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Extending full protection inside existing marine protected areas, or reducing fishing effort outside, can reconcile conservation and fisheries goals

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Running head: Full protection helps rebuild fish stocks and fisheries

Abstract

1 Most fish stocks worldwide are fished at maximum sustainable yield (MSY) or overfished, as many fisheries management strategies have failed to achieve sustainable fishing. Identifying effective fisheries management strategies has now become urgent.

2 Here, we developed a spatially-explicit metapopulation model accounting for population connectivity in the north-western Mediterranean Sea, and parameterized it for three ecologically and economically important coastal fish species: the white seabream *Diplodus sargus*, the two-banded seabream *Diplodus vulgaris* and the dusky grouper *Epinephelus marginatus*.

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

4 *D. sargus* is currently in low overfishing, while *D. vulgaris* and *E. marginatus* are in high overfishing. Stock recovery to B_{MSY} for the last two species requires a reduction of current F around 50%. This would guarantee an increase in both stock biomass (around 50 and 75% for *D. vulgaris* and *E. marginatus*, respectively) and catch (around 15 and 30%) after a transient time of ~15–30 years. Alternatively, doubling the size of fully protected areas over fishable areas within the existing network of MPAs would lead to positive conservation effects for all three species without substantially affecting the overall productivity of the fishery and the total economic value of the catch.

5 *Synthesis and applications.* We provide the first assessment of stock status for three coastal species in the north-western Mediterranean and evaluate the ecological and fisheries outcomes of different management strategies. Extending full protection inside existing multiple-use marine protected areas or reducing fishing effort outside can deliver both conservation and fisheries benefits.

Riassunto

1 La maggior parte degli stock ittici mondiali è sfruttata ai limiti della sostenibilità o sovrasfruttata, poiché molte strategie di gestione della pesca non sono riuscite a realizzare una pesca sostenibile. L'identificazione di strategie efficaci di gestione della pesca è quindi diventata urgente.

2 Abbiamo sviluppato un modello di metapopolazione spazialmente esplicito che tiene conto della connettività tra popolazioni nel Mar Mediterraneo nord-occidentale e lo abbiamo parametrizzato per tre specie ittiche costiere importanti dal punto di vista ecologico ed economico: il sarago maggiore *Diplodus sargus*, il sarago fasciato *Diplodus vulgaris* e la cernia bruna *Epinephelus marginatus*.

3 Abbiamo utilizzato il modello per valutare in che modo la biomassa degli stock e le catture rispondono alle variazioni del tasso di mortalità da pesca (F) e delle dimensioni delle aree a protezione integrale all'interno del sistema esistente di aree marine protette (AMP). Per ogni specie abbiamo stimato la massima produzione sostenibile (MSY) e i corrispondenti valori di biomassa dello stock (B_{MSY}) e del tasso di mortalità da pesca (F_{MSY}) fornendo dei valori di riferimento cruciali per valutare la gestione della pesca.

4 *D. sargus* è attualmente in condizioni di moderato sovrasfruttamento, mentre *D. vulgaris* e *E. marginatus* sono in condizioni di sovrasfruttamento elevato. Per le ultime due specie il recupero degli stock fino a B_{MSY} richiede una riduzione del valore attuale di F pari al 50% circa. Questo garantirebbe un aumento sia della biomassa degli stock (circa +50 e +75% rispettivamente per *D. vulgaris* e *E. marginatus*) che delle catture (+15 e +30% circa) dopo un periodo di circa 15-30 anni. In alternativa, raddoppiare l'estensione delle aree a protezione integrale rispetto alle aree aperte alla pesca all'interno della rete esistente di AMP porterebbe a benefici conservazionistici per tutte e tre le specie senza influenzare sostanzialmente la produttività complessiva della pesca e il valore economico totale delle catture.

5 *Sintesi e applicazioni.* Abbiamo fornito una prima valutazione dello stato degli stock per tre specie costiere nel Mediterraneo nord-occidentale e abbiamo valutato le ripercussioni ecologiche e produttive di diverse strategie di gestione. Estendere le aree a protezione integrale all'interno delle aree marine protette esistenti o ridurre lo sforzo di pesca al loro esterno può offrire vantaggi sia in termini di conservazione che di produttività della pesca.

Keywords

Coastal fish, Fisheries management, Fishing effort regulation, Marine conservation, Marine protected areas, Metapopulation models, Mediterranean Sea, Stock assessment.

1 Introduction

Marine fisheries provide a major source of food and livelihood for hundreds of millions of people worldwide. However, most of the world's fish stocks are maximally sustainably fished (*sensu* FAO 2018, previously called "fully fished") or overfished, with strong cascading impacts on both marine biodiversity (Sala *et al.* 2012; Ortuño Crespo & Dunn 2017) and societies (Golden *et al.* 2016). In particular, the Mediterranean and Black Seas (FAO area 37) are currently the basins with the highest percentage (62%) of stocks fished at biologically unsustainable levels (FAO 2018), and the Mediterranean is one of the regions with the lowest fishery management index scores for management and enforcement globally (Hilborn *et al.* 2020). Several strategies have been proposed to pursue sustainability in fisheries (Hoggarth 2006; Coll *et al.* 2013; Goetze *et al.* 2016; Carvalho *et al.* 2019). Traditional management has focused on adjusting fishing effort to levels guaranteeing maximum sustainable yield (MSY), i.e. the maximum catch that can be removed from a stock over time without depleting it. MSY and its related biological reference points, such as stock biomass (B_{MSY}) and fishing mortality rate (F_{MSY}), are benchmarks used for gauging the status of a stock or fisheries (Hilborn & Ovando 2014). Although many coastal species are key targets for small-scale and recreational fisheries (Lloret *et al.* 2019), for most of them these reference points have never been assessed. Understanding the status of these fisheries is now considered a high priority (Hilborn *et al.* 2020).

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

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

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

2 Materials and Methods

2.1 Case study

The study area covers the north-western Mediterranean Sea, and in particular the region located between latitudes 38.5°N–45°N and longitudes 1°E–12°E. The study area encompasses 62 nationally designated Marine Protected Areas (MPAs): some are fully protected areas, and some are multiple-use MPAs containing one or more fully protected area(s) and one or more partially protected areas (Horta e Costa *et al.* 2016). Overall, protected areas cover 11,255 km^2, 535 of which (~5%) are fully protected. We focused on three fish species of high ecological and economic relevance (Guidetti *et al.* 2014) and vulnerable to small-scale and recreational fishing (Lloret *et al.* 2019): the white seabream *Diplodus sargus*, the two-banded seabream *Diplodus vulgaris*, and the dusky grouper *Epinephelus marginatus*. The three species are common in the Mediterranean Sea: they thrive in littoral rocky bottoms and generally occur from a few meters down to approximately 50 m depth, although they can be found, at lower densities, at greater depths (especially *E. marginatus*; Harmelin & Harmelin-Vivien 1999). Their life cycle is typical of the majority of coastal species, with a pelagic larval phase and a benthic juvenile/adult phase (see section S1 in Supporting Information for further details).

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. The model was parameterized on the basis of the available literature. For some parameters, however, this was not possible due to the lack of reliable information; those parameters were estimated directly from data collected in the field or calibrated via the procedures described in detail in sections S3 and S4. To take into account the major sources of uncertainty affecting parameter estimates, we carried out an uncertainty analysis based on non-parametric statistics (see section 2.2.5 below). Finally, we validated the ability of the model to reproduce the observed patterns of geographic variation in fish population density throughout the study area and under different protection regimes by contrasting the outputs of the model with the observations gathered in the field (see section S4). In the following sections, we concisely summarize the main features of the model; for further details, the reader is referred to the supplementary information.

2.2.1 Habitat suitability

The selected fish species have similar habitat requirements, at least in the adult phase. Therefore, we assumed the same suitable habitat (rocky and hard substrate, encompassing infralittoral reefs, pre-coralligenous and coralligenous formations, down to 50 m depth) for all three species. Habitat was mapped using available information on bathymetry and seabed habitats from the EMODnet portal (www.emodnet.eu). Bathymetry was provided as a high-resolution raster map (1/480°; Populus et al. 2017). Seabed habitat maps were hand-corrected in QGIS software; in fact, although EMODnet maps represent the most updated georeferenced seafloor maps for the Mediterranean Sea, some areas included in our domain were associated to low confidence levels, while others completely lacked any habitat information. For these areas, we first cross-checked information on the EMODnet map with the distribution of coastline substrate types reported in Furlani *et al.* (2014), and then we analysed high-resolution satellite images from Google Earth to ascertain substrate type where the information did not match. In case of mismatch or absence of habitat information in the original map, we added a buffer of rocky substrate along the coast with its extent inversely proportional to the sea bottom slope.

2.2.2 Connectivity assessment

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

2.2.3 Protection

To describe the protection regime of each model cell, we considered three levels of protection: unprotected, partially protected and fully protected areas. Each cell within the spatial domain of the model was associated with at least one protection level. When there was more than one protection level in the same cell, we calculated the relative coverage of each protection level with respect to the total surface of the cell. Partially protected areas were identified with the portion of MPA that is not fully protected. Information on the MPAs (geographical coordinates, names, areas, establishment year, presence of fully protected areas, etc.) was derived from the MAPAMED database (medpan.org/main_activities/mapamed/). MPA perimeters were provided as georeferenced polygons, allowing us to define the geometric intersection with each cell and to calculate the corresponding surface area. The total area covered by the model domain (which includes only the coastal part of the whole geographic range covered by the analysis, see next section) is 23,463 km². Of these, 4,373 km² fall within a protected area, 325 of which (7%) under full protection and 4,047 under partial protection.

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 (i.e. below sea level) 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). The total suitable area covered by the model domain is 1,753 km². Each sub-population 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.

2.2.5 Uncertainty analysis

To account for the uncertainty associated with the estimation of the most critical model parameters, namely those describing natural and fishing mortality processes and the stock-recruitment relationship, we used a non-parametric approach based on bootstrapping. This allowed us to generate an empirical probability distribution for each parameter (see sections S3 and S4 for details). The model was then used to test different fisheries management scenarios for the three model species at the scale of the whole study area (see next section). To this end, we sampled the probability distributions of the bootstrapped parameters to generate new random parameter sets. Model simulations were run 100 times, each time with a different parameter set, to eventually obtain a probability distribution for each model output, from which we derived the statistics of interest to quantify the uncertainty of our estimates.

2.3 Assessment of the current state of stocks

To provide a standard assessment of the current state of each stock, we referred to the assessment guidelines for demersal fisheries proposed by the General Fisheries Commission for the

Mediterranean (GFCM 2014). The level of overfishing was determined on the basis of the ratio $F_c/F_{0.1}$, where F_c is the current rate of fishing mortality and $F_{0.1}$ is one of the most widely used biological target reference points in fisheries (see section S5 for details on its calculation). The following operational classification was used:

- low overfishing, if $F_c/F_{0.1} \leq 1.33$
- intermediate overfishing, if $1.33 < F_c/F_{0.1} < 1.66$
- high overfishing, if $F_c/F_{0.1} \geq 1.66$.

2.4 Fisheries management scenarios

We investigated the response of stock biomass and catch to changes in (i) the fishing mortality rate, and (ii) the extent of fully protected areas in the current system of MPAs. In the first set of experiments, we considered a homogeneous reduction or increase of current fishing mortality rate (F_0) across the study area. In the second, we changed the relative coverage of existing fully protected areas in the MPAs currently established in the study area, keeping the total surface area of each MPA unchanged. The area not included in the fully protected area was considered as partially protected (i.e. with an intermediate level of fishing mortality, namely 55% of that experienced in unprotected areas). 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 projected by the calibrated 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*.

3 Results

3.1 Effects of changing fishing mortality rate

The responses of stock biomass and catch of the three studied species to changes of fishing mortality rate at the scale of the whole study area are shown in Fig. 2. To make species-specific results easier to compare, we normalized biomass and catch values for each species with respect to the baseline simulation (performed under current fishing mortality, as estimated via model calibration). For *D. vulgaris* and *E. marginatus*, normalized maximum sustainable yield (MSY) and the corresponding normalized stock biomass are >1, indicating that there is room for improvement over current management, while for *D. sargus* they are ~1, suggesting that the stock is exploited at its maximum sustainable level. The ratios between baseline biomasses and biomasses at MSY (B_c/B_{MSY}) are 1, 0.66 and 0.57 for *D. sargus*, *D. vulgaris* and *E. marginatus*, respectively. The corresponding ratios between baseline biomasses and unfished biomasses, i.e. with fishing effort set to zero across the whole study area, (B_c/B_0) are 0.44, 0.26 and 0.21, respectively.

Current fishing mortality rates (F_c) for *D. vulgaris* and *E. marginatus* are twice those associated with MSY (F_{MSY}). The values of $F_{0.1}$ calculated from the curves of catch per recruit (Fig. S8) are equal to 0.87, 0.58, 0.29 for *D. sargus*, *D. vulgaris* and *E. marginatus.* The corresponding ratios $F_c/F_{0.1}$ are 1.15, 1.73, and 3.49, respectively, indicating that *D. sargus* is in low overfishing, while the other two species (and especially *E. marginatus*) are in high overfishing.

Fig. 3A shows the temporal dynamics of stock biomass over time under an MSY scenario. At the beginning of the simulations, relative biomass B/B_{MSY} is 0.66 (IQR 0.62–0.71) for *D. vulgaris* and 0.57 (0.52–0.61) for *E. marginatus*, while *D. sargus* is already at MSY. Subsequently, the relative biomasses of *D. vulgaris* and *E. marginatus* grow progressively until reaching their maximum (B/B_{MSY} = 1). The duration of the transient period required to approach B_{MSY} (i.e. for a full recovery of the stock) is ~10–20 years for both species. Fig. 3B shows the temporal dynamics of catch (expressed, in this case, as the ratio between current catch and its present value, C/C_c) under the same scenario (MSY). Relative catches fall, during the first year of implementation of the scenario, from the present level (=1 by definition) to approximately 0.55 for *D. vulgaris* and 0.53 for *E. marginatus*. Afterwards, they grow over time until reaching their maximum value, 1.16 (IQR 1.06–1.28) for *D. vulgaris* and 1.30 (1.20–1.44) for *E. marginatus*. The time required to attain the present levels again ($C/C_c = 1$) is about 7 years for *D. vulgaris* and 9 years for *E. marginatus*.

3.2 Effects of expanding fully protected areas

Predicted responses of stock biomass and catch of the three species to changes in the relative coverage of fully protected areas (keeping fishing mortality rate at its present level F_c) are shown in Fig. 4. The effect of expanding fully protected areas on fish biomass are consistently positive for all species and approximately proportional to the extent of full protection. When the relative coverage of full protection is set to 100% of the total protected area, the predicted increase in stock biomass relative to the baseline is 16% (IQR 15–20%) for *D. sargus*, 58% (40–84) for *D. vulgaris*, and 56% (47–70%) for *E. marginatus*. On the other hand, effects on catch are species dependent. For *D. sargus* and *E. marginatus*, catch is negatively related to the fully protected fraction. In contrast, for *D. vulgaris* the effect of increasing the fully protected fraction is generally positive, except when the fraction is lower than the present one or >80% of the total protected area. In particular, the median catch of *D. vulgaris* is expected to be maximized by a full protection encompassing ~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 between $0.33F_c$ and F_c. The maximum value (+11%, IQR 6–17%) 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 is achieved when the fraction of fully protected area is between 10 and 20%, albeit it does not represent a significant change compared to present (median value +0.06%, IQR from –0.25 to +0.64%). Changes with respect to the current value of catch become negative outside this interval.

4 Discussion

We showed that one of the three fish studied (the white seabream *Diplodus sargus*) is currently in low overfishing in the north-western Mediterranean, while the other two (the two-banded seabream *D. vulgaris* and the dusky grouper *Epinephelus marginatus*) are in high overfishing. Achieving fisheries sustainability requires either a significant reduction of fishing mortality in unprotected areas and/or an increase of the size of fully protected areas while keeping the overall fishing effort constant. Estimated current stock biomasses (B_c) are lower than B_{MSY} for *D. vulgaris* and *E. marginatus*. However, the level of depletion ($B_c > 0.5B_{MSY}$) is such that both species 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 of *D. vulgaris* and *E. marginatus* be significantly reduced (by around 50%). In practice, this could be achieved through a range of management solutions including both input (e.g. gear restrictions, reduction of fishing capacity) and output controls (e.g. reduction in allowable catch; see Anderson *et al.* 2019 for a review of management measures). In the medium/long term (10–20 years), such a prospect of fishery recovery would generate increases in stock biomass [51% (IQR 40–62%) for *D. vulgaris* and 75% (63–91%) for *E. marginatus*], fisheries catch [16% (9–25%) for *D. vulgaris* and 23% (17–40%) for *E. marginatus*] and, consequently, total value of catch [11% (6–17%) overall].

While the positive effects on stock biomass of the two species in high overfishing would be visible immediately after starting the recovery plan, our simulations suggest that the process of rebuilding catch to levels at least equal to the current ones would take more time (7 years for *D. vulgaris* and 9 years for *E. marginatus*). During this relatively long transient period, catches may be substantially reduced, especially in the first year (around –50% for both species). To avoid excessive socioeconomic impacts (Worm *et al.* 2009) or unreported or illegal fishing (Agnew *et al.* 2009), specific accompanying measures should be adopted.

Enforcement of fishing effort control in unprotected areas may be difficult to put into practice, especially in the case of small-scale and recreational fisheries in coastal areas. Therefore, an effective alternative strategy could be to rely on already designated MPAs and extend the coverage of full protection within the existing MPA network, provided that sound enforcement and management is ensured by adequate staff and budget capacity (Gill *et al.* 2017). Increasing the relative size of fully protected areas within multiple-use MPAs, while keeping fishing mortality rate outside MPAs at current levels, can generate positive conservation effects (increase in stock biomass) for the three coastal species. Positive effects of the size of fully protected areas on fish biomass are known (Claudet *et al.* 2008), and can be related to better inclusion of fish home ranges (Di Franco *et al.* 2018) and increase in self-recruitment through larger proportions of retained larvae (Botsford, Micheli & Hastings 2003). From the economic viewpoint, a recent analysis by Brander *et al.* (2020) has shown that the global benefits of expanding MPAs exceed their costs.

Impacts on catch are species-specific and dependent on the size of the fully protected area. In our case, they are positive for the species with the longest dispersal distance (*D. vulgaris*) and negative for those with a narrower dispersion range (*D. sargus* and *E. marginatus*). Given that the three studied coastal species have limited adult movement (La Mesa *et al.* 2011; Di Franco *et al.* 2018), the relatively short pelagic larval phase represents the primary opportunity for dispersal and connectivity (Di Franco *et al.* 2012; Andrello *et al.* 2013; Pujolar *et al.* 2013).

Ensuring that the loss in fishing grounds is offset by gains in catch (Halpern & Warner 2003; Gaines *et al.* 2010) is key for successful fisheries management with MPAs. We showed that an increase of size of fully protected areas within existing multiple-use MPAs can generate positive effects for *D. vulgaris*, both in terms of stock biomass [+20% (IQR 14–28%)] and catch [around +4% (IQR 1–9%)], for levels of full protection between 20% and 50%, respectively, of the total protected area. Despite relatively high levels of uncertainty on the actual magnitude of the effects, their sign is consistently positive. In the case of *D. sargus* and *E. marginatus,* increasing the relative size of the fully protected area would not generate positive effects on catch. However, given that adult spillover was not accounted for in this study, the actual benefits on catch may be underestimated. In any case, the economic viability of the fishery (expressed in terms of total value of catch) would be preserved.

We are aware that the economic component of fisheries sustainability is more complex than how we have described it: a comprehensive description should also account for fisher behaviour, which relates stock dynamics, fishing revenues and costs (Anderson *et al.* 2019). Some fisheries around the world are managed using maximum economic yield (MEY) as a reference, an approach that in many cases guarantees better conservation achievements besides economic optimality, because biomass reference points are generally higher and mortality reference points lower than under a MSY-based approach (Hilborn *et al.* 2020). However, developing a model that accounts explicitly for the economic dynamics of the fishery under study, given the complex context of small-scale coastal fisheries in the Mediterranean and the lack of reliable and comprehensive information, was beyond the scope of our work. In addition, despite its limits as a reference point for fisheries management, MSY is still one of the key targets of the Common Fisheries Policy of the European Union.

Despite the ecological and commercial interests of the studied coastal species, to our knowledge our study is the first modelling effort of its kind, fully integrating the biological and demographic characteristics of the species into a spatially explicit metapopulation model. Although results are affected by manifold sources of uncertainty (including the intrinsic variability of environmental and ecological processes driving the dynamics of the stocks across time and space, as well as the scarcity of data available to build a comprehensive picture), we are confident that our results are robust, at least as regards the general patterns emerging from the analysis. As a further proof of the robustness of our results, it is interesting to note that the reserve effect emerging from our data on *D. sargus* (see Figs. S4 and S5) is fully consistent with what observed by Melià et al. (2020) for the same species inside and outside another Mediterranean MPA (Torre Guaceto, southern Adriatic Sea).

Our findings suggest that responses to management strategies are species-specific. This is in line with previous evidence suggesting that the effects of management measures depend on life history and ecological traits of the species considered (Anderson *et al.* 2019, Hilborn *et al.* 2020). It is also particularly true for the response of different fish species to the establishment of marine protected areas (e.g. Claudet *et al.* 2010, Di Franco et al. 2018). To provide more general and more broadly applicable conclusions, it is therefore crucial to carry out studies encompassing a larger number of species. In this perspective, we believe that our study represents a relevant first step and can help define future research directions.

We have shown that strong conservation benefits can be obtained through non-spatial regulations, by reducing fishing effort in unprotected areas, or via area-based management strategies, by increasing the size of fully protected areas within existing MPAs (hence not increasing the size of MPAs overall). Improving the status of the stocks without significantly affecting the long-term profitability of the fisheries would be very attractive to decision makers and represents a message easily transferable to stakeholders. We believe this study can greatly contribute to more effective management of vulnerable species and help reconcile conservation and fisheries goals.

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.

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Data availability statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.05qfttf0k (Belharet *et al.* 2020)

Supporting information

Additional supporting information may be found online in the Supporting Information section.

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Figure legends

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

Figure 2. Stock biomass and catch of the three studied species (colour coded) as functions of fishing mortality rate *F*. Median values are indicated by coloured dots, while error bars show interquartile ranges. Biomass and catch values (averaged over the last 10 years of a 50-year simulation) are normalized with respect to baseline values for each species (obtained at current fishing mortality rate, F_c). *F* was varied by applying different multipliers to the 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. Median values of Maximum Sustainable Yield (MSY) and stock biomass at MSY (B_{MSY}) for each species are indicated by coloured dots near the axes, while the corresponding levels of fishing mortality (F_{MSY}) are highlighted by black-bordered circles. The white, black-bordered circle identifies the baseline scenario.

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}). Solid lines indicate median trajectories, with shadowed areas showing the corresponding interquartile ranges. Biomasses are normalized with respect to B_{MSY}, while catches are normalized with respect to their estimated current value C_c. Lines for *D. sargus* are flat because the species is already at MSY.

Figure 4. Stock biomass and catch of the three studied species as functions of the percent coverage of fully protected areas within existing MPAs. Median values are indicated by coloured dots, while error bars show interquartile ranges. Biomass and catch values (averaged over the last 10 years of a 50-year 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 current value, A_c). 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. Solid lines indicate median values, with shadowed areas showing the corresponding interquartile ranges.

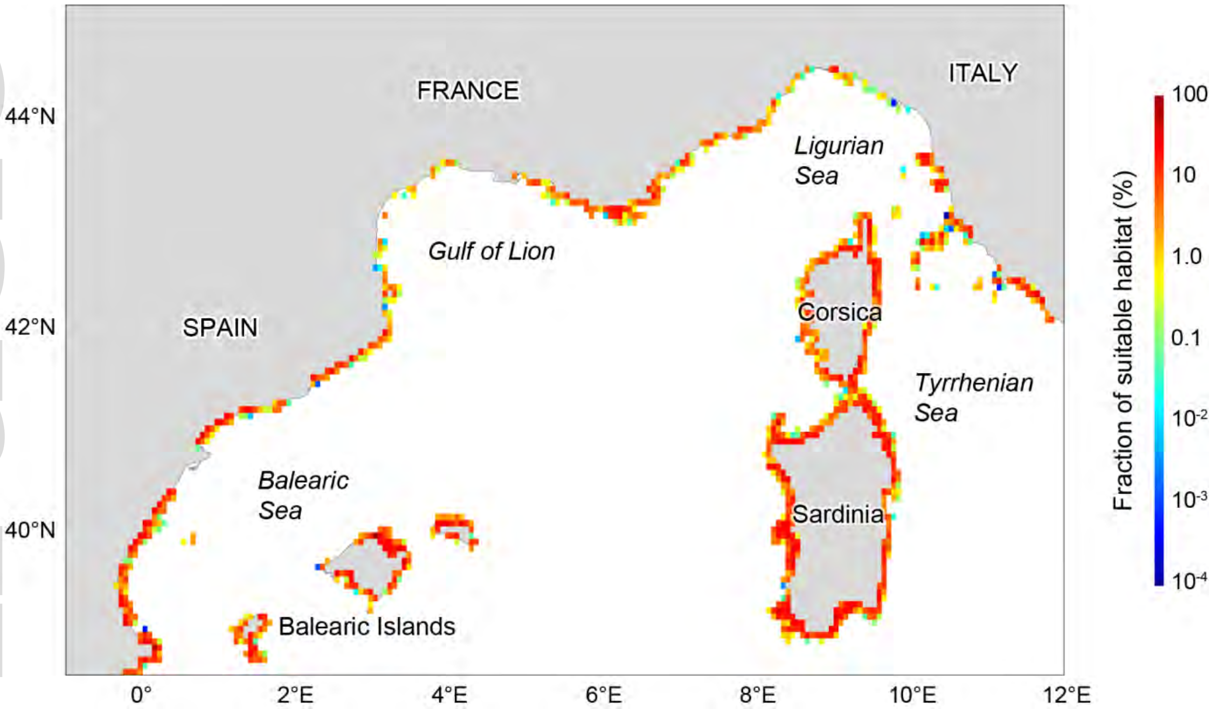

FRANCE
ITALY
SPAIN
Ligurian Sea
Gulf of Lion
Corsica
Tyrrhenian Sea
Balearic Sea
Sardinia
Balearic Islands
44°N
42°N
40°N
0°
2°E
4°E
6°E
8°E
10°E
12°E
Fraction of suitable habitat (%)
100
10
1.0
0.1
10-2
10-3
10-4

Fig. 1

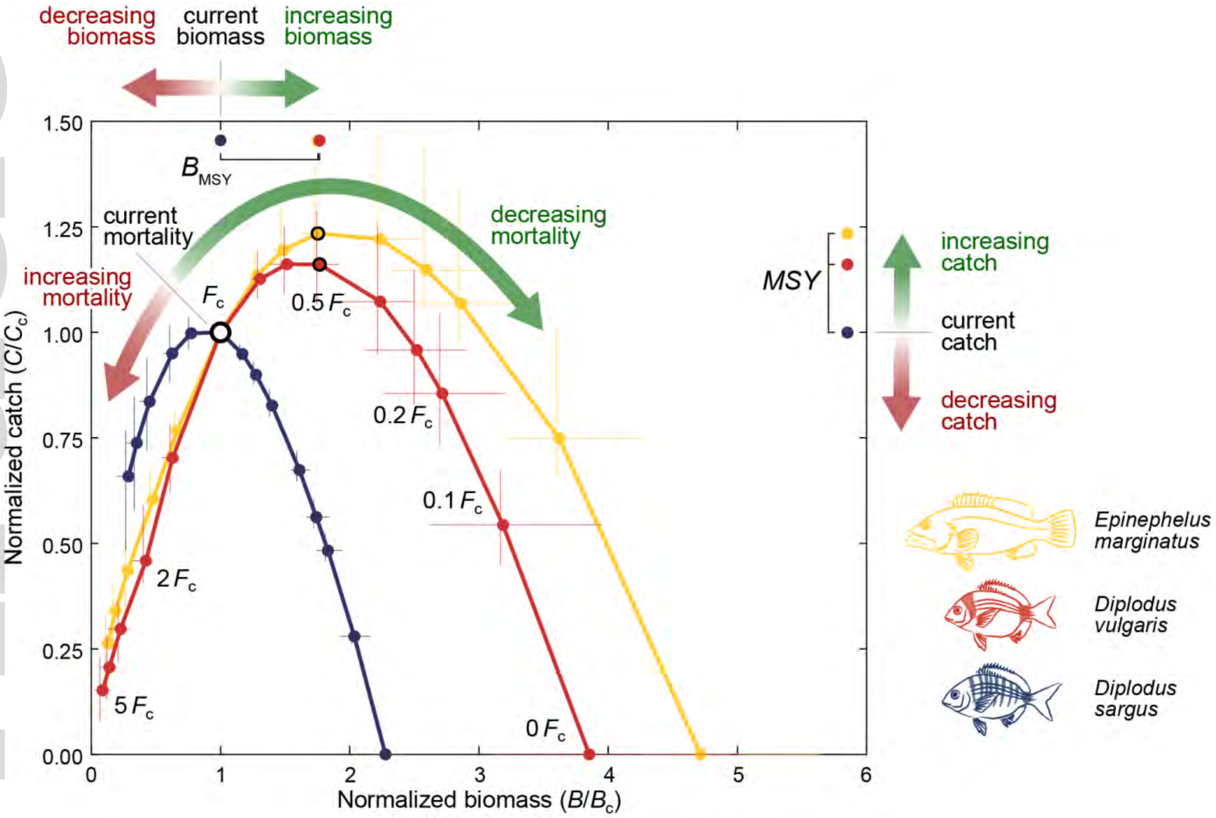

decreasing biomass
current biomass
increasing biomass
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Normalized catch (C/C_c)
B_MSY
current mortality
increasing mortality
F_c
0.5 F_c
decreasing mortality
0.2 F_c
0.1 F_c
2 F_c
5 F_c
0 F_c
0
1
2
3
4
5
6
Normalized biomass (B/B_c)
MSY
increasing catch
current catch
decreasing catch
Epinephelus marginatus
Diplodus vulgaris
Diplodus sargus

Fig. 2

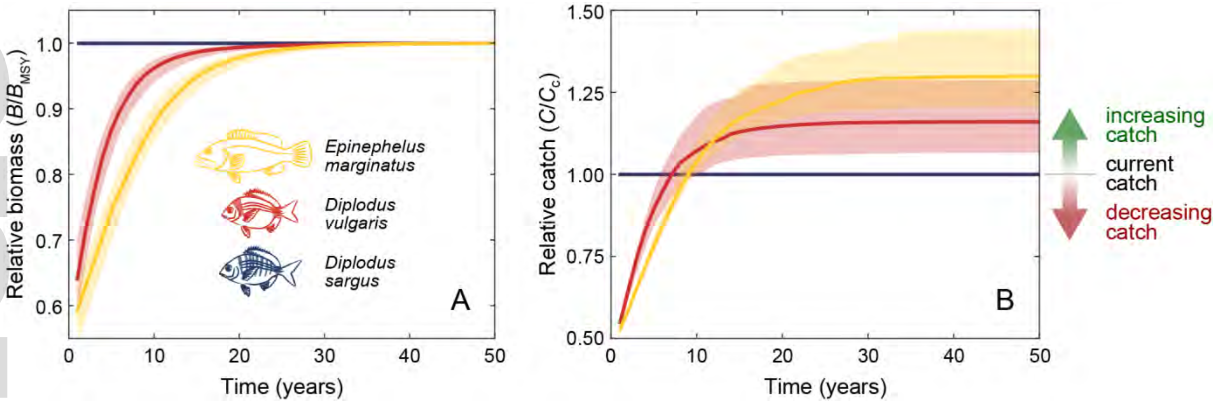

Relative biomass (B/B_{MSY})
1.0
0.9
0.8
0.7
0.6
0
10
20
30
40
50
Time (years)
Epinephelus marginatus
Diplodus vulgaris
Diplodus sargus
A
Relative catch (C/C_c)
1.50
1.25
1.00
0.75
0.50
0
10
20
30
40
50
Time (years)
B
increasing catch
current catch
decreasing catch

Fig. 3

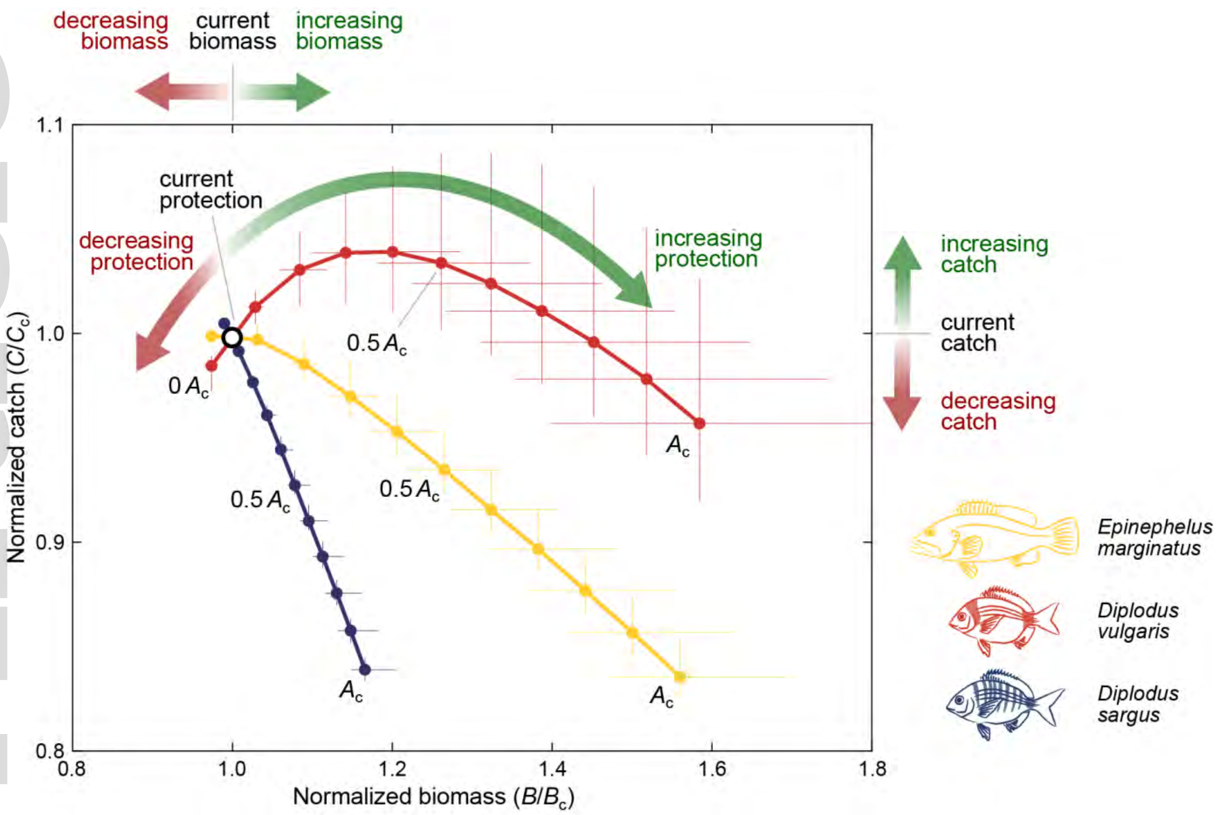
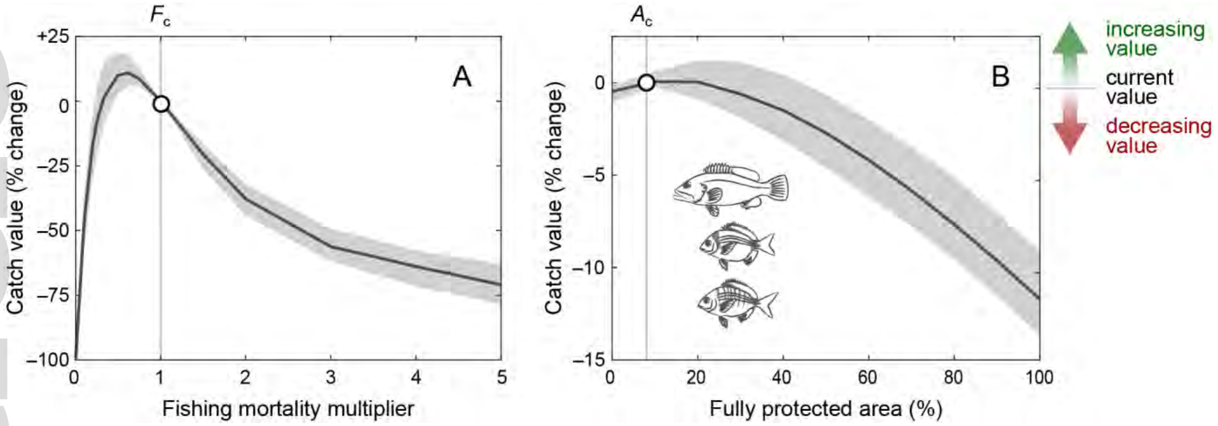

decreasing biomass
current biomass
increasing biomass
current protection
decreasing protection
increasing protection
increasing catch
current catch
decreasing catch
0 A
0.5 A
A
Normalized catch (C/C)
Normalized biomass (B/B)
0.8
0.9
1.0
1.1
1.2
1.4
1.6
1.8
Epinephelus marginatus
Diplodus vulgaris
Diplodus sargus

Fig. 4



F_c
A
Catch value (% change)
+25
0
−25
−50
−75
−100
0
1
2
3
4
5
Fishing mortality multiplier
A_c
B
Catch value (% change)
0
−5
−10
−15
0
20
40
60
80
100
Fully protected area (%)
increasing value
current value
decreasing value

Fig. 5