

The effects of marine protected areas on ecosystem recovery and fisheries using a comparative modelling approach

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Abstract

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The overexploitation of many marine stocks calls for the development and 28 assessment of tools to support recovery, rebuilding and conservation of marine 29 resources. Here, we assessed the potential contributions to fisheries sustainability 30 31 and ecosystem recovery at the local level of three multiple-use Marine Protected Areas (MPAs) in the Northwestern Mediterranean Sea ecosystem. For each MPA, 32 we built a food-web model for each management (MU): the Fully Protected Area 33 (FPA), the Partially Protected Area (PPA) and the Unprotected Area (UPA) 34 35 surrounding the MPA. Using the nine food-web models we characterized and compared the structure and functioning of each MU, we assessed differences and 36 37 similarities within and among the three MPAs, and evaluated if the ecosystem response to full protection led to specific ecosystem functional traits that are 38 shared among the three MPAs. We showed differences among MUs in terms of 39 ecosystem structure and functioning. Overall, FPAs presented most positive effect 40 of protection in terms of ecosystem structure and functioning, and were followed by 41 PPAs. The effects of protection on neighboring non-protected areas were hardly 42 noticeable. Similarities between Cerbère-Banyuls and Medes Islands MPAs were 43 observed, while Cap de Creus MPA showed the least benefits from protection. This 44 is likely due to similarities in the configuration of the protection areas, levels of 45 enforcement and establishment, and the impact of recreational and artisanal 46 47 fisheries. Our study illustrates that well-enforced Mediterranean MPAs can yield local positive impacts on the structure and functioning of marine ecosystems that 48 can contribute to fisheries sustainability. 49

- 50 Keywords: Management units, fully protected areas, partially protected areas,
- 51 Ecopath with Ecosim, NW Mediterranean Sea
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1. Introduction

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Marine ecosystems have been degraded at high rates under the cumulative impact of multiple anthropogenic activities (Costello et al., 2010; Halpern et al., 2015). In 2010, the United Nations' Convention on Biological Diversity (CBD) established a target of 10% of the ocean to be protected by 2020 ("Aichi Target 11") (CBD, 2010). MPAs are an essential

tool for reversing the global degradation of ocean life (Claudet et al. 2008; Babcock et al; 2010). Several studies have shown that protection from fishing leads to rapid increases in abundance, size and biomass of exploited species and, sometimes, to an increase in species diversity (e.g. Claudet et al., 2010; Di Franco et al., 2018; Lester et al., 2009). However, only 3.7% of the world's ocean is protected with implemented marine protected areas (MPAs) (Sala et al. 2018).

MPAs can also provide socioeconomic benefits. Economic benefits may stem from the creation of employment opportunities through the establishment of non-consumptive activities such as tourism and recreation (Roncin et al. 2008), or from securing future jobs by increasing the chances of managing stocks sustainably (Sumaila et al., 2000). Fisheries benefits arise from ecological effects within protected areas spillover the boundaries of the MPA (Di Lorenzo et al. 2016). Empirical studies comprising artisanal (Stelzenmüller et al., 2008), recreational (Font et al., 2012a) and industrial bottom-trawling fishing effort (Murawski et al., 2005) showed a concentration of fishing activities in the close vicinity of the MPA boundaries. This concentration of fishing effort, also known as "fishing the line", can reduce spillover of fish to the surrounding area and can have major implications for the effectiveness of MPAs in achieving ecological and socio-economic goals (Wilcox and Pomeroy, 2003), particularly those concerning wider stock replenishment and fisheries sustainability at a regional level.

Most MPAs are multiple-use MPAs (Claudet 2018). They combine different levels of protection within a spatially zoned management scheme that can be fully protected areas (FPAs), where all extractive activities are prohibited, or a type of partially protected areas (PPAs), where some extractive activities are allowed but with varying restrictions (Horta e Costa et al., 2016; Lubchenco and Grorud-Colvert, 2015) (Giakoumi et al., 2017). How multiple use MPAs are management can have strong implications in terms of the ecosystem and fisheries benefits they can provide at a more regional levels. Recent studies showed that ecological benefits can be observed in fully and highly protected areas, while lower levels of protection do not provide benefits or only when surrounding a fully protected area (Zupan et al. 2018a). In addition, when allowed in a given zone of an MPA, extractive use concentrate and can become a threat for the overall MPA (Zupan et al. 2018b)

While MPAs are an ecosystem-based management tool, it is still unclear how the functioning of ecosystems responds to protection. In particular, do the different levels of

protection in multiple-use MPAs translate into different reorganization of ecosystems? How the ecosystem response of different levels or protection transfer into fisheries benefits? Can the local ecosystem and fisheries response of multiple use-MPAs scale-up at a regional level? Here, using food-web modeling techniques, we present the first attempt to quantitatively model and compare ecosystem structural and functional trait responses to different levels of protection in multiple-use MPA. We used three Mediterranean MPAs as a case study and developed ecosystem models for each management until in each MPA.

2. Material & Methods

Study area

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We examined different management units (MUs) of three different MPAs in the northwestern Mediterranean Sea: the Cerbère-Banyuls MPA in France, and Cap de Creus and Medes Islands MPAs in Spain (Figure 1). Cerbère-Banyuls MPA is located in the southeastern part of France, and it covers a coastal area of 6.50 km². This marine area spans between 0 and 60 meters and it contains three main Mediterranean habitats: calcareous seaweed bottom (Lithophyllum), Mediterranean seagrass meadows (Posidonia oceanica) and coralligenous bottom (Pseudolithophyllum expansum). There are also some protected and emblematic species that inhabit in this MPA, such as the grouper (Epinephelus marginatus) and the red coral (Corallium rubrum). Cap de Creus MPA is located in the northeastern part of Spain, it covers a coastal area of 8.19 km² and spans between 0 and 60 meters. Shallow marine bottoms surrounding the peninsula of Cap Creus are mostly rocky whereas most deep areas are muddy (Sardá et al., 2012). The coastal rocky bottoms of the Cap de Creus continental shelf are dominated by the community of coralligenous, which is mainly characterized by coralline algae and suspension feeders species (gorgonians, sponges, and bryozoans) (lacono et al., 2012). Finally, the Medes Islands MPA is located in the northeastern part of Spain, and it covers a coastal area of 4.64 km². Medes Islands MPA has a depth range between 0 and 60 meters, and it contains a great diversity, constituting a complex ecosystem due to the existence of many different types of habitats such as Posidonia oceanica meadows, gorgonian communities (Eunicella singularis and Paramuricea clavata) and coralligenous bottom (Gili, 1981; Ros and Gili, 2015). It also shelters other important marine species, like the grouper and red coral (Hereu et al., 2012).

The main reason to select these three MPAs was their similar bathymetry range and habitat composition, and the proximity among them. The three MPAs combine

different levels of protection within a spatially zoned management scheme (Table 1 and Figure 1). Fully protected areas (FPAs) are areas where extractive uses are not allowed. Partially protected areas (PPAs) allow restricted uses such as traditional/artisanal fisheries or scuba-diving (Zupan et al. 2018b). Finally, we selected the unprotected areas (UPAs) surrounding the MPAs, in order to model a similar ecosystem without protection but with immediate influence from the protected region. The boundaries of the unprotected areas were set taking into account that they should have similar characteristics to the MPA, and they should be adjacent to the MPA (Figure 1).

Modelling approach

MU models were developed using Ecopath with Ecosim approach (EwE 6.6 version) (Christensen et al., 2008; Christensen and Walters, 2004) and followed the best practices rules (Heymans et al., 2016). Ecopath is a mass-balanced model based on two equations. The first master equation describes the energy balance for each group, so that:

Consumption = production + respiration + unassimilated food

The second Ecopath equation is based on the assumption that the production of one functional group is equal to the sum of all predation, non-predatory losses, exports, biomass accumulations, and catches, as expressed by the following equation:

$$P/B_i \cdot B_i = P/B_i \cdot B_i \cdot (1 - EE_i) + \sum_i (Q/B)_{ii} \cdot B_i \cdot DC_{ii} + Y_i + NM_i + BA_i$$
 Eq. 1

where B_i is the biomass, $(P/B)_i$ is the production rate, $(Q/B)_i$ is the consumption rate, DC_{ji} is the fraction of prey i included in the diet of predator j, NM_i is the net migration of prey i, BA_i is the biomass accumulation of prey i, Y_i is the catch of prey i, and EE_i is the ecotrophic efficiency of prey i, that is, the proportion of production used in the system or exported.

Parametrization

All the models were built using the best available information and represent periods from 2000s to 2010s, mostly limited by the available biomass data on the underwater visual census (UVC). Specifically, the models we built of the Cerbère-Banyuls MPA included most of the information from 2013, while the Cap de Creus MPA and the Medes Islands MPA included most of their information from the period (2005-2008) and (2000-2004), respectively.

Information about species presence and their biomasses were aggregated in functional groups (FGs) of species or groups of species clustered according to key information about their trophic ecology, commercial value, and abundance in the ecosystem. We used the meta-web structure defined for the Western Mediterranean Sea model (Coll et al., 2019a) developed under the SafeNet Project¹ context, which contains ninety functional groups. We adapted this meta-web structure to local conditions and we removed those FGs which did not occur in the study areas. The final food-web structure of Cerbère-Banyuls MPA contains 64 functional groups (2 marine mammals, 3 seabirds, 1 sea turtle, 8 pelagic fish, 25 demersal fish, 3 cephalopods, 14 invertebrates, 2 primary producers, 2 zooplankton, 2 phytoplankton and 2 detritus), and 67 functional groups for Cap de Creus MPA and Medes Islands MPA (2 marine mammals, 3 seabirds, 1 sea turtle, 9 pelagic fish, 25 demersal fish, 3 cephalopods, 14 invertebrates, 4 primary producers, 2 zooplankton, 2 phytoplankton and 2 detritus) (Table 2). Except in the case of FPAs, which do not have discards because all fishing extractions are forbidden, food-web structures of each MU in the same MPA were identical.

FGs' biomasses were obtained from different sources from the study area or surrounding areas (see supplementary material Table S1.1. for details on the parameterization of each functional group). The nine MU models share biomass data on some FGs (marine mammals, seabirds, sea turtles, pelagic fish, some invertebrates' groups, primary producers, zooplankton and phytoplankton) due to the lack of local data and/or the closeness among these MPAs. The rest of the FGs were parameterized with local information available from field studies (supplementary material Table S1.1.).

Biomass estimates for invertebrates' species were not frequently available and therefore we used realistic EE values to estimate the biomass of 4 FG in Cerbère-Banyuls models and 6 in Cap de Creus and Medes Islands models (supplementary material Table S1.1.). Scaling factors were used on biomass data of pelagic fish groups available from the MEDITS oceanographic survey (Bertrand et al., 1997), which does not fully cover coastal areas. Thus, this scaling enabled to adapt the estimates and get more accurate biomass estimations for these coastal areas. The scaling conversions were based on species depth distribution (extracted from *Aquamaps* – www.aquamaps.org) (Kaschner et al., 2013) and took into account their contribution in each FG. MEDITS trawling survey data were extracted with a new released software inside SafeNet Project, which is called MEDITS

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¹ http://www.criobe.pf/recherche/safenet/

data explorer v. 1.5.1 (Steenbeek, 2018a). This tool allowed us to weight the biomass by bathymetric range. We extracted MEDITS trawling survey data from the closest point to each MPA, in order to have biomass data for those species that were not present during UVC.

Production (P/B, year⁻¹) and consumption (Q/B, year⁻¹) rates were either estimated using empirical equations (Heymans et al., 2016), taken from literature or from other model developed in the Mediterranean Sea (Coll et al., 2019b) (supplementary material Table S1.1.). Additionally, local body lengths of reef-associated species obtained from UVC (Di Franco, 2017) were used to estimate those rates using empirical equations and local data (Pauly, 1980). In some cases, these produced different rates between MUs due to changes in the length frequency of species in protected versus not protected areas.

The diet information was compiled using published studies on stomach content analyses, giving preference to local or surrounding areas (supplementary material Table S1.1.). To calculate the Diet Matrix (DC) we used the Diet matrix calculator (Steenbeek, 2018b). This tool automatizes the process of selecting and scaling diet data, and it generates the diet composition matrix and a pedigree index associated with each predator FG (supplementary material appendix 2, Table S2.1., S2.2., S2.3.). Due to the small sizes of the MUs investigated and the capacity to some species to move between MUs (Gell and Roberts, 2003a; Grüss et al., 2011), we set a fraction of the diet composition as import for all MUs based on the time that these species feed outside the areas and their ecological traits. This import was based on the size, behavior and ecology of species of each functional group (Froese and Pauly, 2019).

Fisheries data were obtained from different sources (database, literature and unpublished data) (supplementary material Table S1.1.) and were split into two fishing fleets – recreational and artisanal (except for FPA models where fishing activities are not allowed). Regarding artisanal catches, Cerbère-Banyuls catches were obtained from a local study (Prats, 2016), while for Cap de Creus and Medes Islands the data came from an official dataset of the regional government of Catalonia managed by the Institute of Marine Sciences (ICM-CSIC) (Tudó, 2017). For Cap de Creus, these landings were from Llançà, Port de la Selva, Cadaqués and Roses harbours, where the main fleet operating is coming from, and were scaled by the months fishing inside the MPA (Gómez et al., 2006). For the recreational fisheries, we extracted catches from Ivanhoff *et al.* (2010) in Cerbére-Banyuls. Cap de Creus catches came from Font and Lloret (2011a, 2011b) and Lloret *et*

al. (2008a, 2008b). Whereas, for Medes recreational catches were collected from Sacanell(2012).

Ensuring mass-balance and assessing the quality of the model

In an Ecopath model, the energy input and output of all functional groups must be balanced under some ecological and thermodynamic rules: (1) EE < 1.0; (2) P/Q [production/consumption rate or gross efficiency (GE)] ranges from 0.1 to 0.3 with the exception of fast growing groups such as bacteria; (3) R/A (respiration/food assimilation) < 1; (4) R/B (respiration/biomass) ranges from 1 to 10 for fish and higher values for small organisms; (5) NE (net efficiency of food conversion) > GE and (6) P/R (production/respiration) < 1 (Christensen et al., 2008; Heymans et al., 2016).

Initial values of the MU models showed that the EE > 1 for some functional groups: mainly small pelagic fish groups and invertebrates' groups. This could be due to unfeasible low initial biomass estimates, and two procedures were applied to solve EE higher than 1. For pelagic fish groups (mackerels, horse mackerels, European sardine, European anchovy and other small pelagic fish), we added immigration biomass because studied areas (MUs) are relatively small compared to the dispersal rate of those species (Di Franco et al., 2012). For invertebrate' groups (non-commercial decapods, sea cucumbers and other macrobenthos), EE values were fixed to 0.8 in order to calculate their biomass.

To balance the models, we applied a manual mass-balanced procedure following a top-down approach modifying input parameters starting from the functional groups with higher TL and considering the best practice guidelines (Heymans et al., 2016). We used the PREBAL diagnostics (Link, 2010) in order to ensure that the model followed general ecological and biological principles and to guide the balancing procedure. Several functional groups displayed too low P/Q values (<0.2 or even <0.1 in some cases), and in these cases reasonable P/Q values were assigned based on a previous EwE model developed in the same study area (Corrales et al., 2015).

The quality of the model was evaluated using the pedigree routine, which allows assigning a pedigree value for each input parameter (B, P/B, Q/B, diet and catches) (Christensen et al., 2008; Christensen and Walters, 2004). All pedigree values were established manually except for diet pedigree values, which were obtained from the Diet Calculator software (Steenbeek, 2018b). This software computes a total pedigree value for each diet record, which is a weighted average of four field scores from four diet features

(region, year, type of data and method). Pedigree values were first used to determine which parameters were of lower quality and thus could be modified during the balancing procedure. Afterwards, they were used to calculate the pedigree index of each model, which vary between 0 (lowest quality) and 1 (highest quality) (Christensen and Walters, 2004).

Model analyses and ecological indicators

Flow diagram

The food-web structure of each MU in the three MPAs was visualized using a flow diagram. Flow diagrams were obtained using the *ggplot2* package (Wickham, 2010) implemented in R software (R Core Team, 2017) and were built from the biomass and trophic levels (TL, as outputs) of each FG, and the direct trophic interactions among them. The TL identifies the position of organisms within food webs by tracking the source of energy for each organism, and it is calculated by assigning primary producers and detritus a TL of 1 (e.g. phytoplankton), and consumers to a TL of 1, plus the average TL of their prey weighted by their proportion in weight in the predator's diet (Christensen, 1996).

Ecological indicators

Several ecological indicators were computed to describe the state and functioning of the ecosystems. These indicators were divided into five main groups following (Coll and Steenbeek, 2017):

- **Biomass-based**. These indicators are calculated from the biomass of components. Species biomass data are considered basic information to evaluate effectiveness in marine protected areas (Micheli et al., 2004). We included five biomass-based indicators: total biomass (TB, t·km⁻²·year⁻¹), biomass of commercial species (CB, t·km⁻²·year⁻¹), biomass of
- fish species (FB, t·km⁻²·year⁻¹), and Kempton Q diversity index (KI).
- Trophic-based. These indicators reflect the TLs for different groups of the food web. The trophic level may indicate ecosystem "health" because it reflects fishing pressure due to the removal of predators (Christensen and Walters, 2004). We selected four trophic-based indicators: TL of the community (TLc), TL of the community including organisms with TL \geq 2 (TL2), TL of the community including organisms with TL \geq 3.25 (TL3.25) and TL of the community including organisms with TL \geq 4 (TL4).

Species and size-based. These indicators are based on species traits and conservation status. Increase in species traits such as mean length could be a direct effect of marine protected areas (Claudet et al., 2006). We selected three species-based indicators: biomass of IUCN-endangered species in the community (ES, t·km⁻²·year⁻¹), mean length of fish in the community (ML, cm) and mean life span of fish in the community (MLS, year).

Flow-based. We used the Total System Throughput (TST, t-km-2-year-1), the sum of all flows in the model (consumption, export, respiration, and flow to detritus) and considered an overall measure of the "ecological size" of the system (Finn, 1976). Finn's Cycling Index (FCI, %), the fraction of the ecosystem's throughput that is recycled (Finn, 1976). Average Path Length (APL) defined as the average number of groups that flows passes through and is an indicator of stress (Christensen, 1995). Several additional indicators were selected because of their robustness in front of models' comparison (Heymans et al., 2014): the ratios of consumption (Q), export (Ex) and production (P).

Catch-based. These indicators are based on catch and discard species data in the food web. They can give an idea on the potential effect on adjacent fisheries through spillover of exploited fishes from FPAs (McClanahan and Mangi, 2000). We included six indicators: total catch (TC t·km⁻²·year⁻¹), total discarded catch (TD, t·km⁻²·year⁻¹), trophic level of the catch (TLC), intrinsic vulnerability index of catch (VI), mean length of fish in the catch (MLC, cm) and mean life span of fish in the catch (MLC, year).

Additionally, the mixed trophic impact (MTI) analysis was performed to quantify direct and indirect trophic interactions among functional groups (Ulanowicz and Puccia, 1990). This analysis quantifies the direct and indirect impacts that a hypothetical increase in the biomass of one functional group would have on the biomasses of all the other functional groups, including the fishing fleets. The MTI for living groups is calculated by constructing an $n \times n$ matrix, and quantifying each interaction between the impacting group (j) and the impacted group (i) is:

$$MTI_{ji} = DC_{ji} - FC_{ij},$$
 Eq. 2

where DC_{ji} is the diet composition term expressing how much i contributes to the diet of j, and FC_{ij} is a host composition term giving the proportion of the predation on j that is due to i as a predator.

To identify the keystone species within the ecosystem, we estimated the keystoneness index (KS) of the most important reef FG (Common pandora: *Pagellus*

erythrinus; Sparidae; White seabream: Diplodus sargus; Common two-banded seabream: Diplodus vulgaris; Common dentex: Dentex dentex; Red scorpionfish: Scorpaena scrofa; Groupers: Epinephelus sp; Brown meagre: Sciaena umbra; Labridae and Serranidae; Other commercial medium demersal fish; Salema: Salpa salpa; Mugilidae; Red mullet: Mullus barbatus; and Surmulet: Mullus surmuletus) using 3 different methods. A keystone species is a species that shows relatively low biomass but has a relatively important role in the ecosystem (Power et al., 1996). We used 3 indices: (1) Power keystone indicator (1996) (KS_P) and (2) Libralato's keystone indicator (2006) (KS_I), which are based on a measure of trophic impact derived from the MTI analysis, and a quantitative measure of biomass; and (3) Valls (2015) (KS_V) keystoneness index, in which the biomass component is based on a descending ranking. These indices are calculated as:

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$$KS_{Pi} = \varepsilon_i \frac{1}{p_i}$$
 Eq. 3

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$$KS_{Li} = \log[\varepsilon_i(1 - p_i)]$$
 Eq. 4

$$KS_{Vi} = \log[IC_i \cdot BC_i]$$
 Eq. 5

where ε_i represents the RTI; p_i is the contribution of the group i to the total biomass in the food-web; IC_i is a component estimating the trophic impact of the group i; BC_i is a component estimating the biomass of the group i.

Evaluating MPAs and the role of MUs

In order to determine the role of MUs in the functioning of the MPAs, results from ecological indicators (except catch-based indicators) and keystoneness species were compared among three MUs within an MPA. This comparison among MUs ecological indicators served to capture shifts on ecosystem structure and functioning due to the level of protection (Fortin and Dale, 2005).

To evaluate the differences among the three studied MPAs, results from ecological indicators (except catch-based indicators) and keystoneness species were compared with the same MUs of different MPAs. For instance, considering the FPAs of three MPAs allowed us to capture how different are these MPAs since they officially offer the same level of protection. Despite that each MPA differs on restriction in their PPAs, this multiple comparison procedure was developed for the three MUs because the ecological theory establishes that reserve effects should extend from FPA to beyond its boundaries as a result of spillover (Gell and Roberts, 2003b).

Impact of small-scale fisheries

To evaluate the impact of small-scale fisheries on the MPAs, catch-based indicators were examined between PPAs and UPAs of the three MPAs. The mixed trophic results of recreational and artisanal fishing fleets were examined to quantify the direct and indirect impact of each fleet on the functional groups for PPAs and UPAs of studied MPAs, and their potential competition and trade-offs between them.

3. Results

The pedigree index values of the MU models showed similar values among them (Figure 2), ranging from 0.41 to 0.52. The highest pedigree values were obtained for Cerbère-Banyuls, and regarding MUs, FPAs obtained slightly lower pedigree index than the other MUs.

The flow diagrams displayed high levels of biomass even for some high trophic level groups, especially in FPAs (Fig. 3). Also, results emphasized the complexity of these food webs regarding the number of trophic links among functional groups with important fluxes of energy from phytoplankton (FG 61 and 62) and detritus (FG 63) up to the food web.

Ecosystem structure and functional traits

Overall, biomass-based indicators displayed the same pattern between MUs (Figure 4), with the highest biomass vales found in Cerbère-Banyuls, then Medes Islands and finally Cap de Creus. Conversely, the Kempton's Biodiversity Indicator (KI) decreased from Cap de Creus to Medes Islands and then Cerbère-Banyuls, which had the lowest KI value. Within MUs, the FPAs showed the highest values in terms of total and fish biomass, and they were followed by PPA in all MPAs. In Cap de Creus we observed similar values among MUs for both indicators.

Trophic-based indicators revealed that in general the TL of the community and TL2 was higher for Cerbère-Banyuls, followed by Medes Islands, while Cap de Creus showed the lowest levels (Figure 5). Cerbère-Banyuls and Medes Islands displayed similar values for TL325 and TL4, while Cap de Creus obtained higher variance among these indicators. Specifically, Cap de Creus showed the highest TL325 values and the lowest TL4 value. Within MUs, most trophic-based indicators showed the highest values for FPAs followed by PPAs and UPAs. However, FPA in Cap de Creus displayed the lowest value of TL4 (Fig. 5).

Flows-based indicators showed differences between MPA. Cerbère-Banyuls showed the highest values for Q/TST, TST, FCI and APL, while the lowest values for Ex/TST and P/TST (Figure 6). Inversely Cap de Creus showed the lowest values for Q/TST, whilst the highest values for Ex/TST and P/TST. Medes Islands values were located between these two MPAs. Considering MU values, flow-based results revealed higher values for FPAs followed by PPAs in most of the flows-based indicators. As an exception, Ex/TST and P/TST were higher for UPAs and lower for FPAs.

Results from species and size-based indicators (Figure 7) pointed out that Cerbère-Banyuls got the highest values for IUCN species B, followed by Medes Islands. Regarding ML and MLS, the highest values were also obtained for Cerbère-Banyuls, followed by Cap de Creus and then Medes Islands. Species and size-based indicators were higher for FPAs, except in Cap de Creus, where PPA had higher values of ML and MLS than FPA.

All keystoneness indices (Figure 8; Supplementary material appendix 3) for the nine models identified the same groups as keystone: Groupers, Other commercial medium demersal fish, Common dentex and Labridae & Serranidae. Particularly, Groupers obtained the highest relative total impact. These results confirmed that these functional groups play an important ecological role in these Mediterranean coastal ecosystems. Keystoneness indices showed different patterns among MUs and MPAs. Medes Islands models obtained the highest number of keystone species followed by Cerbère-Banyuls (Figure 8).

Role and impact of small-scale fisheries

Total catch and discards showed similar values between Cap de Creus and Medes Islands, while Cerbère-Banyuls presented the lowest values (Figure 9). IV values were similar for Cap de Creus and Cerbère-Banyuls, and the lowest IV values were found for Medes Islands. TLc was higher for Cerbère-Banyuls and Cap de Creus and lower for Medes Islands (Figure 9), and these results are in line with MLSc results (Figure 7). Also, Cerbère-Banyuls obtained the highest value for MLc while Cap de Creus got the lowest values. TC and discards exhibited higher values for PPAs than UPAs. IV indexes were higher for PPAs than UPAs except for Cerbère-Banyuls. TLc values were similar between PPA and UPA in Cap de Creus and Medes Islands, while it was higher for PPA in Cerbère-Banyuls. ML and MLS results evidenced similar values between MUs for Medes Islands, while PPA obtained higher values in Cap de Creus and lower in Cerbère-Banyuls.

The MTI analysis based on the recreational fisheries (Figure 10) revealed that the impact of recreational fisheries to the functional groups in the ecosystem were clearly higher than the impacts of these groups to recreational fisheries (between -0.86 and 0.84 and -0.15 and 0.26, respectively). The highest impacting and impacted values were found for PPA in Cap de Creus, where impacted values were higher for PPA in Cerbère-Banyuls (positively on Sparidae and negatively on Brown meagre, Common dentex and Groupers) and Medes Islands (positively on Common two-banded seabream and Red scorpionfish). Impacts on recreational fisheries were low (close to zero) for most groups except for Groupers and Sparidae in Cerbère-Banyuls due to their higher catches and thus their importance to recreational fisheries.

In line with impacts of recreational fisheries, impacts of artisanal fisheries (Figure 11) were higher and more fluctuating than impacts of functional groups to artisanal fisheries (ranging from -0.80 to 0.77 and -0.32 to 0.12, respectively). Generally, artisanal impact results did not evidence great differences between MUs. The highest artisanal fisheries impacting values were obtained in Cerbère-Banyuls, with some exceptions for negative impacting values of some groups (Common pandora and Red mullet) in Cap de Creus. Artisanal fisheries impacted results displayed low values (close to zero), except for Groupers group which highly negatively impacted on the artisanal fishery of PPA in Cap de Creus.

Overall, the MTI analysis based on fisheries did not show any pattern among MUs and MPAs, and fisheries impacting values were clearly higher and more fluctuating than impacted values (ranging from -0.86 to 0.84 and -0.32 to 0.26, respectively). Mostly, impacts of recreational fisheries were higher for the PPA of Cap de Creus, while impacts of artisanal fleet were higher for Cerbère-Banyuls. Specifically, MTI analysis revealed that the impacts of recreational fisheries were greater (positively and negatively) for Brown meagre and Groupers. On the other hand, the recreational fishery was highly (positively) impacted by Other commercial medium demersal fish and Sparidae (Figure 10). Regarding artisanal fishery, Brown meagre, Other commercial medium demersal fish and Red mullet were positively impacted by recreational fisheries, while Common dentex and Groupers were negative impacted (Figure 11). Groupers was the most impacting (negatively) group on the artisanal fishery. Recreational and artisanal fishery obtained low impacted and impacting values between them. Among them, the highest impact was for the recreational impact on artisanal in the PPA of Cap de Creus (0.28).

4. Discussion

We built nine quantitative models to investigate the differences among MUs of three MPAs in the NW Mediterranean Sea. To our knowledge, this is the first attempt to develop a food-web model for each MUs within MPA to assess the impact of protection at local scales at the ecosystem level.

The pedigree index values revealed that the input data were qualitatively acceptable compared to the distribution of pedigree values in other existing models (Lassalle et al., 2014; Morissette, 2007). Also, the pedigree values of the models was comparable to that from the available MPA model in the Western Mediterranean Sea (e.g., 0.49 in (Prato et al., 2016b). However, FPAs showed the lowest pedigree values, although they are aimed to be protected and well monitored. Overall, these results highlight the need to further study and monitor MPAs within the Mediterranean Sea.

The flow diagram showed differences among MUs. Although the TL were similar among three MUs in each MPA, some commercial functional groups (e.g. FG 26 – Groupers in Cerbère-Banyuls) showed higher values for FPAs. This pattern could be due to the effect of protection in these areas which may be connected with the complexity of the food web and the maturity of the ecosystem (Odum and Barrett, 1971).

Ecological indicators showed differences among MUs and pointed out de strong benefits of FPAs (Sala et al., 2017). FPAs (also known as no-take areas) are widely recognized as a powerful tool for an ecosystem approach to fisheries management and for biodiversity conservation (Claudet et al., 2008) and several studies described their positive effects on biomass (Guidetti et al., 2014), trophic levels (Guénette et al., 2014), mean length (Claudet et al., 2006), mean life span (Guénette and Pitcher, 1999) and biomass of IUCN species such as groupers (Claudet et al., 2008). In our study, consumption rate over total system flows was higher in FPAs than PPA and UPA, because of the higher the biomass in the ecosystem the higher the consumption in the ecosystem. Libralato et al. (2010) found similar results for another Mediterranean MPA due to the effect of protection. The same pattern was found for TST, APL and FCI, in which the value of the indicator increases with the level of protection. These indicators suggested lower stress, more maturity, more ecological size and higher resilience (Christensen, 1995) for FPAs ecosystems. In line with these results, Sala et al., (Sala et al., 2017) highlighted the potential benefits of FPAs and pointed out that these areas are more resilient than UPAs. In addition, most biomass-based, trophic-based, species-based and flows-based results

obtained from PPAs demonstrated their role as buffer zones (Giakoumi et al., 2017), so they may confer biomass enhancement compared to UPAs although FPAs produce greater benefits (Lester and Halpern, 2008; Sciberras et al., 2015).

In contrast, the biodiversity index (KI) did not show the expected pattern as biodiversity is expected to increase with protection (Costello and Ballantine, 2015). This controversial result could be due to the available data, which came from different studies for each MPA and year. Therefore as more exhaustive species biomass data are available, the biodiversity index becomes more reliable (Claudet, 2013; Hereu Fina et al., 2017). In addition, export ratio and production ratio results showed higher values for UPAs because the biomass of several FGs (such as Sparidae or Groupers) were quite high to support their feeding rates. These FGs would migrate beyond the boundaries of the modelled ecosystem (MU), which are relatively small compared to the dispersal rate of those species (Di Franco et al., 2012).

The indicators displayed differences among MUs within each MPA, especially in the case of Cerbère-Banyuls and Medes Islands MPAs, but not for Cap de Creus. Probably, these pattern could be explained by their enforcement, reported to be a key factor to promote direct and indirect reserve effects (Guidetti et al., 2008). The lack of enforcement is one of the most relevant issues concerning MPAs in the Mediterranean context (Fenberg et al., 2012). Claudet and Guidetti (2010) recognized that an MPA without enforcement and compliance is just a paper park and no reserve effects can be expected. This could be the case of Cap de Creus, in which our results did not show the same pattern found for the other two MPAs. In fact, Lloret et al. (2008b, 2008a) reported a lack of enforcement and a low level of compliance in Cap de Creus, particularly on minimum landing sizes of certain species or lacking fishing license. This is in contrast with Cerbère-Banyuls and Medes Islands MPAs, in which ensuring compliance and enforcement promote a high level of ecological effectiveness (Di Franco et al., 2014). Our results are also consistent with previous studies performed in Cerbère-Banyuls (Harmelin-Vivien et al., 2008) and Medes Islands (Harmelin-Vivien et al., 2008; Sala et al., 2012), which demonstrated reserve effects for those MPAs and reported higher biomass in FPAs with a rapid declining from FPAs outward. Giakoumi et al. (2017) revealed significant stronger biomass effect for FPAs than PPAs and higher fish density in older, better enforced, and smaller MPA. Considering that Cap de Creus has the smallest FPA and is the newest (Table 1) and least enforced MPA in the study, our results suggest that the year of establishment and level of enforcement have a strong effect on MPA effectiveness. These pattern among MPAs were also found by E Costa *et al.* (2016) who presented a novel classification system for MPAs which ranges from 1 (fully protected areas) to 8 (unprotected areas). In this scale, Cerbère-Banyuls obtained a rate of 4.7, being a highly protected area, and Medes 6.4, being less well protected (e Costa et al., 2016). Cap de Creus was not included in this study, but we could assume higher MPA index because of its small FPA and its lack of enforcement. Overall, our results call for enhancement on the regulations, increasing the surface of FPAs and the enforcement of management rules in Medes and Cap de Creus MPA.

All keystoneness indices for the nine models pointed out the same functional groups as keystone. Among them, Grouper and Common dentex were highlighted as keystone groups in previous western Mediterranean MPAs models (Prato et al., 2016a; Valls et al., 2012). KS_L (Libralato et al., 2006) clearly showed that the keystone role of species increases with the level of protection, so the highest KS_L values were found in FPAs. It demonstrates its possible application to capture biological and ecological effects of protection because it tends to underestimate the role of groups with low biomass (as Libralato et al., 2010). KS_P (Power et al., 1996) showed a different pattern because it assigns high keystoneness to FGs with high abundance allowing confusion between dominant and structuring species and overrepresenting rare species (Coll et al., 2013). The KS_V (Valls et al., 2015) showed higher values for species such as Groupers and Common dentex in non-fully protected areas (PPAs and UPAs) because it avoids underrepresenting rare species and aims at better balancing the two components of the keystoneness definition, impact and abundance.

MPAs are considered an important tool to manage coastal fisheries (Claudet et al., 2006), and enforcement is a key aspect to achieve these goals. Our results show that well-enforced MPAs can enhance small-scale fishery (artisanal and recreational) by spillover effect and promote the sustainability of local fisheries (Forcada et al., 2009; Goñi et al., 2011; Sala et al., 2013). According to the spillover effect, total catch and discards were higher in PPAs than in UPAs for all MPAs. Exceptionally, results of MUs in Cap de Creus differed substantially from Cerbère-Banyuls and Medes Islands. This could be related to the position of its FPAs, which is not located in the core of the MPA and surrounded by the PPA, which is the common MPA design in the Mediterranean Sea (Gabrié et al., 2012) and could reduce PPAs effectiveness. High values of total catch and discards in Cap de Creus

could be related to the non-compliance, as well as to the lack of geolocated catch data, which could have biased our results. Non-compliance could result in some fishing inside FPAs and PPAs, which may reduce the effectiveness of their potential biological, ecological and fisheries benefits (Roberts, 2000), in accordance with above conclusions obtained from other ecological indicators (e.g. Biomass-based indicators). In addition, estimates of IV and ML from Cap de Creus could be explained as a failure in the enforcement. On the other hand, we hypothesized that TLc and MLS values were obtained as a result of the targeted species by the recreational fishery in each MPA, and the different level of protection in PPAs (Ivanoff et al., 2010; Sacanell, 2012). Considering the concept of "fishing the line", which can jeopardize the success of an MPA (Kellner et al., 2007), understanding spatial-temporal patterns of fishing effort around a MPA is a key aspect to manage and assess these areas. In this context, Stelzenmüller et al. (Stelzenmüller et al., 2008) found a local concentration of fishing effort around the borders of Cerbère-Banyuls and Medes Islands MPAs, in accordance with our results.

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The mixed trophic impact analysis results highlighted the impact of recreational fisheries in Cap de Creus among the rest of studied MPAs, in agreement with the failure on the sustainable management and its contribution to adjacent fisheries because of nonenforcement (Lloret et al., 2008b, 2008a). PPAs showed higher impacted values than UPAs, which suggest a higher contribution of PPAs to the recreational fishery. Although PPAs may differ on their level of protection (Lester and Halpern, 2008), for example spearfishing is not allowed inside the PPA of Cerbère-Banyuls (Font et al., 2012b), these results confirmed their ecological effects and benefits for adjacent fisheries. For instance, recreational fishery impacted negatively on Groupers in all MPAs, which reflected that this is a target species. The recreational fishery is impacted positively and negatively by Groupers which could be explained by feeding behavior and fleet behavior such as competition between fishery and FG. Groupers were negatively impacted by artisanal fishery because of their catch, especially in Cerbère-Banyuls (Prats, 2016). Regarding the artisanal fishery, the highest negative impacting values were represented by targeted species for this fleet, while positive values may represent FGs which are prey of those targeted species. Cerbère-Banyuls obtained higher impacting values than other MPAs. Since it is a well enforced MPA, it could represent higher benefits or catches than other MPAs. In addition, most highlighted FGs by their high impacting values in artisanal fishery matched with the keystone species, which support that non-enforced marine protected areas may compromise positive effects of these ecosystems (Claudet and Guidetti, 2010).

Our results encourage fishermen compliance, which is key for fisheries' success such as in Torre Guaceto MPA, where co-management involving fishers, scientists and managers increased fisheries catches (Guidetti and Claudet, 2010).

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Even though our work showed that quantitative food-web modelling techniques can be useful to assess MPAs effects on the structural and functional traits of marine ecosystems and their adjacent fisheries, some limitations were found during this study. One of the main hurdles was the lack of local data for some FGs identified in previous MPAs modelling studies (Prato et al., 2016b; Valls et al., 2012). For example, literature including benthonic biomass estimations inside MPAs is mainly focused on sea urchin, gorgonian and Posidonia (e.g. (Hereu et al., 2012; Schvartz and Labbe, 2012). However, studies about other important benthic groups such as sponges or crustaceans are scarce. Additionally, spatial-temporal series of catches and fleet distribution would improve the analysis on the effect of MPA potential benefits on the recreational and artisanal fishery. We did not find studies on artisanal and recreations fishery including estimates of temporal catches in Cap de Creus and Medes Islands MPAs. Collecting time series of fishing activities surrounding MPAs is a monitoring priority, as previously highlighted (Prato et al., 2016b; Valls et al., 2012). A recent published study (Lloret et al., 2019), which focused in the northwestern Mediterranean Sea, emphasized the importance of differentiating between fishing methods or gears when studying the impacts on vulnerable species in MPAs which could be accomplished if data are available. Moreover, our results could be biased by the oceanographic conditions and the structure of the modelled MPAs (Heymans et al., 2016). In addition, and despite that these MPAs are closely located, the biomass estimations to develop the models came from different reference years which could limit the comparison among MPAs as a result of different environmental conditions (Sala et al., 2012). The structure, habitat and design of the MPAs also could represent another limitation (Charton et al., 2000) because we are modelling different environments: archipelago, coastal with covered FPA and coastal exposed FPA.

Despite these limitations, this work represents to our knowledge the first attempt to model management units within a protected area and it provides the basis to assess the role of these areas within a network of MPAs using a food-web modelling approach. These results highlight the capability of the EwE modeling approach to capture protection effects in such small areas despite data limitations. Our results suggest that enforcement can have an impact regarding the potential benefits of MPAs at the local scale, and a lack of

- 606 enforcement is noticeable in surrounding areas. Protected areas can increase their
- 607 maturity and resilience and show potential benefits for small-scale fisheries that act in their
- 608 surroundings when these areas are well-enforced. Future assessments on the role of
- these MUs should assess their role within a network to quantify their impacts at a sub-
- 610 regional (e.g. Northwestern Mediterranean) and regional (e.g. Western Mediterranean)
- 611 geographic scales.

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Supplementary data

- 618 Additional Supplementary material may be found in the online version of this article:
- Appendix 1. Supplementary tables: Cerbère-Banyuls, Cap de Creus and Medes MPAs
- 620 functional groups species composition and methods and references used to estimate the
- basic input parameters of the nine Ecopath model (Table S1.1.); Input parameters and
- outputs estimate for Cerbère-Banyuls (Table S1.2.), Cap de Creus (Table S1.3.) and
- 623 Medes Islands (Table S1.4.) MU models.
- 624 Appendix 2. Supplementary tables: Diet composition matrix for the MU models of
- 625 Cerbère-Banyuls (Table S2.1.), Cap de Creus (Table S2.2.) and Medes Islands (Table
- 626 S2.3.) MPA.
- 627 Appendix 3. Supplementary tables: Keystone indexes and Relative Total Impact values
- for the functional groups included in Cerbère-Banyuls (Table S3.1), Cap de Creus (Table
- 629 S3.2) and Medes Islands (Table S3.3) MU models. FPA: Fully Protected Area; PPA:
- 630 Partially Protected Area; UPA: Unprotected Area.

References

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Figures and Tables

Figure captions

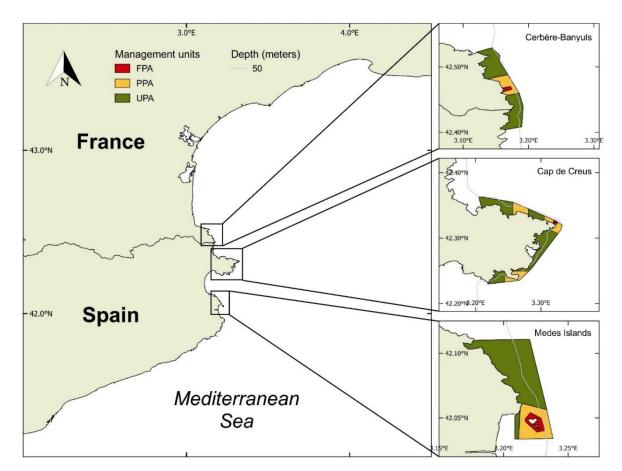


Figure 1. Location of three modelled MPAs and their MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) in Cerbère-Banyuls, Cap de Creus and Medes Islands.

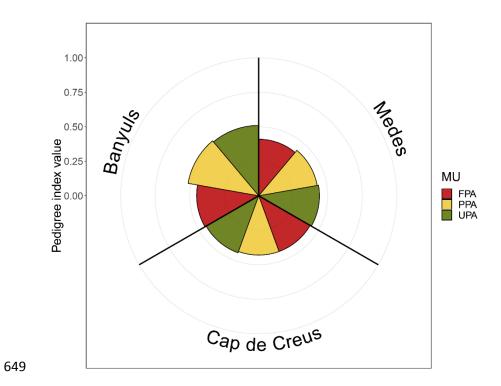
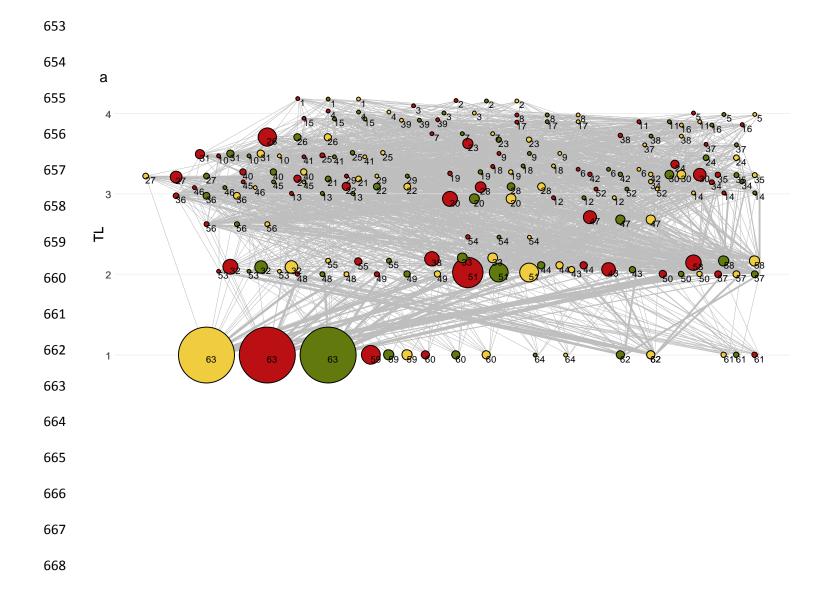
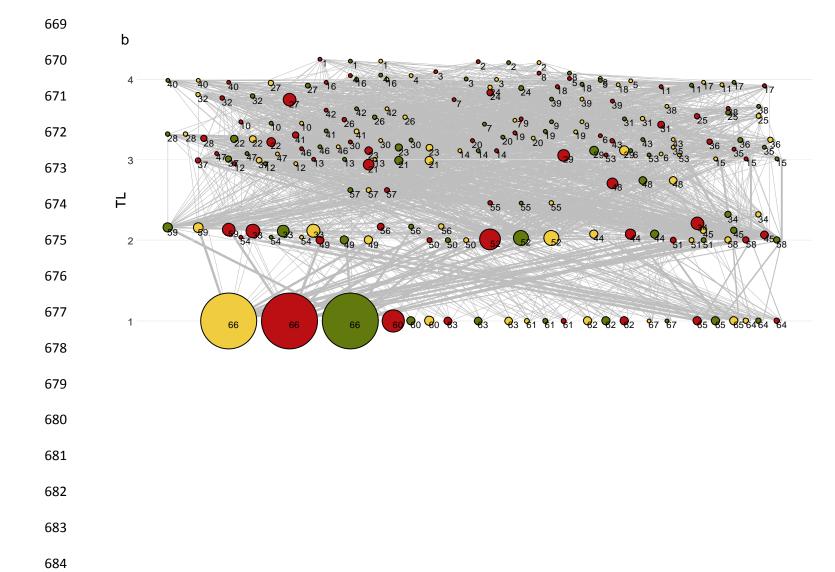


Figure 2. Pedigree index values of three MUs models (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).





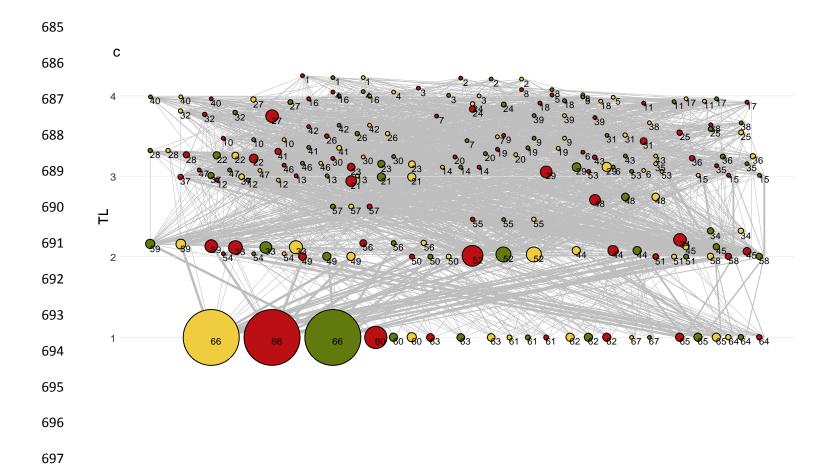


Figure 3. Flow diagram of fully protected areas (FPAs) of (a) Cerbère-Banyuls MPA, (b) Cap de Creus and (c) Medes Islands MPA models organized by Trophic Levels (y-axis). The size of each circle is proportional to the biomass of the functional group. The wideness of the connecting lines is proportional to the magnitude of their flows.

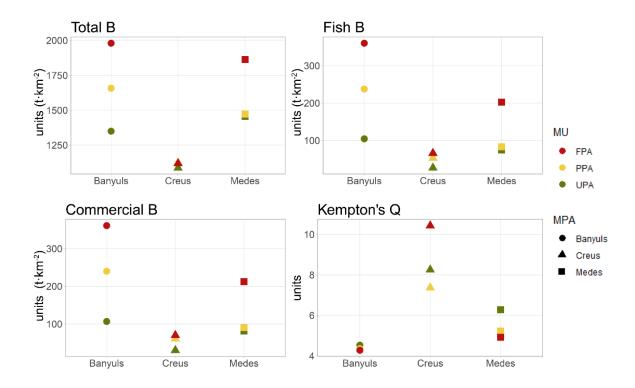


Figure 4. Biomass-based indicators of three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

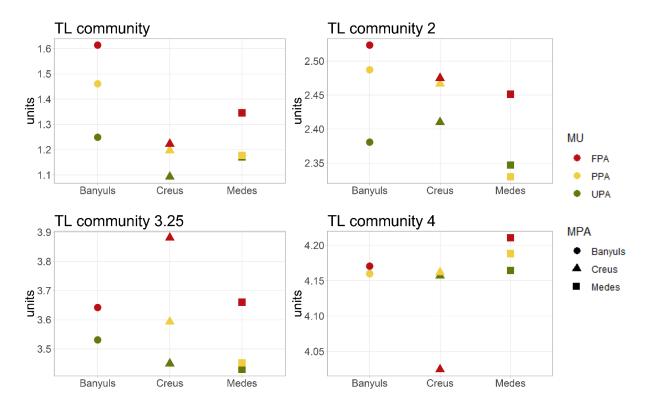


Figure 5. Trophic-based indicators of three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

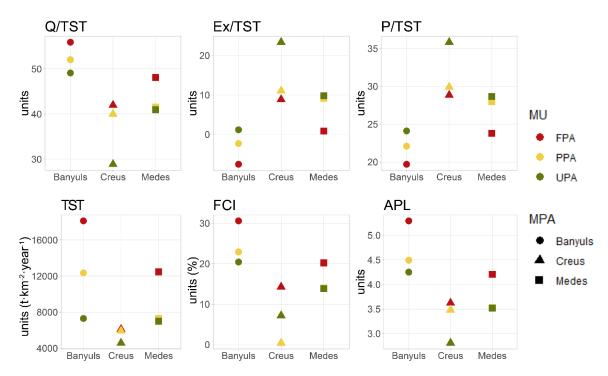


Figure 6. Flow-based indicators of three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

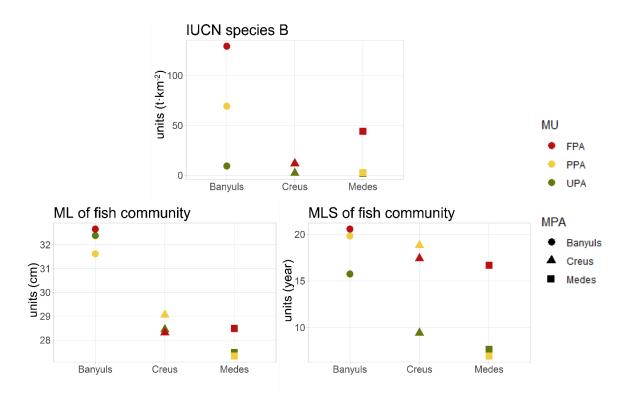


Figure 7. Species-based indicators of three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

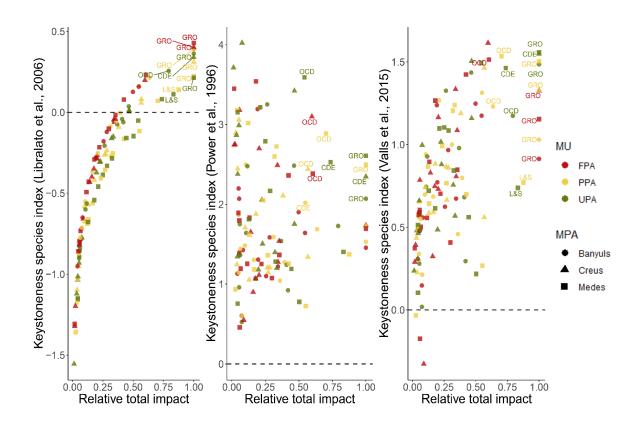


Figure 8. Keystone Index analysis of three MU (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). The acronyms identify the functional group with highest keystoneness index and relative total impact. (GRO – Groupers; CDE – Common dentex; OCD – Other commercial medium demersal fishes; L&S – Labridae and Serranidae).

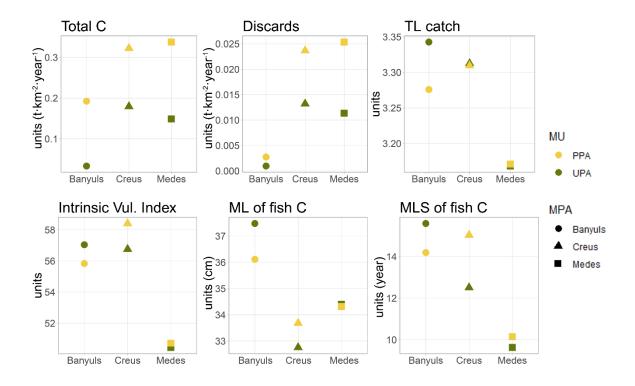


Figure 9. Catch-based indicators of three MUs (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

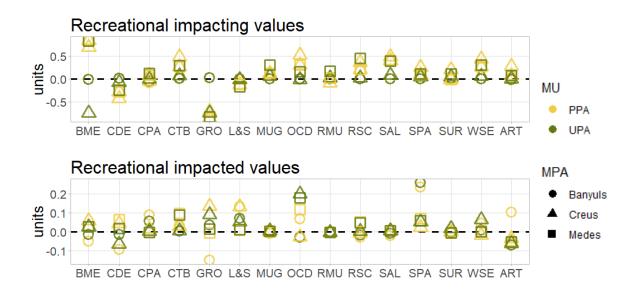


Figure 10. Recreational impacting and impacted values of three MUs (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (BME – Brown meagre; CDE – Common dentex; CPA – Common pandora; CTB – Common two-banded seabream; GRO – Groupers; L&S – Labridae and Serranidae; MUG – Mugilidae; OCD – Other commercial medium demersal fishes; RMU – Red mullet; RSC – Red scorpionfish; SAL – Salema; SPA – Sparidae; SUR – Surmulet; WSE – White seabream; ART – Artisanal fishery).

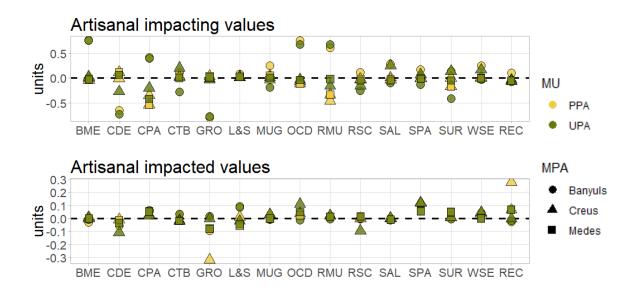


Figure 11. Artisanal impacting and impacted values of three MUs (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (BME – Brown meagre; CDE – Common dentex; CPA – Common pandora; CTB – Common two-banded seabream; GRO – Groupers; L&S – Labridae and Serranidae; MUG – Mugilidae; OCD – Other commercial medium demersal fishes; RMU – Red mullet; RSC – Red scorpionfish; SAL – Salema; SPA – Sparidae; SUR – Surmulet; WSE – White seabream; REC – Recreational fishery).

Tables

Table 1. Surface area (km²) covered by management unit (MU) and year of creation of each marine protected area (MPA) and their year (Cerbère-Banyuls, Cap de Creus and Medes Islands).

MPA	Year of creation	MU		
		FPA	PPA	UPA
Cerbère-Banyuls	1974	0.65	5.85	35.00
Cap de Creus	1998	0.21	7.98	22.37
Medes Islands	1983	0.39	4.24	14.85

Table 2. Functional groups included for the MU models showing those present (P) or absent (A) in each MPA. FG = Functional Group. Discards only are included in PPA and UPA models.

FG number	FG name	Cerbère-Banyuls	Cap de Creus	Medes Islands
1	Bottlenose dolphins	Р	Р	Р
2	Striped dolphins	Р	Р	Р
3	Endangered and pelagic seabirds	Р	Р	Р
4	Gulls and cormorants	Р	Р	Р
5	Terns	Р	Р	Р
6	Loggerhead turtles	Р	Р	Р
7	Non-commercial large pelagic fishes	P	P	P
8	Other large pelagic fishes	Р	Р	Р
9	Mackerels	P	Р	Р
10	Horse mackerels	' P	Р	, P
11	Other medium pelagic fishes	' P	Р	' P
12		r P	P	P
	European sardine	r P		P
13	European anchovy	•	P	
14	Round sardinella	A	Р	P
15	Other small pelagic fish	P	Р	P
16	Anglerfish	P	P	P
17	European conger	Р	Р	Р
18	European hake	Р	Р	Р
19	Poor cod	Р	Р	Р
20	Common pandora	Р	Р	Р
21	Sparidae	Р	Р	Р
22	White seabream	Р	Р	Р
23	Common two-banded seabream	Р	Р	Р
24	Common dentex	Р	Р	Р
25	Red scorpionfish	P	P	P
26	Scorpaenidae	P	P	P
27	Groupers	P	Р	P
28	Brown meagre	P	Р	P
29	Labridae and Serranidae	P	P	P
30	Flatfishes	r P	P	P
		r P	P	
31	Other commercial medium demersal fish			P
32	No commercial medium demersal fish	P	P	P
33	Salema	P	P	Р
34	Mugilidae	P	P	P
35	Red mullet	P	P	P
36	Surmulet	Р	Р	Р
37	No commercial small demersal fish	Р	Р	Р
38	Small-spotted catshark	Р	Р	Р
39	Rays and skates	Р	Р	Р
40	Torpedos	Р	Р	Р
41	Coastal benthic cephalopods	Р	Р	Р
42	Benthopelagic cephalopods	Р	Р	Р
43	Other benthic cephalopods	Р	Р	Р
44	Bivalves	Р	Р	Р
45	Gastropods	Р	Р	Р
46	European lobster	Р	Р	Р
47	Other commercial decapods	P	P	P
48	Non-commmercial decapods	P	Р	P
49	Purple sea urchin	' P	Р	r P
50	Other sea urchin	r P	P	P
50 51		P P	P	P P
	Sea cucumbers			
52	Other macro-benthos	P	P	P
53	Jellyfish	P	P	P
54	Salps and other gelatinous zooplankton	P	Р	P
55	Red coral	Р	Р	Р

56	Other corals and gorgonians	Р	Р	Р
57	Macrozooplankton	Р	Р	Р
58	Meso and microzooplankton	Р	Р	Р
59	Suprabenthos	Р	Р	Р
60	Mediterranean seagrass	Р	Р	Р
61	Other seagrasses	Α	Р	Р
62	Erected algae	Α	Р	Р
63	Seaweeds	Р	Р	Р
64	Small phytoplankton	Р	Р	Р
65	Large phytoplankton	Р	Р	Р
66	Detritus	Р	Р	Р
67	Discards	Р	Р	Р