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

Journal:	<i>Aquatic Conservation: Marine and Freshwater Ecosystems</i>
Manuscript ID	AQC-19-0295.R1
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
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The effects of marine protected areas on ecosystem recovery and fisheries using a comparative modelling approach

Authors

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Abstract

1. The overexploitation of many marine resources and ecosystems calls for the development and implementation of measures to support their recovery and conservation.
2. The potential contributions to support fisheries and ecosystem recovery were assessed at the local level of the three multiple-use Marine Protected Areas (MPAs) of Cerbère-Banyuls, Medes Islands and Cap de Creus, located in the Northwestern Mediterranean Sea.
3. For each MPA, a food-web model accounting for each protection level (PL) was developed: the fully protected area (FPA), the partially protected area (PPA) and the unprotected area (UPA) surrounding the MPA. Using the resulting nine food-web models, the ecosystem structure and functioning of each PL were compared and characterized, differences and similarities within and among the three MPAs were assessed, and ecosystem response to fully protection was evaluated for the three MPAs.

4. Differences in terms of ecosystem structure and functioning were found among PLs. Overall, FPAs presented the most positive effect of protection in terms of ecosystem structure and functioning, followed by PPAs. However, the effects of protection on neighbouring unprotected areas were hardly noticeable.
5. Similarities between Cerbère-Banyuls and Medes Islands MPAs were observed, while Cap de Creus MPA showed the least benefits from protection overall. These results are likely due to similarities in the configuration of the protected areas, the levels of enforcement and compliance, and the impact of recreational and small scale fisheries allowed in the PPAs and UPAs.
6. This study illustrates that well-enforced Mediterranean MPAs, even when small, can yield local positive impacts on the structure and functioning of marine ecosystems that can contribute to support local fisheries.

Keywords: Protection levels, fully protected areas, partially protected areas, Ecopath with Ecosim, NW Mediterranean Sea

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3 72 **1. Introduction**
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5 73 Marine ecosystems have been degraded at high rates under the cumulative
6 74 impact of multiple anthropogenic activities (Costello *et al.*, 2010; Halpern *et al.*,
7 75 2015). In 2010, the United Nations' Convention on Biological Diversity (CBD)
8 76 established a target of 10% of the ocean to be protected by 2020 ("Aichi Target 11")
9 77 (CBD, 2010). Marine protected areas (MPAs hereafter) are an essential tool for
10 78 reversing the global degradation of ocean life (Claudet *et al.*, 2008; Babcock *et al.*,
11 79 2010; McCauley *et al.*, 2015). Several studies have shown that protection from
12 80 fishing leads to rapid increases in abundance, size and biomass of exploited species
13 81 and, sometimes, to an increase in species diversity (e.g. Claudet *et al.*, 2010; Di
14 82 Franco *et al.*, 2018; Lester *et al.*, 2009). However, only 3.7% of the world's ocean is
15 83 currently protected with MPAs (Sala *et al.*, 2018).
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17 84 MPAs can also provide socio-economic benefits. Economic benefits may
18 85 stem from the creation of employment opportunities through the development of non-
19 86 consumptive activities such as tourism and recreation (Roncin *et al.*, 2008), or from
20 87 securing future jobs by increasing the chances of managing stocks sustainably
21 88 (Sumaila *et al.*, 2000). Fisheries benefits arise from ecological effects within
22 89 protected areas in the form of biomass recovery, and subsequent spillover outside
23 90 the boundaries of the MPA (Di Lorenzo *et al.*, 2016) or by increased larval production
24 91 and supply to unprotected areas (Marshall *et al.*, 2019), with MPAs finally
25 92 replenishing external fisheries grounds. Actually, empirical studies comprising small
26 93 scale (Stelzenmüller *et al.*, 2008), recreational (Font *et al.*, 2012a) and industrial
27 94 bottom-trawling fishing effort (Murawski *et al.*, 2005) showed a concentration of
28 95 fishing activities in the close vicinity of the MPA boundaries. This concentration of
29 96 fishing effort, also known as "fishing the line", can reduce the biomass in
30 97 neighbouring unprotected areas.
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32 98 Most MPAs are multiple-use (Claudet, 2018). They combine different levels
33 99 of protection within a spatially zoned management scheme that can encompass fully
34 100 protected areas (FPA, also known as no-take areas), where all extractive activities
35 101 are prohibited, or a type of partially protected areas (PPAs), where some fishing
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activities are allowed but with varying restrictions (Lubchenco and Grorud-Colvert, 2015; Horta e Costa *et al.*, 2016; Giakoumi *et al.*, 2017). Multiple management uses in MPAs can have strong implications in terms of ecosystem and fisheries benefits at the larger scale (i.e. regional). Recent studies showed that ecological benefits can be observed in fully and highly protected areas, while lower levels of protection provide benefits only under specific conditions (i.e. when surrounded by a fully protected area; (Zupan *et al.*, 2018b). In addition, when allowed in a given zone of an MPA, fishing exploitation can become a threat for the overall MPA (Zupan *et al.*, 2018a).

While MPAs are an ecosystem-based management tool, it is still unclear how the functioning of ecosystems is affected by protection - in particular, how different levels of protection in multiple-use MPAs translate into ecosystem reorganizations, and how ecosystem response to different levels of protection transfer into fisheries benefits. Here, using food-web modelling techniques, different levels of protection in multiple-use MPA were quantitatively modeled and their ecosystem structural and functional trait responses were compared. Three Mediterranean MPAs were used as case studies to develop ecosystem models for each protection level in each MPA.

2. Material & Methods

Study areas

Different protection levels (PLs) in three MPAs in the North-western Mediterranean Sea were examined: Cerbère-Banyuls MPA in France, Cap de Creus and Medes Islands MPAs in Spain (Figure 1). A PL was identified as an area included in an MPA or its surroundings which is classified by its level of protection (fully, partially or unprotected).

These three MPAs were selected because of their similar bathymetric ranges, habitat composition, spatial proximity, and because each MPA combines different levels of protection within a spatially zoned management scheme (Table 1 and Figure 1). Each of the three MPAs has a fully protected area (FPA) at its core, where fishing is not allowed. Neighbouring partially protected areas (PPAs) allow restricted

uses such as small-scale (traditional/artisanal) fisheries (Zupan *et al.*, 2018a). Last, unprotected areas (UPAs) surround each MPA.

In order to model the functioning of each MPA and the influence of the protected area on the unprotected area, the FPA, PPA and UPA zones in isolation were modelled. The boundaries of UPAs were selected as all areas adjacent to the MPA with similar ecological characteristics (Figure 1).

Ecosystem modelling approach

PL models were developed using the Ecopath with Ecosim approach (EwE 6.6 version) (Christensen and Walters, 2004; Christensen *et al.*, 2008) and followed the best practices rules (Heymans *et al.*, 2016).

Ecopath is a mass-balanced model based on two main equations. The first master equation describes the energy balance for each functional group in the model, so that:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad \text{Eq. 1}$$

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:

$$P/B_i \cdot B_i = P/B_i \cdot B_i \cdot (1 - EE_i) + \sum_j (Q/B)_{ji} \cdot B_i \cdot DC_{ji} + Y_i + NM_i + BA_i \quad \text{Eq. 2}$$

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.

Model parametrization

An ecosystem model was built for each protection level, i.e. for each combination of the three MPAs and three protection levels (FPA, PPA and UPA).

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

Species presence and their biomass were aggregated in functional groups (FGs) of species or groups of species clustered according to their trophic ecology, commercial value, and abundance in the ecosystem. The meta-web structure previously defined for the Western Mediterranean Sea model (Coll *et al.*, 2019) developed under the SafeNet Project¹ context was followed. This meta-web structure was adapted to local conditions, removing those FGs which did not occur in the study areas. The final food-web structure of Cerbère-Banyuls MPA contained 64 functional groups (two marine mammals, three seabirds, one sea turtle, eight pelagic fish, 25 demersal fish, three cephalopods, 14 invertebrates, 2 primary producers, two zooplankton, two phytoplankton and two detritus), while Cap de Creus MPA and Medes Islands MPA had 67 functional groups each (two marine mammals, three seabirds, one sea turtle, nine pelagic fish, 25 demersal fish, three cephalopods, 14 invertebrates, four primary producers, two zooplankton, two phytoplankton, and two detritus) (supplementary material Table S1.1). Except in the case of FPAs, which do not have discards because all fishing extractions are forbidden, food-web structures of each PL in the same MPA were identical.

FGs' biomass were obtained from different sources from the study area or surrounding areas (see supplementary material Table S2.1. for details on the parameterization of each functional group). The nine PL models share biomass data on some FGs (marine mammals, seabirds, sea turtles, pelagic fish, some invertebrates' groups, primary producers, zooplankton and phytoplankton) for two main reasons: the lack of local data and/or the closeness among these MPAs. The

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

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rest of the FGs were parameterized with local information available from field studies for Cerbère-Banyuls (underwater visual census, UVC) (Claudet, 2013) and literature for Cap de Creus and Medes Islands models (García-Rubies and Zabala i Limousin, 1990; Macpherson *et al.*, 2002; Hereu Fina and Quintana Pou, 2012; Hereu Fina *et al.*, 2017) (supplementary material Table S2.1.) except for some non-reef fish and invertebrates' FG. For these non-reef fish FG (e.g. anglerfish), MEDITS trawling survey (Bertrand *et al.*, 1997) data were extracted with a new software developed for SafeNet Project, MEDITS data explorer v. 1.5.1 (Steenbeek, 2018a). This tool allowed us to extract MEDITS data easily, and to scale biomass data to the area and bathymetric ranges. MEDITS trawling survey data were extracted from the closest point to each MPA, in order to have biomass data for those species that were not present during field studies. Those species are present in the MPAs, but they are less important in MPAs in terms of biomass. This assumption was assessed previously with expert knowledge from the project. For invertebrates' FGs whose biomass estimates were not available, realistic EE values were used to estimate the biomass of four FGs in Cerbère-Banyuls models and six FGs in Cap de Creus and Medes Islands models (supplementary material Table S2.2.). Additionally, scaling factors were used on biomass data of pelagic fish groups available from the MEDITS oceanographic survey, which does not fully cover coastal areas. Thus, this scaling enabled to adapt the estimates and get more accurate biomass values 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.

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 models developed in the Mediterranean Sea (Coll *et al.*, 2019) (supplementary material Table S2.1). Additionally, local body lengths of reef-associated species obtained from UVC (Di Franco, 2018) were used to estimate P/B and Q/B rates using empirical equations and local data (Pauly, 1980).

Diet matrices (supplementary material Appendix 3, Tables S3.1., S3.2. and S3.3.) were built using diet information which was compiled using published studies

on stomach content analyses, giving preference to local or surrounding areas (supplementary material Table S2.1.). Diet Matrix Calculator (Steenbeek, 2018b), a custom-build extraction tool, was used to automatize the process of selecting and scaling diet data. Drawing on a large library of published diet studies, the Diet matrix calculator tool selects the most likely suitable diet studies for a specific model area, based on a range of criteria, and generates a diet composition matrix with accompanying pedigree index for each predatory functional group. Due to the small sizes of the PLs investigated and the capacity of some species to move between PLs (Gell and Roberts, 2003a; Grüss *et al.*, 2011), a fraction of the diet composition of these species was set as import for all PLs based on the time that these species feed outside the areas and their ecological traits. This import was based on the size, behaviour, 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 S2.1) and the information on catches was split into two fishing fleets – recreational and professional small scale (except for FPA models where fishing activities are not allowed). Regarding professional small scale fisheries catches, Cerbère-Banyuls data 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 fleets operating are located, and were scaled by the months of fishing activity of the fleets inside the MPA (Gómez *et al.*, 2006). For recreational fisheries, catches were extracted from Ivanoff *et al.* (2010) in Cerbère-Banyuls. Cap de Creus recreational catches came from Font and Lloret (2011a, 2011b) and Lloret *et al.* (2008a, 2008b). Whereas, for Medes, recreational catches were extracted from Sacanell (2012).

Ensuring mass-balance and assessing the quality of the models

In an Ecopath model, the energy input and output of all functional groups must be balanced under ecological and thermodynamic rules: (1) $EE < 1.0$; (2) P/Q [production/consumption rate or gross efficiency (GE)] should range 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) should range 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). A standardized procedure to ensure the mass-balance of all the models was followed (detailed information can be found at Appendix 5 in the supplementary material).

The quality of the models 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 and Walters, 2004; Christensen *et al.*, 2008). 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).

Models analyses and ecological indicators

The food-web structure of each PL 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, trophic levels (TL, as outputs) of each FG, and the direct trophic interactions among them extracted from EwE. 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).

To describe the state and functioning of the ecosystems, several ecological indicators were derived from modeling procedure. A detailed explanation of the equations to calculate these indicators are described in Christensen *et al.* (2008) and Coll and Steenbeek (2017). These indicators were divided into five main groups following:

- Biomass-based 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), so it is expected that the higher biomass-based indicator value, the more restrictive protection levels and enforced MPAs are. Four biomass-based indicators were included: total biomass ($t \cdot km^{-2}$), biomass of commercial species ($t \cdot km^{-2}$), biomass of fish species ($t \cdot km^{-2}$), and Kempton Q diversity index.
- Trophic-based indicators reflect the TL position of different groups of the food web. Trophic level indicators may reflect ecosystem "health" because fishing pressure resulting in the removal of predators can cause a decline in the trophic level of the catch and/or the community (Christensen and Walters, 2004). Therefore, the higher TL and trophic-based indicators estimates are found in the more restrictive protection levels and enforced MPAs. Four trophic-based indicators were selected: 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) (Pauly and Watson, 2005).
- Species and size-based indicators are based on species traits and conservation status. Increase in species traits such as mean length can be a direct effect of marine protected areas (Claudet *et al.*, 2006), and therefore higher values are expected for more restrictive protection levels and enforced MPAs. Three species-based indicators were selected: biomass of species that are included in the IUCN Red List - Mediterranean regional assessment (www.iucnredlist.org) as threatened (i.e. critically endangered, endangered

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3 307 and vulnerable) and near threatened ($t \cdot km^{-2} \cdot year^{-1}$), mean length (ML) of fish
4 308 in the community (cm) and mean life span (MLS) of fish in the community
5 309 (year).
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8 310 - Flow-based indicators are related to the interactions in the network of the
9 311 system and six were selected. The Total System Throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$)
10 312 is the sum of all flows in the model and it is considered an overall
11 313 measure of the “ecological size” of the system (Finn, 1976). The Finn’s
12 314 Cycling Index (FCI, %) is the fraction of the ecosystem’s throughput that is
13 315 recycled (Finn, 1976). The Average Path Length (APL) is defined as the
14 316 average number of groups that flows pass through and is an indicator of stress
15 317 (Christensen, 1995). Therefore, the higher FCI and APL values are, the more
16 318 resilient, stable and mature the ecosystem is (Christensen, 1995). Additional
17 319 indicators were selected because of their information on the distribution of
18 320 ecosystem flows and their robustness in front of models’ comparison
19 321 (Heymans *et al.*, 2014) and: the ratios of consumption (Q), export (Ex) and
20 322 production (P).
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31 323 - Catch-based indicators are focused on the fishing activity and based on catch
32 324 and discard data. They can give an idea of the potential effect on adjacent
33 325 fisheries through spillover of exploited fishes from FPAs (McClanahan and
34 326 Mangi, 2000), so greater catch-based indicators values are expected on well-
35 327 enforced MPAs. Also, PPA is usually surrounding FPAs and is where higher
36 328 fishing pressure levels occur (Stelzenmüller *et al.*, 2008), so catch-based
37 329 indicators are supposed to be higher in these areas. Six indicators were
38 330 included: total catch ($t \cdot km^{-2} \cdot year^{-1}$), total discarded catch ($t \cdot km^{-2} \cdot year^{-1}$), TL of
39 331 the catch, the intrinsic vulnerability index of catch, ML of fish in the catch (cm)
40 332 and MLS of fish in the catch (year).
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49 333 Additionally, the mixed trophic impact (MTI) analysis was performed to
50 334 quantify direct and indirect trophic interactions among functional groups (Ulanowicz
51 335 and Puccia, 1990). This analysis quantifies the direct and indirect impacts that a
52 336 hypothetical increase in the biomass of one functional group would have on the
53 337 biomass 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:

$$MTI_{ji} = DC_{ji} - FC_{ij}, \quad \text{Eq. 3}$$

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.

Furthermore, keystone analysis was performed for the nine protection levels. A keystone species is a species that shows relatively low biomass but has a relatively important role in the ecosystem (Power *et al.*, 1996). To identify the keystone species within the ecosystem, the keystone 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 spp*; brown meagre: *Sciaena umbra*; Labridae and Serranidae; Other commercial medium demersal fish; salema: *Salpa salpa*; Mugilidae; red mullet: *Mullus barbatus*; and striped red mullet: *Mullus surmuletus*) were estimated using Valls *et al.* (2015) (KS_V) keystone index, in which the biomass component is based on a descending ranking. These indices are calculated as:

$$KS_{Vi} = \log [IC_i \cdot BC_i] \quad \text{Eq. 3}$$

where IC_i is a component estimating the trophic impact of the group i ; and BC_i is a component estimating the biomass of the group i .

Evaluating MPAs and the role of PLs

In order to determine the role of PLs in the functioning of the MPAs, results from ecological indicators (except catch-based indicators) and keystone analysis were compared among the three PLs within each MPA. This comparison among PLs

ecological indicators served to capture shifts in ecosystem structure and functioning due to the level of protection (Dale and Fortin, 2014).

The same above-mentioned indicators were used to evaluate differences among the three studied MPAs, comparing the same PLs of the different MPAs. For instance, considering the FPAs of the three MPAs allowed us to capture how different are these MPAs even although they officially offer the same levels of protection. Despite that each MPA differs in the restrictions in their PPAs, this multiple comparison procedure was developed for the three PLs because ecological theory establishes that reserve effects should extend from FPA 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 impact results of recreational and professional small scale fishing fleets were examined to quantify the direct and indirect impact of each fleet on the functional groups for PPAs and UPAs of the three studied MPAs, and their potential competition and trade-offs between them were identified.

3. Results

The pedigree index values of the PL 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 FPAs had slightly lower pedigree indexes than the other PLs.

The flow diagrams displayed high levels of biomass even for some high trophic level groups, especially in the FPAs (Figure 3 and supplementary material Figure S6.1). Also, the results highlighted the complexity of these food webs with respect to the number of trophic links among functional groups with important fluxes of energy from phytoplankton and detritus up the food web.

Ecosystem structure and functional traits

Overall, biomass-based indicators displayed the same pattern between PLs (Figure 4), with the highest biomass values found in Cerbère-Banyuls, then Medes Islands and finally Cap de Creus. Conversely, the Kempton's biodiversity index decreased from Cap de Creus to Medes Islands and then Cerbère-Banyuls. Within PLs, the FPAs showed the highest values in terms of total and fish biomass, and they were followed by the PPA in all MPAs. In Cap de Creus similar values were observed among PLs for total, fish and commercial biomass. Kempton's biodiversity index values were similar among PLs for Cerbère-Banyuls, while the highest value was obtained by the UPA for Medes Islands and the FPA for Cap de Creus.

Trophic-based indicators revealed that 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 TL3.25 and TL4, while Cap de Creus showed higher variance among these indicators. Specifically, Cap de Creus showed the highest TL3.25 values and the lowest TL4 value. Within PLs, most trophic-based indicators showed the highest values for FPAs followed by PPAs and UPAs. However, the FPA in Cap de Creus displayed the lowest value of TL4 (Figure 5).

Flow-based indicators showed differences between MPAs. 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). In contrast, Cap de Creus showed the lowest values for Q/TST, whilst the highest values were observed for Ex/TST and P/TST. Medes Islands MPA values were located between these two MPAs. Considering PL values, flow-based results revealed higher values for FPAs followed by PPAs in most of the flow-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) revealed that Cerbère-Banyuls had the highest values for IUCN species biomass, followed by Medes Islands. Regarding ML and MLS of fish, 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.

The keystone index (Figure 8; Supplementary material Appendix 4) for the nine models identified as keystone functional groups: groupers, other commercial medium demersal fish, common dentex and Labridae & Serranidae. Particularly, groupers had the highest relative total impact. These results confirmed that groupers play an important ecological role in Mediterranean coastal ecosystems. The keystone index showed different patterns among PLs and MPAs. Medes Islands models had the highest number of keystone species followed by Cerbère-Banyuls (Figure 8).

Role and impact of small-scale and recreational fisheries

Total catch and discards showed similar values between Cap de Creus and Medes Islands, while Cerbère-Banyuls presented the lowest values (Figure 9). Vulnerability index values were similar for Cap de Creus and Cerbère-Banyuls, with the lowest value found for Medes Islands. TL of the catch was higher for Cerbère-Banyuls and Cap de Creus and lower for Medes Islands (Figure 9), and these results are in line with MLS of the catch results (Figure 7). Also, Cerbère-Banyuls showed the highest value for MLc while Cap de Creus had the lowest value. TC and discards exhibited higher values for PPAs than UPAs. IV indexes were higher for PPAs than UPAs except for Cerbère-Banyuls. The catch TL 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 of the catch results showed similar values between PLs for Medes Islands, while PPA showed higher values in Cap de Creus and lower in Cerbère-Banyuls.

Overall, the MTI analysis based on fisheries did not show any pattern among PLs and MPAs, and fisheries impacting values were clearly higher and more fluctuating than impacted values. Mostly, the highest impacts of recreational fisheries were found for the PPA of Cap de Creus, while the highest impacts of smale scale fleet were found 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 small scale 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 small scale fishery. Recreational and small scale fisheries showed low impacted and impacting values between them. Among them, the highest impact was for the recreational fleet on the small scale one in the PPA of Cap de Creus.

4. Discussion

Nine quantitative models were built to investigate the differences among PLs of three MPAs in the NW Mediterranean Sea. This analysis allowed us to assess the impact of protection on the ecosystem at local scale. The input data were qualitatively acceptable if our results are compared to the distribution of pedigree values in other existing models (Morissette, 2007; Lassalle *et al.*, 2014). Also, the pedigree values of the models were comparable to that from other available MPA models in the Western Mediterranean Sea, such as 0.49 in the Portofino MPA (Prato *et al.*, 2016). However, FPAs showed the lowest pedigree values because several P/B parameters were estimated to obtain reasonable P/Q values (Heymans *et al.*, 2016) and so decreasing their pedigree index. These results highlighted the need to develop studies focused on estimating specific growth and consumption ratios for species in Mediterranean MPAs.

The flow diagram showed the first differences among PLs. Although TLs were similar among three PLs in each MPA, some commercial functional groups (e.g. FG 26 – groupers in Cerbère-Banyuls) showed slightly 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 also showed differences among PLs and pointed at the strong benefits of FPAs (Sala *et al.*, 2017). FPAs (also known as no-take areas) are

widely recognized as a powerful tool for ecosystem and biodiversity conservation (Claudet *et al.*, 2008) and several studies have described their positive effects on biomass (Guidetti *et al.*, 2014), trophic levels (Prato *et al.*, 2016), mean length (Claudet *et al.*, 2006), mean life span (Gunette and Pitcher, 1999), condition (Lloret and Planes, 2003) and biomass of IUCN species such as groupers (Claudet *et al.*, 2008).). Not surprisingly, biomass and trophic-based indicators results increased with the level of protection which demonstrated these positive effects of protection. This implies that FPAs promote higher fish weight and marine species abundance (Harmelin-Vivien *et al.*, 2008). The increase in the TLs underlined the applicability of FPAs as a conservation tool for large predatory fish species (Soler *et al.*, 2015).

The same pattern was also 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, larger ecological size and higher resilience (Christensen, 1995) for FPAs ecosystems. In line with these results, Sala *et al.* (2017) highlighted the potential benefits of FPAs and pointed out that these areas are more resilient than UPAs. In line with these results, consumption rate over total system flows was higher in FPAs than PPA and UPA, since the higher the biomass in the ecosystem the higher the consumption. Libralato *et al.* (2010) found similar results for another Mediterranean MPA in the Adriatic Sea due to the effect of protection. In addition, export 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. So, these FGs would migrate beyond the boundaries of the modelled ecosystem (PL) to maintain their feeding rates. The export results are also related to the fact that fisheries occur in UPAs and PPAs in comparison with FPAs, where they are forbidden.

Similarly, species based-indicators results showed a gradient among PLs. reduces population abundance and mostly removing larger and older fish and so decreasing the ML and MLS of fish in UPAs and increasing in the FPAs (Lizaso *et al.*, 2000). In addition, this pattern could also be due to large fish biomass with a dominance of large apex predators such as *Epinephelus marginatus* (Hackradt *et*

511 *al.*, 2014). Similar results were found for several MPAs in the Mediterranean Sea
512 (Guidetti *et al.*, 2014).

513 In addition, most biomass-based, trophic-based, species-based and flows-
514 based results obtained from PPAs demonstrated their role as buffer zones
515 (Giakoumi *et al.*, 2017), so they may confer biomass enhancement compared to
516 UPAs although FPAs produce greater benefits (Lester and Halpern, 2008; Sciberras
517 *et al.*, 2015). In addition, export and production ratio results showed higher values
518 for UPAs because the biomass of several FGs (such as Sparidae or groupers) were
519 quite high to support their feeding rates. So, these FGs would migrate beyond the
520 boundaries of the modelled ecosystem (PL) to maintain their feeding rates. The
521 export results are also related to the fact that fisheries occur in UPAs and PPAs in
522 comparison with FPAs, where they are forbidden.

523 In contrast, the Kempton's biodiversity index did not show the expected
524 pattern as biodiversity is expected to increase with protection (Costello and
525 Ballantine, 2015). This controversial result could be due to the available data, which
526 came from different studies for each MPA. The Kempton's biodiversity index may be
527 biased since Cerbère-Banyuls model differs on the number of functional groups
528 compared to Cap de Creus and Medes Islands model (Ainsworth and Pitcher, 2006).
529 Using multiple studies for each MPA could also bias this result because some studies
530 showed biomass estimates at higher taxonomic levels than others and the time
531 period that these models represent with regard to the creation year of the MPA.
532 Therefore, as more exhaustive species biomass data are available, the biodiversity
533 index becomes more reliable (Claudet, 2013; Hereu Fina *et al.*, 2017). Although
534 some MPAs are not implemented for biodiversity purposes (Day *et al.*, 2012), the
535 great differences of Kempton's biodiversity index between the FPA and the other
536 two PL areas in Cap de Creus could indicate that the PPA and the UPA marine
537 populations are not being replenished by new individuals coming from the FPA and
538 so not achieving the FPA's biodiversity value. The failure on the spillover effect in
539 Cap de Creus may be due to the lack of enforcement (Lloret *et al.*, 2008a, 2008b),
540 high fishing pressure in the area (Lloret *et al.*, 2008b) or the zonation and design of

the MPA which is represented by a fragmented PPA and a non-totally surrounded FPA.

Overall, indicators displayed differences among PLs within each MPA, especially in the case of Cerbère-Banyuls and Medes Islands MPAs, but not for Cap de Creus. Probably, these patterns 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.* (2008a, 2008b) reported a lack of enforcement and a low level of compliance in Cap de Creus, particularly on minimum landing sizes of certain species and lack of fishing licenses. This is in contrast with Cerbère-Banyuls and Medes Islands MPAs, in which compliance and enforcement are ensured to promote a high level of ecological effectiveness (Di Franco *et al.*, 2016). 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 decline 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 MPAs. Considering that Cap de Creus is the least enforced MPA in the study, our results suggest that the level of enforcement and compliance have a strong effect on MPA effectiveness at the ecosystem level. These patterns among MPAs were also found by Horta 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 (Horta e Costa *et al.*, 2016). Cap de Creus was not included in this study, but a higher MPA index can be assumed because of its small FPA and its low compliance which increases the impact of fishing activities. Overall,

our results call for enhancement of the regulations, increasing the extent of FPAs and the enforcement of management rules in Medes and Cap de Creus MPA.

All keystone indices for the nine models pointed at the same functional groups as keystones. Among them, groupers and common dentex were highlighted as keystone groups in previous western Mediterranean MPAs models (Valls *et al.*, 2012; Prato *et al.*, 2016).

MPAs are considered an important tool to manage coastal fisheries (Claudet *et al.*, 2006; Di Franco *et al.*, 2016), and enforcement is a key aspect to achieve these goals. Biomass and catch-based results demonstrated that well-enforced small coastal MPAs can enhance small-scale and recreational fisheries by spillover effect and can 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. Additionally, these differences on catches and discards between PPAs and UPAs can be explained by the concept of “fishing the line”, which can reduce the biomass in neighbouring unprotected areas (Kellner *et al.*, 2007), so understanding spatial-temporal patterns of fishing effort around an MPA is a key aspect to manage and assess these areas. In this context, 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. On the other hand, although small-scale and recreational fisheries are often considered to have a relatively low ecological impact, they do affect vulnerable species in coastal or offshore waters in the western Mediterranean Sea (including MPAs) through, targeted fishing or unintentional bycatch (Lloret *et al.*, 2019).

The results of PLs in Cap de Creus differed substantially from Cerbère-Banyuls and Medes Islands. This could be related to the physical position of its FPA within a multi-use MPA, which for Cap de Creus is not located at the core of the MPA surrounded by PPAs as is the common MPA design in the Mediterranean Sea (Gabrié *et al.*, 2012). This unconventional placement could explain the observed reduction in PPA effectiveness although this interpretation could be biased by the

apparent lack of enforcement in Cap de Creus. In MPAs, the maximum benefit to conservation and ecosystem services will occur when FPAs are surrounded by well-managed fishing grounds (Roberts and Hawkins, 2000). This result suggested the requirement of an implemented and non-fragmented PPA surrounding the FPA in Cap de Creus which complements and ensures the protection of the biodiversity in the FPA, as recommended in IUCN guidelines for applying MPAs (Day *et al.*, 2012).

In addition, high values of total catch and discards in Cap de Creus could be related to non-compliance, as well as to the lack of georeferenced catch data that could have biased our results. Non-compliance could also 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 the lack of enforcement obtained from other ecological indicators (e.g. biomass-based indicators). Additionally, vulnerability index and ML of the catch estimated values from Cap de Creus could be explained as a failure in the enforcement in an MPA supporting high fishing pressure from both small-scale and recreational fishing sectors (Lloret and Font, 2013). Finally, our results highlighted the impact of recreational fisheries in Cap de Creus among the rest of studied MPAs, which could be also reducing MPA benefits (Lloret *et al.*, 2008a, 2008b). On the other hand, the lower values of total catch and discards, the higher values of TL of the catch, ML and MLS of fish in the catch, could reveal potential benefits of protection to adjacent fisheries. Fishing pressure can lead to a decrease of TL of the catch (Shannon *et al.*, 2014) and ML and MLS of fish in the catch (Pelletier *et al.*, 2005). Similarly, Prato *et al.* (2016) demonstrated that a decrease in the fishing effort lead to an increase in the trophic level of the catch because of increasing in fish predators biomass in Portofino MPA (Northwestern Mediterranean Sea).

PPAs showed higher impacted values than UPAs, which suggest a higher contribution of PPAs to the recreational fishery. Although PPAs may differ in 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. Regarding the small scale fishery, the highest negative impacting values were represented by

targeted species for this fleet, while positive values may represent FGs which are preys 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 small scale 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 was identified as a key attribute for fisheries' success such as in Torre Guaceto MPA, where co-management involving fishers, scientists and managers led to an increase in total fish biomass in FPA, an increase in fishermen's revenues when they operate within the PPA and an increase in the commitment of local fishermen to environmental issues (Di Franco *et al.*, 2016).

The stronger benefits of FPAs than PPA and the importance of PPAs as a buffer area may suggest an alternative reorganization on the MPA zonation. An increase on the surface or percentage of area covered by FPA could lead to more resilient and productive MPAs which would enhance the benefits of ecosystem services including adjacent fisheries. Additionally, PPAs must be surrounding the FPA in order to ensure and complement the protection. Accordingly, MPA configuration may obtain greater benefits when increasing the FPA surface and ensuring its protection with a buffer PPA. MPAs and networks of MPAs can be used to enhance the resilience, resistance in front perturbations or ecosystem transformation in the face of climate change (Carr *et al.*, 2017). MPA zonation allows to assess the impacts of each protection level and accommodate multiple objectives, human activities and stakeholder groups, and it is a key aspect of the management of MPAs (Francour *et al.*, 2001; Lester and Halpern, 2008).

Even though our work illustrates that quantitative food-web modelling techniques can be useful to assess coastal MPAs effects on the structural and functional traits of marine ecosystems and their adjacent fisheries, some limitations were faced. One of the main hurdles was the lack of local data for some FGs identified in previous MPA modelling studies (Libralato *et al.*, 2010; Valls *et al.*, 2012; Prato *et al.*, 2016). For example, literature including benthonic biomass estimations

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inside MPAs is mainly focused on sea urchins, gorgonians and *Posidonia* meadows (e.g. Hereu Fina and Quintana Pou, 2012; Schvartz and Labbe, 2012). However, studies on other important benthic groups such as sponges or crustaceans are scarce. During the balancing procedure, higher predation mortalities were found for several FGs in most quantitative models and diet imports were set in order to ensure the mass-balance for each model. Although these import values were set considering ecological and size attributes of each FGs, small and open study areas could represent a limitation of our models due to the lack of data and knowledge. Additionally, spatial-temporal series data of catches and fleet distribution would improve the analysis on the effect of MPA potential benefits on the recreational and small scale fisheries. Collecting time series of fishing activities surrounding MPAs is a monitoring priority, as previously highlighted (Valls *et al.*, 2012; Prato *et al.*, 2016). 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 zonation of the modelled MPAs (Heymans *et al.*, 2016). In addition, and despite the fact 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).

Despite the limitations, this work provides the basis to assess the role of these Mediterranean coastal 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 on the potential benefits of MPAs at the local scale, and a lack of enforcement is noticeable in surrounding areas. MPAs can increase ecosystem maturity and resilience and show potential benefits for small-scale fisheries that act in their surroundings when these areas are well-enforced. Perceptions of ecological and social benefits are key drivers of stakeholder support to MPAs and could therefore reinforce a virtuous loop further enhancing

MPA effects (Bennett *et al.*, 2019). Future assessments on the spatial distribution of marine resources and the role of these PLs within a network should take place in order to quantify their impacts at a sub-regional (e.g. Northwestern Mediterranean) and regional (e.g. Western Mediterranean) geographic scales.

Acknowledgements

This work was funded by EU Research Project SAFENET project (“Sustainable Fisheries in EU Mediterranean Waters through Network of MPAs.” Call for proposals MARE/2014/41, Grant Agreement n. 721708). D. Vilas benefited from a Short Term Scientific Mission by the COST Action MarCons (CA15121).

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Tables

Table 1. Surface area (km²) and the percentage covered by protection level (PL) and year of creation of each marine protected area (MPA) (Cerbère-Banyuls, Cap de Creus and Medes Islands).

MPA	Year of	PL km ² (%)
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	creation	FPA	PPA	UPA
Cerbère-Banyuls	1974	0.65 (1.59)	5.85 (14.32)	35.00 (85.68)
Cap de Creus	1998	0.21 (0.69)	7.98 (26.11)	22.37 (73.20)
Medes Islands	1983	0.39 (2.00)	4.24 (21.77)	14.85 (76.23)

Figures

Figure 1. Location of the three MPAs and their protection levels (PL) (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 the three protection levels (PL) 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 diagrams of three protection levels (PL) (FPA: red; PPA: yellow; UPA: green) of Cerbère-Banyuls MPA model organized by trophic levels (TL) (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. The numbers identify the functional groups of the PL models (Appendix 1 supplementary material) (Flow diagrams of Cap de Creus and Medes Islands MPA can be found in supplementary material Figure S6.1.).

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Figure 4. Biomass-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, Kempton's Q – Kempton's Q diversity index).

Figure 5. Trophic-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (TL – trophic level).

Figure 6. Flow-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (Q/TST – Consumption ratio, Ex/TST – Export ratio, P/TST – Production ratio, TST – Total System Throughput, FCI – Finn Cycle Index and APL – Average Path Length).

Figure 7. Species-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, ML – mean length and MLS – mean life span).

Figure 8. Keystone Index analysis of the three protection levels (PL) (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 keystone 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 the three protection levels (PL) (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (C – Catch; TL – trophic level; ML – mean length; MLS – mean life span).

Figure 10. Recreational impacting and impacted values of three protection levels (PL) models (PPA: partially protected area; UPA: unprotected area) 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 – striped red mullet; WSE – white seabream; ART – Small scale fishery).

Figure 11. Small scale impacting and impacted values of three protection levels (PL) models (PPA: partially protected area; UPA: unprotected area) 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 – striped red mullet; WSE – white seabream; REC – Recreational fishery).

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3 **Supplementary data**
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5 Additional Supplementary material may be found in the online version of this article:
6

7 **Appendix 1.** Supplementary table: Functional groups included for the protection
8 level models showing those present (P) or absent (A) in each MPA (Table S1.1.).
9

10 **Appendix 2.** Supplementary tables: Cerbère-Banyuls, Cap de Creus and Medes
11 MPAs functional groups species composition and methods and references used to
12 estimate the basic input parameters of the nine Ecopath models (Table S2.1.); Input
13 parameters and outputs estimate for Cerbère-Banyuls (Table S2.2.), Cap de Creus
14 (Table S2.3.) and Medes Islands (Table S2.4.) PL models.
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17 **Appendix 3.** Supplementary tables: Diet composition matrix for the protection level
18 models of Cerbère-Banyuls (Table S3.1.), Cap de Creus (Table S3.2.) and Medes
19 Islands (Table S3.3.) MPA.
20

21 **Appendix 4.** Supplementary tables: Keystone index and Relative Total Impact
22 values for the functional groups included in Cerbère-Banyuls (Table S4.1), Cap de
23 Creus (Table S4.2) and Medes Islands (Table S4.3) protection level models. FPA:
24 fully protected area; PPA: partially protected area; UPA: unprotected area.
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27 **Appendix 5.** Additional explanatory text about balancing procedure.
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29 **Appendix 6.** Supplementary figure: Flow diagrams of three protection levels of
30 Cap de Creus and Medes Islands MPA model (Figure S6.1.).
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The effects of marine protected areas on ecosystem recovery and fisheries using a comparative modelling approach

Authors

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Abstract

1. The overexploitation of many marine resources and ecosystems calls for the development and implementation ~~of measure~~ of measures to support their recovery and conservation.
2. ~~We assessed the~~The potential contributions to support fisheries and ecosystem recovery were assessed at the local level of the three multiple-use Marine Protected Areas (MPAs) of Cerbère-Banyuls, Medes Islands and Cap de Creus, located in the Northwestern Mediterranean Sea.
3. ~~For each MPA, we developed~~ a food-web model accounting for each ~~management unit~~protection levels (PLMU) was developed: the fully protected area (FPA), the partially protected area (PPA) and the unprotected area (UPA) surrounding the MPA. Using the resulting nine food-web models, ~~we characterized and compared~~ the ecosystem structure and functioning of each MUPL were compared and characterized, ~~we assessed~~ differences and

similarities within and among the three MPAs were assessed, and ~~the~~ ecosystem response to fully protection was evaluated for the three MPAs.
~~evaluated if the ecosystem response to full protection led to specific~~
~~ecosystem functional traits that are shared among the three MPAs.~~

4. We showed differences Differences among MUs in terms of ecosystem structure and functioning were found among PLs. Overall, FPAs presented the most positive effect of protection in terms of ecosystem structure and functioning, followed by PPAs. However, the effects of protection on neighbouring unprotected areas were hardly noticeable.

5. Similarities between Cerbère-Banyuls and Medes Islands MPAs were ~~obtained~~observed, while Cap de Creus MPA showed the least benefits from protection overall. These results are likely due to similarities in the configuration of the ~~protection~~ protected areas, the levels of enforcement and compliance, and the impact of recreational and small scale fisheries allowed in the PPAs and UPAs.

6. Our ~~This~~ study illustrates that well-enforced Mediterranean MPAs, even when small, can yield local positive impacts on the structure and functioning of marine ecosystems that can contribute to support local fisheries.

Keywords: Management units, Protection levels, fully protected areas, partially protected areas, Ecopath with Ecosim, NW Mediterranean Sea

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1. Introduction

Marine ecosystems have been degraded at high rates under the cumulative impact of multiple anthropogenic activities (Costello et al., 2010; Halpern et al., 2015)(Costello et al., 2010; Halpern et al., 2015)(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)(CBD, 2010)(CBD, 2010). Marine protected areas (MPAs hereafter) are an essential tool for reversing the global degradation of ocean life (Claudet et al., 2008; Babcock et al., 2010; McCauley et al., 2015)(Claudet et al., 2008; Babcock et al., 2010; McCauley et al., 2015)(Babcock et al., 2010; Claudet et al., 2008; McCauley et al., 2015). 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 currently protected with implemented MPAs (Sala et al., 2018)(Sala et al., 2018)(Sala et al., 2018).

MPAs can also provide socio-economic benefits. Economic benefits may stem from the creation of employment opportunities through the development of non-consumptive activities such as tourism and recreation (Roncin et al., 2008)(Roncin et al., 2008)(Roncin et al., 2008), or from securing future jobs by increasing the chances of managing stocks sustainably (Sumaila et al., 2000)(Sumaila et al., 2000)(Sumaila et al., 2000). Fisheries benefits arise from ecological effects within protected areas in the form of biomass recovery, and subsequent spillover outside the boundaries of the MPA (Di Lorenzo et al., 2016)(Di Lorenzo et al., 2016)(Di Lorenzo et al., 2016) or by increased larval production and supply toward unprotected areas (Marshall et al., 2019)(Marshall et al., 2019)(Marshall et al., 2019), with MPAs finally replenishing external fisheries grounds. Actually, empirical studies comprising small scale (Stelzenmüller et al., 2008)(Stelzenmüller et al., 2008)(Stelzenmüller et al., 2008), recreational (Font et al., 2012a)(Font et al., 2012a)(Font et al., 2012a) and industrial bottom-trawling fishing effort (Murawski et al., 2005)(Murawski et al., 2005)(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 the biomass in neighbouring unprotected areas.

Most MPAs are multiple-use (Claudet, 2018)(Claudet, 2018)(Claudet, 2018). They combine different levels of protection within a spatially zoned management scheme that can encompass fully protected areas (FPA, also known as no-take areas), where all extractive activities are prohibited, or a type of partially protected areas (PPAs), where some fishing activities are allowed but with varying restrictions (Lubchenco and Grorud-Colvert, 2015; Horta e Costa *et al.*, 2016; Giakoumi *et al.*, 2017)(Lubchenco and Grorud-Colvert, 2015; Horta e Costa *et al.*, 2016; Giakoumi *et al.*, 2017)(Giakoumi *et al.*, 2017; Horta e Costa *et al.*, 2016; Lubchenco and Grorud-Colvert, 2015). Multiple management uses in MPAs can have strong implications in terms of ecosystem and fisheries benefits at the larger scale (i.e. regional). Recent studies showed that ecological benefits can be observed in fully and highly protected areas, while lower levels of protection provide benefits only under specific conditions (i.e. when surrounded by a fully protected area; (Zupan *et al.*, 2018b)(Zupan *et al.*, 2018b)(Zupan *et al.*, 2018b). In addition, when allowed in a given zone of an MPA, fishing exploitation can become a threat for the overall MPA (Zupan *et al.*, 2018a)(Zupan *et al.*, 2018a)(Zupan *et al.*, 2018a).

While MPAs are an ecosystem-based management tool, it is still unclear how the functioning of ecosystems is affected by protection - in particular, how different levels of protection in multiple-use MPAs translate into ecosystem reorganizations, and how ecosystem response to different levels of protection transfer into fisheries benefits. Here, using food-web modelling techniques, different levels of protection in multiple-use MPA were quantitatively modeled and their ecosystem structural and functional trait responses were compared. Three Mediterranean MPAs were used as case studies to develop ecosystem models for each protection level in each MPA.

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benefits. Here, using food-web modelling techniques, different levels of protection in multiple-use MPA were quantitatively modeled and their ecosystem structural and functional trait responses were compared. the first attempt to quantitatively model and compare ecosystem structural and functional trait responses to different levels of protection in multiple-use MPAs is presented. Three Mediterranean MPAs were used as a case studies and to develop ecosystem models for each management unit in each MPA.

2. Material & Methods

Study areas

Different management units protection levels (MUsPLs) in three MPAs in the North-western Mediterranean Sea were examined: Cerbère-Banyuls MPA in France, Cap de Creus and Medes Islands MPAs in Spain (Figure 1). An PL MU was identified as an area included in an MPA or its surroundings which is classified by its level of protection (fully, partially or unprotected).

These three MPAs were selected because of their similar in bathymetry ranges, habitat composition, spatial proximity, and because each MPA combines different levels of protection within a spatially zoned management scheme (Table 1 and Figure 1). Each of the three MPAs has a fully protected area (FPA) at its core, where where fishing exploitation is not allowed. Neighbouring partially protected areas (PPAs) allow restricted uses such as small-scale (traditional/artisanal) fisheries (Zupan et al., 2018a)(Zupan et al., 2018a)(Zupan et al., 2018a). Last, unprotected areas (UPAs) surround each MPA.

In order to model the functioning of each MPA and the influence of the protected area on the unprotected area, the FPA, PPA and UPA zones in isolation were modelled. The boundaries of UPAs were selected as all areas adjacent to the MPA with similar ecological characteristics (Figure 1).

Ecosystem modelling approach

PLMU models were developed using the Ecopath with Ecosim approach (EwE 6.6 version) (Christensen and Walters, 2004; Christensen et al., 2008)(Christensen

~~and Walters, 2004; Christensen et al., 2008)(Christensen et al., 2008; Christensen and Walters, 2004)~~ and followed the best practices rules ~~(Heymans et al., 2016)(Heymans et al., 2016)(Heymans et al., 2016).~~

Ecopath is a mass-balanced model based on two main equations. The first master equation describes the energy balance for each functional group in the model, so that:

$$\text{Consumption} = \text{production} + \text{respiration} + \text{unassimilated food} \quad \text{Eq. 1}$$

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:

$$P/B_i \cdot B_i = P/B_i \cdot B_i (1 - EE_i) + \sum_j (Q/B)_{ji} \cdot B_i \cdot DC_{ji} + Y_i + NM_i + BA_i \quad \text{Eq. 2}$$

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.

Model parametrization

An ecosystem model was built for each ~~management unit~~ protection level, i.e. for each combination of the three MPAs and three protection levels (FPA, PPA and UPA). The nine ~~PLMU~~ models were built using the best available information and represented periods from 2000s to 2010s, mostly limited by the available biomass data from the underwater visual census (UVC). Specifically, the Cerbère-Banyuls MPA model included most of the data from 2013, while the Cap de Creus MPA and the Medes Islands MPA models included most of their information from the period (2005-2008) and (2000-2004), respectively.

Species presence and their biomass were aggregated in functional groups (FGs) of species or groups of species clustered according to their trophic ecology,

commercial value, and abundance in the ecosystem. The meta-web structure previously defined for the Western Mediterranean Sea model (Coll et al., 2019)(Coll et al., 2019)(Coll et al., 2019a) developed under the SafeNet Project¹ context was followed. This meta-web structure was adapted to local conditions, removing those FGs which did not occur in the study areas. The final food-web structure of Cerbère-Banyuls MPA contained 64 functional groups (~~two~~2 marine mammals, ~~3~~three seabirds, ~~1~~one sea turtle, ~~8~~eight pelagic fish, 25 demersal fish, ~~3~~three cephalopods, 14 invertebrates, 2 primary producers, ~~2~~two zooplankton, ~~2~~two phytoplankton and ~~2~~two detritus), while Cap de Creus MPA and Medes Islands MPA had 67 functional groups each (~~2~~two marine mammals, ~~3~~three seabirds, ~~1~~one sea turtle, ~~9~~nine pelagic fish, 25 demersal fish, ~~3~~three cephalopods, 14 invertebrates, ~~4~~four primary producers, ~~2~~two zooplankton, ~~2~~two phytoplankton, and ~~2~~two detritus) (supplementary material Table S1.12). Except in the case of FPAs, which do not have discards because all fishing extractions are forbidden, food-web structures of each PLMU in the same MPA were identical.

FGs' biomass were obtained from different sources from the study area or surrounding areas (see ~~additional explanatory text in Appedix 4 and~~ supplementary material Table S1.12.1. for details on the parameterization of each functional group). ~~The nine PL models share biomass data on some FGs (marine mammals, seabirds, sea turtles, pelagic fish, some invertebrates' groups, primary producers, zooplankton and phytoplankton) for two main reasons: 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 for Cerbère-Banyuls (underwater visual census, UVC)~~ ~~The nine PL models share biomass data on some FGs (marine mammals, seabirds, sea turtles, pelagic fish, some invertebrates' groups, primary producers, zooplankton and phytoplankton) for two main reasons: 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 for Cerbère-Banyuls (underwater visual census, UVC)~~ (Claudet, 2013)(Claudet, 2013) and literature for Cap de Creus and Medes Islands

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

models (García-Rubies and Zabala i Limousin, 1990; Macpherson *et al.*, 2002; Hereu Fina and Quintana Pou, 2012; Hereu Fina *et al.*, 2017)(García-Rubies and Zabala i Limousin, 1990; Macpherson *et al.*, 2002; Hereu Fina and Quintana Pou, 2012; Hereu Fina *et al.*, 2017) (supplementary material Table S2.1.) except for some non-reef fish and invertebrates' FG. For these non-reef fish FG (e.g. Anglerfish), MEDITS trawling survey (Bertrand *et al.*, 1997)(Bertrand *et al.*, 1997) data were extracted with a new released software insidedeveloped for SafeNet Project, which is called MEDITS data explorer v. 1.5.1 (Steenbeek, 2018a)(Steenbeek, 2018a). This tool allowed us to extract MEDITS data easily, and itto scales biomass data to the area and bathymetric rangesautomatically. We extracted MEDITS trawling survey data were extracted from the closest point to each MPA, in order to have biomass data for those species that were not present during field studies. Those species are present in the MPAs, but they are less important in MPAs in terms of biomass. This assumption was assessed previously withby expert knowledge from the project. For invertebrates' FGs whose biomass estimates were not available, realistic EE values were used to estimate the biomass of four FGs in Cerbère-Banyuls models and six FGs in Cap de Creus and Medes Islands models (supplementary material Table S2.2.). Additionally, scaling factors were used on biomass data of pelagic fish groups available from the MEDITS oceanographic survey, which does not fully cover coastal areas. Thus, this scaling enabled to adapt the estimates and get more accurate biomass values for these coastal areas. The scaling conversions were based on species depth distribution (extracted from Aquamaps – www.aquamaps.org) (Kaschner *et al.*, 2013)(Kaschner *et al.*, 2013) and took into account their contribution in each FG.

Production (P/B, year⁻¹) and consumption (Q/B, year⁻¹) rates were either estimated using empirical equations (Heymans *et al.*, 2016)(Heymans *et al.*, 2016)(Heymans *et al.*, 2016), taken from literature or from other models developed in the Mediterranean Sea (Coll *et al.*, 2019)(Coll *et al.*, 2019)(Coll *et al.*, 2019b) (supplementary material Table S1S2.1). Additionally, local body lengths of reef-

associated species obtained from UVC ([Di Franco, 2018](#))(~~Di Franco, 2018~~)(~~Di Franco, 2018~~) were used to estimate P/B and Q/B rates using empirical equations and local data ([Pauly, 1980](#))(~~Pauly, 1980~~)(~~Pauly, 1980~~).

Diet matrices (supplementary material Appendix 3, Tables S3.1., S3.2. and S3.3.) were built using The diet information which was compiled using published studies on stomach content analyses, giving preference to local or surrounding areas (supplementary material Table ~~S1~~S2.1.). ~~When calculating the Diet Matrix (DC), a pedigree index associated with each predator FG (supplementary material appendix 2, Table S2.1., S2.2., S2.3.) was generated. We used the Diet Matrix Calculator (Steenbeek, 2018b)(Steenbeek, 2018b), a custom-build extraction tool, was used (Steenbeek 2018), a custom-built extraction tool that to automatizes the process of selecting and scaling diet data. Drawing on a large library of published diet studies, the Diet matrix calculator tool selects the most likely suitable diet studies for a specific model area, based on a range of criteria, and generates a diet composition matrix with accompanying pedigree index for each predatory functional group. Due to the small sizes of the MUsPLs investigated and the capacity to of some species to move between MUsPLs (Gell and Roberts, 2003a; Grüss et al., 2011)(Gell and Roberts, 2003a; Grüss et al., 2011)(Gell and Roberts, 2003a; Grüss et al., 2011), a fraction of the diet composition of these species was set as import for all MUsPLs based on the time that these species feed outside the areas and their ecological traits. This import was based on the size, behaviour, and ecology of species of each functional group (Froese and Pauly, 2019)(Froese and Pauly, 2019)(Froese and Pauly, 2019).~~

Fisheries data were obtained from different sources (database, literature and unpublished data) (~~additional explanatory text in Appendix 4 and~~ supplementary material Table ~~S1~~S2.1) and the information on catches was split into two fishing fleets – recreational and professional small scale (except for FPA models where fishing activities are not allowed). Regarding professional small scale fisheries catches, Cerbère-Banyuls data were obtained from a local study Regarding professional small scale fisheries catches, Cerbère-Banyuls data were obtained from a local study (Prats, 2016)(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), 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)(Tudó, 2017). For Cap de Creus, these landings were from Llançà, Port de la Selva, Cadaqués and Roses harbours, where the main fleets operating are located, and were scaled by the months of fishing activity of the fleets inside the MPA For Cap de Creus, these landings were from Llançà, Port de la Selva, Cadaqués and Roses harbours, where the main fleets operating are located, and were scaled by the months of fishing activity of the fleets inside the MPA (Gómez *et al.*, 2006)(Gómez *et al.*, 2006). For recreational fisheries, we extracted catches were extracted from Ivanoff *et al.* (2010)(2010) in Cerbère-Banyuls. Cap de Creus recreational catches came from Font and Lloret (2011a, 2011b)(2011a, 2011b) and Lloret *et al.* (2008a, 2008b)(2008a, 2008b). Whereas, for Medes, recreational catches were extracted from Sacanell (2012)(2012).

Ensuring mass-balance and assessing the quality of the models

In an Ecopath model, the energy input and output of all functional groups must be balanced under ecological and thermodynamic rules: (1) $EE < 1.0$; (2) P/Q [production/consumption rate or gross efficiency (GE)] should range from 0.1 to 0.3 with the exception of ~~fast-fast~~-growing groups such as bacteria; (3) R/A (respiration/food assimilation) < 1 ; (4) R/B (respiration/biomass) should range 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)(Christensen *et al.*, 2008; Heymans *et al.*, 2016)(Christensen *et al.*, 2008; Heymans *et al.*, 2016). A standardized procedure to ensure the mass-balance of all the models was followed (detailed information can be found at Appendix 4-5 in the supplementary material).

The quality of the models 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 and Walters, 2004](#);[Christensen et al., 2008](#))(~~Christensen and Walters, 2004; Christensen et al., 2008~~)(~~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](#))(~~Steenbeek, 2018b~~)(~~Steenbeek, 2018~~). 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](#))(~~Christensen and Walters, 2004~~)(~~Christensen and Walters, 2004~~).

Models analyses and ecological indicators

Flow diagram

The food-web structure of each PLMU in the three MPAs was visualized using a flow diagram. Flow diagrams were obtained using the *ggplot2* package ([Wickham, 2010](#))(~~Wickham, 2010~~)(~~Wickham, 2010~~) implemented in R software ([R Core Team, 2017](#))(~~R Core Team, 2017~~)(~~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 extracted from EwE. 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](#))(~~Christensen, 1996~~)(~~Christensen, 1996~~).

Ecological indicators

~~Several ecological indicators were computed to~~To describe the state and functioning of the ecosystems, several ecological indicators were computed derived from modeling procedure. A detailed explanation of the equations to calculate these indicators are described in Christensen et al. (2008)(2008) and Coll and Steenbeek

(2017). 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)(Micheli *et al.*, 2004)(Micheli *et al.*, 2004), so it is expected that the higher biomass-based indicator value, the more restrictive protection levels and enforced MPAs are. Four biomass-based indicators were included: total biomass (TB, t·km⁻²), biomass of commercial species (CB, t·km⁻²), biomass of fish species (FB, t·km⁻²), and Kempton Q diversity index (KI).
- Trophic-based. These indicators reflect the TL position of different groups of the food web. Trophic level indicators may reflect ecosystem “health” because fishing pressure removing resulting in the removal of predators can cause a decline in the trophic level of the catch and/or the community (Christensen and Walters, 2004)(Christensen and Walters, 2004)(Christensen and Walters, 2004). Therefore, the higher TL and trophic-based indicators estimates are found in the more restrictive protection levels and enforced MPAs. Four trophic-based indicators were selected: TL of the community (TLc), TL of the community including organisms with TL ≥ 2 (TL2), TL of the community including organisms with TL ≥ 3.25 (TL3.25) and TL of the community including organisms with TL ≥ 4 (TL4) (Pauly and Watson, 2005)(Pauly and Watson, 2005)(Pauly and Watson, 2005).
- Species and size-based. These indicators are based on species traits and conservation status. Increase in species traits such as mean length can be a direct effect of marine protected areas (Claudet *et al.*, 2006)(Claudet *et al.*, 2006)(Claudet *et al.*, 2006), and therefore higher values are expected for more restrictive protection levels and enforced MPAs. Three species-based indicators were selected: biomass of species that are included in the IUCN Red List - Mediterranean regional assessment (www.iucnredlist.org) as threatened (i.e. critically endangered, endangered and vulnerable) and near

threatened (~~ES~~, $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$), mean length (~~ML~~) of fish in the community (~~ML~~, cm) and mean life span (~~MLS~~) of fish in the community (~~MLS~~, year).

- ~~Flow-based. Several indicators are related to total flows related to the interactions in the network of the system and six were used selected.~~ The Total System Throughput (TST, $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$) ~~is~~, the sum of all flows in the model (~~consumption, export, respiration, and flow to detritus~~), ~~and~~ it is considered an overall measure of the “ecological size” of the system (~~Finn, 1976~~)(~~Finn, 1976~~)(~~Finn, 1976~~). The Finn’s Cycling Index (FCI, %) is the fraction of the ecosystem’s throughput that is recycled (~~Finn, 1976~~)(~~Finn, 1976~~)(~~Finn, 1976~~), ~~and the higher its value~~. The Average Path Length (APL) is defined as the average number of groups that flows passes through and ~~XXXXX~~ is an indicator of stress (~~Christensen, 1995~~)(~~Christensen, 1995~~)(~~Christensen, 1995~~). ~~Therefore, the higher FCI and APL values are, the more resilient, stable and mature the ecosystem is (Christensen, 1995)(Christensen, 1995).~~ Additional indicators were selected because of ~~their information on the distribution of ecosystem flows and~~ their robustness in front of models’ comparison (~~Heymans et al., 2014~~)(~~Heymans et al., 2014~~)(~~Heymans et al., 2014~~) ~~and their information on the distribution of ecosystem flows~~: the ratios of consumption (Q), export (Ex) and production (P) ~~..~~.

- ~~Catch-based. These indicators are based focused on catch and discard species data the fishing activity and based on catch and discard data.~~ They can give an idea of ~~in~~ the potential effect on adjacent fisheries through spillover of exploited fishes from FPAs (~~McClanahan and Mangi, 2000~~)(~~McClanahan and Mangi, 2000~~)(~~McClanahan and Mangi, 2000~~), ~~so greater catch-based indicators values are expected on well-enforced MPAs.~~ ~~Also, PPAs is usually are surrounding FPAs and is where higher fishing pressure levels occur (Stelzenmüller et al., 2008)(Stelzenmüller et al., 2008), so catch-based indicators are supposed to be higher in these areas.~~ Six indicators were included: total catch (~~TC~~ $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$), total discarded catch (~~TD~~, $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$), ~~trophic level TL~~ of the catch, ~~(TLC)~~, the intrinsic vulnerability index of catch

(VI), ~~mean length~~ ML of fish in the catch (MLC , cm) and ~~mean life span~~ MLS 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)(Ulanowicz and Puccia, 1990)(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 biomass 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:

$$MTI_{ji} = DC_{ji} - FC_{ij}, \quad \text{Eq. 3}$$

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.

Furthermore, keystone analysis was performed for the nine management units protection levels. A keystone species is a species that shows relatively low biomass but has a relatively important role in the ecosystem (Power et al., 1996)(Power et al., 1996)(Power et al., 1996). To identify the keystone species within the ecosystem, the keystone 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 spp*; brown meagre: *Sciaena umbra*; Labridae and Serranidae; Other commercial medium demersal fish; salema: *Salpa salpa*; Mugilidae; red mullet: *Mullus barbatus*; and striped red mullet: *Mullus surmuletus*) were estimated using ~~3 three different methods: (1) Power keystone indicator (Power et al., 1996) (KS_p) and (2) Libralato's keystone indicator (Libralato et al., 2006) (KS_L), which are based on a measure of trophic impact derived from the MTI analysis, and a quantitative measure of biomass; and (3) Valls et al. (2015)(2015)(2015) (KS_V) keystone index, in which the biomass component is based on a descending ranking. These indices are calculated as:~~

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434 $KS_{pi} = \epsilon_i \frac{1}{p_i}$ Eq.4

435 $KS_{Li} = \log [\epsilon_i(1 - p_i)]$ Eq.5

436 $KS_{Vi} = \log [IC_i \cdot BC_i]$ Eq.

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

441 **Evaluating MPAs and the role of MUsPLs**

442 In order to determine the role of MUsPLs in the functioning of the MPAs,
443 results from ecological indicators (except catch-based indicators) and keystone-ness
444 were compared among the three MUsPLs within each MPA. This comparison among
445 MUsPLs ecological indicators served to capture shifts in ecosystem structure and
446 functioning due to the level of protection (Dale and Fortin, 2014)(Dale and Fortin,
447 2014)(Fortin and Dale, 2005).

448 The sSame above-mentioned indicators were used to evaluate differences
449 among the three studied MPAs, comparing the same MUsPLs of the different MPAs.
450 For instance, considering the FPAs of the three MPAs allowed us to capture how
451 different are these MPAs since even although they officially offer the same levels of
452 protection. Despite that each MPA differs on in the restrictions in their PPAs, this
453 multiple comparison procedure was developed for the three MUsPLs because the
454 ecological theory establishes that reserve effects should extend from FPA beyond
455 its boundaries as a result of the spillover (Gell and Roberts, 2003b)(Gell and Roberts,
456 2003b)(Gell and Roberts, 2003b).

457 **Impact of small-scale fisheries**

458 To evaluate the impact of small-scale fisheries on the MPAs, catch-based
459 indicators were examined between PPAs and UPAs of the three MPAs. The mixed
460 trophic impact results of recreational and professional small scale fishing fleets were
461 examined to quantify the direct and indirect impact of each fleet on the functional

groups for PPAs and UPAs of the three studied MPAs, and their potential competition and trade-offs between them were identified.

3. Results

The pedigree index values of the **PLMU** 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 FPAs ~~obtained-had~~ slightly lower pedigree indexes than the other **MUsPLs**.

The flow diagrams displayed high levels of biomass even for some high trophic level groups, especially in the FPAs (Figure 3 and supplementary material Figure ~~S5S6~~.1). Also, ~~the~~ results ~~emphasized-highlighted~~ the complexity of these food webs ~~regarding-with respect to~~ 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 **MUsPLs** (Figure 4), with the highest biomass values found in Cerbère-Banyuls, then Medes Islands and finally Cap de Creus. Conversely, the Kempton's ~~b~~Biodiversity Indicator index (~~KI~~) decreased from Cap de Creus to Medes Islands and then Cerbère-Banyuls. Within **MUsPLs**, the FPAs showed the highest values in terms of total and fish biomass, and they were followed by ~~the~~ PPA in all MPAs. In Cap de Creus similar values were observed among **MUsPLs** for ~~both-indicatorstotal, fish and commercial biomass~~. Kempton's biodiversity index values were similar among PLs for Cerbère-Banyuls, while the highest value was obtained by the UPA for Medes Islands and the FPA for Cap de Creus.

Trophic-based indicators revealed that 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 TL3.25 and TL4, while Cap de Creus ~~obtained-showed~~ higher variance among these indicators. Specifically, Cap de Creus showed the highest TL3.25

values and the lowest TL4 value. Within MUSPLs, most trophic-based indicators showed the highest values for FPAs followed by PPAs and UPAs. However, the FPA in Cap de Creus displayed the lowest value of TL4 (Figure 5).

Flow-based indicators showed differences between MPAs. Cerbère-Banyuls showed the highest values for Q/TST, TST, FCI₁ and APL, while the lowest values for Ex/TST and P/TST (Figure 6). InverselyIn contrast, Cap de Creus showed the lowest values for Q/TST, whilst the highest values were observed for Ex/TST and P/TST. Medes Islands MPA values were located between these two MPAs. Considering PLMU values, flow-based results revealed higher values for FPAs followed by PPAs in most of the flow-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 outrevealed that Cerbère-Banyuls had the highest values for IUCN species Bbiomass, followed by Medes Islands. Regarding ML and MLS of fish, 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 keystone indices~~The keystone index (Figure 8; Supplementary material appendix-Appendix 34) for the nine models identified ~~the same groups as~~ keystone functional groupss: groupers, oOther commercial medium demersal fish, common dentex and Labridae & Serranidae. Particularly, groupers obtained-had the highest relative total impact. These results confirmed that groupers play an important ecological role in Mediterranean coastal ecosystems. ~~The k~~Keystone index~~exices~~ showed different patterns among MUSPLs and MPAs. Medes Islands models obtained-had the highest number of keystone species followed by Cerbère-Banyuls (Figure 8).

517 **Role and impact of small-scale and recreational 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~~ Vulnerability index values were similar for Cap de Creus and Cerbère-Banyuls, and

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

The MTI analysis based on the recreational fisheries (Figure 10) revealed that ~~their impacts on the FGs in the ecosystem were clearly higher than the impacts of FGs to on 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.

In line with impacts of recreational fisheries, impacts of small scale fisheries (Figure 11) were higher and more fluctuating than impacts of FGs to small scale fisheries (ranging from 0.80 to 0.77 and 0.32 to 0.12, respectively). Generally, small scale impact results did not ~~evidence~~ show great differences between ~~MUs~~ PLs. The highest small scale 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). Small scale fisheries impacted results displayed low values (close to zero), except for groupers, which highly negatively impacted on the small scale fishery of PPA in Cap de Creus.

Overall, the MTI analysis based on fisheries did not show any pattern among MUsPLs 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, ~~the highest impacts of recreational fisheries were found for the PPA of Cap de Creus, while the highest impacts of small scale fleet were found for Cerbère-Banyuls impacts of recreational fisheries were higher for the PPA of Cap de Creus, while impacts of small scale 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 small scale 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 small scale fishery. Recreational and small scale fisheries showed low impacted and impacting values between them. Among them, the highest impact was for the recreational fleet on the small scale one in the PPA of Cap de Creus (~~0.28~~).

4. Discussion

Nine quantitative models were built to investigate the differences among MUsPLs of three MPAs in the NW Mediterranean Sea. ~~This analysis allowed us to assess the impact of protection on the ecosystem at local scale. To our knowledge, this is the first attempt to develop a food web model for each MUsPLs within MPAs to assess the impact of protection on the ecosystem at local scale.~~

The input data were qualitatively acceptable if our results are compared to the distribution of pedigree values in other existing models (~~Morissette, 2007; Lassalle et al., 2014~~)(~~Morissette, 2007; Lassalle et al., 2014~~)(~~Lassalle et al., 2014; Morissette, 2007~~). Also, the pedigree values of the models were comparable to that from other available MPA models in the Western Mediterranean Sea, such as 0.49 in the Portofino MPA (~~Prato et al., 2016~~)(~~Prato et al., 2016~~)(~~Prato et al., 2016a~~). However, FPA showed the lowest pedigree values because several P/B parameters were

estimated to ~~estimate—obtain~~ reasonable P/Q values (~~Heymans et al., 2016~~)(~~Heymans et al., 2016~~)(~~Heymans et al., 2016~~) and so decreasing their pedigree index. These results highlight~~ed~~ the need to ~~further develop studies~~ develop studies focused on estimating specific growth and consumption ratios for species in Mediterranean MPAs.~~develop studies focused on estimating specific growth and consumption ratios in Mediterranean MPAs to characterize and monitor MPAs within the Mediterranean Sea.~~

The flow diagram showed the first differences among MUsPLs. Although ~~the~~-TLs were similar among three MUsPLs in each MPA, some commercial functional groups (e.g. FG 26 – groupers in Cerbère-Banyuls) showed slightly 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~~)(~~Odum and Barrett, 1971~~)(~~Odum and Barrett, 1971~~).

Ecological indicators also showed differences among MUsPLs and pointed ~~out~~ at the strong benefits of FPAs (~~Sala et al., 2017~~)(~~Sala et al., 2017~~)(~~Sala et al., 2017~~). FPAs (also known as no-take areas) are widely recognized as a powerful tool for ecosystem and biodiversity conservation (~~Claudet et al., 2008~~)(~~Claudet et al., 2008~~)(~~Claudet et al., 2008~~) and several studies have described their positive effects on biomass (~~Guidetti et al., 2014~~)(~~Guidetti et al., 2014~~)(~~Guidetti et al., 2014~~), trophic levels (~~Prato et al., 2016~~)(~~Guénette et al., 2014~~)(~~Guénette et al., 2014~~), mean length (~~Claudet et al., 2006~~)(~~Claudet et al., 2006~~)(~~Claudet et al., 2006~~), mean life span (~~Guénette and Pitcher, 1999~~)(~~Guénette and Pitcher, 1999~~)(~~Guénette and Pitcher, 1999~~), condition (~~Lloret and Planes, 2003~~)(~~Lloret and Planes, 2003~~)(~~Lloret and Planes, 2003~~) and biomass of IUCN species such as groupers (~~Claudet et al., 2008~~)(~~Claudet et al., 2008~~)(~~Claudet et al., 2008~~).). Not surprisingly, biomass and trophic-based indicators results increased with the level of protection which demonstrated these positive effects of protection. This implies that FPAs promote higher fish weight and marine species abundance ~~Not surprisingly, biomass and trophic-based indicators results increased with the level of protection which demonstrated these positive effects of protection. This implies that FPAs promote higher fish weight and marine species~~

~~abundance (Harmelin-Vivien *et al.*, 2008). The increase in the TLs underlined the applicability of FPAs as a conservation tool for large predatory fish species. The increase in the TLs underlined the applicability of FPAs as a conservation tool for large predatory fish species (Soler *et al.*, 2015).~~

The same pattern was also 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, larger ecological size and higher resilience (Christensen, 1995) for FPAs ecosystems. In line with these results, Sala *et al.* (2017) highlighted the potential benefits of FPAs and pointed out that these areas are more resilient than UPAs. ~~In our study~~ In line with these results, consumption rate over total system flows was higher in FPAs than PPA and UPA, since the higher the biomass in the ecosystem the higher the consumption. Libralato *et al.* (2010)(2010)(2010) found similar results for another Mediterranean MPA in the Adriatic Sea due to the effect of protection. In addition, export 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. So, these FGs would migrate beyond the boundaries of the modelled ecosystem (PL) to maintain their feeding rates. The export results are also related to the fact that fisheries occur in UPAs and PPAs in comparison with FPAs, where they are forbidden. ~~The same pattern was also 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, larger ecological size and higher resilience (Christensen, 1995)(Christensen, 1995) for FPAs ecosystems. In line with these results, Sala *et al.* (2017)(2017) highlighted the potential benefits of FPAs and pointed out that these areas are more resilient than UPAs.~~

Similarly, species based-indicators results showed a gradient among PLs. ~~reduces population abundance and mostly removing larger and older fish and so decreasing the ML and MLS of fish in UPAs and increasing in the FPAs Fishing reduces population abundance and mostly removing larger and older fish and so decreasing the ML and MLS of fish in UPAs and increasing in the FPAs (Lizaso *et*~~

~~al., 2000). In addition, this pattern could also be due to large fish biomass with a dominance of large apex predators such as *Epinephelus marginatus* In addition, this pattern could also due to large fish biomass with a dominance of large apex predators such as *Epinephelus marginatus* (Hackradt et al., 2014). Similar results were found for several MPAs in the Mediterranean Sea (Guidetti et al., 2014).~~

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)(Giakoumi et al., 2017)(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)(Lester and Halpern, 2008; Sciberras et al., 2015)(Lester and Halpern, 2008; Sciberras et al., 2015). In addition, export 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. So, these FGs would migrate beyond the boundaries of the modelled ecosystem (PL) to maintain their feeding rates. The export results are also related to the fact that fisheries occur in UPAs and PPAs in comparison with FPAs, where they are forbidden.

In contrast, the Kempton's biodiversity index did not show the expected pattern as biodiversity is expected to increase with protection In contrast, the Kempton's biodiversity index (KI) did not show the expected pattern as biodiversity is expected to increase with protection (Costello and Ballantine, 2015)(Costello and Ballantine, 2015)(Costello and Ballantine, 2015). This controversial result could be due to the available data, which came from different studies for each MPA. The Kempton's biodiversity index may be biased since Cerbère-Banyuls model differs on the number of functional groups compared to Cap de Creus and Medes Islands model (Ainsworth and Pitcher, 2006). This controversial result could be due to the available data, which came from different studies for each MPA. Using multiple studies for each MPA could also bias this result because some studies showed biomass estimates at higher taxonomic levels than others and the time period that these models represent with regard to the creation year of the MPA. Therefore, as more

exhaustive species biomass data are available, the biodiversity index becomes more reliable. Using multiple studies for each MPA may bias this result because some studies showed biomass estimates at higher taxonomic levels than others and year. Therefore, as more exhaustive species biomass data are available, the biodiversity index becomes more reliable (Claudet, 2013; Hereu Fina *et al.*, 2017)(Claudet, 2013; Hereu Fina *et al.*, 2017)(Claudet, 2013; Hereu Fina *et al.*, 2017). Although some MPAs are not implemented for biodiversity purposes (Day *et al.*, 2012), the great differences of Kempton's biodiversity index between the FPA and the other two PL areas in Cap de Creus could indicate that the PPA and the UPA marine populations are not being replenished by new individuals coming from the FPA and so not achieving the FPA's biodiversity value. The failure on the spillover effect in Cap de Creus may be due to the lack of enforcement, the great differences of Kempton's biodiversity index between the FPA and the other two PL areas in Cap de Creus could indicate that the PPA and the UPA marine populations are not being replenished by new individuals coming from the FPA and so not achieving the FPA's biodiversity value. The failure on the spillover effect in Cap de Creus may be due to the lack of enforcement (Lloret *et al.*, 2008a, 2008b), high fishing pressure in the area (Lloret *et al.*, 2008b) or the zonation and design of the MPA which is represented by a fragmented PPA and a non-totally surrounded FPA. In addition, export 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. So, these FGs would migrate beyond the boundaries of the modelled ecosystem (MU) to maintain their feeding rates. The export results are also related to the fact that fisheries occur in UPAs and PPAs in comparison with FPAs, where they are forbidden.

Overall, indicators displayed differences among MUsPLs within each MPA, especially in the case of Cerbère-Banyuls and Medes Islands MPAs, but not for Cap de Creus. Probably, these patterns could be explained by their enforcement, reported to be a key factor to promote direct and indirect reserve effects (Guidetti *et al.*, 2008)(Guidetti *et al.*, 2008)(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)(Fenberg et al., 2012)(Fenberg et al., 2012)~~. Claudet and Guidetti ~~(2010)(2010)(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.* ~~(2008a, 2008b)(2008a, 2008b)(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 and ~~on lack of~~ fishing licenses. This is in contrast with Cerbère-Banyuls and Medes Islands MPAs, in which compliance and enforcement are ensured to promote a high level of ecological effectiveness ~~(Di Franco et al., 2016)(Di Franco et al., 2016)(Di Franco et al., 2016)~~. Our results are also consistent with previous studies performed in Cerbère-Banyuls ~~(Harmelin-Vivien et al., 2008)(Harmelin-Vivien et al., 2008)(Harmelin-Vivien et al., 2008)~~ and Medes Islands ~~(Harmelin-Vivien et al., 2008; Sala et al., 2012)(Harmelin-Vivien et al., 2008; Sala et al., 2012)(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 decline~~ing~~ from FPAs outward.

Giakoumi *et al.* ~~(2017)(2017)(2017)~~ revealed significant stronger biomass effect for FPAs than PPAs and higher fish density in older, better enforced, and smaller MPAs. Considering that Cap de Creus is the least enforced MPA in the study, our results suggest that the level of enforcement and ~~the~~ compliance have a strong effect on MPA effectiveness at the ecosystem level. These patterns among MPAs were also found by Horta e Costa *et al.* ~~(2016)(2016)(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 ~~(Horta e Costa et al., 2016)(Horta e Costa et al., 2016)(Horta e Costa et al., 2016)~~. Cap de Creus was not included in this study, but ~~a~~ higher MPA index can be assumed because of its small FPA and its low compliance which increases~~s~~ the impact of fishing activities. Overall, our results call for enhancement of the regulations, increasing the ~~surface extent~~ of FPAs and the enforcement of management rules in Medes and Cap de Creus MPA.

All keystone indices for the nine models pointed ~~out~~ at the same functional groups as keystones. Among them, groupers and common dentex were highlighted as keystone groups in previous western Mediterranean MPAs models (~~Valls et al., 2012; Prato et al., 2016~~)(~~Valls et al., 2012; Prato et al., 2016~~)(~~Prato et al., 2016b; Valls et al., 2012~~).

MPAs are considered an important tool to manage coastal fisheries (~~Claudet et al., 2006; Di Franco et al., 2016~~)(~~Claudet et al., 2006; Di Franco et al., 2016~~)(~~Claudet et al., 2006; Di Franco et al., 2016~~), and enforcement is a key aspect to achieve these goals. ~~Our results show~~Biomass and catch-based results demonstrated that well-enforced small coastal MPAs can enhance small-scale and recreational fisheries by spillover effect and can promote the sustainability of local fisheries (~~Forcada et al., 2009; Goñi et al., 2011; Sala et al., 2013~~)(~~Forcada et al., 2009; Goñi et al., 2011; Sala et al., 2013~~)(~~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. Additionally, these differences on catches and discards between PPAs and UPAs can be explained by the concept of “fishing the line”, which can reduce the biomass in neighbouring unprotected areas (~~Kellner et al., 2007~~)(~~Kellner et al., 2007~~)(~~Kellner et al., 2007~~), so understanding spatial-temporal patterns of fishing effort around an MPA is a key aspect to manage and assess these areas. In this context, Stelzenmüller et al. (~~2008~~)(~~2008~~)(~~2008~~) found a local concentration of fishing effort around the borders of Cerbère-Banyuls and Medes Islands MPAs, in accordance with our results. On the other hand, although small-scale and recreational fisheries are often considered to have a relatively low ecological impact, they do affect vulnerable species in coastal or offshore waters in the western Mediterranean Sea (including MPAs) through, targeted fishing or unintentional bycatch (~~Lloret et al., 2019~~)(~~Lloret et al., 2019~~)(~~Lloret et al., 2019~~).

The results of PLs in Cap de Creus differed substantially from Cerbère-Banyuls and Medes Islands. This could be related to the physical position of its FPA

within a multi-use MPA, which for Cap de Creus is not located at the core of the MPA surrounded by PPAs as is the common MPA design in the Mediterranean Sea. The results of MUs in Cap de Creus differed substantially from Cerbère-Banyuls and Medes Islands. This could be related to the physical position of its FPA, which for this MPA is not located at the core surrounded by PPAs as is the common MPA design in the Mediterranean Sea (Gabrié *et al.*, 2012)(Gabrié *et al.*, 2012)(Gabrié *et al.*, 2012). This unconventional placement could explain the observed reduction in PPA effectiveness although this interpretation could be biased by the apparent lack of enforcement in Cap de Creus. In MPAs, the maximum benefit to conservation and ecosystem services will occur when FPAs are surrounded by well-managed fishing grounds (Roberts and Hawkins, 2000)(Roberts and Hawkins, 2000). This result suggested the requirement of an implemented and non-fragmented PPA surrounding the FPA in Cap de Creus which complements and ensures the protection of the biodiversity in the FPA, as recommended in IUCN guidelines for applying MPAs and non-fragmented s (Day *et al.*, 2012)(Day *et al.*, 2012). This unconventional placement could explain the observed reduction in PPA effectiveness.

In addition, high values of total catch and discards in Cap de Creus could be related to non-compliance, as well as to the lack of georeferenced catch data that could have biased our results. Non-compliance could also result in some fishing inside FPAs and PPAs, which may reduce the effectiveness of their potential biological, ecological and fisheries benefits (Roberts, 2000)(Roberts, 2000)(Roberts, 2000), in accordance with the lack of enforcement above conclusions obtained from other ecological indicators (e.g. biomass-based indicators). Additionally, estimates of IV vulnerability index and ML of the catch estimated values from Cap de Creus could be explained as a failure in the enforcement in an MPA supporting a high fishing pressure from both small-scale and recreational fishing sectors (Lloret and Font, 2013)(Lloret and Font, 2013)(Lloret and Font, 2013). Finally, our results highlighted the impact of recreational fisheries in Cap de Creus among the rest of studied MPAs, which could be also reducing MPA benefits (Lloret *et al.*, 2008a, 2008b)(Lloret *et al.*, 2008a, 2008b)(Lloret *et al.*, 2008b, 2008a). On the other hand,

~~the lower values of total catch and discards, the higher values of TL of the catch, ML and MLS of fish in the catch, could reveal potential benefits of protection to adjacent fisheries. Fishing pressure can lead to a decrease of TL of the catch, the higher values of TL of the catch, ML and MLS of fish in the catch, which reveal potential benefits of protection to adjacent fisheries. Fishing pressure can lead to a decrease of TL of the catch (Shannon *et al.*, 2014) and ML and MLS of fish in the catch (Pelletier *et al.*, 2005). Similarly, Prato *et al.* (2016) demonstrated that a decrease in the fishing effort lead to an increase in the trophic level of the catch because of increasing in fish predators biomass in Portofino MPA (Northwestern Mediterranean Sea)demonstrated that a decrease on the fishing effort lead to an increase on the trophic level of the catch because of increasing on fish predators biomass in Portofino MPA (Northwestern Mediterranean Sea).~~

PPAs showed higher impacted values than UPAs, which suggest a higher contribution of PPAs to the recreational fishery. Although PPAs may differ ~~on~~in their level of protection ~~(Lester and Halpern, 2008)(Lester and Halpern, 2008)(Lester and Halpern, 2008)~~, for example, spearfishing is not allowed inside the PPA of Cerbère-Banyuls ~~(Font *et al.*, 2012b)(Font *et al.*, 2012b)(Font *et al.*, 2012b)~~, these results confirmed their ecological effects and benefits for adjacent fisheries. Regarding the small scale fishery, the highest negative impacting values were represented by targeted species for this fleet, while positive values may represent FGs which are preys of those targeted species. Cerbère-Banyuls obtained higher impacting values than other MPAs. Since it is a ~~well~~well-enforced MPA, it could represent higher benefits or catches than other MPAs. In addition, most highlighted FGs by their high impacting values in small scale 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)(Claudet and Guidetti, 2010)(Claudet and Guidetti, 2010)~~. Our results encourage fishermen compliance, which was identified as a key attribute for fisheries' success such as in Torre Guaceto MPA, where co-management involving fishers, scientists and managers led to an increase in total

fish biomass in FPA, an increase in fishermen's revenues when they operate within the PPA and an increase in the commitment of local fishermen to environmental issues (Di Franco *et al.*, 2016)(Di Franco *et al.*, 2016)(Di Franco *et al.*, 2016).

The stronger benefits of FPAs than PPA and the importance of PPAs as a buffer area may suggest an alternative reorganization on the MPA zonation. An increase on the surface or percentage of area covered by FPA could lead to more resilient and productive MPAs which would enhance the benefits of ecosystem services including adjacent fisheries. Additionally, PPAs must be surrounding the FPA in order to ensure and complement the protection. Accordingly, MPA configuration may obtain greater benefits when increasing the FPA surface and ensuring its protection with a buffer PPA. MPAs and networks of MPAs can be used to enhance the resilience, resistance in front perturbations or ecosystem transformation in the face of climate change the e (Sala *et al.*, 2017) (Day *et al.*, 2012)the and so spatial analysis should be included in future studies in order to verify the benefits of new protection level zonations(Carr *et al.*, 2017)(Carr *et al.*, 2017). MPA zonation allows to assess the impacts of each protection level and accommodate multiple objectives, human activities and stakeholder groups, and it is a key aspect of the management of MPAs MPA zonation allows to assess the impacts of each PL and accommodate multiple objectives, human activities and stakeholder groups, and it is a key aspect of the management of MPAs (Francour *et al.*, 2001; Lester and Halpern, 2008).

Even though our work illustrates that quantitative food-web modelling techniques can be useful to assess coastal MPAs effects on the structural and functional traits of marine ecosystems and their adjacent fisheries, some limitations were faced. One of the main hurdles was the lack of local data for some FGs identified in previous MPAs modelling studies (Libralato *et al.*, 2010; Valls *et al.*, 2012; Prato *et al.*, 2016)(Libralato *et al.*, 2010; Valls *et al.*, 2012; Prato *et al.*, 2016)(Libralato *et al.*, 2010; Prato *et al.*, 2016a; Valls *et al.*, 2012). For example, literature including benthonic biomass estimations inside MPAs is mainly focused on

sea urchins, gorgonians and *Posidonia* meadows (e.g. [Hereu Fina and Quintana Pou, 2012; Schwartz and Labbe, 2012](#)~~(Hereu Fina and Quintana Pou, 2012; Schwartz and Labbe, 2012)~~~~(Hereu et al., 2012; Schwartz and Labbe, 2012)~~). However, studies on other important benthic groups such as sponges or crustaceans are scarce. [During the balancing procedure, higher predation mortalities were found for several FGs in most quantitative models and diet imports were set in order to ensure the mass-balance for each model. Although these import values were set considering ecological and size attributes of each FGs, small and open study areas could represent a limitation of our models due to the lack of data and knowledge](#)~~During the balancing procedure, higher predation mortalities were found for several FGs in most quantitative models and diet imports were set in order to ensure the mass-balance. Although these import values were set considering ecological and size attributes of each FGs and did not influence modeling output, small study areas could represent a limitation for food-web modeling.~~ Additionally, spatial-temporal series [data](#) of catches and fleet distribution would improve the analysis on the effect of MPA potential benefits on the recreational and small scale fisheries. Collecting time series of fishing activities surrounding MPAs is a monitoring priority, as previously highlighted ([Valls et al., 2012; Prato et al., 2016](#))~~(Valls et al., 2012; Prato et al., 2016)~~~~(Prato et al., 2016a; Valls et al., 2012)~~. A recent published study ([Lloret et al., 2019](#))~~(Lloret et al., 2019)~~~~(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 zonation of the modelled MPAs ([Heymans et al., 2016](#))~~(Heymans et al., 2016)~~~~(Heymans et al., 2016)~~. In addition, and despite [the fact](#) 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](#))~~(Sala et al., 2012)~~~~(Sala et al., 2012)~~.

Despite the 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 Mediterranean coastal 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 on~~ the potential benefits of MPAs at the local scale, and a lack of enforcement is noticeable in surrounding areas. MPAs can increase ecosystem maturity and resilience and show potential benefits for small-scale fisheries that act in their surroundings when these areas are well-enforced. Perceptions of ecological and social benefits are key drivers of stakeholder support to MPAs and could therefore reinforced a virtuous loop further enhancing MPA effects ~~(Bennett et al., 2019)(Bennett et al., 2019)(Bennett et al., 2019)~~. Future assessments on the spatial distribution of marine resources and the role of these PLs within a network should take place in order to quantify their impacts at a sub-regional (e.g. Northwestern Mediterranean) and regional (e.g. Western Mediterranean) geographic scales.~~Future assessments on the role of these MUs within a network should take place in order to quantify their impacts at a sub-regional (e.g. Northwestern Mediterranean) and regional (e.g. Western Mediterranean) geographic scales.~~

Acknowledgements

This work was funded by EU Research Project SAFENET project ("Sustainable Fisheries in EU Mediterranean Waters through Network of MPAs." Call for proposals MARE/2014/41, Grant Agreement n. 721708). D. Vilas benefited from a Short Term Scientific Mission by the COST Action MarCons (CA15121).

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Tables

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26 1755 **Table 1.** Surface area (km²) and the percentage covered by management-unit
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28 1756 (MU)protection level (PL) and year of creation of each marine protected area (MPA)
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30 1757 (Cerbère-Banyuls, Cap de Creus and Medes Islands).

MPA	Year of creation	PLMU (km ²) (%)		
		FPA	PPA	UPA
Cerbère-Banyuls	1974	0.65 (1.59)	5.85 (14.32)	35.00 (85.68)
Cap de Creus	1998	0.21 (0.69)	7.98 (26.11)	22.37 (73.20)
Medes Islands	1983	0.39 (2.00)	4.24 (21.77)	14.85 (76.23)

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50 1761 **Table 2.** Functional groups included for the MU models showing those present (P)
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52 1762 or absent (A) in each MPA. FG = Functional Group. Discards only are included in
53 1763 PPA and UPA models.
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FG number	FG-name	Cerbère- Banyuls	Cap—de Creus	Medes Islands
1	Bottlenose dolphins	P	P	P
2	Striped dolphins	P	P	P
3	Endangered—and—pelagic seabirds	P	P	P
4	Gulls and cormorants	P	P	P
5	Terns	P	P	P
6	Loggerhead turtles	P	P	P
7	Non-commercial large pelagic fishes	P	P	P
8	Other large pelagic fishes	P	P	P
9	Mackerels	P	P	P
10	Horse mackerels	P	P	P
11	Other medium pelagic fishes	P	P	P
12	European sardine	P	P	P
13	European anchovy	P	P	P
14	Round sardinella	A	P	P
15	Other small pelagic fish	P	P	P
16	Anglerfish	P	P	P
17	European conger	P	P	P
18	European hake	P	P	P
19	Poor cod	P	P	P
20	Common pandora	P	P	P
21	Sparidae	P	P	P
22	White seabream	P	P	P
23	Common—and—two-banded seabream	P	P	P
24	Common dentex	P	P	P
25	Red scorpionfish	P	P	P
26	Scorpaenidae	P	P	P
27	Groupers	P	P	P
28	Brown meagre	P	P	P
29	Labridae and Serranidae	P	P	P
30	Flatfishes	P	P	P
31	Other—commercial—medium demersal fish	P	P	P
32	No—commercial—medium demersal fish	P	P	P
33	Salema	P	P	P
34	Mugilidae	P	P	P
35	Red mullet	P	P	P
36	Striped red mullet	P	P	P
37	No-commercial small demersal fish	P	P	P
38	Small-spotted catshark	P	P	P
39	Rays and skates	P	P	P

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3		40	Torpedos	P	P
4		41	Coastal benthic cephalopods	P	P
5		42	Benthopelagic cephalopods	P	P
6		43	Other benthic cephalopods	P	P
7		44	Bivalves	P	P
8		45	Gastropods	P	P
9		46	European lobster	P	P
10		47	Other commercial decapods	P	P
11		48	Non-commercial decapods	P	P
12		49	Purple sea urchin	P	P
13		50	Other sea urchin	P	P
14		51	Sea cucumbers	P	P
15		52	Other macro-benthos	P	P
16		53	Jellyfish	P	P
17		54	Salps and other gelatinous zooplankton	P	P
18		55	Red coral	P	P
19		56	Other corals and gorgonians	P	P
20		57	Macrozooplankton	P	P
21		58	Meso and microzooplankton	P	P
22		59	Suprabenthos	P	P
23		60	Mediterranean seagrass	P	P
24		61	Other seagrasses	A	P
25		62	Erected algae	A	P
26		63	Seaweeds	P	P
27		64	Small phytoplankton	P	P
28		65	Large phytoplankton	P	P
29		66	Detritus	P	P
30		67	Discards	P	P
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Figures

Figure 1. Location of the three MPAs and their ~~MUs~~ protection levels (PL) ~~PLs~~ (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 the three **MUs** protection levels (PL) 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 diagrams of three management units protection levels (PL) (FPA: red; PPA: yellow; UPA: green) of Cerbère-Banyuls MPA model organized by trophic levels (TL) (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. The numbers identify the functional groups of the PLMU models (Appendix 1 supplementary material) (Flow diagrams of Cap de Creus and Medes Islands MPA can be found in supplementary material Figure S5S6.1.).

Figure 4. Biomass-based indicators of the three MUs protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, Kempton's Q – Kempton's Q diversity index).

Figure 5. Trophic-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (TL – trophic level).

Figure 6. Flow-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (Q/TST – Consumption ratio, Ex/TST – Export ratio, P/TST – Production ratio, TST – Total System Throughput, FCI – Finn Cycle Index and APL – Average Path Length).

Figure 7. Species-based indicators of the three protection levels (PL) (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, ML – mean length and MLS – mean life span).

Figure 8. Keystone Index analysis of the three protection levels (PL) (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 the three protection levels (PL) (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (C – Catch; TL – trophic level; ML – mean length; MLS – mean life span).

Figure 10. Recreational impacting and impacted values of three protection levels (PL)MU models (PPA: partially protected area; UPA: unprotected area) 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 – striped red mullet; WSE – white seabream; ART – Small scale fishery).

Figure 11. Small scale impacting and impacted values of three protection levels (PL)MU models (PPA: partially protected area; UPA: unprotected area) 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 – striped red mullet; WSE – white seabream; REC – Recreational fishery).

Supplementary data

Additional Supplementary material may be found in the online version of this article:

Appendix 1. Supplementary table: Functional groups included for the protection level models showing those present (P) or absent (A) in each MPA (Table S1.1.).

Appendix 12. Supplementary tables: Cerbère-Banyuls, Cap de Creus and Medes MPAs functional groups species composition and methods and references used to estimate the basic input parameters of the nine Ecopath models (Table S1S2.1.); Input parameters and outputs estimate for Cerbère-Banyuls (Table S1S2.2.), Cap de Creus (Table S1S2.3.) and Medes Islands (Table S1S2.4.) PLMU models.

Appendix 23. Supplementary tables: Diet composition matrix for the protection levelMU models of Cerbère-Banyuls (Table S2S3.1.), Cap de Creus (Table S2S3.2.) and Medes Islands (Table S2S3.3.) MPA.

Appendix 34. Supplementary tables: Keystone indexes and Relative Total Impact values for the functional groups included in Cerbère-Banyuls (Table S3S4.1.), Cap de Creus (Table S3S4.2.) and Medes Islands (Table S3S4.3.) protection levelMU models. FPA: fully protected area; PPA: partially protected area; UPA: unprotected area.

Appendix 45. Additional explanatory text about modelling parameterization and balancing procedure.

Appendix 56. Supplementary figure: Flow diagrams of three management unitsprotection levels (FPA: red; PPA: yellow; UPA: green)-of Cap de Creus and Medes Islands MPA model (Figure S6.1.).

For Peer Review