AQUATIC CONSERVATION
Marine and Freshwater Ecosystems

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

Journal:	*Aquatic Conservation: Marine and Freshwater Ecosystems*
Manuscript ID	Draft
Wiley - Manuscript type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Vilas, Daniel; University of Florida Institute of Food and Agricultural Sciences, Nature Coast Biological Station; University of Florida School of Forest Resources and Conservation, Fisheries and Aquatic Sciences Program; Institut de Ciències del Mar, Renewable Marine Resources Coll, Marta; Institut de Ciències del Mar, Renewable Marine Resources; Ecopath International Initiative Corrales, Xavier; Institut de Ciències del Mar, Renewable Marine Resources; Ecopath International Initiative Steenbeek, Jeroen; Ecopath International Initiative Piroddi, Chiara; European Commission Joint Research Centre Ispra Sector, Institute for Environment and Sustainability Calò, Antonio; Université Côte d'Azur, CNRS, UMR ; Università di Palermo Dipartimento di Scienze della Terra e del Mare Di Franco, Antonio; Université Côte d'Azur, CNRS, UMR ; Stazione Zoologica Anton Dohrn, Dipartimento Ecologia Marina Integrata, Sede Interdipartimentale della Sicilia Font, Toni; Universitat de Girona Facultat de Ciencies Guidetti, Paolo; Université Côte d'Azur, CNRS, UMR Ligas, Alessandro; Consorzio per il Centro Interuniversitario di Biologia Marina ed Ecologia Applicata G. Bacci, Lloret, Josep; Universitat de Girona Facultat de Ciencies, Institute of Aquatic Ecology Prato, Giulia; WWF Italy Sahyoun, Rita; WWF France Sartor, Paolo; Consorzio per il Centro Interuniversitario di Biologia Marina ed Ecologia Applicata G. Bacci Claudet, Joachim; National Centre for Scientific Research, CRIOBE
Broad habitat type (mandatory) select 1-2:	coastal < Broad habitat type
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Authors

Daniel Vilas*[1,2,3], Marta Coll[1,4], Xavier Corrales[1,4], Jeroen Steenbeek[4], Chiara Piroddi[5], Antonio Calò[6,7], Antonio Di Franco[6,8], Toni Font[9], Paolo Guidetti[6], Alessandro Ligas[10], Josep Lloret[9], Giulia Prato[11], Rita Sahyoun[12], Paolo Sartor[10] and Joachim Claudet[13]

Affiliations

[1] Institut de Ciències del Mar (ICM-CSIC), P. Marítim de la Barceloneta, 37-49, 08003 Barcelona, Spain.

[2] Nature Coast Biological Station, Institute of Food and Agricultural Sciences, University of Florida, Cedar Key, FL 32625, United States.

[3] Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, United States.

[4] Ecopath International Initiative (EII), Barcelona, Spain.

[5] European Commission, Joint Research Centre, Institute for Environment and Sustainability, Via Fermi 2749, 21027 Ispra, Italy.

[6] Université Côte d'Azur, CNRS, UMR 7035 ECOSEAS, Parc Valrose 28, Avenue Valrose, 06108, Nice, France.

[7] Dipartimento di Scienze della Terra e del Mare (DiSTeM), Università di Palermo, Via Archirafi 20, 90123 Palermo, Italy.

[8] Stazione zoologica Anton Dohrn, Dipartimento Ecologia Marina Integrata, Sede Interdipartimentale della Sicilia, Lungomare Cristoforo Colombo (complesso Roosevelt), 90142 Palermo, Italy.

[9] Universitat de Girona, Girona, Spain.

[10] Consorzio per il Centro Interuniversitario di Biologia Marina ed Ecologia Applicata "G.Bacci", Italy.

[11] WWF Italy, Italy.

[12] WWF France, 35-37 rue Baudin - 93310 Le Pré-Saint-Gervais – France.

[13] National Center for Scientific Research, PSL Université Paris, CRIOBE, USR 3278 CNRS-EPHE-UPVD, Maison des Océans, 195 rue Saint-Jacques 75005 Paris, France.

Abstract

The overexploitation of many marine resources and ecosystems calls for the development and implementation of measure of measures to support their recovery and conservation. We assessed the potential contributions to support fisheries and ecosystem recovery 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. For each MPA, we developed a food-web model accounting for each management units (MU): 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 MU, we assessed differences and similarities within and among the three MPAs, and we evaluated if the ecosystem response to full protection led to specific ecosystem functional traits that are shared among the three MPAs. We showed differences among MUs in terms of ecosystem structure and functioning. 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 neighboring unprotected areas were hardly noticeable. Similarities between Cerbère-Banyuls and Medes Islands MPAs were obtained, 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 areas, the levels of enforcement and compliance, and the impact of recreational and small scale fisheries allowed in the PPAs and UPAs. Our study illustrates that well-enforced Mediterranean MPAs, even small, can yield local positive impacts on the structure and functioning of marine ecosystems that can contribute to support local fisheries.

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

***Contact author:** danielvilasgonzalez@gmail.com

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). 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). Marine protected areas (MPAs hereafter) are an essential tool for reversing the global degradation of ocean life (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 protected with implemented MPAs (Sala et al., 2018).

MPAs can also provide socioeconomic 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), or from securing future jobs by increasing the chances of managing stocks sustainably (Sumaila et al., 2000). Fisheries benefits arise from ecological effects within protected areas in the form of biomass recovery, and subsequent spillover outside the boundaries of the MPA (Di Lorenzo et al., 2016) or by increased larval production and supply toward unprotected areas (Marshall et al., 2019), with MPAs finally replenishing external fisheries grounds. Actually, empirical studies comprising small scale (Stelzenmüller et al., 2008), recreational (Font et al., 2012a) and industrial bottom-trawling fishing effort (Murawski et al., 2005) showed a concentration of fishing activities in the close vicinity of the MPA boundaries. This concentration of fishing effort, also known as "fishing the line", can reduce the biomass in neighboring unprotected areas.

Most MPAs are multiple-use (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 (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 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 or protection transfer into fisheries benefits. Here, using food-web modeling techniques, 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 develop ecosystem models for each management unit in each MPA.

2. Material & Methods

Study areas

Different management units (MUs) of three MPAs in the Northwestern Mediterranean Sea were examined: Cerbère-Banyuls MPA in France, Cap de Creus and Medes Islands MPAs in Spain (Figure 1). An 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, wherewhere fishing exploitation 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 onto 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

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

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

Consumption = production + respiration + unassimilated food 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 management unit, i.e. for each combination of the three MPAs and three protection levels (FPA, PPA and UPA).

The nine MU 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., 2019a) developed under the SafeNet Project[1] 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 (2 marine mammals, 3 seabirds, 1 sea turtle, 8 pelagic fish, 25 demersal fish, 3 cephalopods, 14 invertebrates, 2 primary producers, 2 zooplankton, 2 phytoplankton and 2 detritus), while Cap de Creus MPA and Medes Islands MPA had 67 functional groups each (2 marine mammals, 3 seabirds, 1 sea turtle, 9 pelagic fish, 25 demersal fish, 3 cephalopods, 14 invertebrates, 4 primary producers, 2 zooplankton, 2 phytoplankton and 2 detritus) (Table 2). Except in the case of FPAs, which do not have discards because all fishing extractions are forbidden, food-web structures of each MU in the same MPA were identical.

FGs' biomass were obtained from different sources from the study area or surrounding areas (see additional explanatory text in Appedix 4 and supplementary material Table S1.1. for details on the parameterization of each functional group).

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., 2019b) (supplementary material Table S1.1). Additionally, local body lengths of reef-

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

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).

The diet information was compiled using published studies on stomach content analyses, giving preference to local or surrounding areas (supplementary material Table S1.1.*)*. 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. Due to the small sizes of the MUs investigated and the capacity to some species to move between MUs (Gell and Roberts, 2003a; Grüss et al., 2011), a fraction of the diet composition of these species was set as import for all MUs based on the time that these species feed outside the areas and their ecological traits. This import was based on the size, behavior and ecology of species of each functional group (Froese and Pauly, 2019).

Fisheries data were obtained from different sources (database, literature and unpublished data) (additional explanatory text in Appendix 4 and supplementary material Table S1.1) 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).

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 mass-balance of all the models was followed (detailed information can be found at Appendix 4 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 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, 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).

Models analyses and ecological indicators

Flow diagram

The food-web structure of each MU in the three MPAs was visualized using a flow diagram. Flow diagrams were obtained using the *ggplot2* package (Wickham, 2010) implemented in R software (R Core Team, 2017) and were built from the biomass and trophic levels (TL, as outputs) of each FG, and the direct trophic interactions among them 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).

Ecological indicators

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

Biomass-based. These indicators are calculated from the biomass of components. Species biomass data are considered basic information to evaluate effectiveness in marine protected areas (Micheli et al., 2004). 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 predators can cause a decline in the trophic level of the catch and/or the community (Christensen and Walters, 2004). 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).

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). 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, t·km^{-2}·year^{-1}), mean length of fish in the community (ML, cm) and mean life span of fish in the community (MLS, year).

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

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

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

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

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.

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 keystoneness index (KS) of the most important reef FG (common pandora: *Pagellus erythrinus*; Sparidae; white seabream: *Diplodus sargus*; common two-banded seabream: *Diplodus vulgaris*; Common dentex: *Dentex dentex*; red scorpionfish: *Scorpaena scrofa*; groupers: *Epinephelus 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 different methods: (1) Power keystone indicator (1996) (KS_P) and (2) Libralato's keystone indicator (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 (2015) (KS_V) keystoneness index, in which the biomass component is based on a descending ranking. These indices are calculated as:

$$KS_{Pi} = \varepsilon_{i\frac{1}{p_i}} \qquad \text{Eq.4}$$

$$KS_{Li} = \log\left[\varepsilon_i(1 - p_i)\right] \qquad \text{Eq.5}$$

$$KS_{Vi} = log\left[IC_i{\cdot}BC_i\right] \qquad \text{Eq. 6}$$

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

Evaluating MPAs and the role of MUs

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

Same above-mentioned indicators were used to evaluate differences among the three studied MPAs, comparing the same MUs of the different MPAs. For instance, considering the FPAs of the three MPAs allowed us to capture how different are these MPAs since they officially offer the same levels of protection. Despite that each MPA differs on restriction in their PPAs, this multiple comparison procedure was developed for the three MUs because the ecological theory establishes that reserve effects should extend from FPA beyond its boundaries as a result of the 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 MU models showed similar values among them (Figure 2), ranging from 0.41 to 0.52. The highest pedigree values were obtained for Cerbère-Banyuls, and FPAs obtained slightly lower pedigree index than the other MUs.

The flow diagrams displayed high levels of biomass even for some high trophic level groups, especially in the FPAs (Figure 3 and supplementary material Figure S5.1). Also, results emphasized the complexity of these food webs regarding the number of trophic links among functional groups with important fluxes of energy from phytoplankton (FG 61 and 62) and detritus (FG 63) up to the food web.

Ecosystem structure and functional traits

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

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 higher variance among these indicators. Specifically, Cap de Creus showed the highest TL3.25 values and the lowest TL4 value. Within MUs, most trophic-based indicators showed the highest values for FPAs followed by PPAs and UPAs. However, FPA in Cap de Creus displayed the lowest value of TL4 (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). Inversely, 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 MU 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 out that Cerbère-Banyuls had the highest values for IUCN species B, followed by Medes Islands. Regarding ML and MLS, the highest values were also obtained for Cerbère-Banyuls, followed by Cap de Creus and then Medes Islands. Species and size-based indicators were higher for FPAs, except in Cap de Creus, where PPA had higher values of ML and MLS than FPA.

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

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

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

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 great differences between MUs. 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 MUs and MPAs, and fisheries impacting values were clearly higher and more fluctuating than impacted values (ranging from -0.86 to 0.84 and -0.32 to 0.26, respectively). Mostly, impacts of recreational fisheries were higher for the PPA of Cap de Creus, while impacts of 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 MUs of three MPAs in the NW Mediterranean Sea. To our knowledge, this is the first attempt to develop a food-web model for each MUs within MPA to assess the impact of protection 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 (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., 2016a). However, FPAs showed the lowest pedigree values because several P/B parameters were estimated to estimate reasonable P/Q values (Heymans et al., 2016) and so decreasing their pedigree index. These results highlight the need to further develop studies to charactherize and monitor MPAs within the Mediterranean Sea.

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

Ecological indicators also showed differences among MUs and pointed out 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 (Guénette et al., 2014), mean length

(Claudet et al., 2006), mean life span (Guénette and Pitcher, 1999), condition (Lloret and Planes, 2003) and biomass of IUCN species such as groupers (Claudet et al., 2008). In our study, consumption rate over total system flows was higher in FPAs than PPA and UPA, 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. 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 addition, most biomass-based, trophic-based, species-based and flows-based results obtained from PPAs demonstrated their role as buffer zones (Giakoumi et al., 2017), so they may confer biomass enhancement compared to UPAs although FPAs produce greater benefits (Lester and Halpern, 2008; Sciberras et al., 2015).

In contrast, the biodiversity index (KI) did not show the expected pattern as biodiversity is expected to increase with protection (Costello and Ballantine, 2015). This controversial result could be due to the available data, which came from different studies for each MPA and year. Therefore, as more exhaustive species biomass data are available, the biodiversity index becomes more reliable (Claudet, 2013; Hereu Fina et al., 2017). In addition, export 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 MUs within each MPA, especially in the case of Cerbère-Banyuls and Medes Islands MPAs, but not for Cap de Creus. Probably, these pattern could be explained by their enforcement, reported to be a key factor to promote direct and indirect reserve effects (Guidetti et al., 2008).

The lack of enforcement is one of the most relevant issues concerning MPAs in the Mediterranean context (Fenberg et al., 2012). Claudet and Guidetti (2010) recognized that an MPA without enforcement and compliance is just a paper park and no reserve effects can be expected. This could be the case of Cap de Creus, in which our results did not show the same pattern found for the other two MPAs. In fact, Lloret *et al.* (2008b, 2008a) reported a lack of enforcement and a low level of compliance in Cap de Creus, particularly on minimum landing sizes of certain species and on lacking fishing license. 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 declining from FPAs outward.

Giakoumi *et al.* (2017) revealed significant stronger biomass effect for FPAs than PPAs and higher fish density in older, better enforced, and smaller MPA. Considering that Cap de Creus 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) 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 higher MPA index can be assumed because of its small FPA and its low compliance which increase the impact of fishing activities. Overall, our results call for enhancement of the regulations, increasing the surface of FPAs and the enforcement of management rules in Medes and Cap de Creus MPA.

All keystoneness indices for the nine models pointed out at the same functional groups as keystones. Among them, groupers and common dentex were highlighted as keystone groups in previous western Mediterranean MPAs models (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), and enforcement is a key aspect to achieve these goals. Our results show 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 neighboring unprotected areas (Kellner et al., 2007), so understanding spatial-temporal patterns of fishing effort around a MPA is a key aspect to manage and assess these areas. In this context, Stelzenmüller *et al*. (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 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). 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), in accordance with above conclusions obtained from other ecological indicators (e.g. Biomass-based indicators). In addition, estimates of IV and ML from Cap de Creus could be explained as a failure in the enforcement in an MPA supporting a 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., 2008b, 2008a).

PPAs showed higher impacted values than UPAs, which suggest a higher contribution of PPAs to the recreational fishery. Although PPAs may differ on their level of protection (Lester and Halpern, 2008), for example spearfishing is not allowed inside the PPA of Cerbère-Banyuls (Font et al., 2012b), these results confirmed their ecological effects and benefits for adjacent fisheries. 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 prey of those targeted species. Cerbère-Banyuls obtained higher impacting values than other MPAs. Since it is a well enforced MPA, it could represent higher benefits or catches than other MPAs. In addition, most highlighted FGs by their high impacting values in 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 revenues when the operate within the PPA and increase the commitment of local fishermen to environmental issues (Di Franco et al., 2016).

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; 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 et al., 2012; Schvartz and Labbe, 2012). However, studies on other important benthic groups such as sponges or crustaceans are scarce. Additionally, spatial-temporal series of catches and fleet distribution would improve the analysis on the effect of MPA potential benefits on the recreational and small scale fisheries. Collecting time series of fishing activities surrounding MPAs is a monitoring priority, as previously highlighted (Prato et al., 2016a; Valls et al., 2012). A recent published study (Lloret et al., 2019), which focused in the Northwestern Mediterranean Sea, emphasized the importance of differentiating between fishing methods or gears when studying the impacts on vulnerable species in MPAs which could be accomplished if data are available. Moreover, our results could be biased by the oceanographic conditions and the zonation of the modelled MPAs (Heymans et al., 2016). In addition, and despite that these MPAs are closely located, the biomass estimations to develop the models came from different reference years which could limit the comparison among MPAs as a result of different environmental conditions (Sala et al., 2012).

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 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 virtuos loop further enhancing MPA effects (Bennett et al., 2019). 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.

Acknowledgments

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

MPA	Year of creation	MU (km²)		
		FPA	PPA	UPA
Cerbère-Banyuls	1974	0.65	5.85	35.00
Cap de Creus	1998	0.21	7.98	22.37
Medes Islands	1983	0.39	4.24	14.85

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

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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 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
40	Torpedos	P	P	P
41	Coastal benthic cephalopods	P	P	P
42	Benthopelagic cephalopods	P	P	P
43	Other benthic cephalopods	P	P	P
44	Bivalves	P	P	P
45	Gastropods	P	P	P
46	European lobster	P	P	P
47	Other commercial decapods	P	P	P
48	Non-commmercial decapods	P	P	P
49	Purple sea urchin	P	P	P
50	Other sea urchin	P	P	P
51	Sea cucumbers	P	P	P
52	Other macro-benthos	P	P	P
53	Jellyfish	P	P	P
54	Salps and other gelatinous zooplankton	P	P	P
55	Red coral	P	P	P
56	Other corals and gorgonians	P	P	P
57	Macrozooplankton	P	P	P
58	Meso and microzooplankton	P	P	P
59	Suprabenthos	P	P	P
60	Mediterranean seagrass	P	P	P
61	Other seagrasses	A	P	P
62	Erected algae	A	P	P
63	Seaweeds	P	P	P
64	Small phytoplankton	P	P	P
65	Large phytoplankton	P	P	P
66	Detritus	P	P	P
67	Discards	P	P	P

Figures

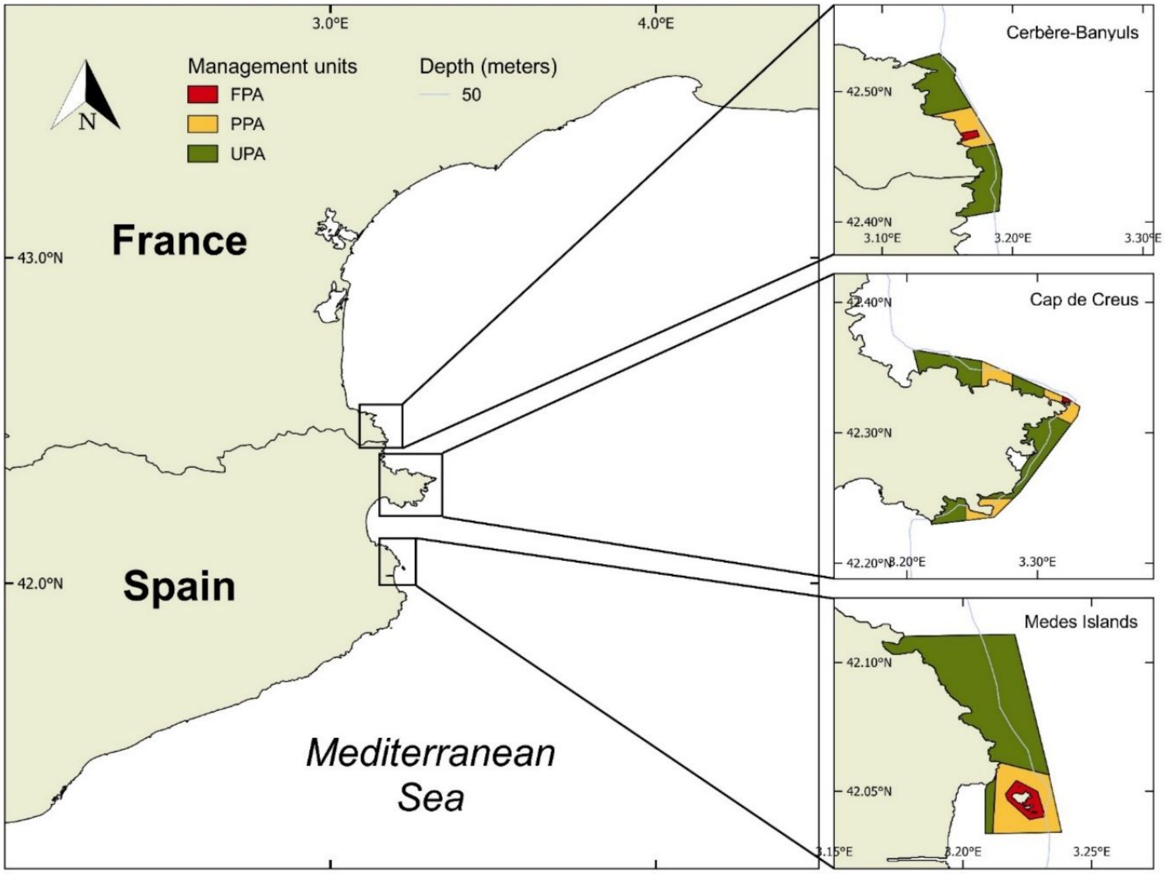

Figure 1. Location of the three MPAs and their MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) in Cerbère-Banyuls, Cap de Creus and Medes Islands.

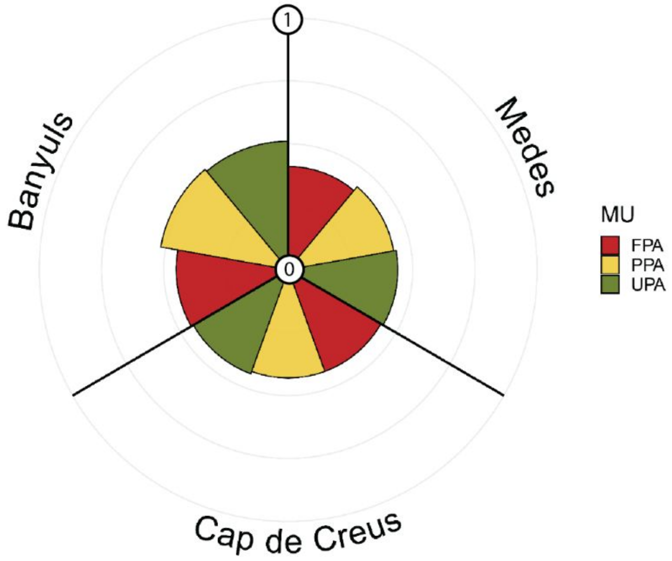

Figure 2. Pedigree index values of the three MUs models (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands).

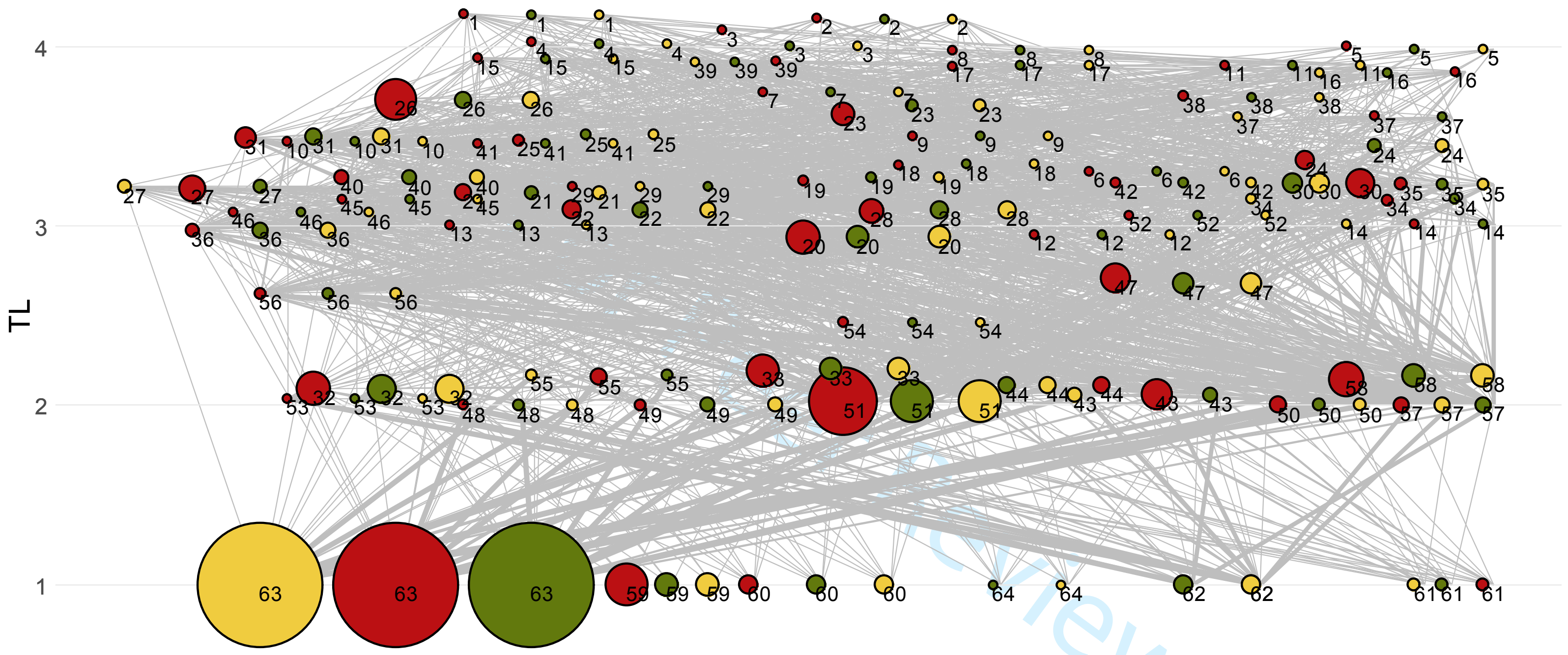

Figure 3. Flow diagrams of three management units (FPA: red; PPA: yellow; UPA: green) of Cerbère-Banyuls MPA model organized by trophic levels (TL) (y-axis). The size of each circle is proportional to the biomass of the functional group. The wideness of the connecting lines is proportional to the magnitude of their flows. The numbers identify the functional groups of the MU models (Appendix 1 supplementary material) (Flow diagrams of Cap de Creus and Medes Islands MPA can be found in supplementary material Figure S5.1.).

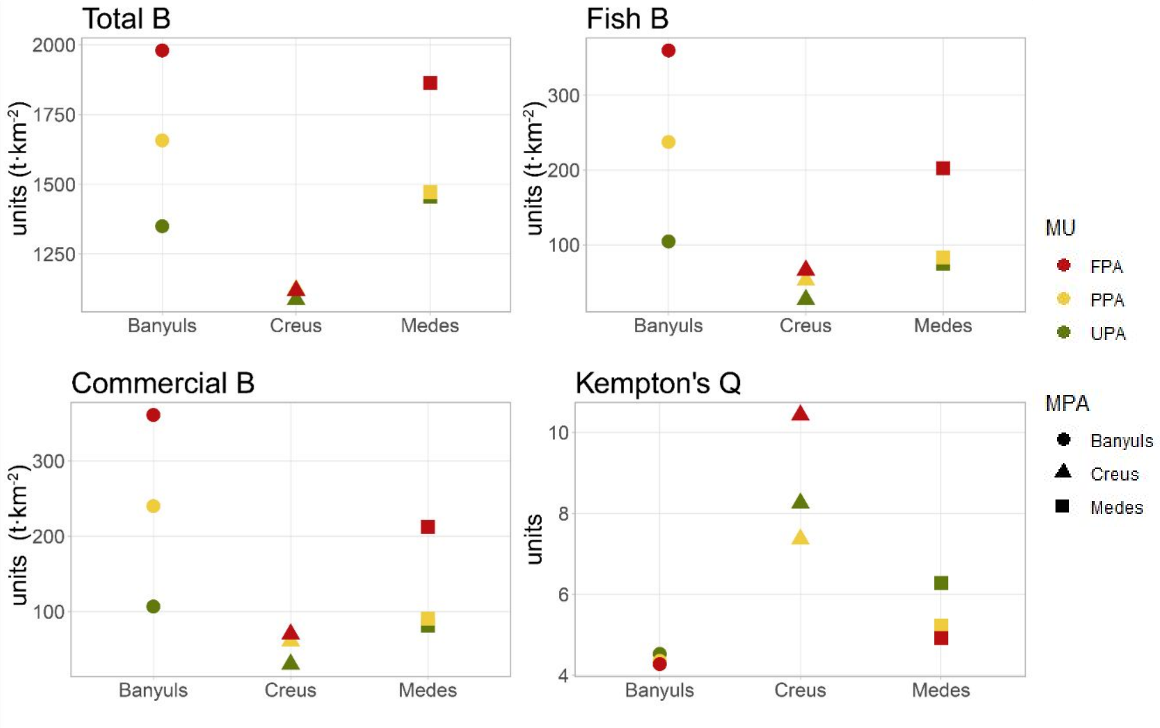

Figure 4. Biomass-based indicators of the three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, Kempton's Q – Kempton Q diversity index).

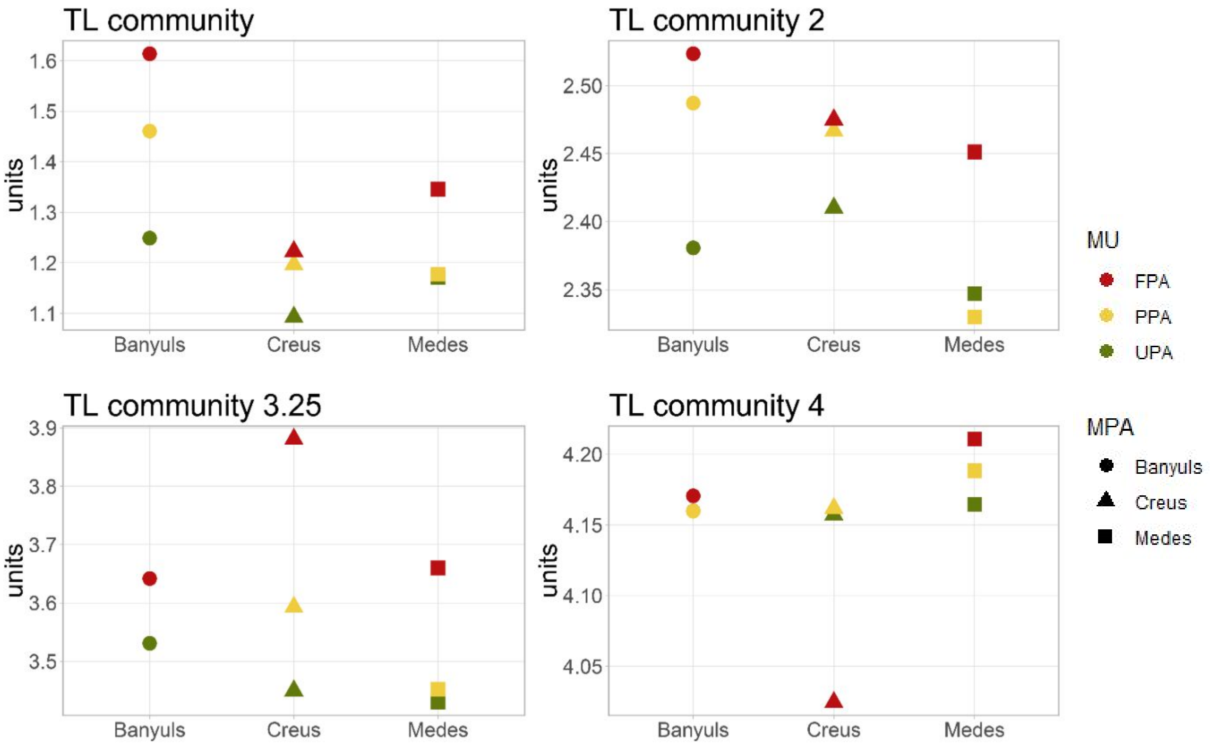

Figure 5. Trophic-based indicators of the three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (TL – trophic level).

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

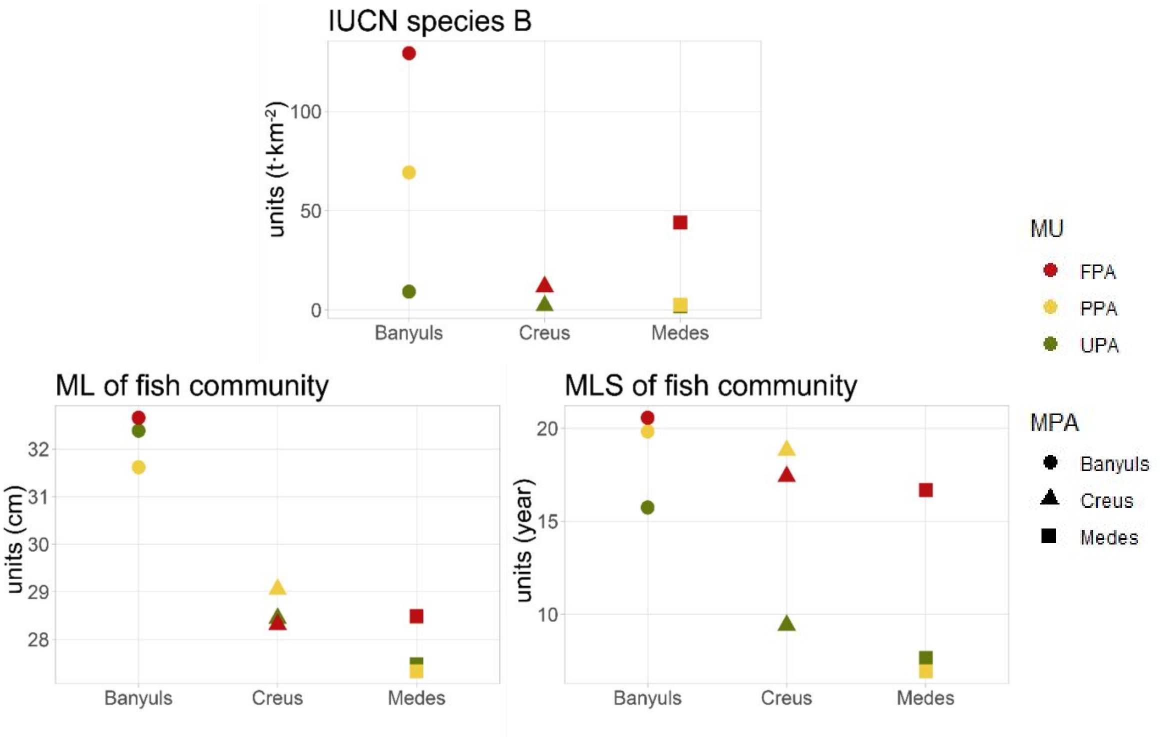

Figure 7. Species-based indicators of the three MUs (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (B – Biomass, ML – mean length and MLS – mean life span).

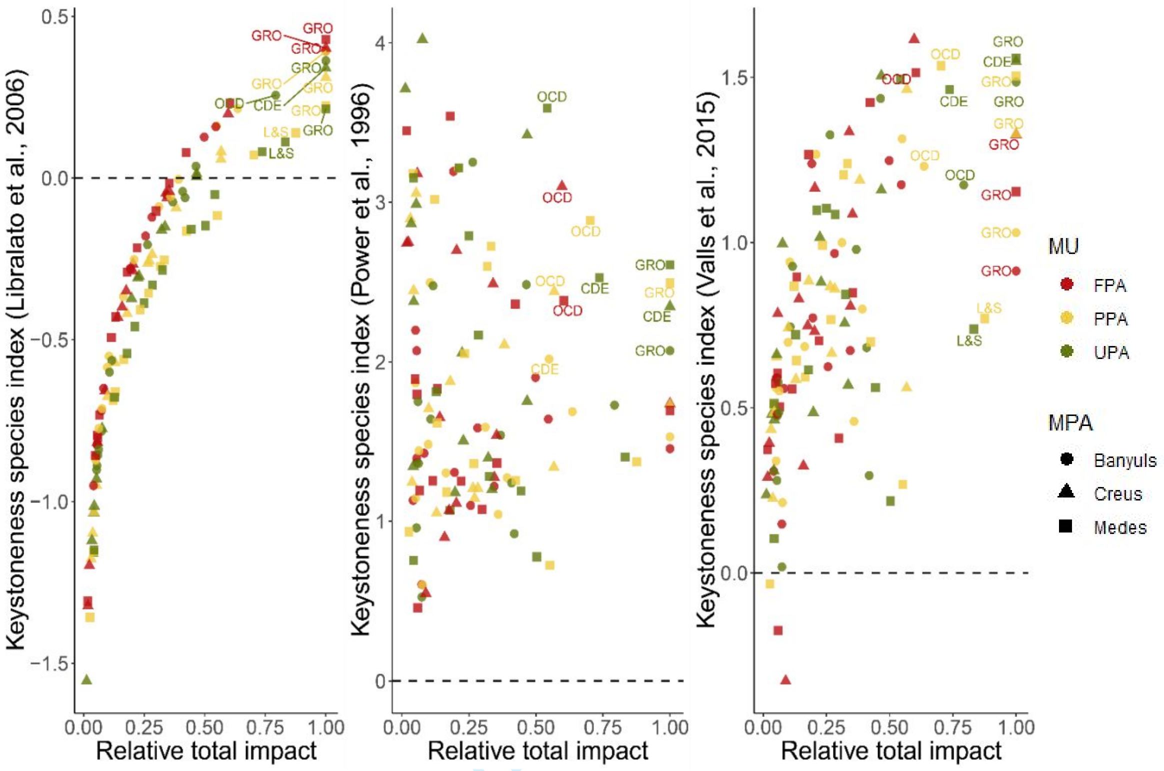

Figure 8. Keystone Index analysis of the three MU (FPA: fully protected area; PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). The acronyms identify the functional group with highest keystoneness index and relative total impact.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

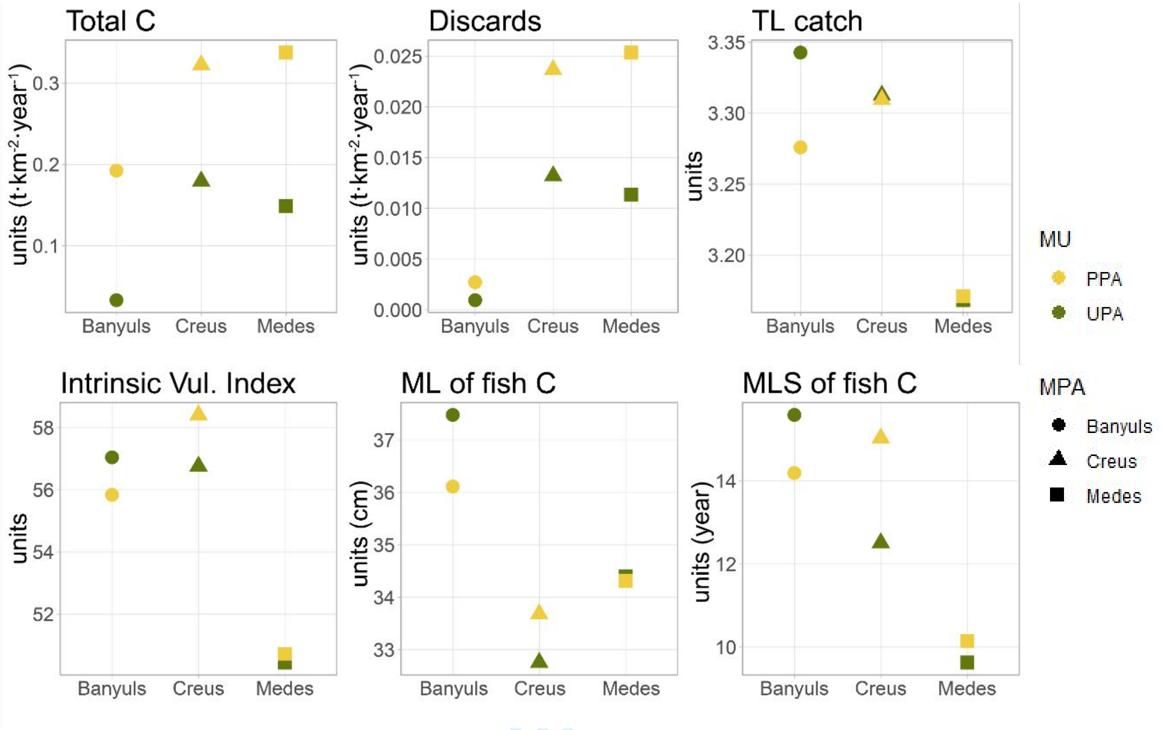

Figure 9. Catch-based indicators of the three MUs (PPA: partially protected area; UPA: unprotected area) models for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (C – Catch; TL – trophic level; ML – mean length; MLS – mean life span).

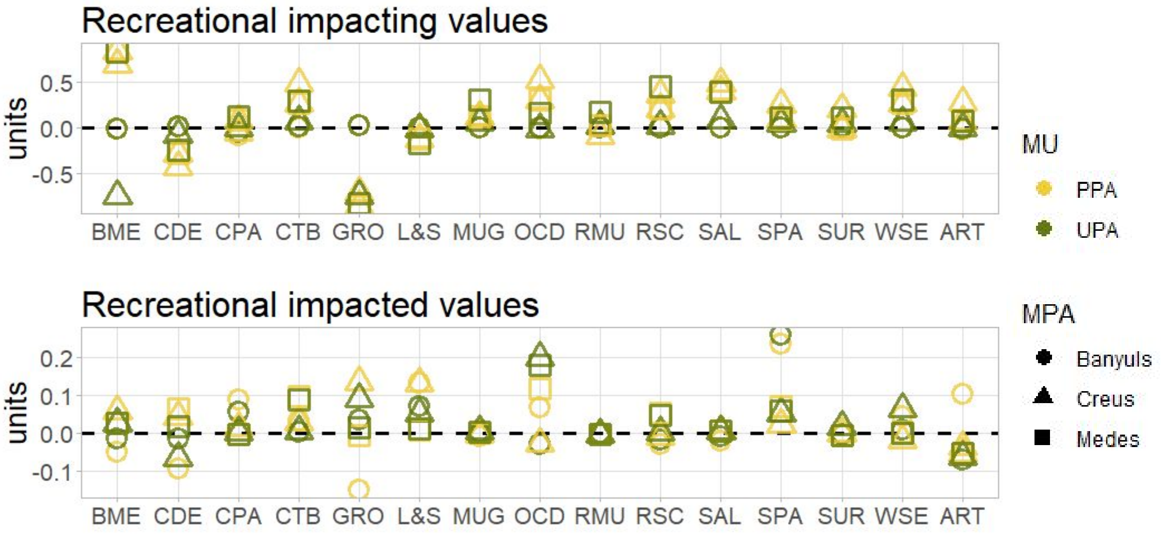

Figure 10. Recreational impacting and impacted values of three MU models (PPA: partially protected area; UPA: unprotected area) for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (BME – brown meagre; CDE – common dentex; CPA – common pandora; CTB – common two-banded seabream; GRO – groupers; 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).

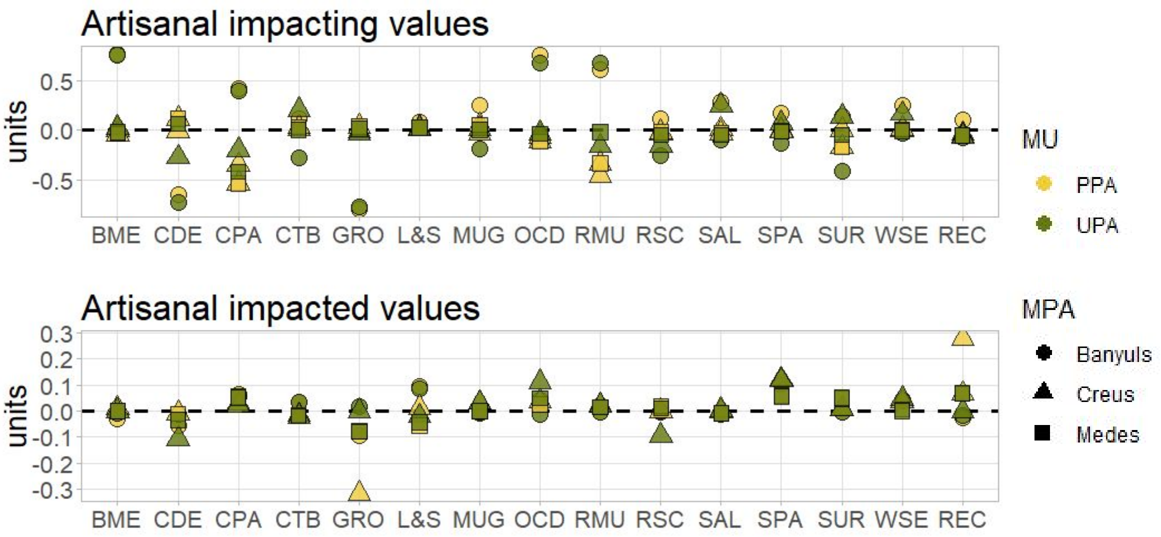

Figure 11. Small scale impacting and impacted values of three MU models (PPA: partially protected area; UPA: unprotected area) for each MPA (Cerbère-Banyuls, Cap de Creus and Medes Islands). (BME – brown meagre; CDE – common dentex; CPA – common pandora; CTB – common two-banded seabream; GRO – groupers; 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 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 S1.1.); Input parameters and outputs estimate for Cerbère-Banyuls (Table S1.2.), Cap de Creus (Table S1.3.) and Medes Islands (Table S1.4.) MU models.

Appendix 2. Supplementary tables: Diet composition matrix for the MU models of Cerbère-Banyuls (Table S2.1.), Cap de Creus (Table S2.2.) and Medes Islands (Table S2.3.) MPA.

Appendix 3. Supplementary tables: Keystone indexes and Relative Total Impact values for the functional groups included in Cerbère-Banyuls (Table S3.1), Cap de Creus (Table S3.2) and Medes Islands (Table S3.3) MU models. FPA: fully protected area; PPA: partially protected area; UPA: unprotected area.

Appendix 4. Additional explanatory text about modelling parameterization and balancing procedure.

Appendix 5. Supplementary figure: Flow diagrams of three management units (FPA: red; PPA: yellow; UPA: green) of Cap de Creus and Medes Islands MPA model.