

# Field monitoring and trophic modelling as management tools to assess ecosystem functioning and the status of high trophic level predators in Mediterranean marine protected areas

Giulia Prato

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#### UNIVERSITE NICE-SOPHIA ANTIPOLIS - UFR Sciences Ecole Doctorale de Sciences Fondamentales et Appliqués

# THESE

pour obtenir le titre de Docteur en Sciences de l'UNIVERSITE Nice-Sophia Antipolis

Discipline : Sciences de l'Environnement présentée et soutenue par Giulia Prato

# Stratégie d'échantillonnage et modélisation trophique : des outils de gestion pour évaluer le fonctionnement des écosystèmes et le statut des prédateurs de haut niveau trophique dans les aires marines protégées méditerranéennes.

Field monitoring and trophic modelling as management tools to assess ecosystem functioning and the status of high trophic level predators in Mediterranean Marine Protected Areas

Thèse dirigée par

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soutenue le 29 janvier 2016

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#### Abstract

The overexploitation of high trophic level predators (HTLP) may trigger trophic cascades, often leading to a simplification of marine food-webs and reducing their resilience to human impacts. Marine protected areas (MPAs) can foster increases of HTLP abundance and biomass, but long time frames are needed to observe a recovery, when possible, of lost trophic interactions.

This PhD aimed to propose integrated management-tools to monitor HTLP recovery and the restoration of trophic interactions in Mediterranean MPAs, and to evaluate the effectiveness of these tools at assessing fishing impacts upon HTLP and the associated food-web. Two often distant approaches were combined: field monitoring and food-web modelling. First, to survey the fish assemblage, we proposed to improve the traditional underwater visual census technique of one size-transects with variable size transects adapted to fish mobility. This improvement increased the accuracy of density and biomass estimates of HTLP at three Mediterranean MPAs. We then evaluated the potential of food-web modelling with the Ecopath with Ecosim and Ecotroph approach as a tool to inform ecosystem-based management in Mediterranean MPAs. We proposed a standard model structure as the best compromise between model complexity, feasibility of model construction in terms of data collection, and reliability of model outputs. Key functional groups for which local accurate biomass data should be collected in priority in order to get reliable model outputs were identified. Applying this approach to an old datarich MPA allowed to highlight the keystone functional role of HTLPs and cephalopods, and to assess the cumulated impact of artisanal and recreational fishing on the food-web. Model outputs highlighted that reducing recreational fishing effort would benefit both the ecosystem and the naturally declining artisanal fishery, through increased availability of higher quality catches. Finally, we estimated the costs of model development for a datapoor reserve and suggested how to cost-efficiently increase model quality.

Overall this PhD work emphasised the potential of combining field monitoring and foodweb modelling tools, which can mutually enhance each other to achieve an effective ecosystem based management in MPAs.

#### Abstract Français

La surexploitation des prédateurs de haut niveau trophique (HTLP) peut déclencher des cascades trophiques qui souvent conduisent à une simplification des réseaux trophiques marins en réduisant leur résistance aux impacts humains. Les aires marines protégées (AMP) peuvent favoriser des augmentations d'abondance et biomasse des HTLP, mais la complète restauration des interactions trophiques, lorsque cela est possible, nécessite des délais importants.

Cette thèse vise à proposer des outils intégrés de gestion pour évaluer le retour des HTLP et la restauration des interactions trophiques dans les AMP méditerranéennes, et à évaluer l'efficacité de ces outils pour estimer les impacts de la pêche sur les HTLP et le réseau trophique associé. Deux approches souvent éloignés ont été combinées : les suivis de terrain et la modélisation des réseaux trophiques. Pour échantillonner la communauté de poissons, nous avons proposé d'améliorer la technique traditionnelle de recensement visuel sous-marin en recourant à des transects de taille variable, adaptée à la mobilité des poissons. Cette méthode a lors permis d'augmenter la précision des estimations de densité et de biomasse des HTLP dans les trois AMP méditerranéennes suivies. Ensuite, nous avons évalué l'apport de la modélisation trophique avec les approches EwE et EcoTroph comme outil de gestion écosystémique pour les AMP méditerranéennes. Une structure standard de modèle a été proposée comme étant le meilleur compromis entre la complexité du modèle, la faisabilité de sa construction et la fiabilité de ses sorties. Les groupes fonctionnels clés pour lesquels des données de biomasse locales exactes devraient être recueillis en priorité afin d'obtenir des sorties de modèles fiables ont été identifiés. L'application de cette approche à une AMP ancienne, riche en données, a permis de mettre en évidence le rôle fonctionnel clé des HTLP et des céphalopodes, et d'évaluer l'impact cumulé de la pêche artisanale et de loisir sur l'ensemble du réseau trophique. Les résultats du modèle ont montré qu'une réduction de l'effort de la pêche de loisir profitait à la fois l'écosystème et améliorait la rentabilité de la pêche artisanale, grâce à une disponibilité accrue des captures de niveau trophique supérieur. Enfin, les coûts de développement d'un tel modèle pour une AMP ne disposant que de peu de données ont été estimés, tout en suggérant des pistes pour améliorer la qualité du modèle.

Globalement, ce travail de thèse a souligné le potentiel d'une approche conjuguant des suivis de terrain et de la modélisation trophique, des outils se renforçant mutuellement, pour parvenir à une gestion écosystémique efficace dans les AMP.

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#### 1. Chapter 1. General introduction

#### 1.1 The ecological importance of high trophic level predators.

At a global scale, the overexploitation of fisheries resources has affected in the first place fish species at the higher trophic levels of the food-web (high trophic level predators, hereafter HTLP), which have been disproportionately targeted for centuries (Jackson et al. 2001, Myers & Worm 2005). Generally characterised by slow growth rates and late sexual maturity, HTLP are highly vulnerable to fishing (Duffy 2002, Gascuel et al. 2014) as shown by their rapid decline in many areas of the world (Pauly et al. 1998). The decline in the abundance of HTLP populations has often triggered trophic cascades (Box 1), eventually leading to large-scale ecosystem shifts (Estes et al. 2011). These dramatic consequences have drawn attention to the key ecological role that HTLP play in shaping marine communities. High trophic levels indeed represent functional 'information' which reveals the energetic efficiency of ecosystems and improves their stability (Jørgensen et al. 2000, Odum 1969). In their absence, the functional diversity and redundancy of many ecosystems are reduced, leading to less complex food-webs, reduced community stability and lower resilience to anthropogenic impacts (Bascompte et al. 2005, Coll et al. 2008, Estes et al. 2011, Britten et al. 2014). The significance of HTLP role has become even more clear observing the few pristine ecosystems left in the world, where unprecedented levels of fish biomass at the higher levels of the food-web have been reported, setting new baselines for evaluating present and historical human impacts and providing new targets for conservation efforts (Stevenson et al. 2007, Sandin et al. 2008). If the depletion of HTLP may lead to trophic cascades, an important build up in their biomass can promote indirect effects and help to re-establish lost trophic interactions and ecosystem functions (Ray et al. 2005). However, indirect effects of HTLP recovery are highly variable depending on several factors and can show conspicuous time lags with respect to direct effects (Micheli et al. 2004, Lester et al. 2009).

#### **BOX 1. Trophic cascades**



Trophic cascades are indirect effects of fishery removals on the food-web. They are described as predatory interactions, involving three or more trophic levels, where the removal of important carnivore predators triggers the release of herbivores and consequently a decrease in primary producers (Menge 1995). In the Mediterranean rocky sublittoral, the overfishing of sea breams (*Diplodus* spp.), the most effective sea urchin predators in this basin, caused an increase in sea urchins abundance (*Paracentrotus lividus*), which overgrazed erect macroalgal assemblages. In areas where sea urchins could reach high densities, overgrazing induced the shift from complex macroalgal assemblages to species-poor coralline barrens (Sala et al.1998, Guidetti 2007). Drawings from the outreach video "The Book of Marine Protected Areas, Prato & Gianni 2015", MMMPA project (see Outreach & Communication)

#### 1.2 High trophic level predators recovery in Mediterranean Marine Protected Areas and related management challenges

In the last century, the Mediterranean was subject to an exponential increase in both commercial fishing and coastal development, causing the overexploitation of most of its fish stocks and the collapse of many of them (Colloca et al. 2013). Overfishing strongly impacted Mediterranean food-webs, which are nowadays deprived of high trophic level predators, with medium-sized fish like sea breams (*Diplodus* spp.) controlling ecosystem shape (Box 1) (Sala 2004). Observation of the dramatic ecosystem shifts caused by changes in the abundance of small and medium-sized predators, in some areas of the Mediterranean, prompted reflections on the changes that food–webs must have experienced over historical time frames after depletion of HTLP, and if recovery to a former level is possible (Sala 2004).

Overfishing and the depletion of HTLP also affected traditional small-scale artisanal fishing, a millenary activity depicted in ancient art catching fish almost the size of a man at the water surface (Guidetti & Micheli 2011).

To face such situation, Marine Protected Areas (MPAs) have spread across the Mediterranean, gaining wide acceptance as efficient tools contributing to an effective ecosystem-based management strategy (Lubchenco et al. 2003). MPAs were indeed established not only as a tool to conserve and restore biodiversity, but also to "achieve the long term conservation of associated ecosystem services and cultural values" (Dudley et al. 2008), thus seeking a balance between biodiversity protection and continued human use (Abdulla et al. 2008). Several large-scale studies and global synthetises have shown that MPAs allowed to increase the density and biomass of the most commonly exploited species and reveal initial trajectories of ecosystem recovery (Halpern & Warner 2002, Lester et al. 2009). When properly managed, Mediterranean MPAs have also allowed to achieve remarkably large fish biomass compared to exploited areas, highlighting the high potential of recovery of Mediterranean ecosystems (Sala et al. 2012, Guidetti et al. 2014).

However, long-term observations from some of the oldest MPAs have shown that abundances of HTLP are still increasing, denoting that long time frames are needed before carrying capacity is reached (Micheli et al. 2004, Babcock et al. 2010, Garcia Rubies et al. 2013).Long time frames are required also to observe indirect changes triggered by HTLP recovery (Micheli et al. 2005), while most Mediterranean reserves are young (established a few decades ago, at most). Long-term management strategies are

thus needed to assess the evolution of MPAs along the observed trajectory of recovery, but are often lacking in the Mediterranean (Garcia Rubies et al. 2013).

Furthermore, management of MPAs should go beyond the monitoring of a subset of species of recognised ecological importance and should account for the complexity of the food-webs they host. Unravelling trophic interactions is essential on one hand to assess the recovery of ecosystem structure and functions (Libralato et al. 2010) and on the other hand to understand and mitigate the influences that multiple human uses might have on food-webs, allowing thus to anticipate or deal with ecosystem shifts (Sala 2004, Plagany et al. 2014, Fulton et al. 2015).

#### 1.3 Thesis objectives and approaches

The above considerations were further developed in the first publication arouse from this PhD work and presented in the second chapter of the manuscript (Prato G, Guidetti P, Bartolini F, Mangialajo L, Francour P (2013) *The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context.* Advances in Oceanography and Limnology 4:176–193). The paper was based upon a literature review aimed at answering the following questions:

- Are high-trophic level predators currently recovering in marine protected areas?
- What are the indirect consequences of such recovery on the food-webs?
- Are increasing levels of these predators a signal of increasing ecosystem health?

Addressing these issues was necessary to introduce the main questions which drove this PhD thesis: if the fundamental role of high trophic level predators in shaping marine communities and food-webs is finally acknowledged, as well as their leading position in ecosystem recovery, how can we, in the context of an efficient MPA management:

- **Q1.** effectively monitor high trophic level predators' recovery?
- **Q2.** unravel and monitor trophic interactions?
- **Q3.** quantify fishing impacts upon HTLP and associated food-webs?

Effective management of Mediterranean ecosystems needs to merge the two often distant disciplines of field ecology and modelling (Pellétier et al. 2008). We thus coupled both approaches in order to answer the above questions and ultimately provide useful and cost-efficient tools for MPAs management.

Underwater visual census (UVC) surveys are to date the only possible non-destructive approach to monitor the fish assemblage in Marine Protected Areas. A challenging objective for both research and management is the development and implementation of consistent UVC methods across the Mediterranean to assess the abundance of the entire fish assemblage, accounting for the different mobility and behaviour of fish, from the smallest crypto-benthic species to the large highly motile predatory fish. This is essential to measure reliable relative values of high-trophic level predators increase and assess variations in fish assemblage composition over time.

But field studies alone cannot aim at unravelling the complexity of food-web interactions, an essential step to evaluate the indirect effects of several and often interacting human impacts (Plaganyi et al. 2014, Fulton et al. 2015). Ecosystem models can help to shed light on these issues. They are increasingly recognised as necessary tools to apply the ecosystem approach to fisheries management (Espinoza-Tenorio et al. 2012), and are more and more used for conservation purposes, i.e to design and holistically evaluate the performance of Marine Protected Areas (Fulton et al. 2015). Food-web modelling in particular is a useful tool to unravel trophic interactions and identify keystone species, describe ecosystem structural traits, derive indexes of ecosystem maturity and complexity and evaluate the consequences of several human impacts on the food-web (Christensen & Walters 2004, Libralato et al. 2010, Heymans et al. 2014, Valls et al. 2015). The tropho-dynamic modelling approach Ecopath with Ecosim (Christensen & Pauly 1992, Christensen & Walters 2004) and its more recent implementation EcoTroph (Gascuel et al. 2009, 2011) fostered more than 400 applications across the world (Colléter et al. 2015), addressing a multitude of issues related to both fisheries management and conservation. However, EwE has not yet gained full attention as a possible tool for the management of small coastal areas, and model applications in MPAs are still few, especially in the Mediterranean (Coll & Libralato 2012). This scarcity is largely due to the large amount of data needed to get reliable models and the associated uncertainties on data precision. Issues of data availability and guality are particularly accentuated in this naturally and geopolitically heterogeneous basin (Katsanevakis et al.

2015), however, if reliable ecosystem models could be built in a cost-effective way, they could provide useful information for the research and management of MPAs.

#### **1.4 Structure of the manuscript**

In order to address the above mentioned challenges we adopted an integrative approach, combining literature synthesis, field studies (Section 1) and theoretical and applied modelling exercises (Section 2), which were alternatively applied in the following chapters to face specific issues:

- A literature review: to assess the state of the art on the importance of high trophic level predators for MPAs management. (Chapter 2)
- A semi-quantitative literature synthesis, integrated with a field survey: to identify the most appropriate and cost-effective UVC method to survey the whole fish assemblage. (Question 1, Chapter 3)
- A field study: to i) evaluate the effectiveness of two UVC transect sizes to survey large mobile predators (Question 1) and ii) combine three transect sizes to assess the whole fish assemblage (Question 2 and 3, Chapter 4)
- A theoretical modelling exercise: to identify an optimal Ecopath model structure that considers trade-offs between feasibility of data gathering, complexity, and uncertainty. (Question 2, Chapter 5)
- An applied modelling exercise, based upon the integration of available local data: to assess artisanal and recreational fishing impacts and conflicts on the food-web associated with a NW Mediterranean MPA. (Question 2 and 3, Chapter 6)
- An applied modelling exercise, based upon collection of new data in the field: to i) unravel trophic interactions and identify keystone species to be monitored in a data poor MPA and ii) evaluate the costs of building a standard trophic model in a data poor MPA, following the guidelines for model structure and data collection developed in chapter 5. (Question 2, Chapter 7)

Overall results of this PhD work are synthetized and discussed in **Chapter 8**, and some perspectives on the possible applications for MPAs management and on potential avenues of research are presented

#### 1. Chapitre 1. Introduction générale français

#### 1.1 L'importance écologique des prédateurs de haut niveau trophique

À l'échelle mondiale, la surexploitation des ressources halieutiques a surtout touché les espèces de poissons des niveaux trophiques supérieurs dans les chaînes trophiques (prédateurs de niveau trophique supérieur, ci-après HTLP), qui ont été ciblées de manière disproportionnée pendant des siècles (Jackson et al. 2001 Myers et Worm 2005). Généralement caractérisés par des taux de croissance lents et une maturité sexuelle tardive, les HTLP sont très vulnérables à la pêche (Duffy 2002, Gascuel et al. 2014), comme en témoigne leur rapide déclin dans de nombreuses régions du monde (Pauly et al., 1998). Ce déclin d'abondance des populations de HTLP a souvent entraîné des cascades trophiques (encadré 1), se traduisant souvent par des changements à grande échelle des écosystèmes (Estes et al., 2011). Ces conséquences dramatiques ont attiré l'attention sur le rôle écologique clé que les HTLP jouent dans la structuration des communautés marines. Les hauts niveaux trophiques représentent en effet l'information fonctionnelle qui témoigne de l'efficacité énergétique des écosystèmes et améliore leur stabilité (Jørgensen et al. 2000, Odum 1969). En leur absence, la diversité fonctionnelle et la redondance de nombreux écosystèmes sont réduits, se qui se traduit par des réseaux trophiques moins complexes, une stabilité réduite de la communauté et une plus faible résilience aux impacts anthropiques (Bascompte et al., 2005, Coll et al. 2008, Estes et al., 2011, Britten et al. 2014).

La signification du rôle des HTLP est devenue encore plus claire en observant les rares écosystèmes vierges encore existant dans le monde. Des niveaux sans précédent de biomasse de poissons en haut du réseau trophique ont été rapportés, établissant de nouveaux niveaux de référence pour l'évaluation actuelle et historique des impacts humains et fournissant de nouveaux seuils à atteindre pour les efforts de conservation (Stevenson et al. 2007, Sandin et al., 2008).

Si l'effondrement des HTLP peut conduire à des cascades trophiques, une accumulation importante de leur biomasse peut promouvoir des effets indirects et aider à rétablir les interactions trophiques perdues et les fonctions des écosystèmes (Ray et al., 2005). Cependant, les effets indirects de la récupération des HTLP varient fortement en fonction de différents facteurs et peuvent nécessiter plus de temps que les effets directs (Micheli et al. 2004, Lester et al., 2009).



Les cascades trophiques sont les effets indirects des prélèvements de la pêche sur le réseau trophique. Ils sont décrits comme des interactions de prédation, impliquant trois ou plusieurs niveaux trophiques : la suppression des prédateurs carnivores importants entraîne une augmentation d'herbivores et, par conséquent, une diminution des producteurs primaires (Menge, 1995). En Méditerranée, en milieu rocheux , la surpêche de sars (*Diplodus* spp.), les prédateurs d'oursins les plus efficaces, a provoqué une augmentation de l'abondance des oursins de mer (*Paracentrotus lividus*), qui a alors entraîné un surpâturage des formations de macroalgues érigées. Dans ces zones de surpâturage où les oursins atteignent des densités élevées, les assemblages initiaux de macroalgues, complexes et diversifiés, laissent place à des peuplements simplifiés, pauvres en espèces (Sala et al.1998, Guidetti 2007). Dessins extraits de la vidéo de sensibilisation "Le Livre des aires marines protégées, Prato et Gianni 2015», projet MMMPA (voir chapitre Sensibilisation et Communication)

# 1.2 Récupération des prédateurs de haut niveau trophique dans les aires marines protégées de Méditerranée et les défis relatifs à la gestion

Au siècle dernier, la Méditerranée a été soumise à une augmentation exponentielle de la pêche commerciale et au développement côtier, provoquant la surexploitation de la plupart de ses stocks de poissons et l'effondrement de beaucoup d'entre eux (Colloca et al. 2013). La surpêche a fortement modifié les réseaux trophiques méditerranéens, qui sont aujourd'hui largement dépourvus de prédateurs de niveaux trophiques élevés, avec des poissons de taille moyenne comme les sars (Diplodus spp.) qui contrôlent l'écosystème (encadré 1) (Sala 2004). L'observation des changements dramatiques de l'écosystème dans certaines régions de la Méditerranée, causés par des changements dans l'abondance des prédateurs de petite et moyenne tailles, a incité des réflexions sur les changements survenus au sein des réseaux trophiques au cours de l'histoire avec la disparition progressive des HTLP et fait se demander si la restauration de leur abondance ancienne est possible (Sala 2004).

La surpêche et l'épuisement des HTLP a également affecté la pêche artisanale aux petits métiers, une activité millénaire, qui a été représentée dans l'art antique comme capable d'attraper des poissons presque de la taille d'un homme dans les eaux de surface (Guidetti & Micheli 2011).

Pour faire face à cette situation, les aires marines protégées (AMP) se sont rapidement développées en Méditerranée, largement acceptées comme outils efficaces contribuant à une stratégie de gestion efficace des écosystèmes (Lubchenco et al., 2003). Les AMP ont en effet été établies non seulement comme un outil pour conserver et restaurer la biodiversité, mais aussi pour "assurer la conservation à long terme des services écosystémiques et des valeurs culturelles associés" (Dudley et al., 2008), cherchant ainsi un équilibre entre la protection de la biodiversité et la poursuite de l'exploitation humaine (Abdulla et al., 2008). Plusieurs études à grande échelle et des synthèses mondiales ont montré que les AMP ont permis d'augmenter la densité et la biomasse des espèces les plus couramment exploitées, révélant les trajectoires initiales de rétablissement de l'écosystème (Halpern et Warner 2002, Lester et al., 2009). Lorsqu'elles sont correctement gérées, les AMP méditerranéennes ont également permis d'aboutir à niveaux remarquables de biomasse de poissons en comparaison avec les zones exploitées, soulignant ainsi le fort potentiel de récupération des écosystèmes méditerranéens (Sala et al. 2012, Guidetti et al. 2014).

Cependant, des observations à long terme de certaines AMP anciennes ont montré que l'abondance des HTLP continue d'augmenter, traduisant alors la nécessité d'une

protection à long terme avant que la capacité de charge de l'écosystème ne soit atteinte (Micheli et al. 2004, Babcock et al. 2010, Garcia Rubies et al., 2013). Des délais importants sont aussi nécessaires avant d'observer les changements indirects provoqués par la récupération des HTLP (Micheli et al., 2005), alors que la plupart des réserves de Méditerranée sont jeunes (créées il y a quelques décennies, tout au plus). Des stratégies de gestion à long terme sont donc nécessaires pour apprécier le degré d'évolution des AMP, mais elles font souvent défaut en Méditerranée (Garcia Rubis et al. 2013).

En outre, la gestion des AMP ne devrait pas se contenter de la surveillance d'un sousensemble d'espèces même d'importance écologique reconnue mais doit tenir compte de la complexité des réseaux trophiques qu'elles hébergent. Comprendre les interactions trophiques est essentiel, d'une part pour évaluer la récupération de la structure et des fonctions des écosystèmes (Libralato et al., 2010) et, d'autre part, pour comprendre et atténuer les influences que les usages multiples pourraient avoir sur les réseaux trophiques, permettant ainsi d'anticiper ou de traiter les changements de l'écosystème (Sala 2004, Plagany et al. 2014, Fulton et al. 2015).

#### 1.3 Objectifs et approches de la thèse

Les considérations ci-dessus ont été développées dans la première publication issue de ce travail de thèse et sont présentées dans le deuxième chapitre du manuscrit (Prato G, Guidetti P, Bartolini F, Mangialajo L, Francour P (2013) *The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context.* Advances in Oceanography and Limnology 4:176–193). Le travail s'appuie sur une revue de la littérature et cherche à répondre aux questions suivantes :

- Est-ce qu'il y a actuellement une récupération des prédateurs de haut niveau trophique dans les aires marines protégées ?
- Quelles sont les conséquences indirectes de cette reprise sur les réseaux trophiques ?
- Est-ce que les niveaux croissants de ces prédateurs sont un signal de l'amélioration de la santé des écosystèmes ?

Aborder ces questions était nécessaire afin d'introduire les questions principales qui ont motivé cette thèse : si le rôle fondamental des prédateurs de haut niveau trophique dans la structuration des communautés marines et des réseaux trophiques est finalement reconnu, ainsi que leur importance clé dans la récupération de l'écosystème, il faut alors se demander, dans un contexte de gestion efficace des AMP, comment il est possible de

- Q1. quantifier efficacement la récupération des prédateurs de haut niveau trophique ?
- Q2. comprendre et suivre les interactions trophiques ?
- Q3. quantifier les impacts de la pêche sur les HTLP et les réseaux trophiques associés ?

Une gestion efficace des écosystèmes méditerranéens nécessite de combiner deux disciplines souvent éloignées : l'écologie de terrain et la modélisation (Pelletier et al., 2008). Nous avons ainsi couplé ces deux approches afin de répondre aux questions cidessus et, finalement, fournir des outils efficaces et utiles pour la gestion des aires marines protégées.

Les comptages visuels en plongée sous-marine (UVC) sont à ce jour la seule approche non destructive possible de suivi des peuplements de poissons dans les aires marines protégées. Un objectif difficile à la fois pour la recherche et la gestion est le développement et la mise en œuvre de méthodes cohérentes à l'échelle de la Méditerranée, pour évaluer l'abondance de l'ensemble du peuplement de poissons. Ces méthodes doivent prendre en considération les différences de mobilité et de comportement des poissons, allant des petites espèces crypto-benthiques aux grandes espèces de poissons prédateurs très mobiles. Cela est essentiel pour mesurer des valeurs relatives fiables de l'augmentation de prédateurs de haut niveau trophique et pour évaluer les modifications de la composition des peuplements de poissons au fil du temps.

Mais les seules études de terrain ne peuvent pas suffire à démêler la complexité des interactions des réseaux trophiques, une étape essentielle pour évaluer les effets indirects de plusieurs impacts humains, qui souvent interagissent (Plagányi et al. 2014,

Fulton et al. 2015). Les modèles écosystémiques peuvent contribuer à éclairer ces questions. Ils sont de plus en plus reconnus comme des outils nécessaires pour appliquer l'approche écosystémique aàa gestion de la pêche (Espinoza-Tenorio et al. 2012) et ils sont de plus en plus utilisés à des fins de conservation pour concevoir et évaluer de manière holistique la performance d'aires marines protégées (Fulton et al., 2015). La modélisation du réseau trophique en particulier est un outil utile pour comprendre les interactions trophiques, identifier les espèces clés, décrire les caractéristiques structurelles de l'écosystème, en tirer des indices de maturité et de complexité de l'écosystème et pour évaluer les conséquences de plusieurs impacts humains sur le réseau trophique (Christensen et Walters 2004, Libralato et al. 2010, Heymans et al. 2014, Valls et al. 2015). L'approche de modélisation tropho-dynamique Ecopath avec Ecosim (Christensen et Pauly 1992, Christensen et Walters 2004), et plus récemment EcoTroph (Gascuel et al. 2009, 2011) a été utilisée plus de 400 fois à travers le monde (Colléter et al. 2015), en abordant une multitude de questions liées à la fois à la gestion des pêches et à la conservation. Cependant, Ecopath n'est pas encore reconnu comme un outil possible de gestion des petites zones côtières et les applications de tels modèles dans les AMP sont encore peu nombreuses, notamment en Méditerranée (Coll & Libralato 2012). Cette rareté est en grande partie due à la grande quantité de données nécessaires pour obtenir des modèles fiables et aux incertitudes associées à la précision des données. Les questions de la disponibilité et de la qualité des données sont particulièrement accentuéers dans ce bassin naturellement et géopolitiquement très hétérogène (Katsanevakis et al. 2015). Cependant, si des modèles écosystémiques fiables pouvaient être construits d'une manière efficace, ils pourraient fournir des informations utiles pour la recherche et la gestion des AMP.

#### 1.4 Structure du manuscrit

Afin de relever les défis mentionnés ci-dessus et répondre aux questions posées, nous avons adopté une approche intégrative, combinant des synthèses de la littérature, des études de terrain (Section 1) et des exercices de modélisation théoriques et appliqués (Section 2) à travers les chapitres suivants :

 Une revue de la littérature : pour évaluer l'état de l'art sur l'importance des prédateurs de haut niveau trophique pour la gestion des aires marines protégées. (Chapitre 2)

- Une synthèse de la littérature semi-quantitative, intégrée à un travail de terrain : pour identifier la méthode UVC la plus appropriée et rentable de quantification de l'ensemble du peuplement de poissons. (Question 1, chapitre 3)
- Une étude de terrain : pour i) comparer l'efficacité de deux largeurs de transects UVC dans l'étude des grands prédateurs mobiles (question 1) et ii) combiner trois largeurs de transects pour évaluer l'ensemble du peuplement de poissons (Question 2 et 3, chapitre 4)
- Un exercice de modélisation théorique : pour identifier une structure de modèle Ecopath optimal permettant un compromis entre la faisabilité de la collecte de données, la complexité du modèle et l'incertitude des résultats. (Question 2, chapitre 5)
- Un exercice de modélisation appliquée fondé sur l'intégration des données locales disponibles : pour évaluer les impacts et les conflits de la pêche artisanale et de loisir sur le réseau trophique d'une AMP en Méditerranée nord-occidentale. (Question 2 et 3, chapitre 6)
- Un exercice de modélisation appliquée, sur la base de la collecte de nouvelles données sur le terrain : pour i) décrire les interactions trophiques et identifier les espèces clés à surveiller dans une AMP pauvre en données ii) évaluer les coûts de construction d'un modèle trophique standard dans une AMP pauvre en données, en suivant les lignes directrices développées dans le chapitre 5 pour la structure du modèle et la collecte de données. (Question 2, chapitre 7)

Les résultats de cette thèse sont synthétisés et discutés dans le chapitre 8 et quelques perspectives sur les applications possibles en terme de gestion des aires marines protégées et sur les développements à venir possibles en recherche sont présentées.

# 2 Chapter 2. The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context.

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#### The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context

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High-level predators have been depleted in the oceans worldwide following centuries of selective fishing. There is widespread evidence that high-level predators' extirpation may trigger trophic cascades leading to the degradation of marine ecosystems. Restoration of large carnivores to former levels of abundance might lead to ecosystem recovery, but very few pristine ecosystems are left as baselines for comparison.

Marine protected areas (MPAs) can trigger initial rapid increases of high-level predator abundance and biomass. Nevertheless, long term protection is needed before the ecosystem's carrying capacity for large carnivores is approached and indirect effects on lower trophic levels are observed.

The Mediterranean is probably very far from its pristine condition, due to a long history of fishing. Today small to medium-sized consumers (e.g. sea breams) are the most abundant predators shaping coastal benthic communities, while historical reconstructions depict abundant populations of large piscivores and sharks inhabiting coastal areas. Mediterranean MPAs are following a promising trajectory of ecosystem recovery, as suggested by a strong gradient of fish biomass increase. Consistent monitoring methods to assess relative variations of high-level predators, together with food-web models aimed at disentangling the indirect effects of their recovery, could be useful tools to help set up appropriate management strategies of MPAs.

**Keywords:** high-level predator; top predator; trophic cascades; MPAs; ecosystem shift; overfishing; baseline; ecosystem recovery

#### 1. Introduction

High-level predators, a category including top predators, are generally large-sized longliving animals like marine mammals, sharks and large teleosts that occupy the higher trophic levels in the food web. They are commonly characterized by late sexual maturity and their abundance, at adult stage, is usually not subject to predator control. Together these characteristics result in low resilience to demographic perturbation and high risk of extinction, conditions making them highly vulnerable to fishing [1]. In a number of regions worldwide, their almost complete extirpation from marine ecosystems is a direct consequence of fishing that has disproportionately targeted them for centuries [2,3]. Today we face a situation where almost no pristine marine ecosystems are left and where historical information on pre-exploitation abundance of high-level predators is very rare. In many places, high-level predators have been absent or rare for so long that scientists and managers have never realized how important they were in the ecosystem. In this con-

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text a clear understanding of their ecological role is limited by the fact that our observations are restricted to already altered ecosystems, affected by the decline and, in some cases, disappearance of top predators. Historical data from coastal ecosystems are more abundant and suggest that losses of large predatory fish and mammals were especially pronounced here and led to marked changes in coastal ecosystems structure and function [2]. In fact, the fauna of predators we have today in many coastal ecosystems is a 'ghost' [4] of what it was before human impacts. Such ecosystems nowadays are often controlled by medium-sized predators, although larger carnivores originally preying upon them likely controlled the trophic web in the past [5]. In terrestrial ecosystems, medium-sized predators have sometimes replaced top predators: i.e. coyotes are mesopredators where wolves have been reintroduced, while they have ascended to the role of apex predators

where larger predators have been extirpated [6-8]. Due to this possible shift between mesopredators and apex predators, we will here use the term 'top predator' to qualify the highest level trophic category of predators.

Management of marine ecosystems should consider how they looked in the presence of top predators to be able to set meaningful conservation targets. The Mediterranean is an especially interesting area in this context. This sea has a history of thousands of years of exploitation. In fact, the first evidence of fishing in the shallow Mediterranean comes from prehistory, with the Mediterranean dusky grouper being among the target fishes fished for more than 10,000 years and the blue fin tuna, being an important part of Mediterranean culture for 12,000 years, for millennia exploited by many coastal artisanal fisheries [9]. Apparently first local fish depletions started during Roman times [10], due to rising human population and food demand. During medieval times, strong human population growth resulted in the depletion of fisheries in coastal waters [11]. In the late nineteenth century fishing capacity grew exponentially and in the twentieth century it expanded offshore and to deeper waters. Today most, if not all, of Mediterranean important stocks are overexploited and this sea is very far from the pristine condition depicted in antiquity.

Here we will analyse the reasons that stand for the largely accepted hypothesis that high-level predators have an important ecological role in shaping marine communities, as shown by empirical observations on the far reaching impacts caused by their depletion, which is especially heavy in coastal ecosystems. Subsequently, we will review the effects of Marine protected areas (MPAs) implementation, in terms of high-level predator recovery and their impact on food webs. We will specifically focus on the Mediterranean region, signed by the previous extinction of many top predators and by a general lack of historical data. As a conclusion we will try to answer the following questions: are high-level predators currently recovering in marine protected areas? What are the indirect consequences of such a recovery? Are increasing levels of these predators a good signal of increasing ecosystem health? We will finally suggest possible ways to overcome the general lack of data and knowledge on high-level predators.

#### 2. The importance of high-level predators

#### 2.1 Trophic cascades and pristine ecosystems

In a seminal paper published in 1960, Hairston, Smith and Slobodkin proposed that predators have the potential to maintain global plant biomass by limiting the densities of herbivores ('The world is green' hypothesis) [12]. For the first time, it was stated that predators at the upper trophic levels might control the abundance of consumers and primary producers at lower trophic levels.

Following the 'The world is green' revolution, the idea that ecosystems might be shaped by apex predators stimulated several avenues of research.

In 1966 Paine stated the hypothesis that 'local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites of one species'. Paine experimentally demonstrated that the removal of the apex sea star predator *Pisaster ochraceus* from the rocky intertidal (Pacific Coast of North America) resulted in a pronounced decrease in diversity, with local extinctions of certain benthic invertebrates and algae due to outcompetition from more efficient space occupiers (mussels) [13]. This was one of the first experimental evidences about the role of a keystone predator and showed that in communities controlled by the natural predation of a top predator, the sea star, prev abundances were controlled and local diversity was higher.

The strength of carnivore effects generally depends on the strength of the link between the predator and its prey [14] and often relates to the predator's body size [15]. In a system of strongly interacting links, large top predators frequently initiate the top-down control leading to indirect effects on food webs (i.e. trophic cascades) [16].

Clearly, experimental demonstration is logistically impractical for large animals. What we observe today in marine systems is a situation of generalized absence of large top predators, which have long been reduced or extirpated from much of the world [2,17,18] and whose depletion has triggered trophic cascades that sometimes led to dramatic ecosystem shifts. Trophic cascades are generally a signature of the vast and growing human impact on natural systems and since the 1960s they have been demonstrated in a wide variety of systems, as witnessed by the number of reviews written on the subject [18–22].

A review from the end of the 1990s [19] provided evidence that trophic cascades were no longer limited to sole simple systems like lakes, streams and intertidal zones, as previously reported [23]. Discoveries of trophic cascades were reported from previously unexpected systems, such as the open ocean, tropical forests, fields, and soils. The amplitude of such phenomenon was assessed in several benthic marine ecosystems [20], showing that trophic cascades range from Mediterranean rocky sublittoral, kelp forests and rocky subtidal to coral reefs, rocky intertidal and soft bottoms. A comparison of six different ecosystems, demonstrated that trophic cascades were strongest in lentic and marine benthos and weakest in marine plankton and terrestrial food webs [21]. Evidence of oceanic top-down control from large high trophic level piscivores was also found [22]. Substantial marine mammal, sharks and large piscivorous fish depletions led to mesopredator and invertebrate predator increases and in some cases to trophic cascades negatively impacting commercial species. A more recent empirical study on top predators [18] revealed the unanticipated impacts of trophic cascades on processes as diverse as the dynamics of disease, wildfire, carbon sequestration, invasive species, and biogeochemical cycles defining the loss of these animals as humankind's most pervasive influence on nature.

When fishery data or ecologists' observations are available from a time when top predators were still present, the far reaching impacts of high-level marine carnivore depletion on the ecosystem appear clear.

One of the most well studied examples of such phenomena comes from the Aleutian Islands, where variations in sea otter abundances due to overfishing and subsequent protection have been responsible for dramatic variations of sea urchin population density. These changes have determined the alternation between the natural kelp forest systems and the impoverished condition of overgrazed rocky reefs. Moreover, diet switching of killer whales in this area and subsequent increased predation on sea otters has demised sea urchins from otter predation ultimately causing the destruction of kelp forests [24,25].

The depletion of cod (*Gadus morhua*) followed by the shifting of the fishery to lower trophic levels (fishing down the food web [26]) caused a transition towards a kelp forests ecosystem that superficially looked like its initial state, but *de facto* was very different [5]. The ecological extinction of cod in Canadian coastal zones led to dramatic increases in sea urchin populations, which overgrazed kelp forests leaving widespread barrens [27]. The subsequent shift of the fisheries towards sea urchins allowed kelp forests to recover [28]. The combination of abundant kelp without high-level predators was ideal for a population increase of the predatory crab *Cancer borealis* [29]. Today this mesopredator crab is the dominant species of the ecosystem and is only limited by the availability of nursery habitats (bottom-up control), as opposed to predation on adults (top-down control) [5].

Sharks are one of the largest predators in the oceans, generally foraging on large areas. Today they are still subject to catch and mortality rates that are far exceeding the estimated rebound rates for many populations, causing their worldwide decline and the consequently relevant ecological consequences [30,31]. In some cases (New England, South Africa) the dramatic depletion of large sharks has resulted in the proliferation of smaller elasmobranchs, of which large sharks were the sole predators, and the decline of bony fish at lower levels in the food web [22].

The diversity of species within each trophic level is a type of insurance against the disruption of the ecological functions that species assemblages perform [32]. A long history of fishing down the food web has left Caribbean coral reefs with low species diversity and few functional players at each trophic level (low functional redundancy) [21]. Predators such as sharks, large groupers and snappers have been extirpated from many reefs and many herbivorous fish have been removed by selective fishing. Thanks to the reduction in population density and the size of its predators and competitors, the sea urchin *Diadema antillarum* was left as the primary herbivore in this system. The very high abundance of *Diadema* favoured the explosion of a disease that induced mass mortality of urchins in the 1980s, with resulting uncontrolled macroalgal growth and overcompetition on hard corals. This was one of the world's most rapid and widespread shifts in community state ever documented [5,33]. This shift was probably possible because of the historical overfishing and consequently reduced low functional redundancy of Caribbean reef communities, a condition that negatively affected the resilience of this ecosystem to catastrophic and unpredictable events [34,35].

In many areas only medium–upper trophic level predators are left to control the ecosystem, since their original predators have long been depleted. These are today the main fishing target and are subject to strong fishing pressures. In Kenyan coral reefs, the main keystone species we can identify today is the triggerfish (*Balistapus undulates*), the single most important predator of sea urchins. Where this fish is overfished, sea urchin densities largely increase and turf filamentous algae overgrow corals bioeroded by the sea urchins' grazing activity. Sea urchins can outcompete important grazer fish such as parrotfishes and hard corals cover decreases sharply [36–39].

Deleterious effects of sea urchin predator depletion have been observed also in the Canary Islands, where it has been demonstrated that losses in the diversity of predatory fish species lead to a loss of functional roles and cascading effects that constrain ecosystem processes, leading to the spread of barren grounds [40].

Although the last mentioned species are not top predators, examples of their effects on the ecosystem need to be mentioned in order to imagine the role that previously abundant and larger top predators probably had. In fact, if removing a few species of small scale fishes can change the underwater landscape so dramatically, it is unavoidable to ask one-self what were the consequences of removing large predators from such ecosystems [41] and how these looked in their presence.

There are very few examples left in the world of pristine ecosystems but their observation has provided fundamental information on the shape of an ecosystem in the presence of top predators.

The observation of Shark Bay, Australia, a remote subtropical location characterized by healthy sea grass communities and large population sizes of many large-bodied taxa [42], released important information on the role of tiger sharks as top predators. It was demonstrated that tiger sharks have widespread risk effects on both large-bodied herbivores and mesopredators (sea turtles, dolphins, dugongs, pied cormorants). Behaviourmediated cascades leading to effects on the micro-habitats of the area have been supposed. In fact risk-induced heavy grazing by large herbivores led to reduced seagrass quality in habitats of lower incidence of tiger sharks, and increased quality in areas of higher shark abundance.

Recent studies revealed the structure of two pristine ecosystems, the Palmyra and Kingman atolls in the Line Islands (central Pacific) and the North Western Hawaiian Islands [43–46]. At both locations large high-level predators (specifically large piscivorous snappers, groupers, carangids and sharks) account for 55% to 85% of total fish biomass, with sharks accounting for 57% and 74% of total piscivore biomass in the Line Islands. Despite enhanced predation, high biomass of herbivores is also supported by the coral reefs, together with higher coral cover when compared to nearby fished islands of the same archipelago [46].

The Palmyra and Kingman atolls and the North Western Hawaiian Islands ecosystems have been described as characterized by an inverted trophic pyramid with most fish biomass at top levels, a structure that, due to historical overfishing of our oceans, had never been observed before by ecologists. Even if the existence of inverted pyramids has recently been questioned due to size-based constraints [47], it is undeniable that these pristine ecosystems set new baselines for evaluating present and historical human impacts and provide new targets for MPA conservation efforts.

# 2.2 High-level predators in the Mediterranean: historical reconstruction and degradation

The actual state of the Mediterranean is characterized by a paucity of high-level predator species both in richness and abundance and with medium-sized fish like sea breams left alone to control ecosystem shape. In fact the Mediterranean harbours a classical example of a trophic cascade controlled by a medium-sized fish [48]. Here the rocky sublittoral is characterized by the shift between a developed community with high fish and macroalgal biomass (e.g. *Cystoseira* forests, the Mediterranean 'kelp') and an overgrazed community with high abundance of sea urchins and low algal biomass (e.g. encrusting coralline algae and barren grounds). It has been largely demonstrated that overfishing of sea breams (*Diplodus* spp.), the most effective sea urchin predators in the Mediterranean, led in many areas to large increases in sea urchin population densities with consequent algal overgrazing and shift to low diversity coralline barrens [49,50].

Our understanding of Mediterranean food webs is actually based on a mix of unnatural, simplified communities, dominated by small species, where megafauna has been virtually eliminated by overfishing. [2,17,41]. This impoverished state is supposedly very far from the pristine conditions.

In fact, the Mediterranean has not been pristine since long before the onset of industrial fishing, but it is signed by a millenary history of exploitation, thus it is very difficult to evaluate the current state of this sea. Historical reconstructions have proved to be a useful strategy to fill this gap for many ecosystems, as already reviewed by several authors [51,52], but they are still scarce in the Mediterranean.

Archaeozoological reconstructions based on the study of fish bone remains (i.e. osteometry) allowed investigation of the history of fishing in times preceding the advent of writing. The data have revealed how Mediterranean shallow waters were once dominated by large sized piscivores which attained much bigger sizes than nowadays [53]. Desse and Desse-Berset proposed that these observations allow us to chronologically set the beginning of overexploitation [53].

The analysis of a large amount of fish bones recovered from a Neolithic coastal site of Cap Andréas Kastros, Cyprus, revealed evidences of early exploitation of pristine populations. Here selective fishing conducted from the coast was directed to large specimens of tunas and groupers [54]. Similarly, other Neolithic coastal Mediterranean sites revealed large specimens, attaining sizes that are not comparable with the mediocre dimensions of fish captured by fishermen today [53]. Fish remains from a Spanish cave revealed how fish fauna diversity and size decreased over the last 12,000 years [55]. Osteometry studies also revealed the presence of almost locally extinct species, such as the sturgeon (*Acipenser sturio*), and some elasmobranch species that appear to have been very abundant in coastal waters, contrary to the current situation.

Until the end of the Mesolithic and during Neolithic eras the groupers were very abundant in the coastal systems between the 35<sup>th</sup> and 40<sup>th</sup> parallel, accounting for 30–80% of the examined bony remains. Sites in Spain, Tunisia, Corse, Cyprus, Sicily and other Italian sites revealed the presence of healthy populations of *Epinephelus* spp., with all size ranges represented [56].

Anecdotal research has also led to very interesting discoveries on this topic. A survey of ancient Greek, Etruscan and Roman mosaics and paintings depicted large groupers often reaching the size of a man, being caught at the water surface by fishermen using poles or harpoons from boats, a technique that would yield no grouper catch today [57]. As illustrated in ancient frescoes many Mediterranean top predators (e.g. dolphinfish *Coryphaena hippurus*) may have been all actively fished in antiquity [51].

An especially striking implication of these studies is that not only in ancient times much larger individuals were commonly fished, but that their abundance in coastal waters was high, allowing humans to fish them directly from land [57] or from little boats [57]. Current groupers' bathymetric distribution shows well how populations actively respond to human exploitations. Largest individuals of this species indeed find refuge at depths that exceed the diving limit of most of the recreational spearfishermen [53,58,59].

A recent study coupling historical reconstruction and modelling delivered a detailed account of successive waves of fish depletions in the Adriatic sea and shows well the trajectory of degradation undergone by the Mediterranean ecosystem [10]. Marine mammals at the top of the food web were largely common in antiquity and have been depleted or are very rare today. The common dolphin (*Delphinus delphis*), bottlenose dolphins and the monk seal were hunted in classical Greek, Roman and medieval times and are today ecologically extinct in almost all the Mediterranean Sea.

Predilection for tuna, sharks, rays, sturgeons, common bass, sea bream and hake on Roman and Greek tables led to a large increase in their exploitation. Bluefin tuna fishery was coastal, subsistence and small scale for millennia. Industrial overexploitation probably started around 1950 with open water purse seining substituting coastal trap fisheries. Today the Atlantic-Mediterranean bluefin tuna stock is considered overfished. Similar fate touched the swordfish and the demersal high-level predator *Merluccius merluccius*. Common dentex (*Dentex dentex*) and common Pandora (*Pagellus erythrinus*) are today considered depleted and the dusky grouper (*Epinephelus marginatus*) may be locally extinct [10]. Lotze's results show that large predators and consumers >1 m in length were reduced to 11% of former abundance, a far more drastic reduction than smaller macrofauna (47%), especially in the last century.

As a result, a process of trophic downgrading [18] was observed in the Adriatic [10], with diversity shifting towards smaller, lower trophic level species. Increased exploitation and functional extinctions have altered and largely simplified food webs by changing the proportions of top predators, intermediate consumers and basal species.

Sharks, rays and chimaeras, are by far the most endangered group of marine fish in the Mediterranean Sea, with 31 species (40% of all) critically endangered, endangered or vulnerable [60]. Another detailed historical reconstruction concerned large predatory sharks in the Northwestern Mediterranean Sea, using a diverse set of historical records dating back to the early nineteenth and twentieth centuries [61]. Records from the 1920s–1930s showed that the Mediterranean Sea sustained abundant populations of large sharks, regularly targeted by many coastal fisheries. The analysed species, mackerel sharks (*I. oxyrinchus* and *Lamna nasus*), requiem shark (*Prionace glauca*), hammerhead shark (*Sphyrna zygaena*), and thresher shark (*Alopias vulpinus*), showed rates of decline up to 99.99%, levels at which they can be considered functionally extinct in coastal and pelagic waters of the Northwestern Mediterranean Sea. Trends of biomass data also showed a significant reduction in mean size over time, which is the lowest in the world [62].

In addition to large predatory sharks and bony fishes, other top predators like cetaceans and the monk seal underwent extreme declines due to a variety of human impacts [63,64].

A concluding remark could be that wherever high-level predators have been extirpated, ecosystems have consequently become degraded and simplified [65]. It is then plausible to assume that a return of high-level carnivores to a system will allow degraded systems to recover [16]. A tempting question is whether conservation of these predators could restore biodiversity and ecological functioning [16]. The science of marine reserves can give insights on this potential.

# 3. Recovery of high-level predators and biodiversity within marine protected areas

#### 3.1 Data from the world

Several studies have demonstrated that marine reserves are an effective tool for the recovery of large piscivorous fish and upper trophic levels (direct effects), but have also shown a large variability of effects in terms of triggered trophic cascades (indirect effects). In fact, while in some temperate ecosystems it was possible to demonstrate that recovery of highlevel predators (sea otters, snappers, spiny lobster, sea bream) can lead to the re-establishment of lost trophic interactions (e.g. sea urchins and macroalgae) [66,67], in more diverse ecosystems like coral reefs a more variable response is observed, depending on conditions such as duration of protection, taxonomic resolution of the study (species or functional group) and possible compensation effects due to functional redundancy [67–76]. Recent meta-analytical studies give a useful global overview of marine reserve protection effects in terms of recovery of upper trophic levels and trophic changes.

A global meta-analysis based on data from 124 reserves demonstrated that protection yielded significant average increases of density, biomass, average organism size and species richness of the communities within reserves [77]. Differential responses were observed among taxonomic groups, with large fish and invertebrates targeted by fishing showing significant increases in density and biomass overall, while algal cover increased in temperate reserves and decreased in tropical reefs, due to the recovery of exploited large herbivores.

Through the analysis of long term time series of ecological data in and out of marine reserves from several regions, it was demonstrated that positive effects on target predatory fish and lobsters occurred rapidly after reserve establishment but continued to increase, in some cases up to 25–40 years after protection (respectively Serranide and Lutjaniae in the Apo islands and triggerfish in Kenyan reserves) [78]. This analysis showed that the ecosystems were still generally far away from their carrying capacity in terms of high-level predators. Large herbivorous fish showed decadal increases in abundance too. Indirect effects through trophic cascades were common especially in terms of sea urchin reductions, but showed conspicuous time lags (average 13 years after protection) with respect to direct effects, probably due to behavioural mechanisms of predation risk reduction [78].

Similar conclusions on the magnitude and timing of protection effects were drawn from a meta-analysis of data from several temperate and tropical locations [79]. The authors observed clear trophic changes in protected ecosystems due to a time lasting build-up of biomass and abundance of upper trophic levels. Indirect negative effects were also evident for low mobility, small sized, and non-target fish species.

Other meta-analytical studies revealed that commercial species including many top predatory fish were observed to increase in density in many southern Europe MPAs [80,81]. Response of commercial exploited fishes to protection depended on species maximum body size, with large species showing the strongest increase in MPAs. Moreover the response of large species increased with time of protection. Commercial exploited fish with a benthic habitat responded positively to protection, while exploited fish with a bentho-pelagic habitat did not show a demonstrable response to protection. For non-commercial unexploited fish with a benthic habitat, densities were higher inside the reserve, probably because positive effects in habitat changes were more important than possible negative trophic cascade effects [80,81]. On the other hand, densities were higher outside the reserve for bentho-pelagic non-exploited species, suggesting possible trophic cascade effects due to predator increases.

A crucial question is whether MPAs are able to protect and restore species performing key ecological functions, but remarkably few studies have evaluated functional recovery after habitat degradation [82]. An interesting study in this regard reported that recovery of species richness and diversity in marine reserves coincided with increases in functional richness and diversity of fish assemblages [83]. Species recovery in reserves resulted in increased representation across different functional categories, particularly key groups like large carnivores and herbivores.

Thus reserves reveal initial trajectories towards recovery, but if compared with the few studied pristine ecosystems, it appears clear that the levels of piscivore biomass observed in recent marine reserves across the world are well below what the ecosystems could sustain. Moreover, for indirect changes to occur in marine reserves an absolute increase in abundance, mean size or biomass of target species, i.e. a restoration or build

up to some (unknown) former level, is necessary [78,84]. Management of marine reserves should thus acknowledge that the potential for recovery of ecosystem functioning through protection is high, but will likely require long time frames [76,78,84]. In this context long-term monitoring is necessary and needs to be carried out for long enough lapses of time to have the chance to detect indirect effects. Special attention should be paid to variations in high-level predator biomass, a variable that can yield useful information on the state of recovery of a system following protection.

#### 3.2 Mediterranean marine protected areas

Mediterranean MPAs, when well enforced [85], have shown to be very effective in leading to increases in the biomass and diversity of large piscivorous and invertebrate feeding fish, especially for serranids, sciaenids, sparids, and the larger labrids [50,58,84, 86–96], as also reviewed in [97].

Due to Mediterranean food web complexity the indirect effects of predator recovery are often masked by many factors, such as local conditions of oceanography, habitat topography and complexity (presence of refuges for prey species) and intensity of fishing outside the reserve. As in the rest of world, moreover, indirect effects can occur with considerable time lags with respect to direct effects [98].

Variable results have been drawn from the observation of indirect protection effects. In the Scandola Marine Reserve lower abundance and species richness of macrozoobenthos were observed [99] where predators attained higher abundance compared to nearby unprotected sites [88]. At the Ustica Marine Reserve, increases in piscivores (groupers) coincided with a decrease of small size microcarnivorous fish [58,100] and a seasonal increase of abundance and species richness of polychaetes and gasteropods [101,102]. Even with regard to the strong trophic interaction sea breams - sea urchin - algae [82], somewhat contradictory results have resulted on the potential for recovery of algal beds in MPAs through sea bream protection [49,92,98]. In fact, densities of fish need to reach a critical threshold in order to reduce sea urchins and drive the transition [50]. It has been demonstrated that when a protected area has the proper physical and biological characteristics (appropriate habitat for sea breams, as well as dimension and duration of protection encompassing their mobility and life cycle) to trigger changes at population and/or community levels, it allows the recovery of the predatory sea bream population, and the reestablishment of predatory control upon sea urchins, as happened in the Torre Guaceto MPA [92]. In the protected zone of Torre Guaceto, moreover, coralline barrens were less extended whereas turf forming and erect-branched algae showed an opposite pattern.

Due to the absence of pristine sites left in the Mediterranean and the few quantitative historical data to set a baseline against which to compare the health of current ecosystems and set precise conservation targets, comparisons among marine protected areas of different age, or between MPAs and fished sites (space for time substitutions) have shown to be useful in setting some reference points.

A recent large-scale study covering several MPAs and fished sites across the Mediterranean revealed a trajectory of degradation and recovery, with high-level predator biomass being significantly larger at protected than at non protected sites [96]. A gradient of 31-fold range increase in fish biomass was observed, reaching a maximum of 115-fold. This is the largest fish biomass gradient ever reported for reef fish assemblages and is probably indicative of the large impact of historical and current fishing pressure in the Mediterranean [96]. Continuous increase of high-level predators (particularly groupers) at the Medes islands, where they reached 49% of fish biomass after 27 years of protection, show that the potential for recovery in Mediterranean MPAs is comparable to other parts of the world and that aiming at achieving fish biomass values similar to those observed in the pristine tropical systems is possible. The authors finally suggest how the marine reserves with highest fish biomass are a useful current baseline against which managers can compare recovery trends for fish assemblages in rocky habitats across the Mediterranean. No clear pattern in the structure of benthic community was associated with the gradient on fish biomass, but three alternative community states were revealed in the trajectory of recovery: large fish biomass and reef dominated by non-canopy algae, lower fish biomass but abundant algal canopies and suspension feeders, and low fish biomass and extensive barrens.

The functional approach is still rare in the Mediterranean. Spanish marine protected areas were shown to support higher functional diversity than adjacent unprotected sites, due to a difference in the trophic structure rather than in species diversity [103]. High-level predators contributed the most to the dissimilarity between protected and unprotected sites. Coupling a functional approach with food web modelling it was also found that protected areas support higher trophic levels and are characterized by more complex food webs than exploited areas [104]. Finally it was demonstrated that the Lavezzi Islands Reserve significantly protects functional originality ('original' species are species that support unique and essential processes) and diversity, with the most original species being the large predator *Seriola dumerili* [105]. Protection of these species is an insurance against functional diversity erosion and a prerequisite to sustain coastal goods and services derived from ecosystem functioning [81,105].

#### 4. Food web modelling in the Mediterranean

The complexity of species interactions in Mediterranean ecosystems together with the long history of exploitation and the variety and intensity of anthropogenic stressors (fishing, pollution, aquaculture, etc.) that differentially impact them, has prompted the need for a holistic approach to the comprehension of this ecosystem and the management of its marine resources. Thus, in the context of an ecosystem-based management of marine resources [106,107], food web modelling, already largely applied across the world especially through the software Ecopath with Ecosym [108–110], has gained growing recognition also in the Mediterranean. As already recently reviewed [110], food web modelling in the Mediterranean has allowed the unification of a large amount of sparse ecological information in order to identify keystone species and disentangle species interactions in different ecosystems, as well as quantify structural and functional ecosystem traits, assess the impacts of human activities and analyse management options for marine resources. While the majority of models in the Mediterranean have described fished ecosystems to assess fishing impact, models applied to marine protected areas are scarce, yet they delivered interesting results. The management of the Port Cros MPA in France was shown to be succeeding in protecting top trophic level groups, and the model released interesting information on dusky grouper export from the MPA [111]. A model built on the Bonifacio Strait natural reserve of Corsica, analysed high-level predator sensitivity to increased artisanal and recreational fishing effort and examined management options for recreational fisheries [112]. Ecosystem effects of protection were analysed by comparing the Miramare Reserve in the Adriatic with an industrially exploited area, revealing higher mean trophic level of the community, higher food web complexity, and higher fish/invertebrates and pelagic/demersal ratios in the MPA [104].
A meta-analysis conducted on results from 39 Ecopath models from the Mediterranean allowed the determination of the main keystone species or functional group from different Mediterranean ecosystems. High-level predators such as marine mammals, seabirds and large fishes ranked high in several models and a higher proportion of keystone groups appeared in non-fished or slightly fished ecosystems with respect to exploited ecosystems [110].

Trophic modelling coupled with historical data allowed assessment of the structural degradation of two food webs in the Mediterranean (the North-Central Adriatic and the South Catalan Sea) from the 1970s to the 1990s, largely consequent to top predator depletion. Clear reductions in the mean and maximum trophic level of the community, decreasing fraction and percentage biomass of top predators, together with reductions in indexes of food web complexity were a clear sign of the degradation due to the overexploitation of higher trophic levels and to food web simplification. The Mediterranean resulted more degraded and less robust to species loss than other non-Mediterranean systems [113].

A previously mentioned study that interestingly analysed palaeontological, archaeological, fisheries and ecological data through food web modelling, delivered dramatic results on the historical degradation of the Adriatic ecosystem [10] and through simulations of species losses showed that today's ecosystems are probably less robust to species extinctions than in the past.

#### 5. Conclusions

Similarly to what happened in terrestrial ecosystems [16,18], we are nowadays witnessing the far reaching impacts of high-level predator depletion in marine ecosystems, impacts that are far more striking when ecological observations are available from a time previous to predator depletion. In these cases we have seen how extirpation of predators may cause prominent ecosystem shifts. Kelp forests were replaced by barren grounds in the Aleutian Islands, and corals were outcompeted by macroalgae on coral reefs, with consequent reductions in species and functional diversity. Moreover, on long time scales, superficially less evident but not less dramatic changes occurred in some ecosystems, like the shift towards the poorly diverse and macroinvertebrate-dominated kelp forests of Canada coastal zones.

The few pristine ecosystems existing in the world show an ecosystem shape with surprisingly high biomass levels at the top of the trophic pyramid, setting new baselines and targets for MPA management.

Nevertheless, for many ecosystems, information on their state prior to the beginning of exploitation does not exist. Most of our knowledge on the state of Mediterranean ecosystems originates from field studies in the last 30 years [96]. At this time, when the first marine protected areas were created (Port Cros, 1963; Scandola, 1975; Medes Islands, 1983) the ecosystem structure of the Mediterranean had already been largely affected by many centuries of exploitation, in some cases dating back to prehistory [56]. Large predators such as sharks, monk seal and large piscivores that were once very common had already been actively fished or hunted. As has been shown for other ecosystems in the world, the communities we observe today in the Mediterranean, with sea breams being the key benthic predators causing habitat shift, are probably not representative of the past and of the natural conditions of this ecosystem. In fact, it was suggested that if recent changes in the abundance of medium-sized predators have caused trophic cascades in coastal communities leading to ecosystem shifts, it is plausible to hypothesize that the dramatic changes in the size and abundance of once common large fish must have caused

significant changes in food web structure over historical periods, as this has been shown for marine food webs worldwide [2,17].

With this background, a crucial question is unavoidable: how would Mediterranean marine ecosystems look in the presence of large predators?

We have seen how historical reconstruction of the abundances and sizes of large animals in the last century is scant in the Mediterranean [61], but may help setting up appropriate conservation and fisheries management goals and targets for assessing the recovery of endangered species, food webs and whole communities [50].

To answer our questions, we have highlighted that marine protected areas across the world and in the Mediterranean are significantly leading to a slow recovery of high-level predators, but even the oldest MPAs have not yet reached their carrying capacity. We have reviewed how these predators can have a major role in strongly shaping communities and modifying ecosystem functions and that they can be a good indicator of the state of recovery of an MPA.

We have seen that for highly complex food webs like the Mediterranean ones, it is difficult to ascertain information on the food web consequences of high-level predator recovery from empirical ecological studies [41]. Food web modelling is largely considered a very useful tool to unravel trophic interactions, describe ecosystem structural traits, derive maturity indexes for comparisons [104,109,114] and also assess the potential for recovery of high-level predators [115], but model applications in marine protected areas are still few, especially in the Mediterranean. This scarcity is largely due to the large amount of data needed to get reliable models and the associated uncertainties on data precision. Nevertheless, if reliable ecosystem models could be built in a cost effective way, they could provide useful information for the research and management of marine protected areas.

If the fundamental role of high-level predators in marine ecosystems is finally acknowledged [18], as well as their leading position in MPA recovery, their monitoring should then be a fundamental point in the design and management plan of MPAs.

Nevertheless the pre-existing disturbance of millennia of exploitation undergone by the Mediterranean Sea, which led to the ecological extinction of large top predators such as many species of sharks and marine mammals, must be acknowledged by MPA management, which should define realistic targets of recovery and conservation thereafter. For some of these wide ranging large animals, recovery is a challenging task, but can be enhanced by comprehensive MPA networks that in order to be effective, should be built on sound scientific data and with the help of advanced scientific tools like predictive habitat modelling and spatial mapping, integrated with life history and behavioural data [116,117]. We have seen that the recovery of high-level predators like large predatory fish in MPAs is an important and realistic target, but their monitoring is not an easy task. A challenging objective for both research and management could be the development and implementation of consistent field monitoring methods to assess the abundance of the entire fish assemblage, from the smallest cryptobenthic species to the large highly motile predatory fish. In this way reliable relative values of high-level predator increase could be obtained. Complementing historical reconstruction, ecosystem modelling and effective long term monitoring of high-level predators in the field could help us to effectively assess the recovery of marine coastal ecosystems.

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#### References

- [1] J.E. Duffy, *Biodiversity and ecosystem function: The consumer connection*, Oikos 99 (2002), pp. 201–219.
- [2] J.B.C. Jackson, M.X. Kirby, W.H. Berger, K.A. Bjorndal, L.W. Botsford, B.J. Bourque, R.H. Bradbury, R. Cooke, J. Erlandson, and J.A. Estes, *Historical overfishing and the recent collapse of coastal ecosystems*, Science 293 (2001), pp. 629–637.
- [3] R.A. Myers and B. Worm, *Extinction, survival or recovery of large predatory fishes*, Philosophical Transactions of the Royal Society B: Biological Sciences 360 (2005), pp. 13–20.
- [4] P.K. Dayton, M.J. Tegner, P.B. Edwards, and K.L. Riser, *Sliding baselines, ghosts, and reduced expectations in kelp forest communities*, Ecological Applications 8 (1998), pp. 309–322.
- [5] R. Steneck and E. Sala, Large marine carnivores: Trophic cascades and top-down controls in coastal ecosystems past and present, University of Maine Sea Grant College Program, 2005.
- [6] K.M. Berger, E.M. Gese, and J. Berger, Indirect effects and traditional trophic cascades: A test involving wolves, coyotes, and pronghorn, Ecology 89 (2008), pp. 818–828.
- [7] G.W. Roemer, M.E. Gompper, and B.V. Valkengurgh, *The ecological role of the mammalian mesocarnivore*, BioScience 59 (2009), pp. 165–173.
- [8] L.R. Prugh, C.J. Stoner, C.W. Epps, W.T. Bean, W.J. Ripple, A.S. Laliberte, and J.S. Brashares, *The rise of the mesopredator*, BioScience 59 (2009), pp. 779–791.
- [9] B.A. Block, Of tuna and tonnaroti, Science 289 (2000), pp. 876–877.
- [10] H.K. Lotze, M. Coll, and J.A. Dunne, *Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean*, Ecosystems 14 (2011), pp. 198–222.
- [11] D.T. Neil, A thousand years of human-coastal interactions in Venice: Lessons from the serene republic. Coast to Coast 2002-Source to Sea, National Coast.
- [12] N.G. Hairston, F.E. Smith, and L.B. Slobodkin, Community structure, population control, and competition, American Naturalist (1960), pp. 421–425.
- [13] R.T. Paine, Food web complexity and species diversity, American Naturalist (1966), pp. 65– 75.
- [14] —, Food webs: Linkage, interaction strength and community infrastructure, Journal of Animal Ecology 49 (1980), pp. 667–685.
- [15] A.R.E. Sinclair, S. Mduma, and J.S. Brashares, *Patterns of predation in a diverse predator-prey system*, Nature 425 (2003), pp. 288–290.
- [16] J. Ray, K.H. Redford, R. Steneck, and J. Berger, *Large Carnivores and the Conservation of Biodiversity*, Island Press, 2005.
- [17] J.B.C. Jackson and E. Sala, Unnatural oceans, Scientia Marina 65 (2001), pp. 273–281.
- [18] J.A. Estes, J. Terborgh, J.S. Brashares, M.E. Power, J. Berger, W.J. Bond, S.R. Carpenter, T.E. Essington, R.D. Holt, J.B.C. Jackson, R.J. Marquis, L. Oksanen, T. Oksanen, R.T. Paine, E.K. Pikitch, W.J. Ripple, S.A. Sandin, M. Scheffer, T.W. Schoener, J.B. Shurin, A.R.E. Sinclair, M.E. Soule, R. Virtanen, and D.A. Wardle, *Trophic downgrading of planet Earth*, Science 333 (2011), pp. 301–306.
- [19] M.L. Pace, J.J. Cole, S.R. Carpenter, and J.F. Kitchell, *Trophic cascades revealed in diverse ecosystems*, Trends in Ecology & Evolution 14 (1999), pp. 483–488.
- [20] J.K. Pinnegar, N.V.C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M.L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, and G. d'Anna, *Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management*, Environmental Conservation 27 (2000), pp. 179–200.
- [21] J.B. Shurin, E.T. Borer, E.W. Seabloom, K. Anderson, C.A. Blanchette, B. Broitman, S.D. Cooper, and B.S. Halpern, A cross-ecosystem comparison of the strength of trophic cascades, Ecology Letters 5 (2002), pp. 785–791.

- [22] J.K. Baum and B. Worm, Cascading top-down effects of changing oceanic predator abundances, Journal of Animal Ecology 78 (2009), pp. 699–714.
- [23] D.R. Strong, Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems, Ecology 73 (1992), pp. 747–754.
- [24] J.A. Estes and J.F. Palmisano, Sea otters: Their role in structuring nearshore communities, Science (New York, NY) 185 (1974), pp. 1058–1060.
- [25] J.A. Estes, M.T. Tinker, T.M. Williams, and D.F. Doak, Killer whale predation on sea otters linking oceanic and nearshore ecosystems, Science 282 (1998), pp. 473–476.
- [26] D. Pauly, V. Christensen, J. Dalsgaard, R. Froese, and F. Torres Jr, *Fishing down marine food webs*, Science 279 (1998), pp. 860–863.
- [27] R.S. Steneck, M.H. Graham, B.J. Bourque, D. Corbett, J.M. Erlandson, J.A. Estes, and M.J. Tegner, *Kelp forest ecosystems: Biodiversity, stability, resilience and future*, Environmental Conservation 29 (2002), pp. 436–459.
- [28] R.S. Steneck, J. Vavrinec, and A.V. Leland, Accelerating trophic-level dysfunction in kelp forest ecosystems of the western North Atlantic, Ecosystems 7 (2004), pp. 323–332.
- [29] A.V. Leland, A new apex predator in the Gulf of Maine? Large, mobile crabs (Cancer borealis) control benthic community structure, (2002).
- [30] F. Ferretti, B. Worm, G.L. Britten, M.R. Heithaus, and H.K. Lotze, *Patterns and ecosystem consequences of shark declines in the ocean*, Ecology Letters 13 (2010), pp. 1055–1071.
- [31] B. Worm, B. Davis, L. Kettemer, C.A. Ward-Paige, D. Chapman, M.R. Heithaus, S.T. Kessel, and S.H. Gruber, *Global catches, exploitation rates, and rebuilding options for sharks*, Marine Policy 40 (2013), pp. 194–204.
- [32] T.P. Hughes, A.H. Baird, D.R. Bellwood, M. Card, S.R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J.B.C. Jackson, and J. Kleypas, *Climate change, human impacts, and the resilience of coral reefs*, Science 301 (2003), pp. 929–933.
- [33] J. Bascompte, C.J. Melián, and E. Sala, *Interaction strength combinations and the overfishing of a marine food web*, Proceedings of the National Academy of Sciences of the United States of America 102 (2005), pp. 5443–5447.
- [34] J.M. Pandolfi, R.H. Bradbury, E. Sala, T.P. Hughes, K.A. Bjorndal, R.G. Cooke, D. McArdle, L. McClenachan, M.J.H. Newman, and G. Paredes, *Global trajectories of the long-term decline of coral reef ecosystems*, Science 301 (2003), pp. 955–958.
- [35] D.R. Bellwood, T.P. Hughes, C. Folke, and M. Nyström, *Confronting the coral reef crisis*, Nature 429 (2004), pp. 827–833.
- [36] T.R. McClanahan and S.H. Shafir, Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons, Oecologia 83 (1990), pp. 362–370.
- [37] T.R. McClanahan, Kenyan coral reef lagoon fish: Effects of fishing, substrate complexity, and sea urchins, Coral Reefs 13 (1994), pp. 231–241.
- [38] T.R. McClanahan, A coral reef ecosystem-fisheries model: Impacts of fishing intensity and catch selection on reef structure and processes, Ecological Modelling 80 (1995), pp. 1–19.
- [39] T.R. McClanahan, N.A. Muthiga, A.T. Kamukuru, H. Machano, and R.W. Kiambo, *The effects of marine parks and fishing on coral reefs of northern Tanzania*, Biological Conservation 89 (1999), pp. 161–182.
- [40] S. Clemente, J.C. Hernández, and A. Brito, Evidence of the top-down role of predators in structuring sublittoral rocky-reef communities in a Marine Protected Area and nearby areas of the Canary Islands, ICES Journal of Marine Science: Journal du Conseil 66 (2009), pp. 64–71.
- [41] E. Sala, *The past and present topology and structure of Mediterranean subtidal rocky-shore food webs*, Ecosystems 7 (2004), pp. 333–340.
- [42] M.R. Heithaus, A.J. Wirsing, and L.M. Dill, *The ecological importance of intact top-predator populations: A synthesis of 15 years of research in a seagrass ecosystem*, Marine and Freshwater Research 63 (2012), pp. 1039–1050.
- [43] A.M. Friedlander and E.E. DeMartini, Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators, Marine Ecology Progress Series 230 (2002), pp. 253–264.
- [44] C. Stevenson, L.S. Katz, F. Micheli, B. Block, K.W. Heiman, C. Perle, K. Weng, R. Dunbar, and J. Witting, *High apex predator biomass on remote Pacific islands*, Coral Reefs 26 (2007), pp. 47–51.

- [45] E.E. DeMartini, A.M. Friedlander, S.A. Sandin, and E. Sala, *Differences in fish-assemblage structure between fished and unfished atolls in the northern Line Islands, central Pacific*, Marine Ecology Progress Series 365 (2008), pp. 199–215.
- [46] S.A. Sandin, J.E. Smith, E.E. DeMartini, E.A. Dinsdale, S.D. Donner, A.M. Friedlander, T. Konotchick, M. Malay, J.E. Maragos, and D. Obura, *Baselines and degradation of coral reefs in the northern Line Islands*, PLoS One 3 (2008).
- [47] R. Trebilco, J.K. Baum, A.K. Salomon, and N.K. Dulvy, *Ecosystem ecology: Size-based con-straints on the pyramids of life*, Trends in Ecology & Evolution 28 (2013), 423–431.
- [48] E. Sala and M. Zabala, Fish predation and the structure of the sea urchin Paracentrotus lividus populations in the NW Mediterranean, Marine Ecology Progress Series 140 (1996), pp. 71–81.
- [49] E. Sala, C.F. Boudouresque, and M. Harmelin-Vivien, Fishing, trophic cascades, and the structure of algal assemblages: Evaluation of an old but untested paradigm, Oikos 82 (1998), pp. 425–439.
- [50] P. Guidetti, Predator diversity and density affect levels of predation upon strongly interactive species in temperate rocky reefs, Oecologia 154 (2007), pp. 513–520.
- [51] J.K. Pinnegar and G.H. Engelhard, *The 'shifting baseline' phenomenon: A global perspec*tive, Reviews in Fish Biology and Fisheries 18 (2008), pp. 1–16.
- [52] H.K. Lotze and B. Worm, *Historical baselines for large marine animals*, Trends in Ecology & Evolution 24 (2009), pp. 254–262.
- [53] J. Desse and N. Desse-Berset, Pêche et surpêche en Méditerranée: le témoignage des os, Exploitation des Animaux Sauvages a Travers le Temps 13 (1993), pp. 332–333.
- [54] J. Desse, and N. Desse-Berset, Osteometry and fishing strategies at Cape Andreas Kastros (Cyprus, 8th millennium BP), Annalen-Koninklijk Museum voor Midden-Afrika-Zoologische Wetenschappen 274 (1994).
- [55] Cueva de Nerja (prov. Malaga): a close look at a twelve thousand year ichthyofaunal sequence from southern Spain [Paleolithic, Neolithic, Chalcolithic], Annales Musee Royal de l'Afrique Centrale Sciences Zoologiques Vol. 274.
- [56] —, Préhistoire du mérou, Marine Life 9 (1999), pp. 19–30.
- [57] P. Guidetti and F. Micheli, Ancient art serving marine conservation, Frontiers in Ecology and the Environment 9 (2011), pp. 374–375.
- [58] G. La Mesa and M. Vacchi, An analysis of the coastal fish assemblage of the Ustica Island marine reserve (Mediterranean Sea), Marine Ecology 20 (2002), pp. 147–165.
- [59] A. Di Franco, S. Bussotti, A. Navone, P. Panzalis, and P. Guidetti, *Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages*, Marine Ecology Progress Series 387 (2009), pp. 275–285.
- [60] M.N. Bradai, B. Saidi, and S. Enajjar, *Elasmobranchs of the mediterranean and black sea: Status, ecology and biology bibliographic analysis*, Food and agriculture organization of the United nations (FAO), 2011.
- [61] F. Ferretti, R.A. Myers, F. Serena, and H.K. Lotze, *Loss of large predatory sharks from the Mediterranean Sea*, Conservation Biology 22 (2008), pp. 952–964.
- [62] P. Megalofonou, Incidental catch and estimated discards of pelagic sharks from the swordfish and tuna fisheries in the Mediterranean Sea, Fishery Bulletin 103 (2005), pp. 620–634.
- [63] W.M. Johnson and D.M. Lavigne, *The Mediterranean monk seal*, Conservation Guidelines. Multilingual Edition. IMMA Inc. Ghelph, Canada. 152p. Internet edition: http://www.monachus.org/library.htm (1998).
- [64] R.R. Reeves, *The status and distribution of cetaceans in the Black Sea and Mediterranean Sea.*
- [65] M.E. Soulé and J. Terborgh, *Continental conservation: Scientific foundations of regional reserve networks*, Island Press, 1999.
- [66] J.A. Estes, Growth and equilibrium in sea otter populations, The Journal of Animal Ecology (1990), pp. 385–401.
- [67] N.T. Shears and R.C. Babcock, Marine reserves demonstrate top-down control of community structure on temperate reefs, Oecologia 132 (2002), pp. 131–142.
- [68] G.R. Russ and A.C. Alcala, Marine reserves: Rates and patterns of recovery and decline of large predatory fish, Ecological applications (1996), pp. 947–961.
- [69] S. Jennings and N.V.C. Polunin, Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities, Coral Reefs 16 (1997), pp. 71–82.

- [70] T.R. McClanahan, Recovery of a coral reef keystone predator, "Balistapus undulatus", in East African marine parks, Biological Conservation 94 (2000), pp. 191–198.
- [71] N.T. Shears and R.C. Babcock, Continuing trophic cascade effects after 25 years of no-take marine reserve protection, Marine Ecology Progress Series 246 (2003), pp. 1–16.
- [72] G.R. Russ and A.C. Alcala, Marine reserves: Rates and patterns of recovery and decline of predatory fish, 1983-2000, Ecological Applications 13 (2003), pp. 1553–1565.
- [73] N.A.J. Graham, R.D. Evans, and G.R. Russ, *The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef*, Environmental Conservation 30 (2003), pp. 200–208.
- [74] T.R. McClanahan, N.A.J. Graham, J.M. Calnan, and M.A. MacNeil, *Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya*, Ecological Applications 17 (2007), pp. 1055–1067.
- [75] K. Kramer and K.L. Heck, Top-down trophic shifts in Florida Keys patch reef marine protected areas, Marine Ecology Progress Series 349 (2007), pp. 111–123.
- [76] G.R. Russ and A.C. Alcala, Decadal-scale rebuilding of predator biomass in Philippine marine reserves, Oecologia 163 (2010), pp. 1103–1106.
- [77] S.E. Lester, B.S. Halpern, K. Grorud-Colvert, J. Lubchenco, B.I. Ruttenberg, S.D. Gaines, S. Airamé, and R.R. Warner, *Biological effects within no-take marine reserves: A global synthesis*, Marine Ecology Progress Series 384 (2009), pp. 33–46.
- [78] R.C. Babcock, N.T. Shears, A.C. Alcala, N.S. Barrett, G.J. Edgar, K.D. Lafferty, T.R. McClanahan, and G.R. Russ, *Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects*, Proceedings of the National Academy of Sciences 107 (2010), pp. 18256–18261.
- [79] F. Micheli, P. Amarasekare, J. Bascompte, and L.R. Gerber, *Including species interactions in the design and evaluation of marine reserves: Some insights from a predator-prey model*, 2004.
- [80] J. Claudet, C.W. Osenberg, L. Benedetti-Cecchi, P. Domenici, J.-A. García-Charton, Á. Pérez-Ruzafa, F. Badalamenti, J. Bayle-Sempere, A. Brito, and F. Bulleri, *Marine reserves: Size and age do matter*, Ecology Letters 11 (2008), pp. 481–489.
- [81] J. Claudet, C.W. Osenberg, P. Domenici, F. Badalamenti, M. Milazzo, J.M. Falcón, I. Bertocci, L. Benedetti-Cecchi, J.A. García-Charton, and R. Goñi, *Marine reserves: Fish life history and ecological traits matter*, Ecological applications 20 (2010), pp. 830–839.
- [82] J. Claudet, P. Guidetti, D. Mouillot, N.T. Shears, and F. Micheli, *Ecological effects of marine protected areas: Conservation, restoration, and functioning*, Marine Protected Areas: A Multidisciplinary Approach (2011).
- [83] F. Micheli and B.S. Halpern, Low functional redundancy in coastal marine assemblages, Ecology Letters 8 (2005), pp. 391–400.
- [84] F. Micheli, B.S. Halpern, L.W. Botsford, and R.R. Warner, *Trajectories and correlates of community change in no-take marine reserves*, Ecological Applications 14 (2004), pp. 1709–1723.
- [85] P. Guidetti, M. Milazzo, S. Bussotti, A. Molinari, M. Murenu, A. Pais, N. Spano, R. Balzano, T. Agardy, and F. Boero, *Italian marine reserve effectiveness: Does enforcement matter?* Biological Conservation 141 (2008), pp. 699–709.
- [86] J.G. Harmelin, and J. Marinopoulos, Recensement de la population de corbs (Sciaena umbra, Linnaeus, 1758: Pisces) du Parc National de Port-Cros (Méditerranée, France) par inventaires visuels, Scientific Report of Port-Cros National Park 15 (1993), pp. 265–276.
- [87] J.G. Harmelin, F. Bachet, and F. Garcia, Mediterranean marine reserves: Fish indices as tests of protection efficiency, Marine Ecology 16 (1995), pp. 233–250.
- [88] P. Francour, Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean), Oceanologica Acta 17 (1994), pp. 309– 317.
- [89] J. Claudet, D. Pelletier, J.Y. Jouvenel, F. Bachet, and R. Galzin, Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators, Biological Conservation 130 (2006), pp. 349–369.
- [90] J. Garcia-Charton and S. Planes, Etude de l'impact de la Réserve Naturelle Marine de Cerbère-Banyuls comme source d'exportation de poissons littoraux adultes vers les zones avoisinantes, Rapport EPHE–Conseil Général des Pyrénées-Orientales, 6 (2002) 43p.

- [91] J.A. García-Charton, A. Pérez-Ruzafa, P. Sánchez-Jerez, J.T. Bayle-Sempere, O. Reñones, and D. Moreno, *Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages*, Marine Biology 144 (2004), pp. 161–182.
- [92] P. Guidetti, Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs, Ecological Applications 16 (2006), pp. 963–976.
- [93] M. Harmelin-Vivien, L. Le Diréach, J. Bayle-Sempere, E. Charbonnel, J.A. García-Charton, D. Ody, A. Pérez-Ruzafa, O. Reñones, P. Sánchez-Jerez, and C. Valle, *Gradients of abun*dance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological conservation 141 (2008), pp. 1829–1839.
- [94] E. Macpherson, A. García-Rubies, and A. Gordoa, *Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve*, Marine Biology 137 (2000), pp. 1067–1076.
- [95] E. Macpherson, A. Gordoa, and A. Garcia-Rubies, *Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean*, Estuarine, Coastal and Shelf Science 55 (2002), pp. 777–788.
- [96] E. Sala, E. Ballesteros, P. Dendrinos, A. Di Franco, F. Ferretti, D. Foley, S. Fraschetti, A. Friedlander, J. Garrabou, H. Güçlüsoy, P. Guidetti, B.S. Halpern, B. Hereu, A.A. Karamanlidis, Z. Kizilkaya, E. Macpherson, L. Mangialajo, S. Mariani, F. Micheli, A. Pais, K. Riser, A.A. Rosenberg, M. Sales, K.A. Selkoe, R. Starr, F. Tomas, and M. Zabala, *The structure of Mediterranean rocky reef ecosystems across environmental and human gradients, and conservation implications*, Plos One 7 (2012).
- [97] J.A. García-Charton, A. Pérez-Ruzafa, C. Marcos, J. Claudet, F. Badalamenti, L. Benedetti-Cecchi, J.M. Falcón, M. Milazzo, P.J. Schembri, B. Stobart, F. Vandeperre, A. Brito, R. Chemello, M. Dimech, P. Domenici, I. Guala, L. Le Diréach, E. Maggi, and S. Planes, *Effectiveness of European Atlanto-Mediterranean MPAs: Do they accomplish the expected effects on populations, communities and ecosystems?* Journal for Nature Conservation 16 (2008), pp. 193–221.
- [98] F. Micheli, L. Benedetti-Cecchi, S. Gambaccini, I. Bertocci, C. Borsini, G.C. Osio, and F. Romano, *Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages*, Ecological Monographs 75 (2005), pp. 81–102.
- [99] C.F. Boudouresque, A. Caltagirone, J.R. Lefevre, V. Rico, and R. Semroud, Macrozoobenthos de la reserve naturelle de Scandola (Corse, Meditérranée nord-occidentale). Analyse pluriannuelle de l'effet reserve, 1992, pp. 15–20.
- [100] M. Vacchi, S. Bussotti, P. Guidetti, and G. La Mesa, *Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea)*, Italian Journal of Zoology 65 (1998), pp. 281–286.
- [101] R. Chemello, Studio della malacofauna costiera dell'isola di Ustica (Gastropoda), Lavori SIM 1 (1986), pp. 51–76.
- [102] F. Badalamenti, G. Cantone, R. Domina, N. Di Pietro, D. Catalano, E. Mollica, and G. D'Anna, *Primi dati sulla fauna a policheti di substrato duro dell'infralitorale fotofilo superiore dell'Isola di Ustica*, Biologia Marina Mediterranea 6 (1999), pp. 230–236.
- [103] A. Villamor and M.A. Becerro, Species, trophic, and functional diversity in Marine Protected and non-Protected Areas, Journal of Sea Research 73 (2012), pp. 109–116.
- [104] S. Libralato, M. Coll, M. Tempesta, A. Santojanni, M. Spoto, I. Palomera, E. Arneri, and C. Solidoro, *Food-web traits of protected and exploited areas of the Adriatic Sea*, Biological Conservation 143 (2010), pp. 2182–2194.
- [105] D. Mouillot, J.M. Culioli, D. Pelletier, and J.A. Tomasini, *Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve*, Biological Conservation 141 (2008), pp. 1569–1580.
- [106] A.M. Duda and K. Sherman, A new imperative for improving management of large marine ecosystems, Ocean & Coastal Management 45 (2002), pp. 797–833.
- [107] P. Cury, L. Shannon, and Y.-J. Shin, *The functioning of marine ecosystems: A fisheries perspective*, Responsible Fisheries in the Marine Ecosystem (2003), pp. 103–123.
- [108] D. Pauly, V. Christensen, and C. Walters, *Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries*, ICES Journal of Marine Science: Journal du Conseil 57 (2000), pp. 697–706.

- [109] V. Christensen and C.J. Walters, Ecopath with Ecosim: Methods, capabilities and limitations, Ecological Modelling 172 (2004), pp. 109–139.
- [110] M. Coll and S. Libralato, Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea, Fish and Fisheries 13 (2012), pp. 60–88.
- [111] A. Valls, D. Gascuel, S. Guénette, and P. Francour, Modeling trophic interactions to assess the effects of a marine protected area: Case study in the NW Mediterranean Sea, Marine Ecology Progress Series 456 (2012), pp. 201–214.
- [112] C. Albouy, D. Mouillot, D. Rocklin, J. Culioli, and F. Le Loc'h, Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model, Marine Ecology Progress Series 412 (2010), pp. 207–221.
- [113] M. Coll, H.K. Lotze, and T.N. Romanuk, Structural degradation in Mediterranean Sea food webs: Testing ecological hypotheses using stochastic and mass-balance modelling, Ecosystems 11 (2008), pp. 939–960.
- [114] V. Christensen, Ecosystem maturity—towards quantification, Ecological Modelling 77 (1995), pp. 3–32.
- [115] V. Christensen, and D. Pauly, Changes in models of aquatic ecosystems approaching carrying capacity, Ecological Applications 8 (1998), pp. 104–109.
- [116] S.K. Hooker and L.R. Gerber, Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna, BioScience 54 (2004), pp. 27–39.
- [117] S.K. Hooker, A. Cañadas, K.D. Hyrenbach, C. Corrigan, J.J. Polovina, and R.R. Reeves, *Making protected area networks effective for marine top predators*, Endanger Species Research 13 (2011), pp. 203–218.

## Section 1. Field monitoring

This section aims at identifying appropriate tecniques to monitor high trophic level predators abundance and biomass in MPAs and evaluate their recovery relative to the whole fish assemblage.



Performing transect visual census. Images from Gianni F, Prato G, The book of Marine Protected Areas, MMMPA outreach video

# 3 Chapter 3. Reviewing fish underwater visual census methods in the Mediterranean Sea: setting a baseline for standardisation.

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#### 3.1 Abstract

Underwater visual census (UVC) is the only non-destructive technique to survey fish assemblages. Several UVC techniques exist and are used across the world in order to pursue different objectives. Choosing the most appropriate technique for a given research and management objective can thus be hampered by the wide range of choices, and inherent advantages and disadvantages of each method should be considered. Moreover, the large availability of methods, which often allow to measure different variables, arouses the need for standardisation in method application, especially if data are to be compared.

Here, we focused on the Mediterranean infralittoral (0-40 m) and aimed at setting a baseline for a standardisation of UVC method selection and application to pursue different research and coastal resource management objectives. We combined a semiquantitative review of the papers adopting UVC techniques in Mediterranean coastal areas, with a field method comparison of different UVC techniques. Based on the variable needed to pursue a specific objective, we evaluated the suitability of each method to measure such variable, as well as its costs and benefits. Finally, we assessed the level of standardisation in the Mediterranean for the most common UVC method adopted to date. Results show that strip transects are the most commonly adopted technique to survey fish communities in the Mediterranean, providing the most complete quantitative description of the fish assemblage at the lower economic and time costs. Standardization in transect surface has not yet been achieved across the Mediterranean, since more than 50% of the studies targeting similar species use different transect dimensions. Other methods, such as video-UVC can be complementary to transects (i.e. to survey fish at depths exceeding diving limits or to study fish behaviour). A synthetic table is provided to guide choice of the most appropriate method depending on the needed variable.

#### 3.2 Introduction

It is a widely accepted notion that monitoring marine ecosystems is a general requirement, preparatory to design sound measures aimed at ensuring conservation and management of biodiversity. Fish communities, as an intrinsic component of marine biodiversity, have been severely impacted worldwide via overfishing and habitat destruction, often leading not only to negative commercial consequences (i.e. overexploited fish stocks) (Pauly et al. 1998, Watson & Pauly 2001), but also to ecosystem-wide degradation through the disruption of trophic interactions (Pace et al. 1999, Pinnegar et al. 2000, Jackson et al. 2001) and loss of ecosystem services fishes may ensure (Holmund & Hammer 1999, Worm et al. 2006).

Preserving fish communities is thus crucial in order to conserve biodiversity, ecosystem functions and ecosystem services (Holmund & Hammer 1999; Jackson et al. 2001). In this perspective, field observations can provide a solid scientific knowledge through which the sustainable use of marine resources can be devised (Carstensen 2014).

Underwater visual census performed by divers (hereinafter UVC) was introduced in 1954 (Brock et al 1954) to guantitatively assess fish communities in coral reefs. UVC was proposed as a non-destructive alternative to extractive monitoring techniques. Since its first introduction, a variety of in situ UVC techniques have been used to study tropical and temperate fish assemblages, including the first video methods already in 1965 (Steinberg et al 1965). The variety in census techniques (Thresher & Gunn, 1986) triggered the development of studies dealing with methods' cost-effectiveness and biases (Bannerot & Bohnsack 1986, Sale & Sharp 1983). In more recent years two global reviews described existing UVC methods, the first one providing a broad picture of existing destructive and visual census methods to monitor fish and associated habitats (Murphy et al. 2010) and the second documenting in detail existing video techniques and their possible applications (Mallet et al. 2014). The large availability of methods, each one with its inherent advantages and disadvantages, arouses the need for standardisation in method application, especially if data are to be compared. Such need was already highlighted in 1986 (Thresher & Gunn, 1986), and the development of standardised monitoring protocols for marine biodiversity in response to specific research and coastal resource management objectives, has been achieved in some areas of the world, such as for some Large Marine Ecosystem (LME) (Sherman & Duda 2002, PISCO 2010). Being areas characterized by distinct bathymetry, hydrography, productivity, and trophically

dependent populations (Sherman & Hempel 2009), LMEs represent units from a management perspective, and shall thus benefit from standardised monitoring programs. In this perspective, coastal resource management in the Mediterranean LME (Sherman & Hempel. 2009), does not yet benefit from standardised monitoring protocols for biodiversity, which would allow for data comparisons on a regional scale. Visual census was introduced in this basin twenty one years after its first appearance. Mediterranean marine communities had been facing centuries of over-exploitation (Guidetti & Micheli 2011), and coastal development along with habitat loss were rapidly intensifying (Airoldi & Beck 2007) arousing the urgency for monitoring. Harmelin-Vivien & Harmelin (1975) first proposed a UVC protocol aimed at inventorying the fish assemblage at an MPA (Port Cros National Park), in an easy, objective and non-destructive way. Since this first publication (Harmelin-Vivien & Harmelin, 1975) and after the review on available UVC practices (among which transects, stationary point counts, random paths, etc.) provided by Harmelin Vivien et al. (1985) UVC techniques have been regularly used across the Mediterranean (Sala & Ballesteros, 1997, Garcia-Charton et al. 2004, Guidetti et al. 2008, Harmelin Vivien et al. 2008, Sala et al. 2012, La Mesa et al. 2013; Guidetti et al., 2014) and have been adapted to pursue different research and management objectives. in different habitats. Like in other temperate and tropical regions, the advent of several underwater video technologies especially in the last 15 years, with Remotely Operated Videos (Andaloro et al. 2013), Baited Underwater Videos (Condal et al. 2012) and Diver Operated Video (Tessier et al. 2013) (see Appendix for definitions), further diversified UVC methods. But different UVC techniques, employing or not videos, often allow for different variables to be measured, and such diversification was not accompanied by a standardization in method selection and application across the Mediterranean LME. In this scenario, our paper focuses on the Mediterranean infralittoral (0-40 m) and aims at

setting the baseline for a standardisation in UVC method selection and application to pursue different research and coastal resource management objectives (e.g. within MPAs).

To achieve such goal, we reviewed semi-quantitatively papers adopting UVC techniques in Mediterranean coastal areas since its first advent, following some key steps:

1) identifying the variables needed to pursue specific objectives

2) analysing the pertinence and the cost-benefits of the methods available to measure such variables

3) assessing the level of standardisation in the Mediterranean for the most common UVC method adopted to date

We further integrated our review by comparing data collected in the field through traditional UVC (transects performed by diving operators) with more recent video techniques (Diver Operated Video and a Remote Rotating Video System), that have already been used in coral reefs (Pelletier et al. 2011, 2012) but are still little applied in the Mediterranean. In particular, to our knowledge this is the first paper in the Mediterranean testing a Remote Rotating Video System to survey the fish community.

#### 3.3 Methods

#### 3.3.1 Bibliographic review

We carried out a bibliographic search in ISI Web of Knowledge on all databases, using the key words "(visual census OR recensement visuel\* OR censiment\* visiv\* OR censo\* visual\*) AND Mediterran\*)", considering the years from 1975 to august 2014. Since ISI Web of knowledge did not find papers older than 1990, we completed the search going through the bibliography of the available papers and pursuing them with google scholar. Overall 256 references resulted from our search. Among these we excluded studies that used only extractive methods (experimental fishing), studies from non-Mediterranean zones and studies not focusing on fish. Finally 179 papers were retained.

The papers were classified according to publication journal, year of publication (using five years categories), country where the study was performed, research topic, considered species or group of species, methods applied, measured variables and habitat. Surface units and time measures of the applied method, when provided, were also noted for further analyses on standardisation across the Mediterranean.

Research topics were divided in the following categories: artificial structures (whenever a paper included artificial reefs, gas platforms, breakwaters, fish farms or FADs), behaviour (only papers including quantitative or semi-quantitative data), human impacts (pollution, tourism impact, fishing impact), methodological studies (methods comparisons or methods evaluations), population dynamics, recruitment and settlement, reserve effect (including papers assessing changes in the living components within a marine protected area when one or several human impacts are excluded, as well as papers dealing with the assessment of the spillover effect to adjacent areas), fish assemblage characterization/spatio-temporal distribution and species occurrence.

Concerning the methods used, the considered categories were: transects, transects coupled with other methods (transect +), circular point counts, video + (all papers dealing with a video method involved comparison with at least one other technique, thus the category was video techniques coupled to other methods), total counts, random counts, spatial census, rapid visual census, and others. A short description for each method is provided in the Annex.

Results of published papers dealing with methods comparisons were also briefly summarised.

#### 3.3.2 Field methods comparison

For comparison in the field we selected the most common UVC method adopted in the Mediterranean according to our previous analysis (strip transects performed by divers) and two video methodologies: diver operated video transects (Tessier et al. 2013) and Staviro (Pelletier et al 2012, Bouchoucha et al. 2013a, 2013b), a remote high-definition un-baited rotating video system (see Appendix for system description).

The three census methods were tested in Bay of Villefranche (SE France) in May 2013. All methods were applied in the same area, between 5 and 15 meters depth, on a predominantly rocky substrate interspersed with *Posidonia oceanica* patches (rocky coverage  $\geq$  70 %). Multiple operators performed UVC within the same temporal window. When multiple census have been done, a minimum distance (> 25 m) was kept among operators in order to reasonably reduce the risk of reciprocal disturbance and spatial dependence of data.

Among 3 close days of similar good weather and visibility conditions we carried out 18 strip transects (Harmelin-Vivien & Harmelin 1975) of 25 meter length and 5 meter width, 21 video transects 25 meter long, and 27 Staviro deployments at randomly selected sites over the study area. Strip transects were carried out by two expert operators swimming at constant speed (approx. 8-10 min/25 m) and close distance from the sea floor.

Concerning video transects, the same operator swam at a constant speed (approx. 3 min/25 m) at 1.5 m from the bottom, keeping the video camera steady, horizontal and toward the end of the transect, thus recording in front of himself (Tessier et al. 2013).

The Staviro system was set on the sea floor and programmed so that the camera housing rotated from 60° every 30 seconds, at a fixed angle. Hence, six observation sectors were recorded per 360° rotation, each rotation lasting approximately 3 minutes. The system was left in place for 12 minutes, in order to complete three whole rotations (making one replicate) and account for one minute before and after each triplet, in order

to minimise disturbances due to boat presence, engine noise and setting and retrieval of the system. Further technical details on the Staviro system can be found in (Pelletier et al. 2012, Bouchoucha et al. 2013).

For the three methods, fish were recognized to the lowest taxonomic level possible. For isolated fish and small groups (<10 individuals) the actual number of fish was counted, while schools of fish (> 10 individuals) were recorded as follow: in strip transects Harmelin-Vivien (1985) categories of abundance were used (i.e. 11–30,31–50, 51–200, 201–500, >500 ind.) and the mid point of each category was retained, while in both video methods freeze frames were used and the maximum number of individuals among freeze frames for the same school was retained. During Staviro video analysis, individuals were counted per sector, and then summed up for each 360 rotation. For each species and each sampling unit, the maximum abundance observed over the three rotations was retained.

Since we could not measure surface area in video methods, direct comparison of density data was not possible. Multivariate analyses were thus performed on the fish assemblage with presence-absence data. Methods could not equally identify all fish seen to the species level, thus analysis were carried out at different levels of taxonomical scale-up (species, genus and functional group), in order not to lose possibly relevant information. For each level of aggregation, data were analysed for differences among methods through a multivariate PERMANOVA (Anderson 2001) with one fixed factor "method" (fixed factor, 3 levels) and based on Jaccard distance measure. We used Montecarlo permutations whenever number of possible permutations was low, <500. A Permdisp analysis was carried out to assess differences in data dispersion among methods. Results were graphically represented with an unconstrained principal coordinate analysis (PCO) and vectors of presence-absence variables were superposed to the ordination through Spearman correlation to identify the taxonomic groups principally responsible for differences between methods. Species accumulation plots allowed discriminating which method captured the most complete image of the fish assemblage with the least time cost (where time cost = field time + analysis time). The PRIMER 6 and PERMANOVA + package (Plymouth Marine Laboratory) was used to perform the analyses.

#### 3.3.3 Integration of bibliographic and field work

Bibliographic and field work were integrated in a final table in order to provide a synthesis of indications to guide the choice of the most suitable method for each variable that was analysed in the reviewed papers. A compendium of factors was integrated in the table: as

a proxy for method appropriateness we referred to the number of published papers using the specific method to assess the variable in question, plus field and lab time requirements, training and costs. We coded semi-guantitative variables to highlight the level of appropriateness of each method according to the previous factors. Thus, in order to code the factor "number of papers using the specific method to assess a given variable", we assigned the following 3 categories: maximum number of papers, minimum number of papers, number of papers within the two extremes. Additionally, to treat the "zero" case (when zero papers used a method to measure a given variables), we further defined three categories based on expert judgement: "0" was assigned when no paper in the literature had applied the method for the given variable, although it would have been feasible. "Feasible"(F) was assigned when the given variable could be assessed by the method, but with some limitations (i.e. density could be estimated by fixed video methods by setting two fixed land marks at a known distance and angle from the camera, and calculating the arrival time of each fish species) (Stobart et al. 2005). "NA" was assigned when the method does not allow for the computation of the variable. The factors time, training and equipment costs were classified each in three categories based respectively on expert knowledge and a survey. Time included field and lab work per sample: < 15 minutes (1), between 15 and 30 minutes (2) and between 30 minutes and 2 hours (3). Training was classified by listing all the skills needed to carry out a fish visual census with each method, i.e.: diving, underwater fish identification, fish counting, fish size estimation, sampling surface estimation, video-equipment handling and video analysis. For each method we summed the number of skills needed, and coded three categories with the following criteria: maximum number of skills (3), minimum number of skills (1), number of skills within the two extremes (2). To quantify equipment costs we provided rough price estimates for each method, including selling price and material amortization, and classified them from 1 (lowest costs) to 3 (highest costs). We did not include an estimate of costs for boat rental, assuming each method would need a boat to reach the sampling spot. We then filled the table cells with colours grading from bright green (max number of papers, least sampling time, least training and least equipment costs) to light grey (0 papers) and to dark grey (NA).

## 3.4 Results

#### 3.4.1 Bibliographic review

Most studies were carried out in Italy (84 papers), followed by Spain (37 papers) and France (30 papers). Fewer studies came from the eastern Mediterranean, with Greece (4 papers), Turkey (3 papers), and scattered papers from Croatia, Slovenia, Israel and Lebanon. Only 8 studies interested more than one country.

Published studies adopting UVC methods dramatically increased after 1994. Maximum number of published papers was reached in the last 5 years. From 1995, research objectives and applied visual census methods became more diversified (Fig. 1).



Fig. 1 Evolution in time in the number of papers, research topics and methods applied, resulting from the literature research in Isi Web of Knowledge "(visual census OR recensement visuel\* OR censiment\* visiv\* OR censo\* visual\*) AND Mediterranean", plus authors archives.

According to our review the most common research objective addressed through UVC (26% of published papers) was the spatial and/or temporal characterization of the fish assemblage (either the whole assemblage or a subset of species), followed by reserve effect (22%) and artificial structures (20%). Less addressed issues were methodological assessments (10%) and the study of fish recruitment and settlement (8%) (Tab. 1).

Tab. 1 Total number of papers measuring each variables (rows) within each research objective (columns). Numbers in parenthesis indicate the percentage of papers addressing each research topic (head line) or measuring each variable (head column). Scores along columns are assigned a gradation of colours from bright green (best score) to grey (worst score).

		Spatio-temporal distribution, characterization	Reserve effect	Artificial structure	Method	Recruitment settlement	Human impact	Population dynamics	Species occurrence	Behaviour
		(26 %)	(22 %)	(20 %)	(9 %)	(8 %)	(4 %)	(3 %)	(2 %)	(3 %)
Density	(77 %)	42	33	23	11	13	5	2	1	4
Size / Biomass	(50 %)	16	30	16	9	9	1	4	0	3
Sp. richness, Community metrics	(49 %)	33	19	17	11	1	3	0	1	0
Abundance, pres/abs	(19 %)	4	6	13	4	3	1	1	1	1
Functional categories	(15 %)	8	5	6	6	0	1	0	0	0
Frequency of occurrence	(11 %)	3	3	9	1	1	1	0	0	1
Semi-quant. behaviour obs.	(8 %)	2	2	2	3	2	1	1	0	1
N, Max N, Spp/ minute	(2 %)	0	0	0	1	0	3	0	0	0

Table 1 summarizes the main variables measured by the reviewed papers according to the research objective. For each objective, density was the most commonly measured variable (77% of the papers), followed by size (50 % of the papers), retained in particular by reserve effect studies, and species richness/community metrics (49% of the papers). This last variable was the most used (11 papers) in methodological evaluation studies. Most of the reviewed papers used transects (64%), either alone (87 papers), either complemented by other methods (e.g. experimental fishing - 10 papers, random or total counts - 6 papers, and others (see Appendix for method description) (27 papers) (Fig.2). Stationary point counts were the second most used method, but were large behind transects in terms of papers adopting them (11), followed by total counts and video methods (10 papers) (Fig.2).



Fig.2 Number of papers adopting each method. See the Annex for description of each method. Transect + and video + stand for transect and videos coupled with other techniques (e.g. experimental fishing, random paths, FAST, etc.). "Other" includes methods used only by one or two papers, such as quadrats or mobile point counts.

### Methodological comparisons in the literature

Methodological comparisons among UVC techniques in the Mediterranean were not common (8 papers), but showed an increasing trend in the latest years, with the advent of improved video techniques.

The 1975 study by Harmelin-Vivien & Harmelin set the basis for the expansion of quantitative UVC techniques in the Mediterranean. Harmelin-Vivien & Harmelin introduced strip transects of 5 meter width and fish counting through 5 abundance classes and 4 size classes. Codified procedures for behaviour annotation were also proposed. Ten years later, the same authors published a review on UVC (Harmelin-Vivien et al., 1985), presenting the methods adopted in temperate and tropical regions until then, and analysing the criticalities and biases of each (random walks, transects, quadrats and fixed points). According to this review, random paths were more efficient than transects and fixed points to describe species richness, but they did not allow to estimate fish abundance nor biomass. Fixed points were suggested mainly to study fish around isolated structures or in heterogeneous/patchy habitats. Transects, instead, were considered more appropriate for homogenous habitats and to study the whole fish assemblage, keeping in mind that transect width should be adapted to the mobility of the species, to visibility conditions and to the habitat type. UVC limits due to scuba diving, such as depth, time and noise influence on fish, were also discussed.

In 1997, Francour compared transects, stationary point counts and total counts (meaning counts of all the individuals inhabiting a given area, see Appendix) to assess the density of a subset of species in a *Posidonia oceanica* meadow at the Port Cros national park. Density estimates obtained with the different methods were compared for selected species, differing for mobility and behaviour. For each species, small size class fishes (total length < 1/3 maximum total length) were recorded mostly by transects and circular points, and medium and large size class fishes by circular points or total count. Differences among methods were dependent on the season of sampling and from species behaviour: schooling fish were better detected by fixed points, and very mobile species were mainly recorded through transects.

The paper by D'Anna et al. (1999) showed the logic applied to select the most appropriate UVC technique to assess fish biomass and assemblage structure in both natural and artificial habitats: substrates were first classified and then appropriate techniques were chosen accordingly. Horizontal transects were applied to *P. oceanica* meadows and homogenous sandy bottoms, while vertical transects were used for vertical cliffs. Point counts were preferred to survey scattered *P. oceanica* patches on the sandy bottom and for mixed substrates of sand and stones. Finally, spatial census (a mixed technique including point counts and circular transects) was chosen to assess the fish assemblage around artificial structures (artificial reef and FAD). The study stressed the importance of choosing coherent units of measures for comparative studies, concluding that density related to volumes (m<sup>3</sup>) resulted more appropriate than density related to surfaces (m<sup>2</sup>) for assessments of fish assemblages around artificial structures.

The paper by De Girolamo & Mazzoldi (2001) was the first one to attempt a methodological assessment of some biases in UVC transect on rocky habitats. Main results from the study were that i) separate survey methods adapted to different fish behaviour (a higher speed transect for epi-benthic species followed by a lower speed survey for benthic fish) although more time consuming, provided more realistic fish counts by better detecting cryptic fish. And ii) continuous size estimates were more advantageous than size classes estimates, yielding the best biomass assessments.

The only statistical comparison conducted in the Mediterranean between strip transects (25x5 m, 8 min/transect) and stationary point counts (radius = 5m, 8 min/point count) came by Guidetti et al. 2005. Results showed that, once results from both methods were adjusted for surface area, strip transects yielded higher number of fish taxa and fish densities, both with and without including gregarious species. The authors thus confirmed

what suggested by Harmelin-Vivien et al. (1985) that strip transects should be preferred when working on homogenous habitats.

The following methodological assessments were mainly comparisons between video techniques and underwater visual census.

Baited Underwater Video (BUV) was adopted only once in the Mediterranean shallow habitats by Stobart et al. 2007 in order to assess its performance in estimating fish abundance and diversity on rocky reefs. The studied variables were species richness, maximum number of species at the bait and maximum % presence of species at different sampling sites. BUV resulted to be an effective tool when estimation of species richness is the prime objective, while UVC using 25x5 m transects was more suitable to estimate fish abundance and size at sites not constrained by diving limits, especially given the higher time costs of BUV.

In Tessier et al. 2013 the effectiveness of Diver operated underwater video (DOV) along transects was compared to transects UVC to assess reserve effect. Results showed that DOV was able to detect significant but weaker effects of protection than UVC on abundance and species richness of the fish assemblage. According to the authors, when reserve effect is weaker, DOV might fail to detect it due to some limitations of videos such lower camera field of view compared to human eye and lower species identification chance linked both to image quality and to the avoidance behaviour of shy species. In fact, when fleeing away or keeping a large distance from the operator, shy species are more difficult, if not impossible, to identify through image analysis. On the other hand DOV allowed to archive and thus further analyse data without spending extra time underwater, for example quantifying fish aggregations, a potentially useful parameter to assess reserve effect, or classifying substrate types and quantifying their percentage cover.

The study by Andaloro et al. (2013a) compared ROV with mobile point counts UVC (see Appendix for description) to describe the fish assemblage around gas platforms. Estimates of abundance, species richness and frequency of occurrence were compared, and fish were categorized in ecological categories on the basis of their spatial organisation in the water column. ROV overall failed to give a truthful representation of the fish assemblage being more limited in the detection of crypto-benthic and necto-benthic fish, thus providing lower species richness and abundances estimates than UVC. ROV proved nevertheless to be useful in detecting low mobile and abundant planktonivorous species and was thus suggested to be used in complementarity to UVC, especially at depths and sampling times not affordable to the latter.

An interesting contribution by Bulleri & Benedetti-Cecchi (2014) investigated the potential of spearfishermen videos to assess the structure of fish assemblages. Videos from the sit-and-wait fishing technique were compared with transect UVC. The measured parameter was the maximum number of species seen at any one time over the whole duration of one video. Density estimates were derived by accounting for maximum visibility. Although fish assemblage composition differed, spearfishing videos and transects provided comparable estimates of species richness. Videos in particular were able to detect relatively uncommon and shy species like *Dentex dentex* and *Sparus aurata*, but they underestimated sedentary species. The authors stressed how the large availability of fishing videos all over the Mediterranean would make them an invaluable source of information on fish assemblages on shallow rocky reefs.

## 3.4.2 Field methods comparison

Overall 39 fish taxa were identified by the three methods, most of which were detected by strip transects (32 detected in total, 7 uniquely detected by transect), followed by Staviro (26 total, 3 unique) and video transects (10 total, 1 unique) (Tab.2)

Таха	Method
Boops boops	S
Mugilidae	S
Sciaena umbra	S
Blenniidae	Т
Epinephelus marginatus	Т
Labrus viridis	Т
Scorpaena porcus	Т
Scorpaena scrofa	Т
Spondyliosoma canthaurus	Т
Thalassoma pavo	Т
Oblada melanura	V
Labrus merula	S,T
Mullus surmuletus	S,T
Muraena helena	S,T
Serranus cabrilla	S <i>,</i> T
Serranus scriba	S,T
Sparus aurata	S,T
Symphodus cinereus	S,T
Symphodus doderleinii	S <i>,</i> T
Symphodus mediterraneus	S <i>,</i> T
Symphodus melanocercus	S <i>,</i> T
Symphodus ocellatus	S,T
Symphodus roissali	S,T
Tripterygiidae	S,T
Chromis chromis	S,T,V
Coris julis	S,T,V
Diplodus annularis	S,T,V
Diplodus puntazzo	S,T,V
Diplodus sargus	S,T,V
Diplodus vulgaris	S,T,V
Sarpa salpa	S,T,V
Serranus spp.	S,T,V
Spicara spp.	S,T,V
Symphodus rostratus	S,T,V
Symphodus spp.	S,T,V
Symphodus tinca	S,T,V

Tab. 2 Species unique to each method and combination of methods. T= transects, S= Staviro, V= video transects

Permanova analysis on presence/absence of each taxon identified to lowest level possible (Blennidae, Trypterigidae, *Spicara* spp. and Mugilidae were never identified at species level), showed significant differences among the three methods and among each pair of methods (P<0.001) (post-hoc pair-wise tests). Difference among the three methods was best described by the first axis of the PCO (30%), although a large percentage of variability remained unexplained (Fig. 3a). Here, strip transect data displayed the least dispersion among samples, as opposed to the more scattered video transect data, as confirmed from the Permdisp analysis (P < 0.017, with pairwise tests showing significant differences between transects v Staviro and transects v video transects, but not between staviro v video transect). Only vectors of variables with correlations > 0.5 as well as vectors for gregarious species were visualised. Transect and Staviro were positively correlated to the first axis of the PCO and were the methods capturing most of the fish species (Fig. 3a). Schooling fish like *Boops boops* showed a slight correlation trend with video methods.



Fig.3 PCO at the species (a), genus (b), and functional group aggregation level (c)

When aggregating presence-absence by genus, differences among methods were still significant (PERMANOVA, P<0.001) although they were less evident in the PCO representation, where Staviro was slightly overlapping both with video transects and strip transects. Here, *Sarpa, Serranus, Apogon, Mullus* and *Diplodus* were more related to transects, *Boops* was again slightly more related to video methods (Fig. 3b).

When aggregating presence-absence by functional group, PERMANOVA highlighted significant differences among methods (P<0.005) and pairwise tests showed significant differences between strip transects and Staviro, as well between strip transects and video transects (Pmc < 0.005 and Pmc <0.007 respectively), while no significant differences were detected between Staviro and video transects. Samples where less discriminated by the PCO at this level of functional aggregation of the variables, and differences among methods, in particular among transects and video transect, were better visible along the vertical axis. Carnivorous crypto-benthic and necto-benthic fish were more related to transects, while planktonivorous schooling fish characterised video methods (Fig. 3c).

Species accumulation plots showed that at the achieved level of replication none of the three methods alone could record all the species detected by the sum of the three methods and that at an equal effort in terms of sampling and analysis time, strip transects detected a much higher proportion of species than the video methods. Moreover, even increasing sampling and analysis time, the two video methods won't reach transects in terms of number of species recorded (Fig. 4). In terms of functional groups, transects and Staviro could detect most of them (5/6), contrary to video transects (3/6). Only strip transects recorded higher trophic level predators (*E. marginatus*), while only Staviro detected schooling detritivors (mugilidae) (Tab 2).



Fig. 4 Species accumulation plots. Cumulated time includes field and analysis time for each method.

### 3.4.3 Integration of bibliographic and field work

Tab. 3 displays the classification of each method according to time needed per each replicate, training and equipment costs. UVC methods such as transects, point counts, rapid visual census and spatial census require the highest number of skills underwater (higher training), but are less time consuming and less expensive than video methods. UVC through random counts, total counts and fast are slightly more time consuming but require less skills underwater than the previous methods, not needing estimates of surface area or, in the case of random counts, size estimates (Tab. 3). Video methods require video equipment handling skills and video analysis skills (such as species identification a posteriori, which can be guided through books), but are more time consuming especially in terms of video-analysis time and, in average, more expensive (Tab.3)

	TRAINING									TIME		EQUIPMEN	EQUIPMENT		
	Diving	Underwater species identification	Underwater individual counts	Underwater fish size estimation	Underwater area estimation	Video equipment handling	Video analysis	Total	Training index	Time cost (min)	Time cost index	Equipment cost (€)	Equipment cost index		
Transect	1	1	1	1	1	0	0	5	3	< 15	1	1000-2000	1		
Stationary point counts	1	1	1	1	1	0	0	5	3	< 15	1	1000-2000	1		
Rapid Visual Census	1	1	1	1	1	0	0	5	3	< 15	1	1000-2000	1		
Spatial census	1	1	1	1	1	0	0	5	3	< 15	1	1000-2000	1		
Total counts	1	1	1	1	0	0	0	4	2	15-30	2	1000-2000	1		
Random counts	1	1	0	0	0	0	0	2	2	15-30	2	1000-2000	1		
Fast	1	1	0	1	0	0	0	3	2	15-30	2	1000-2000	1		
Video transect	1	0	0	0	0	1	1	3	2	30-120	3	3000-4000	2		
BUV	0	0	0	0	0	1	1	2	1	30-120	3	3000-4000	2		
Staviro	0	0	0	0	0	1	1	2	1	30-120	3	3000-4000	2		

Tab.3 Classification of methods according to training (based on the number of skills required), time (including field and digitisation time), and equipment costs. For each attribute, three categories were defined (see Methods section)

Results of the bibliographic review, field survey and costs analysis were integrated in Table 4. For each analysed variable (as density, biomass, species richness, etc), transects showed the highest score (highlighted in bright green) for most of the factors considered: largest number of papers adopting them, reduced time and costs of application. In particular, transects were adopted with large majority respect to other methods to measure density (96), biomass (59) and species richness and/or community metrics (54), given the relative ease of surface estimates. Concerning this last variable, our field comparison confirmed the higher efficiency of transects respect to remote high-definition rotating video systems and DOV. In fact, the same variables were measured with other methods in less than 10 papers for each method. On the other hand, to perform UVC by transects highly skilled and trained specialists working underwater are needed (Harmelin-Vivien et al., 1985). Stationary point counts (Harmelin-Vivien et al., 1985) followed transects, sharing similar time, training and equipment costs, but showing lower success in the literature (Fig. 2).

Rapid Visual Census (RVC) (Dempster et al. 2002) and spatial census (D'Anna et al. 1999b) are adaptations of fixed points and transects specifically designed for fish farms and artificial structures, sharing thus similar field time, costs and training needs of the two previous methods.

Total counts (Macpherson et al. 1997, Biagi et al. 1998) did allow for a range of variables to be measured, and require less strict training than previous methods, given that underwater surface area estimation is not generally required. However, they were less adopted in the literature, likely because these are not properly sampling techniques. Sampling implies the random selection of a subset of individuals from a statistical population, from which estimates can be derived. A relevant portion of statistical techniques (e.g. ANOVA, MANOVA, t-tests, etc) are based on sampling data. Standardization and comparison of data collected with this kind of approach is thus difficult.

Random paths (Harmelin-Vivien et al. 1985, La Mesa et al. 2010), have always been applied in concomitance to other methods, given the possibility to reach a wider spectrum of species. Assuming that the same detail of species identification is required in transects and point counts, random paths required less skills underwater (lower training), not needing any surface estimate, but consequently not allowing to derive variables related to surface.

Most video techniques adopted in the Mediterranean (video transects, Remote Operated Vehicles, Baited Underwater Video, Staviro, cabled observatories) did not allow to derive

surface related variables (density and biomass respectively derived from abundance and size measured in the field) and were mainly used to derive estimates of species richness and of total or relative abundance. This, together with the longer time required for video analysis and the generally higher costs, resulted in few papers adopting such techniques in visual census studies. Nevertheless, density and biomass estimates would be feasible if field of view is known and if stereo-videos are used, allowing to measure size of fish and observation distance. Training with fish silhouettes of known size at different distances prior to video analysis would also be a solution (Cheal & Thompson 1997, Francour 1999, Mallet et al. 2014). Other variables that have been measured or can be easily measured through video methods are species/minute, frequency of occurrence and behavioural observations. These are particularly suited to video methods due to the possibility of leaving instruments in the field for prolonged times (Mallet et al. 2014) (Tab. 4). Among video methods, a remote high-definition rotating video system like Staviro is more successful than diver operated videos in detecting the species composition of the fish assemblage, as shown from our field observation. This, together with the need for a diver in DOV, reduces the advantage of such method respect both to traditional transects or point counts (higher time and equipment costs, less variables to be possibly derived), and to remotely operated video methods. For remotely operated videos, training requirements are lower than traditional UVC (Tab. 3) and scuba diving time and depth limits can be overcome. Data archiving moreover allows for further data analysis and double-checks from different observers.

Two citizen science methods are also proposed in the table: fish census through spearfishermen videos has been used to assess density, species richness and species/minute, and has the advantage of having extremely low costs (no diving involved, large availability of videos on youtube) and allowing large-scale geographical assessments. The Fish Assemblage Sampling Technique (FAST) is a random walk used to quantify few variables (presence/absence, frequency of occurrence and size) for a reduced set of easy-to recognize target species (Seytre & Francour 2008, 2009). This method allows for computation of several indices useful to monitor the healthiness of fish assemblages, and its relatively low cost and training needed make it a good candidate method for citizen science.

Table 4 Total number of papers using a given method to measuring a given variable. Numbers in parenthesis are the total number of papers found in the literature for each method. BUV = baited underwater video, ROV = remote operated vehicle. Scores are assigned a gradation of colours from bright green (best score) to dark grey (worst score). 0 = feasible/appropriate but not applied in the available literature (light grey). F= feasible with conditions (medium grey) NA not feasible (dark grey)

			VARIA	BLES		COSTS					
	Density	Size Biomass	Abundance pres/abs	S/Comm. metrics	N,Spp/min	Freq. of occurrence	Semi- quant. Behav.	TIME	TRAINING	EQUIPMENT	COMMENTS
Transect (112)	10 0	62	13	57	1	7	9	1	3	1	Best in homogeneous habitats (Harmelin Vivien 1985)
Stationary point count (12)	11	4	1	8	0	2	1	1	3	1	Best in heterogeneous habitats (Harmelin Vivien 1985)
Rapid Visual Census (5)	5	5	4	3	NA	0	NA	1	3	1	Specific for fish farms (Dempster et al. 2002)
Spatial census (8)	4	3	6	3	0	6	1	1	3	1	Specific for artificial reefs (D'Anna et al. 1999)
Total counts (10)	4	6	3	2	0	1	1	2	2	1	
Random counts (5)	N A	0	3	3	0	1	0	2	2	1	Always combined with other method
Video transect (2)	N A	F	2	1	0	0	0	3	2	2	Data archiving, allows to quantify fish aggregations (Tessier et al. 2013)
FAST (2)	N A	2	NA	NA	0	2	NA	2	2	1	
BUV (1)	F	1	0	1	1	0	0	3	1	3	Data archiving, no depth limit (Stobart et al. 2007)
ROV (1)	N A	F	1	1	0	1	0	3	1	3	Data archiving, no depth limit (Andaloro et al. 2013)
Cabled observatory (2)	F	F	2	1	0	1	0	3	1	3	Data archiving ,Continuous deployment, no depth limit (Condal et al. 2012)
Spearfishing video (1)	1	NA	0	1	1	0	NA	1	1	1	Citizen science, free and large samples availability (Bulleri et al. 2014)
Staviro (this paper)	F	F	0	1	1	1	0	3	1	3	Data archiving, no depth limit (Pelletier et al. 2012)

#### 3.4.4 Transects standardisation across the Mediterranean

Since strip transects are the most commonly adopted method according to our review, we assessed if standard measures were adopted across the Mediterranean, and if not, which measures had been mostly applied. Moreover we assessed how often and in which way transect counts had been modified to account for the different mobility and behaviour of fish. Eighty-six out of the 116 papers focusing on the whole fish assemblage used transects, and 22% of these used transects of 25x5 meters, 19% of 50x5 m and 6% of 20x2 m. The remaining 53% used a variety of measures, ranging mostly from 2 to 6 meters width and from 10 to 200 meters length. Similarly, 33% of the studies focusing on just one or few necto-benthic species used 25x5 meter transects. Among the 9 papers focusing on recruits and juveniles through transects, different measures were used (25x2 m, 10x2 m, 20x1 m, 2x1 m and 1x1m). Similarly also 66% of the studies focusing on high trophic level predators used transects of different widths such as 50 x 15 m, 50 x 5 m, 100 x 10 m. Finally transects to assess crypto-benthic fish (6 studies over 7) measured 30x1, 50x1,50x2.5 and 25x 5 m.

Among the 86 studies adopting transects to assess the whole fish assemblage, only 13 modified the method to assess different parts of the fish assemblage. Nine papers used separate swims on the same transect, either swimming at different speeds, through a second observer, or on the swim back to record more sedentary and cryptic fish. Only 2 papers modified transect widths, using narrower transects to assess crypto-benthic fish.

#### 3.5 Discussion

Focusing on the Mediterranean our study has highlighted some main conclusions concerning the use of fish UVC methods in this basin up to date: 1) density is the most commonly measured variable, allowing to address several research objectives, followed by biomass and species richness; 2) diver – UVC through transects is up to date the most regularly used method, allowing to effectively measure the widest range of possible quantitative and qualitative variables; 3) standardization of transect dimensions in the Mediterranean has not yet been achieved, since more than 50% of the studies targeting the whole fish assemblage use different and varying transect dimensions. Standardization seems however to be an ongoing process, with 5 meters being the preferred width measure (47% of the studies).

Density is a key variable that allows for comparisons in time and space. If coupled with species richness, size distribution and biomass (which can be derived from size), a

comprehensive picture of the fish assemblage can be provided and its evolution consequent to management actions (i.e. fishery or protection) can be assessed. Size and, consequently, biomass, is necessary if the protection effect of conservation areas needs to be assessed (Lester & Halpern 2008, Di Franco et al. 2009, Sala et al. 2012, Guidetti et al. 2014) and if energy flows in food-webs is to be quantitatively described (MSFD, Christensen & Pauly 1993,2004, Prato et al 2014). Information on size for key species in protected areas can also be coupled to economic studies to evaluate the income resulting from the diving attraction caused by abundant and large-sized individuals (Bassu et al. 2007).

Comparisons of UVC techniques with experimental fishing (Harmelin-Vivien & Francour 1992, Andaloro et al. 2011) often led to the common result that both methods differ in their ability to detect species with different mobility or behaviour and thus if used alone lead to a different and incomplete description of the fish community. Similar conclusions derived from comparisons of traditional UVC methods and video methods, as highlighted both from the literature review and from our field observations. To date, transects are the census method that allow for the more accurate and complete estimates of density, biomass and species richness, with least costs, and thus gained the most success in Mediterranean research.

Stationary circular points also allow for computation of such variables, but comparisons among the these and transects showed that, once adjusted for surface, stationary points reach lower density estimates (Guidetti et al. 2005). Moreover, when this method is used (for example in specific cases like isolated artificial structures), care should be given to perform instantaneous counts. Observations through fixed points sometimes lasted up to several minutes in the literature, and such practice was generally not accompanied by an adequate calculation of density, since during such lapse of time the diver is in fact observing a flux of fish entering and exiting the survey area, instead than a snapshot of the fish assemblage (Francour, 1999). Such risk is less evident during transects where the observer swims forward, instantaneously scanning the area immediately in front of himself.

Diver - UVC practices have been more successful than video methods, in Mediterranean even more than elsewhere (Cappo et al. 2003, Mallet et al. 2014). This tendency, although partially due to the more recent advent of video methods, has still not being inverted, for several reasons. A proper estimate of surface area (and thus density) and size of fish (and thus biomass) is more complicated and often not possible using video techniques. Video systems alone generally detect lower fish abundances and do not

allow to assess the whole fish community, failing to properly record crypto-benthic and necto-benthic fish, due to their inherent limitations (lower field of view, image quality, harder identification of shy species). Their technological costs and the long time needed to perform video analysis are an additional important limitation to their application. Their higher success in many areas of the world (Mallet et al. 2014), other than their more ancient introduction, is probably linked to the need of surveying fish communities in limiting oceanic conditions, like strong currents and/or presence of sharks, that might affect divers safety much more than in Mediterranean conditions.

Despite their limits nonetheless, video methods can be a useful complement to traditional UVC methods also in the Mediterranean. Fixed video methods for instance, if the surveyed area is known, they could allow to quantify highly abundant planktonivorous fish, characterized by lower mobility and tendency to aggregation (Andaloro et al. 2013b). Moreover they allow to monitor fish assemblages at depths exceeding diving limits, are well suited to study fish behaviours over long time intervals and to monitor the ecosystem on a long temporal scale through fixed observatories (Condal et al. 2012, Azzurro et al. 2013). In particular, as we observed in the field, remote rotating video systems like Staviro are promising complementary methods to UVC, since they provide a good description of the fish assemblage in terms of functional groups, while not requiring specialised staff on the field. Lastly, they give the possibility to collect several replicates thanks to the short time needed for each one (12 minutes).

Our analysis clearly showed that transects had the highest success in the Mediterranean, being the most effective technique to address a variety of objectives and variables with the least cost, but it also pointed out that their application for monitoring fish assemblages still needs improvement.

Firstly, more than 50% of the analysed studies that aimed at surveying the whole fish assemblage, differed among them for the adopted transect sizes. Different transect size can affect the efficiency of the method in detecting a given species, according to the species' behaviour and mobility (Cheal & Thompson 1997, Kulbicki 1998, Bozec at al. 2011). When different studies target the same species or group of species, standardisation in transect size is necessary, or else comparisons of density and biomass values could be biased. Secondly, if a study targets the whole fish assemblage, thus species with very different mobility (i. e large mobile fish, necto-benthic fish or crypto-benthic fish) different transect widths should be adopted for each mobility group. To date this has seldom been done in the Mediterranean, while it is a more common practice in coral (Sandin et al 2008). Overall, standardization of transect size should be

achieved if regional monitoring programs want to be developed for the Mediterranean, as in other Large Marine Ecosystems of the world (Pisco 2002).

If training is not available or cannot be provided, or if dive limits are concerned, alternatives to transects should be considered. The spread of more advanced technologies such as stereo-videos (Harvey & Shortis 1995) together with increased image quality and more achievable prices, will allow to increase the success of video methods also in our basin, as it is happening at a global scale (Mallet et al. 2014).

In structurally complex habitats moreover UVC is often not sufficient to survey cryptobenthic fish, and options of other methods should be considered, such as lure assisted transects (Kruschel & Shultz 2012) or sampling with anaesthetic (Kovacic et al 2012, Thiriet et al 2014). Finally, both if a single method is modified to account for fish behaviour, or if several methods are used complementarily to assess the whole fish community, issues such as the integration of data collected from different units of measure arise and shall be solved prior to field effort, in order to permit a full exploitation of the collected data

To conclude, in a management perspective, choice of the most suitable method is driven not only by accuracy, but also by its feasibility and effectiveness, including time, costs and training needed. The type of data needed and the use that will be made of it should be clearly stated in order to properly select the best method. Tab.5 provides a synthesis of our results and aims to facilitate the choice of the most appropriate method depending on the needed variable. Tab. 5 Synthetic scores for each method according to the variables to be measured and to their cost-efficiency. Scores are assigned a gradation of colours from bright green (best score) to dark grey (worst score). Asterisks :method aptness to measure the given variable, based on the number of papers adopting the method in the literature. \*low aptness, \*\*\* high aptness, F= feasible with conditions. NA= not feasible.

- Time : T= < 15 min, TT= >15,<30 min, TTT= 30 120 min
- Training : S = skills in video analysis and video equipment handling, SS = skills in in diving and species identification, SSS= skills in diving, species identification, enumeration of fish, estimation of fish size, estimation of sampling surface area).
- Costs: € = 1000-2000 € , €€= 3000-4000 €, €€€ = 4000-10000 €

		Transect	Circular fixed point	Total counts	Random counts	FAST	Video transect	Staviro	BUV	ROV	Cabled observatory	Spearfishing video
Variables/surface	Density, Size/Biomass	***	**	**	NA	NA	NA	NA	F	NA	F	*
Total variables	Abundance, pres/abs, Sp. richness and community metrics, Freq. of occurrence, Behaviour	***	**	**	**	NA	*	*	*	*	*	*
Variables/time	Tot N, Max N, Spp/min	*	*	*	*	*	*	*	*	*	*	*
	Time	т	Т	TT	TT	Т	TTT	TTT	TTT	TTT	TTT	TT
	Training	SSS	SSS	SS	SS	SS	SS	S	S	S	S	S
	Costs	€	€	€	€	€	€€	€€	€€	€€€	€€€	€

## 3.6 References

- Addis P, Cau A, Massuti E, Merella P, Sinopoli M, Andaloro F (2006) Spatial and temporal changes in the assemblage structure of fishes associated to fish aggregation devices in the Western Mediterranean. Aquat Living Resour 19:149–160
- Airoldi L, M W Beck (2007). Loss, status and trends for coastal marine habitats of Europe. Oceanography and Marine Biology 45:345–405.
- Andaloro F, Castriota L, Ferraro M, Romeo T, Sarà G, Consoli P (2011) Evaluating fish assemblages associated with gas platforms: evidence from a visual census technique and experimental fishing surveys. Cienc Mar 37:1–9
- Andaloro F, Ferraro M, Mostarda E, Romeo T, Consoli P (2013a) Assessing the suitability of a remotely operated vehicle (ROV) to study the fish community associated with offshore gas platforms in the Ionian Sea: a comparative analysis with underwater visual censuses (UVCs). Helgol Mar Res 67:241–250
- Andaloro F, Ferraro M, Mostarda E, Romeo T, Consoli P (2013b) Assessing the suitability of a remotely operated vehicle (ROV) to study the fish community associated with offshore gas platforms in the Ionian Sea: a comparative analysis with underwater visual censuses (UVCs). Helgol Mar Res 67:241–250
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. Can J Fish Aquat Sci 58:626–639
- Azzurro E, Aguzzi J, Maynou F, Chiesa JJ, Savini D (2013) Diel rhythms in shallow Mediterranean rocky-reef fishes: a chronobiological approach with the help of trained volunteers. J Mar Biol Assoc U K 93:461–470
- Bannerot SP, Bohnsack JA (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report NMFS 41:1–15
- Bassu V, Porcu C, Niccolini F (2007) Studio sul valore economico delle popolazioni di cernie nell' Area Marina Protetta di Tavolara Punta Coda Cavallo. Rapporto finale 2008, Intervento E1.
- Biagi F, Gambaccini S, Zazzetta M (1998) Settlement and recruitment in fishes: the role of coastal areas. Ital J Zool 65:269–274
- Boland GS, Lewbel GS (1986) Estimation of demersal fishdensities in biological surveys using underwater television systems. Oceans 2: 9–13
- Bombace G, Fabi G, Fiorentini L, Spagnolo A (1995) Assessment of the ichthyofauna of an artificial reefe through visual census and trammel net: comparison between the two sampling techiques
- Bouchoucha B, Pelletier D, Herves, G. H, Roman W, Mallet D (2013) Guide méthodologique simplifié pour la mise en oeuvre des STAVIRO et l'analyse des images.
- Bouchoucha M, Witkowski F, Mallet D, Roman W, Hervé G, Pelletier D (2013) Remote rotating video for fast spatial survey of coastal Mediterranean macrofauna and habitats.

- Bozec Y-M, Kulbicki M, Laloë F, Mou-Tham G, Gascuel D (2011) Factors affecting the detection distances of reef fish: implications for visual counts. Marine Biology 158:969–981
- Brock VE (1954). A preliminary report on a method of estimating reef fish popula-tion. J. Wildlife Manag. 18: 297–308.
- Bulleri F, Benedetti-Cecchi L (2014) Chasing fish and catching data: recreational spearfishing videos as a tool for assessing the structure of fish assemblages on shallow rocky reefs. Mar Ecol Prog Ser 506:255–265
- Cappo M, Harvey E, Malcolm H, Speare P, others (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. Aquat Prot Areas-What Works Best We Know:455–464
- Cardona L, Lopez D, Sales M, Caralt S De, Diez I (2007) Effects of recreational fishing on three fish species from the Posidonia oceanica meadows off Minorca (Balearic archipelago, western Mediterranean). Sci Mar 71:811–820
- Carstensen J (2014) Need for monitoring and maintaining sustainable marine ecosystem services. Frontiers in Marine Science 1:33
- Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. Mar Ecol Prog Ser 158:241–248
- Christensen V, Pauly D (1993) Trophic Models of Aquatic Ecosystems. The World Fish Center
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological modelling 172:109–139
- Clarke KR, Green RH (1988) Statistical design and analysis for a" biological effects" study. Mar Ecol Prog Ser 46:213–226
- Coll M, Piroddi C, Albouy C, Rais Lasram F Ben, Cheung WWL, Christensen V, Karpouzi VS, Guilhaumon F, Mouillot D, Paleczny M, others (2011) The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Glob Ecol Biogeogr 24:12
- Condal F, Aguzzi J, Sarda F, Nogueras M, Cadena J, Costa C, Rio J Del, Manuel A (2012) Seasonal rhythm in a Mediterranean coastal fish community as monitored by a cabled observatory. Mar Biol 159:2809–2817
- D'Anna G, Lipari Ro, Badalamenti F, Cuttitta A (1999a) Questions arising from the use of visual census in natural and artificial habitats. Fish Vis Census Mar Prot Areas II Nat Sicil 23:187–204
- D'Anna G, Lipari Ro, Badalamenti F, Cuttitta A (1999b) Questions arising from the use of visual census in natural and artificial habitats. Fish Vis Census Mar Prot Areas II Nat Sicil 23:187–204
- Dempster T, Sanchez-Jerez P, Bayle-Sempere JT, Giménez-Casalduero F, Valle C (2002) Attraction of wild fish to sea-cage fish farms in the south-western Mediterranean Sea: spatial and short-term temporal variability. Mar Ecol Prog Ser 242:237–252
- Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P (2009) Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. Mar Ecol Prog Ser 387:275–285
- Fedra K, Machan R (1979) A Self-Contained Underwater Time-Lapse Camera for in situ Long-Term Observations. Marine Biology 55: 239-246
- Francour P (1997) Fish assemblages of Posidonia oceanica beds at Port-Cros (France, NW Mediterranean): Assessment of composition and long-term fluctuations by visual census. Mar Ecol 18:157–173
- Francour P (1999a) A critical review of adult and juvenile fish sampling techniques in Posidonia oceanica seagrass beds. Nat Sicil 23:33–57
- Francour P (1999b) A critical review of adult and juvenile fish sampling techniques in Posidonia oceanica seagrass beds. Nat Sicil 23:33–57
- Giakoumi S, Kokkoris GD (2013) Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean sea. Mediterranean Marine Science 14:58–68
- De Girolamo M, Mazzoldi C (2001) The application of visual census on Mediterranean rocky habitats. Mar Environ Res 51:1–16
- Guidetti P, Baiata P, Ballesteros E, Di Franco A, Hereu B, Macpherson E, Micheli F, Pais A, Panzalis P, Rosenberg AA, Zabala M, Sala E (2014) Large-Scale Assessment of Mediterranean Marine Protected Areas Effects on Fish Assemblages. PLoS ONE 9:e91841
- Guidetti P, Micheli F (2011) Ancient art serving marine conservation. Frontiers in Ecology and the Environment 9:374–375
- Guidetti P, Verginella L, Viva C, Odorico R, Boero F (2005) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. J Mar Biol Assoc U K 85:247–255
- Harmelin-Vivien ML, Francour P (1992) Trawling or visual censuses? Methodological bias in the assessment of fish populations in seagrass beds. Mar Ecol 13:41–51
- Harmelin-Vivien M, Harmelin J (1975) Présentation d'une méthode d'évaluation in situ de la faune ichtyologique. Trav Sci Parc Nation Port-Cros 1:47–52
- Harmelin-Vivien M, Harmelin J, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. Rev Décologie 40:467–539
- Harvey E, Shortis M (1995) A system for stereo-video measurement of sub-tidal organisms. Mar Technol Soc J 29:10–22
- Holmlund CM, Hammer M (1999) Ecosystem services generated by fish populations. Ecological Economics, 29: 253–268
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA (2001) Historical overfishing and the recent collapse of coastal ecosystems. science 293:629–637
- Kingsford MJ, CN Battershil. (1998): Procedures for establishing a study. Studying temperate marine environments-A handbook for ecologists. Canterbury University Press, Christchurch 29-48.
- Kovačić M, Patzner RA, Schliewen U (2012) A first quantitative assessment of the ecology of cryptobenthic fishes in the Mediterranean Sea. Mar Biol 159:2731–2742

- Kruschel C, Schultz ST (2012) Use of a lure in visual census significantly improves probability of detecting wait-ambushing and fast cruising predatory fish. Fisheries Research 123–124:70–77
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. Journal of Experimental Marine Biology and Ecology 222:11–30
- La Mesa G, Molinari A, Tunesi L (2010) Coastal fish assemblage characterisation to support the zoning of a new Marine Protected Area in north-western Mediterranean. Ital J Zool 77:197–210
- La Mesa G, Guidetti P, Bussotti S, Cattaneo-Vietti R, Manganaro A, Molinari A, Russo GF, Spano N, Vetrano G, Tunesi L (2013) Rocky reef fish assemblages at six Mediterranean marine protected areas: broad-scale patterns in assemblage structure, species richness and composition. Italian Journal of Zoology 80:90–103
- Lester SE, Halpern BS (2008) Biological responses in marine no-take reserves versus partially protected areas. Marine Ecology Progress Series 367:49–56
- Macpherson E, Biagi F, Francour P, García-Rubies A, Harmelin J, Harmelin-Vivien J, Jouvenel J, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. Mar Ecol Prog Ser 160:135–147
- Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). Fish Res 154:44–62
- Mallet D, Wantiez L, Lemouellic S, Vigliola L, Pelletier D (2014) Complementarity of Rotating Video and Underwater Visual Census for Assessing Species Richness, Frequency and Density of Reef Fish on Coral Reef Slopes. PLoS ONE 9:e84344
- Moreno I (2006) Artificial reefs as a tool for coastal management in Balearic Islands (Western Mediterranean). J Coast Res:1843–1846
- Murphy HM, Jenkins GP (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Mar Freshw Res 61:236
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr F (1998) Fishing down marine food webs. Science 279:860–863
- Pelletier D, Leleu K, Mou-Tham G, Guillemot N, Chabanet P (2011) Comparison of visual census and high definition video transects for monitoring coral reef fish assemblages. Fisheries Research 107:84–93
- Pelletier D, Leleu K, Mallet D, Mou-Tham G, Hervé G, Boureau M, Guilpart N (2012) Remote High-Definition Rotating Video Enables Fast Spatial Survey of Marine Underwater Macrofauna and Habitats (SJ Goldstien, Ed.). PLoS ONE 7:e30536
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, Anna G d' (2000) Trophic cascades in benthic

marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200

- Pisco (2010) Monitoring MPAs by SCUBA in waters off Central California. Partnership for Interdisciplinary Studies of Coastal Oceans. <u>www.piscoweb.org</u>.
- Prato G, Gascuel D, Valls A, Francour P (2014) Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints. Mar Ecol Prog Ser 512:71–88
- Relini M, Torchia G, Relini G (1994) Seasonal variation of fish assemblages in the Loano artificial reef (Ligurian Sea Northwestern-Mediterranean). Bull Mar Sci 55:2–3
- Rilov G, Benayahu Y (2000) Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective. Mar Biol 136:931–942
- Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Güçlüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications. PLoS ONE 7:e32742
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37–42
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS One 3: e1458
- Seytre C, Francour P (2008) Is the Cape Roux marine protected area (Saint-Raphael, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. Aquat Living Resour 21:297–305
- Seytre C, Francour P (2009) The Cap Roux MPA (Saint-Raphael, French Mediterranean): changes in fish assemblages within four years of protection. ICES J Mar Sci 66:180–187
- Sherman K, Duda A (2002). Large marine ecosystem monitoring, assessment, and management across the global north-south divide. ICES Council Meeting Papers CM 2002/W:2
- Sherman K, Hempel G (Editors) 2009. The UNEP Large Marine Ecosystem Report: A perspective on changing conditions in LMEs of the world Regional Seas. UNEP Regional Seas Report and Studies No. 182. United Nations Environment Programme. Nairobi, Kenya.
- Steele JH, Schumacher M (2000) Ecosystem structure before fishing. Fish Res 44:201– 205
- Steinberg JC, Koczy FF, (1964). An acoustic-video system for marine biologicalresearch: objectives and requirements. In: Tavolga WN (Ed.), Marine Bio-Acoustics. Pergamon Press, New York, pp. 1–9
- Stobart B, García-Charton JA, Espejo C, Rochel E, Goñi R, Reñones O, Herrero A, Crec'hriou R, Polti S, Marcos C, Planes S, Pérez-Ruzafa A (2007) A baited

underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. J Exp Mar Biol Ecol 345:158–174

- Tessier A, Pastor J, Francour P, Saragoni G, Crec'hriou R, Lenfant P (2013) Video transect as a complement to underwater visual census to study reserve effect on fish assemblages. Aquat Biol
- Thiriet P (2014) Comparison of fish assemblage structure and underlying ecological processes, between Cystoseira forests and less structurally complex habitats of North-Western Mediterranean rocky subtidal. PhD diss., Université Nice Sophia Antipolis
- Thresher RE, Gunn JS (1986) Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). Environ Biol Fish 17:93–116
- UNEP-MAP-RAC/SPA: Strategic Action Programme For The Conservation Of Biological Diversity (SAP BIO) InThe Mediterranean Region, Tunis, 2003
- Vacchi M, La Mesa G, Boyer M, Bearzi P (1999) fish visual census in marine protected areas. Il Naturalista Sicilano 23,Proceedings of the International workshop, Ustica
- Vacchi M, Tunesi L (1993) Stationary visual census: A technique for the assessment of fish assemblages in Mediterranean protected coastal areas. Boll Oceanol Teor Appl 11:225–229
- Watson R, Pauly D (2001) Systematic distortions in world fisheries catch trends. Nature 414:534–536
- Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science 314:787–790

# 3.7 Annex

**Transects** (Harmelin Vivien 1975): visual census along transects involves a trained diver swimming at constant speed along a straight path of known length and recording all fish visible within a pre-determined distance at each side of the path. Transect width can be adapted according to fish mobility (generally 1 m width for cryptic fish, 5 meter width for nectobenthic fish).

**Stationary point counts** (Bohnsack & Bannerot 1986; Vacchi & Tunesi 1993): this technique involves a diver who sets on the seafloor and records all fish visible within an imaginary cylinder of pre-determined radius length, extending from the bottom to the surface. When all species within his field of view are recorded, the diver rotates to scan another sector, until the full circle is completed. A whole circle count lasts 5 minutes. Possible adaptations are different radius lengths or different total sampling time due to separation of functional groups counts (i.e at the first rotation necto-benthic fish are counted, then cryptic fish in a second rotation) (La Mesa et al. 2013)

**Mobile point counts** (Rilov & Benayahu 2000): this technique was specifically developed to census the fish community at gas platforms and consisted in swimming along an imaginary circle of 3 meters radius with the pillar as centre and counting all fish within the circle.

**Rapid Visual Census (RVC)** (Kingsford & Battershill 1998, Dempster et al 2002): Method designed to census fish around fish farm cages. Swimming through the water mass adjoining fish farm cages, the diver counts all fish present within a strip 15 m wide, 50 length and 15 m deep, covering a volume of approximatively 11 250 m<sup>3</sup>. Each count lasts 5 minutes.

**Spatial counts** (Charbonnel et al 1997, D'Anna et al 1999): mixed technique designed to census fish around artificial reefs, including line transects, circular transects and point counts. First phase: a diver sets on top of the artificial pyramid and counts all fish present around the complete perimeter of the pyramid during 5-8 minutes. Second phase: the diver swims around the perimeter of the pyramid (circular transect) and then through one of its internal passages (line transect), to record more sedentary and cryptic fish (10 minutes).

Last phase: the diver swims through a transect 25 m x 6 m to reach the second pyramid, where the census operations are repeated in the same way. Length of the transects and duration of the census are adapted according to artificial reefs structure.

**Total counts** (Harmelin Vivien 1985, Planes et al 1998): the principle of this method is to count all target fish within a given area, generally defined by a trait of coastline of known length and a given isobath.

**Random paths** (Harmelin Vivien 1985, Francour 1999): technique involving counts of fixed or varying duration made on random paths across the selected area. Data collected in this way provide information on species diversity and spatial distribution. This method is generally used in concomitance to other census techniques were the sampled surface is known (allowing estimates of density).

**Fish assemblage survey technique (FAST)** (Seytre & Francour 2009): this technique is a modification of random counts consisting in six 15 min random visual censuses covering all kind of substrata (sand, seagrass, rock). Census are performed on a presence-absence basis and on a two size class basis (large fish >2/3 of fish total length, and small to medium fish <2/3 total length). Only a predetermined set of species are recorded, which are those targeted by professional and/or recreational fishing. The so collected data are treated in a standard way in order to compute a set of indices describing the health of the fish assemblage. Being very easy to apply this technique is well adapt for citizen science.

**Diver Operated Video transects (DOV)** (Boland and Leubel 1986, Tessier et al 2013): the method involves a diver holding a camera and swimming 1.5 m above the bottom at constant speed, along a transect of fixed length. The operator keeps the video camera steady and perpendicular to the bottom, recording in front of himself. A reference bar attached to the camera housing is sometimes used to control the camera elevation.

**Remotely Operated Video (ROV)** (Fedra & Machan 1979, Stokesbury et al 2004): ROV systems are equipped with HD camera and can be stationary and linked to a vessel or platform, autonomous and thus set on the seafloor, or finally towed by a vessel. Towed systems are towed by the vessel at low speed in order to film along a predefined trajectory of known length. Systems can be deployed in the water column at a constant

elevation from the seafloor or above the seabed using a sledge, depending on the targeted fish assemblage. The cameras can be set vertically in order to face the sea floor or with a fixed downward angle. ROV systems can also be adapted to record fish around gas platform pillars, simulating the trajectory of a mobile point count (Andaloro et al 2013)

**Remote rotating video system (Staviro**, **STAtion Video ROtative in French)** (Pelletier et al 2012, Bouchacha et al 2013): The Staviro is a remote high definition rotating video system fixed on a tripod, dropped from the boat onto the seabed, and retrieved using buoys and rigging. The rotation affords a 360° providing panoramic images and a much larger surveyed area than fixed ROV systems, while avoiding the image distortion characteristic of fisheye lenses (Pelletier et al 2012). Potential double counting is minimized by paying particular attention to the direction of fish movement with respect to rotation, and by calculating the mean abundance over rotations, to average out the variability between rotations. More details on image analysis are given in the methods section.

**Baited Underwater Video (BUV)** (Cappo et al 2004, Stobart et al 2007): a BUV ystem consists in one or two HD video cameras sheltered by a video housing firmly mounted within a protective cage. The cameras film the sea surrounding the bait, which is placed close to the camera, at a distance that can range from 0.5 to 1.5 m. The choice of the bait depends on the species that want to be attracted. The orientation of the system can be either horizontal or vertical to the bottom, resulting in different abundances and species compositions of the observed fish assemblage (Langlois et al., 2006; Wraith, 2007).

**Cabled observatory** (Condal et al 2012): these structures are permanent video platforms using cables for energy supply, data transfer and instrument control. They are equipped with cameras that can continuously acquire digital images of the surrounding environment at 360, for long periods (months-years). For image analysis the field of view of interest can be selected. This system has been used to document seasonal rhythms of fish communities over long time windows.

**Spearfishing video**: while spearfishing, videos are generally recorded using Go-pro HD micro cameras mounted on a spear gun, recording footage with a given angle. Bulleri et al

2014 proposed to use widely available spearfishing videos to monitor fish assemblage at large spatial and temporal scales with low costs.

# References of reviewed papers

- Addis P, Cau A, Massuti E, Merella P, Sinopoli M, Andaloro F (2006) Spatial and temporal changes in the assemblage structure of fishes associated to fish aggregation devices in the Western Mediterranean. Aquatic Living Resources 19:149–160
- Addis P, Secci M, Cau A (2013) The effect of Mistral (a strong NW wind) episodes on the occurrence and abundance of Atlantic bluefin tuna (Thunnus thynnus) in the trap fishery of Sardinia (W Mediterranean). Scientia Marina 77:419–427
- Andaloro F, Castriota L, Ferraro M, Romeo T, Sara G, Consoli P (2011) Evaluating fish assemblages associated with gas platforms: Evidence from a visual census technique and experimental fishing surveys. Ciencias Marinas 37:1–9
- Andaloro F, Ferraro M, Mostarda E, Romeo T, Consoli P (2013) Assessing the suitability of a remotely operated vehicle (ROV) to study the fish community associated with offshore gas platforms in the Ionian Sea: a comparative analysis with underwater visual censuses (UVCs). Helgoland Marine Research 67:241–250
- Arechavala-Lopez P, Uglem I, Sanchez-Jerez P, Fernandez-Jover D, Bayle-Sempere JT, Nilsen R (2010) Movements of grey mullet Liza aurata and Chelon labrosus associated with coastal fish farms in the western Mediterranean Sea. Aquaculture Environment Interactions 1:127–136
- Arigoni S, Francour P, Harmelin-Vivien M, Zaninetti L (2002) Adaptive colouration of Mediterranean labrid fishes to the new habitat provided by the introduced tropical alga Caulerpa taxifolia. Journal of Fish Biology 60:1486–1497
- Azzurro E, Aguzzi J, Maynou F, Chiesa JJ, Savini D (2013) Diel rhythms in shallow Mediterranean rocky-reef fishes: a chronobiological approach with the help of trained volunteers. Journal of the Marine Biological Association of the United Kingdom 93:461–470
- Azzurro E, Matiddi M, Fanelli E, Guidetti P, Mesa G La, Scarpato A, Axiak V (2010) Sewage pollution impact on Mediterranean rocky-reef fish assemblages. Marine environmental research 69:390–397
- Azzurro E, Pais A, Consoli P, Andaloro F (2007) Evaluating day-night changes in shallow Mediterranean rocky reef fish assemblages by visual census. Marine Biology 151:2245–2253
- Bayle-Sempere JT, Ramos-Espla AA, Garcia Charton JA (1994) Intra-annual variability of an artificial reef fish assemblage in the marine reserve of Tabarca (Alicante, Spain, SW Mediterranean). Bulletin of Marine Science 55:2–3
- Bell JD (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. Journal of Applied Ecology:357–369
- Bellier E, Neubauer P, Monestiez P, Letourneur Y, Ledireach L, Bonhomme P, Bachet F (2013) Marine reserve spillover: Modelling from multiple data sources. Ecological Informatics 18:188–193

- Biagi F, Gambaccini S, Zazzetta M (1998) Settlement and recruitment in fishes: the role of coastal areas. Italian Journal of Zoology 65:269–274
- Bodilis P, Louisy P, Draman M, Arceo HO, Francour P (2014) Can Citizen Science Survey Non-indigenous Fish Species in the Eastern Mediterranean Sea? Environmental Management 53:172–180
- Bodilis P, Seytre, C. C, Charbonnel E, Francour, P. F (2011) Monitoring of the artificial reef fish assemblages of the Gulf Juan marine protected area (France, North Western Mediterranean). Brazilian Journal of Oceanography 59:167–176
- Bombace G, Fabi G, Fiorentini L, Spagnolo A (1995) Assessment of the ichthyofauna of an artificial reefe through visual census and trammel net: comparison between the two sampling techiques
- Bonaca MO, Lipej L (2005) Factors affecting habitat occupancy of fish assemblage in the Gulf of Trieste (Northern Adriatic Sea). Marine Ecology-an Evolutionary Perspective 26:42–53
- Bonaviri C, Fernández TV, Badalamenti F, Gianguzza P, Lorenzo M Di, Riggio S (2009) Fish versus starfish predation in controlling sea urchin populations in Mediterranean rocky shores. Marine Ecology Progress Series 382:129–138
- Bubic TS, Grubisic L, Ticina V, Katavic I (2011) Temporal and spatial variability of pelagic wild fish assemblages around Atlantic bluefin tuna Thunnus thynnus farms in the eastern Adriatic Sea. Journal of Fish Biology 78:78–97
- Bulleri F, Benedetti-Cecchi L (2014) Chasing fish and catching data: recreational spearfishing videos as a tool for assessing the structure of fish assemblages on shallow rocky reefs. Marine Ecology Progress Series 506:255–U569
- Bussotti S, Denitto F, Guidetti P, Belmonte G (2002) Fish Assemblages in Shallow Marine Caves of the Salento Peninsula (Southern Apulia, SE Italy). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 23:11–20
- Bussotti S, Guidetti P (1999) Fish communities associated with different seagrass systems in the Mediterranean Sea. Naturalista siciliano 23:245–259
- Bussotti S, Guidetti P (2005) Distribution patterns of the golden goby, Gobius auratus, in Mediterranean sublittoral rocky cliffs. Italian Journal of Zoology 72:305–309
- Bussotti S, Guidetti P (2009) Do Mediterranean fish assemblages associated with marine caves and rocky cliffs differ? Estuarine Coastal and Shelf Science 81:65–73
- Bussotti S, Guidetti P (2011) Timing and habitat preferences for settlement of juvenile fishes in the Marine Protected Area of Torre Guaceto (south-eastern Italy, Adriatic Sea). Italian Journal of Zoology 78:243–254
- Bussotti S, Guidetti P, Belmonte G (2003) Distribution patterns of the cardinal fish, Apogon imberbis, in shallow marine caves in southern Apulia (SE Italy). Italian Journal of Zoology 70:153–157
- Cardona L, Lopez D, Sales M, Caralt S De, Diez I (2007) Effects of recreational fishing on three fish species from the Posidonia oceanica meadows off Minorca (Balearic archipelago, western Mediterranean). Scientia Marina 71:811–820
- Cecchi E, Piazzi L, Balata D (2007) Interaction between depth and protection in determining the structure of Mediterranean coastal fish assemblages. Aquatic Living Resources 20:123–129

- Cenci E, Pizzolon M, Chimento N, Mazzoldi C (2011) The influence of a new artificial structure on fish assemblages of adjacent hard substrata. Estuarine Coastal and Shelf Science 91:133–149
- Charbonnel E, Francour P, Harmelin J (1996) Finfish population assessment techniques on artificial reefs: a review in the European Union. In: p 261–278
- Charbonnel E, Francour P, Harmelin J, Ody D (1995) Les problèmes d'échantillonnage et de recensement du peuplement ichtyologique dans les récifs artificiels. Biol Mar Med 2:85–90
- Charbonnel E, Serre C, Ruitton S, Harmelin JG, Jensen A (2002) Effects of increased habitat complexity on fish assemblages associated with large artificial reef units (French Mediterranean coast). ICES Journal of Marine Science 59:S208–S213
- Charton JG, Williams I, Ruzafa AP, Milazzo M, Chemello R, Marcos C, Kitsos M-S, Koukouras A, Riggio S (2000) Evaluating the ecological effects of Mediterranean marine protected areas: habitat, scale and the natural variability of ecosystems. Environmental Conservation 27:159–178
- Cheminee A, Sala E, Pastor J, Bodilis P, Thiriet P, Mangialajo L, Cottalorda JM, Francour P (2013) Nursery value of Cystoseira forests for Mediterranean rocky reef fishes. J Exp Mar Biol Ecol 442:70–79
- Ciriaco S, Costantini M, Italiano C, Odorico R, Picciulin M, Verginella L, Spoto M (1998) Monitoring the Miramare Marine Reserve: assessment of protection efficiency. Italian Journal of Zoology 65:383–386
- Claudet J, Pelletier D, Jouvenel JY, Bachet F, Galzin R (2006) Assessing the effects of marine protected area (MPA) on a reef fish assemblage in a northwestern Mediterranean marine reserve: Identifying community-based indicators. Biological Conservation 130:349–369
- Coll J, Abad R, Alvarez E, Deudero S, Mas R, Riera F, Moreno I (2009) Dtate of fish populations and influence on the trammel net fishery at three balearic island (Western Mediterranean) artificial reefs a decade after their deployment. Bulletin of Marine Science 85:77–100
- Coll J, Garcia-Rubies A, Morey G, Reñones O, Álvarez-Berastegui D, Navarro O, Grau AM (2013) Using no-take marine reserves as a tool for evaluating rocky-reef fish resources in the western Mediterranean. ICES Journal of Marine Science: fst025
- Coll J, Moranta J, Renones O, Garcia-Rubies A, Moreno I (1998) Influence of substrate and deployment time on fish assemblages on an artificial reef at Formentera Island (Balearic Islands, western Mediterranean). Hydrobiologia 385:139–152
- Condal F, Aguzzi J, Sarda F, Nogueras M, Cadena J, Costa C, Rio J Del, Manuel A (2012) Seasonal rhythm in a Mediterranean coastal fish community as monitored by a cabled observatory. Marine Biology 159:2809–2817
- Consoli P, Romeo T, Ferraro M, Sara G, Andaloro F (2013) Factors affecting fish assemblages associated with gas platforms in the Mediterranean Sea. Journal of Sea Research 77:45–52
- Consoli P, Romeo T, Giongrandi U, Andaloro F (2008) Differences among fish assemblages associated with a nearshore vermetid reef and two other rocky habitats along the shores of Cape Milazzo (northern Sicily, central Mediterranean

Sea). Journal of the Marine Biological Association of the United Kingdom 88:401–410

- Claudet J, Garcia Charton JA, Lenfant P (2011) Combined effects of levels of protection and environmental variables at different spatial resolutions on fish assemblages in a marine protected area. Conservation Biology 25:105–114
- Consoli P, Sara G, Mazza, G. M, Battaglia, P. B, Romeo, T. R, Incontro, V. I, Andaloro, F A (2013) The effects of protection measures on fish assemblage in the Plemmirio marine reserve (Central Mediterranean Sea, Italy): A first assessment 5 years after its establishment. Journal of Sea Research 79:20–26
- D'Anna G, Badalamenti F, Lipari R, Cuttitta A, Pipitone C (1995) Fish assemblage analysis by means of a visual census survey on an artificial reef and on natural areas in the Gulf of Castellammare (NW Sicily). In: p 27–31
- D'Anna G, Giacalone VM, Badalamenti F, Pipitone C (2004) Releasing of hatchery-reared juveniles of the white seabream Diplodus sargus (L., 1758) in the Gulf of Castellammare artificial reef area (NW Sicily). Aquaculture 233:251–268
- D'Anna G, Lipari Ro, Badalamenti F, Cuttitta A (1999) Questions arising from the use of visual census in natural and artificial habitats. Fish Visual Census in Marine Protected Areas II Naturalista Siciliano 23:187–204
- Dempster T, Sanchez-Jerez P, Bayle-Sempere JT, Giménez-Casalduero F, Valle C (2002) Attraction of wild fish to sea-cage fish farms in the south-western Mediterranean Sea: spatial and short-term temporal variability. Marine Ecology Progress Series 242:237–252
- Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P (2009) Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. Marine Ecology Progress Series 387:275–285
- Di Franco A, Coppini G, Pujolar JM, Leo GA De, Gatto M, Lyubartsev V, Melia P, Zane L, Guidetti P (2012) Assessing Dispersal Patterns of Fish Propagules from an Effective Mediterranean Marine Protected Area. PLoS ONE 7
- Di Franco A, Di Lorenzo M, Guidetti P (2013) Spatial patterns of density at multiple life stages in protected and fished conditions: an example from a Mediterranean coastal fish. Journal of Sea Research 76:73–81
- Di Franco A, Graziano M, Franzitta G, Felline S, Chemello R, Milazzo M (2011) Do small marinas drive habitat specific impacts? A case study from Mediterranean Sea. Marine Pollution Bulletin 62:926–933
- Di Martino V, Stancanelli B, Molinari A (2007) Fish community associated with *Halophila stipulacea* meadow in the Mediterranean Sea. Cybium 31:451–458
- Dufour V, Jouvenel JY, Galzin R (1995) Study of a Mediterranean rocky reef fish assemblage comparisons of population-distributions between depths in protected and unprotected areas over one decade. Aquatic Living Resources 8:17–25
- Fasola M, Canova L, Foschi F, Novelli O, Bressan M (1997) Resource use by a Mediterranean rocky slope fish assemblage. Marine Ecology 18:51–66
- Felix-Hackradt FC, Hackradt CW, Trevino-Oton J, Perez-Ruzafa A, Garcia-Charton JA (2013) Temporal patterns of settlement, recruitment and post-settlement losses in

a rocky reef fish assemblage in the South-Western Mediterranean Sea. Marine Biology 160:2337–2352

- Fernández TV, D'Anna G, Badalamenti F, Perez-Ruzafa A (2008) Habitat connectivity as a factor affecting fish assemblages in temperate reefs. Aquatic Biology 1:239–248
- Fernandez-Jover D, Sanchez-Jerez P, Bayle-Sempere JT, Valle C, Dempster T (2008) Seasonal patterns and diets of wild fish assemblages associated with Mediterranean coastal fish farms. ICES Journal of Marine Science 65:1153–1160
- Forcada A, Bayle-Sempere JT, Valle C, Sanchez-Jerez P (2008) Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. Marine environmental research 66:536–547
- Franco A, Perez-Ruzafa A, Drouineau H, Franzoi P, Koutrakis ET, Lepage M, Verdiell-Cubedo D, Bouchoucha M, Lopez-Capel A, Riccato F, Sapounidis A, Marcos C, Oliva-Paterna FJ, Torralva-Forero M, Torricelli P (2012) Assessment of fish assemblages in coastal lagoon habitats: Effect of sampling method. Estuarine Coastal and Shelf Science 112:115–125
- Francour P (1997) Fish assemblages of Posidonia oceanica beds at Port Cros (France, NW Mediterranean): Assessment of composition and long-term fluctuations by visual census. Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 18:157–173
- Francour P (1999) A critical review of adult and juvenile fish sampling techniques in Posidonia oceanica seagrass beds. Naturalista sicil 23:33–57
- Francour P (2000) Long term monitoring of Posidonia oceanica fish assemblages of the Scandola Marine Reserve (Corsica, northwestern Mediterranean). Cybium 24:85– 95
- Garcia-Charton JA, Perez-Ruzafa A (1998) Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 19:111–128
- García-Charton J, Pérez-Ruzafa A, Sánchez-Jerez P, Bayle-Sempere J, Reñones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Marine Biology 144:161–182
- Garcia-Rubies A (1999) Effects of fishing on community structure and on selected populations of Mediterranean coastal reef fish. Naturalista siciliano 23:59–81
- Garcia-Rubies A, Hereu B, Zabala M (2013) Long-Term Recovery Patterns and Limited Spillover of Large Predatory Fish in a Mediterranean MPA. PLoS ONE 8
- García-Rubies A, Macpherson E (1995) Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Marine Biology 124:35–42
- García-Rubies A, Zabala i Limousin M (1990) Effects of total fishing prohibition on the rocky fish assemblages of Medes Islands marine reserve (NW Mediterranean). Scientia Marina, 1990, vol 54, num 4, p 317-328
- Georgiadis M, Mavraki N, Koutsikopoulos C, Tzanatos E (2014) Spatio-temporal dynamics and management implications of the nightly appearance of Boops boops (Acanthopterygii, Perciformes) juvenile shoals in the anthropogenically modified Mediterranean littoral zone. Hydrobiologia 734:81–96

- Giakoumi S, Grantham HS, Kokkoris GD, Possingham HP (2011) Designing a network of marine reserves in the Mediterranean Sea with limited socio-economic data. Biological Conservation 144:753–763
- Giakoumi S, Kokkoris GD (2013) Effects of habitat and substrate complexity on shallow sublittoral fish assemblages in the Cyclades Archipelago, North-eastern Mediterranean sea. Mediterranean Marine Science 14:58–68
- Girolamo M De, Mazzoldi C (2001) The application of visual census on Mediterranean rocky habitats. Marine environmental research 51:1–16
- Girolamo M De, Scaggiante M, Rasotto M (1999) Social organization and sexual pattern in the Mediterranean parrotfish Sparisoma cretense (Teleostei: Scaridae). Marine Biology 135:353–360
- Guidetti P (2000) Differences among fish assemblages associated with nearshore Posidonia oceanica seagrass beds, rocky-algal reefs and unvegetated sand habitats in the Adriatic Sea. Estuarine Coastal and Shelf Science 50:515–529
- Guidetti P (2001) Population dynamics and post-settlement mortality of the ornate wrasse, Thalassoma pavo, in the Tyrrhenian Sea (western Mediterranean). Italian Journal of Zoology 68:75–78
- Guidetti P (2002) Temporal changes in density and recruitment of the Mediterranean ornate wrasse Thalassoma pavo (Pisces, Labridae). Archive of Fishery and Marine Research 49:259–267
- Guidetti P (2004) Fish assemblages associated with coastal defence structures in southwestern Italy (Mediterranean Sea). Journal of the Marine Biological Association of the United Kingdom 84:669–670
- Guidetti P, Bianchi CN, Chiantore M, Schiaparelli S, Morri C, Cattaneo-Vietti R (2004) Living on the rocks: substrate mineralogy and the structure of subtidal rocky substrate communities in the Mediterranean Sea. Marine Ecology Progress Series 274:57–68
- Guidetti P, Bianchi CN, Mesa G La, Modena M, Morri C, Sara G, Vacchi M (2002) Abundance and size structure of Thalassoma pavo (Pisces: Labridae) in the western Mediterranean Sea: variability at different spatial scales. Journal of the Marine Biological Association of the United Kingdom 82:495–500
- Guidetti P, Boero F (2001) Occurrence of the Mediterranean parrotfish Sparisoma cretense (Perciformes: Scaridae) in south-eastern Apulia (south-east Italy). Journal of the Marine Biological Association of the United Kingdom 81:717–718
- Guidetti P, Boero F (2002) Spatio-temporal variability in abundance of the parrotfish, Sparisoma cretense, in SE Apulia (SE Italy, Mediterranean Sea). Italian Journal of Zoology 69:229–232
- Guidetti P, Bussotti S (1997) Recruitment of Diplodus annularis and Spondyliosoma cantharus (Sparidae) in shallow seagrass beds along the Italian coasts (Mediterranean Sea). Marine Life 7:47–52
- Guidetti P, Bussotti S (2000) Fish fauna of a mixed meadow composed by the seagrasses Cymodocea nodosa and Zostera noltii in the Western Mediterranean. Oceanologica Acta 23:759–770

- Guidetti P, Bussotti S (2002) Effects of seagrass canopy removal on fish in shallow Mediterranean seagrass (Cymodocea nodosa and Zostera noltii) meadows: a local-scale approach. Marine Biology 140:445–453
- Guidetti P, Bussotti S, Boero F (2005) Evaluating the effects of protection on fish predators and sea urchins in shallow artificial rocky habitats: a case study in the northern Adriatic Sea. Marine environmental research 59:333–348
- Guidetti P, Cattaneo-Vietti R (2002) Can mineralogical features influence distribution patterns of fish? A case study in shallow Mediterranean rocky reefs. Journal of the Marine Biological Association of the United Kingdom 82:1043–1044
- Guidetti P, Fanelli G, Fraschetti S, Terlizzi A, Boero F (2002) Coastal fish indicate humaninduced changes in the Mediterranean littoral. Marine environmental research 53:77–94
- Guidetti P, Milazzo M, Bussotti S, Molinari A, Murenu M, Pais A, Spano N, Balzano R, Agardy T, Boero F, Carrada G, Cattaneo-Vietti R, Cau A, Chemello R, Greco S, Manganaro A, Sciara GN di, Russo GF, Tunesi L (2008) Italian marine reserve effectiveness: Does enforcement matter? Biological Conservation 141:699–709
- Guidetti P, Terlizzi A, Fraschetti S, Boero F (2002) Spatio-temporal variability in fish assemblages associated with coralligenous formations in south eastern Apulia (SE Italy). Italian Journal of Zoology 69:325–331
- Guidetti P, Terlizzi A, Fraschetti S, Boero F (2003) Changes in Mediterranean rocky-reef fish assemblages exposed to sewage pollution. Marine Ecology Progress Series 253:269–278
- Guidetti P, Verginella L, Viva C, Odorico R, Boero F (2005) Protection effects on fish assemblages, and comparison of two visual-census techniques in shallow artificial rocky habitats in the northern Adriatic Sea. Journal of the Marine Biological Association of the United Kingdom 85:247–255
- Gul B, Lok A, Ozgul A, Ulas A, Duzbastilar FO, Metrin C (2011) Comparison of fish community structure on artificial reefs deployed at different deothe on turkish aegean coast. Brazilian Journal of Oceanography 59:27–32
- Harmelin J (1987) Structure et variabilité de l'ichtyofaune d'une zone rocheuse protégée en Méditerranée (Pare national de Port-Cros, France). Marine Ecology 8:263–284
- Harmelin J (1990) Ichthyofauna of the Mediterranean rocky bottoms: Structure of the coralligenous ground assemblage of Port-Cros Island(National Park, France). MARSEILLE 50:23–30
- Harmelin J-G (1999) Visual assessment of indicator fish species in Mediterranean marine protected areas. Il Naturalista siciliano 23:83–104
- Harmelin JG, Bachet F, Garcia F (1995) Mediterranean marine reserves: Fish indices as tests of protection efficiency. Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 16:233–250
- Harmelin-Vivien ML, Bitar G, Harmelin JG, Monestiez P (2005) The littoral fish community of the Lebanese rocky coast (eastern Mediterranean Sea) with emphasis on Red Sea immigrants. Biological Invasions 7:625–637
- Harmelin-Vivien M, Direach L Le, Bayle-Sempere J, Charbonnel E, Garcia-Charton JA, Ody D, Perez-Ruzafa A, Renones O, Sanchez-Jerez P, Valle C (2008) Gradients

of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? Biological Conservation 141:1829–1839

- Harmelinvivien ML, Francour P (1992) Trawling or visual census methodological bias in the assessment of fish populations in seagrass beds. Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 13:41–51
- Harmelin-Vivien M, Harmelin J (1975) Présentation d'une méthode d'évaluation in situ de la faune ichtyologique. Trav Sci Parc Nation Port-Cros 1:47–52
- Harmelin-Vivien M, Harmelin J, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G,
  Blanc F, Chevalier R, Duclerc J (1985) Evaluation visuelle des peuplements et
  populations de poissons: méthodes et problèmes. Revue d'écologie 40:467–539
- Harmelin-Vivien M, Harmelin J, Leboulleux V (1995) Microhabitat requirements for settlement of juvenile sparid fishes on Mediterranean rocky shores. In: Space Partition within Aquatic Ecosystems. Springer, p 309–320
- Illich IP, Kotrschal K (1990) Depth distribution and abundance of North Adriatic littoral roky reef bellioid fishes (Blennidae and Trypterigion). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 11:277–289
- Jouvenel JY (1997) Inventory of Cerbere/Banyuls-sur-Mer marine reserve ichtyofauna (N.-W. Mediterranean, France). Vie Et Milieu-Life and Environment 47:77–84
- Jouvenel J-Y, Pollard DA (2001) Some effects of marine reserve protection on the population structure of two spearfishing target-fish species, Dicentrarchus labrax (Moronidae) and Sparus aurata (Sparidae), in shallow inshore waters, along a rocky coast in the northwestern Mediterranean Sea. Aquatic Conservation: Marine and Freshwater Ecosystems 11:1–9
- Koeck B, Tessier A, Brind'Amour A, Pastor J, Bijaoui B, Dalias N, Astruch P, Saragoni G, Lenfant P (2014) Functional differences between fish communities on artificial and natural reefs: a case study along the French Catalan coast. Aquatic Biology 20:219–234
- Kruschel C, Schultz ST (2012) Use of a lure in visual census significantly improves probability of detecting wait-ambushing and fast cruising predatory fish. Fisheries Research 123:70–77
- La Mesa G, Guidetti P, Bussotti S, Cattaneo-Vietti R, Manganaro A, Molinari A, Russo GF, Spano N, Vetrano G, Tunesi L (2013) Rocky reef fish assemblages at six Mediterranean marine protected areas: broad-scale patterns in assemblage structure, species richness and composition. Italian Journal of Zoology 80:90–103
- La Mesa G, Longobardi A, Sacco F, Marino G (2008) First release of hatchery juveniles of the dusky grouper Epinephelus marginatus (Lowe, 1834) (Serranidae: Teleostei) at artificial reefs in the Mediterranean: results from a pilot study. Scientia Marina 72:743–756
- La Mesa G, Micalizzi M, Giaccone G, Vacchi M (2004) Cryptobenthic fishes of the "Ciclopi Islands" marine reserve (central Mediterranean Sea): assemblage composition, structure and relations with habitat features. Marine Biology 145:233–242

- La Mesa G, Molinari A, Bava S, Finoia MG, Cattaneo-Vietti R, Tunesi L (2011) Gradients of abundance of sea breams across the boundaries of a Mediterranean marine protected area. Fisheries Research 111:24–30
- La Mesa G, Molinari A, Gambaccini S, Tunesi L (2011) Spatial pattern of coastal fish assemblages in different habitats in North-western Mediterranean. Marine Ecology-an Evolutionary Perspective 32:104–114
- La Mesa G, Molinari A, Tunesi L (2010) Coastal fish assemblage characterisation to support the zoning of a new Marine Protected Area in north-western Mediterranean. Italian Journal of Zoology 77:197–210
- La Mesa G, Vacchi M (1999) An analysis of the coastal fish assemblage of the Ustica Island marine reserve (Mediterranean Sea). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 20:147–165
- Lenfant P, Louisy P, Licari ML (2003) Inventory of dusky groupers (Epinephelus marginatus) in the marine reserve of Cerbere-Banyuls (France, North-Western Mediterranean Sea) after 17 years of protection. Cybium 27:27–36
- Letourneur Y, Ruitton S, Sartoretto S (2003) Environmental and benthic habitat factors structuring the spatial distribution of a summer infralittoral fish assemblage in the north-western Mediterranean Sea. Journal of the Marine Biological Association of the UK 83:193–204
- Lipej L, Bonaca MO, Šiško M (2003) Coastal fish diversity in three marine protected areas and one unprotected area in the Gulf of Trieste (Northern Adriatic). Marine Ecology 24:259–273
- Macpherson E (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. Journal of Experimental Marine Biology and Ecology 220:127–150
- Macpherson E, Biagi F, Francour P, García-Rubies A, Harmelin J, Harmelin-Vivien J, Jouvenel J, Planes S, Vigliola L, Tunesi L (1997) Mortality of juvenile fishes of the genus Diplodus in protected and unprotected areas in the western Mediterranean Sea. Marine Ecology Progress Series 160:135–147
- Macpherson E, Garcia-Rubies A, Gordoa A (2000) Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. Marine Biology 137:1067–1076
- Macpherson E, Gordoa A, Garcia-Rubies A (2002) Biomass size spectra in littoral fishes in protected and unprotected areas in the NW Mediterranean. Estuarine, Coastal and Shelf Science 55:777–788
- Macpherson E, Raventos N (2005) Settlement patterns and post-settlement survival in two Mediterranean littoral fishes: influences of early-life traits and environmental variables. Marine Biology 148:167–177
- Macpherson E, Zike U (1999) Temporal and spatial variability of settlement success and recruitment level in three blennoid fishes in the northwestern Mediterranean. Marine Ecology Progress Series 182:269–282
- Mazzoldi C, Girolamo M De (1998) Littoral fish community of the Island Lampedusa (Italy): a visual census approach. Italian Journal of Zoology 65:275–280

- Milazzo M, Anastasi I, Willis TJ (2006) Recreational fish feeding affects coastal fish behavior and increases frequency of predation on damselfish *Chromis chromis* nests. Marine Ecology Progress Series 310:165–172
- Milazzo M, Badalamenti F, Fernandez TV, Chemello R (2005) Effects of fish feeding by snorkellers on the density and size distribution of fishes in a Mediterranean marine protected area. Marine Biology 146:1213–1222
- Milazzo M, Palmeri A, Falcon JM, Badalamenti F, Garcia-Charton JA, Sinopoli M, Chemello R, Brito A (2011) Vertical distribution of two sympatric labrid fishes in the Western Mediterranean and Eastern Atlantic rocky subtidal: local shore topography does matter. Marine Ecology-an Evolutionary Perspective 32:521–531
- Moreno I (2002) Effects of substrate on the artificial reef fish assemblage in Santa Eulalia Bay (Ibiza, western Mediterranean). ICES Journal of Marine Science 59:S144– S149
- Moreno I (2006) Artificial reefs as a tool for coastal management in Balearic Islands (Western Mediterranean). Journal of Coastal Research:1843–1846
- Mouillot D, Culioli JM, Lepretre A, Tomasini JA (1999) Dispersion statistics and sample size estimates for three fish species (*Symphodus ocellatus, Serranus scriba* and *Diplodus annularis*) in the Lavezzi Islands Marine Reserve (South Corsica, Mediterranean Sea). Marine Ecology-Pubblicazioni Della Stazione Zoologica Di Napoli I 20:19–34
- Nieder J, Mesa G La, Vacchi M (2000) Blenniidae along the Italian coasts of the Ligurian and the Tyrrhenian Sea: Community structure and new records of *Scartella cristata* for northern Italy. Cybium 24:359–369
- Ordines F, Moranta J, Palmer M, Lerycke A, Suau A, Morales-Nin B, Grau AM (2005) Variations in a shallow rocky reef fish community at different spatial scales in the western Mediterranean Sea. Marine Ecology Progress Series 304:221–233
- Pais A, Azzurro E, Chessa LA (2004) Distribution patterns of coastal fish assemblages associated with different rocky substrates in Asinara Island National Park (Sardinia, Italy). Italian Journal of Zoology 71:309–316
- Pais A, Azzurro E, Guidetti P (2007) Spatial variability of fish fauna in sheltered and exposed shallow rocky reefs from a recently established Mediterranean Marine Protected Area. Italian Journal of Zoology 74:277–287
- Pastor J, Francour P (2010) Occurrence and distribution range of *Parablennius pilicornis* (Actynopterigii: perciformes: blennidae) along the french Mediterranean. Acta Ichthyologica Et Piscatoria 40:179–185
- Pastor J, Koeck B, Astruch P, Lenfant P (2013a) Coastal man-made habitats: Potential nurseries for an exploited fish species, Diplodus sargus (Linnaeus, 1758). Fisheries Research 148:74–80
- Pelaprat C (1999) Influence of protection measures on the seasonal and annual variations of densities and biomasses within the no invigilated fishing reserve of Calvi. Nat Sic 23:223–242
- Piazzi L, Cecchi E, Serena F (2012) Spatial and temporal patterns of diversity in Mediterranean rocky reef fish assemblages. Vie Et Milieu-Life and Environment 62:129–136

- Pizzolon M, Cenci E, Mazzoldi C (2008) The onset of fish colonization in a coastal defence structure (Chioggia, Northern Adriatic Sea). Estuarine Coastal and Shelf Science 78:166–178
- Planes S, Jouvenel J-Y, Lenfant P (1998) Density dependence in post-recruitment processes of juvenile sparids in the littoral of the Mediterranean Sea. Oikos:293–300
- Planes S, Macpherson E, Biagi F, Garcia-Rubies A, Harmelin J, Harmelin-Vivien M, Jouvenel JY, Tunesi L, Vigliola L, Galzin R (1999) Spatio-temporal variability in growth of juvenile sparid fishes from the Mediterranean littoral zone. Journal of the Marine Biological Association of the United Kingdom 79:137–143
- Raedemaecker F De, Miliou A, Perkins R (2010a) Fish community structure on littoral rocky shores in the Eastern Aegean Sea: Effects of exposure and substratum. Estuarine Coastal and Shelf Science 90:35–44
- Raedemaecker F De, Miliou A, Perkins R (2010b) Fish community structure on littoral rocky shores in the Eastern Aegean Sea: Effects of exposure and substratum. Estuarine Coastal and Shelf Science 90:35–44
- Relini G, Relini M, Montanari M (2000) An offshore buoy as a small artificial island and a fish-aggregating device (FAD) in the Mediterranean. Hydrobiologia 440:65–80
- Relini G, Relini M, Palandri G, Merello S, Beccornia E (2007) History, ecology and trends for artificial reefs of the Ligurian sea, Italy. Hydrobiologia 580:193–217
- Relini G, Relini M, Torchia G (1998) Fish biodiversity in a Caulerpa taxifolia meadow in the Ligurian Sea. Italian Journal of Zoology 65:465–470
- Relini G, Relini M, Torchia G (2000) Fish population changes following the invasion of the allochthonous alga Caulerpa taxifolia in the Ligurian Sea (NW Mediterranean). ICES Documents, CM:1–17
- Relini G, Relini M, Torchia G, Palandri G (2002) Ten years of censuses of fish fauna on the Loano artificial reef. ICES Journal of Marine Science: Journal du Conseil 59:S132–S137
- Relini M, Torchia G, Relini G (1994) Seasonal variation of fish assemblages in the Loano artificial reef (Ligurian Sea Northwestern-Mediterranean). Bulletin of Marine Science 55:2–3
- Relini M, Torchia G, Relini G (1995) Fish population patterns in a coastal artificial habitat in the north-western Mediterranean. Biology and ecology of shallow coastal waters, Olsen & Olsen, Denmark, Fredensborg:359–368
- Reñones O, Goñi R, Pozo M, Deudero S, Moranta J (1999) Effects of protection on the demographic structure and abundance of Epinephelus marginatus (Lowe, 1834).
  Evidence from Cabrera Archipelago National Park (West-central Mediterranean).
  Marine Life 9
- Renones O, Moranta J, Coll J, Morales-Nin B (1997) Rocky bottom fish communities of Cabrera Archipelago National Park (Mallorca, western Mediterranean). Scientia Marina 61:495–506
- Rius M (2007) The effect of protection on fish populations in the Ses Negres Marine Reserve (NW Mediterranean, Spain). Scientia Marina 71:499–504

- Sala E, Ballesteros E (1997) Partitioning of space and food resources by three fish of the genus Diplodus (Sparidae) in a Mediterranean rocky infralittoral ecosystem. Oceanographic Literature Review 44
- Sanchez-Jerez P, Gillanders BM, Rodriguez-Ruiz S, Ramos-Espla AA (2002) Effect of an artificial reef in Posidonia meadows on fish assemblage and diet of Diplodus annularis. ICES Journal of Marine Science 59:S59–S68
- Sanchez-Jerez P, Ramos-Espla A (2000) Changes in fish assemblages associated with the deployment of an antitrawling reef in seagrass meadows. Transactions of the American Fisheries Society 129:1150–1159
- Seytre C, Francour P (2008) Is the Cape Roux marine protected area (Saint-Raphael, Mediterranean Sea) an efficient tool to sustain artisanal fisheries? First indications from visual censuses and trammel net sampling. Aquatic Living Resources 21:297–305
- Seytre C, Francour P (2009) The Cap Roux MPA (Saint-Raphael, French Mediterranean): changes in fish assemblages within four years of protection. ICES Journal of Marine Science 66:180–187
- Seytre C, Francour P (2013) A long-term survey of Posidonia oceanica fish assemblages in a Mediterranean Marine Protected Area: emphasis on stability and no-take area effectiveness. Marine and freshwater research
- Seytre C, Vanderklift MA, Bodilis P, Cottalorda JM, Gratiot J, Francour P (2013) Assessment of commercial and recreational fishing effects on trophic interactions in the Cap Roux area (north-western Mediterranean). Aquatic Conservation-Marine and Freshwater Ecosystems 23:189–201
- Spanier E (2000) Changes in the ichthyofauna of an artificial reef in the southeastern Mediterranean in one decade. Scientia Marina 64:279–284
- Stobart B, Garcia-Charton JA, Espejo C, Rochel E, Goni R, Renones O, Herrero A, Crec'hriou R, Polti S, Marcos C, Planes S, Perez-Ruzafa A (2007) A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. Journal of Experimental Marine Biology and Ecology 345:158–174
- Tessier A, Pastor J, Francour P, Saragoni G, Crec'hriou R, Lenfant P (2013) Video transects as a complement to underwater visual census to study reserve effect on fish assemblages. Aquatic Biology 18:229–241
- Tunesi L, Molinari A, Salvati E (2006) Fish assemblage of the marine protected area of Cinque Terre (NW Mediterranean Sea): First characterization and assessment by visual census. Chemistry and Ecology 22:245–253
- Ulas A, Duzbastilar FO, Aydin C, Lok A, Metin C (2011) Determining Density of Caulerpa racemosa (Forsskal) J. Agardh and its Effects on Catch Compositions of Fishing Gears. Turkish Journal of Fisheries and Aquatic Sciences 11:385–391
- Vacchi M, Boyer M, Bussotti S, Guidetti P, Mesa G La (1999a) Some interesting species in the coastal fish fauna of Ustica Island (Mediterranean Sea). Cybium 23:323–331
- Vacchi M, Boyer M, Bussotti S, Guidetti P, Mesa G La (1999b) Some interesting species in the coastal fish fauna of Ustica Island (Mediterranean Sea). Cybium 23:323–331

- Vacchi M, Bussotti S, Guidetti P, Mesa G La (1998) Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea). Italian Journal of Zoology 65:281–286
- Vacchi M, Tunesi L (1993) Stationary visual census: A technique for the assessment of fish assemblages in Mediterranean protected coastal areas. Boll Oceanol Teor Appl 11:225–229
- Valle C, Bayle-Sempere JT (2009) Effects of a marine protected area on fish assemblage associated with Posidonia oceanica seagrass beds: temporal and depth variations. Journal of Applied Ichthyology 25:537–544
- Valle C, Bayle-Sempere JT, Dempster T, Sanchez-Jerez P, Gimenez-Casalduero F (2007) Temporal variability of wild fish assemblages associated with a sea-cage fish farm in the south-western Mediterranean Sea. Estuarine Coastal and Shelf Science 72:299–307
- Vigliola L, Harmelin-Vivien M, Biagi F, Galzin R, García-Rubies A, Harmelin J, Jouvenel J, Direach-Boursier L, Macpherson E, Tunesi L (1988) Spatial and temporal patterns of settlement among sparid fishes of the genus Diplodus in the north-western Mediterranean. Marine Ecology Progress Series 168:45–56
- Villamor A, Becerro MA (2012) Species, trophic, and functional diversity in Marine Protected and non-Protected Areas. Journal of Sea Research 73:109-116
- Zabala M, Louisy P, GarciaRubies A, Garcia V (1997) Socio-behavioural context of reproduction in the Mediterranean dusky grouper Epinephelus marginatus (Lowe, 1834) (Pisces, Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). Scientia Marina 61:79–98

# 4 Chapter 4. Combining multiple underwater visual census transect sizes to survey the whole fish assemblage in Mediterranean marine protected areas: an application in 3 case studies

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### 4.1 Abstract

Monitoring fish communities in Marine Protected Areas (MPAs) is necessary to assess if MPAs are meeting the goals for which they have been designed, allowing to detect changes in the abundance and size of exploited species and recovery of associated communities. High trophic level predators (HTLP) in particular play an important functional role in marine ecosystems and monitoring them within MPAs is essential to assess if the ecosystem is recovering. Monitoring techniques based on underwater visual census (UVC) should be adapted to fish mobility and behaviour, which can largely affect fish detectability to the survey technique. In the Mediterranean however, UVC transects of one dimension (often 25 x 5 m) are commonly used to survey the whole fish assemblage, from large mobile predators to crypto-benthic fish. Large mobile predators and shy species (often corresponding to HTLP) seldom approach the diver at such short distances, thus their abundances are likely under-estimated. Here we propose a simple improvement to traditional transect surveys to better account for the different mobility of species. First we compared the effectiveness of two transects surfaces (35 x 20 m and 25 x 5 m) both in i) quantifying large mobile predators and shy species within and outside Mediterranean MPAs, and ii) assessing the effect of protection on these species. Both transect sizes detected a significant protection effect on large mobile predators and more accurate density and biomass estimates were obtained with larger transects in MPAs. We thus combined three transect surfaces (10 x 1, 25 x 5, 35 x 25 m) in order to assess the recovery of HTLP relative to the full fish assemblage. We evidenced a significant effect of protection on HTLP, whose response was always higher in magnitude than that of other functional groups. Relative contribution of each functional group to total fish biomass differed within and outside MPAs and HTLP displayed the largest biomass ratios,

dominating trophic pyramids in MPAs. This was especially marked at older and highly enforced MPAs. Surveys with multiple transect sizes would allow for a more realistic assessment of HTLP and associated fish assemblage recovery within MPAs.

### 4.2 Introduction

The spread of marine protected areas (MPAs) across the world as conservation and fisheries management tools encouraged the development of non-destructive methods to monitor biodiversity and assess MPAs performance (Harmelin-Vivien et al. 1985, Murphy & Jenkins 2010, Mallet & Pelletier 2014). One of the most largely documented effects of protection within MPAs is the recovery (in terms of increased density, size and biomass) of species usually targeted by fishing. Monitoring programs based on underwater visual census (UVC) surveys have spread to assess such recovery (Harmelin et al. 1995, Samoilys & Carlos 2000, Colvocoresses & Acosta 2007, Murphy & Jenkins 2010, Mallet & Pelletier 2014). Fish at the higher trophic levels of the food web (hereafter high trophic level predators, HTLP) are typically the most targeted and the most sensible to exploitation (Myers & Worm 2003, Garcia-Rubies et al. 2013, Britten et al. 2014). HTLP play keystone roles in marine ecosystems, and their recovery within MPAs can trigger indirect effects encompassing all levels of the food web, through the re-establishment of lost trophic interactions (Pace et al. 1999, Pinnegar et al. 2000, Shears & Babcock 2002, Guidetti 2006a, Prato et al. 2013). To track such changes in the food web monitoring programs are needed to survey not only a selection of commercial fish species, but the whole fish community, from high trophic level predators and target fish, to non-commercial species, like small crypto-benthic fish.

Several visual census techniques have been developed across the world to survey fish assemblages in coastal areas, ranging from UVC by transects or fixed points (Brock 1954, Harmelin-Vivien & Harmelin 1975, Harmelin-Vivien et al. 1985, Bannerot & Bohnsack 1986) to video techniques operated by SCUBA divers or remote operated vehicles (ROV) (Murphy & Jenkins 2010, Mallet & Pelletier 2014). For shallow areas, UVC with transects and fixed points are often more convenient than video methods. Despite their known biases (i.e. observer effects, errors in size and width estimation) (Willis 2001, Edgar et al. 2004, Williams et al. 2006) and SCUBA-diving-related constraints (depth and time divelimits), these techniques usually combine lower economic and time costs, allowing to detect and identify a higher number of species, and to quantitatively describe the fish assemblage composition by assessing density and biomass variables, which is complicated if not impossible with video methods (Tessier et al. 2013, Mallet & Pelletier 2014, Prato et al. in prep). Nonetheless, it is often agreed that methods aiming at quantifying fish abundance through observation within a fixed surface area (i.e. until a

fixed distance from the observer, as strip transects or fixed points) provide underestimates of density, due to problems in detecting subjects within the sample surface (Thresher & Gunn 1986). More recently, it was also pointed out that if UVC counts are not instantaneous, the density of fast swimming fish can be over-estimated (Ward-Paige et al. 2010). Overall, the magnitude of the error varies widely depending on the species' moniltiy, behaviour (Mintevera et al. 2008) and morpho-anatomy.

Some studies have compared the effectiveness of different transect widths and/or, radius length of fixed points to survey fish species, generally concluding that dimensions of sampling surfaces should be adapted to the different fish mobility, accounting for the minimum distance of species approach and for species detectability based on size, body shape (e.g. flat fish), colors (e.g. sandy gobids) and behaviours (Cheal & Thompson 1997, Kulbicki 1998, Samoilys & Carlos 2000, MinteVera et al. 2008). According to fish mobility and size for instance, most fish species can be broadly grouped in three categories, and the surface of a visual census sampling unit should be adapted differently to each (Harmelin et al. 1995, Kulbicki 1998, Bozec et al. 2011): (1) crypto-benthic fish spending most of their life cycle hidden within macrophytes stands, holes and crevasses, or resting motionless but camouflaged upon the substrate, thanks to coloration and/or suitable bodyshape. The detectability of these species is low and reduces sharply as a function of distance from the observer, thus they should generally be surveyed within small surfaces (0.5 - 1 meter from the observer) (Kovačić et al. 2012). (2) small-medium necto-benthic fish (< 40 cm total length) that are generally easy to detect, are not strongly affected by diver presence (Kulbicki 1998) and whose abundance is large enough to be surveyed at a medium distance from the observer. (3) large mobile necto-benthic fish (> 40 cm total length), that are easy to detect but are shy and/or generally occur at low abundances, thus they need to be surveyed within a larger surface than the previous group (Kulbicky 1998, Bozec et al. 2011). Distances from the observer adopted in the literature for these fish range from 5 to 15 meters (Harmelin et al. 1985, Tresher & Gunn 1986, Kulbicky 1998, Colvocoresses & Acosta 2007).

While in monitoring programs for coral reefs, transects of different widths have been adopted to survey fish of different size and behaviour (Halford & Thompson 1994, Mapstone et al. 1998, Sandin et al. 2008), this is not a common practice in the Mediterranean sea. To our knowledge no study in the Mediterranean has compared the effect of different surface units for the same method in quantifying fish density and biomass, nor have different surfaces been combined to survey the whole fish assemblage.

UVC by strip transects, the most widely adopted method in this basin (Prato et al. in prep), has been seldom adapted to different fish mobility. Variable transect widths were used in studies specifically targeting both cryptic (1-2 meters) and necto-benthic fish (4-5 meters) (De Girolamo & Mazzoldi 2001, Di Franco et al. 2013), but a single transect width was always used to target both small-medium necto-benthic fish (< 40 cm total length) and larger and more mobile fish. The most common transect widths adopted here ,moreover, do not exceed 5 meters, meaning a distance of 2.5 meters from the observer (Prato et al in prep), thus possibly underestimating the abundance of large mobile and shy fish that seldom approach the observer at such short distance. These fish generally correspond to the high trophic level predators, most sensible to fishing.

Monitoring programs adopting variable transect widths to survey crypto-benthic, nectobenthic and large mobile fish are thus particularly needed to more realistically assess the abundance of high trophic level predators and their relative contribution to total fish biomass, an important indicator of ecosystem health and recovery (Russ & Alcala 2003, Garcia-Rubies et al. 2013, Prato et al. 2013), as well as to investigate the indirect effects of protection on the whole fish assemblage. Based on these premises, this study has two main objectives: first to compare the effectiveness of two transects surfaces (35 x 20 m and 25x 5 m) both in i) quantifying the density and biomass of large mobile predators and species highly sensible to fishing within and outside Mediterranean MPAs, and ii) assessing the effect of protection on these species. Secondly, to integrate three transect surfaces (small, medium and large) in order to survey the whole fish assemblage, in particular to i) evaluate the response of HTLP to protection in comparison to the other functional groups, ii) quantify the relative contribution of each functional group to total fish biomass.

# 4.3 Methods

## 4.3.1 Study area



This study was performed at three MPAs in the Western Mediterranean (Fig.1). The Tavolara-Punta Coda Cavallo MPA (hereafter Tavolara MPA) is located in north-east Sardinia (Italy, 40° 35' N, 09° 49' E) and was established in 1997, but enforcement became effective around 2003-04. It includes 76 km of coastline, covers 15,357 ha, and is divided into three subareas characterised by different levels of protection. In the zone of integral reserve (no-take zone, 529 ha) only research activities are allowed, while in the two zones of partial protection different activities are allowed under regulations. Spearfishing is not allowed within the MPA borders.

The Cabo de Palos-Islas Hormigas MPA (herafter Cabo de Palos MPA) is located in southeastern Spain, and was established in 1995. Enforcement is high in the MPA since its establishment (Hackradt et al. 2014). The MPA extends from the coast to the Islas

Hormigas archipelago (37° 38' N, 0° 42' W), for a total surface of 1,898 ha divided into two zones: a no-take zone of 270 ha, surrounding the Hormigas islands archipelago, where only scientific research activities are allowed, and a zone of partial reserve where small scale fishing, recreational diving and boating are allowed with some limitations. Recreational fishing, including spearfishing, is not allowed within the MPA borders.

The Scandola MPA is located in north-west Corsica (France) and was established in 1975, with regular enforcement (Francour et al. 2001). It extends over 25 km of coastline, for a total area of 1,000 ha. It is divided into a no-take zone of 122 ha and a buffer zone where professional fishing is allowed under authorizations. In the no-take zone only scientific research activities are allowed and boating respecting speed limits (anchoring is forbidden). Recreational fishing, including spearfishing, is not allowed within the MPA borders. In the zones outside the three MPAs all activities are allowed.

### 4.3.2 Sampling design and data collection

Fish assemblage surveys were conducted at each MPA during 3-4 consecutive days in the warm season under optimal visibility conditions, respectively in summer 2013 for the Tavolara and Cabo de Palos MPAs and in summer 2014 for the Scandola MPA. At each MPA, on rocky habitats, four sites inside the no-take zone and four sites outside the MPA were randomly selected at a distance of about 500 m between each other. Visual census transects of three different surfaces were used in order to account for different fish mobility and to allow assessments on the whole fish community, as required by our second objective. Firstly, large transects 35 x 20 m<sup>2</sup> transects were used to record only large mobile necto-benthic fish and species very sensible to fishing (i.e. Sciaena umbra, Epinephelus marginatus). A transect width of 20 meters (i.e. 10 meters on each side of the diver) was chosen to encompass a large enough sample area for these shy species. Similar distances were selected in UVC studies including large mobile fish, although in some of those cases fixed points were used (Thresher & Gunn 1986, Samoilys & Carlos 2000).

Secondly, medium transects 25 x 5 m<sup>2</sup>, which is the most common transect in Mediterranean (Prato et al, in prep.) were adopted to record all necto-benthic fish (>5 cm total length). The species previously recorded in larger transect were also counted in medium transects to allow transect sizes comparison, as required by our first objective. Thirdly, small transects 10x1 m<sup>2</sup> were adopted to survey crypto-benthic fish (e.g. Blenniidae, Gobiidae, Scorpaenidae) and juveniles of necto-benthic fish (<5 cm total

length). Chromis chromis, Boops boops and Spicara spp juveniles were counted in small transects starting from < 4 cm total length, since it is the size at which these are more commonly seen near refuges (Pinnegar & Polunin 2000), while at greater sizes they are more commonly observed in the water column, and thus better surveyed with the 25 x 5 m transects.

Actual number of fish encountered was recorded up to 10 individuals, whereas larger groups were recorded using categories of abundance (i.e. 11–30, 31–50, 51–200, 201– 500,500-1000 ind.; see Harmelin-Vivien et al.1985). Fish size (total length) was recorded within 5 cm size classes for large sized fish (maximum size >50 cm), 2 cm size classes for necto-benthic fish and 1 cm for small crypto-benthic fish. Fish wet weight was estimated from size data by means of length–weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (www.fishbase.org).

At each site, four replicates of each transect size were completed between 5 and 15 meters depth, obtaining 4 replicate "triplets" per site. Each "triplet" of transects was completed in the following order: one large transect, one medium transect at 4-5 meters distance from the former and one small transect on the swim back of the medium transect, while rewinding the reel thread. Distance among adjacent triplets was approximatively 30-40 meters.

# 4.3.3 Data analysis

Each species was assigned to one of five functional groups following (Guidetti et al. 2008). Groups were: high trophic level predators, small piscivores, invertebrate feeders group 1 (major predators of sea urchins), invertebrate feeders group 2 (whose diet seldom includes sea urchins), small carnivorous crypto-benthic fish (including also juveniles of all species < 5 cm total length), planktonivores and herbivores (Tab.1). We split invertebrate feeders into two groups similarly to Guidetti et al. 2008 because of the major role the few fish species of group 1 can have in regulating sea urchin populations and hence potentially controlling ecosystem states (Sala et al. 1998, Guidetti 2006b). The same species (*Sparus aurata*, *Diplodus sargus*, *Diplodus vulgaris*) are also important fishery targets. Tab. 1 Surveyed taxa and corresponding functional group and transect type adopted to recorded them. HTLP= high trophic level Pedator, INV1= Invertebrate feeder type 1 (feeding mainly on sea urchins) INV 2= invertebrate feeder type 2, CA\_CB = carnivore cryptobenthic, PLA = planktonivore, HE = herbivore.

A = 35 x 20 m transects, B= 25 x 5 m transects, C = 10 x 1 m transects. For each species, juveniles (total length <5 cm and < 4 cm *for Chromis chromis, Boops boops* and *Spicara spp*.) were classified as carnivore cryptobenthic and recorded with transect C.

		Transect
Taxon	Functional group	type
Anthias anthias	PLA	В
Apogon imberbis	PLA	В
Boops boops	PLA	В
Chromis chromis	PLA	В
Coris julis	INV 1	С
Dentex dentex	HTLP	А
Diplodus annularis	INV 2	В
Diplodus cervinus cervinus	INV 2	А
Diplodus puntazzo	INV 2	В
Diplodus sargus sargus	INV 1	В
Diplodus vulgaris	INV 1	В
Epinephelus costae	HTLP	А
Epinephelus marainatus	HTLP	А
Labrus merula	INV 2	В
Labrus viridis	INV 2	В
Mullus surmuletus	INV 2	В
Mycteroperca rubra	HTLP	А
Ohlada melanura	PLA	В
Parahlennius aattoruaine	CA CB	С
Parahlennius nilicornis	CA CB	C
Parahlennius rouxi		C
Parahlennius tentacularis	CA CB	C
Parahlennius zvonimiri		C
Sarna salna	HF	В
Sciaena umbra	INV 2	А
Scorngeng spp	SP	С
Scorpaena scrofa	SP	C
Serranus cabrilla	SP	B
Serranus scriba	SP	B
Sparus aurata	INIV 1	A
Sphuraena viridensis		Δ
Spirgraena vinuensis		B
Spiculu spp.		B
Symphodus cinereus		B
Symphodus dodarlaini		B
Symphodus moditorranous		B
Symphodus mediterruneus		B
Symphodus melanocercus		D
Symphodus ocenatus		D
Symphodus roissall		D
Sympnoaus rostratus		D
Symphoaus tinca	INV 2	В
i nalassoma pavo	INV 2	В
Tripterygion delaisi	CA_CB	L C
i ripterygion tripteronotus	CA_CB	C

## Effectiveness of two transect sizes to survey large mobile fish

First we analysed the effectiveness of using large  $(35 \times 20 \text{ m}^2)$  or medium size  $(25 \times 5 \text{ m}^2)$  transects to survey 8 large mobile fish species and species sensible to fishing (Tab. 1). To compare the effectiveness of the two transect sizes at surveying large mobile fish we analysed two null hypothesis: i) the two transect sizes detected similar density, biomass and species richness at each level of protection and ii) the two transect sizes were equally effective in detecting an effect of protection. Accuracy and precision were the metrics used to select the most appropriate transect size. We used higher density and biomass estimates as a proxy for accuracy (Sale & Sharp 1983, Colvocoresses & Acosta 2007, Mintevera et al. 2008). We quantified precision using the 95% confidence interval of the mean estimates.

We analysed the data (8 species, 188 samples, 94 samples per each transect size) as density (n/m<sup>2</sup>) and biomass (g/m<sup>2</sup>) using 4-way permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) based on Bray-Curtis dissimilarity matrix. "Region" (R) was treated as a random factor with three levels (Corse, Sardinia and Spain), "Protection" (P) and "Transect size" (T) were treated as fixed orthogonal factors both with two levels, respectively IN and OUT for P, and A (large transects) and B (medium transects) for M. Site was treated as random factor with 4 levels nested in Region and Protection. The interaction between the two fixed factors P and T was tested first, and, if interactions were significant, post-hoc pairwise tests with Montecarlo test were performed to compare among transect sizes (T) for each protection level (P), and among protection levels for each transect size.

Non metric multidimensional scaling (nMDS) was used to visualise multivariate patterns. Species relevant for contributing to the significant differences among levels of the interaction factor were identified using similarity percentage (SIMPER) (Clarke & Warwick 2001).

Univariate metrics describing large mobile/shy fish (tab.1) assemblage structure - species richness, density and biomass for all fish pooled, and for each species - were individually compared between transect sizes by using univariate permutational analysis of variance based on Euclidean distance to avoid any assumption on the distribution of the data. Since our objective was to select the transect size allowing to identify most species of a fish assemblage in a given area, we considered raw estimates of species richness per transect, instead of standardizing it per transect surface.

Finally, in order to assess if Permanova results were due to differences among means and/or to differences among variances, we performed a PERMDISP analysis over the hierarchy of scales (following Di Franco et al 2014). We first calculated in PERMDISP the individual deviation values for each transect from centroids of the combined factor Transect size-Site-Protection-Region (i.e. the distances, in the normalized Euclidean space, of the individual replicates from the centroids of the 4 replicates in each site and transect). The individual deviation values obtained were then analysed using PERMANOVA under the same sampling design used above. The analysis was performed both on univariate and multivariate abundance and biomass data.

#### High trophic level predators contribution to total fish assemblage

Once the difference among transect sizes was tested, we analysed protection effect considering the whole fish assemblage, with univariate and multivariate analyses. For these analyses, the 8 large mobile/shy species sampled by using both large and medium transects, were removed from medium transects data matrix, in order to avoid overlap among large and medium transect data matrix. Thus, 3 matrix were obtained, containing data related to, respectively, (1) the 8 large mobile species sampled within large transects, (2) all necto-benthic fish (> 5 cm TL) sampled within medium transects, excluding the 8 large mobile species that were sampled also within large transect, (3) crypto-benthic fish and juveniles (<5 cm for necto-benthic fish and < 4 cm for the planktonivores C. chromis, S. spicara and B. boops) sampled only in small transects. The three matrices were then bind into one matrix accounting for the whole fish assemblage, and since species were surveyed on different surface units and thus had different variance scales, we performed the analysis on total counts and total biomass after down-weighting the dispersion measure of each species, in order to obtain data with comparable variance scales (Clarke et al 2006). This procedure consisted in dividing the counts/biomasses for each species by their dispersion index D, i.e. the variance to mean ratio calculated from replicates within a group (in our case the group was defined by the finest spatial scale, i.e. factor Site nested in Protection x Region). The resulting dispersion-weighted data matrix had a common (Poisson-like) variance structure across species, but unchanged relative responses of a species in different groups (Clarke et al. 2006). Permutational multivariate analysis of variance based on Bray Curtis dissimilarity were performed on down-weighted and then square root transformed abundance and biomass data, Permutational univariate analysis of variance based on Euclidean distance measure were performance on total abundance

and biomass data. As before, to assess if Permanova results were due to real differences among means or to differences in the variance, we assessed dispersion variability across the hierarchy of levels of our sampling design ( Di Franco et al 2014). We calculated in PERMDISP the individual deviation values for each down-weighted transect from centroids of the combined factor Site-Protection-Region (i.e. the distances, in the normalized Euclidean space, of the individual replicates from the centroids of the 4 replicates in each site). The individual deviation values obtained were then analysed using PERMANOVA under the same sampling design used above. The analysis was performed both on univariate and multivariate dispersion-downweighted abundance and biomass data.

In order to evaluate the magnitude of the reserve effect for each functional group, we analysed average effect sizes (ES) for each species based on Cohen's index (Cohen 1988) calculated as the difference between the mean biomass inside the MPAs and the mean biomass outside the MPAs, divided by the cumulated standard deviations of the two means. To test for significance of effect sizes we computed 95% confidence intervals and assessed if they overlapped or not with 0 (no overlap = significant ES). Finally, the contribution of each functional group to total fish density and biomass was analysed at the three MPAs, and relative contributions were compared between protected and non-protected zones in each MPA.

Analyses were performed using the R 3.1.0 software (R Development Core Team 2014) and the Primer 6 and PERMANOVA multivariate statistics package (Clarke & Gorley 2006).

## 4.4 Results

### 4.4.1 Effectiveness of two transect sizes to survey large mobile fish

Multivariate analysis on density and biomass data showed a significant interaction among Region, Protection and Transect size (p=0.001 and p=0.002 respectively) (Tab. 2). Pairwise tests on the interaction were performed between levels of Transect size and between levels of Protection. Transect sizes A and B significantly differed for biomass data inside the reserve both in Corsica (p=0.02) and Spain (p=0.002), while no significant differences among transect size resulted in Sardinia nor outside the 3 MPAs (Tab. 3, Fig. 2). When density data was considered p values were close to significance for the same regions (p=0.05 in Corsica and p=0.06 in Spain). Concerning the Protection factor, a significant reserve effect on density data was detected by both transect sizes in the

Tavolara MPA (Sardinia), and only by large transects in Cabo de Palos (Spain) (Tab. 3). When biomass data was analysed, both transect sizes detected a significant protection effect in all regions. Permdisp at the multiple scale showed that variances were homogenous for the interaction factor Region x Protection x Transect size for both density and biomass data (respectively p = 0.074 and p = 0.267).

Tab. 2 Multivariate Permanova on square root transformed density  $(n/m^2)$  and biomass data  $(g/m^2)$ . Only high trophic level predators and shy/mobile species are included in the analysis. Significant results are highlighted in bold.R= region, P = protection, T ) transect size, S= site

			D (n/m²)			B (g/m <sup>2</sup> )	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
R	2	96.58	2.1763	0.019	4551.5	2.2742	0.019
Р	1	435.48	8.1415	0.087	45653	28.302	0.115
т	1	78.976	0.84384	0.554	4480.8	1.413	0.403
RxP	2	53.492	1.2054	0.322	1613.1	0.80601	0.624
RxT	2	93.597	6.2932	0.001	3171.4	6.7217	0.001
PxT	1	68.065	1.0383	0.404	3388	1.8305	0.279
S(RxP)	18	44.431	2.1757	0.001	2003.1	2.1827	0.001
RxPxT	2	65.56	4.408	0.001	1851	3.9231	0.002
TxS(RxP)	18	14.86	0.7277	0.889	471.1	0.51334	1
Rs	143	20.421			917.72		
Total	190						

Tab. 3 Pairwise tests with Monte-carlo permutations for the combined factor Region x Potection x Method (multivariate Permanova) on square root transformed density (D,  $n/m^2$ ) and biomass data (B,  $g/m^2$ ). Tests were performed among levels of the factor Protection and among levels of the factor Method. Significant results are highlighted in bold.

	Levels	D	В
Inside MPA vs Outside MPA	Corsica, Transect A	0.087	0.035
	Corsica, Transect B	0.1471	0.046
	Sardinia, Transect A	0.036	0.009
	Sardinia, Transect B	0.013	0.001
	Spain, Transect A	0.029	0.001
	Spain, Transect B	0.077	0.022
Transect A vs Transect B	Corsica, IN	0.0512	0.019
	Corsica, OUT	0.1448	0.215
	Sardinia, IN	0.2515	0.739
	Sardinia, OUT	0.728	0.342
	Spain, IN	0.0603	0.002
	Spain, OUT	0.204	0.124



Fig. 2 Assemblage structure (in terms of biomass) of the eight high trophic level predators and rare species selected for comparison of transect sizes. Two-dimensional nMDS ordinations of centroids for the combined factor Region x Protection x Transect size are shown.

SIMPER for multivariate density and biomass on the combined factor Region x Protection x Transect size showed that species responsible for transect size difference inside Cabo de Palos were *Epinephelus marginatus*, *Sciaena umbra* with higher abundance and biomass detected with large transects (Fig.3), *Sparus aurata* detected with higher estimates in medium transects and *Sphyraena viridensis*, *Diplodus cervinus* and *Mycteroperca rubra* detected only with large transects (Fig.3). *E. marginatus*, *Dentex dentex* and *S. umbra* were also responsible for differences among transect size in the Scandola MPA (Corse): more and larger individuals of *E. marginatus* and *D. dentex* were detected with large transects, while *S. umbra* was better detected with medium transects.



Fig.3 Average density and biomass  $\pm$  SE detected by method A (large transects 35x20 m) and B (medium transects 25x5 m) for each of the 8 large mobile species, at each protection level and region.

Univariate Permanova on total density and biomass and on species richness also revealed a significant interaction among the factors Region, Protection and Transect size (p=0.002 for density and p=0.001 for biomass and species richness of the large mobile fish; Tab.4). Pairwise post-hoc tests were run for the interaction P x R x T, both among levels of the factor Transect size (to analyse differences among transect sizes in surveying the fish assemblage) and among levels of Protection (to analyse differences in the effectiveness of both transect sizes in detecting a protection effect). Transect size A and B resulted significantly different inside the Cabo de Palos MPA, with large transects (Transect A) detecting higher density (n/m<sup>2</sup>), biomass (g/m<sup>2</sup>) and species richness (S) than medium transects (Transect B) (Tab.5, Fig.4). Inside the Scandola MPA large transects detected significantly higher species richness than medium transects (Tab.5, Fig.4), while inside the MPAs there was no significant difference among the transect sizes, although in Cabo de Palos and Scandola there was a trend of higher biomass and species richness detected with large transects. For Tavolara, where fish biomass and species richness were lower than the

other case studies, the trend was opposite, with medium transects showing a trend of higher biomass, density and species richness than large transects (Fig. 4). Permdisp at the multiple scale on univariate density data showed that variances were homogenous for the interaction factor RxPxT (p = 0.234), while significant differences among variances were found for biomass data for the same interaction factor (p=0.001). Pairwise post-hoc tests among levels of the factor Transect size revealed that variances were not homogenous among the two transect sizes inside Cabo de Palos MPA (p=0.03).



Fig.4 Mean total density  $(n.m^{-2})$ , biomass  $(g.m^{-2})$  and species richness (S) ± SE detected by Transect size A (large transects 35x20 m) and B (medium transects 25x5 m) at each protection level and region. Asterisks indicate significant differences among methods.
Tab. 4 Univariate Permanova on square root transformed density (D;  $n/m^2$ ) and biomass data (B;  $g/m^2$ ) and on raw species richness data (S; number of species per replicate). Only high trophic level predators and shy/mobile species are included in the analysis. Re = Region, T= transect size, P= protection, S = site. Significant results are highlighted in bold.

			D			В		_	S	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
R	2	0.009	0.75	0.526	28.41	0.74	0.565	3.79	5.36	0.013
Р	1	0.231	41.14	0.074	567.69	27.51	0.073	35.52	14.79	0.167
т	1	0.006	0.24	0.583	35.85	0.96	0.582	14.32	1.98	0.280
RxP	2	0.006	0.46	0.693	20.65	0.53	0.696	2.40	3.40	0.050
RxT	2	0.023	11.92	0.002	37.18	40.02	0.001	7.23	36.64	0.001
PxT	1	0.013	0.83	0.435	31.59	1.00	0.412	10.65	2.64	0.277
S(RxP)	18	0.012	2.55	0.001	38.78	4.15	0.001	0.71	1.20	0.264
RxPxT	2	0.016	8.33	0.002	31.54	33.95	0.001	4.04	20.49	0.001
TxS(RxP)	18	0.002	0.40	0.987	0.88	0.09	1.000	0.19	0.33	0.997
Rs	140	0.005			9.35			0.59		
Total		188.00								

Tab. 5 Pairwise tests with Montecarlo permutations for the combined factor Region x Potection x Transect size (univariate Permanova) on square root transformed density (D;  $n/m^2$ ) and biomass data (B;  $g/m^2$ ) and on raw species richness (S) of the large mobile fish. Tests were performed among levels of the factor Potection and among levels of the factor transect size Significant results are highlighted in bold.

	Levels	D	В	S
	Corsica, Transect A	0.113	0.154	0.028
side MPA vs itside MPA	Corsica, Transect B	0.092	0.118	0.086
	Sardinia, Transect A	0.002	0.01	0.008
	Sardinia, Transect B	0.005	0.013	0.002
u Ou	Spain, Transect A	0.008	0.002	0.001
	Spain, Transect B	0.219	0.061	0.128
	Corsica, IN	0.636	0.934	0.03
A B	Corsica,OUT	0.684	0.56	0.399
ect s ect	Sardinia,IN	0.429	0.865	0.615
ans v rans	Sardinia,OUT	0.104	0.162	0.204
μμ	Spain,IN	0.016	0.002	0.003
	Spain,OUT	0.824	0.097	0.083

Concerning levels of the factor Protection, when univariate density and biomass data were analysed, both transect sizes detected a significant effect of protection in Tavolara, while in Cabo de Palos only transect A detected a significant effect of protection (Tab. 5). In Scandola protection effect was never significant. When Permdisp pairwise post-hoc tests were performed among levels of the factor Protection, variances were never homogenous among inside and outside each MPA. When species richness was analysed results were consistent for Cabo de Palos and Tavolara, while for Scandola a significant protection effect (p=0.03) was detected with transect A (Tab. 5).

When evaluating the precision of different transect sizes through the analysis of 95% confidence intervals (Fig. 5), differences among the two transect sizes appeared highly variable depending on the region and protection level. Inside the three MPAs larger transects showed a trend of larger confidence intervals (thus lower precision) than medium transects, with the exception of Tavolara for biomass data, where the trend was opposite. Outside the three MPAs, when density data was considered larger transect resulted more precise than medium ones. Considering biomass data this trend was confirmed only for Tavolara, while outside Scandola and Cabo de Palos larger transects appeared less precise.



Fig. 5. 95 % confidence intervals on the mean density and biomass estimates within and outside the three marine protected areas

# 4.4.2 Fish assemblage analysis

Multivariate analysis revealed a significant interaction among the factors Region and Protection for both abundance and biomass data (p = 0.001, Tab. 6). Pairwise tests showed a significant effect of protection in Sardinia and Spain, while no significant protection effect was highlighted in Corsica.(Tab. 7, Fig. 6).

Permdisp at the multiple scale showed that after dispersion weighting, variances were homogenous for all interaction factors and for the protection factor, while significant differences among variances were found only for the factor Region.

Tab. 6 Multivariate Permanova on square root transformed abundance (n) and biomass (g) data for the whole fish assemblage. Significant results are highlighted in bold.

			N			В			
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)		
R	2	9472.7	4.6514	0.001	9735.3	4.2272	0.001		
Р	1	12392	3.0522	0.146	14166	3.1114	0.154		
RxP	2	4082.3	2.0046	0.003	4577.1	1.9875	0.003		
S(RxP)	18	2059.6	1.6959	0.001	2326	1.5638	0.001		
Rs	67	1214.5			1487.4				
Total	90								

Tab. 7 Pairwise tests with Montecarlo permutations for the combined factor Region x Potection on dispersion weighted and square root transforTd abundance (n) and biomass (g) data . Tests were performed among levels of the factor Potection. Significant results are highlighted in bold.

		Ν	В
1PA MPA	Corsica	0.272	0.232
nside N Vs utside	Sardinia	0.002	0.001
= 0	Spain	0.001	0.001



Fig.

6 Fish assemblage structure for dispersion down-weighted and square root transformed biomass data. Twodimensional nMDS ordinations for the centroids of the combined factor Region x Protection are shown.

Univariate analysis for the whole fish assemblage revealed no significant effect of protection, although for biomass data the probability approached the threshold (p = 0.089) (Tab.8). Permdisp at the multiple scale showed significant differences among variances only for the factor Site.

			Ν			В	
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
R	2	106.2	0.52357	0.674	4.3569	1.7429	0.189
Р	1	1158.9	25.302	0.103	28.174	34.772	0.089
RxP	2	45.658	0.2251	0.871	0.81091	0.32438	0.783
S(RxP)	18	206.74	3.2346	0.002	2.5498	3.5203	0.001
Rs	67	63.915			0.72431		
Total	90						

Tab. 8 Univariate Peranova on dispersion weighted and square root transformed abundance (n) and biomass (g) data for the whole fish assemblage. Significant results are highlighted in bold.

The analysis of effect size showed that high trophic level predators (HTLP) were always significantly responding positively to protection (95 % confidence intervals of the effect size not overlapping 0), with the exception of *Muraena helena* (Fig. 7). In average, the magnitude of HTLP response (Significant effect size = 0.43) was the highest compared to all other functional groups. *Epinephelus marginatus* had one of the largest effect sizes compared to all other species (E.S.= 0.84). Invertebrate feeders 1 and 2 were the only

other groups showing a significantly positive response to protection. While all species of group 1 had positive effect sizes, the magnitude and direction of the response in group 2 was highly species-specific. The response of small piscivores, crypto-benthic fish and planktonivores was also highly variable, with most species not showing significant increases within the no-take zones. Some species showed higher biomasses outside the MPAs (negative E.S.) (*Scorpaena scrofa, Diplodus annularis, Parablennius gattorugine* and the two planktonivores *Anthias anthias* and *Boops boops*), although significance could not be assessed for most of them since these species were not recorded at all three MPAs in this study and therefore was not possible to calculate confidence intervals. The largest positive response to protection was shown by the crypto-benthic fish *Tripterygion delaisi* with an effect size of 0.87 (Fig. 7).



Fig.7 Average effect size  $\pm$  IC 95% calculated for each species (points) and trophic group (squares) based on Cohen's Index. Black points stand for significantly positive effect size, meaning error bars not overlapping 0, or markedly positive effect sizes (when confidence intervals could not be computed). Grey points stand for non-significant effect size, or just negative or null effect sizes when error bars could not be computed. Bright red squares mean significantly positive effect size for trophic class, opaque red means non-significant effect size.

Analysis of functional groups percentage composition showed that in terms of density, the relative contribution of functional groups to total fish assemblage did not vary markedly within and outside the three MPAs, with planktonivorous and carnivorous crypto-benthic and juvenile fish always dominating, followed by invertebrate feeders of type 1 (Fig. 8).

When biomass data were considered, the high trophic level predators showed larger contributions within than outside the three MPAs: almost 50% within vs 2% outside Cabo de Palos MPA, 25% vs <2% in Scandola and 9% vs <1% in Tavolara. In the no-take zone of the Cabo de Palos MPA (Spain) (148  $\pm$  26 g/m<sup>2</sup> total biomass), the HTLP biomass was the highest, followed by that of invertebrate feeders of group 2 (18%). Outside the MPA  $(70 \pm 16 \text{ g/m}^2 \text{ total biomass})$ , fish assemblage biomass was more equally partitioned among invertebrate feeders and planktonivorous fish (36 % and 32 % respectively). In the no-take zone of the Scandola MPA (Corse) (218 ± 52 g/m2 total biomass), high trophic level predators reached 25 % of the total fish biomass, but the trophic pyramid was dominated by necto-benthic carnivorous fish (58% of total biomass). Outside this MPA (79  $\pm$  12 g/m<sup>2</sup> total biomass) the biomass of carnivorous necto-benthic fish showed the highest percentage (53%), followed by planktonivores and herbivores (31% and 11 % respectively). Finally, in the no-take zone of Tavolara MPA (Italy) (83 ± 12 g/m<sup>2</sup> total biomass), the necto-benthic carnivorous fish dominated (49%) followed by herbivores and planktonivores (approximatively 20% each). Outside this MPA ( $18 \pm 3 \text{ g/m}^2$  total biomass) the relative proportions of the groups, except HTLP, were fairly consistent with the no-take zone (Fig. 8).



Fig. 8 Functional groups density and biomass percentage inside and outside the three MPAs. For each species, juvenile fish (total length <5 cm and < 4 cm for *Chromis chromis, Spicara spp* and *Boops boops*) were classified as small crypto-benthic carnivores.

### 4.5 Discussion

Here, we highlight how adopting large size transects (20 x 35 m) instead of standard 5 x 25 m transects to survey large mobile and shy fish within MPAs increases the accuracy of density and biomass estimates, allowing to reduce the bias of under-estimation due to the common avoidance behaviour of these fish. Next, through the adoption of three transect sizes to survey the whole fish assemblage at three Mediterranean MPAs, we highlighted a significant effect of protection on high trophic level predators, whose response was always higher in magnitude than that of other functional groups. Trophic pyramids differed within and outside MPAs due to the larger contribution of HTLP to total fish biomass at protected sites. This, coupled with the highest contribution of HTLP to total fish biomass at older MPAs, suggests this metric as an effective indicator of MPA performance.

### 4.5.1 Effectiveness of two transect sizes to survey large mobile fish

Achieving a realistic estimate of fish assemblage density and biomass through visual census is an arduous task. On one hand, many authors agree that UVC underestimates the true abundance of fish, since a human observer will likely always miss a small percentage of fish that are really on the census area (e.g. Sale & Douglas 1981, Sale & Sharp 1983, Short & Bayliss 1985). Thus, when several visual census methods are compared, greater accuracy is generally assumed to be represented by the highest density of fish recorded (Samoylis & Carlos 2000, Mintevera et al. 2008). On the other hand, other authors suggest that underwater visual census may overestimate the abundance of fish because of non-instantaneous counts being performed (Ward-Paige et al. 2010, Trebilco et al. 2013). This bias can occur especially in presence of predator fishes displaying high swimming speed and attractive behaviour towards divers (Ward-Page et al. 2010). The mobility of fish relative to the census area is likely to have the greatest effect on the accuracy of the visual census method (Myers 1989): simultaneously counting a range of species with different mobility leads to lesser accuracy in estimates than if species groups are counted separately using the most adapted method to their mobility ((Smith 1989, De Girolamo & Mazzoldi 2001). In this perspective, we analysed the effectiveness of large sized transects and medium sized transects at recording large mobile and shy fish, that in the Mediterranean are generally surveyed using the same transect dimensions adopted for all necto-benthic fish (Prato et al. in prep). Strip transects of larger size resulted more accurate than medium ones in no-take zones of older MPAs

(Cabo de Palos and Scandola), detecting higher abundance and biomass of large mobile fish. In particular, Dentex dentex, Sphyraena viridensis and Mycteroperca rubra were always more accurately surveyed with larger transects (i.e. higher abundances and biomass in large transects). Large transects also reached higher density and biomass estimates for Epinephelus marginatus in Scandola and Cabo de Palos MPAs. By comparing dispersion of the data across the full hierarchy of scales we could moreover confirm that identified differences among transects sizes for the single species were actually due to real differences in the estimated means and not to differences in their dispersion. These results well agree with what observed by Kulbicky (1998), i.e that larger numbers of shy fish would be observed further away from the observer than directly on the transect path. Even where these species are abundant, such as in our above-mentioned case studies, they will still keep at a "safety distance" from the observer, thus the probability of detection (sensu Kulbicky, 1989) within a distance of 10 m is higher than that of detecting them within 2.5 from each side of the observer. Larger transect size could thus help reducing the bias of under-estimation due to fish behaviour. Additionally, the possible overestimation bias of non-instantaneous visual counts due to the higher speed of the large mobile fish with respect to the speed of the observer (Ward-Page et al. 2010), is unlikely to insist here. As stated also in Guidetti et al. 2014 in fact, the large mobile fish in the analysed ecosystem are not particularly fast-swimming species that can be attracted by divers. Moreover, larger transects were surveyed at an average speed (700m<sup>2</sup> / 5min) approximatively 8 times higher than the speed of survey on medium transects (125m<sup>2</sup> / 8min), thus overestimation bias due to fish flux across the sampling surface is likely reduced. Nonetheless, further testing would be needed to formally assess this issue.

In unprotected areas and in the Tavolara MPA, finally the two transect sizes did not significantly provide different estimates , although a trend of higher density estimates was observed with smaller transects. This trend could be due to the smaller individuals observed in the external sites and in Tavolara MPA. Indeed, smaller dusky grouper individuals tend to be more hidden in crevices and thus be less visible, which might explain why an observer having to survey a larger surface would miss them (Cheal & Thompson 1997, Bozec et al. 2011). In medium transects a smaller area can be more easily searched and thus it is more probable to detect more sedentary and hidden species (Mintevera et al. 2008), such as, in our case, smaller individuals of the dusky grouper. Although large mobile fish were not considered in their study, Mintevera et al 2008 compared nested cylinders of varying radius length to survey fish of different size classes, showing that best

density estimates for small sized individuals were obtained on smaller surfaces, while larger individuals were recorded with higher accuracy and precision in larger surface units. The same is likely happening in our case, and although we did not directly test it, the approach would possibly benefit from a separation among size classes for the large mobile fish.

Both transect sizes were effective in detecting a protection effect at the three MPAs, although the lower abundance estimates provided by small transects did not allow to reach significance when total density estimates were analysed. Finally, differences in precision among the two transect sizes did not show clear univocal trends within and outside the MPAs. The trend of lower precision shown by large transects within MPAs is likely due to the detection of more rare and shy species (i.e. *M. rubra*, *E. costae*, *S. viridensis*,) that are always missed by medium transects, and generally absent outside the MPAs due to their avoidance behaviour. The choice of the transect size to be adopted should thus balance the trade-offs of detecting higher number of species, while achieving lower precision.

### 4.5.2 Fish assemblage analysis

Overall, the higher accuracy (i.e. biomass) and species richness on large transects in two of the three MPAs, coupled to the non-significance in transect differences in Tavolara led us to select the combination of large, medium and small transect sizes, as the best option to analyse the full fish assemblage and assess the relative contribution of high trophic level predators to fish biomass within the three MPAs.

A significant effect of protection was detected both for large mobile fish analysed alone and for the whole fish assemblage at both the Cabo de Palos and Tavolara MPAs, in agreement with previous studies (García-Charton et al. 2004, Di Franco et al. 2009). For the Scandola MPA instead, a protection effect was detected only for large mobile fish, and not when the whole fish assemblage was analysed. This result was probably a consequence of the high among-site variability in this MPAs, as confirmed by a significant difference among dispersions at the site scale. Within the no-take zone in fact remarkably high biomass estimates were concentrated in one particular site (Palazzu). On one hand, the exposure and structural complexity of this site make it a refuge zone for the dusky grouper in particular (Francour 1994). Striking differences in fish biomass have indeed been observed since few years after the MPA establishment, when this site was compared with the same external sites we surveyed (Francour 1989). Since 1995 moreover, an almost exponential increase in the abundance of dusky groupers has been observed at the

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same site, highlighting the occurrence of a strong refuge effect after fishing was banned (Seytre et al. in prep). On the other hand, one site within the no-take zone showed biomass values in the same range of those observed outside the MPA, which were relatively high for a non-protected area. The protection effect in this MPA is thus likely masked by a combination of factors: a high inter site variability within the no take zone, probably linked to differences in the geomorphological complexity of the habitat, and a relatively high abundance and biomass of fish outside the MPA (79 g/m2 outside Scandola, a higher value than what observed in a multitude of non-protected areas across the Mediterranean (Sala et al. 2012, Guidetti et al. 2014).

Overall, the average response of HTLP to protection was always positive at the three MPAs, and was higher in magnitude than the response of other functional groups. Invertebrate feeders of group 1 were also always favoured by protection since they included species usually targeted by fishing. Lower trophic level species (many of which are also non - commercial species) showed high variability in response, including reduction of some species in the MPAs, which highlighted the occurrence of possible indirect effects of protection through predation or competition for resources. These results were similar to meta-analytical studies encompassing several Mediterranean MPAs (Micheli et al. 2004, Guidetti 2007), and well corresponded to the response observed by the same trophic groups in well enforced MPAs (Guidetti et al. 2008). Nonetheless, although cascading trophic interactions are likely occurring at the species level, at the trophic group level there was no significant evidence of biomass reduction within the MPAs compared to the exploited sites. Exploitation at the non-protected sites is thus likely to have larger impact across the food-web than the top-down control exerted by high trophic level predators at protected sites (Soler et al. 2015).

Finally, analysis of trophic pyramids showed that biomass contribution of high trophic level predators is larger within each MPA than outside compared to other functional groups, markedly contributing to total fish biomass in the total protection zones. As also suggested by Soler et al 2015, such disparity in biomass ratios between MPAs and open access sites for the different trophic groups implies a trophic re-organisation that is likely to have substantial consequences for ecological functions. This is likely to be more evident at older and highly enforced MPAs like Scandola (1975) and Cabo de Palos (1995), where HTLP contribution to total fish biomass eventually led to top heavy trophic pyramids and was higher than in the more recently established and enforced Tavolara MPA (1997, but enforced in 2003). Similar trends were observed in a study covering 13 MPAs and 17

unprotected sites across the Mediterranean (Guidetti et al 2014), suggesting that this metric is a useful indicator of MPA performance.

# 4.6 Conclusion

It has been demonstrated that high trophic level predators keep increasing in MPAs up to several years after protection (Garcia Rubies et al. 2013), and long term monitoring programs are thus essential to establish whether carrying capacity has been reached or not for these species (Garcia Rubies et al. 2013). On the basis of our results, we additionally suggest that such monitoring programs should adopt transects of variable surface adapted to fish mobility and behaviour, as it is has long been suggested (Harmelin Vivien et al. 1985). Although the use of the 20 m transect width we proposed might be limited by lower visibility conditions in the cold season and increase the chance of errors in surface estimations, we suggest that the necto-benthic fish and large mobile fish should be counted separately, especially in MPAs with high fish abundance, and that the size of the transects should be larger for large mobile fish than for necto-benthic fish. We did not test if separating the counts for large mobile fish and necto-benthic fish would also increase the accuracy of counts for the latter, but this is very likely to be the case especially in MPAs with high abundances of both groups. Counting a small number of fish is in fact generally more accurate than counting a large number (Cheal & Thompson 1997, De Girolamo & Mazzoldi 2001).

Adoption of transects of variable surface respectively for large mobile fish, necto-benthic fish and cryptic fish, in monitoring programs would be a simple improvement to traditional one-size transect surveys, and would allow to increase the accuracy of total fish assemblage estimates within MPAs, especially when the abundance of high trophic level predators within them is significantly recovering.

# 4.7 References

- Bannerot SP, Bohnsack JA (1986) A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Tech Rep NMFS 41:1–15
- Britten GL, Dowd M, Minto C, Ferretti F, Boero F, Lotze HK (2014) Predator decline leads to decreased stability in a coastal fish community. Ecol Lett 17:1518–1525
- Brock VE (1954) A preliminary report on a method of estimating reef fish populations. J Wildl Manag:297–308

- Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. Mar Ecol Prog Ser 158:241–248
- Clarke KR, Chapman MG, Somerfield PJ, Needham HR (2006) Dispersion-based weighting of species counts in assemblage analyses. Mar Ecol Prog Ser 320:11–27
- Clarke KR, Gorley RN (2006) User manual/tutorial. Primer-E Ltd Plymouth:93
- Cohen J (1988) The effect size index: d. Stat Power Anal Behav Sci 2nd Ed N J Lawrence Erl-Baum Assoc:20–26
- Colvocoresses J, Acosta A (2007) A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations. Fish Res 85:130–141
- Bozec Y-M, Kulbicki M, Laloë F, Mou-Tham G, Gascuel D (2011) Factors affecting the detection distances of reef fish: implications for visual counts. Marine Biology 158:969–981
- De Girolamo M, Mazzoldi C (2001) The application of visual census on Mediterranean rocky habitats. Mar Environ Res 51:1–16
- Di Franco A, Bulleri F, Pennetta A, De Benedetto G, Clarke KR, Guidetti P (2014) Within-Otolith Variability in Chemical Fingerprints: Implications for Sampling Designs and Possible Environmental Interpretation (S Thrush, Ed.). PLoS ONE 9:e101701
- Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P (2009) Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. Mar Ecol Prog Ser 387:275–285
- Di Franco A, Di Lorenzo M, Guidetti P (2013) Spatial patterns of density at multiple life stages in protected and fished conditions: an example from a Mediterranean coastal fish. J Sea Res 76:73–81
- Edgar GJ, Barrett NS, Morton AJ (2004) Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. J Exp Mar Biol Ecol 308:269–290
- Francour P (1989) Les peuplements ichtyologiques de la réserve de Scandola: influence de la réserve intégrale. Trav Sci Nat Régional Réserves Nat Corse:33–93
- Francour P (1994) Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). Oceanol Acta 17:309–317
- Francour P, Harmelin JG, Pollard D, Sartoretto S (2001) A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquat Conserv Mar Freshw Ecosyst 11:155–188
- García-Charton JA, Pérez-Ruzafa A, Sánchez-Jerez P, Bayle-Sempere JT, Reñones O, Moreno D (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. Mar Biol 144:161–182
- Garcia-Rubies A, Hereu B, Zabala M (2013) Long-Term Recovery Patterns and Limited Spillover of Large Predatory Fish in a Mediterranean MPA. PLoS ONE 8
- Guidetti P (2006a) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol Appl 16:963–976

Guidetti P (2006b) Marine reserves reestablish lost predatory interactions and cause community changes in rocky reefs. Ecol Appl 16:963–976

- Guidetti P (2007) Potential of Marine Reserves to Cause Community-Wide Changes beyond Their Boundaries. Conserv Biol 21:540–545
- Guidetti P, Baiata P, Ballesteros E, Di Franco A, Hereu B, Macpherson E, Micheli F, Pais A, Panzalis P, Rosenberg AA, Zabala M, Sala E (2014) Large-Scale Assessment of Mediterranean Marine Protected Areas Effects on Fish Assemblages. PLoS ONE 9:e91841
- Guidetti P, Milazzo M, Bussotti S, Molinari A, Murenu M, Pais A, Spano N, Balzano R, Agardy T, Boero F, Carrada G, Cattaneo-Vietti R, Cau A, Chemello R, Greco S, Manganaro A, Sciara GN di, Russo GF, Tunesi L (2008) Italian marine reserve effectiveness: Does enforcement matter? Biol Conserv 141:699–709
- Hackradt CW, García-Charton JA, Harmelin-Vivien M, Pérez-Ruzafa Á, Le Diréach L, Bayle-Sempere J, Charbonnel E, Ody D, Reñones O, Sanchez-Jerez P, others (2014) Response of rocky reef top predators (Serranidae: Epinephelinae) in and around marine protected areas in the Western Mediterranean Sea.
- Halford AR, Thompson AA (1994) Visual census surveys of reef fish. Australian Institute of Marine Science
- Harmelin J-G, Bachet F, Garcia F (1995) Mediterranean Marine Reserves: Fish Indices as Tests of Protection Efficiency. Mar Ecol 16:233–250
- Harmelin-Vivien M, Harmelin J (1975) Présentation d'une méthode d'évaluation in situ de la faune ichtyologique. Trav Sci Parc Nation Port-Cros 1:47–52
- Harmelin-Vivien M, Harmelin J, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G,
   Blanc F, Chevalier R, Duclerc J (1985) Evaluation visuelle des peuplements et
   populations de poissons: méthodes et problèmes. Rev Décologie 40:467–539
- Kovačić M, Patzner RA, Schliewen U (2012) A first quantitative assessment of the ecology of cryptobenthic fishes in the Mediterranean Sea. Mar Biol 159:2731–2742
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J Exp Mar Biol Ecol 222:11–30
- Mallet D, Pelletier D (2014) Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). Fish Res 154:44–62
- Mapstone BD, Ayling T, Great Barrier Reef Marine Park Authority (1998) An investigation of optimum methods and unit sizes for the visual estimation of abundances of some coral reef organisms. Great Barrier Reef Marine Park Authority, Townsville, Qld.
- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. Ecol Appl 14:1709–1723
- Mintevera CV, Moura RL de, Francini-Filho RB (2008) Nested sampling: an improved visual-census technique for studying reef fish assemblages. Mar Ecol Prog Ser 367:283–293
- Myers (1989) Micronesian reef fishes. A practical guide to the identification of coral reef fishes of the tropical Central and Western Pacific. Coral Graphics. Guam. 298 pp

- Murphy HM, Jenkins GP (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review. Mar Freshw Res 61:236
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283
- Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483–488
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, Anna G d' (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200
- Prato G, Guidetti P, Bartolini F, Mangialajo L, Francour P (2013) The importance of highlevel predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context. Adv Oceanogr Limnol 4:176–193
- Russ GR, Alcala AC (2003) Marine reserves: rates and patterns of recovery and decline of predatory fish, 1983-2000. Ecol Appl 13:1553–1565
- Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Guclusoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications. Plos One 7:e32742
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos:425–439
- Sale PF, Douglas WA (1981) Precision and accuracy of visual census technique for fish assemblages on coral patch reefs. Environ Biol Fishes 6:333–339
- Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37–42
- Samoilys MA, Carlos G (2000) Determining Methods of Underwater Visual Census for Estimating the Abundance of Coral Reef Fishes. Environ Biol Fishes 57:289–304
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS One 3:e1548
- Shears NT, Babcock RC (2002) Marine reserves demonstrate top-down control of community structure on temperate reefs. Oecologia 132:131–142
- Short J, Bayliss P (1985) Bias in aerial survey estimates of kangaroo density. J Appl Ecol:415–422
- Smith MPL (1989) Improving multispecies rocky reef fish censuses by counting different groups of species using different procedures. Environ Biol Fishes 26:29–37
- Soler GA, Edgar GJ, Thomson RJ, Kininmonth S, Campbell SJ, Dawson TP, Barrett NS, Bernard ATF, Galván DE, Willis TJ, Alexander TJ, Stuart-Smith RD (2015) Reef

Fishes at All Trophic Levels Respond Positively to Effective Marine Protected Areas. PLOS ONE 10:e0140270

- Tessier A, Pastor J, Francour P, Saragoni G, Crec'hriou R, Lenfant P (2013) Video transect as a complement to underwater visual census to study reserve effect on fish assemblages. Aquat Biol
- Thresher RE, Gunn JS (1986) Comparative analysis of visual census techniques for highly mobile, reef-associated piscivores (Carangidae). Environ Biol Fishes 17:93–116
- Trebilco R, Baum JK, Salomon AK, Dulvy NK (2013) Ecosystem ecology: size-based constraints on the pyramids of life. Trends Ecol Evol
- Ward-Paige C, Flemming JM, Lotze HK (2010) Overestimating fish counts by noninstantaneous visual censuses: consequences for population and community descriptions. Plos One 5:e11722
- Williams ID, Walsh WJ, Tissot BN, Hallacher LE (2006) Impact of observers' experience level on counts of fishes in underwater visual surveys. Mar Ecol Prog Ser 310:185–191
- Willis TJ (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. J Fish Biol 59:1408–1411

# Section 2. Food web modelling

The trophic re-organization observed within MPAs linked to the large increase in high trophic level predators biomass, as highlighted in Chapter 4, is likely to affect ecosystem functions and their reponse to human impacts (Soler et al 2015). Food-web modelling allows to unravel trophic interactions and to dig deeper on the effects of protection/exploitation on ecosystem functions (Libralato et al. 2010, Plagany et al. 2014). In this section we aim to test the potential of food web modelling with Ecopath and EcoTroph as a management tool within MPAs. If the process of model building is simplified and standardised while kept reliable (Chapter 5), EwE modelling could be incorporated to the management of MPAs., both as an integrative approach to make the most of existing data and build upon it according to management needs (Chapter 6), as well as a driver and guide for efficient monitoring (Chapter 7)



Location of the MPAs for which models where developed (Portofino, Cap Roux) or analysed (Port Cros) in the chapters of this section.

# Ecopath and EcoTroph core principles and equations

# Ecopath

The EwE modelling approach (Christensen & Pauly 1992, Christensen & Walters 2004) is founded on the Ecopath model, which provides a quantitative representation of the studied ecosystem in terms of trophic flows and biomasses for a defined time period (a snap-shot).

The ecosystem is represented by trophically linked functional groups, which can be composed of species, groups of species with ecological similarities, or ontogenetic fractions of a species.

The key principle of Ecopath is mass balance: for each group represented in the model, the energy removed from that group, for example by predation or fishing, must be balanced by the energy consumed, i.e. consumption. Two linear equations represent the the energy balance among groups (Eq.1) and the energy balance within a group (Eq.2) :

$$P/B_{i} \times B_{i} = B_{i} \times P/B_{i} \times (1 - EE_{i}) + \Sigma^{N}{}_{j} (Q/B)_{ji} \times Bi \times DC_{ji} + Y_{i} + NM_{i} + Ba_{i}$$
(1)  

$$Qi=P_{i} + R_{i} + UA_{i}$$
(2)

N is the number of functional groups in the model, B is the biomass, P/B is the production rate, Q/B is the consumption rate,  $DC_{ji}$ , the diet composition is the fraction of prey i included in the diet of predator j, NM<sub>i</sub> is the net migration of prey I, BA<sub>i</sub> is the biomass accumulation of prey i, Y<sub>i</sub> is the catch of prey i and EEi is the ecotrophic efficiency of prey i, i.e. the fraction of production which is used in the system, R the respiration, P the production, Q the consumption, and UA the unassimilated consumption because of egestion and excretion. The quantity  $(1 - EE) \times P/B$  is the 'other mortality' rate unexplained by the model.

Ecopath parameterizes the model by describing a system of linear equations for all the functional groups in the model. For each functional group, three of the basic parameters: Bi, (P/B)i, (Q/B)i or EEi have to be known in addition to the fisheries yield (Yi) and the diet composition. The energy balance within each group is ensured when consumption by group (i) equals production by (i), respiration by (i) and food that is unassimilated by (i) (see Eq. 2). The units of the model are expressed in terms of nutrient or energy related currency by unit of surface (frequently expressed as tons x km<sup>-2</sup> x yr<sup>-1</sup>).

One of the main outputs that Ecopath provides is the trophic level of each group, which characterizes their position within ecosystem's food web (Lindeman, 1942; Odum & Heald, 1975). By convention, primary producers and detritus have TL = 1, while values for consumer groups are calculated from the weighted average TL of their prey.

The TL is computed as follows:

$$\tau_j = 1 + \Sigma (DC_{ji} \times \tau_i)$$
(3)

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Where j is the predator of prey i,  $DC_{ji}$  is the fraction of prey i in the diet o fpredator j and  $\tau_i$  is the trophic level of prey i.

### **Ecotroph**

The EcoTroph model is based on two key ideas. The first key idea is that an ecosystem can be represented by the distribution of its biomass across trophic levels (TLs). This distribution is called the biomass trophic spectrum (Gascuel et al. 2005). The biomass enters the food web at TL=1, generated by primary producers or recycled by the microbial loop (Figure 3.1). Between TL=1 and TL=2, There is no biomass between TLs 1 and 2, all animals being at a TL equal to (for herbivores and detritivores) or higher than 2. At TLs>2, the biomass is composed by heterotrophic organisms with mixed diet and fractional TLs resulting in a continuous distribution of biomass along TLs (the biomass trophic spectrum, Gascuel et al. 2005)

The second key idea is that the trophic functioning of marine ecosystems is modelled as a biomass flow surging up the food web from lower to higher trophic levels (Figure 3.1). Each organic particle moves more or less rapidly up the food web according to abrupt jumps caused by predation and to continuous processes (ontogenic changes in TLs). All particles jointly constitute a biomass flow which is considered together using a continuous model (Gascuel et al. 2008).

Based on the traditional equations of fluid dynamics, the flow of the biomass present in the ecosystem at  $TL\tau$  under steady-state conditions is expressed as:

$$\phi(\tau) = \mathsf{D}(\tau) \times \mathsf{K}(\tau) \tag{4}$$

Where  $\phi(\tau)$  refers to the amount of biomass that moves up the food-web through TL $\tau$  (expressed in tons per year), D( $\tau$ ) is the density of biomass at trophic level  $\tau$  (expressed in tons per trophic level) and K( $\tau$ ) is the speed of flow, which quantifies the velocity of biomass transfers in the food-web (expressed as the numbers of TLs crossed per year).

The continuous distribution of the biomass across a trophic level is calculated using a discrete approximation based on small trophic classes. EcoTroph conventionally considers trophic classes of width  $\Delta \tau$  equal to 0.1 *TL*, from Trophic Level 2 (corresponding to first-order consumers) to Trophic Level 5 (value considered sufficient to cover all top predators likely to occur in marine ecosystems). Thus, the mean biomass  $B_{\tau}$  (in t), which is present

in the  $[\tau,\tau+\Delta\tau]$  trophic class under steady-state conditions, can be estimated as  $\int D(\tau) \times d\tau$ or  $D(\tau) \times \Delta\tau$  for a small interval  $\Delta\tau$ . Therefore:

$$B\tau = \phi\tau \times \Delta\tau / K\tau$$
(5)

where  $\phi \tau$  and  $K \tau$  are the mean biomass flow and mean speed of flow within the  $[\tau, \tau + \Delta \tau]$  trophic class, respectively.

As natural losses occur during trophic transfers (through non-predation mortality, respiration, and excretion), the biomass flow  $\Phi_{\tau}$  is a decreasing function of TL. Exploitation by fisheries can be considered a diversion of one part of the trophic flow, which adds to this negative natural trend. Therefore, from one trophic class to the next, the biomass flow is calculated as

$$\phi \tau + 1 = \phi \tau \times \exp[-(\mu_{\tau} + \phi_{\tau}) \times \Delta \tau]$$
(6)

where  $\mu_{\tau}$  is the natural loss rate (related to excretion and respiration) and  $\phi_{\tau}$  is the fishing loss rate (with  $\phi_{\tau} = F_{\tau} / K_{\tau}$ , where F is the fishing mortality). Eq. (6) implies that the biomass flow at a given TL depends on the flow from lower TLs. Thus, it implicitly introduces a bottom–up control of prey on predators in the model. Eq. (6) also defines the net transfer efficiency (NTE) between continuous TLs as exp(- $\mu\tau$ ).

The speed of the biomass flow  $K_{\tau}$  (flow kinetic) depends on the turnover of the biomass, and must be estimated for each trophic class. It is expressed as

$$\mathsf{K}\tau = (\mathsf{P}/\mathsf{B}) \tau \tag{7}$$

 $K_{\tau}$  is first estimated for a reference state (usually the current state). Then, starting with values defined for the reference state, the speed of flow for a given simulated state is calculated using the top-down equation:

$$K_{\tau} = \left[K_{ref,\tau} - F_{ref,\tau}\right] \left[1 + \alpha_{\tau} x \frac{B_{pred}^{\gamma} - B_{ref,pred}^{\gamma}}{B_{ref,pred}^{\gamma}}\right] + F_{\tau}$$
(8)

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This equation takes into account the effect of fishing on flow kinetics  $K_{\tau}$  and the effect of predators on prey. Fishing reduces the life expectancy of individuals; animals spend less time in their trophic class and hence the speed of flow is increased, according to the term of fishing mortality  $F_{\tau}$ . The speed of flow at TL  $\tau$  depends partly also on the abundance of predators ( $B_{pred}$ ), since the more predators there are, the faster prey are likely to be eaten. The coefficient  $\propto_{\tau}$  defines the intensity of this control and may vary between 0 (no top-down control) and 1 (all natural mortality  $M_{\tau}$  depends on predator abundance). The coefficient  $\gamma$  is a shape parameter varying between 0 and 1, defining the functional relationship between prey and predators.

Equations (5), (6), and (8) are used to calculate the biomass trophic spectrum Bt for any simulated fishing pattern

Finally, catches per time unit (in tons x year<sup>-1</sup>) are derived from earlier equations, as follows:

$$Y\tau = \varphi\tau \,\varphi\tau \,\Delta\tau \text{ or } Y\tau = F\tau B\tau \tag{9}$$

where  $F\tau$  is the usual fishing mortality (year<sup>-1</sup>), defined as the ratio  $Y\tau/B\tau$  and equal to  $\phi\tau$  $\Delta\tau$  (from Equations (5) and (9)). Since only a fraction of ecosystem biomass is usually accessible to fisheries, a selectivity coefficient  $S\tau$  estimated from field observations or from a theoretical selectivity function (see Gascuel et al. 2011 for details) is added to the model. Hence,  $B\tau$  and  $F\tau$  are replaced by the accessible biomass  $B^*\tau$  and the accessible biomass flow  $F^*\tau$  in Equation (9). Two distinct kinetics of trophic transfer are used to characterize the speed of flow in the reference state, one for the entire biomass ( $K_{ref, \tau}$ ), and the other for the accessible biomass only ( $K^*_{ref, \tau}$ ) ,accounting for the fact that exploited species usually do not have the same characteristics as the unexploited ones.

Equations presented here constitute the core of the ET-Transpose and ET-Diagnosis routines accessible through an R package which was used in this PhD work.

# 5 Chapter 5. Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints.

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Contribution to the Theme Section 'Trophodynamics in marine ecology'



# Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints

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ABSTRACT: Mass-balance trophic models (Ecopath and EcoTroph) are valuable tools that can be used to describe ecosystem structure and functioning, identify target species to be monitored, and allow comparisons of ecosystem states under different management options. Nevertheless, the Ecopath modelling approach is constrained by 2 major sources of uncertainty: model complexity and input data quality. We developed an approach for identifying the optimum model structure that considers trade-offs between feasibility, complexity, and uncertainty, using a Mediterranean coastal ecosystem as a case study. We began with an existing well-documented and good-quality food-web model comprising 41 functional groups at Port-Cros National Park, France. Based on this model, we assessed the effects of different aggregation choices, driven by a simplification of sampling effort, on the Ecopath and EcoTroph model outputs. We identified the functional groups in which imprecise biomass input significantly influenced the food-web model, and measured the relative effects on the ecosystem trophic structure and ecosystem maturity and complexity indices. A simplified model comprising 32 functional groups was identified as the best compromise between model complexity and reliability. High trophic level predators, abundant primary producers, and groups with a high biomass and/or diversified diet significantly influenced the model structure. We concluded that the collection of local and accurate biomass data, especially for the most influential functional groups we identified, should be a priority when developing food-web models for similar ecosystems. Our method enables simplified and standardized models, while considering both the feasibility and reliability of the Ecopath and EcoTroph applications for Mediterranean coastal ecosystems.

KEY WORDS: Aggregation  $\cdot$  Uncertainty  $\cdot$  Complexity  $\cdot$  Trophic spectrum  $\cdot$  Ecosystem indices  $\cdot$  Biomass  $\cdot$  Ecopath  $\cdot$  EcoTroph  $\cdot$  Mediterranean Sea

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#### INTRODUCTION

With the oceans facing increasing impacts by humans, unravelling the complexity of marine ecosystem functioning and species interactions has gradually become a pressing necessity. Single species approaches are not sufficient to ensure a sustainable exploitation of marine resources (Botsford et al. 1997, Hofmann & Powell 1998). Instead, ecosystembased approaches enable a deeper understanding of the consequences of human exploitation by considering the whole ecosystem, and assist managers in implementing the sustainable use of natural resources (Coll et al. 2013a).

The development of the ecosystem approach to fisheries has triggered an exponential growth of

modelling tools worldwide (Plagányi 2007, Espinoza-Tenorio et al. 2012). Originally developed by Polovina (1984), Ecopath with Ecosim (EwE) (Christensen & Pauly 1992, Walters et al. 1997, Christensen & Walters 2004) is the most widely used approach to represent marine food webs. About 400 EwE models with different objectives and representing a wide variety of ecosystems worldwide have been published (Colléter et al. 2013), ranging from exploring foodweb interactions to computing ecosystem indicators useful for cross-system comparisons, as well as for assessing the impact of fishing or marine protected areas (MPAs) on the ecosystem (Pauly et al. 2000, Christensen & Walters 2005, Guénette et al. 2014). Ecopath is a mass-balanced and species-based model in which species with similar life cycles and diets are aggregated into functional groups. The descriptive Ecopath model is the key initialization step in the EwE modelling process, from which further dynamic and spatial predictions can be simulated with Ecosim and Ecospace for policy scenario testing (Walters et al. 1997, 1999). EcoTroph, a trophodynamic model recently integrated as a plug-in in the EwE software (Gascuel 2005, Gascuel & Pauly 2009, Gascuel et al. 2009, 2011), is based on the idea that an ecosystem can be represented by the distribution of its biomass across trophic levels (TLs), called the biomass trophic spectrum. The simplified picture of ecosystem functioning provided by EcoTroph has proven to be very useful for exploring theoretical aspects of ecosystems, as well as for analysing the impacts of fishing or protection (Colléter et al. 2012, Gasche & Gascuel 2013).

The use of ecosystem models such as the EwE model is generally constrained by 2 major sources of uncertainty: (1) structural complexity (Abarca-Arenas & Ulanowicz 2002, Fulton et al. 2003, Pinnegar et al. 2005, Johnson et al. 2009), and (2) the amount and quality of the input data (Essington 2007, Link 2010, Fulton 2010, Kearney et al. 2013, Lassalle et al. 2014). Structural complexity in Ecopath models is measured as the number of compartments in the model, the way species are aggregated in these compartments, and the inclusion of stanzas, i.e. groups representing different life history stages for species that have a complex trophic ontogeny. In fact, it is unrealistic to include all interactions at the species level in a food web model. Moreover, adding complexity does not necessarily improve a model's performance, but generally increases uncertainty (Fulton et al. 2003). Species aggregation is thus necessary, but can strongly influence the model outputs. The over-aggregation of certain components of the food web, at either the

upper or lower trophic levels, produces models with very different behaviours (Pinnegar et al. 2005) and has sometimes led to dissimilar and conflicting recommendations for management action (Punt & Butterworth 1995, Yodzis 2001). In addition, Ecopath models require a large amount of input data, the quality of which can vary significantly. An in-depth evaluation of the sensitivity of Ecopath models to imprecise input data showed that the Ecopath modelling process is most sensitive to biomass and production rate parameters, and only occasionally sensitive to consumption rate and diet (Essington 2007). In our analysis, we decided to focus on the biomass input parameter. Biomass is of direct relevance to marine resource management, yet it is not easy to estimate accurately for the totality of the food web components due to the costs and constraints of sampling in the marine environment.

In the Mediterranean Sea, several Ecopath models have been built with various levels of detail, depending on the research questions and data availability (Table 1). For some exploited ecosystems (e.g. Northern Adriatic Sea, South Catalan Sea, Northern Aegean Sea, and Greek Ionian Sea), rather comprehensive models have been developed that include more than 30 functional groups based on the high availability of biomass data from industrial fishing monitoring (experimental trawling) (Table 1). In contrast, few models (e.g. Libralato et al. 2006, Albouy et al. 2010, Valls et al. 2012) representing coastal zones in the Mediterranean Sea have been developed and used to analyse MPAs (Table 1). The scarcity of foodweb models for the Mediterranean coastal MPAs is likely due to the high diversity and complexity of their food webs (Sala 2004), and the many challenges in terms of data collection. A protected area is a zone in which fishing and other human impacts are restricted to achieve conservation objectives. Thus, destructive sampling methods such as experimental fishing (i.e. trawl surveys), which could provide extensive data on the studied ecosystem, are generally prohibited or limited. However, less destructive methods also have limitations. Underwater monitoring techniques, such as visual censusing to assess fish and mega-invertebrate biomass or suction pumps to sample macrofauna, are time consuming and require a considerable workload for collecting the samples in the field and analysing them at the laboratory. Thus, field-based estimates of biomass are generally available only for a subset of species of recognized ecological importance in coastal zones and/or of particular management relevance in protected areas. For instance, in the Mediterranean,

Table 1. Origin of biomass input data for 22 models of the Mediterranean. The 4th column lists the number of groups included in the related model (excluding non-living The next columns express the percentages of functional groups for which biomass data were Estifor marine mammals field-based local studies. surveys derived from the method specified in column header. Sampling-based data are derived from either experimental fishing, monitoring or and extrapolation from visual personal communications, include data obtained from empirical models, groups, i.e. detritus, bycatch/discards and dissolved organic matter). method mates from the indirect

list of models was derived from Coll & Libralato (2012) and Colleter et al. (2013). Art.: artisanal; Ind.: industrial Source estimate Model literature/ Non-local method Indirect Local field Experimental fishina/ Sampling Functional adrioup Fishing turtles and birds. The ea Location A

			(n)		monitoring	studies	momon	other model	Commo	
	Miramare Natural Marine Reserve 2000–2003	None/Art.	23	78.3	65.2	13.0	21.7	0	0	Libralato et al. (2006, 2010)
2	Bonifacio Straits Natural Reserve, Corsica 2000–2001	None/Art.	31	48.4	48.4	0	0	9.7	32.3	Albouy et al. (2010)
e	Port-Cros National Park 1998–2008	None/Art.	40	57.5	0	57.5	15.0	0	27.5	Valls et al. (2012)
4	Bay of Calvi, Corsica 1998	None/Art.	26	61.5	0	61.5	7.7	30.8	0	Pinnegar (2000)
2	Arancy Bay, Sardinia 2006	Ind.	12	25.0	25.0	0	25.0	0	50.0	Diaz Lopez et al. (2008)
9	Santa Pola Bay, Spain 2001–2007	Ind.	39	100	0	100	0	0	0	Bayle-Sempere (2013)
Ł	Southern Catalan Sea 1994	Ind.	36	86.1	66.7	19.4	2.8	0	11.1	Coll et al. (2006)
∞	N Adriatic Sea 1997–2000	Ind.	17	100	0	100	0	0	0	Zucchetta et al. (2003)
6	NC Adriatic Sea 1975–1980	Ind.	37	100	81.1	18.9	0	0	0	Coll et al. (2008)
1(	) N Adriatic Sea 1990	Ind.	32	84.4	53.1	31.3	6.3	0	9.4	Barausse et al. (2009)
-	N Adriatic Sea 1997–2000	Ind.	17	100	0	100	0	0	0	Pranovi & Link (2009)
1	NE Ionian Sea 1964	Ind.	17	23.5	5.9	17.6	76.5	0	0	Piroddi et al. (2010)
1	8 N Aegean Sea 2003–2006	Ind.	38	76.3	68.4	7.9	18.4	2.6	2.6	Tsagarakis et al. (2010)
1	Greek Ionian Sea 1998–2006	Ind.	37	70.3	70.3	0	10.8	13.5	5.4	Moutopolous (2013)
Ţ.	5 Black Sea 1960	Ind.	13	100	0	100	0	0	0	Daskalov (2002)
1(	b Black Sea 1960	Ind.	9	66.7	0	66.7	0	0	33.3	Gucu (2002)
1	7 Black Sea 1980, 1990	Ind.	9	50.0	0	50.0	0	0	50.0	Gucu (2002)
1	Betang de Thau Lagoon 1980s	Ind.	10	30.0	0	30.0	0	0	70.0	Palomares et al. (1993)
1	<ul> <li>Veniče Lagoon – Palude della Rosa 1990s</li> </ul>	None/Art.	15	73.3	66.7	6.7	26.7	0	0	Carrer & Opitz (1999)
2(	) Venice Lagoon 1990s	Ind.	19	26.3	0	26.3	0	73.7	0	Libralato et al. (2002)
2	Venice Lagoon 1998	Ind.	25	72.0	36.0	36.0	20.0	8.0	0	Pranovi et al. (2003)
5	? Orbetello Ľagoon 1995, 1996	Ind.	11	0	0	0	18.2	0	81.8	Brando et al. (2004)

there is extensive knowledge on the trophic interactions between sea bream, sea urchins, and macroalgae and their role in controlling coastal ecosystem states (Sala et al. 1998, Guidetti 2007). These groups are thus common monitoring targets in Mediterranean MPAs, while we face a lack of data and knowledge for many other functional groups (Sala 2004). Consequently, the application of food-web modelling has remained relatively limited in coastal Mediterranean ecosystems.

The objective of this work was to determine an optimum and standardized model structure to represent a northwestern Mediterranean coastal food web that accounts for the trade-offs between feasibility, complexity, and uncertainty. To do so, we selected the Ecopath model representing the MPA of Port-Cros, a French marine national park in the northwestern Mediterranean Sea (Valls et al. 2012). This model was originally built to synthesize all available data and identify knowledge gaps regarding the described ecosystem. Thus, the study presents detailed information on species aggregation into the 41 defined functional groups (Table 2), which makes it the most detailed model available representing a Mediterranean coastal food web (Table 1). Such a comprehensive synthesis was made possible by the many years of research and monitoring that produced a significant amount of data for this old MPA, created in 1963 (e.g. Khoury 1987, Francour 1990). Hence, the biomass parameters were estimated from local field-based studies for 57.5% of the functional groups, which is a relatively high score compared to similar modelled ecosystems (Table 1). We used the original Port-Cros model as our control state, and we simplified its trophic structure by applying different levels of species aggregation, the choice of which was driven by sampling feasibility conTable 2. The 41 functional groups of the Port-Cros control model. Details in Valls et al. (2012). Only the least destructive methods were considered: visual survey (VS), visual census (VC), acoustics (Ac), suction sampler (SS), scraping (SC), plankton nets/bottles (PNB), chlorophyll remote sensing (CRS), corer (Co), and net fishing (NF). The groups in **bold** are those considered for aggregation

Sampling method	Functional group
VS	Seabirds
VC	Amberiack+
VC	Dusky grouper – medium
VC	Dusky grouper – large
VC	Dusky grouper – small
VC. NF	Ravs
VC. NF	Large-scaled scorpionfish+
VC. NF	Scorpionfishes+
VC, NF	Striped red mullet+
VC, NF	Pagellus
VC, Ac, NF	Horse mackerels+
VC, NF	Diplodus+
VC, NF	Wrasses
VC, NF	Mullets
VC, C	Cephalopods
VC, SS	Blennies
VC, SS	Pipefishes+
VC, SS	Gobies
SS, SC	Gastropods
SS	Small crustaceans
SS	Amphipods
SS	Brittle stars+
SS, SC	Suspensivores
SS, VC	Crabs
SS, VC	Decapods
SS, Co, SC	Polychaetes
SS, VC, SC	Bivalves
VC	Sea stars
VC	Sea cucumbers
VC	Sea urchins
PNB	Large zooplankton
PNB	Small zooplankton
VC	Gorgonians
VC, NF	Salema – adults
VC	Salema – juveniles
Co, SC	Foraminifera
A, SC	Posidonia
SC	Shallow seaweeds
SC	Deep seaweeds
PNB, CRS	Phytoplankton
Co, SS	Detritus

siderations. We then identified the functional groups for which local and accurate biomass data should be collected as a priority, as they have the most significant influence on the model outputs. Specifically, we focused on 3 main questions: (1) how do samplingdriven aggregation choices alter the model description of ecosystem functioning; (2) to what level of aggregation can the model be simplified without significantly altering its accuracy; and (3) what are the functional groups in the simplified model for which imprecise biomass input significantly influences the biomass calculations of other groups, and thus the overall description of the ecosystem functioning.

By addressing these issues, we intended to propose some priority guidelines, in terms of model structure and data collection, that could enable the development of standardized models of complex Mediterranean coastal ecosystems.

#### **METHODS**

Two food-web modelling approaches were used in our analysis: the species-based Ecopath model and the TL-based EcoTroph model. Ecopath was used to build several versions based on the control model, with different levels of aggregation and different input biomass values, while EcoTroph was used to compute the trophic spectra for each new model. Sensitivity analyses were performed on selected ecosystem maturity and complexity indices computed by Ecopath, and on the trophic description of the ecosystem provided by EcoTroph.

#### **Ecopath**

Ecopath uses a mass-balanced food-web model, assuming 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:

$$P/B_i \times B_i = P/B_i \times B_i \times (1 - EE_i) + \Sigma j (Q/B)_{ii} \times B_i \times DC_{ii} + Y_i + NM_i + BA_i$$
(1)

where *B* is the biomass,  $P/B_i$  is the production rate, *Q*/*B* is the consumption rate,  $DC_{ji}$  is the diet composition representing the fraction of prey *i* 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*<sub>i</sub> is the catch of prey *i*, and *EE*<sub>i</sub> is the ecotrophic efficiency of prey *i* (the proportion of production that is used in the system, e.g. through predation and harvest). Assuming there is no export and no biomass accumulation, and the catches are known, only 3 of the 4 remaining parameters (*B*,  $P/B_{ii}$ , *Q*/*B*, and *EE*<sub>i</sub>) have to be set initially for each group. The parameterization routine solves the equations for each missing parameter iteratively (Christensen et al. 2008).

A comprehensive Ecopath model was built by Valls et al. (2012) for the Port-Cros MPA (Table 2), which covers a surface area of 13 km<sup>2</sup> and reaches a maximum depth of 50 m. Biotopes are typical of the northwestern Mediterranean, with nearshore rocky reefs, large Posidonia oceanica meadows, and a coralligenous habitat, hosting a high biodiversity of commercially important fish and decapod crustaceans; only 5% of the reserve is a no-take area, outside of which fishing is permitted with severe restrictions (Francour et al. 2001). The Ecopath model represents an average situation for the period from 1998 to 2008, defined by the data used in the model. Large amounts of data were available for this old and well-studied MPA, which allowed for the development of a relatively detailed model, including 40 living functional groups (plus one detrital group). More precisely, the model comprises 18 groups of fish, 17 groups of invertebrates, 4 groups of primary producers, and 1 group of seabirds. In addition, the model is well documented in terms of both species aggregation choices and species-level information for each functional group. Moreover, all fish biomass data are of good quality as they were derived from visual censusing and scientific trawling in the area. Local fieldbased biomass data were also available for some invertebrate and primary producer groups. Details on the species composition of each functional group in the control Port-Cros model, as well as the input parameters for each group, can be found in Valls et al. (2012). Finally, the model respected Link's recommendations of data quality (Link 2010), and its representation of the Port-Cros ecosystem was in accordance with the current available knowledge (Valls et al. 2012).

#### EcoTroph

The trophic level-based EcoTroph model assumes that biomass has a continuous distribution in an ecosystem as a function of continuous TLs. The biomass is represented as entering the system at TL = 1, generated by the photosynthetic activity of primary producers or recycled from the detritus by the microbial loop. Then, at TLs >2, the biomass is distributed along a continuum of TL values and all fractional TLs are filled due to the diet variability of the various consumers. The resulting biomass distribution constitutes the biomass trophic spectrum (Gascuel et al. 2005). The functioning of the ecosystem is then modelled as a continuous flow of biomass, surging up the food web from lower to higher TLs, through predation and ontogenic processes.

Based on the usual equations of fluid dynamics, the flow of the biomass present in the ecosystem at TL  $\tau$  under steady-state conditions is expressed as:

$$\varphi(\tau) = D(\tau) \times K(\tau) \tag{2}$$

where  $\varphi(\tau)$  refers to the amount of biomass that moves up the food web through TL  $\tau$  (metric t per year),  $D(\tau)$  is the density of biomass at TL  $\tau$  (metric t per trophic level), and  $K(\tau)$  is the speed of flow, which quantifies the velocity of biomass transfers in the food web (number of TLs crossed per year).

The continuous distribution of the biomass across a TL is calculated using a discrete approximation based on small trophic classes. EcoTroph conventionally considers trophic classes of width  $\Delta \tau$  equal to 0.1 TL, from TL 2 (corresponding to first-order consumers) to TL 5 (a value considered sufficient to cover all top predators likely to occur in marine ecosystems). Thus, the mean biomass  $B_{\tau}$  (in metric t), which is present in the  $[\tau, \tau + \Delta \tau]$  trophic class under steady-state conditions, can be estimated as  $\int D(\tau) \times d\tau$  for a small interval  $\Delta \tau$ . Therefore,

$$B_{\tau} = \varphi_{\tau} \times \Delta_{\tau} / K_{\tau} \tag{3}$$

where  $\varphi_{\tau}$  and  $K_{\tau}$  are the mean biomass flow and mean speed of flow within the  $[\tau, \tau + \Delta \tau]$  trophic class, respectively; see the supplementary material in Valls et al. (2012) for further explanation.

In this study, we used the ET-Transpose routine described in Gascuel et al. (2009) to translate the outputs of the original Ecopath model into an EcoTroph model and to build the biomass trophic spectrum. The biomass of each functional Ecopath group was distributed over a range of trophic classes around the mean TL of the group (estimated by Ecopath), assuming a log-normal distribution. The trophic spectrum is the curve obtained by summing the biomass parameter over all functional groups and provides a synthetic view of the trophic structure of the ecosystem.

We then used the ET-Diagnosis routine to conduct sensitivity testing. We simulated how the baseline ecosystem would be impacted by increasing or decreasing the fishing effort. Fishing effort can be modified per fleet by applying various effort multipliers, and the structure of the trophic spectrum will vary under different efforts (Gascuel et al. 2011, Gasche & Gascuel 2013).

#### Aggregated models and comparisons

The original version of the Ecopath model for the Port-Cros National Park's MPA, described by Valls et

al. (2012), was selected as the control model in our simplification procedure, and 6 models were derived from this, using successive aggregation steps. Purely taxonomical aggregations were avoided. Aggregation choices were driven by sampling efficiency considerations; for each functional group, the most adequate and least destructive sampling methods were assigned, and groups that shared at least one common sampling method were considered for aggregation. Thus, aggregation choices were also consistent with the habitat use among groups, so that species in the same group occupied the same habitat. Aggregation choices were also constrained by diet composition overlap and similarities in production and consumption (P/B and Q/B rates), which should differ by less than 3-fold between groups (Fulton et al. 2003). Small cryptobenthic fish (blennies, pipefishes, and gobies) were grouped based on the difficulty in sampling them and because they share similar lifehistory parameters. The other fish functional groups were not further aggregated relative to the original model, in which they were grouped according to their TL, maximum length, and feeding type (Valls et al. 2012).

Starting from the first aggregated model (the one with the broadest aggregation of the invertebrate groups), a biomass trophic spectrum was computed, and the trophic spectra ratios between this first model and the control were compared. The TLs corresponding to the widest changes in the trophic spectrum were identified, and the corresponding functional groups were isolated in the subsequent model, in which different levels of aggregation were tested. For each new model, static ecosystem indices were computed and the percentage difference between each aggregated model and the control were compared. This procedure was repeated stepwise until the aggregation with the fewest differences from the control in the trophic spectra and ecosystem indices was identified. *P*/*B* and *Q*/*B* ratios were computed for the newly aggregated groups; they were weighted with the biomass and summed over all of the groups to be aggregated. Similarly, the new diet compositions were obtained by weighting the food intake of each group with the consumption of the group, and then summing the food intakes over all of the groups to be aggregated.

To evaluate the successive species aggregations, we compared the ecosystem indices that are most widely accepted as indicators of ecosystem maturity and complexity in the literature: Finn's cycling index (FCI), system omnivory index (SOI), relative ascendency (%A), and TL of the community ( $TL_{co}$ ) (Chris-

tensen 1995, Libralato et al. 2010). Because the total amount of matter flowing in each model was maintained constant and equal to the original, the maturity indices related to the flows and biomasses were not considered. FCI measures the fraction of the ecosystem's throughput that is recycled. The degree of energy and nutrient recycling in an ecosystem is assumed to increase as ecosystems mature and develop routes for nutrient conservation (Odum 1969). SOI is defined as the average omnivory index of all consumers, weighted by the logarithm of the food intakes (Christensen & Pauly 1992). It expresses the variance in the TLs of the consumers' prey groups (Pauly et al. 1993) and is considered a measure of food-web complexity. Ascendency is a measure of the average mutual information in a system, scaled by system throughput, and is derived from information theory (Ulanowicz & Norden 1990). If one knows the location of a unit of energy, the uncertainty about where it will flow to next is reduced by an amount known as the 'average mutual information'. The amount of the average mutual information multiplied by the total system throughput (TST) gives the ascendancy (A). There is an upper limit for the development of the ascendancy, which is called the 'development capacity'. Here, we are considering %A, defined as the ratio between A and the development capacity that was demonstrated to be clearly correlated with maturity sensu Odum (Christensen 1994). The average  $TL_{co}$  is estimated as the biomassweighted average TL for all functional groups of the web, excluding those at TL = 1. Libralato et al. (2010) showed that TL<sub>co</sub> was consistently lower in a fished food web compared to an adjacent unexploited one. Given the similarity of fishing patterns in coastal Mediterranean waters, we retained  $TL_{co}$  as a good indicator of the fishing effects.

The model that showed the smallest differences from the control in the trophic spectra and ecosystem indices was considered to offer the best species aggregation scheme, and was therefore selected for further analysis. The ET-Diagnosis function was applied to test whether the selected model would behave differently from the control in terms of assessing the fishing impact on the ecosystem. For both the control and the selected model, we built 2 different fishing scenarios by applying 2 effort multipliers (mF) to the current fishing mortality of each trophic class. Specifically, we applied an mF = 0 to simulate a closure of the fishery and an mF = 12 to simulate an increase in fishing effort. The latter value of mF was shown to be of the same order of magnitude as those observed in surrounding and similar

unprotected areas (Valls et al. 2012). We then compared the simulation outputs to the unexploited state and identified the differences between the patterns of the 2 models.

# Sensitivity to error in input biomass and identification of the most influential species

The model selected after aggregation was set as the new reference (ref. model) to test the effects of variation in each group's input biomass on the biomass estimates of the other groups, and to evaluate the impact of these errors on the overall model outputs; 31 new models were built by increasing the biomass of each group by 10% and obtaining the biomass of the other groups (except primary producers) from the Ecopath equation solutions (with ecotrophic efficiencies fixed). During this process, the biomass of the primary producers was not obtained from the Ecopath equation solutions, but instead was kept at its original value, because it was input data in the original model and therefore avoided a potential modelling artefact: i.e. strong increases in primary producer biomass to sustain increased consumer abundance due to the Ecopath routine estimation of the primary production required to sustain consumption. Thus, we were conservative by evaluating the minimum impact that imprecise input biomass for consumers would have on the model outputs. Subsequently, the biomass of each primary producer was also varied by 10%, and the biomasses of all other groups were obtained from the Ecopath equation solutions to test the influence of an error in the primary producer input biomass.

A variation of 10% was assumed to be small enough to keep the models mass-balanced and large enough to create differences between the models. To test the model sensitivity to the biomass increments, the biomass trophic spectra and maturity indices were compared between each new model and the ref. model. The trophic spectra of the ratios between the new model and the ref. model were plotted, and 3 indices were derived: the number of trophic levels affected by a variation in the biomass of >1% (i.e. the width of the trophic spectra, Width\_TS); the maximum level of biomass increase (i.e. the peak of the trophic spectra, Peak\_TS), and the total biomass increase (i.e. the area of the trophic spectra, B\_TS); the latter was expressed as the percentage difference from the ref. model biomass and was increased for several functional groups simultaneously to test for any amplifying effect on the trophic spectra. The percentage

differences from the ref. model were compared for %A, SOI, FCI,  $TL_{co}$ , and 2 additional flow indices: the ratio of total primary production to total respiration (TPP/R) and the ratio of total biomass to total system throughput (B/TST). The latter 2 flow-related maturity indices were included at this step of the analysis because variations in the functional groups' biomass inputs induced variations in the amount of matter flowing in the model.

A principal component analysis (PCA) was conducted to visualize the impact of each functional group on the ecosystem attributes. The previously mentioned indices of maturity, complexity, and trophic structure were the explicative variables of the PCA, while the different models obtained by 10% increases in the biomass of each functional group were the samples. All variables were standardized to a zero mean and unit variance to compensate for differences in the value ranges. TL and biomass were included in the PCA as supplementary continuous variables and trophic class was included as a supplementary categorical variable, so that they would not be considered in the computation of the principal components. The groups were then ranked according to their contribution to each of the first 3 principal components, and their mean ranking was computed. Thus, summarized information was obtained for the functional groups with the most impact on the variables overall. The functional groups were then plotted in decreasing order of their mean rank (a rank of 1 was attributed to the group having the greatest impact). The groups with the highest rankings were identified and selected as those having the most impact on the model's output, and thus requiring local and accurate biomass input data.

#### RESULTS

#### Model aggregations and comparisons

Model A included 33 living groups (Table 3) and was characterized by the largest aggregation of invertebrate groups that can be sampled with suction devices (gastropods, small crustaceans, amphipods, brittle stars, suspensivores, crabs, decapods, and polychaetes comprised a new Epifauna+ group). Sea stars and sea cucumbers were not included, because their constant production and consumption rates differ significantly from the other invertebrates, and estimates of their biomass are more commonly obtained from a visual census. Model B (34 living groups) differed from Model A by the separation of a

Sampling	Control	Model A	Model B	Model C	Model D	Model E	Model F
VC, SS	Blennies	Blennies	Blennies	Blennies+	Blennies+	Blennies+	Gobies+
VC, SS	Pipefishes+	Pipefishes+	Pipefishes+	pipefishes)	pipefishes)	pipefishes)	pipefishes,
VC, SS	Gobies	Gobies	Gobies	Gobies	Gobies	Gobies	gobles)
SS, SC	Gastropods	Epifauna	Epifauna	Epifauna	Epifauna	Epifauna	Epifauna
SS	Small crustaceans	(gastropods, small	(gastropods, small	(gastropods, small	(gastropods, small	(gastropods, small	(gastropods, small
SS	Amphipods	amphipods,	amphipods,	amphipods,	amphipods,	amphipods,	amphipods,
SS	Brittle stars+	suspensivore,	suspensivore,	polychaetes)	Sittle stars)	suspensivore,	bittle stars)
SS, SC	Suspensivores	decapods, polychaetes)	ls, etes)	Suspensivores+ (bivalves, suspensivores)	Suspensivores+ (bivalves, suspensivores)		Suspensivores+ (bivalves, suspensivores)
SS, VC	Crabs		Decapods+	Decapods+	Decapods+	Decapods+	Decapods+
SS, VC	Decapods		decapods)	decapods)	decapods)	decapods)	decapods)
SS, Co, SC	Polychaetes				Polychaetes	Polychaetes	Polychaetes
SS,VC, SC	Bivalves	Bivalves	Bivalves				
VC	Sea stars	Sea stars	Sea stars	Echinoderms+	Echinoderms+	Echinoderm+	Echinoderms+
VC	Sea cucumbers	Sea cucumbers	Sea cucumbers	cucumbers)	cucumbers)	cucumbers)	cucumbers)
SC	Shallow seaweeds	Shallow seaweeds	Shallow seaweeds	Seaweeds+ (shallow	Seaweeds+ (shallow	Seaweeds+ (shallow	Seaweeds+ (shallow
SC	Deep seaweeds	Deep seaweeds	Deep seaweeds	deep seaweeds)	deep seaweeds)	deep seaweeds)	deep seaweeds)
No. of groups	40	33	34	31	32	31	31

Table 3. Aggregation schemes. The groups that were not modified from the control model are not listed. Number of functional groups (excluding detritus) given at bottom. Grey boxes indicate functional groups that have been mapped to an aggregate group listed higher in the table. Co: corer; SC: scraping; SS: suction sampler; VC: visual census

pooled crab and decapod group (Decapods+) from the Epifauna+ group. In Model C, suspensivores were excluded from the Epifauna+ group as well, and aggregated with bivalves (Suspensivores+). Moreover, sea stars were grouped with sea cucumbers (Echinoderms+), blennies with pipefishes (Blennies+), and shallow seaweeds with deep seaweeds (Seaweeds+), resulting in an overall aggregation into 31 living groups. Model D (32 living groups) was equal to Model C, except for the polychaetes, which were excluded from the Epifauna+ group and defined as a separate group. In Model E (31 living groups), the suspensivores and bivalves were added to the Epifauna+ group, while the polychaetes were kept separated. Finally, Model F (31 living groups) was characterized by an Epifauna+ group that included gastropods, small crustaceans, amphipods,

and brittle stars. The previously defined groups of Decapods+, Suspensivores+, Echinoderms+, and Seaweeds+ remained as separate groups, while a Gobies+ group was created to aggregate gobies, blennies, and pipefishes.

For every aggregated model, FCI and %A were higher than in the control model, while the SOI was systematically lower. The differences in  $TL_{co}$  were either negative or null. The aggregation that caused the largest variations in ecosystem indices (Fig. 1) and trophic spectra (Fig. 2) was that of crabs and decapods with Epifauna+ (Model A), causing a 30% increase in FCI (Fig. 1) and negative biomass differences for TL > 3.5 (Fig. 2a). Suspensivores+ and polychaetes also significantly affected ecosystem indices and trophic spectra when aggregated with the Epifauna+ group; Mod-



Fig. 1. Percentage differences in the system indices between the aggregated models and the control model

els D and F showed the least differences from the control (Figs. 1 & 2b). The aggregations of Echinoderms, Seaweeds+ and Gobies+ caused no major modifications in model properties. Model F, with 31 living functional groups, had the most simplified species aggregation scheme, i.e. the smallest variations in the ecosystem indices and trophic structure relative to the control for the highest level of species aggregation possible.

The simulation test confirmed that the behaviour of Model F was similar to that of the control, when both closure (mF = 0) and increased fishing effort (mF = 12) were simulated. The exploitation effect was significant only at TL > 3.5, and in neither the original nor the aggregated model did the exploitation cause major biomass variations at the lower TLs (Fig. 3). Model F was thus selected for successive analysis.

# Sensitivity to error in the input biomass

A sensitivity analysis was applied to Model F. The analyses of the trophic spectra (Fig. 4) and the differences in the ecosystem indices due to biomass variations (see Appendix 1) showed that the high TL predator groups, Amberjack+ and Dusky grouper – large, had the largest impacts on the biomass of the other groups, and thus most influenced the trophic spectra and ecosystem indices. Increments of 10% in the biomass of these 2 large fish



Fig. 2. Trophic spectra of the ratios of the biomass between the control model and (A) aggregated Models A, B, and C or (B) aggregated Models D, E, and F, in relative values

groups affected the biomass of all other trophic groups by more than 1%, with most TLs affected by more than 5% (Fig. 4A). The trophic spectra sensitivity to Dusky grouper – large increased when TL  $\geq$ 4, since this was the only group occupying the highest TLs. The trophic spectra for both Amberjack+ and Dusky grouper – large reached peaks with an approximately 9% increase in biomass, and overall biomass increased (B\_TS) by 0.25 and 0.28%, respectively, relative to Model F. With regard to the other fish groups, the highest impact in terms of number of TLs affected and shifts in biomass was caused by



Fig. 3. Simulation scenarios for Model F and the control model. Relative biomass values were obtained from the trophic spectra ratios, with effort multipliers mF = 12 (Sim12) and mF = 0 (Sim0) applied to both models



Fig. 4. Biomass ratios between the trophic spectra of each model obtained after an increase of 10% to the biomass of one functional group and the trophic spectra of the reference model (represented by the solid line at relative biomass = 1). The dotted line corresponds to the threshold value of a 1% variation in biomass. (A) Higher trophic level predators; (B) other fish groups; (C) invertebrates

Horse mackerels+ (Width\_TS = 21, Peak\_TS = 7.5%, B\_TS = 0.09%), followed by Scorpionfishes+ and Wrasses (Fig. 4B).

Among the invertebrates (Fig. 4C), Cephalopods+ affected the largest number of trophic levels (Width\_TS = 19), followed by Decapods (Width\_TS = 9). Decapods was the group with the most impact on the Peak\_TS index; under their influence, the trophic spectrum reached the maximum peak resulting from a 10% increment in the biomass. An increase of 10% in the biomass of Sea worms and Echinoderms+ led to high biomass peaks in the trophic spectra (Peak\_TS = 8.8, Peak\_TS = 8.4%, respectively), but their impacts were limited to a very narrow range of TLs corresponding to their own range (Width\_TS = 4, Width\_TS = 2, respectively). A simultaneous biomass increase of several functional groups resulted in a simple additive effect on the trophic spectra and thus was not considered further.

Similar to the trophic spectra analysis, a 10% increment in the biomass of the Dusky grouper - large and Amberjack+ groups caused the largest variations in absolute terms in all ecosystem indices, especially impacting FCI (7.2 and 8.1%, respectively), TPP/R (6.4 and 7.2%, respectively), and %A (2.1% for both). As for the Epifauna+, Decapods+, Cephalopods, and Horse mackerels+ groups, the biomass increments caused large variations in FCI (max. value = 7.0% for Epifauna+) and SOI (max. value = 1.6% for Horse mackerels+). Increments in the biomass of Foraminifera and Small zooplankton had a strong influence on FCI (6.3 and 6.6%, respectively). Posidonia oceanica had a high overall impact and principally caused large variations in the flow indices TPP/R (4.7%) and B/TST (6.1%), and in %A (2.1%).

#### **Principal component analysis**

A PCA on all indices was performed (Fig. 5). The first PC accounted for almost 50% of the variability of the data, and the second PC accounted for 25% (Fig. 5A). The first PC summarized the variability explained by 2 sets of variables: recycling



Fig. 5. Principal component analysis (PCA) plots. (A) Variables and (B) individual factors for the first 2 principal components. (C) Individual factors for principal components 1 and 3. In the variables plot (A), B and TL are the supplementary variables (blue). In the individual factor plots (B,C), only the non-overlapping points were labelled to improve visualization. B: biomass; B\_TS: biomass of the trophic spectra; B/TST: biomass/total system throughput; FCI: Finn's cycling index; Peak\_TS: peak of the trophic spectra; SOI: system omnivory index; TC: trophic class; TL<sub>co</sub>: mean trophic level of the community; TL: trophic level; TPP/R: total primary production/total respiration; TS: trophic spectra; Width\_TS: width of the trophic spectra

(FCI), %A, and trophic spectra structure (Width\_TS and Peak\_TS) on the one hand, and the energy flux indices (TPP/R and B/TST) and trophic spectraderived biomass index (B\_TS) on the other. Within each set, the variables appeared to be highly correlated to one another. The influence of the functional groups on the variables (i.e. their effect on the indices) was related to their biomass. Several species which cover the whole range of trophic levels, but with low biomass, influenced the variables less than average (Fig. 5b). In contrast, the top predators Dusky grouper – large and Amberjack+ (TL >4), having higher biomasses, strongly affected many ecosystem indices, particularly the trophic spectra indices (Width\_TS, Peak\_TS), ecosystem maturity (FCI, %A), and flow indices (TPP/R, B/TST) summarized by PC1. Groups feeding on a wide range of trophic levels and with consistent biomass (Decapods, Epifauna+, Horse mackerels+ and Cephalopods) affected the ecosystem complexity indices (SOI and TLco), while the Posidonia group affected the flow and biomass related indices (TPP/R,B/TST, and B\_TS).

When the third PC was visualized (Fig. 5C), the functional groups were ordered by TL. Following the high TL predator groups, the Scorpionfishes+, Cephalopods, and Horse mackerels+ were arranged in decreasing order of TL and contributed equally to PC1. On the positive side of PC3, the TL of the groups decreased, and biomass became the dominant supplementary variable. Thus, Decapods+ and Epifauna+ contributed equally to both PC1 and PC3 in terms of the ecosystem complexity indices (SOI and  $TL_{co}$ ), while *Posidonia*, having the highest biomass, showed the highest contribution to PC1 and PC3 in terms of overall biomass increase (B\_TS), and to PC1 for %A.

The first 3 PCs summarized approximately 80% of the variability explained by the indices, so the functional groups were ranked according to their contributions to these axes. By plotting the species in decreasing order of their mean rank (rank of 1 for the species having the highest impact) (Fig. 6), we highlighted 2 major gaps among the ranking scores. The first and most evident gap separated *Posidonia*, Amberjack+, Epifauna+, Decapods+ and Dusky grouper – large, which had the highest ranking on all 3 PCs, from Cephalopods. The second gap separated the Cephalopods and Horse mackerels+ from the other groups. The rankings gradually decreased after these groups, so no further groups were selected.

#### DISCUSSION

We have addressed 2 issues in this paper related to model uncertainty: functional group aggregation and sensitivity to biomass data input. Our intent was to improve the feasibility of Ecopath applications for complex Mediterranean coastal ecosystems by accounting for the constraints that field sampling and monitoring impose on the collection of reliable data. We evaluated how these constraints might lead to an altered description of ecosystem functioning and proposed a model structure that allows for a compromise between reliability and feasibility.



Fig. 6. Ranking of the functional groups based on their contributions to the first 3 principal components. Red boxes separate the first and second groups with the highest rankings

#### Aggregating trophic groups

Initially, we dealt with the effects of aggregation on food-web properties. The issue of the ecosystem indices' dependence upon the model structure has been largely discussed in the literature. Many studies have concluded that food-web properties are affected not only by the reduction in the number of compartments, but also and primarily by the way the functional groups are aggregated in such compartments (Christensen 1995, Abarca-Arenas & Ulanowicz 2002, Fulton et al. 2003, Pinnegar et al. 2005). Until further knowledge is obtained, models built in a standardized way, at least for similar ecosystems, could increase the reliability of model comparisons over time and/or space (Dame & Christian 2006, Fulton 2010).

Focusing on a northwestern Mediterranean coastal ecosystem, we identified which species aggregation choices, defined on the basis of sampling efficiency considerations, caused major modifications in the model description of the ecosystem state and should therefore be avoided. We mainly focused on lower TL groups that are often less studied and overly aggregated in ecosystem models.

From our analysis, it appeared that some indices (SOI and %A) vary significantly less than others (FCI) among the different model configurations (Fig. 1). These configurations primarily differed for the invertebrate functional groups. Pinnegar et al. (2005) tested aggregation schemes emphasizing different parts of the food web (fish, marine mammals, and invertebrates) and reported greater variation for the same 2 indices compared to our results. Nevertheless, in a recent meta-analysis on 105 food-web models from different areas of the world, %A proved to be robust to the model construction in terms of the number of functional groups (Heymans et al. 2014). FCI showed the strongest variations among all our model configurations.

Decapods, crabs, suspensivores, and polychaetes were responsible for the main differences between the ecosystem structures described by the models. These groups show different degrees of connection within the food web in comparison to the other macrofaunal invertebrates (amphipods, small crustaceans, gastropods, and brittle stars) and have different predators (low predator overlap index). Consequently, aggregating them together increased the connections between the primary producers and the upper levels of the food web, and it introduced cannibalism within the group. By altering the feedback cycles in the model, it is likely that this pooling affects the overall stability of the system (Dambacher et al. 2003). This aggregation thus led to an erroneous and increased quantification of FCI, which might affect interpretation of the ecosystem's resilience and maturity. This result agrees with the analysis in Pinnegar et al. (2005), in which the fish-centred model, including a compartment equivalent to our epifaunal group, showed the greatest increase in FCI. In addition, SOI largely decreased, because the variety of the TLs upon which the upper consumers feed is reduced. Species interactions in the food web might thus appear less complex than they are in reality. More particularly, given the important biomass of decapods and their connections with higher TLs, their inclusion in the Epifauna group significantly altered the biomass trophic spectrum, impacting the distribution of biomass up to higher TLs and causing a general decrease in the mean TL of the community. Trophic spectra are now recognized as a useful tool with which to analyse the impacts of fisheries and/or protection on the whole trophic network (Gascuel et al. 2009, Libralato et al. 2010, Colléter et al. 2012, Lassalle et al. 2012), but if they are initially altered by a biased model structure, inaccurate conclusions could be derived from their observation. The inclusion of polychaetes and suspensivores in the Epifauna group should be avoided, although it would simplify sampling. This confirms the existing knowledge that groups accessing primarily different food sources within the system should not be overaggregated (Fulton et al. 2003, Pinnegar et al. 2005).

The groupings that did not significantly affect the model behaviour were the amphipods with small crustaceans, gastropods, and brittle stars; decapods with crabs; suspensivores with bivalves; sea stars with sea cucumbers; and grouping all small cryptobenthic fishes together (i.e. gobies, blennies, and pipefishes). Some of these results may be explained by the similar functional role of the groups (amphipods, small crustaceans, and gastropods), while others are possibly due to the very low biomass of one of the 2 groups in the control model (i.e. bivalves and sea stars). It would be interesting to compare such results with other aggregation approaches used in ecosystem modelling. The regular coloration algorithms applied in Johnson et al. (2001), for example, formalize the aggregation procedure by collapsing groups that have ties to equivalent prey and predators, with equivalent groups being those that pertain to the same TL.

The simplified trophic structure implied a substantial reduction in complexity and a simplification of the data collection process due to greater aggregation than in the control model (31 living groups instead of 40). Nevertheless, even after applying a simulated increase in the fishing effort, the level of aggregation did not noticeably affect the distribution of biomass across the TLs. The simplified model is still rather detailed in comparison to other models of the Mediterranean, such as the Miramare Natural Marine Reserve model (Libralato et al. 2006), which has 23 functional groups, or the Bonifacio Strait Natural Reserve model (Albouy et al. 2010), which has 31 groups.

#### **Prioritizing groups for biomass estimates**

Next, we assessed the model uncertainty related to the quality of the biomass input data. Based on Essington's conclusions on biomass input data being the parameter that most affects the model output estimations, we wanted to identify which groups our model was most sensitive to after a variation in their biomass. The most influential species we identified were all characterized by a high biomass, a high TL and a diversified diet, or a combination of the two. Abundant high TL predators, such as the large dusky grouper Epinephelus marginatus and species in the Amberjack group (including Seriola dumerili, Sphyraena viridensis, Dicentrarchus labrax, Conger conger, and Muraena helena; see Appendix 1), comprised the groups with the most impact on the trophic spectra and ecosystem maturity indices (%A, FCI, TPP/R, and TB/TST). Thus, inaccurate input biomass data for these groups would alter the biomass estimates of all other groups. As demonstrated by the biomass trophic spectra, higher prey biomass would be required to sustain a higher biomass for these predators, consequently affecting the trophic structure of the ecosystem. Our results were similar to Christensen & Pauly's (1998) simulations, where the top predators' biomass was increased to assess the carrying capacity of an ecosystem. A 10-fold increase in the top predators' biomass, given a fixed primary production, increased FCI and TPP/R approached 1, meaning less sedimentation, better utilization of the detritus, and nutrient recycling within the food web, which corresponds to an image of a more mature system sensu Odum (1969). Our results on the influence of high TL predators on food-web properties are in accordance with the general knowledge that these predators are good indicators of ecosystem health and maturity (Ray et al. 2005, Prato et al. 2013), and their recovery in a protected zone is the first sign of improved ecosystem health (Sandin & Sala 2012). As we demonstrated, models built with inaccurate biomass data for high TL predators and fixed primary

producer values would depict a significantly altered food web.

Epifauna, Decapods+, Horse mackerels+, and Cephalopods were the groups that most influenced the ecosystem complexity by modifying the SOI and the mean TL of the community. Epifauna and decapods are abundant in the ecosystem and are the main prey items of many other groups (high ecotrophic efficiencies), and therefore act as connectors between the primary producers and the upper TLs. The planktivorous fish group (including horse mackerels, Chromis chromis, Spicara spp., Boops boops, and Oblada melanura) and cephalopods significantly affected the biomass trophic spectra, causing biased biomass estimates for a wide range of functional groups. Indeed, planktivorous fish represent up to 32% of fish biomass and are responsible for up to 40% of all fish throughput in some Mediterranean ecosystems (Pinnegar & Polunin 2004). These fishes are important prey for coastal predators, as well as important detritus producers (Pinnegar 2000, Pinnegar & Polunin 2004). They may also be involved in wasp-waist control mechanisms, similar to those in the South Catalan Sea (Coll et al. 2006). Cephalopods have high consumption rates (the highest among all upper TLs), a widely diversified diet, and are a preferred prey for many predatory fish. Thus, this group is very likely playing a significant role in the energy and material flow of marine ecosystems (Coll et al. 2013b). However, it is often difficult to assess their abundance and role in marine ecosystems, primarily due to logistical problems (Piatkowski et al. 2001).

The strong influence of *Posidonia oceanica* on the maturity indices related to flow measures was probably due to its high biomass, which was an order of magnitude greater than any other functional group. Moreover, given the low consumption rate of *P. oceanica* by other functional groups (low ecotrophic efficiency), an increase in its biomass might cause an increased flow to detritus, thereby affecting FCI.

Our study was based on the single example of the Port-Cros ecosystem, for which a large amount of information was available. Nonetheless, useful insights can be derived from an in-depth analysis of a well-known complex food web and applied to comparable ecosystems (i.e. northwestern Mediterranean) (Sala 2004).

The identification of high TL predators and *P. oceanica* as the most influential groups in our study is in agreement with Mediterranean monitoring programs (Moreno et al. 2001, Levin & Grimes 2002, Coll et al. 2008, Montefalcone 2009, Di Franco et al. 2009, Prato et al. 2013). Nevertheless, accurate methods to
assess their biomass are still a challenging issue, especially for high TL predators. In addition to these groups, our results highlighted the important role in the food web of groups that are usually poorly detailed, such as epifauna, decapods, planktivorous fish, and cephalopods. Although the importance of these groups has been demonstrated in Mediterranean coastal ecosystems (Sala 1997, Pinnegar 2000, Piatkowski et al. 2001, Goñi et al. 2006), they are rarely included in monitoring programs for many reasons, e.g. the challenges in obtaining good quality data, the absence of commercial value or of a protection status, and the lack of public awareness for noncharismatic species.

#### CONCLUSIONS

Food-web modelling enables setting reference levels for indicators of ecosystem structure and functioning (Dame & Christian 2006, Heymans et al. 2014), which is very useful in the context of the ecosystem approach to marine resource management. In this study, we showed that ecosystem indicators largely depend on model structure and that the reliability of the reference levels for the ecosystem indicators may be improved by developing standardized models that account for input data quality.

We identified a level of trophic aggregation that simplifies the model structure and data collection, without significantly altering the model results. The priority functional groups requiring accurate biomass estimates were also identified (Dusky grouper large, Amberjack+, Posidonia oceanica, Decapods+, Epifauna+, Horse mackerels+, and Cephalopods). Link et al. (2012) stated that if the component of model uncertainty linked to observation error needs to be overcome, sampling designs should be improved in a cost-effective way; priority should be given to increasing the data accuracy for poorly known components of the food web, rather than adding further precision to already well-known groups. However, we should acknowledge that obtaining accurate biomass data for all functional groups is not always feasible in complex and highly diverse Mediterranean coastal ecosystems. Thus, we suggest focusing on better documenting the biomass of the poorly known but important groups (such as those we identified), which could help to increase the reliability of the Ecopath-standardized applications in such complex ecosystems.

The methodological approach proposed here to address the issue of model simplification is of interest

for 2 reasons: (1) it increases the feasibility of model building in terms of data collection; and (2) it adds to our knowledge of the modelled system by analysing the effects of simplification and imprecise biomass data on the ecosystem indices, trophic structure, and the capacity of the model to assess fishery impacts. This approach is easily applicable, and it could help foster the development of standardized Ecopath models to represent complex Mediterranean food webs.

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#### LITERATURE CITED

- Abarca-Arenas LG, Ulanowicz RE (2002) The effects of taxonomic aggregation on network analysis. Ecol Model 149:285–296
- Albouy C, Mouillot D, Rocklin D, Culioli J, Le Loc'h F (2010) Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model. Mar Ecol Prog Ser 412:207–221
- Barausse A, Duci A, Mazzoldi C, Artioli Y, Palmeri L (2009) Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. Estuar Coast Shelf Sci 83:577–590
- Bayle-Sempere JT, Arreguín-Sánchez F, Sanchez-Jerez P, Salcido-Guevara LA, Fernandez-Jover D, Zetina-Rejón MJ (2013) Trophic structure and energy fluxes around a Mediterranean fish farm. Ecol Model 248:135–147
- Botsford LW, Castilla JC, Peterson CH (1997) The management of fisheries and marine ecosystems. Science 277: 509–515
- Brando VE, Ceccarelli R, Libralato S, Ravagnan G (2004) Assessment of environmental management effects in a shallow water basin using mass-balance models. Ecol Model 172:213–232
- Carrer S, Opitz S (1999) Trophic network model of a shallow water area in the northern part of the Lagoon of Venice. Ecol Model 124:193–219
- Christensen V (1994) On the behavior of some proposed goal functions for ecosystem development. Ecol Model 75–76:37–49
- Christensen V (1995) Ecosystem maturity—towards quantification. Ecol Model 77:3–32
- Christensen V, Pauly D (1992) Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61:169–185
- Christensen V, Pauly D (1998) Changes in models of aquatic ecosystems approaching carrying capacity. Ecol Appl 8: S104–S109
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 172: 109–139

- Christensen V, Walters CJ (2005) Using ecosystem modeling for fisheries management: where are we. ICES CM / M:19
- Christensen V, Walters CJ, Pauly D, Forrest R (2008). Ecopath with Ecosim version 6 user guide. Lenfest Ocean Futures Project, University of British Columbia, Vancouver
- Coll M, Libralato S (2012) Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish Fish 13:60–88
- Coll M, Palomera I, Tudela S, Sardà F (2006) Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, northwestern Mediterranean. J Mar Syst 59:63–96
- Coll M, Lotze HK, Romanuk TN (2008) Structural degradation in Mediterranean Sea food webs: testing ecological hypotheses using stochastic and mass-balance modelling. Ecosystems 11:939–960
- Coll M, Cury P, Azzurro E, Bariche M and others (2013a) The scientific strategy needed to promote a regional ecosystem-based approach to fisheries in the Mediterranean and Black Seas. Rev Fish Biol Fish 23:415–434
- Coll M, Navarro J, Olson RJ, Christensen V (2013b) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep-Sea Res II 95:21–36
- Colléter M, Gascuel D, Ecoutin JM, Tito de Morais L (2012) Modelling trophic flows in ecosystems to assess the efficiency of marine protected area (MPA), a case study on the coast of Senegal. Ecol Model 232:1–13
- Colléter M, Guitton J, Gascuel D (2013) An introduction to the EcoTroph R package: analyzing aquatic ecosystem trophic networks. R Journal 5:98–107
- Dambacher JM, Luh H, Li HW, Rossignol PA (2003) Qualitative stability and ambiguity in model ecosystems. Am Nat 161:876–888
- Dame JK, Christian RR (2006) Uncertainty and the use of network analysis for ecosystem-based fishery management. Fisheries 31:331–341
- Daskalov GM (2002) Overfishing drives a trophic cascade in the Black Sea. Mar Ecol Prog Ser 225:53–63
- Di Franco A, Bussotti S, Navone A, Panzalis P, Guidetti P (2009) Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. Mar Ecol Prog Ser 387:275–285
- Díaz López B, Bunke M, Bernal Shirai JA (2008) Marine aquaculture off Sardinia Island (Italy): ecosystem effects evaluated through a trophic mass-balance model. Ecol Model 212:292–303
- Espinoza-Tenorio A, Wolff M, Taylor MH, Espejel I (2012) What model suits ecosystem-based fisheries management? A plea for a structured modeling process. Rev Fish Biol Fish 22:81–94
- Essington TE (2007) Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Can J Fish Aquat Sci 64:628–637
- Francour P (1990) Dynamique de l'écosystème à *Posidonia* oceanica dans le Parc National de Port-Cros. Analyse des compartiments matte, litière, faune vagile, échinodermes et poissons. PhD thesis, Université Pierre et Marie Curie, Paris
- Francour P, Harmelin JG, Pollard D, Sartoretto S (2001) A review of marine protected areas in the northwestern Mediterranean region: siting, usage, zonation and management. Aquat Conserv Mar Freshw Ecosyst 11: 155–188

- Fulton EA (2010) Approaches to end-to-end ecosystem models. J Mar Syst 81:171–183
- Fulton EA, Smith ADM, Johnson CR (2003) Effect of complexity on marine ecosystem models. Mar Ecol Prog Ser 253:1-16
- Gasche L, Gascuel D (2013) EcoTroph: a simple model to assess fishery interactions and their impacts on ecosystems. ICES J Mar Sci 70:498–510
- Gascuel D (2005) The trophic-level based model: a theoretical approach of fishing effects on marine ecosystems. Ecol Model 189:315–332
- Gascuel D, Bozec YM, Chassot E, Colomb A, Laurans M (2005) The trophic spectrum: theory and application as an ecosystem indicator. ICES J Mar Sci 62:443–452
- Gascuel D, Pauly D (2009) EcoTroph: modelling marine ecosystem functioning and impact of fishing. Ecol Model 220:2885–2898
- Gascuel D, Tremblay-Boyer L, Pauly D (2009) EcoTroph (ET): a trophic level based software for assessing the impacts of fishing on aquatic ecosystems. Res Rep 17, Fisheries Centre, University of British Columbia, Canada
- Gascuel D, Guénette S, Pauly D (2011) The trophic-levelbased ecosystem modelling approach: theoretical overview and practical uses. ICES J Mar Sci 68:1403–1416
- Goñi R, Quetglas A, Reñones O (2006) Spillover of spiny lobsters *Palinurus elephas* from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219
- Gucu AC (2002) Can overfishing be responsible for the successful establishment of *Mnemiopsis leidyi* in the Black Sea? Estuar Coast Shelf Sci 54:439–451
- Guénette S, Meissa B, Gascuel D (2014) Assessing the contribution of marine protected areas to the trophic functioning of ecosystems: a model for the Banc d'Arguin and the Mauritanian Shelf. PLoS ONE 9:e94742
- Guidetti P (2007) Predator diversity and density affect levels of predation upon strongly interactive species in temperate rocky reefs. Oecologia 154:513–520
- Heymans JJ, Coll M, Libralato S, Morissette L, Christensen V (2014) Global patterns in ecological indicators of marine food webs: a modelling approach. PLoS ONE 9: e95845
- Hofmann EE, Powell TM (1998) Environmental variability effects on marine fisheries: four case histories. Ecol Appl 8:S23–S32
- Johnson JC, Borgatti SP, Luczkovich JJ, Everett MG (2001) Network role analysis in the study of food webs: an application of regular role coloration. J Social Struct 2: 1–15
- Johnson GA, Niquil N, Asmus H, Bacher C, Asmus R, Baird D (2009) The effects of aggregation on the performance of the inverse method and indicators of network analysis. Ecol Model 220:3448–3464
- Kearney KA, Stock C, Sarmiento JL (2013) Amplification and attenuation of increased primary production in a marine food web. Mar Ecol Prog Ser 491:1–14
- Khoury C (1987) Ichtyofaune des herbiers de posidonies du Parc National de Port-Cros: composition, éthologie alimentaire et rôle dans le réseau trophique. PhD thesis, Université Aix-Marseille II, France
- Lassalle G, Gascuel D, Le Loc'h F, Lobry J and others (2012) Assessing the effects of fisheries on marine top predators: the Bay of Biscay case study. ICES J Mar Sci 69: 925–938
- Levin PS, Grimes CB (2002) Reef fish ecology and grouper conservation and management. In: Sale PF (ed) Coral

reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, p 377–390

- Libralato S, Pastres R, Pranovi F, Raicevich S, Granzotto A, Giovanardi O, Torricelli P (2002) Comparison between the energy flow networks of two habitats in the Venice Lagoon. Mar Ecol 23:228–236
- Libralato S, Tempesta M, Solidoro C, Spoto M (2006) An ecosystem model applied to Miramare natural marine reserve: limits, advantages and perspectives. Biol Mar Mediterr 13:386–395
- Libralato S, Coll M, Tempesta M, Santojanni A and others (2010) Food-web traits of protected and exploited areas of the Adriatic Sea. Biol Conserv 143:2182–2194
- Link JS (2010) Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecol Model 221:1580–1591
- Link JS, Ihde TF, Harvey CJ, Gaichas SK and others (2012) Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. Prog Oceanogr 102:102–114
- Montefalcone M (2009) Ecosystem health assessment using the Mediterranean seagrass *Posidonia oceanica*: a review. Ecol Indic 9:595–604
- Moreno D, Aguilera PA, Castro H (2001) Assessment of the conservation status of seagrass (*Posidonia oceanica*) meadows: implications for monitoring strategy and the decision-making process. Biol Conserv 102:325–332
- Moutopoulos DK, Libralato S, Solidoro C, Stergiou KI (2013) Toward an ecosystem approach to fisheries in the Mediterranean Sea: multi-gear/multi-species implications from an ecosystem model of the Greek Ionian Sea. J Mar Syst 113-114:13–28
- Odum EP (1969) The strategy of ecosystem development. Science 164:262–270
- Palomares MLD, Reyes-Marchant P, Zainure L, Barnabe G, Lasserre G (1993) A trophic model of a Mediterranean lagoon, Etang de Thau, France. In: Christensen V, Pauly D (eds), Trophic models of aquatic ecosystems. ICLARM Conf Proc 26:153–158
- Pauly D, Bartz MS, Palomares MLD (1993) Improved construction, parametrization and interpretation of steadystate ecosystem models. In: ICLARM Conf Proc 26: 224–229
- Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57:697–706
- Piatkowski U, Pierce GJ, Morais da Cunha M (2001) Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fish Res 52:5–10
- Pinnegar JK (2000) Planktivorous fishes: links between the Mediterranean littoral and pelagic. PhD thesis, University of Newcastle, UK
- Pinnegar JK, Polunin NVC (2004) Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecol Model 172: 249–267
- Pinnegar JK, Blanchard JL, Mackinson S, Scott RD, Duplisea DE (2005) Aggregation and removal of weak-links in food-web models: system stability and recovery from disturbance. Ecol Model 184:229–248
- Plagányi ÉE (2007) Models for an ecosystem approach to fisheries. Fish Tech Pap 477, FAO, Rome
- Polovina JJ (1984) Model of a coral reef ecosystem. Coral Reefs 3:1–11

- Piroddi C, Giovanni B, Christensen V (2010) Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. Ecol Model 221:1526–1544
- Pranovi F, Link JS (2009) Ecosystem exploitation and trophodynamic indicators: a comparison between the northern Adriatic Sea and southern New England. Prog Oceanogr 81:149–164
- Pranovi F, Libralato S, Raicevich S, Granzotto A, Pastres R, Giovanardi O (2003) Mechanical clam dredging in Venice Lagoon: ecosystem effects evaluated with a trophic mass-balance model. Mar Biol 143:393–403
- Prato G, Guidetti P, Bartolini F, Mangialajo L, Francour P (2013) The importance of high-level predators in marine protected area management: consequences of their decline and their potential recovery in the Mediterranean context. Adv Oceanogr Limnol 4:176–193
- Punt AE, Butterworth DS (1995) The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. S Afr J Mar Sci 16:255–285
- Ray J, Redford KH, Steneck R, Berger J (2005) Large carnivores and the conservation of biodiversity. Island Press, Washington, DC
- Sala E (1997) The role of fishes in the organization of a Mediterranean sublittoral community. II. Epifaunal communities. J Exp Mar Biol Ecol 212:45–60
- Sala E (2004) The past and present topology and structure of Mediterranean subtidal rocky-shore food webs. Ecosystems 7:333–340
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos 82:425–439
- Sandin SA, Sala E (2012) Using successional theory to measure marine ecosystem health. Evol Ecol 26:435–448
- Tsagarakis K, Coll M, Giannoulaki M, Somarakis S, Papaconstantinou C, Machias A (2010) Food-web traits of the North Aegean Sea ecosystem (eastern Mediterranean) and comparison with other Mediterranean ecosystems. Estuar Coast Shelf Sci 88:233–248
- Ulanowicz RE, Norden JS (1990) Symmetrical overhead in flow networks. Int J Syst Sci 21:429–437
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Vasconcellos M, Mackinson S, Sloman K, Pauly D (1997) The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol Model 100:125–134
- Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev Fish Biol Fish 7:139–172
- Walters C, Pauly D, Christensen V (1999) Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems 2:539–554
- Yodzis P (2001) Must top predators be culled for the sake of fisheries? Trends Ecol Evol 16:78–84
- Zucchetta M, Libralato S, Granzotto A, Pranovi F, Raicevich S (2003) Modelling approach for the evaluation of the efficacy of MPA in the northern Adriatic Sea. In: Özhan E (ed) Proc 6th Int Conf Mediterranean Coast Environ, MEDCOAST, Ravenna, Vol 3, p 433–444

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Table A1. The sensitivity of the model indices to 10% increments in functional group biomass. The values of the system indices are given as the percentage difference from the control model. TL: trophic level: TS: trophic spectra

Functional groups	Trophic level	Biomass	Width_TS	Peak_TS	Biomass_TS	Relative ascendancy	Finn's cycling index	System omnivory index	TL community	Biomass/ total system throughput	Total primary production/ respiration
Rays	4.37	0.03	0	0.073	0.002	0.412	0.154	0.094	0.000	0.015	0.050
Grouper large	4.37	4.32	31	9.333	0.256	2.058	7.220	0.003	0.052	1.953	6.379
Grouper medium	4.25	0.43	26	2.201	0.076	0.823	2.304	0.026	0.003	0.610	2.043
Large-scale scorpionfish+	4.20	0.49	4	1.126	0.018	0.412	0.768	0.024	0.024	0.190	0.589
Seabirds	4.09	0.29	0	0.230	0.002	0.000	0.154	0.050	0.006	0.059	0.136
Amberjack+	4.08	5.55	31	8.796	0.283	2.058	8.141	0.071	0.002	2.212	7.162
Grouper small	3.99	0.25	2	1.061	0.033	0.412	1.075	0.020	0.011	0.266	0.905
Scorpionfishes+	3.78	4.29	20	4.140	0.101	1.235	3.533	0.008	0.014	0.980	3.186
Pagellus	3.66	0.65	0	0.596	0.014	0.412	0.461	0.000	0.005	0.116	0.397
Striped mullet+	3.62	0.24	0	0.211	0.007	0.412	0.307	0.049	0.004	0.056	0.190
Cephalopods	3.59	3.00	19	2.434	0.079	0.823	6.670	1.565	0.058	0.227	0.550
Horse mackerels+	3.52	20.00	21	7.538	0.089	0.823	6.750	1.550	0.137	0.228	0.548
Gobies+	3.34	0.58	0	0.445	0.010	0.412	0.307	0.015	0.010	0.087	0.304
Diplodus+	3.10	3.63	10	3.879	0.053	0.412	0.768	0.033	0.081	0.183	0.727
Large zooplankton	3.04	2.19	c	2.311	0.009	0.412	3.072	0.070	0.005	0.810	1.693
Wrasses+	2.95	5.04	12	6.158	0.066	0.823	1.690	0.031	0.069	0.430	1.558
Decapods+	2.66	17.21	6	9.907	0.168	1.646	6.880	1.518	0.280	0.227	0.545
Sea worms	2.33	27.83	4	8.822	0.058	0.823	2.458	0.011	0.072	0.633	1.982
Mullets+	2.27	4.50	0	0.537	0.005	0.412	0.154	0.002	0.006	0.021	0.066
Suspensivores	2.26	27.89	2	3.330	0.032	0.412	1.690	0.021	0.042	0.445	1.347
Gorgonians	2.23	40.56	2	4.834	0.044	0.412	0.154	0.014	0.064	0.003	0.092
Epifauna+	2.18	72.45	5	6.177	0.150	2.058	6.950	1.513	0.305	0.227	0.545
Sea urchins	2.15	38.27	1	3.087	0.045	0.412	0.307	0.017	0.099	0.029	0.274
Small zooplankton	2.10	9.70	1	3.850	0.058	0.000	6.605	0.061	0.136	1.350	2.230
Echinoderms+	2.06	77.79	2	8.436	0.129	0.412	0.461	0.045	0.364	0.040	0.294
Foraminifera	2.00	4.84	1	3.088	0.050	0.823	6.298	0.057	0.118	0.990	1.823
Salema large	2.00	00.00	0	0.583	0.006	0.412	0.000	0.057	0.022	0.003	0.028
Salema small	2.00	00.00	0	0.442	0.004	0.000	0.154	0.057	0.017	0.000	0.040
Posidonia	1.00	8666.85	1	9.677	9.281	2.058	4.455	0.000	0.000	6.068	4.673
Phytoplankton	1.00	20.16	0	0.023	0.022	0.412	3.994	0.000	0.000	2.625	4.082
Seaweeds+	1.00	182.98	0	0.204	0.196	0.000	1.229	0.000	0.000	0.626	1.245

# 6 Chapter 6. A trophic modelling approach to assess artisanal and recreational fisheries impacts and conflicts in MPAs

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#### Abstract

Marine Protected Areas (MPAs) have spread across the Mediterranean to protect its rich biodiversity and manage human activities for a more sustainable coastal development. Within MPAs, traditional artisanal fishing is competing for space and resources with increasing recreational fishing, likely leading to interacting ecological effects. Such effects are difficult to unravel given the multispecies character of both fisheries and the complexity of the food-webs upon which they both impact. In order to address these issues, we developed an Ecopath and Ecotroph trophic model for the Portofino MPA case study (NW Mediterranean), in particular to i) identify keystone species and assess fishing impact on them, ii) analyse the interacting impact of artisanal and recreational fishing on ecosystem biomass and trophic structure, iii) assess the potential for biomass recovery in the MPA under different scenarios of fisheries management iv) assess the impact of recreational fishing on artisanal fishing catches. Two high trophic level predators (HTLP) groups coupled important keystone roles with strong fishing pressure, and should thus be prioritised for the definition of management actions. Recreational fishing had the widest impact on the food-web, strongly impacting HTLP. Simulation of different mortality scenarios for each fishery highlighted that the ecosystem is far from its carrying capacity for HTLP. Forbidding recreational fishing allowed a 24% increase in HTLP biomass, and benefited artisanal fishing by increased HTLP catches availability. Artisanal fishing alone could be maintained with a moderate impact on the food-web. Overall Ecopath and Ecotroph modelling is a valuable tool to advise MPAs management, but it is essential to

increase data availability and quality by developing long-term monitoring programs on key species and on artisanal and recreational fishing.

**Keywords:** Marine Protected Area, food-web, artisanal fishing, recreational fishing, Ecopath, EcoTroph

# Highlights:

- MPAs lack tools to unravel artisanal and recreational fishing interacting impacts
- We modelled the Portofino MPA food-web (NW Mediterranean) to assess such impacts
- High trophic level predators (HTLP) couple keystone roles and high fishing losses
- Limiting recreational fishing increases HTLP biomass, benefiting artisanal fishing
- We prove that Ecopath and EcoTroph are useful tools to advise management of MPAs

#### 6.1 Introduction

In the last decade the ecosystem-based management approach has become the major call of action in the marine research context. Ignoring the nature, strength and complexity of species interactions, single species approaches have generally failed to cope with the increasing human impacts on the world's oceans that often cause dramatic changes in marine ecosystems (Roux et al. 2013, Travis et al. 2014). The Mediterranean, hosting an estimated 7% of the world's marine biodiversity (Coll et al. 2010, 2011), exemplifies the scarce success of these approaches, since most of its fish stocks are currently overfished (Colloca et al. 2013, Vasilakopoulos et al. 2014) and irreversible ecosystem changes have occurred in some areas open to fishing (Sala et al. 1998, 2012). The overexploitation of fish stocks also affected traditional activities like small-scale artisanal fishing by reducing the availability of catches. Artisanal fishing is usually operated by relatively small vessels (less than 12 meters total length, with low-power engine) typically fishing within the first three nautical miles from the coast (Coppola 2006, Guyader et al. 2013). Usually, artisanal fisheries are highly multi-specific (Farrugio et al. 1993) and multi-métier, using a broad range of gears and techniques selected according to seasonal availability of target species (the concept of "métier" denotes a combination of fishing gear, target species, area and season; Mesnil & Shepherd 1990, Biseau 1998). Such activity has long played a fundamental role in both the economy and society (Farrugio et al. 1993) of the Mediterranean, with considerable cultural and historical significance, but is now declining in many areas with a downward trend in the number of vessels and licenses, catches and net revenues (Gómez et al. 2006, Guyader et al. 2013, Lloret & Font 2013, Di Franco et al. 2014).

In addition to commercial fishing, Mediterranean coastal ecosystems are facing a boom in leisure activities, particularly recreational fishing. An increasing number of studies supported the idea that the increasing recreational fishing effort can have similar or even higher effects on fish populations as commercial fishing (Cooke & Cowx 2004, 2006, Lewin et al. 2006). Nonetheless, recreational fishing is not as controlled nor as well investigated as commercial fishing, especially in the Mediterranean, where it would represent more than 10% of the total fishing catches (Coll et al. 2004, Morales-Nin et al. 2005, Font et al. 2012).

To face this situation and in the perspective of an ecosystem-based approach to coastal management (Lubchenco et al. 2003), Marine Protected Areas have spread across the

coastal zones of the Mediterranean as a tool to protect the ecosystem and manage human activities for a more sustainable coastal development (Abdulla et al. 2008, Forcada et al. 2008). Where they are well managed and enforced, MPAs have proved to be effective in protecting exploited fish and invertebrate stocks (Goñi et al. 2006, Guidetti et al. 2008, Sala et al. 2012), and have in some successful cases helped to enhance artisanal fisheries (Guidetti & Claudet 2010, Fenberg et al. 2012). Nonetheless, Mediterranean MPAs are often small and competition for space and resources is increasingly causing conflicts among artisanal and recreational fishermen, the activity of these latter within MPAs being often less regulated and controlled (Edgar GJ, 2011). Artisanal and recreational fishing pressure are indeed likely to have interacting ecological effects, which are difficult to unravel given the multispecies character of both fisheries and the complexity of the protected food webs upon which they both impact (Baskett et al. 2007).

Ecosystem models could help to shed light on such issues by accounting for the direct and indirect trophic interactions among multiple species (Colléter et al. 2012, Travis et al. 2014) The use of EwE (Ecopath with Ecosim) modelling software (Christensen & Pauly 1992, Christensen & Walters 2004) has grown significantly in the last 15 years (Fulton 2010, Colléter et al. 2015) and is by now gaining widespread acceptance as a tool to apply the EAM (Ecosystem Approach to Management) (Coll et al. 2015). Ecopath was largely demonstrated to be useful in unravelling trophic relationships and providing a picture of ecosystem functioning, that can be updated in time. The more recent plug-in EcoTroph (Gascuel et al. 2005, 2011) provides a simplified representation of ecosystem functioning and allows to evaluate fisheries impacts and analyse the conflicts among interacting fishing fleets (Gasche & Gascuel 2013, Colléter et al. 2014).

Thus, the objective of this study was to show how Ecopath and EcoTroph trophic models can be used to assess impacts of artisanal and recreational fisheries on the marine food web within a coastal MPA, and to analyse interactions and potential conflicts between fisheries. As a case study, we focussed on the Portofino MPA (Ligurian Sea). This MPA was established with the objective of conserving marine biodiversity around the Portofino promontory, and in the last years has also become the promoter of a sustainable socio-economic development of the area. Traditionally, the area hosted a well-developed artisanal fishing fleet, which, although declining naturally because of the old age of local fishermen, is increasingly competing for space with recreational fishing (Salmona & Verardi 2001, Catteneo-Vietti et al. 2010, Markantonatou et al., 2015).

We thus approached these issues by building an Ecopath and Ecotroph model for the Portofino MPA on the basis of the standard model structure proposed in Prato et al (2014). In particular we aimed at:

1 unravelling trophic relationships in the model area, identifying keystone groups and assessing how these are affected by artisanal and recreational fishing;

2 analysing the interacting impact of artisanal and recreational fishing on ecosystem biomass and fish assemblage, and assess the potential for biomass recovery in the MPA under different scenarios of fisheries management;

3 analysing the impact of recreational fishing on artisanal fishing, both quantitatively and qualitatively.

#### 6.2 Methods

#### 6.2.1 Study area



Fig. 1 Habitat map and zoning of the Portofino MPA. The modelled area is surrounded by the black rectangle, and includes zones A, B and partially C around the southern front of the promontory. Habitat map retrieved from Diviaco and Coppo (2006; updated to 2012)

The promontory of Portofino is located 25km east from Genoa in the Ligurian Gulf and extends over 13 km of coastline (Salmona & Verardi 2001) (Fig.1). The Portofino MPA was established in 1999 to safeguard the marine biodiversity around the promontory and promote a traditional and sustainable use of its natural resources (Cappanera et al. 2013). Currently it is the third smallest Italian MPA (374 ha) and is managed by a Consortium comprised of the three municipalities of Camogli, Portofino and Santa Margherita Ligure, the Metropolitan City of Genoa and the University of Genoa. Similarly to other Italian MPAs, it is divided into different subzone types: no-take/no-access A zone, a B zone of

general reserve and a C zone of partial protection, where different restrictions regulate human uses. Artisanal fishing involves 35 operating vessels <10 meters in length (MARTE + project, 2011) and is allowed in zones B and C only for the residents of the three municipalities. This fishery is multi-métier and multi-specific, and fixed nets including gill nets, trammel nets and combined nets are the mostly used gears (70% of total used gears), followed by longlines and surrounding net, locally named "lampara" and hereafter referred to as "small purse seine" (both around 20% of total used gears). Other traditional fishing gears (e.g. tonnarella targeting small pelagic, and mugginara, specifically targeting mugilids) are allowed during specific periods and are restricted to a single site within zone C of the MPA (Cattaneo-Vietti et al., 2014). Recreational fishing is permitted for residents of the three municipalities under authorization in Zones B and C and for non-residents only in Zone C. For both recreational and artisanal fishing other restrictions such as the fishing of some species, spatial closures, prohibitions or modifications of fishing techniques, regulations in fishing effort and minimum landing sizes are also implemented in the MPA in order to control the activities, according to the MPA Regulation (2008), (Markantonatou et al. 2014). The modeled surface (57 ha) thus includes the southern front of the MPA, encompassing zones A and B and two sectors of zone C (Fig.1) and is characterized mainly by hard bottoms (51% rocky habitat, 31% coralligenous habitat ), with some Posidonia oceanica meadows and shallow sands (overall 18% of the area). This area supports most of the artisanal and recreational fishing pressure in the MPA, with highest overlap between coralligenous habitat and fishing footprint around 30-40 meters depth (Markantonatou et al. 2014). The southern submerged steep cliffs of the promontory and the particular hydrodynamic conditions of the area (Doglioli et al. 2004) create in fact a unique system where rocky reefs, caves, and massive blocks support a very diversified benthic community, including extended coralligenous habitat cover (Cattaneo-Vietti et al. 2010). This in turn, provides food and shelter for a rich coastal fish community. The hydrodynamic conditions also attract large pelagic fish that are frequently fished in this small area (Cattaneo-Vietti et al. 2014). In the model area main fishing activities are fixed nets and surrounding net fishing ("Lampara"), in addition to recreational fishing.

# 6.2.2 Ecopath model structure

The species-based Ecopath model and the trophic levels (TLs)-based EcoTroph model were used in this study. The Data-rely toolbox developed by (Lassalle et al. 2014) was applied to evaluate data reliability and robustness of the Ecopath model predictions.

Ecopath is a mass-balanced model 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:

#### $P/Bi \times Bi = P/Bi \times Bi \times (1 - EEi) + \Sigma j (Q/B)ji \times Bi \times DCji + Yi + NMi + Bai$ (1)

B is the biomass, P/Bi is the production rate, Q/B is the consumption rate, DCji is the fraction of prey i included in the diet of predator *j*, *NMi* is the net migration of prey *i*, *BAi* is the biomass accumulation of prey *i*, *Yi* is the catch of prey *i* and *EEi* is the ecotrophic efficiency of prey *i*, that is the proportion of production used in the system. The model represents an average situation of the southern front of the Portofino MPA for the period 2007-2014, to ensure that protection effects were already in place. A simplified model structure developed by (Prato et al. 2014) for the Port Cros MPA with the intent of standardizing Ecopath modelling for Mediterranean MPAs was used in our study. Three new functional groups specific of the Portofino area were added to the standard model structure: small tuna-like fishes (hereafter small tunas), dolphins and horse mackerels. Small tuna-like fishes include species such as Sarda sarda, Auxis rochei and Euthynnus alletteratus, which, although pelagic, are often caught within the MPA boundaries and are thus important fishery resources. A group of dolphins of the species Tursiops truncatus permanently lives in the waters just in front of the MPA (Alessi et al. 2011), and are very likely interacting with the modeled food-web. The "horse mackerels and sand smelts+" group (the notation "+" following the name of each functional group signifies that several species are included in the group) (Valls et al. 2012, Prato et al. 2014) was split in two to account for some additional pelagic species frequently reported in the catches within the MPA (Scomber spp., Sardinella aurita), that have different diets from the "sand smelts +" group. An import component was added to the diet of migratory and pelagic species that are not present during the whole year in the study area. Similarly, due to the small size of the study area and the mixing of currents characteristic of this zone, we had to integrate zooplankton and phytoplankton advection in the model, which are likely continually imported and exported from the zone (Pinnegar et al. 2000). We thus added a component of import both in the diet of zooplankton and of benthic invertebrates which feed on zooplankton and phytoplankton. Finally, due to the absence of biomass data, together with their likely weak interaction with the shallow food web, some fish caught in the modelled area but known to live at depths >50 m were excluded from the model (Lophius piscatorius, Scyliorhinus canicula and Merluccius merluccius).

Details on the origins of all input parameters are given in Annex 1.

## Catches estimates

The MPA partially monitors artisanal fishing effort and catches. Only available fishing catches within the model area were thus considered, including catches from fixed nets (trammel nets, gill nets and combined nets), small purse seine and recreational fishing.

In order to obtain an annual picture of catches in the model area we had to attain from two main sources of data:

- A dataset of fishermen interviews (MARTE+ project, 2011) from which effort in the model area in one year was estimated, computed as total number of boats and days of fishing for fishing metier.
- The available logbooks from three boats (two boats monitored in 2012, one in 2013-2014), from which catches in kg/day for each fishing métier were estimated.

Thus, data from the logbooks (kg/day of fishing for each species and fishing métier) were multiplied for the total number of fishing days/year for the same métier.

Recreational fishermen must fill logbooks concerning catches within the MPA boundaries. From the logbooks we computed average catches expressed as kg /hour within our model area and multiplied for the total number of hours of recreational fishing in the MPA in one year (Cappanera et al. 2013).

From these estimates, we derived alternative data sets, using 2 multiplier coefficients for professional fishing (0.5 and 2) and 7 coefficients (0.5 and from 2 to 7) for recreational fishing, in order to account for larger uncertainty. Resulting values were then proposed to the evaluation of the MPA staff fishing experts, responsible for the monitoring of professional and recreational fishing. For each species, the most realistic estimate according to the expert's knowledge was retained. These expert-modified values were used to build our reference model. Two other models were then built with expert's estimates both multiplied and divided by the coefficient 1.5 to account for uncertainty in the data, and a fourth model was also built with the original logbook's estimates, to identify differences and data gaps. Accounting for uncertainty, we aimed at highlighting the potential of Ecopath and Ecotroph as a tool for advising MPAs management, and thus

stress on the urgent need to improve monitoring strategies and increase ecological and fisheries data quality and availability.

## 6.2.3 Species interactions, keystonness scores and fisheries impact

The mixed trophic impact routine (MTI) of Ecopath assesses the relative impact of a slight increase in abundance of any group on the biomass of other groups on the food-web (Christensen & Pauly 1992).

Keystone species are defined as the species having the highest and widest impact on the food web despite a low biomass. They were identified by applying the new keystonness index developed by (Valls et al. 2015). The index is characterized by an impact component (IC, defining the trophic impact of a group on the other groups) and a biomass component (BC), according to the following equation:

$$KS = Ln (IC \times BC)$$
(2)

Where IC is defined from (Libralato et al. 2006) as:

$$IC_{i} = \sqrt{\sum_{j \neq i} m_{ij}^{2}}$$
(3)

Parameter  $IC_i$  represents the overall effect of group *i* on all the other groups in the food web (and is expressed as the sum of the squared values of  $m_{ij}$  (the MTI score) of group *i*, paired with each of the other living group *j* in the food web. The mixed-trophic impact of group *i* on itself ( $m_{ij}$ ) is excluded, as well as the mixed-trophic impact on non-living groups such as detritus (Libralato et al. 2006).

The biomass component is defined as the rank of the group's biomass in descending order:

$$BC = drank(Bi)$$
(4)

Fishing loss (*Floss*) is an indicator of fishing impact given by the ratio between catches and the production of each functional group (*Y*/*P*). After obtaining production (*P*) from *P*/*B* x *B* we computed Floss for each functional group, in order to analyze the impact of fishing on keystone groups. Fishing fleets are treated as predators in the MTI routine, thus we analysed direct and indirect fisheries impacts within the ecosystem by computing and cumulatively plotting the MTI index of each fleet.

#### 6.2.4 Data quality and MTI sensitivity analysis

Since data availability and quality is the main limitation to EwE, like for any ecosystem model (Prato et al. 2014, Lassalle et al. 2014), data quality was assessed applying the food web diagnostics proposed by Link 2010 and the Data-Reli toolbox developed by Lassalle et al 2014. The Pedigree index (Morissette 2007) of the model was computed to summarise the uncertainty related to each input value and was used to assess if model quality was sufficient (Pedigree >0.4) to pursue with the analysis (Lassalle et al. 2014). Respiration / consumption ratio was not ecologically correct for sea urchins and cephalopods, thus their Q/B ratio was slightly increased.

Robustness of MTI results was tested through a sensitivity analysis (Lassalle et al 2014). We rebuilt the original net impact matrix where  $q_{ij}$  is the net impact of *i* on *j* and is given by the difference between positive effects (quantified by the fraction of prey *i* in the diet of predator *j* j), and negative effects  $f_{ij}$  (evaluated as the fraction of total consumption of *j* used by predator *i*). Then, in the analysis routine, 5000 Q matrices are created by drawing qij values from independent uniform distributions defined by original  $q_{ij} \pm 20\%$  (Richardson et al. 2006). The  $m_{ij}$  values for each pairwise intersection of the Q matrices are then calculated, their signs recorded and the percentage of  $m_{ij}$  values with the same sign as in the original MTI matrix (SMTI) is estimated. Results were summarized into one matrix recording the sign of the original  $m_{ij}$  values and the SMTI percentages that are categorized into four classes:[0; 50], [50; 75], [75; 95] and [95; 100].

## 6.2.5 Ecotroph model

The EcoTroph model summarizes the ecosystem functioning as a flow of biomass surging up the food web from lower to higher Trophic Levels (TL), through predation and ontogenic processes. The biomass enters the system at TL = 1, generated by primary producers or recycled from the detritus. For TLs > 2, the biomass is distributed along a continuum of TL due to the diet variability of the various consumers. The resulting biomass distribution is called trophic spectrum (Gascuel et al. 2005). EcoTroph thus allows to simulate various fishing scenarios and their impact on the biomass trophic spectrum.

On the basis of usual equations of fluid dynamics, the flow of the biomass present in the ecosystem at  $TL\tau$  under steady-state conditions is expressed as:

$$\mathbf{\Phi}(\tau) = \mathsf{D}(\tau) \times \mathsf{K}(\tau) \tag{5}$$

Where  $\phi(\tau)$  refers to the amount of biomass that moves up the food-web through TL $\tau$  (expressed in tons per year),  $D(\tau)$  is the density of biomass at trophic level  $\tau$  (expressed in tons per trophic level) and  $K(\tau)$  is the speed of flow, which quantifies the velocity of biomass transfers in the food-web (expressed as the numbers of TLs crossed per year). The continuous distribution of the biomass across a trophic level is calculated using a discrete approximation based on small trophic classes. EcoTroph conventionally considers trophic classes of width  $\Delta \tau$  equal to 0.1 *TL*, from Trophic Level 2 (corresponding to first-order consumers) to Trophic Level 5 (value considered sufficient to cover all top predators likely to occur in marine ecosystems). Thus, the mean biomass  $B\tau$  (in t), which is present in the [ $\tau,\tau+\Delta\tau$ ] trophic class under steady-state conditions, can be estimated as  $\int D(\tau) \times d\tau$  or  $D(\tau) \times \Delta\tau$  for a small interval  $\Delta\tau$ . Therefore:

$$B\tau = \Phi\tau \times \Delta\tau / K\tau$$
(5)

where  $\phi_{\tau}$  and  $K_{\tau}$  are the mean biomass flow and mean speed of flow within the  $[\tau, \tau + \Delta \tau]$  trophic class, respectively.

The flow of biomass from one trophic class to the next is non conservative and is thus expressed as:

$$\mathbf{\Phi}\tau + 1 = \mathbf{\Phi}\tau \times \exp[-(\mu_{\tau} + \phi_{\tau}) \times \Delta\tau]$$
(7)

where  $\mu_{\tau}$  is the natural loss rate (related to excretion and respiration) and  $\varphi_{\tau}$  is the fishing loss rate (with  $\varphi_{\tau} = F_{\tau} / K_{\tau}$ , where *F* is the fishing mortality). We refer to the Appendix in Gascuel et al. 2011 for further explanation of EcoTroph dynamics.

#### 6.2.6 Scenarios of fisheries closures and analysis of interacting impacts

For each functional group, accessibility to fishing was defined according to the number of targeted species within the functional group (if none of the species within the group is fished, then the accessibility value is zero). Afterwards, we used the ET-transpose routine described in Gascuel et al. (2009) to translate the outputs of the original Ecopath model

into an ET model and to build the trophic spectra of the cumulated catches and the trophic spectra of the fishing loss for each fishing fleet.

We simulated the unexploited state of the ecosystem by setting fishing loss ( $\varphi$ ) to 0 for all fleets in the ET-diagnosis routine. The current condition and two alternative fishing scenarios were compared to the unexploited state: no recreational fishing ( $\varphi_{\tau}=Y_{\tau}^{com}/P_{\tau}$ , where  $Y_{\tau}^{com}$  is the catch of commercial fisheries only, at trophic level  $\tau$ ) to test the effect of an interdiction of this activity, and double artisanal and recreational fishing ( $\varphi_{\tau}=2\cdot Y_{\tau}/P_{\tau}$ , where  $Y_{\tau}$  is the total catch at trophic level  $\tau$ ) to assess the impact that an increase in the fishing effort could have in the ecosystem.

Finally, we plotted artisanal and recreational fisheries' mixed impact on accessible biomass, TL of the accessible biomass, catches of the artisanal fishery and mean TL of the artisanal fishery's catch.

#### 6.3 Results

#### 6.3.1 Food web structure

The pedigree index of the model was 0.49. Biomass estimates were available for 60% of the groups (including most of the higher trophic levels, and the primary producers) while the remaining 40% (benthic compartments) were estimated by the model (Tab. 1). Biomasses of fish, invertebrates and primary producers were respectively 2%, 15% and 83% of total biomass in the system (5126 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup> including *Posidonia oceanica*).

Tab.1 Parameters of the balanced Ecopath model. Parameters in bold were obtained through the mass-balance calculations of the model. TL: Trophic level; B: biomass; ...

	Group name	TL	В	P/B	Q/B	EE	P/Q	F	Y Fixed nets	Y Small purse seine	Y Recreational	Discards Fixed nets
1	Dolphins	4.95	0.03	0.07	13.49	0.00	0.01	-	-	-	-	-
2	Small tunas +	4.64	1.23	0.35	8.19	0.50	0.04	0.18	0.11	0.00	0.10	0.00
3	Amberjack & dentex +	4.31	6.00	0.47	3.58	0.65	0.13	0.27	0.14	0.45	1.06	0.00
4	Dusky grouper L	4.39	4.60	0.18	0.81	0.00	0.22	-	-	-	-	-
5	Dusky grouper M	4.26	1.26	0.47	1.66	0.13	0.28	0.06	0.08	0.00	0.00	0.00
6	Dusky grouper S	3.98	0.62	1.34	4.40	0.09	0.30	-	-	-	-	-
7	Large-scaled scorpionfishes +	3.79	2.50	0.54	4.62	0.68	0.12	0.21	0.19	0.00	0.32	0.00
8	Scorpionfishes&combers +	3.69	1.18	0.65	6.60	0.97	0.10	0.27	0.03	0.00	0.29	0.00
9	Stripped red mullets +	3.72	2.14	0.88	7.84	0.70	0.11	0.05	0.05	0.00	0.06	0.00
10	Horse mackerels +	3.76	8.09	0.97	7.57	0.90	0.13	0.03	0.00	0.18	0.03	0.00
11	Sand smelts +	3.53	15.11	0.83	10.41	0.43	0.08	0.06	0.00	0.62	0.24	0.00
12	Pagellus	3.45	0.31	0.67	6.96	0.79	0.10	0.41	0.03	0.00	0.10	0.00
13	Diplodus +	3.08	29.70	0.73	6.46	0.24	0.11	0.11	1.40	0.00	1.94	0.00
14	Gobies +	3.26	6.00	1.12	8.54	0.90	0.13	0.01	0.00	0.00	0.06	0.00
15	Wrasses +	3.23	2.49	0.96	9.56	0.75	0.10	0.03	0.02	0.00	0.05	0.00
16	Mullets	2.32	1.17	0.36	14.99	0.39	0.02	0.01	0.00	0.00	0.01	0.00
17	Salema S	2.35	3.17	0.95	5.30	0.25	0.18	-	-	-	-	-
18	Salema L	2.00	6.10	0.60	2.54	0.64	0.24	0.31	0.00	1.84	0.04	0.00
19	Decapods +	2.65	12.61	2.64	18.89	0.90	0.14	0.01	0.14	0.00	0.00	0.00
20	Cephalopods	3.61	3.43	2.34	7.80	0.70	0.30	0.13	0.05	0.00	0.40	0.00
21	Zooplankton L	3.02	3.12	22.71	60.47	0.95	0.38	-	-	-	-	-
22	Zooplankton S	2.10	7.52	35.44	109.43	0.95	0.32	-	-	-	-	-
23	Sea worms	2.31	40.16	2.58	15.27	0.95	0.17	-	-	-	-	-
24	Macrofauna +	2.16	49.71	4.10	47.60	0.90	0.09	-	-	-	-	-
25	Echinoderms +	2.36	21.38	0.59	1.67	0.50	0.35	-	-	-	-	-
26	Suspensivores +	2.19	74.23	2.63	11.20	0.90	0.23	-	-	-	-	-
27	Gorgonians	2.23	500.80	0.20	0.53	0.02	0.38	-	-	-	-	-
28	Sea urchins	2.15	64.95	0.57	2.70	0.60	0.21	-	-	-	-	-
29	Meiofauna	2.00	<b>19.84</b> 3674.0	10.00	33.33	0.95	0.30	-	-	-	-	-
30	Posidonia	1.00	0	0.55	-	0.24	-	-	-	-	-	-
31	Seaweeds	1.00	557.00	4.43	-	0.14	-	-	-	-	-	-
32	Phytoplankton	1.00	7.14	179.60	-	0.46	-	-	-	-	-	-
33	Detritus	1.00	65.25	-	-	0.28	-	-	-	-	-	-

The analysis of the energy fluxes and biomass repartition (Fig. 2) allowed to discern among a main bentho-pelagic path, connecting primary producers and detritus to the higher trophic levels in the food-web through the benthic compartments, and a pelagic path connecting phytoplankton, zooplankton, planktonivorous fish and pelagics. The biomass of first order producers was dominated by Posidonia oceanica and seaweeds, which were the largest source of energy for Salemas and Sea urchins, the main herbivores in the system. The detritus compartment exhibited strong energy connections with many (Macrofauna+, Sea benthic invertebrate groups worms, Echinoderms+ and Suspensivores). Gorgonians dominated the biomass of benthic invertebrates, but their contribution to the energy fluxes of the food-web was limited, due to the low number of groups feeding on them. Suspensivores+ held the second position in the biomass ranking of benthic compartments, followed by Sea urchins, Macrofauna+, Sea worms and Echinoderms+ (sea stars and sea cucumbers).

Cephalopods played an important role in connecting the pelagic and bentho-pelagic paths, showing a high degree of connections both with benthic invertebrates, planktonivorous fish and high trophic level predators. Fish biomass was high in the modelled system (91.6 tons·km<sup>-2</sup>·year<sup>-1</sup>), which supported in particular very high biomasses of the Diplodus+ group (29 tons · km<sup>-2</sup> ·year<sup>-1</sup>) and also significant biomass of the high trophic level predator groups Amberjack&dentex+ and Dusky grouper. Planktonivorous fish were also important (15 tons km<sup>-2</sup> year<sup>-1</sup> for Sand smelts+ and 8 tons ·km<sup>-2</sup> year<sup>-1</sup> for Horse mackerels+), being preys of many higher trophic level groups, thus connecting the pelagic pathway to the bentho-pelagic one.

Finally, artisanal and recreational fisheries catches were respectively 53% and 47% of total landings, estimated to be 10 tons  $\cdot \text{ km}^{-2} \cdot \text{year}^{-1}$ , corresponding to 9% of total fish and fished invertebrates biomass.



Fig. 2 Flow diagram of the modelled ecosystem. Size of the nodes is proportional to the biomass of the functional groups. Lines represent the flux of energy among groups. Colours are proportional to the magnitude of the flux.

#### 6.3.2 Species interactions and keystonness scores

The keystonness analysis (Fig. 3) showed that three groups play an especially important role in the functioning of the food web: Amberjack&dentex+, Large scaled scorpionfishes+ and the Small dusky grouper, followed by Stripped red mullets+ and Cephalopods. The analysis of the MTI signs for these groups allowed to unravel both their negative impacts on the food web through direct predation, but also positive cascade effects that they triggered on some species by releasing them from meso-predation (Fig.4). Amberjack&dentex+ had the overall largest trophic impact, with a significant negative impact on the Small dusky grouper, but also on Horse mackerels+, highlighting the connection of this group with both the pelagic and bentho-pelagic pathways. The Small dusky grouper and Large scale scorpionfish+ on their turn negatively impacted many necto-benthic fish groups. Positive indirect effects of Amberjack&dentex+ and the Small

dusky grouper, although slight, mainly concerned benthic invertebrates groups (Sea urchins, Macrofauna+, Suspensivores+ and Decapods+), which were released from mesopredation. A slight increase in Large scaled scorpionfish+ biomass led to larger indirect positive effects than the two previous groups, mainly favouring Cephalopods+, Decapods+, Large zooplankton, and Gobies+ (Fig.4)

Cephalopods+ also had a high KS score (Fig.3), showing the largest overall positive impact on the food-web, both directly as preferred preys of the Medium and Large dusky groupers, but also indirectly, positively affecting several invertebrates as Sea urchins, Gorgonians, Suspensivores+, Macrofauna+, and Echinoderms+ (divers effects +) (Fig.4). These indirect positive effects were mainly consequent to meso-predation release from Decapods, Diplodus+, and Sand smelts+, all preys of Cephaopods+. Among negative effects, indirect competition for preys with necto-benthic fish like Large scale scorpionfish+ and Scorpionfish and combers+ was unravelled (Fig.4).

Dolphins and small tunas+, although having higher trophic levels and smaller biomasses, did not result as keystone predators likely because of the large import component in their diets, that attenuated their trophic impact in the modelled area.



Fig. 3 Functional groups plotted against keystone index and trophic level. Size of the bubbles is scaled to the biomass of the group.



Fig. 4 Cumulative plot of the mixed trophic impact indices of the species with highest keystonnes scores. Values on the positive axis represent positive impacts of the keystone groups on each functional group in the food-web, values on the negative axis represent negative impacts. Impacts <0.05 were grouped together under divers effects (both negative and positive).

Analysis of fishing loss rates (Fig. 5) showed that six groups encompass a high fishing pressure, with annual catch higher than 35% of their natural production. Among these 6 groups, two were previously identified as keystone species: the Amberjack&dentex+ and the Large scaled scorpionfishes+. In contrast, Pagellus, Salema L, Small tunas+ and Scorpionfish&combers+ are strongly exploited, but seem to play a limited role in the functioning of the food-web. Concerning the other groups, fishing pressure was lower, with annual catch lower than 20%.



Fig. 5 Fishing loss rate for each functional group. Fishing loss= Y/P

The sensitivity analysis performed on the MTI matrix revealed that MTI signs were robust to a variation of +/-20% in the original net impact value: 85 % of the pairwise intersections in the original MTI matrix had a sign equal to that of the original matrix with a confidence percentage > 95% (70% of the pairwise intersections reached 100% confidence) (Tab. 1, Annex).

#### 6.3.3 Current catch and fishing loss rates by fishery

Trophic spectra of the cumulated fisheries catches showed overlap among the three fisheries, in particular for trophic levels > 3.5 (Fig.6a). Recreational fishing catches targeted trophic levels > 3 (mean TL catch = 3.56), while artisanal fixed nets catches concentrated mainly around TL 3 (mean TL catch = 3.35). Purse seine fishing caught high biomasses at TL 2 (Salemas), and also at TL > 3.5 (mean TL catch= 2.75). The overlap of the three fisheries on high trophic levels resulted in the strongest fishing losses for trophic levels higher than 4, due to the lower turnover rates of these predators (Fig. 6b). On the contrary, high catches at TL 2 and 3 did not translate into strong fishing impact. When confidence intervals were added according to the two alternative estimates provided by the

MPA fishery experts, results kept consistent. When the analysis was run on the model based on non-corrected logbook fishing data, fishing loss by recreational fishing was consistently lower, due to an underestimation of total fishing catches (Fig. A1 Annex.). However, the general trend of major impact from the three fisheries overlap on high trophic levels was maintained.





When fisheries were considered as predators in the MTI analysis (Fig.7), they had both direct negative impacts on the species they targeted, but also indirect negative impacts by reducing the prey availability for some species (competition) and indirect positive impacts due to release from predation. In particular, the recreational fishing fleet had the strongest total impact on the food web. Species directly targeted by this fishery were the high trophic level groups Small tunas+, Amberjack&dentex+ and Large scaled scorpionfish+. Release

from predation from these high trophic level predators favoured some species such as the Small and medium dusky grouper, Horse mackerels+, Wrasses+ and several benthic invertebrates. Professional fishery with fixed nets negatively impacted the Medium dusky grouper, partly due to direct fishing and partly to competition, since many species targeted by fixed nets were also preys of the Medium dusky grouper. Sea urchins and most benthic invertebrates (except Decapods+) were also favoured by an increase in this fishery. Professional fishery with small purse seine had the lowest overall trophic impact, with a large negative impact mainly on Salemas and Amberjack and dentex+ (targeting barracudas), and a consequent positive impact on the Small dusky grouper and benthic invertebrates.



Fig. 7 Cumulative plot of the mixed trophic impact indices of the fishing fleets. Values on the positive axis represent positive impacts of the fishery on the functional groups in the food-web, values on the negative axis represent negative impacts. Impacts <0.05 were grouped together under diverse effects (both negative and positive).

## 6.3.4 Simulation of fisheries closures

Simulation of fishing scenarios (Fig. 8) showed that the system was far from its unexploited condition for the higher trophic level groups (TL>4), whose biomass in the unexploited state would be 44% higher than current biomass. When recreational fishing

mortality was set to 0, the total biomass of high trophic level fish increased of 24%. When fishing mortality was doubled for all fisheries high trophic levels were again the most impacted. When logbook data were also considered, at the current state the system resulted closer to the unexploited condition. This was again due to the underestimation of recreational fishing catches, since when recreational fishing mortality was set to 0 results were equal to the reference model (Fig. A2 Annex).



Fig.8 Trophic spectra of relative biomass (dimensionless) by fishing scenario. Relative biomass was calculated by dividing absolute biomass values of each scenario by the absolute biomass values of the unexploited state. Expert uncertainty relates to the two alternative estimates of catches, according to experts knowledge (see text)

The analysis of fisheries interactions showed that artisanal fisheries quantitatively impacted the biomass accessible to fisheries more than recreational fisheries (Fig.9a). Indeed, setting respectively artisanal or recreational fisheries to zero, the accessible biomass would increase about 22 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year <sup>-1</sup> (+ 47%) and 12 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year <sup>-1</sup> (+ 25%), respectively.

On the other hand, recreational fishing had a stronger impact on the composition of the fish assemblage, affecting the mean TL of the accessible biomass (Fig.9b). Forbidding recreational fisheries would, in fact, lead to an increase in the mean TL from approximately 3.15 to 3.35, while a reduction in artisanal fisheries would not modify the mean TL of the accessible biomass.

Quantitative impact of recreational fishing on professional fishing catches resulted in a potential increase of 1.2 tons  $\cdot$  km<sup>2</sup>  $\cdot$  year <sup>-1</sup> in the catches of the latter (+23 %) if the former was set to 0 (Fig. 9c). Prohibiting recreational fishing moreover would increase the mean TL of the professional catches from 2.95 to 3.15 (Fig.9d)



Fig. 9 Isopleths of scenarios showing the effects of a variation in fishing effort on a) the total accessible biomass of the system, b) the mean trophic level of the accessible biomass, c) the artisanal fishery catches and d) the mean trophic level of the artisanal fishery catches. mE= multiplier of the fishing effort. Artisanal fishery included fixed nets and small purse seine.

#### 6.4 Discussion

#### 6.4.1 Building a trophic model in the context of Mediterranean MPAs

Scientific ecological knowledge on Mediterranean MPAs, when available, is often dispersed among several sources of information, ranging from local or foreign universities or environmental agencies, to local/traditional ecological knowledge, historical archives, and expert opinions. Integration of this wealth of information is essential for a holistic understanding of protection effects on ecosystem functioning and thus a fully informed management of MPAs. The trophic modelling approach adopted here is a useful tool to accomplish such integration, allowing us to fit largely scattered data into a coherent picture of ecosystem functioning for the Portofino MPA. In particular, a snapshot of the highly productive area surrounding the southern promontory of the MPA was provided, representing an average year between 2007 and 2014. This model provides a baseline that can be easily updated in the years to come, when more geo-referenced data on key species biomass.

Similarly to most ecosystem models, it was not possible to obtain local data for all functional groups (Pedigree index = 0.46), but model-derived estimates were in accordance with ecological knowledge of the area. Biomass ranking of benthic invertebrates was confirmed by expert opinion (C. Cerrano pers comm.) with highest biomasses of gorgonians, followed by suspensivores+, macrofauna+, sea worms and echinoderms+ (sea stars and sea cucumbers). Trophic levels computed by the model fell also within the range of results for the Mediterranean (Stergiou & Karpouzi 2001).

The analysis of the energy fluxes allowed to unravel a complex food-web despite the relatively small area, with a main bentho-pelagic energy path exchanging energy with a more pelagic path through some key groups like cephalopods, planktonivorous fish and high trophic level predators. Comparison of relative biomass partitioning among primary producers, benthic invertebrates and fish with another modelled Mediterranean MPA (Port Cros, Valls et al 2012) allowed highlighting the peculiarities of Portofino. This area supports high benthic community biomass (15% of total biomass) when compared to the Port Cros MPA (3.5%), sustaining high biomass of fish at all trophic levels (2% of total biomass, against 0.65% in Port Cros). The fish biomass observed was particularly high especially for high trophic level predators (10 tons  $\cdot \text{ km}^{-2} \cdot \text{ year}^{-1}$ ) and sea breams (29 tons  $\cdot \text{ km}^{-2} \cdot \text{ year}^{-1}$ ) in comparison to the Port Cros MPA (9 and 3 tons  $\cdot \text{ km}^{-2} \cdot \text{ year}^{-1}$ )

respectively, Valls et al 2012). Sea breams biomass in the MPA was in fact shown to be higher than the accepted threshold of 12 individuals per 125 m<sup>2</sup> necessary to maintain sea urchins abundance low and avoid rocky reef ecosystem shifts towards barrens (Guidetti & Sala 2007, Guidetti et al 2008). Indeed, extended sea-urchin barrens are absent in the Portofino MPA (Sala et al. 2012). The identification of high trophic level predators (Amberjack&dentex+ group and Dusky grouper) as keystone groups supports current conservation strategies aiming at protecting these target fish within Mediterranean MPAs. It is noteworthy that cephalopods have also shown a high keystonness index in the Portofino MPA, similarly to the Port Cros model (Valls et al. 2012) and to a subsequent sensitivity analysis performed on it, which highlighted the impact that uncertain input biomass data for cephalopods can have on biomass estimates of other groups (Prato et al. 2014). Being both a preferred prey for many high trophic level predators, but also predators acting on a wide range of trophic levels, cephalopods occupy an important functional role in both coastal and pelagic ecosystems (Piatkowski et al. 2001, Coll et al. 2013). Large variations in cephalopods biomass can indeed lead to strong effects on the marine food-webs, both through bottom up and top down impacts. In the Portofino MPA they are subject to some artisanal and recreational fishing pressure, which is likely underestimated due to the presence of illegal fishing in the MPA. This is a common issue in most Mediterranean coastal areas, but is generally difficult to address. If the exploitation state of cephalopods is not controlled, their biomass could become a limiting food item for their predators, especially for the protected Dusky grouper. Cephalopods should thus be regarded as an important monitoring target in the context of Mediterranean MPAs.

#### 6.4.2 Interacting fishing impacts on the food-web

This study was the first attempt to assess the impact of recreational fisheries on a Mediterranean MPA food-web, and its interaction with the artisanal fishery, starting from available although limited local logbook data. Estimates of artisanal fishing catches within the MPA zones surrounding the southern promontory front (3.35 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>) were much higher than catches in the Port Cros MPA (0.3 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>) and Bonifacio Straits Natural Reserve (0.09 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>) for which similar Ecopath models had been built (Valls et al 2012, Albouy et al 2010). Estimates of recreational fishing (3.56 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>) were also markedly higher when compared to Bonifacio (0.1 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup>), although in Bonifacio these were indirectly derived by applying a percentage to professional fishing catches (Albouy et al 2010). Total estimates were instead similar to 162

those from the Cote Bleu Marine Park (SW France), comparable to Portofino in terms of number of fishing boats and metiers, with 4.6 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup> landed by coastal artisanal fisheries operating with fixed nets, and approximately 3.6 tons · km<sup>-2</sup> · year<sup>-1</sup>of recreational fishing catches (from boat and shore) (Leleu et al. 2014, Cote bleu Scientific Report 2013-2014). The catches overlap among artisanal and recreational fisheries in the Portofino MPA led to strong fishing losses on high trophic level predators, due to the lower turnover rates of these groups. Although the Portofino MPA was demonstrated to be effective in sustaining a recovery of fish biomass within its borders (Guidetti et al. 2008), as also shown by the high biomass levels within it, fishing losses on high trophic level predators are still high within the MPA. Recreational fishing, in particular, contributed for approximately half of these fishing losses, leading to the largest impact on the whole food web, as shown by the mixed trophic impact analysis. Fisheries primarily targeting high trophic level predators often lead to such wide impacts on the ecosystem, as it has been shown to happen in the whole Ligurian sea (Britten et al. 2014). An analysis of 25 years of landings (1950-1974) from the tuna trap ("tonnarella") situated in the zone C of the Portofino MPA, just outside our modelled area, revealed the occurrence of a strong depletion of top predators, including sharks, tunas and other large piscivores associated with this coastal area, which were gradually replaced by lower trophic levels (Britten et al. 2014). Such trophic downgrading was parallel to an intensification of fishing effort and ultimately led to a decrease in the stability of the fish community due to a release from topdown control. The community became dominated by intermediate trophic levels with variable life history (mainly herbivores, cephalopods and planktonivores), subject to wide oscillations in time (Britten et al. 2014). Here, the analysis of the mixed trophic impact of the recreational fishery showed that the similar intermediate trophic level groups also benefited from a slight increase in its effort.

#### 6.4.3 Management applications of trophic modelling

The presented modelling approach can provide some useful outcomes for the management of MPAs. First, it allows identifying species that play important keystone roles in the food-web, but are at the same time subject to strong fishing impact. These species (included in the Amberjack&dentex+ and Large Scaled Scorpionfishes+ groups for the Portofino case study) can be considered as "sentinels" of the condition of the food-web and their monitoring should therefore be regarded as a priority within MPAs. Monitoring should take place both by assessing their biomass state in the ecosystem, but also 163

evaluating their exploitation status through the survey of artisanal and recreational fishing catches. These species could also be a reference for the definition of management actions (for instance, calculating the reduction of fishing mortality needed to attain predefined conservation objectives) and for the assessment of their efficiency.

The model also revealed that regarding high trophic level predators, the ecosystem is likely far away from its carrying capacity, assumed to be equal to our simulated condition of no fishing. An eventual interdiction of recreational fishing would lead to a significant increase in the biomass of this group (TL>4), up to 24%. A similar analysis performed on the Port Cros MPA showed that the ecosystem was very near to its simulated unexploited state (Valls et al. 2012). The habitat and ecological differences among the two areas, but also the older age of the Port Cros MPA (more than 50 years), and the lower fishing pressure within this area are probably influencing this difference. MPA carrying capacity for high trophic level predators for instance generally needs between 13 and 30 years depending on the species (Garcia-Rubies et al. 2013). According to our results, the potential carrying capacity for high trophic level predators in the Portofino MPA is likely to be high, but the current level of fishing within the MPA borders should be reduced in order to pursue the MPAs conservation objectives.

Finally, the model allowed to inform about the impact of recreational fishing on artisanal fisheries catches. The competition for target fish among recreational and artisanal fishing is a growing issue in many Mediterranean coastal areas, but few MPAs assess such impact. In the Cote Bleu Marine Park for example the long term assessment of both fisheries highlighted a strong competition of resources, where over 36 species highly targeted by artisanal fishermen, 25 were also a spearfishing target and 17 were targeted by recreational fishing from boat. Moreover, recreational fishing was less selective, targeting both the prey of species normally targeted by artisanal fishermen and also the large carnivores (Leleu et al 2014, Charbonnel et al. 2014). Such trend was also highlighted in our study, and is likely to be more intense given the probable underestimation of recreational fishing catches. Illegal spearfishing is in fact likely occurring in the MPA, and monitoring recreational fishermen is further complicated by the mismatch among logbooks and local expert's estimates in our study.

Artisanal fishery is a conservation target for many Mediterranean MPAs, which often promote a sustainable socio-economic development and the conservation of traditional activities, when carried on in a sustainable way, and of local identities/cultures (Di Franco et al. 2014). Our results suggested that the artisanal fishery alone would have moderate impact on the food web, reducing by less than 15% the biomass of top predators (TL>4.0), with almost no effect on the total biomass of lower trophic levels. Limiting recreational fishing effort could therefore allow the MPA to pursue both its conservation and socio-economic development targets, by i) reducing the impact on high trophic level predators and thus benefiting the whole ecosystem and ii) increasing the availability of catches at higher trophic levels for artisanal fishing. This type of catch is generally more valuable on the market, thus providing economic benefits to the naturally-declining artisanal fishing activity.

Lastly, integrating these results to other impact assessments on the Portofino MPA (Markantonatou et al. 2014), which highlighted the high spatial overlap among artisanal and recreational fishing activities on the coralligenous habitat, allows to provide a holistic set of information that could help driving management actions within the MPA.

#### 6.5 Conclusions

The trophic modelling approach with Ecopath and Ecotroph provided useful insights on the food-web structure associated with the Portofino MPA. Amberjack&dentex+ and Largescaled scorpionfishes+ were identified as sentinel groups, cumulating high keystonness and a currently high fishing impact. The interacting impacts of artisanal and recreational fishing on the food-web were also unravelled. Despite some limits in input data availability, application of pre-balancing rules (Link 2010), coupled with the novel sensitivity analysis on the mixed trophic impact matrix (Lassalle et al. 2014) and the comparisons of 4 different models based on alternative catch estimates, provided consistent trends in the results. The potential of the approach is thus high, not only to assess large scale ecosystem impacts such as those of industrial fisheries and climate change (Fouzai et al. 2012, Albouy et al. 2014, Coll et al. 2015) but also at a more local scale to address crucial issues such as those of users conflicts, common to most coastal ecosystems and MPAs. Nonetheless, it is essential that coastal Mediterranean MPAs develop long term monitoring programs on key species and on extractive professional and recreational activities. Only by increasing data availability and integration it will be possible to develop more robust food-web models and enhance their potential as management tools, by integrating dynamic simulations and bridging them with spatial modelling approaches (Steenbeek et al. 2013, Levin et al. 2014).

# 6.6 References

- Abdulla A, Gomei M, Maison E, Piante C (2008) Status of marine protected areas in the Mediterranean Sea. IUCN Malaga WWF Fr
- Albouy C, Velez L, Coll M, Colloca F, Loc'h F, Mouillot D, Gravel D (2014) From projected species distribution to food-web structure under climate change. Glob Change Biol 20:730–741
- Baskett ML, Micheli F, Levin SA (2007) Designing marine reserves for interacting species: Insights from theory. Biol Conserv 137:163–179
- Biseau A (1998) Definition of a directed fishing effort in a mixed-species trawl fishery, and its impact on stock assessments. Aquat Living Resour 11:119–136
- Britten GL, Dowd M, Minto C, Ferretti F, Boero F, Lotze HK (2014) Predator decline leads to decreased stability in a coastal fish community (G De Leo, Ed.). Ecol Lett 17:1518–1525
- Cappanera V, Venturini S, Campodonico P (2013) Valutazione dell'impatto antropico legato alle attività svolte nell'area Marina Protetta Portofiino. Le attività di fruizione 2012-2013
- Cattaneo-Vietti R, Albertelli G, Aliani S, Bava S, Bavestrello G, Cecchi LB, Bianchi CN, Bozzo E, Capello M, Castellano M, others (2010) The Ligurian Sea: present status, problems and perspectives. Chem Ecol 26:319–340
- Cattaneo-Vietti R, Cappanera V Castellano M, Povero P. (2014) Yield and catch changes in a Mediterranean Small Tuna Trap: a climate change effect? Marine Ecology **35:** 1-12
- Charbonnel E, Bachet F, Monin M, Bellan-Santini D (2014). Rapport sur les travaux scientifiques du Parc Marin de la Côte Bleue. Années 2012-2014. Rapport Parc Marin de la Côte Bleue Agence de l'Eau RMC, Fr.: 1-180.
- Christensen V, Pauly D (1992) Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61:169–185
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 172:109–139
- Coll M, Akoglu E, Arreguín-Sánchez F, Fulton EA, Gascuel D, Heymans JJ, Libralato S, Mackinson S, Palomera I, Piroddi C, others (2015) Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. Rev Fish Biol Fish 25:413–424
- Colléter M, Gascuel D, Albouy C, Francour P, Tito de Morais L, Valls A, Le Loc'h F (2014) Fishing inside or outside? A case studies analysis of potential spillover effect from marine protected areas, using food web models. J Mar Syst 139:383–395
- Colléter M, Gascuel D, Ecoutin JM, Tito de Morais L (2012) Modelling trophic flows in ecosystems to assess the efficiency of marine protected area (MPA), a case study on the coast of Senegal. Ecol Model 232:1–13
- Colléter M, Walters CJ, Gatti P, Gascuel D (2015) Including foraging arena and top-down controls improves the modeling of trophic flows and fishing impacts in aquatic food webs. Mar Ecol Prog Ser 534:17–37

- Coll J, Linde M, García-Rubies A, Riera F, Grau AM (2004) Spear fishing in the Balearic Islands (west central Mediterranean): species affected and catch evolution during the period 1975–2001. Fish Res 70:97–111
- Coll M, Navarro J, Olson RJ, Christensen V (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Res Part II Top Stud Oceanogr 95:21–36
- Colloca F, Cardinale M, Maynou F, Giannoulaki M, Scarcella G, Jenko K, Bellido JM, Fiorentino F (2013) Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish Fish 14:89–109
- Coll M, Piroddi C, Albouy C, Ben Rais Lasram F, Cheung WWL, Christensen V, Karpouzi VS, Guilhaumon F, Mouillot D, Paleczny M, others (2011) The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. Glob Ecol Biogeogr
- Coll M, Piroddi C, Steenbeek J, Kaschner K, Ben Rais Lasram F, Aguzzi J, Ballesteros E, Bianchi CN, Corbera J, Dailianis T, Danovaro R, Estrada M, Froglia C, Galil BS, Gasol JM, Gertwagen R, Gil J, Guilhaumon F, Kesner-Reyes K, Kitsos M-S, Koukouras A, Lampadariou N, Laxamana E, López-Fé de la Cuadra CM, Lotze HK, Martin D, Mouillot D, Oro D, Raicevich S, Rius-Barile J, Saiz-Salinas JI, San Vicente C, Somot S, Templado J, Turon X, Vafidis D, Villanueva R, Voultsiadou E (2010) The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats. PLoS ONE 5:e11842
- Cooke SJ, Cowx IG (2004) The role of recreational fishing in global fish crises. BioScience 54:857–859
- Cooke SJ, Cowx IG (2006) Contrasting recreational and commercial fishing: searching for common issues to promote unified conservation of fisheries resources and aquatic environments. Biol Conserv 128:93–108
- Coppola SR (2006) Inventory of Artisanal Fishery Communities in the Western and Central Mediterranean. Food & Agriculture Org.
- Di Franco A, Bodilis P, Piante C, Thiriet P, Francour P, Guidetti P. (2014) Fishermen engagement, a key element to the success of artisanal fisheries management in Mediterranean marine protected areas. MedPAN North Project. WWF-France.
- Diviacco G, Coppo S (2006). Atlante degli habitat marini della Liguria. Region Liguria, Genova, Italy, pp. 205
- Doglioli AM, Griffa A, Magaldi MG (2004) Numerical study of a coastal current on a steep slope in presence of a cape: The case of the Promontorio di Portofino. J Geophys Res Oceans 1978–2012 109
- Edgar GJ (2011). Does the global network of marine protected areas provide an adequate safety net for marine biodiversity? Aquatic Conserv: Mar. Freshw. Ecosyst. 21: 313–316. doi:10.1002/aqc.1187
- Farrugio H, Oliver P, Biagi F (1993) An overview of the history, knowledge, recent and future research trends in Mediterranean fisheries. Sci Mar 57:105–119
- Fenberg PB, Caselle JE, Claudet J, Clemence M, Gaines SD, García-Charton JA, Gonçalves EJ, Grorud-Colvert K, Guidetti P, Jenkins SR, others (2012) The

science of European marine reserves: Status, efficacy, and future needs. Mar Policy 36:1012–1021

- Font T, Lloret J, Piante C (2012) Recreational fishing within Marine Protected Areas in the Mediterranean. MedPAN North Proj WWF Fr
- Forcada A, Bayle-Sempere JT, Valle C, Sanchez-Jerez P (2008) Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. Mar Environ Res 66:536–547
- Fouzai N, Coll M, Palomera I, Santojanni A, Arneri E, Christensen V (2012) Fishing management scenarios to rebuild exploited resources and ecosystems of the Northern-Central Adriatic (Mediterranean Sea). J Mar Syst 102-104:39–51
- Fulton EA (2010) Approaches to end-to-end ecosystem models. J Mar Syst 81:171–183
- Garcia-Rubies A, Hereu B, Zabala M (2013) Long-Term Recovery Patterns and Limited Spillover of Large Predatory Fish in a Mediterranean MPA. PLoS ONE 8
- Gasche L, Gascuel D (2013) EcoTroph: a simple model to assess fishery interactions and their impacts on ecosystems. ICES J Mar Sci J Cons
- Gascuel D, Bozec Y-M, Chassot E, Colomb A, Laurans M (2005) The trophic spectrum: theory and application as an ecosystem indicator. ICES J Mar Sci J Cons 62:443–452
- Gascuel D, Guénette S, Pauly D (2011) The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. ICES J Mar Sci J Cons 68:1403–1416
- Gascuel D, Tremblay-Boyer L, Pauly D (2009) EcoTroph (ET): a trophic level based software for assessing the impacts of fishing on aquatic ecosystems. Fisheries Centre Research Reports 17:83 p
- Gómez S, Lloret J, Demestre M, Riera V (2006) The decline of the artisanal fisheries in Mediterranean coastal areas: the case of Cap de Creus (Cape Creus). Coast Manag 34:217–232
- Goñi R, Quetglas A, Renones O (2006) Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219
- Guidetti P, Claudet J (2010) Comanagement practices enhance fisheries in marine protected areas. Conserv Biol 24:312–318
- Guidetti P., M. Milazzo, S. Bussotti, A. Molinari, M. Murenu, A. Pais, N. Spano, R. Balzano, T. Agardy, F. Boero, G. Carrada, R. Cattaneo-Vietti, A. Cau, R. Chemello, S. Greco, A. Manganaro, G. Notarbartolo di Sciara, G. Russo, L. Tunesi, 2008. Italian marine reserve effectiveness: does enforcement matter? Biol Conserv, 41: 699-709.
- Guyader O, Berthou P, Koutsikopoulos C, Alban F, Demaneche S, Gaspar MB, Eschbaum R, Fahy E, Tully O, Reynal L, others (2013) Small scale fisheries in Europe: A comparative analysis based on a selection of case studies. Fish Res 140:1–13
- Lassalle G, Bourdaud P, Saint-Béat B, Rochette S, Niquil N (2014) A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. Ecol Model 285:13–21

- Leleu K, Pelletier D, Charbonnel E, Letourneur Y, Alban F, Bachet F, Boudouresque CF (2014) Métiers, effort and catches of a Mediterranean small-scale coastal fishery: The case of the Côte Bleue Marine Park. Fish Res 154:93–101
- Levin N, Coll M, Fraschetti S, Gal G, Giakoumi S, Göke C, Heymans JJ, Katsanevakis10 S, Mazor T, Öztürk11 B, others (2014) Biodiversity data requirements for systematic conservation planning in the Mediterranean Sea. Mar Ecol Prog Ser 508:261–281
- Lewin W-C, Arlinghaus R, Mehner T (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev Fish Sci 14:305–367
- Libralato S, Tempesta M, Solidoro C, Spoto M (2006) An ecosystem model applied to Miramare natural Marine Reserve: limits, advantages and perspectives. Biol Mar Mediterr 13: 386-395
- Link JS (2010) Adding rigor to ecological network models by evaluating a set of prebalance diagnostics: A plea for PREBAL. Ecol Model 221:1580–1591
- Lloret J, Font T (2013) A comparative analysis between recreational and artisanal fisheries in a Mediterranean coastal area. Fish Manag Ecol 20:148–160
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves 1. Ecol Appl 13:3–7
- Marte + Progetto Strategico (2011) La pesca artigianale nel territorio trans-frontaliero: capacita', sforzo di pesca e caratterizzazione dei principali metiers. In: Modelli di governance e Monitoraggio per la salvaguardia e valorizzazione delle risorse ittiche; Componente 4:monitoraggio delle risorse ittiche e acquacoltura sostenibile
- Markantonatou V, Noguera P, Semitiel-Garcia M, Hogg K, Sano M, 2015. Social networks and information flow: building the ground for collaborative marine conservation planning in Portofino Marine Protected Area (MPA). Journal of Ocean and Coastal Management. *In press.*
- Mesnil B, Shepherd JG (1990) A hybrid age-and length-structured model for assessing regulatory measures in multiple-species, multiple-fleet fisheries. J Cons ICES J Mar Sci 47:115–132
- Morales-Nin B, Moranta J, García C, Tugores MP, Grau AM, Riera F, Cerdà M (2005) The recreational fishery off Majorca Island (western Mediterranean): some implications for coastal resource management. ICES J Mar Sci J Cons 62:727–739
- Morissette L (2007) Complexity, cost and quality of ecosystem models and their impact on resilience. PhD thesis, University of British Columbia
- Piatkowski U, Pierce GJ, Morais da Cunha M (2001) Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fish Res 52:5–10
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien ML, Hereu B, Milazzo M, Zabala M, Anna G d' (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200
- Prato G, Gascuel D, Valls A, Francour P (2014) Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints. Mar Ecol Prog Ser 512:71–88
- Richardson TL, Jackson GA, Ducklow HW, Roman MR (2006) Spatial and seasonal patterns of carbon cycling through planktonic food webs of the Arabian Sea determined by inverse analysis. Deep Sea Res Part II Top Stud Oceanogr 53:555–575
- Roux J-P, Van Der Lingen CD, Gibbons MJ, Moroff NE, Shannon LJ, Smith AD, Cury PM (2013) Jellyfication of marine ecosystems as a likely consequence of overfishing small pelagic fishes: lessons from the Benguela. Bull Mar Sci 89:249–284
- Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Güçlüsoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The Structure of Mediterranean Rocky Reef Ecosystems across Environmental and Human Gradients, and Conservation Implications (TN Romanuk, Ed.). PLoS ONE 7:e32742
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos:425–439
- Salmona P, Verardi D (2001) The marine protected area of Portofino, Italy: a difficult balance. Ocean Coast Manag 44:39–60
- Steenbeek J, Coll M, Gurney L, Mélin F, Hoepffner N, Buszowski J, Christensen V (2013) Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial-temporal data. Ecol Model 263:139–151
- Stergiou KI, Karpouzi VS (2001) Feeding habits and trophic levels of Mediterranean fish. Rev Fish Biol Fish 11:217–254
- Travis J, Coleman FC, Auster PJ, Cury PM, Estes JA, Orensanz J, Peterson CH, Power ME, Steneck RS, Wootton JT (2014) Integrating the invisible fabric of nature into fisheries management. Proc Natl Acad Sci 111:581–584
- Valls A, Coll M, Christensen V (2015) Keystone species: toward an operational concept for marine biodiversity conservation. Ecol Monogr 85:29–47
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Vasilakopoulos P, Maravelias CD, Tserpes G (2014) The alarming decline of Mediterranean fish stocks. Curr Biol 24:1643–1648

## 6.7 Annex

Tab.A1 Origin of input parameters for each functional group. Biomass and catches are provided in tons  $\cdot \ km^{2} \cdot \ year^{-1}$ 

Fixed nets catches: since the mesh size of trammel nets differed depending on the main target species (large mesh size of 50-60 mm targeting lobster and small mesh size of 20-30 mm targeting mullets) trammel nets catches for both mesh sizes were treated separately. Same procedure was applied for the bycatch data available from the logbooks. Purse seine catch (\*): Species caught by purse seine fishing were known from the logbooks, while caught kg were derived from the equation Y= F/B assuming a fishing mortality (F) of 0.2. These estimates were then multiplied for the total number of fishing days/ year

0	Functional group	Value	References	Observations
1	Dolphins			
	В	0.03	Alessi unpublished data, Alessi et al. 2014 Gnone et al. 2011	Abundance of dolphins from acoustic data (Alessi et al. 2014) and visual surveys around the area (Alessi unpublished data). Data were related to the surface occupied by the eastern subpopulation of <i>T.truncatus</i> in the Pelagos sanctuary (Gnone et al: 2011). Density was transformed to biomass with the mean body weight of <i>T. truncatus</i> (Fiori unpublished data)
	Р/В	0.07	Coll et al. 2006	
	Q/B	13.49	Coll et al. 2006	
	Diet		Blanco et al. 2001	
2	Small tunas +			
	В		Estimated by Ecopath	
	P/B	0.35	Coll et al. 2006	
	Q/B	8.19	Empirical equation from Palomares & Pauly 1998	
	Diet		Stergiou & Karpouzi 2001, Falautano et al. 2007, Mostarda et al. 2007	
	Y	0.10,0.15	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
3	Amberjack & dentex +			
	В	6.00	MPA monitoring data 2010 and 2013-2014	Bergeggi MPA (nearby similar protected and monitored ecosystem) was used as an additional sampling site to gather data of rare or migratory species not observed in the available monitoring data of Portofino ( <i>S.viridensis, S.dumerili,</i> <i>C.conger</i> ), although known to inhabit the area due to frequent sightings/fisheries catches.
	Р/В	0.36	Z = F + M , M= Empirical equation from Gislason et al. 2008, assuming F= 0.2 for lampara	
	Q/B	3.58	Empirical equation from Palomares & Pauly 1998	
	Diet		Badalamenti et al. 1995, Morales-Nin & Moranta 1997, Barreiros et al. 2002, Matic-Skoko et al. 2010, Rogdakis et al. 2010, Anastasopoulou et al. 2013	

۰	Functional group	Value	References	Observations
	Y	1.06,0.14,0.45 1	Recreational fishing, artisanal fixed nets, artisanal purse seine	Logbooks + interviews + staff correction for fixed nets, F=0.2 + staff correction for purse seine * (see text for details)
4	Dusky grouper			
	В	6.45	MPA monitoring 2010 and 2013-2014*	
	P/B	0.17	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B Diet	2.56	Empirical equation from Palomares & Pauly 1998 Valls et al. 2012	
	Υ	0.08	Artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
5	Large-scaled			
	scorpionfishes + B	2 50	MPA monitoring 2010 and 2013-2014*	
	P/B	0.49	Z = F + M, $M = Empirical equation from Gislason et al 2008$	
	Q/B	4.62	Palomares & Pauly, 1998	
	Diet		Bradai & Bouain 1990, Karpouzi &	
	Y	0.33,0.19	Stergiou 2003, Cresson et al. 2014 Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff
6	Scorpionfishes & combers			correction (see text for details)
	+	1 1 7	MDA monitoring 2010 and 2012 2014*	
	B D/P	1.17	MPA monitoring 2010 and 2013-2014" Z = E + M M= Empirical equation from	
	r/b	0.47	Gislason et al 2008	
	Q/B	6.60	Palomares & Pauly, 1998	
	Diet		Stergiou & Karpouzi 2001, Relini et al. 2002	
	Y	0.29,0.03	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
7	Stripped red mullets +			
	B		Estimated by Ecopath	
	Р/В	0.88	Gislason et al 2008 , assuming F for the group = F Mullus surmuletus	
	Q/B	7.84	Palomares & Pauly, 1998	
	Diet		Stergiou & Karpouzi 2002	Loghooks Lintonious Listoff
8	<sup>Y</sup> Horse mackerels +	0.06,0.05	Recreational fishing, artisanal fixed nets	correction (see text for details)
_	В		Estimated by Ecopath	
	P/B	0.97	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B	7.57	Palomares & Pauly, 1998	
	Diet		Tsikliras et al. 2005, Stergiou & Karpouzi, 2002	
	Y	0.03,0.0006,0. 18	Recreational fishing, artisanal fixed nets, artisanal purse seine	Logbooks + interviews + staff correction for fixed nets ((see text for details).F=0.2 + staff correction for purse seine *
9	Sand smelts +			
	В	15.11	MPA monitoring 2010 and 2013-2014*	

٥	Functional group	Value	References	Observations
	Р/В	0.79	Z = F + M, M= Empirical equation from Gislason et al. 2008, assuming F= 0.2 for purse seine Palomares & Pauly, 1998	
	Diet	10.41	Pinnegar & Polunin 2000, Stergiou &	
	Y	0.24,0.002,0.6 2	Rarpouzi 2001, Cresson et al. 2014 Recreational fishing, artisanal fixed nets, artisanal purse seine	Logbooks + interviews + staff correction for fixed nets (see text for details). F=0.2 + staff correction for purse seine*
10	Pagellus			
	В	0.28	MPA monitoring 2010 and 2013-2014*	Biomass of the group was obtained multiplying the biomass of <i>Pagellus</i> <i>erythrinus</i> x 3 to account for <i>Pagellus</i> <i>bogaraveo and Pagellus acarne,</i> which are fished in the area, but were not detected during visual census
	P/B	0.88	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B	6.96	Palomares & Pauly, 1998	
	Diet		Stergiou & Karpouzi, 2002	
	Υ	0.1,0.03	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
11	Diplodus +			
	В	29.70	MPA monitoring 2010 and 2013-2014*	
	Р/В	0.70	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B	6.46	Palomares & Pauly, 1998	
	Diet		Sala 1997, Pita et al. 2002	
12	Y Gabias +	1.94,1.4	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
12	B	0.14	Estimated by Econath	Understimated by visual census
	D	0.14		onderstimated by visual census
	P/B	1.19	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B	8.54	Palomares & Pauly, 1998	
	Diet		Pita et al. 2002, Karpouzi & Stergiou 2003, Velasco et al. 2010	
	Υ	0.06	Recreational fishing	Logbooks + interviews + staff correction (see text for details)
13	Wrasses +			
	В	2.49	MPA monitoring 2010 and 2013-2014*	
	Р/В	0.94	Z = F + M , M= Empirical equation from Gislason et al 2008	
	Q/B	9.56	Palomares & Pauly, 1998	
	Diet		Cresson et al. 2014, Stergiou & Karpouzi 2002, Velasco et al. 2010	
	Υ	0.06,0.02	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
14	wullets	1.00		
	в В	1.06	WIPA MONITORING 2010 and 2013-2014*	
	٢/٢	0.45	z = F + W, $W = Empirical equation from Gislason et al 2008$	

0	Functional group	Value	References	Observations
	Q/B	14.99	Palomares & Pauly, 1998	
	Diet		Valls et al., 2012	
	Υ	0.01	Recreational fishing	Logbooks + interviews + staff correction (see text for details)
15	Salema			
	В	9.20		
	Р/В	0.58	Z = F + M , M= Empirical equation from Gislason et al 2008 , assuming F= 0.2 for LamparaLampara	
	Q/B	23.90	Palomares & Pauly, 1998	
	Diet		Verlaque 1990, Dobroslavić et al. 2013	
	Y	0.04,1.84	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
16	Decapods +			
	В	0.12	estimated by Ecopath	Local estimate available only for <i>P.</i> elephans
	Р/В	2.64	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	18.89	Pinnegar 2000,	
	Diet		Valls et al. 2012	
	Y	0.14	Artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
17	Cephalopods			
	В	3.43	Betti 2013	Biomass <i>O. vulgaris from</i> Betti 2013, biomass <i>T. sagittatus</i> from B= Y/F,
	Р/В	2.34	Valls et al. 2012	assuming F 1.suyittutus – F O.vulguns
	Q/B	5.18	Estimated by Ecopath	Pinnegar 2000
	Diet		Valls et al. 2012	
	Y	0.4,0.05	Recreational fishing, artisanal fixed nets	Logbooks + interviews + staff correction (see text for details)
18	Zooplankton - large			
	В		Estimated by Ecopath	
	Р/В	22.71	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	60.47	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Diet		Valls et al. 2012	
19	Zooplankton - small			
	В		Estimated by Ecopath	
	Р/В	35.44	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	109.43	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Diet		Valls et al. 2012	
20	Sea worms			
	B	3.50	Estimated by Ecopath	Data from local studies not complete / underestimated
	Р/В	2.58	valls et al. 2012, Pinnegar 2000	Average of literature values
	Q/В	15.27	valls et al. 2012, Pinnegar 2000	Average of literature values
	Diet		valls et al. 2012	
21	Macrotauna +	24.62		
	В	24.62	Estimated by Ecopath	oata from local studies not complete / underestimated

٥	Functional group	Value	References	Observations
	P/B	4.10	Coll et al. 2006, Pinnegar 2000, Valls et	Average of data
	O/B	47 60	al. 2012 Coll et al. 2006. Pinnegar 2000. Valls et	
		47.00	al. 2012	
	Diet		Valls et al. 2012	
22	Echinoderms +			
	В		Estimated by Ecopath	
	P/B	0.59	Coll et al. 2006, Pinnegar 2000, Valls et	Average of literature values
	Q/B	2.70	al. 2012 Pinnegar 2000	
	Diet		Valls et al. 2012	
23	Suspensivores +			
	В	4.45	Estimated by Ecopath	Data from local studies not complete
	2 /2			/ underestimated
	Р/В	2.63	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	11.20	Pinnegar 2000, Valls et al. 2012	Estimated by the model for $a P/Q =$
	Diat		Valle et al. 2012	0,3
24	Gergenians			
24		500.80	Corrange at al. 2005. Revestralle at al	
	D	500.80	2014	
	P/B	0.20	Mistri & Ceccherelli 1994, Weinbauer &	
	0/0	0.53	Velimirov 1995	
	Q/B Diat	0.53		
25	Diel Sociurching		Valis et al. 2012	
25		64.95	Chiantoro et al 2009	
	D D/R	04.95	Coll et al. 2006 Pinnegar 2000 Valls et	Average of literature values
	170	0.57	al. 2012	Average of incrutare values
	Q/B	2.77	Pinnegar 2000	
	Diet		Valls et al. 2012	
26	Meiofauna			
	В		Estimated by Ecopath	
	P/B	10.00	Danovaro et al. 2002	
	Q/B		Estimated by Ecopath for a P/Q of 0.3	
	Diet		Valls et al. 2012	
27	Posidonia			
	В	3674.00	Montefalcone et al. 2015	Leaf,frond,rhyzome,roots. Conversion factors AFDW = 80% DW from (Westlake 1964), WW = 5.7 x DW from Valls et al. 2012
	P/B	0.55	Francour 1990	
28	Seaweeds			
	В	557.00	Mangialajo et al. 2008, Montefalcone et	Biomass of macrophytes + biomass of
			al. 2015	algal epiphytes on P.oceanica leafs
	D /D	4.42	Valle at al. 2012	
20	r/b Dhutonlankton	4.43	valis et al. 2012	
29	Phytopiankton			

0	Functional group	Value	References	Observations
	В	7.14	Marine ecosystem regional monitoring network, Liguria Region	Monitoring of Chla from 2007 to 2012 at 15 and 50 m depth. Conversion factors used: Chla/m <sup>3</sup> > C g/m <sup>3</sup> from De Jong 1991, C g/m3> WW g/m3 from (Shannon & Jarre-Teichmann 1999) Transformation from g/m <sup>3</sup> to g/m <sup>2</sup> for an average depth of 30 m, assuming a uniform distribution of Chla in the water column (Palomares & Pauly 2004)
	Р/В	179.50	Lazzara et al. 2010	PP= 90 gC/m2 Lazzara et al. converted to WW from Shannon & Jarre- Teichmann 1999.
30	Detritus			
	В	65.25	Empirical equation from Christensen & Pauly 1993	Using the primary production estimate from Lazzara et al. 2010 for the Ligurian sea

## 6.7.1 Model balancing

The model was balanced by acting mainly on diets, since these derived from studies in other Mediterranean areas, and were often not sufficiently detailed. Biomass values were modified only for the most uncertain cases.

Initial ecotrophic Efficiencies of fish groups were > 1 for Scorpionfish and combers+, Pagellus, Gobids+ and Mullets. Predation on these groups was reduced by shifting small percentages of the diet of Amberjack + and Large-scale scorpionfishes+ to Wrasses+, Sand smelts+, Gobids+ and cephalopods.

Biomass of Gobids+ was too low to sustain predation, probably because underwater visual census underestimates these cryptic fish (Kovacic et al. 2012), and was thus let to model estimate by setting EE=0.9.

Similar reasoning was applied to Mullets and Pagellus, who are likely underestimated by visual census, thus their biomass was increased of 10% (within the pedigree range).

Initial biomass estimates for invertebrates (Decapods+, Sea worms and Macrofauna+) were too low to sustain predation. The field biomass available for Decapods+ related only to *P. elephans*, while a wider range of species are included in this group, upon which many predators feed. Sea worms and Macrofauna+ estimates derived from local field studies (Thrush et al 2011, Misic et al. 2011) that had assessed the abundance of invertebrates only in some specific spots of the MPA for specific study purposes. These estimates were probably not representative of the abundance in the whole model area, thus we preferred to estimate the biomass of these groups by setting the value of Ecotrophic efficiency.

Sea urchins did not cope with predation from the highly abundant Diplodus + group, although biomass estimates for both were considered reliable. We thus increased the P/B ratio of sea urchins which was very low when compared to other literature values and adopted an average of these.

## 6.7.2 Sensitivity analysis

**6.7.3** Tab. A2 MTI sensitivity analysis. Bright green cells: effects with high confidence percentage (>95%); medium green cells: [95–75[; pink cells: [75–50[; red cells: <50% (this means the average sign from the sensitivity analysis is opposed to the one of the original MTI matrix).

	Dolphins	Small tunas+	Amberjack & dentex +	Dusky grouper - large	Dusky grouper - medium	Dusky grouper - small	Large-scaled scorpionfishes +	Scorpionfishes & combers +	Stripped red mullets +	Hor se mackerels +	Sand smelts +	Pagellus	Diplodus+	Gobies +	Wrasses +	Mullets	Salema - juveniles	Salema - adults	Decapods +	Cephalopods	Zooplankton - large	Zooplankton - small	Sea worms	Macrofauna +	Echinoderms +	Suspensivores +	Gorgonians	Sea ur chins	Meiofauna	Posidonia	Seaweeds	Phytoplankton	Detritus	Landings	
Dolphins	100	100	100	100	100	100	100	100	100	100	92	100	100	51	100	100	100	100	90	100	67	100	63	98	100	100	100	100	100	99	100	81	100	100	
Small tunas +	100	100	100	100	100	100	100	37	100	100	87	100	97	99	100	100	95	97	100	100	83	99	91	100	100	100	99	99	78	98	64	69	85	100	
Amberjack & dentex +	100	100	100	100	100	100	100	100	100	100	99	100	100	61	99	100	100	100	77	100	55	97	52	96	100	100	100	100	100	99	100	64	100	100	
Dusky grouper - large	100	100	100	100	100	100	100	100	100	100	100	100	100	63	59	100	100	100	100	100	100	55	94	100	87	100	100	100	100	100	100	93	100	100	
Dusky grouper - medium	100	100	100	100	100	100	100	100	90	100	100	100	100	77	89	100	100	100	99	100	100	83	80	91	100	100	100	100	100	96	83	87	96	98	
Dusky grouper - small	100	86	99	90	100	100	100	100	100	100	100	100	100	53	100	100	100	99	100	100	100	100	73	100	100	100	100	100	100	100	61	65	100	100	
Large-scaled scorpionfishes +	58	100	88	100	100	100	100	100	100	77	100	89	100	100	100	99	100	100	100	100	100	100	100	64	100	100	100	100	100	100	88	94	99	100	
Scorpionfishes & combers +	100	89	100	99	100	100	96	100	100	100	100	96	99	100	100	64	100	100	100	100	64	98	100	100	94	100	100	100	100	100	100	100	100	89	
Stripped red mullets +	100	100	100	100	100	100	100	100	100	100	71	71	100	100	100	85	85	100	100	100	100	100	100	100	100	100	99	97	100	100	100	100	100	100	
Horse mackerels +	100	100	100	98	77	100	100	100	100	100	100	100	100	88	96	100	100	100	89	99	100	54	96	100	100	98	100	100	100	100	100	71	100	100	
Sand smelts +	69	67	80	100	100	48	100	97	100	100	100	100	100	100	100	87	100	100	100	98	100	83	100	100	91	98	84	100	55	99	95	81	100	100	
Pagellus	100	100	99	100	100	100	100	57	76	97	100	100	100	100	100	99	100	100	100	100	100	100	65	100	100	99	70	92	100	100	100	95	100	100	
Diplodus +	77	100	100	100	100	100	100	100	100	100	100	86	100	100	66	100	100	99	69	100	100	100	80	72	74	100	100	100	100	100	100	100	100	100	
Gobies +	100	99	100	80	100	100	100	100	100	100	100	100	84	100	100	100	100	87	100	100	100	100	100	89	100	100	100	100	100	63	100	97	100	100	
Wrasses +	100	100	100	72	77	100	100	100	100	100	98	67	100	98	100	98	100	100	100	100	100	100	99	100	100	100	100	100	100	100	100	100	100	100	
Mullets	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	84	100	100	100	100	100	100	100	70	100	54	99	100	100	100	100	99	
Salema - juveniles	79	100	100	100	100	100	100	100	100	100	92	100	100	100	100	100	100	99	100	100	100	100	100	100	100	100	100	100	99	100	100	100	73	98	
Salema - adults	100	100	100	100	100	100	100	100	100	100	99	54	100	100	100	100	73	100	100	100	100	100	100	100	81	100	100	100	100	100	100	100	100	100	
Decapods +	100	100	78	100	100	100	86	100	100	100	100	100	91	100	100	80	100	100	100	58	100	69	100	100	100	100	100	100	100	100	100	100	100	100	
Cephalopods	65	76	100	100	100	65	100	100	100	100	100	100	100	100	100	100	62	100	100	100	98	83	89	100	100	100	100	100	100	100	100	99	100	56	
Zooplankton - large	100	100	100	100	99	100	100	100	100	100	100	100	64	57	100	100	99	100	100	100	100	100	100	83	100	100	100	95	100	85	96	100	100	100	
Zooplankton - small	100	100	100	100	100	100	98	100	100	100	100	100	100	99	100	100	27	100	100	100	100	100	100	98	100	100	100	100	100	78	100	100	96	100	
Sea worms	100	100	100	100	98	100	91	95	100	100	100	100	69	100	88	81	100	100	100	100	100	77	100	100	73	100	66	100	96	100	66	100	52	100	
Macrofauna +	83	93	100	100	100	100	100	99	71	100	100	93	100	98	100	100	88	100	69	100	73	100	100	100	100	100	100	100	100	100	100	100	100	100	
Echinoderms +	100	100	100	70	100	100	100	100	100	100	100	100	100	100	100	86	100	96	100	63	100	100	100	100	100	100	100	84	95	100	100	100	76	94	
Suspensivores +	100	100	100	100	100	100	98	100	100	74	100	100	100	79	100	90	99	100	100	100	100	100	100	80	100	100	100	100	100	100	100	100	100	100	
Gorgonians	100	100	100	100	100	100	94	100	100	100	100	94	100	100	100	100	100	100	100	100	100	84	100	100	100	100	100	60	100	100	100	100	100	97	
Sea urchins	100	100	100	100	99	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	96	100	100	100	98	100	100	100	100	99	
Meiofauna	100	88	100	100	100	100	100	100	100	82	91	100	65	100	98	100	100	100	100	100	90	97	100	95	100	53	100	94	100	99	100	100	100	55	
Posidonia	100	100	100	100	100	100	99	100	97	100	100	100	100	100	100	100	100	100	100	100	100	100	78	100	97	89	100	100	79	100	100	72	100	100	
Seaweeds	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	98	100	100	100	93	100	100	100	100	100	100	100	100	
Phytoplankton	100	100	100	100	65	97	87	95	100	100	100	84	100	100	100	100	99	100	100	100	100	100	100	94	100	100	99	100	75	68	76	100	100	100	
Detritus	100	100	94	100	100	100	100	100	100	99	98	100	100	100	100	100	100	100	100	100	100	99	100	100	100	100	100	100	100	100	100	100	100	91	
Landings	100	100	100	100	100	100	100	78	99	100	94	83	100	100	100	100	85	100	100	100	100	100	100	100	98	100	100	100	100	96	100	100	100	100	



Fig. A1 Trophic spectra of the fishing loss including logbook data not corrected by MPA staff experts.



Fig. A2 Trophic spectra of the relative biomass by fishing scenarios, including logbook data not corrected by MPA staff experts.

## 6.7.4 References input parameters

- Alessi J, Bianchi CN, Bozzini G, Brunoldi M, Cappanera V, Casale A, Corvisiero P, Fanciulli G, Grosso D, Magnoli N, Melchiorre C, Morri C, Povero P, Stasi N, Taiuti M, Viano G, Wurtz M (2014) ARION: a tool for real time bottlenose dolphin monitoring in the Portofino MPA, 28th Annual Conference of the European Cetacean Society, Liége
- Anastasopoulou A, Mytilineou C, Lefkaditou E, Kavadas S, Bekas P, Smith CJ, Papadopoulou KN, Christides G (2013) The diet and feeding ecology of Conger conger (L. 1758) in the deep waters of the Eastern Ionian Sea. Mediterr Mar Sci 14
- Badalamenti F, D'Anna G, Lopiano L, Scilipoti D, Mazzola A (1995) Feeding habits of young-of-the-year greater amberjack Seriola dumerili (Risso, 1810) along the N/W Sicilian Coast. Sci Mar 59:317–323
- Barreiros JP, Santos RS, Borba AES (2002) Food habits, schooling and predatory behaviour of the Yellowmouth Barracuda, Sphyraena viridensis Cuvier, 1829 (Perciformes: Sphyraenidae) in the Azores. Cybium 26(8):83-88
- Bavestrello G, Bo M, Bertolino M, Betti F, Cattaneo-Vietti R (2014) Long-term comparison of structure and dynamics of the red coral metapopulation of the Portofino Promontory (Ligurian Sea): a case-study for a Marine Protected Area in the Mediterranean Sea. Mar Ecol
- Blanco C, Salomón O, Raga JA (2001) Diet of the bottlenose dolphin (Tursiops truncatus) in the western Mediterranean Sea. J Mar Biol Assoc UK 81:1053–1058
- Bradai MN, Bouain A (1990) Régime alimentaire de Scorpaena porcus et de S. scrofa (Teleostei, Scorpaenidae) du Golfe de Gabès, Tunisie. Cybium 14:207–216
- Cappanera V, Venturini S, Campodonico P (2013) Valutazione dell'impatto antropico legato alle attività svolte nell'area Marina Protetta Portofiino. Le attiiviità dii fruizione 2012-2013
- Cerrano C, Arillo A, Azzini F, Calcinai B, Castellano L, Muti C, Valisano L, Zega G, Bavestrello G (2005) Gorgonian population recovery after a mass mortality event. Aquat Conserv Mar Freshw Ecosyst 15:147–157
- Chiantore M, Vielmini I, Privitera D, Mangialajo L, Cattaneo-Vietti R (2008) Habitat effects on the population structure of Paracentrotus lividus and Arbacia lixula. Chem Ecol 24:145–157
- Christensen V, Pauly D (1993) Trophic Models of Aquatic Ecosystems. The WorldFish Center
- Coll M, Palomera I, Tudela S, Sardà F (2006) Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J Mar Syst 59:63–96
- Cresson P, Ruitton S, Ourgaud M, Harmelin-Vivien M (2014) Contrasting perception of fish trophic level from stomach content and stable isotope analyses: A Mediterranean artificial reef experience. J Exp Mar Biol Ecol 452:54–62
- Danovaro R, Gambi C, Mirto S, others (2002) Meiofaunal production and energy transfer efficiency in a seagrass Posidonia oceanica bed in the western Mediterranean. Mar Ecol Prog Ser 234
- De Jong, S.A, Haufman, PAG., Sandee AJJ. and Nienhuis PH, 1991. Community oxygen budgets on seagrass beds and microbial mats on the Banc d'Arguin, Mauritania, p. 67-68. In: PMJ. Herman and CHR. Heip (eds.) Report on the workshop, 'Modeling the benthos', Yerseke, The Netherlands, 20-22 March 1991. Delta Institute for Hydrobiological Research, Yerseke
- Dobroslavić T, Zlatović A, Bartulović V, Lučić D, Glamuzina B (2013) Diet overlap of juvenile salema (Sarpa salpa), bogue (Boops boops) and common two-

banded sea bream (Diplodus vulgaris) in the south-eastern Adriatic. J Appl Ichthyol 29:181–185

- Falautano M, Castriota L, Finoia MG, Andaloro F (2007) Feeding ecology of little tunny Euthynnus alletteratus in the central Mediterranean Sea. J Mar Biol Assoc UK 87:999
- Francour P (1990) Dynamique de l'écosystème à Posidonia oceanica dans le Parc National de Port-Cros.Analyse des compartiments matte, litière, faune vagile, échinodermes et poissons. Doctorat, Université Pierre et Marie Curie, Paris
- Gislason H, Daan N, Rice J, Pope J (2008) Does natural mortality depend on individual size. ICES CM
- Gnone G, Bellingeri M, Dhermain F, Dupraz F, Nuti S, Bedocchi D, Moulins A, Rosso M, Alessi J, McCrea RS, Azzellino A, Airoldi S, Portunato N, Laran S, David L, Di Meglio N, Bonelli P, Montesi G, Trucchi R, Fossa F, Wurtz M (2011) Distribution, abundance, and movements of the bottlenose dolphin (Tursiops truncatus) in the Pelagos Sanctuary MPA (north-west Mediterranean Sea): The bottlenose dolphin in the pelagos sanctuary MPA. Aquat Conserv Mar Freshw Ecosyst 21:372–388
- Karpouzi VS, Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. J Fish Biol 62:1353–1365
- Mangialajo L, Chiantore M, Cattaneo-Vietti R (2008) Loss of fucoid algae along a gradient of urbanisation, and structure of benthic assemblages. Mar Ecol Prog Ser 358:63–74
- Matic-Skoko S, Tutman P, Marcejla E, Skaramuca D, \DJikic D, Lisicic D, Skaramuca B (2010) Feeding habits and trophic status of Mediterranean moray eel, Muraena helena L., 1758 in the Adriatic Sea—preliminary approach. Rapp Comm Int Pour Mer Méditerranée 39:583
- Misic C, Castellano M, Harriague AC (2011) Organic matter features, degradation and remineralisation at two coastal sites in the Ligurian Sea (NW Mediterranean) differently influenced by anthropogenic forcing. Marine environmental research. 72(1):67-74.
- Mistri M, Ceccherelli VU (1994) Growth and secondary production of the Mediterranean gorgonian Paramuricea clavata. Mar Ecol-Prog Ser 103:291– 291
- Montefalcone M, Vassallo P, Gatti G, Parravicini V, Paoli C, Morri C, Bianchi CN (2015) The exergy of a phase shift: Ecosystem functioning loss in seagrass meadows of the Mediterranean Sea. Estuar Coast Shelf Sci 156:186–194
- Morales-Nin B, Moranta J (1997) Life history and fishery of the common dentex (Dentex dentex) in Mallorca (Balearic Islands, western Mediterranean). Fish Res 30:67–76
- Mostarda E, Campo D, Castriota L, Esposito V, Scarabello MP, Andaloro F (2007) Feeding habits of the bullet tuna Auxis rochei in the southern Tyrrhenian Sea. J Mar Biol Assoc UK 87:1007
- Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar Freshw Res 49:447–453
- Palomares Ld, Pauly D (2004) West African Ecosystems. Fish Cent Res Rep 12:4
- Pinnegar JK, Polunin NVC (2000) Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399–409
- Pita C, Gamito S, Erzini K (2002) Feeding habits of the gilthead seabream (Sparus aurata) from the Ria Formosa (southern Portugal) as compared to the black seabream (Spondyliosoma cantharus) and the annular seabream (Diplodus annularis). J Appl Ichthyol 18:81–86

- Relini G, Relini M, Torchia G, De Angelis G (2002) Trophic relationships between fishes and an artificial reef. ICES J Mar Sci J Cons 59:S36–S42
- Rogdakis Y, Ramfos A, Koukou K, Dimitriou E, Katselis G (2010) Feeding habits and trophic level of sea bass (Dicentrarchus labrax) in the Messolonghi-Etoliko lagoons complex (Western Greece). J Biol Res 13:13–26
- Sala E (1997) Fish predators and scavengers of the sea urchin Paracentrotus lividus in protected areas of the north-west Mediterranean Sea. Mar Biol 129:531– 539
- Shannon LJ, Jarre-Teichmann A (1999) A model of trophic flows in the northern Benguela upwelling system during the 1980s. South Afr J Mar Sci 21:349– 366
- Stergiou KI, Karpouzi VS (2001) Feeding habits and trophic levels of Mediterranean fish. Rev Fish Biol Fish 11:217–254
- Thrush S, Chiantore M, Asnagi V, Hewitt J, Fiorentino D, Cattaneo-Vietti R (2011) Habitat–diversity relationships in rocky shore algal turf infaunal communities. Marine Ecology Progress Series 424:119–132
- Tsikliras AC, Torre M, Stergiou KI (2005) Feeding habits and trophic level of round sardinella (Sardinella aurita) in the northeastern Mediterranean (Aegean Sea, Greece). J Biol Res 3:67–75
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Velasco EM, Gómez-Cama MC, Hernando JA, Soriguer MC (2010) Trophic relationships in an intertidal rockpool fish assemblage in the gulf of Cádiz (NE Atlantic). J Mar Syst 80:248–252
- Verlaque M (1990) Relations entre Sarpa salpa (Linnaeus, 1758)(Téléostéen, Sparidae), les autres poissons brouteurs et le phytobenthos algal méditerranéen. Oceanol Acta 13:373–388
- Weinbauer M, Velimirov B (1995) Biomass and secondary production of the temperate gorgonian coral Eunicella cavolini (Coelenterata:Octocorallia). Mar Ecol Prog Ser 121:211–216
- Westlake DF (1964) Light extinction, standing crop and photosynthesis within weed beds.

# 7 Building a standard trophic model for a data-poor marine reserve: cost-benefit analysis.

## 7.1 Abstract

Mediterranean coastal ecosystems support a great diversity of habitats, species and communities, being a major challenge for an ecosystem management approach. In particular, effective management of Marine Protected Areas should account for the complexity of the food-webs they host to properly evaluate priority actions. The application of food-web modelling through the Ecopath with Ecosim software (EwE) may allow to unravel such a complexity and could thus help to better pursue the conservation and management objectives of Mediterranean MPAs. Unfortunately, whilst widely applied at larger ecosystem scales where the presence of industrial fisheries allows for large data availability covered by global databases, EwE has not yet gained full attention as a possible tool for the management of smaller and highly diverse coastal areas. At this small scale fine resolution local data is needed in order to develop useful models for management, but is costly to obtain for all functional groups. Here we evaluate costs associated with the development of a standard Ecopath model for a recently established coastal fishery reserve, where no quantitative biological data is available (Cap Roux, NW Mediterranean sea). Field campaigns were designed to obtain local data in priority for a selection of groups for which imprecise biomass input can widely affect model outputs (Prato et al. 2014). Trophic interactions were unravelled and keystone functional groups such as high trophic level predators and cephalopods were identified, highlighting the need for monitoring these groups. Costs associated with all steps of model building, from data collection to model balancing, were provided and evaluated in relation to the achieved model quality. The least cost-efficient surveys were identified and the benefits of integrating regular monitoring programs with food-web models development were discussed.

#### 7.2 Introduction

Marine protected areas (MPAs) have spread worldwide in response to the increasing calls for an ecosystem based fisheries management (EBFM), as an alternative or additional measure to policies focused on single species (Browman et al 2005, Gaines et al 2010). Up to date the performance of MPAs in achieving their conservation and fisheries management objectives has been generally assessed through empirical studies analysing the direct effects of protection, such as the response of single species or groups of species (Lester et al 2009, Guidetti & Sala 2007) or the spillover effect for adjacent fisheries (Murawski et al al 2005, Goni et al 2008, Colléter et al. 2014). The complex linkages and interactions among species instead, can hardly be unravelled through observational studies, but are a key component of the EBFM and essential to fully comprehend the mechanisms driving species response to protection (Kellner et al. 2010).

The limits of empirical studies concerning these issues can be overcome with ecosystem modelling, a tool that has the high potential to assess both the conservation performance of MPAs at the ecosystem scale, but also their outcomes in fisheries management (Pelletier et al. 2005). In this context, the "Ecopath with Ecosim" (EwE, Christensen & Walters 2004) modelling approach is increasingly gaining interest as a management-advice tool, in both areas of fisheries management and conservation, and has been widely applied worldwide thanks to its capability of integrating ecological, economic and social aspects and analysing trade-offs, both temporally and spatially (Christensen et al. 2009). Yet, the development of EwE models, like all ecosystem models, is burdened by the amount of data needed and the uncertainty associated with it (Dame and Christian 2005, Morisette 2007). Sensitivity analysis on model outputs are thus increasingly becoming part of the model building routine (Link et al. 2010, Lassalle et al. 2014, Steenbeek 2015).

Efforts have also been implemented to provide standard model structures facilitating the construction of EwE models (Christensen et al 2009). Standard model structures have for instance been used to model Large Marine Ecosystems (Piroddi et al 2015), based on data available in global databases (Christensen et al. 2009, Piroddi et al. 2015). Nonetheless, to be considered as tools to advise management in MPAs, models must achieve a trade-off between parsimony and complexity, and, essentially, must be grounded on local fine-resolution data (Pelletier et al. 2005, Prato et al. 2014). If more realistic models are developed, the long-lasting gap

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between empirical studies and modelling could be overcome and the two approaches would more often be integrated, allowing more representative and thorough assessments of MPA effects (Pelletier et al. 2005).

The few existing Ecopath models built for Mediterranean MPAs largely differ in model complexity. In Prato et al. 2014 we proposed a simplified and standardised model structure to be applied to Mediterranean coastal MPAs and we identified the functional groups for which accurate local biomass data are needed in priority to develop a reliable model (high trophic level predators, planktonivorous fish, decapods, cephalopods, macrofauna and abundant primary producers). Here we take a step forward, and analyse the feasibility and costs of building a trophic model grounded on newly collected local data, based on the simplified and standardised structure proposed in Prato et al. 2014. We selected the case study of the Cap Roux fishery reserve (NW Mediterranean, France) representative of recently established Mediterranean MPAs where few if none quantitative biological data are available, and designed a monitoring program targeted specifically to collect biomass data for the above mentioned groups. We then evaluated the costs associated with all steps of model building, from data collection to model balancing, and discussed model costs in relation to the achieved model quality. Providing this effort and cost analysis, we aim to assess if EwE can be realistically considered as a management tool for Mediterranean MPAs.

## 7.3 Methods

## 7.3.1 Study area

The Cap Roux fishery reserve (Fig. 1) comprises 450 ha and extends from the shore out to the 80 m isobath. The area has been protected from all kinds of extractive activities (both commercial and recreational) since December 2003, but daily enforcement surveys were implemented in 2008 in summer time. As part of of the Natura 2000 site of the Esterel, the Cap Roux reserve includes priority habitats for conservation such as extensive *Posidonia oceanica* meadows and coralligenous formations (Bonhomme et al. 2010). The modelled area (145 ha, Fig.1) represents the subtidal portion of the reserve including the following habitats: soft bottoms (7%), *Posidonia oceanica* (75%), corallogenous bioconcretions (10%), rocky infralittoral (6%) and coralligenous (2%). Coastal detritic habitat, extending from approximatively

40 m depth, was excluded from the model. The model was built to represent the average summer condition of the Cap Roux reserve in 2014 (July-September).



Fig.1 Habitat map and sampling sites of the modelled area (dashed area in the central map) within the Cap Roux fishery reserve (SW France).. Habitat map modified from Bonhomme et al. 2010.

# 7.3.2 Field sampling

Tab.1 Sampling sites for each habitat and method. Refer to Fig.1 for location of sampling sites.N = number of replicates

	Coastal Hard bottom (5 m)		Roc bar (5-15	ky nk 5 m)	Biocono (12	cretions m)	Posido ocear (12 i	onia nica m)	Sofi botto (5m	t om )	Target taxa
	Sites	N	Sites	N	Sites	N	Sites	N	Sites	N	
Transect 25 x 5 m	HB1	4	RB1	8	CB1	4	P1	4			
Market LE	HB2	4	RB2	8	CB2	4	P2	4			Fish
	HB3	4					Р3	4			
Transect 25 x 1 m	HB1	4	RB1	8	CB1	4					Cephalopods
	HB2	4	RB2	8	CB2	4					Decapods Sea stars
	HB3	4									
Circles r=5 m	HB1	6	RB1	6	CB1	3					Cephalopods
A. Company	HB2	6	RB2	6	CB2	3					Decapods Sea stars
	HB3	6									
Quadrats 1x1 m	HB1	20	RB1	20			P1	10			Sea urchins
	HB2	20	RB2	20			P2	10			Holothurians Ophiuroids
	HB3	20					Р3	10			
Air lift device r=40cm	HB1	3	RB1	6			P1	3	S1	3	Macrofauna
C	HB2	3					P2	3	S2	3	

Location of sampling sites was determined using a stratified random sampling approach where sites were assigned randomly to each of 3 major habitat types (Coastal hard bottoms, *Posidonia oceanica*, coralligenous bioconcretions) plus two rocky banks (characterised by rocky and coralligenous habitat). Habitats were distributed along a depth gradient from the coast to 30 meters depth. Three sites were randomly selected within coastal hard bottoms at 5 meters depth (HB 1-3), three sites within *P. oceanica* beds at 15 meter depth (P 1-3), and two sites within the coralligenous bioconcretions at 15 m depth (CB 1-2). Finally, two sites were selected at each rocky bank, respectively between 5 and 10 meters and between 15 and 30 meters depth (RB 1-2) (Fig.1, Tab.1).

Field data were collected for fish, echinoderms (including sea urchins, holothurians sea stars and ophiuroids), decapods, octopus and macrofauna. Tab. 1 synthetises the sampling scheme for each functional group.

Fish were surveyed monthly (July, August and September 2014), while invertebrate surveys were conducted only in July and September. Fish and echinoderms (excluding sea stars) surveys were carried out at all habitats and sites. Surveys for sea stars, decapods and cephalopods were not carried out in *P*; oceanica habitat, given the low abundances of such organisms in this habitat (pers. obs. P. Francour) and accounting for the too long time needed to search through dense *P. oceanica* meadows. Macrofauna was sampled in two sites for each habitat, excluding coralligenous bioconcretions to avoid damage of this fragile habitat. Two sites at soft bottoms (S 1-2, Fig.1) were also sampled, since macrofauna was expected to be abundant in such habitat.

Fish abundance, species composition and size (recorded using 2 cm size classes) were recorded along 4 replicate transects 25 x 5 meters long.

Sea urchins, holothurians and ophiuroids were identified, counted and measured within 1  $m^2$  quadrats. Twenty replicates were performed at coastal hard bottom sites to account for the heterogeneity of the substrate (rocks and pebbles), while 10 replicates were sampled in *P. oceanica* and rocky banks sites. Sea urchins and holothurians were recognised to the species level and measured with a calliper to nearest mm. Recorded measures were respectively the largest radius of the disk and the contracted body length. Ophiuroids disk was estimated to the nearest cm due to the difficulty at catching the organism.

Two methods were used to record mobile mega-invertebrates (sea stars, octopus and decapods) (Tab.1). The first method consisted in 25x1 meter transect (4 replicates/site), which were coupled with the fish transects, where a diver searched the substrate behind the fish counts operator. Since we could not detect any decapods or octopuses with transects, we then designed a method characterised by replicate circles of 5 m radius, allowing to easily survey a wider surface for each replicate and thus better accounting for the mobility and distribution of these organisms. The method was characterised by replicate circles of 5 m radius, where two operators searched the substrate while swimming around an iron pole. Each operator held respectively the extremity and the mid-point of a 5 m rope, which was fixed to the iron pole with a rotating ring. In such way the operators could define the surface to be sampled while holding tight the rope and swimming around the pole (Tab.1). Three replicate circles were completed at each depth in rocky bank (6 in total per each rocky bank) and at each coralligenous bioconcretion site, while 6 replicates were carried out on coastal hard bottoms to account for the heterogeneity of the substrate (3 on rock and 3 on pebbles). Sea stars were measured for the maximum arm length from the tip of the longest arm to the centre of the disk; for decapods we recorded carapace length and for cephalopods we visually estimated cephalothorax length.

To survey macrofauna (> 1mm), three replicates of 40 cm diameter were sampled at each site with an air lift pump fixed at one extremity to interchangeable nylon nets of 1 mm mesh size (Tab.1). We did not select smaller mesh sizes since these would significantly increase sorting time (Jameson 1995, Ferraro et al 2011) while not significantly affecting biomass estimates (Bachelet 1990, Covazzi-Harriague 2006). Samples were then sieved through 0.50 mm sieves and preserved under 6% formalin and seawater solution. At sand and *P. oceanica* sites we used an inox steel cylinder to define our sampling area. The cylinder (40 m diameter) was equipped with handles on the upper side and a sharp cut edge on the bottom side, specifically realised to facilitate insertion in the substrate. Two divers were needed at each operation : one diver pressed the cylinder in the sediment up to ca 30 cm depth and the other diver activated the air lift pump during 2 minutes (Vassapollo et al 2009, Michel et al 2010), moving the tube in circles within the walls of the cylinder for sand samples, and vertically for *P. oceanica* samples. To sample in rocky habitat, a hard plastic cylinder (40 cm diameter) with handles was used. An extra tissue strip was fixed all around

the base of the cylinder (like a skirt) with galvanized chain at its perimeter, so that the base could be moulded to the substrate, thus preventing organisms to escape from underneath. While one diver moved the air lift tube, the other one held the cylinder on the bottom while scraping algae from the substrate, which were thus directly aspired by the air lift pump. This technique was preferred to previous scraping and collection of algae since many vagile macroinvertebrates could fly away during the scraping process.

#### 7.3.3 Ecopath model structure

The species-based Ecopath model was used in this study.

Ecopath is a mass-balanced model 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:

$$P/B_i \times B_i = B_i \times P/B_i \times (1 - EE_i) + \Sigma_j^N (Q/B)_{ji} \times Bi \times DC_{ji} + Y_i + NM_i + Ba_i$$
(1)  

$$Qi=P_i + R_i + UA_i$$
(2)

Where N the number of functional groups in the model, B is the biomass, P/Bi is the production rate, Q/B is the consumption rate, DCji is the fraction of prey i included in the diet of predator j, NMi is the net migration of prey I, BAi is the biomass accumulation of prey I, Yi is the catch of prey i and EEi is the ecotrophic efficiency of prey i, that is the proportion of production used in the system. The model represents the average summer condition of the Cap roux fishery reserve ecosystem in 2014. The simplified model structure developed by Prato et al. (2014) for the Port Cros MPA was used in our study. Seabirds and rays were not included in the model, since their biomasses are likely to be very low in the model area. We thus preferred to exclude them instead of estimating their biomasses through the mass-balance calculations.

#### Input parameters

Fish wet weight was estimated from size data by means of length-weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (from www.fishbase.org). Echinoderms wet weight was also estimated using available length-weight relationships from the

literature and, where needed, dry weight-wet weight conversion factors from Brey et al 2010 were used (Annex, Tab. 1). Macrofauna samples were sorted and identified to the genus level when possible. Ash free dry weight was obtained by drying organisms at 60°C and incinerating them at 450°C. Ash free dry weight was converted to wet weight using conversion factors from Brey et al.2 010. Algae wet weight was measured after blotting for water in excess. Per each species, the calculation of biomass in the model area accounted for the surface of its habitat types inside the model area.

Biomass of *Posidonia oceanica* (leaves, frond, rhizome and root) was calculated using the average biomass (g/m<sup>2</sup>) of a Mediterranean *Posidonia oceanica* meadow (Montefalcone et al. 2015) extrapolated for habitat surface at Cap Roux (Bonhomme et al. 2010). Biomass of phytoplankton was estimated from the value of primary productivity in the Ligurian sea (Lazzara et al 2010) divided by the P/B rate of phytoplankton used in Valls et al. 2012 for the Port Cros ecopath model. Biomass of detritus was estimated through an empirical relationship (Christensen & Pauly 1993). For consumers that were not quantified on the field (since we prioritised data collection for sensible groups for which imprecise input biomass values can affect model outputs) (Prato et al. 2014), biomass was estimated through the mass-balance calculations of the model.

Production to biomass ratio (P/B) of fish corresponds to the total mortality rate Z (Allen 1971), the sum of natural (M) and fishing (F) mortality rates. F was assumed to be null, while M was calculated with an empirical equation (Gislason et al. 2008). Fish consumption per unit biomass Q/B was calculated with the empirical equation from Palomares & Pauly 1998, while for invertebrates' production and consumption rates we used the average of the best literature values available for similar coastal Mediterranean ecosystems (Pinnegar et al. 2000, Albouy et al. 2010, Valls et al. 2012).

Diet composition of fish and invertebrates were based on available Mediterranean literature and, for aggregation into functional groups, were weighted for the local biomass and consumption rates of each species. All input parameters and empirical equations used are listed in Tab.2 in the Annex.

#### 7.3.4 Keystone groups analysis

The mixed trophic impact routine (MTI) of Ecopath assesses the relative impact of a slight increase in abundance of any group on the biomass of other groups on the food-web (Christensen et al 2005). Keystone species are defined as the species having the highest and widest impact on the food web despite a low biomass. They were identified by applying the new keystonness index developed by Valls et al 2015. The index is characterized by an impact component (IC, defining the trophic impact of a group on the other groups) and a biomass component (BC), according to the following equation:

$$KS = Ln(IC \times BC)$$
(2)

Where IC is defined from Libralato et al 2006 as:

$$\varepsilon_{i} = \sqrt{\Sigma_{i \neq i} m_{ij}^{2}}$$
(3)

Parameter  $\mathcal{E}_i$  represents the overall effect of group i on all the other groups in the food web (without including the effect of the group on itself) and is expressed as the sum of the squared values of  $m_{ij}$  (the MTI score) of group i, paired with each of the other living group j in the food web. The mixed-trophic impact of group I on itself (mii) is excluded, as well as the mixed-trophic impact on dead groups such as detritus (Libralato et al.2006).

The biomass component is defined as the rank of the group's biomass in descending order:

$$BC = drank(Bi)$$
(4)

We calculated the KS index for each group in the model (excluding fisheries) and plotted the groups according to their KS index and biomass, scaled by trophic level.

### 7.3.5 Data quality and MTI sensitivity analysis

Data quality was assessed applying the food web diagnostics proposed by Link 2010 and Lassalle et al 2014. The Pedigree routine to summarise the uncertainty around the input data, based on a set of qualitative choices relative to the origin of biomass,

*P/B*, *Q/B*, catch and diet input for each functional group. The range of uncertainty of biomass data, for example, varies from  $\pm$  10% (locally sampled high precision data, low uncertainty,) to  $\pm$  80% (model estimate, high uncertainty) (Morissette 2007). An overall pedigree of the model is then calculated as the average of the individual pedigree values (Pauly *et al.* 2000). According to Lassalle et al. 2014, a Pedigree index > 0.4 testifies sufficient quality to pursue with model analysis.

Robustness of MTI results was tested through a sensitivity analysis (Lassalle et al 2014). We rebuilt the original net impact matrix where qij is the net impact of i on j and is given by the difference between positive effects (quantified by the fraction of prey i in the diet of predator j), and negative effects fij (evaluated as the fraction of total consumption of j used by predator i). Then, in the analysis routine, 5000 Q matrices are created by drawing qij values from independent uniform distributions defined by original qij± 20% (Richardson et al. 2006). The mij values for each pairwise intersection of the Q matrices are then calculated, their signs recorded and the percentage of mij values with the same sign as in the original MTI matrix (SMTI) is estimated. Results were summarized into one matrix recording the sign of the original mij values and the SMTI percentages that are categorized into four classes:[0; 50], [50; 75], [75; 95] and [95; 100].

#### 7.3.6 Cost analysis

Effort devoted to the construction of the model was guantified as total hours of field work, total hours of lab. work for macrofaunal sample treatment (sorting and identification) and total hours of computer work for data analysis and model building. Costs for field work were quantified assuming a flat rate of 500 € per dive for a scientific underwater operator (including fees, field trip, and diving material amortization). Analysis of macrofaunal samples was carried out by a specialised laboratory, thus we reported the total cost invested for such service, selected after a market analysis. Cost of computer work was guantified on the basis of 35 € / hour, calculated from the average 2014 annual salary of a researcher enrolled at the French national centre for scientific research ( CNRS, <u>www.cnrs.fr</u>).

Field and lab costs were also analysed separately for each ecological group, reporting number of campaigns to survey each group within the warm season, total number of samples (replicates) performed, total hours of field and lab work and total cost.

Finally, the minimum unit of effort was provided in terms of hours/replicate in the field for each ecological group sampled. Cost for equipment amortization was also considered, including amortization for boat maintainance and diving equipment and data recording equipment (including reels 25m long, pvc quadrats, plastic callipers, underwater writing slates and papers, pencils, and macrofauna and algae sampling equipment: inox steel cylinder, plastic cylinder with embedded chain, airlift sampler device, nylon collecting bags, scalpel).

## 7.4 Results

A total of 35 fish species were recorded and grouped in 11 functional groups following the standard model structure proposed in Prato et a. 2014 (Tab.2a). Two sea urchin species, three holothurian species and two sea star species were also identified. Ophiuroids were not identified to the species level. Holothurians, stars and ophiuroids were aggregated into one functional group (echinoderms+), while sea urchins in another (sea urchins+), again following Prato et al. 2014. Sampling with the air lift device allowed to identify 12 invertebrate taxa aggregated in two separate functional groups (polychaetes and macrofauna + , Tab. 2b), 11 dominant seaweed taxa (aggregated in 1 functional group). Overall, the model was made of 18 functional groups, for 78 % of which we could use biomass estimates collected in the field (10 groups of fish, echinoderms, sea urchins, macrofauna and algae). Tab.2b shows the list of the recorded taxa and their aggregation into the 18 functional groups for model building. We were not able to obtain estimates of biomass for decapods and cephalopods, since field surveys allowed to record only very few individuals of *Palinurus elephas* and *Octopus vulgaris*.

Tab.2a List and composition of the fish functional groups for which bion	nass
data was collected in the field, and sampling method used.	

Functional group	Species	Method
Amberjack & dentex +	Dentex dentex	fish transects
Amberjack & dentex +	Muraena Helena	fish transects
Gobids +	Apogon imberbis	fish transects
Gobids +	Diplodus annularis	fish transects
Gobids +	Parablennius rouxi	fish transects
Diplodus +	Diplodus puntazzo	fish transects
Diplodus +	Diplodus sargus	fish transects
Diplodus +	Diplodus vulgaris	fish transects
Diplodus +	Sparus aurata	fish transects
Diplodus +	Spondyliosoma cantharus	fish transects
Dusky grouper +	Epinephelus marginatus	fish transects
Large-scaled scorpionfishes +	Labrus merula	fish transects
Large-scaled scorpionfishes +	Labrus viridis	fish transects
Large-scaled scorpionfishes +	Sciaena umbra	fish transects
Mullets	Mugilidae	fish transects
Salema +	Sarpa salpa	fish transects
Sand smelts +	Anthias anthias	fish transects
Sand smelts +	Boops boops	fish transects
Sand smelts +	Chromis chromis	fish transects
Sand smelts +	Oblada melanura	fish transects
Sand smelts +	Spicara spp.	fish transects
Scorpionfishes & combers +	Scorpaena spp.	fish transects
Scorpionfishes & combers +	Serranus cabrilla	fish transects
Scorpionfishes & combers +	Serranus scriba	fish transects
Stripped red mullets +	Mullus surmuletus	fish transects
Wrasses +	Coris julis	fish transects
Wrasses +	Symphodus cinereus	fish transects
Wrasses +	Symphodus doderleini	fish transects
Wrasses +	Symphodus mediterraneus	fish transects
Wrasses +	Symphodus melanocercus	fish transects
Wrasses +	Symphodus ocellatus	fish transects
Wrasses +	Symphodus roissali	fish transects
Wrasses +	Symphodus rostratus	fish transects
Wrasses +	Symphodus tinca	fish transects
Wrasses +	Thalassoma pavo	fish transects

Functional group	Species	Method
Decapods +	Palinurus elephas	invertebrate transects and circles
Cephalopods	Octopus vulgaris	invertebrate transects and circles
Echinoderms +	Echinaster sepositus	invertebrate transects and circles
Echinoderms +	Marthasterias glacialis	invertebrate transects and circles
Echinoderms +	Holothuria forskali	quadrats
Echinoderms +	Holothuria poli	quadrats
Echinoderms +	Holothuria tubulosa	quadrats
Sea urchins	Arbacia lixula	quadrats
Sea urchins	Paracentrotus lividus	quadrats
Macrofauna+	Ophiura	quadrats
Macrofauna+	Arthropoda	air lift pump
Macrofauna+	Briozoa	air lift pump
Macrofauna+	Chordata	air lift pump
Macrofauna+	Cnidaria	air lift pump
Macrofauna+	Echinodermata	air lift pump
Macrofauna+	Mollusca	air lift pump
Macrofauna+	Porifera	air lift pump
Polychaetes	Anellida	air lift pump
Polychaetes	Nermertea	air lift pump
Polychaetes	Plathyelminthe	air lift pump
Polychaetes	Sipuncula	air lift pump
Sea weeds	Cladostephus spongiosus	air lift pump
Sea weeds	Corallinacea	air lift pump
Sea weeds	Cystoisera compressa	air lift pump
Sea weeds	Cystoseira brachycarpa	air lift pump
Sea weeds	Dictyota spp.	air lift pump
Sea weeds	Halopteris filicina	air lift pump
Sea weeds	Jania spp.	air lift pump
Sea weeds	Padina pavonica	air lift pump
Sea weeds	Peyssonnelia sp.	air lift pump
Sea weeds	Stypocaulon scoparia	air lift pump
Sea weeds	Lithothamnion sp	air lift pump

Tab.2b List and composition of the invertebrate and primary producers functional groups for which biomass data was collected in the field, and sampling method used.

## 7.4.1 Model balancing

Ecotrophic efficiency was >1 for six fish groups (Amberjack&dentex +, Scorpionfish and combers +, Striped red mullets +, Gobies and Mullets) and two invertebrate groups (Polychaetes and Macrofauna+).

Predation mortality on Amberjack and dentex + from Dusky grouper medium was reduced shifting 4% of grouper's diet from the mentioned group to other preys through proportional rescaling. Cannibalism on Scorpionfish and combers+ was reduced by shifting their diet to Wrasses +, a known prey of this group (Thiriet et al

2014). The proportion of diet of Dusky grouper small on Striped red mullets+ was reduced of 3% and diet was rescaled proportionally. Transect visual census is not appropriate to detect small cryptic species, and in fact gobies biomass was too low to sustain predation. It was thus calculated through the model's mass-balance equations. Mullets were subject to a strong predation mortality from cephalopods, which was reduced by rescaling a 5% of cephalopod's diet to their other preys.

Sea worms input biomass estimated on the field (1.6 tons/km<sup>2</sup>) was far too low to sustain predation. Biomass was very low compared to other similar ecosystem models (Albouy et al 2010, Valls et al 2012, Prato et al. in prep) and likely strongly underestimated, since our field sampling did not occur on coralligenous concretions. This habitat is likely hosting high abundance of sea worms, but is also very fragile, thus it would have been damaged by the air lift pump sampling. We thus estimated sea worms biomass through the mass balance calculations of the model.

Macrofauna input biomass was low to sustain predation from Decapods+. Our input biomass value was probably underestimated since we did not sample in coralligenous concretions, thus we increased input biomass by 40% according to the standard pedigree range provided for low precision-local sampling data (Morisette 2007). Then, by reducing Decapods diet on macrofauna by 20%, we reached a reasonable biomass estimate that satisfied the mass-balance requisite.

#### 7.4.2 Ecopath model

The balanced model had a pedigree of 4.1 and respected all pre-balancing rules (Link et al 2010, Lassalle et al. 2014). Final model parameters are provided in Tab.3. Biomasses of fish, invertebrates and primary producers were respectively 0.07%, 0.64% and 99% of total biomass in the system ( tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup> including *Posidonia oceanica*). Analysis of fluxes showed that the food-web was mainly organised around a bentho-pelagic pathway, with limited exchanges with the pelagic domain (Fig. 2). Biomass of first order producers was dominated by *Posidonia oceanica* and seaweeds, which were the largest source of energy for Salemas and Sea urchins, the main herbivores in the system (Fig. 2). Strong energy fluxes connected the detritus compartment with many benthic invertebrate groups (Meiofauna, Suspensivores+ and Echinoderms+) and Mullets. Main fluxes connecting the benthic and fish groups were those between Macrofauna+ and

Wrasses+, Suspensivores and Diplodus+ and Decapods with Scorpionfish&combers+. Decapods were also an important source of energy for many intermediate and higher trophic levels (3.5-4). Cephalopods exhibited strongest connection with high trophic level predators (large and medium dusky grouper and Amberjack&dentex+), whose biomass was not very high (0.88 tons  $\cdot$  km<sup>-2</sup>  $\cdot$  year<sup>-1</sup> in total).

	Group name	TL	В	P/B	Q/B	EE	P/Q
1	Amberjack & dentex +	4.27	0.14	0.20	3.78	1.00	0.05
2	Dusky grouper - large	4.38	0.60	0.12	1.13	0.00	0.11
3	Dusky grouper - medium	4.20	0.32	0.36	1.48	0.00	0.24
4	Dusky grouper - small	3.93	0.29	1.34	3.12	0.06	0.43
5	Large-scaled scorpionfishes +	3.51	0.83	0.48	6.24	0.15	0.08
6	Scorpionfishes & combers +	3.64	0.57	0.42	8.12	0.80	0.05
7	Stripped red mullets +	3.68	0.20	0.42	8.95	0.84	0.05
8	Sand smelts +	3.75	3.57	0.54	11.33	0.31	0.05
9	Diplodus +	3.15	3.46	0.61	10.24	0.11	0.06
10	Gobies +	3.27	1.96	1.25	9.94	0.90	0.13
11	Wrasses +	3.22	2.68	0.85	10.21	0.16	0.08
12	Mullets	2.32	0.17	0.35	18.24	0.49	0.02
13	Salema - juveniles	2.35	0.54	0.81	6.06	0.41	0.13
14	Salema - adults	2.00	4.40	0.25	2.54	0.05	0.10
15	Decapods +	2.53	9.84	2.64	18.89	0.90	0.14
16	Cephalopods	3.62	0.83	2.34	5.18	0.90	0.45
17	Zooplankton - large	3.04	1.94	22.71	60.47	0.95	0.38
18	Zooplankton - small	2.10	7.29	35.44	109.43	0.95	0.32
19	Sea worms	2.32	9.55	3.36	15.27	0.90	0.22
20	Macrofauna +	2.18	24.50	4.10	47.60	0.97	0.09
21	Echinoderms +	2.36	8.54	0.59	2.70	0.67	0.22
22	Suspensivores +	2.19	25.33	2.63	11.20	0.80	0.23
23	Gorgonians	2.23	35.09	0.20	0.53	0.05	0.38
24	Sea urchins	2.15	40.00	0.57	2.77	0.19	0.21
25	Meiofauna	2.00	21.91	10.00	33.33	0.95	0.30
26	Posidonia	1.00	27391.56	0.55	0.00	0.04	
27	Seaweeds	1.00	586.51	4.43	0.00	0.11	
28	Phytoplankton	1.00	11.45	112.60	0.00	0.62	
29	Detritus	1.00	86.35			0.08	

Tab.3 Outputs of the balanced model. Parameters in bold were estimated through the model's massbalance calculations



Fig.2 Flow diagram of the modelled ecosystem. Size of the nodes is proportional to the biomass of the functional groups. Lines represent the flux of energy among groups. Colours are proportional to the magnitude of the flux.

## 7.4.3 Keystone groups and mixed trophic impact

Keystone species analysis (Fig.3) highlighted high trophic level predators pertaining to the group Amberjack&dentex+, and the small and large dusky groupers with highest keystonnes index, followed by Cephalopods and Diplodus+, while primary producers groups characterised by large biomasses ranked lowest. MTI analysis showed that top down effects prevail in the Cap Roux reserve, with consequent trophic cascades. Predation of the Amberjack&dentex+ group on the small Dusky grouper and on the Large scale scorpionfish + group, positively affects many intermediate trophic levels (i.e. Scorpionfishes and combers, Salema juveniles, Gobies+, Diplodus + ) through release from predation. On the other hand, the Amberjack&dentex+ group is consumed by the large Dusky grouper, which indirectly favours the small Dusky grouper. Cephalopods (similarly to decapods) have positive impacts on all size classes of the Dusky grouper, contributing importantly to their diet, while they compete with the Amberjack&dentex+ group for predation on sand smelts.

Furthermore, they negatively impact many groups through direct predation and/or competition, such as Decapods +, Macrofauna +, Gobies + and Sand smelts +. A competition effect also arises with Diplodus +, due to the overlap among their diets on the macroafaunal component. Finally, the model allows to identify the typical Mediterranean trophic cascade, since a slight increase in the biomass of Diplodus + negatively impacts sea urchins, indirectly allowing for an increase in seaweeds biomass.

The sensitivity analysis on the results of the mixed trophic impact routine showed that 60 % of the pairwise intersections in the original MTI matrix had a sign with a confidence percentage of 100% (Annex, Tab.3). For 83 % of the combinations the confidence interval was superior to 95% and only 10 pairwise combinations (1%) had a confidence interval < 50%. None of these involved the identified keystone groups.



Fig.3 Ordination of functional groups according to their keystone index and trophic level. The diameter of the circles is proportional to the biomass of the group.

#### 7.4.4 Effort and cost analysis

In order to collect the needed data for building a trophic model of the Cap Roux fishery reserve representing the warm season, 51 diving hours were completed corresponding to a cost of 25500  $\in$  and four operators were employed, including one skipper (Tab.4). Treatment and identification of macrofaunal samples required an effort of approx. 1500 hours at an expense of 16000  $\in$ . Data analysis and model building were carried out in 120 hours, correspondin to a cost 4200  $\in$ . Overall, 200

including  $2000 \in$  for equipment amortization and if scientific underwater operators must be contracted for field data collection, on the basis of our salary assumption  $45700 \in$  would need to be invested to build a model for the Cap Roux reserve.

Tab.4 Total effort and cost covering the whole process of model building. Effort was quantified as hours/process, and staff employed. Prices were calculated assuming a flat rate of  $500 \notin$  per dive for a scientific underwater operator (approx. 60 min/dive and including material amortization) and  $35 \notin$  per hour of computer work for a researcher (based on 2014 annual salary for a CNRS researcher)

	Hours	Cost (€)	Staff
Field work	51	25500	2-3 scientific divers, 1 skipper
Macrofauna + algae sorting, identification	1500	16000	2 biologists
Data analysis + model building	120	4200	1 biologist
Equipment amortization		2000	
Total cost		47700	

The least cost-efficient field surveys in terms of cost per total replicates were surveys for mega-invertebrates and macrofauna (respectively  $6500 \notin / 78$  replicates and  $5000 \notin / 50$  replicates, against  $8000 \notin / 150$  fish transects and  $6000 \notin / 260$  echinoderm quadrats) (Tab. 5). When the cost for lab. work was added, the most expensive process was data collection for macrofauna and algae, reaching an overall investment of  $21000 \notin$  for data collection, sample sorting and taxa identification (Tab. 5).

Tab.5 Total data collection cost for each ecological group. Lab cost for fish and invertebrates inlcudes data digitalisation and standardisation.

Total cost / group	Campaigns	Replicates	Field hours	Field cost (€)	Lab cost (€)	Total cost (€)
Fish	3	150	16	8000	560	8560
Mega-invertebrates	2	78	13	6500	560	7060
Echinoderms	2	260	12	6000	280	6280
Macrofauna + algae	2	50	10	5000	16000	21000

Efficiency of fish and echinoderms surveys was related to the short time needed to survey one replicate (6 min / transect, 3 min / quadrat) (Tab. 6). Both could be performed by one operator. Sampling with circles for sea stars, decapods and cephalopods required longer time per replicate, since it allowed to sample a larger surface (78.5 m<sup>2</sup>/replicate circle against 25 m<sup>2</sup>/replicate transect). One operator was needed per transect replicate, while two operators were needed for each circle replicate (Tab. 6).To sample macrofauna and algae four operators were needed: two underwater operators collected the sample, and two operators on-board (other than

the skipper) transferred the samples from the nets to plastic bags. Macrofauna analysis (sorting, identification and weighting) was carried out by specialists with an effort of 30 hours/sample at a cost of 320 €/sample.

Field	Fish	Mega-invertebrates		Echinoderms	Macrofauna + algae		
	Transects	Circles	Transects	Quadrats	Suction sampling	Sorting, Id	
Posidonia	0.10	-	-	0.10	0.22	30	
Rock/pebble	0.10	0.15	0.13	0.05	0.20	30	
Coralligenous concretion	0.10	0.23	0.17	-	-	-	
Sand	-	-	-	-	0.15	30	
Staff/replicate	1	2	1	1	2 divers, 2 on boat	2	

Tab.6 Effort for each sampling method quantified as hours/replicate

## 7.5 Discussion

The Ecopath model of the Cap Roux fishery reserve represented a snapshot of this ecosystem during the warm season of 2014, and was built on the basis of biomass data collected in the field specifically for this purpose. To our knowledge this is the first attempt to quantify the costs involved in the process of Ecopath modelling, from data collection in the field to model construction. Values provided are not absolute, but are an example for the Cap roux ecosystem in the warm season.

The overall quality of the model assessed through the pedigree index (Christensen and Walters 2004) was in the range considered satisfactory for model outputs analysis (Pedigree 0.4-0.6, Lassalle et al 2014), although at its lower limit. The sensitivity analysis of the MTI outputs showed that results concerning the trophic interactions of keystone groups are robust to variations in input data and can be interpreted with fair confidence. The total cost of building this model was 47700  $\in$ , leading to exploitable biomass data for 78% of the functional groups.

Several considerations must be taken into account to properly evaluate this amount.

First of all total cost was calculated assuming a flat rate of  $500 \in x$  dive for a scientific underwater operator, enrolled specifically for the purpose of data collection for modelling. This kind of data, however, shall not serve only for modelling, and should be collected during standard monitoring programs by the MPA staff.

Moreover, when comparing costs invested for data collection and quality of the data obtained, sampling for macrofauna, decapods and cephalopods were the least cost effective processes, each for different reasons. Sampling for decapods and cephalopods with both tested visual census methods was not successful, since very few individuals were recorded. This was possibly due to insufficient sampling effort or

for the paucity of these species in the studied area, in agreement with declarations of fishermen from the surrounding area (Lepetit 2014). Non-destructive surveys for decapods and cephalopods biomass are rare in the literature. In most modelling studies for Mediterranean coastal areas indeed, the biomass for these groups is generally estimated through model mass-balance calculations or is derived from other areas of the Mediterranean (Valls et al 2012, Albouy et al. 2010, Pinnegar et al 2000, Diaz et al. 2008).

Sampling for macrofaunal and polychaetes biomass data required a total expense of 21 000 €, 16 000 € of which were needed only for sample sorting and identification. The biomass value obtained with this sampling effort was too low to balance the model without some modifications. While for the macrofauna group model balance could be reached increasing input biomass within the pedigree range, biomass of polychaetes (1.60 tons km<sup>2</sup>·year<sup>-1</sup>) was far too low and had to be estimated by the mass-balance calculations of the model. In other models from coastal Mediterranean (Valls et al 2012, Albouy et al 2010, Pinnegar et al 2000), macrofauna and polychaetes biomass are much higher than our input values (respectively 60-100 tons km<sup>2</sup> year <sup>-1</sup> for macrofauna and 30-60 tons km<sup>2</sup> year <sup>-1</sup> but similarly to decapods and cephalopods these values were either obtained through model estimation or derived from studies in other Mediterranean areas. Local values for these groups were never available in any model we considered.

The question thus arises whether uncertainty resides in the input biomass value for macrofauna and polychaetes, or in the structure of the model itself, such as the number and composition of functional groups or the input parameters (i.e diet composition) of other groups preying upon macrofauna and polychaetes. For instance, biomass of macrofauna and polychaetes was possibly underestimated in our study for reasons such as insufficient sampling effort, lack of sampling on the probably rich coralligenous bioconcretions and lack of sampling for infaunal polychaetes on rocky reefs. Another bias could be related to the spatial extension of our model, which did not include deeper areas dominated by coastal detritic habitat, also part of the Cap Roux reserve (30-40 m until 80 m isobath). Fish from the shallower zone might rely on macrofauna from the deeper coastal detritic habitat for a non-negligible portion of their diet. Although it would be interesting to investigate the trophic functioning of such deeper zone and its exchanges with the shallower habitats, its study is hampered by the complexity and costs of sampling at depths

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exceeding diving limits. Experimental trawling would be useful in this view, but is not advisable in a protected area. For all these reasons we decided to exclude coastal detritic from the model.

However, the cost implied in increasing sampling effort for macrofauna, both at shallower and deeper areas, would be substantial, and it would thus be more advantageous to invest for increased quality of input data for higher trophic levels feeding on it, including decapods and cephalopods, that are of more direct relevance for MPA management. Moreover, the development of models with standard structure, thus same number and similar composition of functional groups and similar input diet values (Christensen et al 2009) (that are anyway often obtained from the Mediterranean literature) might allow to isolate this potential source of error when model comparisons are performed, either among different seasons or years for the same area or among different coastal Mediterranean areas.

If these cost-benefit issues are considered and macrofauna is not sampled, total costs for model building lower to approximatively 26 700  $\in$ . 8000  $\in$  of these would be devolved to fish monitoring, but generally this activity is already part of standard monitoring programs in Mediterranean MPAs. An additional 6500  $\in$  (24% of total cost) should then be invested in monitoring decapods and cephalopods. Considering the ecological importance of both decapods and cephalopods, as well as their commercial interest for both artisanal and recreational fishing, it would be worth to establish appropriate monitoring surveys which would allow more comprehensive assessment of the effects of protection, while providing valuable data for modelling. Finally 6000  $\in$  should be invested into echinoderms monitoring, which, too, is often already carried on in Mediterranean MPAs, in particular to assess the biomass of sea urchins (key actors in the trophic cascade sea breams – sea urchins – seaweeds characteristic of the Mediterranean) (Sala et al 1998, Guidetti & Sala 2007).

Overall, if collection of biomass data of some key groups like fish (especially high trophic level predators), cephalopods and decapods is integrated to regular monitoring activities implemented by qualified MPA staff, model building costs can be reduced to only computer work (4200 €).Once a first model is built moreover, much less effort is needed to update it in time, providing outputs useful for informing management decisions (Christensen and Pauly 1993, Dame & Christian 2005, Coll et al 2010). In our case study for example, the investment in model building allowed to identify the keystone groups of the studied area, such as high trophic level predators (including the dusky grouper, *Epinephelus marginatus*) and cephalopods (i.e. mainly

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*Octopus vulgaris*) and to unravel the trophic interactions among these, with interesting possible management applications.

The dusky grouper for instance is a species protected by moratorium in France and also a flag species in Mediterranean MPAs, being a strong attraction for diving tourism (Bassu et al 2007). The Ecopath model showed that its biomass is positively affected by that of cephalopods, which on the other hand are an important target of both artisanal and recreational fishing within Mediterranean MPAs. In the Cap roux reserve they are likely subject to a considerable amount of illegal fishing, due to the absence of regular surveillance in the area (estimates for these illegal catches were ot available), as it is often the case in the Mediterranean. Implementing management measures such as intensified surveillance or reduction of artisanal and/or recreational fishing catches for cephalopods would have the double effect of protecting a functional group of recognised ecological importance (Piatkowski et al 2001,Coll et al 2013), with additional beneficial effects for the groupers population.

Building an EwE model thus offers a standardised framework both to define monitoring programs as well as to organise the so-collected ecological information into a coherent picture of ecosystem functioning. As we have seen moreover, highlighting the uncertainties of a model is important to correctly interpret model results, but should not discourage their construction (Dame & Christian 2011). Investing in the construction of a first model would provide an MPA with an ecosystem-based management tool which can be easily updated in time, and which can deliver useful information, such as the identification of priority species to be targeted by management actions, or the evaluation of fisheries impact on the ecosystem and on key species (Prato et al. in prep), and the quantification of spill over from the MPA (Colléter et al 2014). The more the availability of data in Mediterranean MPAs increases, the more applications can be envisaged, up to spatial and temporal simulations of the effects of management actions on the food-web (Dame & Christian 2011, Coll et al 2015).
- Albouy C, Mouillot D, Rocklin D, Culioli J, Le Loc'h F (2010) Simulation of the combined effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using a trophic model. Mar Ecol Prog Ser 412:207–221
- Bassu V, Porcu C, Niccolini F (2007) Studio sul valore economico delle popolazioni di cernie nell' Area Marina Pr otetta di Tavolara Punta Coda Cavallo. Rapporto finale 2008, Intervento E1
- Bonhomme D, Astruch P, Antonioli PA, Bonhomme P, Perez T, Ruitton S, Ivanisevic J, 2010. Inventaire et Cartographie des Habitats Naturels, des espèces végétales et animales du Site Natura 2000 « l'Estérel et des abords de Fréjus (FR9301628) » Lot 2 : Milieux marins. Contrat GIS Posidonie Ville de Saint Raphaël,267 p.
- Brey T, Müller-Wiegmann C, Zittier ZMC, Hagen W (2010) Body composition in aquatic organisms — A global data bank of relationships between mass, elemental composition and energy content. Journal of Sea Research 64:334– 340
- Christensen V, Ferdaña Z, Steenbeek J (2009) Spatial optimization of protected area placement incorporating ecological, social and economical criteria. Ecol Model 220:2583–2593
- Christensen V, Pauly D (1992) Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological modelling 61:169–185
- Christensen V, Pauly D (1993) Trophic Models of Aquatic Ecosystems. The WorldFish Center
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological modelling 172:109–139
- Christensen V, Walters CJ, Ahrens R, Alder J, Buszowski J, Christensen LB, Cheung WWL, Dunne J, Froese R, Karpouzi V, Kaschner K, Kearney K, Lai S, Lam V, Palomares MLD, Peters-Mason A, Piroddi C, Sarmiento JL, Steenbeek J, Sumaila R, Watson R, Zeller D, Pauly D (2009) Database-driven models of the world's Large Marine Ecosystems. Ecol Model 220:1984–1996
- Christensen V, Walters CJ, Pauly D. Ecopath with Ecosim: a user's guide (2005).. Fisheries Centre, University of British Columbia, Vancouver 154
- Coll M, Akoglu E, Arreguín-Sánchez F, Fulton EA, Gascuel D, Heymans JJ, Libralato S, Mackinson S, Palomera I, Piroddi C, others (2015) Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. Rev Fish Biol Fish 25:413–424
- Colléter M, Gascuel D, Albouy C, Francour P, Tito de Morais L, Valls A, Le Loc'h F (2014) Fishing inside or outside? A case studies analysis of potential spillover effect from marine protected areas, using food web models. J Mar Syst 139:383–395
- Coll M, Libralato S (2012) Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish Fish 13:60–88

- Coll M, Navarro J, Olson RJ, Christensen V (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Res Part II Top Stud Oceanogr 95:21–36
- Dame JK (2005). Evaluation of ecological network analysis for ecosystem-based management. PhD diss. East Carolina University
- Dame JK, Christian RR (2006) Uncertainty and the Use of Network Analysis for Ecosystem-Based Fishery Management. Fisheries 31:331–341
- Dame JK, Christian RR (2011) Uncertainty and the Use of Network Analysis for Ecosystem-Based Fishery Management. Fisheries 31:331–341
- Díaz López B, Bunke M, Bernal Shirai JA (2008) Marine aquaculture off Sardinia Island (Italy): ecosystem effects evaluated through a trophic mass-balance model. Ecol Model 212:292–303
- Gascuel D, Bozec Y-M, Chassot E, Colomb A, Laurans M (2005) The trophic spectrum: theory and application as an ecosystem indicator. ICES J Mar Sci 62:443–452
- Gascuel D, Morissette L, Palomares MLD, Christensen V (2008) Trophic flow kinetics in marine ecosystems: toward a theoretical approach to ecosystem functioning. ecological modelling 217:33–47
- Gascuel D, Guénette S, Pauly D (2011) The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. ICES J Mar Sci 68:1403–1416
- Gislason H, Daan N, Rice J, Pope J (2008) Does natural mortality depend on individual size. ICES CM
- Goñi R, Adlerstein S, Alvarez-Berastegui D, Forcada A, Reñones O, Criquet G, Polti S, Cadiou G, Valle C, Lenfant P, others (2008) Spillover from six western Mediterranean marine protected areas: evidence from artisanal fisheries. Mar Ecol Prog Ser 366:159–174
- Guidetti P, Sala E (2007) Community-wide effects of marine reserves in the Mediterranean Sea. Mar Ecol Prog Ser 335:43–56
- Kellner JB, Litvin SY, Hastings A, Micheli F, Mumby PJ (2010) Disentangling trophic interactions inside a Caribbean marine reserve. Ecol Appl 20:1979–1992
- Lassalle G, Bourdaud P, Saint-Béat B, Rochette S, Niquil N (2014) A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. Ecol Model 285:13–21
- Lazzara L, Marchese C, Massi L, Nuccio C, Maselli F, Santini C, Pieri M, Sorani V (2010) Sub-regional patterns of primary production annual cycle in the Ligurian and North Tyrrhenian seas, from satellite data. Italian Journal of Remote Sensing 42:87–102
- Lepetit A, 2014. Quel avenir pour le cantonnement du Cap Roux ? Etude du contexte et des différents scenarii possibles d'évolution du cantonnement pour assurer son efficacité et sa pérennité. Master diss., Agrocampus Ouest Rennes
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Mar Ecol Prog Ser 384:33–46
- Lindeman RL (1942) The trophic-dynamic aspect of ecology. Ecology 23:399-417

- Link JS (2010) Adding rigor to ecological network models by evaluating a set of prebalance diagnostics: A plea for PREBAL. Ecol Model 221:1580–1591
- Michel L, Lepoint G, Dauby P, Sturaro N (2010) Sampling methods for amphipods of *Posidonia oceanica* meadows: a comparative study. Crustaceana 83:39–47
- Montefalcone M, Vassallo P, Gatti G, Parravicini V, Paoli C, Morri C, Bianchi CN (2015) The exergy of a phase shift: Ecosystem functioning loss in seagrass meadows of the Mediterranean Sea. Estuarine, Coastal and Shelf Science 156:186–194
- Morissette L (2007) Complexity, cost and quality of ecosystem models and their impact on resilience. PhD diss., University of British Columbia
- Murawski SA, Wigley SE, Fogarty MJ, Rago PJ, Mountain DG (2005) Effort distribution and catch patterns adjacent to temperate MPAs. ICES Journal of Marine Science: Journal du Conseil 62:1150–1167
- Odum WE, Heald EJ, (1975). The detritus-based food web of an estuarine community, in: Cronin LE (Ed.), Estuarine Research. Academic Press, New York, pp. 265–286
- Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar Freshw Res 49:447–453
- Pelletier D, Claudet J, Ferraris J, Benedetti-Cecchi L, Garcia-Charton JA (2008) Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. Can J Fish Aquat Sci 65:765–779
- Piatkowski U, Pierce GJ, Morais da Cunha M (2001) Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fish Res 52:5–10
- Pinnegar, J.K., 2000. Planktivorous Fishes: Links Between the Mediterranean Littoral and Pelagic. Ph.D. diss. University of Newcastle, 213 pp.
- Pinnegar JK, Polunin NVC (2004) Predicting indirect effects of fishing in Mediterranean rocky littoral communities using a dynamic simulation model. Ecol Model 172:249–267
- Piroddi C, Coll M, Steenbeek J, Macias Moy D, Christensen V (2015) Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity. Mar Ecol Prog Ser 533:47–65
- Prato G, Gascuel D, Valls A, Francour P (2014) Balancing complexity and feasibility in Mediterranean coastal food-web models: uncertainty and constraints. Mar Ecol Prog Ser 512:71–88
- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos:425–439
- Steenbeek J, Buszowski J, Christensen V, Akoglu E, Aydin K, Ellis N, Felinto D, Guitton J, Lucey S, Kearney K, others (2015) Ecopath with Ecosim as a model-building toolbox: Source code capabilities, extensions, and variations. Ecol Model
- Thiriet P (2014)Comparisons of fish assemblage structure and underlying ecological processes, between *Cystoseira* forests and less structurally complex habitats

of North-Western Mediterranean subtidal rocky reefs. PhD diss. Université Nice Sophia Antipolis, Nice.

- Valls A, Coll M, Christensen V (2015) Keystone species: toward an operational concept for marine biodiversity conservation. Ecological Monographs 85:29–47
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Vasapollo C (2009) Spatio-temporal variability of plant features and motile invertebrates in Posidonia oceanica seagrass meadows. PhD diss. Open University.Milton Keynes (UK)

# 7.7 Annex

Tab.1 Parameters used for the length-weight conversions of echinoderms, according to the power function WW =a  $L^{A^b}$ , where WW is the wet weight expressed in grams or mg depending on the size unit of measure. For *Echinaster sepositus* dry weight (DW) was converted to WW with a conversion factor = 0.283 (Brey et al. 2010)

			Powe	r function		
			para	ameters		
	Size				Biomass	
Species	unit	Size measure	а	b	unit	References
Holothuria polii	Cm	contracted length	0.48	1.66	g WW	Francour 1990
Holothuria tubulosa	Cm	contracted length	0.05	2.53	g WW	Francour 1990
Arbacia lixula	Mm	maximum diameter without spines	0.00	2.53	g WW	Pais et al. 2007
Paracentrotus lividus	Mm	maximum diameter without spines	0.00	2.48	g WW	Pais et al. 2007
Spharechinus granularis	Mm	maximum diameter without spines	0.00	2.75	g WW	Dance 1987
Marthasterias glacialis	Cm	length of the longest arm from the centre of the disk	0.31	2.74	mg WW	O' Gormann 2009
Echinaster sepositus	Cm	length of the longest arm from the centre of the disk	0.05	2.29	g DW	Schiebling 1981
Ophiouroids	Cm	disk diameter	0.00	2.41	g WW	Robinson 2010

#### Tab. 2 Origin of input parameters for each functional group

N°	Funtional group	Value	References	Observations
1	Amberjack & dentex +			
	В	0.14	Underwater visual census in the study area	
			Z = M when fishing mortality is null. M=	
	P/B	0.20	Empirical equation from Gislason et al	
			2008	
	O/B	3.78	Empirical equation from Palomares &	
			Pauly 1998	
			Badalamenti et al. 1995, Morales-Nin &	
	Diet		Moranta, 1997, Barreiros et al. 2002, Anastasonoulou et al. 2013 Matic-Skoko	
			et al., 2010. Rogdakis et al 2010	
2	Dusky grouper			
	B	1.21	Underwater visual census in the study area	
	2		Z = M when fishing mortality is null. M=	
	P/B	0.16	Empirical equation from Gislason et al	
			2008	
	O/B	2 1 2	Empirical equation from Palomares &	
	QB	5.12	Pauly 1998	
	Diet		Valls et al., 2012	
3	Large-scaled scorpionfishes +			
	В	0.83	Underwater visual census in the study area	
			Z = M when fishing mortality is null. M=	
	P/B	0.48	Empirical equation from Gislason et al	
	- 1		2008	
	Q/B	6.24	Palomares & Pauly, 1998	
	Diet		Stergiou & Karpouzi 2002, Cresson et al.	
А	Scornionfishes & combers +		2014	
-	R	0.57	Underwater visual census in the study area	
	D	0.57	7 = M when fishing mortality is null $M =$	
	P/B	0.42	Empirical equation from Gislason et al	
			2008	
	Q/B	8.12	Palomares & Pauly, 1998	
	Diet		Relini et al 2002, Stergiou & Karpouzy 2002	
5	Stripped red mullets +			
	В	0.20	Underwater visual census in the study area	
			Z = M when fishing mortality is null. M=	
	P/B	0.42	Empirical equation from Gislason et al	
			2008	
	Q/B	8.95	Palomares & Pauly, 1998	
	Diet		Stergiou & Karpouzi 2002	
6	Sand smelts +			
	В	3.57	Underwater visual census in the study area	
			Z = M when fishing mortality is null. M=	
	P/B	0.54	Empirical equation from Gislason et al	
			2008	
	Q/B	11.33	Palomares & Pauly, 1998	
	Diet		Pinnegar 2000, Stergiou & Karpouzi 2002,	
] _	Dialadua		Cresson et al. 2014,	
<b>′</b>	Diploaus +	2.46		
1	D	3.40	onderwater visual census in the study area	

N°	Funtional group	Value	References	Observations
			Z = M when fishing mortality is null. M=	
	Р/В	0.61	Empirical equation from Gislason et al 2008	
	Q/B	10.24	Palomares & Pauly, 1998	
	Diet		Sala 1997, Pita et al. 2002	
8	Gobies +			
	В	1.96	Estimated by Ecopath	Understimated by visual census
			Z = M when fishing mortality is null. M=	
	Р/В	1.25	Empirical equation from Gislason et al 2008	
	Q/B	9.94	Palomares & Pauly, 1998	
	Diet		Pita et al.2002, Velasco et al. 2010,	
٥	Wrassos +		Stergiou & Karpouzi, 2002	
5	R	2 68	Underwater visual census in the study area	
	0	2.00	Z = M when fishing mortality is null. M=	
	Р/В	0.85	Empirical equation from Gislason et al	
	Q/B	10.21	Palomares & Pauly. 1998	
			Stergiou & Karpouzi 2002, Velasco et al.	
	Diet		2010, Cresson et al. 2014	
10	Mullets			
	В	0.17	Underwater visual census in the study area	
	P/B	0.35	Z = M when fishing mortality is null. M= Empirical equation from Gislason et al	
	0/0	10.24	2008	
	Q/B Diot	18.24	Valls at al. 2012	
11	Saloma		Valis et al., 2012	
	R	1 00	Underwater visual census in the study area	
	U	4.55	7 = M when fishing mortality is null M=	
	P/B	0.38	Empirical equation from Gislason et al 2008	
	Q/B	29.00	Palomares & Pauly, 1998	
	Diet		Dobroslavic et al. 2013, Verlaque, 1990	
12	Decapods +			
	В		estimated by Ecopath	
	Р/В	2.64	Coll et al 2006, Pinnegar, 2000, Valls et al., 2012	Average of literature values
	Q/B	18.89	Pinnegar 200,	
	Diet		Valls et al. 2012	
13	Cephalopods			
	В		estimated by Ecopath	
	P/B	2.34	Valls et al 2012	
	Q/B		Estimated by Ecopath setting P/Q= 0.3	
	Diet		Valls et al. 2012	
14	Zooplankton - large			
	В		Estimated by Ecopath	
	P/B	22.71	Coll et al 2006, Pinnegar, 2000, Valls et al., 2012	Average of literature values

N°	Funtional group	Value	References	Observations
	Q/B	60.47	Coll et al 2006, Pinnegar, 2000, Valls et al., 2012	Average of literature values
	Diet		Valls et al. 2012	
15	Zooplankton - small			
	В		Estimated by Ecopath	
	P/B	35.44	Coll et al 2006, Pinnegar, 2000, Valls et al., 2012	Average of literature values
	Q/B	109.43	Coll et al 2006, Pinnegar, 2000, Valls et al., 2012	Average of literature values
	Diet		Valls et al. 2012	
16	Sea worms			
	В	1.63	Estimated by Ecopath	
	P/B	2.58	Valls et al 2012, Pinnegar 2000	Average of literature values
	Q/B	15.27	Valls et al 2012, Pinnegar 2001	Average of literature values
	Diet		Valls et al. 2012	
17	Macrofauna +			
	В	17.53	Sampling in the study area	
	P/B	4.10	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	47.60	Coll et al. 2006, Pinnegar 2000, Valls et al. 2013	
	Diet		Valls et al. 2012	
18	Echinoderms +			
	В	8.54	Underwater visual census in the study area	
	P/B	0.59	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	2.70	Pinnegar 2000	
	Diet		Valls et al. 2012	
19	Suspensivores +			
	В		Estimated by Ecopath	
	P/B	2.63	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B		Pinnegar 2000, Valls et al. 2012	Estimated by the model for a $P/Q = 0.3$
	Diet		Valls et al., 2012	
23	Gorgonians			
	В		Estimated by Ecopath	
	P/B	0.20	Mistri & Ceccarelli 1993, Weinbauer & Velimirov 1995	
	Q/B	0.53	Valls et al., 2012	
	Diet		Valls et al., 2012	
24	Sea urchins			
	В	40.00	Underwater visual census in the study area	
	P/B	0.57	Coll et al. 2006, Pinnegar 2000, Valls et al. 2012	Average of literature values
	Q/B	2.77	Pinnegar 2000	
	Diet		Valls et al., 2012	
25	Meiofauna			

N°	Funtional group	Value	References	Observations
	В		Estimated by Ecopath	
	P/B	10.00	Danovaro et al. 2002	
	Q/B		Estimated by Ecopath for a P/Q of 0.3	
	Diet		Valls et al. 2012	
26	Posidonia			
	В	27391.56	Montefalcone et al. 2015	Leaf,frond,rhyzome,roots. Conversion factors AFDW = 80% DW from Westlake 1964, WW = 5.7 x DW from Valls et al 2012
	Р/В	0.55	Francour 1990	
27	Seaweeds			
	В	586.51	Sampling in the study area	
	P/B	4.43	Valls et al. 2012	
28	Phytoplankton			
	В	11.45	Indirect estimation from PP	
	Р/В	179.50	Lazzara et al. 2010	PP= 90 gC/m2 Lazzara et al. 2010 converted to WW from Shannon &
				Jarre-Teichmann 1999.
29	Detritus			
	В	86.35	Empirical equation from Christensen & Pauly 1993	Using a primary production estimate of 175 gC/m2 x year for the Mediterranean sea (Chassot et al. 2007)

Tab. 3 MTI sensitivity analysis. Bright green cells: effects with high confidence percentage (>95%); medium green cells: [95–75[; pink cells: [75–50[; red cells: <50% (this means the average sign from the sensitivity analysis is opposed to the one of the original MTI matrix).

	Amberjack & dentex +	Dusky grouper - large	Dusky grouper - medium	Dusky grouper - small	Large-scaled scorpionfishes +	Scorpionfishes & combers +	Stripped red mullets +	Sand smelts +	Diplodus +	Gobies +	Wrasses +	Mullets	Salema - juveniles	Salema - adults	Decapods +	Cephalopods	Zooplankton - large	Zooplankton - small	Sea worms	Macrofauna +	Echinoderms +	Suspensivores +	Gorgonians	Sea urchins	Meiofauna	Posidonia	Seaweeds	Phytoplankton	Detritus
Amberjack & dentex +	100	100	98.4	100	100	100	92.9	100	100	98.6	90.2	99	100	100	83.3	100	100	100	100	91.3	100	100	100	100	95.1	99.8	100	99	100
Dusky grouper - large	100	100	100	100	56.6	100	100	99.5	99.8	91.7	100	83	100	100	100	100	99.9	97.6	60.7	98.7	99.9	99.8	99.9	99.9	39.3	99.7	66.7	100	96.4
Dusky grouper - medium	100	98.9	100	100	99.1	100	100	82.8	99.6	99.8	100	96.3	100	100	52.5	45.8	82.2	58.7	50.1	99.9	100	99.8	99.7	99.7	63.1	45.8	51.4	83.9	46.7
Dusky grouper - small	100	100	96.8	100	52.1	100	100	100	100	100	74.7	100	100	100	91.3	100	100	100	98.1	92.3	100	100	100	100	100	100	100	100	100
Large-scaled scorpionfishes +	100	100	100	99.5	100	100	100	100	100	99.1	100	86.7	64.8	100	90.4	100	100	100	100	99.6	63.4	100	100	100	100	100	100	100	100
Scorpionfishes & combers +	88.4	100	99.8	72.4	85.9	100	100	100	95.6	100	100	99.3	75.2	99.4	97.9	100	100	100	93.2	100	100	100	100	100	100	100	100	100	100
Stripped red mullets +	100	100	80.7	97	100	44.7	100	100	100	100	70.9	99.6	97	99.2	100	100	100	100	57.4	99.8	100	95.6	100	77.1	98.5	99.9	100	100	100
Sand smelts +	100	99.4	100	99.4	60.4	100	100	100	100	91.1	100	100	100	100	100	75.9	100	100	100	100	99.7	99.9	86.7	100	100	99.8	72.5	100	99.9
Diplodus +	100	100	100	71.1	100	73.9	100	100	100	87.4	100	100	100	100	100	100	100	100	100	64.6	100	100	100	100	100	100	100	93	100
Gobies +	100	100	95.2	85.7	92.2	100	99.9	94.3	95.1	100	99.8	99.9	74.7	100	100	100	84.7	85.2	100	100	100	99.8	61.5	100	100	100	97.1	100	100
Wrasses +	100	100	87.2	100	100	49.9	100	100	100	100	100	100	100	100	99	100	85.9	100	50.1	100	100	99.5	100	100	100	100	100	100	100
Mullets	100	100	100	28.2	100	80.8	100	100	76.6	100	99.4	100	97.9	100	100	94	100	100	100	86.6	99.4	65.7	92.7	62	99.9	88.3	100	100	100
Salema - juveniles	100	100	100	100	100	100	100	100	100	100	98.9	100	100	100	99.7	99.2	100	69.7	100	100	100	100	100	100	100	100	100	100	100
Salema - adults	98.3	100	100	99.3	100	70.6	99.8	100	100	100	88.7	39.4	78.7	100	100	100	100	99.9	99.7	100	100	99	100	100	100	100	100	81.5	100
Decapods +	100	100	100	100	100	100	100	100	100	100	100	100	100	95.7	100	100	74.6	66.5	90.4	100	100	100	100	100	100	100	100	100	100
Cephalopods	100	100	100	99.1	100	98.1	85.5	100	100	87.7	100	100	100	100	100	100	100	100	99.8	77.7	100	100	100	100	47.1	99.9	100	100	100
Zooplankton - large	94.7	100	100	99.6	100	100	100	100	66.6	94.8	99.3	100	100	100	100	100	100	100	100	100	100	100	100	99.2	100	100	98.6	100	74.1
Zooplankton - small	93.4	100	100	100	74	99.4	99.9	100	100	100	99.7	100	100	100	100	100	100	100	57.8	74.9	76.8	100	100	100	100	98.1	100	100	80.5
Sea worms	97.1	74.7	99.9	99.2	92.6	97.8	100	98.5	100	100	96.4	99.9	99.9	100	88	64.2	100	100	100	100	100	100	65.4	78.1	99.9	100	99.4	100	100
Macrofauna +	74.6	99.6	89	100	97.5	53.8	98.4	100	100	100	100	100	53.2	100	100	100	87.1	100	100	100	100	100	100	100	100	100	100	100	100
Echinoderms +	100	100	100	100	100	100	100	88.3	99.2	60.3	100	100	99	100	100	79.1	100	100	98.6	100	100	100	100	100	100	100	100	72.6	100
Suspensivores +	100	100	100	50.8	100	98	66	84.6	100	100	89.6	87.4	100	100	96.7	100	100	100	99	96.3	53.5	100	100	100	100	100	100	100	99.1
Gorgonians	99.9	100	100	100	85.1	95.7	100	100	100	100	100	100	100	100	100	100	100	100	100	99.5	100	100	100	100	100	100	100	89.9	100
Sea urchins	90.5	98.9	100	100	100	100	100	100	96.4	82.6	100	100	100	100	100	54.7	100	100	100	100	99.8	100	45.1	100	99.1	100	100	100	100
Meiofauna	94	100	100	100	100	100	100	94.7	90.5	100	95.6	100	100	60.7	100	99.3	98.7	100	100	97.5	100	99.9	100	99.6	100	94.4	72.6	100	100
Posidonia	74.4	100	100	100	100	100	100	100	76.2	98.7	100	100	100	100	100	100	62.6	79.5	97.5	100	100	96	100	100	100	100	100	99.7	100
Seaweeds	95	100	100	100	100	98.9	56.7	100	94.9	100	99.6	99.8	100	100	100	99.4	63.5	91.5	100	100	53.8	100	74.7	100	97.3	100	100	99.9	99
Phytoplankton	98.3	100	100	100	97.8	54.9	100	100	100	100	59	100	100	99.3	98	95.7	100	100	100	96.4	97	100	100	100	99.1	99.9	100	100	98.8
Detritus	77.3	100	100	100	100	100	100	90	100	100	97.5	100	100	100	100	98.4	86.9	100	100	99.8	100	100	100	100	100	99.9	100	100	100

## Annex references

- Anastasopoulou A, Mytilineou C, Lefkaditou E, Kavadas S, Bekas P, Smith CJ, Papadopoulou KN, Christides G (2013) The diet and feeding ecology of Conger conger (L. 1758) in the deep waters of the Eastern Ionian Sea. Mediterr Mar Sci 14
- Badalamenti F, D'Anna G, Lopiano L, Scilipoti D, Mazzola A (1995) Feeding habits of young-of-the-year greater amberjack Seriola dumerili (Risso, 1810) along the N/W Sicilian Coast. Sci Mar 59:317–323
- Barreiros JP, Santos RS, Borba AES (2002) Food habits, schooling and predatory behaviour of the Yellowmouth Barracuda, Sphyraena viridensis Cuvier, 1829 (Perciformes: Sphyraenidae) in the Azores. Cybium 26(8):83-88
- Bavestrello G, Bo M, Bertolino M, Betti F, Cattaneo-Vietti R (2014) Long-term comparison of structure and dynamics of the red coral metapopulation of the Portofino Promontory (Ligurian Sea): a case-study for a Marine Protected Area in the Mediterranean Sea. Mar Ecol
- Blanco C, Salomón O, Raga JA (2001) Diet of the bottlenose dolphin (Tursiops truncatus) in the western Mediterranean Sea. J Mar Biol Assoc UK 81:1053–1058
- Chassot E, Mélin F, Le Pape O, Gascuel D (2007) Bottom-up control regulates fisheries production at the scale of eco-regions in European seas. Marine Ecology Progress Series 343:45–55
- Christensen V, Pauly D (1993) Trophic Models of Aquatic Ecosystems. The WorldFish Center
- Coll M, Palomera I, Tudela S, Sardà F (2006) Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. J Mar Syst 59:63–96
- Cresson P, Ruitton S, Ourgaud M, Harmelin-Vivien M (2014) Contrasting perception of fish trophic level from stomach content and stable isotope analyses: A Mediterranean artificial reef experience. J Exp Mar Biol Ecol 452:54–62
- Dance C, Kuiper N (1987) Size weight relations in the sea urchin Sphaerechinus granularis in Port-Cros island (Var, French Mediterranean). Colloque international sur Paracentrotus lividus et les oursins comestibles. Gis Posidonie. Faculté des Sciencies de Luminy. Marseille.
- Danovaro R, Gambi C, Mirto S, others (2002) Meiofaunal production and energy transfer efficiency in a seagrass Posidonia oceanica bed in the western Mediterranean. Mar Ecol Prog Ser 234
- De Jong, S.A, Haufman, PAG., Sandee AJJ. and Nienhuis PH, 1991. Community oxygen budgets on seagrass beds and microbial mats on the Banc d'Arguin, Mauritania, p. 67-68. In: PMJ. Herman and CHR. Heip (eds.) Report on the workshop, 'Modeling the benthos', Yerseke, The Netherlands, 20-22 March 1991. Delta Institute for Hydrobiological Research, Yerseke
- Dobroslavić T, Zlatović A, Bartulović V, Lučić D, Glamuzina B (2013) Diet overlap of juvenile salema (Sarpa salpa), bogue (Boops boops) and common twobanded sea bream (Diplodus vulgaris) in the south-eastern Adriatic. J Appl Ichthyol 29:181–185
- Francour P (1990) Dynamique de l'écosystème à Posidonia oceanica dans le Parc National de Port-Cros.Analyse des compartiments matte, litière, faune vagile, échinodermes et poissons. Doctorat, Université Pierre et Marie Curie, Paris
- Gislason H, Daan N, Rice J, Pope J (2008) Does natural mortality depend on individual size. ICES CM

- Karpouzi VS, Stergiou KI (2003) The relationships between mouth size and shape and body length for 18 species of marine fishes and their trophic implications. J Fish Biol 62:1353–1365
- Matic-Skoko S, Tutman P, Marcejla E, Skaramuca D, \DJikic D, Lisicic D, Skaramuca B (2010) Feeding habits and trophic status of Mediterranean moray eel, Muraena helena L., 1758 in the Adriatic Sea—preliminary approach. Rapp Comm Int Pour Mer Méditerranée 39:583
- Mistri M, Ceccherelli VU (1994) Growth and secondary production of the Mediterranean gorgonian Paramuricea clavata. Mar Ecol-Prog Ser 103:291–291
- Montefalcone M, Vassallo P, Gatti G, Parravicini V, Paoli C, Morri C, Bianchi CN (2015) The exergy of a phase shift: Ecosystem functioning loss in seagrass meadows of the Mediterranean Sea. Estuar Coast Shelf Sci 156:186–194
- Morales-Nin B, Moranta J (1997) Life history and fishery of the common dentex (Dentex dentex) in Mallorca (Balearic Islands, western Mediterranean). Fish Res 30:67–76
- Mostarda E, Campo D, Castriota L, Esposito V, Scarabello MP, Andaloro F (2007) Feeding habits of the bullet tuna Auxis rochei in the southern Tyrrhenian Sea. J Mar Biol Assoc UK 87:1007
- O'Gorman EJ, Emmerson MC (2009) Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences 106:13393–13398
- Pais A, Chessa LA, Serra S, Ruiu A, Meloni G, Donno Y (2007) The impact of commercial and recreational harvesting for Paracentrotus lividus on shallow rocky reef sea urchin communities in North-western Sardinia, Italy. Estuarine, Coastal and Shelf Science 73:589–597
- Palomares MLD, Pauly D (1998) Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. Mar Freshw Res 49:447–453
- Palomares Ld, Pauly D (2004) West African Ecosystems. Fish Cent Res Rep 12:4
- Pinnegar JK, Polunin NVC (2000) Contributions of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122:399–409
- Pita C, Gamito S, Erzini K (2002) Feeding habits of the gilthead seabream (Sparus aurata) from the Ria Formosa (southern Portugal) as compared to the black seabream (Spondyliosoma cantharus) and the annular seabream (Diplodus annularis). J Appl Ichthyol 18:81–86
- Relini G, Relini M, Torchia G, De Angelis G (2002) Trophic relationships between fishes and an artificial reef. ICES J Mar Sci J Cons 59:S36–S42
- Robinson LA, Greenstreet SPR, Reiss H, Callaway R, Craeymeersch J, Boois I de, Degraer S, Ehrich S, Fraser HM, Goffin A, Kröncke I, Jorgenson LL, Robertson MR, Lancaster J (2010) Length–weight relationships of 216 North Sea benthic invertebrates and fish. Journal of the Marine Biological Association of the United Kingdom 90:95
- Rogdakis Y, Ramfos A, Koukou K, Dimitriou E, Katselis G (2010) Feeding habits and trophic level of sea bass (Dicentrarchus labrax) in the Messolonghi-Etoliko lagoons complex (Western Greece). J Biol Res 13:13–26
- Sala E (1997) Fish predators and scavengers of the sea urchin Paracentrotus lividus in protected areas of the north-west Mediterranean Sea. Mar Biol 129:531– 539
- Scheibling RE, Lawrence JM (1982) Differences in reproductive strategies of morphs of the genus Echinaster (Echinodermata: Asteroidea) from the Eastern Gulf of Mexico. Marine Biology 70:51–62

- Shannon LJ, Jarre-Teichmann A (1999) A model of trophic flows in the northern Benguela upwelling system during the 1980s. South Afr J Mar Sci 21:349– 366
- Stergiou KI, Karpouzi VS (2001) Feeding habits and trophic levels of Mediterranean fish. Rev Fish Biol Fish 11:217–254
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Velasco EM, Gómez-Cama MC, Hernando JA, Soriguer MC (2010) Trophic relationships in an intertidal rockpool fish assemblage in the gulf of Cádiz (NE Atlantic). J Mar Syst 80:248–252
- Verlaque M (1990) Relations entre Sarpa salpa (Linnaeus, 1758)(Téléostéen, Sparidae), les autres poissons brouteurs et le phytobenthos algal méditerranéen. Oceanol Acta 13:373–388
- Weinbauer M, Velimirov B (1995) Biomass and secondary production of the temperate gorgonian coral Eunicella cavolini (Coelenterata:Octocorallia). Mar Ecol Prog Ser 121:211–216
- Westlake DF (1964) Light extinction, standing crop and photosynthesis within weed beds.

# 8 General discussion

## 8.1 The initial questions

Centuries of selective fishing on high trophic level predators (HTLP) caused a gradual simplification of Mediterranean food-webs, which are nowadays mostly controlled by smaller and lower trophic level species (Sala et al. 2004). The depletion of HTLP affected the overall stability of Mediterranean ecosystem and reduced its resilience to human impacts (Coll et al. 2008, Britten et al. 2014). The protection from fishing within MPAs allowed to trigger a recovery in HTLP abundance and biomass, but long time frames are needed in order to re-establish lost trophic interactions and ecosystem functions (Sala et al. 2012, Guidetti et al. 2014). Long-term monitoring of both HTLP and trophic interactions is thus essential to assess if MPAs are effectively promoting an overall ecosystem recovery and to adapt management consequently.

This PhD aimed at evaluating and proposing effective and operational managementtools to: Q1) effectively monitor high trophic level predators recovery, Q2) unravel and monitor trophic interactions and Q3) quantify fishing impacts upon HTLP and associated food-webs within Mediterranean MPAs.

## 8.2 Main results

The chapters of this thesis developed interconnected steps necessary to pursue the final management-oriented objectives, and provided at the same time results that further elucidate the important functional role of HTLP in marine ecosystems and the state of their recovery in MPAs. We will summarise here the main outcomes of each section of the thesis: field monitoring and food web modelling.

## Underwater visual census (UVC) to survey high trophic level predators

Results from our literature analysis (Chapter 3) highlighted that UVC transects are by far the most commonly adopted technique to survey fish communities in the Mediterranean. Compared with other methods, such as video – UVC, transects provide the most complete quantitative description of the fish assemblage, detecting the highest number of species and allowing to measure several variables (i.e. density, size), at the lower economic and time costs. They are thus better suited for the regular monitoring activities of coastal Mediterranean MPAs, where the

quantification of fish density and biomass is necessary to assess the efficiency of protection. Despite the success of transect UVC across the Mediterranean however, standardization in transect surface is not yet achieved, with more than 50% of the analysed studies that aimed at surveying the whole fish assemblage, differing for the adopted transect sizes. Different transect size can affect the efficiency of the method in detecting a given species, according to its behaviour and mobility (Cheal & Thompson 1997, Kulbicki 1998, Bozec et al. 2011). On one hand thus, standardisation is needed, since comparisons of density or biomass values obtained with different transect width for the same species could be biased. On the other hand, different transect widths should be applied to survey fish species differing for mobility and behaviour (Harmelin-Vivien et al. 1985, Bozec et al. 2011). This is seldom done in the Mediterranean, where the same transect width has been always used to survey both large mobile fish and less mobile necto-benthic fish (Chapter 3).

This evidence encouraged us to evaluate if transects of larger dimensions than those most commonly adopted across the Mediterranean (25 x 5 m), would better account for the behaviour of large mobile and shy predators (often corresponding to HTLP), that seldom allow the observer to approach at such short distance. Results from our field comparison (Chapter 4) showed that within MPAs large size transects (20 x 35 m) provided more accurate density and biomass estimates for large mobile and shy fish than medium transects (5 x 25 m), allowing to reduce under-estimation bias due to the common avoidance behaviour of these fish. Precision of density and biomass estimates tended to be lower when large transects were used within MPAs, because more rare and shy species or species with shoaling behaviour (i.e, *Mycteroperca rubra, Epinephelus costae, Sphyraena viridensis*) were detected. The choice of the transect size to be adopted should thus balance the trade-offs of detecting higher number of species, while achieving lower precision.

Following these results we opted for the combination of three transect sizes (20 x 35 m, 5 x 25 m and 1 x 10 m), adapted respectively to large mobile predators, nectobenthic fish and small crypto-benthic fish, to survey the whole fish assemblage at three Mediterranean MPAs. We evidenced a significant effect of protection on HTLP, whose response in terms of increased biomass within the MPA was always higher in magnitude than that of other functional groups. Trophic pyramids differed within and outside MPAs in terms of relative contribution of each functional group to total fish biomass, with HTLP displaying the largest inside vs outside biomass ratios. This was especially marked at older and highly enforced MPAs (Cabo de Palos, Spain, and Scandola, Corsica-France), suggesting this metric as an effective indicator of HTLP recovery.

In the context of monitoring the recovery of HTLP within MPAs, detecting higher density, biomass and species number for this group should be the priority in the selection of a UVC method. In light of our results we suggested that the combination of large, medium and small transect sizes (respectively for large mobile fish, nectobenthic fish and cryptic fish) in monitoring programs is a simple improvement to traditional one-size transect surveys, allowing to increase the accuracy of total fish assemblage estimates within MPAs, and should thus be considered to assess recovery of HTLP in relation to total fish biomass.

The trophic re-organization we observed caused by the large increase of HTLP within MPAs, is likely to affect the ecosystem functions (Soler et al. 2015). Food-web modelling allows to unravel trophic interactions and to dig deeper on the effects of protection/exploitation on ecosystem functions (Libralato et al. 2010, Plagányi et al. 2014). If the process of model building is simplified and standardised while kept reliable, food-web models can be effective tools for an ecosystem based management in MPAs.

#### Food web modelling

The second section of this PhD was introduced by a theoretical modelling exercise (Chapter 5) where, starting from the most detailed model available for a Mediterranean MPA (Port Cros, Valls et al. 2012), we identified an optimal level of functional groups aggregations which was the best compromise between model complexity, feasibility of model construction in terms of data collection, and reliability of model outputs. In particular the aggregation of several benthic taxa sharing similar predators into one unique macrofaunal group, allows for a substantial simplification in the data collection process, without significantly affecting model outputs. We also identified the key functional groups for which small variations in input biomass data mostly influenced model outputs. These include high trophic level predators, species with a high level of connections in the trophic network such as macrofauna and decapods and primary producers generally present in high biomasses in the Mediterranean, such as *Posidonia oceanica*. We concluded that local and accurate

biomass data should be collected in priority for these groups when developing foodweb models for similar Mediterranean ecosystems.

This model structure was then applied to two case studies representative of Mediterranean data-availability: the older and relatively data rich Portofino MPA (Chapter 6) and the more recently established and data-poor Cap Roux fishery reserve (Chapter 7). Model structure was kept standard in terms of species aggregation into functional groups, but necessarily had to be adapted to the local conditions of each case study, by adding or deleting functional groups depending on their presence or absence at each MPA.

The Portofino MPA food-web model allowed to identify the HTLP groups *Epinephelus marginatus*, Amberjack&dentex+ (including *Dentex dentex, Seriola dumerili, Sphyraena viridensis, Dicentrarchus labrax, Muraena helena, Conger conger*) and Large scaled scorpionfish+ (*Scorpaena scrofa, Sciaena umbra, Labrus merula, Labrus viridis, Pagrus pagrus* and *Phycis phycis*) as keystone species in the food-web, followed by Cephalopods. At the same time, a strong fishing pressure was highlighted on Amberjack&dentex+ and Large scaled scorpionfish+, which were thus considered "sentinel species", i.e species combining high ecological importance and highly fishing pressure in the ecosystem under study, that should thus be prioritised for monitoring and could be "anchor points' for the definition of management actions that deserve to be taken (ex. to calculate the reduction of fishing mortality needed to attain predefined conservation objectives) and for the assessment of their efficiency.

The interacting impacts of artisanal and recreational fishing were unravelled showing that HTLP were mostly threatened by the recreational fishing, which also had the widest effect on the food-web. The ecosystem was far from reaching carrying capacity for HTLP, whose biomass could still increase of 44 %, confirming the high sensitivity of this group to fishing and thus also to protection measures. According to model results, additionally, measures aiming at forbidding recreational fishing would not only benefit the ecosystem by increasing HTLP biomass (24%), but would also increase the mean trophic level (and thus the quality) of the catch of the artisanal fishery. Artisanal fishing alone reduced the biomass of HTLP by less than 15% and could instead be maintained with a moderate impact on the ecosystem.

Overall, some useful insights for MPA management were derived from this study: limiting recreational fishing effort for example would allow the MPA to pursue both its

conservation and socio-economic development targets, by i) reducing the impact on HTLP and thus encouraging their further recovery within the MPA, whose carrying capacity is far to be reached ii) increasing the availability of catches at higher trophic levels for artisanal fishing, thus providing economic benefits to this naturally-declining traditional fishing activity.

Despite the uncertainties associated with some input biomass and fishing data, extensive sensitivity analysis through recently developed routines (Data-reli toolbox, Lassalle et al 2014 and pre-balancing rules, Link 2010) and the comparison of alternative models with varying input data, allowed to increase the confidence in model results.

Modelling the food-web associated with the Cap roux fishery reserve (Chapter 7) also allowed to identify HTLP (Amberjack&dentex+ group and *E. marginatus*) as well as cephalopods as keystones groups in the ecosystem, further stressing the need for monitoring these species. No biological data was available on the area, thus input biomass data was collected on the field, prioritising the functional groups identified in Chapter 5, for which imprecise biomass data can widely affect model outputs. Cost and effort analysis on the full process of model construction pointed out where it would be advisable to invest, in order to increase model quality costefficiently: rather than concentrating effort and resources onto macrofauna sampling, for instance, at least in the first place it would be more advisable to invest in sampling effort for HTLP, as well as decapods and cephalopods. The two latter groups are very seldom included in MPAs monitoring programs, despite their ecological and economical importance, being targets of both artisanal and recreational fishing. (Piatkowski et al. 2001, Goñi et al. 2006, Wagner 2008). It would be thus worth to establish appropriate monitoring surveys for these groups, which would allow more comprehensive assessments of the effects of protection, while providing valuable data for modelling. Excluding sampling for macrofauna, the average estimate for model development costs for an area of 145 ha totalled 26 700 €, including field data collection for fish and mobile mega-invertebrates (decapods, cephalopods and echinoderms), data analysis and model building. If monitoring programs are already in place in an MPA and thus data is already available, model building (data integration and analysis) would require an investment of ca 4 200 €, i.e. less than 1/6 of the previous amount.

## 8.3 Further discussion and perspectives

#### Making food-web models operational in MPAs

By providing a standard model structure and identifying the most sensitive groups for which local biomass data should be collected in priority (Chapter 5), we aimed at simplifying the process of model development and encouraging its application within MPAs. However, other sources of uncertainty were not addressed in this manuscript. While reviewing the literature of Mediterranean models for our analysis (Chapter 5) we noted that not only biomass is often not locally estimated, but also other required input parameters are often derived from the literature, such as diet compositions, or P/B and Q/B ratios for invertebrate groups. Local studies providing estimates for these parameters are indeed very rare and this often causes circular referencing among models, eventually leading to a literature source which often pertains to another time period and a far-away and different ecosystem. These uncertain input data could bias the biomass estimates of groups for which local data is not available or cannot be measured in the field, and that are thus obtained from the model massbalance equations (Morissette 2007, Lassalle et al. 2014). For instance, in Chapter 7 we evidenced how data collected in the field for some groups (macrofauna, cephalopods and decapods) did not provide realistic values to feed the model, and more sampling effort would have been needed to increase quality of these data, at very high costs for some groups. When comparing our values, we evidenced that in other studies from coastal Mediterranean macrofaunal biomass was always estimated by the model. In each study, moreover, P/B, Q/B and diet compositions of many groups feeding on macrofauna were often derived from other models, often relative to other areas of the Mediterranean or even further away.

On one hand, it is paramount that models are grounded on local data. They have the important function of highlighting eventual inconsistencies in such data, and can serve to encourage the upgrading of estimates. Investing on data collection and monitoring is thus needed (Carstensen 2014). However, it shall also be acknowledged that obtaining local estimates for all parameters and groups is often not feasible and that costs to increase data quality for some groups can be very high in a management perspective. Alternative solutions can be those of 1) simplifying and standardising model structure and use models to identify groups for which local biomass should be collected in priority, as we did (Chapter 5) 2) developing a

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Mediterranean data-base with the most updated and reliable estimates for diets, P/B and Q/B (the latter two especially for invertebrates, since empirical equations can be used to derive these parameters for fish) to which modellers could refer as a start. Christensen et al. (2009) provided guidelines to develop database-driven models of large marine ecosystems starting from common default values of input parameters. While they suggested to use the approach as a draft model for improvement, that would make it easier to get started with the modelling process, they also cautioned from the use of these models for management advice, stressing that, for such use, models should be enriched with as much as finer scale data is available. For smallscale models of Mediterranean MPAs high resolution data is essential, however, a Mediterranean data-base to be used as a common reference for critical parameters (very unlikely to be available locally) could help to further standardise the process of model development, and would allow to isolate some of the sources of uncertainty related with input data, eventually increasing models comparability. If, for instance, in every MPA model developed with a standard structure, P/B, Q/B and diet were derived from a common source, when models are compared the eventual differences in the biomass of estimated groups would be more probably due to each MPA's particular environmental or management characteristics, than to a bias in model structure and parameters. A Mediterranean database for these parameters would also largely simplify the process of model construction, where a large amount of time is spent in integrating and transforming data from different sources, allowing a large gain in time and thus efficiency in a management perspective.

#### The complementarity of monitoring and modelling

Monitoring is an essential management tool per-se, allowing to assess if MPAs are meeting the goals for which they have been designed, by detecting change in the abundance and growth rate of species and communities of concern and evaluating how well a reserve fulfils the goal of enhancing a local fishery. But data derived from monitoring can also bridge the gap between field ecology and modelling. On one hand, monitoring data can feed food-web models, needed to investigate issues that cannot be addressed by field studies alone. On the other hand, food-web models can help to identify priority targets for monitoring and to bring to light data gaps or inconsistencies in local data, thus they can re-direct monitoring, in a feed-back loop that shall be accordingly translated into adaptive management. Models developed in

this study for instance, either built with newly collected data (Chapter 7) or with data from past monitoring (Chapter 5 and 6), highlighted the keystone role of high trophic level predators in the protected ecosystems (Valls et al. 2015). This further emphasised the importance of monitoring HTLP and to obtain more accurate estimates of their abundance and biomass in MPAs through appropriate non-destructive techniques (Chapter 4). Additionally, in all the presented case studies, food-web models agreed in assigning a keystone role to cephalopods, which are often (or totally) overlooked when designing monitoring plans in the Mediterranean. Cephalopods play an important functional role in both coastal and pelagic ecosystems (Piatkowski et al. 2001, Coll et al. 2013), being a preferred prey for many high trophic level predators, but also predators acting on a wide range of trophic levels. Moreover, they are economically important artisanal and recreational fishing targets. Studies are needed to assess their abundance and biomass in coastal areas, appropriate non-destructive techniques should be identified and monitoring should be implemented. Fishing pressure on this group should also be regularly monitored.

Finally, modelling can build upon monitoring data to develop ecosystem based indicators, such as food-web indicators, as also required by the Marine Strategy Framework Directive, in order to achieve the Good Environmental Status (Heymans et al. 2014, Guesnet et al. 2015). In this view, MPAs and corresponding models could be very useful to define targets for indicators and to provide reference values corresponding to different conservation states. Indicators based on trophic levels, for example, are increasingly being used to assess fisheries impact on the whole ecosystem (Shannon et al. 2014) and modelling can serve to generate reference values for indicators through dynamic simulations, which would need very long time series if only monitoring data were used (Pelletier et al. 2008). In this perspective, a further development of our study could be the application of the recently proposed Apex Predator Indicator (API) and High Trophic Indicator (HTI) (Bourdaud et al. 2015). Both are trophic level based indicators centred on the proportion of apex and/or high trophic level predators in the ecosystem, as a proxy for the good functioning of the whole food web, and ecosystem-specific targets could be proposed for each indicator through simulation (Bourdaud et al. 2015).

# Perspectives on food web models as operative ecosystem based management tools in MPAs,

On the basis of the data we had strengthened by extensive sensitivity analysis, we proved the potential of food-web models for MPAs management in i) identifying keystone and sentinel species in the ecosystem ii) highlighting the MPA's possible carrying capacity for HTLP iii) unravelling the food-web consequences of variations in HTLP biomass iv) advising for a reduction of recreational fishing effort on HTLP and evaluating the impact of recreational fishing on artisanal fishing.

If 1) exhaustive monitoring programs are implemented in MPAs, targeting both biological resources but also, importantly, human impacts (local fisheries catches and effort), and 2) food web modelling becomes a regular step to integrate data from monitoring, the range of the possible management applications of food web models developed with the EwE – EcoTroph - Ecospace package is extremely wide, and is in continuous expansion (Coll et al. 2015). Here we provide some examples of possible perspectives.

The spread of invasive species in the Mediterranean is widely recognised as a critical threat to its biodiversity and ecosystem functioning and to the provision of ecosystem services in this basin (Katsanevakis et al. 2014). Food web models could help to address this issue, allowing to understand the role and impact of invasive species on the food web and to analyse management scenarios (Arias-González et al. 2011) Although the interest for this approach is growing (Coll et al. 2015), in the Mediterranean applications are still scant.

EwE-Ecotroph models have been used in a couple of studies to assess biomass spillover from MPAs (Valls et al. 2012, Colléter et al. 2014) and, in one study, to quantify the contribution of an MPA to the trophic functioning and productivity of the larger surrounding ecosystem (Guénette et al. 2014). MPAs are often very small in the Mediterranean, it could be thus interesting to assess if extending their borders could increase their contribution in terms of spillover to adjacent systems and also to the total production and catches of the surrounding ecosystem. Through the dynamic modules Ecosim and Ecospace, moreover, it is possible to explore the potential effects on ecosystem structure and on fisheries production of alternative fisheries management (and also climate change) scenarios, to model energy exchanges from MPAs to external areas and to quantify MPAs impact on larger ecosystems. Finally, if several MPA food-web models are developed, large-scale analysis could be carried

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out in Ecospace to assess the effects of different spatial configurations of MPAs networks and/or different fisheries management scenarios on ecosystem structure, functioning and fisheries production.

In order to fully exploit this high potential, MPAs should start integrating food-web modelling as a regular tool in their management plan, using it in the first place to direct monitoring and integrate data into a coherent picture of ecosystem functioning, and then, once a reliable basis is set, to build upon this picture according to management needs.

## **8 Discussion Generale**

#### 8.1 Les questions initiales

Des siècles de pêche ciblant les prédateurs de haut niveau trophique (HTLP) ont provoqué une simplification progressive de réseaux trophiques de Méditerranée, avec un contrôle exercé aujourd'hui principalement par de petites espèces de plus bas niveau trophique (Sala et al., 2004). L'épuisement des HTLP a affecté la stabilité globale des écosystème méditerranéens et réduit sa capacité de résistance aux impacts humains (Coll et al. 2008, Britten et al. 2014). L'interdiction de pêche dans les AMP a favorisé une augmentation de l'abondance et de la biomasse des HTLP. Toutefois, les délais nécessaires afin de rétablir les interactions trophiques perdues et les fonctions des écosystèmes sont assez importants (Sala et al. 2012, Guidetti et al. 2014). La surveillance à long terme des HTLP et des interactions trophiques est donc essentielle pour apprécier si les AMP peuvent efficacement favoriser une restauration globale de l'écosystème et adapter en conséquence leur gestion.

Cette thèse visait à évaluer et proposer des outils de gestion efficaces et opérationnels pour : Q1) quantifier efficacement la récupération des prédateurs de haut niveau trophique, Q2) comprendre et suivre les interactions trophiques et Q3) quantifier les impacts de la pêche sur les HTLP et les réseaux trophiques associés.

## 8.2 Principaux résultats

Les différents chapitres de cette thèse ont permis d'apporter des résultats complémentaires nécessaires pour répondre aux objectifs affichés de gestion des AMP en élucidant en particulier l'importance du rôle fonctionnel des HTLP dans le fonctionnement des écosystèmes marins et en appréciant leur degré de restauration dans les AMP. Nous allons résumer ici les principaux résultats des deux sections de la thèse : suivis de terrain et modélisation du réseau trophique.

# Suivi des prédateurs de haut niveau trophique avec comptage visuel en plongée (UVC)

Les résultats de notre analyse de la littérature (chapitre 3) ont confirmé que les transects UVC sont de loin la technique la plus couramment adoptée pour étudier les communautés de poissons en Méditerranée. Comparés à d'autres méthodes, telles que la vidéo en plongée sous-marine, les transects fournissent la description quantitative la plus complète des peuplements de poissons, détectant le plus grand nombre d'espèces et permettant de mesurer plusieurs variables (i.e. densité, taille),

avec des coûts économiques faibles et des temps d'acquisition réduits. Ils sont donc mieux adaptés aux activités régulières de surveillance des AMP côtières méditerranéennes, où la quantification de la densité et de la biomasse des poissons est nécessaire pour évaluer l'efficacité de la protection. Malgré le succès des comptages visuels sur transects, aucune normalisation de leur surface n'a encore été réalisée en Méditerranée : plus de 50% des études analysées prenant en compte l'ensemble du peuplement de poissons, adoptent des tailles de transects variables. Selon le comportement et la mobilité des espèces, des largeurs de transect non adaptées peuvent affecter l'efficacité de la méthode dans leur prise en compte (Cheal & Thompson 1997, Kulbicki 1998, Bozec et al., 2011). D'un côté donc, la normalisation est nécessaire, car les comparaisons de densité ou de biomasse, obtenues pour le même jeu d'espèces pourraient varier selon la largeur de transect retenue,. D'autre part, il est nécessaire de retenir des transects de différentes largeurs pour étudier des espèces de poissons dont la mobilité et le comportement diffèrent (Harmelin-Vivien et al., 1985, Bozec et al., 2011). Ceci est rarement le cas en Méditerranée, où une largeur unique de transect a toujours été utilisée pour échantillonner à la fois les espèces mobiles de grande taille mais aussi les poissons necto-benthiques moins mobiles (chapitre 3). Ce constat nous a encouragé à évaluer si des transects de dimensions supérieures à celles plus communément adoptées en Méditerranée, à savoir 25 x 5 m, permettraient de mieux prendre en compte le comportement des prédateurs de grande taille, mobiles (généralement des HTLP) et craintifs (se laissant rarement approcher par un plongeur sous-marin à courte distance). Les résultats de notre comparaison sur le terrain (Chapitre 4) ont montré que, dans les AMP, les transects de grande taille (35 x 20 m) fournissent des estimations de densité et de biomasse plus réalistes pour les poissons de grande taille, mobiles et craintifs que les transects classiques (25 x 5 m). Ceci permet de réduire le biais de sous-estimation dû au comportement d'évitement communément observé avec ces espèces. Cependant, la précision des estimations de densité et de biomasse tend à être plus faible (plus forte variance) lorsque des transects de grande taille sont utilisés au sein des AMP, car plus d'espèces rares et craintives ou espèces au comportement grégaire (i.e. Mycteroperca rubra, Epinephelus costae, Sphyraena viridensis) sont détectées. Le choix de la taille de transect à adopter est donc un compromis entre la détection d'un plus grand nombre d'espèces et la diminution de la précision des estimations. Suite à ces résultats, nous avons opté pour la combinaison de trois tailles de transects (L x I : 35 x 20 m, 25 x 5 m et 10 x 1

m), adaptées respectivement aux grands prédateurs mobiles, aux espèces nectobenthiques et aux petites espèces crypto-benthiques, pour échantillonner le plus complètement possible la totalité du peuplement de poissons. Dans les trois AMP méditerranéennes suivies, nous avons montré un effet significatif de la protection sur les HTLP : leur réponse en termes d'augmentation de biomasse dans la zone protégée est toujours meilleure que pour les autres groupes fonctionnels. Les pyramides trophiques diffèrent au sein et en dehors des AMP en termes de contribution relative de chaque groupe fonctionnel à la biomasse totale de poissons. Les HTLP en particulier présentent les plus forts ratios intérieur/extérieur en biomasse. Cela est particulièrement marqué dans les AMP les plus âgées et les mieux surveillées (Cabo de Palos, Espagne et Scandola, en Corse-France), et suggère que ce ratio est un indicateur pertinent du degré de récupération des HTLP. Dans le contexte du suivi de la récupération des HTLP au sein des AMP, être capable de mesurer efficacement une densité, une biomasse ou une richesse spécifique d'HTLP doit être une priorité dans la sélection de la méthode de comptage à retenir. Compte tenu de nos résultats, nous avons suggéré que l'adoption d'une combinaison de transects de taille variable (respectivement pour les espèces mobiles de grande taille, les espèces necto-benthiques et les espèces cryptiques) dans les programmes de surveillance représente une amélioration des suivis traditionnels effectués avec des transects de largeur unique. Cette amélioration de la méthode permet d'augmenter la précision globale des estimations des peuplements de poissons au sein des AMP et devrait donc être retenue pour apprécier le taux de récupération de HTLP en utilisant le rapport biomasse des HTLP/biomasse totale de poissons.

Les modifications trophiques que nous avons observées, dues à l'augmentation importante des HTLP au sein des AMP, sont susceptibles d'affecter les fonctions des écosystèmes (Soler et al. 2015). La modélisation du réseau trophique permet de comprendre les interactions trophiques et d'analyser plus en détail les effets de la protection et/ou de l'exploitation sur les fonctions de l'écosystème (Libralato et al. 2010, Plagányi et al. 2014). Si les étapes de construction des modèles sont simplifiées et standardisées, tout en respectant la fiabilité des modèles, ces derniers peuvent être alors des outils efficaces d'une gestion écosystémique des AMP.

#### La modélisation du réseau trophique

La deuxième partie de cette thèse a débuté par un exercice de modélisation théorique (Chapitre 5). A partir du modèle disponible le plus détaillé pour une AMP méditerranéenne (Port-Cros, Valls et al. 2012), nous avons identifié le niveau optimal d'agrégation en groupes fonctionnels, respectant le compromis entre la complexité du modèle, la faisabilité de la construction du modèle en termes de collecte de données et la fiabilité des sorties du modèle. En particulier, l'agrégation de plusieurs taxons benthiques qui partagent des prédateurs similaires en un seul groupe de macrofaune permet une simplification importante dans le processus de collecte de données, sans affecter significativement les résultats du modèle. Nous avons également identifié les groupes fonctionnels clés pour lesquels de petites variations dans les données de biomasse d'entrée influencent fortement les résultats issus du modèle. Ces groupes comprennent les prédateurs de niveau trophique supérieur, les espèces ayant un niveau élevé de connexion dans le réseau trophique, telles que la macrofaune et décapodes, et les producteurs primaires généralement présents avec de fortes biomasses en Méditerranée comme Posidonia oceanica. Nous avons conclu que des données locales et précises de biomasse devraient être collectées en priorité pour ces groupes lors de l'élaboration des modèles trophiques dans des écosystèmes méditerranéens similaires.

Cette structure de modèle a ensuite été appliquée en Méditerranée à deux cas d'étude représentatifs de la disponibilité préalable des données : l'AMP de Portofino, assez ancienne et pour laquelle de nombreuses données sont disponibles (chapitre 6) et le cantonnement de pêche du Cap Roux, établi plus récemment et ne disposant que de peu de données (chapitre 7). La structure du modèle a été conservée en termes d'agrégation d'espèces en groupes fonctionnels, mais a nécessairement dû être adaptée aux conditions locales de chaque cas d'étude, en ajoutant ou supprimant des groupes fonctionnels en fonction de leur présence ou de leur absence dans chaque AMP.

Le modèle trophique de l'AMP de Portofino a permis d'identifier les groupes de HTLP Epinephelus marginatus, Amberjack & dentex + (comprenant Dentex dentex, Seriola dumerili, Sphyraena viridensis, Dicentrarchus labrax, Muraena helena, Conger conger) et Large scale scorpionfish + (Scorpaena scrofa, Sciaena umbra, Labrus merula, Labrus viridis, Pagrus pagrus et Phycis Phycis) comme des groupes-clés dans le réseau trophique, suivis par les céphalopodes. Dans le même temps,

une forte pression de pêche a été mise en évidence sur Amberjack & dentex + et Large scale scorpionfish +, qui ont donc été considérés comme des «espèces sentinelles», c'est-à-dire des espèces alliant une grande importance écologique et une forte sensibilité aux pressions de pêche dans l'écosystème à l'étude. Ces espèces devraient donc être prioritaires pour la surveillance et pourraient servir de pierres angulaires à la définition des mesures de gestion à prendre (ex. pour calculer la réduction de la mortalité par pêche nécessaire pour atteindre les objectifs de conservation prédéfinis) et pour l'évaluation de leur efficacité.

Les effets croisés de la pêche artisanale et de loisir ont été étudiés et ont montré que les HTLP étaient pour la plupart menacés par la pêche récréative. Cette dernière a également l'effet le plus important sur le réseau trophique. L'écosystème n'a pas encore atteint sa capacité de charge pour les HTLP : leur biomasse pourrait encore augmenter de 44%, confirmant la forte sensibilité de ce groupe à la pêche et donc aussi aux mesures de protection. En outre, selon les résultats du modèle, des mesures visant à interdire la pêche récréative bénéficieraient l'écosystème non seulement en augmentant la biomasse de HTLP (24%), mais également en augmentant le niveau trophique moyen (et donc la qualité) des captures de la pêche artisanale. La pêche artisanale à elle seule réduit la biomasse de HTLP de moins de 15% et pourrait donc être maintenue avec un impact modéré sur l'écosystème.

Dans l'ensemble, des indications utiles pour la gestion de l'AMP découlent de cette étude : une limitation de l'effort de pêche récréative, par exemple, permettrait à l'AMP de poursuivre ses objectifs à la fois de conservation et de développement socioéconomique par i) la réduction de l'impact sur les HTLP, favorisant ainsi leur restauration au sein de l'AMP dont la capacité de charge est loin d'être atteinte, ii) l'accroissement de la disponibilité de captures à des niveaux trophiques supérieurs pour la pêche artisanale, équivalant alors à des avantages économiques pour cette activité de pêche traditionnelle naturellement en déclin.

Malgré les incertitudes associées à certaines données initiales en termes de biomasse ou de pêche, l'analyse de sensibilité réalisée à l'aide des routines développées récemment (la boîte à outils Data-Reli, Lassalle et al. 2014 et les règles de pré-équilibrage, Link 2010) et la comparaison de modèles alternatifs avec des données d'entrée variables, a permis d'accroître la confiance dans les résultats du modèle.

La modélisation du réseau trophique associé à la réserve de pêche du Cap Roux (chapitre 7) a également permis d'identifier les HTLP (les groupes Amberjack & dentex + et Epinephelus marginatus) ainsi que les céphalopodes comme groupes clés dans l'écosystème, soulignant en outre la nécessité d'un suivi de ces espèces. Aucune donnée biologique n'était disponible sur la zone, donc les données de biomasse ont été recueillies sur le terrain, focalisant en priorité sur les groupes fonctionnels identifiés dans le chapitre 5 et pour lesquels des données de biomasse imprécises peuvent largement influer les sorties du modèle. L'analyse des coûts associés et des efforts d'échantillonnage nécessaires au processus de construction du modèle a permis d'identifier comment il serait souhaitable d'investir pour augmenter la qualité du modèle de façon économiquement efficace. Au lieu de concentrer les efforts et les ressources sur l'échantillonnage de la macrofaune, par exemple, au moins dans un premier temps, il serait plus judicieux d'investir dans l'échantillonnage des HTLP, mais aussi des décapodes et des céphalopodes. Les deux derniers groupes sont très rarement inclus dans les programmes de surveillance des AMP, en dépit de leur importance écologique et économique en tant qu'espèces cibles de la pêche artisanale et récréative (Piatkowski et al., 2001, Goñi et al. 2006, Wagner 2008). Il serait donc intéressant de mettre en place des programmes de suivis appropriés pour ces groupes, ce qui permettrait des évaluations plus complètes des effets de la protection, tout en fournissant des données précieuses pour la modélisation. Sans compter l'échantillonnage de la macrofaune, l'estimation moyenne des coûts de développement du modèle pour une superficie de 145 ha s'élève à 26 700 €, comprenant la collecte de données sur le terrain pour les poissons et les méga-invertébrés mobiles (décapodes, céphalopodes et échinodermes), l'analyse des données et la construction du modèle. Si des programmes de suivis sont déjà en place dans une AMP et que des données sont déjà disponibles, la construction d'un modèle (incluant l'intégration et l'analyse des données) ne représenterait alors qu'un investissement de 4 200 € ca, soit moins de 1/6ème du montant précédent.

#### 8.3 Synthèse et perspectives

#### Rendre les modèles de réseau trophique opérationnels au sein des AMP

En proposant une structure standard de modèle et en identifiant les groupes les plus sensibles pour lesquels des données locales de biomasse doivent être recueillies en priorité (chapitre 5), nous avons cherché à simplifier le processus de développement des modèles et à favoriser leur utilisation au sein des AMP. Cependant, d'autres sources d'incertitude n'ont pas été abordées dans ce manuscrit. Lors de l'analyse critique de la littérature sur les modèles méditerranéens (chapitre 5), nous avons constaté que non seulement la biomasse est rarement estimée localement, mais aussi que d'autres paramètres d'entrée requis proviennent souvent de la littérature, en particulier le régime alimentaire, ou le rapport P/B et Q/B pour les groupes d'invertébrés. Les études locales fournissant des estimations pour ces paramètres sont en effet très rares, ce qui se traduit souvent par un référencement circulaire entre modèles, entraînant finalement le recours à une référence qui se rapporte initialement à une période de temps et/ou un écosystème complètement différent. Ces données d'entrée incertaines pourraient biaiser les estimations de biomasse des groupes pour lesquels des données locales ne sont pas disponibles ou ne peuvent pas être mesurées sur le terrain, et qui ont ainsi été obtenues à partir des équations de bilan de masse du modèle (Morissette 2007, Lassalle et al. 2014). Par exemple, dans le chapitre 7, nous avons souligné que les données recueillies sur le terrain pour certains groupes (macrofaune, céphalopodes et décapodes) n'étaient pas réalistes pour alimenter le modèle. Un effort d'échantillonnage supplémentaire aurait donc été nécessaire pour améliorer la qualité de ces données, mais cela avec des coûts très élevés pour certains groupes. La comparaison de nos données avec celles de la littérature a montré que dans certaines études les biomasses de macrofaune ont toujours été estimées par les modèles. De plus, dans ces études, les données de P/B, Q/B et de régime alimentaire de nombreux groupes se nourrissant de la macrofaune ont souvent été dérivées d'autres modèles, le plus souvent issus d'autres régions de la Méditerranée ou d'encore plus loin.

Il est donc primordial que les modèles soient développés avec des données locales. Ces modèles sont importants car ils permettent de mettre en évidence les incohérences éventuelles parmi ces données et peuvent servir à encourager l'amélioration des estimations. Investir sur la collecte des données et le suivi est donc nécessaire (Carstensen 2014). Cependant, il est également reconnu que l'obtention d'estimations locales pour tous les paramètres et les groupes est souvent impossible et que dans une perspective de gestion les coûts nécessaires pour améliorer la qualité des données de certains groupes peuvent être très élevés. Des solutions alternatives peuvent être : 1) simplifier et standardiser la structure des modèles et utiliser ces modèles pour identifier les groupes pour lesguels les données de biomasse doivent être obtenues de façon prioritaire en local, comme nous l'avons fait (chapitre 5); 2) élaborer une base de données pour l'ensemble de la Méditerranée avec une estimation des régimes alimentaires et des rapports P/B et Q/B la plus fiable et actualisée possible (en particulier les deux dernières variables pour les invertébrés, puisque des équations empiriques sont disponibles pour les calculer pour les poissons). Les modélisateurs pourraient donc se rapporter à cette base de données pour une version initiale de leur modèle. Christensen et al. (2009) ont fourni des lignes directrices pour développer des modèles de grands écosystèmes marins en utilisant pour les paramètres d'entrée des valeurs par défaut tirées de bases de données. Ils ont d'un côté suggéré d'utiliser cette approche pour développer une version initiale du modèle avant de l'améliorer en raison d'une facilitation des différents processus de modélisation; ils ont toutefois mis en garde contre l'utilisation de tels modèles dans le cas d'une politique de gestion. Dans ce dernier cas, ils ont souligné que les modèles devraient alors être enrichis avec autant des données locales que possible. Dans le cas des modèles développés pour des AMP de petite taille en Méditerranée, des données à haute résolution sont donc essentielles. Cependant, une base de données méditerranéenne qui serait utilisée comme référence commune pour les paramètres critiques (probablement très peu disponibles localement) pourrait aider à normaliser davantage le processus de développement d'un modèle et permettrait aussi d'isoler certaines des sources d'incertitude liées aux données d'entrée, tout en augmentant éventuellement la comparabilité entre modèles. Si, par exemple, dans chaque modèle d'AMP développé avec une structure standard, les données de P/B, Q/B et de régime alimentaire sont obtenues à partir d'une source commune, lorsque les modèles seront comparés les éventuelles différences de biomasse des groupes estimés seraient plus probablement dues à des caractéristiques environnementales ou de gestion, spécifiques à chaque AMP, plutôt qu'à un biais dans la structure et les paramètres du modèle. Une base de données méditerranéenne pour ces paramètres pourrait aussi largement simplifier le processus de construction du modèle, en évitant une perte certaine de temps passé à intégrer et transformer des données provenant de différentes sources. Ceci permettrait un gain de temps certain, et donc d'efficacité, dans une perspective de gestion.

## La complémentarité des approches suivi de terrain et modélisation

Le suivi est un outil de gestion essentiel per-se, permettant d'évaluer si les AMP atteignent les objectifs pour lesquels elles ont été conçues, en détectant les changements dans l'abondance et les taux de croissance des espèces et des communautés d'intérêt et donc de juger dans guelle mesure une réserve atteint son objectif d'amélioration de la pêche locale. Mais les données issues des suivis peuvent également permettre de combler le fossé entre l'écologie de terrain et la modélisation. D'une part, les données de suivis peuvent alimenter des modèles du réseau trophique, nécessaires pour aborder des guestions que les seules études de terrain ne peuvent pas traiter. D'autre part, les modèles trophiques peuvent aider à identifier des cibles prioritaires à suivre et à mettre en lumière des lacunes ou des incohérences dans les données locales. Ils peuvent ainsi réorienter les suivis avec, en retour, une nouvelle traduction en mesures de gestion plus adaptées. Les modèles développés dans notre étude par exemple, qu'ils soient construits avec des données nouvellement recueillies (chapitre 7) ou avec des données de suivis préexistants (chapitre 5 et 6), ont souligné le rôle-clé des prédateurs de haut niveau trophique dans les écosystèmes de zones protégées (Valls et al. 2015). Cela a en outre mis en relief l'importance des suivis de HTLP et permis d'obtenir des estimations plus précises de leur abondance et de leur biomasse dans les AMP grâce à des techniques non destructives appropriées (chapitre 4). En outre, dans toutes les études de cas présentées, les modèles de réseau trophique reconnaissaient également un rôle clé aux céphalopodes, alors qu'ils sont souvent (ou totalement) négligés lors de la conception des stratégies de suivis en Méditerranée. Les céphalopodes jouent un rôle fonctionnel important dans les écosystèmes côtiers et pélagiques (Piatkowski et al., 2001, Coll et al. 2013), comme proie privilégiée pour de nombreux prédateurs de niveau trophique supérieur, mais aussi comme prédateurs agissant sur un large éventail de niveaux trophiques. Ils sont par ailleurs des cibles économiquement importantes de la pêche artisanale et récréative. Des suivis devraient être mis en œuvre impérativement pour évaluer leur abondance et biomasse dans les zones côtières, après identification de techniques non destructives appropriées. Les pressions de pêche sur ce groupe pourraient alors être régulièrement contrôlées.

Enfin, la modélisation peut s'appuyer sur et mettre à profit les données de suivis pour élaborer des indicateurs à l'échelle de l'écosystème, tels que les indicateurs de réseau trophique. Ceux-ci sont en effet requis par la directive-cadre sur la stratégie du milieu marin, afin de parvenir à un bon état écologique (Good Ecological Status) (Heymans et al. 2014, Guesnet et al. 2015). Dans cette perspective, les AMP et les modèles correspondants pourraient être très utiles pour définir des seuils pour les indicateurs et pour proposer des valeurs de référence correspondant à différents états de conservation. Les indicateurs fondés sur les niveaux trophiques, par exemple, sont de plus en plus utilisés pour évaluer l'impact de la pêche sur l'ensemble de l'écosystème (Shannon et al. 2014). La modélisation peut servir à générer des valeurs de référence pour les indicateurs à travers des simulations dynamiques. Cela nécessiterait des très longues séries temporelles si seules les données de suivis sont utilisées (Pelletier et al., 2008). Dans cette perspective, un nouveau développement à notre étude pourrait être l'application des indicateurs proposés récemment comme l'Apex Predator Indicateur (API) et le High Trophic Indicator (HTI) (Bourdaud et al. 2015). Ces deux indicateurs sont fondés sur les niveaux trophiques, et en particulier sur la proportion des prédateurs apicaux et/ou de niveaux trophiques supérieurs dans l'écosystème, utilisés comme proxy du bon fonctionnement de l'ensemble du réseau trophique. Des objectifs spécifiques à l'écosystème pourraient donc être proposés pour chaque indicateur par simulation (Bourdaud et al. 2015).

# <u>Perspectives sur les modèles du réseau trophique comme outils de gestion</u> <u>écosystémiques opérationnels dans les AMP</u>

Sur la base des données collectées, complétées par des analyses de sensibilité approfondies, nous avons démontré le potentiel des modèles de réseau trophique en termes d'outils de gestion des AMP pour i) identifier les espèces clés et sentinelles de l'écosystème ii) mettre en évidence la capacité de charge possible de l'AMP pour les HTLP, iii) analyser les conséquences des variations de biomasse des HTLP dans le réseau trophique iv) recommander une réduction de l'effort de pêche récréative sur les HTLP et évaluer l'impact de la pêche récréative sur la pêche artisanale.

Si 1) des programmes de suivi exhaustifs sont mis en œuvre dans les AMP, ciblant à la fois les ressources biologiques, mais aussi et surtout, les impacts humains (captures et effort des pêcheries locales) et si 2) la modélisation du réseau trophique devient une étape régulière pour intégrer les données des suivis, la gamme des applications de gestion possibles des modèles trophiques développés avec l'ensemble EwE-EcoTroph-Ecospace est extrêmement large, et en expansion

continue (Coll et al 2015). Quelques applications possibles sont données ici à titre de perspectives.

La propagation des espèces envahissantes en Méditerranée est largement reconnue comme une grave menace pour la biodiversité et le fonctionnement de l'écosystème et pour la fourniture de services écosystémiques (Katsanevakis et al. 2014). Les modèles trophiques pourraient aider à aborder ce problème pour mieux comprendre le rôle des espèces envahissantes et leur impact sur le réseau trophique et analyser des scénarios de gestion (Arias-González et al., 2011). Bien que l'intérêt de cette approche soit en pleine croissance (Coll et al . 2015), les applications en Méditerranée sont encore rares.

Les modèles EwE-EcoTroph ont été utilisés dans quelques études pour évaluer l'export de biomasse à partir des AMP (Valls et al. 2012, Colleter et al. 2014) et, dans une étude, pour quantifier la contribution d'une AMP au fonctionnement et à la productivité trophique de l'écosystème environnant (Guénette et al. 2014). Les AMP sont souvent très petites en Méditerranée, il pourrait donc être intéressant d'évaluer si l'extension de leurs frontières permettrait d'accroître leur contribution en termes d'export aux systèmes adjacents et à la production totale ou en termes de captures dans les écosystèmes environnants. D'ailleurs, à travers les modules dynamiques Ecosim et Ecospace, il est possible d'explorer les effets potentiels des scénarios de gestion alternative de la pêche (et aussi du changement climatique) sur la structure de l'écosystème et sur la production de la pêche, de modéliser les échanges d'énergie à partir des AMP vers les zones externes et de quantifier l'impact des AMP sur les écosystèmes plus vastes. Enfin, si plusieurs modèles de réseau trophique sont développés dans plusieurs AMP, une analyse à grande échelle pourrait être effectuée avec Ecospace pour évaluer les effets des différentes configurations spatiales de réseaux d'AMP et / ou de différents scénarios de gestion des pêches sur la structure et le fonctionnement de l'écosystème et sur la production par pêche.

Afin d'exploiter pleinement ce potentiel élevé, les AMP devraient commencer à intégrer la modélisation du réseau trophique comme un outil régulier dans leur plan de gestion, en l'utilisant en premier lieu pour mieux orienter les suivis et intégrer les données en une image cohérente du fonctionnement de l'écosystème pour ensuite, une fois cette base fiable disponible, optimiser et améliorer cette image en fonction des besoins de gestion.

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# 9 References

- Abdulla A, Gomei M, Maison E, Piante C (2008) Status of marine protected areas in the Mediterranean Sea. IUCN, Malaga and WWF, FranceBabcock RC, Shears NT, Alcala AC, Barrett NS, Edgar GJ, Lafferty KD, McClanahan TR, Russ GR (2010) Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. PNAS 107:18256–18261
- Arias-González JE, González-Gándara C, Cabrera JL, Christensen V (2011) Predicted impact of the invasive lionfish Pterois volitans on the food web of a Caribbean coral reef. Environ Res 111:917–925
- Bascompte J, Melián CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. PNAS 102:5443–5447
- Bourdaud P, Gascuel D, Bentorcha A, Brind'Amour A (2015) New trophic indicators and target values for an ecosystem-based management of fisheries. Ecol Indic
- Bozec Y-M, Kulbicki M, Laloë F, Mou-Tham G, Gascuel D (2011) Factors affecting the detection distances of reef fish: implications for visual counts. Mar Biol 158:969–981
- Britten GL, Dowd M, Minto C, Ferretti F, Boero F, Lotze HK (2014) Predator decline leads to decreased stability in a coastal fish community. Ecology Letters 17:1518–1525
- Carstensen J (2014) Need for monitoring and maintaining sustainable marine ecosystem services. Front Mar Sci 1:33
- Cheal AJ, Thompson AA (1997) Comparing visual counts of coral reef fish: implications of transect width and species selection. Mar Ecol Prog Ser 158:241–248
- Christensen V, Pauly D (1992) Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological modelling 61:169–185
- Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological modelling 172:109–139
- Christensen V, Walters CJ, Ahrens R, Alder J, Buszowski J, Christensen LB, Cheung WWL, Dunne J, Froese R, Karpouzi V (2009) Database-driven models of the world's Large Marine Ecosystems. Ecol Model 220:1984– 1996
- Coll M, Akoglu E, Arreguín-Sánchez F, Fulton EA, Gascuel D, Heymans JJ, Libralato S, Mackinson S, Palomera I, Piroddi C, others (2015) Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. Rev Fish Biol Fish 25:413–424
- Coll M, Libralato S (2012) Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish and Fisheries 13:60–88

- Coll M, Lotze HK, Romanuk TN (2008) Structural degradation in Mediterranean Sea food webs: testing ecological hypotheses using stochastic and massbalance modelling. Ecosystems 11:939–960
- Coll M, Navarro J, Olson RJ, Christensen V (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep Sea Res Part II Top Stud Oceanogr 95:21–36
- Colléter M, Valls A, Guitton J, Gascuel D, Pauly D, Christensen V (2015) Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecological Modelling 302:42–53
- Colloca F, Cardinale M, Maynou F, Giannoulaki M, Scarcella G, Jenko K, Bellido JM, Fiorentino F (2013) Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish and Fisheries 14:89–109
- Dudley N, Stolton S (2008). Defining protected areas: an international conference in Almeria, Spain. Gland, Switzerland: IUCN. 220pp.
- Duffy JE (2002) Biodiversity and ecosystem function: the consumer connection. Oikos 99:201–219
- Espinoza-Tenorio A, Wolff M, Taylor MH, Espejel I (2012) What model suits ecosystem-based fisheries management? A plea for a structured modeling process. Reviews in Fish Biology and Fisheries 22:81–94
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soule ME, Virtanen R, Wardle DA (2011) Trophic Downgrading of Planet Earth. Science 333:301–306
- Fulton EA, Bax NJ, Bustamante RH, Dambacher JM, Dichmont C, Dunstan PK, Hayes KR, Hobday AJ, Pitcher R, Plagányi ÉE, Punt AE, Savina-Rolland M, Smith ADM, Smith DC (2015) Modelling marine protected areas: insights and hurdles. Philosophical Transactions of the Royal Society B: Biological Sciences 370:20140278
- Garcia-Rubies A, Hereu B, Zabala M (2013) Long-Term Recovery Patterns and Limited Spillover of Large Predatory Fish in a Mediterranean MPA. PLoS ONE 8
- Gascuel D, Coll M, Fox C, Guénette S, Guitton J, Kenny A, Knittweis L, Nielsen JR, Piet G, Raid T, Travers-Trolet M, Shephard S (2014) Fishing impact and environmental status in European seas: a diagnosis from stock assessments and ecosystem indicators. Fish and Fisheries
- Gascuel D, Guénette S, Pauly D (2011) The trophic-level-based ecosystem modelling approach: theoretical overview and practical uses. ICES J Mar Sci 68:1403–1416
- Gascuel D, Pauly D (2009) EcoTroph: modelling marine ecosystem functioning and impact of fishing. Ecological Modelling 220:2885–2898
- Goñi R, Quetglas A, Renones O (2006) Spillover of spiny lobsters Palinurus elephas from a marine reserve to an adjoining fishery. Mar Ecol Prog Ser 308:207–219
- Guénette S, Meissa B, Gascuel D (2014) Assessing the Contribution of Marine Protected Areas to the Trophic Functioning of Ecosystems: A Model for the Banc d'Arguin and the Mauritanian Shelf. PloS One 9:e94742
- Guesnet V, Lassalle G, Chaalali A, Kearney K, Saint-Béat B, Karimi B, Grami B, Tecchio S, Niquil N, Lobry J (2015) Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. Ecol Model 313:29–40
- Guidetti P (2007) Predator diversity and density affect levels of predation upon strongly interactive species in temperate rocky reefs. Oecologia 154:513– 520
- Guidetti P, Baiata P, Ballesteros E, Di Franco A, Hereu B, Macpherson E, Micheli F, Pais A, Panzalis P, Rosenberg AA, Zabala M, Sala E (2014) Large-Scale Assessment of Mediterranean Marine Protected Areas Effects on Fish Assemblages. PLoS ONE 9:e91841
- Guidetti P, Micheli F (2011) Ancient art serving marine conservation. Frontiers in Ecology and the Environment 9:374–375
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. Ecology letters 5:361–366
- Harmelin-Vivien M, Harmelin J, Chauvet C, Duval C, Galzin R, Lejeune P, Barnabé G, Blanc F, Chevalier R, Duclerc J (1985) Evaluation visuelle des peuplements et populations de poissons: méthodes et problèmes. Rev Décologie 40:467–539
- Heymans JJ, Coll M, Libralato S, Morissette L, Christensen V (2014) Global Patterns in Ecological Indicators of Marine Food Webs: A Modelling Approach. PLoS ONE 9:e95845
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA (2001) Historical overfishing and the recent collapse of coastal ecosystems. science 293:629–637
- Jørgensen SE, Patten BC, Straškraba M (2000) Ecosystems emerging:4. Growth. Ecological Modelling 126:249–284
- Katsanevakis S, Coll M, Piroddi C, Steenbeek J, Ben Rais Lasram F, Zenetos A, Cardoso AC (2014) Invading the Mediterranean Sea: biodiversity patterns shaped by human activities. Marine Ecosystem Ecology 1:32
- Kulbicki M (1998) How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. J Exp Mar Biol Ecol 222:11–30
- Lassalle G, Bourdaud P, Saint-Béat B, Rochette S, Niquil N (2014) A toolbox to evaluate data reliability for whole-ecosystem models: Application on the Bay of Biscay continental shelf food-web model. Ecol Model 285:13–21
- Lester SE, Halpern BS, Grorud-Colvert K, Lubchenco J, Ruttenberg BI, Gaines SD, Airamé S, Warner RR (2009) Biological effects within no-take marine reserves: a global synthesis. Marine Ecology Progress Series 384:33–46
- Libralato S, Coll M, Tempesta M, Santojanni A, Spoto M, Palomera I, Arneri E, Solidoro C (2010) Food-web traits of protected and exploited areas of the Adriatic Sea. Biological Conservation 143:2182–2194

- Link JS (2010) Adding rigor to ecological network models by evaluating a set of prebalance diagnostics: A plea for PREBAL. Ecol Model 221:1580–1591
- Lubchenco J, Palumbi SR, Gaines SD, Andelman S (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecological applications 13:3–7Menge BA (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecological monographs 65:21–74
- Morissette L (2007) Complexity, cost and quality of ecosystem models and their impact on resilience. PhD diss. University of British Columbia
- Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Osio GC, Romano F (2005) Cascading human impacts, marine protected areas, and the structure of Mediterranean reef assemblages. Ecological Monographs 75:81–102
- Micheli F, Halpern BS, Botsford LW, Warner RR (2004) Trajectories and correlates of community change in no-take marine reserves. Ecological Applications 14:1709–1723Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Philosophical Transactions of the Royal Society B: Biological Sciences 360:13–20
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr F (1998) Fishing down marine food webs. Science 279:860–863
- Pelletier D, Claudet J, Ferraris J, Benedetti-Cecchi L, Garcìa-Charton JA (2008) Models and indicators for assessing conservation and fisheries-related effects of marine protected areas. Canadian Journal of Fisheries and Aquatic Sciences 65:765–779
- Plagányi E, Ellis N, Blamey L, Morello E, Norman-Lopez A, Robinson W, Sporcic M, Sweatman H (2014) Ecosystem modelling provides clues to understanding ecological tipping points. Marine Ecology Progress Series 512:99–113
- Piatkowski U, Pierce GJ, Morais da Cunha M (2001) Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. Fish Res 52:5–10
- Prato G, Guidetti P, Bartolini F, Mangialajo L, Francour P (2013) The importance of high-level predators in marine protected area management: Consequences of their decline and their potential recovery in the Mediterranean context. Advances in Oceanography and Limnology 4:176– 193
- Odum EP (1969) The strategy of ecosystem development. Science 164:262–270
- Ray J, Redford KH, Steneck R, Berger J (2005) Large Carnivores and the Conservation of Biodiversity. Island Press, Washington
- Sala E (2004) The past and present topology and structure of Mediterranean subtidal rocky-shore food webs. Ecosystems 7:333–340
- Sala E, Ballesteros E, Dendrinos P, Di Franco A, Ferretti F, Foley D, Fraschetti S, Friedlander A, Garrabou J, Guclusoy H, Guidetti P, Halpern BS, Hereu B, Karamanlidis AA, Kizilkaya Z, Macpherson E, Mangialajo L, Mariani S, Micheli F, Pais A, Riser K, Rosenberg AA, Sales M, Selkoe KA, Starr R, Tomas F, Zabala M (2012) The Structure of Mediterranean Rocky Reef

Ecosystems across Environmental and Human Gradients, and Conservation Implications. Plos One 7:e32742

- Sala E, Boudouresque CF, Harmelin-Vivien M (1998) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos:425–439
- Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D (2008) Baselines and degradation of coral reefs in the northern Line Islands. PLoS One 3:e1548
- Shannon L, Coll M, Shin Y, others (2014) Trophic level-based indicators to track fishing impacts across marine ecosystems. Mar Ecol Prog Ser 512:115–140
- Soler GA, Edgar GJ, Thomson RJ, Kininmonth S, Campbell SJ, Dawson TP, Barrett NS, Bernard ATF, Galván DE, Willis TJ, Alexander TJ, Stuart-Smith RD (2015) Reef Fishes at All Trophic Levels Respond Positively to Effective Marine Protected Areas. PLOS ONE 10:e0140270
- Stevenson C, Katz LS, Micheli F, Block B, Heiman KW, Perle C, Weng K, Dunbar R, Witting J (2007) High apex predator biomass on remote Pacific islands. Coral Reefs 26:47–51
- Valls A, Coll M, Christensen V (2015) Keystone species: toward an operational concept for marine biodiversity conservation. Ecological Monographs 85:29–47
- Valls A, Gascuel D, Guénette S, Francour P (2012) Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. Mar Ecol Prog Ser 456:201–214
- Wagner HP (2008) Lobsters: biology, management, aquaculture and fisheries. Crustaceana 81:381–381

## The Book of Marine Protected Areas.

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This short movie wants to tell the story of depletion of the Mediterranean Sea following the increase of human population and fish demand. The overexploitation of larger predators and the fishing down the food web caused ecosystem shifts in many coastal areas, where important macroalgal habitats were replaced by marine deserts overgrazed by sea urchins. A succession of drawings that come to life in videos show how marine protected areas where the collaboration among managers, stakeholders and scientists is achieved represent one of the best solutions to prevent and sometimes reverse this negative trend and restore our sea.