

# Accepted Manuscript

Ecosystem structure and fishing impacts in the northwestern Mediterranean Sea using a food web model within a comparative approach

Xavier Corrales, Marta Coll, Samuele Tecchio, José María Bellido, Ángel Mario Fernández, Isabel Palomera

PII: S0924-7963(15)00054-8  
DOI: doi: [10.1016/j.jmarsys.2015.03.006](https://doi.org/10.1016/j.jmarsys.2015.03.006)  
Reference: MARSYS 2692

To appear in: *Journal of Marine Systems*

Received date: 13 May 2014  
Revised date: 4 March 2015  
Accepted date: 15 March 2015



Please cite this article as: Corrales, Xavier, Coll, Marta, Tecchio, Samuele, Bellido, José María, Fernández, Ángel Mario, Palomera, Isabel, Ecosystem structure and fishing impacts in the northwestern Mediterranean Sea using a food web model within a comparative approach, *Journal of Marine Systems* (2015), doi: [10.1016/j.jmarsys.2015.03.006](https://doi.org/10.1016/j.jmarsys.2015.03.006)

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

**To be resubmitted to the Journal of Marine Systems**

**Ecosystem structure and fishing impacts in the northwestern Mediterranean Sea using a food web model within a comparative approach**

Xavier Corrales<sup>a,b\*</sup>, Marta Coll<sup>a,c,d</sup>, Samuele Tecchio<sup>a,e</sup>, José María Bellido<sup>f,g</sup>, Ángel Mario Fernández<sup>f</sup>, Isabel Palomera<sup>a,c</sup>

- a. Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta, nº 37-49. 08003. Barcelona, Spain.
- b. Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. P.O. Box 447, Migdal 14950, Israel.
- c. Ecopath International Initiative Research Association, Barcelona, Spain.
- d. Institut de Reserche pour le Développement, UMR EME 212. Centre de Reserche Halieutique Méditerranéenne et tropicale. Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France.
- e. Normandie Université UNICAEN, UMR BOREA (MNHN, UPMC, CNRS-7208, IRD-207), Esplanade de la Paix, 14032 Caen CEDEX 5, France
- f. Instituto Español de Oceanografía (IEO). Centro Oceanográfico de Murcia. Murcia, Spain.
- g. School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, AB24 2TZ Aberdeen, Scotland, UK.

\*Corresponding author: Xavier Corrales

Present address: Kinneret Limnological Laboratory, Israel Oceanographic & Limnological Research. P.O. Box 447, Migdal 14950, Israel. + 972 4 6721444  
E-mail address: corrales@icm.csic.es; xcrportbou@gmail.com

**Abstract**

We developed an ecological model to characterize the structure and functioning of the marine continental shelf and slope area of the northwestern Mediterranean Sea, from Toulon to Cape La Nao (NWM model), in the early 2000s. The model included previously modeled areas in the NW Mediterranean (the Gulf of Lions and the Southern Catalan Sea) and expanded their ranges, covering 45547 km<sup>2</sup>, with depths from 0 to 1000 m. The study area was chosen to specifically account for the connectivity between the areas and shared fish stocks and fleets.

Input data were based on local scientific surveys and fishing statistics, published data on stomach content analyses, and the application of empirical equations to estimate consumption and production rates. The model was composed of 54 functional groups, from primary producers to top predators, and Spanish and French fishing fleets were considered. Results were analyzed using ecological indicators and compared with outputs from ecosystem models developed in the Mediterranean Sea and the Gulf of Cadiz prior to this study.

Results showed that the main trophic flows were associated with detritus, phytoplankton, zooplankton and benthic invertebrates. Several high trophic level organisms (such as dolphins, benthopelagic cephalopods, large demersal fishes from the continental shelf, and other large pelagic fishes), and the herbivorous salema fish, were identified as keystone groups within the ecosystem. Results confirmed that fishing impact was high and widespread throughout the food web. The comparative approach highlighted that, despite productivity differences, the ecosystems shared common features in structure and functioning traits such as the important role of detritus, the dominance of the pelagic fraction in terms of flows and the importance of benthic-pelagic coupling.

**Keywords:** northwestern Mediterranean Sea, Ecopath model, mass-balance model, fishing impacts, Ecosystem Approach to Fisheries, comparative approach.

## 1. Introduction

Global marine catches increased from the 1950s to a maximum of 90 million tonnes at the end of the 1980s. For many years, the total reported global landings have stagnated at around 80 million tonnes per year (FAO, 2012), with another 20 million tonnes of additional illegal/unreported catch (Agnew et al., 2009). This stagnation has occurred despite increased fishing efforts and efficiency, and the geographic and bathymetric expansion of fishing activities (Pauly and Palomares, 2010; Swartz et al., 2010; Watson et al., 2013; Watson and Morato, 2013). The overall limits of sustainable exploitation have long been exceeded (Pitcher and Cheung, 2013; Worm and Branch, 2012).

The Mediterranean Sea has been strongly influenced by human activities since ancient times (Lotze et al., 2011). However, since the industrial revolution these impacts have grown exponentially due to technological improvements in fishing fleets and the demographic explosion in the area (Lotze et al., 2011). The high impact of fishing is evidenced by several stock assessments, indicating that most demersal and pelagic stocks are fully exploited or overexploited (Colloca et al., 2013; GFCM, 2013). In addition, the Mediterranean Sea has been altered by other human effects such as habitat loss and degradation, pollution, climate change, eutrophication, aquaculture and the introduction of alien species (Coll et al., 2012; Coll et al., 2010).

The current situation of exploited resources and marine ecosystems shows that management based on single species, the dominant in the last 50 years, has not been sufficient to ensure the proper management of exploited resources. Therefore, there is a pressing need to move towards an Ecosystem-based Approach to Fisheries (EAF) (Cochrane and de Young, 2008; Garcia et al., 2003).

The EAF framework has aroused a great interest among the scientific community and new tools have been developed in recent decades, including ecological models and ecological indicators (Link, 2011; Plagányi, 2007). These tools provide a framework for integrating ecological and ecosystem issues into management programs by assessing, for example, the impacts of interactions between species and fisheries and their implications in marine fisheries management.

In the Mediterranean Sea, several ecological models using the *Ecopath with Ecosim* approach (EwE) (Christensen and Walters, 2004) have been developed (Coll and

Libralato, 2012). These models have been used for a diversity of applications such as analysing fishing impacts (Coll et al., 2006a; Coll et al., 2007), comparing ecosystem structure and functioning traits (Hattab et al., 2013; Tsagarakis et al., 2010), exploring management options (Fouzai et al., 2012), assessing the impact of aquaculture (Forestal et al., 2012), evaluating the effects of the environment (Coll et al., 2008; Piroddi et al., 2010) and exploring the effects of invasive species in the food web (Daskalov, 2002).

The NW Mediterranean Sea is exploited by French and Spanish fleets and is one of the most impacted regions in the basin (Coll et al., 2012; Micheli et al., 2013). Previous ecosystem models developed in the study area indicated intense exploitation of the marine ecosystem (Banaru et al., 2013; Coll et al., 2006a) and changes in the trophic structure of the ecosystem (Coll et al., 2008).

In this study, we developed a food web model in a large area of the NW Mediterranean Sea including the Gulf of Lions and part of the Balearic Sea. Previously, various smaller models were developed in this area (Banaru et al., 2013; Coll et al., 2006a), but the new model includes a larger area considering important hydrodynamic events that enhance the connectivity between the two regions. Also included were several submarine canyons of the area, which are mainly located in the Gulf of Lions and the northern part of the Balearic Sea. These canyons play an important ecological role and are associated with important fishing activities (Würtz, 2012). From a fisheries point of view, there are also some 'shared stocks' in the area, which motivated the development of the larger model. Shared stocks include the important commercial populations of hake (*Merluccius merluccius*) and anchovy (*Engraulis encrasicolus*).

With this new modeling effort we aimed to develop a useful modeling tool to contribute to the fisheries management in the region through an ecosystem approach. In this study, we present the new ecological model and use it to update previous knowledge of the area by:

- a) Characterizing the structure and functioning of the ecosystem during the early 2000s;
  - b) Assessing the impact of fishing activity on the ecosystem using ecological indicators;
- and
- c) Comparing the results with other food web models developed in several areas of the Mediterranean Sea and adjacent waters of the Gulf of Cadiz.

## 2. Material and methods

### 2.1. Study area and period

Despite the fact that the Mediterranean Sea is considered an oligotrophic region, the NW Mediterranean is a rather productive area (Bosc et al., 2004; Estrada, 1996). This is due to the upwelling activity influenced by wind conditions and the fresh water inputs from the Rhone and Ebro Rivers (Agostini and Bakun, 2002; Salat, 1996). General marine circulation is characterized by the presence of the wide Northern current running along the continental slope from the Ligurian Sea to the continental shelf of the Balearic Sea (Millot, 1999).

Several parts of the area have been identified as important ecological habitats, and spawning and nursery areas, for small pelagic and demersal fish (Lleonart et al., 2008; Palomera et al., 2007). Moreover, this area is home to abundant seabird colonies, such as in the Gulf of Lions and the Ebro Delta (Arcos et al., 2009; Cadiou et al., 2004). Several species of mammals and sea turtles are also present in the area (Gómez de Segura et al., 2006a; Gómez de Segura et al., 2006b).

Mediterranean fisheries are characterized by multi-specificity (targeting a variety of fish and invertebrate species), particularly in the demersal regime, and use of a large number of landing sites (Lleonart and Maynou, 2003). Catches are landed on a daily basis and are made near the coast, on the continental shelf down to the mid-continental slope. Three different types of fleets can be identified: artisanal, industrial and semi-industrial (Farrugio and Papaconstantinou, 1998). Although the artisanal fleet is still important, the most important fleets are semi-industrial and industrial, composed of bottom trawlers, purse seiners and longliners, and include the tuna fishery (Lleonart and Maynou, 2003).

This study includes the Gulf of Lions and part of the Balearic Sea, specifically the continental shelf and upper slope from Toulon (France) to Cabo de la Nao (Spain) (Fig. 1). The NW Mediterranean Sea model (NWM model) represents the early 2000s and covers an area of 45.547 km<sup>2</sup>, with depths from 0 to 1000 m.

The selection of the bathymetry in the model is justified for fishery and biological reasons. The limit of 0-50 m represents an important feeding area for most species or functional groups and is essential for the inclusion in the model of *Posidonia oceanica*,

macrophytes and microphytobenthos, and the artisanal fleet. The limit of 1000 m is the boundary at which bottom trawling fleet is allowed to operate (Regulation EC 1967/2006).

The northern and southern boundaries are justified because part of the northern Catalonia (Spain) fishing fleets exploits the fishing resources in the Gulf of Lions (Aldebert et al., 1993; Leonart et al., 2008), resulting in a number of shared stocks, as is the case of hake and anchovy. The hydrodynamic events in the region indicate connectivity between the Gulf of Lions and the Balearic Sea, due to the general southward circulation mainly illustrated by anchovy larvae transport (Ospina-Alvarez et al., 2012; Sabatés et al., 2001). The model does not include the Balearic Islands as this area has different ecological and fisheries features (Quetglas et al., 2012) and is considered another GSA (Geographical Sub-Areas) for management purposes by the General Fisheries Commission for the Mediterranean (GFCM).

## 2.2. Modeling approach

The food web model of the NWM was constructed using the *Ecopath with Ecosim* (EwE) software version 6.3 (Christensen and Walters, 2004; Christensen et al., 2008). We used the static Ecopath model that provides a “snapshot” of the trophic flows in the ecosystem during a specific period. The Ecopath model is parameterized with two master equations for each functional group or “box” in the model: one describes the biological production and the other describes the energy balance. A functional group consists of ontogenic fractions of a species, single species or groups of species sharing common ecological traits such as habitat or feeding (Christensen et al., 2008).

The first equation of the production of each functional group (i) is:

$$P_i = \sum_j B_j \cdot M2_{ij} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \quad \text{Eq. (1)}$$

where  $M2_{ij}$  is the predation mortality caused by the biomass of the predators ( $B_j$ );  $Y_i$  are exports from the system due to fishing activity;  $E_i$  is the net migration rate (emigration – immigration);  $BA_i$  is the biomass accumulation in the ecosystem; and  $P_i \cdot (1 - EE_i)$  is other natural mortality excluding predation ( $M0$ ).  $M0$  is a catch-all term including all mortality not elsewhere included, e.g. mortality due to disease or old age. In Ecopath,  $M0$  is not entered directly, as it is unknown, but is computed from the Ecotrophic Efficiency (EE). EE is the production of group (i) that is utilized within the system or is

exported due to catches or migration (Christensen and Walters, 2004; Christensen et al., 2008).

Eq. (1) can be re-expressed as:

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum_j B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i)$$

Eq. (2)

where  $(P/B)_i$  is the production of (i) per unit of biomass and is equivalent to total mortality, or  $Z$ , in the steady-state condition (Allen, 1971);  $(Q/B)_i$  is the consumption of (i) per unit of biomass; and  $(DC_{ij})$  is the proportion of (i) in the diet composition of predator (j) in terms of biomass.

For each equation three of the four basic parameters ( $B_i$ ,  $P/B_i$ ,  $Q/B_i$ ,  $EE_i$ ) are required. Moreover, the catch by fleet and functional group ( $Y_j$ ) and the diet ( $DC_{ij}$ ) of all groups are also needed.

The energy balance within each group is ensured when the consumption by group (i) equals the production by (i), respiration by (i) and food that is unassimilated by (i). Further details on the algorithms and equations are described in Christensen and Walters (2004) and Christensen et al. (2008).

### 2.3. Functional groups and input data

The definition of the functional groups for the NWM model was based on biological and ecological characteristics of the species such as food, size, habitat and depth distribution, on the commercial importance of the species and on data availability (especially biomass, diet and catch) (Table 1). The groups were based on previously developed models in the South Catalan Sea (Coll et al., 2006a) and the Gulf of Lions (Banaru et al., 2013), and on data from the Marine Strategy Framework Directive (MSFD) of the Spanish Government (Ordines et al., 2012).

The NWM model was composed of 54 functional groups, including 3 primary producers, 17 groups of invertebrates, 27 groups of fish, 1 group of sea turtles, 1 group of seabirds, 2 groups of marine mammals and 3 groups of detritus (natural detritus, discards and by-catch of sea turtles, seabirds and cetaceans) (Table 1).



Three species were split into two multi-stanza groups: hake (adult hake, i.e. > 25 cm total length, TL, and juvenile hake, i.e.  $\leq 25$  cm TL, with a transition age of 24 months), anchovy (adult anchovy, i.e. > 11 cm TL and juvenile anchovy, i.e.  $\leq 11$  cm TL, with a transition age of 12 months), and sardine (*Sardina pilchardus*) (adult sardine, i.e. > 12 cm TL and juvenile sardine, i.e.  $\leq 12$  cm TL, with a transition age of 15 months) (Table 1).

The input parameters for the model initialization were obtained following a similar procedure as documented in Coll et al. (2006a) and Coll et al. (2007). Published and unpublished information from the Institute of Marine Science (ICM-CSIC), the Spanish Institute of Oceanographic (IEO) and the French Research Institute for Exploration of the Sea (IFREMER) in the study area and from other literature sources (see Supplement Online Information section 1 and Corrales (2013)) was collected, analyzed and integrated. Biomass was estimated using data from (1) bottom trawl surveys (swept-area method) conducted in the area (Fig. 2), which included MEDITS surveys from Spain (IEO) and France (IFREMER) and several trawl surveys conducted by the ICM in Spain for benthic, benthopelagic and demersal fish and megafaunal invertebrates; (2) acoustic surveys for small pelagic fish; (3) plankton nets (for micro- and mesozooplankton); and (4) other information available in the literature (see Supplement Online Information section 1 and Corrales (2013)). Biomass estimates were calculated first by each bathymetric stratum (Fig. 1) and a mean biomass was estimated taking into account the weight of each stratum in the total surface area. Seasonal information was used when available.

Production/biomass (P/B) and consumption/biomass (Q/B) ratios were either taken from the literature, or estimated by applying empirical equations or using assumptions from other models and corrected for temperature changes following Opitz (1996) (see Supplement Online Information section 1 and Corrales (2013)).

The diet composition matrix ( $DC_{ij}$ ) was compiled using published information on stomach content analyses from the region or ecologically-similar areas, and a database of diet information was built (references are cited in the Supplement Online Information section 1 and Corrales (2013)).

The migratory patterns of some species (Atlantic bluefin tuna (*Thunnus thynnus*), other large pelagic fishes, sea turtles, seabirds and mammals) were taken into account by

modeling a proportion of their diet compositions as imports to the ecosystem (Coll et al., 2006a; Christensen et al., 2008). The microbial food web was only indirectly considered in the model modifying the zooplankton diet and detritus dynamics as done previously (Coll et al., 2006a). To do this, the percentage of the diet of micro- and mesozooplankton belonging to the microbial food web was defined considering the results of Calbet et al. (2002) in the Alboran Sea, which generally indicates that the contribution of ciliates to the micro- and mesozooplankton diet is around 30%. This was included as part of the detritus dynamics without directly modeling this food web segment into the model. We chose this parameterization because (1) inputs for the microbial food web are scarce and difficult to estimate and (2) their flows could overshadow other trophic flows in the system (Christensen et al., 2008).

The fishing fleet was divided according to its characteristics and the area where fleets operate. The Spanish fleet was divided into bottom trawlers, purse seiners, longliners and the artisanal fleet; and the French fleet into bottom and mid-water trawlers, purse seiners and the artisanal fleet. The longline fleet, superficial and bottom, was joined in the same Spanish fleet, because the available information did not allow their distinction. A recreational fleet was included due to its importance and impact on the Mediterranean Sea (Gaudin and de Young, 2007). However, due to the scarcity of data this fleet was included only for the Spanish area.

Official landings were obtained from the statistical yearbooks of the Valencian regional government, the official dataset of the regional government of Catalonia managed by the ICM-CSIC and from the R3 report for the Gulf of Lions (Demaneche et al., 2009). Because data in the R3 report corresponds to 2007-2008, we reconstructed the catches for 2000-2003 using the evolution of catches in the Catalan region, from which we had data from 2000 to 2012. For the Atlantic bluefin tuna catch for the French fleet, we used the value from Banaru et al. (2013). Percentages of discards and recreational fisheries catch were incorporated using data from a literature review based on the Spanish Mediterranean and Gulf of Cadiz region (Coll et al., 2014) and were extrapolated for the French area. Although the socio-economic conditions of the two areas differ substantially, we assumed that it was better to apply the results of one area to the other, rather than ignore the existence of discards.

The main steps of the balancing process followed for the NWM model are described in the Supplementary Online Information section 2 and in Corrales (2013).

#### **2.4. Model analysis and ecosystem indicators**

We calculated several ecological indicators to provide information on the quality of the model, the ecological roles of the functional groups, key structural and functional traits of the ecosystem, and the impacts of fishing and fishing fleets on the ecosystem (Coll and Libralato, 2012; Christensen and Walters, 2004).

##### **a) Pedigree index and quality of the model**

We used the pedigree routine of the Ecopath model to quantify the uncertainty associated with the input parameters (Christensen and Walters, 2004; Christensen et al., 2008). We recorded the origin and quality of the data assigning to each input a value of uncertainty or a confidence interval, which we used to calculate the pedigree index. The pedigree index varies between 0 (low quality) and 1 (high quality), allowing a description of the quality of the model that can be compared to other models. The pedigree information was also used to determine which parameters were of lower quality and therefore could be modified during the balancing procedure. The confidence intervals and index values used to describe the uncertainty of the balanced Ecopath model are described in the Supplementary Information 3.

##### **b) Ecological indicators by functional group and trophic interactions**

To analyze the ecological position of the functional groups of the NWM model we used the Trophic Level (TL) defined by the model. The TL identifies the position of the species within the food web. By convention, primary producers and detritus have TL=1, while the TL of consumer groups (j) are calculated from the TL average of their prey (i), weighted by the proportion of each prey in the diet (j) ( $DC_{ij}$ ) (Lindeman, 1942; Stergiou and Karpouzi, 2001). The Omnivory Index (OI) of each group was also included, which indicates trophic specialization and is calculated as the variance of the TL of their prey (i) (Christensen et al., 2008).

The Mixed Trophic Impact (MTI) analysis was used to quantify the relative impact that a hypothetical small increase in the biomass of one functional group would have on the biomasses of each functional group of the ecosystem, including the fishing fleets (Christensen et al., 2008; Ulanowicz and Puccia, 1990).

To identify the key species within the ecosystem (both keystone and structuring species), we calculated the keystone index (KS) using two methods (Libralato et al., 2006; Power et al., 1996). A keystone group plays an important role in the ecosystem regardless of its relatively low biomass (Power et al., 1996). On the contrary, a dominant or structuring group would play an important role due to its large biomass. Both methods use the relative overall effect ( $\varepsilon_i$ ) calculated from the MTI analysis. In the first method (Libralato et al., 2006) the KS is calculated as:

$$KS1_i = \text{Log} [\varepsilon_i (1 - p_i)] \quad \text{Eq. (3)}$$

where  $p_i$  is the contribution of each functional group (i) to the total biomass of the food web. In this case, key groups are those with  $KS_i$  values closer to zero and a high relative overall effect.

The second method (Power et al., 1996) expresses the  $KS_i$  as:

$$KS2_i = \text{Log} [\varepsilon_i \cdot (1/p_i)] \quad \text{Eq. (4)}$$

In this case, key groups are those with higher  $KS_i$  values and/or high relative overall effect.

### c) Ecosystem structure and functioning

We used the following indicators related to the development and maturity of ecosystems (Odum, 1969, 1971) to analyze the structure and functioning of the food web: (1) Total System Throughput (TST,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), estimated as the total flows in the ecosystem (sum of all consumption (TQ,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), Exports (E,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), Total Respiration (TR,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ), Total Flow to Detritus (TFD,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ); (2) Total Biomass (TB,  $\text{t}\cdot\text{km}^{-2}$ ); (3) Total Production (TP,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ); (4) Net Production (NP,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ); (5) total Primary production/total Respiration (Pp/R); (6) total Primary production/ total Biomass (Pp/B,  $\text{t}\cdot\text{km}^{-2}\cdot\text{year}^{-1}$ ); (7) the System Omnivory Index (SOI), defined as the average of the OIs of each consumer group, weighted by the logarithm of their consumption; (8) the Finn's Cycling Index (FCI, %), which is the fraction of the throughput that is recycled; and (9) the Finn's mean Path Length (PL), that represents the number of functional groups that a flow connects within the ecosystem (Finn, 1976).

We calculated the Transfer Efficiency (TE), the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem (e.g., by the fishing activity)

or transferred to higher trophic levels through consumption. The TE is calculated using the trophic flows and the discrete trophic levels with the ratio between the production of current TL and previous TL (Lalli and Parsons, 1993; Pauly and Christensen, 1995) and summarizes the inefficiencies or energy dissipation that is produced along the food web due to respiration, excretion, egestion and natural mortality (Lindeman, 1942).

In addition, the flows and biomass of the NWM model were aggregated for each discrete trophic level to draw a Lindeman spine, a graphical and simple representation of the food web (Lindeman, 1942). The detritus box was separated from the primary producers to show the amount of energy that was flowing through it.

We also calculated the mean Trophic Level of the community (mTLco) weighting the TL of each functional group by its biomass. We calculated the mTLco by taking into account all trophic levels of the ecosystem and by excluding the TL<II (thus excluding primary producers and detritus).

#### **d) Fishing impacts**

To assess the role and impact of fishing, we use several ecological indicators. The MTI analysis was used to quantify the direct and indirect impact of each fleet on the functional groups. The exploitation rate ( $F/Z$ ), the proportion of the total mortality ( $Z$ ) that is induced by fishing mortality ( $F$ ), was also calculated by functional group. We calculated the Primary Production Required to sustain the fisheries (% PPR), which can be estimated from primary producers (% PPRa) and from primary producers and detritus (% PPRb), the Gross Efficiency of the fishery (GE), and the mean Trophic Level of the catch (mTLc) (Christensen et al., 2008; Pauly and Christensen, 1995).

#### **e) Comparison of results with other food web models**

Finally, the ecological indicators obtained from the NWM model were compared with those from several ecosystem models previously developed in the Mediterranean Sea and the Gulf of Cadiz area (Fig. 3). These models are the South Catalan Sea (SCS, Coll et al. (2006a)), and the Gulf of Lions (GoL, Banaru et al. (2013)), both included in the NWM model area, the Northern and Central Adriatic Sea (NCAS, Coll et al. (2007)), the North Aegean Sea (NAS, Tsagarakis et al. (2010)), the lower continental slope of the Catalan Sea or Deep Catalan Sea (DCS, Tecchio et al. (2013)), the Greek Ionian Sea (IS, Moutopoulos et al. (2013) ), the Gulf of Gabes (GoG, Hattab et al. (2013)), and the

Gulf of Cadiz (GoC, Torres et al. (2013)), the latter in the adjacent waters of the Atlantic Ocean.

With the exception of the GoL, IS and GoG models, these Ecopath models were developed following similar criteria to the NWM model to define the functional groups and to estimate the input data and share similar ecological structures. However, to minimize the potential biases of indicators that are more susceptible to model structure, we included in the comparison only those indicators that are sufficiently robust for a comparative approach following Coll and Libralato (2012).

### 3. Results

#### 3.1. Pedigree index and quality of the model

The pedigree index calculated for the NWM model was 0.62 (Table 4). This value indicates that the input data used in this model was of acceptable quality when compared to the distribution of pedigree values in other existing models (Morissette, 2007). The pedigree of the NWM model is comparable to those from other available models of the Mediterranean Sea (Table 4).

#### 3.2. Ecological indicators by functional group and trophic interactions

The EE values in the NWM model were generally high (Table 2), indicating that a high proportion of the production of each functional group is consumed (preyed upon) within the ecosystem or is exported (as catches or migration). The fish groups showed high values except for the top predators (other large pelagic fishes, functional groups or f.g. 47, and adult hake, f.g. 26), with the exception of those species that are heavily exploited, such as anglerfish (*Lophius spp.*, f.g. 24), conger (*Conger conger*, f.g. 28) and Atlantic bluefin tuna (f.g. 46). The lower EE values for primary producers (f.g. 1-4) and planktonic groups (f.g. 5 and 7) indicated that a larger percentage of production from these groups flows to detritus.

The functional groups ranged from TL = 1 for primary producers (f.g. 1-4) and detritus groups (f.g. 52-54) to TL = 4.44 for dolphins (Table 2). Most of the invertebrate groups showed TL lower than 3, except for the red shrimp (*Aristeus antennatus*, f.g. 12) and benthic and benthopelagic cephalopod groups (f.g. 17-20). The salema fish (*Sarpa salpa*, f.g. 21) showed the lowest TL value for fish groups, as its diet is based on benthic

primary producers. The TLs of small pelagic fishes (f.g. 38-43) were also low, due to the importance of phytoplankton and zooplankton in their diet (Table 2, Fig. 4).

The quantification of the trophic flows among the functional groups illustrated the importance of the pelagic-benthic coupling (Fig. 4). For example, it was observed that many groups from the pelagic compartment were consumed by groups in the benthic compartment, for example, the macrozooplankton (f.g. 6), gelatinous plankton (f.g. 7), small pelagic fishes (f.g. 38-43) and benthopelagic and mesopelagic fishes (f.g. 33 and 34) (Fig. 4). In addition, demersal groups such as anglerfish (f.g. 24), juvenile and adult hake (f.g. 25 and 26) and conger (f.g. 28) feed on organisms from the pelagic compartment. In addition, the detritus was shown to be an important compartment as most of the biomass and production in the demersal habitat was associated with it (Table 3, Fig. 4).

The highest flows to detritus corresponded to phytoplankton (f.g. 1), micro- and mesozooplankton (f.g. 5) and annelids (f.g. 8) (Table 2). The highest values regarding fish groups corresponded to anchovy (f.g. 38 and 39) and sardine (f.g. 40 and 41) (Table 2).

The lower values of OI were observed for micro- and mesozooplankton (f.g. 5), the salema fish (f.g. 21) and small pelagic fish (f.g. 38-43), suggesting high specialization. These groups exert a high predation on primary producers (f.g. 1-4) and zooplanktonic groups (f.g. 5 and 6).

Most of the functional groups presented high predation mortalities (M2), except large predators organisms, such as anglerfish (f.g. 24), demersal sharks (f.g. 35 and 36), Atlantic bluefin tuna (f.g. 46), other large pelagic fishes (f.g. 47) and dolphins (f.g. 50), as well as the baleen whales (f.g. 51) and rays and skates (f.g. 37) (Table 2). Other natural mortality excluding predation (M0) was low in most of the functional groups. However, phytoplankton (f.g. 1), micro- and mesozooplankton (f.g. 5), gelatinous plankton (f.g. 7), adult hake (f.g. 26), demersal sharks from the continental shelf (f.g. 35), mackerel (*Scomber spp.*, f.g. 45) and seabirds (f.g. 49) presented a high M0 (Table 2).

The MTI analysis (Fig. 5) indicated that several functional groups showed a low impact on the ecosystem, such as the spottail mantis shrimp (*Squilla mantis*, f.g. 10), the

Norway lobster (*Nephrops norvegicus*, f.g. 11), the red shrimp (f.g. 12), demersal sharks from the continental shelf (f.g. 35), rays and skates (f.g. 37), sea turtles (f.g. 48), seabirds (f.g. 49) and baleen whales (f.g. 51). We also observed that most of the functional groups would have a negative impact on themselves due to within-group competition for food resources and impacts on their main prey. Numerous functional groups were impacted positively by the groups at the base of the food web such as primary producers (f.g. 1-4), zooplankton groups (f.g. 5 and 6), suprabenthos (f.g. 9), benthic invertebrates (f.g. 8, 15 and 16) and detritus (f.g. 52-54). Also, small pelagic fishes (f.g. 38-43), especially anchovy (f.g. 38 and 39) and sardine (f.g. 40 and 41), had a remarkable impact on various functional groups at higher and lower trophic levels.

Results from the MTI also allowed us to identify some coupled pelagic-demersal relationships. For example, it highlighted the relationship of juvenile hake (f.g. 25) and large demersal fishes from the continental shelf (f.g. 31) to benthopelagic cephalopods (f.g. 18), or, between adult hake (f.g. 26) and horse mackerel (f.g. 44). In addition, the results from the MTI highlighted a strong relation of adult hake (f.g. 26) to demersal fishes from the upper slope (f.g. 32) and benthopelagic cephalopods (f.g. 18) to juvenile anchovy (f.g. 38) and juvenile sardine (f.g. 40).

The MTI analysis was also used to detect indirect impacts through trophic cascades and beneficial predation. For example an increase in the biomass of large demersal fishes from the continental shelf (f.g. 31) could cause a decrease in salema fish (f.g. 21) and small demersal fishes from the continental shelf (f.g. 30), which in turn would cause an increase in benthic primary producers (f.g. 2-4).

Results from the two keystone indexes (Fig 6) indicated that dolphins (f.g. 50), large demersal fishes from the continental shelf (f.g. 31), benthopelagic cephalopods (f.g. 18 and 20), other large pelagic fishes (f.g. 47) and salema fish (f.g. 21) could be keystone species based on Libralato et al. (2006) (Fig. 6). In the case of the index proposed by Power et al. (1996), seabirds and anglerfish were also highlighted as keystone. Moreover, some groups with low TL were also identified as structuring species due to their high biomass and high trophic impact, such as phytoplankton (f.g. 1), micro- and mesozooplankton (f.g. 5), macrozooplankton (f.g. 6) and benthic invertebrates (f.g. 16).



### 3.3. Ecosystem structure and functioning of Mediterranean marine food webs

27.88% of the flows of the NWM model was consumed, 28.95% was exported, 7.44% was respired and 39.73% was flowing to detritus (Table 4). The TST of the NWM model was similar to those obtained for the SCS, NCAS and GoG models; lower than the GoC model and higher than other models (Table 4).

The total biomass supported by the ecosystem (excluding detritus) was mainly divided into benthic invertebrates (f.g. 8, 15 and 16; 38.9%), phytoplankton (f.g. 1; 19.7%), pelagic fishes (f.g. 38-47; 16.7%), zooplankton groups (f.g. 5-7; 11.1%), benthic and demersal fishes (f.g. 21-37; 6.1%), benthic primary producers (f.g. 2-4; 2.9%), crustaceans (f.g. 10-14; 2.3%) and cephalopods (f.g. 17-20; 1.9%) (Table 2). In addition, most of the total production came from phytoplankton (f.g. 1; 85%) and micro- and mesozooplankton (f.g. 5; 10%) (Table 2). Disregarding these two groups, the annelids (f.g. 8; 43%), macrozooplankton (f.g. 6; 16.25%), crustaceans (f.g. 10-14; 6.7%), sardine (f.g. 40 and 41; 6.63%), benthic primary producers (f.g. 2-4; 5.77%), gelatinous plankton (f.g. 7; 4.61%) and anchovy (f.g. 38 and 39; 3.1%) were also important. In turn, 79.5% of total consumption flows was concentrated in the micro- and mesozooplankton (f.g. 5; 52.5%) and annelids (f.g. 8; 27%) (Table 2). Sardine (f.g. 40 and 41; 4.11%), macrozooplankton (3.42%), crustacean (f.g. 10-14; 3.05%) and anchovy (f.g. 38 and 39; 2.47%) were also important contributors. These results highlight the importance of the pelagic compartment of the ecosystem.

The TE in the NWM model was 14.3% (Table 4), so on average 14% of the production of one TL became a production of its upper TL. This value was in line with the value from DCS, IS and GoC models, it was lower than GoL, NAS and GoG models and higher than SCS and NCAS models. The average TE in the primary producers' food web (15.4%) was higher than the average TE of the detritus food web (13.3%) (Table 4 and Fig. 7).

The Lindeman spine showed that most of the flows were located between TL I and TL III, which collectively represented about 95% of the TST. The consumption of detritus by TL II was high. In addition, this representation highlighted the importance of TL II and III in terms of biomass, which together accounted for 71.38% of total biomass if detritus was excluded. Exporting flows were higher from TL III than from the rest of the other trophic levels due to the fisheries exports.

The mTLco for the NWM model when taking into account all the groups included in the model was 1.38. If groups with  $TL < 2$  were excluded, the mTLco was 2.48 (Table 4). These values were similar to the other models compared (Table 4). However, the mTLco was slightly higher in the NAS, GoL, GoG and GoC models.

### 3.4. Fishing impacts

Fishing mortality values ( $F$ ) were high ( $F > 0.5$ ) for several exploited functional groups (Table 2), including spottail mantis shrimp (f.g. 10), mullets (*Mullus spp.*, f.g. 22), juvenile hake (f.g. 25), poor cod (*Trisopterus minutus*, f.g. 27), flatfishes (f.g. 29) and Atlantic bluefin tuna (f.g. 46). When looking at exploitation rates ( $F/Z$ ) several exploited groups showed high values ( $> 0.5$ ), indicating that more than 50% of total mortality in the group was due to fishing (Table 2).

The MTI analysis focusing on fishing fleets showed that the 8 fleets included in the NWM model had negative impacts on themselves and, in general, lower negative impacts on other fleets. The trawling fleets from Spain and France had the most widespread impact on the ecosystem and the highest impact on some demersal groups (Fig. 5). In addition, the French bottom-mid water trawling fleet had a strong impact on anchovy (f.g. 38 and 39) due to their pelagic catch. Purse seiners from Spain and France presented significant impacts on sardine (f.g. 40 and 41) and dolphins (f.g. 50). In addition, the Spanish purse seiner fleet had a large impact on anchovy (f.g. 38 and 39), round sardinella (*Sardinella aurita*, f.g., 42) and other large pelagic fish (f.g. 47), while the French fleet had larger impacts on Atlantic bluefin tuna (f.g. 46).

The longliner fleet had large negative impacts on seabirds and other large pelagic fishes (f.g. 47). The Spanish artisanal fleet had a high negative impact on other large pelagic fishes (f.g. 47) and a remarkably positive impact on European sprat (f.g. 43), horse mackerel (f.g. 44) and mackerel (f.g. 45) due to the removal of their principal predators (other large pelagic fishes). The French artisanal fleet showed a high negative impact on conger (f.g. 28), flatfishes (f.g. 29), rays and skates (f.g. 37), Atlantic bluefin tuna (f.g. 46) and sea turtles (f.g. 48). The recreational fleet presented the lowest impact with the largest negative impact on other large pelagic fishes. The MTI analysis also showed that sea turtles (f.g.48), seabirds (f.g. 49) and dolphins (f.g. 50) had a low negative impact on the fishing fleets in general, while these groups were heavily impacted by several of the fleets.

Total catch in the area was lower in the NWM model than the SCS and GoC models and higher than the GoL, NCAS, NAS, IS and GoG models (Table 4). The mTLc value of the NWM model was in line with the SCS and NCAS models and lower than the GoL, NAS, GOG, IS and GoC models (Table 4). The analysis of the total catch by fleet indicated that the Spanish purse seiners and French bottom and mid-water trawlers have the highest catches in the area (Table 5). The mTLc by fleet indicated that the Spanish purse seiners and the French artisanal fleet had the lowest values. The longliners presented the highest mTLc, indicating that this fishing activity played an important role as a “predator” fishery in the ecosystem.

The GE of the fishery was higher in the NWM model than the SCS, GoL, NCAS, GoG and GoC models, lower than the NAS model and similar to the IS model (Table 4). PPR was 12.08% when only considering primary production from primary producers (% PPRa), and 17.36% when also taking into account the detritus (% PPRb) (Table 4), in line with the SCS, GoL and GoC models and higher than those from NCAS, GoG, IS and NAS models (Table 4).

#### **4. Discussion**

This study allowed us to characterize the structure and functioning of the ecosystem in the NW Mediterranean Sea and to estimate the fishing impacts during the early 2000s. This ecosystem model is not the first developed in the study area, as previous models have been developed in smaller areas of the Catalan Sea (SCS, Coll et al. (2006a); DCS, Tecchio et al. (2013)) and in the Gulf of Lions (GoL, Banaru et al., 2013). However, these models focused on smaller areas, while hydrodynamic events indicate connectivity over a larger area (Ospina-Alvarez et al., 2012). In addition, there are some shared stocks between Spanish and French fleets (for example, Aldebert et al. (1993)).

The main differences between the four models developed in the study area (SCS, GoL, DCS and NWM) can be related to primary production (influenced by the inputs from primary rivers and wind conditions), the modeled years and the modelled bathymetric range. For example, the SCS model did not include the coastal area (0-50 m), reached up to 400 m and represented a period from the past (Table 4).

The relatively high Pedigree value of the NWM model indicates that the available information in the study area was sufficient to parameterize the model with an

acceptable quality. However, in order to develop the Ecosim and Ecospace modules and test different scenarios, some input data should be improved.

For example, some information gaps were identified, especially for low trophic level organisms such as benthic primary producers, suprabenthos, annelids, bivalves-gastropods, benthic invertebrates and gelatinous plankton, which should inform future scientific research objectives in the area.

Obtaining realistic official catch data is a difficult challenge in the Mediterranean Sea and, in our case, especially in the French area. The reconstruction of the catches of French fleets using the catch trends in the Catalan region represents a limitation of the present study. We nevertheless considered that this assumption offered a more realistic catch estimation than the assumption that the available catch data (only for the 2007-2008 period) is a sufficient representation for the modeled years (2000-2003), especially considering that during this period (2000-2008) there was a noticeable decline in Spanish catches. In addition, this assumption was justified by the behaviour of part of the Catalan fleets, which also exploit the main stocks of the Gulf of Lions, such as hake, sardine and anchovy. Thus, we assumed that the evolution of the catches for the two regions is similar to obtain a better catch estimation. Furthermore, the illegal, unreported and unregulated (IUU) catch, which is significant on the Spanish side of the study area (Coll et al., 2014; Pauly et al., 2014) and the French recreational fleet were not included. This represents an obstacle to understanding the real impacts of fishing activity (Zeller and Pauly, 2007). As new information is being generated, the present model will be updated and its quality will be improved.

#### **4.1. Ecological indicators by functional group and trophic interactions**

In general, trophic levels obtained for crustacean, benthic invertebrate, fish and cetacean functional groups were consistent with the results obtained for these organisms in the Mediterranean Sea (Stergiou and Karpouzi, 2001) and several modeled Mediterranean ecosystems (e.g., Coll et al. (2006a); Banaru et al. (2013)).

Mortality rates obtained for the model were split into fishing mortality (F), predation mortality (M2) and other natural mortality excluding predation (M0). The natural mortality (M0 + M2) values obtained in the NWM model were in accordance with the range of values from stock assessments (García et al., 2011a, b; Jadaud et al., 2011b;

Lleonart, 1990) and other ecosystem models (Banaru et al., 2013; Coll et al., 2006a; Tecchio et al., 2013). However, some differences were detected. For example, in the case of adult anchovy, adult sardine and adult hake, the values from the NWM model were higher than values from stock assessments (García-Rodríguez et al., 2010; García et al., 2011a, b; Jadaud et al., 2011a). These differences were also observed in other ecological models developed in the Iberian Peninsula ecosystem (Coll et al., 2006a; Sánchez and Olaso, 2004; Torres et al., 2013) and can be explained by the fact that ecological models calculated the predation mortality ( $M_2$ ) more accurately than traditional assessments.

In addition, most groups had low levels of other natural mortality excluding predation ( $M_0$ ). This was in line with SCS and GoL models and suggests that for these groups the NWM model was able to explain their population dynamics to a good extent, as low  $M_0$  values highlight that a large percentage of total mortality is explained by the model. However, some groups had high  $M_0$  values. This is because they were not consumed in the ecosystem or were not fished. We also observed high values of  $M_0$  associated with species/groups that spend part of their time outside of the study area, such as seabirds and large pelagic fishes, or that are very abundant, such as planktonic organisms. In addition, some groups without complete information also showed high  $M_0$ , such as gelatinous plankton. This may be related to the difficulty in parameterizing this group (Pauly et al., 2009), especially in regards to predation, as there is limited information about potential predators because of the difficulty of identifying these organisms in stomach contents studies (Stergiou and Karpouzi, 2001).

The MTI analysis obtained for the NWM model highlighted the importance of groups that form the base of the food chain (phytoplankton, detritus, zooplankton groups, suprabenthos and benthic invertebrates). These groups may be related to possible bottom-up interactions (Hunter and Price, 1992). Additionally, this analysis showed the high impact of small pelagic fish (especially sardine and anchovy) on the higher and lower trophic levels, suggesting a wasp-waist control of these organisms in the system (Cury et al., 2000), in line with results from previous research and ecological models (e.g., Coll et al. (2006a); Palomera et al. (2007); Tsagarakis et al. (2010); Banaru et al. (2013); Hattab et al. (2013)). In addition, some top-down processes within the ecosystem were observed, such as between dolphins and benthopelagic cephalopods or

between benthopelagic cephalopods and sardine and anchovy, confirming the important role of benthopelagic cephalopods on marine ecosystems (Coll et al., 2013a).

Our results identified some important links between the benthic and pelagic domains. This coupling is characteristic of upwelling areas (Moloney et al., 2005) and highly exploited temperate ecosystems (e.g., Sánchez and Olaso (2004); Coll et al. (2006a); Tsagarakis et al. (2010); Torres et al. (2013)). The interactions between the two domains can affect demersal fish production as a result of changes in primary productivity and zooplankton abundance (Ware and Thomson, 2005). At the same time, changes in the demersal fish abundance can cause cascading effects on pelagic fish (Frank et al., 2005). Therefore, the existence of these links reinforces the need to establish ecosystem-based management in the Mediterranean Sea.

When comparing the two keystone indices (KS), the same species were identified: dolphins, large demersal fishes from the continental shelf, benthopelagic cephalopods, other large pelagic fishes and salem fish. However, according to the method proposed by Power et al. (1996), seabirds and anglerfish were also suggested as a keystone species. This is due to the different biomass weights in the calculations of the indices (Coll et al., 2013b; Valls et al., In press). Dolphins, benthopelagic cephalopods and other large pelagic fishes were identified as keystone species/groups in Mediterranean ecosystems previously (Table 6a). However, salem fish were not identified in other models. The NWM model showed that this species had a large impact on benthic primary producers and predation on benthic primary producers can cause strong impacts on other groups because benthic primary producers are a source of food and protection for many species on the ecosystem. In addition, some groups with low TL were identified as key groups, as in other Mediterranean ecosystems (Table 6b). These groups play a fundamental role due to their abundance and, therefore, can be defined as structuring groups within the ecosystem (Coll et al., 2013b; Heymans et al., 2012).

#### **4.2. Ecosystem structure and functioning of Mediterranean marine food webs**

The magnitude of trophic flows of the NWM model (TST) was in line with the other models developed in the Western Mediterranean Sea (SCS and GoL) and with NCAS and GoG models. The differences between models in the study area (SCS, GoL and NWM) were mainly related to the productivity of the region (high productivity areas are located in the Gulf of Lions and in the Ebro Delta due to river runoffs and local

upwelling) and differences in the bathymetric ranges included in the different modeling applications (deeper in the GoL model and shallower in the SCS model). The NCAS and GoG models have high values of TST as they represent coastal areas located in high productivity continental shelves of the Mediterranean Sea. The highest TST value corresponded to the GoC model, due to the input of nutrient-rich waters from the Mediterranean Sea and the Guadiana and Guadalquivir River inputs on the Atlantic side (Ramos et al., 2012); while the lowest value corresponded to the DCS model, due to the oligotrophic nature of deep-sea systems (Gage and Tyler, 1991). A larger number of models in southern Mediterranean areas are needed to analyze the latitudinal gradient with ecological indicators.

Results regarding total biomass and trophic flows, in terms of consumption and production, showed that the NWM model is dominated by the pelagic domain as a large percentage of biomass is located in this compartment and this is where flows mainly occurred. This was also observed in other ecological models developed in the Mediterranean Sea (SCS, GoL, NCAS, NAS and GoG) and the adjacent Atlantic region (GoC).

Detritus flows to TL II were similar to primary producers flows to TL II. This highlighted an important link between phytoplankton and benthic invertebrate groups (annelids (f.g. 8), suprabenthos (f.g. 9), bivalves-gastropods (f.g. 15) and benthic invertebrates (f.g. 16)) via detritus. Plankton groups contributed significantly to the detritus compartment, as described in other Mediterranean ecological models (SCS, NCAS, NAS, GoG and GoC) and could be identified as a key functioning process of Mediterranean ecosystems. In fact, the relationship between detritus and organisms at TL II seemed to be an essential trophic pathway.

Total flows in the ecosystem decreased with the increase of TL, in line with the ecological theory (Lalli and Parsons, 1993). The transfer efficiencies (TE) obtained for the NWM model were within the common values recorded in other aquatic ecosystems (Odum, 1971; Pauly and Christensen, 1995). However, these values were higher than the average reported worldwide (10%), as well as the values obtained in other Mediterranean ecosystems, except in the NCAS ecosystem, clearly indicating the oligotrophic character of the Mediterranean Sea, in contrast to more eutrophic ecosystems (Coll et al., 2006b; Shannon et al., 2003). The TE of the primary producers

food web was higher than the TE of the detritivore food web, indicating that the ecosystem was more limited by primary production than by detritus (Shannon et al., 2003). However, in the NWM model the TE between TL III – IV increased, as described in the SCS, NCAS and GoC models. This has previously been explained by the high fishing impacts in the upper trophic levels of marine ecosystems (Coll et al., 2009).

In general, the indices related to the ecosystem development theory suggested that the NWM ecosystem is at a low ecosystem development state (Christensen, 1995; Odum, 1969, 1971). For example, the Pp/R was higher than 1, indicating that there was more energy produced than respired within the ecosystem; the Pp/B reflected a low level of biomass accumulation within the ecosystem compared to productivity; and the indicators related to the food web complexity (SOI and PL) showed low values, indicating that the ecosystem was more chain-like than web-like.

#### **4.3. Fishing impacts**

The results of this study confirmed that commercial fishing was an important component of the NWM ecosystem dynamics. The total catch in the early 2000s was high and in line with the SCS model, indicating high exploitation of the ecosystem. However, the value was higher value than the GoL ecosystem because a complete estimation of discards was not included in that model (Banaru et al., 2013). This estimation is very important to obtain real estimates of the fishing mortality and impact (Zeller and Pauly, 2007). In addition, the catch in the NWM ecosystem was larger than the other ecological models from Central and Eastern Mediterranean compared in this study. This may be related to the large proportion of small-scale fisheries in central and eastern areas (Bas, 2002), in addition to a lower quality of fisheries statistics (Pauly et al., 2014).

The lower mTLc values indicated high exploitation based on low trophic level organisms, mainly those that feed on plankton (principally small pelagic fish and juvenile fish) and benthic invertebrates. This implies a high risk of ecosystem overfishing (Libralato et al., 2008).

The F/Z for sardine was larger than the reference point of 0.4 recommended for small pelagic fishes (Patterson, 1992) and anchovy and round sardinella had a high value as



well. In addition, several demersal functional groups presented higher F/Z than the reference point of 0.5 proposed for demersal stocks (Rochet and Trenkel, 2003). From an ecosystem point of view these results corroborated some stock assessments made in the study area, indicating the overexploitation of several marine resources in the Mediterranean Sea (Colloca et al., 2013; GFCM, 2013).

Results from fishing fleets indicated that the fleets act as top predators on the ecosystem, impacting all exploitable TL. Fishing activities had a negative impact on many predators. This was also observed in other Mediterranean Sea ecosystems (Banaru et al., 2013; Coll et al., 2006a; Tsagarakis et al., 2010). On the contrary, the MTI analysis suggested that these groups are not important competitors of fishing activity in the area, but the fishing effects on these species were disproportionately high due to their low reproductive rate and impacts on their prey.

The GE was higher than the mean global value (0.0002) calculated from a wide range of marine ecosystems (Christensen et al., 2008) but similar to other Mediterranean ecosystems (SCS, GoL, NCAS, IS, NAS and GoG) and the Gulf of Cadiz ecosystem. This indicates that the impact of fishing activity was high.

## 5. Conclusions

The ecosystem model of the NWM represents an advance in the analysis of the exploited NW Mediterranean ecosystem as it includes a larger area allowing the integration of Spanish and French fishing activities and updates previous results. This model sets the baseline to investigate further issues related to the productivity of the area, the fish distribution and habitats (Giannoulaki et al., 2013; Giannoulaki et al., 2011), the connectivity (Ospina-Alvarez et al., 2012), fleet dynamics and future scenarios of global change (including changes in climate, fishing and the introduction of invasive species).

In the future, the calibration of the model and development of temporal simulations (Christensen and Walters, 2004; Walters et al., 1997) will help to improve the NWM model and explore how environmental factors and fisheries can affect the ecosystem in the future (Coll et al., 2009; Coll et al., 2008). In addition, a spatial version using the Ecospace module (Walters et al., 1999) can be used to analyze and compare the potential impacts on the marine ecosystem of the implementation of different

management measures in time and space, such as the implementation of Marine Protected Areas (MPAs) (Fouzai et al., 2012). Future plans include the investigation of the ecological impacts of the Fisheries Restricted Area (FRA) in the Gulf of Lions declared by the GFCM (Leonart et al., 2008), the impact of the establishment of seasonal closures of purse seine activities in recruitment and/or spawning areas of anchovy, such as Bay of Roses, Gulf of Sant Jordi and the areas influenced by the input of the Rhone and Ebro Rivers (Palomera et al., 2007), and the impact of a reduction of fishing efforts in the area.

### **Acknowledgements**

The authors wish to acknowledge the scientific researchers from the Institut de Ciències del Mar (Barcelona, Spain), the Instituto Español de Oceanografía (Murcia and Cádiz, Spain) and the Institut Français de Recherche pour l'Exploitation de la Mer (Sète, France) for providing data used in this study and advice, with special mention to Daniella Banaru, Francesc Sardà, Joan B. Company, Joan Navarro, María Ángeles Torres, Jordi Leonart and Francesc Maynou. We also address special thanks to Chiara Piroddi and Gideon Gal for their constructive remarks on the manuscript. We are grateful to the Editor and the reviewer for their helpful comments on our manuscript. Xavier Corrales was partially supported by an IOLR scholarship. Marta Coll was partially supported by the EC Marie Curie CIG grant to BIOWEB and the Spanish Research Program Ramon y Cajal. This is a contribution to ECOTRANS Spanish PN project and to DESSIM Israeli project.

**Table legends**

**Table 1.** Input data of the NWM model by functional group.  $B_i$  = initial biomass ( $t \cdot km^{-2}$ );  $P/B$  = production/biomass ( $year^{-1}$ );  $Q/B$  = consumption/biomass ( $year^{-1}$ );  $U/Q$  = unassimilated food/consumption; landings and discards ( $t \cdot km^{-2} \cdot years^{-1}$ ).

**Table 2.** Modified input parameters and outputs obtained from the NWM model. TL = trophic level;  $B_f$  = Final Biomass ( $t \cdot km^{-2}$ ); EE = Ecotrophic Efficiency;  $P/Q$  = Production/Consumption ratio;  $R/B$  = Respiration/Biomass ratio;  $R/A$  = Respiration/Assimilation ratio;  $P/R$  = Production/Respiration ratio; NE = Net Efficiency;  $F$  = Fishing Mortality ( $years^{-1}$ );  $M_2$  = Predation Mortality ( $years^{-1}$ );  $M_0$  = Other Natural Mortality ( $years^{-1}$ );  $F/Z$  = Exploitation Rate;  $P$  = Production ( $t \cdot km^{-2} \cdot years^{-1}$ );  $Q$  = Consumption ( $t \cdot km^{-2} \cdot years^{-1}$ );  $O_i$  = Omnivory Index;  $FD$  = Flow to Detritus ( $t \cdot km^{-2} \cdot years^{-1}$ ).

**Table 3.** Diet composition matrix for the NWM model. Cells in grey represent values lower than 0.01.

**Table 4.** Characteristics, statistics and ecological indicators for the NWM and other neighbouring models compared. NWM = Northwestern Mediterranean Sea; SCS = South Catalan Sea (Coll et al., 2006); GoL = Gulf of Lions (Banaru et al., 2013); DCS = Lower continental slope of the Catalan Sea (Tecchio et al., 2013); NCAS = North-Central Adriatic Sea (Coll et al., 2007); NAS = North Aegean Sea (Tsagarakis et al., 2010); IS = Greek Ionian Sea (Moutolopoulos et al., 2013); GoG = Gulf of Gabes (Hattab et al., 2013); GoC = Gulf of Cadiz (Torres et al., 2013).

**Table 5.** Catch ( $t \cdot km^{-2} \cdot year^{-1}$ ) and mean trophic level of the catch (mTLc) for the fleets in the NWM model

**Table 6.** Functional groups identified as a) keystone and b) structuring species/groups in the Mediterranean Sea and the adjacent Atlantic area (GoC). NWM = Northwestern Mediterranean Sea; SCS = South Catalan Sea (Coll et al., 2006); GoL = Gulf of Lions (Banaru et al., 2013); DCS = Lower continental slope of the Catalan Sea (Tecchio et al., 2013); NCAS = North-Central Adriatic Sea (Coll et al., 2007); NAS = North Aegean Sea (Tsagarakis et al., 2010); IS = Greek Ionian Sea (Moutolopoulos et al., 2013); GoG = Gulf of Gabes (Hattab et al., 2013); GoC = Gulf of Cadiz (Torres et al., 2013).

**Figure legends**

- Fig. 1.** The NW Mediterranean Sea (GSA 6 and 7), showing the modelled area (0-1000m) and depth ranges.
- Fig. 2.** Location of hauls of MEDITS surveys used to parameterize the initial values of demersal and benthic groups in the NWM model.
- Fig. 3.** Location of Ecopath models used in the comparative analysis.
- Fig. 4.** Flow diagram of the NWM model. The size of each circle is proportional to the biomass of the functional group. The numbers identify the functional groups of the NWM model (Table 1). The wideness of the connecting lines is proportional to the magnitude of their flows.
- Fig. 5.** Mixed trophic Impact (MTI) analysis of the NWM model. Negative (red) and positive (blue) impacts are represented.
- Fig. 6.** Keystone Index analysis of the NWM model. The size of each circle is proportional to the biomass of the functional groups (a) indicator *sensu* Libralato et al. (2006), and (b) indicator *sensu* Power et al. (1996). The numbers identify the functional groups of the NWM model (Table 1).
- Fig. 7.** Trophic flows of the NWM model organized by integer trophic levels (TL) in the form of Lindeman spine. TL I is split into primary producers (P) and detritus (D). The flows are represented in  $t \cdot km^{-2} \cdot year^{-1}$ .

## References

- Agnew, D., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J.R., Pitcher, T.J., 2009. Estimating the worldwide extent of illegal fishing. *PLoSOne* 4, e4570.
- Agostini, V.N., Bakun, A., 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fisheries Oceanography* 11, 129-142.
- Aldebert, Y., Lleonart, J., Recasens, L., 1993. Analysis of gear interactions in a hake fishery: The case of the Gulf of Lions (NW Mediterranean). *Scientia Marina* 57, 207-217.
- Arcos, J.M., Bécarea, B., Rodríguez, B., Ruiz, A., 2009. Áreas Importantes para la Conservación de las Aves marinas en España. LIFE04NAT/ES/000049-Sociedad Española de Ornitología (SEO/Birdlife). Madrid.
- Banaru, D., Mellon-Duval, C., Roos, D., Bigot, J.-L., Souplet, A., Jadaud, A., Beaubrun, P., Fromentin, J.-M., 2013. Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. *Journal of Marine Systems* 111-112, 45-68.
- Bas, C., 2002. El mar Mediterráneo: recursos vivos y explotación Ariel Ciencia, Barcelona.
- Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Global Biogeochemical Cycles* 18, doi:10.1029/2003GB002034.
- Cadiou, B., Pons, J.-M., Yésou, P., 2004. Oiseaux marins nicheurs de France métropolitaine (1960-2000). In Cadiou, B.; Pons, J.-M.; Yésou, P. (Eds). Editions Biotope, Mèze. 218 pp.
- Calbet, A., Broglio, E., Saiz, E., Alcaraz, M., 2002. Low grazing impact of mesozooplankton on the microbial communities of the Alboran Sea: a possible case of inhibitory effects by the toxic dinoflagellate *Gymnodinium catenatum*. *Aquatic microbial ecology* 26, 235-246.
- Cochrane, K., de Young, C., 2008. Ecosystem approach to fisheries management in the Mediterranean. United Nations Food and Agriculture Organization. Options Mediterranean Series 62, 71-85.
- Coll, M., Carreras, M., Cornax, M., Massutí, E., Morote, E., Pastor, X., Quetglas, A., Sáez, R., Silva, L., Sobrino, I., 2014. Closer to reality: Reconstructing total removals in mixed fisheries from Southern Europe. *Fisheries Research* 154, 179-194.
- Coll, M., Libralato, S., 2012. Contributions of food-web modelling for an Ecosystem Approach of Marine Resource Management in the Mediterranean Sea. *Fish and Fisheries* 13, 60-88.
- Coll, M., Navarro, J., Olson, R., Christensen, V., 2013a. Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. *Deep Sea Research II: Topical Studies in Oceanography* 95, 21-36.
- Coll, M., Navarro, J., Palomera, I., 2013b. Ecological role of the endemic Starry ray *Raja asterias* in the NW Mediterranean Sea and management options for its conservation. *Biological Conservation* 157, 108-120.
- Coll, M., Palomera, I., Tudela, S., 2009. Decadal changes in a NW Mediterranean Sea food web in relation to fishing exploitation. *Ecological Modelling* 220, 2088-2102.

- Coll, M., Palomera, I., Tudela, S., Dowd, M., 2008. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978-2003. *Ecological Modelling* 217, 95-116.
- Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006a. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *Journal of Marine Systems* 59, 63-96.
- Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W., Christensen, V., Karpouzi, V., Le Loc, F., Mouillot, D., Paleczny, M., Palomares, M.L., Steenbeek, J., Trujillo, P., Watson, R., Pauly, D., 2012. The Mediterranean Sea under siege: spatial overlap between marine biodiversity, cumulative threats and marine reserves. *Global Ecology and Biogeography* 21, 465-480.
- Coll, M., Piroddi, C., Kaschner, K., Ben Rais Lasram, F., Steenbeek, J., Aguzzi, J., Ballesteros, E., Nike Bianchi, C., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Frogliola, C., Galil, B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-S., Koukouras, A., Lampadariou, N., Laxamana, E., López-Fé de la Cuadra, C.M., Lotze, H.K., Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., 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, doi:10.1371.
- Coll, M., Santojanni, A., Palomera, I., Tudela, S., Arneri, E., 2007. An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. *Journal of Marine Systems* 67, 119-154.
- Coll, M., Shannon, L.J., Moloney, C.L., Palomera, I., Tudela, S., 2006b. Comparing trophic flows and fishing impacts of a NW Mediterranean ecosystem with coastal upwelling systems by means of standardized models and indicators. *Ecological Modelling* 198, 53-70.
- Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M., Fiorentino, F., 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish and Fisheries* 14, 89-109.
- Corrales, X., 2013. Modelización ecológica del Mediterráneo Noroccidental: estructura del ecosistema e impactos de la pesca, Master en Gestión Pesquera Sostenible, 4a edición. Universidad de Alicante, p. 186 pp.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J., Verheye, H.M., 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp-waist" ecosystems. *ICES Journal of Marine Science* 57, 603.
- Christensen, V., 1995. Ecosystem maturity - towards quantification. *Ecological Modelling* 77, 3-32.
- Christensen, V., Walters, C., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 72, 109-139.
- Christensen, V., Walters, C., Pauly, D., Forrest, R., 2008. Ecopath with Ecosim version 6. User Guide - November 2008. Lenfest Ocean Futures Project 2008, 235 pp.
- Daskalov, G.M., 2002. Overfishing drives a trophic cascade in the Black Sea. *Marine Ecology Progress Series* 225, 53-63.
- Demaneche, S., Merrien, C., Berthou, P., Lespagnol, P., 2009. Rapport R3 Méditerranée continentale, échantillonnage des marées au débarquement. Méthode d'évaluation et évaluation des captures et de l'effort de pêche des flottilles de la façade Méditerranée continentale sur la période 2007-2008. Programme P6

- AESYPECHE “Approche écosystémique de l’halieutique” Project Système d’Informations Halieutiques. IFREMER, France, p. 54 pp.
- Estrada, M., 1996. Primary production in the northwestern Mediterranean. *Scientia Marina* 60, 55-64.
- FAO, 2012. The State of World Fisheries and Aquaculture, Rome.
- Farrugio, H., Papaconstantinou, C., 1998. The status of fisheries resources in the Mediterranean. In: R. Robles and Ph. Ferlin (mod.). Workshop on gaps in Fishery Science. CIESM Workshop Series No 5: 13-24.
- Finn, J.T., 1976. Measures of ecosystem structure and function derived from analysis of flows. *Journal of Theoretical Biology* 56, 363-380.
- Forestal, F., Coll, M., Christensen, V., Die, D., 2012. Ecosystem effects of Bluefin Tuna (*Thunnus thynnus thynnus*) aquaculture in the North-Western Mediterranean Sea. *Marine Ecology Progress Series* 456, 215-231.
- 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). *Journal of Marine Systems* 102-105, 39-51.
- Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308, 1621-1623.
- Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor. Cambridge University Press, Cambridge.
- García-Rodríguez, M., Fernández, A.M., Pérez-Gil, J.L., Esteban, A., 2010. Stock assesment of the Hake (*Merluccius merluccius*) in the Northern Spain. GFCM-SAC.
- García, E., Bellido, J.M., Torres, P., Quintanilla, L., Giráldez, A., Alemany, F., Iglesias, M., González, M., 2011a. Stock assessment of the anchovy (*Engraulis encrasicolus*) stock of the Northern Spain. GFCM-SAC.
- García, E., Bellido, J.M., Torres, P., Quintanilla, L., Giráldez, A., Alemany, F., Iglesias, M., González, M., 2011b. Stock assessment of the sardine (*Sardina pilchardus*) stock of the Northern Spain. GFCM-SAC.
- Garcia, S.M., Zerbi, A., Aliaume, C., Do Chi, T., Lasserre, G., 2003. The ecosystem approach to fisheries. Issues, terminology, principles, institutional foundations, implementation and outlook. FAO Fisheries Technical Paper 443, 71.
- Gaudin, C., de Young, C., 2007. Recreational fisheries in the Mediterranean countries: a review of existing legal frameworks. *Studies and Reviews. FAO-GFCM* 81, 104.
- GFCM, 2013. Report of the 15th Session of the Scientific Advisory Committee (SAC). , Rome, 8-11 April 2013., p. 87 pp.
- Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., Bigot, J.-L., Tičina, V., Pyrounaki, M., 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fisheries Oceanography* 22, 69-89.
- Giannoulaki, M., Pyrounaki, M.M., Liorzou, B., Leonori, I., Valavanis, V.D., Tsagarakis, K., Bigot, J.L., Roos, D., De Felice, A., Campanella, F., 2011. Habitat suitability modelling for sardine juveniles (*Sardina pilchardus*) in the Mediterranean Sea. *Fisheries Oceanography* 20, 367-382.
- Gómez de Segura, A., Crespo, E.A., Pedraza, S.N., Hammond, P.S., Raga, J.A., 2006a. Abundance of small cetaceans in waters of the central Spanish Mediterranean. *Marine Biology* 150, 149-160.
- Gómez de Segura, A., Tomás, J., Pedraza, S.N., Crespo, E.A., Raga, J.A., 2006b. Abundance and distribution of the endangered loggerhead turtle in Spanish

- Mediterranean waters and the conservation implications. *Animal Conservation* 9, 199-206.
- Hattab, T., Ben Rais Lasram, F., Albouy, C., Romdhane, M.S., Jarboui, O., Halouani, G., Cury, P., Le Loc'h, F., 2013. An ecosystem model of an exploited southern Mediterranean shelf region (Gulf of Gabes, Tunisia) and a comparison with other Mediterranean ecosystem model properties. *Journal of Marine Systems*.
- Heymans, J.J., Coll, M., Libralato, S., Christensen, V., 2012. 9.06. Ecopath theory, modelling and application to coastal ecosystems, in: Editors-in-Chief, E.W.D.M.a.V.E.D.B.A.M. (Ed.), *In Treatise on Estuarine and Coastal Science*, pp. 93-113.
- Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 723-732.
- Jadaud, A., Guijarro, B., Massutí, E., Farrugio, H., 2011a. Stock assessment of the French-Spanish shared stock of hake (*Merluccius merluccius*) in the Gulf of Lions. GFCM-SAC.
- Jadaud, A., Guijarro, B., Massutí, E., Farrugio, H., 2011b. Stock assessment of the French-Spanish shared stock of *Mullus barbatus* in the Gulf of Lions. GFCM-SAC.
- Lalli, C.M., Parsons, T.R., 1993. *Biological oceanography: An Introduction*. Pergamon Press.
- Libralato, S., Coll, M., Tudela, S., Palomera, I., Pranovi, F., 2008. Novel index for quantification of ecosystem effects of fishing as removal of secondary production. *Marine Ecology Progress Series* 355, 107-129.
- Libralato, S., Christensen, V., Pauly, D., 2006. A method for identifying keystone species in food web models. *Ecological Modelling* 195, 153-171.
- Lindeman, R.L., 1942. The trophic-dynamic aspect of ecology. *Ecology* 23, 399-418.
- Link, J., 2011. *Ecosystem-based fisheries Management: confronting tradeoffs*. Cambridge University Press, Cambridge.
- Lotze, H.K., Coll, M., Dunne, J., 2011. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea. *Ecosystems* 14, 198-222.
- Lleonart, J., 1990. *La pesquería de Cataluña y Valencia: descripción global y planteamiento de bases para su seguimiento*. Final Report to EC DG XIV.
- Lleonart, J., Maynou, F., 2003. Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina* 67, 37-49.
- Lleonart, J., Salat, J., Olivar, P., Puig, P., Moranta, J., Le Corre, G., Sacchi, J., Franquesa, R., Tudela, S., 2008. Standard format for the submission of proposals for GFCM Fisheries Restricted Areas (FRA) in the Mediterranean: Continental slope of the Eastern Gulf of Lions.
- Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R., Nykjaer, L., Rosenberg, A.A., 2013. Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PLoS ONE* 8, e79889.
- Millot, C., 1999. Circulation in the Western Mediterranean Sea. *Journal of Marine Systems* 20, 423-442.
- Moloney, C.L., Jarre, A., Arancibia, H., Bozec, Y.-M., Neira, S., Roux, J.-P., Shannon, L.J., 2005. Comparing the Benguela and Humboldt marine upwelling ecosystems with indicators derived from inter-calibrated models. *ICES Journal of Marine Science: Journal du Conseil* 62, 493-502.



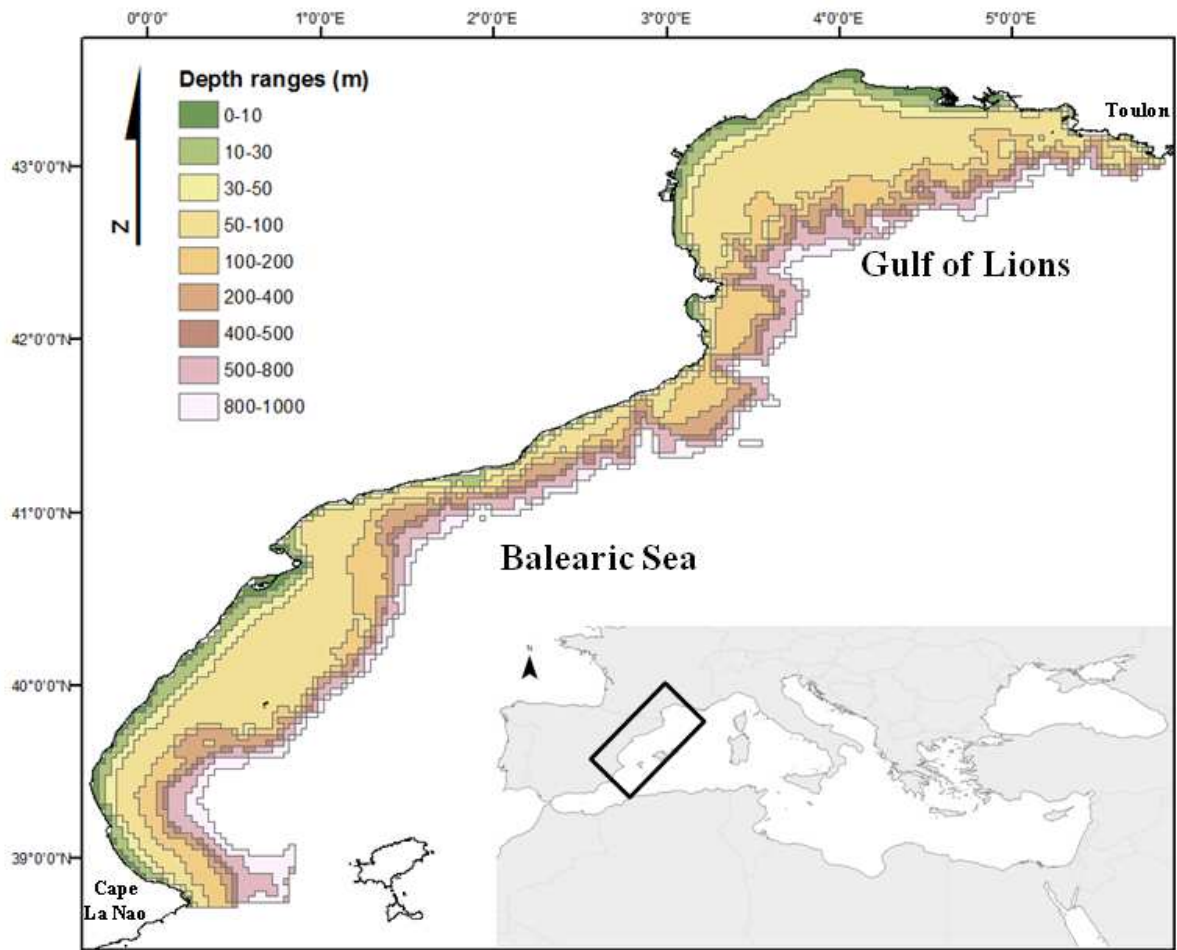
- Morissette, L., 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the gulf of St. Lawrence. University of British Columbia, Vancouver, p. 260.
- Moutopoulos, D.K., Libralato, S., Solidoro, C., Stergiou, K.I., 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. *Journal of Marine Systems*.
- Odum, E.P., 1969. The strategy of ecosystem development. *Science* 104, 262-270.
- Odum, E.P., 1971. *Fundamentals of Ecology*. Saunders, Philadelphia, PA (USA).
- Opitz, S., 1996. *Quantitative Models of Trophic Interactions in Caribbean Coral Reefs*. ICLARM. Manila, Philippines.
- Ordines, F., Quetglas, A., Massutí, E., Gil de Sola, L., Preciado, I., Farriols, M.A., 2012. Estrategia Marina. Demarcación Marina Levantino-Balear. Parte IV: Descriptores del buen estado ambiental. Descriptor 4: Redes tróficas. Evaluación inicial y buen estado ambiental. Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA) and Instituto Español de Oceanografía (IEO). p. 72 pp.
- Ospina-Alvarez, A., Parada, C., Palomera, I., 2012. Vertical migration effects on the dispersion and recruitment of European anchovy larvae: From spawning to nursery areas. *Ecological Modelling* 231, 65-79.
- Palomera, I., Olivar, M.P., Salat, J., Sabates, A., Coll, M., Garcia, A., Morales-Nin, B., 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography* 74, 377-396.
- Patterson, K., 1992. Fisheries for small pelagic species: an empirical approach to management targets. *Reviews in Fish Biology and Fisheries* 2, 321-338.
- Pauly, D., Christensen, V., 1995. Primary Production Required to Sustain Global Fisheries. *Nature* 374, 255-257.
- Pauly, D., Graham, W., Libralato, S., Morissette, L., Palomares, M.L.D., 2009. Jellyfish in ecosystems, online databases, and ecosystem models. *Hydrobiologia* 616, 67-85.
- Pauly, D., Palomares, M.L.D., 2010. An empirical equation to predict annual increases in fishing efficiency. Fisheries Centre University of British Columbia. Working Paper Series 07.
- Pauly, D., Ulman, A., Piroddi, C., Bultel, E., Coll, M., 2014. 'Reported' versus 'likely' fisheries catches of four Mediterranean countries. *Scientia Marina* 78, 11-17.
- Piroddi, C., Bearzi, G., Christensen, V., 2010. Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. *Ecological Modelling* 221, 1526-1544.
- Pitcher, T., Cheung, W.W.L., 2013. Fisheries: Hope or despair? *Marine Pollution Bulletin* 74, 506-516.
- Plagányi, É., 2007. *Models for an Ecosystem Approach to Fisheries*. Food and Agriculture Organization, Rome, Italy.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. *BioScience* 46, 609-620.
- Quetglas, A., Guijarro, B., Ordines, F., Massutí, E., 2012. Stock boundaries for fisheries assessment and management in the Mediterranean: the Balearic Islands as a case study. *Scientia Marina* 76, 17-28.
- Ramos, F., Gil, J., Torres, M.A., Silva, L., Vila, Y., Sánchez, R., Jiménez, M.P., Baldó, F., Fernández-Salas, L.M., Rueda, J.L., Díaz del Río, V., Vázquez, J.T., López-

- González, N., Lens, S., Bellas, J., Besada, V., Viñas, L., González-Quijano, A., Franco, M.A., Fumega, J., 2012. Estrategias Marinas. Demarcación Marina Sudatlántica. Parte I. Marco General: Características de la demarcación marina. Ministerio de Agricultura, Alimentación y Medio Ambiente (MAGRAMA), Instituto Español de Oceanografía (IEO), p. 127 pp.
- Rochet, M.-J., Trenkel, V.M., 2003. Which community indicators can measure the impact of fishing? A review and proposals. *Canadian Journal of Fisheries and Aquatic Sciences* 60, 86-99.
- Sabatés, A., Salat, J., Olivar, M.P., 2001. Advection of continental water as an export mechanism for anchovy, *Engraulis encrasicolus*, larvae. *Scientia Marina* 65, 77-87.
- Salat, J., 1996. Review of hydrographic environmental factors that may influence anchovy habitats in Northwestern Mediterranean. *Scientia Marina* 60, 21– 32.
- Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. *Ecological Modelling* 172, 151-174.
- Shannon, L.J., Moloney, C.L., Jarre, A., Field, J.G., 2003. Trophic flows in the southern Benguela during the 1980s and 1990s. *Journal of Marine Systems* 39, 83-116.
- Stergiou, K.I., Karpouzi, V.S., 2001. Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries* 11, 217-254.
- Swartz, W., Sala, E., Tracey, S., Watson, R., Pauly, D., 2010. The Spatial Expansion and Ecological Footprint of Fisheries (1950 to Present). *PLoS ONE* 5, e15143.
- Tecchio, S., Coll, M., Christensen, V., Company, J.B., Ramírez-Llodra, E., Sardà, F., 2013. Food web structure and vulnerability of a deep-sea ecosystem in the NW Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 75, 1-15.
- Torres, M.A., Coll, M., Heymans, J.J., Christensen, V., Sobrino, I., 2013. Food-web structure of and fishing impacts on the Gulf of Cadiz ecosystem (South-western Spain). *Ecological Modelling* 265, 26-44.
- 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. *Estuarine, Coastal and Shelf Science* 88, 233-248.
- Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. *Coenos* 5, 7-16.
- Valls, A., Coll, M., Christensen, V., In press. Keystone species: towards an operational concept for marine biodiversity conservation. *Ecological Monographs*.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in Fish Biology and Fisheries* 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.
- Ware, D.M., Thomson, R.E., 2005. Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. *science* 308, 1280-1284.
- Watson, R.A., Cheung, W.W.L., Anticamara, J.A., Sumaila, R.U., Zeller, D., Pauly, D., 2013. Global marine yield halved as fishing intensity redoubles. *Fish and Fisheries* 14, 493-503.
- Watson, R.A., Morato, T., 2013. Fishing down the deep: Accounting for within-species changes in depth of fishing. *Fisheries Research* 140, 63-65.

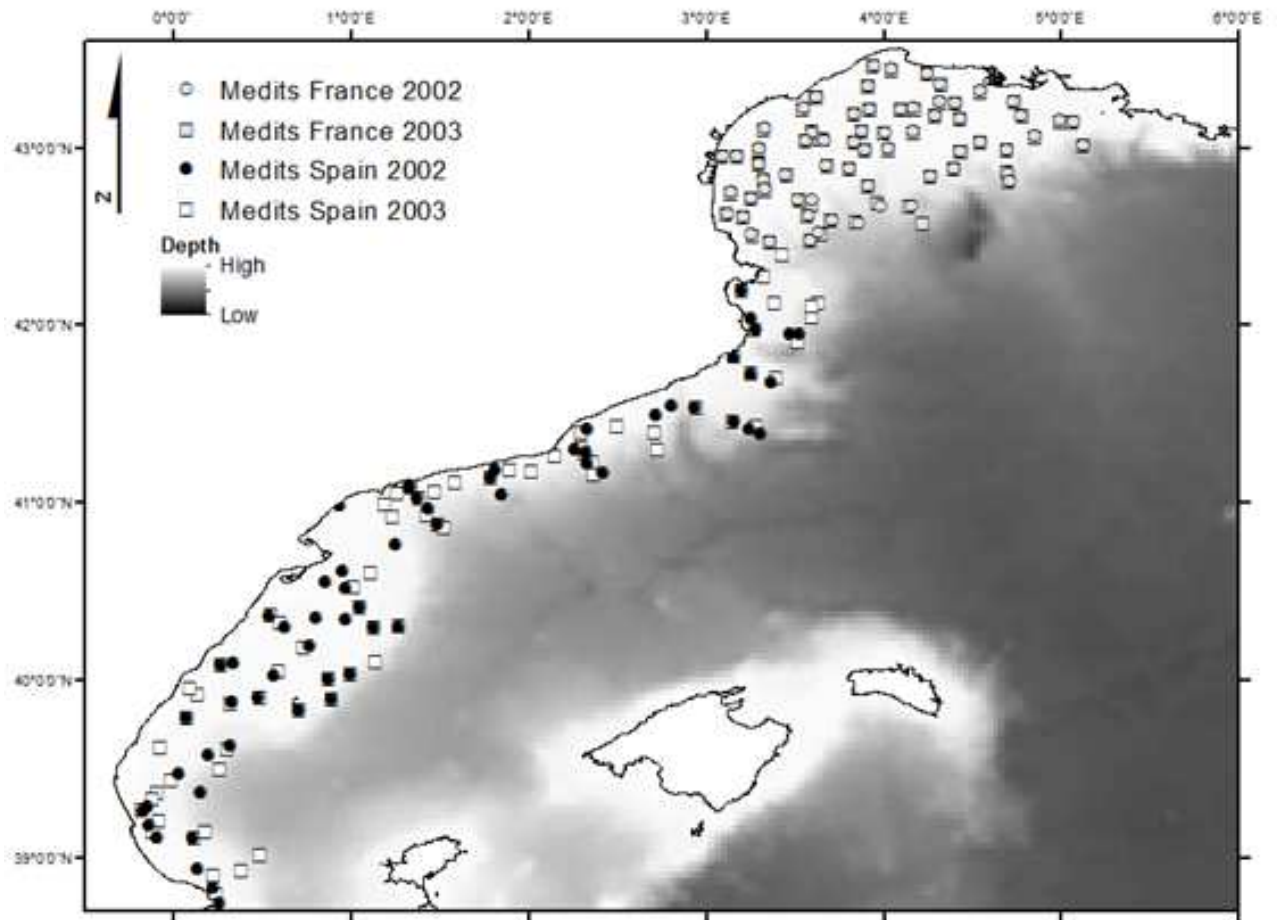
- Worm, B., Branch, T.A., 2012. The future of fish. *Trends in Ecology & Evolution* 27, 594-599.
- Würtz, M., 2012. Mediterranean submarine canyons: Ecology and governance. IUCN.
- Zeller, D., Pauly, D., 2007. Reconstruction of marine fisheries catches for key countries and regions (1950-2005). *Fisheries Centre Research Report* 15, 163.

ACCEPTED MANUSCRIPT

**Fig. 1.** The NW Mediterranean Sea (GSA 6 and 7), showing the modelled area (0-1000m) and depth ranges.

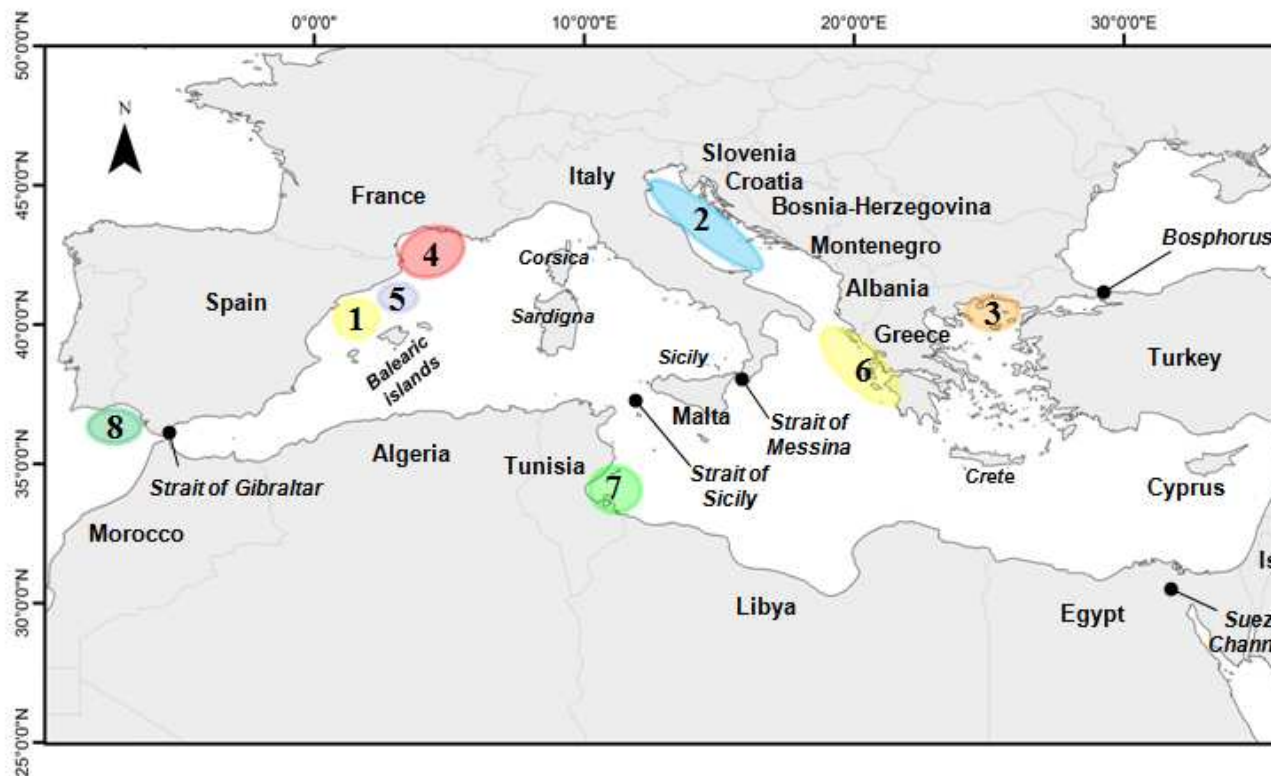


**Fig. 2.** Location of hauls of MEDITS surveys used to parameterize the initial values of demersal and benthic groups in the NWM model.

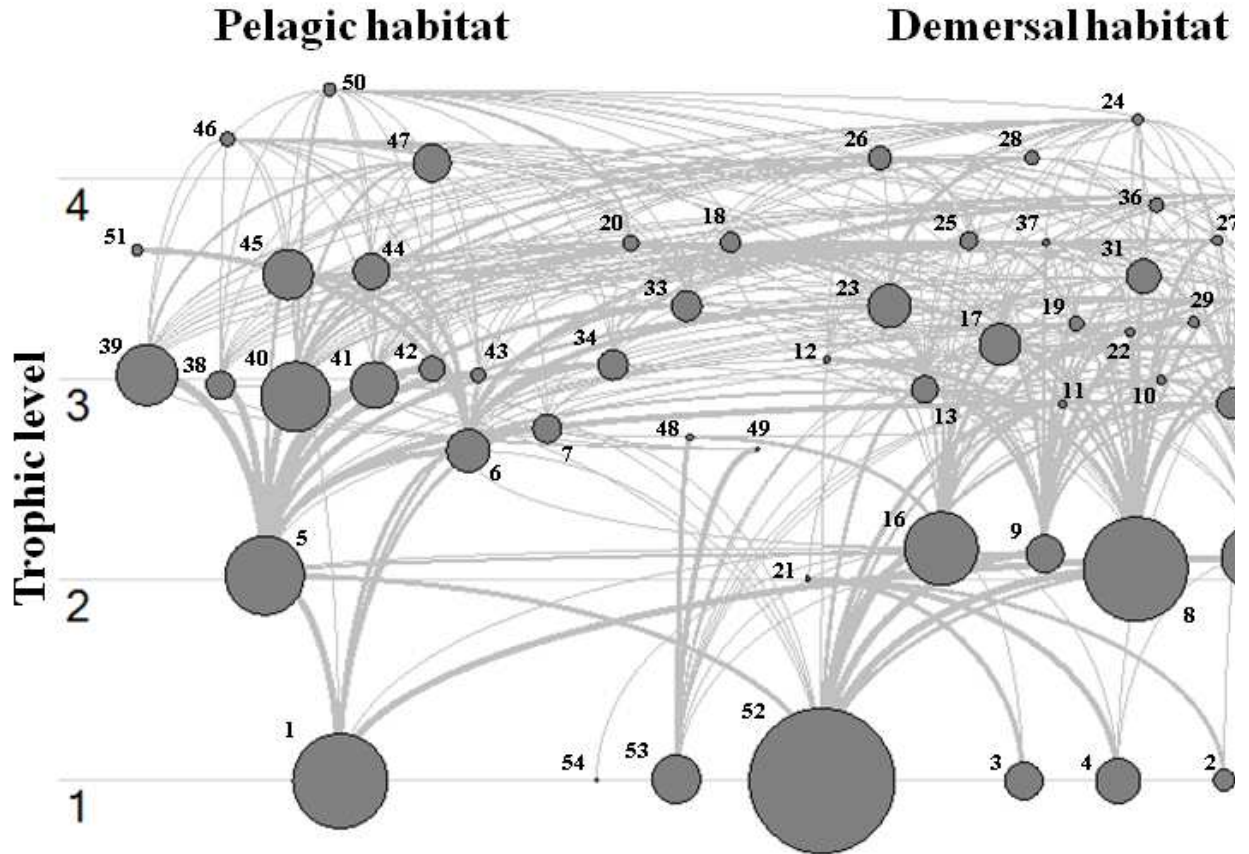


**Fig. 3.** Location of Ecopath models used in the comparative analysis.

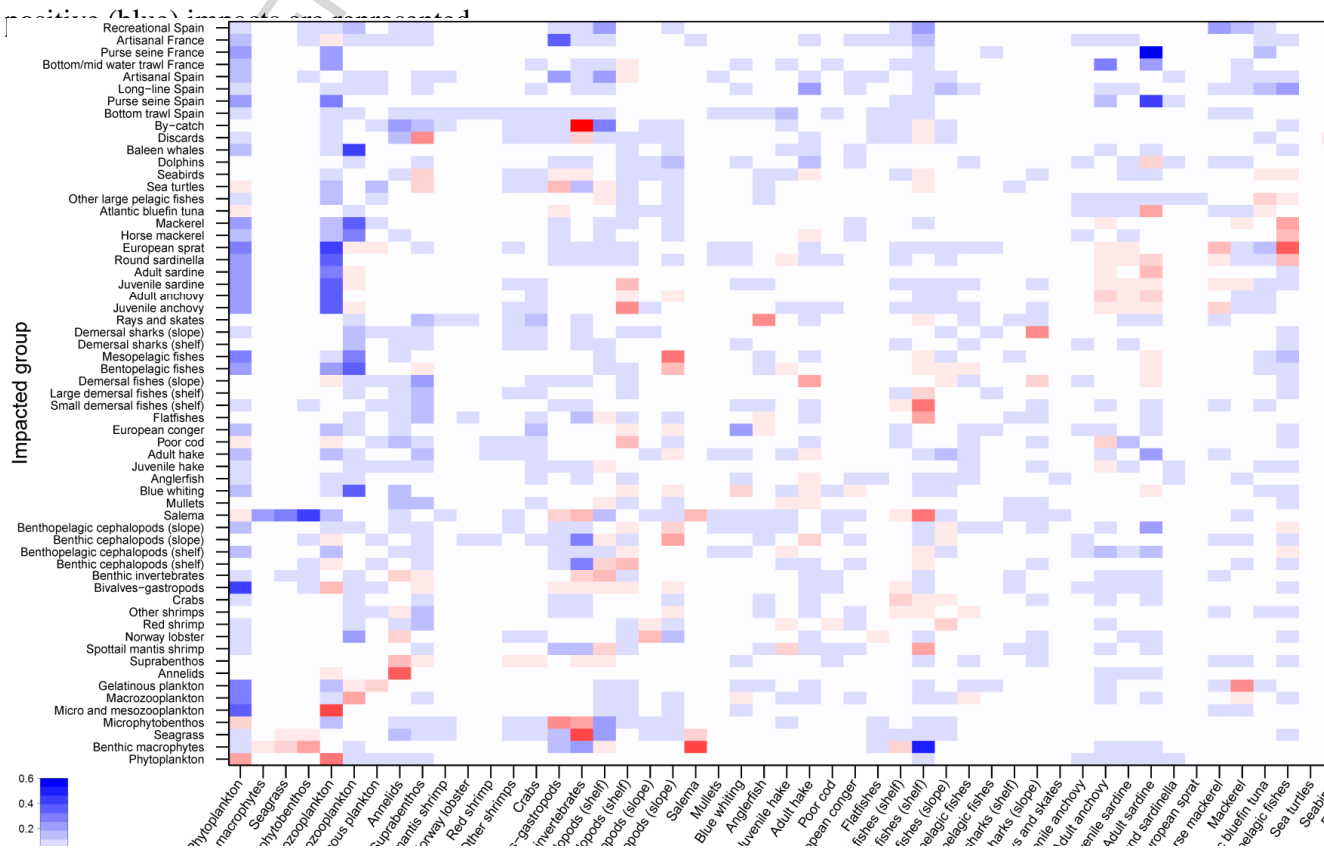
1: South Catalan Sea (SCS, Coll et al. (2006a)); 2: North-Central Adriatic Sea (NCAS, Coll et al. (2007)); 3: North Aegean Sea (NAS, Tsagarakis et al. (2010)); 4: Gulf of Lions (GoL, Banaru et al. (2013)); 5: Lower continental slope of the Catalan Sea (DCS, Tecchio et al. (2013)); 6: Greek Ionian Sea (IS, Moutopoulos et al. (2013)); 7: Gulf of Gabes (GoG, Hattab et al. (2013)); 8: Gulf of Cadiz (GoC, Torres et al. (2013)).



**Fig. 4.** Flow diagram of the NWM model. The size of each circle is proportional to the biomass of the functional group. The numbers identify the functional groups of the NWM model (Table 1). The wideness of the connecting lines is proportional to the magnitude of their flows.

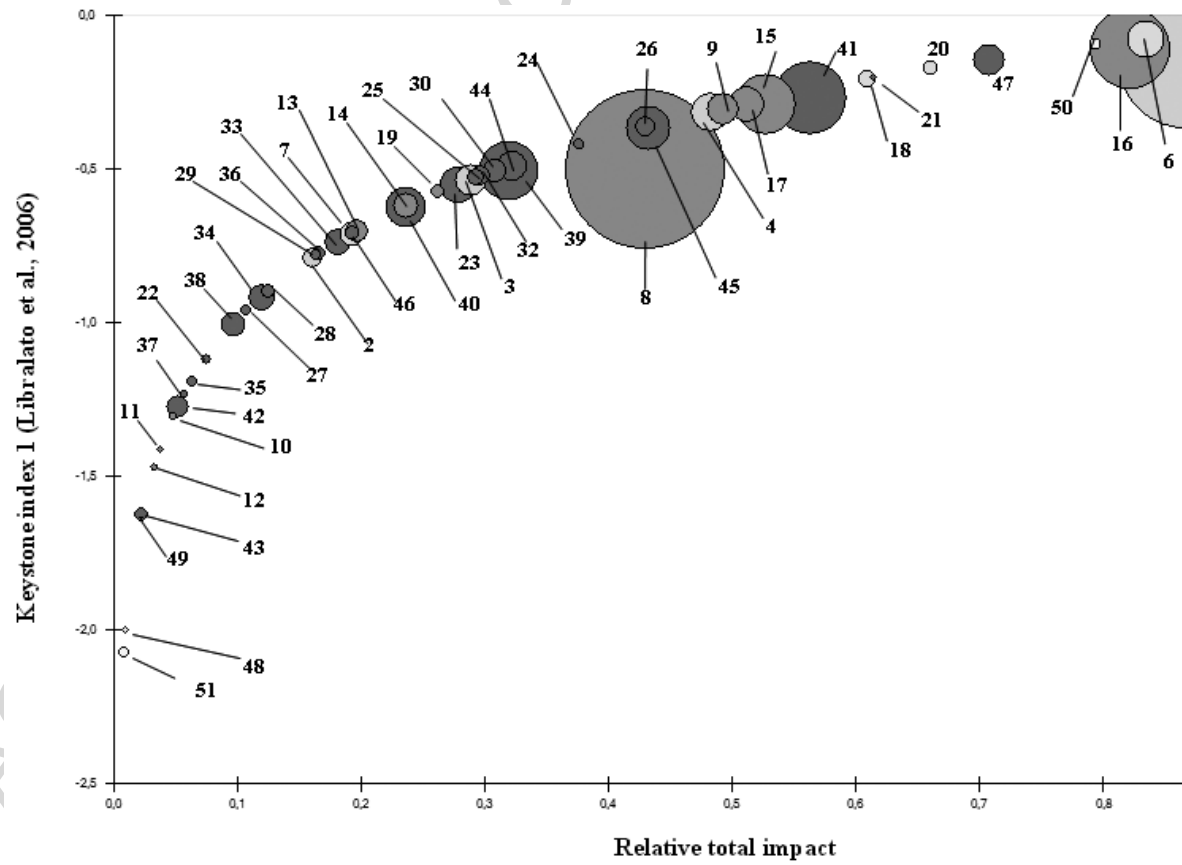


**Fig. 5.** Mixed trophic Impact (MTI) analysis of the NWM model. Negative (red) and



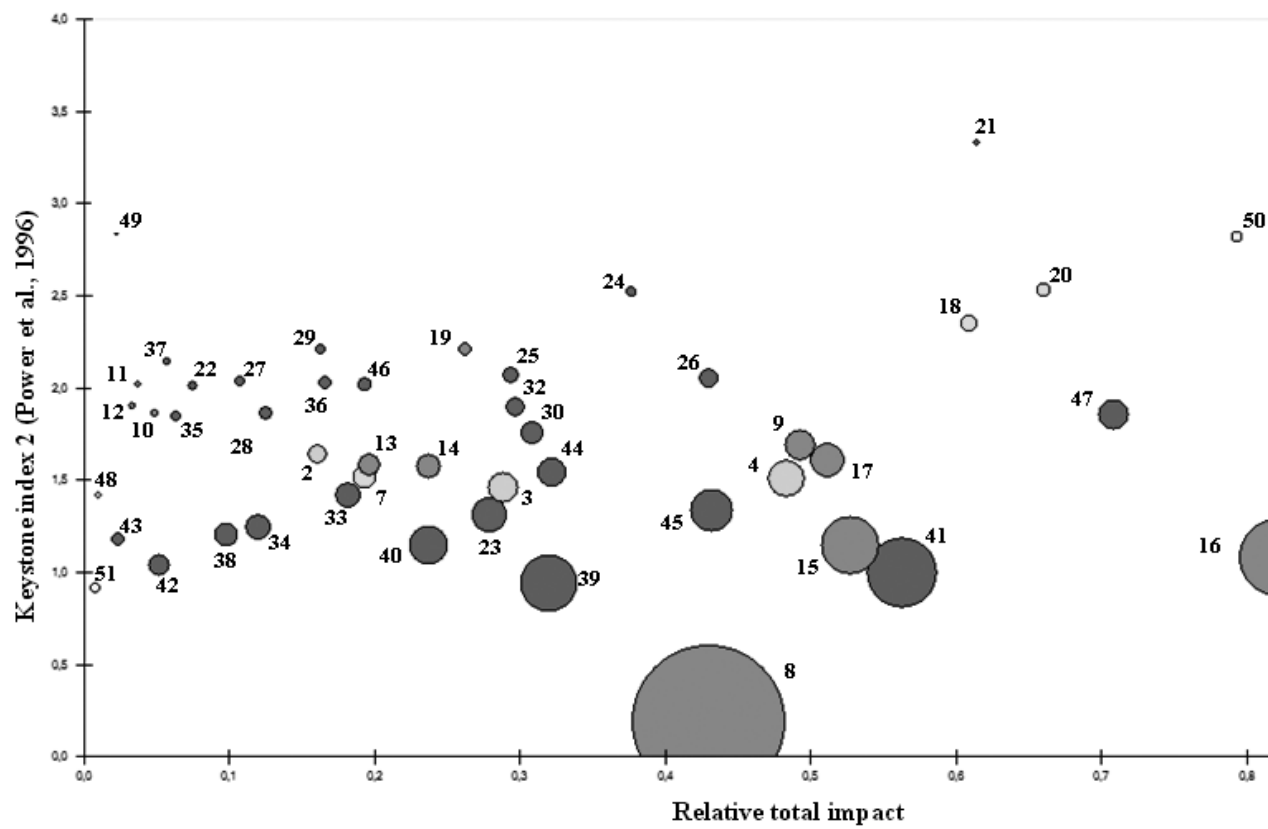
**Fig. 6.** Keystone Index analysis of the NWM model. The size of each circle is proportional to the biomass of the functional groups (a) indicator *sensu* Libralato et al. (2006), and (b) indicator *sensu* Power et al. (1996). The numbers identify the functional groups of the NWM model (Table 1).

a)



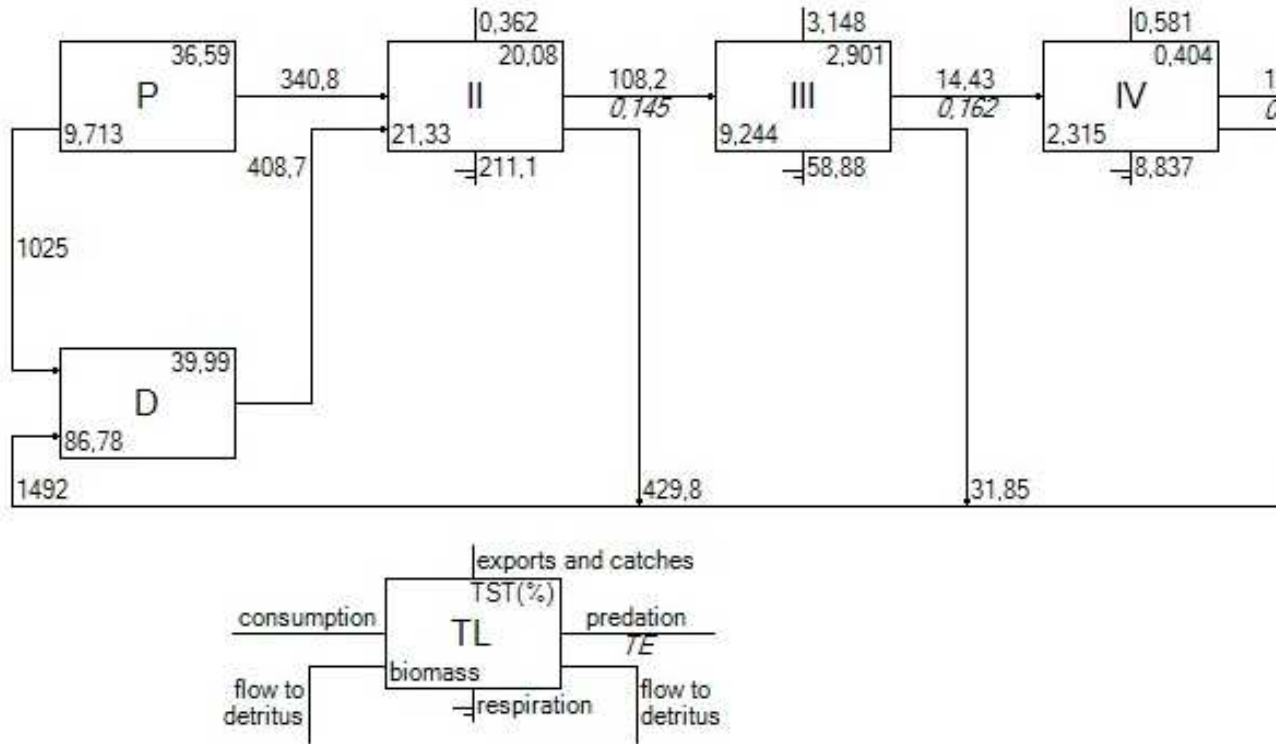


b)



ACCE

**Fig. 7.** Trophic flows of the NWM model organized by integer trophic levels (TL) in the form of Lindeman spine. TL I is split into primary producers (P) and detritus (D). The flows are represented in  $t \cdot km^{-2} \cdot year^{-1}$ .



## Tables

**Table 1.** Input data of the NWM model by functional group.  $B_i$  = initial biomass ( $t \cdot km^{-2}$ );  $P/B$  = production/biomass ( $year^{-1}$ );  $Q/B$  = consumption/biomass ( $year^{-1}$ );  $U/Q$  = unassimilated food/consumption; landings and discards ( $t \cdot km^{-2} \cdot years^{-1}$ ).

FG	Functional group	Bi	P/B	Q/B	U/Q	Landings	Discards
1	Phytoplankton	8.46	161.72	-	-	-	-
2	Benthic macrophytes	0.16	1.08	-	-	-	-
3	Seagrass	0.44	2.35	-	-	-	-
4	Microphytobenthos	0.66	4.20	-	-	-	-
5	Micro and mesozooplankton	3.90	41.70	120.82	0.40	-	-
6	Macrozooplankton	0.62	19.96	49.82	0.20	-	-
7	Gelatinous plankton	0.26	13.57	49.38	0.20	-	-
8	Annelids	12.01	2.71	20.15	0.60	-	-
9	Suprabenthos	0.44	7.87	52.12	0.30	-	-
10	Spottail mantis shrimp	0.0005	57.30	8.59	0.20	0.020	0.006
11	Norway lobster	0.02	1.13	7.26	0.20	0.010	0.003
12	Red shrimp	0.02	1.35	8.72	0.20	0.011	0.002
13	Other shrimps	0.02	1.71	8.49	0.20	0.013	0.005
14	Crabs	0.03	1.93	7.07	0.20	0.023	0.007
15	Bivalves-gastropods	1.66	1.00	4.09	0.40	0.138	0.015
16	Other benthic invertebrates	1.99	0.44	2.75	0.40	0.005	0.001
17	Benthic cephalopods (continental shelf)	0.06	5.06	4.41	0.13	0.185	0.051
18	Benthopelagic cephalopods (continental shelf)	0.02	1.41	26.47	0.40	0.019	0.006
19	Benthic cephalopods (upper slope)	0.01	0.91	4.41	0.13	0.003	0.001
20	Benthopelagic cephalopods (upper slope)	0.01	1.60	26.47	0.40	0.008	0.003
21	Salema	0.001	7.98	10.59	0.20	0.006	0.001
22	Mulletts	0.03	2.66	7.14	0.20	0.047	0.017
23	Blue whiting	0.28	0.74	5.80	0.20	0.074	0.023
24	Anglerfish	0.05	0.92	3.03	0.20	0.028	0.007
25	Juvenile hake	0.06	2.69	7.22	0.20	0.102	0.016
26	Adult hake	0.02	2.17	3.05	0.20	0.039	0.005
27	Poor cod	0.04	1.97	6.83	0.20	0.045	0.011
28	European conger	0.02	2.53	2.82	0.20	0.037	0.007
29	Flatfishes	0.02	4.39	7.46	0.20	0.052	0.009
30	Small demersal fishes (continental shelf)	0.07	1.63	7.60	0.20	0.046	0.010
31	Large demersal fishes (continental shelf)	0.14	2.09	5.95	0.20	0.190	0.038
32	Demersal fishes (upper slope)	0.16	0.55	5.85	0.20	0.021	0.007
33	Benthopelagic fishes	0.14	0.64	8.58	0.30	0.005	0.001
34	Mesopelagic fishes	0.05	0.78	7.13	0.30	0.013	0.003
35	Demersal sharks (continental shelf)	0.04	0.40	4.49	0.20	0.003	0.001
36	Demersal sharks (upper slope)	0.07	0.30	4.93	0.20	0.003	0.001
37	Rays and skates	0.02	0.60	6.05	0.20	0.005	0.001
38	Juvenile anchovy	0.27	1.45	21.30	0.30	0.019	0.005
39	Adult anchovy	1.61	1.21	10.22	0.30	0.565	0.156
40	Juvenile sardine	0.74	1.70	19.72	0.30	0.038	0.013
41	Adult sardine	2.46	1.43	9.08	0.30	1.209	0.345
42	Round sardinella	0.21	1.14	7.81	0.30	0.059	0.030
43	European sprat	0.07	0.94	11.18	0.30	0.0004	0.0001
44	Horse mackerel	0.40	0.68	5.76	0.20	0.089	0.019
45	Mackerel	0.88	0.79	4.99	0.20	0.087	0.024
46	Atlantic bluefin tuna	0.08	1.26	1.70	0.20	0.080	0.011

47	Other large pelagic fishes	0.44	0.54	4.01	0.20	0.021	0.003
48	Sea turtles	0.02	0.17	2.48	0.20	-	0.0006
49	Seabirds	0.001	4.47	70.89	0.20	-	0.00002
50	Dolphins	0.05	0.03	12.32	0.20	-	0.0005
51	Baleen whales	0.04	0.04	4.11	0.30	-	-
52	Detritus	85.92	-	-	-	-	-
53	Discards	0.86	-	-	-	-	-
54	By-catch	0.00	-	-	-	-	-

---

ACCEPTED MANUSCRIPT

**Table 2.** Modified input parameters and outputs obtained from the NWM model. TL = Trophic Level; Bf = Final Biomass ( $t \cdot km^{-2}$ ); EE = Ecotrophic Efficiency; P/Q = Production/Consumption ratio; R/B = Respiration/Biomass ratio ( $year^{-1}$ ); R/A = Respiration/Assimilation ratio; P/R = Production/Respiration ratio; NE = Net Efficiency; F = Fishing Mortality ( $years^{-1}$ ); M2= Predation Mortality ( $years^{-1}$ ); M0 = Other Natural Mortality ( $years^{-1}$ ); F/Z = Exploitation Rate; P = Production ( $t \cdot km^{-2} \cdot years^{-1}$ ); Q = Consumption ( $t \cdot km^{-2} \cdot years^{-1}$ ); Oi = Omnivory Index; FD = Flow to Detritus ( $t \cdot km^{-2} \cdot years^{-1}$ ).

F G	Functional group	T L	Bf	E E	P / Q	R/ B	R / A	P / R	N E	F	M 2	M 0	F / Z	P	Q	O I	FD
1	Phytoplankton	1. 0 0	8. 46 5	0. 2 -	- -	- -	- -	- -	- -	- -	40 .1 7	12 0.8 3	-	136 1.7 3	- -	- -	102 2.0 2
2	Benthic macrophytes	1. 0 0	0. 16 1	0. 2 -	- -	- -	- -	- -	- -	- -	0. 22 6	0.8 6 -	-	0.1 7 -	- -	- -	0.1 4 -
3	Seagrass	1. 0 0	0. 44 5	0. 1 -	- -	- -	- -	- -	- -	- -	0. 36 9	1.9 9 -	-	1.0 3 -	- -	- -	0.8 7 -
4	Microphytobenthos	1. 0 0	0. 66 7	0. 2 -	- -	- -	- -	- -	- -	- -	1. 29 3	3.5 3 -	-	3.1 6 -	- -	- -	2.3 1 -
5	Micro and mesozooplankton	2. 0 2	3. 90 1	0. 6 3	30 .7 9	0. 4 2	1. 3 5	0. 5 8	- -	- -	25 .6 2	16. 08 -	-	162 .64 3	47 1.2 3	0 2 2	251 .20 -
6	Macrozooplankton	2. 6 4	0. 62 1	0. 9 0	0. 4 0	19 .9 0	0. 5 0	1. 0 0	0. 5 0	- -	18 .2 2	1.7 4 -	-	12. 28 66	30. 66 9	0. 2 9	7.2 0 0
7	Gelatinous plankton	2. 7 5	0. 26 9	0. 2 7	0. 2 3	25 .9 6	0. 5 2	0. 3 4	0. 3 -	- -	3. 96 1	9.6 1 -	-	3.4 9 71	12. 71 7	2 2 7	5.0 2 2
8	Annelids	2. 0 5	12. .0 1	0. 5 8	0. 1 3	5. 35 6	0. 6 1	0. 5 4	0. 3 4	- -	1. 57 4	1.1 4 -	-	32. 54 7	24 1.9 7	0 0 5	158 .92 -
9	Suprabenthos	2. 1 3	0. 44 4	0. 9 5	0. 1 1	28 .6 8	0. 7 8	0. 2 2	0. 2 -	- -	7. 36 1	0.5 1 -	-	3.4 8 03	23. 03 2	1 1 2	7.1 3 -
10	Spottail mantis shrimp	3. 0 0	0. 03 8	0. 9 0	0. 3 71	3. 6 3	0. 6 0	0. 3 8	0. 9 0	0. 9 28	1. 28 4	0.0 4 0	0.	0.0 7 2	0.2 2 2	0. 2 2	0.0 4 -
11	Norway lobster	2. 8 8	0. 02 0	0. 9 6	0. 2 92	3. 6 8	0. 4 8	0. 3 3	0. 8 0	0. 8 0	0. 89 0	0.2 0 2	0.	0.0 3 1	0.1 6 2	0. 6 2	0.0 3 -
12	Red shrimp	3. 1 0	0. 02 7	0. 9 4	0. 3 98	3. 5 7	0. 7 5	0. 4 3	0. 7 1	0. 4 1	2. 19 0	0.1 0 4	0.	0.0 5 6	0.1 6 0	0. 2 0	0.0 3 -
13	Other shrimps	2. 9 4	0. 22 3	0. 9 7	0. 3 69	3. 5 4	0. 8 4	0. 4 6	0. 0 8	0. 0 8	2. 79 3	0.2 3 3	0.	0.6 9 9	1.8 9 5	0. 3 5	0.4 3 -
14	Crabs	2. 8 8	0. 28 5	0. 9 8	0. 3 96	2. 5 2	0. 9 1	0. 4 8	0. 1 8	0. 4 1	2. 47 3	0.1 3 4	0.	0.7 5 6	1.9 6 3	0. 3 3	0.4 3 -
15	Bivalves-gastropods	2. 1 1	1. 66 0	0. 8 4	0. 2 45	1. 5 9	0. 6 9	0. 4 1	0. 0 9	0. 0 9	0. 70 0	0.2 0 9	0.	1.6 6 8	6.7 8 0	0. 1 0	3.0 5 -
16	Benthic invertebrates	2. 1	3. 00	0. 8	0. 2	1. 33	0. 5	0. 7	0. 4	0. 0	0. 81	0.2 0	0.	2.9 1	11. 18	0. 1	5.3 2

		6	0	6	7	6	3	0		0		8					
1	Benthic cephalopods	3.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.			
7	(continental shelf)	1	0.	9	4	2.	5	8	4	4	1.	0.1	2	0.9	2.4	0	0.3
		7	55	4	0	07	4	5	6	3	22	1	4	7	3	8	8
1	Benthopelagic	3.	0.	0.	0.	13	0.	0.	0.	0.	1.	0.0	0.	0.2	3.1	0.	1.2
8	cephalopods	6	12	9	0	.7	8	1	1	2	80	9	1	5	8	2	8
	(continental shelf)	8	6	8	8	7	5	3	1	1	0	0	0	1	1	1	1
1	Benthic cephalopods	3.	0.	0.	0.	2.	0.	0.	0.	0.	1.	0.0	0.	0.1	0.3	0.	0.0
9	(upper slope)	2	0.	9	4	07	5	8	4	0	65	6	3	3	1	1	5
		8	07	6	0	07	4	5	6	5	65	6	3	3	1	1	5
2	Benthopelagic	3.	0.	0.	0.	13	0.	0.	0.	0.	1.	0.0	0.	0.1	2.2	0.	0.9
0	cephalopods (upper	6	0.	9	0	.7	8	1	1	1	97	1	6	8	6	2	1
	slope)	8	09	9	8	8	7	5	3	3	97	1	6	8	6	4	1
2	Salema	2.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.1	3	0.0	0.0	0.	0.0
1		0	0.	9	1	6.	8	2	1	5	0.	0.1	3	1	5	0	3
		0	01	0	5	88	1	3	9	9	84	6	7	1	5	0	3
2	Mulletts	3.	0.	0.	0.	3.	0.	0.	0.	2.	0.	0.2	0.	0.0	0.2	0.	0.0
2		2	0.	9	3	05	5	8	4	0	0.	0.2	7	8	3	1	5
		4	03	1	7	05	3	7	7	4	39	3	7	8	3	0	5
2	Blue whiting	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.0	0.	0.5	3.4	0.	0.7
3		3	0.	9	1	71	8	2	2	1	75	2	8	6	9	1	0
		6	60	8	6	71	0	5	0	6	75	2	8	6	9	0	0
2	Anglerfish	4.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.0	0.	0.0	0.1	0.	0.0
4		2	0.	9	3	1.	6	6	3	7	0.	0.0	7	5	5	1	3
		9	05	7	0	50	2	1	8	1	18	3	8	5	5	6	3
2	Juvenile hake	3.	0.	0.	0.	4.	0.	0.	0.	1.	0	0.0	0.	0.1	0.7	0.	0.1
5		6	0.	9	2	22	7	3	2	0	33	5	4	6	8	2	6
		9	11	7	1	22	4	5	6	8	33	5	4	6	8	3	6
2	Adult hake	4.	0.	0.	0.	1.	5	8	4	2	0.	0.5	2	0.2	0.5	1	0.2
6		1	0.	5	3	40	3	9	7	7	41	7	1	1	5	6	0
		1	17	4	8	40	3	9	7	7	41	7	1	1	5	6	0
2	Poor cod	3.	0.	0.	0.	3.	0.	0.	0.	1.	0.	0.0	0.	0.0	0.2	0.	0.0
7		6	0.	9	2	49	6	5	3	3	58	8	6	8	9	2	6
		9	04	6	9	49	4	6	6	0	58	8	6	8	9	7	6
2	European conger	4.	0.	0.	0.	1.	5	0	5	5	0.	0.0	0.	0.0	0.2	0.	0.0
8		1	0.	9	4	13	0	0	0	9	51	3	2	8	1	1	4
		0	08	7	0	13	0	0	0	9	51	3	2	8	1	0	4
2	Flatfishes	3.	0.	0.	0.	3.	0.	0.	0.	1.	0.	0.0	0.	0.0	0.3	0.	0.0
9		2	0.	9	2	88	6	5	3	4	65	4	6	9	3	1	7
		8	04	8	8	88	5	4	5	0	65	4	7	9	3	1	7
3	Small demersal fishes	3.	0.	0.	0.	4.	0.	0.	0.	0.	1.	0.0	0.	0.3	1.7	0.	0.3
0	(continental shelf)	1	0.	9	2	45	7	3	2	2	36	3	4	8	8	1	7
		6	24	8	1	45	3	7	7	3	36	3	4	8	8	7	7
3	Large demersal fishes	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.0	0.	0.3	2.3	0.	0.4
1	(continental shelf)	5	0.	9	1	75	7	2	2	6	0.	0.0	6	9	0	2	3
		1	35	8	7	75	9	7	1	4	35	2	4	9	0	9	3
3	Demersal fishes	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.0	0.	0.1	0.9	0.	0.2
2	(upper slope)	4	0.	9	1	69	7	2	2	1	76	7	7	6	5	1	0
		0	3	7	69	9	7	1	7	7	76	7	7	6	5	1	0
3	Benthopelagic fishes	3.	0.	0.	0.	4.	7	2	2	0	1.	0.0	0.	0.3	2.5	1	0.7
3		3	0.	9	1	72	9	7	1	2	24	3	2	9	7	0	8
		7	30	8	5	72	9	7	1	2	24	3	2	9	7	0	8
3	Mesopelagic fishes	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.0	0.	0.3	2.1	0.	0.6
4		0	0.	9	1	92	7	2	2	0	97	5	5	2	4	3	6
		7	30	5	5	92	9	7	1	5	97	5	5	2	4	6	6
3	Demersal sharks	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.3	0.	0.0	0.1	0.	0.0
5	(continental shelf)	9	0.	2	0	19	8	1	1	0	0.	0.3	2	2	8	2	5
		2	04	2	9	19	9	3	1	9	00	1	2	2	8	0	5
3	Demersal sharks	3.	0.	0.	0.	3.	0.	0.	0.	0.	0.	0.1	0.	0.0	0.3	0.	0.0
6	(upper slope)	8	0.	5	0	64	9	0	0	0	10	4	0	2	3	2	8
		7	07	3	6	64	2	8	8	6	10	4	0	2	3	8	8
3	Rays and skates	3.	0.	0.	0.	4.	0.	0.	0.	0.	0.	0.1	0.	0.0	0.1	0.	0.0
7		6	0.	7	1	24	8	1	1	2	16	5	7	1	1	2	2
		8	02	4	0	24	8	4	2	8	16	5	7	1	1	5	2
3	Juvenile anchovy	2.	0.	0.	0.	13	0.	0.	0.	0.	1.	0.0	0.	0.3	5.7	0.	1.7
8		9	0.	9	0	.4	9	1	1	0	34	2	6	9	1	0	2
		7	27	9	7	6	0	1	0	9	34	2	6	9	1	5	2

3 9	Adult anchovy	3. 0 2	1. 61 9	0. 9 2	0. 1 9	0. 5 2	0. 8 3	0. 2 0	0. 1 7	0. 4 5	0. 0 76	0.0 1 1	3 5 7	1.9 5 4	16. 46 0	0. 0 0	4.9 5 5
4 0	Juvenile sardine	2. 9 7	0. 74 4	0. 9 9	0. 0 0	12 .1 0	0. 8 4	0. 1 2	0. 1 7	0. 0 7	0. 0 0	1. 0.1 0	0 0 4	1.2 6 6	14. 61 5	0. 0 5	4.4 6 6
4 1	Adult sardine	2. 9 1	2. 46 8	0. 9 6	0. 1 6	4. 93 8	0. 7 8	0. 2 9	0. 2 2	0. 6 3	0. 6 77	0.0 0 3	4 4 4	3.5 22. 34	22. 1 0	0. 1 0	6.7 8 8
4 2	Round sardinella	3. 0 5	0. 21 8	0. 9 5	0. 1 5	4. 33 9	0. 7 6	0. 2 1	0. 2 2	0. 4 2	0. 0 69	0.0 0 3	0 3 7	0.2 4 4	1.6 4 4	0. 0 2	0.5 0 0
4 3	European sprat	3. 0 2	0. 07 2	0. 9 2	0. 1 5	3. 45 9	0. 7 7	0. 2 1	0. 2 1	0. 0 1	0. 0 86	0.0 0 7	0 0 1	0.0 0.4 6	0.4 3 0	0. 0 0	0.1 3 3
4 4	Horse mackerel	3. 5 4	0. 40 8	0. 9 2	0. 1 93	3. 8 5	0. 8 7	0. 1 5	0. 1 7	0. 2 7	0. 0 40	0.0 0 1	0 4 0	0.2 7 0	2.3 0 5	0. 1 5	0.4 7 7
4 5	Mackerel	3. 5 2	0. 88 9	0. 4 6	0. 1 20	3. 20 0	0. 8 5	0. 2 0	0. 1 3	0. 1 0	0. 26 0	0.4 0 6	1 9 6	0.6 9 7	4.3 7 0	0. 1 0	1.2 3 3
4 6	Atlantic bluefin tuna	4. 2 0	0. 08 1	0. 9 1	0. 3 1	1. 96 1	0. 6 4	0. 6 9	0. 3 5	0. 1 0	0. 00 1	0.1 1 1	0 1 1	0.1 0 2	0.3 2 3	0. 1 0	0.0 7 7
4 7	Other large pelagic fishes	4. 8 8	0. 44 2	0. 1 3	0. 1 67	2. 67 3	0. 8 0	0. 2 7	0. 1 6	0. 0 7	0. 01 0	0.4 8 0	1 3 0	0.2 3 4	1.7 4 8	0. 0 8	0.5 6 6
4 8	Sea turtles	2. 7 1	0. 02 0	0. 2 7	0. 0 81	1. 81 1	0. 9 9	0. 0 9	0. 0 3	0. 0 3	0. 00 4	0.1 4 0	2 0 0	0.0 0 4	0.0 4 2	0. 5 2	0.0 1 1
4 9	Seabirds	2. 6 5	0. 00 0	0. 0 6	0. 0 4	52 .2 2	0. 9 2	0. 0 9	0. 0 8	0. 0 1	0. 00 0	4.4 6 0	0 0 0	0.0 1 0	0.1 7 7	0. 0 3	0.0 3 3
5 0	Dolphins	4. 4 4	0. 05 3	0. 3 0	0. 0 83	9. 83 0	0. 0 0	0. 0 0	0. 0 1	0. 0 1	0. 00 00	0.0 2 3	3 0 3	0.0 0 4	0.6 4 7	0. 1 7	0.1 3 3
5 1	Baleen whales	3. 6 4	0. 04 0	0. 0 1	0. 0 84	2. 84 9	0. 9 1	0. 0 1	0. 0 0	0. 0 0	0. 00 00	0.0 4 0	0 0 0	0.0 0 8	0.1 0 5	0. 0 5	0.0 6 6
5 2	Detritus	1. 0 0	0.85 .9 2	0. 2 7	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0. 3 0	0.0 0 0
5 3	Discards	1. 0 0	0. 86 9	0. 5 9	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0. 0 0	0.3 5 5
5 4	By-catch	1. 0 0	0. 00 1	0. 1 1	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	0. 0 0	0.0 0 0

**Table 3.** Diet composition matrix for the NWM model. Cells in grey represent values lower than 0.01.

	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	
1	0.	0.	0.									0.	0.												
	6	3	2									6	0												
	8	0	0									0	5												
2																							0.		
																							2		
																						0			
3																							0.		
																							0		
																							3		
																							0		

4									0.	0.									0.	0.		
5	0.	0.	0.	0.	0.				0.	0.									0.	0.		
6	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
7	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
8	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
9	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.
10																						
11																						
12																						
13																						
14																						
15																						
16																						
17																						
18																						
19																						
20																						
21																						
22																						
23																						
24																						
25																						
26																						
27																						
28																						
29																						
30																						



31																		0	0	0	0	0	
32																		1	2	1	1	5	4
33																		0.	0.	0.	0.	0.	0.
34																		1	0	0	0	0	0
35																		0	1	3	2	7	7
36																		0.	0.	0.	0.	0.	0.
37																		0	7	0	1	0	2
38																		0.	0.	0.	0.	0.	0.
39																		0	0	0	0	0	0
40																		0.	0.	0.	0.	0.	0.
41																		0	0	0	0	0	0
42																		1	1	8	2	5	7
43																		0.	0.	0.	0.	0.	0.
44																		0	0	0	0	0	0
45																		1	1	1	1	1	1
46																		0.	0.	0.	0.	0.	0.
47																		0	6	1	0	0	0
48																		0.	0.	0.	0.	0.	0.
49																		1	1	1	1	1	1
50																		0.	0.	0.	0.	0.	0.
51																		1	1	1	1	1	1
52																		0	0	0	0	0	0
53																		0	0	0	0	0	0
54																		1	1	1	1	1	1
IM																							
PO																							
RT																							
TO																							
TA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
L																							

**Table 3.** Diet composition matrix for the NWM model (continuation). Cells in grey represent values lower than 0.01.

	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
1						0.20							0.11										
2																							
3																							
4		0.05																					
5		0.03			0.35	0.29				0.95	1.00	0.95	0.89	0.95	1.00	0.24	0.25						
6	0.10	0.05	0.07	0.07	0.53	0.41	0.10	0.15	0.03					0.05		0.37	0.51	0.04					0.50
7		0.03		0.05				0.05									0.11		0.10	0.10			
8	0.26	0.36	0.26	0.21	0.11	0.10	0.10	0.10	0.11							0.10	0.02						
9	0.20	0.21	0.17	0.25			0.07	0.08	0.12														
10			0.01						0.01														
11	0.01								0.01														
12				0.01				0.01															
13	0.01	0.03	0.05	0.05	0.02		0.03	0.11	0.09														
14	0.06	0.06	0.09	0.08			0.06	0.04	0.17														
15	0.10	0.07	0.05	0.05				0.02	0.10														
16	0.21	0.09	0.03	0.12				0.03	0.07														
17		0.01	0.07				0.16	0.02	0.04						0.03		0.01						0.02
18			0.02					0.05										0.03	0.02				0.09
19				0.01				0.04															0.04
20				0.02														0.04	0.02				0.15
21																							
22									0.01														
23							0.10	0.01															0.06
24																							
25																							0.01
26																							0.10
27																							
28																							0.05



**Table 4.** Characteristics, statistics and ecological indicators for the NWM and other neighbouring models compared. NWM = North-western Mediterranean Sea; SCS = South Catalan Sea (Coll et al., 2006); GoL = Gulf of Lions (Banaru et al., 2013); DCS = Lower continental slope of the Catalan Sea (Tecchio et al., 2013); NCAS = North-Central Adriatic Sea (Coll et al., 2007); NAS = North Aegean Sea (Tsagarakis et al., 2010); IS = Greek Ionian Sea (Moutolopoulos et al., 2013); GoG = Gulf of Gabes (Hattab et al., 2013); GoC = Gulf of Cadiz (Torres et al., 2013).

Indicators	NWM	SCS	GoL	DCS	NCAS	NAS	IS	GoG	GoC	Units
Years	1999-2003	1994	2000-2009	2009	1990s	2003-2006	1998-2006	2000-2005	2009	
Depth range	0-1000	50-400	0-2500	1000-1400	10-280	20-300	50-1100	20-200	15-800	m
Area modelled	45547	4500	20400	850	55500	8374	49149	35900	7224	km <sup>2</sup>
Number of functional groups	54	40	40	20	40	40	39	41	43	
Number of primary producers	4	1	5	0	1	1	2	3	1	
Number of alive functional groups	51	37	38	18	37	38	37	39	41	
Sum of all Consumptions (TQ)	897.27	851.73	1480.1	51.36	1305.04	868.83	348.07	1442.63	1946.9	t·km <sup>-2</sup> ·year <sup>-1</sup>
Sum of all Exports (E)	1088.08	1251.89	251.7	20.09	730.15	274.81	1.69	735.81	2233.7	t·km <sup>-2</sup> ·year <sup>-1</sup>
Sum of all Respiratory Flows (TR)	279.55	326.86	498.7	20.19	421.09	269.48	174.84	524.62	955.1	t·km <sup>-2</sup> ·year <sup>-1</sup>
Sum of all Flows to Detritus (TFD)	1493.14	1607.52	764.63	65.84	1387.46	562.53	508.91	1137.51	2599.2	t·km <sup>-2</sup> ·year <sup>-1</sup>
Total System Throughput (TST)	3758.03	4038	2995.13	157.48	3843.74	1975.65	1033.51	3840.57	7734.9	t·km <sup>-2</sup> ·year <sup>-1</sup>
Sum of all Production (TP)	1599.93	1851.31	1572.80	14.83	1566	791	599.05	1809.63	3704.4	t·km <sup>-2</sup> ·year <sup>-1</sup>
Calculated Total Net Primary Production	1366.1	1577	1042.4	0	1149.85	535.48	495.44	1259.54	3187.7	t·km <sup>-2</sup> ·year <sup>-1</sup>
Total Primary production/Total Respiration (Pp/R)	4.89	4.82	2.09	0	2.73	1.99	2.83	2.41	3.3	
Net System Production (NP)	1086.55	1250.14	543.70	-20.19	728.76	265.99	320.59	734.92	2231.6	t·km <sup>-2</sup> ·year <sup>-1</sup>
Total Primary Production/Total Biomass (Pp/B)	32.00	26.74	15.10	0	8.82	16.21	23.25	16.75	39.8	
System Omnivory Index (SOI)	0.19	0.19	0.21	0.29	0.19	0.18	0.36	-	0.18	
Finn's cycling index (of total throughput) (FCI)	9.12	6.77	11.87	4.2	14.7	14.6	14.33	7.35	3	% of TST
Finn's mean Path Length (PL)	2.75	2.56	3.99	-	5.41	3.63	5.85	3.05	2.43	
Total Biomass (excluding detritus) (TB)	42.69	58.97	68.90	3.93	130.3	33.04	21.31	75.36	80.02	t·km <sup>-2</sup>

Mean Trophic Level of the community (mTLco)	1.38	1.5	1.43	1.10	1.39	1.69	-	2.03	1.61	
mTLco (excluding TL=1)	2.48	2.36	2.67	2.85	2.13	2.57	-	2.69	2.55	
Total Catches (TC)	4.18	5.36	2.13	0	2.45	2.35	1.69	1.72	4.55	t·km <sup>-2</sup> ·year <sup>-1</sup>
Mean Trophic Level of the Catch (mTLc)	3.13	3.12	3.24	0	3.07	3.47	3.33	3.44	3.32	
Primary Production Required to sustain the fishery (PPR, considering PP)	12.08	9.54	13.58	0	6.59	3.45	5.54	3.66	12.97	%
Primary Production Required to sustain the fishery (PPR, considering PP + detritus)	17.36	10.6	-	0	15	6.76	-	7.2	16.45	%
Gross Efficiency of the fishery (GE)	0.003	0.01	0.002	0.000	0.002	0.004	0.003	0.001	0.001	
Transfer Efficiency (TE)										
Mean	14.3	12.2	19.7	15.7	10	17.4	13.1	19.24	14.9	%
From primary producers	15.4									%
From detritus	13.3									%
Ecopath pedigree index	0.62	0.67	0.67	0.54	0.66	0.61	0.54	0.65	0.63	

**Table 5.** Catch ( $t \cdot km^{-2} \cdot year^{-1}$ ) and mean trophic level of the catch (mTLc) for the fleets in the NWM model

<b>Fleet</b>	<b>Catch</b>	<b>mTLc</b>
Spanish bottom trawl	0.71	3.40
Spanish purse seine	1.16	2.99
Spanish longline	0.03	3.76
Spanish artisanal	0.15	3.22
French bottom and mid-water trawl	1.13	3.12
French purse seine	0.60	3.06
French artisanal	0.35	2.99
Recreational	0.05	3.46

**Table 6.** Functional groups identified as a) keystone and b) structuring species/groups in the Mediterranean Sea and the adjacent Atlantic area (GoC). NWM = North-western Mediterranean Sea; SCS = South Catalan Sea (Coll et al., 2006); GoL = Gulf of Lions (Banaru et al., 2013); DCS = Lower continental slope of the Catalan Sea (Tecchio et al., 2013); NCAS = North-Central Adriatic Sea (Coll et al., 2007); NAS = North Aegean Sea (Tsagarakis et al., 2010); IS = Greek Ionian Sea (Moutolopoulos et al., 2013); GoG = Gulf of Gabes (Hattab et al., 2013); GoC = Gulf of Cadiz (Torres et al., 2013).

a)

	NWC S	SCS	GoL	DCS	NCA S	NAS	IS	GoG	GoC
Dolphins	X	X	X		X				X
Benthopelagic cephalopods	X	X	X			X			X
Large pelagic fish	X					X			
Sharks				X			X	X	

b)

	NWC S	SCS	GoL	DCS	NCA S	NAS	IS	GoG	GoC
Phytoplankton	X	X			X	X		X	X
Micro- and mesozooplankton	X	X	X		X	X	X	X	X
Macrozooplankton	X	X	X			X		X	X
Benthic invertebrates	X		X	X	X		X	X	

**Highlights**

- We characterized the structure and functioning of the NW Mediterranean Sea with an ecological food-web model
- The model highlighted the dominance of the pelagic fraction and the importance of the benthic-pelagic coupling
- Several food-web indicators showed that the NWM ecosystem was heavily impacted by fishing
- The trawl fleet had the greatest impact on the ecosystem
- Compared Mediterranean ecosystems shared common features in the structure and functioning

ACCEPTED MANUSCRIPT