ECOSYSTEM BASED MANAGEMENT IN THE MEDITERRANEAN SEA: SCIENTIFIC CHALLENGES AND ADVANCES

LA GESTIÓN BASADA EN LOS ECOSISTEMAS EN EL MAR MEDITERRÁNEO: RETOS CIENTÍFICOS Y AVANCES

Chiara Piroddi, PhD Thesis

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LA GESTIÓN BASADA EN LOS ECOSISTEMAS EN EL MAR MEDITERRÁNEO: RETOS CIENTÍFICOS Y AVANCES

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ECOSYSTEM BASED MANAGEMENT IN THE MEDITERRANEAN SEA: SCIENTIFIC CHALLENGES AND ADVANCES

ABSTRACT

RESUMEN

RESUM

In this thesis I investigated the status of the Mediterranean Sea ecosystem and the sustainability of its marine resources using an interdisciplinary approach, which combined data integration and modelling approaches. Results highlighted a series of commonalities for Mediterranean marine ecosystems: they indicate that 'small pelagic fishes', mainly European pilchards and anchovies, both with high biomasses and high proportions in catches, are important structuring species for the Mediterranean ecosystem (at regional, sub-regional and local scales). 'Large pelagic fishes' are the main keystone species for both the past and current Mediterranean ecosystem configuration, while 'sharks' and 'medium pelagic fishes' played a key role in the past, but their ecological role is currently replaced by benthopelagic and benthic cephalopods. In addition, the 'Mediterranean monk seal' "*Monachus monachus*", where it still occurs, is the species with the highest TL followed by 'piscivorous cetaceans' and 'large pelagic fish'.

Looking at temporal ecosystem dynamics, biomass trends and ecological indicators (e.g., community biomass, trophic levels of the community, catch and diversity indicators) reveal that the combined effect of excessive fishing pressure and changes in primary productivity altered the Mediterranean marine ecosystem over time, especially reducing the proportions of top predators (e.g., pinnipeds, large pelagic fish) and mid trophic level organisms (e.g., small pelagic fishes) and increasing the abundance of groups at lower trophic levels (e.g., invertebrates). The Western and the Adriatic Seas are the most degraded ecosystems with biomasses declines among all the species compartments assessed (from forage fish to sharks/rays and skates, except for invertebrates that remained stable in time). The Ionian Sea was found to be the area with less biomass changes historically in comparison with available survey data. Even at a more local scale (Amvrakikos Gulf), both ecological indicators and biomass trends highlight a degradation of the demersal compartments of the food web but a relative stability of the pelagic ones mainly due to high eutrophication levels.

Fishing pressure and changes in primary production (PP) play an important role in driving species temporal dynamics; yet, PP seems to be the strongest driver upon the Mediterranean Sea ecosystem. Fisheries data (mainly catch and effort) are found to be under-reported and under-estimated at regional, sub-regional and local scale. For example, fishing mortalities (and so landings data obtained from Food and Agriculture Organization [FAO] fisheries statistics) of three most important commercial species (European pilchard '*Sardina pilchardus*', anchovy '*Engraulis encrasicolus*' and hake '*Merluccius merluccius*') were in fact observed in early decades (1950s), in all the Mediterranean sub-regions, between 5 and 10 times inferior from the average reference values reported in stock assessment for these fish stocks in the Mediterranean Sea. Even in the assessment of the Italian fisheries, the reconstructed total catches were 2.6 times the landings officially reported by the FAO on behalf of Italy for the same period and same area, with unreported commercial landings (from both industrial and artisanal sectors) contributing 50% to the total catch (in relation to FAO reporting) and discards contributing another 7%.

In Europe, several models and associated indicators exist that could be used in support of European policies (MSFD); yet, Ecopath with Ecosim (EwE) is the most applied tool for modelling marine and aquatic ecosystems and the one that can produce the largest number of indicators useful for the Marine Strategy Framework Directive (MSFD). Since anthropogenic pressures are rapidly expanding in the basin, this work constitutes an important first step to advance further in the regional assessment of the Mediterranean Sea ecosystem and to inform conservation plans and management actions.

En esta tesis he investigado el estado ambiental del mar mediterráneo y la sostenibilidad de sus recursos marinos mediante un enfoque interdisciplinario que combina la integración de datos y la modelización de ecosistemas. Los resultados ponen de relieve una serie de puntos en común de los ecosistemas marinos mediterráneos: el grupo de "peces pelágicos de tamaño pequeño", principalmente compuesto por sardinas y boquerones, con grandes biomasas y capturas, es un grupo importante en relación con la estructura del ecosistema mediterráneo (a nivel regional, sub regional y a escalas locales). El grupo de "peces pelágicos de gran tamaño" destaca por ser importante como grupo clave del ecosistema, tanto en el pasado como en el presente, mientras que el grupo de "tiburones" y "peces pelágicos de tamaño medianos" han jugado un rol ecológico clave en el pasado, pero éste es actualmente reemplazado por los grupos de peces bentopelágicos y cefalópodos bentónicos. Además, la foca monje del mediterráneo "*Monachus monachus*", en aquellas zonas donde todavía existe, es la especie con el nivel trófico más alto, seguida por el grupo de "cetáceos que se alimentan de peces" y "peces pelágicos de gran tamaño".

En cuanto a la dinámica temporal del ecosistema, las tendencias de la biomasa y de los indicadores ecológicos (por ejemplo, la biomasa de la comunidad, los niveles tróficos de la comunidad, las capturas y los indicadores de diversidad) revelan que el efecto combinado de una presión pesquera excesiva y los cambios en la productividad primaria ha alterado el ecosistema marino del mediterráneo a través del tiempo, especialmente en cuanto a una reducción de las proporciones de los depredadores superiores (por ejemplo, pinnípedos, y peces pelágicos de gran tamaño) y organismos de niveles tróficos mediados (por ejemplo, peces pelágicos de tamaño pequeño), y el aumento en abundancia de grupos de organismos en niveles tróficos inferiores (por ejemplo, invertebrados). El mar mediterráneo occidental y el mar adriático son los ecosistemas más degradados con bajadas de biomasas para todas las especies evaluadas (desde los peces pelágicos de tamaño pequeño a los tiburones y rayas, con excepción de los invertebrados que se mantienen estables en el tiempo). El mar jónico es el área con menos cambios históricos en términos de biomasa en comparación con los datos disponibles de muestreos. Incluso a una escala más local (en el Golfo de Amvrakikos), tanto los indicadores ecológicos como las biomasas evidencian una degradación de los

compartimentos demersales de la red trófica, aunque se observa una relativa estabilidad de los compartimentos pelágicos, principalmente debido a los altos niveles de eutrofización. La presión pesquera elevada y los cambios en la producción primaria (PP) juegan un papel importante en la dinámica temporal de las especies; sin embargo, cambios en la PP parecen ser los principales impulsores de la dinámica temporal en el ecosistema del mar mediterráneo.

Los datos pesqueros (principalmente la captura y el esfuerzo pesquero) se encuentran sub-estimados y consecuentemente sub-registrados a escala regional, sub-regional y local. Por ejemplo, la mortalidad por pesca (y por tanto los datos de desembarque que se obtienen de las estadísticas de pesca de la Organización para la Agricultura y la Alimentación [FAO]) de tres de las especies comerciales más importantes (Sardina europea '*Sardina pilchardus*', anchoa '*Engraulis encrasicolus*' y merluza "*Merluccius merluccius*') para las primeras décadas de este estudio (1950), y en todas las sub-regiones mediterráneas analizadas, era entre 5 y 10 veces inferior a los valores de referencia promedio registrados en evaluaciones del stock de estas poblaciones en el mar mediterráneo. Incluso en la evaluación de las pesquerías italianas, la reconstrucción de las capturas totales muestra que las capturas totales son 2,6 veces mayores que los desembarques registrados oficialmente por la FAO durante el mismo período y la misma zona, con desembarques comerciales no declarados (de los sectores industriales y artesanales) que contribuyen el 50 % de la captura total (en relación a los informes de la FAO) y los descartes que contribuyen otro 7%.

En Europa, existen varios modelos e indicadores asociados que podrían ser utilizados en apoyo de las políticas europeas de gestión medioambiental, como la Directiva Marco sobre la Estrategia Marina (MSFD); sin embargo, Ecopath with Ecosim (EwE) es la herramienta más aplicada para la modelización de los ecosistemas marinos y acuáticos y la que puede producir un mayor número de indicadores útiles para la MSFD. Dado que las presiones antropogénicas se están expandiendo rápidamente en la cuenca mediterránea, este trabajo constituye un primer paso importante para avanzar en la evaluación regional del estado ambiental del ecosistema marino mediterráneo y para informar a los planes de conservación y acciones de manejo presentes y futuros.

En aquesta tesi he investigat l'estat ambiental del mar mediterrani i la sostenibilitat dels seus recursos marins mitjançant un enfoc interdisciplinari que combina la integració de dades i la modelització d'ecosistemes. Els resultats posen en relleu una sèrie de punts en comú dels ecosistemes marins mediterranis: el grup de "peixos pelàgics de mida petita", principalment compost per sardines i seitons, amb grans biomasses i captures, és un grup important en relació amb l'estructura de l'ecosistema mediterrani (tant a nivell regional, sub regional i a escales locals). El grup de "peixos pelàgics de gran mida" destaca per ser important com a grup clau de l'ecosistema, tant en el passat com en el present, mentre que el grup dels "taurons" i "peixos pelàgics de mida mitjana" han jugat un paper ecològic clau en el passat, però aquest és actualment reemplaçat pels grups de peixos bentopelàgicos i cefalòpodes bentònics. A més, el vell marí del mediterrani "*Monachus monachus*", en aquelles zones on encara existeix, és l'espècie amb el nivell tròfic més alt, seguida pel grup de "cetacis que s'alimenten de peixos" i "peixos pelàgics de grans dimensions".

Pel que fa a la dinàmica temporal de l'ecosistema, les tendències de la biomassa i dels indicadors ecològics (per exemple, la biomassa de la comunitat, els nivells tròfics de la comunitat, les captures i els indicadors de diversitat) revelen que l'efecte combinat d'una pressió pesquera excessiva i els canvis en la productivitat primària ha alterat l'ecosistema marí mediterrani a través del temps, especialment pel que fa a una reducció de les proporcions dels depredadors superiors (per exemple, pinnípedes, i peixos pelàgics de grans dimensions) i organismes de nivells tròfics mitjans (per exemple, peixos pelàgics de mida petita), i l'augment en abundància de grups d'organismes en nivells tròfics inferiors (per exemple, invertebrats). El mar mediterrani occidental i el mar adriàtic són els ecosistemes més degradats amb baixades de biomasses per a totes les espècies avaluades (des dels peixos pelàgics de mida petita als taurons i ratjades, amb excepció dels invertebrats que es mantenen estables en el temps). El mar jònic és l'àrea amb menys canvis històrics en termes de biomassa en comparació amb les dades disponibles de mostrejos. Fins i tot a una escala més local (en el Golf de Amvrakikos), tant els indicadors ecològics com les biomasses evidencien una degradació dels compartiments demersals de la xarxa tròfica, encara que s'observa una relativa estabilitat dels compartiments pelàgics, principalment a causa dels alts nivells d'eutrofització. La pressió pesquera elevada i els canvis en la producció primària (PP) juguen un paper important en la dinàmica temporal de les espècies; però, els canvis en la PP semblen ser els principals impulsors de la dinàmica temporal de l'ecosistema del mar mediterrani.

Les dades pesquers (principalment la captura i l'esforç pesquer) es troben subestimats i conseqüentment registrats de forma errònia a escala regional, sub regional i local. Per exemple, la mortalitat per pesca (i per tant les dades de desembarcament que s'obtenen de les estadístiques de pesca de l'Organització per a l'Agricultura i l'Alimentació [FAO]) de tres de les espècies comercials més importants (Sardina europea "*Sardina pilchardus*", anxova "*Engraulis encrasicolus*" i lluç "*Merluccius merluccius*") per a les primeres dècades d'aquest estudi (1950), i en totes les sub regions mediterrànies analitzades, era entre 5 i 10 vegades inferior als valors de referència mitjana registrats en avaluacions de l'estoc d'aquestes poblacions al mar mediterrani. Fins i tot en l'avaluació de les pesqueries italianes, la reconstrucció de les captures totals mostra que les captures totals són 2,6 vegades més grans que els desembarcaments registrats oficialment per la FAO durant el mateix període i per la mateixa zona, amb desembarcaments comercials no declarats (dels sectors industrials i artesanals) que contribueixen al 50% de la captura total (en relació als informes de la FAO) i els descarts que contribueixen un altre 7%.

A Europa hi ha diversos models i indicadors associats que podrien ser utilitzats en suport de les polítiques europees de gestió mediambiental, com la Directiva Marc sobre l'Estratègia Marina (MSFD); de totes formes, Ecopath with Ecosim (EwE) és l'eina més aplicada per a la modelització dels ecosistemes marins i aquàtics i la que pot produir un major nombre d'indicadors útils per a la MSFD. Atès que les pressions antropogèniques s'estan expandint ràpidament a la conca mediterrània, aquest treball constitueix un primer pas important per avançar en l'avaluació regional de l'estat ambiental de l'ecosistema marí mediterrani i per informar els plans de conservació i gestió presents i futurs.

CHAPTER 1.

INTRODUCTION

MAJOR PRESSURES ON THE MARINE ENVIRONMENT

Covering 71% of the Earth's surface, the oceans are important to humankind in multiple ways: they are key in regulating global climate and biochemical processes (Rahmstorf 2002) and, hosting a variety of complex marine ecosystems, they provide important good and services (e.g., seafood, leisure and recreation; Worm et al. 2006, Halpern et al. 2012). Until recently, because of their magnitude, the oceans were thought to offer inexhaustible marine resources (Costanza et al. 1999). However, as human populations kept growing and migrating along the coasts (~40% of the world's population lives within 100 km of the coast; Agardy et al. 2005, Ferrario et al. 2014), many resources and associated habitats have diminished and/or have been altered by the pressure of increased human activities (Halpern et al. 2015). Among major threats affecting marine ecosystems are fisheries and aquaculture, pollution, eutrophication, climate change and species invasions (Figure 1: Halpern et al. 2008, Halpern et al. 2015).

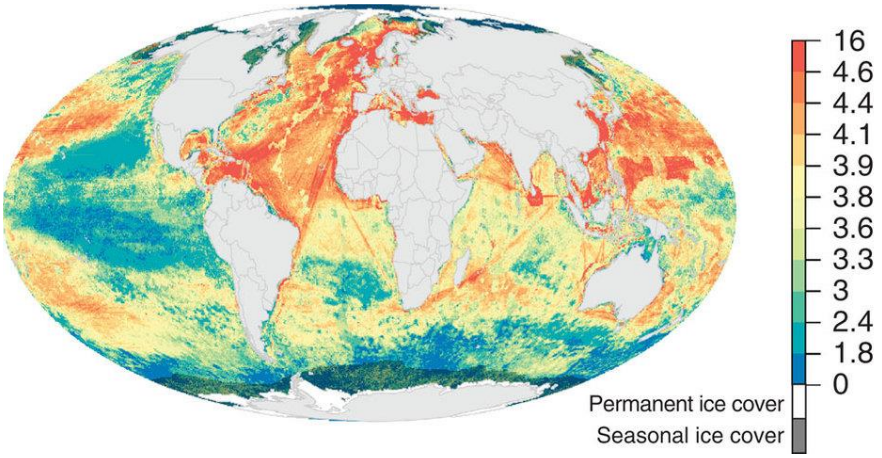

Figure 1. Cumulative human impact to marine ecosystems as of 2013 (source: Halpern, 2015). Impact scores are based on 19 anthropogenic stressors. Colours are assigned to 10-quantiles in the data, except the highest scores which are the top 5% of scores. Areas of permanent sea ice are shaded white and the area within maximum sea ice extent is masked to indicate where scores are less certain because change in sea ice extent could not be included.

Global fisheries, by removing target and non-target species and deteriorating marine habitats, are one of the major responsible of significant and profound ecological changes in the structure and function of marine ecosystems (Pauly et al. 1998, Worm et al. 2006). The collapse of cod stocks off the coasts of New England and eastern Canada (Myers & Worm 2003), the large decline of sardines across the Pacific Ocean (Chavez et al. 2003), the declines of sharks in the northwest Atlantic Ocean (Myers et al. 2007) or the depletion of sea turtles in the Carribean Sea (McClenachan et al. 2006) are only few examples of the detrimental direct and indirect impact of fisheries on marine resources (Pauly et al. 2002). Nevertheless, despite clear evidences of taxa collapses throughout the world, fishing effort continues to increase well beyond sustainable levels (Pauly et al. 2002, Watson et al. 2013), pressuring not only historical fishing grounds (e.g., continental shelves) but also reaching new untouched areas of the oceans (e.g., high seas and deep sea floors, Swartz et al. 2010).

Moreover, global aquaculture (of both farmed fish and shellfish) has more than doubled in the past 15 years (FAO 2016). Even though aquaculture is often perceived as a pressure relief for ocean fisheries in sustaining world fish supplies, several concerns still remains in its management practices and its impact on marine ecosystems (Naylor et al. 2000). For example, the large use of wild fish for feeding farmed carnivorous species or the reduction of wild fish supply through habitat modification (Naylor & Burke 2005) are factors that are continuously of concern for marine ecosystems and their resources.

Marine pollution, consisting of contaminants as persistent organic pollutants, oils, radionuclides, heavy metals, pathogens, litters and debris (Williams 1996), did not receive much attention until recently when clear signs of negative impacts were observed on ecosystems and organisms (Islam & Tanaka 2004). Despite the fact that monitoring and regulating pollution have been identified as fundamental to sustainably manage and preserve marine resources, work is still needed to properly tackle this issue (Williams 1996). In fact, regardless of the existence of international legislations on marine pollution (e.g., the 1972 Convention on the Prevention of Marine Pollution by Dumping Wastes and Other Matter and the 1978 Protocol to the International Convention for the Prevention of Pollution from Ships (MARPOL)), many nations are still producing large pollution loads which are directly or indirectly negatively impacting the ocean (Derraik 2002).

Marine eutrophication occurs when large quantities of nutrients enter in the ecosystems mainly from riverine discharges, agriculture and atmospheric deposition from burning fossil fuels (Smith et al. 1999). A major threat caused by eutrophication is the formation of so called “dead zones”, areas characterized by decreased levels of dissolved oxygen (DO) in bottom waters that induce hypoxia and in worst cases anoxia events (Diaz & Rosenberg 2008). The most known and studied areas where dead zones occur are the Baltic, Kattegat, Black Sea, Gulf of Mexico, and East China Sea. Since global population is expected to keep growing, energy use and agricultural production are expected to intensify, increasing levels of eutrophication, hypoxia and thus the formation of dead zones (Diaz & Rosenberg 2008).

Over the past 30 years, oceans, acting as the planet's sink, have absorbed most of the added atmospheric temperature and carbon dioxide produced by green gas emissions and other human activities with the result that currently oceans are warmer (increase of ~0.1°C per decade) and more acidic (decrease of ~0.02 pH per decade) (Bakun 1990, Overland et al. 2010). These changes have already altered the structure and function of marine ecosystems; for example, by decreasing ocean productivity, increasing ocean acidification, altering food web dynamics, reducing abundance of habitat-forming species, shifting species distributions, and increasing the greater incidence of diseases (Hoegh-Guldberg & Bruno 2010).

Global warming together with shipping and aquaculture are also the major causes of increasing invasive species into our oceans. The impacts of invasive species on marine ecosystems are diverse and mostly related to the modification of marine habitats either by displacing or removing native species, or community structure and food webs changes, or the alteration of fundamental processes, such as nutrient cycling and sedimentation (Ruiz et al. 1997). Some studies have also showed a negative effect of invasive species on fisheries by diminishing catches and some also on human health by causing disease (Weber et al. 1994, Bax et al. 2003).

ECOSYSTEM BASED MANAGEMENT

As anthropogenic pressures are rapidly increasing, understanding how stressors interact with each other and influence marine ecosystems and how such dynamics affect the sustainability of goods and services they provide is of urgent importance (Halpern et al. 2012). Up to now, a large body of studies have focused on the impact of a single stressor on specific compartments of marine and coastal environments; however, following the collapse of many marine resources worldwide and the difficulties to properly manage them individually, a move toward an "Ecosystem-Based Management" (EBM) approach has been identified as a necessary step (Pikitch et al.

2004). This approach recognizes the need to assess the ecosystem as a whole, rather than focusing on single resources, and considering the impact of multiple stressors on the system, instead of individual ones, for responsible resource management decisions to be made (Pikitch et al. 2004).

Despite the fact that the EBM concept is relatively new to management plans, the foundations of EBM are deep-rooted within many international agreements. For example, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), in 1980, described it as an approach that:

> *"takes into account all the delicate and complex relationships between organisms (of all sizes) and physical processes (such as currents and sea temperature) that constitute the Antarctic marine ecosystem" (19)*

while the United Nations Convention on Biological Diversity (CBD) in 1982 defined it as:

> *"a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way" [20]*

Only recently (2005), though, the Communications Partnership for Science and the Sea (COMPASS) gave a more in-depth inclusive definition of EBM:

> *"an integrated approach to management that considers the entire ecosystem, including humans. The goal of EBM is to maintain an ecosystem in a healthy, productive and resilient condition so that it can provide the services humans want and need. EBM differs from current approaches that usually focus on a singlespecies, sector or activity or concern; it considers the cumulative impacts of different sectors" [21]*

Because of the failure in managing individual species, the EBM approach has seen increased popularity in many management initiatives with the result that its implementation is now taking place in several different sectors (e.g., forestry, fisheries) with sector-specific variations (e.g., Ecosystem Approach to Fisheries) (Levin et al. 2009). In particular, international regulations such as the Convention of Biological Diversity, [CBD], the Reykjavık Declaration of 2001, the European Marine Strategy Framework Directive [MSFD; 2008/56/EC], and the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), are pushing policies towards the integration of effective and operational EBM procedures, using robust and appropriate tools. Some of these tools are modelling frameworks and indicators (Fulton et al. 2011). As highlighted in these regulations, in fact, indicators can be used to evaluate whether an ecosystem and its services are well maintained and sustainably used (Layke 2009, Walpole et al. 2009, TEEB 2010) and can help translating ecosystem impacts and changes into management measure (Shin et al. 2010a, Rombouts et al. 2013).

In the marine environment, several efforts have been undertaken to evaluate marine ecosystem structure and their response to human activities through the use of key indicators (Link et al. 2010, Shin et al. 2010b, Coll et al. 2016). At the European level, for example, these initiatives have been carried out to assist the European Marine Strategy Framework Directive [MSFD; 2008/56/EC], the environmental pillar of the European marine policy. The MSFD aims at assessing the status of an ecosystem under anthropogenic pressures and the required interventions to bring the system back to its desired good status, making human activities sustainable, since this is one of the objectives of the MSFD. In particular, the Directive requires Member States (MSs) to take the necessary measures to achieve or maintain Good Environmental Status (GEnS; Borja et al. 2011) in the marine environment, by the year 2020 at the latest, through the assessment of descriptors and indicators related to biological, physico-chemical characteristic of the system and associated pressures (e.g., fishing, hazardous substances, hydrological alterations, litter and noise, and biological disturbance such as introduction of non-indigenous species) (Cardoso et al. 2010).

ECOSYSTEM MODELLING AS A KEY TOOL TO EBM

The development and application of ecosystem models have increased in the last decades (Plagányi 2007) because they are recognised as powerful tools to quantify baseline conditions of marine ecosystems, estimate the impact of pressures and the suitability of management measures, integrate scarce survey datasets and, ultimately, provide explicit support to decision-making processes complementing single species modelling approaches (Fulton & Smith 2004, Shin et al. 2004, Christensen & Walters 2005, Fulton 2010). Different types of modelling techniques exist that can describe and assess the whole ecosystem, and can consider the different components that characterize it including human and/or climate impacts (Christensen & Walters 2004, Shin et al. 2010c, Fulton et al. 2011).

These models include: (a) whole ecosystem models that take into account all trophic levels in the ecosystem and are mainly represented by Atlantis (Fulton & Smith 2004) and the Ecopath with Ecosim (EwE) software (Christensen & Walters 2004); (b) individual based models (IBMs) that track fate of single species or, in some instances, multi species (e.g., OSMOSE; Shin et al. 2004) through their life cycle with the assumption that their behaviour has an effect on the population's dynamics; and (c) minimally realistic models (MRM), that represent a limited number of species that have important interactions with a target species of interest and include MSVPA (Multi-Species Virtual Population Analysis; Sparre 1991), GADGET (Taylor & Stefansson 2004), CCAMLR predator-prey models (Mori & Butterworth 2006). In recent years, also, under the growing need to provide guidance for biodiversity conservation and ecosystem-based management, hydrological, hydrodynamic and biogeochemical models have been coupled with multi-species models (Travers et al. 2009, Kaplan et al. 2012). These so called end-to-end (E2E) models combine physico-chemical oceanographic processes with ecological processes into a single modelling framework (Figure 2) (Travers et al. 2009) to better represent/understand the whole food web while accounting for dynamic forcing effects of anthropogenic impacts (e.g., fishing) and climate (Cury et al. 2008).

Coupling can been achieved in different ways (Travers et al. 2007). For example, hydrodynamic models have been linked to bioenergetics-population dynamic models to examine how climate forcing propagates through the food web (Megrey et al. 2007) or hydrodynamic-biogeochemical models have been coupled to food web models (Beecham et al. 2015) to better assess the dynamics of the entire ecosystem. The coupling between these different model-classes should, in principle, be two way interactions, meaning that there is always feedback between the different environmental processes. When this happens models represent at best the nature of the processes. When the feedback is offline (one way interaction) instead, coupling is applied to reduce the computational effort while still achieving a valid approximation of the processes (Beecham et al. 2015).

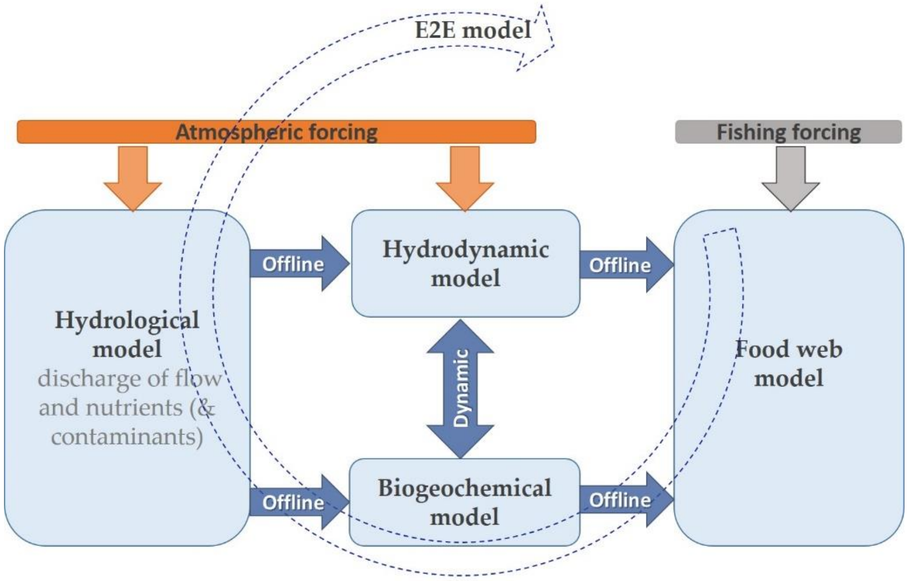

Figure 2. Marine ecosystem model types (boxes) and way of coupling between them (arrows). End to End model encompasses all of the models as it is represented by the the dashed arrow (source: this thesis).

When developing and applying an ecosystem model, several problems may rise, generally associated with the accuracy and the uncertainty of model inputs and outputs (Fulton et al. 2003, Jørgensen 2008). One of the main criticisms to ecosystem models is in fact related to the large complexity of the system (Fulton et al. 2003, Plagányi 2007) that make model predictions highly uncertain. Despite the fact that ecosystem models are highly complex by nature and uncertainty remains high, they are considered the best tools capable of answering ecosystem related questions. Since erroneous conclusions may be drawn if ignoring food web dynamics and the forces driving them, the advantages of applying such models can outweigh their potential pitfalls (Fulton et al. 2003). In any case, the issue of uncertainty is generally overcome by testing the robustness of model outputs (through a calibration process, for example) against a range of other models or against survey data. This approach permits the identification of weak components across different levels of complexity, underlying system and model assumptions (Fulton 2001).

ECOPATH WITH ECOSIM APPROACH

The Ecopath with Ecosim (EwE) approach (Christensen & Walters 2004) is used in this thesis to build Mediterranean ecosystem models and simulate dynamic changes of species/functional groups and catches over time. This software combines ecosystem trophic mass balance (biomass and flow) analysis (Ecopath) with dynamic (Ecosim) and spatial-dynamic (Ecospace) modeling capabilities (Christensen & Walters 2004, Christensen et al. 2014, www.ecopath.org). Since its origins (Polovina 1984), this modeling tool has advanced considerably (Coll et al. 2015, Steenbeek et al. 2016, Villasante et al. 2016), making it, now, one of the most suitable tools for exploring changes in marine biodiversity/ecosystem services (Sukhdev 2008) and for ecosystem-approach to fisheries and marine resources (Coll et al. 2015, Villasante et al. 2016). This is also reflected by the number of ecosystem models (~500) using the EwE approach that are currently published (Colléter et al. 2015) throughout the world.

The software has three main modules: Ecopath that is a mass balance model that provides a static description of an ecosystem at a given time period (Christensen & Walters 2004), describing all the principal autotrophic and heterotrophic species individually or by aggregating them into functional groups (species with similar trophic role). Ecosim, the tropho-dynamic simulation module, that has the capability to conduct multispecies simulations to explore changes in ecosystem structure and functioning, the impact of fishing and policy exploration (Christensen & Walters 2004). Ecospace, the spatial-temporal dynamic module, that represents the dynamics of marine species/functional groups over a two-dimensional space grid (Walters et al. 1999) linking the habitat attributes of an ecosystem (e.g., depth, temperature, pH, bottom type) to the trophic dynamics established in the food web (Christensen et al. 2014). Details about the available programing environments, recent developments and limitations of the EwE approach can be found extensively described in the literature (Christesen and Walters 2004; Steenbeek et al. 2016).

EwE has been widely used to understand various aspects of ecosystem based management. For example, assessing the structure and functioning of marine ecosystems (e.g., Heymans et al. 2004) from freshwater estuarine, coastal, to deep sea habitats (e.g., Harvey et al. 2003, Tsagarakis et al. 2010, Tecchio et al. 2013); performing ecosystem comparisons through the use of modelled derived indicators (e.g., Heymans et al. 2014); evaluating ecosystem-wide impacts of fishing strategies (e.g., Ainsworth et al. 2008), environmental changes (e.g., Mackinson et al. 2009, Mackinson 2014) and invasive species (Langseth et al. 2012, Libralato et al. 2015); analysing management options for marine resources (e.g., Lynam & Mackinson 2015) and describing bioaccumulation of toxins in the food web (e.g., Booth & Zeller 2005).

ECOLOGICAL INDICATORS

Ecosystem models can be used to derive useful ecological indicators to inform/support management decisions (Shin et al., 2010a, Shin et al., 2010b). In the marine research field, and particularly in the context of EBM, several efforts have been undertaken to define, test and evaluate indicators capable of capturing the status of marine ecosystems against changes in pressures (Shin et al. 2010a, Halpern et al. 2012, Rombouts et al. 2013). These initiatives have been carried out to assist several international organizations/regulations (e.g., the European Marine Strategy Framework Directive [MSFD; 2008/56/EC]; the Convention of Biological Diversity [CBD]; the UNEP Marine and Coastal Strategy (UNEP, 2011); the Intergovernmental Platform on Biodiversity and Ecosystem Services [IPBES]), with the aim of improving and/or maintaining the state of the environment and monitoring the rate of progress in achieving ecological objectives or targets.

Accordingly to Rice (2003), there are approximately 200 indicators (from cellular to ecosystem level) that can describe marine ecosystem health and that can be tractable and meaningful to all stakeholders (scientists, policy makers, the media, and the general public). These indicators include both empirical and model-based indicators. In particular, empirically-based indicators are used as proxies to indicate community response to change (e.g., state of fish stocks for fisheries management: Rice & Rochet 2005, or benthic community structure for habitat quality assessment: Borja & Dauer 2008), while model-based indicators are primarily developed and used to resolve ecosystem management questions (e.g., impact of specific pressures on marine ecosystems [Cury et al. 2008, Coll et al. 2016]; socio-economic and governance issues [Ehler 2003, Rice & Rochet 2005]; cumulative impacts of multiple human activities [Halpern et al. 2012, Coll et al. 2016]).

In this context and with the goal of informing management processes, in this thesis I use the EwE modelling approach to calculate modelled-derived indicators for the Mediterranean Sea ecosystem. The selection of the indicators follows mainly the work of IndiSeas (“Indicators for the Seas”; www.indiseas.org; see e.g., Shannon et al.

[2014] and Coll et al. [2016]), an international initiative that has developed and assessed ecological indicators for cross ecosystem comparisons to inform on the impacts of fishing on marine ecosystems woldwide. Among these indicators, are fisheries and ecology-based indicators (e.g., Shin et al., 2010), biodiversity and conservation indicators (Shannon et al. 2014, Coll et al. 2016), environmental (Fu et al. 2015), and socioeconomic and governance indicators (e.g., Bundy et al. in press). A summary of the initiative can be found at www.indiseas.org and in Shin et al. (2012).

THE MEDITERRANEAN SEA

The Mediterranean Sea extends from 30°N to 45°N and from 6°W to 36°E, and constitutes the world's largest (2 522 000 km^2) and deepest (average 1460 m, maximum 5267 m) enclosed sea on Earth. It is connected to the Atlantic Ocean via the Strait of Gibraltar in the west, to the Black Sea via the Bosporus, and the Dardanelles in the north-east and to the Red Sea via the Suez Canal in the south-east (Figure 3).

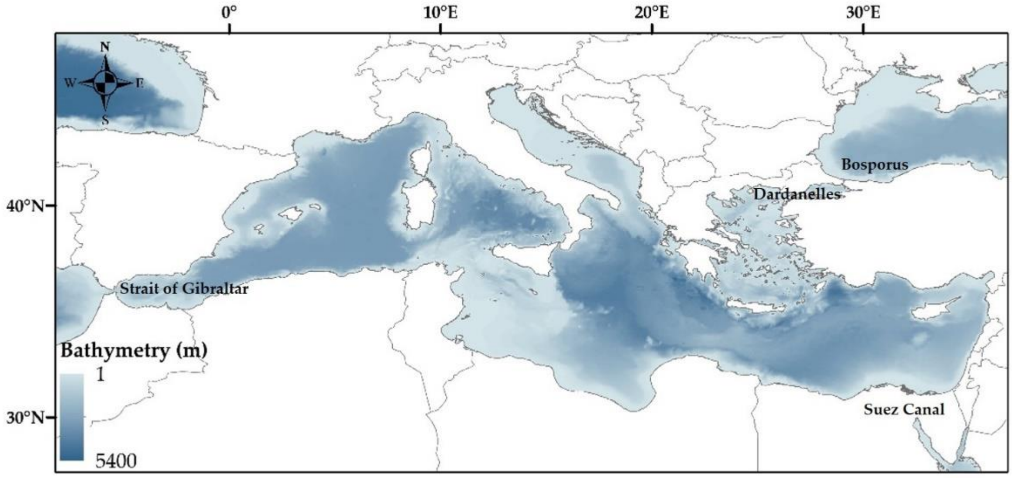

Figure 3. The Mediterranean Sea with the bathymetry profile (in meters (m)).

Overall, the basin is considered oligotrophic with some exceptions along coastal areas due mainly to river discharges (Barale & Gade 2008) and frontal mesoscale activity (Siokou-Frangou et al. 2010). Phosphorous, rather than nitrogen, is the limiting nutrient especially towards the eastern basin (Krom et al. 1991). Biological productivity decreases from north to south and west to east whilst an opposite trend is observed for temperature and salinity. In particular, the mean sea surface temperature varies between a minimum of 14–16°C (west to east) in winter and a maximum of about 20–26°C (w-e) in the summer (with the exception of the shallow Adriatic Sea where the range is between the 8–10°C in winter and 26–28°C in summer) (Barale & Gade 2008). Evaporation greatly exceeds precipitation and river runoff decreases from west to east, causing sea surface height to decrease and salinity to increase eastward (Bethoux 1980, Garrett et al. 1993). The Mediterranean Sea has a topographically diverse continental shelf that generally varies from south (mainly narrow and steep) to north (wider areas). In some instances, though, narrow shelves can be also found in some coasts of Turkey, in the Aegean, Ligurian and northern Alboran Seas, while extended shelves are also present in the Tunisian shelf and near the Nile Delta (Pinardi et al. 2006). Shelf waters represent 20% of the total Mediterranean surface, and the rest is open sea (Coll et al. 2010).

Despite the fact that the Mediterranean Sea covers only 0.32% of the world ocean volume, it shows a relatively high marine species richness and a high rate of endemism (Coll et al. 2010). However, individual species abundance remains quite low, suffering from a degree of dwarfism, related to the general oligotrophic nature of the Mediterranean, that decreases again from northwest to southeast (Sonin et al. 2007).

Currently, approximately 17 000 species have been recorded in the basin (Bianchi & Morri 2000, Coll et al. 2010): of these, at least 26% are prokaryotic (Bacteria and Archaea) and eukaryotic (Protists) marine microbes. The phytoplankton community is composed predominantly of Coccolithophores, Dinoflagellata and Bacillariophyaceae and includes more than 1 500 species. Among microzooplankton, foraminifera is the main group with more than 600 species. Still, it is within the Animalia group that the majority of the species are described (~11 500) with the greatest contribution coming from the Crustacea (13.2%) and Mollusca (12.4%) (Coll et al. 2010). Among the vertebrates, there are 650 marine species of fishes of which approximately 80 are elasmobranchs and the rest are mainly from actinopterygians (86%) (Coll et al. 2010). Nine species of marine mammals (five Delphinidae, and one each to the Ziphiidae, Physeteridae, Balaenopteridae, and Phocidae) and three species of sea turtles (the green *Chelonia mydas*, the loggerhead *Caretta caretta* and leatherback *Dermochelys coriacea* turtle) are encountered regularly in the Mediterranean Sea. Among the seabirds, 15 species frequently occur in the Mediterranean Sea, 10 gulls and terns (Charadriiformes), four shearwaters and storm petrels (Procellariiformes), and one shag (Pelecaniformes) (Coll et al. 2010). These estimates make the Mediterranean Sea one of Earth's hotspot areas for marine biodiversity (Coll et al. 2010, Costello et al. 2010); unfortunately, because of the extensive alteration throughout history of combined multiple human stressors, such as fishing practises, habitat loss and degradation, eutrophication, and the introduction of alien species (Coll et al. 2012, Micheli et al. 2013), the basin is also among the most impacted ecoregions of the world (Costello et al. 2010, Halpern et al. 2015).

These pressures have resulted in major alterations of Mediterranean marine ecosystems with signs of biodiversity loss observed throughout the food web, from top to bottom (Lotze et al. 2006, Lotze et al. 2011). Previously common species, such as the monk seal (*Monachus monachus*) (Panou et al. 1993), short-beaked common dolphin (*Delphinus delphis*) (Bearzi et al. 2003), Atlantic bluefin tuna (*Thunnus thynnus*) (MacKenzie et al. 2009) and several shark species (Ferretti et al. 2008), are currently endangered or critically endangered (Hilton-Taylor 2000, Bearzi 2012, Karamanlidis & Dendrinos 2015). In addition, the *Posidonia oceanica*, the most common and endemic sea grass species of the Mediterranean Sea, is showing alarming signs of disappearance, especially in the northern parts of the basin (Marbá et al. 1996).

A number of regional organisations, agreements and initiatives are involved in the protection of the Mediterranean marine biodiversity and ecosystem and in the maintenance of a sustainable economic development. Among all, the most important ones are the Barcelona Convention - including its seven implementing protocols and the United Nations Environment Programme (UNEP)'s Mediterranean Action Plan (MAP) -, the Agreement on the Conservation of Cetaceans in the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS), the Food and Agriculture Organization (FAO) with several sectoral agreements and initiatives - such as the FAO Compliance Agreement, the General Fisheries Commission for the Mediterranean (GFCM) and the International Commission for the Conservation of Atlantic Tunas (ICCAT) -, the Convention on Biological Diversity and other biodiversity related agreements and conventions - such as the Bern Convention -, and the EU's sectoral and environment policies (e.g., MSFD) and regional programmes and initiatives like the EU Mediterranean Strategy. Yet, despite the presence of such frameworks, agreements and initiatives, difficulties exist in governing and managing Mediterranean marine resources. The major cause behind it is related to the socio-political complexity of the region, being surrounded by twenty one countries from Europe, Asia and Africa, all having highly different political and cultural systems and associated legal jurisdictions. As a consequence of this complexity and lack of regional management strategies that take this complexity into account, Mediterranean ecosystems keep degrading and many marine species are over-exploited or depleted (Papaconstantinou & Farrugio 2000, Colloca et al. 2013, Tsikliras et al. 2013, Vasilakopoulos et al. 2014).

1.1 Thesis Objective (Thesis Outline)

The overarching objective of this thesis is to contribute to the scientific component needed to advance an ecosystem-based management approach in the Mediterranean Sea. This thesis adopts an interdisciplinary approach, combining data integration, modelling approaches and the analysis of the model-based indicators, to investigate the status of the Mediterranean Sea ecosystem and the sustainability of its marine resources in order to inform future conservation and management actions.

To achieve the overall objective, this thesis is organized around five main topics: a review about the use of ecological models to assess marine ecosystem status in support of European policies (*Chapter 2.1*); the reconstruction of Italy's marine fisheries removals and fishing capacity (*Chapter 2.2*); and the development and use of an ecosystem modelling approach to: a) assess ecosystem health changes of a semi-enclosed embayment of the Mediterranean Sea (*Chapter 2.3*); b) develop a quantitative description of the whole Mediterranean marine ecosystem in two periods of time representing past and present conditions (*Chapter 2.4*); and c) evaluate historical impact of environmental and fisheries drivers on the whole Mediterranean marine ecosystem (*Chapter 2.5*). Annexes 1-5 compile the original peer reviewed articles (and supplementary materials) that have resulted from this PhD thesis (4 published and 1 submitted for publication), while Annex 6 lists additional peer-reviewed publications which I contributed as co-author (6 published or accepted).

Specific objectives of each chapter:

CHAPTER 2.1: ECOLOGICAL MODELS TO ASSESS MARINE ECOSYSTEM STATUS IN SUPPORT OF EU POLICIES

Since the European Union's Marine Strategy Framework Directive (MSFD) seeks to achieve, for all European seas a "Good Environmental Status" (GEnS, Borjia et al., 2011) by 2020, and ecological models are currently one of the strongest approaches used to predicting and understanding the consequences of anthropogenic and climate-driven changes in the natural environment, the objectives of the chapter were to:

- review the current capabilities of the modelling community to inform on indicators outlined in the Marine Strategy Framework Directive (MSFD), focusing on biodiversity (D1), food webs (D4), non-indigenous species (D2) and seafloor integrity (D6) descriptors of the MSFD;

- assess which models were able to demonstrate the linkages between indicators and ecosystem structure/function and the impact of pressures on state and indicators;
- and report on gaps in model capability and suggest needs for development.

This chapter highlighted EwE as the modelling toolbox associated with the largest number of model-derived biodiversity indicators that could be used to support the MSFD. For this reason, this modelling approach was chosen and applied in this thesis to the Mediterranean Sea as shown in Chapters 2.3, 2.4 and 2.5.

CHAPTER 2.2: RECONSTRUCTION OF ITALY'S MARINE FISHERIES

An important step when building an ecosystem model is the collection of biological, environmental and human related data. This chapter developed a method for reconstructing long time series of catches for one of the most important fisheries of the Mediterranean Sea, the Italian fisheries. This work was conducted as part of an overall effort to reconstruct global fisheries catches (Pauly & Zeller 2016) by the Sea Around Us (www.seaaroundus.org), which also included other Mediterranean countries (Coll et al. 2014; Pauly et al. 2014; Tsikliras et al. 2007; Ulman et al. 2013).

Thus, using all available data sources and accounting for reported and unreported commercial landings, recreational and subsistence landings and discards, this Chapter estimated for the 1950-2010 period:

- catches for all marine Italian fishing sectors;
- fishing capacity for major Italian fishing fleets; and
- total catch per unit of effort.

In the near future, Mediterranean catch reconstructions will be integrated in the modelling effort developed for the Mediterranean Sea, as in Chapters 2.4 and 2.5, to reduce data gaps and better capture the impact of fishing pressure on the Mediterranean marine ecosystem.

CHAPTER 2.3: ECOSYSTEM HEALTH FOR A MEDITERRANEAN SEMI-ENCLOSED EMBAYMENT

Using the ecosystem modelling approach Ecopath with Ecosim (EwE; Christensen & Walters 2004), this chapter assesses and quantifies the health status of a semi-enclosed embayment of the Mediterranean Sea, the Amvrakikos Gulf (Ionian Sea).

With this chapter I wanted to highlight the importance of assessing also local ecosystem dynamics (in this case an embayment of the Mediterranean Sea) and associated stressors that might or not differ from the regional scale model. Thus, a food web model of the Amvrakikos Gulf ecosystem for the 1980 was built and fitted to time series from 1980 to 2013. The aim of the study was to:

- investigate temporal dynamics of marine resources in the last three decades considering the effect of changes in rivers run off, development of fish farming and changes in fisheries as the major anthropogenic drivers affecting the system; and
- assess structural and functional changes of the Amvrakikos Gulf, using model derived indicators obtained from temporal simulations.

CHAPTER 2.4: MODELLING THE MEDITERRANEAN MARINE ECOSYSTEM

Using the EwE modelling framework, and the Ecopath food web model in particular (Christensen & Walters 2004), this chapter assesses the Mediterranean marine ecosystem structure and function as a whole. In particular two EwE food web models for the 1950s and 2000s periods were built to investigate:

- the main structural and functional characteristics of the Mediterranean food-web during these two time periods;
- the key species/functional groups and interactions;
- the role of fisheries and their impact; and
- the ecosystem properties of the Mediterranean Sea in comparison with other European Regional Seas.

The main challenge of this chapter is to represent the Mediterranean Sea ecosystem as whole, which is characterized by different biological and environmental characteristics, and to retrieve/integrate available regional data. However, due to the complexity of the region, a sub-regional approach was also developed to investigate the food web structural and functional properties at two geographical levels: the sub-regional (dividing the Mediterranean Sea in four areas: Western Mediterranean Sea, Adriatic Sea, Ionian and Central Mediterranean Sea and Aegean and Levantine Sea) and the regional level (considering the whole Mediterranean Sea).

CHAPTER 2.5: HISTORICAL CHANGES OF THE MEDITERRANEAN SEA ECOSYSTEM

In order to inform future management policies and develop plausible scenarios, this chapter quantifies temporal dynamics of marine species in the Mediterranean Sea ecosystem as a whole and by sub-region as indicated above, evaluating past and current dynamics and status. The specific goals are to investigate:

- temporal evolution of the Mediterranean marine ecosystem from 1950 to 2011 by fitting the Mediterranean food web model (previously developed in chapter 2.4) to available time series, developing a hind-cast scenario analysis, which includes changes in primary productivity, fisheries activities and food web dynamics; and
- structural and functional changes of the Mediterranean Sea ecosystem using specific modelled-derived indicators from 1950 to 2011 using the hind-cast scenario analysis of the best fitted model.

CHAPTER 2.

RESULTS

Chapter 2.1

Ecological models to assess marine ecosystem status in support of EU policies

ECOLOGICAL INDICATORS 58 (2015) 175-191

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Using ecosystem models to assess biodiversity indicators in support of the EU Marine strategy framework directive

El uso de modelos basados en el ecosistema para evaluar indicadores de biodiversidad que sirvan de soporte a la Directiva Marco sobre la Estrategia Marina

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Abstract

The European Union's Marine Strategy Framework Directive (MSFD) seeks to achieve, for all European seas, "Good Environmental Status" (GEnS), by 2020. Ecological models are currently one of the strongest approaches used to predicting and understanding the consequences of anthropogenic and climate-driven changes in the natural environment. We assess the most commonly used capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity descriptors. We built a catalogue of models and their derived indicators to assess which models were able to demonstrate: (1) the linkages between indicators and ecosystem structure and function and (2) the impact of pressures on ecosystem state through indicators. Our survey identified 44 ecological models being implemented in Europe, with a high prevalence of those that focus on links between hydrodynamics and biogeochemistry, followed by end-to-end, species distribution/habitat suitability, bio-optical (remote sensing) and multispecies models. Approximately 200 indicators could be derived from these models, the majority of which were biomass and physical/hydrological/chemical indicators. Biodiversity and food webs descriptors, with ~49% and ~43% respectively, were better addressed in the reviewed modelling approaches than the non-indigenous species (0.3%) and sea floor integrity (~8%) descriptors. Out of 12 criteria and 21 MSFD indicators relevant to the abovementioned descriptors, currently only three indicators were not addressed by the 44 models reviewed. Modelling approaches showed also the potential to inform on the complex, integrative ecosystem dimensions while addressing ecosystem fundamental properties, such as interactions between structural components and ecosystems services provided, despite the fact that they are not part of the MSFD indicators set. The cataloguing of models and their derived indicators presented in this study, aim at helping the planning and integration of policies like the MSFD which require the assessment of all European Seas in relation to their ecosystem status and pressures associated and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020.

Resumen

La Directiva Marco sobre la Estrategia Marina (DMEM) de la Unión Europea pretende alcanzar el "buen estado medioambiental" (BEE) de todos los mares europeos en el 2020. Los modelos ecológicos son actualmente uno de los enfoques más potentes que se utilizan para predecir y entender las consecuencias de cambios antropogénicos y climáticos en el medio natural. En este artículo evaluamos las capacidades más utilizadas en la modelización para proporcionar información sobre los indicadores contenidos en la DMEM, en particular sobre los descriptores de biodiversidad, redes alimentarias,

especies no indígenas e integridad del fondo marino. Hemos construido un catálogo de modelos con sus indicadores para evaluar qué modelos son capaces de demostrar: (1) los vínculos entre indicadores y la estructura y función del ecosistema y (2) el impacto de las distintas presiones sobre el estado de los ecosistemas usando indicadores. Este estudio ha identificado 44 modelos ecológicos que se están aplicando en Europa; hay una gran prevalencia de modelos que se centran en la relación entre la hidrodinámica y la biogeoquímica, seguidos de otros modelos "de principio a fin" (end-to-end), de distribución de especies/hábitats, de bio-óptica (teledetección) y de múltiples especies. Con estos modelos se pueden calcular aproximadamente unos 200 indicadores, la mayoría de los cuales están relacionados con biomasa o con aspectos físicos/hidrológicos/químicos. Los descriptores de biodiversidad y redes tróficas, con el ~49% y ~43% respectivamente, están mejor estudiados en los modelos revisados que los de especies no indígenas (0,3%) y los de integridad del fondo marino (~ 8%). De los 12 criterios y 21 indicadores pertinentes para los descriptores que mencionamos antes de la DMEM, en la actualidad sólo 3 indicadores no son abordadas por ninguno de los 44 modelos analizados. Los modelos muestran también la posibilidad de informar sobre la complejidad del ecosistema de un modo global, y al mismo tiempo analizar las propiedades fundamentales de los ecosistemas, como por ejemplo las interacciones entre los componentes estructurales y los servicios que proporcionan los ecosistemas, a pesar de que estas interacciones no son parte de los indicadores establecidos por la DMEM. El catálogo de modelos e indicadores presentado en este estudio tiene por objetivo ayudar en la planificación e integración de políticas como la DMEM, que requiere analizar el estado de los ecosistemas y las presiones en todos los mares europeos y establecer objetivos ambientales (a través de indicadores) para lograr el BEE en 2020.

1. Introduction

The use of robust and appropriate indicators that can assess whether an ecosystem and its services are well maintained and sustainably used (Layke, 2009; Walpole et al., 2009; TEEB, 2010) has been recognised as an essential step for the practical implementation of conservation and management policies (Rombouts et al., 2013). Several efforts have been undertaken at a European scale to evaluate marine ecosystem structure and their response to human activities, using key indicators to assess and sustain "Good Environmental Status" (GEnS; Borja et al., 2011). These initiatives have been carried out to assist the Marine Strategy Framework Directive (MSFD, 2008/56/EC; European Commission, 2008), the main European Directive that focuses on marine waters and aims at assessing the status of an ecosystem under anthropogenic pressures and the required interventions to bring the system back to its desired good status, making human activities sustainable, since this is one of the objectives of the MSFD. To achieve GEnS, 11 descriptors, 29 associated criteria and 56 indicators (from biological, physico-chemical indicators as well as pressure indicators—including hazardous substances, hydrological alterations, litter and noise, and biological disturbance such as introduction of non-indigenous species) have been identified (Cardoso et al., 2010; European Commission, 2010) (Tables 2 and 4).

Despite the fact that several attempts have been made to assess the environmental status of marine waters in an integrative manner (Borja et al., 2011; Halpern et al., 2012; Tett et al., 2013), significant gaps still exist on understanding marine ecosystem structures and functions and their response to human pressures (Katsanevakis et al., 2014; Borja et al., 2013). Currently, ecological models have been recognised as powerful tools to evaluate ecosystem structure and function and predict the impacts of human activities (Fulton and Smith, 2004; Shin et al., 2004; Christensen and Walters, 2005; Plagányi, 2007; Fulton, 2010) and climate change (Tomczak et al., 2013; Chust et al., 2014) on marine systems. Thus, this study aims to assess the most commonly used capability of the modelling community to inform on indicators outlined in the EU MSFD (2008/56/EC), focusing particularly on biodiversity related descriptors: biological diversity (D1), non-indigenous species (D2), food webs (D4), and seafloor integrity (D6). To date, there has been no thorough evaluation of the capabilities of ecological models to provide information as explicitly outlined by the MSFD indicator structure, this task has been only partially undertaken (e.g., Reiss et al., 2014). With this work, we aim to fill in this knowledge gap by providing an inventory of models in EU regional seas that could assess MSFD indicators associated with biodiversity, non-indigenous species, food webs and seafloor integrity. For this reason, we have built a model catalogue ranging from lower to higher trophic levels, including those that successfully couple the two compartments and associated ecosystem processes. This inventory, developed as part of the DEVOTES FP7 Project (http://www.devotes-project.eu/), serves to highlight the vast potential of model-derived indicators that can be associated with MSFD descriptors and aims to provide a thorough assessment of their relevance and degree of "operationality."

Yet, we acknowledge that this study does not aim to serve as review of all the existing models available in the literature, but instead highlight a process of exploring modelling potential to support specific European policies. Because of the nature of these issues, though, similar case studies conducted elsewhere are likely to lead to similar outcomes, conclusions, and recommendations (e.g., because of similar/same model availability and/or process understanding). Thus, this work emphasises several types of ecological modelling and derived indicators that exist at EU level stressing how such diversity of modelling approaches could be useful to support management policies and the limitations that still occur to achieve this task.

In particular, this study is divided into six sections, comprising (1) catalogue structure; (2) a general overview of model characteristics; (3) model potential to address MSFD GEnS descriptors and indicators (including the ability to address biodiversity components and habitat types); (4) geographical coverage of models; (5) ability to address pressures; and (6) gaps in models type/modelling capability and needs for further development.

2. Catalogue structure

The catalogue has been built primarily with models/areas targeted by the DEVOTES partners (which represent 23 research institutions from EU and non EU countries), yet with an effort to integrate available models/areas from other inventories (e.g., the MEECE project http://www.meece.eu/Library.aspx) and scientific literature.

The catalogue has been structured with several fields following the MSFD Commission Decision 2010/477/EU (European Commission, 2010) and grouped into six main categories:

i. Model/Indicator properties with the following sub-categories:
    a. MSFD descriptor/indicator, descriptor/indicator outlined in the directive
    b. Model derived indicator (MDI), indicator resultant from model output
    c. MDI type defined as 1. Static (e.g., snapshot of the indicator at a precise period of time), 2. Dynamic (e.g., indicator which changes in time) or 3. Spatial dynamic (e.g., indicator which changes in time and space)
    d. MDI status of development defined as 1. Operational, when the indicator is developed, tested and validated (e.g., it could be either an indicator used by the Member States (MS) for national environmental monitoring; or in EU/International Conventions' monitoring programmes; or validated with observed/survey data although not necessarily approved by any national/international law or convention); 2. Under development, an indicator proposal exists, but not yet validated in field/real data (e.g., indicator not yet used for MS national environmental monitoring or for EU/International Conventions' monitoring programmes; or not yet validated with survey data); 3. Conceptual, an indicator idea, supported by theoretical grounds, although no practical measure/metric is yet available (e.g., indicator not yet tested)
    e. MDI target/reference values and unit defined as thresholds/limits representing boundaries between an acceptable and unacceptable status
    f. Model name referring to the label used to identify a particular model
    g. Model type referring to model characteristics/properties and/or to the technique used to assess specific ecosystems
    h. Data requirements referring to data needed to run a certain model
    i. Confidence/uncertainty referring to the ability of models to assess uncertainty for the input/output data and it is defined as the type of statistical analysis used to evaluate it
    j. Source Scientific literature and or Institutional report supporting selected

MDI/models entries

ii. Model/MDI in relation to MSFD Descriptors: referring to models and MDI broad capability to address the 11 descriptors of the directive (D1–D11).

iii. Model/MDI correspondence with MSFD Biodiversity Indicators: referring to models and MDI assessed in relation to their capability to provide information for the specific indicators listed under the criteria of the four descriptors (D1/D2/D4/D6) as officially outlined in the European Commission (2010).

iv. Model/MDI correspondence with biodiversity components referring to which biodiversity components (e.g., microbes, phytoplankton and fish) the indicator was related to or was evaluated with. Categories adopted for biodiversity components followed those of the European Commission (2010) and EU Commission Staff Working Paper (CSWP, 2012).

v. Model/MDI coverage of specific habitat types and geographical range/scale referred to whether an MDI was related to certain habitats and geographical areas. Categories adopted for Habitat Types followed those of the European Commission (2010) and EU Commission Staff Working Papers (CSWP, 2011, 2012). Concerning geographical coverage, we have adopted well-established international criteria for smaller scale subdivisions or ecological assessment areas in order to increase the spatial detail on the information collected (e.g., the International Council for the Exploration of the Sea (ICES) and General Fisheries Commission for the Mediterranean (GFCM) subdivisions).

vi. Model/MDI relation to specific pressures: referring to whether there was scientific evidence of a relationship between a pressure and a specific indicator. Indicators were related to pressures either as responsive/sensitive to, or affected by a given pressure (state indicators, e.g., mainly through changes in trends) or indicators were actually pressure indicators themselves. The considered pressures follow the list of pressures and impacts of Annex 3 of the MSFD.

3. Model characteristics

The model catalogue revealed that currently 44 models have been applied with outputs relevant to MSFD descriptors (Table 1). These ecological models being used to describe or understand ecosystem processes can be categorised under seven types of modelling approaches described below:

3.1. Biogeochemical models

The bulk properties of biogeochemical fluxes in marine ecosystems are combined with information on physical forcing, chemical cycling and ecological structure to simulate the response of lower trophic level groups (phytoplankton and zooplankton) to environmental conditions, including climate variability and change (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011). Such models typically have very simplified representations of biological organisms, and associated trophic structure (Anderson, 2005).

3.2. Multispecies models

These models represent populations of dynamically interacting species or functional groups. Some models also resolve multiple stages or size-classes within populations (Christensen and Walters, 2004; Hollowed et al., 2000; Shin and Cury, 2001). Focus of these models is on understanding the implication of the indirect interactions in ecosystems that result from the complex networks of direct predator–prey interactions in marine communities. The models aim to represent, for example, top-down or bottom-up effects along marine food chain ranging from primary producers (e.g. phytoplankton) to top predators (e.g., marine mammals), or the role of indirect competitive interactions among species (Fung et al., 2015). Effects of exploitation by fisheries and environmental change are also frequently described by these models.

3.3. Species Distribution Models (SDM)/Habitat Suitability Models (HSM)

SDM combine observations of species occurrence or abundance with environmental explanatory variables to develop ecological and evolutionary understanding and to predict distribution across selected habitats (Elith and Leathwick, 2009; Reiss et al., 2014). HSM relate field observations to a set of environmental variables (e.g., reflecting key factors of the ecological niche like climate, topography, geology) to produce spatial predictions on the suitability of locations for a target species, community or biodiversity (Hirzel et al., 2006). A new generation of SDM/HSM – i.e. dynamic bioclimatic envelope models – now provide greater links to the mechanistic understanding of niche ecology. Such models typically include additional model components that describe physiological responses of species to the environment, population dynamics and dispersal, to further constrain the distribution of suitable habitat and provide more realistic species distribution projections (Cheung et al., 2011).

3.4. Meta-community models

Meta-community is a set of interacting communities which are linked by the dispersal of multiple, potentially interacting species. In this context, meta-community models are theoretical frameworks describing specific mechanistic processes in order to predict empirical community patterns. They deal mainly with species composition and abundance and their variation within a meta-community (Hugueny et al., 2007).

3.5. Bio-optical models

The optical properties of biological materials, such as phytoplanktonic or heterotrophic unicellular organisms, are analysed and then modelled to predict distributions of biological communities over wide spatial areas (with remote sensing data) or in terms of expected depth limitations that can be inferred from modelling studies. Bio-optical models are based on various fundamental theories of optics which apply to a single particle making use of a set of equations/algorithms (Morel and Maritorena, 2001; IOCCG, 2006).

3.6. Hydrodynamic–biogeochemical models

These are mainly coupled hydrodynamic and biogeochemical models to capture global scale patterns in physical–chemical components affecting lower trophic level groups (e.g., phytoplankton and zooplankton) (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011).

3.7. End-to-end models

In recent years, hydrodynamic-biogeochemical models (or just biogeochemical models) have been coupled with multispecies models. These so called end-to-end (E2E) models combine physico-chemical oceanographic processes with organisms ranging from low trophic level (LTL) to higher trophic level organisms (HTL) into a single modelling framework (Travers et al., 2009).

Of the models reported in this study, more than half were coupled ecological models (Table 1). The most common type of models currently in the catalogue were hydrodynamic-biogeochemical models (36%) followed by end-to-end (18%), species distribution/habitat suitability, bio-optical and multispecies (14% each), biogeochemical and meta-community (2% each) models (Table 1).

In the framework of ecological studies, physical–biological interactions are the main factors that can better describe ecosystem properties and the spatial and/or temporal evolution in function of relevant pressures identified, climate change or anthropogenic impacts. This is reflected in the choice of modelling approaches and in the growing need to couple different types of models within a single modelling framework (Travers et al., 2009; Rose et al., 2010). This is particularly true if the models are intended to predict changes and provide guidance in a framework of biodiversity conservation and ecosystem-based management (Travers et al., 2009; Kaplan et al., 2012).

Recent software developments, within the current (DEVOTES) and former EU projects (e.g., MEECE http://www.meece.eu/), have shown that these models (hydrodynamic-biogeochemical and multispecies models) can be coupled to run together. This represents a powerful tool for scenario testing of climate change and anthropogenic impacts simultaneously. There is a growing trend for E2E modelling, which includes anthropogenic and physical drivers behind observed changes, identifying both direct and indirect causes (Fulton, 2010; Shin et al., 2010b; Travers-Trolet et al., 2014), and so better facilitates the setting of targets and implementation of management measures (Cury et al., 2008; Kaplan et al., 2012).

Fig. 1 illustrates the capacity of the seven model types to represent the different components of marine ecosystems, including or excluding, human components and/or climate impacts. Coupled (both E2E and hydrodynamic-biogeochemical models) and bio-optical (remote sensing) models included in this catalogue were primarily spatially dynamic and 5 out of 30 models were also dynamic. The remaining models were mainly static with only 5 out of 14 models presenting dynamic and spatial modules as well (Table 1). This is an important and interesting result since spatial-dynamic models are able to provide greater capacity for forecasting of ecosystem dynamics, although they require a more data intensive calibration (e.g., the initial testing and tuning of a model) and validation (e.g., the comparison/fitting of model with a data set representing “local” field data) approaches (Jørgensen, 2008).

A total of 201 model-derived indicators (see S1 of supplementary materials) were included in this catalogue, of which more than half were considered to be “operational”

(64%), while the majority of the remainder were still “under development” (33%), with only a few “conceptual” approaches (3%) presented (Table 2). We acknowledge that some indicators might have changed their status since the time of this survey (e.g., some indicators “under development” may have been assessed and now classified as ”operational”) but for the purpose of this work we decided to keep them in the status of development that they were reported during the survey.

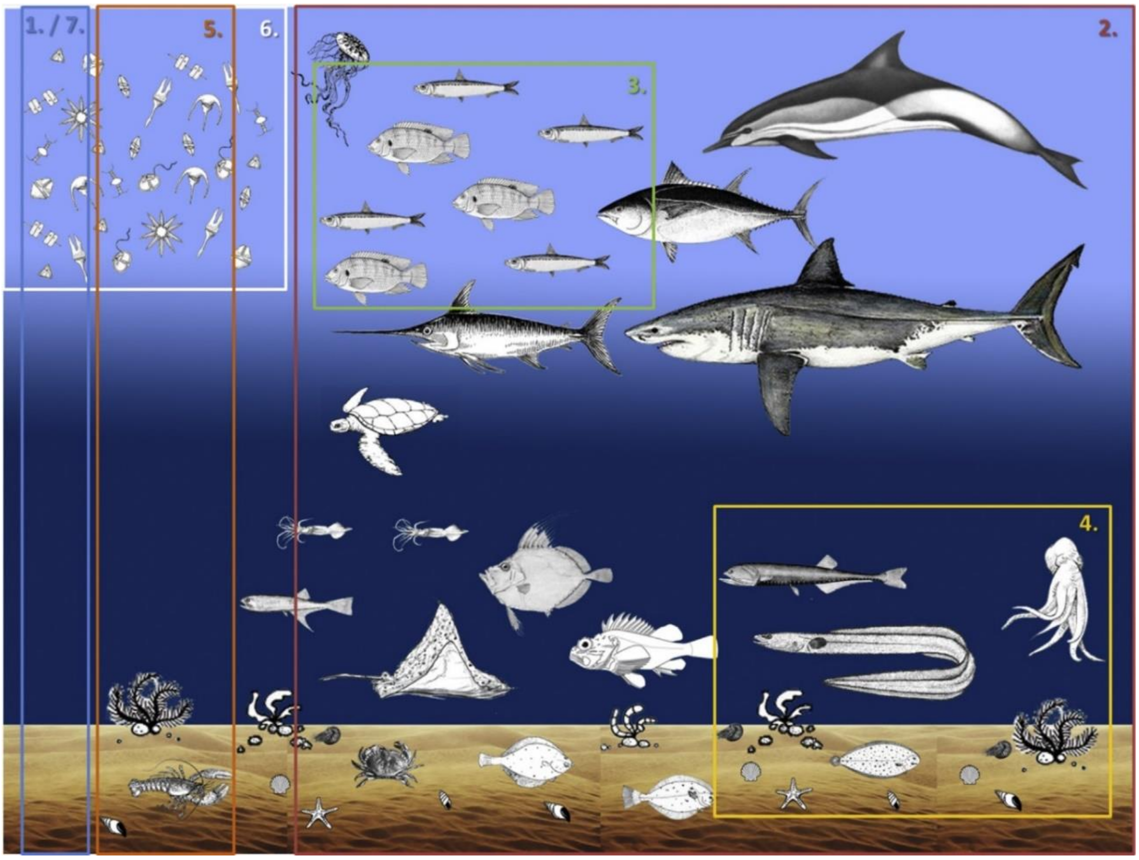

Fig. 1. Illustration of models capacity to describe the ecosystem, from specific processes integrating biological compartments and the associated abiotic environment to the entire ecosystem including, or not, human components or climate impacts. In particular, 1 and 7 – refer to biogeochemical and coupled physical–biogeochemical models; 2 and 3 – refer to multispecies models (either at species or at food web level); 4 – Species distribution/Habitat Suitability; 5 – meta-community models and 6 – bio-optical models. E2E models encompass all of them.

Ecopath with Ecosim (EwE) was notably associated with the largest number of model-derived biodiversity indicators (Table 2). However, the majority of these biodiversity indicators were biomasses of species or groups of species at different trophic levels of the food web. For ease of characterisation/evaluation, model-derived indicators were grouped into seven major categories (see Table 3 for the detailed list).

Table 1

Summary table of models library showing models' name, acronym, data type (SP: spatial; DY: dynamic; ST: static), number of model derived indicators and uncertainty (VOD: validated with observed data; VOD*: some of the indicators still need to be validated with observed data; NA: not available; STAT: statistical analysis; BOOT: bootstrap; PE: pedigree).

#	Model name	Model acronym	Type of the model	Coupled	Data type	Model derived indicators	Uncertainty
1	European Regional Seas Ecosystem Model (ERSEM)	ERSEM	Biogeochemical	No	SP-DY	2	VOD
2	Black Sea chlorophyll and coloured dissolved/detrital matter (Chl & CDM) model	BS-Chl & CDM	Bio-optical models (remote sensing)	No	SP-DY	4	VOD*
3	Black Sea model of downwelling radiance (BS-PAR Model)	BS-PAR	Bio-optical models (remote sensing)	No	SP-DY	1	VOD
4	Black Sea Particle Size Distribution (PSD) model	BS-PSD (PSC)	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
5	Black Sea spectral Primary Production (SPP) model	BS–SPP	Bio-optical models (remote sensing)	No	SP-DY	1	VOD*
6	Black Seal Inherent Optical Properties model (IOPs)	BS-IOPs	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
7	North Sea Optical Properties (NSOP)	NSOP	Bio-optical models (remote sensing)	No	DY	1	STAT
8	1D General Ocean Turbulence Model (GOTM) and European Regional Seas Ecosystem Model (ERSEM) and Ecopath with Ecosim (EwE)	GOTM-ERSEM-EwE	End to end	Yes	DY	6	NA
9	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO) and Ecopath with Ecosim (EwE)	POM-BIMS-ECO-EwE	End to end	Yes	DY	3	NA
10	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-BioEBUS-OSMOSE	End to end	Yes	SP-DY	5	NA
11	Regional Ocean Model System (ROMS) and $N_2 P_2 Z_2 D_2$ biogeochemical model and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-$N_2 P_2 Z_2 D_2$-OSMOSE	End to end	Yes	SP-DY	12	NA
12	Norwegian Sea Ecosystem, End-to-End	NORWECOM.E2E	End to end	Yes	SP-DY	6	NA
13	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM) and Fish Model	ERGOM + MOM + Fish	End to end	Yes	DY	2	VOD
14	ECOSystem Model (ECOSMO) and Stochastic Multi-Species model (SMS)	ECOSMO-SMS	End to end	Yes	SP-DY	2	NA
15	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ERSEM-POM-OSMOSE	End to end	Yes	SP-DY	10	NA
16	Hubbell's neutral model of biodiversity (HNM)	HNM	Meta-community	No	ST	1	NA
17	Ecopath with Ecosim (EwE)	EwE	Multispecies	No	ST-DY-SP	136	PE-VOD*
18	North Sea Threshold general additive models (NS tGAM)	NS tGAM	Multispecies	No	DY	4	BOOT
19	Population-Dynamical Matching Model (PDMM)	PDMM	Multispecies	No	DY	1	VOD
20	Bay of Biscay Qualitative trophic model	BoB Qualit	Multispecies	No	ST	1	NA
21	Length-based multispecies model (LeMANS)	LeMANS	Multispecies	No	DY	2	VOD
22	Stochastic Multi-Species model (SMS)	SMS	Multispecies	No	DY	2	VOD
23	Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) and European Regional Seas	POLCOMS-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA

	Ecosystem Model (ERSEM)						
24	3D General Estuarine Transport Model (GETM) and European Regional Seas Ecosystem Model (ERSEM)	GETM-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	16	VOD*
25	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO)	POM-BIMS-ECO	Physical (hydrodynamic)–biogeochemical	Yes	DY	4	NA
26	St. Petersburg Eutrophication Model (SPBEM)	SPBEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
27	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM)	ERSEM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	11	NA
28	3D General Estuarine Transport Model (GETM) and Ecological Regional Ocean Model (ERGOM)	GETM-ERGOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	8	VOD*
29	BAltic Sea Long-Term large-Scale Eutrophication Model (BALTSEM)	BALTSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
30	Biogeochemical Flux Model (BFM) and Princeton Ocean Model (POM)	BFM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	5	NA
31	Black Sea Ecosystem Model	BSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	13	VOD*-STAT
32	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM)	ERGOM + MOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
33	ECOSystem Model (ECOSMO)	ECOSMO	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
34	MOHID and Pelagic Biogeochemical Model (LIFE)	MOHID-LIFE	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	4	VOD*
35	Nucleus for European Modelling of the Oceans (NEMO) and Biogeochemical Flux Model (BFM)	NEMO-BFM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	10	NA
36	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS)	ROMS-BioEBUS	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
37	Regional Ocean Model System (ROMS) and $N_2P_2Z_2D_2$ biogeochemical model	ROMS-$N_2P_2Z_2D_2$	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	12	NA
38	Swedish Coastal and Ocean Biogeochemical model (SCOBI) and Rossby Center Ocean circulation model (RCO)	RCO-SCOBI	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
39	Ecological Niche Factor Analysis (ENFA)	ENFA	SDM/Habitat Suitability Models	No	ST	1	NA
40	Bay of Biscay Habitat suitability based on Generalised Additive Models (GAM)	BoB GAM	SDM/Habitat Suitability Models	No	ST	1	NA
41	Bay of Biscay Habitat suitability based on Generalised Linear Models (GLM)	BoB GLM	SDM/Habitat Suitability Models	No	ST	1	NA
42	Habitat suitability based on MaxEnt (Maximum Entropy)	MaxEnt	SDM/Habitat Suitability Models	No	ST	2	NA
43	Niche-Trait Model (NTM)	NTM	SDM/Habitat Suitability Models	No	ST	1	NA
44	Process-driven habitat model	PDH	SDM/Habitat Suitability Models	No	ST	1	NA

Not surprisingly, biomass indicators constituted the largest group with approximately 57% followed by diversity indices (13%) and physical, hydrological and chemical indicators (12%). Regarding targets and/or reference values associated with model-derived indicators, the catalogue highlights that only few models in few areas had assigned target or reference values, despite the fact that the majority were considered "operational" (i.e. developed, tested and validated). This is the case of fully developed models for which validated outputs exist (e.g., BSEM by Dorofeev et al., 2012), but under policy contexts such as the MSFD, lack tested and validated reference values or targets compliant with specific legal requirements.

Also, very few of the reported models have been used to clearly assess the effects of measures to meet the targets that will eventually be established. For instance, multispecies models have been applied in the Ionian Sea and in the North Sea ecosystems to assess the reduction in fishing effort as a measure to (a) bounce back common dolphin populations (e.g., EwE model by Piroddi et al., 2011); (b) assess the response of selected biodiversity indicators (e.g., PDMM by Shephard et al., 2013; Fung et al., 2013, or EwE model by Lynam and Mackinson, in press); (c) test the effect of selective fishing on community biodiversity conservation (e.g., LeMANS model by Rochet et al., 2011) and implemented in the Bay of Biscay (e.g., OSMOSE model by Chifflet et al., 2014) to evaluate the effect of different fishing scenarios on small pelagic fish stocks.

In addition, not all the models were able to address uncertainty; the majority (61%) lacked an approach to determine confidence intervals/range of uncertainty or required further validation work for indicators. This is a reflection, as mentioned above, of the type of data present in the catalogue which are more spatial-dynamic than static and for which validation is more difficult to obtain. From the models that reported addressing uncertainty (39%), data comparison and data validation (e.g., model outputs fitted to surveyed data) was the most common method reported (Table 1).

4. Model potential to address descriptors and indicators for biological descriptors

In terms of supporting the MSFD, ecological models can be the most effective means to model relationships between activities, pressures, state and thus indicators

(Jørgensen, 2008; Jørgensen and Fath, 2011). This is because of the integrative character of these modelling approaches that often consider many ecosystem components from abiotic factors to biotic interactions and processes. The 44 models available in the catalogue were capable of addressing indicators in 8 of the 11 descriptors of the MSFD (Table 2) although, due to the focus of this survey which primarily dealt with the four biodiversity related descriptors, their modelling potential was stronger for two of these biodiversity descriptors: biological diversity (D1) and food webs (D4). Nevertheless, human induced eutrophication (D5), hydrographical conditions (D7) and commercial fish and shellfish (D3) were well addressed by the models in this catalogue. Within the biodiversity related descriptors, non-indigenous species (D2) and seafloor integrity (D6) were the most poorly addressed by the models currently in the catalogue (Table 2). However, Pinnegar et al. (2014) shows how EwE models can be useful in assessing the response of an ecosystem to the introduction of invasive species (D2). Similarly, increasing the spatial resolution of many of the current models would further improve our understanding of the direct effect of fishing and other activities (such as decommissioning of oil rigs or development of a wind farm) on seafloor integrity (D6). In several cases, models have been used to investigate the impacts of trawling and test fisheries scenarios (e.g., high resolution ERSEM-POM model, Petihakis et al. (2007)). However, most of the models considered in this catalogue do not explicitly include descriptions of these types of pressures on the marine environment, they do not link to benthic habitat layers, and their understanding of pressures and impacts is in many cases still limited by scarce empirical information (Hooper and Austen, 2014).

Typically, a single model was capable of addressing more than one MSFD descriptor and sometimes up to six, as is the case of EwE (Table 2). As a result, the same model may be noted for having indicators in multiple stages of development (e.g., operational, under developed or conceptual) either across descriptors or within the same descriptor. This is because the reported status of development relates not to the model itself but to the different indicators that can be derived from the model. The potential of the available models to address MSFD indicators specifically those within biological descriptors was evaluated by extracting the number of indicators (outlined in the European Commission (2010)) that each model can inform on (Table 2).

All models could address multiple indicators, from the set of 21 MSFD indicators under these 4 descriptors. In fact, 20 models in the catalogue had the potential to address at least half of these indicators. Despite the high potential of the models to address MSFD indicators, not all of the available model-derived indicators were fully operational (see Section 2 for definition and Table 4).

The mean percentage of operational model-derived indicators across all MSFD indicators was 64%. Our analysis also revealed that there were three indicators required under the biodiversity descriptors for which no model-derived indicators were available in the catalogue (Table 4): D1C3-I2: population genetic structure; D2C2-I1: Ratio between invasive non-indigenous species and native species and D2C2-I2: Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

Additionally, it is noteworthy that the potential of modelling approaches to address ecosystem fundamental properties such as D1C8I1 "Interactions between structural components" and D1C8I2 "Services provided" (Table 4) was high. These aspects, despite being clearly mentioned in the European Commission (2010), were not part of the MSFD indicators set, most probably due to the difficulty in defining them through specific indicators. Nevertheless, the majority of the model-derived indicators included in this catalogue (189 out of the 201) have the potential to inform on these complex, integrative ecosystem dimensions. In any case, although the catalogue shows the potential of models to address Ecosystem Services (ES, sensu Liquete et al., 2013), the survey performed cannot inform adequately on the capacity of the indicators to support policy-makers' use of these ES concepts.

This is a current limitation of the MSFD set of indicators (Table 4) which does not clearly require the assessment of ecosystems services, despite the fact that in 2011, as a party of the Convention on Biological Diversity (CBD), the European Union (EU) adopted a new strategy (the Biodiversity Strategy to 2020), which integrates ES as key elements for the conservation approach to biodiversity (Maes et al., 2012). The role of ES in supporting conservation initiatives and socio-economic activities calls for action to monitor, quantify and value trends in these services, so as to ensure that they are adequately considered in decision making processes.

Table 2
Models' capability per the 11 Marine Strategy Framework Directive descriptors (D) assessed by the number of indicators provided by each model (for names, see Table 1). The development status of the indicators is indicated (op: operational, ud: under development, co: conceptual). The last column summarises the number of MSFD official indicators (European Commission, 2010) of D1, D2, D4 and D6 (check Table 4) that the model-derived indicators can inform on. [a] New proposals for Descriptor 4 Food Webs, not yet considered under the set of Indicators outlined in the EU Commission Decision (European Commission, 2010).

		D1 Biological diversity	D2 Non-ind. species	D3 Commercial fish	D4 Food webs	D5 Eutrophication	D6 Seafloor integrity	D7 Hydrological alterations	D8 Contaminants	D9 Contaminants in food	D10 Marine litter	D11 Energy/ noise	# MSFD indicators addressed under D1, D2, D4, D6
1	BALTSEM	7op			5op	3op		2op					16
2	BFM-POM	5op			3op	2op		2op					14
3	BSEM	6op/7ud	1op/1ud		1op/7ud	4ud		3op					9
4	EwE	82op/82ud/7co	1ud	53op/57ud/4co	82op/82ud/7co	13op/14ud/2co	17op/25ud/4co						13 (+1[a])
5	ECOSMO	6op			3op	2op		3op					14
6	ECOSMO-SMS	2ud		2ud	2ud								8
7	ENFA	1op		1op	1op								14
8	ERGOM + MOM	7op			5op	3op		2op					16
9	ERGOM + MOM + fish	2op		2op	2op								7
10	ERSEM	2ud			2ud	1ud							12
11	ERSEM-POM	11op			6op	3op		5op					14
12	ERSEM-POM-OSMOSE	10ud		10ud	10ud								9
13	BoB GAM	1op		1op	1op								16
14	GETM-ERGOM	8ud			2ud	4ud		6ud					14
15	GETM-ERSEM	16ud			5ud	8ud	2ud	11ud					19
16	BoB GLM	1op		1op	1op								16
17	GOTM-ERSEM-EWE	6ud		4ud	6ud					3ud			8
18	HNM	1co			1co	1co	1co						16
19	BS-IOPs	3ud			2ud	3ud							8
20	LeMANS	2op		2op	2op								7
21	MaxEnt	2op	1op	1op	2op								17
22	MOHID–LIFE	4op			3op	3op		1op					10
23	NEMO-BFM	10ud			7ud	4ud		3ud					17
24	NSOP	1ud			1ud	1ud							8
25	NStGAM	4ud		2ud	4ud	1ud							10
26	NORWECOM.E2E	6op			3op	2op		3op					14
27	NTM	1ud			1ud		1ud						9
28	PDMM	1op		1op	1op								7
29	POLCOMS-ERSEM	6op			3op	2op		3op					14
30	POM-BIMS-ECO	4op			3op	2op		1op					14
31	POM-BIMS-ECO-EWE	3ud		3ud	3ud								9
32	PDH	1ud			1ud		1ud						11
33	BS-PSD (PSC)	3ud			3ud	3ud							5
34	BoB Qualit	1co		1co	1co								8 (+1[a])
35	RCO-SCOBI	7op			5op	3op		2op					16
36	BS-Chl & CDM	4ud			4ud	4ud							6
37	BS-PAR	1ud											3

38	BS-S PP	1ud			1ud	1ud						3
39	ROMS-BioEBUS	6op			3op	2op		3op				14
40	ROMS-BioEBUS-OSMOSE	5ud		5ud	5ud							9
41	ROMS-$N_2P_2Z_2D_2$	12op			8op	5op		4op				13
42	ROMS-$N_2P_2Z_2D_2$-OSMOSE	12op		12op	12op							11
43	SMS	2op		2op	2op							7
44	SPBEM	7op			5op	3op		2op				16
Number of models per descriptor		44	3	17	43	26	5	17	0	1	0	0

Table 3
The model-derived indicators grouped into 7 major categories, based on what the indicators inform on, with their overall percentages in the DEVOTES Catalogue of model-derived indicators.

	Type of indicators		**%**
1	Biomass		57
2	Diversity indicators	Biodiversity indices (*e.g.* Kempton diversity index, trophic level of the community) and species/habitat diversity, proportions in community	13
3	Primary or secondary production		9
4	Spatial distribution indicators	Species spatial distribution	6
5	Species life-history	Traits such as for e.g. length, weight or life span	1
6	Ecological Network Analysis (ENA) indicators	Flows, energies and efficiencies	2
7	Physical, hydrological and chemical	Describing either habitat integrity or pressures	12

To do so, a clear linkage needs to be established between biodiversity and ecosystem functioning and the diversity and complexity of the benefits they provide, i.e. the ecosystems services (be it provisioning, regulating or cultural), in order to allow the development of operational indicators. Yet, the indicators available are not comprehensive and are often inadequate to characterise ES; data are often either insufficient or the linkages are poorly understood to support the use of these indicators (Liquete et al., 2013).

4.1. Biodiversity components and habitats

Habitats and species are key attributes of biological diversity and their occurrence, distribution and abundance is used as criteria to assess the ecosystem status (Table 5). To attain GEnS for D1, as stated in the MSFD, "no further loss of biodiversity at ecologically relevant scale should occur, and, if it does, restoration measures should be put in place". The definition of GEnS is dependent on the ecological relevance and is approached at different scales of complexity, from species to habitats, communities and ecosystem (see Borja et al., 2013). Biodiversity components indicated in the MSFD include microbes, phytoplankton, zooplankton, angiosperms, macroalgae, benthic invertebrates, fishes, cephalopods, marine mammals, reptiles and birds, with specific subgroups within the last four categories. Their inclusion in ecological models listed in the catalogue was highly heterogeneous. Operational model-derived indicators concerned mainly fish, phytoplankton, zooplankton, benthic and pelagic invertebrates and marine mammals (total 64, 45, 31, 23, and 17, respectively) (Fig. 3), while the remaining biodiversity components were covered with less than 10 indicators each.

This reflects the traditional focus of marine ecosystem modelling, driven mainly by the wide spread use of low trophic level models related to the bottom-up forcing of production, and in parallel, motivated by fisheries oriented policies and conservation interests in particular species (Rose et al., 2010; Shin et al., 2010b). As expected, the various models have used similar components differently and, depending on their final goal, the resolution of the biodiversity components differed greatly: from single to multi-species models, inclusion of single or multiple functional groups and integrating both LTL and HTL key organisms (e.g., Oguz et al., 1999; Lewy and Vinther, 2004; Schrum et al., 2006; Coll et al., 2008; Rossberg et al., 2010; Lassalle et al., 2011; Mateus et al., 2012;

Tsiaras et al., 2012). Of the models catalogued, only Hubbell's neutral model and the Population-Dynamical Matching Model (PDMM) resolve biodiversity at species level, and only the PDMM does so through the entire marine food chain (Fung et al., 2013). EwE model-derived indicators, either operational, conceptual or still under development, have been used to model all types of biodiversity components (excluding microbes), with fish being the most frequently assessed group (25%) followed by benthic invertebrates (15%), marine mammals (12%) and cephalopods (11%).

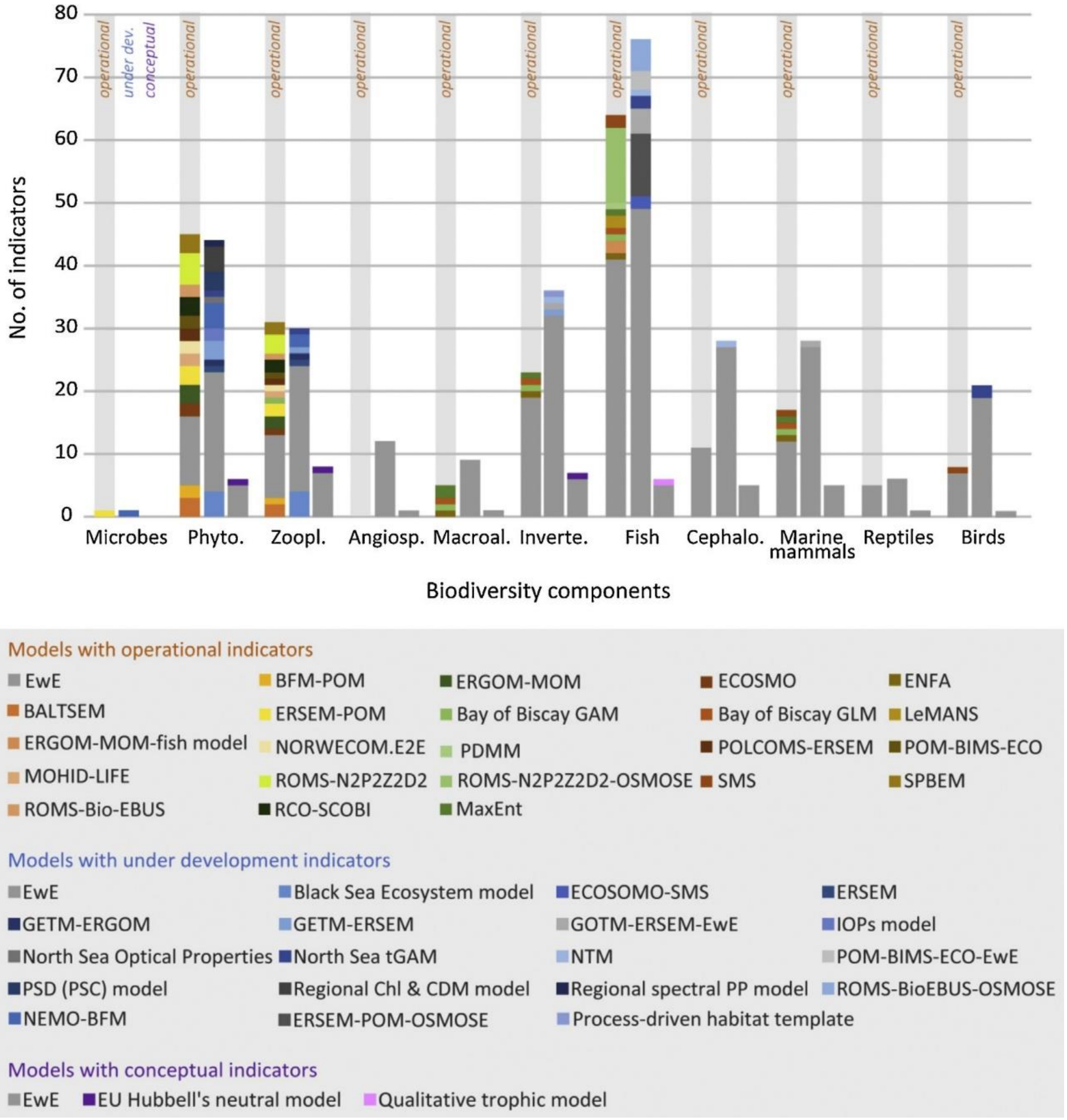

Fig. 3. Number of model-derived indicators available per biodiversity component. For each biological group the indicators are organised by columns according to their development status: operational, under development and conceptual. The different colours and patterns identify the models providing the indicators.

Table 4

Model derived indicators and models available per MSFD descriptor/indicator for biodiversity related descriptors (D1, D2, D4, D6), with particular emphasis on the number of operational indicators (op) out of the indicators available for each MSFD indicator.

MSFD descriptor	Criteria	MSFD indicator	Model derived indicators from DEVOTES catalogue		Comments
			Operational/available indicators	Number of models	
D1	C1	I1 Distributional range	33 op/45	27	
D1	C1	I2 Distributional pattern within range	4 op/10	15	
D1	C1	I3 Area covered by the species (for sessile/benthic species)	1 op/2	5	
D1	C2	I1 Population (1) abundance and/or (2) biomass	93 op/163	37	
D1	C3	I1 Population demographic characteristics: (1) body size; (2) age class structure; (3) sex ratio; (4) fecundity rates; (5) survival/mortality rates; (6) other	14 op/37	15	
D1	C3	I2 Population genetic structure	No indicators available	No models available	*D1 Biodiversity/C3 Population condition*
D1	C4	I1 Distributional range	6 op/9	21	*The exact same indicators are proposed as suitable to address both I1 and I2 from D1C4 Com. Dec.*
D1	C4	I2 Distributional pattern	6 op/9	21	
D1	C5	I1 Area	6 op/7	20	*Nearly the same indicators as in D1C4 are also reported as suitable to address both I1 and I2 from D1C5 Com. Dec.*
D1	C5	I2 Volume	4 op/4	15	
D1	C6	I1 Condition of the typical (1) species and (2) communities	89 op/174	39	
D1	C6	I2 Relative (1) abundance and/or (2) biomass	11 op/25	7	
D1	C6	I3 (1) Physical, (2) hydrological and (3) chemical conditions	12 op/39	23	
D1	C7	I1 Composition of ecosystem components: (1) habitats and (2) species	96 op/168	39	
D1	C7	I2 Relative proportions of ecosystem components: (1) habitats and (2) species	100 op/186	43	
D1	(C8)	I1 Interactions between structural components	108 op/198	44	*Not defined under Com. Dec. list but in its text.*
D1	(C8)	I2 Services provided	105 op/183	39	
D2	C1	I1 Trends in: (1) abundance; (2) temporal occurrence; (3) spatial distribution	2 op/4	3	
D2	C2	I1 Ratio between invasive non-indigenous species and native species	No indicators available	No models available	*D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species*
D2	C2	I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem	No indicators available	No models available	
D4	C1	I1 Performance of (1) key predator species determined from their productivity; (2) other trophic group	3 op/7	19	
D4	C2	I1 (1) Large fish (by weight); (2) other species	18 op/40	10	
D4	C3	I1 Abundance trends of functionally important selected: (1) groups with fast turnover rates; (2) groups/species that are targeted by human activities or that are indirectly affected by them; (3) habitat-defining groups/species; (4) groups/species at the top of the food web; (5) long-distance anadromous and catadromous migrating species; (6) groups/species that are tightly linked to specific groups/species at another trophic level	100 op/181	42	
D4	*(C4)*	*(not defined)*	None operational/3	2	*D4 Food webs: new proposals*

D6	C1	I1 Biogenic substrate: (1) type; (2) abundance; (3) biomass; (4) areal extent	2 op/5	6
D6	C1	I2 Extent of seabed significantly affect by human activities for the different substrate types	None operational/1	1
D6	C2	I1 Presence of particularly sensitive and/or tolerant species	None operational/1	1
D6	C2	I2 Multi-metric indexes assessing benthic community condition and functionality, such as (1) species diversity and (2) richness, (3) proportion of opportunistic to sensitive species	1 op/4	6
D6	C2	I3 Proportion of (1) biomass or (2) number of individuals in the macrobenthos above some specified length/size	17 op/38	3
D6	C2	I4 Parameters describing the characteristics of the benthic community	None operational/1	1

The microbial component, as reported in the catalogue, was only evaluated by ERSEM-POM in the Aegean Sea and under development by NEMO-BFM in the Baltic Sea. When models were organised according to model type, multispecies models assessed the majority of biodiversity components with the exception of microbes that were mostly evaluated by coupled hydrodynamic–biogeochemical models (Fig. 3). The predominant habitat types that should be assessed within the evaluation of the status under the MSFD are water-column, seabed and ice habitats, with ecological models referring to one or several of these habitats. In our catalogue, of all predominant habitats, water-column was the most comprehensively evaluated habitat, either on its own, or in relation to the other two habitats.

Table 5
Number of model-derived indicators for each biodiversity component per habitat type (only habitats addressed by the models are included).

Biodiversity components	Seabed			Water column				ICE
	Littoral rock and reef	Shallow sublittoral mixed sediment	Shelf sublittoral mud	Marine coastal	Marine shelf	Marine oceanic	Variable salinity estuarine water	Ice-habitats
Microbes				1	1			1
Phytoplankton		9	1	4	42	13	2	4
Zooplankton	1	10	1	3	34	12	1	2
Angiosperms					12	7		
Macroalgae	1			1	11	1		
Invertebrates	1	11	1	1	45	15		1
Fish								
Coastal fish				2				
Pelagic fish				12	18	12		1
Pelagic				1	2	2		
Demersal fish				7	13			1
Demersal					1	11		
Other	1	14			34	11		
Cephalopods								
Coastal/shelf		13			27	6		
Other					7	1		
Marine								
Toothed		13		1	23	2		
Baleen whales					1	1		
Seals					3	1		1
Other	1				8	6		
Reptiles								
Sea turtles					10	1		
Birds								
Inshore pelagic feeding		13			13			
Offshore pelagic feeding				1	1			
Other					10	5		

There were only two instances where seabed habitats were evaluated on their own. Ice-associated habitats were assessed by hydrodynamic–biogeochemical and multispecies models while seabed habitats were evaluated in multispecies and SDM/Habitat suitability/Community models. Multispecies as well as coupled (both hydrodynamic–biogeochemical and E2E) models were mainly used for the assessment of species or groups of species/organisms that can be linked to water-column habitats. Examining the intersection between model-derived indicators and habitats, the water column was the most widely covered habitat, specifically the continental shelf where all components of biodiversity were covered (Table 5). The marine oceanic water column was also widely covered; however, in this case microbes were not evaluated. In estuaries, only phytoplankton and zooplankton were assessed, which were also the main components modelled in ice-associated habitats. In the seabed habitat, shallow sublittoral mixed sediments were the most commonly evaluated with model-derived indicators assessing 7 out of the 11 biodiversity components. Invertebrates were mainly studied in relation to the water column over the continental shelf although they are also considered in models that include a benthic component, for example, ERSEM. The least addressed biodiversity components were microbes, coastal fish, pelagic elasmobranchs, baleen whales, seals and offshore pelagic birds. When looking at habitat representation in model-derived indicators, ice associated habitats, estuarine water column and shelf sublittoral mud were seldom covered (Table 5).

5. Models geographical coverage

Ecological models can be applied to many different areas with adequate customization (Henry et al., 2012; Mateus et al., 2012). The models in the catalogue have not been applied with the same spatial scale in all European regional seas (Fig. 2). The majority of reported indicators related to the Mediterranean Sea, representing more than half of the indicators entered in the catalogue (137), followed by the North-East Atlantic Ocean (78), Black Sea (29), Baltic Sea (18), non-EU regional seas (11) and EU scale (2). The EwE software was the most widely used model and has been applied in each EU regional sea area and most sub-regions; the second most commonly used model was ECOSMO, which has been implemented for the Baltic Sea, the North-East Atlantic Ocean and one non-EU regional sea (Barents Sea).

In most regional seas, the proportion of model-derived indicators considered operational was high (ranging between 60 and 80%), except for the Black Sea where a suite of ecological models had been developed but using model-derived indicators still under development (about 70%) at the time of the assessment. Conceptual models were mainly reported for the North-East Atlantic region. As stated by the MSFD, Member

States (MS) need to cooperate to ensure a coordinated effort in the study and development of management strategies for the different marine regions and sub-regions. This is the case for ecological models developed for understanding and forecasting the marine ecosystem response to pressures. This catalogue demonstrates that the geographical coverage of ecological models in European marine waters is extensive and that the assessment of the environmental status can benefit considerably from greater use of ecological modelling. However, the use of differing models in different regions constrains the possibility of comparisons and inference of robust conclusions on causalities and scenarios (Chust et al., 2014).

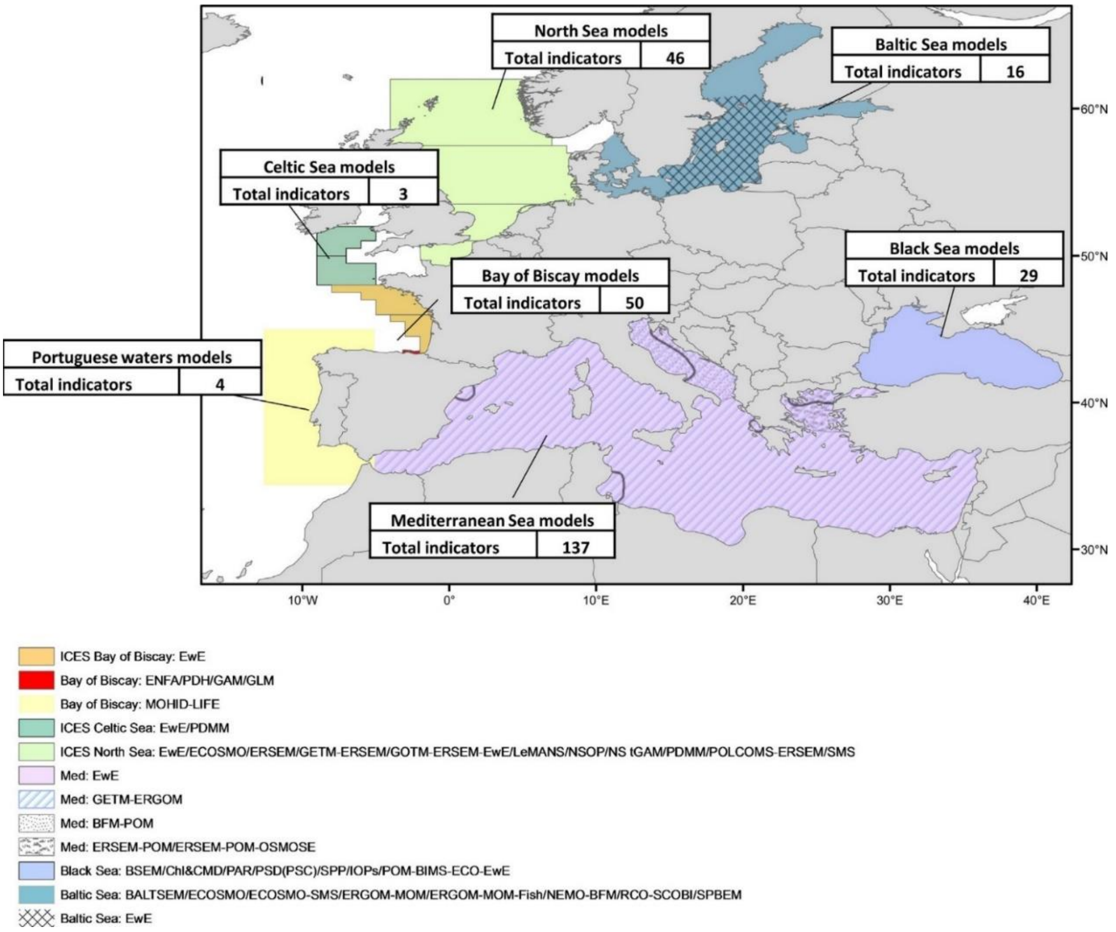

Fig. 2. Geographical distribution and spatial coverage of the models in the catalogue, when applicable. ECOSMO, ROMS-BioEBUS and ROMS-BioEBUS-OSMOSE are not displayed since are occurring in areas (Barents Sea and Benguela) outside the European Seas. EU Hubbell's neutral model and Maxent since they are applied to all EU regional seas are not represented.

6. Addressing pressures with models

Models are powerful tools for scenario testing of climate and anthropogenic impacts both separately and simultaneously (Jørgensen and Fath, 2011). All 44 available models included in the present catalogue, have been used to address at least one pressure or its impact on state of the ecosystem or its components. Most of the model-derived indicators compiled in the catalogue are state indicators (91%), meaning that they inform on the condition of the ecosystem, its components or its functioning, while reflecting the impacts of single or multiple pressures in the environment. The majority do not provide a direct measure of the pressure(s) affecting the system, so they can only indirectly be associated to the pressures mentioned above. And despite strong scientific evidence for the overall cause–effect relationships between many of these pressures and the state of the ecosystem (Shin et al., 2005, 2010a; Fulton, 2011), the identification and quantification of the pressure(s) cannot be achieved through these indicators. On the other hand, a few of the indicators produced by the models are actually pressure indicators (9%), which means that they act as proxies for relevant pressures.

For instance, temperature or pH can act as a proxies for climate change; nutrients concentration and oxygen levels as proxies for eutrophication; biomass of an invasive species (e.g., *Mnemiopsis leidyi*, Dorofeev et al., 2012) as a proxy for non-indigenous species pressure; and also 'Inverse fishing pressure' which measures the total fishing pressure on an ecosystem using landings over biomass, could be considered as a proxy for exploitation rate and therefore a potential pressure indicator (Shin et al., 2010). Of all the pressures listed in the MSFD, 'Interference with the hydrological regime' was the most frequently addressed (in terms of numbers of models), with all 44 models reported and currently being used in monitoring or research associated with this pressure (Fig. 4). The 'Input of nutrients and organic material' and 'Marine acidification' (pH change) followed as pressures that could be addressed by more than half of the models. On the other hand, 'Non-indigenous species', 'Marine litter' and 'Underwater noise' were the least addressed pressures by the type of models included in our survey, with just four models able to inform on the responses to one, or maximum two, of these pressures.

The pressures 'Physical loss of marine habitat' and 'Physical damage to marine habitats' (combined as 'sum of Physical damage' in Fig. 4), could primarily be addressed using E2E, multispecies and SDM/Habitat suitability types of models. The Meta-community model could also produce indicators related to these pressures. A total of 20 models provided 114 indicators to address these pressures, with EwE able to provide 95 of these indicators. Such indicators were mostly state indicators, primarily related to biomass of different trophic levels, with a small number also relating to species distribution, primary and secondary production. Two physico-chemical indicators from the GETM-ERSEM model were the only pressure indicators reported: denitrification layer depth and oxygen penetration depth. 'Underwater noise' and 'Marine litter' were both addressed by the same two models (GOTM-ERSEM-EwE and EwE), and through a similar set of model-derived indicators (in a total of 19 state indicators), all relating to top predator biomass such as large fish, marine mammals, reptiles and seabirds. This is a common thread for many of the pressures acting particularly on higher trophic groups and therefore their impacts are better evidenced by models encompassing such trophic levels.

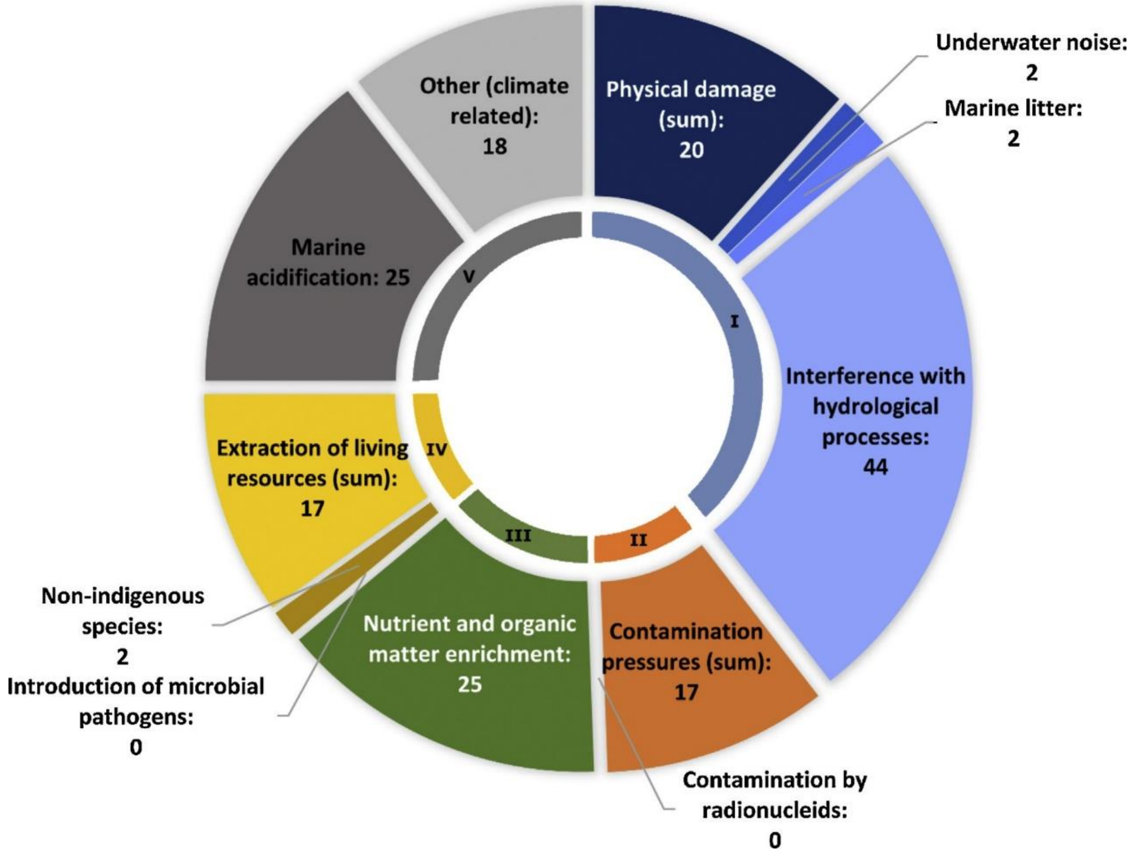

Fig. 4. Capability of models in the DEVOTES catalogue to address pressures outlined in the Marine Strategy Framework Directive (Annex III); the number of models available per major type of pressure is indicated: I – physical disturbance type of pressures; II – contamination by hazardous substances; III – nutrient and organic matter enrichment; IV – biological disturbance; and V – climate related pressures.

The pressure 'Interference with the hydrological processes' could be addressed by 190 indicators from all models in our catalogue. Such changes in hydrological regime (namely thermal and salinity), were perceived as pressures related closely to climate change, although climate change is also accounted for by other pressures such as 'Marine acidification'. In this sense, the large majority of the state indicators in the catalogue were reported as able to reflect the impact of these regime-shifts with strong ecological implications throughout the food web. Only 19 are pressure indicators, essentially physical–chemical indicators derived from coupled models with physical (hydrodynamic)–biogeochemical modules. The EwE food web and the BS-PAR bio-optical (remote sensing) were the other type of models providing two of these pressures indicators (respectively, '1/(landings/biomass)–Inverse fishing pressure' and 'Habitat condition–water transparency'). The pressures 'Contamination by synthetic compounds', 'Contamination by non-synthetic substances & compounds' and 'Acute pollution' (represented as 'Sum of contamination Pressures' in Fig. 4) were addressed by a total of 17 models of different types (multispecies, meta-community, SDM/habitat suitability and coupled models).

Up to 132 model-derived indicators were identified, with the EwE model able to provide the highest number. The majority of these were indicators of biomass with a small proportion of indicators relating to energy flow and primary/secondary production. One pressure indicator '1/(landings/biomass)–Inverse fishing pressure' has also been reported under this pressure type. The majority of the 25 models assessing 'Inputs of nutrients and organic matter' (Fig. 4) were spatial-dynamic coupled models (both E2E and hydrodynamic–biogeochemical) and, less frequently, biogeochemical, multispecies and bio-optical models. The total number of indicators that could address this pressure is 42, focusing on various measures of primary production and parameters relating to zooplankton. Only two of them are pressure indicators: 'Population size (as biomass) of a non-indigenous species–*Mnemiopsis leidyi*' and 'Habitat condition as water transparency'. 'Non-indigenous species' were only addressed by two models, the BSEM physical (hydrodynamic)–biogeochemical coupled model and the EwE food web model, through the indicators 'Population size (as biomass) of a non-indigenous species – *Mnemiopsis leidyi*' and 'Alien shrimps biomass", respectively.

A total of 17 models, essentially food web and coupled models, have been applied in the context of 'Selective extraction of living resources' (encompassing extraction of fish and shellfish through direct catch, by-catch and discards and extraction of maërl, seaweed harvesting and the extraction of any other species) (Fig. 4). Overall, 143 indicators were associated collectively with these models. The majority of these were indicators of biomass, being associated with the EwE model. Only one pressure indicator was reported ('1/(landings/biomass)–Inverse fishing pressure') from EwE. 'Marine acidification (pH change)' was currently addressed by 25 models (Fig. 4), essentially coupled models (both E2E and hydrodynamic–biogeochemical) with a dynamic or spatial-dynamic nature, but also multispecies, bio-optical models, and biogeochemical models. A total of 56 indicators capable of assessing the effects of this pressure, relating also to climate change, could be derived by these models. These indicators are predominantly related to biomass of lower trophic groups and primary production.

Finally, other pressures not listed in the MSFD Annex III, related to climate and inter-annual meteorology, were also mentioned by the modellers, reporting 18 models that could provide 30 indicators responsive to such pressures. The majority were state indicators, such as low trophic groups biomass, but also some production, diversity or species life-history indicators. As pressure indicators, six physical–chemical proxies of climate pressures were mentioned (see S1 in the online version).

7. Gaps and development needs

This work summarises the current capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity. The cataloguing of models and their derived indicators presented in this study aim to help the planning and the implementation of objectives defined in the MSFD particularly in relation to which models and indicators exist and the missing components to support such policy.

This is particularly important in the MSFD framework that requires the assessment of all European Seas in relation to their ecosystem status and pressures associated, and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020. Overall it was evident from the analysis of the model catalogue that some descriptors (and their requirements) within the MSFD (Table 4) are best assessed by modelling (e.g., D4 food webs), while other indicators are better assessed by "traditional" empirically derived ecological indices. For instance, many models potentially addressing D6 (seafloor integrity) lacked specific indicators of substrate type or seabed extent (Table 4) mainly because of their inability to express benthic habitat as some form of component. D2 (non-indigenous species) is currently poorly addressed by the models even though some of them would have the capability to provide useful indicators for this descriptor. Similarly indicators for D8 (contaminants), D9 (contaminants in food), D10 (marine litter), D11 (underwater noise) outlined by the European Commission (2010) are not currently addressed by any of the models reported here; however, these descriptors were not the target of our survey.

Three indicators related to the four biodiversity related descriptors (D1, D2, D4, D6) had no model-derived indicator in the catalogue (Table 4):

- D1 Biodiversity/C3 Population condition.
    - I2 Population genetic structure
- D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species
    - I1 Ratio between invasive non-indigenous species and native species
    - I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

With respect to the gaps addressed to pressures, the majority of models require further work to show how sensitive and specific to pressures they are. Underwater noise, marine litter and contamination by microbial pathogens are poorly addressed by existing models and those that have been reported to produce indicators that are sensitive to these pressures require further development. It is emphasised that this summary of model use does not reflect model adequacy, data quality or the overall quality and effectiveness of the monitoring and research programmes under which the models are applied.

Focusing on model features, two main gaps were identified that require further development: one related to the setting of targets, and the other to uncertainty associated with model results. Targets exist when objectives have been clearly identified and their translation into operational performance metrics agreed to, which involves a socio-political decision process that occurs independently of model development. If the models have been developed independently of such processes, which is the case for most of the models listed in the study, targets for selected variables may not be available (despite the indicator being operational) reflecting the context in which they have been developed. Thus, because the models in the catalogue were not developed with the aim of supporting MSFD, and because the MSFD does not set clear targets or aims, it is not surprising that model developers often reported difficulties in setting targets and/or reference values for their models.

Two main barriers were identified. First, the process of association of ecologically meaningful targets to model outputs (derived indicators) without a clear vision of where and what the model would be used for in a specific MSFD context. Second, the level of demand required by the targets: should thresholds and/or reference values reflect the good condition of the assessed component in isolation (for e.g., for each indicator used) or reflect a compromise between ecological integrity and the use of the marine environment, as implicit in the MSFD GEnS definition?

The level at which GEnS should be defined, either at indicator or at the descriptor level, or even for all eleven descriptors together, will influence the way thresholds setting is perceived and established (Borja et al., 2013). This will ultimately affect the final assessment as discussed in depth in Claussen et al. (2011) and Borja et al. (2013). For the last point, it can be argued that there is not enough information at this stage for model developers to set meaningful targets for MSFD purpose. Therefore, threshold setting should be guided by clear objectives and end goals as achievable targets and these are not known at present.

In this context, several initiatives have been created to support and address, at least partly, most of the issues arise above; for example FP7 projects such as MEECE (completed) and DEVOTES (in progress) have been developed to explore the use of ecological models in assessing ecosystem status and in support of decision making and EU policy. More recently, MIDAS, a modelling inventory database with models currently in use by the European Commission, allows the assessment of how models are used and/or support impact assessments at EU level.

In addition, not all the models were able to address uncertainty; the majority lacked confidence intervals or an approach to evaluate uncertainty of the model outputs. Marine system models are indeed becoming increasingly complex and sophisticated, but far too little attention has been paid to model errors and the extent to which model outputs actually relate to ecosystem processes (Allen et al., 2007). Further developments on this would produce more robust assessments and forecasts and therefore more reliable indicators.

European geographical coverage is also very heterogeneous with several identified marine areas with enormous potential for improvement. Also certain habitats (e.g., ice-associated habitats or continental shelf sublittoral mud) and biodiversity components (e.g., microbes) are underrepresented in the modelling approaches presently in the catalogue. As mentioned before, this is mostly due to the emphasis that has been given historically to particular flag species, commercially important organisms or particularly endangered species/habitats. However, the relative importance of modelling such components can change according to the system studied. Current gaps should, therefore, be evaluated on a regional scale basis.

Looking at current modelling gaps from a regional seas perspective, one of the limitations observed is the focus of the participants in the review process that may have shown a bias in the selection of models/model types. An example of this is Atlantis, a E2E model not currently operational in Europe, or the Bioenergetics and Dynamic Energy Budget (DEB) type of models currently not included in this catalogue but widely used in the regions covered by DEVOTES (Teal et al., 2012). These models describe how individuals acquire and utilise energy, in addition to how physiological performance is influenced by environmental variables, and can serve as a link between different levels of biological organisation (Nisbet et al., 2000, 2012). Considering them would thus increase the potential to address MSFD Descriptors/Indicators that focus particularly on properties at the individual level and physiological level, usually responding to pressures whose impacts operate or can primarily be detected at that scale (e.g., biological disturbance, such as food resource depletion; contamination; or effects of climate change, namely marine acidification).

In addition, regional model runs identified the need to improve the existing models with regards to species diversity (e.g., adding certain species or refining subgroups), spatial resolution for selected species and for better description of the direct effect of anthropogenic pressures on ecosystems. Model response towards the impact of certain pressures still requires further testing. Relevance of certain pressures differs across regional marine areas. Broadly speaking, those that could benefit from further research are for physical damage to marine habitats, underwater noise, marine litter, contamination by radio-nuclides, introduction of microbial pathogens, extraction of species (maërl, seaweed and others), marine acidification, acute pollution events and nutrient and organic matter enrichment.

Data availability is also a constraint. This could partially explain why the number of 'under development' indicators is still quite high suggesting that this requires particular efforts to increase the potential to address MSFD descriptors.

To assess the environmental status descriptors adequately, the gap analysis conducted here highlights that further refining of the current models and their associated indicators as well as the adoption of new modelling techniques are needed. The information (data) needs for model development and the results provided (outputs), is very heterogeneous. Two main modelling approaches can be distinguished: statistical (i.e. SDMs) and mechanistic (i.e. multispecies and biogeochemical models) (Kendall et al., 1999). In general terms, spatial mechanistic models require large amounts of computational resources, and can only be applied when demographical, physiological, and life traits of species are well known. On the other hand, statistical (i.e. SDMs) modelling studies often neglect dispersal-limitation and advection, although they can play an important role on spatial distribution, while spatial dynamical models minimise the role of environmental factors on species distribution (Robinson et al., 2011). Taking a balanced view between the importance of dispersal-limitation and of niche partitioning on the species spatial distribution, we suggest that research efforts should focus on integrating the two mechanisms into ecological modelling.

Finally, in some instances, the gaps identified may not need to be filled. This is the case for component(s) and/or pressure(s) considered 'un-manageable' (e.g., the target for zooplankton biomass or distribution). However, given the complex interactions within ecosystems, management of some components may have unexpected effects on 'unmanageable' components. Thus, ecological models should be developed to encompass all components, to the extent that they are known, wherever possible.

See original publication in Annex 1

Chapter 2.2

Reconstruction of Italy's marine fisheries

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Reconstruction of Italy’s marine fisheries removals and fishing capacity, 1950-2010.

Reconstrucción de las capturas pesqueras marinas italianas y la capacidad de pesca, 1950-2010.

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Abstract

Italy has the highest catches of all countries fishing in the Mediterranean Sea. Despite the availability of fisheries statistics at the national level, reported catch amounts account only for a portion of total fisheries removals. This study aims to provide an estimate of 1) catches for all marine fishing sectors; 2) fishing effort in the major Italian fishing fleets; and 3) catch per unit of effort from 1950 to 2010. Catches were estimated using a catch-reconstruction approach that looked at all types of fisheries removals: from reported and unreported landings (from both industrial and artisanal fisheries) to recreational landings and discards. The reconstructed total catch for the 1950-2010 time period was 2.6 times the amount reported by the FAO on behalf of Italy. Illegal, unreported and unregulated (IUU) landings constituted 53.9% of the reconstructed total catch, followed by reported catches (38.8%) and unreported discards (7.3%). Industrial fisheries were dominant, with 79.1% of the reconstructed total removals, followed by the artisanal catch (16.8%), with recreational (3.2%) and subsistence (0.9%) fisheries making very small contributions. Catch per unit of effort declined since the early 1950s. Our study is the first that estimated total Italian fisheries removals and fishing capacity using a holistic approach; such approach is particularly important in areas like the Mediterranean Sea, where the multi-species and multi-gear nature of fisheries make the assessment of single-species fisheries resources and their management difficult.

Resumen

Italia cuenta con las mayores capturas de todos los países que pescan en el mar Mediterráneo. A pesar de la disponibilidad de estadísticas pesqueras a nivel nacional, las capturas registradas representan sólo una parte del total de las extracciones pesqueras. Este estudio tiene como objetivo proporcionar una estimación de 1) las capturas de todos los sectores de pesca marina; 2) la explotación pesquera (o esfuerzo) de las grandes flotas italianas; y 3) las capturas por unidad de esfuerzo entre 1950 y 2010. Las capturas se han estimado utilizando una reconstrucción que contempla todo tipo de extracción por pesquerías: desde desembarques declarados y no declarados (tanto de pesquerías industriales como artesanales) hasta desembarques recreativos y descartes. Las capturas totales reconstruidas del período 1950-2010 representan 2,6 veces la cantidad reportada por la FAO en nombre de Italia. Los desembarcos por pesca ilegal, no declarada y no reglamentada (INDNR) constituyeron el 53,9% de las capturas totales reconstruidas, seguido por las capturas declaradas (38,8%) y los descartes no declarados (7,3%). La pesca industrial domina estas cifras, con el 79,1% de las extracciones reconstruidas totales, seguida por la captura artesanal (16,8%), y con muy pequeñas contribuciones de la pesca recreativa (3,2%) y de subsistencia (0,9%). La captura por unidad de esfuerzo disminuyó desde principios del decenio de 1950. Nuestro estudio es el primero que calcula el total de las extracciones pesqueras italianas y la capacidad de pesca utilizando un enfoque holístico. Este enfoque es particularmente importante en áreas como el mar Mediterráneo, donde las múltiples especies y la diversidad de artes pesqueras hacen difícil la evaluación y gestión de recursos pesqueros de forma mono-específica.

1. Introduction

The Mediterranean Sea has been described as "under siege" due to the effects of multiple stressors such as fishing, habitat loss and degradation, pollution, eutrophication, and the incidental introduction of alien species (Coll et al., 2011). Fishing is one of the strongest pressures, and has caused changes in ecosystem structure, declines in major fish stocks and in overall biodiversity in many parts of the Mediterranean Sea (Colloca et al., 2011; Farrugio et al., 1993; Papaconstantinou and Farrugio, 2000; Vasilakopoulos et al., 2014). Although the exploitation of marine resources has a long history in the Mediterranean basin (Thompson, 1947), fisheries research and management has only developed post-World War II, particularly in the northwest of the basin (Farrugio et al., 1993). Italian fisheries are among the most important fisheries in the Mediterranean, constituting, according to the Food and Agriculture Organization of the United Nations (FAO) statistics, roughly 30% of its all catches. In recent decades, the Italian fishing industry has faced declines, both in terms of catch, due to a decrease in the major fisheries resources (4th Multi-Annual Guidance Plans; MAGPs), and also in fishing effort, as a result of European Commission regulations, which attempt to adjust the fishing fleet to the available fishing resources (Iborra Martin, 2006). In contrast, since the late 1980s, there has been a steady increase in farmed fish production. The majority of mariculture production consists of Mediterranean mussels (*Mytilus galloprovincialis*) and Manila clams (*Tapes philippinarum*), followed by gilt-head seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*) (Cataudella and Spagnolo, 2011; OECD, 2010). The present reconstruction is solely concerned with marine capture fisheries of finfish and invertebrates (excluding sponges, turtles, jellyfish and marine mammals), and thus does not address aquaculture trends and associated issues.

Given the growing emphasis on ecosystem-based management issues in fisheries (Pikitch et al., 2004), a comprehensive understanding of total fisheries removals and fishing capacity is fundamental to understanding the ecosystem resources trends and thus contribute to policy on future resource use. This, however, becomes challenging in a Mediterranean country whose statistical reports of catch and effort are often unreliable, and where actual catches are often underestimated (European Commission, 2003;

Garibaldi, 2012; Garibaldi and Kebe, 2005; Moutopoulos and Koutsikopoulos, 2014). Commercially valuable species often go directly to public markets and regional auctions, and these catches often are not included in the official records and hence go unreported (OECD, 1994). Also, there is limited monitoring and enforcement, especially with regard to illegal nets and mesh sizes, the landing and marketing of undersized fish, and compliance with restrictions on fishing season and areas (OECD, 1994). Available fisheries statistics exist at the national level, i.e., from the Italian National Statistical Institute (ISTAT) and the Institute for Economic Research in Fishery and Aquaculture (IREPA), and the data from these two organizations are sent to FAO. These reported catches account only for part of total fisheries removals and have never been harmonized and/or compared with estimates of total fisheries removals. This is particularly true for small-scale fisheries, whose catches are generally underestimated, and for recreational and subsistence fisheries, which are often not accounted for in countries' official statistics (Pauly, 2006; Pauly et al., 2014).

As part of an overall effort to reconstruct global fisheries catches (Zeller et al., 2007) by the Sea Around Us (www.seaaroundus.org; Pauly, 2007), which also includes Mediterranean countries (Coll et al., 2014; Pauly et al., 2014; Tsikliras et al., 2007; Ulman et al., 2013), this study aims to provide estimates of fishing capacity for the major Italian fishing fleets and catches for all marine fishing sectors from 1950 to 2010, using all available data sources and accounting for reported and unreported commercial landings, recreational and subsistence landings and discards. Reconstructed catches and effort presented here are for the whole of Italy. Results by sub-regional seas: 1) Ligurian; 2) Northern, Central and Southern Tyrrhenian; 3) Ionian; 4) Northern, Central and Southern Adriatic Sea; 5) Sicilian and 6) Sardinian waters can be found in Piroddi et al. (2014).

2. Materials and methods

2.1 *Study area*

Italy is located in southern Europe and covers an area of approximately 301,270 km^2. It includes the Italian peninsula, Sicily and Sardinia (the two largest Mediterranean islands), and 71 other smaller islands. The country consists of 21 regions, 15 of which are coastal (Fig. 1). The territorial waters extend to 12 nautical miles from the coast and have a surface area of 7210 km^2 and the continental shelf has a surface area of 201310 km^2 (Iborra Martin, 2006). The Italian Exclusive Economic Zone (EEZ), as delineated by Claus et al. (2014) (see also www.vliz.be), covers nearly 538,000 km^2. Due to its central Mediterranean Sea location, four of the seven Mediterranean Sea subdivisions surround the peninsula: the Tyrrhenian and Ligurian Sea in the west, the Ionian Sea in the south and the Adriatic Sea in the east. This geographic positioning leads to important biophysical differences of the waters around Italy. For example, the distribution of the continental shelf is very uneven; it is very broad and shallow in the Adriatic Sea, but changes to very narrow shelves with steep slopes in the other seas (Cataudella and Spagnolo, 2011; Francalanci, 1993). Also, the waters range from being highly eutrophic in the northern Adriatic Sea to oligotrophic in most other areas. The diversity of these biophysical conditions also leads to a high biodiversity: Italian waters host important commercial species such as the Atlantic bluefin tuna (*Thunnus thynnus*), charismatic megafauna such as the endangered Mediterranean monk seal (*Monachus monachus*) and habitat-forming species, such as seagrass (*Posidonia oceanica*) (Giakoumi et al., 2013; MacKenzie et al., 2009; Reijnders et al., 1997).

Italy has a population of 61 million people (ISTAT, 2012), over half of which reside in coastal regions (Cori, 1999; ISTAT, 2012). Fishing occurs along the entire coastline and catches are landed at over 800 sites (Cataudella and Spagnolo, 2011; Iborra Martin, 2006; OECD, 2010). Despite their marginal contribution to the national economy, both in terms of income and employment opportunities, fisheries play a fundamental role in certain regions (e.g., in Sicily). The Italian fishing industry is characterized by the predominance of small and older vessels, a diversity of fishing gear, and consequently a diverse array of multi-species catches (Cataudella and Spagnolo, 2011; FAO, 2010; OECD, 2010). The commercial fisheries are represented by the following types of fleets: bottom trawlers, mid-water trawlers, purse seiners, longliners, dredges, multi-purpose vessels and an artisanal fishery.

2.2 *Italian fisheries management*

A comprehensive fisheries management scheme was initiated in 1982 with the Law 41/1982; prior to that, only certain restrictions such as minimum mesh size, minimum legal landing size, and closed areas were mandated by national authorities.

With the introduction of Law 41/1982, national triennial plans were established. In particular, all professional fishing vessels had to possess a license managed by the Directorate General for Fishery and Aquaculture of the Ministry of Agriculture Policy. The license includes characteristics of the vessel (e.g., the name of the vessel, the EU number, GT), limitations of fishing areas, gear use and spatial licensing (e.g., over-seas and ocean-going fishing, Mediterranean fishing, and in-shore coastal fishing; OECD, 2010). Currently, the licensing scheme limits fishing effort mainly in the form of temporal restrictions which are set each year in relation to spawning seasons.

In addition, the closure is compulsory for the eastern fishing grounds and voluntary in the western grounds. Starting in 1996 and re-enforced in 2000, a seasonal closure was also initiated for tuna. In addition, in 1992, the European Union (EU) put a 2.5 km limit on the length of driftnets; in 1998, the EU fully banned the use of driftnets in the Mediterranean Sea and the northeast Atlantic Ocean, which became fully effective on January 1, 2002. Additionally, in 1994, the EU established a set of restrictions for the main gear types (EU Rule 1626/94) to preserve fisheries resources in the Mediterranean Sea. For instance, the operation of trawls and seines was prohibited within three nautical miles (nm) from the coast except for "special fisheries" for which derogation by the national legislation was put in place. For example, the "Bianchetto" (juvenile of *Sardina pilchardus*), "Rossetto" (*Aphia minuta mediterranea*) and "Cicerello" (juvenile of *Gymnammodytes cicerelus*) fisheries operate only in winter (January 15–March 15 as a rule) for a period of 60 days.

These fisheries have a long history at the local level and are one of the most important small-scale activities with large socio-economic impacts. Since 2010, the EU has banned these fisheries (small trawling boats using mesh size <40 mm) throughout the Mediterranean for their unsustainability, stating that only vessels of other gear types with a proper management plan would be allowed to fish (Reg. (CE) n. 1967/2006).

In Italy, to date, no quotas or TACs (total allowable catch) have been established, except for sedentary species such as clams or highly migratory species such as Atlantic bluefin tuna, due to the multi-species nature of the fisheries, which does not allow fishers to easily shift their target species from one to the other (Cataudella and Spagnolo, 2011; Iborra Martin, 2006; OECD, 2010). Also, few fisher consortia exist in the country, such as for the management of molluscs (CO.GE.MO) and of small-scale fisheries (CO.GE.PA.), introduced by the Italian Ministry, to empower fishers and local fishing enterprises to manage and regulate specific stocks in limited areas (Spagnolo, 2006).

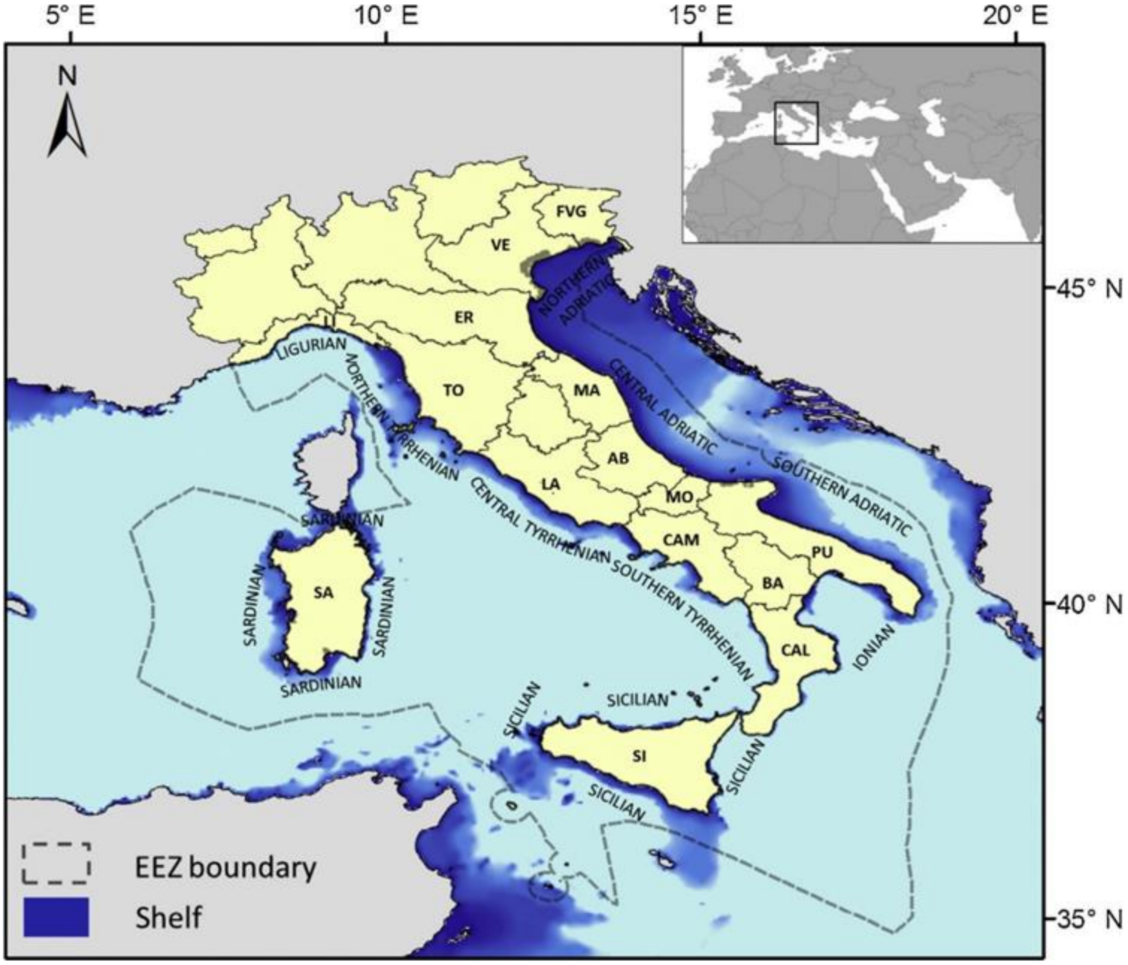


Fig. 1. Italy with its coastal regions (LI: Liguria; TO: Toscany; LA: Lazio; CAM: Campania; CAL: Calabria; SI: Sicily; SA: Sardinia; BA: Basilicata; PU: Apulia; MO: Molise; AB: Abruzzo; MA: Marches; ER: Emilia Romagna; VE: Veneto; FVG: Friuli Venezia Giulia) and the four surrounding sub-regionals seas: Ligurian; (Northern, Central and Southern) Tyrrenian; Ionian and (Northern, Central and Southern) Adriatic Sea. For the scope of the report Sicilian and Sardinian waters have been considered separately.

2.3 *Catch reconstruction approach*

The reconstruction of Italy’s total fisheries catches for the 1950–2010 period was completed by following the same approach as described and applied in Zeller et al. (2007). Since this method is well known and well described, refer to Zeller et al. (2007) for a more detailed description.

2.4 *Data sources*

A general description of data sources used in the reconstruction is detailed in

Table 4. In particular, we presented the fishing sectors considered, years of data availability, associated references, anchor points and estimated uncertainty (see below).

2.4.1 *Official landings*

The baseline used for reported catches was the time-series of capture production from the two Italian national statistical organizations (ISTAT and IREPA) which were compared to the FAO FishStat database. Two other FAO databases were also used: the global capture production dataset available for 1950–2010 and the regional dataset from the General Fisheries Commission for the Mediterranean (GFCM) available for 1970–2010 (FAO, 2012). Since the two trends were identical for the same time period (1970–2010) we decided to use and present here only the FAO global dataset, which had longer time series. As previously mentioned, ISTAT and IREPA were the responsible authorities which collected the data.

In particular, the official catch statistics were first provided by ISTAT from 1950 to 2001, and only recently the Italian Ministry of Agriculture and Forestry Policies (MIPAAF) transferred management of the fishery sector to IREPA from 2005 onwards. In 2000, IREPA, before becoming the official national fisheries statistical organization, under a mandate of MIPAAF, and with respect to European legislative requirements, took the coordinating role of optimizing the fisheries statistical scheme to obtain detailed and harmonized fisheries data collection along the entire Italian coast. This new survey methodology collects other relevant data on important aspects of the fisheries, namely, total landings per species; prices obtained by species; fishing effort; fishing hours; and fishing typologies. This is carried out on a weekly basis by 'local observers' from within the fisheries sector, i.e., biologists, ship owners, ex-fishers, and business consultants distributed along the major Italian fishing ports (of which there are approximately 800).

The structure of our reconstruction data followed the spatial allocation outlined in Table 1. Here, the Adriatic and the Tyrrhenian Seas were split into Northern, Central and Southern sections to account for their large extent and for significant differences in reported landings. Sicilian and Sardinian waters were considered separately for the same reason (Fig. 1). Among the sub-regional divisions, Sicily, followed by Central Adriatic, and South and North Tyrrhenian had the most incomplete catch datasets (Fig. 2). Due to this sub-regional division, gaps and inconsistencies with the data were easier to address and correct (most of the time to species-level) through literature searches. In particular, using the scientific literature (Cappuccinelli, 2005, 2011), we were able to reconstruct the last 11 years of the catches of European anchovy (*Engraulis encrasicolus*) and European pilchard (*S. pilchardus*) around the coasts of Sardinia (Supplementary materials, Fig. S1).

Table 1.
Catch allocation reconstruction following ISTAT-IREPA structure.

Sub-regional division	**Coastal regions**
1. Ligurian	Liguria
2. Tyrrhenian	
- Northern	Tuscany
- Central	Lazio
- Southern	Campania and Calabria West
3. Ionian	Calabria East; Apulia West; Basilicata
4. Adriatic	
- Northern	Emilia Romagna; Veneto; Friuli Venetia Giulia
- Central	Abruzzi; Marches; Molise; Emilia Romagna
- Southern	Apulia East
5. Sardinian	Sardinia
5. Sicilian	Sicily

We were also able to complement our compiled dataset or officially reported landings, i.e., the integration of IREPA and ISTAT datasets, with catch data of Atlantic bluefin tuna, frigate tuna (*Auxis thazard*), Atlantic bonito (*Sarda sarda*) and swordfish (*Xiphias gladius*), using the ICCAT statistical database for the main Italian sub-regions. In particular, we tried to use a conservative approach by taking into account the maximum landing estimates for each of these taxa from each dataset. The difference between ICCAT and IREPA–ISTAT catches regarding these large pelagic fishes and the reconstructed trends are displayed in Fig. S2.

In addition, once completed, each regionally compiled dataset of reported landings (corresponding to each of the six sub-regional divisions) was sent for validation to national experts (from local Universities: Universita' degli Studi di Sassari/Genova, respectively, in Sardinia and Liguria; from the National Research Council (CNR): Ancona and Mazaro del Vallo; and/or from local research institutes: Arpat Toscana).

The taxonomic breakdown of the commercial species used in the reconstruction was taken from ISTAT and IREPA (Supplementary materials, Table S1). Most of the species were commonly represented, although in a few occasions, some adjustments were made, for example, 'goatfishes' were one group for ISTAT, which IREPA split into red mullet (*Mullus barbatus*) and striped red mullet (*Mullus surmuletus*). In these cases, we decided to use the most detailed list of species, and apply the proportion of presence observed in one source to the other list. In addition, due to the high amount of the very uninformative group 'marine fishes nei' in the data, we decided to split this group into several species and/or groups of species according to the catch composition in the data disseminated by FAO on behalf of Italy. Thus, the reported data were allocated to 82 species or taxa for this reconstruction (Table S1).

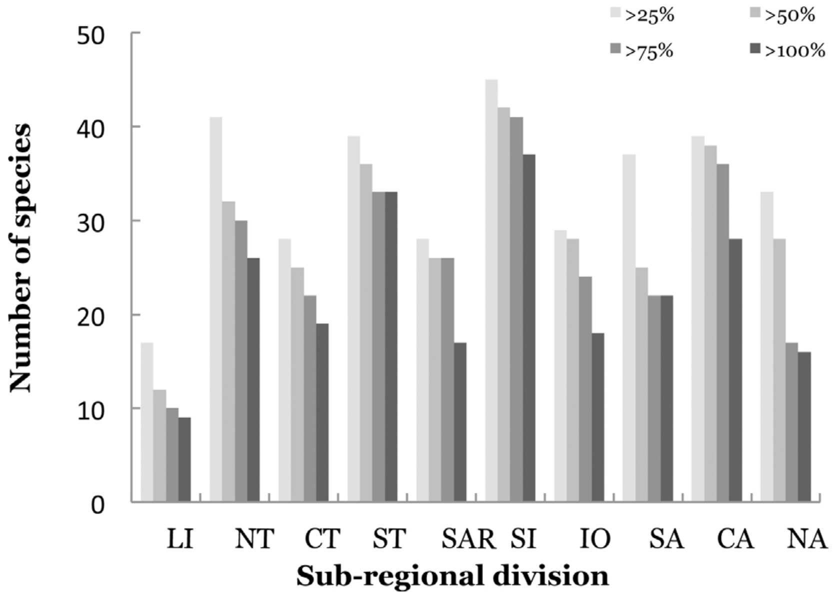


Fig. 2. Number of species per each sub-regional division present in the IREPA dataset with catch values greater than 25%, 50%, 75% and 100% compared to the ISTAT dataset.

2.4.2 *Fishing effort*

Fishing effort (here in kW days^{-1}) was estimated by taking the product of the number of fishing vessels, kW per vessel (inferred from their GT), and the number of days spent fishing. This information was obtained from ISTAT and IREPA. From 1950 to 1983, the type of vessels reported by ISTAT consisted of only four groups: trawlers, gillnetters, longliners and 'various gears'. From 1984 to 2001, vessel classification was extended to incorporate four additional groups: mid-water trawlers, purse seiners, dredges, and multiple-use vessels. From 1996, IREPA assigned the following classifications to vessel-type:

- Trawl;
- Purse seine;
- Mid-water trawl;

- Mechanical dredges (hydraulics dredge);
- Longlines (drifting or fixed longlines with vessel length >12m);
- Artisanal fishery (fixed gears such as set nets, hooks and traps with vessel length <12 m);
- Passive multi-use vessels (fixed gears with vessel length >12m);
- Multi-technique vessels (both fixed and mobile gears).

This classification takes into account the high degree of multi-gear use by the Italian fishing fleets and their wide dispersal rate along the entire coastline. More than 80% of vessels are authorized to fish with a variety of fishing gears, particularly for small-sized vessels, due to their limited range, which forces them to depend on the seasonal availability of coastal resources. Similar to the reported catches, there were some discrepancies between the two primary sources (ISTAT and IREPA) for the number of fishing vessels and GT values, as a result, the more detailed list of fleets (in this case, from IREPA) was used.

The data began in 1984 and in order to include estimates for the missing years (1950–1983) in the absence of effort data from earlier years, the proportion of observed fleets for earlier years was taken as the same as for 1984. The reason why we decided to keep the same proportion as 1984, and not the average ratio between 1984 and 2010, was due to the reduction in effort observed in the country from the mid-1980s onward, mainly as a result of EU regulations and declines in marine resources. The number of days at sea and number of fishers were available only from 1996 to 2010 through the IREPA dataset; thus, to estimate the missing years (1950–1995), we maintained kept the ratio of days at sea and the ratio of fishers per type of fleet observed in 1996. GT was used to estimate fishing power in kW for each vessel using the equation developed by Anticamara et al. (2011), i.e., $kW = 11.26\ GT^{0.71}$, which expresses the relationship between GT and kW as an exponential relationship. As for days at sea and number of fishers, GT was available per type of fleets only for the period 1996–2010 and thus it was extrapolated for the missing years as the average ratio of GT in the observed time period. Changes in technology have increased fishing capacity on board the same vessel over time (Pauly and Palomares, 2010). To account for improvements in technology that are not be captured by kW as a measure of effort, a technological "creep factor" of 1% was applied since 1980 (Table 2), as derived from the empirical relationship by Pauly and Palomares (2010).

Table 2.
Technological coefficients of fishing vessels by gear type as reported by (Pauly and Palomares 2010).

	Technological coefficient		
Vessel type	**1950-1980**	**1981-1995**	**1995-2010**
Trawlers	0.5	1	1.8
Mid water trawlers	0.5	1	1.8
Dredges	0.5	1	1.4
Purse seiners	0.5	1	1.8
Artisanal	0.5	1	1.3
Multiple gears	0.5	1	2.5
Longliners	0.5	1	2.8

Finally, we calculated catch per unit of effort (CPUE) expressed as kg kW^{-1} $days^{-1}$ by dividing the total reconstructed catches by the total reconstructed effort for the whole of Italy. For comparison, we also calculated CPUE using the official catch statistics (FAO) divided by the total reconstructed effort.

2.4.3 *Unreported landings I: Recreational catches*

While recreational fishing can be practiced both at sea and from land, the present study concerns only boat-based recreational activities, and therefore excludes shore-based angling, spear fishing and shellfish collection. Until 2010, recreational catches had never been assessed or included in national fishery statistics. To fulfill recent EU legislative requirements, the Italian Ministry of Agriculture and Forestry (MIPAAF) first surveyed recreational fishing activities (particularly the number of fishers and gear types). To date, there are only a few sources of information regarding Italian recreational fisheries. The first preliminary assessment was conducted in 1996 by Anagnopoulos et al. (1998), who described recreational fisheries in Italy and Greece with respect to their fleet size, number of fishers, landings, and fishing effort, here used as anchor points for 1996. Based on more recent sources of information (Cisneros-Montemayor and Sumaila, 2010; Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007), three additional anchor points representing the number of fishers for the years 1989, 1993 and 2003, were developed. Population statistics for the 1950–2010 period were extracted from

ISTAT (2012) and used to indirectly estimate total recreational catches by local residents. For instance, we used the percentage of observed number of fishers (from the four anchor points) in the total population (1989: 2.2%; 1993: 2.7%; 1996: 2.6% and 2003: 2.7%) to establish a time series of number of recreational fishers for the missing years. Thus, for the 1950–1988 period, it was assumed that 2.2% of the total population fished recreationally, while for 1990–1992, 1994–1995 and 1997–2002, we interpolated the estimates of the four anchor points, and for the last period (2004–2010), the percentage observed in 2003 (2.7%) was held constant to 2010. We assumed that the proportions of recreational fishing fleets for each sub-regional division observed in 1996 were constant throughout the years (Table S2), and that two fishers per boat caught 1.6 t year^{-1} of fish (Anagnopoulos et al., 1998), to derive total Italian boat-based recreational catches from 1950 to 2010. To allocate recreational catches to species-level, we used the ratio found in Anagnopoulos et al. (1998) for each sub-divisional region (Table S3). Also, since there is also an illegal aspect to the recreational fisheries, (e.g., undersized fish, catch above the permitted limits, etc., Table S4), an additional illegal component was estimated (see below for further details).

2.4.4 *Unreported landings II: Illegal, subsistence catches and discards*

In Italy, as in many other parts of the Mediterranean Sea (Coll et al., 2014; Ulman et al., 2013), unreported commercial catches are almost always associated with illegal fishing activities and are thus of concern. In Italy, the most common infringements include the use of illegal fishing gears, trawlers operating closer to shore than permitted, fishing in 'no take' marine protected areas, and the catching of 'bianchetto' or other undersized specimen (ISMEA, 2006). Although the approach carried out by IREPA, with observers inspecting landings at the main harbors along the Italian coasts, should minimize the quantity of unreported landings, we decided to search for additional information coming from NGO reports and from Italian newspaper accounts and TV documentaries. The most widely-known and 'observed' illegal fishing activity along the entire Italian coast is the use of driftnets. At the end of the 1980s, the driftnet fishery was the largest fishery in the Mediterranean Sea with over 700 vessels, driftnets of up to 40 km in length and annual reported catches of 5000 t of swordfish and 1000 t of tuna (Tudela, 2004). Despite the maximum length limit of 2.5 km prescribed by the EU in 1992, approximately 650 driftnet boats continued operating with nets measuring on average between 10 and 12 km (Tudela, 2004).

The unreported catches from 1992 to 2001 were assumed to be based on a constant number of 650 vessels from 1992 to 1998 (Tudela, 2004) and 299 vessels (Cornax, 2007) from 1999 to 2001, 5% of which operated from Liguria, 49% in the Tyrrhenian Sea, 31% from Sicily, 7% from Sardinia as well as from the Ionian Sea. A catch rate per vessel of 7 t year^{-1} of swordfish and 1.4 t year^{-1} of tunas was assumed based on Tudela (2004) and Cornax et al. (2006). From 2002 onwards, after driftnet fishing was officially banned, surveys conducted by different NGOs in major Italian ports identified over 150 driftnet boats still in operation (fish were landed at night to avoid controls). Also, in 2008, the journalist Sabrina Giannini conducted a series of interviews with fishers, and documented the illegal driftnet activities for an Italian TV program ("Report: Mare Nostrum: sfruttamento marino"). To estimate these unreported driftnet catches for the 2002–2010 period, the following sources were used: OCEANA (Cornax, 2007; Cornax and Pardo, 2009; Cornax et al., 2006), RSPCA in collaboration with Humane Society International and the Whale and Dolphin Conservation Society (2005), and the interview conducted by Sabrina Giannini. The number of boats observed (~150) was kept constant for the 2002–2010 period and a constant catch rate per boat of 2 t year^{-1} of swordfish and 0.5 t year^{-1} of tunas was used.

Regarding other illegal activities occurring in the artisanal, industrial and recreational fisheries, only recently have Italian media/newspapers begun to report on them. The majority of this news refers to the confiscation of illegal gear by the Italian Coast Guard, and only a few accounts refer to quantities of confiscated species (Table S4). Since 2010, the Italian Coast Guard has started to report on illegal operations at sea and on land. We used the information from the Italian Coast Guard database, combined with direct interviews conducted with LT Commander Alessio Morelli, Head of the Fisheries National Control Unit-Coast Guard, to derive a rough estimate of illegal activity in the area. We were not able to identify any sources of data relating to personal consumption (i.e., the subsistence fishery). Thus, to develop such an estimate indirectly, and in a conservative manner, we used and held constant the lowest value (1 kg fisher^{-1} day^{-1}) estimated by Coll et al. (2014) for the Spanish subsistence fishery (since Spain shares similar fish consumption patterns and maritime policies), and applied this to Italian commercial fishers per fleet type and the number of fishing days per type of fleet, per year and per each sub-division. Italian discards for the 1950–2010 period were estimated using two main anchor points, one by Vassilopoulou (2012) and the other by the European Commission (2011a). Additional scientific papers were used in regards to local studies (Table S5). Due to the multi-species nature of Italian fisheries, which allows for the catching of several species at the same time, the high demand of seafood in local markets, and the high enforcement costs required for the monitoring of restrictions, fishers rarely discard fish, but retain and land their by-catch, which is an important component of unreported landings. The rates of by-catch and discards were determined by the type of fleet of each sub-regional division and the total catch per type of fleet (Table S5). We then separated the retained by-catch from discards, using data in the literature, of which, approximately 60% was retained and 40% discarded (Sánchez et al., 2007; Sartor et al., 2003).

2.4.5 Uncertainty

We assessed the uncertainty associated with the reconstruction using a scoring procedure, utilizing uncertainty criteria developed and used by the Intergovernmental Panel on Climate Change (Mastrandrea et al., 2010) to assess uncertainty of input data used in their assessments, which were further calibrated using the results of Monte Carlo simulation in Ainsworth and Pitcher (2005) and Tesfamichael and Pitcher (2007). In particular, this approach consisted of assigning a score, ranging between 1 (very low evidence or less robust data) and 4 (very high evidence and robust data), to the reconstructed catch data of each fishing sector for three different decades (1950–1969; 1970–1989; 1990–2010) (See Table 3 and Table S6 in Supplementary materials). Average scores (and hence percentage confidence intervals) for each time period were derived through catch-weighted averaging of sector scores. This scoring procedure was previously used in a 'blind' scoring session for 22 Pacific Island countries and territories (Zeller et al., 2015) in which each score was independently (blind) given by three separate research staff. This procedure showed little differences between scorers, and generally reflected the score given by the lead researcher who had conducted each island's reconstruction. Hence, for Italy, the leading author scored each sector for each of the three time periods, as she was most familiar with the underlying data sources and their level of reliability or trustworthiness.

Table 3.
Score' for evaluating the quality of time series of reconstructed catches, with their confidence intervals.

Score		**-%**	**+%**	**Corresponding IPCC criteria***
4	Very high	10	20	High agreement & robust evidence
3	High	20	30	High agreement & medium evidence **or** medium agreement & robust evidence
2	Low	30	50	High agreement & limited evidence **or** medium agreement & medium evidence **or** low agreement & robust evidence.
1	Very low	50	90	Less than high agreement & less than robust evidence

*(IPCC criteria from Figure 1 of Mastrandrea et al. (2010), which note that "confidence increase" [and hence confidence intervals are reduced] "when there are multiple, consistent independent lines of high-quality evidence").

3. Results

3.1 Reconstructed total catches

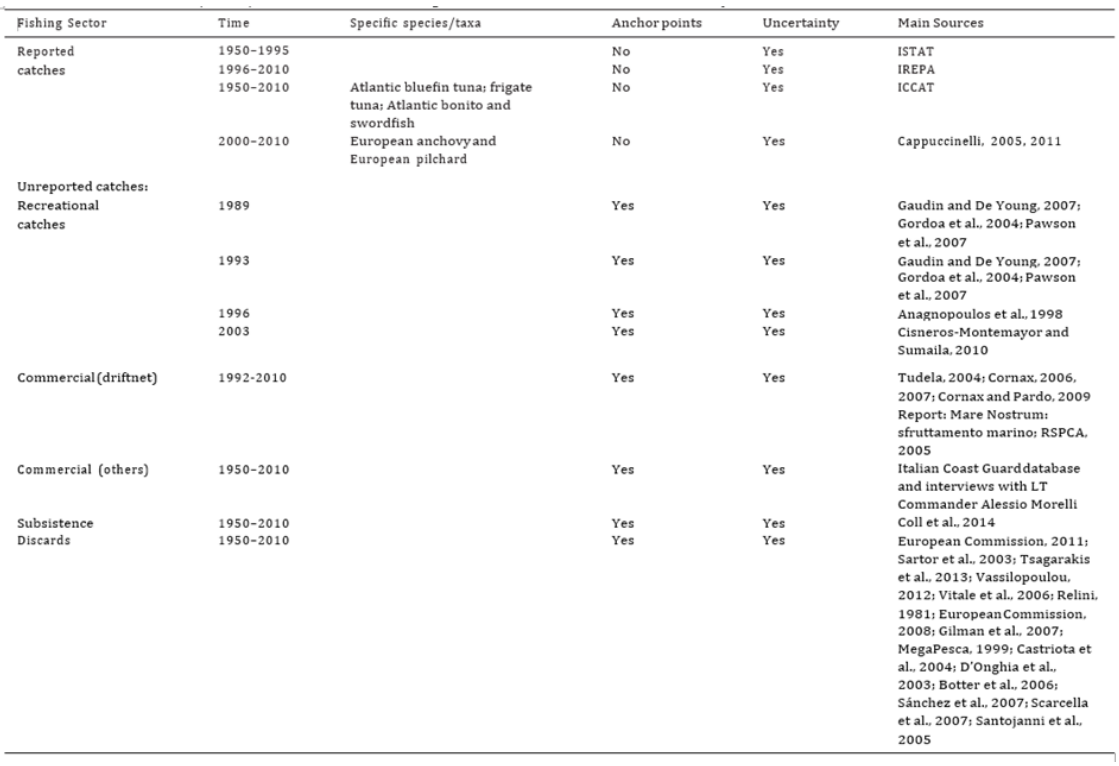
The reconstructed total catch for the 1950–2010 period exceeded by a factor of 2.6 the official catches reported by the FAO on behalf of Italy. Of this, approximately 79% was caught by industrial fisheries, 17% by artisanal fisheries, 3% by recreational fisheries and <1% by subsistence fisheries, while discards (7% of the total) were predominately (95%) from industrial fisheries (Fig. 3a). Reconstructed total catches were relatively stable throughout the 1950s and 1960s, averaging about 700,000 t year^{-1}, before increasing between 1971 and 1979 to 1.1 million t year^{-1}. Thereafter, the annual catch plateaued at an average of 1.06 million t year^{-1} until 1986, then sharply decreased to 676,000 t year^{-1} by 1990. Annual catches remained steady in the early 1990s, with a small increase to 741,000 t in 1998, before again sharply decreasing and continuing the declining trend to the end of the time series in 2010, when catches were just 374,000 t (Fig. 3a).

Catches consisted of 92 taxa, of which 65 were identified to species, including higher pooled groups such as 'marine fishes nei' and 'marine invertebrates nei'. In terms of total tonnage, catches were dominated by small pelagic fishes, notably European anchovy (*E. encrasicolus*), which accounted for 18.1% of all catches (Fig. 3b). The second most important taxon, in terms of tonnage (at least in earlier decades) was the European pilchard (*S. pilchardus*), which accounted for 12.5% of total catches overall, but has since declined substantially (Fig. 3b). The remaining taxa, grouped by family, contributing the most to the catches were molluscs (12.4%), Scombridae (9.0%), Sparidae (7.4%), crustaceans (5.6%), Carangidae (4.0%) and sharks and rays (3.9%; Fig. 3b).

3.2 *Official landings*

For the reported landings, we compared our assessment with the two national sources of statistics (ISTAT and IREPA) and the FAO, and found that data sets were similar only for the last six years (2005–2010, Fig. 4), which corresponds to the period when IREPA became the official national statistical source. Most of the catches per species and per sub-regional division in the ISTAT dataset were on at least 30–40% lower than the one provided by IREPA. In particular, when comparing the years 2000 and 2001 between the two national sources, of the 58 taxa in the IREPA dataset, 49 had catch values greater than 25%, 43 greater than 50%, 33 greater than 75% and 26 greater than 100%, while the remaining had similar values between the two sources.

Table 4
Italian reconstruction of the catches highlighting the fishing sector considered, the period of data available (Time), the source, anchor points, and estimated uncertainty.



Fishing Sector	Time	Specific species/taxa	Anchor points	Uncertainty	Main Sources
Reported catches	1950–1995		No	Yes	ISTAT
	1996–2010		No	Yes	IREPA
	1950–2010	Atlantic bluefin tuna; frigate tuna; Atlantic bonito and swordfish	No	Yes	ICCAT
	2000–2010	European anchovy and European pilchard	No	Yes	Cappuccinelli, 2005, 2011
Unreported catches:					
Recreational catches	1989		Yes	Yes	Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007
	1993		Yes	Yes	Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007
	1996		Yes	Yes	Anagnopoulos et al., 1998
	2003		Yes	Yes	Cisneros-Montemayor and Sumaila, 2010
Commercial (driftnet)	1992-2010		Yes	Yes	Tudela, 2004; Cornax, 2006, 2007; Cornax and Pardo, 2009 Report: Mare Nostrum: sfruttamento marino; RSPCA, 2005
Commercial (others)	1950–2010		Yes	Yes	Italian Coast Guard database and interviews with LT Commander Alessio Morelli
Subsistence	1950–2010		Yes	Yes	Coll et al., 2014
Discards	1950–2010		Yes	Yes	European Commission, 2011; Sartor et al., 2003; Tsagarakis et al., 2013; Vassilopoulou, 2012; Vitale et al., 2006; Relini, 1981; European Commission, 2008; Gilman et al., 2007; MegaPesca, 1999; Castriota et al., 2004; D'Onghia et al., 2003; Botter et al., 2006; Sánchez et al., 2007; Scarcella et al., 2007; Santojanni et al., 2005

These data were visibly higher (on average more than two times higher) than the data reported to FAO for the same time period which ranged from 171,000 to 430,000 t year⁻¹. Overall, there was a slight decrease in national reported landings between 1950 and the beginning of the 1960s, followed by an increase in the middle of the 1980s and a general and continuous decline to 2010. This differs from the trend in the FAO data which increases steadily in 1950 with a peak in 1985 and then fairly steadily declines in 2010 (Fig. 3a).

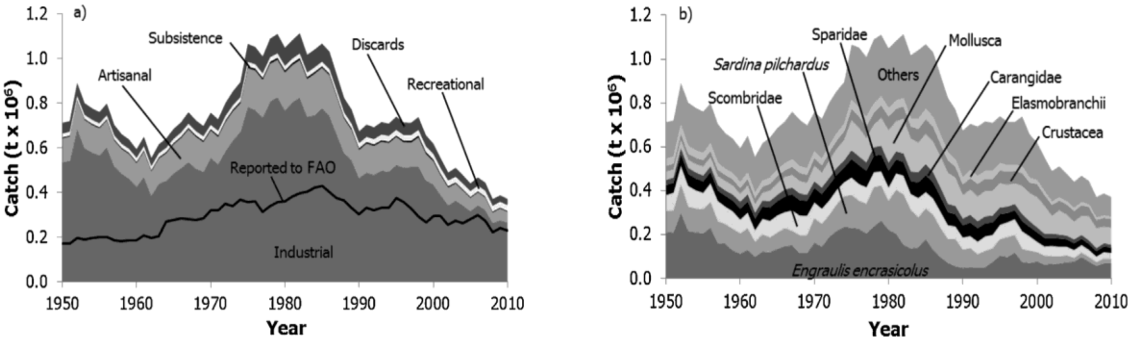


Fig. 3. Reconstructed total catches for the whole of Italy: a) by fishing sector and discards, with reported FAO catches overlaid as black line graph for 1950–2010 period; and b) by taxa (the 'Others' grouping contains 82 taxa).

European anchovies and European pilchards were the main fish species reported in the national data throughout the different sub-regions, which began to decline in the beginning of 1980s (Fig. 3b). All the other major taxa, (e.g., Scombridae, Mollusca, Sparidae and Carangidae) presented similar trends with declines commencing from the 1980s or beginning of 1990s (Fig. 3b).

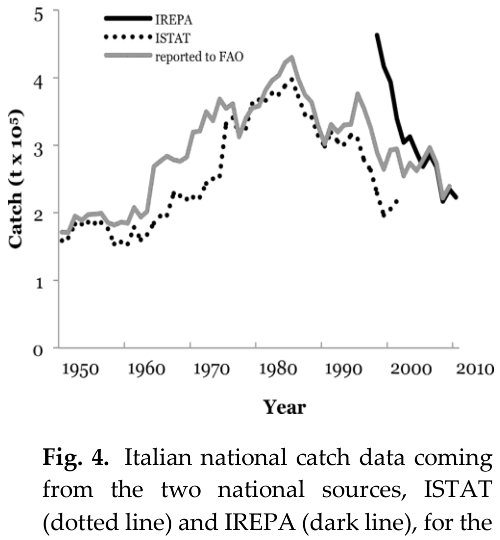


Fig. 4. Italian national catch data coming from the two national sources, ISTAT (dotted line) and IREPA (dark line), for the 1950–2010 period in comparison with the ones reported to FAO (grey line).

3.3 *Fishing effort and catch per unit of effort*

Results indicated that artisanal vessels dominated in terms of vessels numbers, followed by trawlers and multiple gears (Fig. 5a). Trawlers, on the other hand, had the highest fishing effort, in term of cumulative engine power (kWdays⁻¹), followed by purse seiners and artisanal fisheries (Fig. 5b). With regards to all fishing fleet and their trends, number of vessels and fishing effort, decreased over time, after the maximum from the late 1970s to mid-1980s (with only multiple gears having their highest peak in the 1990s) and a steady decline thereafter. The CPUE trend showed a continuous decline since the 1950s with a maximum of ~9kg kW^{-1} $days^{-1}$ in the early 1950s and a minimum of ~3kg kW $days^{-1}$ in the late 2000s (Fig. 6).

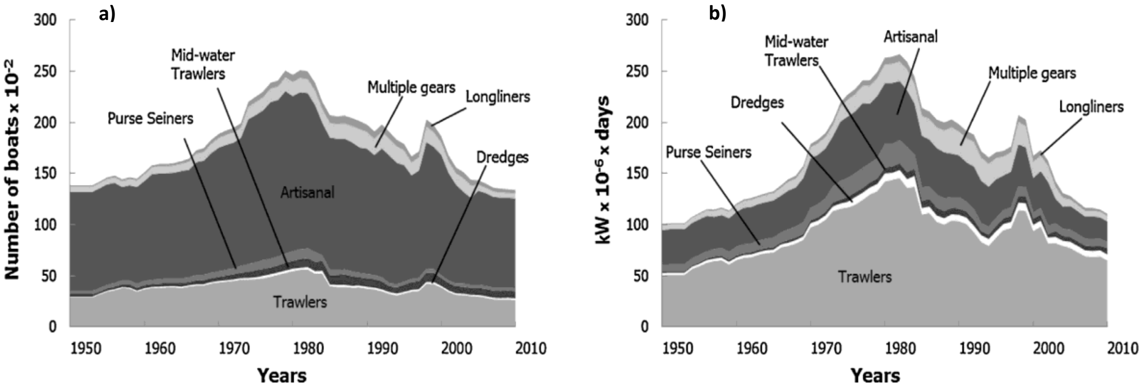


Fig. 5. For the whole of Italy: a) reconstructed total number of fishing boats; and b) reconstructed total fishing effort (kW 10^{-6} $days^{-1}$) per gear type.

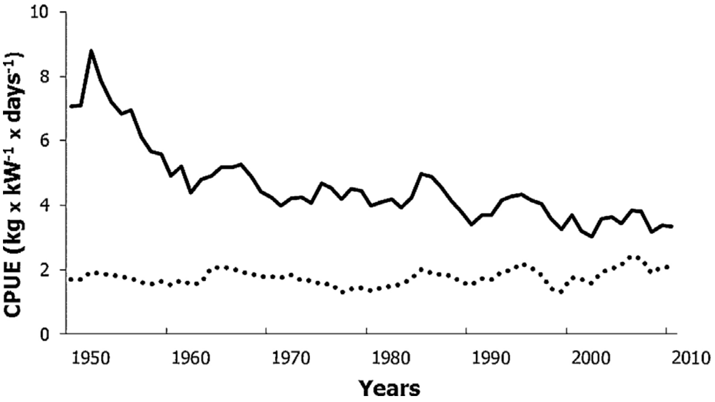


Fig. 6. Catch per unit of effort (kg kW^{-1} $days^{-1}$) for the whole of Italy for the 1950–2010 period using the reconstructed catches and effort time series (black line) and catches reported by the FAO on behalf of Italy with the reconstructed effort (dotted line).

3.4 *Unreported landings: Recreational fisheries*

The estimated recreational catches for 1950–2010 were around 1.45 million t, which increased from 19,200 t in 1950 to 29,800 t in 2010 with a pronounced growth during the last three decades (Fig. 3a). The Adriatic Sea accounted for 597,000 t (41.4%); the Tyrrhenian Sea sub-division 497,000 (34.3%); the Ligurian 194,000 t (13.4%); Sardinia 77,300 t (5.3%); Sicily 68,100 t (4.7%) and Ionian Sea 16,700 t (1.2%). The major species caught in Italy by the recreational sector were tuna (Scombridae) with 232,000 t (15.4%), bogue with 155,000 t (10.7%), Atlantic bonito with 107,000 t (7.4%) and Mediterranean horse mackerel (*Trachurus mediterraneus*) with 97,300 t (6.7%).

3.5 *Unreported landings: Subsistence catches*

The estimated subsistence catches for the 1950–2010 time period averaged 6400 t year^{-1}, with a maximum of 9100 t in 1982 and minimum of 4000 t in 2010, contributing only 0.9% of the reconstructed total catch (Fig. 3a). In this case, the Central Adriatic Sea and Sicily had the highest removals, with approximately 91,400 t (23%) and 85,600 t (22%), respectively. Given our assumption of same catch compositions for subsistence catches and reported landings, the subsistence catch was assumed to consist mainly of European anchovy (13.5%), European pilchard (10.7%) and molluscs (14.8%).

3.6 *Unreported commercial catches and discards*

The estimated unreported catches for the illegal driftnet fishing fleet for the 1992–2010 period totaled 49,130 t, which consisted to 83% of swordfish and 17% of tuna species. The regions in which this illegal activity was prevalent were the South Tyrrhenian Sea and Sicily, which contributed 46% and 31% of the 49,130 t, respectively. Also, an illegal component from other industrial fishing fleets and the artisanal sector was added. In particular, a total of approximately 6 million t was estimated for the period 1950–2010, of which 76% and 24% came from industrial and artisanal fisheries, respectively. Retained unreported by-catch per fleet type and per subdivision for the period 1950–2010 accounted for approximately 5 million t, averaging about 82,500 t year^{-1}, most of which came from industrial fisheries (95%) and from the Central Adriatic (~1.6 million t; 33%) and Sicily (1.2 million t; 25%). The major by-catch taxa were clams (Bivalvia; 604,000 t; 12.0%), sharks (Selachimorpha; 446,000 t; 8.9%), jacks (Trachurus spp.; 335,000 t; 6.7%) and rays (Rajidae; 283,000 t; 5.6%). Discards, on the other hand, were 3.4 million t. Since we applied a proportional rate to separate the retained by-catch from discards, the same patterns were observed for the regional subdivisions and discarded taxa. Discards and by-catch from bottom trawling represented the largest component, totaling 3.8 million t (Fig. 3a).

3.7 *Uncertainty*

The ranges of uncertainty estimated for the reconstructed total catches showed wider confidence intervals in the first two estimation periods (1950–1969; 1970–1989) and a reduction only in the last period (1990–2010; Fig. 7).

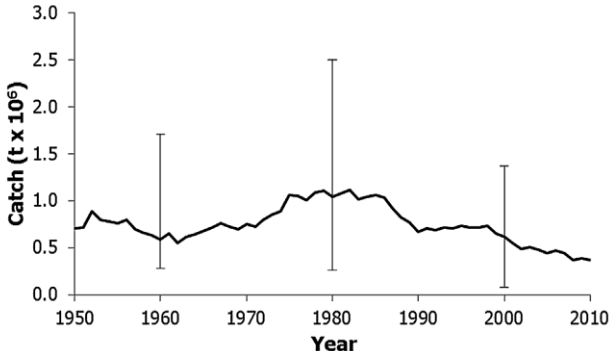


Fig. 7. Estimated reconstructed total catches with confidence intervals. The values of the error bars are displayed for each time period (1960 for 1950–1969, 1980 for 1970–1989, and 2000 for 1990–2010).

4. Discussion

This study represents the first attempt to estimate total fisheries removals for the whole of Italy in the Mediterranean Sea, for the period 1950–2010. Our reconstructed total catches were 2.6 times the landings officially reported by the FAO on behalf of Italy for the same period and same sea. This difference was mainly caused by poor reporting of commercial catches, with unreported commercial landings (from both industrial and artisanal sectors) contributing 50% to the total catch (in relation to FAO reporting) and discards contributing another 7%. This gap in the official national statistics (mainly related to the earlier period of the ISTAT datasets) was previously observed by other studies (AdriaMed, 2003; Cataudella and Spagnolo, 2011) which documented that about 30–40% of catches remained unreported, and pointed to changes in data collection, systematic approach and absence of data verification and/or analysis as the causes of this discrepancy. Our reconstruction agrees with these studies, with an even higher discrepancy for industrial fisheries (53%). We recognize that, because of the nature of our approach used here, which requires assumption-based inferences and interpolations, uncertainties remain (see below), for example in our estimates of underreported catches or in the disaggregation of the taxonomic catch composition and further studies should be conducted to reduce this uncertainty. However, we believe that our approach is justified by the unacceptability of the alternative, yet common default approach, of interpreting non-reported or missing data components as zero removals (Pauly et al., 1998). Thus, by documenting and justifying each step of our approach, our study represents the first important step towards the integrated understanding of total fisheries removals for all of Italy.

Our reconstructed commercial catches and fishing effort showed a remarkable decline starting around the 1980s as a consequence of the decline of the living marine resources (Arneri, 1996; Iborra Martin, 2006), the increase in fishing costs (e.g., fuel;

Sacco, 2011) and the EU regulations to reduce fishing capacity (Iborra Martin, 2006). In Italy, it has been observed that, after the 1980s, catches rapidly declined, primarily as a result of a decrease in the biomass of small pelagic fishes, particularly European anchovy and European pilchard (Iborra Martin, 2006) and many other important demersal and pelagic fish stocks (Arneri, 1996; Iborra Martin, 2006). An indicator of the overexploitation of the marine resources in the region is also given by our reconstructed CPUE trend, which steadily declined since the early 1950s, while the opposite trend is obtained if one uses official catch statistics. Some caution should be applied when interpreting these data. In fact, despite evidence of marine resource reductions in Italian waters, it is worth emphasizing how high uncertainties still exist for fishing effort (e.g., number of days at sea and the number of observed vessels), particularly for early years, and catch data. Unfortunately, at the time this research was undertaken, no information was available to fill these gaps. Recent efforts have been undertaken regionally to address at least partly this issue (e.g., EVOMED, 2011), and thus further development of this work is required.

Our study highlights the importance of artisanal fisheries in Italy, which is similar to other parts of the Mediterranean (Coll et al., 2014; Piroddi et al., 2011; Tudela 2004; Ulman et al., 2013). However, while artisanal fisheries had the largest number of vessels (around 60% of all Italian fishing vessels), from a catch volume perspective, trawlers caught the most, and, despite accounting for only 21% of the fishing boats, they had the greatest impact on commercial and non-commercial taxa in the region (Pranovi et al., 2000; Sánchez et al., 2007; Sartor et al., 2003). As for the increase of multiple gears observed here, this might be an artifact derived from the different criteria of grouping vessels, as done by IREPA in past years. In fact, vessels were roughly aggregated by prevalent fishing gear, and whenever their prevalent gear was not obvious, they were included in the "multiple gear" category.

Besides reported commercial catches, the recreational fisheries were assessed; since no official/reported time series of catches exist, this fishing sector was considered unreported from 1950 to 2010. In Italy, only a few sources of information are available (Anagnopoulos et al., 1998; Cisneros-Montemayor and Sumaila, 2010; Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007), and thus, for a few regions, high uncertainty still exists with regards to total catch. Since this sector has increased in Italy, particularly in the north-west (Anagnopoulos et al., 1998; Pawson et al., 2007), more effort should be invested to assess the impact of recreational fisheries on marine resources and ultimately to refine the estimates of the total Italian catch.

Illegal catches and unreported catches (including discards), despite being a serious issue in Italian fisheries, have never been previously assessed. We consider these components the least studied among all the different Italian fishery sectors, and with the highest uncertainty. Since they are key components for understanding and evaluating the impact of fishing on commercial and non-commercial taxa (Zeller et al., 2007) specific studies (e.g., structured interviews with fishers) should be implemented to properly assess them. Despite these caveats, our study indicates that unreported catches are very significant, accounting for over half of total fisheries removals. These results are in line with other catch reconstruction studies conducted in the Mediterranean Sea that have shown high percentages of unreported and illegal catches in their assessment of fisheries removals, e.g., 40% in Spain (Coll et al., 2014), 35% in Greece (Tsikliras et al., 2007), 63% in Turkey (Ulman et al., 2013).

In Italy, one of the major causes of illegal/unreported catches is the continuous use of prohibited driftnets. The loss of revenue due to changes in fishing gears is probably the major reason behind such constant fishing practice (swordfish and tuna species are important and high valued products of the Italian market); in fact, the profits that one driftnet boat could obtain are generally 25% higher than the net added value from an average vessel (Spagnolo and Sabatella, 2004). Regarding other illegal activities, no historical information was found. In 2010, the Italian Coast Guard started collecting and reporting infringements at sea and on land in relation to the use of illegal gears or undersized species (European Commission, 2011b). Unfortunately, this database is still an under-representation of what is happening along the Italian coastline (Alessio Morelli pers. comm.) and therefore our reconstruction might not reflect entirely the situation occurring in the region. Subsistence catches present another limitation in terms of an existing fishing sector for which no direct data are available. Specific studies focusing on this component are fundamental in order to improve our estimate of total catch removal of the Italian fisheries. Unreported discards is another aspect of under-reported resource mortality, and are considered pressing issues for marine conservation and fisheries management (Caddy, 2009; Hall and Mainprize, 2004). In Italy, studies on discards and by-catch have increased in recent years, partly due to the implementation of the EU Data Collection Regulation [Commission Regulation (EC) No 1639/2001; currently, Data Collection Framework, Council Regulation (EC) No 199/2008] and partly also to the establishment of the ecosystem approach to fisheries (EAF) (Garcia, 2003; Tsagarakis et al., 2013). However, limited studies still exist or have been found in the area that differentiate between the proportions of retained by-catch and of discards per gear type, thus more effort should be dedicated to fill this gap. Required also would be detailed information on survival rates of discarded species by gear type. Our results show that, on average, retained by-catch accounts for 11% and discards for 7% of total removals, with bottom trawling having the highest impact followed by longline and dredges. These percentages agree with other studies conducted in the Mediterranean Sea, which have looked at the contribution of discards and by-catch and estimated a range on average between 10% and 20% (Coll et al., 2014; Tsagarakis et al., 2013; Ulman et al., 2013).

5. Conclusion

Our estimates of total fisheries removals for the whole of Italy (1950–2010) illustrated a decrease in catch and effort that began in the mid-1980s and continued until 2010. This overall pattern aligns with FAO and national statistics trends, highlighting a severe degradation of marine resources in the region. Yet, our results exceed the officially reported amount by a factor of 2.6, which suggests substantial problems in the collection and reporting of actual catch data and quite a considerable amount of under-reported catches. Such prevalence of under-reported catches highlights significant management, monitoring and enforcement shortcomings. Official catch statistics are in fact used in stock assessments for policy making decision, and the exclusion of under-reported catches (or total fisheries removal) could bias the resulting scientific advice given to policy-makers. Since the impact of fisheries is considered one of the most pressuring threat affecting marine life, their underestimation poses a serious concern not only to the conservation of valuable marine resource but also to the success of future fisheries. Despite the limitations explained above, the estimates of total fisheries removals presented in this study represent an improvement over official estimates, and should be taken into account when dealing with fisheries management, despite the substantial uncertainty associated with the present estimates. With many key fish stocks declining, it is necessary for fisheries management to fully capture how much the resources have been and are being removed and from which sector, so that appropriate decisions for the future can be made (Pauly et al., 2014). Our study is the first that attempted to estimate the Italian fisheries removals using a holistic approach; these methods are particularly important in areas like the Mediterranean Sea, where the multi-species and multi-gear nature of fisheries make the assessment of single-species fisheries resources and their management difficult and likely inappropriate.

See original publication in Annex 2

Chapter 2.3

Ecosystem health for a Mediterranean semi-enclosed embayment

CONTINENTAL SHELF RESEARCH 121 (2016) 61-73

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Ecosystem health for a Mediterranean semi-enclosed embayment (Amvrakikos Gulf, Greece): assessing changes using a modelling approach

Salud ambiental de una golfo semi-cerrado del Mediterráneo (Golfo de Amvrakikos, Grecia): evaluación de cambios temporales mediante el uso de modelización ecológica

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Abstract

Marine and coastal ecosystems are important for human wellbeing in multiple ways and yet they are subject to increasing anthropogenic stressors which pose serious threats to their health status. In this context, we used an ecosystem modeling approach to assess and quantify the health status of a semi-enclosed embayment of the Mediterranean Sea, the Amvrakikos Gulf (surface: 405 km^2; maximum depth: 60 m) (Ionian Sea). In particular, we built a food web model of the Gulf ecosystem for the 1980 and we fit it to time series from 1980 to 2013. The aim of the study was to: (1) investigate dynamics of marine resources in the last three decades considering the effect of changes in rivers run off, development of fish farming and dynamics of fisheries as the major anthropogenic drivers affecting the system; (2) assess structural and functional changes of the Gulf, using model derived indicators obtained from temporal simulations. Results indicated that the strongest drivers in the Amvrakikos food web were changes in nutrients and organic matter mostly from the loads of two local rivers. Trends in ecological indicators, which explained changes in the structure of the Gulf, highlighted a degradation of the demersal compartments of the food web and a relative stability of the pelagic ones mainly due to high eutrophication levels. By including several ecosystem drivers into

the model, the present study is intended as a tool for assessing Amvrakikos ecosystem health and for developing future management policies in the Gulf.

Resumen

Los ecosistemas marinos y costeros son importantes para el bienestar humano por múltiples razones, y sin embargo, están sujetos a crecientes impactos antropogénicos que plantean serias amenazas de salud ambiental. En este contexto, hemos utilizado la modelización ecológica basada en el ecosistema para evaluar y cuantificar el estado de salud ambiental de una bahía semi-cerrada del Mar Mediterráneo, en el Golfo de Amvrakikos (superficie: 405 km^2, profundidad máxima: 60 m) (Mar Jónico). En particular, hemos desarrollado un modelo de red trófica del ecosistema durante los años 80 y lo hemos calibrado con series temporales de datos desde 1980 a 2013. Los objetivos concretos del estudio han sido: (1) investigar la dinámica de los recursos marinos en las últimas tres décadas considerando como principales impulsores de los cambios ambientales el efecto sobre el ecosistema de los cambios en la escorrentía de los ríos, el desarrollo de la acuicultura y las pesquerías; y (2) evaluar los cambios estructurales y funcionales en el ecosistema utilizando una serie de indicadores obtenidos a partir de simulaciones temporales realizadas con el modelo ecológico. Los resultados indicar que los principales impulsores de la red trófica del Golfo de Amvrakikos fueron los cambios en la cantidad de nutrientes y materia orgánica en la escorrentía de los ríos locales. La evolución de los indicadores ecológicos, los cuáles se utilizan para explicar los cambios en la estructura del ecosistema, han evidenciado una degradación de los compartimentos demersal de la red trófica, principalmente debido a los altos niveles de eutrofización, y una relativa estabilidad en los compartimentos pelágicos. Mediante la inclusión de varios impulsores de cambio ambiental en el modelo ecológico, el presente estudio ilustra la utilidad del modelo ecológico como una herramienta para evaluar la salud ambiental del ecosistema marino de la bahía de Amvrakikos y para desarrollar futuras políticas de gestión en la zona.

1. Introduction

Marine ecosystems are increasingly impacted worldwide by a series of threats that include overfishing (e.g., Pauly et al., 2005), aquaculture (e.g., Naylor et al., 2000), eutrophication (e.g., Diaz and Rosenberg, 2008), habitat loss and degradation (e.g., Dobson et al., 2006), climate change (e.g., Overland et al., 2010), pollution (e.g., Islam and Tanaka, 2004) and species invasion (e.g., Libralato et al., 2015). Possible irreversible impacts and synergies among these threats are posing doubts on the long term sustainability of goods and services currently provided by marine ecosystems (Halpern et al., 2012), with the result that many national and international regulations (e.g., European Marine Strategy Framework Directive, [MSFD; 2008/56/EC]; Convention of Biological Diversity, [CBD]) are intervening to assess, control and reduce stress induced by the aforementioned threats. Yet, while a large body of studies focus on the impact of a single factor on specific compartments of marine and coastal environments, the assessment of cumulative and cascading effects of different threats remains poorly studied as well as the trade-offs that might rise when managing them in an integrated framework (Link et al., 2010). For this reason, there has been a growing interest to develop more comprehensive tools capable of assessing the effects of anthropogenic impacts within a single common framework (Halpern et al., 2008; Libralato and Solidoro, 2009; Travers et al., 2009) in order to facilitate the setting of targets and implementation of management measures (Cury et al., 2008; Kaplan et al., 2012; Piroddi et al., 2015). The development of ecosystem models, despite requiring a large amount of multidisciplinary data to be accurate, has increased in the last decades (Heymans et al., 2014; Piroddi et al., 2015) mainly driven by a worldwide movement toward ecosystem-based management approach (Levin et al., 2009; Pikitch et al., 2004). Ecosystem modeling approaches are particularly valuable in the context of European policies like the MSFD which requires an integrative assessment of the health status of marine and coastal ecosystems in relation to the cumulative effect of different pressures (Cardoso et al., 2010). In the following Directive, the assessment of ecosystem status and the setting of reference values and targets to achieve “Good Environmental Status” (GEnS) should be done through the use of indicators (Borja et al., 2014) which are already, at least partly, important ecosystem model outputs (Piroddi et al., 2015). Model derived indicators can in fact serve to evaluate whether an ecosystem and its services are well maintained and sustainably used so that the suitable management measures can be proposed (Piroddi et al., 2015; Shin et al., 2010).

Here we assessed the health status of the Amvrakikos Gulf (Greece, Fig. 1) which has been defined an ideal "natural laboratory" for ecosystem assessments (Bearzi et al., 2008) due to its small size, its semi-enclosed morphology (Katselis et al., 2013), its richness of charismatic megafauna (Bearzi et al., 2008) and because it provides several goods and services (EC, 2009). The Gulf is the final receptor of freshwater and nutrient loads from surrounding areas and from two important rivers, hosts several aquaculture sites (mostly fish farms active since the end of the 80s), and its resources are exploited by local small-scale fisheries. Nevertheless, despite being protected by national, European and international regulations for its diverse wildlife and wetlands (EC, 2009; Gonzalvo et al., 2014), the Gulf has undergone in the past decades through severe changes that have degraded rapidly the entire ecosystem (Katselis et al., 2013; Spyratos, 2008). It has indeed become seasonally hypoxic/anoxic (Kountoura and Zacharias, 2013) resulting in more than 50% of habitat loss on the seafloor (Ferentinos et al., 2010). Under such complex scenario, the Gulf represents a perfect case-study for applying ecosystem modeling approach and its model can be possibly of interest for other world's ecosystems facing similar pressures. The aims of our work were twofold: (1) investigate the dynamics of marine resources in the Amvrakikos Gulf from 1980 to 2013 considering the effect of rivers run off, fish farms and fisheries as major anthropogenic drivers affecting the system and (2) look at structural and functional changes of the ecosystem using model derived indicators obtained from temporal simulations.

2. Materials and methods

2.1 *Study area*

The Gulf of Amvrakikos (Fig. 1) is a semi-enclosed embayment of approximately 405 km^2 (excluding marshes and lagoons), situated in north-western Greece that communicates with the Ionian Sea through the Preveza Channel: a narrow (minimum width of 370m) and shallow (< 5 m at the shallowest point and ~ 20 m at the deepest) 3 km-long corridor. Its fjord-like hydrographic regime, because of a shallow sill, reduces deep water exchange with the open sea; the mean depth of the Gulf is approximately 30 m (its maximum is 60 m), with a seabed mostly covered by mud or sand (Ferentinos et al., 2010). Surface salinity fluctuates widely but remains low throughout the year (17–35%: Friligos et al., 1997) while sea-surface temperatures range between 9.0 °C and 30.6 °C (Friligos et al., 1997; Panayotidis et al., 1994). Water quality of the Gulf is influenced by the runoff of two rivers (Louros and Arachthos), located in the northern shore (Friligos et al., 1997; Kountoura and Zacharias, 2013), which is controlled by dams operating since 1953 and 1980 for Louros and Arachthos respectively (Ferentinos et al., 2010). Moreover, the Gulf is affected by fish farms, agriculture, livestock and discharges from domestic sewage from coastal towns and villages (Ferentinos et al., 2010; Gonzalvo et al., 2014). In the last 20–30 years, the deeper layers of the water column have become seasonally hypoxic/anoxic, with the western side seasonally hypoxic and the eastern seasonally anoxic (Kountoura and Zacharias, 2013), while the epipelagic layers are still characterized by abundant marine life (Bearzi et al., 2008; Gonzalvo et al., 2014; Panayotidis et al., 1994).

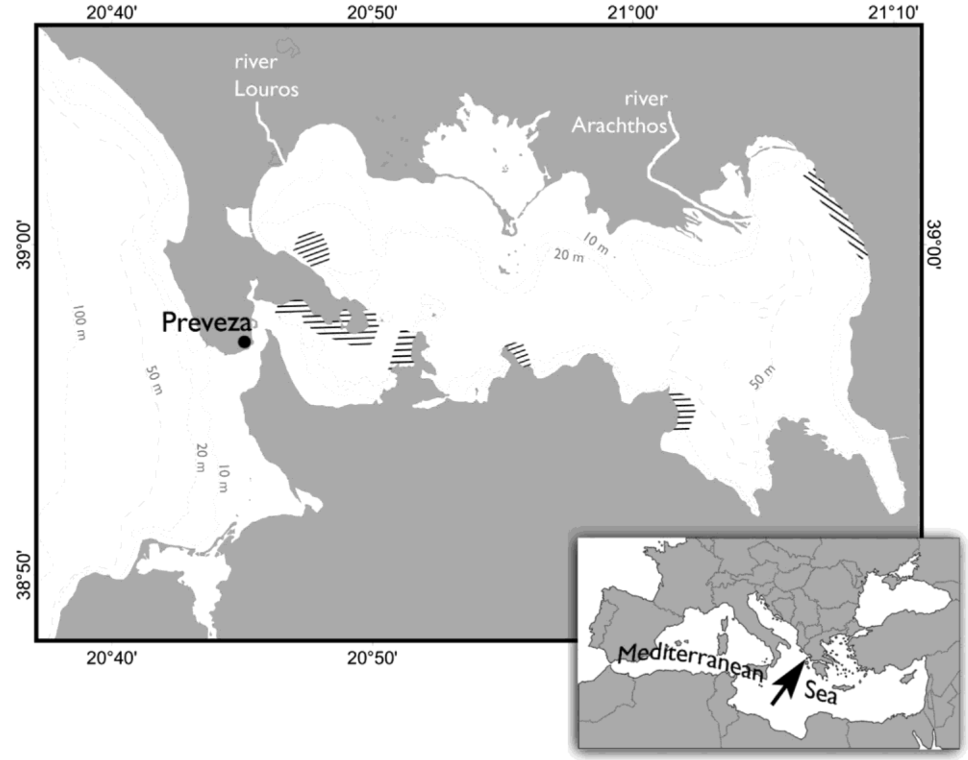


Fig. 1. The Amvrakikos Gulf map with depth profile and the location of fish farms represented by black lines.

Commercial fisheries operating in the study area include only small-scale fisheries working mainly with set nets (i.e., trammel and gill nets). According to the Royal Fishing Law 23.3/8-4-53 trawling and purse-seining are prohibited within the Gulf all year round since 1953. Currently the active fishing fleet includes ~ 280 boats fishing exclusively inside the Gulf and targeting mainly European pilchard (*Sardina pilchardus*), red mullet (*Mullus barbatus*), sand steenbras (*Lithognathus mormyrus*), caramote prawn (*Penaeus kerathurus*), common cuttlefish (*Sepia officinalis*), mugilidae and Solea spp. (EC, 2009; Koutsikopoulos et al., 2008).

2.2 *The food web model*

A food web model was constructed for the Amvrakikos Gulf using the Ecopath with Ecosim (EwE) software version 6 (Christensen et al., 2008). In Ecopath, all principal autotroph and heterotroph species can be represented either individually or aggregated into functional groups considering their ecological roles. Ecopath, the static module of the software that permits definition of initial conditions for the dynamic module Ecosim (Christensen and Walters, 2004), is based on two main equations. In the first one, the biological production of each functional group is equal to the sum of fishing mortality, predation mortality, net migration, biomass accumulation, and other unexplained mortality as follows:

$$(P/B)_i \cdot B_i = Y_i + \sum_j [B_j \cdot (Q/B)_j \cdot DC_{ji}] + E_i + BA_i + (P/B)_i \cdot B_i (1 - EE_i) \quad (1)$$

where (P/B) is the production to biomass ratio for a certain functional group (i), B_i is the biomass of a group (i), Y_i the total fishery catch of group (i), $(Q/B)_j$ is the consumption to biomass ratio for each predator (j), DC_{ji} is the proportion of the group (i) in the diet of predator (j), E_i is the net migration (emigration – immigration), BA_i is the biomass accumulation for the group (i), EE_i is the ecotrophic efficiency, and $(1-EE_i)$ represents mortality due to factors other than predation and fishing.

In the second equation, the consumption (Q) of each functional group (i) is equal to the sum of production (P), respiration (R), egestion (GS) and unassimilated food (GS·Q).

$$Q_i = P_i + R_i + GS_i \cdot Q_i \quad (2)$$

The implication of these two equations is that the model is mass-balanced; under this assumption, Ecopath uses and solves a system of linear equations estimating missing parameters (see also Christensen and Walters (2004) and Pauly et al. (2000)). In Ecosim the system of algebraic equations of Ecopath (Eq. (1)) is used to set up a system of differential equations to estimate biomass fluxes as follows:

$$dB_i / dt = g_i \sum_j Qji - \sum_j Qij + I_i - (M_i + F_i + e_i)B_i \tag{3}$$

where dBi/dt is the biomass growth rate of group (i) during the interval dt, gi is the net growth efficiency (production/consumption ratio), Ii is the immigration rate, Mi and Fi are natural and fishing mortality rates of group (i), ei is emigration rate (Christensen and Walters, 2004). Consumption rates (Qji) are calculated in Ecosim based on the "foraging arena" theory where Bi's are divided into vulnerable and invulnerable fractions to account for hiding and other behavior strategies adopted by animals for balancing predation risk with foraging (Ahrens et al., 2012). In particular, Ecosim describes the interactions between each predators (j) and prey (i) by attributing a vulnerability term (vij) for each of these interactions. This vulnerability parameter sets the maximum increase in predation mortality a given predator can cause on a given prey. Low values of vulnerability (close to 1) mean that prey production determines the predation mortality ('bottom-up' control) while high values of vulnerability (e.g., 100) mean that predator biomass determines how much prey is consumed (top-down control) (Christensen and Walters, 2004). Mixed effect (vulnerability = 2) is set as the default value in Ecosim.

Also, in Ecosim, trophic interactions can be described as flow rates using the following formula:

Flow rate = aij/Aij ·vij·Pj (4)

where aij is the "rate of effective search" parameter, Aij the restricted area where predator j forages on prey i, vij vulnerable prey biomass and Pj the predator abundance. This equation recognizes that predators search for prey only over restricted foraging arenas and that the vulnerable prey biomass is distributed only over such areas (Christensen et al., 2008).

2.3 *Model parameterization and functional groups*

The Ecopath model constructed for the Amvrakikos Gulf represents an annual average of the years 1980–1981, being this the first years of available time series of catches (1980–2011) and river discharge (1981–2008). To describe both high trophic level (HTL) and low trophic level (LTL) organisms/compartments, a total of 34 functional groups were considered, including marine mammals (1), seabirds (3), sea turtle (1), fishes (15), invertebrates (6), benthos (1), zooplankton (1), bacterioplankton (1), primary producers (1), fish farms (1) and detritus (3). Biomasses (expressed as tonnes of wet weight per km^2) for benthic invertebrates, phytoplankton and zooplankton were available from scientific literature and for seabirds species also through global international databases (Birdlife www.birdlife.org and the Sea Around Us Database www.searoundus.org). Common bottlenose dolphins (*Tursiops truncatus*) biomass was available for the years 2003–2013 (Bearzi et al., 2008, Gonzalvo, unpulished data). To estimate the biomass of 1980 we used the study of Gonzalvo et al. (2014) on population abundance changes during the last 20 years based on fishers interviews. Surveys or stock assessments to estimate biomass of commercially important groups (functional groups 6–20 and 22–26 in Table S1) were not available for the area. Thus, for each of these functional groups, Catch per Unit of Effort (CPUE) estimates were used as a proxy of their relative biomass, assuming proportionality between CPUE and biomass (Myers and Worm, 2003; Watson et al., 2013). CPUEs, expressed as tonnes kW^{-1}year^{-1}, were calculated by dividing the reconstructed catches by the total reconstructed effort (see section below). Despite being abundant in the Gulf, no biomass estimate was available for jellyfish, thus it was estimated from the model by imposing EE equal to 0.95 under the conservative assumption that most of its production was used in the system, reducing possibilities to overestimate its abundance and effects (Christensen and Pauly, 1998; Pauly et al., 2009). In order to represent over time nutrients and organic matter loads affecting the eutrophication state of the system, we incorporated in the model fish farms and particulate organic matter (POM) as functional groups. The biomass of fish farms was represented as the total fish produced from the cages and was available from late 1980s from the Fisheries Department of Preveza Prefecture. Thanks to detailed local information on cage productivity, feed given, average feed composition and feed loss (Fisheries Department of Preveza Prefecture), we quantified organic matter and nutrient released from cages (Lupatsch and Kissil, 1998) from 1981 to 2008.

Organic matter release from cages were represented by opportunely setting unassimilated fraction (including also uneaten feed) and detritus fate (to POM) for the fish farm functional group and forcing its biomass with fish farm production over time. POM initial biomass was derived from biochemical oxygen demand (BOD) estimates in water samples while net migration parameter from river and human-related discharges was used to represent annual input to the Gulf (Albanis et al., 1995; Katselis and Ramfos, 2015; Zacharias et al., 2009). Abiotic data consisted of monthly total river outflows of Louros and Arachthos (1980–2008) and was provided by the Public Power Corporation SA. Moreover, nutrient released by the rivers and by fish farm cages were used to determine nutrient inputs to the Gulf. We considered nitrogen as limiting nutrient (typical for coastal shallow ecosystems; Libralato and Solidoro, 2009) and used its estimated dynamics as forcing function for phytoplankton primary production. Bacterioplankton was included in the model to mimic main biogeochemical cycles and possible oxygen consumption due to organic matter degradation. Bacterioplankton biomass and rates, not available for the study area, were taken from similar ecosystems (Harvey et al., 2003; Libralato and Solidoro, 2009).

P/B and Q/B ratios for finfish and invertebrates were estimated using empirical equations (Christensen et al., 2008) or were taken from 2003 to 2007 for a fraction of the total number of fishing vessels. To estimate total catch for the 1979–2007 period we first searched in the literature for total fishing fleet size. Based on public sources of data (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009), six anchor points representing the number of fishing vessels for the years 2011, 2009, 2001, 2000, 1991 and 1980 were found. To get the overall trend of fishing fleet size for the 1979–2011 period we used the six anchor points and interpolated the estimates of the anchor points for the missing years following the same approach as described and applied in Zeller et al. (2007). We then estimated the total catch by species for 1979–2007 for the entire Amvrakikos from literature and expressed as annual rates ($year^{-1}$) (Table S1).

A diet composition matrix was constructed using either field studies (e.g., stomach contents) or diet data obtained from the literature for the same species in similar ecosystems (Table S2). For some functional groups, when the information was lacking, we also integrated the outputs parameters (DC, P/B, Q/B) of previously built EwE models available for the Ionian Sea (Moutopoulos et al., 2013; Piroddi et al., 2010; Piroddi et al., 2011) and the adjacent Adriatic Sea (Coll et al., 2009b). In the case of fish farm, P/B and Q/ B represented respectively the production of fish and the consumption of feed per year from the cages while the diet was opportunely set in order to represent the feed coming from outside the system (Katselis and Ramfos, 2015; Zacharias et al., 2009).

Catch data was reconstructed from a number of different sources. In particular, catch by species and total catch was available from the Preveza Department of Fisheries from 1979 to 2001 and from Koutsikopoulos et al. (2008) and local fishers interviews, from 2003 to 2007, for a fraction of the total number of fishing vessels. To estimate total catch for the 1979–2007 period we first searched in the literature for total fishing fleet size. Based on public sources of data (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009), six anchor points representing the number of fishing vessels for the years 2011, 2009, 2001, 2000, 1991 and 1980 were found. To get the overall trend of fishing fleet size for the 1979–2011 period we used the six anchor points and interpolated the estimates of the anchor points for the missing years following the same approach as described and applied in Zeller et al. (2007). We then estimated the total catch by species for 1979–2007 for the entire Amvrakikos fishing fleet using the catch/vessel ratio given by the Department of Fisheries of Preveza and applied it to the reconstructed fishing vessels time series. Fishing effort (kW) was estimated for the 1979–2011 period by taking the product of the reconstructed number of fishing vessels, kW per vessel (calculated using GT; EC, 2009), and the number of days spent fishing (Koutsikopoulos et al., 2008). Also, to account for improvements in technology not captured by kW as a measure of effort, a technological "creep factor" of 1% was applied since 1980 (Table 2), as derived from the empirical relationship by Pauly and Palomares (2010). Since no discards data were available for the Gulf, we assumed same discard ratio provided by Moutopoulos et al. (2013) for an ecosystem model of the neighboring open waters of the Ionian Sea. A detailed description of the functional groups, data to parameterize the model and associated references are listed in Tables S1, S2, S3 of Supplementary materials.

2.4 *Model and data quality*

In order to assess the quality of the model we reported the overall pedigree index, that ranges from 0 to 1 (see Table 1). The pedigree is calculated on the basis of the presumed quality of data entered in the model with larger weight for local experimental data and lower weight for parameters derived from other models or extrapolated from other systems. Low overall pedigrees (0.1–0.3) imply a model constructed with low-precision data and/or with data coming from areas outside the studied region, while higher values (close to 1) indicate a model constructed with locally-derived data (Christensen et al., 2008; Morissette, 2007). The highest pedigree values observed in Ecopath models ranged be- tween 0.7 and 0.8 (Christensen et al., 2008; Morissette, 2007).

2.5 *Ecosim fitting procedure*

We used Ecosim to fit the model to observed time-series of data using the sum of squares (SS) deviations between predicted and observed data as a metric for assessing model performance (Christensen et al., 2008). The time-series used to fit the model were mainly biomasses, catch per unit effort (CPUE) and catches for those functional groups with available information (Table S3) while main forcings were fishing effort over time, nutrient loads and organic matter (estimated from biochemical oxygen demand [BOD] measurements) coming from fish farms, rivers run off and other diffuse sources (Fig. 2a and b). The fitting procedure followed the same methodology as described and applied in Mackinson et al. (2009), which consisted of 7 general steps:

1) Baseline model: trophic interactions with default vulnerabilities (vij = 2; mixed effect), no environmental or fishery data were used to drive the model;
2) Baseline and trophic interactions: trophic interaction modifications were included while no environmental or fishery changes were used. In particular, different of vulnerabilities were tested (5, 10, 15, 20, 25, 30);
3) Baseline and environment: different environmental drivers such as the limiting nutrient (in our case nitrogen) and BOD trends coming from rivers and fish farms (Figure 2) were used to force primary production and POM concentrations. No fishery data were used to drive the model;
4) Baseline, trophic interactions and environment: no fishery data were used;
5) Fishery: Fishing effort was included as a model driver (Figure 2). Trophic interactions were set as default and no environmental data were used;
6) Changes in trophic interactions and fishery: no environmental data was used;
7) Trophic interactions, environment and fishery were jointly included in the model as drivers.

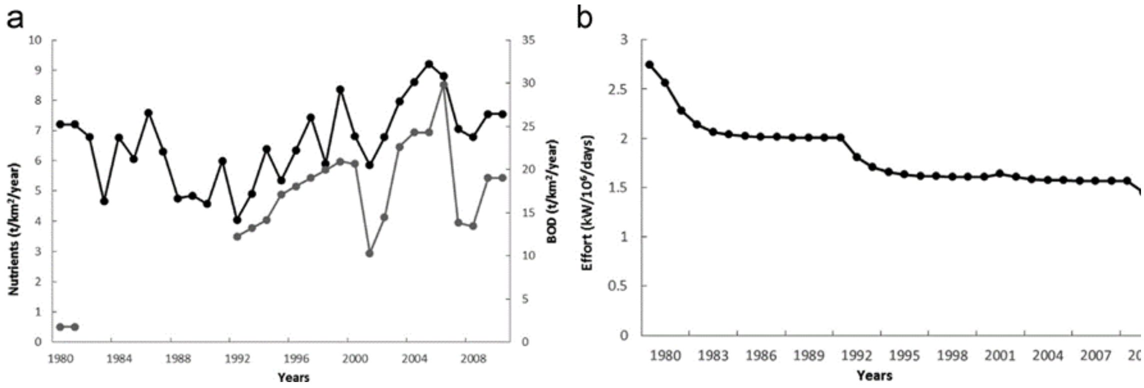


Fig. 2. a. Changes in nutrients concentration (black line) and biogeochemical oxygen demand (gray line); **b.** fishing effort (kW/10^{-6}/days) used as main drivers for the fitting procedure.

To select the best model, at each step, the Akaike's information criterion (AIC) that takes into account the predictive accuracy (sum of squares, SS) and complexity (number of parameters, trophic interactions and environmental drivers e.g., PP) of the model, was calculated (Mackinson et al., 2009).

In addition, once the best model was chosen, to account for anoxia/hypoxia in the system, a 'mediation function' was applied (Christensen et al., 2008). In Ecosim, the mediation function allows a third variable (in our case bacterioplankton) to influence the trophic interaction between two other variables (here seabirds and marine mammals with each of their prey) by altering either the area (Aij), the rate of effective search (aij) or the vulnerability exchange rate (vij). In our case, we applied the mediation function to change both Aij and vij together to assess if, in the presence of oxygen depletion in bottom layers, available preys would concentrate in a shallower stratum making them more available to predators (seabirds and marine mammals). Given that oxygen is not a modeled state variable, we used bacterioplankton dynamics as a proxy for oxygen depletion. This permits to evaluate if an increase in POM in the system through fish farms and river runoff, would affect bacterioplankton and oxygen concentrations with effects on bottlenose dolphins and seabirds abundance by increasing prey abundance at the surface due to the reduction of O_2 on the seafloor.

2.6 *Model analysis*

The Amvrakikos food web was represented graphically with a flow diagram that included information on trophic levels, biomasses and estimated flows (Fig. 3). Ecosystem structure and exploitation status of the Gulf were assessed through a series of indicators (Table 1) derived from network analysis and ecological studies.

Table 1

Detailed description of the ecological indicators examined in this paper with acronyms, typology (state or trend), definitions and/or references.

Ecological Indicator	Acronym	State (S); Trend (T)	Definition and/or references
Total system throughput	TST	*S*	Sum of all the flows (consumption, export, respiration, detritus). It indicates whole ecosystem size (Christensen et al., 2008)
Total primary production/total system respiration	TPP/TR	*S*	It relates to community energetic attributes of ecosystem maturity. In the early stages of ecosystem development primary production (TPP) is expected to exceed respiration (TR) (values greater than 1). As the system matures the ratio is expected to move towards 1 (Christensen et al., 2008)
Total primary production/total biomass	TPP/TB	*S*	It relates to community energetic attributes of ecosystem maturity. As system matures, biomass accumulates, therefore TPP/TB ratio is expected to be high in developing systems and diminish as the system mature (Christensen et al., 2008)
Finn's Cycling Index	FCI	*S*	Percentage of flows recycled in the food web and path length (Finn, 1976)
Ascendancy	A	*S*	Measurement of system growth and development of network links (Monaco and Ulanowicz, 1997)
Overhead	O	*S*	Energy in reserve of an ecosystem that reflects system's strength when it is under unexpected perturbations (Ulanowicz, 1986)
System omnivory index	SOI	*S*	Weighted average of the variance of the TL of consumer's prey. It is an index of trophic specialization showing how feeding interactions are distributed between trophic levels (Libralato, 2008)
Mean Transfer Efficiency	TE	*S*	Efficiency in which energy is transferred between TLs, calculated as the geometric mean of TE for each of the integer trophic levels II to IV (Christensen et al., 2008)
Trophic levels	TL	*S*	(Christensen et al., 2008)
Trophic level of the catches	TL_C	*S*	(Christensen et al., 2008)
Primary production required	%PPR	*S, T*	Calculated as primary production required divided by the total primary production of the system to sustain the catch. Used to evaluate the sustainability of fisheries (Pauly and Christensen, 1995; Tudela et al., 2005)
Kempton's index of biodiversity	Q	*T*	Expresses biomass species diversity by considering those organisms with trophic levels 3 or higher (Kempton and Taylor, 1976)
Total pelagic versus total demersal biomass	P/D	*T*	Ratio between small pelagic species (plankton feeder group) and the piscivores species (predator and benthic groups) (Caddy, 1993, 2000)
Mean trophic level of the community	mTLco	*T*	Excluding those functional groups with TL=1 and calculated as the weighted average of the TL of all the species within the ecosystem (Shannon et al., 2014)
Mean trophic level of groups with TL between 2 and 3	mTL_{2-3}	*T*	
Mean trophic level of groups with TL >3.25	$mTL_{3.25}$	*T*	In our case excluding marine mammals, seabirds and sea turtles (mTL3.25; Pauly and Watson, 2005)
Mean trophic level of top predators	mTL_{TP}	*T*	In our case including marine mammals and seabirds
Mean trophic level of the catches	mTLc	*T*	Weighted average of the TL of fisheries target species (Pauly et al., 1998)
Fishing in Balance index	FIB	*T*	Ratio between the energy required to sustain the fishery landings and the baseline value (the first year of the time series, Pauly et al., 2000)

3. Results

3.1 *Mass-balancing*

To obtain mass balance we adjusted the input parameters of those functional groups (#10) with EE values >1. In particular, for pelagic fish, *Sardina pilchardus*, other clupeidae, other benthopelagic fish, benthopelagic cephalopods, other crustaceans, benthic invertebrates and zooplankton we adjusted the diet matrix, being the data with higher uncertainty. For example, the predation caused by pelagic fish on *Sardina pilchardus* and other clupeidae was decreased because too high (from 35% to 25% and from 0.5% to 0.2% respectively), while the consumption of benthopelagic cephalopods on crustaceans group was overestimated and was reduced by redistributing the proportions in the predator's diet. Crustacean, bivalve and gastropod biomasses were the only biomasses that had to be modified from the original input data: the values taken from closed systems (see Section 2) were indeed too low and had to be increased.

Once balanced, ecotrophic efficiencies (EE) showed high values for the majority of the functional groups, indicating that total mortality in the system was mainly driven by predation and fishing. The gross food conversion efficiency (P/Q) and the respiration over assimilation (R/A) were within the expected ranges (Christensen et al., 2008). The resulting output parameters and the final diet matrix are shown in Table S1, S2 and S3 in Supplementary materials.

3.2 *Model analysis*

3.2.1 *Trophic levels*

Trophic flows, trophic levels and relative biomasses of the Amvrakikos Gulf ecosystem are represented in Fig. 3, Table 2 and Table S1. In particular, the highest trophic levels (TL) were observed for *Tursiops truncatus* (TL=4.07), pelagic fish (mainly large pelagics, TL=4.05) and demersal fish 3 (mainly large demersals, TL=3.91). In contrast, annular seabream (*Diplodus annularis*), European sardine (*Sardina pilchardus*), European sole (*Solea vulgaris*), mullidae, demersal fish 2 (mainly sparidae species), mugilidae, other crustaceans zooplankton, benthic invertebrates, bivalves and gastropods and bacterioplankton had lower TL values ranging between 2.13 and 2.99. It should be also noted that loggerhead sea turtle (*Caretta caretta*) presented a quite low TL (3.27) due to the presence of discarded fish in its diet as it was observed in the Gulf

(Zbinden et al., 2011; Gonzalvo direct observation) and in neighboring areas (White, 2004).

Table 2
Summary statistics and network analysis indicators for the Amvrakikos Gulf food web.

Indicators		Units
Summary statistics		
Sum of all consumption	4421	t·km^{-2}year^{-1}
Sum of all exports	960	t·km^{-2}year^{-1}
Sum of all respiratory flows	1806	t·km^{-2}year^{-1}
Sum of all flows into detritus	4605	t·km^{-2}year^{-1}
Total system throughput	11792	t·km^{-2}year^{-1}
Mean trophic level of the catch	2.77	
Gross efficiency (catch/net p.p.)	0.004	
Total primary production	2583	t·km^{-2}year^{-1}
Total primary production/total respiration	1.43	
Proportion of primary production required to sustain fisheries (PPR%= PPR/PP*100)	8	%
Primary production required to sustain fisheries (PPR)	575	t·km^{-2}year^{-1}
Total primary production/total biomass	10.43	
Total biomass (excluding detritus)	247.66	t·km^{-2}
Total catch	9.53	t·km^{-2}year^{-1}
Network analysis		
System Omnivory Index	0.27	
Finn's cycling index	15.85	%
Ascendancy	34.5	%
Overhead	65.5	%
Mean Transfer Efficiency	13.8	%
Pedigree Index		
Pedigree	0.57	

3.2.2 Time series fitting

The best performances in fitting observed data were obtained when trophic interactions as well as fishing and environmental variables were included all together in the fitting procedure. The best model, which was the one with the lowest AICc, explained 78% of the variance of the data (Table 3). Environmental drivers in combination with trophic interactions were able to explain the majority of the variability observed in the ecosystem (77.2%) while fishing marginally contributed with a 1.8%.

Different vulnerabilities were also tested and the largest improvement was obtained with 30 trophic interactions. The best model reflected quite well the biomass trends for the apex predators of the Amvrakikos Gulf. In particular, Ecosim was able to predict *Tursiops truncatus*, *Phalacrocorax carbo* and *Pelican crispus* abundance trends for the surveyed periods (Fig. 4). A slight improvement was found for seabirds when the mediation function was incorporated in the model, assuming an increased availability of prey on the surface of the water column.

Table 3
Model fits following the seven steps proposed by Mackinson et al. (2009) including trophic interactions, fishery and environmental drivers. Vulnerabilities are shown only for those models with the lowest Akaike Information Criterion (AICc). The "best" model (shown in italics) was the one yielding the lowest AICc.

Steps	vulnerabilities	min SS	AICc	%improved
1. Baseline	0	524.9	71.3	
2. Baseline and trophic interactions	5	524.9	81.4	-14.2
3. Baseline and environment	0	453.0	51.6	37.6
4. Baseline, trophic interactions and environment	30	211.9	16.2	77.2
5. Fishery	0	519.9	70	1.8
6. Trophic interactions and fishery	3	501.1	71.1	0.2
7. Trophic interactions, environment and fishery	*30*	*218.6*	*15.7*	*78.0*

For bottlenose dolphins, on the other hand, the trend improved when a decrease in prey and feeding area was assumed. For forage fish species like *Sardina pilchardus* the model reproduced quite well the fluctuations in CPUE observed between 1980 and 2004, while predicted trends between 2005 and 2007 were overestimated. A similar scenario was also observed for mugilidae. A good reproduction of CPUE time series data was shown for *Trachurus trachurus*, *Diplodus annularis*, mullidae and benthopelagic cephalopods. For these groups, however, the increase in biomass observed in the early 2000s was not picked up by the model. Ecosim was not able to represent well the fluctuations observed for *Penaeus kerathurus*. As for the other commercially important groups only few data points (from 2003 to 2007) were available resulting also in a poor fit (S4 in Supplementary material).

Regarding landings, Ecosim generally underestimated observed values, had difficulties in capturing the changes in catches although trends were vaguely captured for the majority of the groups (Fig. 5).

3.2.3 *Ecological indicators*

Ecological state indicators calculated by Ecopath for the Amvrakikos Gulf (Table 2) revealed that the main flows in the system were flow to detritus (39%) and consumption (37%) followed by respiration (15%) and exports (8%). In addition, indicators addressing community energetics and cycling of nutrients such as the ratio between total primary production (PP) and total respiration (R) (Christensen, 1995; Odum, 1969), primary production/biomass ratio (PP/B) and the SOI (System Omnivory

Index) suggested the system to be at an intermediate-low level developmental stage. The FCI (Finn's Cycling Index), the mean transfer efficiency (TE) and overhead showed relatively high values while ascendancy was quite low. Fishing indicators such as the primary production required (PPR) of the Gulf and the mean trophic level of the catches were respectively 8% and 2.77. The pedigree index of the model was 0.57.

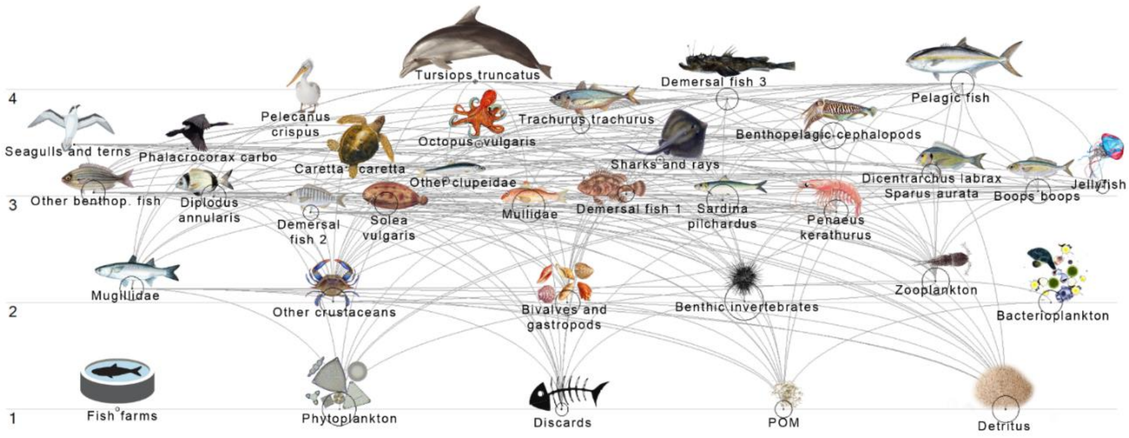


Fig. 3. Flow diagram of the Amvrakikos Gulf ecosystem (early 1980s). Each functional group is shown as a circle, with size approximately proportional to the log of its biomass. All the functional groups are represented by their trophic levels (y-axis) and linked to each other by predator-prey relationships expressed as light gray lines.

Trends in ecological indicators calculated by Ecosim revealed changes through time in the structure of the Amvrakikos Gulf ecosystem (Fig. 6). In particular, trophic level indicators mTLco and mTL_{2-3} increased since the beginning of 1980s. Similar trend was observed also for the ratio between pelagic and demersal species. The other two trophic level indicators, $mTL_{3.25}$ and mTL_{Tp}, showed clear decrease in time, with $mTL_{3.25}$ though increasing again from middle of 2000s. Kempton's biodiversity index fluctuated in time with a certain stability and no clear trend. On the contrary, mean trophic level of the catches (mTLc), fishing in balance index and relative PPR decreased since the beginning of the studied period.

4. Discussion

A food web model was implemented for the Amvrakikos Gulf ecosystem with the aim of reproducing and quantifying main energy and matter flows in the system and dominant food–web dynamics. To do so, we integrated in the model the most important HTL and LTL organisms/compartments characterizing the ecosystem and we represented the major pressures, both from anthropogenic and environmental sources (e.g., river run off, fish farming and fishing), affecting the Gulf.

Some uncertainties, which are discussed below, are still present in this model, particularly when looking at temporal changes in diet composition, discards and biomass of commercially important species. Although further research effort should increase its accuracy, we consider that the model presented here exploits at best the available information and data, sheds light in many factors affecting the complex ecosystem of the Amvrakikos Gulf and provides key ecosystem information that can be useful also for other Mediterranean coastal enclosed ecosystems (e.g., lagoons and gulfs/bays).

4.1 *Model quality and limitation*

Our Ecopath model fell within the medium-high range of the pedigree index estimated by Morissette (2007), who assessed globally the quality of 150 EwE models. The robustness of the baseline period (1980s) was mainly due to available survey data for several species/functional groups (e.g., seabirds and LTL organisms -phytoplankton, benthic invertebrates, zooplankton) of the ecosystem. Yet, data deficiencies still exist. The major gaps were related to poor quality of fisheries data (effort, catch and discards), which limited the reconstruction of the relative biomass of commercially important functional groups and the trends associated to their biomass and catch. In Greece, as well as in many other Mediterranean areas (Pauly et al., 2014), fisheries statistics are generally incomplete and have low reliability (Moutopoulos and Koutsikopoulos, 2014; Tsikliras et al., 2007) since it is not rare that fishermen deliberately misreport their catches to avoid stricter regulations or higher taxation (Bearzi et al., 2006), as it has been also observed in our study area. A recent study by Moutopoulos and Koutsikopoulos (2014) analyzing the landings as well as the fishing effort data per fishing gear reported by the Hellenic Statistical Authority over the period 1982–2010, showed abrupt changes of both recorded species and species landings per subarea, spurious correlations of landings among different species groups and misreporting of fishing gear and/or of fishing vessel characteristics.

Other limiting factors were related to kW or other measures of fishing capacity (tonnage, length over all, number of boats) which are not necessarily good estimates of real fishing effort (Lleonart and Maynou, 2003): meteorological, economic and legislative conditions that hamper fishing are not considered to change over time, whereas they might be all important factors in determining exerted effort.

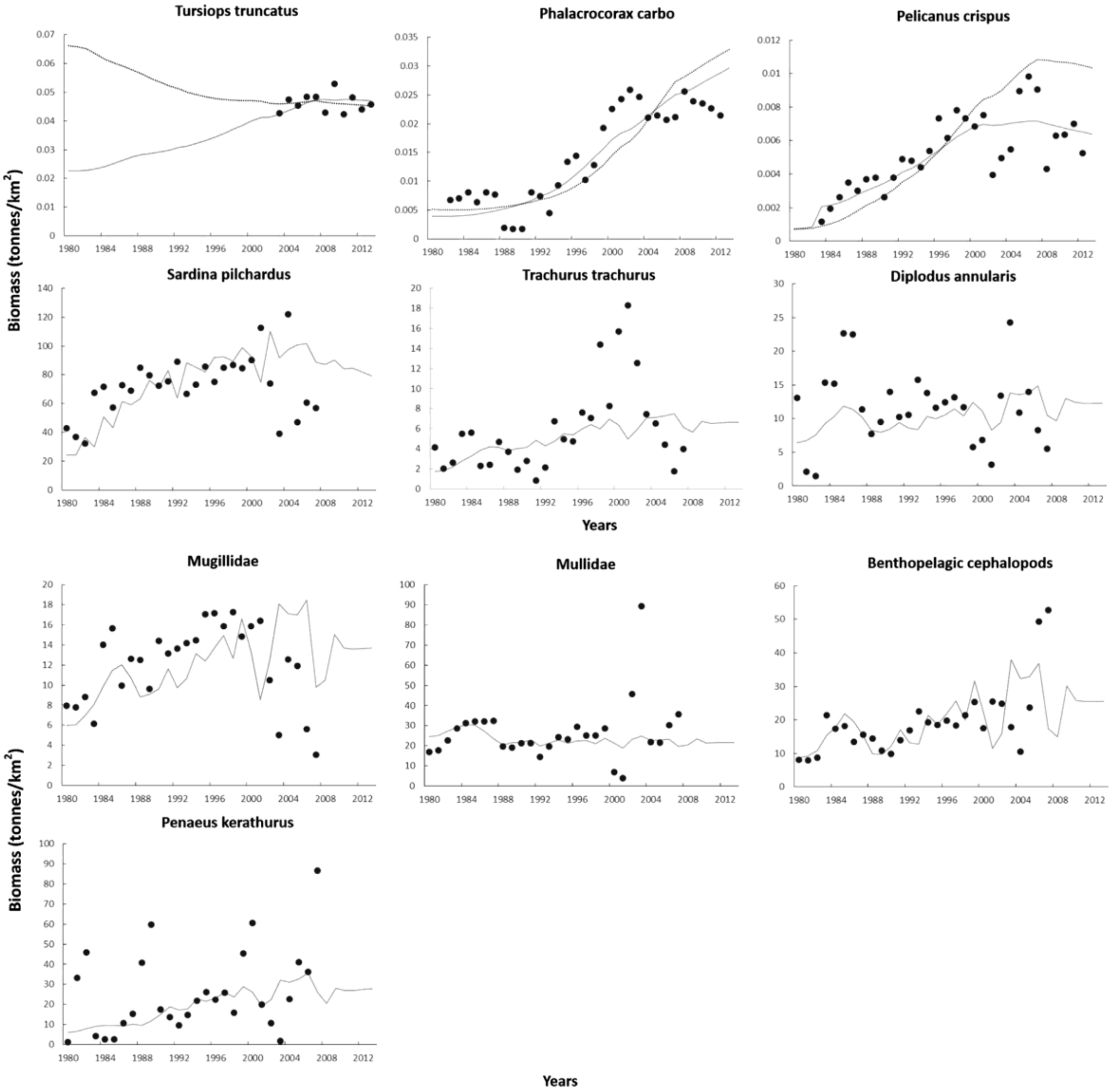


Fig. 4. Predicted (solid lines) versus observed (dots) biomass (t/km^2) for the main functional groups of the Amvrakikos ecosystem for the period 1980-2013. For the megafauna (*Tursiops truncatus*, *Phalacrocorax carbo*, *Pelicanus crispus*) the predicted model is also shown with the inclusion of mediation function (dotted line).

No discard data were available for the study area. Despite the fact that further effort should be conducted to evaluate the impact of discards on commercial and non-commercial taxa, several studies have shown how discard rates in Greek small-scale fishery are relatively low and with a small impact on marine resources (Tsagarakis et al., 2013; Tzanatos et al., 2007; Vassilopoulou, 2012). Not surprisingly, therefore, fishery components in our model have the highest uncertainty. This limits the accuracy of our results, particularly in relation to CPUE trends that were used to calibrate the model.

Unfortunately, this uncertainty is common to many Mediterranean areas (Coll et al., 2008; Moutopoulos et al., 2013; Piroddi et al., 2010) where stock assessments or surveys are not in place or inaccessible and where fisheries statistics are in most cases erroneously recorded (Moutopoulos and Koutsikopoulos, 2014). Despite these limitations, reconstructed CPUE trends, being the only form of available data, are the most commonly used to represent relative biomass (Coll et al., 2008; Piroddi et al., 2010). Here, to limit this uncertainty, we tried to incorporate best available fisheries statistics complemented with local fishers interviews. Fishers' ecological knowledge (FEK) is gaining attention for understanding and evaluating changes in the structure and function of marine ecosystems (Bunce et al., 2008; Saenz-Arroyo et al., 2005). FEK data, obtained from fishers interviews, can be transformed into quantitative data (e.g., numerical trends) using different techniques (e.g., fuzzy logic: Ainsworth et al., 2008; Brotz et al., 2012) in order to ease their implementation in ecosystem modelling approaches (Ainsworth, 2011).

Thus, we recognize that further interviews should be conducted to fill knowledge gaps and possibly move toward more realistic data, increasing model accuracy. Yet, with the data currently available, our model represents the best approximation to provide an integrated understanding of the Amvrakikos Gulf marine ecosystem.

4.2 *Model analysis*

4.2.1 *Time series fitting*

The model was able to reproduce available time series of biomass and catch data when applying nutrient, organic matter and fishing effort as main drivers. Changes in nutrient loads, however, seemed to be the strongest driver, explaining around 38% of the variability in the food web of the Gulf, highlighting the importance of bottom-up forces in the dynamics of this ecosystem. The explicit representation of establishment and development of fish farm from 1980 to today permitted to highlight that, during the last decades, fish farms represented a secondary contribution to nutrients and organic matter to the Gulf, whereas the two main rivers were the main drivers of the Gulf eutrophication. The strong demand for irrigation waters to the surrounding agricultural farms and the consequent runoff of minerals represented also important non-point contribution (Spyratos, 2008).

When looking at overall dynamic changes of the main functional groups of the Amvrakikos Gulf for the period 1980–2013, the model showed a relative stability of the species/functional groups at the top of the food web and fluctuations with sign of decrease for the ones at the bottom, which is in accordance with previous studies pointing at eutrophication and contaminants as the main reason for such differences (Ferentinos et al., 2010; Koutsikopoulos et al., 2008). Only 2–3 decades ago the Gulf occasionally had hypoxic conditions at depths greater than 40 m (HCMR, 1988); currently the situation has worsened and these conditions are observed in waters up to 23 m of depth (EC, 2009). This trend constitutes a serious concern not only for demersal and benthic species but also for those on top of the food web, with effects beyond trophic interactions. For instance, Gonzalvo et al. (2015) have documented epidermal lesions on the main top predator of the Gulf, the bottlenose dolphin, suggesting environmental, such as the increase of local temperature (Philandras et al., 2008) and salinity (Feidas et al., 2007), as well human-related stressors (e.g., pollution) as their likely cause. Contaminants influencing dolphins' reproductive rates might also be the reason why this species, the only marine mammal present in the Gulf, remains currently stable (Gonzalvo, unpublished data) and not increasing since the only potential "dolphin predator" in the area is small-scale fishing fleet but evidences of by-catch were rarely observed in the Gulf. The only two species that seem to thrive in this type of ecosystem, showing an increase in population, are the *Phalacrocorax carbo* and the *Pelican crispus*. The most likely causes for such positive trend, as observed in other European wetlands (Cowx, 2013), are attributed to the legal protection granted to both species and their habitats and the presence of hot-spot areas for fish-eating birds (i.e. lagoons, fish farms) (BirdLife International, 2004; Liordos et al., 2014).

No significant results were obtained for the catches of the main commercially important groups of the ecosystem. This could be attributed, as mentioned above, to misreporting of fisheries statistics in terms of both catches and fishing fleet composition, but also to illegal, unregulated and unreported catches. Although fishery is the secondary most important component driving the system (after riverine nutrients and organic loads), as shown in this study, this poses a serious handicap for understanding the dynamics of the fishing fleet and generally of the ecosystem.

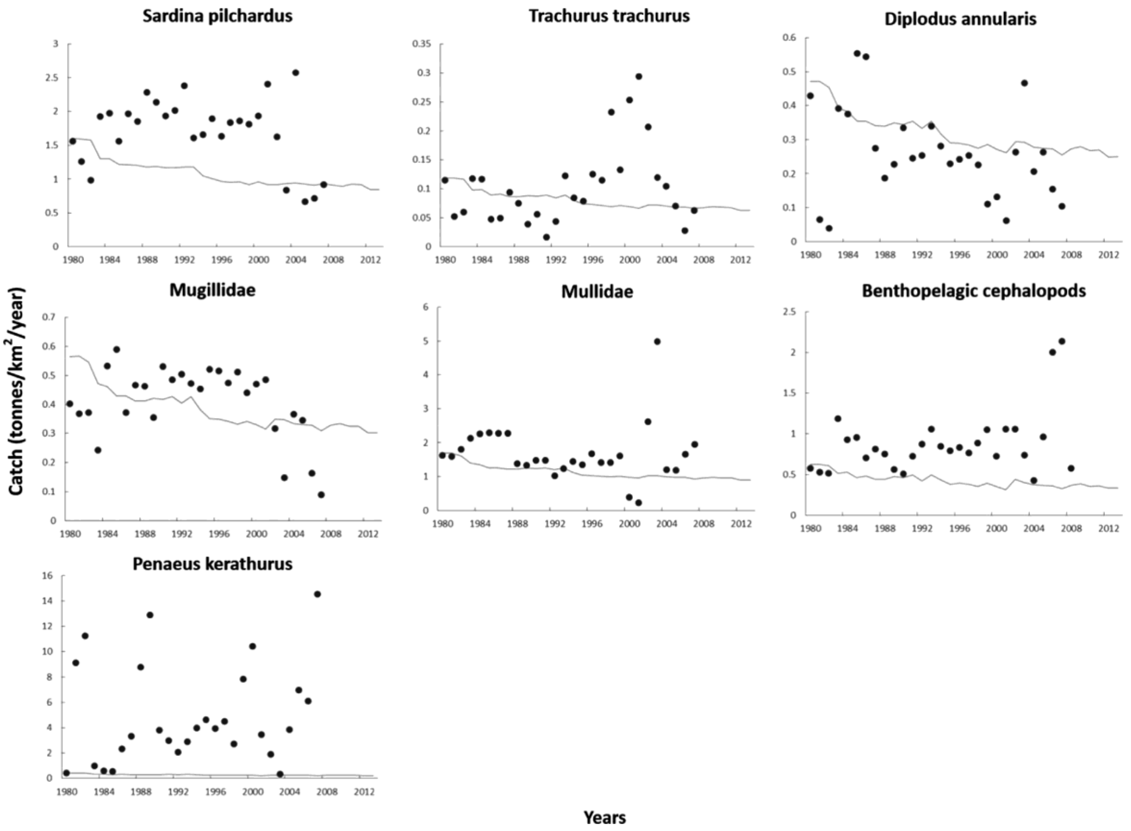


Fig. 5. Predicted (solid lines) versus observed (dots) catches (t/km^2/year) for the main commercially important functional groups of the Amvrakikos ecosystem.

4.2.2 *Ecological indicators*

The results obtained from our baseline model (year 1980), mainly regarding type of flows and cycling indices, already indicated the Amvrakikos Gulf to be an immature and perturbed system, typical of "closed" ecosystems (e.g., like estuaries, lagoons and bays) where bottom-up processes drive the system, and where possibly high levels of community stress are induced by anthropogenic and environmental forces. These results are in line with the estimates obtained for other large eutrophic ecosystems with similar historical evolutions (Ferentinos et al., 2010) and general patterns such as the Black and the Baltic Seas (Akoglu et al., 2014; Tomczak et al., 2012). These three semi-enclosed systems share, indeed, similar patterns as they have undergone in the last decades through severe ecosystem changes such as: (a) eutrophication with frequent hypoxia/anoxia events, mainly caused by the increasing concentration of human activities in the coastal zone such as industrial and agricultural waste (Akoglu et al., 2014; Readman et al., 1993; Tomczak et al., 2012), (b) local environmental changes such as the increase in the average annual air temperature (Philandras et al., 2008) and the reduction of the mean annual rainfall (Feidas et al., 2007) and (c) increasing fishery activities (Akoglu et al., 2014; Koutsikopoulos et al., 2008; Tomczak et al., 2012). Further similarities are found in their high levels of total primary production per unit of surface (t km^{-2} year^{-1}; Amvrakikos Gulf: 2583; Black Sea: 3483; Baltic Sea: 2434) and low levels of the mean TL of the catches (Amvrakikos Gulf: 2.78; Black Sea: 3.07; Baltic Sea: 3.3). Also, it is noteworthy not only the importance of small pelagic fish in the fisheries landings of all three areas, but also the dominance of these forage fish due to high levels of productivity in the epipelagic layers of the water column (Ferentinos et al., 2010; Oguz and Gilbert, 2007; Tomczak et al., 2012). The high values of total primary production and eutrophication levels in Amvrakikos, which are comparable to those of most eutrophic and heavily polluted gulfs of Greece, such as Saronikos and Thermaikos Gulfs (Nikolaidis et al., 2005), are indicative of the fragile health status of the Gulf of Amvrakikos.

Trends in ecological indicators gave some explanations on changes in the structure of the Amvrakikos Gulf across the 1980– 2013 period. In particular, when looking at ecosystem indicators such as the mean trophic level of the community, those groups with TL between 2 and 3, and the ratio between pelagic and demersal groups, a consistent pattern was delineated with increasing trends from the beginning of 1980. These positive trends over time reflected an increase of small pelagics and some of their predators (e.g., seabirds) and a decrease of demersal groups that might be related to the synergetic effects of nutrient enrichments and overfishing (Caddy, 1993; Libralato et al., 2004). However, since local fishery resulted to have a marginal role in the Gulf's food web and on its dynamics, a dominant effect of overfishing appears unlikely while eutrophication seems to be the only major player affecting the system.

Regarding catch related indicators, both the mean trophic level of the catches, the FIB index and PPR/PP decreased over time. Similar trend in the FIB index has been observed in another heavily degraded and highly eutrophic ecosystem as the Adriatic Sea suggesting a progressive deterioration of the ecosystem over time with a contraction of the fishery sector (Coll et al., 2009b). In particular, these trends might be a symptom of crisis in the local artisanal fishery, rather than overfishing, as observed in other areasf the Mediterranean Sea (Coll et al., 2009a; Coll et al., 2007; Piroddi et al., 2010).

Fig 6. Ecological and network indicators (Kempton's index of biodiversity (Q); Pelagic/Demersal ratio (P/D); Mean trophic level of the community (mTLco); Mean trophic levels of groups having trophic level between 2 and 3 (mTL_{2-3}); Mean trophic levels of groups having trophic level >3.25 ($mTL_{3.25}$; excluding marine mammals, sea turtles and seabirds); Mean trophic level of top predators (mTL_{TP}); Mean trophic level of the catches (mTLc); Fishing in balance index (FIB); Primary production required/PP (%PPR)) calculated from Ecosim model for the period 1980–2013. The estimated trends (solid line) are shown with the value of the slope and the coefficient of variation (R^2) for the regression model.

This crisis is also manifested by the fact that younger generations do not see any future in fisheries and that the traditionally oriented fishing community is rapidly changing (Gonzalvo et al., 2014). Moreover, the observed P/D trend might indicate a shift in the ecosystem trophic state (i.e., eutrophication; Caddy, 1993) that mime the overfishing effects (Libralato et al., 2004). Observed changes in biomasses, catches, FIB and PPR, however, seemed not to have influenced the Kempton's Q diversity index that shows relative stability over time (Fig. 6) suggesting rearrangement of species densities and interactions in a way to maintain system biodiversity, possibly indicating that the system as a whole is still resilient to large driver changes. A completely different question is for how long this increasingly fragile ecosystem will be showing such resilience unless some adequate management measures are implemented.

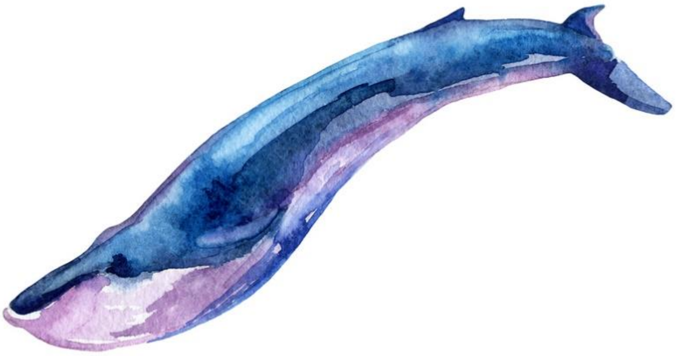
5. Conclusion

The construction of a food web model enabled us to assess and quantify changes in the structure of the Amvrakikos ecosystem and the cumulative impacts of the major factors affecting the system. Our results highlighted a general degradation of the demersal compartments of the food web and a relative stability of the pelagic ones mainly due to high eutrophication levels, which was confirmed by ecological indicators. The notorious degradation of the Gulf of Amvrakikos, particularly acute during the past 20 years, calls for action and is urgently needed if we want to preserve this increasingly fragile ecosystem. In order to produce a more accurate picture of the ecosystem dynamics of the Gulf, future initiatives should be dedicated to improve data deficiencies and to farther develop temporal simulations. Robust hind cast simulations are necessary in order to forecast ecosystem dynamics and explore different management policies and future scenarios.

See original publication in Annex 3

Chapter 2.4

Modelling the Mediterranean Sea ecosystem



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Modelling the Mediterranean marine ecosystem: addressing the challenge of complexity.

Modelización del ecosistema marino del Mediterráneo: abordando el desafío de la complejidad.

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Abstract

An ecosystem modelling approach was used to understand and assess the Mediterranean marine ecosystem structure and function as a whole. In particular, 2 food web models for the 1950s and 2000s were built to investigate: (1) the main structural and functional characteristics of the Mediterranean food web during these 2 time periods; (2) the key species/functional groups and interactions; (3) the role of fisheries and their impact; and (4) the ecosystem properties of the Mediterranean Sea in comparison with other European regional seas. Our results show that small pelagic fishes, mainly European pilchards and anchovies, prevailed in terms of biomasses and catches during both periods. Large pelagic fishes, sharks and medium pelagic fishes played a key role in the 1950s ecosystem, and have been replaced in more recent years by benthopelagic and benthic cephalopods. Fisheries showed large effects on most living groups of the ecosystem in both time periods. When comparing the Mediterranean results to those of other European regional seas modelling initiatives, the Mediterranean stood alone in relation to the type of flows (e.g. Mediterranean Sea, flow to detritus: 42%; other EU seas, consumption: 43–48%) driving the system and the cycling indices. This suggested higher levels of community stress induced by intensive fishing activities in the Mediterranean basin. This study constitutes the first attempt to build an historical and current food web model for the whole Mediterranean Sea.

Resumen

En este estudio se ha utilizado un enfoque de modelización ecológica basado en el ecosistema para describir y evaluar la estructura del ecosistema marino del Mediterráneo en su conjunto. En particular, se han desarrollado dos modelos de redes tróficas representativos de los años 1950 y 2000 y se han analizado: (1) las principales características estructurales y funcionales de la red trófica del Mediterráneo durante estos dos períodos de tiempo; (2) las especies / grupos e interacciones tróficas clave; (3) el rol de la pesca y su impacto; y (4) las propiedades ecológicas del ecosistema marino del Mediterráneo en comparación con las que presentan otros mares europeos. Los resultados muestran que los peces pelágicos de tamaño pequeño, principalmente sardinas y anchoas, prevalecen en términos de biomasa y capturas durante ambos períodos. Además, los peces pelágicos de gran tamaño, los tiburones y los peces pelágicos de tamaño medianos juegan un rol ecológico clave en el ecosistema durante los años 1950, y este rol se ve sustituido en los últimos años por los peces bentopelágicos y los cefalópodos bentónicos. La actividad pesquera tiene un impacto importante en la mayoría de los grupos ecológicos del modelo en ambos períodos. Al comparar los resultados del Mediterráneo con los de otras iniciativas de modelización de mares europeos, los resultados muestran la singularidad del mar Mediterráneo en relación con el tipo de flujos tróficos del sistema y el reciclaje de materia y energía (por ejemplo, el mar Mediterráneo, el flujo trófico hacia los detritos es de 42% en relación con el total, en otros mares de la UE el consumo es de 43-48%). Estos resultados evidencian un nivel mayor de estrés en el ecosistema Mediterráneo causado por las actividades pesqueras, muy intensas en esta región. El estudio constituye el primer intento de desarrollar un modelo de red trófica marina del ecosistema del Mediterráneo en su conjunto representativa de una época pasada y presente.

Introduction

Marine ecosystem models have been progressively employed worldwide to investigate the structure and functioning of marine systems and the effects of anthropogenic pressures such as fishing, climate change and pollution on marine ecosystems (Christensen & Walters 2004, Shin et al. 2004, Fulton 2010). Understanding the mechanisms behind diverse ecological networks (e.g. trophic interactions and flows) and the roles of human activities on marine structure and function is critical when managing marine resources (Cury et al. 2003). The development of ecosystem models to explore ecosystem functions and responses to anthropogenic and/or environmental changes has been driven by the so called 'ecosystem-based management' (EBM) approach, which aims at managing the whole ecosystem rather than focusing on a single resource, helping researchers and policy makers to answer questions for responsible resource management decisions (Pikitch et al. 2004). Currently, among the most used ecological modelling tools for EBM in the aquatic environment is the software package 'Ecopath with Ecosim' (EwE, Christensen & Walters 2004; www.ecopath.org). EwE models have been widely used to describe the structure and functioning of marine ecosystems, evaluate the effects of anthropogenic activities and environmental changes and explore fishing management policy options (Coll et al. 2009a, Piroddi et al. 2011, Heymans et al. 2012). Here we applied the EwE approach to describe and assess the Mediterranean marine ecosystem structure and functioning as a whole.

The Mediterranean Sea is a semi-enclosed basin with unique characteristics: it is oligotrophic (Barale & Gade 2008), highly diverse in species richness (Coll et al. 2010) and yet is considered a sea 'under siege' due to multiple uses and stressors (Coll et al. 2012). Twenty-one countries in Europe, Asia and Africa surround and share this enclosed sea. Their different cultural, social and economic characteristics pose significant challenges to sustainable management of Mediterranean marine resources. As a consequence of this complexity and lack of management strategies that take this complexity into account, the Mediterranean ecosystem has degraded, and many marine species are overexploited or depleted (Papaconstantinou & Farrugio 2000, Lleonart & Maynou 2003, Colloca et al. 2013, Tsikliras et al. 2013b, Vasilakopoulos et al. 2014).

Thus, there has been an urgent need to employ EBM as a complementary management framework to address current and future threats to the Mediterranean marine ecosystems. Several research activities have already been conducted in the region to address this issue at the basin scale. In particular, Coll et al. (2012) and Micheli et al. (2013) investigated the cumulative impacts of specific anthropogenic threats to Mediterranean marine biodiversity. Here, we applied a different approach, that is, the description of the structure and functioning of the whole Mediterranean ecosystem in terms of trophic linkages, trophic flows and biomasses, and between 2 post-World War II decades. Compared to Coll et al. (2012) and Micheli et al. (2013), who used spatial analysis and expert knowledge to assess the impacts on the ecosystem, our study quantifies the trophic interactions and effects of pressures (e.g. in this case fishing) occurring in the whole area, using the best available data to date.

A recent study by Coll & Libralato (2012) highlighted that more than 40 EwE models describing local or regional Mediterranean ecosystems exist (including lagoons, marine reserves and coastal and shelf areas), but none of these past efforts focussed on the Mediterranean Sea as a whole. This is likely due to the complexity of building such an ecosystem model while being able to capture the differences in environmental and biological characteristics of the Mediterranean region, and due to difficulties regarding data mining and integration.

Therefore, our study is the first attempt to comprehensively model the Mediterranean basin. Studies like this one become critically important in support of policies like the Marine Strategy Framework Directive (MSFD; 2008/56/EC), the main European Directive on marine waters that requires the assessment of all European seas at regional scales in relation to their ecosystem status and associated pressures, and the establishment of environmental targets (through the use of indicators) to achieve 'Good Environmental Status' by 2020 (Cardoso et al. 2010).

Specifically, in this study we investigated (1) the main structural and functional characteristics of the Mediterranean food web during 2 different time periods, i.e. the 1950s and 2000s; (2) the key species/ functional groups and interactions for both time periods; (3) the role of fisheries and their effects; and (4) the ecosystem properties of the

Mediterranean Sea in comparison with other European regional seas, namely the North Sea, Baltic Sea and Black Sea, which have already been modelled at the regional basin scale (Tomczak et al. 2012, 2013, Akoglu et al. 2014, Mackinson 2014).

Materials and methods

Mediterranean Sea

The Mediterranean Sea extends from 30° to 45° N and from 6° W to 36° E, and constitutes the world's largest (2 522 000 km^2) and deepest (average 1460 m, maximum 5267 m) enclosed sea. It is connected to the Atlantic Ocean via the Strait of Gibraltar in the west, to the Black Sea via the Bosporus and the Dardanelles in the north-east, and to the Red Sea via the Suez Canal in the south-east (Fig. 1). Overall, the basin is considered oligotrophic with some exceptions along coastal areas due mainly to river discharges (Barale & Gade 2008) and frontal mesoscale activity (Siokou-Frangou et al. 2010). Phosphorus, rather than nitrogen, is the limiting nutrient, especially towards the eastern basin (Krom et al. 1991). Biological productivity decreases from north to south and west to east, whereas an opposite trend is observed for temperature and salinity. In particular, the mean sea surface temperature varies between a minimum of 14–16°C (west to east) in winter and a maximum of ca. 20–26°C (west to east) in the summer (with the exception of the shallow Adriatic Sea, where the range is between 8–10°C in winter and 26–28°C in summer) (Barale & Gade 2008). Evaporation greatly exceeds precipitation, and river runoff decreases from west to east, causing sea surface height to decrease and salinity to increase eastward (Coll et al. 2010). The Mediterranean Sea has a topographically diverse continental shelf that generally varies from south (mainly narrow and steep) to north (wider areas). In some instances, however, narrow shelves can also be found on some coasts of Turkey, in the Aegean, Ligurian and northern Alboran Seas, while extended shelves are also present on the Tunisian shelf and near the Nile Delta (Pinardi et al. 2006). Shelf waters represent 20% of the total Mediterranean surface, and the rest is open sea (Coll et al. 2010).

Mediterranean marine species richness is relatively high; to date, approximately 17 000 species have been recorded in the Mediterranean Sea, with a gradient of species richness that decreases from northwest to southeast (Bianchi & Morri 2000, Coll et al.

2010, 2012). Of these 17 000 species, at least 26% are prokaryotic (Bacteria and Archaea) and eukaryotic (protists) marine microbes. The phytoplankton community is composed predominantly of coccolithophores, dinoflagellates and Bacillariophyceae and includes more than 1500 species. Among microzooplankton, foraminiferans comprise the main group, with more than 600 species. However, the majority of species are described within the Animalia (~11 500 species), with the greatest contribution coming from the Crustacea (13.2%) and Mollusca (12.4%) (Coll et al. 2010). Among the vertebrates, 650 species of marine fishes have been recorded, of which approximately 80 are elasmobranchs and the rest are mainly actinopterygians (86%) (Coll et al. 2010). Nine species of marine mammals (5 Delphinidae, 1 Ziphiidae, 1 Physeteridae, 1 Balaenopteridae and 1 Phocidae) and 3 species of sea turtles (the green turtle *Chelonia mydas*, the loggerhead *Caretta caretta* and the leatherback *Dermochelys coriacea*) are encountered regularly in the Mediterranean Sea. Among seabirds, 15 species frequently occur in the Mediterranean Sea, including 10 gulls and terns (Charadriiformes), 4 shearwaters and storm petrels (Procellariiformes) and 1 shag (Pelecaniformes) (Coll et al. 2010).

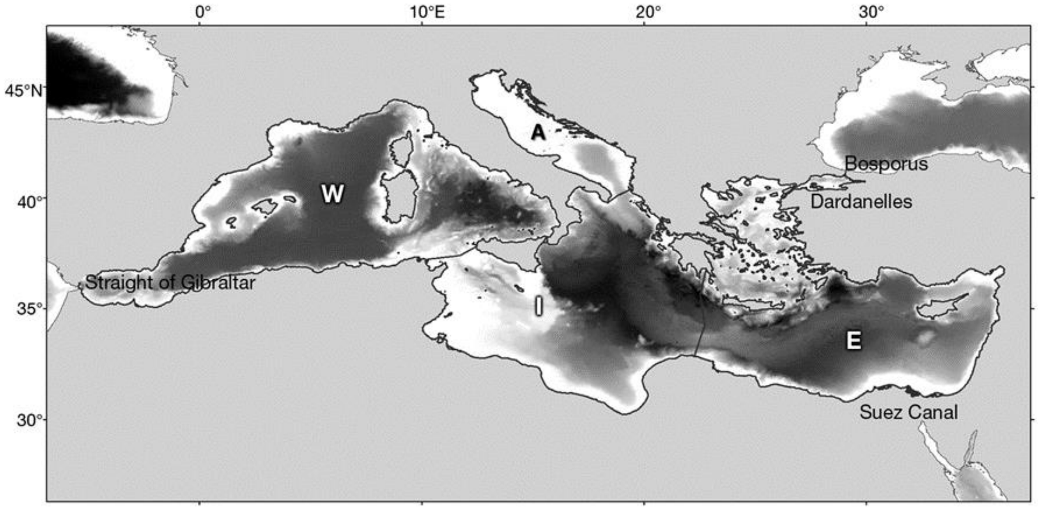


Fig. 1. Mediterranean Sea, showing depth profile (darker shading indicates greater depth) and the 4 Marine Strategy Framework Directive (MSFD) areas: Western Mediterranean Sea (W); Adriatic Sea (A); Ionian and Central Mediterranean Sea (I); Aegean and Levantine Sea (E).

Ecosystem modelling approach

Two food web models of the entire Mediterranean Sea were constructed using the EwE software version 6 (Christensen et al. 2008) representing annual average biomasses and trophic flows for the 1950s and the 2000s. The analysis was restricted to Ecopath, the static component of the software that describes the ecosystem and its resources at a precise period in time (Christensen & Walters 2004). In Ecopath, all principal autotroph and heterotroph species can be represented either individually or aggregated into functional groups considering their ecological roles.

The EwE model is based on 2 main equations. In the first one, the biological production of a functional group is equal to the sum of fishing mortality, predation mortality, net migration, biomass accumulation and other unexplained mortality as follows:

$$(P/B)i \cdot Bi = Yi + \sum j \, [Bj \cdot (Q/B)\, j \cdot DCji\,] + Ei + BAi + (P/B)\, i \cdot Bi\,(1 - EEi) \qquad (1)$$

where P/B is the production to biomass ratio for a certain functional group i, Bi is the biomass of a group i, Yi is the total fishery catch rate of group i, (Q/B)j is the consumption to biomass ratio for each predator j, DCji is the proportion of group i in the diet of predator j, Ei is the net migration rate (emigration − immigration), BAi is the biomass accumulation rate for the group i, EEi is the ecotrophic efficiency, and (1 − EEi) represents mortality other than predation and fishing.

In the second equation, the consumption (Q) of a functional group (i) is equal to the sum of production (P), respiration (R) and unassimilated food (GS · Q).

$$Qi = Pi + Ri + GSi \cdot Qi \qquad (2)$$

The implication of these 2 equations is that the model is mass balanced; under this assumption, Ecopath uses and solves a system of linear equations (1 for each functional group present in the system) estimating the missing parameters. To ensure the mass balance, we applied a manual mass-balanced procedure following a top-down approach, adjusting the input parameters of those groups ‘out of balance’ (EE > 1), occurring when total energy demand placed on those groups either by predation or fishing exceeds total production. In particular, we changed those parameters associated with higher uncertainty, i.e. diet matrix, P/B and, to a lesser extent, biomass (Christensen & Walters 2004). The ecological models were considered balanced when (1) estimated EE values were <1; (2) gross food conversion efficiency (P/Q) was < 0.5; and (3) respiration over assimilation (R/A) was <1 (Christensen & Walters 2004).

Parameterization and functional groups

Two food web models were constructed for the decades of 1950 and 2000, respectively. The reason for choosing these 2 time periods was related to best data collection in the case of the last decade and available catch time series (starting in the 1950s) and biogeochemical/stock assessment model outputs (e.g. biomasses for phytoplankton and fish stocks) for the first decade. To best represent the entire Mediterranean Sea ecosystem, while still considering sub-regional differences in environmental and biological characteristics, both models were divided in 4 sub-models following the 4 sub-regional divisions defined by the Marine Strategy Framework Directive (MSFD; 2008/56/EC): (1) Western Mediterranean Sea (W); (2) Adriatic Sea (A); (3) Ionian and Central Mediterranean Sea (I); (4) Aegean and Levantine Sea (E) (Fig. 1).

To separate each MSFD area within the full single Mediterranean model, we assigned a habitat area which corresponds to the fraction of the total area where the functional groups occur. In particular, if a functional group occurs throughout the total Mediterranean Sea, the biomass is scaled by a factor of 1; otherwise biomass is scaled by the fraction of the Mediterranean Sea area occupied (see Tables S1 & S2 in the Supplement Materials). To define functional groups, we used all available data to parameterize the model and ecological traits of species to establish the groups (see Tables S1−S4 in the Supplement).

We divided marine mammals into 'piscivorous cetaceans' (mainly dolphins), 'other cetaceans' (mainly whales) and 'pinnipeds' (monk seal *Monachus monachus*). Fishes were divided into 'sharks', 'rays and skates', 'deep-sea fishes' (mainly mesopelagic, bathypelagic and bathydemersal), pelagic fishes and demersal fishes. Pelagic and demersal fishes were further divided in 'small' (common total length < 30 cm), 'medium' (30−89 cm) and 'large' (≥ 90 cm) following a similar approach used by Christensen et al. (2009), which simplified the definition of the fish groups (e.g. piscivores, benthivores and herbivores) in the model parameterization but still considered fish based on their asymptotic length, feeding habitats and vertical distribution characteristics. Invertebrate species were separated into 'benthopelagic' and 'benthic cephalopods', 'bivalves and gastropods', 'crustaceans', 'jellyfishes', 'benthos' and ‘zooplankton’. Primary producers were divided in ‘phytoplankton’ and ‘seagrass’.

Each MSFD area had the same functional group categories except for highly migratory species such as the ‘other cetaceans’ group, the ‘large pelagic fishes’ (e.g. tuna species and swordfish *Xiphias gladius*) and the ‘sea turtles’ that were allowed to move and feed in all 4 areas. ‘European hake’ *Merluccius merluccius*, ‘European pilchard’ *Sardina pilchardus* and ‘European anchovy’ *Engraulis encrasicolus* were considered individually due to their importance as commercial species, and thus individual groups were created to represent these species within the model. A total of 103 functional groups were described to represent the whole Mediterranean Sea model.

For each group, 5 input parameters were estimated: biomass (B), production rate per unit of biomass (P/B), consumption rate per unit of biomass (Q/B), diet composition (DC) and fisheries catch rate (Y). The biomass of each functional group, expressed as tonnes (t) of wet weight per km^2, was obtained from field surveys, estimated from empirical equations of population reconstruction or assessed by biogeochemical models. For the scope of this work, we searched mainly for data available at regional scales (either from survey campaigns or from other model outputs), and when this information was not available, local case studies were used instead (e.g. ‘seagrass’ biomass; see Tables S1 & S2 in the Supplement). For the 1950s model, which lacked surveyed data, the biomasses of commercially important groups (functional groups 6 to 21 in Table 1) were estimated from stock assessments (e.g. International Commission for the Conservation of Atlantic Tunas ICCAT; https://www. iccat.int/en/pubs_CVSP.htm for the large pelagic fishes) or by applying a logistic growth model (Schaefer 1954) as in previous studies (Walters et al. 2008, Piroddi et al. 2010). In particular, this last method, also called surplus production model, expressed as:

$$Nt + 1 = Nt + rNt\,(1 - Nt/k) - Ct \qquad (3)$$

allows estimating the size of a given population/stock (N) at certain time (t) knowing the historical catch time series (Ct), the intrinsic rate of population growth (r; obtained from Fishbase, Froese & Pauly 2010) and the carrying capacity (k).

‘Phytoplankton’ biomass was taken from the outputs of a biogeochemical model developed for the entire Mediterranean Sea (Macias et al. 2014), while ‘zooplankton’ was obtained from a global database available from the National Oceanic and Atmospheric Administration (www.st.nmfs.noaa.gov). For the other functional groups, information was available either through the literature (e.g. 'pinnipeds' and 'sea turtles') or reconstructed from global databases (e.g. seabird biomass from the Sea Around Us Project; www.seaaroundus.org). The P/B and Q/B ratios were estimated using empirical equations (Christensen et al. 2008) or taken from the literature and were expressed as annual rates (t km^{-2} yr^{-1}) (Tables S1 & S2 in the Supplement).

A diet composition matrix was constructed using either field studies (e.g. stomach contents) or diet data obtained from the literature for the same species in similar ecosystems (Table S3 in the Supplement). For highly migratory species ('large pelagic fishes', 'other cetaceans' and'sea turtles') and 'seabirds' groups, we accounted for a percentage of the diet being outside the marine ecosystem, assuming that those species also move outside the studied system for feeding (Coll et al. 2006, 2007, Christensen et al. 2008, Piroddi et al. 2010). In some instances, we integrated parameters (B, DC, P/B and Q/B) from previously built EwE models for different areas of the Mediterranean Sea (Adriatic Sea: Coll et al. 2007, 2009c; Catalan Sea: Coll et al. 2006, 2008, Tecchio et al. 2013; Ionian Sea: Piroddi et al. 2010, 2011, Moutopoulos et al. 2013; Aegean Sea: Tsagarakis et al. 2010; Gulf of Lions: Banaru et al. 2013; Tunisia: Hattab et al. 2013). In particular, the output of these models was used as a starting point for the reconstruction of those parameters for which information was lacking. Detailed descriptions of the functional groups and data used to parameterize the model are given in Tables S1−S5 in the Supplement.

The official landing data by species and by country were taken from the United Nation's Food and Agriculture Organization (FAO) database (FishStat: http:// data.fao.org/database?entryId=babf3346-ff2d-4e6c- 9a40-ef6a50fcd422) and available from 1950 to 2010. This time series was then complemented with data (available per country) from the Sea Around Us database (www.seaaroundus.org) to assign species to fishing fleet. We considered 6 commercial fisheries defined by gear types: bottom trawlers, bottom dredges, mid-water trawlers, purse seiners, long liners and the artisanal fisheries.

Table 1. Functional groups and fisheries included in the models together with their abbreviations.

No.	Functional groups/fisheries	Abbreviation
1	Piscivorous cetaceans	PC
2	Other cetaceans	OC
3	Pinnipeds	PI
4	Seabirds	SB
5	Sea turtles	ST
6	Large pelagic fishes	LP
7	Medium pelagic fishes	MP
8	European pilchard	EP
9	European anchovy	EA
10	Other small pelagic fishes	SP
11	Large demersal fishes	LD
12	European hake	HK
13	Medium demersal fishes	MD
14	Small demersal fishes	SD
15	Deep-sea fishes	DF
16	Sharks	SK
17	Rays and skates	RS
18	Benthopelagic cephalopods	BPC
19	Benthic cephalopods	BC
20	Bivalves and gastropods	BG
21	Crustaceans	CR
22	Jellyfish	JF
23	Benthos	BE
24	Zooplankton	ZO
25	Phytoplankton	PH
26	Seagrass	SE
27	Discards	DS
28	Detritus	DE
29	Trawlers	TR
30	Dredges	DR
31	Mid-water trawlers	MT
32	Purse seiners	PS
33	Long liners	LL
34	Artisanal fisheries	AR
35	Recreational fisheries	RC

Species were assigned to the following gear types by assuming the same proportion per year as observed in the Sea Around Us database (data accessed in November 2013). In the case of Italy, which is surrounded by 3 of the 4 MSFD areas, we used a detailed reconstruction of catches (Piroddi et al. 2014) available for sub-regional seas (MFSD area: [1] Ligurian; [2] Northern, Central and Southern Tyrrhenian; [3] Ionian; [4] Northern, Central and Southern Adriatic Sea; [3] Sicilian; and [4] Sardinian waters), while for Greece, which has waters both in the Ionian and in the Eastern Mediterranean Sea, we used the same proportions as calculated by Tsikliras et al. (2007, 2013a).

A recreational fishery was also included in the analysis using data coming from the Sea Around Us database (in the case of Italy and Spain) and from literature reviews (Anagnopoulos et al. 1998, Gordoa et al. 2004, Pawson et al. 2007, Cisneros-Montemayor & Sumaila 2010). We estimated the percentage of discards and the species discarded using reports and scientific papers available in the literature (Megalofonou 2005, EC 2011, Vassilopoulou 2012, Tsagarakis et al. 2013) and data from previous EwE Mediterranean models available cited above. Fisheries landings and discards, expressed as annual rates (t km^{-2} yr^{-1}), for both models and for each sub-region are shown in Tables S8–S11 in the Supplement. A list of functional groups and fisheries included in both models, together with their abbreviations, is given in Table 1 and in Table S5.

Pedigree index and model quality

The pedigree of the data refers to the uncertainty associated with the input values of the model. In general, higher pedigrees are associated with higher levels of data quality and with data coming from the study areas. Ecopath can take the pedigree values for all of the data entered in the model (e.g. biomass, P/B, Q/B, diets) into account and can calculate an overall pedigree index, ranging from 0 to 1. Lower pedigree values imply a model constructed with low precision data and with data coming from areas outside the studied region, while higher values indicate a model constructed with locally derived data (Morissette 2007, Christensen et al. 2008). Thus, to assess the quality of our input data, we calculated the overall pedigree index for both models. In addition, the pedigree was also used to guide the balancing procedure of both models, such that the lower pedigree inputs were the first to be modified while balancing the models.

Model analysis and indices

Trophic flows in terms of total production, consumption, respiration, catches and flow to detritus were estimated to represent ecosystem structure and exploitation status (Odum 1969, Ulanowicz 1986, Christensen & Pauly 1993). In particular, the following indicators were evaluated: (1) Total system throughput (TST), calculated as the sum of all flows as an indication of the whole ecosystem size. (2) Total primary production/total system respiration (TPP/TR) and total primary production/total biomass (TPP/TB), as a metric of system maturity. (3) Finn’s cycling index (FCI), as the percentage of flows recycled in the food web (Finn 1976), and the predatory cycling index (PCI), as the percentage of production recycled after the removal of detritus (Christensen et al. 2008). (4) Ascendancy (A), as a measurement of system growth and development of network links (Monaco & Ulanowicz 1997). (5) Overhead (O), as the energy in reserve of an ecosystem that reflects the system’s strength when it experiences unexpected perturbations (Ulanowicz 1986). (6) System omnivory index (SOI), based on the average omnivory index (OI), which is calculated as the variance of the trophic levels (TLs) of a consumer’s prey groups indicating predatory specialization (Christensen & Pauly 1993). (7) Mean transfer efficiency (TE), as the efficiency in which energy is transferred between TLs. The mean TE is calculated as the geometric mean of TE for each of the integer TLs

II to IV. (8) TL of each functional group expressed as:

$$TL_j = 1 + \sum_{i=1}^{n} DC_{ji} \cdot TL_i \qquad (4)$$

where j is the predator of prey i, DCji is the fraction of prey i in the diet of each predator j, and TLi is the TL of prey i. By definition, TL I is attributed to primary producers and detritus, TL II to herbivores, TL III to first order carnivores and TL IV to second-order carnivores. (9) TL of the catches (TLC), as:

$$TL_{Ci} = \frac{\sum_{i=1}^{n} TL_i \cdot Y_i}{\sum_{i=1}^{n} Y_i} \qquad (5)$$

where Yi refers to the landings of species (group) i.

(10) Primary production required (PPR) to sustain the catch, to evaluate the sustainability of fisheries (Pauly & Christensen 1995).

To better represent trophic flows, TLs and biomasses of the Mediterranean marine ecosystem, we used 2 different graphical representations: a flow diagram and a Lindeman spine (Lindeman 1942, Ulanowicz 1995). In the Lindeman spine, primary producers and detritus (both with TL = 1) were separated to better represent the different flows going to the different compartments. To highlight differences in total biomass and mean TL of the community, we also plotted these 2 variables for each MSFD area for the 2 time periods.

Mixed trophic impact and keystone species analyses

The mixed trophic impact (MTI) analysis, expressed as:

$$MTIij = DCij - FCji \qquad (6)$$

where DCij is the diet composition term expressing how much j contributes to the diet of i, and FCji is the proportion of predation on j that is due to i as a predator, allows the quantification of the impacts that a theoretical change of a unit in the biomass of a group (including fishing activities) would have on other groups in the ecosystem (Christensen et al. 2008). It can assess both direct and indirect trophic impacts in the food web, which are either positive or negative, indicating an increase or decrease in the quantity of the affected group. Here we looked at the MTI for each MSFD area and for the 2 different time periods. In addition, and building from the MTI analysis, the keystoneness index (KS) assesses the potential roles of each functional group as keystones in the system. Normally, keystone species are species with a relative low biomass but whose biomass changes would have a disproportionately large effect on the ecosystem structure (Power et al. 1996). Here, for both time periods, we used the index proposed by Libralato et al. (2006):

$$KS_i = \log(\varepsilon_i \times 1/p_i) \quad (7)$$

where ε_i is the overall effect expressed as the square root of the sum of mij square (with mij being the relative impact of a slight increase in biomass of impacting group i on biomass of impacted group j), and pi is the contribution of the functional group to the total biomass of the food web.

Comparison with other European regional seas models

In an effort to support the MSFD, we compared a selection of ecological, fishing and network analysis indicators derived from the Mediterranean Sea model with those obtained from Ecopath models built for other European regional seas: the North Sea (Mackinson 2014), the Baltic Sea (Tomczak et al. 2012, 2013) and the Black Sea (Akoglu et al. 2014). This comparative analysis was done to obtain an overview, at the European scale, of similarities and differences between these exploited ecosystems. We are aware that a few limitations in confronting these models may occur due to differences in model criteria and construction (e.g. definition of certain groups, time periods), and for this reason we present model results with structural differences of the models for a better interpretation of the analysis. In addition, only those indicators more robust to model configurations (e.g. TST, mean TL of the catch, PPR to sustain fisheries, ascendancy and overhead; see Table 2 for the complete list of indicators), as previously assessed by Moloney et al. (2005) and Heymans et al. (2014), were used for the comparison.

Results

Functional group input, data quality and mass balancing

Each MSFD area had 26 living groups (i.e. excluding detritus and discards), if we also consider the 3 migratory groups as part of each area.

Of those 26 groups, the main mass balancing problems were encountered among 'other small' and 'medium' pelagic fishes, 'small' and 'medium' demersal fishes, 'European pilchard' and 'anchovy', 'benthopelagic cephalopods', 'crustaceans', 'benthos' and 'zooplankton', with EE values >1. To obtain mass balance for these groups, we primarily adjusted the diet matrix as the data source with higher uncertainty. For instance, the predation caused by 'large pelagic fish' on 'European pilchard' and 'anchovy', 'medium' and 'other small' pelagic fishes and 'benthopelagic predators' diets. Biomasses of 'crustaceans' and 'bivalves and gastropods' were the only biomasses that were modified from the original input data. The biomasses of these groups were indeed too low and had to be increased. This is a common problem in prebalanced EwE models, where invertebrate biomass estimates are frequently too low to support predation mortality (Christensen et al. 2008).

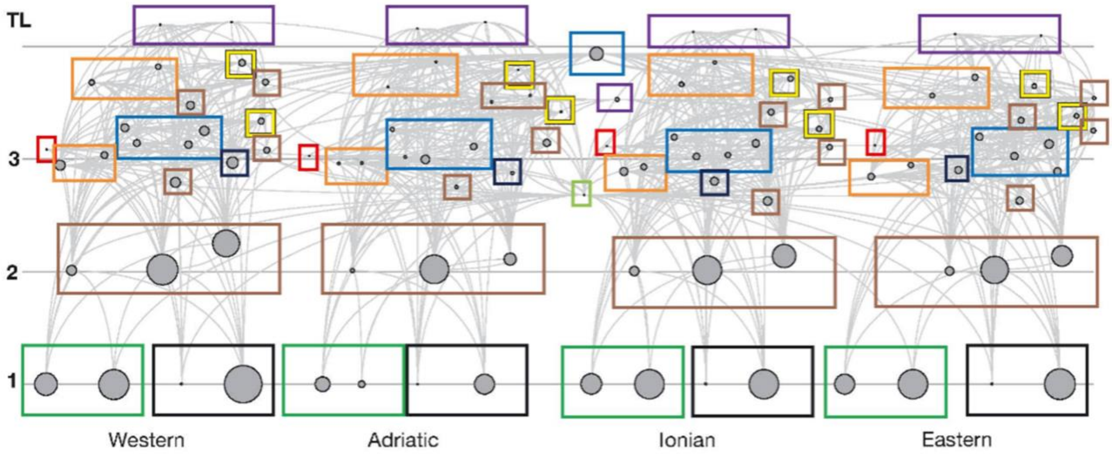


Fig. 2. Flow diagram of the Mediterranean Sea ecosystem (in the 2000s) with the Western part being at the far left followed by the Adriatic, the Ionian and the Eastern (see Fig. 1). Each functional group is shown as a circle whose size is approximately proportional to the log of its biomass. All functional groups are represented by their trophic levels (TL; y-axis) and linked to each other by predator–prey relationships expressed as light grey lines. Coloured boxes define the main functional groups: marine mammals (purple); pelagic fishes (blue); demersal fishes (orange); sharks/rays and skates (yellow); deep-sea fishes (dark blue); seabirds (red); invertebrates (brown); sea turtles (light green); primary producers (dark green); detritus groups (black). Individual flow diagrams of the 4 Marine Strategy Framework Directive (MSFD) areas are presented in Table S6.

Once balanced, EE values were high for the majority of the functional groups, indicating that total mortality in the system was mainly driven by predation and fishing. The gross food conversion efficiency (P/Q) and the respiration over assimilation (R/A) were within the expected ranges (Christensen et al. 2008).

The resulting output parameters and the final diet matrix are shown for each model in Tables S1−S4 in the Supplement. Pedigree indices were different for each time period and increased from the 1950s (0.391) to the 2000s (0.594). Individual results of the pedigree index can be found in Table S7 in the Supplement.

TLs and flows

Trophic flows, TLs and relative biomasses of the Mediterranean Sea ecosystem for the 2000s model are represented in Fig. 2 and in Table S6 (flow diagrams) in the Supplement. In the latter, flow diagrams are separated for each MSFD area. Functional groups are illustrated by their TLs ranging from 1 (primary producers) to 4.22 (marine mammals); the highest TLs were found for 'piscivorous cetaceans' and 'monk seals' (TL ≥ 4). The other marine mammal group, 'other cetaceans', showed a TL of 3.53 (mainly because of the presence of 'zooplankton' and 'benthopelagic cephalopods' in their diet). 'Seabirds', despite being considered a top predator, showed a relatively low TL due to the presence of discards (mainly small pelagic fishes, Oro & Ruiz 1997, Bozzano & Sardà 2002) in their diet. Similarly, 'sea turtles' might have a higher TL than estimated by the model, but their diet also includes discards (Tomas et al. 2001, Gómez de Segura et al. 2003, Casale et al. 2008), and thus, they presented a fairly low TL (2.68) in the model. This is an artifact of EwE that considers discards as a detritus group with TL = 1 and thus tends to lower the TL of those groups that feed considerably on discards (Christensen et al. 2008), as previously seen in other food web models of Mediterranean areas (Coll et al. 2006, 2007, Piroddi et al. 2010). For the fish groups, 'large pelagic fishes' showed a relatively high TL (3.94), followed by 'European hake' (between 3.86 and 3.73), 'large demersal fishes' (between 3.68 and 3.56), 'sharks' (between 3.85 and 3.64) and 'rays and skates' (between 3.41 and 3.27). 'Medium' and 'other small' pelagic fishes were given a TL between 3.28 and 3.19 and between 3.14 and 2.89, respectively. 'European pilchard' and 'European anchovy' had TL values ranging between 3.25 and 3, while the lowest TLs were observed for 'medium' and 'small' demersal fishes and 'deep-sea fishes' (between 3.04 and 2.80). Of the remaining functional groups, 'benthopelagic' and 'benthic cephalopods' and 'jellyfish' reached TL> 3, 'crustaceans' showed values between 2.79 and 2.63, and 'zooplankton', 'bivalves and gastropods' and 'benthos' had

TL values close to 2. Looking at the 4 MSFD areas, comparing total biomass and mean TL of the community, the Adriatic and the Western Mediterranean Sea were the areas with the highest total biomass, followed by the Ionian and Eastern Seas (Fig. 3). During the 2000s, the mean TL of the community (TLco) differed considerably whether calculated using TLco ≥ 1 or TLco > 1 (i.e. excluding detritus and primary producers). For TLco≥ 1, the Adriatic was the area with highest mean TLco (1.86) followed by the Ionian (1.56), Eastern (1.5) and Western Mediterranean (1.49). For TLco > 1, the Western had the highest TLco (2.36), followed by the Eastern (2.34), Ionian (2.28) and Adriatic Seas (2.18) (Fig. 3). Several differences in TLs were also found between the 2 modelled time periods, with declines observed particularly in the Ionian and Eastern Mediterranean Sea in the 2000s compared to the 1950s (Fig. 4). However, to be able to assess changes in TL of the community in the Mediterranean Sea, a more accurate analysis is needed (such as fitting the model to time series data that will reduce the noise around the parameters; Christensen & Walters 2004).

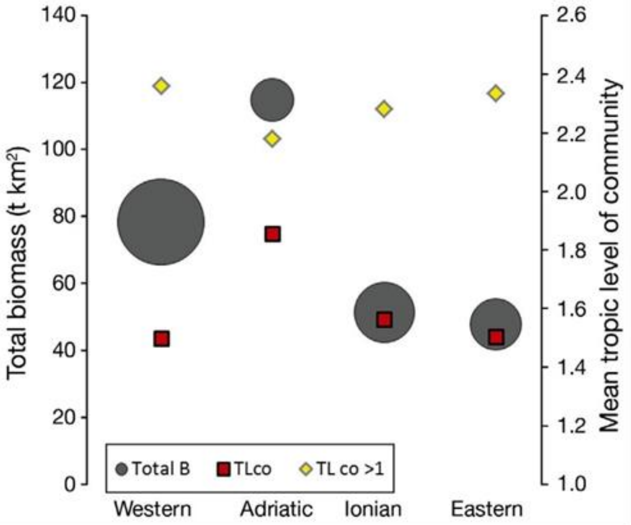
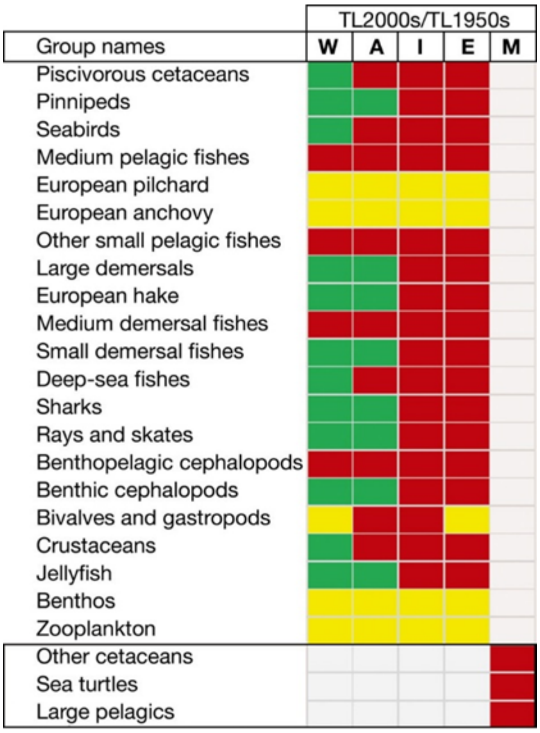


Fig. 3. Total biomass and mean trophic level of the community (TLco) with and without detritus and primary producers (TLco > 1) for each MSFD area (see Fig. 1) for the 2000s. Total biomass is shown as a circle whose size is proportional to the area of the MSFD.



	TL2000s/TL1950s				
Group names	W	A	I	E	M
Piscivorous cetaceans	🟩	🟥	🟥	🟥	⬜
Pinnipeds	🟩	🟩	🟥	🟥	⬜
Seabirds	🟩	🟥	🟥	🟥	⬜
Medium pelagic fishes	🟥	🟥	🟥	🟥	⬜
European pilchard	🟨	🟨	🟨	🟨	⬜
European anchovy	🟨	🟨	🟨	🟨	⬜
Other small pelagic fishes	🟥	🟥	🟥	🟥	⬜
Large demersals	🟩	🟩	🟥	🟥	⬜
European hake	🟩	🟩	🟥	🟥	⬜
Medium demersal fishes	🟥	🟥	🟥	🟥	⬜
Small demersal fishes	🟩	🟩	🟥	🟥	⬜
Deep-sea fishes	🟩	🟥	🟥	🟥	⬜
Sharks	🟩	🟩	🟥	🟥	⬜
Rays and skates	🟩	🟩	🟥	🟥	⬜
Benthopelagic cephalopods	🟥	🟥	🟥	🟥	⬜
Benthic cephalopods	🟩	🟩	🟥	🟥	⬜
Bivalves and gastropods	🟨	🟥	🟥	🟨	⬜
Crustaceans	🟩	🟥	🟥	🟥	⬜
Jellyfish	🟩	🟩	🟥	🟥	⬜
Benthos	🟨	🟨	🟨	🟨	⬜
Zooplankton	🟨	🟨	🟨	🟨	⬜
Other cetaceans	⬜	⬜	⬜	⬜	🟥
Sea turtles	⬜	⬜	⬜	⬜	🟥
Large pelagics	⬜	⬜	⬜	⬜	🟥

Fig. 4. Changes in trophic levels (TLs) between the 1950s and the 2000s for each functional group for each Marine Strategy Framework Directive (MSFD) area (W: Western; A: Adriatic; I: Ionian/Central; E: Aegean/Levantine) and the whole Mediterranean Sea (M: Mediterranean). Green cells represent increased TLs (> 0), yellow cells indicate stable TLs (=0), and red cells show decreased TLs (< 0). Grey cells indicate 'not applicable'.

In the Lindeman spine analysis (Fig. 5), similar patterns were observed for both time periods. Most trophic flows fell within TL I, II and III, and TL I was the pool that generated the majority of the total system throughput (1950s: 78.4% and 2000s: 79.3%) followed by TL II, with 20.2% for the 1950s and 19.6% for the 2000s. In both time periods, primary producers and TL II organisms had the highest biomasses, and comparing the 2 decades, a decline in biomasses was observed in the 2000s versus the 1950s particularly for those groups having TLs higher than III. In both systems, exports as catches were mainly concentrated within TL III.

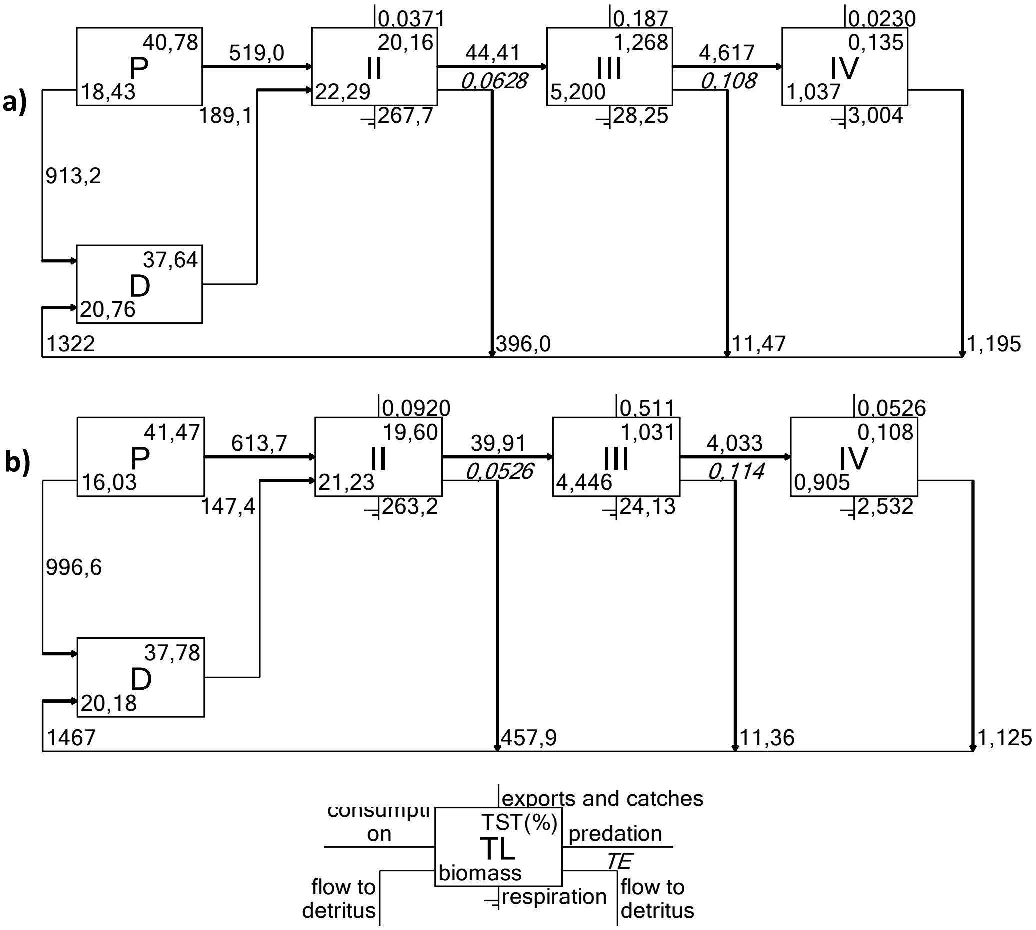


Fig. 5. A Lindeman spine representation of trophic flows (t·km^{-2}·year^{-1}) and biomasses (t·km^{-2}) for the entire Mediterranean Sea ecosystem (a: year 1950 and b: year 2000s).

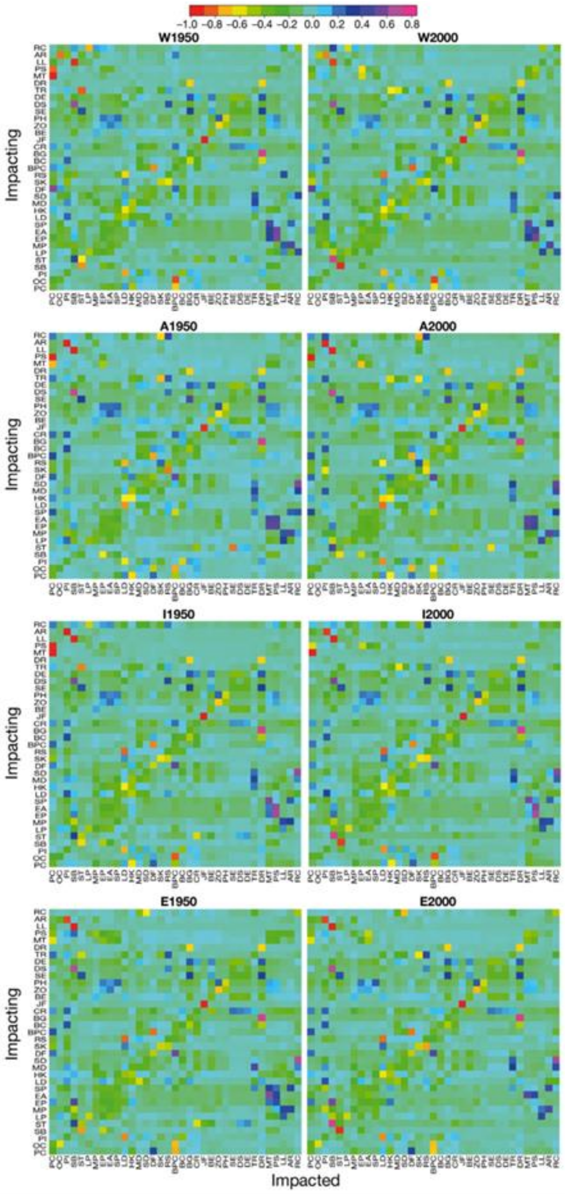


Fig. 6. Mixed trophic impact relationships between functional groups and fisheries in the 4 different Marine Strategy Framework Directive (MSFD) areas (W: Western; A: Adriatic; I: Ionian/Central; E: Aegean/ Levantine). Positive values (from light blue to purple) indicate positive impacts; negative values (from light green to red) indicate negative impacts. The colors should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups. For group abbreviations, refer to Table1.

Trophic impact and keystone species

For a better interpretation of the MTI analysis, results are presented separating each MSFD area (Fig. 6). Several general patterns can be observed in all 4 areas. Among all MSFD areas, most predators had a direct negative impact on their prey through their diet preferences; functional groups negatively impacted themselves due to cannibalism/within group competition; demersal functional groups had a greater impact (either negatively or positively) on the majority of the other groups than pelagic functional groups, and ‘zooplankton’ and ‘phytoplankton’ groups most positively affected all other groups in the system (e.g. through a bottom-up effect). MTI analysis in both time periods revealed changes in the role of ‘pinnipeds’ in the West, Adriatic and Ionian Seas, with a higher impact in the food web during the 1950s and almost no impact in the 2000s. In the Eastern Mediterranean, where the species still occurred in greater numbers, the impact on the food web was greater in 2000s than in the other 3 MSFD areas but still reduced compared to the 1950s. Similar trends were observed for ‘piscivorous cetaceans’ in all MSFD areas, where the group had a large effect in the 1950s but because of their reduced biomass, only had a limited effect in the 2000s. For fishes, ‘European anchovy’ and ‘European pilchard’similarly affected the Mediterranean food web with greater positive impact on top predators, pelagic fishes and fisheries (particularly mid-water trawlers and purse seiners). Interestingly, 'sharks' were negatively impacting marine mammals either through direct competition for the same resources or niche overlap. Overall, lower TL organisms, namely 'benthos', 'crustaceans' and particularly 'seagrass', positively affected the rest of the food web. Results also revealed that the role of fisheries in the different MSFD areas has changed with time, growing in impact from 1950s to 2000s, and affecting several groups in the different food webs. In general, if only the commercially exploited functional groups were considered, results showed a greater impact of bottom trawlers, mid-water trawlers and purse seiners (Fig. 7b).

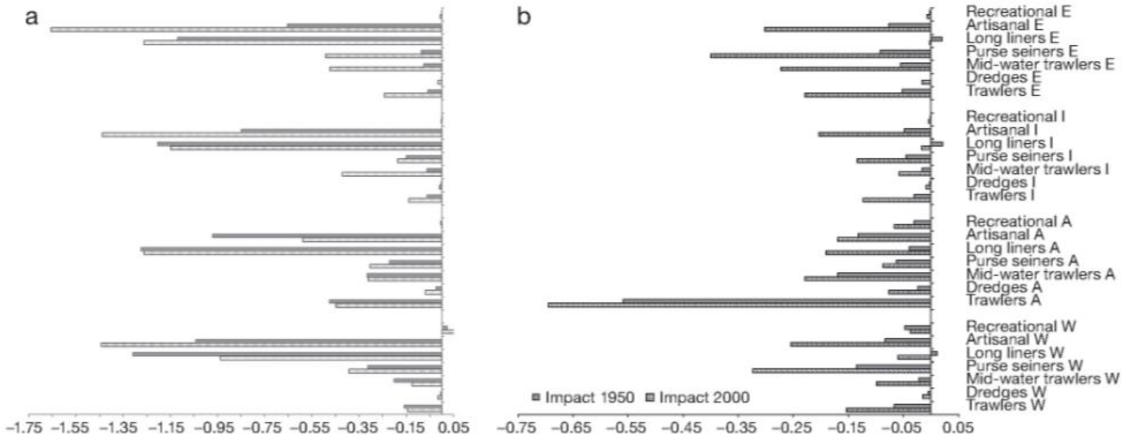


Fig. 7. Cumulative impact (either direct or through a cascade effect) of each fishing gear on (a) all functional groups of the ecosystem and (b) all commercially important species/groups of the ecosystem (see Table 1, numbers 6 to 14 and 16 to 21), in the different Marine Strategy Framework Directive (MSFD) areas (see Fig. 1) and for each studied period. The cumulative impacts were calculated from the mixed trophic impact calculations. Negative values on the x-axis represent negative impact to a positive change in fishery harvest.

More specifically, bottom trawlers and dredges had large negative impacts on targeted demersal species (mainly demersal fishes and 'molluscs') and on 'sea turtles' (incidental catches), while longline fisheries had large negative impacts on 'large pelagic fishes' (target species) and, through incidental catches, on 'sea turtles', dolphins and 'seabirds'. Mid-water trawlers and purse seiners showed negative impacts on targeted small pelagic fishes and, through direct competition for the same resources, on marine mammals and 'seabirds'. When all functional groups in the ecosystem were included in the analysis, artisanal fisheries seemed to be the fleets with greater negative impact, particularly in the Western, Ionian and Eastern Mediterranean Seas (Fig. 7a).

Recreational fisheries had a negative impact on 'large pelagic fishes' and 'sharks' in the Western, Adriatic and Ionian Seas and on 'medium' and 'small' demersal and 'medium' and small pelagic fishes in the Eastern Mediterranean. The results obtained from the keystoneness analysis (Fig. 8 and Table S6 in the Supplement) revealed that in the 1950s ecosystem, 'large pelagic fishes' had the highest overall keystoneness role followed by 'sharks' and 'medium pelagic fishes' groups, whereas in the 2000s ecosystem, 'medium pelagic fishes' were replaced by 'benthic' and 'benthopelagic cephalopods'. Interestingly lower TL groups (e.g. 'zooplankton', 'phytoplankton' and 'benthos') were also identified in both time periods as keystone groups, probably caused by their overall low biomass and high P/B (characteristic of oligotrophic systems) and important role in the ecosystem. In both time periods, marine mammals, in particular 'pinnipeds' and 'piscivorous cetaceans', appeared within the least important keystone groups.

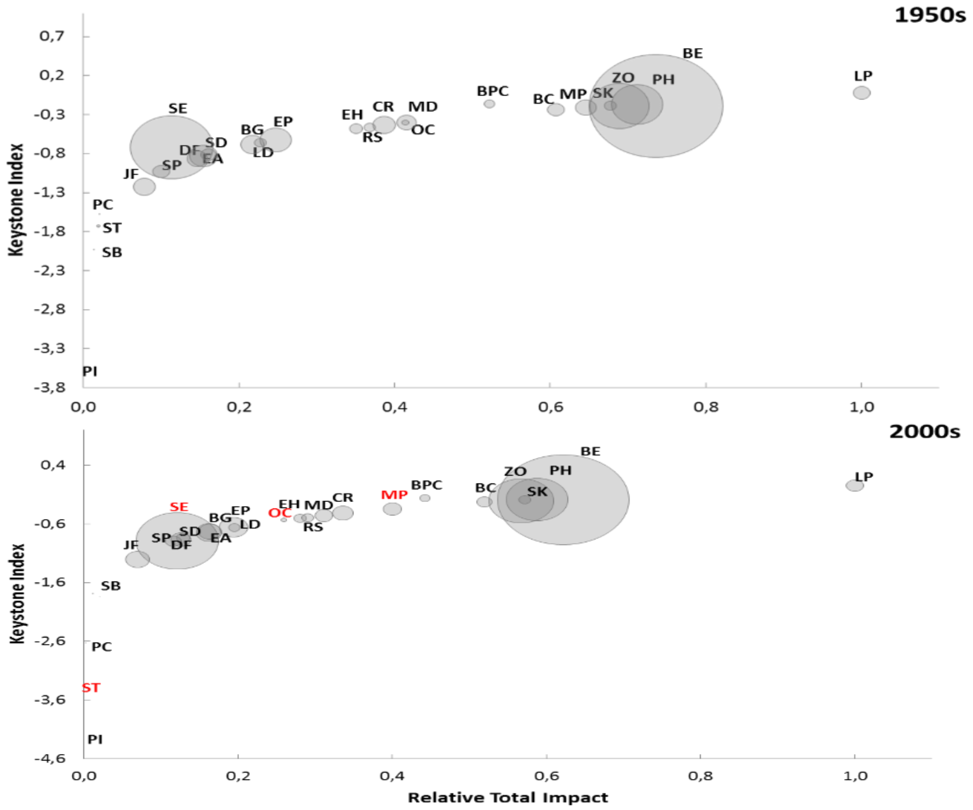


Fig. 8. Relative total impact (εi) versus keystoneness (KSi) showing the role of species/groups in the ecosystem for both time periods (1950s and 2000s). The size of the circles is proportional to the species/group biomass. Functional groups that showed a decline in their keystone role in comparison to the 1950s are shown in red. For abbreviations, refer to Table 1.

Comparison among European regional seas

The statistics and main indicators calculated from the whole Mediterranean Sea ecosystem model representing the 2000s were compared with other modelled European regional seas for the same or similar period (Table 2). The TST revealed that the main flows driving the Mediterranean Sea were flow to detritus (42%) and exports (39%) followed by consumption (15%) and respiration (5%). In the Baltic, North and Black Seas, on the other hand, consumption seemed to be the flow with the highest importance (around 43–48%) followed by flow to detritus (22–30%), respiration (20–23%; in the Black Sea, this flow constituted the second most important flow, with 29%) and exports (1–6%).

Table 2. Summary statistics for the Mediterranean Sea food web model in comparison with the North Sea, Baltic Sea and Black Sea.

Indicators	Mediterranean Sea (this study)	North Sea (Mackinson et al. 2014)	Baltic Sea (Tomczak et al. 2012)	Black Sea (Akoglu et al. 2014)	Units
Main ecosystem features					
Area	2512000	570000	240000	150000	km^2
Studied period	2000s	1991	2000s	1995–2000	Year
Functional groups	103	68	21	10	No.
Main indicators					
Sum of all consumption	923	6157	3435	4500	tkm^{-2} yr^{-1}
Sum of all exports	1320	105	476	490	tkm^{-2} yr^{-1}
Sum of all respiratory flows	290	2658	1851	2990	tkm^{-2} yr^{-1}
Sum of all flows into detritus	1467	3867	2246	2230	tkm^{-2} yr^{-1}
Total system throughput	4000	12786	8007	10210	tkm^{-2} yr^{-1}
Mean trophic level of the catch	3.08	3.7	3.30	3	
Gross efficiency (catch/net primary production)	0.00026	0.00226	0.0016	0.001	
Total primary production	1610	2609	2434	3483	tkm^{-2} yr^{-1}
Total primary production/total respiration	5.55	0.98	1.26	1.16	
Primary production required to sustain fisheries (PPR, considering primary production)	1.46	5.88	52.57	28.93	%
Total primary production/total biomass	37.67	4.71	22.54	90	
Total biomass (excluding detritus)	42.74	554	108	38.7	t km^{-2}
Connectance index	0.10	0.22	0.22	2.5	
System omnivory index	0.27	0.23	0.15	0.116	
Predatory cycling index	10.96	–	0.41	–	%
Finn's cycling index	4.98	20.24	6.98	15.01	%
Mean transfer efficiency	9.2	30.2	12	7.4	%
Ascendancy	42.9	20.6	30.82	31.7	%
Overhead	57.1	79.4	69.18	68.3	%

Looking at ecological indicators addressing community energetics and cycling of nutrients, under Odum's theory (Odum 1969), our results suggest that the Mediterranean Sea ecosystem is at an early developmental stage. This was visible, for example, in the ratio between total primary production (PP) and total respiration (R) (Odum 1969, Christensen 1995) or in the primary production/biomass ratio (PP/B). On the other hand, the indicators from the other European Seas suggested that systems fell within an intermediate-low level developmental stage. For the SOI, despite the low general values, the Mediterranean Sea showed the highest value, while in relation to the 2 cycling indices, the Mediterranean basin had the highest values in PCI and the lowest in FCI. For each European regional sea, ascendancy was relatively low, whereas overhead was high. As for fishing indicators, the PPR% of the Mediterranean was 0.81%, the lowest among the other seas, while TLc was 3.04 in the Mediterranean Sea, similar to the Black Sea and lower in comparison to the other European Seas with higher TL values (between 3.3 and 3.7).

Discussion

This study constitutes the first attempt to build an historical and current food web model for the whole Mediterranean Sea with the challenging effort to integrate available spatial and temporal (in terms of comparing the 1950s and 2000s) biological data and modelling outputs in a coherent manner. We acknowledge that data gaps still exist, for example on temporal changes in diet composition, temporal estimates of discards and biomasses of non-commercially important species and deep sea organisms. Thus, further efforts should be made to reduce this uncertainty and increase the quality of these models.

Quality of the models

As expected, the 1950s model showed a lower pedigree index, scoring in the lower range (0.164–0.676) when compared to the 150 balanced EwE models previously assessed globally by Morissette (2007). This is because the 1950s model was constructed using mainly data obtained from other modelling approaches (e.g. biogeochemical models to estimate phytoplankton biomasses and stock recruitment models to estimate biomass of fish stocks; refer to Table S5 in the Supplement for details of each functional group). Models that have tried to represent the past have always been associated with higher uncertainty, as was observed in other studies (Coll et al. 2008, 2009c, Piroddi et al. 2010, Christensen et al. 2014, Macias et al. 2014), and their outputs should be always taken with caution. To limit this uncertainty, we tried to use models for which outputs have been tested and when possible validated (Macias et al. 2014), or that have been widely utilized to assess temporal biomasses as done for fish stocks (e.g. surplus production models; Walters et al. 2008, Piroddi et al. 2011). In contrast, the 2000s model, due to its higher data quality, showed a relatively higher pedigree. This was due to the availability, in more recent years, of survey data (e.g. trawl surveys such as the MEDITS campaign) and the increase in biodiversity assessments (e.g. Coll et al. 2010) that have improved the level of knowledge in the basin. Nevertheless, data deficiencies exist, particularly in African and Arabic countries, where survey data remain either inaccessible or absent. Despite these limitations, the models developed in this study represent an important step towards an integrated understanding of the Mediterranean Sea marine ecosystem structure and function.

Biomasses, trophic flows and TLs

Results presented here show how the Mediterranean Sea is mainly dominated, in terms of biomass, by lower TL organisms, particularly ‘benthos’, ‘zooplankton’ and ‘phytoplankton’. These groups dominate most of the system flows and, as observed at smaller scales in other Mediterranean food web models (Coll et al. 2006, 2007, Tsagarakis et al. 2010, Moutopoulos et al. 2013, Torres et al. 2013), constantly appear as important key species. This is probably because of the relatively low biomass at higher TLs and a relatively high mean TE overall in the food web, in line with previous studies (Pauly & Christensen 1995, Coll & Libralato 2012). This phenomenon is called the ‘Mediterranean paradox’ for the fact that despite the oligotrophic condition of the basin that constrains the reproduction and feeding of zooplankton, the ecosystem is capable of producing a relatively high fish abundance (Sournia 1973, Macias et al. 2014). In addition, the high TEs have been suggested as a sign of overexploitation of the Mediterranean Sea due to high production exports (Coll et al. 2009b). Marine mammals and large pelagic fishes, on the other hand, are the top predators of the Mediterranean marine ecosystem. In particular, the Mediterranean monk seal *Monachus monachus* is the species with the highest TL followed by 'piscivorous cetaceans' and 'large pelagic fishes'. These outcomes are very interesting since the Mediterranean monk seal and several dolphin populations (e.g. the short-beaked common dolphin *Delphinus delphis*) have dramatically declined over the centuries because of a variety of anthropogenic pressures (e.g. fisheries interactions, habitat loss and pollution) and are now classified either as Critically Endangered (the Mediterranean monk seal is almost extinct), Endangered, or Vulnerable by the International Union for Conservation of Nature (IUCN) Red List of Threatened Animals (UNEP/MAP 1994, Johnson & Lavigne 1998, Reeves & Notarbartolo di Sciara 2006, Bearzi et al. 2008, Piroddi et al. 2011). Large pelagic fishes (mainly tuna species and swordfish), the main keystone group in our modelling approach, have consistently been exploited for thousands of years in the Mediterranean Sea, and these species are also at low levels of abundance (Abdul Malak et al. 2011). This severe decline in biodiversity at the top of the food web particularly in recent decades (Briand 2000, Bearzi et al. 2008, Coll et al. 2008, 2009c, Piroddi et al. 2010, 2011, Lotze et al. 2011), as also shown in our study by their reduced biomass levels, could have induced a cascade effect throughout the food web, with effects on the complexity, connectivity and robustness of the system against further species loss (Briand 2000, Heithaus et al. 2008, Lotze et al. 2011, Piroddi et al. 2011). Defined as umbrella, sentinel, keystone or flagship species, they reflect ecosystem changes and degradation over time, as is also clear from our keystone and MTI analysis, and ensuring their survival would lead to ways of enhancing marine ecosystems and ensure sustainable human activities (Bossart 2006, Boyd et al. 2006, Trites et al. 2006, Sergio et al. 2008).

Ecological role of species and changes with time

The results of our keystone analysis for both time periods also revealed changes over time in other important keystone species. After 'large pelagic fishes', 'sharks' and 'medium pelagic fishes' have played a key role in the past ecosystem, replaced in more recent years by 'benthopelagic cephalopods'. This is not the first time that cephalopods have been identified as a keystone group in Mediterranean food webs (Coll et al. 2006, Tsagarakis et al. 2010, Banaru et al. 2013, Hattab et al. 2013, Torres et al. 2013). This functional group, the role of which in the overall structure and functioning of marine ecosystems remains poorly understood, has an important trophic position (being both predator and prey), and because it can proliferate in highly exploited ecosystems, it constitutes a key element of present marine food webs (Pierce et al. 2008, Coll et al. 2013). As for 'sharks', particularly large predatory sharks, several studies have pointed at strong declines in species over the last centuries mainly due to intensive overexploitation (both for consumption and as discarded species; Megalofonou 2005, Ferretti et al. 2008, Maynou et al. 2011, Coll et al. 2014a). The present study suggests that these species were important in the past Mediterranean ecosystem and confirms a diminishing role within the current food web as a consequence of a reduction in their abundance.

Small and 'medium' pelagic fishes, both with high biomasses and high proportions in catches, show an important role in the Mediterranean ecosystem as structuring species of the food web (Coll et al. 2006, 2007, Piroddi et al. 2010, Tsagarakis et al. 2010). Yet, our results highlight how these organisms, despite being essential for transferring energy from lower to higher TL organisms (Cury et al. 2000, Pikitch et al. 2014), have diminished considerably between the 2 time periods and between sub-regions, causing a reduction in their ecological role.

Fishing impact and the quality of data

From the MTI analysis, bottom trawling and dredges were the fisheries with the widest impact on the food web, particularly on the demersal community. This has been observed in sub-areas of the Mediterranean Sea representing continental shelf and upper slopes (Coll et al. 2006, 2007, Banaru et al. 2013, Hattab et al. 2013). Therefore, our results highlight the effect of bottom trawlers and dredges on marine resources and ecosystems of the Mediterranean Sea as an important issue that should be addressed if sustainable management of fisheries is to be achieved within the region (Puig et al. 2012).

The impacts of artisanal fisheries on the ecosystem have also increased over time, particularly in the Ionian and Eastern Mediterranean Seas, and are probably caused by increased fishing effort in the EU, northern African and Arabic countries (Anticamara et al. 2011). This also has clear implications for the management of marine resources in the Mediterranean Sea because the artisanal fleet dominates the fishing activity in many

Mediterranean countries but is poorly monitored.

Overall, our results show that over time, fisheries have exerted a negative pressure on the food web as a consequence of increased and intensive overexploitation. Yet, several interpretations of these results could be drawn: first, fisheries might not display a greater negative impact (than the one presented here) on commercially important species because of the inclusion in the analysis of developing countries (e.g. North African and Arabic countries) and developed countries together. Completely different spatio-temporal patterns/trends characterize these 2 sides of the Mediterranean Sea that might lead to a masking effect scenario. A reflection of this is visible in the increased impact of artisanal fisheries in the Ionian and Eastern Mediterranean Seas, possibly as a consequence of increased fishing effort in southern Mediterranean countries. This distortion might also be caused by discards, which we kept constant in time due to lack of information, and by Illegal, Unregulated, and Unreported (IUU) activities that, despite being a serious issue in the Mediterranean Sea (Ulman et al. 2013, Coll et al. 2014b), were not included in this study due to the lack of a global estimate for the Mediterranean Sea.

Also, recreational catches are not included in national fishery statistics, and only recently a European Union legislation (Council Regulation [EC] No. 1224/2009) has required the survey of recreational fishing activities. Since only few sources of information exist, which have been incorporated into the model, catches may well have been underestimated. Using fisheries statistics supplied to the FAO by individual countries could be another limiting factor. Several studies have indeed confirmed that most of these statistics largely underestimate their likely true catch by a factor of 2 or more (Zeller & Pauly 2007, Pauly et al. 2014). This could be particularly true for the Southern Mediterranean, where mechanisms to collect fisheries data are less available (FAO 2010) and for some Mediterranean countries where this factor is even higher (Pauly et al. 2014).

An unrealistic scenario is also observed regarding mid-water trawling in the Eastern Mediterranean Sea, where this gear shows an impact on marine resources, despite the fact that it does not operate in most of the Eastern Mediterranean countries

(Sacchi 2011). Obviously this is an error in the Sea Around Us project database, which at the time it was accessed was still under development. These caveats represent the major weaknesses of the Mediterranean fisheries data, and some caution should be taken when interpreting the data. Currently, a database on global fisheries reconstruction from 1950 to 2010, which aims at looking at all types of fisheries removals (from reported and unreported landings to recreational landings and discards) is being constructed, including Mediterranean countries (Le Manach et al. 2011, Ulman et al. 2013, Coll et al. 2014b, Pauly et al. 2014). In the near future, this information on catch reconstructions could be integrated in modelling efforts to reduce the limitations explained above, and to capture better the fishing pressure on current and past Mediterranean marine ecosystems.

Similarities and differences among European regional seas

The relative total biomass per km^2 and per each individual sea reveals that the Adriatic and Western Mediterranean are the areas with the highest biomass followed by the Ionian and Eastern Mediterranean. This confirms a decrease gradient of richness from west to east, as observed in other studies (Bosc et al. 2004), influenced by changes in environmental parameters (e.g. productivity, temperature and salinity) that define and characterize the Mediterranean Sea. Comparing our results to other European seas illustrates that European regional seas are quite diverse. In particular, the Mediterranean Sea stands alone in relation to the type of flows that drive the system and the cycling indices that suggest higher levels of community stress induced by intensive fishing activities, as previously illustrated (Costello et al. 2010).

In regards to ecosystems development, the Mediterranean Sea appears to be in an early development stage, different from the other systems, probably because the ecosystem has been perturbed continuously over a long period of time. Indeed, when ecosystems develop, biomasses and complexity tend to increase and mature, whereas when they are disturbed, e.g. by fishing, they show the opposite trend and stay ‘young’ (Odum 1969). One similarity with the other EU ecosystems is given by the TLs of the catches, which are low in the Mediterranean Sea, in the Black Sea and recently in the Baltic Sea (e.g. herrings and sprats have replaced the collapsed Eastern Baltic cod *Gadus* *morhua* in the landings; Tomczak et al. 2012), highlighting the importance of small pelagics in the fisheries activities of these areas. Although differences may have occurred in the way models were constructed (such as the number of functional groups and links), these outcomes are in line with other studies that pointed at differences in physical and biological features (from highly eutrophic with frequent hypoxia events to moderately eutrophic and productive or relatively oligotrophic regions; Coll et al. 2010, Tomczak et al. 2012, Mackinson 2014) as the reasons for these differences in diversity among European regional seas (Barale & Gade 2008, Narayanaswamy et al. 2013).

Concluding remarks

Overall, our study is the first to provide a basis for understanding and quantifying the structure and functioning of the whole Mediterranean Sea ecosystem, including main marine organisms, from low to high TLs, and considering fishing activity. This is also the first Ecopath model that tries to integrate sub-regions within a unified model to take into consideration differences in biological and environmental characteristics. The construction of 2 food web models (for the past and for current years) enabled us to assess changes in the food web and impacts (in this case fishing) affecting the system. However, further developments of spatial and temporal hind- and forecast analysis are necessary to further model the dynamics of the ecosystem (such as movements of species within and between areas and large migrations) and evaluate the exploitation status of the Mediterranean Sea and explore different management policies and future scenarios. Temporal simulations to hindcast food web dynamics have been developed in regional areas of the Mediterranean Sea such as the Catalan Sea (Coll et al. 2008), the Adriatic Sea (Coll et al. 2009c) and the Ionian Sea (Piroddi et al. 2010). Quantifying the impact of important threats (e.g. climate change and fishing pressure) on a system that is considered 'under siege' (Coll et al. 2012) becomes critically important for ensuring the sustainability of marine resources and the services they provide to humans, and the conservation of this vulnerable ecosystem. This is a step further for the regional assessment of the Mediterranean Sea ecosystem.

See original publication in Annex 4

Chapter 2.5

Historical changes of the Mediterranean Sea ecosystem

SUBMITTED to SCIENTIFIC REPORTS

Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time

Modelización temporal del impacto de los cambios en la producción primaria y la pesca en el ecosistema marino del Mediterráneo

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Abstract

The Mediterranean Sea has been defined as a sea “under siege” because of intense pressures from multiple human activities; yet there is still a lack of information on the cumulative impact of these stressors on the ecosystem and its resources. In this study, we evaluate how the historical trends of various ecosystems groups or species have been impacted by changes in environmental productivity combined with fishing pressure. We do this for the whole Mediterranean Sea, using a food web modelling approach. Results indicate that both fishing pressure and changes in primary production (PP) played an important role in driving species dynamics; yet, PP seems to have been the strongest driver upon the Mediterranean Sea ecosystem. The food web model is able to satisfactorily reproduce historical trajectories of biomasses and catches of several species and functional groups over time, suggesting that the combined effect of an intensive fishing pressure and changes in the environment have modified the Mediterranean marine ecosystem. In general, we observe a reduction of biomasses of important fish stocks (e.g., forage fish) and top predators (e.g., large pelagic fish and pinnipeds) while biomass increased for organisms at the bottom of the food web (e.g., invertebrates). Ecological indicators, such as community biomass, trophic levels of the community, and catch and diversity indicators reflect such ecosystem changes and show an overall degradation over time. Although further efforts are needed to improve the modelling approach, this study constitutes an important step toward a regional assessment of the Mediterranean Sea ecosystem as a whole, and may contribute to inform and implement conservation plans and management actions.

Resumen

El mar Mediterráneo se ha definido como un mar "en estado de sitio" debido a las intensas presiones de múltiples usos y factores de estrés de origen antropogénico. Sin embargo, pocos estudios se han desarrollado para cuantificar el impacto acumulado sobre el ecosistema y sus recursos de estas amenazas. En este estudio se ha evaluado como los cambios temporales de varios grupos o especies del ecosistema han sido impactados por cambios en la produccion primaria en combinación con la presion pesquera. Este es el primer estudio que realiza dicho analisis para el Mediterráneo en su conjunto. Los resultados indican que tanto la presión pesquera como los cambios en la producción primaria (PP) juegan un rol importante en la descripción de la dinámica temporal; sin embargo, el cambio en PP parece ser el principal impulsor del cambio en el Mar Mediterráneo. El modelo ecológico aquí desarrollado es capaz de reproducir a nivel temporal la información disponible sobre varias especies en términos de biomasa y captura, lo que sugiere que el efecto combinado de la presión pesquera excesiva y los cambios en la producción primaria han modificado el ecosistema marino de forma notable. Los principales efectos de estos cambios a nivel del ecosistema han sido la reducción de la biomasa de las poblaciones de peces predadores (por ejemplo, peces pelágicos de gran tamaño) y otros depredadores apicales (por ejemplo, pinnípedos) y el aumento de organismos de tamaño menor que se sitúan en posiciones bajas de la red trófica (por ejemplo, invertebrados). Los indicadores ecológicos como la biomasa de la comunidad, los niveles tróficos medios y la diversidad también son capaces de reflejar el deterioro general del ecosistema en el tiempo. Cabe destacar que, aunque se requiere

un mayor esfuerzo para mejorar el modelo ecológico desarrollado en este estudio, los resultados constituyen un importante paso adelante para contribuir a la evaluación regional del estado de salud ambiental del ecosistema del Mar Mediterráneo y podrian ser utilizados para informar y implementar futuros planes de conservación y gestión.

Introduction

Marine ecosystems around the world are increasingly pressured by a diversity of human stressors, which include fisheries and aquaculture impacts, pollution, climate change, habitat loss and degradation, and species invasions (Halpern et al. 2008, Côté et al. 2016). Since human stressors change over time (Halpern et al. 2015), the assessment of their temporal cumulative effects has been poorly studied and remains a challenging task (Côté et al. 2016). Because these stressors are rapidly increasing, understanding how human interactions, the environment, and marine species interact and influence each other, and how such dynamics affect the sustainability of goods and services they provide, is of urgent importance. Currently this is a priority of many national and international regulations/initiatives (e.g., European Marine Strategy Framework Directive [MSFD; 2008/56/EC]; Convention of Biological Diversity, [CBD], Intergovernmental Platform on Biodiversity and Ecosystem Services [IPBES]) which aim to contribute to the preservation and sustainability of biodiversity use, ensuring long-term human well-being and sustainable development.

In support of these regulations, new comprehensive scientific tools have been developed with the goal of integrating the effects of the above-mentioned human and environmental stressors into a single common framework in order to better guide policy decisions (Halpern et al. 2008, Travers et al. 2009, Collie et al. 2014). Particularly in the context of ecosystem-based management approach (EBM), which assesses ecosystem dynamics rather than focusing on single resources and managing a single threat, there has been a growing use of ecosystem models. These tools are improving their ability to predict complex system dynamics considering the impact of multiple pressures (Christensen & Walters, 2011) and assessing different policy objectives sought by management authorities (Levin et al. 2009, Collie et al. 2014, Piroddi et al. 2015c). Through hind-cast and forecast scenarios, ecosystem models allow to quantitatively assess the role of different stressors on ecosystem dynamics and calculate model-based indicators able to evaluate whether an ecosystem and its services are maintained and used sustainably. Model-based indicators can complement data-based indicators (Shannon et al. 2014) and have been widely developed and used to capture the impact of specific pressures on marine ecosystems (Cury et al. 2008, Coll et al. 2016), such as fishing or eutrophication, and more recently to assess socio-economic and governance issues (Ehler 2003, Rice & Rochet 2005), as well as the cumulative impacts of multiple human activities (Halpern et al. 2012, Coll et al. 2016), informing management processes (Levin et al. 2009, Shin et al. 2010a).

This study applies the Ecopath with Ecosim (EwE) food web model approach to the Mediterranean Sea ecosystem as a whole, with the aim to evaluate temporal responses of species abundances and ecosystem dynamics to the combined effect of historical changes in primary productivity patterns and fisheries. The Mediterranean Sea is a highly diverse marine ecosystem that hosts 7-10% of the world's marine biodiversity (Bianchi & Morri 2000, Coll et al. 2010), and is "under siege" by historical and current impacts of combined multiple human stressors (Coll et al. 2012), mainly fishing practises, habitat loss and degradation, eutrophication, and more recently, the introduction of alien species and climate change effects (Coll et al. 2010, Costello et al. 2010, Coll et al. 2012). Since the intensity of these stressors is increasing throughout the Mediterranean basin, temporal analyses are increasingly needed in order to inform effective current and future marine policies and management actions. In this study, we first quantify temporal dynamics of marine species in the Mediterranean Sea ecosystem as a whole, evaluating their historical dynamics. We then calculate a series of ecological indicators to analyse past ecosystem dynamics.

Our specific goals are to investigate: 1) the temporal evolution of the Mediterranean marine ecosystem from 1950 to 2011 by developing a hind-cast scenario analysis that includes primary productivity, fisheries activities and food web dynamics; and 2) the structural and functional changes of the Mediterranean Sea ecosystem using specific model-based indicators.

Studies such as the present are essential in support of European policies like the Marine Strategy Framework Directive (MSFD; 2008/56/EC) that requires EU member states to assess the environmental status of their territorial waters developing strategies to achieve ''Good Environmental Status (GES)'' by 2020. They can also support regional policies like the UNEP's Mediterranean Action Plan (MAP) that aims at moving towards an ecosystem based management approach (EBM) for both EU and non-EU Mediterranean countries.

This study sets a baseline to further develop ecosystem analyses in order to facilitate the implementation of management policies and explore future plausible scenarios.

Materials and methods

The baseline food web model of the Mediterranean Sea

We used a previously developed food web model (Piroddi et al. 2015a) constructed with the Ecopath with Ecosim approach (EwE) using the Ecopath mass-balance module (Christensen & Walters 2004) representing the whole Mediterranean ecosystem in the 1950 decade. We used the Ecopath model as a baseline to run temporal hind-cast (1950-2011) analyses, assessing the response of the Mediterranean marine ecosystem to changes in primary productivity and fishing effort. The baseline Ecopath model consisted of 103 functional groups, ranging from phytoplankton and invertebrates to top predator species, and it was divided in four sub-models representing the four MSFD areas: 1) Western Mediterranean Sea (W); 2) Adriatic Sea (A); 3) Ionian and Central Mediterranean Sea (I); and 4) Aegean Sea and Levantine Sea (E) to account for sub-regional differences in environmental and biological characteristics of the ecosystem (Fig 1).

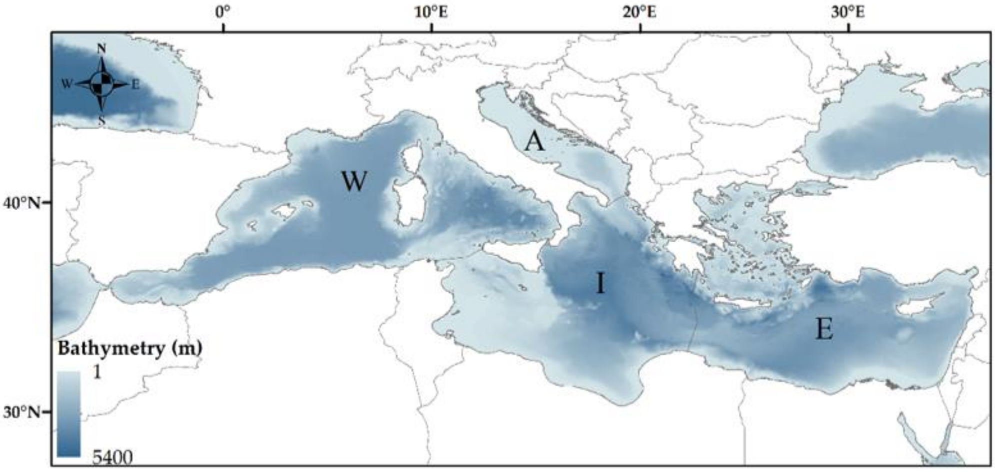

Fig 1. A representation of the Mediterranean Sea with the bathymetry and the four MSFD areas: Western Mediterranean Sea (W); Adriatic Sea (A); Ionian and Central Mediterranean Sea (I); Aegean and Levantine Sea (E).

The food web model had the following key input variables: biomass (B), production/biomass ratio (P/B), consumption/biomass ratio (Q/B), diet composition, and fisheries catches and discards. The main trophic structure of the Mediterranean Sea EwE model is shown in Figure 2 and species and/or functional groups included in the model are listed in Table S1. A full description and sources of information of the input and output parameters of the baseline Ecopath model are available in Piroddi et al. (2015a) and are presented in S2-S3 Tables in the Supporting Information.

A set of pre-balancing (PREBAL; Link 2010) analyses are presented in Figure S4 with the purpose of showing the coherency of the basic input parameters with respect to general rules/principles of ecosystem ecology. In particular, these rules include: 1. biomass estimates by functional group in the model, which span 5–7 orders of magnitude when arranged against their trophic levels; 2. slope of biomass (on a log scale) by functional group, which declines by 5–10% across all the taxa when arranged against trophic levels; 3. vital rates (P/B; Q/B) across taxa/trophic levels, which decline with increasing trophic level (Link 2010, Heymans et al. 2016). The Ecopath model constructed in Piroddi et al. (2015a) included seven types of fishing fleets: trawlers, dredges, mid water trawlers, purse seiners, longliners, artisanal and recreational activities.

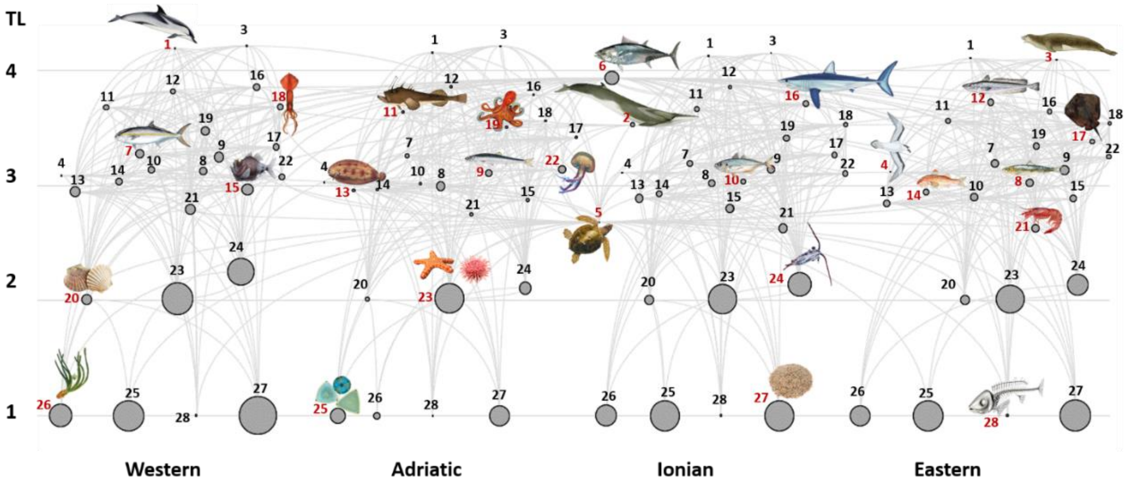

Fig 2. Flow diagram of the Mediterranean Sea ecosystem (year 1950s) with the Western part being at the far left followed by the Adriatic, the Ionian and the Eastern. Each functional group is shown as a circle and its size is proportional to the log of its biomass. The functional groups are represented by their trophic levels (y-axis) and linked by predator-prey relationships shown as light grey lines. Numbers refer to functional group codes, which are reported in the legend, while those in red are graphically represented with a drawing. Numbers in the figure: 1. Piscivorous cetaceans; 2. Other cetaceans; 3. Pinnipeds; 4. Seabirds; 5. Sea turtles; 6. Large pelagics; 7. Medium pelagics; 8. European pilchard; 9. European anchovy; 10. Other small pelagics; 11. Large demersals; 12. European hake; 13. Medium demersals; 14. Small demersals; 15. Deep sea fish; 16. Sharks; 17. Rays and skates; 18. Benthopelagic cephalopods; 19. Benthic cephalopods; 20. Bivalves and gastropods; 21. Crustaceans; 22. Jellyfish; 23. Benthos; 24. Zooplankton; 25. Phytoplankton; 26. Seagrass; 27. Detritus; 28. Discards.

In this study, these fleets were adapted due to a lack of time series of data regarding the number of vessels and gross tonnage (GT) for some of the fleets, which are important for estimating historical fishing effort. In particular, while recreational fishery was retained from the previous model, main commercial fisheries were divided in: 1. trawlers (which included trawlers and dredges); 2. purse seiners; 3. longliners and 4. artisanal fisheries. This new fishing fleets configuration was created to follow the same structure as in Sacchi et al., (2011), the main source of information for temporal time series data of number of vessels and gross tonnage (GT) for the above-mentioned fleets for each Mediterranean country for the period 1990-2010. For Italy and Greece, we were able to get longer time series data using detailed reconstructions respectively from Piroddi et al. (2015a) for the 1950-2010 period, from Stergiou et al. (2007) for 1964-1989, and Moutopoulos et al. (2014) for 1990-2010.

To estimate an overall trend of number of fishing vessels for the 1950-2010 period, for those countries with missing years, we assumed same trends as observed by Greer (2014) who reported the number of fishing vessels for each country of the world for 1950-2010. GT was extrapolated, for the missing years, as the average ratio of GT in the observed time periods, while number of days spent fishing were kept as the ratio of days at sea observed respectively in Sacchi et al., (2011) for the majority of the countries, Piroddi et al., (2015a) for Italy, and Moutopoulos et al., (2014) for Greece. For Spanish and Italian trawlers, we complemented our trends with data from EVOMED (2011), a European project that assessed the evolution and technological improvement of fishing capacity for the major countries of the Mediterranean Sea for the early 1900-2010 period.

Fishing effort (kW*days^{-1}) was calculated as the product of the number of fishing vessels kW per vessel (inferred from their GT), and the number of days spent fishing. To account for improvements in technology (e.g., mobile phone, GPS, sonar, radio) that were not captured by kW as a measure of effort (Figure S5), a conservative technological “creep factor” of 1% as observed by Damalas et al., (2015) and EVOMED (2011) was applied from 1980 to 1995 while for the remaining periods (1950-1979 and 1996-2010) a 0.5% and ~ 1.9% (this value varied with gear type; see S6 Table) were respectively used following the work of Pauly and Palomares (2010).

Temporal dynamic modelling and model derived indicators

The dynamic module of the EwE software, Ecosim (Walters et al. 1997, Christensen & Walters 2004), uses a set of differential equations to estimate biomass fluxes for each species and/or functional group of the ecosystem as follows:

$$dB_i/dt = g_i \sum_j Qji - \sum_j Qij + I_i - (M_i + F_i + e_i)B_i \quad (1)$$

where dBi/dt is the biomass growth rate of group (i) during the interval dt, gi is the net growth efficiency (production/consumption ratio), Ii is the immigration rate, Mi and Fi are natural and fishing mortality rates of group (i), ei is emigration rate, and Bi the biomass (Christensen & Walters 2004). Calculations of consumption rates (Qij) are based on the "foraging arena" theory (Ahrens et al. 2012) where the biomass of prey i is divided between a vulnerable and a non-vulnerable fraction. This is represented as:

$$\text{Qij}= \frac{\text{vij}\cdot \text{aij}\cdot \text{Bi}\cdot\text{Bj}\cdot \text{Ti}\cdot \text{Tj}\cdot \text{Sij}\cdot \text{Mij/Dj}}{\text{vij}\cdot + \text{v'ij}\cdot \text{T}\cdot \text{Mij} + \text{aij}\cdot \text{Mij}\cdot \text{Bj}\cdot \text{Sij}\cdot\text{Tj/Dj}} \quad (2)$$

where vij and v'ij is the vulnerability and expresses the rate with which prey move between being vulnerable and not vulnerable, respectively, aij is the effective search rate for i by j, Ti and Tj are the relative feeding time for prey and predator, Sij are the seasonal or long term forcing effects, Mij are the mediation forcing effects and Dj are the effects of handling time as a limit to consumption rate. One important feature in Ecosim is the use of a vulnerability term for each interaction between a predator and a prey. Low values of vulnerability (close to 1) indicate that prey production determines the predation mortality (phenomenon also known as 'bottom-up' control) and that the predator is close to carrying capacity, while high values of vulnerability (e.g., 100) indicate that predator biomass determines how much prey is consumed (top-down control) and that predators are far away from carrying capacity (Christensen & Walters 2004). Mixed effect (vulnerability = 2) is set as the default value in Ecosim.

The Ecosim approach was used here to fit the model to observed time-series of data using the sum of squares (SS) ratio between predicted and observed data as a metric for assessing model performance (Christensen et al. 2008). We used survey biomasses and catches for those functional groups with available information to compare predicted and observed data (S1). In particular, biomass time series for sea turtles, pinnipeds, benthic invertebrates and deep sea fish were taken from scientific literature, whereas for demersal species (functional groups nº 12-14; 16-19 and 21 in Figure 2), European anchovy, European pilchard and large pelagic fishes, we used scientific surveys (e.g., MEDITS trawl survey and MEDIAS acoustic survey) and stock assessments data (S2). Catch data was taken from the United Nation's Food and Agriculture Organization (FAO) database (FishStat: http://data.fao.org/database) available from 1950 to 2010. These time series were complemented with data (available per country) from the Sea Around Us Project (www.searoundus.org) to assign species to fishing fleet.

When applying the fitting procedure, we noticed that the baseline fishing mortality (Ecopath baseline in 1950s) for the most commercially important target species (European pilchard, anchovy and hake) was relatively low (between 0.02 and 0.05) compared to the reference levels reported in the literature (Patterson 1992, Colloca et al. 2013, Vasilakopoulos et al. 2014). This initially caused a very low reaction of these species to changes in historical fishing effort and primary productivity. To correct these estimates and reflect a more appropriate fishing mortality for these three species, we used the reconstruction of the catches of the Sea Around Us Project and, in particular, for each country of the Mediterranean Sea, we considered the proportion of catch of these species relative to the total catch and applied it respectively in each of our sub-areas.

To fit the temporal dynamic model accounting for data quality/reliability in available time series, we weighted the time series using a factor either of 0.5 or 1 (0 indicating that time series are not considered in the calculation of SS and 1 indicating that they are fully considered; Christensen et al. 2008). For all catch time series and for European pilchards and anchovies biomass in the Ionian and Eastern Mediterranean Seas, we used a weight of 0.5, while the rest of the time series were assigned a weight of 1. This was done to consider questionable catch statistics reporting (as identified in previous research studies [Ulman et al. 2013, Coll et al. 2014, Pauly et al. 2014, Piroddi et al. 2015b]), and to consider poor data availability for forage fish in the Ionian and Eastern Mediterranean Sea (i.e., long time series of European anchovies and pilchards were available only for the Aegean: Jardim et al. 2015, and the Strait of Sicily: Patti et al. 2004, Fiorentino et al. 2013). The choice of using these weights (0.5 and 1) puts less/more emphasis on selected species/functional groups of the ecosystem; still, since there are different methods to determine weighting factors (Heymans et al. 2016), further work should be developed to assess the outcome of the fit procedure using alternative weights.

Fishing effort (Figure S5) and primary production (PP) anomaly over time were used as main forcing time series to drive the model. The PP anomaly results from an Ecosim automated procedure that searches for time-series relative values of annual production (expressed as P/B ratio) of producer groups. This routine considers that if primary production changes over time then the total amount of energy that enters in the ecosystem changes, causing a cascading-up effect that increases or decreases food availability through the ecosystem (Preikshot 2007). Once estimated by Ecosim, the predicted relative PP anomaly was tested against the relative PP time-series data obtained from a biogeochemical model (GETM-ERGOM: Macias et al. 2014) for the same time period using the Spearman's rank-order correlation test (suitable for non-parametric data). Also, we re-run the Ecosim model using the relative PP time-series data from the biogeochemical model to compare and assess the model fit and results using the two different PP time series data (relative PP anomaly from Ecosim, and relative PP data from the biogeochemical model). As for fishing effort, since our reconstruction was done up to 2010 but the majority of our biomass time series were available until 2011, we decided to keep fishing efforts observed in 2010 constant until 2011.

The fitting procedure consisted of seven general steps (Table 1) following the same approach as described and applied by Mackinson et al. (Mackinson 2014). This method uses the Akaike Information criterion (AIC) (Akaike 1974, Burnham & Anderson 2003):

$$AIC = n\log(minSS/n) + 2k \qquad (3)$$

where n is number of observations, minSS is the minimum sum of squares resulting from the comparison of predicted with observed datasets, and k is the number of parameters, to test statistical hypotheses related to changes in predator-prey dynamics (also called vulnerabilities: Vs); changes in primary production (PP anomaly, considering the number of PP spline points (sPP) for smoothing the time series); impact of fishing and possible combinations of the above-mentioned factors (Table 1). The AIC is a tool used for model selection that penalizes for fitting too many parameters, and which is used to choose the "best" model (the one yielding the lowest AIC) considering a good fit and the least number of estimated parameters to do so. In this study, we used the second-order Akaike Information Criterion (AICc) calculated as follow:

$$AICc = AIC + 2k(k-1)/(n-k-1) \qquad (4)$$

to account for small sample sizes (n of observations) in the dataset.

In our case, the fitting procedure was conducted five times: individually for the four sub-models (Western, Adriatic, Ionian and Eastern Mediterranean) as the majority of the functional groups are restricted to one sub-area only, and one extra time for the model representing the whole basin to fit highly migratory species ('large pelagics' and 'sea turtles' groups) that are allowed to move and feed in all four areas.

Once the temporal dynamic fitting procedure was completed, we used the "best" fitted models to calculate model-based indicators by sub-area and for the whole Mediterranean Sea. To be able to compare these indicators with available ones from other regional seas, model-based indicators were selected from a list of indicators previously tested and assessed by international initiatives, mainly IndiSeas ("Indicators for the Seas"; www.indiseas.org; see e.g., Shannon et al., (2014) and Coll et al., (2016)). The list of indicators that were selected is presented in Table 2. Once estimated, we used the Spearman's rank correlation to assess the significance and correlation between our suite of ecological indicators and time.

Table 1. Model fits following the seven steps proposed by Mackinson et al., (Mackinson 2014), which include trophic interactions, fishery and environmental drivers (here changes in primary productivity).

#	Steps	Description
1	Baseline	Trophic interactions with default prey-predator vulnerabilities (vij=2; mixed effect). No environmental or fishery data are used to drive the model.
2	Baseline and trophic interaction	Trophic interactions with different vulnerabilities. No environmental or fishery changes are used to drive the model.
3	Baseline and environment	The "PP anomaly" is used to drive the model. No fishery data are used to drive the model.
4	Baseline, trophic interactions and environment	No fishery data are used.
5	Fishery	Fishing effort is included as model driver. Trophic interactions are set as default and no environmental data are used.
6	Trophic interaction and fishery	No environmental data are used.
7	Trophic interactions, environment and fishery	All the components are jointly included in the model as drivers.

Addressing uncertainty

The Monte Carlo routine built into EwE (Christensen & Walters 2004) was applied in Ecosim to assess sensitivity of Ecosim's output to the basic Ecopath input parameters (B, P/B, Q/B, EE), drawing input parameters from a normal distribution centered on the base Ecopath value and using a defined coefficient of variation, in this case set to 0.1 (Christensen et al. 2008, Coll & Steenbeek 2014). Here, we run 1000 iterations, and the range of outputs (the 5th and 95th percentile) were plotted for both the fitted results (in our case time series of biomasses) and the model-based ecological indicators.

Table 2. Detailed description of modelled derived indicators with acronyms, definitions and references.

Ecological Indicator	Acronym	Definition and references
Community biomass	*Cm*	Index calculated at community level as the sum of the biomass only for those groups fitted to time series data (Unit: t/km^2) (Heymans et al. 2014).
Kempton Q species diversity index	*Qi*	Expresses biomass species diversity by considering those organisms with trophic levels 3 or higher (Kempton & Taylor 1976, Ainsworth & Pitcher 2006).
Mean trophic level of community	*mTLco*	TL of the modelled community spans the whole ecosystem (living groups) (Shin et al. 2010b) including all functional groups (fitted and not fitted).
Mean trophic level of groups with TL >3.25	$\text{mTL}_{3.25}$	Calculated as the mTLco but including all functional groups (fitted and not fitted), excluding only marine mammals, seabirds and sea turtles (mTL3.25; Pauly & Watson 2005)
Total Catch	TC	Sum of all catches (Unit: t/km^2/year) (Bundy et al. 2010).
Trophic level of the catch	TL_C	TL of the catch for all retained species. Retained species are species caught in fishing operations, although not necessarily targeted by a fishery and which are retained because they are of commercial interest (i.e. not discarded) (Shin et al. 2010b).

Results

Time series from the model fitting

The most statistically significant results in our model fitting exercise were obtained when trophic interactions, fishing and the primary productivity changes were included together in the model run (Step 7 in Table 3). Differences were found among the five areas with the "best" fitted models (lowest AICc) explaining between 50% and

69% of the variance of the data (Table 3). By looking at each area separately, the Ionian Sea sub-model was the one that showed the smallest improvement of prediction capabilities (thus the AICc estimates declined the least), while the Eastern followed by the Western Mediterranean were the areas with the biggest improvement from the baseline AICc estimates. Both fishing and primary productivity drivers, when considered individually, were able to enhance the fit of all areas by ~16% to ~50% (when using the predicted PP anomaly) and by ~10% to ~37% when using fishing effort (steps 3 and 5 in Table 1). The addition of trophic interactions to changes in PP anomaly alone (step 4 in Table 1) provided the second largest improvement for the Western, Ionian and the whole Mediterranean Seas (AICc reduced further by ~10%). For the Adriatic Sea this was obtained with the addition of trophic interactions to fishing effort (step 6 in Table 1). Also, different vulnerabilities were tested, and the largest enhancement was obtained using high vulnerabilities (step 7 in Table 3) for both the four sub-models (maximum predator prey-interactions or Vs: #24) and the additional Mediterranean model as a whole (maximum predator prey-interactions or Vs: #2).

When we checked for correlation between the PP anomaly resulting from the Ecosim fitting procedure and the PP from the biogeochemical model, in all the areas except for the Adriatic Sea both PP time series were positively correlated with high significance. On the contrary, the Adriatic Sea showed a negative correlation and highly significant (Table 4 and S7 Figure). Using the "best" fitted models, Ecosim reproduced satisfactorily the biomasses trends for some of the functional groups with available survey data in all sub-areas (Fig 3 and Fig 4). Overall, forage fishes (functional groups nº 8-9), demersal fishes (nº 12-14) and invertebrates (nº 18-19 and 21) showed a good fit in the different sub-models, while deep sea fish (nº 15) and benthos (nº 23) were the least well fitted (Fig 3, Fig 4 and S7 Figures). These latter groups are the ones with the fewest data points. A satisfactory fit was also shown for sharks and rays/skates groups (nº 16-17), and, despite only few observed records, also for pinnipeds (nº 3) (Fig 3, Fig 4 and S8 Figures).

Based on the biomass trends by area, in the Western Mediterranean, the predicted time series suggested a decreasing pattern for the biomasses of several functional groups (Fig 3 and S8 Figure). European pilchard showed a decline from the beginning of our study period (1950), which became more pronounced in the last years of the surveyed period. A similar result was also observed for medium and small demersal fishes, and pinnipeds, although the model was not able to capture the sharp decline of these marine mammals in the 70s. As for sharks, rays/skates the model confirmed a decrease in trends until the end of the 1990s and a slightly increase in the 2000s decade. For European anchovy and hake, Ecosim had difficulties reflecting observed variations in their biomass, although suggesting a decreasing trend for both species.

Table 3. Results of the temporally dynamic fitting procedure of the Ecopath model from 1950s to 2011 following the procedure suggested by Mackinson et al., (Mackinson 2014) (Table 1). Vs is the number of vulnerabilities included in each iteration, sPP the number of primary production spline points (for smoothing of the time series) k is the number of parameters and %IF is the improved fit compared to the baseline AICc (#1). V and sPP are shown only for those models with the lowest Akaike Information Criterion (AICc). The "best" models (shown in bold and italics) are the ones yielding the lowest AICc and the one used to calculate model-based indicators.

Steps	Vs	sPP	min SS	k	AICc	%IF
1. Baseline						
West	0	0	191.0	0	-1768.0	
Adriatic	0	0	245.9	0	-1603.3	
Ionian	0	0	153.5	0	-1995.9	
Eastern	0	0	322.6	0	-1285.1	
Med	0	0	31.9	0	-227.9	
2. Baseline and trophic interactions						
West	1	0	190.9	1	-1766.7	-0.1
Adriatic	1	0	245.9	1	-1601.3	-0.1
Ionian	1	0	153.5	1	-1993.9	-0.1
Eastern	1	0	322.6	1	-1283.3	-0.2
Med	1	0	17.94	1	-226.1	-0.8
3. Baseline and environment						
West	0	6	144.1	6	-2049.7	15.9
Adriatic	0	28	156.1	28	-2037.2	27.1
Ionian	0	32	62.6	32	-2863.6	43.5
Eastern	0	28	167.2	28	-1931.4	50.3
Med	0	10	7.8	10	-306.5	34.5
4. Baseline, trophic interactions and environment						
West	23	3	103.0	26	-2357.7	33.4
Adriatic	23	13	136.7	36	-2164.0	34.9
Ionian	20	34	52.3	54	-3004.6	50.5
Eastern	22	29	137.8	51	-2089.1	62.6
Med	1	5	8.2	6	-308.9	35.6
5. Fishery						
West	0	0	160.8	0	-1946.9	10.1
Adriatic	0	0	172.7	0	-1985.7	23.8
Ionian	0	0	75.2	0	-2738.6	37.2
Eastern	0	0	211.6	0	-1736.6	35.1
Med	0	0	11.6	0	-280.2	22.9
6. Trophic interactions and fishery						
West	23	0	114.2	23	-2256.9	27.7
Adriatic	23	0	121.9	23	-2315.5	44.4
Ionian	23	0	62.9	23	-2876.7	44.1
Eastern	20	0	189.9	20	-1811.7	40.9
Med	2	0	9.5	2	-300.5	31.9
7. Trophic interactions, environment and fishery						
West	***22***	***5***	***60.1***	***27***	***-2917.2***	***65.0***
Adriatic	***23***	***6***	***104.5***	***29***	***-2469.2***	***54.0***
Ionian	***22***	***5***	***55.7***	***27***	***-2996.4***	***50.1***
Eastern	***21***	***12***	***133.1***	***33***	***-2165.0***	***68.5***
Med	***1***	***4***	***5.8***	***5***	***-353.8***	***55.3***

Table 4. Spearman's rank-order correlations between the PP anomaly time series calculated by Ecosim and the PP from the biogeochemical model. For a graphical representation of the correlation please refer to S7 Figure in the Supporting Information.

Sub-model	rho	p-value
West	0.37	7.5E-03
Adri	-0.59	6.5E-06
Ion	0.42	2.5E-03
East	0.49	3.0E-04
Med	0.82	2.2E-16

A poor fit was observed for benthos and deep sea fish, where only few data points were available. A good reproduction of biomass time series was found for crustaceans and benthopelagic cephalopods where the model was able to follow the majority of the fluctuations in time (Fig 3 and S8 Figure). When the model was run using the PP from the biogeochemical model as an alternative primary productivity driver, we observed similar pattern (red dashed in Fig. 3 and 4) as the ones obtained using the PP Ecosim anomaly, and for certain species/functional groups (nº 8 and nº 21 in Fig.3) the fit improved.

As for the Western Mediterranean, also in the Adriatic Sea, Ecosim suggested a more/less pronounced decline for demersal and pelagic fish and for some invertebrates (Fig 3 and S8 Figure). In particular, the model was able to capture the steep decline of pinnipeds observed in the area since mid-1970s and a less marked decrease of medium and small demersal fish observed in mid 1990s. Ecosim captured some of the pattern observed for European hake, sharks, rays/skates suggesting a decline of the groups until the end of the 1990s, followed by a slight increase or by fluctuations (in the case of European hake) in the last years of the studied period. An overall satisfactory match between predicted and available data was found for benthopelagic cephalopods where a decrease was captured since the beginning of the survey period, and for benthic cephalopods and crustacean where the model followed some of the fluctuation of the groups and a slight increase at the end of 2000s. Again, the model did not represent the trends well for deep sea fish (S8 Figure). Regarding forage fish, when we run the model using PP anomaly as driver, Ecosim was not able to reflect the decreasing biomass trend observed in European anchovies, while it was able to pick up a general decline for European pilchards. However, it was when we applied the PP from the biogeochemical model in the model run that Ecosim was able to follow the steep decline observed in European anchovies in mid 1970s and improve also slightly the decline of European pilchard. For the other species/functional groups, different trends were observed using the two different PPs particularly in the decades before the beginning of our time series of observations (Fig 3 and S8 Figure).

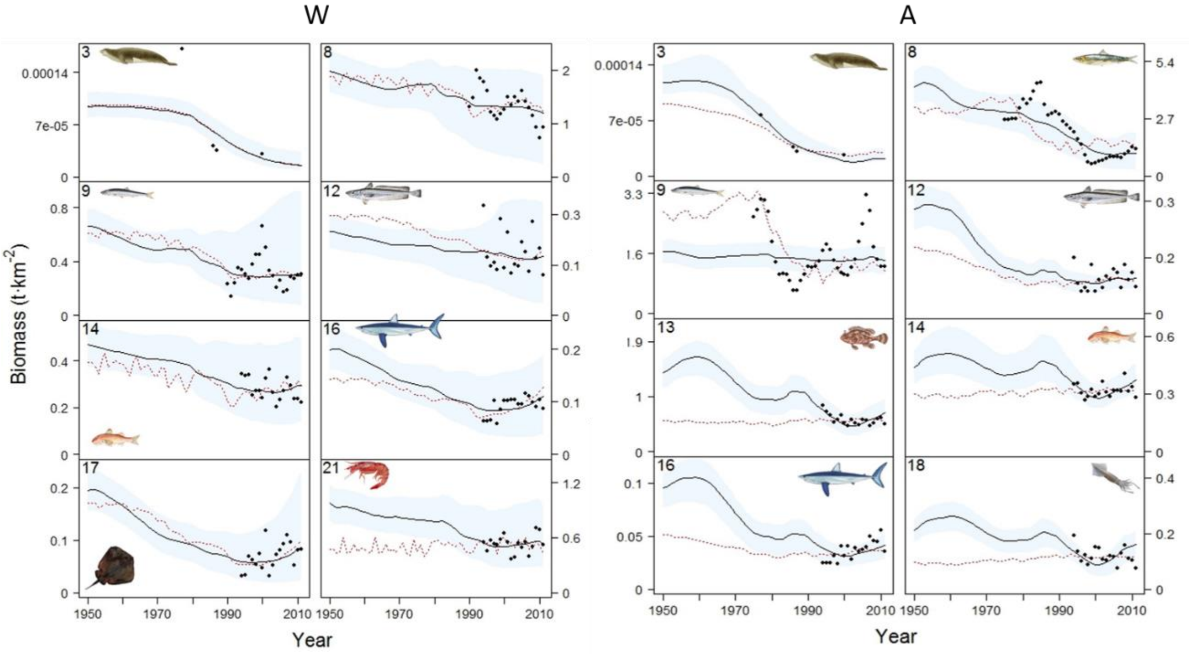

Fig 3. Representation of modelling fitting results for some functional groups occurring in the Western and Adriatic Seas for the period 1950-2011 (results for the rest of the groups are shown in S8 Figure). Predicted biomass (t·km^{-2}) is shown as solid black lines, while observed data is represented as black dots. Functional groups codes correspond to those given in Fig 2. The predicted model (dashed red line) using modelled biogeochemical PP is also shown. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.

The Ionian Sea resulted to be the area with less biomass changes during the years with available survey data (Fig 4 and S8 Figure). Except for pinnipeds, where the model was able to pick up the decline since the late 1970, despite the presence of only few data points, all the other groups didn't show any directional variation in time resulting mainly in a series of fluctuations. However, by looking at the overall time period (1950-2011), the model suggested a small increase in biomass since the beginning of 1990s for small demersal fish and crustaceans. The model partly underestimated and was not able to capture the biomass trends for European pilchards and medium demersals (Fig 4 and S8 Figure), and it did not represent well the trend for benthos (S8 Figure). The use of PP from the biogeochemical model improved slightly the fit for crustaceans, sharks and benthopelagic cephalopods while maintaining the same pattern observed with the PP anomaly.

In the Eastern Mediterranean, different trends among species/functional groups were detected (Fig 4 and S8 Figure). Ecosim represented relatively well the biomass declines of European pilchards and anchovies since the 1990s, despite underestimating the high peaks observed at the beginning of this decade. The model was able to capture the biomass trends for European hake, sharks, small demersals, rays/skates, benthic cephalopods and crustaceans. All these groups showed similar patterns with signs of decrease in the 1990s and fluctuations afterwards.

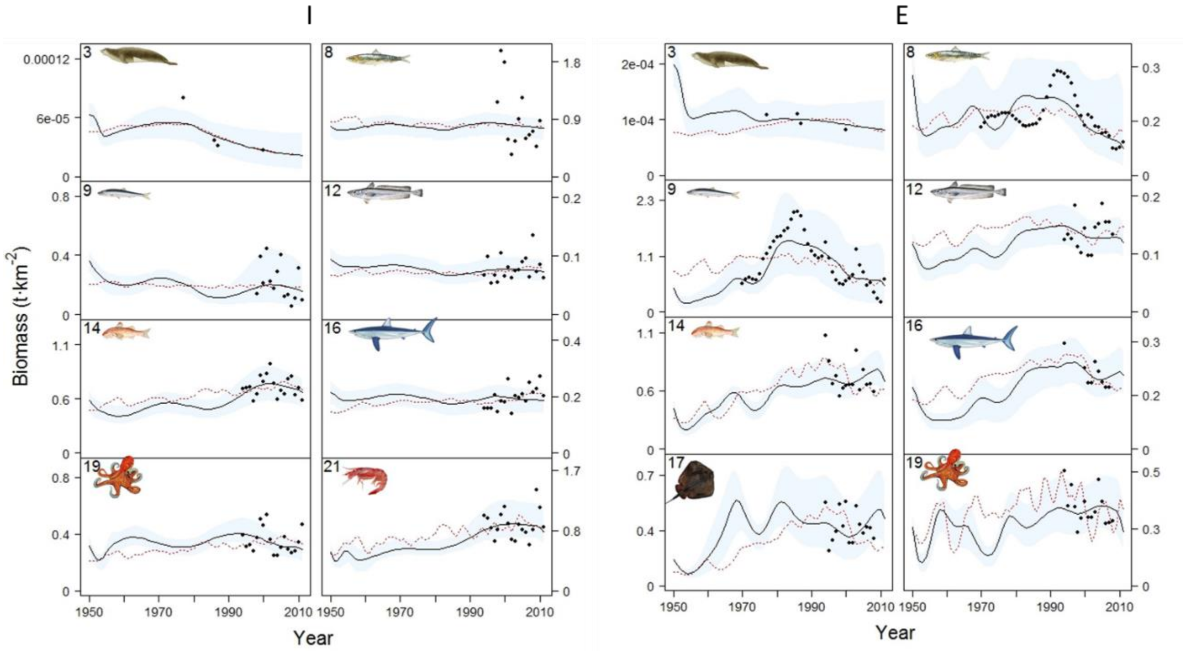

Fig 4. Representation of modelling fitting results for some functional groups occurring in the Ionian and Eastern Seas for the period 1950-2011 (results for the rest of the groups are shown in S8 Figure). Predicted biomass (t·km^{-2}) is shown as solid black lines, while observed data is represented as black dots. Functional groups codes correspond to those given in Fig 2. The predicted model (dashed red line) using modelled biogeochemical PP is also shown. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.

An underestimation of biomass by the model was predicted for medium demersal fish, benthopelagic cephalopods, deep sea fish and benthos where the model was not able to reproduce observed trends and fluctuations (Fig S8). A good fit, even though for only few data points, was found for pinnipeds where the model was able to represent the fluctuation of these marine mammals over time (Fig 4). The predicted trends obtained using PP from the biogeochemical model were similar to the ones found using the PP anomaly and for European hake, sharks, small demersals, benthic cephalopods and crustaceans the fit

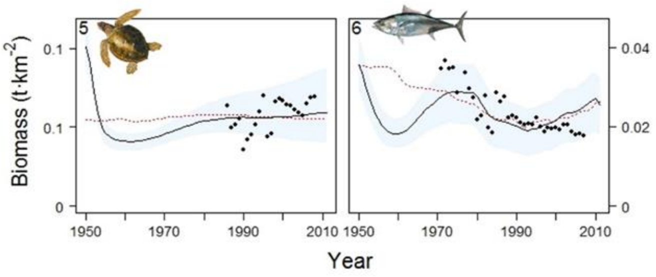

Fig 5. Representation of modelling fitting results for large pelagics and sea turtles in the Mediterranean Sea as whole for the period 1950-2011. Predicted biomass (t·km^{-2}) is shown as solid black lines, while observed data is represented as black dots. Functional groups codes correspond to those given in Fig 2. The predicted model (dashed red line) using modelled biogeochemical PP is also shown. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.

slightly improved. Ecosim was able to represent the decrease in biomass of large pelagic fish particularly since the 80s, while it failed to capture the fluctuation observed at the end of the 2000s in the whole Mediterranean model for the two highly migratory species for which we had survey data: large pelagics and sea turtles. In the case of the sea turtles, the model approximated the general increasing biomass trend of this reptile, but it failed to reproduce its fluctuations over time (Fig 5). We observed similar results with the PP from the biogeochemical model as a driver.

The time series of catch trends estimated for the five areas, when compared with independent data, showed a general satisfactory match (Fig 6 and S9 Figure): the sub-models overestimated or underestimated some fractions of the time series trends, but overall they were able to capture long-term trends similar to those observed (Fig. 6).

In the Western Mediterranean, an increase (up to the end of the 1990s) and posterior decrease in catches were predicted for the majority of the groups with the exception of small pelagic fish, large demersal, and benthic cephalopods that continued to increase even afterwards. Non-significant trend was simulated for rays/skates, while the model was not able to reflect the trend observed for benthopelagic cephalopods. Regarding large pelagic fishes, catches predicted for the whole Mediterranean were similar to those observed until the 1980s, but the predicted catches did not reflect the increase observed in the last two decades (Fig 6a).

In the Adriatic, as for the Western Mediterranean, the model simulated the decrease in catches observed in the beginning of the 1990s for the majority of the functional groups while it did not manage to pick up the sharp decline of European anchovies in mid 1970s, and of European hake and sharks in the 1990s (Fig 6b). In the Ionian Sea, predicted results reflected the increase in catches until the end of 2000s for the majority of the functional groups. For European hake, medium demersal benthic cephalopods, sharks and rays/skates, though, such increase turned into a decrease approximately around the 1990s (Fig. S9c). In the Eastern Mediterranean Sea, predicted results reproduced quite well the increase in catches for the majority of the functional groups until the 1990s and the decline afterwards and they also captured the continuous increase for benthopelagic cephalopods and small pelagic fishes. On the other hand, simulated results did not match the sharp decline of sharks observed since the 1980s in the region (Fig. S9d).

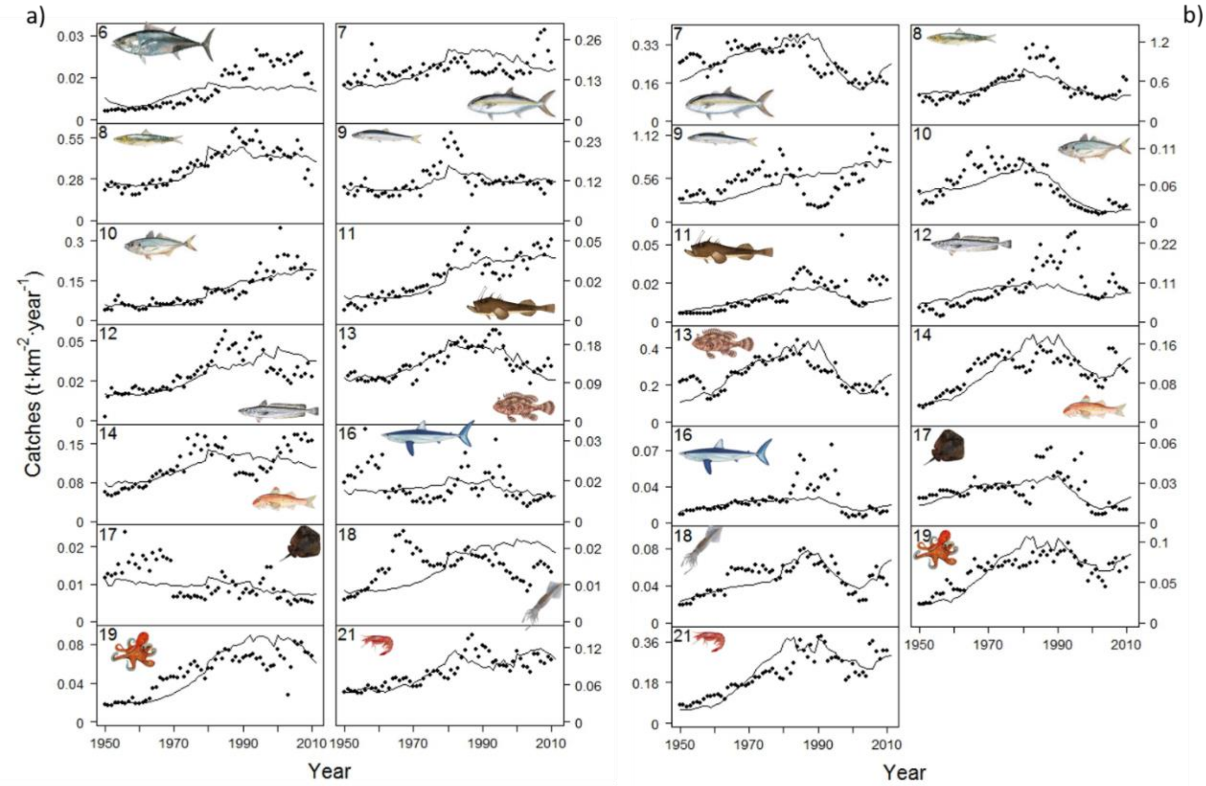

Fig 6. Predicted (solid lines) versus observed (dots) catches (t·km^{-2}·year^{-1}) for main commercially important functional groups of the Western Mediterranean (a) and Adriatic (b) ecosystems (1950-2011). Predictions obtained with the Mediterranean Sea model as whole for large pelagic catches are included in the Western Mediterranean plot (a. #6). Results for the Ionian and Aegean catches are shown in S9 Figure.

Temporal model-based ecological indicators

Trends in ecological indicators calculated from Ecosim temporal outputs showed different patterns if we looked at each sub-regional sea individually or at the Mediterranean ecosystem as a whole. For example, considering the entire Mediterranean Sea, a clear decreasing trend was observed in community biomass indicators like the forage fish biomass and, to less extent, for demersal fish, the Kempton's biodiversity index and in all the trophic level indicators considered (TLco, TL≥3.25 and TL Catch) (Fig 7). On the contrary, an increase was predicted for invertebrate biomass while no clear trend was visible for sharks and rays/skates. Total catch was the only indicator that clearly increased in time (until 1990s) and that gradually decreased afterwards. These patterns were also reflected through the Spearman correlation test (Fig. 8). Considering sub-regional seas (S10-S13 Figures), we observed a clear decline of forage fish, demersal fish and sharks/rays-skates biomasses in the Western and Adriatic Seas, a fluctuation of these groups in the Ionian Sea while in the Eastern Mediterranean they respectively decreased, increased and fluctuated. Invertebrate biomass slightly decreased in the Adriatic Sea; fluctuated in the Western and Ionian Seas; and increased in the Eastern Mediterranean. The Kempton biodiversity index decreased in the Western and in the Ionian Sea, it showed a slight increase in the Adriatic while no clear trend was visible in the Eastern Mediterranean. Total catch increased in all the areas until the beginning of 1990s but in the Western and Ionian Seas started to fluctuate afterwards while in the Eastern and Adriatic Sea it gradually declined. As for the different trophic level indicators assessed, the mean TL of the community slightly increased in the Western Mediterranean and decreased in the other sub-regions, while the mean TL ≥3.25 and mean TL catches decreased in all the seas except in the Eastern Mediterranean where they respectively fluctuated with no clear trend and slightly increased (S10-S13 Figures). When we tested the significance and correlation of our suite of temporal ecological indicators we noticed that in the Western and the Adriatic Seas the majority of the time series were negatively correlated with high significance (respectively 6 and 7 out of 9 indicators; Fig 8). On the contrary, in the Ionian Sea and Eastern Mediterranean Sea, the community indicators (except for forage fishes in the Ionian that showed a weak negative correlation) were highly significant and positively correlated (Fig 8). Also, we observed no significant and weakly correlated trends for mean TL ≥3.25 and Kempton biodiversity index in the Eastern Mediterranean Sea.

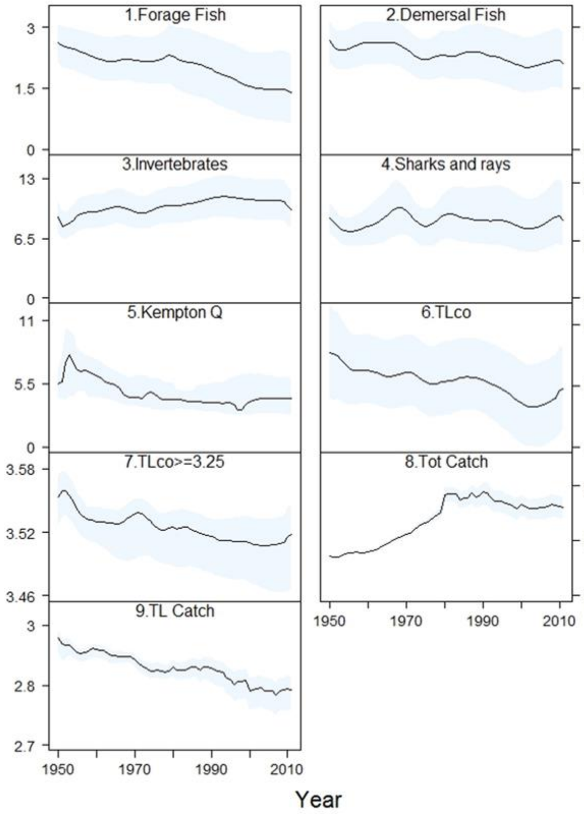

Fig 7. Ecological indicators (1. Forage Fish biomass (t·km^{-2}); 2. Demersal fish biomass (t·km^{-2}); 3. Invertebrates biomass (t·km^{-2}); 4. Sharks/rays and skate biomass (t·km^{-2}); 5. Kempton Q: Kempton's index of biodiversity; 6. mTLco: Mean trophic level of the community; 7. mTL≥3.25: Mean trophic levels of groups having trophic level ≥3.25 (excluding marine mammals, sea turtles and seabirds); 8. Tot Catch: Total Catch (t· km^{-2} ·year^{-1}); 9 TLc: Mean trophic level of the catches) estimated from the Ecosim results for the period 1950-2011 for the whole Mediterranean Sea. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.

Discussion

This study quantified, for the first time for the whole Mediterranean Sea ecosystem, temporal patterns and responses of species/functional groups abundances to the historical combined effect of changes in primary productivity and fisheries.

Model assumptions and limitations

Modelling the Mediterranean Sea ecosystem is a challenging task, not only because of the complex dynamics that characterize this Large Marine Ecosystem (e.g., differences in environmental and biological features), but also because of the difficulties of gathering and integrating regional data (2015a). Several gaps have been already identified and described in the previous work of Piroddi et al. (2015a) which identified the lack of trophic information with a temporal dimension, lack of biomass estimates (especially of those non-commercially important species and deep-sea organisms), and lack of reliable catch data, particularly for southern Mediterranean countries. Also, lack in historical data series (particularly between 1950s and 1970s) and problems with data accessibility limit the development of EBM approaches (Coll et al. 2013, Katsanevakis et al. 2015, Piroddi et al. 2015a). Therefore, more efforts should be dedicated to improve data quality, and to make data better accessible for the region. This study includes the best available regional data (see Supplementary Information) and highlights, when necessary, gaps and difficulties encountered in the modelling process (see below). To account for the uncertainty around the model parameters, we applied a Monte Carlo routine to evaluate model outputs sensitivity (in our case for biomasses and model derived indicators) to data uncertainty. Considering input data uncertainty in model development is critical if the purpose of modelling is to inform policy/management processes (Collie et al. 2014, Heymans et al. 2016). Still, the majority of available modelling tools lack an approach to take uncertainty of modelled data (both input and output) (Allen et al. 2007, Piroddi et al. 2015c) into account. Although some time series were not well replicated and uncertainty analyses can be improved as higher quality data becomes available, our modelling exercise reproduced several surveyed datasets in a satisfactory way and, as such, it is to date the best available representation of historical trends from the Mediterranean Sea, and a first step towards the integrated and historical understanding of this complex ecosystem.

Historical ecosystem drivers of the Mediterranean Sea ecosystem

Modelling results explained between 50% and 69% of the variability of available time series of data. Both fishing pressure and PP anomaly played an important role in improving the model fit. In addition, our results indicated that the PP anomaly, representing the temporal variation of the primary productivity of the system, was the strongest driver upon the Mediterranean Sea ecosystem. This confirms the results obtained from other studies (Coll et al. 2009a, Macias et al. 2014) that have shown how the Mediterranean Sea is driven by bottom-up processes where nutrient availability controls the biological characteristics of the region. The use of relative PP trends from a regional biogeochemical model helped validating our predicted PP anomaly trend and improved the temporal dynamics of selected species in the ecosystem (particularly for small pelagic fish). This was clearly visible, for example, in the Adriatic Sea where PP anomaly unsuccessfully reproduced the trends of European anchovies while PP from the biogeochemical model was able to capture the trends. This confirms the importance and need of coupling hydro-dynamic biogeochemical models with ecosystem models (such as EwE), particularly in complex areas like the Adriatic Sea that has different physical and biological oceanographic characteristics (e.g., eutrophic in the north, oligotrophic in the south; Polimene et al. 2006) and is also subjected to strong anthropogenic pressures (e.g., fishing) (Coll et al. 2009b, Steenbeek et al. 2013). Currently there is a growing interest in this coupling modelling framework (Travers et al. 2009, Rose et al. 2010) in order to improve our capability to predict future ecosystem changes, and provide guidance for the setting of targets and implementation of management measures (Kaplan et al. 2012, Piroddi et al. 2015c).

Our study also highlights that fishing was an important driver affecting the dynamics of fish populations and invertebrates of the Mediterranean Sea ecosystem. This is in line with previous studies that highlighted the increasing impact of fishing in the Mediterranean Sea and the overexploitation of its marine resources (Lotze et al. 2006, Colloca et al. 2013, Vasilakopoulos et al. 2014, Tsikliras et al. 2015). Simulations, in fact, were able to reflect the impact of increased fishing effort in the basin starting, in all the four sub-areas, since the beginning of 1950. Nominal fishing effort showed decreasing trends only after 2000; the only exception was found in the Eastern Mediterranean Sea where fishing effort showed a fluctuating trend in the 2000s decade.

Historical trends of biomass, catch and ecological indicators

We provide interesting results regarding temporal dynamics of major marine species/functional groups of the Mediterranean Sea ecosystem. In general, both biomass trends and ecological indicators revealed that the combined effect of excessive fishing pressure and changes in the primary productivity have altered the Mediterranean marine ecosystem over time, especially reducing the proportions of top predators (e.g., pinnipeds, large pelagic fish) and increasing the abundance of groups at lower trophic levels (e.g., invertebrates). This was already observed from west to east in other studies, for example, in the Catalan (Coll et al. 2006), Adriatic (Coll et al. 2009b, Lotze et al. 2011) and Ionian (Piroddi et al. 2010, Piroddi et al. 2011) Seas. Our results also show that forage fish species were observed to decrease, at a different time scale, in the majority of the studied Mediterranean sub-areas; with the only exception in the Ionian Sea where no clear trends were observed. These small pelagic fish (mainly European pilchard and anchovy) constitute the bulk of fish catches in the Mediterranean Sea, accounting for almost 40% of total landings (FAO 2012) and they are highly commercial. Therefore, an increase of fishing mortality, together with changes in productivity, have affected these stocks throughout the Mediterranean Sea. As for the Ionian Sea, the results obtained here should be taken with caution. Our fitting analysis for the majority of the species/functional group in this area didn’t show any clear trend besides fluctuations over time. These results for the Ionian Sea disagree with several studies that have shown decreasing trend in the abundance of many commercial and uncommercial species in the area (Patti et al. 2004, Machias et al. 2008, Piroddi et al. 2010). Poor model performance could be related to poor quality of the available data used in our study (e.g., for forage fish species, long time series were available only from Sicily), or to the fact that important additional factors were missing from our modelling analysis (e.g., changes in oceanographic and physical characteristics, quality of prey availability, etc.) that could be affecting Ionian Sea populations. This will need further research. Trends in demersal fish stocks also show signs of decrease, both at regional and sub-regional scale (specifically in the Western and Adriatic Sea), while sharks (which in our model were mainly represented by demersal species, see S1) and rays/skates seemed to have declined in the Western and Adriatic regions, but not at the regional scale. Part of these results are in line with historical (Aldebert 1997) and recent studies (Ferretti et al. 2008, Colloca et al. 2013, Vasilakopoulos et al. 2014), which pointed to increased fishing pressure and lack in gear selectivity as the reason why 85% of the assessed demersal stocks (including demersal sharks, rays and skates) are currently overexploited. A clear sign of change in the structure of the Mediterranean Sea ecosystem is visible from results of the mean trophic level of the community, mean TL≥3.25 and Q diversity index (which includes those species or groups with TL≥3) showing a decline since 1950s and reflecting the decline of large predators/fish stocks and increase of lower trophic level organisms. These results are in line with previous ecosystem assessments (Lotze et al. 2006, Coll et al. 2010), although it is important to bear in mind that these results were assessed considering both fitted and non-fitted groups. Caution should be taken when interpreting the results. Differences in ecological indicators were found among the different sub-regions, and we would like to stress the need to further develop these results. Regarding catches, the fitting procedure enabled us to detect issues related to landings data at the beginning of our survey period. Low fishing mortalities were observed in the 1950s, in each sub-area, for three very important commercial species (European pilchard, anchovy and hake). Mortalities for these species were between 5 and 10 times lower than the average reference values reported for these fish stocks in the Mediterranean Sea (Patterson 1992, Colloca et al. 2013, Tsikliras et al. 2015). This confirms the hypothesis, already highlighted by several studies (EC 2003, Garibaldi 2012, Moutopoulos & Koutsikopoulos 2014, Pauly et al. 2014), of poor quality of fisheries

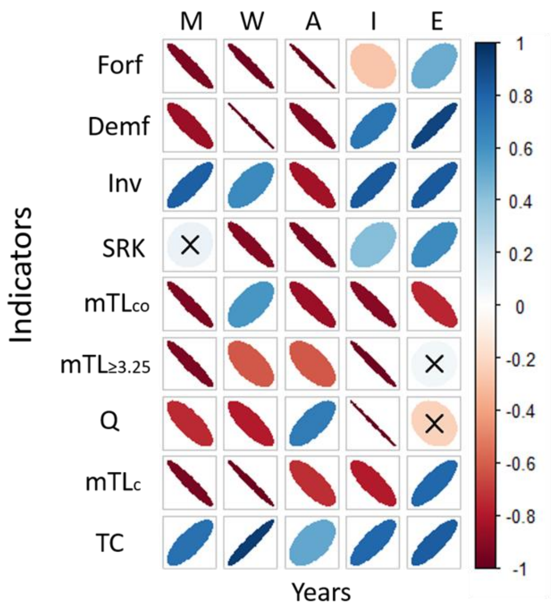

Fig 8. Spearman's rank-order correlations representation between the suite of ecological indicators (**Forf**: Forage fish biomass (t·km^{-2}); **Demf:** Demersal fish biomass (t·km^{-2}); **Inv:** Invertebrates biomass (t·km^{-2}); **SRK:**; Sharks/rays and skate biomass (t·km^{-2}); **mTLco:** Mean trophic level of the community; **mTL≥3.25:** Mean trophic levels of groups having trophic level >3.25 (excluding marine mammals, sea turtles and seabirds); **Q:** Kempton's index of biodiversity; **mTLc:** Mean trophic level of the catches; **TC:** Total catch (t·km^{-2} ·year^{-1}) and time for the four sub-areas (Western: W; Adriatic: A; Ionian: I; Eastern and Levantine: E) and for the additional Mediterranean Sea as whole (Mediterranean: M). Positive correlations are displayed in blue and negative correlations in red color. Color intensity and the size of the eclipses are proportional to the correlation coefficients. At the right side of the graph, the legend color shows the correlation coefficients and the corresponding colors. When the indicators are non-significant (>0.05), they are represented with an X symbol.

statistics, particularly in historical times (1950-1970). Part of this problem could be related to the different way fisheries data were collected and aggregated by the different countries and regional institutions (Katsanevakis et al. 2015). Poor data quality could also be explained by high intensity illegal, unreported and unregulated (IUU) fishing activities occurring in the region (Ulman et al. 2013, Coll et al. 2014, Pauly et al. 2014, Piroddi et al. 2015b) especially with regard to illegal nets and mesh sizes, the landing and marketing of undersized fish, and compliance with restrictions on fishing season and areas (Colloca et al. 2013). This highlights the need to utilize better catch data in modelling exercises in the Mediterranean Sea in order to account for more realistic fishing mortality estimates and trends, and guide/inform proper management decisions. Recent catch reconstruction efforts, which aim at considering all types of fisheries removals (from reported and unreported landings to recreational landings and discards), have been constructed and are now available (www.seaaroundus.org) for the different countries of the Mediterranean Sea (Pauly & Zeller 2016). Therefore, a necessary further step of this study should be the integration of such catch reconstruction in the input modelling parameters to compare results.

Despite limitations, our model was able to reflect the temporal trends of fisheries across the Mediterranean Sea, with a general increase in the total catch and a decline in the mean TL catch. Such patterns could reflect that catch composition, with a highly diversified targeted species, continues to change in time as a result of fisheries expansion to further and deeper fishing grounds (Coll et al. 2014, Pauly et al. 2014). A different picture emerges when looking at total catches per sub-regional area, where clear signs of decrease are noticeable mainly in the Adriatic and the Eastern Mediterranean Sea and for the last simulation years also in the Western Mediterranean and Ionian Seas. These results are in line with previous studies that have pointed out excessive fishing mortality and food web degradation caused by fishing in the Eastern and Adriatic fisheries (Libralato et al. 2010, Lotze et al. 2011, Tsikliras et al. 2015). On the other hand, the more stable catches observed in the Western Mediterranean and Ionian Sea could be the result of exploiting new species, as observed for the Mediterranean as a whole (Coll et al. 2014).

The trophic level of the catches for the whole Mediterranean Sea and as well for the majority of the sub-areas (Western, Adriatic and Ionian Seas) presented a clear 'fishing down' effect (Pauly et al. 1998) that occurs when top predators and large sized fish are removed from the ecosystem and gradually replaced by lower trophic level organisms. Similar trends had been observed in the Mediterranean Sea, both at regional (Pauly et al. 1998), sub-regional (Tsikliras et al. 2015) and more local scale (Stergiou 2005 , Shannon et al. 2014). The only exception was found in the Eastern Mediterranean Sea where, contrary to the rest of areas, a situation of fishing up was found. Accordingly to Stergiou and Tsikliras (2011), though, this might be a 'false fishing up effect' occurring when small pelagic fishes and invertebrates, with a low trophic level, and larger-size predators fish are both intensely fished and/or depleted.

Management and conservation implications of our results and conclusions

The Mediterranean has been exploited for centuries, suffering the impacts of continuous and multiple anthropogenic pressures (Coll et al. 2012, Micheli et al. 2013). Because of increasing signs of deteriorations and degradations at species-, community- and ecosystem levels (Coll et al. 2012, Colloca et al. 2013, Micheli et al. 2013), evidenced as well by this study, the basin is now of particular concern, and is a clear candidate for management actions to halt further decline and increase the sustainable use of marine resources (Katsanevakis et al. 2015). Hindcasting analyses, as performed in this study, allow assessing historical changes in the ecosystem and in its marine resources, and are necessary pieces of the tool kit needed to support management and conservation processes. Yet, to move toward more complete regional policy and conservation plans, several additional steps should be developed from this study in the near future.

First, spatial-temporal analyses able to identify spatial patterns that can directly assist spatial management actions (e.g., by prioritizing specific areas of concern), and facilitate the communication between scientists and policy makers, environmental managers, conservationists and the general public (Micheli et al. 2013) are needed to contribute to the recent Maritime Spatial Planning Directive (MSPD) of the European Commission (EC 2014a). A first attempt has been made in a recent study by Liquete et al (in press), which assessed temporally and spatially the delivery of five marine ecosystem services for the whole Mediterranean basin using several modelling approaches, including EwE and the preliminary results of the present research. However, as pointed out by these authors more work is needed to be able to support management decisions.

Second, the integration of additional human stressors (e.g., aquaculture, invasive species, changes in climate) as driving forces of species dynamics is needed to increase the reliability of this modelling exercise since marine ecosystems are impacted by simultaneous cumulative threats (Coll et al. 2012, Micheli et al. 2013). Currently the recent MSPD, which include the EU's Blue Growth Strategy (EC 2014b) that supports sustainable growth in emergent marine sectors (e.g., aquaculture, coastal tourism, marine energies), is expected to impose further pressures on the Mediterranean Sea (Coll et al. 2012, Piante 2015).

Third, the development of forecast scenarios, including different future management actions, is crucial for the implementation of management plans. Future scenarios should follow the Intergovernmental Panel on Climate Change (IPCC) projections on climate-induced changes in sea surface temperature. They should also consider the relevant elements of the Common Fisheries Policy (CFP) on commercially important stocks to exploit them at Maximum Sustainable Yield (MSY) levels and the reduction of fishing effort needed to develop effective and appropriate policy and conservation plans in the region (Colloca et al. 2013, Tsikliras et al. 2015).

To conclude, with anthropogenic pressures rapidly expanding in the Mediterranean Sea, there is a serious concern that these may push the system beyond the “point of no-return”, with consequence for marine biodiversity and the economies that depend on it, seriously constraining the ecosystem service options available to future generations. Ecosystem modelling tools can play a key role as suitable tools to analyse the suitable options towards ensuring the coexistence of sustainable human activities and the protection of healthy marine ecosystems like the Mediterranean Sea. Temporal hind-cast analysis has enabled us to assess changes in the historical dynamics of species/functional groups inhabiting this system, quantifying the role and impact of changes in primary productivity and fishing pressure. This constitutes an important first step further to advance in the regional assessment of the Mediterranean Sea ecosystem to inform conservation plans and management actions.

See Supplementary Information in Annex 5

Chapter 2.6

Summary of Results

Chapter 2.1

Models and modelled derived indicators potential to support the MSFD

Of the models (#44) reported in this study, more than half were coupled ecological models (Table 1 of Chapter 2.1). The most common type of models currently in the catalogue were hydrodynamic-biogeochemical models (36%) followed by end-to-end (18%), species distribution/habitat suitability, bio-optical and multispecies (14% each), biogeochemical and meta-community (2% each) models (Table 1 of Chapter 2.1). Coupled (both E2E and hydrodynamic-biogeochemical models) and bio-optical (remote sensing) models included in this catalogue were primarily spatially dynamic and 5 out of 30 models were also dynamic. The remaining models were mainly static with only 5 out of 14 models presenting dynamic and spatial modules as well (Table 1 of Chapter 2.1). Ecopath with Ecosim (EwE) was notably associated with the largest number of model-derived biodiversity indicators (Table 2 of Chapter 2.1). Not all the models were able to address uncertainty; the majority (61%) lacked an approach to determine confidence intervals/range of uncertainty or required further validation work for indicators. From the models that reported addressing uncertainty (39%), data comparison and data validation (e.g., model outputs fitted to surveyed data) was the most common method reported (Table 1 of Chapter 2.1). As for the model potential to support MSFD, the models were capable of addressing indicators in 8 of the 11 descriptors of the MSFD (Table 2 of Chapter 2.1). Within the biodiversity related descriptors, which was the focus of the study, non-indigenous species (D2) and seafloor Integrity (D6) were the most poorly addressed by the models currently in the catalogue (Table 2 of Chapter 2.1).

Regarding model based indicators, a total of 201 were included in this catalogue, of which more than half were considered to be “operational” (64%), while the majority of the remainder were still “under development” (33%), with only a few “conceptual” approaches (3%) presented (Table 2 of Chapter 2.1). Biomass indicators constituted the largest group with approximately 57% followed by diversity indices (13%) and physical, hydrological and chemical indicators (12%). The indicators concerned mainly fish, phytoplankton, zooplankton, benthic and pelagic invertebrates and marine mammals (total 64, 45, 31, 23, and 17, respectively) (Fig. 3 of Chapter 2.1), while the remaining biodiversity components were covered with less than 10 indicators each. EwE model-derived indicators, either operational, conceptual or still under development, have been used to model all types of biodiversity components (excluding microbes), with fish being the most frequently assessed group (25%) followed by benthic invertebrates (15%), marine mammals (12%) and cephalopods (11%). Looking at model type, multispecies models assessed the majority of biodiversity components with the exception of microbes that were mostly evaluated by coupled hydrodynamic–biogeochemical models (Fig. 3 of Chapter 2.1). The least addressed biodiversity components were microbes, coastal fish, pelagic elasmobranchs, baleen whales, seals and offshore pelagic birds. In relation to habitat, water-column was the most comprehensively evaluated habitat, specifically the continental shelf, while ice associated habitats, estuarine water column and shelf sublittoral mud were seldom covered (Table 5 of Chapter 2.1).

The majority of reported indicators related to the Mediterranean Sea, representing more than half of the indicators entered in the catalogue (137), followed by the North-East Atlantic Ocean (78), Black Sea (29), Baltic Sea (18), non-EU regional seas (11) and EU scale (2). The EwE software was the most widely used model and has been applied in each EU regional sea area and most sub-regions; the second most commonly used model was ECOSMO, which has been implemented for the Baltic Sea, the North-East Atlantic Ocean and one non-EU regional sea (Barents Sea). In most regional seas, the proportion of model-derived indicators considered operational was high (ranging between 60 and 80%), except for the Black Sea where a suite of ecological models had been developed but using model-derived indicators still under development (about 70%) at the time of the assessment.

Chapter 2.2

Reconstructed total catches

The reconstructed total catch for the 1950–2010 period exceeded by a factor of 2.6 the official catches reported by the FAO on behalf of Italy. Of this, approximately 79% was caught by industrial fisheries, 17% by artisanal fisheries, 3% by recreational fisheries and <1% by subsistence fisheries, while discards (7% of the total) were predominately (95%) from industrial fisheries (Fig. 3a of Chapter 2.2). Reconstructed total catches were relatively stable throughout the 1950s and 1960s, averaging about 700,000 t year^{-1}, before increasing between 1971 and 1979 to 1.1 million t year^{-1}. Thereafter, the annual catch plateaued at an average of 1.06 million t year^{-1} until 1986, then sharply decreased to 676,000 t year^{-1} by 1990. Annual catches remained steady in the early 1990s, with a small increase to 741,000 t in 1998, before again sharply decreasing and continuing the declining trend to the end of the time series in 2010, when catches were just 374,000 t (Fig. 3a of Chapter 2.2). Catches consisted of 92 taxa, of which 65 were identified to species, including higher pooled groups such as 'marine fishes nei' and 'marine invertebrates nei'. In terms of total tonnage, catches were dominated by small pelagic fishes, notably European anchovy (*E. encrasicolus*), which accounted for 18.1% of all catches (Fig. 3b of Chapter 2.2). The second most important taxon, in terms of tonnage (at least in earlier decades) was the European pilchard (*S. pilchardus*), which accounted for 12.5% of total catches overall, but has since declined substantially (Fig. 3b). The remaining taxa, grouped by family, contributing the most to the catches were molluscs (12.4%), Scombridae (9.0%), Sparidae (7.4%), crustaceans (5.6%), Carangidae (4.0%) and sharks and rays (3.9%; Fig. 3b of Chapter 2.2).

Official landings

In total, for the 1950–2010 period, Italian reported national landings ranged between approximately 220,000 and 721,000 t year^{-1}. These data were visibly higher (on average more than two times higher) than the data reported to FAO for the same time period which ranged from 171,000 to 430,000 t year^{-1}. Overall, there was a slight decrease in national reported landings between 1950 and the beginning of the 1960s, followed by an increase in the middle of the 1980s and a general and continuous decline to 2010. This differs from the trend in the FAO data which increases steadily in 1950 with a peak in 1985 and then fairly steadily declines in 2010 (Fig. 3a of Chapter 2.2). European anchovies and European pilchards were the main fish species reported in the national data throughout the different sub-regions, which began to decline in the beginning of 1980s (Fig. 3b of Chapter 2.2).

Fishing effort and Catch per unit of effort

Results indicated that artisanal vessels dominated in terms of vessels numbers, followed by trawlers and multiple gears (Fig. 5a of Chapter 2.2). Trawlers, on the other hand, had the highest fishing effort, in term of cumulative engine power (kWdays^{-1}), followed by purse seiners and artisanal fisheries (Fig. 5b of Chapter 2.2). With regards to all fishing fleet and their trends, number of vessels and fishing effort, decreased over time, after the maximum from the late 1970s to mid-1980s (with only multiple gears having their highest peak in the 1990s) and a steady decline thereafter. The CPUE trend showed a continuous decline since the 1950s with a maximum of ~9kg $kW^{-1}days^{-1}$ in the early 1950s and a minimum of ~3kg $kWdays^{-1}$ in the late 2000s (Fig. 6 of Chapter 2.2).

Unreported landings – Subsistence catches

The estimated subsistence catches for the 1950–2010 time period averaged 6400 t $year^{-1}$, with a maximum of 9100 t in 1982 and minimum of 4000 t in 2010, contributing only 0.9% of the reconstructed total catch (Fig. 3a of Chapter 2.2). In this case, the Central Adriatic Sea and Sicily had the highest removals, with approximately 91,400 t (23%) and 85,600 t (22%), respectively.

Unreported landings – Unreported commercial catches and discards

The estimated unreported catches for the illegal driftnet fishing fleet for the 1992–2010 period totaled 49,130 t, which consisted to 83% of swordfish and 17% of tuna species. The regions in which this illegal activity was prevalent were the South Tyrrhenian Sea and Sicily, which contributed 46% and 31% of the 49,130 t, respectively. Also, an illegal component from other industrial fishing fleets and the artisanal sector was added. In particular, a total of approximately 6 million t was estimated for the period 1950–2010, of which 76% and 24% came from industrial and artisanal fisheries, respectively.

Retained unreported by-catch per fleet type and per subdivision for the period 1950–2010 accounted for approximately 5 million t, averaging about 82,500 t $year^{-1}$, most of which came from industrial fisheries (95%) and from the Central Adriatic (~1.6 million t; 33%) and Sicily (1.2 million t; 25%). The major by-catch taxa were clams (Bivalvia; 604,000 t; 12.0%), sharks (Selachimorpha; 446,000 t; 8.9%), jacks (Trachurus spp.; 335,000 t; 6.7%) and rays (Rajidae; 283,000 t; 5.6%). Discards, on the other hand, were 3.4 million t. Since we applied a proportional rate to separate the retained by-catch from discards, the same patterns were observed for the regional subdivisions and discarded taxa. Discards and by-catch from bottom trawling represented the largest component, totaling 3.8 million t (Fig. 3a of Chapter 2.2).

Uncertainty

The ranges of uncertainty estimated for the reconstructed total catches showed wider confidence intervals in the first two estimation periods (1950–1969; 1970–1989) and a reduction only in the last period (1990–2010; Fig. 7 of Chapter 2.2).

Chapter 2.3

Trophic levels

The highest trophic levels (TL) were observed for *Tursiops truncatus* (TL=4.07), pelagic fish (mainly large pelagics, TL=4.05) and demersal fish 3 (mainly large demersals, TL=3.91). In contrast, annular seabream (*Diplodus annularis*), European sardine (*Sardina pilchardus*), European sole (*Solea vulgaris*), mullidae, demersal fish 2 (mainly sparidae species), mugilidae, other crustaceans zooplankton, benthic invertebrates, bivalves and gastropods and bacterioplankton had lower TL values ranging between 2.13 and 2.99.

Time series fitting

The best performances in fitting observed data were obtained when trophic interactions as well as fishing and environmental variables were included all together in the fitting procedure. The best model, which was the one with the lowest AICc, explained 78% of the variance of the data (Table 3 of Chapter 2.3). Environmental drivers in combination with trophic interactions were able to explain the majority of the variability observed in the ecosystem (77.2%) while fishing marginally contributed with a 1.8%. Different vulnerabilities were also tested and the largest improvement was obtained with 30 trophic interactions. The best model reflected quite well the biomass trends for the apex predators of the Amvrakikos Gulf. In particular, Ecosim was able to predict *Tursiops truncatus*, *Phalacrocorax carbo* and *Pelican crispus* abundance trends for the surveyed periods (Fig. 4 of Chapter 2.3). A slight improvement was found for seabirds when the mediation function was incorporated in the model, assuming an increased availability of prey on the surface of the water column. For bottlenose dolphins, on the other hand, the trend improved when a decrease in prey and feeding area was assumed. For forage fish species like *Sardina pilchardus* the model reproduced quite well the fluctuations in CPUE observed between 1980 and 2004, while predicted trends between 2005 and 2007 were overestimated. A similar scenario was also observed for mugilidae. A good reproduction of CPUE time series data was shown for *Trachurus*

trachurus, *Diplodus annularis*, mullidae and benthopelagic cephalopods. For these groups, however, the increase in biomass observed in the early 2000s was not picked up by the model. Ecosim was not able to represent well the fluctuations observed for *Penaeus kerathurus*. As for the other commercially important groups only few data points (from 2003 to 2007) were available resulting also in a poor fit (S4 in Supplementary material).

Regarding landings, Ecosim generally underestimated observed values, had difficulties in capturing the changes in catches although trends were vaguely captured for the majority of the groups (Fig. 5 of Chapter 2.3).

Ecological Indicators

Ecological state indicators calculated by Ecopath for the Amvrakikos Gulf (Table 2 of Chapter 2.3) revealed that the main flows in the system were flow to detritus (39%) and consumption (37%) followed by respiration (15%) and exports (8%). In addition, indicators addressing community energetics and cycling of nutrients such as the ratio between total primary production (PP) and total respiration (R) (Christensen, 1995; Odum, 1969), primary production/biomass ratio (PP/B) and the SOI (System Omnivory Index) suggested the system to be at an intermediate-low level developmental stage. The FCI (Finn's Cycling Index), the mean transfer efficiency (TE) and overhead showed relatively high values while ascendancy was quite low. Fishing indicators such as the primary production required (PPR) of the Gulf and the mean trophic level of the catches were respectively 8% and 2.77. The pedigree index of the model was 0.57. Trends in ecological indicators calculated by Ecosim revealed changes through time in the structure of the Amvrakikos Gulf ecosystem (Fig. 6 of Chapter 2.3). In particular, trophic level indicators mTLco and mTL_{2-3} increased since the beginning of 1980s. Similar trend was observed also for the ratio between pelagic and demersal species. The other two trophic level indicators, $mTL_{3.25}$ and mTL_{Tp}, showed clear decrease in time, with $mTL_{3.25}$ though increasing again from middle of 2000s. Kempton's biodiversity index fluctuated in time with a certain stability and no clear trend. On the contrary, mean trophic level of the catches (mTLc), fishing in balance index and relative PPR decreased since the beginning of the studied period.

Chapter 2.4

TLs and flows

The highest TLs were found for 'piscivorous cetaceans' and 'monk seals' (TL ≥ 4) while the other marine mammal group, 'other cetaceans', showed a TL of 3.53 (mainly because of the presence of 'zooplankton' and 'benthopelagic cephalopods' in their diet). 'Seabirds', despite being considered a top predator, showed a relatively low TL due to the presence of discards (mainly small pelagic fishes, Oro & Ruiz 1997, Bozzano & Sardà 2002) in their diet. Similarly, 'sea turtles' might have a higher TL than estimated by the model, but their diet also includes discards (Tomas et al. 2001, Gómez de Segura et al. 2003, Casale et al. 2008), and thus, they presented a fairly low TL (2.68) in the model. For the fish groups, 'large pelagic fishes' showed a relatively high TL (3.94), followed by 'European hake' (between 3.86 and 3.73), 'large demersal fishes' (between 3.68 and 3.56), 'sharks' (between 3.85 and 3.64) and 'rays and skates' (between 3.41 and 3.27). 'Medium' and 'other small' pelagic fishes were given a TL between 3.28 and 3.19 and between 3.14 and 2.89, respectively. 'European pilchard' and 'European anchovy' had TL values ranging between 3.25 and 3, while the lowest TLs were observed for 'medium' and 'small' demersal fishes and 'deep-sea fishes' (between 3.04 and 2.80). Of the remaining functional groups, 'benthopelagic' and 'benthic cephalopods' and 'jellyfish' reached TL> 3, 'crustaceans' showed values between 2.79 and 2.63, and 'zooplankton', 'bivalves and gastropods' and 'benthos' had TL values close to 2.

Looking at the 4 MSFD areas, comparing total biomass and mean TL of the community, the Adriatic and the Western Mediterranean Sea were the areas with the highest total biomass, followed by the Ionian and Eastern Seas (Fig. 3 of Chapter 2.4). During the 2000s, the mean TL of the community (TLco) differed considerably whether calculated using TLco ≥ 1 or TLco > 1 (i.e. excluding detritus and primary producers). For TLco≥ 1, the Adriatic was the area with highest mean TLco (1.86) followed by the Ionian (1.56), Eastern (1.5) and Western Mediterranean (1.49). For TLco > 1, the Western had the highest TLco (2.36), followed by the Eastern (2.34), Ionian (2.28) and Adriatic Seas (2.18) (Fig. 3 of Chapter 2.4). Several differences in TLs were also found between the 2 modelled time periods, with declines observed particularly in the Ionian and Eastern Mediterranean Sea in the 2000s compared to the 1950s (Fig. 4 of Chapter 2.4).

Trophic impact and keystone species

Among all MSFD areas, most predators had a direct negative impact on their prey through their diet preferences; functional groups negatively impacted themselves due to cannibalism/within group competition; demersal functional groups had a greater impact (either negatively or positively) on the majority of the other groups than pelagic functional groups, and 'zooplankton' and 'phytoplankton' groups most positively affected all other groups in the system (e.g. through a bottom-up effect).

MTI analysis in both time periods revealed changes in the role of 'pinnipeds' in the West, Adriatic and Ionian Seas, with a higher impact in the food web during the 1950s and almost no impact in the 2000s. In the Eastern Mediterranean, where the species still occurred in greater numbers, the impact on the food web was greater in 2000s than in the other 3 MSFD areas but still reduced compared to the 1950s. Similar trends were observed for 'piscivorous cetaceans' in all MSFD areas, where the group had a large effect in the 1950s but because of their reduced biomass, only had a limited effect in the 2000s. For fishes, 'European anchovy' and 'European pilchard' similarly affected the Mediterranean food web with greater positive impact on top predators, pelagic fishes and fisheries (particularly mid-water trawlers and purse seiners). Interestingly, 'sharks' were negatively impacting marine mammals either through direct competition for the same resources or niche overlap. Overall, lower TL organisms, namely 'benthos', 'crustaceans' and particularly 'seagrass', positively affected the rest of the food web.

Results also revealed that the role of fisheries in the different MSFD areas has changed with time, growing in impact from 1950s to 2000s, and affecting several groups in the different food webs. In general, if only the commercially exploited functional groups were considered, results showed a greater impact of bottom trawlers, mid-water trawlers and purse seiners (Fig. 7b of Chapter 2.4). More specifically, bottom trawlers and dredges had large negative impacts on targeted demersal species (mainly demersal fishes and 'molluscs') and on 'sea turtles' (incidental catches), while longline fisheries had large negative impacts on 'large pelagic fishes' (target species) and, through incidental catches, on 'sea turtles', dolphins and 'seabirds'. Mid-water trawlers and purse seiners showed negative impacts on targeted small pelagic fishes and, through direct competition for the same resources, on marine mam- mals and 'seabirds'. When all functional groups in the ecosystem were included in the analysis, artisanal fisheries seemed to be the fleets with greater negative impact, particularly in the Western, Ionian and Eastern Mediterranean Seas (Fig. 7a of Chapter 2.4). Recreational fisheries had a negative impact on 'large pelagic fishes' and 'sharks' in the Western, Adriatic and Ionian Seas and on 'medium' and 'small' demersal and 'medium' and small pelagic fishes in the Eastern Mediterranean.

The results obtained from the keystoneness analysis (Fig. 8 and Table S6 in the Supplement of Chapter 2.4) revealed that in the 1950s ecosystem, 'large pelagic fishes' had the highest overall keystoneness role followed by 'sharks' and 'medium pelagic fishes' groups, whereas in the 2000s ecosystem, 'medium pelagic fishes' were replaced by 'benthic' and 'benthopelagic cephalopods'. Interestingly lower TL groups (e.g. 'zooplankton', 'phytoplankton' and 'benthos') were also identified in both time periods as keystone groups, probably caused by their overall low biomass and high P/B (characteristic of oligotrophic systems) and important role in the ecosystem. In both time periods, marine mammals, in particular 'pinnipeds' and 'piscivorous cetaceans', appeared within the least important keystone groups.

Comparison among European regional seas

The statistics and main indicators calculated from the whole Mediterranean Sea ecosystem model representing the 2000s were compared with other modelled European regional seas for the same or similar period (Table 2 of Chapter 2.4). The TST revealed that the main flows driving the Mediterranean Sea were flow to detritus (42%) and exports (39%) followed by consumption (15%) and respiration (5%). In the Baltic, North and Black Seas, on the other hand, consumption seemed to be the flow with the highest importance (around 43−48%) followed by flow to detritus (22−30%), respiration (20−23%; in the Black Sea, this flow constituted the second most important flow, with 29%) and exports (1−6%). Looking at ecological indicators addressing community energetics and cycling of nutrients, under Odum's theory (Odum 1969), our results suggest that the Mediterranean Sea ecosystem is at an early developmental stage. This was visible, for example, in the ratio between total primary production (PP) and total respiration (R) (Odum 1969, Christensen 1995) or in the primary production/biomass ratio (PP/B). On the other hand, the indicators from the other European Seas suggested that systems fell within an intermediate-low level developmental stage. For the SOI, despite the low general values, the Mediterranean Sea showed the highest value, while in relation to the

2 cycling indices, the Mediterranean basin had the highest values in PCI and the lowest in FCI. For each European regional sea, ascendancy was relatively low, whereas overhead was high. As for fishing indicators, the PPR% of the Mediterranean was 0.81%, the lowest among the other seas, while TLc was 3.04 in the Mediterranean Sea, similar to the Black Sea and lower in comparison to the other European Seas with higher TL values (between 3.3 and 3.7).

Chapter 2.5

Time series from the model fitting

The most statistically significant results in our model fitting exercise were obtained when trophic interactions, fishing and the primary productivity changes were included together in the model run (Step 7 in Table 3 of Chapter 2.5). Differences were found among the five areas with the "best" fitted models (lowest AICc) explaining between 50% and 69% of the variance of the data (Table 3). By looking at each area separately, the Ionian Sea sub-model was the one that showed the smallest improvement of prediction capabilities (thus the AICc estimates declined the least), while the Eastern followed by the Western Mediterranean were the areas with the biggest improvement from the baseline AICc estimates. Both fishing and primary productivity drivers, when considered individually, were able to enhance the fit of all areas by ~16% to ~50% (when using the predicted PP anomaly) and by ~10% to ~37% when using fishing effort (steps 3 and 5 in Table 1 of Chapter 2.5). The addition of trophic interactions to changes in PP anomaly alone (step 4 in Table 1 of Chapter 2.5) provided the second largest improvement for the Western, Ionian and the whole Mediterranean Seas (AICc reduced further by ~10%). For the Adriatic Sea this was obtained with the addition of trophic interactions to fishing effort (step 6 in Table 1 of Chapter 2.5). Also, different vulnerabilities were tested and the largest enhancement was obtained using high vulnerabilities (step 7 in Table 3 of Chapter 2.5) for both the four sub-models (maximum predator prey-interactions or Vs: #24) and the additional Mediterranean model as a whole (maximum predator prey-interactions or Vs: #2).

When we checked for correlation between the PP anomaly resulting from the Ecosim fitting procedure and the PP from the biogeochemical model, in all the areas except for the Adriatic Sea both PP time series were positively correlated with high significance. On the contrary, the Adriatic Sea showed a negative correlation and highly significant (Table 4 and S7 Figure of Chapter 2.5). Using the "best" fitted models, Ecosim reproduced satisfactorily the biomasses trends for some of the functional groups with available survey data in all sub-areas (Fig 3 and Fig 4 of Chapter 2.5). Overall, forage fishes (functional groups nº 8-9), demersal fishes (nº 12-14) and invertebrates (nº 18-19 and 21) showed a good fit in the different sub-models, while deep sea fish (nº 15) and benthos (nº 23) were the least well fitted (Fig 3, Fig 4 and S7 Figures of Chapter 2.5). These latter groups are the ones with the fewest data points. A satisfactory fit was also shown for sharks and rays/skates groups (nº 16-17), and, despite only few observed records, also for pinnipeds (nº 3).

By looking at biomass trends per area, in the Western Mediterranean, the predicted time series suggested a decreasing pattern for the biomasses of several functional groups (Fig 3 and S8 Figure of Chapter 2.5). European pilchard showed a decline from the beginning of our study period (1950), which became more pronounced in the last years of the surveyed period. A similar result was also observed for medium and small demersal fishes, and pinnipeds, although the model was not able to capture the sharp decline of these marine mammals in the 70s. As for sharks, rays/skates the model confirmed a decrease in trends until the end of the 1990s and a slightly increase in the 2000s decade. For European anchovy and hake, Ecosim had difficulties reflecting observed variations in their biomass, although suggesting a decreasing trend for both species. A poor fit was observed for benthos and deep fish, where only few data points were available. A good reproduction of biomass time series was found for crustaceans and benthopelagic cephalopods where the model was able to follow the majority of the fluctuations in time (Fig 3 and S8 Figure of Chapter 2.5). When the model was run using the PP from the biogeochemical model as an alternative primary productivity driver, we observed similar pattern as the ones obtained using the PP Ecosim anomaly and for certain species/functional groups (nº 8 and nº 21 in Fig.3 of Chapter 2.5) the fit improved.

As for the Western Mediterranean, also in the Adriatic Sea, Ecosim suggested a more/less pronounced decline for demersal and pelagic fish and for some invertebrates (Fig 3 and S8 Figure of Chapter 2.5). In particular, the model was able to capture the steep decline of pinnipeds observed in the area since mid-1970s and a less marked decrease of medium and small demersal fish observed in mid 1990s. Ecosim captured some of the pattern observed for European hake, sharks, rays/skates suggesting a decline of the groups until the end of the 1990s, followed by a slight increase or by fluctuations (in the case of European hake) in the last years of the studied period. An overall satisfactory match between predicted and available data was found for benthopelagic cephalopods where a decrease was captured since the beginning of the survey period, and for benthic cephalopods and crustacean where the model followed some of the fluctuation of the groups and a slight increase at the end of 2000s. Again, the model did not represent the trends well for deep sea fish (S8 Figure in Supplementary materials of Chapter 2.5). Regarding forage fish, when we run the model using PP anomaly as driver, Ecosim was not able to reflect the decreasing biomass trend observed in European anchovies, while it was able to pick up a general decline for European pilchards. However, it was when we applied the PP from the biogeochemical model in the model run that Ecosim was able to follow the steep decline observed in European anchovies in mid 1970s and improve also slightly the decline of European pilchard. For the other species/functional groups, different trends were observed using the two different PPs particularly in the decades before the beginning of our time series of observations (Fig 3 and S8 Figure of Chapter 2.5). The Ionian Sea resulted to be the area with less biomass changes during the years with available survey data (Fig 4 and S8 Figure of Chapter 2.5). Except for pinnipeds, where the model was able to pick up the decline since the late 1970, despite the presence of only few data points, all the other groups didn’t show any directional variation in time resulting mainly in a series of fluctuations. However, by looking at the overall time period (1950-2011), the model suggested a small increase in biomass since the beginning of 1990s for small demersal fish and crustaceans. The model partly underestimated and was not able to capture the biomass trends for European pilchards and medium demersals (Fig 4 and S8 Figure of Chapter 2.5) and it did not represent well the trend for benthos (S8 Figure in Supplementary materials of Chapter 2.5). The use of PP from the biogeochemical model improved slightly the fit for crustaceans, sharks and benthopelagic cephalopods while maintaining the same pattern observed with the PP anomaly.

In the Eastern Mediterranean, different trends among species/functional groups were detected (Fig 4 and S8 Figure of Chapter 2.5). Ecosim represented relatively well the biomass declines of European pilchards and anchovies since the 1990s, despite underestimating the high peaks observed at the beginning of this decade. The model was able to capture the biomass trends for European hake, sharks, small demersals, rays/skates, benthic cephalopods and crustaceans. All these groups showed similar patterns with signs of decrease in the 1990s and fluctuations afterwards. An underestimation of biomass by the model was predicted for medium demersal fish, benthopelagic cephalopods, deep sea fish and benthos where the model was not able to reproduce observed trends and fluctuations (Fig S8 in Supplementary materials of Chapter 2.5). A good fit, even though for only few data points, was found for pinnipeds where the model was able to represent the fluctuation of these marine mammals in time (Fig 4 of Chapter 2.5). The predicted trends obtained using PP from the biogeochemical model were similar to the ones found using the PP anomaly and for European hake, sharks, small demersals, benthic cephalopods and crustaceans the fit slightly improved. Ecosim was able to represent the decrease in biomass of large pelagic fish particularly since the 80s, while it failed to capture the fluctuation observed in the end of the 2000s when looking at results from the whole Mediterranean model for the two highly migratory species for which we had survey data: large pelagics and sea turtles. In the case of the sea turtles, the model approximated the general increasing biomass trend of this reptile, but it failed to reproduce its fluctuations over time (Fig 5 of Chapter 2.5). We observed similar results with the PP from the biogeochemical model as a driver.

The time series of catch trends estimated for the five areas, when compared with independent data, showed a general satisfactory match (Fig 6 and S9 Figure of Chapter 2.5): the sub-models overestimated or underestimated some fractions of the time series trends, but overall they were able to capture long-term trends similar to those observed (Fig. 6 of Chapter 2.5). In the Western Mediterranean, an increase (up to the end of the 1990s) and posterior decrease in catches were predicted for the majority of the groups with the exception of small pelagic fish, large demersal and benthic cephalopods that continued to increase even afterwards. Non-significant trend was simulated for rays/skates, while the model was not able to reflect the trend observed for benthopelagic cephalopods. Regarding large pelagic fishes, catches predicted for the whole

Mediterranean were similar to those observed until the 1980s, but the predicted catches did not reflect the increase observed in the last two decades (Fig 6a of Chapter 2.5).

In the Adriatic, as for the Western Mediterranean, the model simulated the decrease in catches observed in the beginning of the 1990s for the majority of the functional groups while it did not managed to pick up the sharp decline of European anchovies in mid 1970s and of European hake and sharks in the 1990s (Fig 6b of Chapter 2.5). In the Ionian Sea, predicted results reflected the increase in catches until the end of 2000s for the majority of the functional groups. For European hake, medium demersal benthic cephalopods, sharks and rays/skates, though, such increase turned into a decrease approximately around the 1990s (Fig. S9c in Supplementary materials of Chapter 2.5). In the Eastern Mediterranean Sea, predicted results reproduced quite well the increase in catches for the majority of the functional groups until the 1990s and the decline afterwards and they also captured the continuous increase for benthopelagic cephalopods and small pelagic fishes. On the other hand, simulated results did not match the sharp decline of sharks observed since the 1980s in the region (Fig. S9d in Supplementary materials of Chapter 2.5).

Temporal model-based ecological indicators

Trends in ecological indicators calculated from Ecosim temporal outputs showed different patterns if we looked at each sub-regional sea individually or at the Mediterranean ecosystem as a whole. For example, considering the entire Mediterranean Sea, a clear decreasing trend was observed in community biomass indicators like the forage fish biomass and, to less extent, for demersal fish, the Kempton's biodiversity index and in all the trophic level indicators considered (TLco, TL≥3.25 and TL Catch) (Fig 7 of Chapter 2.5). On the contrary, an increase was predicted for invertebrate biomass while no clear trend was visible for sharks and rays/skates. Total catch was the only indicator that clearly increased in time (until 1990s) and that gradually decreased afterwards. These patterns were also reflected through the Spearman correlation test (Fig. 8 of Chapter 2.5).

Considering sub-regional seas (S10-S13 Figures in Supplementary materials of Chapter 2.5), we observed a clear decline of forage fish, demersal fish and sharks/rays-skates biomasses in the Western and Adriatic Seas, a fluctuation of these groups in the

Ionian Sea while in the Eastern Mediterranean they respectively decreased, increased and fluctuated. Invertebrate biomass slightly decreased in the Adriatic Sea; fluctuated in the Western and Ionian Seas; and increased in the Eastern Mediterranean. The Kempton biodiversity index decreased in the Western and in the Ionian Sea, it showed a slight increase in the Adriatic while no clear trend was visible in the Eastern Mediterranean. Total catch increased in all the areas until the beginning of 1990s but in the Western and Ionian Seas started to fluctuate afterwards while in the Eastern and Adriatic Sea it gradually declined. As for the different trophic level indicators assessed, the mean TL of the community slightly increased in the Western Mediterranean and decreased in the other sub-regions, while the mean TL ≥3.25 and mean TL catches decreased in all the seas except in the Eastern Mediterranean where they respectively fluctuated with no clear trend and slightly increased (S10-S13 Figures in Supplementary materials of Chapter 2.5).

When we tested the significance and correlation of our suite of temporal ecological indicators we noticed that in the Western and the Adriatic Seas the majority of the time series were negatively correlated with high significance (respectively 6 and 7 out of 9 indicators; Fig 8 of Chapter 2.5). On the contrary, in the Ionian Sea and Eastern Mediterranean Sea, the community indicators (except for forage fishes in the Ionian that showed a weak negative correlation) were highly significant and positively correlated (Fig 8 of Chapter 2.5). Also, we observed no significant and weakly correlated trends for mean TL ≥3.25 and Kempton biodiversity index in the Eastern Mediterranean Sea.

CHAPTER 3.

GENERAL DISCUSSION

In this thesis I investigate the status of the Mediterranean Sea ecosystem and the sustainability of its marine resources using an interdisciplinary approach, which combine data integration and modelling approaches. During this study a number of specific objectives were addressed, together with the identification of important data gaps/limitations. Before focusing on the Mediterranean Sea ecosystem, I reviewed the capabilities of ecological models developed for European seas to support main European Union policies, highlighting gaps, development needs and recommendation to undertake for further analysis (Chapter 2.1). Results from this first chapter guided the methodological approach used during the rest of the PhD thesis. In Chapter 2.2, I presented one of the important steps needed when building an ecosystem model of a marine ecosystem, which is related to data collection and analysis and, in this particular case, to data regarding fisheries in Italian waters. This second chapter evidenced the limitiations of some data availability regarding fishing exploitation in the Mediterranean Sea, limitations that were taken into account in the following chapters. The core of the thesis was the use of an ecosystem modelling approach (Ecopath with Ecosim [EwE]), applied first to a small area of the Mediterranean Sea, the Amvrakikos Gulf, Greece (Chapter 2.3) and then to the Mediterranean Sea ecosystem as a whole (Chapters 2.4 and 2.5). Results from chapters 2.3, 2.4 and 2.5 highlight the importance of considering local vs regional scale assessments when dealing with the study of marine ecosystem processes and translating relevant results to management processes. In these last three Chapters I evaluated past and current exploitation status of targeted commercial species and important functional groups of the Mediterranean marine ecosystem, putting a special effort in the historical role and impact of fisheries and primary production changes on the dynamics of the marine ecosystems and on specific compartments of the food web (such as top predators, forage fish and invertebrates).

1. Data gaps/limitations

When building Mediterranean ecosystem models both at regional scale but also at more local scales, an important issue is that data availability, accessibility and quality is a major constraint. However, because of the complex nature of ecosystem models that require large amount of multidisciplinary and good quality data (Mora et al. 2016), such limitation was found common not only in the Mediterranean Sea but also in many ecosystems models around the world (Chapter 2.1; Piroddi et al. 2015, Mora et al. 2016).

In the Mediterranean Sea region, in particular, the major pitfalls encountered were related to temporal changes in diet composition, the availability of biomass estimates for specific species or groups (e.g., non-commercially important species, deep-sea organisms) and fisheries data. This is particularly relevant for early decades (1950s-1970s) and for southern Mediterranean countries, where survey data remains still either inaccessible or absent (Chapters 2.3-2.5). Differences in data gaps were found when working at local (Chapter 2.3) and regional scales (Chapter 2.4-2.5). Among all, temporal biomass data for marine mammals and seabirds that were available in the small area of the Mediterranean Sea modelled in this thesis, the Amvrakikos Gulf (in Greece), were lacking for the regional scale. This is not surprising since local studies tend to have more empirical data for specific components of the ecosystem (Guarnieri et al. 2016), whereas regional/global studies have more aggregated and sparse data (Halpern et al. 2015). Such limitation increased the difficulty of building an ecosystem model for the Mediterranean Sea as a whole capable of capturing sub-regional differences in environmental and biological characteristics. This raises the need to increase effort in regional survey/assessments as already highlighted before in the course of other integrated assessments and projects (Coll et al. 2010, Coll et al. 2013a, Micheli et al. 2013, Katsanevakis et al. 2015). It also points out an important limitation at the whole Mediterranean scale to perform regional assessments: the lack of common and standardized datasets regarding important ecosystem components that could be used as ecological indicators to assess the good environmental status of the basis (Katsanevakis et al. 2015, Chapter 2.1: Piroddi et al. 2015).

A common limitation found among the different scales, local (Amvrakikos Gulf; Chapter 2.3), national (Italy; Chapter 2.2) and regional (Mediterranean Sea; Chapter 2.4-2.5), was related to fisheries data (e.g., effort, catch and discards). For example, the fitting procedure utilized in Chapter 2.5 enabled to detect issues related to landings data at the beginning of our survey period (in the 1950s as established in our Ecopath baseline). Low fishing mortalities for the three most important commercial species (European pilchard '*Sardina pilchardus*', anchovy '*Engraulis encrasicolus*', and hake '*Merluccius merluccius*') were, in fact, observed in the 1950s, in each Mediterranean sub-area, between

5 and 10 times lower than the average reference values reported for these fish stocks in the Mediterranean Sea (Patterson 1992, Colloca et al. 2013, Tsikliras et al. 2015). Even the assessment of the Italian fisheries (Chapter 2.2) was able to highlight such discrepancies. In particular, the reconstructed total catches were 2.6 times the landings officially reported by the FAO on behalf of Italy for the same period and same sea, with unreported commercial landings (from both industrial and artisanal sectors) contributing 50% to the total catch (in relation to FAO reporting) and discards contributing another 7%.

In the Mediterranean areas, several studies, included work developed in this thesis (Chapter 2.2), have demonstrated how fisheries statistics are generally incomplete and unreliable (Coll et al. 2013a, Moutopoulos & Koutsikopoulos 2014, Pauly et al. 2014). This is especially true in relation to the catches that are often un-reported and underestimated (EC 2003, Garibaldi & Kebe 2005, Garibaldi 2012) and makes the assessment of fisheries impacts on Mediterranean marine ecosystems a challenging task. For this reason, I decided to reconstruct the Italian fisheries (both reported and un-reported catches and effort), as shown in Chapter 2.2, with the goal to include this assessment in the Mediterranean modelling work. In particular, this study was conducted as part of an overall effort to reconstruct global fisheries catches (Pauly & Zeller 2016) by the Sea Around Us (www.seaaroundus.org), which also included other Mediterranean countries such as Spain (Coll et al. 2014), Greece (Tsikliras et al. 2007, Moutopoulos & Koutsikopoulos 2014), and Turkey (Ulman et al. 2013). Unfortunately at the time of developing this study, the catch reconstruction for the entire Mediterranean Sea was not completed and publically available, therefore it was not possible to integrate the Mediterranean reconstruction information, including Italy, in the modelling work at the regional scale of Chapter 2.4-2.5. The catch time series used in those last two chapters is based on official data distributed by the Food and Agriculture Organization (FAO) of the United Nations. In the near future and when available, the alternative database regarding catch reconstruction will be integrated in the regional modelling effort started under this thesis to reduce the above-mentioned data gaps and the impact of fishing pressure on the Mediterranean marine ecosystem using the two data sources will be compared.

I recognize that, because of the caveats explained above, uncertainties in the modelling results remain high. However, studies presented here include the best available data at the time (see Supplementary material of Chapters 2.2-2.5), use models for which outputs have been tested, and when possible validated (Macias et al. 2014), or that have been widely utilized to assess temporal biomasses for fish stocks (Walters et al. 2008) and highlight main gaps and difficulties encountered along the modelling process (Chapters 2.2-2.5). Also, when possible, uncertainties are assessed and presented. In the reconstruction of the Italian catches (Chapter 2.2), for example, a scoring factor (ranging between 1 -less robust data, to 4- more robust data), is assigned to each fishing sector and then converted to percentage confidence intervals following same criteria developed and used by the Intergovernmental Panel on Climate Change (Mastrandrea et al. 2010). In Chapter 2.3 and 2.5, respectively the Amvrakikos Gulf and the Mediterranean Sea, models are statistically fit to observed data; and in Chapter 2.5 a Monte Carlo routine is applied to assess model output sensitivity around the input parameters of the Mediterranean Sea ecosystem model, on the temporal analysis related to biomass estimates of species and functional groups and on model-based indicators.

Despite the fact that the majority of ecosystem models in European waters still lack a standardized approach that takes into account the uncertainty of modelled data (both input and output parameters), as shown in Chapter 2.1, statistically fit models with measure of uncertainties in model parameters (such as biomass) are critical if the purpose of modelling is to inform policy and management processes (Fulton et al. 2003). Further effort should be conducted to fill knowledge and data gaps. Yet, with the data currently available, this thesis presents the best approximation to assess the historical and current environmental status of Mediterranean marine exploited ecosystems, with emphasis on local to regional scales.

2. Major findings

The Mediterranean marine ecosystem: structural and functional traits

Results from both the static (Chapter 2.4) and dynamic (Chapter 2.5) components of the modelling effort developed for the entire Mediterranean Sea ecosystem have highlighted that the trophic flow dynamics of the Mediterranean marine ecosystem is mainly dominated by lower trophic level organisms, particularly 'benthic invertebrates', ‘zooplankton’ and ‘phytoplankton’ and driven by bottom up processes. This has been observed at regional, sub-regional (this study) and at smaller scales (e.g., this study, Coll et al. 2006, Coll et al. 2007, Tsagarakis et al. 2010, Moutopoulos et al. 2013, Torres et al. 2013) and named as the ‘Mediterranean paradox’ for the capability of the ecosystem to produce relatively high fish abundance despite the oligotrophic characteristic of the basin (Sournia 1973, Macias et al. 2014). Among the top predators, marine mammals and large pelagic fish resulted to be the groups with the highest trophic levels, with the ‘Mediterranean monk seal’ (*Monachus monachus*) being on top of the food web followed by ‘piscivorous cetaceans’ and ‘large pelagic fish’. As shown by the temporal trend analysis of Chapter 2.5, these large predators (in our case monk seals, large pelagic fish and partially sharks) have undergone drastic declines in time due to anthropogenic pressures (mainly fisheries), followed by an increase in abundance of groups at lower trophic levels (e.g., invertebrates). This has been already observed in other studies (Ferretti et al. 2008, Coll et al. 2009a, Coll et al. 2009c, Piroddi et al. 2010, Maynou et al. 2011). Part of these declines are also reflected in the results of the keystone analysis of Chapter 2.3 where top predators (except ‘large pelagic fishes’) have shown a diminishing ecological role in the ecosystem and been replaced, in recent years, by cephalopods. Cephalopods have been identified as a keystone group in many local Mediterranean food webs (Catalan Sea: Coll et al. 2006, North Aegean Sea: Tsagarakis et al. 2010, Gulf of Lion: Bănaru et al. 2013, Gulf of Gabes: Hattab et al. 2013, Gulf of Cadiz: Torres et al. 2013). Despite the fact that the role of cephalopods in the overall structure and functioning of marine ecosystems remains poorly understood, this study confirms that they are a key element in current marine food webs (Coll et al. 2013b).

The regional assessment presented in Chapters 2.4 and 2.5 has also revealed signs of decrease for organisms located in the middle of the Mediterranean food web. For example, forage fish (‘European sardine ‘*Sardina pilchardus*’, and anchovy ‘*Engraulis encrasicolus*’), which are important structuring species of the Mediterranean food web having high biomasses and high proportions in the catches (almost 40% of total landings; FAO 2012) were observed to decrease, at different time scale, in the majority of the Mediterranean Sea. This is likely due to excessive fishing pressures and changes in primary productivity, confirming the trends already highlighted in smaller areas of the

Mediterranean Sea (Coll et al. 2007, Palomera et al. 2007, Piroddi et al. 2010, Tsagarakis et al. 2010, Van Beveren et al. 2016). The local (Chapter 2.3) and regional scales (Chapters 2.4 and 2.5) models showed similar results in relation to demersal fish stocks which were observed decline. However, while for the regional Mediterranean Sea assessment, increase fishing pressure seemed to have been the major player impacting these stocks, as observed by other studies (Colloca et al. 2013, Vasilakopoulos et al. 2014), a degradation of the ecosystem, mainly caused by eutrophication and contaminants, was the major reason for the decline of demersal fish in the Amvrakikos Gulf (Koutsikopoulos et al. 2008, Ferentinos et al. 2010).

When comparing the Mediterranean Sea to other European seas (North, Baltic and Black Seas; Chapter 2.4) several differences were observed. In particular, the Mediterranean Sea stood alone in relation to the type of energy and matter flows (mainly flow to detritus and exports) and the cycling indices (Predatory cycling index; Finn's cycling index) (Odum 1969, Christensen 1995) suggesting higher levels of community stress induced by intensive fishing activities, as previously illustrated (Costello et al. 2010). In regards to ecosystems development, the Mediterranean Sea appeared to be in an early development stage, different from the other systems, probably because the ecosystem has been perturbed continuously over a long period of time. Indeed, when ecosystems develop, biomasses and complexity tend to increase and mature, whereas when they are disturbed, e.g. by fishing, they show the opposite trend and stay 'young' (Odum 1969, Christensen 1995). This was also observed in the Amvrakikos Gulf (Chapter 2.3), suggesting that such conditions (young and less complex), typical of "semi-closed" ecosystems, occur where bottom-up processes drive the system and where possibly high levels of community stress are induced by anthropogenic (e.g., fishing) and environmental forces (e.g., changes in primary production [PP]) (Heymans et al. 2014).

The Mediterranean marine ecosystem: ecosystem drivers

Both fishing pressure and primary production (PP) changes played an important role in describing the temporal dynamics of the Mediterranean marine ecosystem. Results presented in this study (Chapters 2.3, 2.4 and 2.5) indicate that temporal variation of PP in the system was the strongest driver upon the Mediterranean Sea ecosystem. This confirms the results obtained from other local studies (Coll et al. 2009b, Macias et al. 2014) that have shown how the Mediterranean Sea is driven by bottom-up processes where nutrient availability controls the biological characteristics of the region. The use of relative PP trends from a regional biogeochemical model in this study helped validating the predicted PP anomaly trend from the ecological model and improved the temporal dynamics of selected species in the ecosystem (particularly for small pelagic fish) (Chapter 2.5). This was clearly visible, for example, in the Adriatic Sea where PP anomaly unsuccessfully reproduced the trends of European anchovies while PP from the biogeochemical model was able to capture the trends. Since there are no official long-trend (from the 1950s) records of primary production in the region (Macias et al. 2014), using coupling hydro-dynamic biogeochemical models with ecosystem models (e.g., EwE) becomes critically important, particularly in complex areas like the Adriatic Sea that has diverse physical and biological oceanographic characteristics (e.g., eutrophic in the north, oligotrophic in the south; Polimene et al. 2006) and it is also subjected to strong anthropogenic pressures (e.g., fishing) (Coll et al. 2009c, Steenbeek et al. 2013).

In this study, historical changes in PP at regional, sub-regional and local scale were used to assess the response of the Mediterranean Sea ecosystem to changes in the environment. However, other environmental factors (e.g., SST, O_2) influence the dynamics of the Mediterranean Sea ecosystem (Stergiou et al. 2016) and they should be taken into account in future modelling efforts. This might improve the description of the dynamics of certain groups and areas (e.g., Ionian Sea) that were not well captured by the current Mediterranean models (Chapters 2.3, 2.4 and 2.5). Thus, future work will be dedicated to develop this part of the modelling approach further.

This thesis also highlights that fishing was an important driver affecting the dynamics of fish populations and invertebrates of the Mediterranean Sea ecosystem. This is in line with previous studies that highlighted the increasing impact of fishing in the Mediterranean Sea and the overexploitation of its marine resources (Colloca et al. 2013, Vasilakopoulos et al. 2014, Tsikliras et al. 2015). Simulations of Chapter 2.5, in fact, are able to reflect the impact of increased fishing effort in the basin starting, in all the four sub-areas (Western Mediterranean, Adriatic, Ionian and Central Mediterranean and Eastern and Levantine), since the beginning of 1950s. Nominal fishing effort showed decreasing trends only after 2000; the only exception was found in the Eastern Mediterranean Sea where fishing effort was observed fluctuating in the 2000s decade. Similar decreasing trends in fishing effort observed in the Mediterranean Sea were also found in Italy (Chapter 2.2) and the Amvrakikos Gulf (Chapter 2.3) despite the decline that started at the beginning of 1980s. Since official records and statistics of fishing effort are often unable to capture real trends in fishing capacity (because of biases and misreporting), as observed for example in the Catalan Sea (Gorelli et al. 2016), reconstructing fishing effort, as shown in Chapters 2.2, 2.3 and 2.5, becomes critically important for understanding its historical evolution and impact on marine resources and for effective management measures to be placed (Hilborn & Walters 1992).

Fishing, as presented in Chapters 2.2, 2.4 and 2.5, was shown to be an important driver affecting the abundance of the Mediterranean stocks over time. For example, the mixed trophic impact analysis of Chapter 4, indicated bottom trawling and dredges to be the fisheries with the widest impact on the Mediterranean food web, particularly on the demersal community. This has been observed in several smaller areas of the Mediterranean Sea representing continental shelf and upper slopes (e.g., Coll et al. 2006, Coll et al. 2007, Puig et al. 2012, Bănaru et al. 2013, Hattab et al. 2013). In the same analysis the impact by artisanal fisheries on the ecosystem is shown to have increased in time.

Overall, our results for the entire Mediterranean Sea reveals a continuous increase in catches with a slight downtrend from mid 1990s showing high level of exploitation in the region. Since signs of deteriorations are continuously recorded in the region (Lotze et al. 2006, Vasilakopoulos et al. 2014), such pattern could mean that catch composition, having highly diversified targeted species, continues to change in time as a result of fisheries expansion to further and deeper fishing grounds (Coll et al. 2014, Pauly et al. 2014). A different picture was detected when looking at total catches per sub-regional area, where clear signs of decrease are noticed mainly in the Adriatic and the Eastern Mediterranean Sea and only in the last years also in the Western Mediterranean and Ionian Seas. These results are in line with previous works that point out the excessive fishing mortality and food web degradation caused by fishing in the Eastern and Adriatic fisheries (Coll et al. 2009, Libralato et al. 2010, Lotze et al. 2011, Tsikliras et al. 2015). On the other hand, the more stable catches observed in the Western

Mediterranean and Ionian Sea could be the result of exploiting new species, as observed for the Mediterranean as a whole (Coll et al. 2014). Trends in trophic level of the catches both at regional, sub-regional and local scale presented a clear 'fishing down' effect (Pauly et al. 1998) that occurs when top predators and large sized fish are removed from the ecosystem and gradually replaced by lower trophic level organisms. Such patterns were observed by other studies in the Mediterranean Sea both at regional (Pauly et al. 1998), sub-regional (Tsikliras et al. 2015) and more local scale (Stergiou 2005 , Shannon et al. 2014). The only exception was found in the Eastern Mediterranean Sea where, contrary to the rest of areas, a situation of fishing up has been described. Accordingly to Stergiou and Tsikliras (2011), though, this might be a 'false fishing up effect' occurring when small pelagic fishes and invertebrates, with a low trophic level, and larger-size predators fish are both intensely fished and/or depleted.

Ecological processes at regional vs sub-regional vs local

Ecological indicators (Chapter 2.5) for the Mediterranean Sea ecosystem as a whole confirmed the historical changes in the structure of the Mediterranean Sea ecosystem and an overall ecosystem degradation over time caused by the combined effect of excessive fishing pressure and changes in productivity. In particular, decreasing trends were observed for forage and demersal fish biomasses, while an increase and a series of fluctuations were found respectively for invertebrates and sharks/rays and skates.

Difference patterns were instead depicted when considering the sub-regional seas individually (Western, Adriatic, Ionian, Eastern). The Western and the Adriatic Seas resulted to be the most degraded ecosystems with the largest biomasses declines among all the communities assessed (from forage fish to sharks/rays and skates except for invertebrates that remained stable in time). The Ionian Sea resulted to be the area with less biomass changes that didn't show any clear trends but instead a series of fluctuations in time. Since there are no additional studies that have looked at biomass and ecological indicators trends per sub-regional sea, it is difficult to validate these results. However, our overall findings are in line with other assessments conducted for smaller areas of the Mediterranean Sea (Catalan: Coll et al. 2006, Coll et al. 2008, Adriatic Sea: Coll et al. 2009c). The only exception is the Ionian Sea; several studies in the area have shown decreasing trend in the abundance of many commercial and no commercial species (Patti et al. 2004, Machias et al. 2008, Piroddi et al. 2010) that were not well captured in this work. Among the possible causes of such differences are the poor quality of the data and/or some missing components (e.g., oceanographic characteristics) not accounted for in our modelling framework. For this reason, this aspect should be explored further in future research.

Differences were also found between results from the regional Mediterranean Sea ecosystem study and the one performed in the smaller area of Greece, the Amvrakikos Gulf (Chapter 2.3). In fact, despite being both two semi-enclosed basins, they differed in many ways as presented by our modelling results (Chapters 2.3-2.5). In particular, the mean trophic level of the community and Kempton Q Diversity Index, declined in the Mediterranean Sea as a whole while in the gulf they respectively increased and fluctuated. The main reason for differences is related to high abundance of top predatory species and of forage fish in the gulf, because of high levels of productivity in the epipelagic layers of the water column and moderate fishing pressure in the area (industrial fisheries are prohibited) (Koutsikopoulos et al. 2008, Ferentinos et al. 2010). In the Mediterranean Sea, instead, the observed decline of top predatory species and forage fish is linked due to intensive fishing pressure and changes in PP. Kempton Q was relative stable in the gulf, despite clear signs of degradation at the bottom of the food web, as shown in Chapter 2.3, and this may be due to the fact that the system is still resilient to large driver changes. This raises an important question: "how resilient are these marine ecosystems, and how will their current functioning be modified in the future? This thesis has shown that the Mediterranean Sea is subjected to high levels of ecosystem stress (from species, to community and population level) and that the degradation is mainly caused by excessive overexploitation of the marine resources and by changes in PP, as observed already at regional (Coll et al. 2012, Micheli et al. 2013, Tsikliras et al. 2015) and smaller scale (Coll et al. 2008, Coll et al. 2009c, Piroddi et al. 2010). However, in light of increasing cumulative impacts, more effort should be put in place to quantify the magnitude of these disturbances and their cumulative impacts, and the capability of the Mediterranean Sea ecosystem to potentially absorbed them without losing its overall structure and function.

3. Policy and conservation implication

The final aim of this thesis was to develop a series of relevant results that could inform current and future policy and conservation frameworks at regional and European level. For example, the Marine Strategy Framework Directive (MSFD; 2008/56/EC), which is the main European regulation for addressing the ecological quality of marine waters, aims at assessing, by 2020, the environmental status of European marine ecosystems under anthropogenic pressures and the required interventions to bring the systems back to its desired good status. To be able to implement the Marine Directive, in 2010, a set of detailed criteria and indicators (from biological, physico-chemical indicators as well as pressure indicators—including hazardous substances, hydrological alterations, litter and noise, and biological disturbance such as introduction of non-indigenous species) were selected with the goal of assessing the "good environmental status" of selected systems (Cardoso et al., 2010; European Commission, 2010). Alongside these environmental measures, other EU policies that focus on the marine environment are represented by the Common Fisheries Policy (CFP), that aims at ensuring the sustainable exploitation of living aquatic resources, including measures to protect sensitive species and habitats from the impacts of fishing. In addition, the new Directive 2014/89/EC (Marine Spatial Planning Directive, MSPD), that provides a framework for Maritime Spatial Planning to support the sustainable development of seas and oceans whilst supporting current and future policies, in particular the implementation of the MSFD (2008/56/EC).

To support environmental regulations and because of the complexity in understanding marine ecosystem structures and functions and their responses to human pressures (Borja et al. 2013, Katsanevakis et al. 2015), ecological models and their modelled derived indicators have been increasingly used to evaluate ecosystems and predict impacts of human pressures on the environment (Fulton & Smith 2004, Shin et al. 2004, Christensen & Walters 2005, Plagányi 2007, Collie et al. 2014). However, since the models, in most cases, are not developed with the aim of supporting management strategies, like the MSFD, there are still difficulties in using models and interpreting their results for policy support (Piroddi et al. 2015; Chapter 2.1). For this reason, I coordinated a review (Chapter 2.1) of models and their derived indicators with the goal of presenting their potential to help the planning and the implementation of objectives defined in the MSFD, particularly in relation to which models and indicators exist and the missing components to support such policy. Results from this analysis showed that there is an extensive number of models (#44) and model derived indicators (#201) in Europe that could be used to support the MSFD, in particular, coming from coupled ecological models (end-to-end). As has been highlighted in Chapter 2.5, this coupling modelling framework, which links hydrodynamic-biogeochemical models with multi-species models, is a powerful tool that can better describe ecosystem properties and include anthropogenic and physical drivers behind observed changes, identifying both direct and indirect causes (Fulton 2010, Shin et al. 2010, Travers-Trolet et al. 2014).

Also, among all the models assessed, Ecopath with Ecosim (EwE) was notably the one associated with the largest number of model-derived biodiversity indicators and, although the majority of the indicators in the catalogue were static, it proves that it is one of the most applied tool for modelling marine and aquatic ecosystems (Colléter et al. 2015, Heymans et al. 2016). Despite the fact that EwE can produce temporal dynamic and spatial dynamic indicators, at the time the review (Chapter 2.1) was conducted only few areas of the European Seas (Coll & Libralato 2012) had spatial and temporal indicators assessed and publicly available. This explains why the catalogue had the majority of the indicators 'static'. In particular, of the 11 descriptors of the MSFD, EwE potential was stronger for two of the biodiversity descriptors: biological diversity (D1) and food webs (D4). Nevertheless, commercial fish and shellfish (D3) and to less extent, seafloor integrity (D6) and human induced eutrophication (D5) descriptors were well addressed by the EwE approach. Non-indigenous species (D2) was poorly addressed by the EwE models of the catalogue. However, recent studies have shown how EwE models can be useful in assessing ecosystem's respond to the introduction of invasive species (Langseth et al. 2012, Pinnegar et al. 2014, Libralato et al. 2015) and new spatial temporal capabilities of the approach have broaden the possibilities to apply this framework to derive temporal-spatial indicators (Steenbeek et al. 2013, Christensen et al. 2014, Coll et al. 2015, Villasante et al. 2016).

Regarding the model derived indicators that EwE was able to produce, 'biomass' (e.g., species/community in the food web) constituted the largest group (57%) followed by ‘diversity’ (13%; e.g., Kempton diversity index, trophic level of the community, species/habitat diversity, proportions in community), ‘primary or secondary production’ (9%), ‘ecological network analysis’ (ENA) (2%; flows, energies and efficiencies) and ‘species life-history’ (1%; traits such as for e.g., length, weight or life span) indicators. Few of the abovementioned indicators were used in this thesis (Chapters 2.3, 2.4 and 2.5), and few more will be integrated or improved in the next phase of the modelling work presented here (e.g., Shannon index; TL of community). Particularly temporal modelled derived indicators (as the ones shown in Chapters 2.3 and 2.5), which are able to detect changes in the structure and function of the ecosystem over time, are necessary pieces of the puzzle if the aim is to inform management processes. Also, the evaluation of these indicators at different spatial scale, as presented in this study, it is essential if we want to provide context-specific actions and guidelines for policy decisions (Guarnieri et al. 2016).

In addition, other factors not presented in this study but which I believe are important factors to account for in policy and conservation plans are the following and can be included in future developments of this work:

1. the development of spatial-temporal analyses able to identify spatial changes of species distribution, biodiversity patterns and threats that can directly assist management actions (e.g., by prioritizing specific areas of concern) and facilitate the communication between scientists and policy makers, environmental managers, conservationists and the general public (Micheli et al. 2013) as also highlighted in the recent European Commission Maritime Spatial Planning Directive (MSPD) (EC 2014a);
2. the integration of additional stressors (e.g., aquaculture, invasive species) as driving forces of species dynamics in the modelling tool since marine ecosystems are impacted by simultaneous cumulative threats (Coll et al. 2012, Micheli et al. 2013). Currently the recent MSPD, which include the EU’s Blue Growth Strategy (EC 2014b) that supports sustainable growth in emergent marine sectors (e.g., aquaculture, coastal tourism, marine energies), is expected to impose further pressure on the Mediterranean ecosystem (Coll et al. 2012, Piante 2015);

3. the development of future scenarios including different management actions into the future are crucial for the implementation of management plans. Future scenarios should follow the Intergovernmental Panel on Climate Change (IPCC) and the Platform on Biodiversity and Ecosystem Services (IPBES) projections on climate-induced changes in sea surface temperature. They should also consider the relevant elements of the Common Fisheries Policy (CFP) on commercially important stocks to exploit them at maximum sustainable yield (MSY) levels (where population size is maintained at a maximum growth rate, allowing the population to continue to be productive indefinitely), and the reduction of fishing effort needed to develop effective and appropriate policy and conservation plans in the region (Colloca et al. 2013, Tsikliras et al. 2015).

CHAPTER 4.

CONCLUSION

This study is the first to provide a basis for understanding and quantifying the structure and functioning of the whole Mediterranean Sea ecosystem, including main marine organisms, from low to high TLs, and considering changes in primary production and fishing activity driving the ecosystem dynamics. This is also the first study that integrates Mediterranean sub-regions within a unified model to take into consideration differences in biological and environmental characteristics. Since anthropogenic pressures are rapidly expanding in the basin, this work constitutes an important first step to further advance in the regional assessment of the Mediterranean Sea ecosystem with the aim to inform conservation plans and management actions.
Main conclusions derived from this study can then be summarized as follow:

1. 'Small pelagic fishes', mainly European pilchards and anchovies, both with high biomasses and high proportions in catches, are important structuring species for the Mediterranean ecosystem (at regional, sub-regional and local scales). On the other hand, the 'Mediterranean monk seal' is the species with the highest TL followed by 'piscivorous cetaceans' and 'large pelagic fish'.
2. 'Large pelagic fishes' is the main keystone group for both the past and current Mediterranean ecosystem while 'sharks' and 'medium pelagic fishes' played a key role in the past, and are currently replaced by benthopelagic and benthic cephalopods.
3. When comparing the Mediterranean to other European regional seas, the Mediterranean stands alone in relation to the type of flows driving the system and the cycling indices, suggesting higher levels of community stress induced by intensive fishing activities in the Mediterranean basin.
4. Looking at ecosystem dynamics, biomass trends and ecological indicators (e.g., community biomass, trophic levels of the community, catch and diversity indicators) reveal that the combined effect of excessive fishing pressure and changes in the primary productivity altered the Mediterranean marine ecosystem over time, especially reducing the proportions of top predators (e.g., pinnipeds, large pelagic fish) and mid trophic level organisms and increasing the abundance of groups at lower trophic levels (e.g., invertebrates).

5. The Western and the Adriatic Seas are the most degraded areas with biomasses declines among all the communities assessed (from forage fish to sharks/rays and skates except for invertebrates that remained stable in time) while the Ionian Sea seems to be the area with less biomass changes historically in comparison with available survey data.
6. In the Amvrakikos Gulf, both ecological indicators and biomass trends highlight a degradation of the demersal compartments of the food web and a relative stability of the pelagic ones mainly due to high eutrophication levels.
7. Fishing pressure and changes in primary production (PP) play an important role in driving species dynamics; yet, PP was the strongest historical driver upon the Mediterranean Sea ecosystem. In Amvrakikos, the strongest historical drivers were changes in nutrients and organic matter mostly from the loads of two local rivers.
8. Fisheries data (mainly catch and effort) are under-reported and under-estimated at regional, sub-regional and local scale. Fishing mortalities for three most important commercial species (European pilchard '*Sardina pilchardus*', anchovy '*Engraulis encrasicolus*' and hake '*Merluccius merluccius*') were, in fact, in 1950s and in all the sub-regions, between 5 and 10 times lower than the average reference values reported for these fish stocks in the Mediterranean Sea by stock assessment analyses. Even in the assessment of the Italian fisheries, the reconstructed total catches were 2.6 times the landings officially reported by the FAO on behalf of Italy for the same period and same sea, with unreported commercial landings (from both industrial and artisanal sectors) contributing 50% to the total catch (in relation to FAO reporting) and discards contributing another 7%.
9. In Europe, several models and associated indicators exist that could be used in support of European policies (MSFD); yet, Ecopath with Ecosim (EwE) seems to be the most applied tool for modelling marine and aquatic ecosystems and the one that can produce the largest number of indicators useful for MSFD.
10. Yet, to move toward more complete regional policy and conservation plans, several additional steps should be developed from this study in the near future:

a) spatial-temporal analyses able to identify spatial patterns that can directly assist spatial management actions and ease the communication between scientists and policy makers; b) the integration of additional human stressors (e.g., aquaculture, invasive species, and changes in climate) as driving forces of species dynamics to increase the reliability of this modelling exercise since marine ecosystems are impacted by simultaneous cumulative threats; c) the development of forecasting scenarios including different management actions (e.g., climate-induced changes in sea surface temperature or reduction of fishing effort) to support the implementation of management plans.

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ANNEXES

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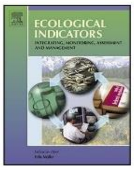

Review

Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive

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ABSTRACT

The European Union's Marine Strategy Framework Directive (MSFD) seeks to achieve, for all European seas, "Good Environmental Status" (GEnS), by 2020. Ecological models are currently one of the strongest approaches used to predicting and understanding the consequences of anthropogenic and climate-driven changes in the natural environment. We assess the most commonly used capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity descriptors. We built a catalogue of models and their derived indicators to assess which models were able to demonstrate: (1) the linkages between indicators and ecosystem structure and function and (2) the impact of pressures on ecosystem state through indicators. Our survey identified 44 ecological models being implemented in Europe, with a high prevalence of those that focus on links between hydrodynamics and biogeochemistry, followed by end-to-end, species distribution/habitat suitability, bio-optical (remote sensing) and multispecies models. Approximately 200 indicators could be derived from these models, the majority of which were biomass and physical/hydrological/chemical indicators. Biodiversity and food webs descriptors, with ∼49% and ∼43% respectively, were better addressed in the reviewed modelling approaches than the non-indigenous species (0.3%) and sea floor integrity (∼8%) descriptors. Out of 12 criteria and 21 MSFD indicators relevant to the abovementioned descriptors, currently only three indicators were not addressed by the 44 models reviewed. Modelling approaches showed also the potential to inform on the complex, integrative ecosystem dimensions while addressing ecosystem fundamental properties, such as interactions between structural components and ecosystems services provided, despite the fact that they are not part of the MSFD indicators set. The cataloguing of models and their derived indicators presented in this study, aim at helping the planning and integration of policies like the MSFD which require the assessment of all European Seas in relation to their ecosystem status and pressures associated and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020.

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Contents

1. Introduction

The use of robust and appropriate indicators that can assess whether an ecosystem and its services are well maintained and sustainably used (Layke, 2009; Walpole et al., 2009; TEEB, 2010) has been recognised as an essential step for the practical implementation of conservation and management policies (Rombouts et al., 2013). Several efforts have been undertaken at a European scale to evaluate marine ecosystem structure and their response to human activities, using key indicators to assess and sustain "Good Environmental Status" (GEnS; Borja et al., 2011). These initiatives have been carried out to assist the Marine Strategy Framework Directive (MSFD, 2008/56/EC; European Commission, 2008), the main European Directive that focuses on marine waters and aims at assessing the status of an ecosystem under anthropogenic pressures and the required interventions to bring the system back to its desired good status, making human activities sustainable, since this is one of the objectives of the MSFD. To achieve GEnS, 11 descriptors, 29 associated criteria and 56 indicators (from biological, physico-chemical indicators as well as pressure indicators—including hazardous substances, hydrological alterations, litter and noise, and biological disturbance such as introduction of non-indigenous species) have been identified (Cardoso et al., 2010; European Commission, 2010) (Tables 2 and 4).

Despite the fact that several attempts have been made to assess the environmental status of marine waters in an integrative manner (Borja et al., 2011; Halpern et al., 2012; Tett et al., 2013), significant gaps still exist on understanding marine ecosystem structures and functions and their response to human pressures (Katsanevakis et al., 2014; Borja et al., 2013). Currently, ecological models have been recognised as powerful tools to evaluate ecosystem structure and function and predict the impacts of human activities (Fulton and Smith, 2004; Shin et al., 2004; Christensen and Walters, 2005; Plagányi, 2007; Fulton, 2010) and climate change (Tomczak et al., 2013; Chust et al., 2014) on marine systems.

Thus, this study aims to assess the most commonly used capability of the modelling community to inform on indicators outlined in the EU MSFD (2008/56/EC), focusing particularly on biodiversity related descriptors: biological diversity (D1), non-indigenous species (D2), food webs (D4), and seafloor integrity (D6). To date, there has been no thorough evaluation of the capabilities of ecological models to provide information as explicitly outlined by the MSFD indicator structure, this task has been only partially undertaken (e.g., Reiss et al., 2014). With this work, we aim to fill in this knowledge gap by providing an inventory of models in EU regional seas that could assess MSFD indicators associated with biodiversity, non-indigenous species, food webs and seafloor integrity. For this reason, we have built a model catalogue ranging from lower to higher trophic levels, including those that successfully couple the two compartments and associated ecosystem processes. This inventory, developed as part of the DEVOTES FP7 Project (http://www.devotes-project.eu/), serves to highlight the vast potential of model-derived indicators that can be associated with MSFD descriptors and aims to provide a thorough assessment of their relevance and degree of "operationality." A detailed description of models and associated references together with the full catalogue are provided as supplementary materials (S1 and S2).

Yet, we acknowledge that this study does not aim to serve as review of all the existing models available in the literature, but instead highlight a process of exploring modelling potential to support specific European policies. Because of the nature of these issues, though, similar case studies conducted elsewhere are likely to lead to similar outcomes, conclusions, and recommendations (e.g., because of similar/same model availability and/or process understanding). Thus, this work emphasises several types of ecological modelling and derived indicators that exist at EU level stressing how such diversity of modelling approaches could be useful to support management policies and the limitations that still occur to achieve this task.

In particular, this study is divided into six sections, comprising (1) catalogue structure; (2) a general overview of model characteristics; (3) model potential to address MSFD GEnS descriptors and indicators (including the ability to address biodiversity components and habitat types); (4) geographical coverage of models; (5) ability to address pressures; and (6) gaps in models type/modelling capability and needs for further development.

2. Catalogue structure

The catalogue has been built primarily with models/areas targeted by the DEVOTES partners (which represent 23 research institutions from EU and non EU countries), yet with an effort to integrate available models/areas from other inventories (e.g., the MEECE project http://www.meece.eu/Library.aspx) and scientific literature (see S1).

The catalogue has been structured with several fields following the MSFD Commission Decision 2010/477/EU (European Commission, 2010) and grouped into six main categories:

i. Model/Indicator properties with the following sub-categories:
    a. *MSFD descriptor/indicator*, descriptor/indicator outlined in the directive

b. *Model derived indicator (MDI)*, indicator resultant from model output
c. *MDI type* defined as 1. *Static* (e.g., snapshot of the indicator at a precise period of time), 2. *Dynamic* (e.g., indicator which changes in time) or 3. *Spatial dynamic* (e.g., indicator which changes in time and space)
d. *MDI status of development* defined as 1. *Operational*, when the indicator is developed, tested and validated (e.g., it could be either an indicator used by the Member States (MS) for national environmental monitoring; or in EU/International Conventions' monitoring programmes; or validated with observed/survey data although not necessarily approved by any national/international law or convention); 2. *Under development*, an indicator proposal exists, but not yet validated in field/real data (e.g., indicator not yet used for MS national environmental monitoring or for EU/International Conventions' monitoring programmes; or not yet validated with survey data); 3. *Conceptual*, an indicator idea, supported by theoretical grounds, although no practical measure/metric is yet available (e.g., indicator not yet tested)
e. *MDI target/reference values and unit* defined as thresholds/limits representing boundaries between an acceptable and unacceptable status
f. *Model name* referring to the label used to identify a particular model
g. *Model type* referring to model characteristics/properties and/or to the technique used to assess specific ecosystems
h. *Data requirements* referring to data needed to run a certain model
i. *Confidence/uncertainty* referring to the ability of models to assess uncertainty for the input/output data and it is defined as the type of statistical analysis used to evaluate it
j. *Source* Scientific literature and or Institutional report supporting selected MDI/models entries

ii. Model/MDI in relation to MSFD Descriptors: referring to models and MDI broad capability to address the 11 descriptors of the directive (D1–D11).
iii. Model/MDI correspondence with MSFD Biodiversity Indicators: referring to models and MDI assessed in relation to their capability to provide information for the specific indicators listed under the criteria of the four descriptors (D1/D2/D4/D6) as officially outlined in the European Commission (2010).
iv. Model/MDI correspondence with biodiversity components referring to which biodiversity components (e.g., microbes, phytoplankton and fish) the indicator was related to or was evaluated with. Categories adopted for biodiversity components followed those of the European Commission (2010) and EU Commission Staff Working Paper (CSWP, 2012).
v. Model/MDI coverage of specific habitat types and geographical range/scale referred to whether an MDI was related to certain habitats and geographical areas. Categories adopted for Habitat Types followed those of the European Commission (2010) and EU Commission Staff Working Papers (CSWP, 2011, 2012). Concerning geographical coverage, we have adopted well-established international criteria for smaller scale subdivisions or ecological assessment areas in order to increase the spatial detail on the information collected (e.g., the International Council for the Exploration of the Sea (ICES) and General Fisheries Commission for the Mediterranean (GFCM) subdivisions; see maps under S1).
vi. Model/MDI relation to specific pressures: referring to whether there was scientific evidence of a relationship between a pressure and a specific indicator. Indicators were related to pressures either as responsive/sensitive to, or affected by a given pressure (state indicators, e.g., mainly through changes in trends) or indicators were actually pressure indicators themselves. The considered pressures follow the list of pressures and impacts of Annex 3 of the MSFD (see S3).

3. Model characteristics

The model catalogue revealed that currently 44 models have been applied with outputs relevant to MSFD descriptors (Table 1). These ecological models being used to describe or understand ecosystem processes can be categorised under seven types of modelling approaches described below:

3.1. Biogeochemical models

The bulk properties of biogeochemical fluxes in marine ecosystems are combined with information on physical forcing, chemical cycling and ecological structure to simulate the response of lower trophic level groups (phytoplankton and zooplankton) to environmental conditions, including climate variability and change (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011). Such models typically have very simplified representations of biological organisms, and associated trophic structure (Anderson, 2005).

3.2. Multispecies models

These models represent populations of dynamically interacting species or functional groups. Some models also resolve multiple stages or size-classes within populations (Christensen and Walters, 2004; Hollowed et al., 2000; Shin and Cury, 2001). Focus of these models is on understanding the implication of the indirect interactions in ecosystems that result from the complex networks of direct predator–prey interactions in marine communities. The models aim to represent, for example, top-down or bottom-up effects along marine food chain ranging from primary producers (e.g. phytoplankton) to top predators (e.g., marine mammals), or the role of indirect competitive interactions among species (Fung et al., 2015). Effects of exploitation by fisheries and environmental change are also frequently described by these models.

3.3. Species Distribution Models (SDM)/Habitat Suitability Models (HSM)

SDM combine observations of species occurrence or abundance with environmental explanatory variables to develop ecological and evolutionary understanding and to predict distribution across selected habitats (Elith and Leathwick, 2009; Reiss et al., 2014). HSM relate field observations to a set of environmental variables (e.g., reflecting key factors of the ecological niche like climate, topography, geology) to produce spatial predictions on the suitability of locations for a target species, community or biodiversity (Hirzel et al., 2006). A new generation of SDM/HSM – i.e. dynamic bioclimatic envelope models – now provide greater links to the mechanistic understanding of niche ecology. Such models typically include additional model components that describe physiological responses of species to the environment, population dynamics and dispersal, to further constrain the distribution of suitable habitat and provide more realistic species distribution projections (Cheung et al., 2011).

3.4. Meta-community models

Meta-community is a set of interacting communities which are linked by the dispersal of multiple, potentially interacting species. In this context, meta-community models are theoretical frameworks describing specific mechanistic processes in order to predict empirical community patterns. They deal mainly with species

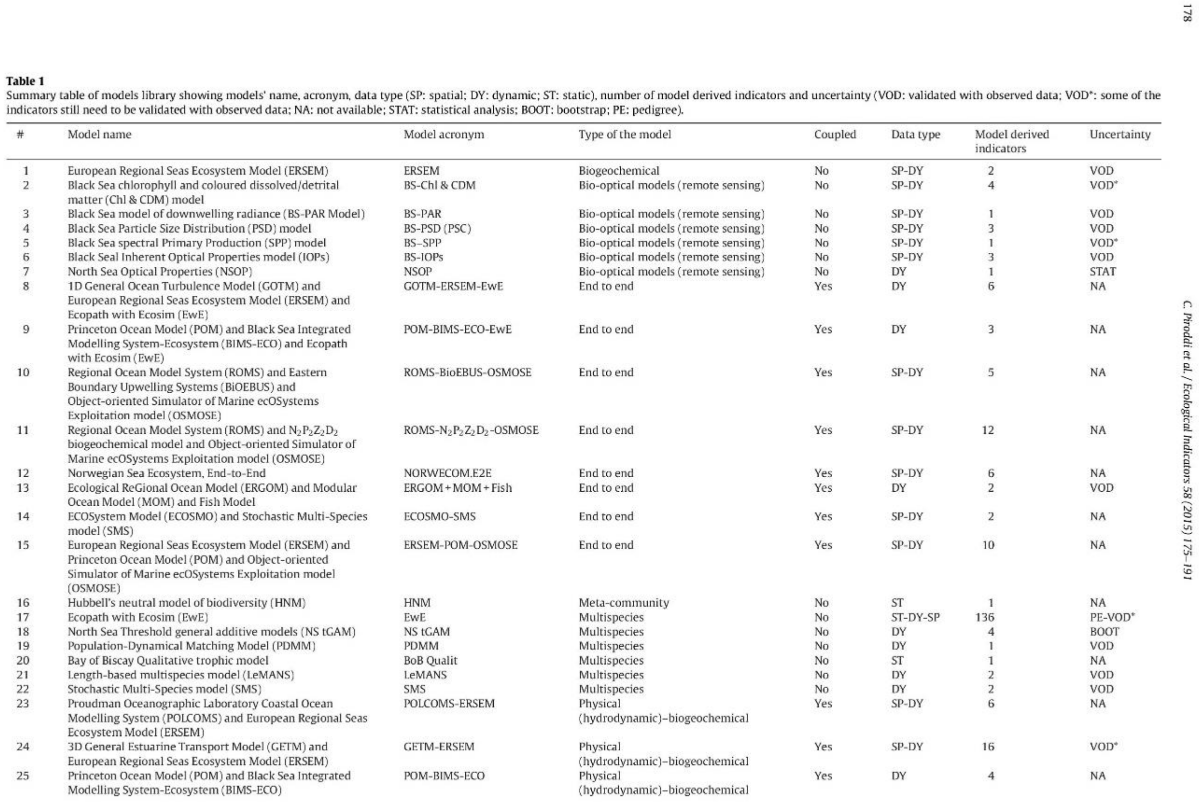

Table 1

Summary table of models library showing models' name, acronym, data type (SP: spatial; DY: dynamic; ST: static), number of model derived indicators and uncertainty (VOD: validated with observed data; VOD*: some of the indicators still need to be validated with observed data; NA: not available; STAT: statistical analysis; BOOT: bootstrap; PE: pedigree).

#	Model name	Model acronym	Type of the model	Coupled	Data type	Model derived indicators	Uncertainty
1	European Regional Seas Ecosystem Model (ERSEM)	ERSEM	Biogeochemical	No	SP-DY	2	VOD
2	Black Sea chlorophyll and coloured dissolved/detrital matter (Chl & CDM) model	BS-Chl & CDM	Bio-optical models (remote sensing)	No	SP-DY	4	VOD*
3	Black Sea model of downwelling radiance (BS-PAR Model)	BS-PAR	Bio-optical models (remote sensing)	No	SP-DY	1	VOD
4	Black Sea Particle Size Distribution (PSD) model	BS-PSD (PSC)	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
5	Black Sea spectral Primary Production (SPP) model	BS–SPP	Bio-optical models (remote sensing)	No	SP-DY	1	VOD*
6	Black Seal Inherent Optical Properties model (IOPs)	BS-IOPs	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
7	North Sea Optical Properties (NSOP)	NSOP	Bio-optical models (remote sensing)	No	DY	1	STAT
8	1D General Ocean Turbulence Model (GOTM) and European Regional Seas Ecosystem Model (ERSEM) and Ecopath with Ecosim (EwE)	GOTM-ERSEM-EwE	End to end	Yes	DY	6	NA
9	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO) and Ecopath with Ecosim (EwE)	POM-BIMS-ECO-EwE	End to end	Yes	DY	3	NA
10	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-BioEBUS-OSMOSE	End to end	Yes	SP-DY	5	NA
11	Regional Ocean Model System (ROMS) and $N_2P_2Z_2D_2$ biogeochemical model and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-$N_2P_2Z_2D_2$-OSMOSE	End to end	Yes	SP-DY	12	NA
12	Norwegian Sea Ecosystem, End-to-End	NORWECOM.E2E	End to end	Yes	SP-DY	6	NA
13	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM) and Fish Model	ERGOM + MOM + Fish	End to end	Yes	DY	2	VOD
14	ECOSystem Model (ECOSMO) and Stochastic Multi-Species model (SMS)	ECOSMO-SMS	End to end	Yes	SP-DY	2	NA
15	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ERSEM-POM-OSMOSE	End to end	Yes	SP-DY	10	NA
16	Hubbell's neutral model of biodiversity (HNM)	HNM	Meta-community	No	ST	1	NA
17	Ecopath with Ecosim (EwE)	EwE	Multispecies	No	ST-DY-SP	136	PE-VOD*
18	North Sea Threshold general additive models (NS tGAM)	NS tGAM	Multispecies	No	DY	4	BOOT
19	Population-Dynamical Matching Model (PDMM)	PDMM	Multispecies	No	DY	1	VOD
20	Bay of Biscay Qualitative trophic model	BoB Qualit	Multispecies	No	ST	1	NA
21	Length-based multispecies model (LeMANS)	LeMANS	Multispecies	No	DY	2	VOD
22	Stochastic Multi-Species model (SMS)	SMS	Multispecies	No	DY	2	VOD
23	Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) and European Regional Seas Ecosystem Model (ERSEM)	POLCOMS-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
24	3D General Estuarine Transport Model (GETM) and European Regional Seas Ecosystem Model (ERSEM)	GETM-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	16	VOD*
25	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO)	POM-BIMS-ECO	Physical (hydrodynamic)–biogeochemical	Yes	DY	4	NA
26	St. Petersburg Eutrophication Model (SPBEM)	SPBEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
27	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM)	ERSEM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	11	NA
28	3D General Estuarine Transport Model (GETM) and Ecological Regional Ocean Model (ERGOM)	GETM-ERGOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	8	VOD*
29	BAltic Sea Long-Term large-Scale Eutrophication Model (BALTSEM)	BALTSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
30	Biogeochemical Flux Model (BFM) and Princeton Ocean Model (POM)	BFM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	5	NA
31	Black Sea Ecosystem Model	BSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	13	VOD*-STAT
32	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM)	ERGOM + MOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
33	ECOSystem Model (ECOSMO)	ECOSMO	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
34	MOHID and Pelagic Biogeochemical Model (LIFE)	MOHID-LIFE	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	4	VOD*
35	Nucleus for European Modelling of the Oceans (NEMO) and Biogeochemical Flux Model (BFM)	NEMO-BFM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	10	NA
36	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS)	ROMS-BioEBUS	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
37	Regional Ocean Model System (ROMS) and $N_2P_2Z_2D_2$ biogeochemical model	ROMS-$N_2P_2Z_2D_2$	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	12	NA
38	Swedish Coastal and Ocean Biogeochemical model (SCOBI) and Rossby Center Ocean circulation model (RCO)	RCO-SCOBI	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
39	Ecological Niche Factor Analysis (ENFA)	ENFA	SDM/Habitat Suitability Models	No	ST	1	NA
40	Bay of Biscay Habitat suitability based on Generalised Additive Models (GAM)	BoB GAM	SDM/Habitat Suitability Models	No	ST	1	NA
41	Bay of Biscay Habitat suitability based on Generalised Linear Models (GLM)	BoB GLM	SDM/Habitat Suitability Models	No	ST	1	NA
42	Habitat suitability based on MaxEnt (Maximum Entropy)	MaxEnt	SDM/Habitat Suitability Models	No	ST	2	NA
43	Niche-Trait Model (NTM)	NTM	SDM/Habitat Suitability Models	No	ST	1	NA
44	Process-driven habitat model	PDH	SDM/Habitat Suitability Models	No	ST	1	NA

composition and abundance and their variation within a meta-community (Hugueny et al., 2007).

3.5. Bio-optical models

The optical properties of biological materials, such as phytoplanktonic or heterotrophic unicellular organisms, are analysed and then modelled to predict distributions of biological communities over wide spatial areas (with remote sensing data) or in terms of expected depth limitations that can be inferred from modelling studies. Bio-optical models are based on various fundamental theories of optics which apply to a single particle making use of a set of equations/algorithms (Morel and Maritorena, 2001; IOCCG, 2006).

3.6. Hydrodynamic–biogeochemical Models

These are mainly coupled hydrodynamic and biogeochemical models to capture global scale patterns in physical–chemical components affecting lower trophic level groups (e.g., phytoplankton and zooplankton) (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011).

3.7. End-to-end models

In recent years, hydrodynamic-biogeochemical models (or just biogeochemical models) have been coupled with multispecies models. These so called end-to-end (E2E) models combine physicochemical oceanographic processes with organisms ranging from low trophic level (LTL) to higher trophic level organisms (HTL) into a single modelling framework (Travers et al., 2009).

Of the models reported in this study, more than half were coupled ecological models (Table 1). The most common type of models currently in the catalogue were hydrodynamic-biogeochemical models (36%) followed by end-to-end (18%), species distribution/habitat suitability, bio-optical and multispecies (14% each), biogeochemical and meta-community (2% each) models (Table 1).

In the framework of ecological studies, physical–biological interactions are the main factors that can better describe ecosystem properties and the spatial and/or temporal evolution in function of relevant pressures identified, climate change or anthropogenic impacts. This is reflected in the choice of modelling approaches and in the growing need to couple different types of models within a single modelling framework (Travers et al., 2009; Rose et al., 2010). This is particularly true if the models are intended to predict changes and provide guidance in a framework of biodiversity conservation and ecosystem-based management (Travers et al., 2009; Kaplan et al., 2012).

Recent software developments, within the current (DEVOTES) and former EU projects (e.g., MEECE http://www.meece.eu/), have shown that these models (hydrodynamic-biogeochemical and multispecies models) can be coupled to run together. This represents a powerful tool for scenario testing of climate change and anthropogenic impacts simultaneously. There is a growing trend for E2E modelling, which includes anthropogenic and physical drivers behind observed changes, identifying both direct and indirect causes (Fulton, 2010; Shin et al., 2010b; Travers-Trolet et al., 2014), and so better facilitates the setting of targets and implementation of management measures (Cury et al., 2008; Kaplan et al., 2012). Fig. 1 illustrates the capacity of the seven model types to represent the different components of marine ecosystems, including or excluding, human components and/or climate impacts.

Coupled (both E2E and hydrodynamic-biogeochemical models) and bio-optical (remote sensing) models included in this catalogue were primarily spatially dynamic and 5 out of 30 models were also dynamic. The remaining models were mainly static with only 5 out of 14 models presenting dynamic and spatial modules as well (Table 1). This is an important and interesting result since spatial-dynamic models are able to provide greater capacity for forecasting of ecosystem dynamics, although they require a more data intensive calibration (e.g., the initial testing and tuning of a model) and validation (e.g., the comparison/fitting of model with a data set representing "local" field data) approaches (Jørgensen, 2008).

A total of 201 model-derived indicators (see S1 of supplementary materials) were included in this catalogue, of which more than half were considered to be "operational" (64%), while the majority of the remainder were still "under development" (33%), with only a few "conceptual" approaches (3%) presented (Table 2). We acknowledge that some indicators might have changed their status since the time of this survey (e.g., some indicators "under development" may have been assessed and now classified as "operational") but for the purpose of this work we decided to keep them in the status of development that they were reported during the survey.

Ecopath with Ecosim (EwE) was notably associated with the largest number of model-derived biodiversity indicators (Table 2). However, the majority of these biodiversity indicators were biomasses of species or groups of species at different trophic levels of the food web. For ease of characterisation/evaluation, model-derived indicators were grouped into seven major categories (see Table 3 for the detailed list). Not surprisingly, biomass indicators constituted the largest group with approximately 57% followed by diversity indices (13%) and physical, hydrological and chemical indicators (12%). Regarding targets and/or reference values associated with model-derived indicators, the catalogue highlights that only few models in few areas had assigned target or reference values, despite the fact that the majority were considered "operational" (i.e. developed, tested and validated). This is the case of fully developed models for which validated outputs exist (e.g., BSEM by Dorofeev et al., 2012), but under policy contexts such as the MSFD, lack tested and validated reference values or targets compliant with specific legal requirements.

Also, very few of the reported models have been used to clearly assess the effects of measures to meet the targets that will eventually be established. For instance, multispecies models have been applied in the Ionian Sea and in the North Sea ecosystems to assess the reduction in fishing effort as a measure to (a) bounce back common dolphin populations (e.g., EwE model by Piroddi et al., 2011); (b) assess the response of selected biodiversity indicators (e.g., PDMM by Shephard et al., 2013; Fung et al., 2013, or EwE model by Lynam and Mackinson, in press); (c) test the effect of selective fishing on community biodiversity conservation (e.g., LeMANS model by Rochet et al., 2011) and implemented in the Bay of Biscay (e.g., OSMOSE model by Chifflet et al., 2014) to evaluate the effect of different fishing scenarios on small pelagic fish stocks.

In addition, not all the models were able to address uncertainty; the majority (61%) lacked an approach to determine confidence intervals/range of uncertainty or required further validation work for indicators. This is a reflection, as mentioned above, of the type of data present in the catalogue which are more spatial-dynamic than static and for which validation is more difficult to obtain. From the models that reported addressing uncertainty (39%), data comparison and data validation (e.g., model outputs fitted to surveyed data) was the most common method reported (Table 1).

4. Model potential to address descriptors and indicators for biological descriptors

In terms of supporting the MSFD, ecological models can be the most effective means to model relationships between activities, pressures, state and thus indicators (Jørgensen, 2008; Jørgensen

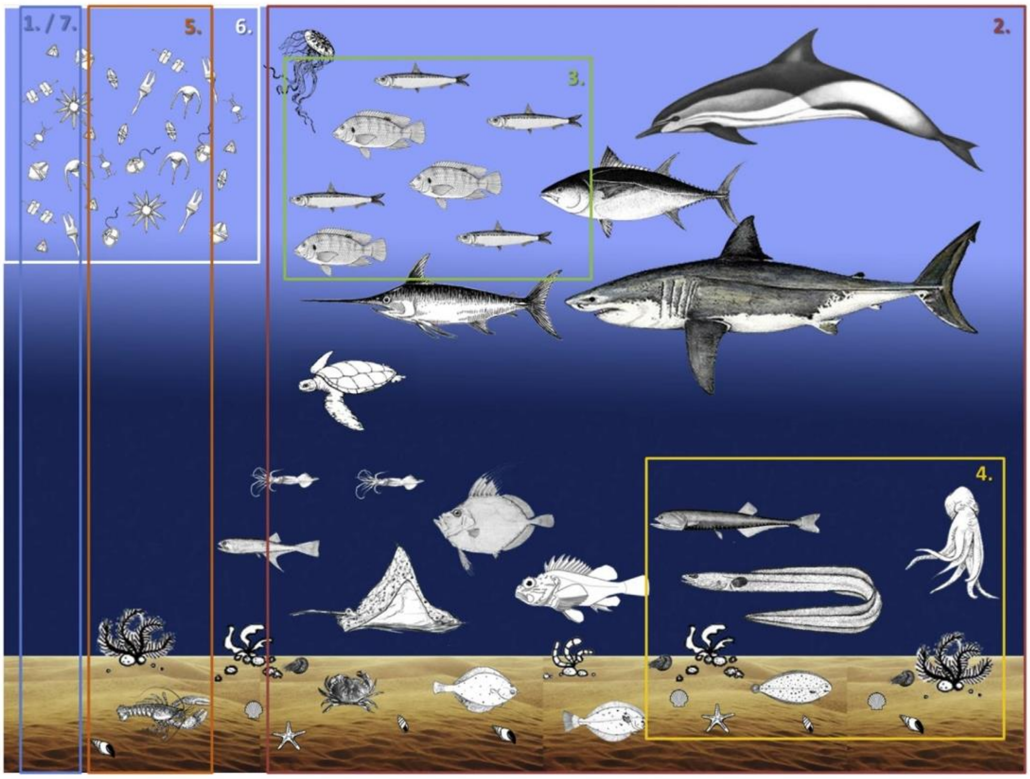

Fig. 1. Illustration of models capacity to describe the ecosystem, from specific processes integrating biological compartments and the associated abiotic environment to the entire ecosystem including, or not, human components or climate impacts. In particular, 1 and 7 – refer to biogeochemical and coupled physical–biogeochemical models; 2 and 3 – refer to multispecies models (either at species or at food web level); 4 – Species distribution/Habitat Suitability; 5 – meta-community models and 6 – bio-optical models. E2E models encompass all of them.

and Fath, 2011). This is because of the integrative character of these modelling approaches that often consider many ecosystem components from abiotic factors to biotic interactions and processes. The 44 models available in the catalogue were capable of addressing indicators in 8 of the 11 descriptors of the MSFD (Table 2) although, due to the focus of this survey which primarily dealt with the four biodiversity related descriptors, their modelling potential was stronger for two of these biodiversity descriptors: biological diversity (D1) and food webs (D4). Nevertheless, human induced eutrophication (D5), hydrographical conditions (D7) and commercial fish and shellfish (D3) were well addressed by the models in this catalogue.

Within the biodiversity related descriptors, non-indigenous species (D2) and seafloor Integrity (D6) were the most poorly addressed by the models currently in the catalogue (Table 2). However, Pinnegar et al. (2014) shows how EwE models can be useful in assessing the response of an ecosystem to the introduction of invasive species (D2). Similarly, increasing the spatial resolution of many of the current models would further improve our understanding of the direct effect of fishing and other activities (such as decommissioning of oil rigs or development of a wind farm) on seafloor integrity (D6). In several cases, models have been used to investigate the impacts of trawling and test fisheries scenarios (e.g., high resolution ERSEM-POM model, Petihakis et al. (2007)). However, most of the models considered in this catalogue do not explicitly include descriptions of these types of pressures on the marine environment, they do not link to benthic habitat layers, and their understanding of pressures and impacts is in many cases still limited by scarce empirical information (Hooper and Austen, 2014).

Typically, a single model was capable of addressing more than one MSFD descriptor and sometimes up to six, as is the case of EwE (Table 2). As a result, the same model may be noted for having indicators in multiple stages of development (e.g., operational, under developed or conceptual) either across descriptors or within the same descriptor. This is because the reported status of development relates not to the model itself but to the different indicators that can be derived from the model. The potential of the available models to address MSFD indicators specifically those within biological descriptors was evaluated by extracting the number of indicators (outlined in the European Commission (2010)) that each model can inform on (Table 2). All models could address multiple indicators, from the set of 21 MSFD indicators under these 4 descriptors. In fact, 20 models in the catalogue had the potential to address at least half of these indicators. Despite the high potential of the models to address MSFD indicators, not all of the available model-derived indicators were fully operational (see Section 2 for definition and Table 4). The mean percentage of operational model-derived indicators across all MSFD indicators was 64%. Our analysis also revealed that there were three indicators required under the biodiversity descriptors for which no model-derived indicators were available in the catalogue (Table 4): D1C3-I2: population genetic structure; D2C2-I1: Ratio between invasive non-indigenous species and native species and D2C2-I2: Impacts of non-indigenous

Table 2
Models' capability per the 11 Marine Strategy Framework Directive descriptors (D) assessed by the number of indicators provided by each model (for names, see Table 1). The development status of the indicators is indicated (op: operational, ud: under development, co: conceptual). The last column summarises the number of MSFD official indicators (European Commission, 2010) of D1, D2, D4 and D6 (check Table 4) that the model-derived indicators can inform on.

		D1 Biological diversity	D2 Non-indigenous species	D3 Commercial fish	D4 Food webs	D5 Human-induced eutrophication	D6 Seafloor integrity	D7 Hydrological alterations	D8 Contaminants	D9 Contaminants in food	D10 Marine litter	D11 Energy/ noise	# MSFD indicators addressed under D1, D2, D4, D6
1	BALTSEM	7op			5op	3op		2op					16
2	BFM-POM	5op			3op	2op		2op					14
3	BSEM	6op/7ud	1op/1ud		1op/7ud	4ud		3op					9
4	EwE	82op/82ud/7co	1ud	53op/57ud/4co	82op/82ud/7co	13op/14ud/2co	17op/25ud/4co						13 (+1[a])
5	ECOSMO	6op			3op	2op		3op					14
6	ECOSMO-SMS	2ud		2ud	2ud								8
7	ENFA	1op		1op	1op								14
8	ERGOM + MOM	7op			5op	3op		2op					16
9	ERGOM + MOM + fish	2op		2op	2op								7
10	ERSEM	2ud			2ud	1ud							12
11	ERSEM-POM	11op			6op	3op		5op					14
12	ERSEM-POM-OSMOSE	10ud		10ud	10ud								9
13	BoB GAM	1op		1op	1op								16
14	GETM-ERGOM	8ud			2ud	4ud		6ud					14
15	GETM-ERSEM	16ud			5ud	8ud	2ud	11ud					19
16	BoB GLM	1op		1op	1op								16
17	GOTM-ERSEM-EWE	6ud		4ud	6ud					3ud			8
18	HNM	1co			1co	1co	1co						16
19	BS-IOPs	3ud			2ud	3ud							8
20	LeMANS	2op		2op	2op								7
21	MaxEnt	2op	1op	1op	2op								17
22	MOHID–LIFE	4op			3op	3op		1op					10
23	NEMO-BFM	10ud			7ud	4ud		3ud					17
24	NSOP	1ud			1ud	1ud							8
25	NStGAM	4ud		2ud	4ud	1ud							10
26	NORWECOM.E2E	6op			3op	2op		3op					14
27	NTM	1ud			1ud		1ud						9
28	PDMM	1op		1op	1op								7
29	POLCOMS-ERSEM	6op			3op	2op		3op					14
30	POM-BIMS-ECO	4op			3op	2op		1op					14
31	POM-BIMS-ECO-EWE	3ud		3ud	3ud								9
32	PDH	1ud			1ud		1ud						11
33	BS-PSD (PSC)	3ud			3ud	3ud							5
34	BoB Qualit	1co		1co	1co								8 (+1[a])
35	RCO-SCOBI	7op			5op	3op		2op					16
36	BS-Chl & CDM	4ud			4ud	4ud							6
37	BS-PAR	1ud											3
38	BS-S PP	1ud			1ud	1ud							3
39	ROMS-BioEBUS	6op			3op	2op		3op					14
40	ROMS-BioEBUS-OSMOSE	5ud		5ud	5ud								9
41	ROMS-$N_2P_2Z_2D_2$	12op			8op	5op		4op					13
42	ROMS-$N_2P_2Z_2D_2$-OSMOSE	12op		12op	12op								11
43	SMS	2op		2op	2op								7
44	SPBEM	7op			5op	3op		2op					16
Number of models per descriptor		44	3	17	43	26	5	17	0	1	0	0	

[a] New proposals for Descriptor 4 *Food Webs*, not yet considered under the set of Indicators outlined in the EU Commission Decision (European Commission, 2010).

Table 3
The model-derived indicators grouped into 7 major categories, based on what the indicators inform on, with their overall percentages in the DEVOTES Catalogue of model-derived indicators.

	Type of indicators		%
1	Biomass		57
2	Diversity indicators	Biodiversity indices (e.g., Kempton diversity index, trophic level of the community) and species/habitat diversity, proportions in community	13
3	Primary or secondary production		9
4	Spatial distribution indicators	Species spatial distribution	6
5	Species life-history	Traits such as for e.g., length, weight or life span	1
6	Ecological Network Analysis (ENA) indicators	Flows, energies and efficiencies	2
7	Physical, hydrological and chemical	Describing either habitat integrity or pressures	12

invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

Additionally, it is noteworthy that the potential of modelling approaches to address ecosystem fundamental properties such as D1C8I1 "Interactions between structural components" and D1C8I2 "Services provided" (Table 4) was high. These aspects, despite being clearly mentioned in the European Commission (2010), were not part of the MSFD indicators set, most probably due to the difficulty in defining them through specific indicators. Nevertheless, the majority of the model-derived indicators included in this catalogue (189 out of the 201) have the potential to inform on these complex, integrative ecosystem dimensions. In any case, although the catalogue shows the potential of models to address Ecosystem Services (ES, *sensu* Liquete et al., 2013), the survey performed cannot inform adequately on the capacity of the indicators to support policy-makers' use of these ES concepts. This is a current limitation of the MSFD set of indicators (Table 4) which does not clearly require the assessment of ecosystems services, despite the fact that in 2011, as a party of the Convention on Biological Diversity (CBD), the European Union (EU) adopted a new strategy (the Biodiversity Strategy to 2020), which integrates ES as key elements for the conservation approach to biodiversity (Maes et al., 2012). The role of ES in supporting conservation initiatives and socio-economic activities calls for action to monitor, quantify and value trends in these services, so as to ensure that they are adequately considered in decision making processes. To do so, a clear linkage needs to be established between biodiversity and ecosystem functioning and the diversity and complexity of the benefits they provide, i.e. the ecosystems services (be it provisioning, regulating or cultural), in order to allow the development of operational indicators. Yet, the indicators available are not comprehensive and are often inadequate to characterise ES; data are often either insufficient or the linkages are poorly understood to support the use of these indicators (Liquete et al., 2013).

4.1. Biodiversity components and habitats

Habitats and species are key attributes of biological diversity and their occurrence, distribution and abundance is used as criteria to assess the ecosystem status (Table 5). To attain GEnS for D1, as stated in the MSFD, "no further loss of biodiversity at ecologically relevant scale should occur, and, if it does, restoration measures should be put in place". The definition of GEnS is dependent on the ecological relevance and is approached at different scales of complexity, from species to habitats, communities and ecosystem (see Borja et al., 2013).

Biodiversity components indicated in the MSFD include microbes, phytoplankton, zooplankton, angiosperms, macroalgae, benthic invertebrates, fishes, cephalopods, marine mammals, reptiles and birds, with specific subgroups within the last four categories. Their inclusion in ecological models listed in the catalogue was highly heterogeneous. Operational model-derived indicators concerned mainly fish, phytoplankton, zooplankton, benthic and pelagic invertebrates and marine mammals (total 64, 45, 31, 23, and 17, respectively) (Fig. 3), while the remaining biodiversity components were covered with less than 10 indicators each. This reflects the traditional focus of marine ecosystem modelling, driven mainly by the wide-spread use of low trophic level models related to the bottom-up forcing of production, and in parallel, motivated by fisheries oriented policies and conservation interests in particular species (Rose et al., 2010; Shin et al., 2010b).

As expected, the various models have used similar components differently and, depending on their final goal, the resolution of the biodiversity components differed greatly: from single to multi-species models, inclusion of single or multiple functional groups and integrating both LTL and HTL key organisms (e.g., Oguz et al., 1999; Lewy and Vinther, 2004; Schrum et al., 2006; Coll et al., 2008; Rossberg et al., 2010; Lassalle et al., 2011; Mateus et al., 2012; Tsiaras et al., 2012). Of the models catalogued, only Hubbell's neutral model and the Population-Dynamical Matching Model (PDMM) resolve biodiversity at species level, and only the PDMM does so through the entire marine food chain (Fung et al., 2013). EwE model-derived indicators, either operational, conceptual or still under development, have been used to model all types of biodiversity components (excluding microbes), with fish being the most frequently assessed group (25%) followed by benthic invertebrates (15%), marine mammals (12%) and cephalopods (11%). The microbial component, as reported in the catalogue, was only evaluated by ERSEM-POM in the Aegean Sea and under development by NEMO-BFM in the Baltic Sea. When models were organised according to model type, multispecies models assessed the majority of biodiversity components with the exception of microbes that were mostly evaluated by coupled hydrodynamic–biogeochemical models (Fig. 3).

The predominant habitat types that should be assessed within the evaluation of the status under the MSFD are water-column, seabed and ice habitats, with ecological models referring to one or several of these habitats. In our catalogue, of all predominant habitats, water-column was the most comprehensively evaluated habitat, either on its own, or in relation to the other two habitats. There were only two instances where seabed habitats were evaluated on their own. Ice-associated habitats were assessed by hydrodynamic–biogeochemical and multispecies models while seabed habitats were evaluated in multispecies and SDM/Habitat suitability/Community models. Multispecies as well as coupled (both hydrodynamic–biogeochemical and E2E) models were mainly used for the assessment of species or groups of species/organisms that can be linked to water-column habitats.

Examining the intersection between model-derived indicators and habitats, the water column was the most widely covered habitat, specifically the continental shelf where all components of biodiversity were covered (Table 5). The marine oceanic water column was also widely covered; however, in this case microbes were not evaluated. In estuaries, only phytoplankton and zooplankton were assessed, which were also the main components modelled in ice-associated habitats. In the seabed habitat, shallow sublittoral mixed sediments were the most commonly evaluated with model-derived indicators assessing 7 out of the 11 biodiversity components. Invertebrates were mainly studied in relation to the water column over the continental shelf although they are also

Table 4
Model derived indicators and models available per MSFD descriptor/indicator for biodiversity related descriptors (D1, D2, D4, D6), with particular emphasis on the number of operational indicators (op) out of the indicators available for each MSFD indicator (I).

MSFD descriptor	Criteria	MSFD indicator	Model derived indicators from DEVOTES catalogue		Comments
			Operational/available indicators	Number of models	
D1	C1	I1 Distributional range	33 op/45	27	
D1	C1	I2 Distributional pattern within range	4 op/10	15	
D1	C1	I3 Area covered by the species (for sessile/benthic species)	1 op/2	5	
D1	C2	I1 Population (1) abundance and/or (2) biomass	93 op/163	37	
D1	C3	I1 Population demographic characteristics: (1) body size; (2) age class structure; (3) sex ratio; (4) fecundity rates; (5) survival/mortality rates; (6) other	14 op/37	15	
D1	C3	I2 Population genetic structure	No indicators available	No models available	*D1 Biodiversity/C3 Population condition*
D1	C4	I1 Distributional range	6 op/9	21	*The exact same indicators are proposed as suitable to address both I1 and I2 from D1C4 Com. Dec.*
D1	C4	I2 Distributional pattern	6 op/9	21	
D1	C5	I1 Area	6 op/7	20	*Nearly the same indicators as in D1C4 are also reported as suitable to address both I1 and I2 from D1C5 Com. Dec.*
D1	C5	I2 Volume	4 op/4	15	
D1	C6	I1 Condition of the typical (1) species and (2) communities	89 op/174	39	
D1	C6	I2 Relative (1) abundance and/or (2) biomass	11 op/25	7	
D1	C6	I3 (1) Physical, (2) hydrological and (3) chemical conditions	12 op/39	23	
D1	C7	I1 Composition of ecosystem components: (1) habitats and (2) species	96 op/168	39	
D1	C7	I2 Relative proportions of ecosystem components: (1) habitats and (2) species	100 op/186	43	
D1	(C8)	I1 Interactions between structural components	108 op/198	44	*Not defined under Com. Dec. list but in its text.*
D1	(C8)	I2 Services provided	105 op/183	39	
D2	C1	I1 Trends in: (1) abundance; (2) temporal occurrence; (3) spatial distribution	2 op/4	3	
D2	C2	I1 Ratio between invasive non-indigenous species and native species	No indicators available	No models available	*D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species*
D2	C2	I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem	No indicators available	No models available	
D4	C1	I1 Performance of (1) key predator species determined from their productivity; (2) other trophic group	3 op/7	19	
D4	C2	I1 (1) Large fish (by weight); (2) other species	18 op/40	10	
D4	C3	I1 Abundance trends of functionally important selected: (1) groups with fast turnover rates; (2) groups/species that are targeted by human activities or that are indirectly affected by them; (3) habitat-defining groups/species; (4) groups/species at the top of the food web; (5) long-distance anadromous and catadromous migrating species; (6) groups/species that are tightly linked to specific groups/species at another trophic level	100 op/181	42	
D4	*(C4)*[a]	*(not defined)*[a]	None operational/3	2	*D4 Food webs: new proposals*
D6	C1	I1 Biogenic substrate: (1) type; (2) abundance; (3) biomass; (4) areal extent	2 op/5	6	
D6	C1	I2 Extent of seabed significantly affect by human activities for the different substrate types	None operational/1	1	
D6	C2	I1 Presence of particularly sensitive and/or tolerant species	None operational/1	1	
D6	C2	I2 Multi-metric indexes assessing benthic community condition and functionality, such as (1) species diversity and (2) richness, (3) proportion of opportunistic to sensitive species	1 op/4	6	
D6	C2	I3 Proportion of (1) biomass or (2) number of individuals in the macrobenthos above some specified length/size	17 op/38	3	
D6	C2	I4 Parameters describing the characteristics (shape, slope and intercept) of the size spectrum of the benthic community	None operational/1	1	

[a] New proposals for Descriptor 4 Food webs, not considered under the set of indicators outlined in the Com Dec. 2010.

Table 5
Number of model-derived indicators for each biodiversity component *per* habitat type (only habitats addressed by the models are included).

Biodiversity components	Seabed			Water column				ICE
	Littoral rock and biogenic reef	Shallow sublittoral mixed sediment	Shelf sublittoral mud	Marine water: coastal	Marine water: shelf	Marine water: oceanic	Variable salinity estuarine water	Ice-associated habitats
Microbes				1	1			1
Phytoplankton		9	1	4	42	13	2	4
Zooplankton	1	10	1	3	34	12	1	2
Angiosperms					12	7		
Macroalgae	1			1	11	1		
Invertebrates	1	11	1	1	45	15		1
Fish								
Coastal fish				2				
Pelagic fish				12	18	12		1
Pelagic elasmobranchs				1	2	2		
Demersal fish				7	13			1
Demersal elasmobranchs					1	11		
Other	1	14			34	11		
Cephalopods								
Coastal/shelf pelagic		13			27	6		
Other					7	1		
Marine mammals								
Toothed whales		13		1	23	2		
Baleen whales					1	1		
Seals					3	1		1
Other	1				8	6		
Reptiles								
Sea turtles					10	1		
Birds								
Inshore pelagic feeding		13			13			
Offshore pelagic feeding				1	1			
Other					10	5		

considered in models that include a benthic component, for example, ERSEM. The least addressed biodiversity components were microbes, coastal fish, pelagic elasmobranchs, baleen whales, seals and offshore pelagic birds. When looking at habitat representation in model-derived indicators, ice associated habitats, estuarine water column and shelf sublittoral mud were seldom covered (Table 5).

5. Models geographical coverage

Ecological models can be applied to many different areas with adequate customization (Henry et al., 2012; Mateus et al., 2012). The models in the catalogue have not been applied with the same spatial scale in all European regional seas (Fig. 2). The majority of reported indicators related to the Mediterranean Sea, representing more than half of the indicators entered in the catalogue (137), followed by the North-East Atlantic Ocean (78), Black Sea (29), Baltic Sea (18), non-EU regional seas (11) and EU scale (2). The EwE software was the most widely used model and has been applied in each EU regional sea area and most sub-regions; the second most commonly used model was ECOSMO, which has been implemented for the Baltic Sea, the North-East Atlantic Ocean and one non-EU regional sea (Barents Sea). In most regional seas, the proportion of model-derived indicators considered operational was high (ranging between 60 and 80%), except for the Black Sea where a suite of ecological models had been developed but using model-derived indicators still under development (about 70%) at the time of the assessment. Conceptual models were mainly reported for the North-East Atlantic region.

As stated by the MSFD, Member States (MS) need to cooperate to ensure a coordinated effort in the study and development of management strategies for the different marine regions and sub-regions. This is the case for ecological models developed for understanding and forecasting the marine ecosystem response to pressures. This catalogue demonstrates that the geographical coverage of ecological models in European marine waters is extensive and that the assessment of the environmental status can benefit considerably from greater use of ecological modelling. However, the use of differing models in different regions constrains the possibility of comparisons and inference of robust conclusions on causalities and scenarios (Chust et al., 2014).

6. Addressing pressures with models

Models are powerful tools for scenario testing of climate and anthropogenic impacts both separately and simultaneously (Jørgensen and Fath, 2011). All 44 available models included in the present catalogue, have been used to address at least one pressure or its impact on state of the ecosystem or its components. Most of the model-derived indicators compiled in the catalogue are state indicators (91%; S1), meaning that they inform on the condition of the ecosystem, its components or its functioning, while reflecting the impacts of single or multiple pressures in the environment. The majority do not provide a direct measure of the pressure(s) affecting the system, so they can only indirectly be associated to the pressures mentioned above. And despite strong scientific evidence for the overall cause–effect relationships between many of these pressures and the state of the ecosystem (Shin et al., 2005, 2010a; Fulton, 2011), the identification and quantification of the pressure(s) cannot be achieved through these indicators. On the other hand, a few of the indicators produced by the models are actually pressure indicators (9%; S1), which means that they act as proxies for relevant pressures. For instance, temperature or pH can act as a proxies for climate change; nutrients concentration and oxygen levels as proxies for eutrophication; biomass of an invasive species (e.g., *Mnemiopsis leidyi*, Dorofeev et al., 2012) as a proxy for non-indigenous species pressure; and also 'Inverse fishing pressure' which measures the total fishing pressure on an ecosystem

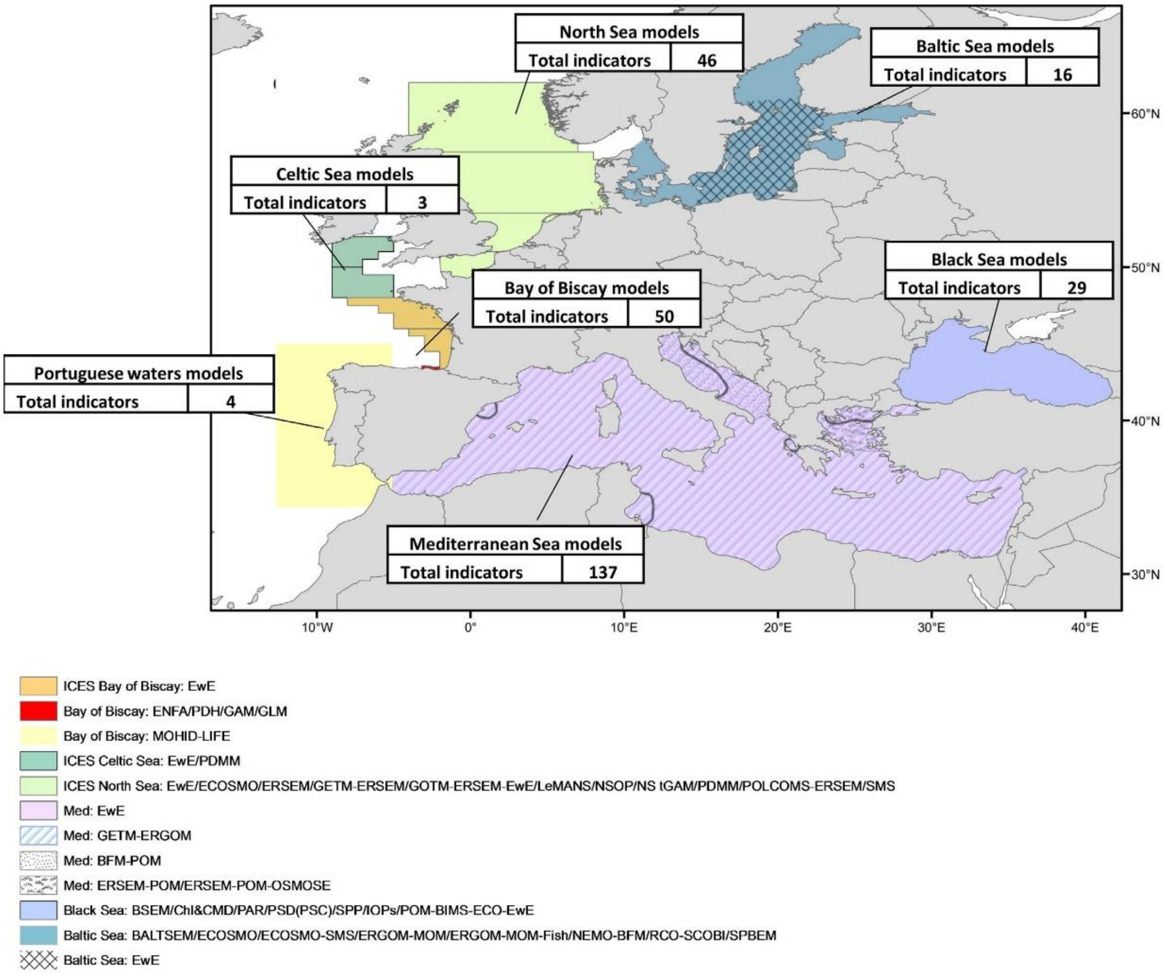

Fig. 2. Geographical distribution and spatial coverage of the models in the catalogue, when applicable. ECOSMO, ROMS-BioEBUS and ROMS-BioEBUS-OSMOSE are not displayed since are occurring in areas (Barents Sea and Benguela) outside the European Seas. EU Hubbell's neutral model and Maxent since they are applied to all EU regional seas are not represented.

using landings over biomass, could be considered as a proxy for exploitation rate and therefore a potential pressure indicator (Shin et al., 2010a).

The survey showed that, collectively, these models had the capacity to address (i.e. respond to, in most cases) all pressures except two ('*Contamination by radio-nuclides*' and '*Microbial pathogens*') of those outlined in the Directive (S3) and summarised in Fig. 4. The potential for the models to inform on the effects of pressures on the ecosystem was heterogeneous and whilst the majority addressed at most five pressures, a few models, mainly represented by multispecies and E2E models, were reported as capable of addressing up to fifteen different pressures (see S1 for a detailed list of pressures addressed by each model). Often pressures were of very different nature: from physical disturbance, to contamination by hazardous substances, nutrient and organic matter enrichment, biological disturbance and climate change (Fig. 4).

Of all the pressures listed in the MSFD, '*Interference with the hydrological regime*' was the most frequently addressed (in terms of numbers of models), with all 44 models reported and currently being used in monitoring or research associated with this pressure (Fig. 4). The '*Input of nutrients and organic material*' and '*Marine acidification*' (pH change) followed as pressures that could be addressed by more than half of the models. On the other hand, '*Non-indigenous species*', '*Marine litter*' and '*Underwater noise*' were the least addressed pressures by the type of models included in our survey, with just four models able to inform on the responses to one, or maximum two, of these pressures.

The pressures '*Physical loss of marine habitat*' and '*Physical damage to marine habitats*' (combined as '*sum of Physical damage*' in Fig. 4), could primarily be addressed using E2E, multispecies and SDM/Habitat suitability types of models (S1). The Meta-community model could also produce indicators related to these pressures. A total of 20 models provided 114 indicators to address these pressures, with EwE able to provide 95 of these indicators. Such indicators were mostly state indicators, primarily related to biomass of different trophic levels, with a small number also relating to species distribution, primary and secondary production. Two physico-chemical indicators from the GETM-ERSEM model were the only pressure indicators reported (S1): denitrification layer depth and oxygen penetration depth.

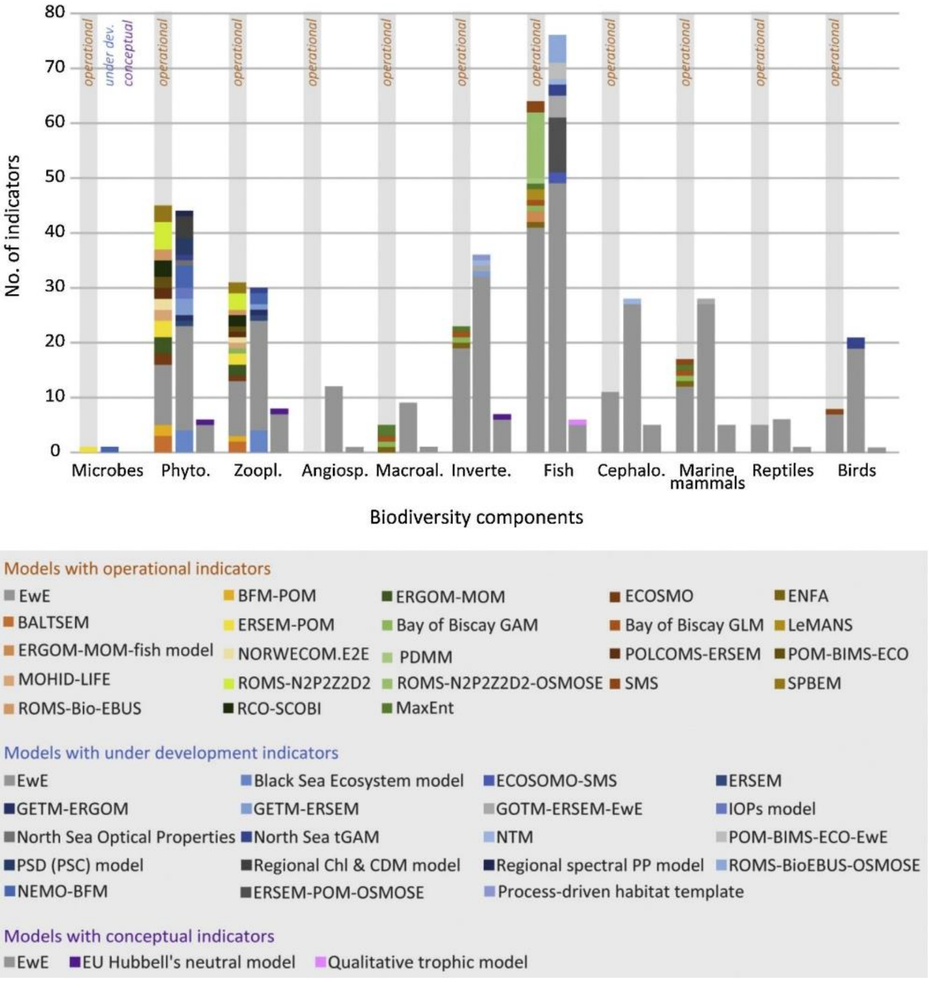

Fig. 3. Number of model-derived indicators available per biodiversity component. For each biological group the indicators are organised by columns according to their development status: operational, under development and conceptual. The different colours and patterns identify the models providing the indicators.

'*Underwater noise*' and '*Marine litter*' were both addressed by the same two models (GOTM-ERSEM-EwE and EwE), and through a similar set of model-derived indicators (in a total of 19 state indicators; S1), all relating to top predator biomass such as large fish, marine mammals, reptiles and seabirds. This is a common thread for many of the pressures acting particularly on higher trophic groups and therefore their impacts are better evidenced by models encompassing such trophic levels.

The pressure '*Interference with the hydrological processes*' could be addressed by 190 indicators from all models in our catalogue. Such changes in hydrological regime (namely thermal and salinity), were perceived as pressures related closely to climate change, although climate change is also accounted for by other pressures such as '*Marine acidification*'. In this sense, the large majority of the state indicators in the catalogue (S1) were reported as able to reflect the impact of these regime-shifts with strong ecological implications throughout the food web. Only 19 are pressure indicators, essentially physical–chemical indicators derived from coupled models with physical (hydrodynamic)–biogeochemical modules. The EwE food web and the BS-PAR bio-optical (remote sensing) were the other type of models providing two of these pressures indicators (respectively, '1/(landings/biomass) – Inverse fishing pressure' and 'Habitat condition – water transparency').

The pressures 'Contamination by synthetic compounds', 'Contamination by non-synthetic substances & compounds' and 'Acute pollution' (represented as 'Sum of contamination Pressures' in Fig. 4) were addressed by a total of 17 models of different types (multispecies, meta-community, SDM/habitat suitability and coupled models). Up to 132 model-derived indicators were identified, with the EwE model able to provide the highest number (S1). The majority of these were indicators of biomass with a small proportion of indicators relating to energy flow and primary/secondary production. One pressure indicator '1/(landings/biomass) – Inverse fishing pressure' has also been reported under this pressure type.

The majority of the 25 models assessing '*Inputs of nutrients and organic matter*' (Fig. 4) were spatial-dynamic coupled models (both E2E and hydrodynamic–biogeochemical) and, less frequently, biogeochemical, multispecies and bio-optical models. The total number of indicators that could address this pressure is 42, focusing on various measures of primary production and

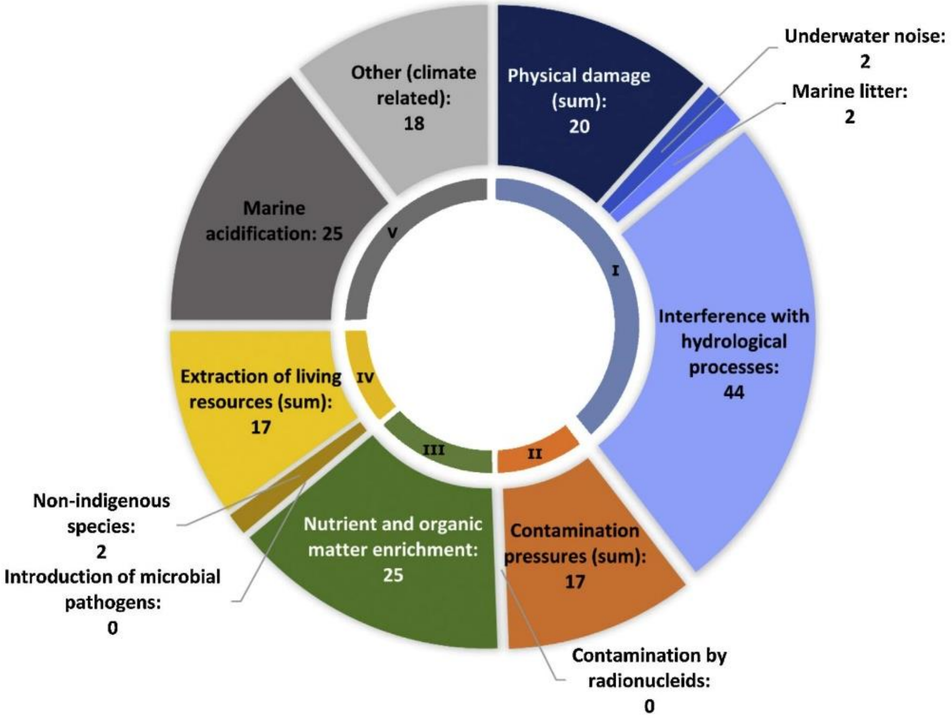

Fig. 4. Capability of models in the DEVOTES catalogue to address pressures outlined in the Marine Strategy Framework Directive (Annex III; see S3); the number of models available per major type of pressure is indicated: I – physical disturbance type of pressures; II – contamination by hazardous substances; III – nutrient and organic matter enrichment; IV – biological disturbance; and V – climate related pressures.

parameters relating to zooplankton. Only two of them are pressure indicators: 'Population size (as biomass) of a non-indigenous species – *Mnemiopsis leidyi*' and 'Habitat condition as water transparency'.

'*Non-indigenous species*' were only addressed by two models, the BSEM physical (hydrodynamic)–biogeochemical coupled model and the EwE food web model, through the indicators 'Population size (as biomass) of a non-indigenous species – *Mnemiopsis leidyi*' and 'Alien shrimps biomass'', respectively.

A total of 17 models, essentially food web and coupled models, have been applied in the context of '*Selective extraction of living resources*' (encompassing extraction of fish and shellfish through direct catch, by-catch and discards and extraction of maërl, seaweed harvesting and the extraction of any other species) (Fig. 4). Overall, 143 indicators were associated collectively with these models (S1). The majority of these were indicators of biomass, being associated with the EwE model. Only one pressure indicator was reported ('1/(landings/biomass) – Inverse fishing pressure') from EwE.

'*Marine acidification (pH change)*' was currently addressed by 25 models (Fig. 4), essentially coupled models (both E2E and hydrodynamic–biogeochemical) with a dynamic or spatial-dynamic nature, but also multispecies, bio-optical models, and biogeochemical models. A total of 56 indicators capable of assessing the effects of this pressure, relating also to climate change, could be derived by these models. These indicators are predominantly related to biomass of lower trophic groups and primary production.

Finally, other pressures not listed in the MSFD Annex III, related to climate and inter-annual meteorology, were also mentioned by the modellers, reporting 18 models that could provide 30 indicators responsive to such pressures. The majority were state indicators, such as low trophic groups biomass, but also some production, diversity or species life-history indicators. As pressure indicators, six physical–chemical proxies of climate pressures were mentioned (S1).

7. Gaps and development needs

This work summarises the current capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity. The cataloguing of models and their derived indicators presented in this study aim to help the planning and the implementation of objectives defined in the MSFD particularly in relation to which models and indicators exist and the missing components to support such policy. This is particularly important in the MSFD framework that requires the assessment of all European Seas in relation to their ecosystem status and pressures associated, and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020.

Overall it was evident from the analysis of the model catalogue that some descriptors (and their requirements) within the MSFD (Table 4) are best assessed by modelling (e.g., D4 food webs), while other indicators are better assessed by "traditional" empirically derived ecological indices. For instance, many models potentially addressing D6 (seafloor integrity) lacked specific indicators of substrate type or seabed extent (Table 4) mainly because of their inability to express benthic habitat as some form of component. D2 (non-indigenous species) is currently poorly addressed by the models even though some of them would have the capability to provide useful indicators for this descriptor. Similarly indicators for D8 (contaminants), D9 (contaminants in food), D10 (marine litter), D11 (underwater noise) outlined by the European Commission (2010) are not currently addressed by any of the models reported here; however, these descriptors were not the target of our survey. Three indicators related to the four biodiversity related descriptors (D1, D2, D4, D6) had no model-derived indicator in the catalogue (Table 4):

- D1 Biodiversity/C3 Population condition.
  - o I2 Population genetic structure
- D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species
  - o I1 Ratio between invasive non-indigenous species and native species
  - o I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

With respect to the gaps addressed to pressures, the majority of models require further work to show how sensitive and specific to pressures they are. Underwater noise, marine litter and contamination by microbial pathogens are poorly addressed by existing models and those that have been reported to produce indicators that are sensitive to these pressures require further development. It is emphasised that this summary of model use does not reflect model adequacy, data quality or the overall quality and effectiveness of the monitoring and research programmes under which the models are applied.

Focusing on model features, two main gaps were identified that require further development: one related to the setting of targets, and the other to uncertainty associated with model results. Targets exist when objectives have been clearly identified and their translation into operational performance metrics agreed to, which involves a socio-political decision process that occurs independently of model-development. If the models have been developed independently of such processes, which is the case for most of the models listed in the study, targets for selected variables may not be available (despite the indicator being operational) reflecting the context in which they have been developed. Thus, because the models in the catalogue were not developed with the aim of supporting MSFD, and because the MSFD does not set clear targets or aims, it is not surprising that model developers often reported difficulties in setting targets and/or reference values for their models. Two main barriers were identified. First, the process of association of ecologically meaningful targets to model outputs (derived indicators) without a clear vision of where and what the model would be used for in a specific MSFD context. Second, the level of demand required by the targets: should thresholds and/or reference values reflect the good condition of the assessed component in isolation (for e.g., for each indicator used) or reflect a compromise between ecological integrity and the use of the marine environment, as implicit in the MSFD GEnS definition? The level at which GEnS should be defined, either at indicator or at the descriptor level, or even for all eleven descriptors together, will influence the way thresholds setting is perceived and established (Borja et al., 2013). This will ultimately affect the final assessment as discussed in depth in Claussen et al. (2011) and Borja et al. (2013). For the last point, it can be argued that there is not enough information at this stage for model developers to set meaningful targets for MSFD purpose. Therefore, threshold setting should be guided by clear objectives and end goals as achievable targets and these are not known at present.

In this context, several initiatives have been created to support and address, at least partly, most of the issues arise above; for example FP7 projects such as MEECE (completed) and DEVOTES (in progress) have been developed to explore the use of ecological models in assessing ecosystem status and in support of decision making and EU policy. More recently, MIDAS, a modelling inventory database with models currently in use by the European Commission, allows the assessment of how models are used and/or support impact assessments at EU level.

In addition, not all the models were able to address uncertainty; the majority lacked confidence intervals or an approach to evaluate uncertainty of the model outputs. Marine system models are indeed becoming increasingly complex and sophisticated, but far too little attention has been paid to model errors and the extent to which model outputs actually relate to ecosystem processes (Allen et al., 2007). Further developments on this would produce more robust assessments and forecasts and therefore more reliable indicators.

European geographical coverage is also very heterogeneous with several identified marine areas with enormous potential for improvement. Also certain habitats (e.g., ice-associated habitats or continental shelf sublittoral mud) and biodiversity components (e.g., microbes) are underrepresented in the modelling approaches presently in the catalogue. As mentioned before, this is mostly due to the emphasis that has been given historically to particular flag species, commercially important organisms or particularly endangered species/habitats. However, the relative importance of modelling such components can change according to the system studied. Current gaps should, therefore, be evaluated on a regional scale basis. Looking at current modelling gaps from a regional seas perspective, one of the limitations observed is the focus of the participants in the review process that may have shown a bias in the selection of models/model types. An example of this is Atlantis, a E2E model not currently operational in Europe, or the Bioenergetics and Dynamic Energy Budget (DEB) type of models currently not included in this catalogue but widely used in the regions covered by DEVOTES (Teal et al., 2012). These models describe how individuals acquire and utilise energy, in addition to how physiological performance is influenced by environmental variables, and can serve as a link between different levels of biological organisation (Nisbet et al., 2000, 2012). Considering them would thus increase the potential to address MSFD Descriptors/Indicators that focus particularly on properties at the individual level and physiological level, usually responding to pressures whose impacts operate or can primarily be detected at that scale (e.g., biological disturbance, such as food resource depletion; contamination; or effects of climate change, namely marine acidification). In addition, regional model runs identified the need to improve the existing models with regards to species diversity (e.g., adding certain species or refining subgroups), spatial resolution for selected species and for better description of the direct effect of anthropogenic pressures on ecosystems. Model response towards the impact of certain pressures still requires further testing.

Relevance of certain pressures differs across regional marine areas. Broadly speaking, those that could benefit from further research are for physical damage to marine habitats, underwater noise, marine litter, contamination by radio-nuclides, introduction of microbial pathogens, extraction of species (maërl, seaweed and others), marine acidification, acute pollution events and nutrient and organic matter enrichment.

Data availability is also a constraint. This could partially explain why the number of 'under development' indicators is still quite high suggesting that this requires particular efforts to increase the potential to address MSFD descriptors. To assess the environmental status descriptors adequately, the gap analysis conducted here highlights that further refining of the current models and their associated indicators as well as the adoption of new modelling techniques are needed.

The information (data) needs for model development and the results provided (outputs), is very heterogeneous. Two main modelling approaches can be distinguished: statistical (i.e. SDMs) and mechanistic (i.e. multispecies and biogeochemical models)

(Kendall et al., 1999). In general terms, spatial mechanistic models require large amounts of computational resources, and can only be applied when demographical, physiological, and life traits of species are well known. On the other hand, statistical (i.e. SDMs) modelling studies often neglect dispersal-limitation and advection, although they can play an important role on spatial distribution, while spatial dynamical models minimise the role of environmental factors on species distribution (Robinson et al., 2011). Taking a balanced view between the importance of dispersal-limitation and of niche partitioning on the species spatial distribution, we suggest that research efforts should focus on integrating the two mechanisms into ecological modelling.

Finally, in some instances, the gaps identified may not need to be filled. This is the case for component(s) and/or pressure(s) considered 'un-manageable' (e.g., the target for zooplankton biomass or distribution). However, given the complex interactions within ecosystems, management of some components may have unexpected effects on 'unmanageable' components. Thus, ecological models should be developed to encompass all components, to the extent that they are known, wherever possible.

Acknowledgements

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.05.037

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Reconstruction of Italy's marine fisheries removals and fishing capacity, 1950–2010

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ABSTRACT

Italy has the highest catches of all countries fishing in the Mediterranean Sea. Despite the availability of fisheries statistics at the national level, reported catch amounts account only for a portion of total fisheries removals. This study aims to provide an estimate of 1) catches for all marine fishing sectors; 2) fishing effort in the major Italian fishing fleets; and 3) catch per unit of effort from 1950 to 2010. Catches were estimated using a catch-reconstruction approach that looked at all types of fisheries removals: from reported and unreported landings (from both industrial and artisanal fisheries) to recreational landings and discards. The reconstructed total catch for the 1950–2010 time period was 2.6 times the amount reported by the FAO on behalf of Italy. Illegal, unreported and unregulated (IUU) landings constituted 53.9% of the reconstructed total catch, followed by reported catches (38.8%) and unreported discards (7.3%). Industrial fisheries were dominant, with 79.1% of the reconstructed total removals, followed by the artisanal catch (16.8%), with recreational (3.2%) and subsistence (0.9%) fisheries making very small contributions. Catch per unit of effort declined since the early 1950s. Our study is the first that estimated total Italian fisheries removals and fishing capacity using a holistic approach; such approach is particularly important in areas like the Mediterranean Sea, where the multi-species and multi-gear nature of fisheries make the assessment of single-species fisheries resources and their management difficult.

1. Introduction

The Mediterranean Sea has been described as "under siege" due to the effects of multiple stressors such as fishing, habitat loss and degradation, pollution, eutrophication, and the incidental introduction of alien species (Coll et al., 2011). Fishing is one of the strongest pressures, and has caused changes in ecosystem structure, declines in major fish stocks and in overall biodiversity in many parts of the Mediterranean Sea (Colloca et al., 2011; Farrugio et al., 1993; Papaconstantinou and Farrugio, 2000; Vasilakopoulos et al., 2014). Although the exploitation of marine resources has a long history in the Mediterranean basin (Thompson, 1947), fisheries research and management has only developed post-World War II, particularly in the northwest of the basin (Farrugio et al., 1993). Italian fisheries are among the most important fisheries in the Mediterranean, constituting, according to the Food and Agriculture Organization of the United Nations (FAO) statistics, roughly 30% of its all catches. In recent decades, the Italian fishing industry has faced declines, both in terms of catch, due to a decrease in the major fisheries resources (4th Multi-Annual Guidance Plans; MAGPs), and also in fishing effort, as a result of European Commission regulations, which attempt to adjust the fishing fleet to the available fishing resources (Iborra Martin, 2006). In contrast, since the late 1980s, there has been a steady increase in farmed fish production. The majority of mariculture production consists of Mediterranean mussels (*Mytilus galloprovincialis*) and Manila clams (*Tapes philippinarum*), followed by gilt-head seabream (*Sparus aurata*) and European seabass (*Dicentrarchus labrax*) (Cataudella and Spagnolo, 2011; OECD, 2010). The present reconstruction is solely concerned with marine capture fisheries of finfish and invertebrates (excluding sponges, turtles, jellyfish and marine mammals), and thus does not address aquaculture trends and associated issues.

Given the growing emphasis on ecosystem-based management issues in fisheries (Pikitch et al., 2004), a comprehensive understanding of total fisheries removals and fishing capacity is

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fundamental to understanding the ecosystem resources trends and thus contribute to policy on future resource use. This, however, becomes challenging in a Mediterranean country whose statistical reports of catch and effort are often unreliable, and where actual catches are often underestimated (European Commission, 2003; Garibaldi, 2012; Garibaldi and Kebe, 2005; Moutopoulos and Koutsikopoulos, 2014). Commercially valuable species often go directly to public markets and regional auctions, and these catches often are not included in the official records and hence go unreported (OECD, 1994). Also, there is limited monitoring and enforcement, especially with regard to illegal nets and mesh sizes, the landing and marketing of undersized fish, and compliance with restrictions on fishing season and areas (OECD, 1994). Available fisheries statistics exist at the national level, i.e., from the Italian National Statistical Institute (ISTAT) and the Institute for Economic Research in Fishery and Aquaculture (IREPA), and the data from these two organizations are sent to FAO. These reported catches account only for part of total fisheries removals and have never been harmonized and/or compared with estimates of total fisheries removals. This is particularly true for small-scale fisheries, whose catches are generally underestimated, and for recreational and subsistence fisheries, which are often not accounted for in countries' official statistics (Pauly, 2006; Pauly et al., 2014).

As part of an overall effort to reconstruct global fisheries catches (Zeller et al., 2007) by the *Sea Around Us* (www.seaaroundus.org; Pauly, 2007), which also includes Mediterranean countries (Coll et al., 2014; Pauly et al., 2014; Tsikliras et al., 2007; Ulman et al., 2013), this study aims to provide estimates of fishing capacity for the major Italian fishing fleets and catches for all marine fishing sectors from 1950 to 2010, using all available data sources and accounting for reported and unreported commercial landings, recreational and subsistence landings and discards. Reconstructed catches and effort presented here are for the whole of Italy. Results by sub-regional seas: 1) Ligurian; 2) Northern, Central and Southern Tyrrhenian; 3) Ionian; 4) Northern, Central and Southern Adriatic Sea; 5) Sicilian and 6) Sardinian waters can be found in Piroddi et al. (2014).

2. Materials and methods

2.1. Study area

Italy is located in southern Europe and covers an area of approximately 301,270 km^2. It includes the Italian peninsula, Sicily and Sardinia (the two largest Mediterranean islands), and 71 other smaller islands. The country consists of 21 regions, 15 of which are coastal (Fig. 1). The territorial waters extend to 12 nautical miles from the coast and have a surface area of 7210 km^2 and the continental shelf has a surface area of 201310 km^2 (Iborra Martin, 2006). The Italian Exclusive Economic Zone (EEZ), as delineated by Claus et al. (2014) (see also www.vliz.be), covers nearly 538,000 km^2. Due to its central Mediterranean Sea location, four of the seven Mediterranean Sea subdivisions surround the peninsula: the Tyrrhenian and Ligurian Sea in the west, the Ionian Sea in the south and the Adriatic Sea in the east. This geographic positioning leads to important biophysical differences of the waters around Italy. For example, the distribution of the continental shelf is very uneven; it is very broad and shallow in the Adriatic Sea, but changes to very narrow shelves with steep slopes in the other seas (Cataudella and Spagnolo, 2011; Francalanci, 1993). Also, the waters range from being highly eutrophic in the northern Adriatic Sea to oligotrophic in most other areas. The diversity of these biophysical conditions also leads to a high biodiversity: Italian waters host important commercial species such as the Atlantic bluefin tuna (*Thunnus thynnus*), charismatic megafauna such as the endangered Mediterranean monk seal (*Monachus monachus*) and habitat-forming species, such as seagrass (*Posidonia oceanica*) (Giakoumi et al., 2013; MacKenzie et al., 2009; Reijnders et al., 1997).

Italy has a population of 61 million people (ISTAT, 2012), over half of which reside in coastal regions (Cori, 1999; ISTAT, 2012). Fishing occurs along the entire coastline and catches are landed at over 800 sites (Cataudella and Spagnolo, 2011; Iborra Martin, 2006; OECD, 2010). Despite their marginal contribution to the national economy, both in terms of income and employment opportunities, fisheries play a fundamental role in certain regions (e.g., in Sicily). The Italian fishing industry is characterized by the predominance of small and older vessels, a diversity of fishing gear, and consequently a diverse array of multi-species catches (Cataudella and Spagnolo, 2011; FAO, 2010; OECD, 2010). The commercial fisheries are represented by the following types of fleets: bottom trawlers, mid-water trawlers, purse seiners, longliners, dredges, multi-purpose vessels and an artisanal fishery.

2.2. Italian fisheries management

A comprehensive fisheries management scheme was initiated in 1982 with the Law 41/1982; prior to that, only certain restrictions such as minimum mesh size, minimum legal landing size, and closed areas were mandated by national authorities. With the introduction of Law 41/1982, national triennial plans were established. In particular, all professional fishing vessels had to possess a license managed by the Directorate General for Fishery and Aquaculture of the Ministry of Agriculture Policy. The license includes characteristics of the vessel (e.g., the name of the vessel, the EU number, GT), limitations of fishing areas, gear use and spatial licensing (e.g., overseas and ocean-going fishing, Mediterranean fishing, and in-shore coastal fishing; OECD, 2010). Currently, the licensing scheme limits fishing effort mainly in the form of temporal restrictions which are set each year in relation to spawning seasons. In addition, the closure is compulsory for the eastern fishing grounds and voluntary in the western grounds. Starting in 1996 and re-enforced in 2000, a seasonal closure was also initiated for tuna. In addition, in 1992, the European Union (EU) put a 2.5 km limit on the length of driftnets; in 1998, the EU fully banned the use of driftnets in the Mediterranean Sea and the northeast Atlantic Ocean, which became fully effective on January 1, 2002. Additionally, in 1994, the EU established a set of restrictions for the main gear-types (EU Rule 1626/94) to preserve fisheries resources in the Mediterranean Sea. For instance, the operation of trawls and seines was prohibited within three nautical miles (nm) from the coast except for "special fisheries" for which derogation by the national legislation was put in place. For example, the "Bianchetto" (juvenile of *Sardina pilchardus*), "Rossetto" (*Aphia minuta mediterranea*) and "Cicerello" (juvenile of *Gymnammodytes cicerelus*) fisheries operate only in winter (January 15–March 15 as a rule) for a period of 60 days. These fisheries have a long history at the local level and are one of the most important small-scale activities with large socio-economic impacts. Since 2010, the EU has banned these fisheries (small trawling boats using mesh size <40 mm) throughout the Mediterranean for their unsustainability, stating that only vessels of other gear types with a proper management plan would be allowed to fish (Reg. (CE) n. 1967/2006).

In Italy, to date, no quotas or TACs (total allowable catch) have been established, except for sedentary species such as clams or highly migratory species such as Atlantic bluefin tuna, due to the multi-species nature of the fisheries, which does not allow fishers to easily shift their target species from one to the other (Cataudella and Spagnolo, 2011; Iborra Martin, 2006; OECD, 2010).

Also, few fisher consortia exist in the country, such as for the management of molluscs (CO.GE.MO) and of small-scale fisheries (CO.GE.PA.), introduced by the Italian Ministry, to empower fishers

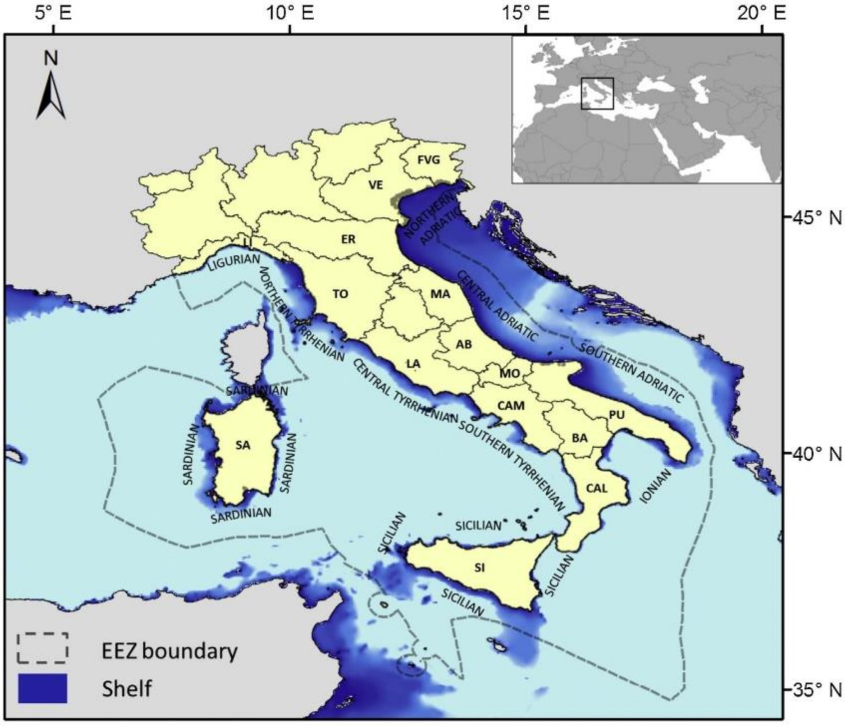

Fig. 1. Italy with its coastal regions (LI: Liguria; TO: Toscany; LA: Lazio; CAM: Campania; CAL: Calabria; SI: Sicily; SA: Sardinia; BA: Basilicata; PU: Apulia; MO: Molise; AB: Abruzzo; MA: Marches; ER: Emilia Romagna; VE: Veneto; FVG: Friuli Venezia Giulia) and the four surrounding sub-regionals seas: Ligurian; (Northern, Central and Southern) Tyrrenian; Ionian and (Northern, Central and Southern) Adriatic Sea. For the scope of the report Sicilian and Sardinian waters have been considered separately.

Table 1
Catch allocation reconstruction following ISTAT-IREPA structure.

Sub-regional division	Coastal regions
1. Ligurian	Liguria
2. Tyrrhenian	
- Northern	Tuscany
- Central	Lazio
- Southern	Campania and Calabria West
3. Ionian	Calabria East; Apulia West; Basilicata
4. Adriatic	
- Northern	Emilia Romagna; Veneto; Friuli Venetia Giulia
- Central	Abruzzi; Marches; Molise; Emilia Romagna
- Southern	Apulia East
5. Sardinian	Sardinia
6. Sicilian	Sicily

and local fishing enterprises to manage and regulate specific stocks in limited areas (Spagnolo, 2006).

2.3. Catch reconstruction approach

The reconstruction of Italy's total fisheries catches for the 1950–2010 period was completed by following the same approach as described and applied in Zeller et al. (2007). Since this method is well known and well described, refer to Zeller et al. (2007) for a more detailed description.

2.4. Data sources

A general description of data sources used in the reconstruction is detailed in Table 4. In particular, we presented the fishing sectors considered, years of data availability, associated references, anchor points and estimated uncertainty (see below).

2.4.1. Official landings

The baseline used for reported catches was the time-series of capture production from the two Italian national statistical organizations (ISTAT and IREPA) which were compared to the FAO FishStat database. Two other FAO databases were also used: the global capture production dataset available for 1950–2010 and the regional dataset from the General Fisheries Commission for the Mediterranean (GFCM) available for 1970–2010 (FAO, 2012). Since the two trends were identical for the same time period (1970–2010) we decided to use and present here only the FAO global dataset, which had longer time series.

As previously mentioned, ISTAT and IREPA were the responsible authorities which collected the data. In particular, the official catch statistics were first provided by ISTAT from 1950 to 2001, and only recently the Italian Ministry of Agriculture and Forestry Policies (MIPAAF) transferred management of the fishery sector to IREPA from 2005 onwards. In 2000, IREPA, before becoming the official national fisheries statistical organization, under a mandate of MIPAAF, and with respect to European legislative requirements, took the coordinating role of optimizing the fisheries statistical scheme to obtain detailed and harmonized fisheries data collection along the entire Italian coast. This new survey methodology collects other relevant data on important aspects of the fisheries, namely, total landings per species; prices obtained by species; fishing effort; fishing hours; and fishing typologies. This is carried out on a weekly basis by 'local observers' from within the fisheries sector, i.e., biologists, ship owners, ex-fishers, and business consultants distributed along the major Italian fishing ports (of which there

Table 2
Technological coefficients of fishing vessels by gear type as reported by Pauly and Palomares (2010).

	Technological coefficient		
Vessel type	1950–1980	1981–1995	1996–2010
Trawlers	0.5	1	1.8
Mid water trawlers	0.5	1	1.8
Dredges	0.5	1	1.4
Purse seiners	0.5	1	1.8
Artisanal	0.5	1	1.3
Multiple gears	0.5	1	2.5
Longliners	0.5	1	2.8

are approximately 800). The structure of our reconstruction data followed the spatial allocation outlined in Table 1. Here, the Adriatic and the Tyrrhenian Seas were split into Northern, Central and Southern sections to account for their large extent and for significant differences in reported landings. Sicilian and Sardinian waters were considered separately for the same reason (Fig. 1).

Among the sub-regional divisions, Sicily, followed by Central Adriatic, and South and North Tyrrhenian had the most incomplete catch datasets (Fig. 2). Since this inconsistency was already noted in other studies (AdriaMed, 2003; Cataudella and Spagnolo, 2011), the IREPA dataset was used from 1996 to 2010, while for the remaining time series (1950–1995), ISTAT catch trend and species composition was used. Due to this sub-regional division, gaps and inconsistencies with the data were easier to address and correct (most of the time to species-level) through literature searches. In particular, using the scientific literature (Cappuccinelli, 2005, 2011), we were able to reconstruct the last 11 years of the catches of European anchovy (*Engraulis encrasicolus*) and European pilchard (*S. pilchardus*) around the coasts of Sardinia (Supplementary materials, Fig. S1). We were also able to complement our compiled dataset or officially reported landings, i.e., the integration of IREPA and ISTAT datasets, with catch data of Atlantic bluefin tuna, frigate tuna (*Auxis thazard*), Atlantic bonito (*Sarda sarda*) and swordfish (*Xiphias gladius*), using the ICCAT statistical database for the main Italian sub-regions. In particular, we tried to use a conservative approach by taking into account the maximum landing estimates for each of these taxa from each dataset. The difference between ICCAT and IREPA–ISTAT catches regarding these large pelagic fishes and the reconstructed trends are displayed in Fig. S2.

In addition, once completed, each regionally compiled dataset of reported landings (corresponding to each of the six sub-regional divisions) was sent for validation to national experts (from local Universities: Universita' degli Studi di Sassari/Genova, respectively, in Sardinia and Liguria; from the National Research Council (CNR): Ancona and Mazaro del Vallo; and/or from local research institutes: Arpat Toscana).

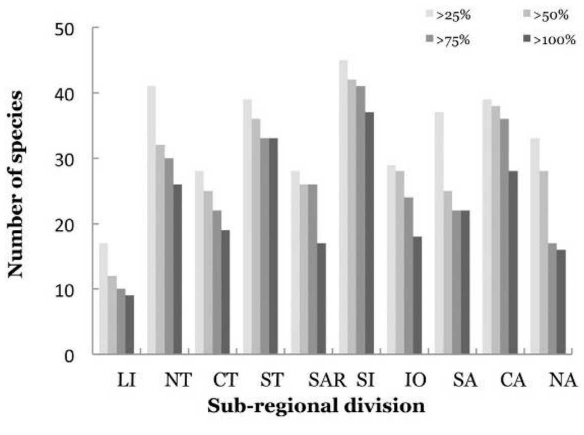

Fig. 2. Number of species per each sub-regional division present in the IREPA dataset with catch values greater than 25%, 50%, 75% and 100% compared to the ISTAT dataset.

The taxonomic breakdown of the commercial species used in the reconstruction was taken from ISTAT and IREPA (Supplementary materials, Table S1). Most of the species were commonly represented, although in a few occasions, some adjustments were made, for example, 'goatfishes' were one group for ISTAT, which IREPA split into red mullet (*Mullus barbatus*) and striped red mullet (*Mullus surmuletus*). In these cases, we decided to use the most detailed list of species, and apply the proportion of presence observed in one source to the other list. In addition, due to the high amount of the very uninformative group 'marine fishes nei' in the data, we decided to split this group into several species and/or groups of species according to the catch composition in the data disseminated by FAO on behalf of Italy. Thus, the reported data were allocated to 82 species or taxa for this reconstruction (Table S1).

2.4.2. Fishing effort

Fishing effort (here in kW days^{-1}) was estimated by taking the product of the number of fishing vessels, kW per vessel (inferred from their GT), and the number of days spent fishing. This information was obtained from ISTAT and IREPA. From 1950 to 1983, the type of vessels reported by ISTAT consisted of only four groups: trawlers, gillnetters, longliners and 'various gears'. From 1984 to 2001, vessel classification was extended to incorporate four additional groups: mid-water trawlers, purse seiners, dredges, and multiple-use vessels. From 1996, IREPA assigned the following classifications to vessel-type:

- Trawl;
- Purse seine;
- Mid-water trawl;
- Mechanical dredges (hydraulics dredge);
- Longlines (drifting or fixed longlines with vessel length >12 m);
- Artisanal fishery (fixed gears such as set nets, hooks and traps with vessel length <12 m);
- Passive multi-use vessels (fixed gears with vessel length >12 m);
- Multi-technique vessels (both fixed and mobile gears).

This classification takes into account the high degree of multi-gear use by the Italian fishing fleets and their wide dispersal rate along the entire coastline. More than 80% of vessels are authorized to fish with a variety of fishing gears, particularly for small-sized vessels, due to their limited range, which forces them to depend on the seasonal availability of coastal resources. Similar to the reported catches, there were some discrepancies between the two primary sources (ISTAT and IREPA) for the number of fishing vessels and GT values, as a result, the more detailed list of fleets (in this case, from IREPA) was used. The data began in 1984 and in order to include estimates for the missing years (1950–1983) in the absence of effort data from earlier years, the proportion of observed fleets for earlier years was taken as the same as for 1984. The reason why we decided to keep the same proportion as 1984, and not the average ratio between 1984 and 2010, was due to the reduction in effort observed in the country from the mid-1980s onward, mainly as a result of EU regulations and declines in marine resources. The number of days at sea and number of fishers were available only from 1996 to 2010 through the IREPA dataset; thus, to estimate the missing years (1950–1995), we maintained kept the ratio of days at sea and the ratio of fishers per type of fleet observed in 1996.

GT was used to estimate fishing power in kW for each vessel using the equation developed by Anticamara et al. (2011), i.e., $kW = 11.26\,GT^{0.71}$, which expresses the relationship between GT

Table 3
'Score' for evaluating the quality of time series of reconstructed catches, with their confidence intervals.

Score	−%	+%	Corresponding IPCC criteria[a]	
4	Very high	10	20	High agreement & robust evidence
3	High	20	30	High agreement & medium evidence or medium agreement & robust evidence
2	Low	30	50	High agreement & limited evidence or medium agreement & medium evidence or low agreement & robust evidence
1	Very low	50	90	Less than high agreement & less than robust evidence

[a] (IPCC criteria from Fig. 1 of Mastrandrea et al. (2010), which note that "confidence increase" [and hence confidence intervals are reduced] "when there are multiple, consistent independent lines of high-quality evidence").

and kW as an exponential relationship. As for days at sea and number of fishers, GT was available per type of fleets only for the period 1996–2010 and thus it was extrapolated for the missing years as the average ratio of GT in the observed time period. Changes in technology have increased fishing capacity on board the same vessel over time (Pauly and Palomares, 2010). To account for improvements in technology that are not be captured by kW as a measure of effort, a technological "creep factor" of 1% was applied since 1980 (Table 2), as derived from the empirical relationship by Pauly and Palomares (2010).

Finally, we calculated catch per unit of effort (CPUE) expressed as $\text{kg}\,\text{kW}^{-1}\,\text{days}^{-1}$ by dividing the total reconstructed catches by the total reconstructed effort for the whole of Italy. For comparison, we also calculated CPUE using the official catch statistics (FAO) divided by the total reconstructed effort.

2.4.3. *Unreported landings I: Recreational catches*

While recreational fishing can be practiced both at sea and from land, the present study concerns only boat-based recreational activities, and therefore excludes shore-based angling, spear fishing and shellfish collection. Until 2010, recreational catches had never been assessed or included in national fishery statistics. To fulfill recent EU legislative requirements, the Italian Ministry of Agriculture and Forestry (MIPAAF) first surveyed recreational fishing activities (particularly the number of fishers and gear types). To date, there are only a few sources of information regarding Italian recreational fisheries. The first preliminary assessment was conducted in 1996 by Anagnopoulos et al. (1998), who described recreational fisheries in Italy and Greece with respect to their fleet size, number of fishers, landings, and fishing effort, here used as anchor points for 1996. Based on more recent sources of information (Cisneros-Montemayor and Sumaila, 2010; Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007), three additional anchor points representing the number of fishers for the years 1989, 1993 and 2003, were developed. Population statistics for the 1950–2010 period were extracted from ISTAT (2012) and used to indirectly estimate total recreational catches by local residents. For instance, we used the percentage of observed number of fishers (from the four anchor points) in the total population (1989: 2.2%; 1993: 2.7%; 1996: 2.6% and 2003: 2.7%) to establish a time series of number of recreational fishers for the missing years. Thus, for the 1950–1988 period, it was assumed that 2.2% of the total population fished recreationally, while for 1990–1992, 1994–1995 and 1997–2002, we interpolated the estimates of the four anchor points, and for the last period (2004–2010), the percentage observed in 2003 (2.7%) was held constant to 2010. We assumed that the proportions of recreational fishing fleets for each sub-regional division observed in 1996 were constant throughout the years (Table S2), and that two fishers per boat caught $1.6\,\text{t}\,\text{year}^{-1}$ of fish (Anagnopoulos et al., 1998), to derive total Italian boat-based recreational catches from 1950 to 2010. To allocate recreational catches to species-level, we used the ratio found in Anagnopoulos et al. (1998) for each sub-divisional region (Table S3).

Also, since there is also an illegal aspect to the recreational fisheries, (e.g., undersized fish, catch above the permitted limits, etc., Table S4), an additional illegal component was estimated (see below for further details).

2.4.4. *Unreported landings II: Illegal, subsistence catches and discards*

In Italy, as in many other parts of the Mediterranean Sea (Coll et al., 2014; Ulman et al., 2013), unreported commercial catches are almost always associated with illegal fishing activities and are thus of concern. In Italy, the most common infringements include the use of illegal fishing gears, trawlers operating closer to shore than permitted, fishing in 'no take' marine protected areas, and the catching of '*bianchetto*' or other undersized specimen (ISMEA, 2006). Although the approach carried out by IREPA, with observers inspecting landings at the main harbors along the Italian coasts, should minimize the quantity of unreported landings, we decided to search for additional information coming from NGO reports and from Italian newspaper accounts and TV documentaries.

The most widely-known and 'observed' illegal fishing activity along the entire Italian coast is the use of driftnets. At the end of the 1980s, the driftnet fishery was the largest fishery in the Mediterranean Sea with over 700 vessels, driftnets of up to 40 km in length and annual reported catches of 5000 t of swordfish and 1000 t of tuna (Tudela, 2004). Despite the maximum length limit of 2.5 km prescribed by the EU in 1992, approximately 650 driftnet boats continued operating with nets measuring on average between 10 and 12 km (Tudela, 2004). The unreported catches from 1992 to 2001 were assumed to be based on a constant number of 650 vessels from 1992 to 1998 (Tudela, 2004) and 299 vessels (Cornax, 2007) from 1999 to 2001, 5% of which operated from Liguria, 49% in the Tyrrhenian Sea, 31% from Sicily, 7% from Sardinia as well as from the Ionian Sea. A catch rate per vessel of $7\,\text{t}\,\text{year}^{-1}$ of swordfish and $1.4\,\text{t}\,\text{year}^{-1}$ of tunas was assumed based on Tudela (2004) and Cornax et al. (2006). From 2002 onwards, after driftnet fishing was officially banned, surveys conducted by different NGOs in major Italian ports identified over 150 driftnet boats still in operation (fish were landed at night to avoid controls). Also, in 2008, the journalist Sabrina Giannini conducted a series of interviews with fishers, and documented the illegal driftnet activities for an Italian TV program ("Report: Mare Nostrum: sfruttamento marino").[2] To estimate these unreported driftnet catches for the 2002–2010 period, the following sources were used: OCEANA (Cornax, 2007; Cornax and Pardo, 2009; Cornax et al., 2006), RSPCA in collaboration with Humane Society International and the Whale and Dolphin Conservation Society (2005), and the interview conducted by Sabrina Giannini. The number of boats observed (~150) was kept constant for the 2002–2010 period and a constant catch rate per boat of $2\,\text{t}\,\text{year}^{-1}$ of swordfish and $0.5\,\text{t}\,\text{year}^{-1}$ of tunas was used.

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[2] Available at: http://www.report.rai.it/dl/Report/puntata/ContentItem-1c6411c7-2f60-490d-bd5a-2829c1d233ff.html.

Table 4
Italian reconstruction of the catches highlighting the fishing sector considered, the period of data available (Time), the source, anchor points, and estimated uncertainty.

Fishing Sector	Time	Specific species/taxa	Anchor points	Uncertainty	Main Sources
Reported catches	1950–1995		No	Yes	ISTAT
	1996–2010		No	Yes	IREPA
	1950–2010	Atlantic bluefin tuna; frigate tuna; Atlantic bonito and swordfish	No	Yes	ICCAT
	2000–2010	European anchovy and European pilchard	No	Yes	Cappuccinelli, 2005, 2011
Unreported catches:					
Recreational catches	1989		Yes	Yes	Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007
	1993		Yes	Yes	Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007
	1996		Yes	Yes	Anagnopoulos et al., 1998
	2003		Yes	Yes	Cisneros-Montemayor and Sumaila, 2010
Commercial (driftnet)	1992-2010		Yes	Yes	Tudela, 2004; Cornax, 2006, 2007; Cornax and Pardo, 2009 Report: Mare Nostrum: sfruttamento marino; RSPCA, 2005
Commercial (others)	1950–2010		Yes	Yes	Italian Coast Guard database and interviews with LT Commander Alessio Morelli
Subsistence	1950–2010		Yes	Yes	Coll et al., 2014
Discards	1950–2010		Yes	Yes	European Commission, 2011; Sartor et al., 2003; Tsagarakis et al., 2013; Vassilopoulou, 2012; Vitale et al., 2006; Relini, 1981; European Commission, 2008; Gilman et al., 2007; MegaPesca, 1999; Castriota et al., 2004; D'Onghia et al., 2003; Botter et al., 2006; Sánchez et al., 2007; Scarcella et al., 2007; Santojanni et al., 2005

Regarding other illegal activities occurring in the artisanal, industrial and recreational fisheries, only recently have Italian media/newspapers begun to report on them. The majority of this news refers to the confiscation of illegal gear by the Italian Coast Guard, and only a few accounts refer to quantities of confiscated species (Table S4). Since 2010, the Italian Coast Guard has started to report on illegal operations at sea and on land. We used the information from the Italian Coast Guard database, combined with direct interviews conducted with LT Commander Alessio Morelli, Head of the Fisheries National Control Unit-Coast Guard, to derive a rough estimate of illegal activity in the area.

We were not able to identify any sources of data relating to personal consumption (i.e., the subsistence fishery). Thus, to develop such an estimate indirectly, and in a conservative manner, we used and held constant the lowest value (1 kg fisher^{-1} day^{-1}) estimated by Coll et al. (2014) for the Spanish subsistence fishery (since Spain shares similar fish consumption patterns and maritime policies), and applied this to Italian commercial fishers per fleet type and the number of fishing days per type of fleet, per year and per each sub-division.

Italian discards for the 1950–2010 period were estimated using two main anchor points, one by Vassilopoulou (2012) and the other by the European Commission (2011a). Additional scientific papers were used in regards to local studies (Table S5). Due to the multi-species nature of Italian fisheries, which allows for the catching of several species at the same time, the high demand of seafood in local markets, and the high enforcement costs required for the monitoring of restrictions, fishers rarely discard fish, but retain and land their by-catch, which is an important component of unreported landings. The rates of by-catch and discards were determined by the type of fleet of each sub-regional division and the total catch per type of fleet (Table S5). We then separated the retained by-catch from discards, using data in the literature, of which, approximately 60% was retained and 40% discarded (Sánchez et al., 2007; Sartor et al., 2003).

2.4.5. Uncertainty

We assessed the uncertainty associated with the reconstruction using a scoring procedure, utilizing uncertainty criteria developed and used by the Intergovernmental Panel on Climate Change (Mastrandrea et al., 2010) to assess uncertainty of input data used in their assessments, which were further calibrated using the results of Monte Carlo simulation in Ainsworth and Pitcher (2005) and Tesfamichael and Pitcher (2007). In particular, this approach consisted of assigning a score, ranging between 1 (very low evidence or less robust data) and 4 (very high evidence and robust data), to the reconstructed catch data of each fishing sector for three different decades (1950–1969; 1970–1989; 1990–2010) (See Table 3 and Table S6 in Supplementary materials). Average scores (and hence percentage confidence intervals) for each time period were derived through catch-weighted averaging of sector scores.

This scoring procedure was previously used in a 'blind' scoring session for 22 Pacific Island countries and territories (Zeller et al., 2015) in which each score was independently (blind) given by three separate research staff. This procedure showed little differences between scorers, and generally reflected the score given by the lead

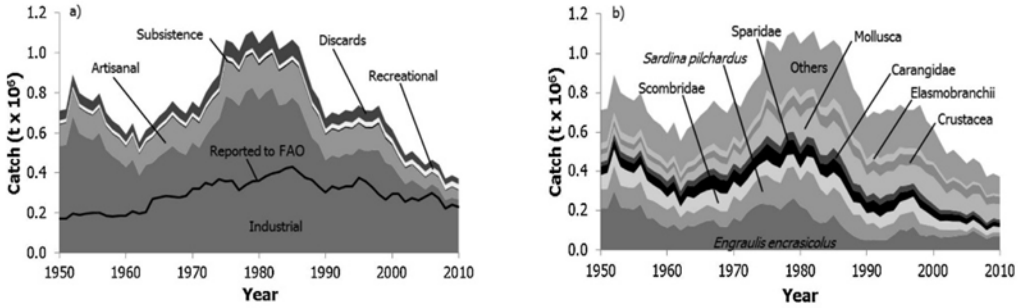

Fig. 3. Reconstructed total catches for the whole of Italy: a) by fishing sector and discards, with reported FAO catches overlaid as black line graph for 1950–2010 period; and b) by taxa (the 'Others' grouping contains 82 taxa).

researcher who had conducted each island's reconstruction. Hence, for Italy, the leading author scored each sector for each of the three time periods, as she was most familiar with the underlying data sources and their level of reliability or trustworthiness.

3. Results

3.1. Reconstructed total catches

The reconstructed total catch for the 1950–2010 period exceeded by a factor of 2.6 the official catches reported by the FAO on behalf of Italy. Of this, approximately 79% was caught by industrial fisheries, 17% by artisanal fisheries, 3% by recreational fisheries and <1% by subsistence fisheries, while discards (7% of the total) were predominately (95%) from industrial fisheries (Fig. 3a). Reconstructed total catches were relatively stable throughout the 1950s and 1960s, averaging about 700,000 t year^{-1}, before increasing between 1971 and 1979 to 1.1 million t year^{-1}. Thereafter, the annual catch plateaued at an average of 1.06 million t year^{-1} until 1986, then sharply decreased to 676,000 t year^{-1} by 1990. Annual catches remained steady in the early 1990s, with a small increase to 741,000 t in 1998, before again sharply decreasing and continuing the declining trend to the end of the time series in 2010, when catches were just 374,000 t (Fig. 3a).

Catches consisted of 92 taxa, of which 65 were identified to species, including higher pooled groups such as 'marine fishes nei' and 'marine invertebrates nei'. In terms of total tonnage, catches were dominated by small pelagic fishes, notably European anchovy (*E. encrasicolus*), which accounted for 18.1% of all catches (Fig. 3b). The second most important taxon, in terms of tonnage (at least in earlier decades) was the European pilchard (*S. pilchardus*), which accounted for 12.5% of total catches overall, but has since declined substantially (Fig. 3b). The remaining taxa, grouped by family, contributing the most to the catches were molluscs (12.4%), Scombridae (9.0%), Sparidae (7.4%), crustaceans (5.6%), Carangidae (4.0%) and sharks and rays (3.9%; Fig. 3b).

3.2. Official landings

For the reported landings, we compared our assessment with the two national sources of statistics (ISTAT and IREPA) and the FAO, and found that data sets were similar only for the last six years (2005–2010, Fig. 4), which corresponds to the period when IREPA became the official national statistical source. Most of the catches per species and per sub-regional division in the ISTAT dataset were on at least 30–40% lower than the one provided by IREPA. In particular, when comparing the years 2000 and 2001 between the two national sources, of the 58 taxa in the IREPA dataset, 49 had catch values greater than 25%, 43 greater than 50%, 33 greater than 75% and 26 greater than 100%, while the remaining had similar values between the two sources. Also, no adjustments were required to the six catch datasets after they were sent for validation to the national experts.

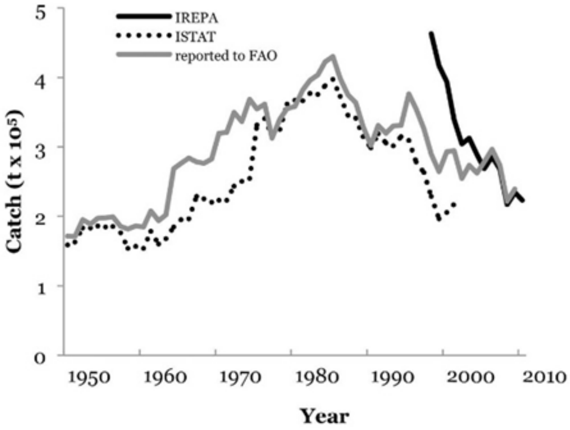

Fig. 4. Italian national catch data coming from the two national sources, ISTAT (dotted line) and IREPA (dark line), for the 1950–2010 period in comparison with the ones reported to FAO (grey line).

In total, for the 1950–2010 period, Italian reported national landings ranged between approximately 220,000 and 721,000 t year^{-1}. These data were visibly higher (on average more than two times higher) than the data reported to FAO for the same time period which ranged from 171,000 to 430,000 t year^{-1}. Overall, there was a slight decrease in national reported landings between 1950 and the beginning of the 1960s, followed by an increase in the middle of the 1980s and a general and continuous decline to 2010. This differs from the trend in the FAO data which increases steadily in 1950 with a peak in 1985 and then fairly steadily declines in 2010 (Fig. 3a). European anchovies and European pilchards were the main fish species reported in the national data throughout the different sub-regions, which began to decline in the beginning of 1980s (Fig. 3b). All the other major taxa, (e.g., Scombridae, Mollusca, Sparidae and Carangidae) presented similar trends with declines commencing from the 1980s or beginning of 1990s (Fig. 3b).

3.3. Fishing effort and catch per unit of effort

Results indicated that artisanal vessels dominated in terms of vessels numbers, followed by trawlers and multiple gears (Fig. 5a). Trawlers, on the other hand, had the highest fishing effort, in term of cumulative engine power (kW days^{-1}), followed by purse seiners

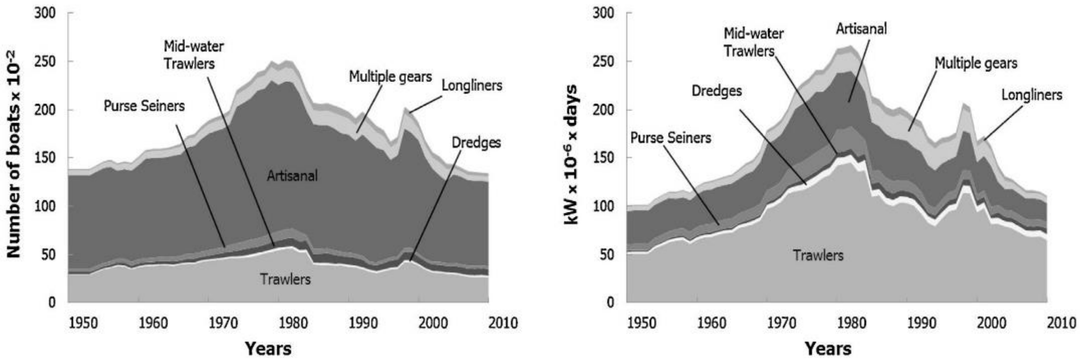

Fig. 5. For the whole of Italy: b) reconstructed total number of fishing boats; and b) reconstructed total fishing effort (kW days^{-1}) per gear type.

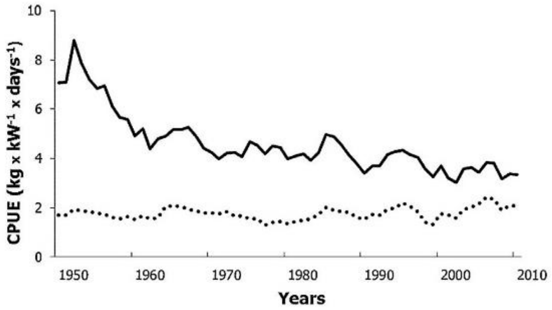

Fig. 6. Catch per unit of effort (kg kW^{-1} days^{-1}) for the whole of Italy for the 1950–2010 period using the reconstructed catches and effort time series (black line) and catches reported by the FAO on behalf of Italy with the reconstructed effort (dotted line).

and artisanal fisheries (Fig. 5b). With regards to all fishing fleet and their trends, number of vessels and fishing effort, decreased over time, after the maximum from the late 1970s to mid-1980s (with only multiple gears having their highest peak in the 1990s) and a steady decline thereafter.

The CPUE trend showed a continuous decline since the 1950s with a maximum of ~9kg kW^{-1} days^{-1} in the early 1950s and a minimum of ~3kg kW days^{-1} in the late 2000s (Fig. 6).

3.4. *Unreported landings: Recreational fisheries*

The estimated recreational catches for 1950–2010 were around 1.45 million t, which increased from 19,200 t in 1950 to 29,800 t in 2010 with a pronounced growth during the last three decades (Fig. 3a). The Adriatic Sea accounted for 597,000 t (41.4%); the Tyrrhenian Sea sub-division 497,000 (34.3%); the Ligurian 194,000 t (13.4%); Sardinia 77,300 t (5.3%); Sicily 68,100 t (4.7%) and Ionian Sea 16,700 t (1.2%). The major species caught in Italy by the recreational sector were tuna (Scombridae) with 232,000 t (15.4%), bogue with 155,000 t (10.7%), Atlantic bonito with 107,000 t (7.4%) and Mediterranean horse mackerel (*Trachurus mediterraneus*) with 97,300 t (6.7%).

3.5. *Unreported landings: Subsistence catches*

The estimated subsistence catches for the 1950–2010 time period averaged 6400 t year^{-1}, with a maximum of 9100 t in 1982 and minimum of 4000 t in 2010, contributing only 0.9% of the reconstructed total catch (Fig. 3a). In this case, the Central Adriatic Sea and Sicily had the highest removals, with approximately 91,400 t (23%) and 85,600 t (22%), respectively. Given our assumption of same catch compositions for subsistence catches and reported landings, the subsistence catch was assumed to consist mainly of European anchovy (13.5%), European pilchard (10.7%) and molluscs (14.8%).

3.6. *Unreported commercial catches and discards*

The estimated unreported catches for the illegal driftnet fishing fleet for the 1992–2010 period totaled 49,130 t, which consisted to 83% of swordfish and 17% of tuna species. The regions in which this illegal activity was prevalent were the South Tyrrhenian Sea and Sicily, which contributed 46% and 31% of the 49,130 t, respectively. Also, an illegal component from other industrial fishing fleets and the artisanal sector was added. In particular, a total of approximately 6 million t was estimated for the period 1950–2010, of which 76% and 24% came from industrial and artisanal fisheries, respectively.

Retained unreported by-catch per fleet type and per subdivision for the period 1950–2010 accounted for approximately 5 million t, averaging about 82,500 t year^{-1}, most of which came from industrial fisheries (95%) and from the Central Adriatic (~1.6 million t; 33%) and Sicily (1.2 million t; 25%). The major by-catch taxa were clams (Bivalvia; 604,000 t; 12.0%), sharks (Selachimorpha; 446,000 t; 8.9%), jacks (*Trachurus* spp.; 335,000 t; 6.7%) and rays (Rajidae; 283,000 t; 5.6%). Discards, on the other hand, were 3.4 million t. Since we applied a proportional rate to separate the retained by-catch from discards, the same patterns were observed for the regional subdivisions and discarded taxa. Discards and by-catch from bottom trawling represented the largest component, totaling 3.8 million t (Fig. 3a).

3.7. *Uncertainty*

The ranges of uncertainty estimated for the reconstructed total catches showed wider confidence intervals in the first two estimation periods (1950–1969; 1970–1989) and a reduction only in the last period (1990–2010; Fig. 7).

4. Discussion

This study represents the first attempt to estimate total fisheries removals for the whole of Italy in the Mediterranean Sea, for the period 195–2010. Our reconstructed total catches were 2.6 times the landings officially reported by the FAO on behalf of Italy for the same period and same sea. This difference was mainly caused by poor reporting of commercial catches, with unreported commercial landings (from both industrial and artisanal sectors) contributing

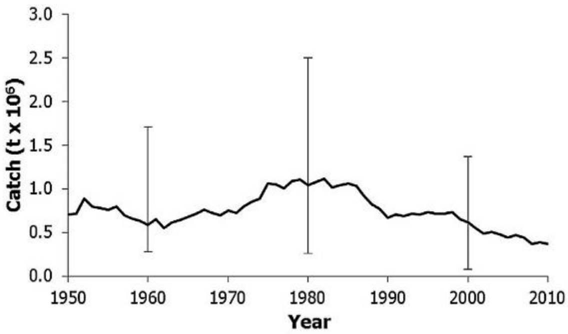

Fig. 7. Estimated reconstructed total catches with confidence intervals. The values of the error bars are displayed for each time period (1960 for 1950–1969, 1980 for 1970–1989, and 2000 for 1990–2010).

50% to the total catch (in relation to FAO reporting) and discards contributing another 7%. This gap in the official national statistics (mainly related to the earlier period of the ISTAT datasets) was previously observed by other studies (AdriaMed, 2003; Cataudella and Spagnolo, 2011) which documented that about 30–40% of catches remained unreported, and pointed to changes in data collection, systematic approach and absence of data verification and/or analysis as the causes of this discrepancy. Our reconstruction agrees with these studies, with an even higher discrepancy for industrial fisheries (53%). We recognize that, because of the nature of our approach used here, which requires assumption-based inferences and interpolations, uncertainties remain (see below), for example in our estimates of underreported catches or in the disaggregation of the taxonomic catch composition and further studies should be conducted to reduce this uncertainty. However, we believe that our approach is justified by the unacceptability of the alternative, yet common default approach, of interpreting non-reported or missing data components as zero removals (Pauly et al., 1998). Thus, by documenting and justifying each step of our approach, our study represents the first important step towards the integrated understanding of total fisheries removals for all of Italy.

Our reconstructed commercial catches and fishing effort showed a remarkable decline starting around the 1980s as a consequence of the decline of the living marine resources (Arneri, 1996; Iborra Martin, 2006), the increase in fishing costs (e.g., fuel; Sacco, 2011) and the EU regulations to reduce fishing capacity (Iborra Martin, 2006). In Italy, it has been observed that, after the 1980s, catches rapidly declined, primarily as a result of a decrease in the biomass of small pelagic fishes, particularly European anchovy and European pilchard (Iborra Martin, 2006) and many other important demersal and pelagic fish stocks (Arneri, 1996; Iborra Martin, 2006). An indicator of the overexploitation of the marine resources in the region is also given by our reconstructed CPUE trend, which steadily declined since the early 1950s, while the opposite trend is obtained if one uses official catch statistics. Some caution should be applied when interpreting these data. In fact, despite evidence of marine resource reductions in Italian waters, it is worth emphasizing how high uncertainties still exist for fishing effort (e.g., number of days at sea and the number of observed vessels), particularly for early years, and catch data. Unfortunately, at the time this research was undertaken, no information was available to fill these gaps. Recent efforts have been undertaken regionally to address at least partly this issue (e.g., EVOMED, 2011), and thus further development of this work is required.

Our study highlights the importance of artisanal fisheries in Italy, which is similar to other parts of the Mediterranean (Coll et al., 2014; Piroddi et al., 2011; Tudela 2004; Ulman et al., 2013). However, while artisanal fisheries had the largest number of vessels (around 60% of all Italian fishing vessels), from a catch volume perspective, trawlers caught the most, and, despite accounting for only 21% of the fishing boats, they had the greatest impact on commercial and non-commercial taxa in the region (Pranovi et al., 2000; Sánchez et al., 2007; Sartor et al., 2003). As for the increase of multiple gears observed here, this might be an artifact derived from the different criteria of grouping vessels, as done by IREPA in past years. In fact, vessels were roughly aggregated by prevalent fishing gear, and whenever their prevalent gear was not obvious, they were included in the "multiple gear" category.

Besides reported commercial catches, the recreational fisheries were assessed; since no official/reported time series of catches exist, this fishing sector was considered unreported from 1950 to 2010. In Italy, only a few sources of information are available (Anagnopoulos et al., 1998; Cisneros-Montemayor and Sumaila, 2010; Gaudin and De Young, 2007; Gordoa et al., 2004; Pawson et al., 2007), and thus, for a few regions, high uncertainty still exists with regards to total catch. Since this sector has increased in Italy, particularly in the north-west (Anagnopoulos et al., 1998; Pawson et al., 2007), more effort should be invested to assess the impact of recreational fisheries on marine resources and ultimately to refine the estimates of the total Italian catch.

Illegal catches and unreported catches (including discards), despite being a serious issue in Italian fisheries, have never been previously assessed. We consider these components the least studied among all the different Italian fishery sectors, and with the highest uncertainty. Since they are key components for understanding and evaluating the impact of fishing on commercial and non-commercial taxa (Zeller et al., 2007) specific studies (e.g., structured interviews with fishers) should be implemented to properly assess them. Despite these caveats, our study indicates that unreported catches are very significant, accounting for over half of total fisheries removals. These results are in line with other catch reconstruction studies conducted in the Mediterranean Sea that have shown high percentages of unreported and illegal catches in their assessment of fisheries removals, e.g., 40% in Spain (Coll et al., 2014), 35% in Greece (Tsikliras et al., 2007), 63% in Turkey (Ulman et al., 2013). In Italy, one of the major causes of illegal/unreported catches is the continuous use of prohibited driftnets. The loss of revenue due to changes in fishing gears is probably the major reason behind such constant fishing practice (swordfish and tuna species are important and high-valued products of the Italian market); in fact, the profits that one driftnet boat could obtain are generally 25% higher than the net added value from an average vessel (Spagnolo and Sabatella, 2004). Regarding other illegal activities, no historical information was found. In 2010, the Italian Coast Guard started collecting and reporting infringements at sea and on land in relation to the use of illegal gears or undersized species (European Commission, 2011b). Unfortunately, this database is still an under-representation of what is happening along the Italian coastline (Alessio Morelli pers. comm.) and therefore our reconstruction might not reflect entirely the situation occurring in the region. Subsistence catches present another limitation in terms of an existing fishing sector for which no direct data are available. Specific studies focusing on this component are fundamental in order to improve our estimate of total catch removal of the Italian fisheries.

Unreported discards is another aspect of under-reported resource mortality, and are considered pressing issues for marine conservation and fisheries management (Caddy, 2009; Hall and Mainprize, 2004). In Italy, studies on discards and by-catch have increased in recent years, partly due to the implementation of the EU Data Collection Regulation [Commission Regulation (EC) No 1639/2001; currently, Data Collection Framework, Council Regulation (EC) No 199/2008] and partly also to the establishment of the ecosystem approach to fisheries (EAF) (Garcia, 2003; Tsagarakis et al., 2013). However, limited studies still exist or have been found in the area that differentiate between the proportions of retained by-catch and of discards per gear type, thus more effort should be dedicated to fill this gap. Required also would be detailed information on survival rates of discarded species by gear type. Our results show that, on average, retained by-catch accounts for 11% and discards for 7% of total removals, with bottom trawling having the highest impact followed by longline and dredges. These percentages agree with other studies conducted in the Mediterranean Sea, which have looked at the contribution of discards and by-catch and estimated a range on average between 10% and 20% (Coll et al., 2014; Tsagarakis et al., 2013; Ulman et al., 2013).

5. Conclusion

Our estimates of total fisheries removals for the whole of Italy (1950–2010) illustrated a decrease in catch and effort that began in the mid-1980s and continued until 2010. This overall pattern aligns with FAO and national statistics trends, highlighting a severe degradation of marine resources in the region. Yet, our results exceed the officially reported amount by a factor of 2.6, which suggests substantial problems in the collection and reporting of actual catch data and quite a considerable amount of under-reported catches. Such prevalence of under-reported catches highlights significant management, monitoring and enforcement shortcomings. Official catch statistics are in fact used in stock assessments for policy making decision, and the exclusion of under-reported catches (or total fisheries removal) could bias the resulting scientific advice given to policy-makers. Since the impact of fisheries is considered one of the most pressuring threat affecting marine life, their underestimation poses a serious concern not only to the conservation of valuable marine resource but also to the success of future fisheries.

Despite the limitations explained above, the estimates of total fisheries removals presented in this study represent an improvement over official estimates, and should be taken into account when dealing with fisheries management, despite the substantial uncertainty associated with the present estimates. With many key fish stocks declining, it is necessary for fisheries management to fully capture how much the resources have been and are being removed and from which sector, so that appropriate decisions for the future can be made (Pauly et al., 2014). Our study is the first that attempted to estimate the Italian fisheries removals using a holistic approach; these methods are particularly important in areas like the Mediterranean Sea, where the multi-species and multi-gear nature of fisheries make the assessment of single-species fisheries resources and their management difficult and likely inappropriate.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2015.06.028

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Table S1. Taxonomic breakdown of the commercial species used in the reconstruction by the two national statistical organizations (ISTAT and IREPA).

	Common name	**Scientific name**	**ISTAT**	**IREPA**	**FAO**
1	Albacore	*Thunnus alalunga*		X	
2	Angler	*Lophius piscatorius*	X	X	
3	Atlantic bluefin tuna	*Thunnus thynnus*		X	
4	Atlantic bonito	*Sarda sarda*	X	X	
5	Atlantic Mackerel	*Scomber scombrus*	X	X	
6	Billfishes	*Istiophoridae*			X
7	Big-scale sand smelt	*Atherina boyeri*	X		
8	Black seabream	*Spondyliosoma cantharus*			X
9	Blue whiting	*Micromesistius poutassou*	X	X	
10	Bogue	*Boops boops*	X	X	
11	Chub mackerel	*Scomber japonicus*		X	
12	Common dentex	*Dentex dentex*	X		
13	Common dolphinfish	*Coryphaena hippurus*			X
14	Common pandora	*Pagellus erythrinus*	X	X	
15	Common sole	*Solea solea*	X	X	
16	European anchovy	*Engraulis encrasicolus*	X	X	
17	European barracuda	*Sphyraena sphyraena*			X
18	European conger	*Conger conger*	X		
19	European eel	*Anguilla anguilla*			X
20	European hake	*Merluccius merluccius*	X	X	
21	European pilchard	*Sardina pilchardus*	X	X	
22	European seabass	*Dicentrarchus labrax*	X		
23	European sprat	*Sprattus sprattus*			X
24	Flathead mullet	*Mugil cephalus*	X	X	
25	Flounder	*Platichthys flesus*			X
26	Forkbeard	*Phycis phycis*			X
27	Frigate tuna	*Auxis thazard thazard*	X		
28	Garfish	*Belone belone*	X		
29	Gilthead seabream	*Sparus aurata*	X		
30	Goatfishes	*Mullidae*	X		
31	Gobies	*Gobiidae*	X		
32	Greater forkbeard	*Phycis blennoides*			X
33	Groupers	*Serranus spp.*	X		
34	Horse mackerels	*Trachurus spp.*	X	X	
35	John dory	*Zeus faber*			X
36	Leerfishes and amberjacks	*Carangidae*	X	X	
37	Marine fishes	Marine fishes not identified	X	X	
38	Anglerfishes	*Lophius* spp.			X
39	Pearly razorfish	*Xyrichtys novacula*			X
40	Picarel	*Spicara smaris*	X	X	
41	Pilotfish	*Naucrates ductor*			X
42	Poor cod	*Trisopterus minutus*		X	
43	Porbeagle	*Lamna nasus*			X
44	Rays	Rajidae	X	X	
45	Red mullet	*Mullus barbatus barbatus*		X	
46	Round sardinella	*Sardinella aurita*			X
47	Saddled seabream	*Oblada melanura*			X
48	Salema	*Sarpa salpa*			X
49	Striped seabream	*Lithognathus mormyrus*			X
50	Sandlances	*Ammodytes spp.*			X
51	Scorpionfishes and gurnards	*Scorpaenidae*	X	X	
52	Sharks	*Selachiimorpha*	X	X	
53	Shortbill spearfish	*Tetrapturus angustirostris*			X
54	Shi drums and brown meagre	Sciaenidae	X		
55	Silver scabbardfish	*Lepidopus caudatus*			X
56	Stargazer	*Uranoscopus* spp.			X
57	Striped red mullet	*Mullus surmuletus*		X	
58	Swordfish	*Xiphias gladius*	X	X	
59	Thresher sharks	*Alopias* spp.			X
60	Tunas	Scombridae		X	

61	Turbots	Scophthalmidae	X	X	
62	Weeverfishes	Trachinidae			X
63	White seabream	*Diplodus sargus sargus*	X		
64	Whiting	*Merlangius merlangus*		X	
65	Clams	Bivalvia	X	X	
66	Common octopus	*Octopus vulgaris*	X	X	
67	Cuttlefishes	Sepiida	X	X	
68	European flying squid	*Todarodes sagittatus*	X	X	
69	Great Mediterranean scallop	*Pecten jacobaeus*		X	
70	Horned octopus	*Eledone cirrhosa*		X	
71	Marine molluscs	Miscellaneous marine molluscs	X	X	
72	Musky octopus	*Eledone moschata*		X	
73	Mutable nassa	*Nassarius mutabilis*		X	
74	Squids	Teuthida	X	X	
75	Blue and red shrimp	*Aristeus antennatus*		X	
76	Caramote prawn	*Melicertus kerathurus*	X	X	
77	Deepwater rose shrimp	*Parapenaeus longirostris*	X	X	
78	European and spiny lobster	*Homarus gammarus; Palinurus vulgaris*	X	X	
79	Giant red shrimp	*Aristaeomorpha foliacea*	X	X	
80	Marine crabs	Brachyura		X	
81	Marine crustaceans	Miscellaneous marine crustaceans	X	X	
82	Norway lobster	*Nephrops norvegicus*	X	X	
83	Spottail mantis shrimp	*Squilla mantis*	X	X	

Table S2. Percentage of Italian recreational fishing fleets observed in 1996 (Anagnopoulos et al., 1998) per each sub-regional division.

Sub-regional division	**Recreational fishing fleets (%)**
1. Ligurian	13.4
2. Tyrrhenian	
- Northern	12.8
- Central	12.9
- Southern	8.6
3. Ionian	1.2
4. Adriatic	
- Northern	25.6
- Central	9.4
- Southern	6.1
5. Sardinian	5.3
6. Sicilian	4.7
Total	100

Table S3. Percentage of recreational species caught (Anagnopoulos et al., 1998) per each sub-regional division: Ligurian (LI); Northern, Central and Southern Tyrrhenian (NT, CT, ST); Sardinian (SAR); Sicilian (SI); Ionian (IO); Southern Northern, Central and Adriatic Sea (NA, CA, SA).

Scientific name	**LI**	**NT**	**CT**	**ST**	**SAR**	**SI**	**IO**	**NA**	**SA**	**CA**
Carangidae	0	0	10	10	2	3	0	0	0	0
Sarda sarda	4	4	19	19	5	3	8	2	8	8
Boops boops	18	18	0	0	13	22	4	14	4	4
Teuthida	1	1	1	1	1	3	0	0	0	0
Prionace glauca	0	0	0	0	1	0	0	3	0	0
Serranus spp.	2	2	1	1	1	2	1	1	1	1
Sciaenidae	0	0	0	0	1	1	0	2	0	0
Dentex dentex	1	1	11	11	2	1	0	0	0	0
Trachinotus ovatus	1	1	5	5	1	1	0	0	0	0
Coryphaena hippurus	1	1	4	4	1	2	0	0	0	0
Dicentrarchus labrax	0	0	0	0	1	1	3	2	3	3
Platichthys flesus	0	0	0	0	1	0	0	2	0	0
Belone belone	2	2	1	1	6	2	1	15	1	1
Sparus aurata	4	4	0	0	2	0	1	4	1	1
Gobiidae	5	5	0	0	3	0	4	7	4	4
Zosterisessor ophiocephalus	0	0	0	0	1	0	0	3	0	0
Merluccius merluccius	0	0	0	0	1	0	0	2	0	0
Trachurus spp.	15	15	1	1	7	11	7	2	7	7
Scomber spp.	0	0	3	3	7	4	16	7	16	16
Mugilidae	1	1	0	0	3	0	0	9	0	0
Pagellus erythrinus	5	5	6	6	6	14	0	1	0	0
Pagrus pagrus	3	3	0	0	1	0	0	0	0	0
Spicara smaris	2	2	0	0	1	1	0	0	0	0
Mullus barbatus	0	0	0	0	0	0	2	0	2	2
Oblada melanura	7	7	0	0	5	5	2	6	2	2
Scorpaenidae	0	0	2	2	1	2	1	0	1	1
Diplodus spp.	8	8	3	3	7	16	1	2	1	1
Lithognathus mormyrus	0	0	0	0	8	4	28	6	28	28
Xiphias gladius	0	0	3	3	1	1	0	0	0	0
Alopias spp.	0	0	0	0	1	0	2	2	2	2
Chelidonichthys lucerna	0	0	0	0	1	0	7	0	7	7
Thunnus spp.	20	20	30	30	7	1	12	5	12	12
Labridae	0	0	0	0	1	0	0	3	0	0

Table S4. List of illegal catch by species (when specified) reported by Italian media. UN=unknown; BFT=Atlantic bluefin tuna; SWO=swordfish; ALB=albacore; AN=European anchovy; SB=European seabass, OCT=common octopus; CT=cuttlefishes; SO=common sole; CL=clams; PD=common pandora; SU=sea urchins; SA=sardines; MA=Atlantic mackerel; LT=little tunny; TU=tunas (species); CBR=cicerello/bianchetto/rossetto.

Species	Tonnes	Gear	Time	Area	Source
UN	0.045	Trawler (no licence)	Dec 2008	Sicily	http://www.iloveagrigento.it/pesca-illegale-a-porto-empedocle-sequestrati-45-kg-di-pesce/
BFT	7	Unknown (no tuna license)	Jun 2009	Sicily	http://www.lombardiaatavola.it/articolo.aspx?id=10361
BFT	43	Unknown (no tuna license)	Jun 2009	South Tyrrhenian -Sicily	http://lombardiaatavola.it/articolo.aspx?id=10458
SWO	3	Unknown (undersized)	Jul 2009	South Tyrrhenian -Sicily	http://www.politicheagricole.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/2405
BFT	0.5	Unknown	Jul 2009	South Tyrrhenian -Sicily	http://www.politicheagricole.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/2405
ALB	0.1	Unknown	Jul 2009	South Tyrrhenian -Sicily	http://www.politicheagricole.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/2405
AN	90	Unknown	Oct 2009	South Adriatic	http://www.traniweb.it/trani/informa/11024.html
SB	1	Unknown	Oct 2009	South Adriatic	http://www.traniweb.it/trani/informa/11024.html
OCT;CT;SO	8	Unknown	Oct 2009	South Adriatic	http://www.traniweb.it/trani/informa/11024.html
CL	5	Dredges	Nov 2009	North Adriatic	http://www.conipiediperterra.com/sequestrate-a-chioggia-5-tonnellate-di-vongole-1125.html
UN	0.19	Recreational sale to restaurant	Mar 2010	Liguria	http://www.riviera24.it/articoli/2010/03/16/81567/operazione-besugo-sequestrati-190-kg-di-prodotto-ittico-in-vendita-proveniente-da-pesca-sportiva
PD	0.12	Recreational sale to restaurant	Mar 2010	Liguria	http://www.riviera24.it/articoli/2010/03/16/81567/operazione-besugo-sequestrati-190-kg-di-prodotto-ittico-in-vendita-proveniente-da-pesca-sportiva
BFT	2	PS (no tuna licenses)	Apr 2010	Ionian Sea	http://www.lecceprima.it/cronaca/porto-cesareo-sequestrate-2-tonnellate-di-tonno-rosso.html
SU	0.6 (above permitted limit)	Recreational fisher	Aug 2010	South Tyrrhenian	http://www.adnkronos.com/IGN/Regioni/Abruzzo/?id=3.1.825584595
BFT	0.65 (500 juveniles)	PS	Oct 2010	South Tyrrhenian	http://www.italiaatavola.net/articolo.aspx?id=17544
CL	0.48	Dredge	Oct 2010	Central Adriatic	http://www.geapress.org/mare/operazione-talasso/7816
BFT	0.3	Dredge	Oct 2010	South Adriatic	http://www.geapress.org/mare/operazione-talasso/7816
SA; MA	2	PS	Oct 2010	Liguria	http://www.geapress.org/mare/operazione-talasso/7816
LT	0.02	Mid-water trawl (no license)	Oct 2010	Ionian Sea	http://www.geapress.org/mare/operazione-talasso/7816
AN	0.011	Mid-water trawl (no license)	Oct 2010	Ionian Sea	http://www.geapress.org/mare/operazione-talasso/7816
UN	0.09	Gillnet	Jun 2011	Liguria	www.guardiacostiera.it

SU	1.2	Unknown	2012	Sicily	http://www.agricolae.it/pesca-illegale-il-bilancio-dellattivita-di-contrasto-nel-2012-80603/
TU; SWO	1.4 (undersized)	Longline	Oct 2012	South Adriatic	http://www.statoquotidiano.it/25/10/2012/vieste-sequestro-14-quintali-tonno-rosso-e-pesce-spada/107443/
SWO	0.085 (20 juveniles)	Unknown	Oct 2012	Sicily	http://livesicilia.it/2012/10/26/porto-empedocle-sequestrati-20-esemplari-di-pesce-spada_203673/
CBR	0.715	Unknown	Jan 2013	South Adriatic	http://www.foggiatoday.it/cronaca/sequestro-bianchetto-manfredonia-calabria-14-gennaio-2013.html
CBR	0.126	Seine	Mar 2013	Ionian Sea	http://bari.repubblica.it/cronaca/2013/01/20/news/incastrati_i_predoni_del_mare-50950505/
CBR	0.1	Unknown	Mar 2013	Ionian Sea	http://www.cn24tv.it/news/65331/pesca-illegale-guardia-costiera-sequestrati-oltre-100-kg-di-bianchetto.html
CBR	0.02	Seine	Apr 2013	Ionian Sea	http://www.lentelocale.it/cronaca/1718-lotta-alla-pesca-illegale-numerosi-sequestri-di-bianchetto-e-cicerello-da-parte-della-guardia-costiera
CBR	0.13	Unknown	Apr 2013	South Tyrrhenian	http://www.ansa.it/web/notizie/regioni/calabria/2013/04/12/Sequestrati-130-chili-novellame_8543000.html
CBR	0.15	Trawlers	Apr 2013	South Adriatic	http://www.manfredonianews.it/sequestro-di-reti-illegali-e-bianchetto

Table S5. Discard and bycatch rates (in %) given to each type of fishing fleet per sub-regional division. Fishing fleet types: T: trawlers; MT: mid-water trawlers; D: dredges; P: purse seiners; AF: artisanal fisheries; MG: multiple gears and L: longline. N/A = not applicable is related to a fishing fleet not being present in a given sub-regional division.

	T	MT	D	P	AF	MG	L
1. Ligurian							
	20[a,b,c,d,e,f]	N/A	N/A	8.5 [a,c,d,g]	5[a,c,d,g]	18.4[a,b,c,d,g,h]	40[a,c,d,h,i]
2. Tyrrhenian							
North	20[a,b,c,d,e,f]	N/A	N/A	8.5[a,c,d,g]	5[a,c,d,g]	18.4[a,b,c,d,g,h]	40[a,c,d,h,i]
Central	20[a,b,c,d,e,f]	N/A	20[a,c,d,j]	8.5[a,c,d,g]	5[a,c,d,g]	18.4[a,b,c,d,g,h]	40[a,c,d,h,i]
South	20[a,b,c,d,e,f]	N/A	20[a,c,d,j]	8.5[a,c,d,g]	5[a,c,d,g]	18.4[a,b,c,d,g,h]	40[a,c,d,h,i]
3. Ionian							
	35[a,c,d,g,k]	N/A	N/A	7.5[a,c,d,g]	5[a,c,d,g]	18.6[a,c,d,g]	40[a,c,d,g]
4. Adriatic							
North	67.4[a,d,l,m,n]	18.3[a,d,g,o]	68.5[a,c,d,g,k]	8.5[a,c,d,o]	7[a,c,d,g]	42.9[a,c,d,l]	50[a,c,d,h,i]
Central	67.4[a,d,l,m,n]	18.3[a,d,g,o]	68.5[a,c,d,g,k]	8.5[a,c,d,o]	7[a,c,d,g]	42.9[a,c,d,l]	50[a,c,d,h,i]
South	67.4[a,d,l,m,n]	18.3[a,d,g,o]	68.5[a,c,d,g,k]	8.5[a,c,d,o]	7[a,c,d,g]	42.9[a,c,d,l]	50[a,c,d,h,i]
5. Sardinian							
	20[a,b,c,d,e,f]	N/A	N/A	8.5[a,c,d,g]	5[a,c,d,g]	18.4[a,b,c,d,g,h]	40[a,c,d,h,i]
6. Sicilian							
	20[a,b,c,d,e]	28.3[a,c,d]	N/A	8.5[a,c,d,g]	5[a,c,d,g]	17.5[a,b,c,d,g,h]	50[a,c,d,h,i]

[a] European Commission (2011); [b] Sartor et al. (2003); [c] Tsagarakis et al. (2013); [d] Vassilopoulou (2012); [e] Vitale et al. (2006); [f] Relini (1981); [g] European Commission (2008); [h] Gilman et al. (2007); [i] MegaPesca (1999); [j] Castriota et al. (2004); [k] D'Onghia et al. (2003); [l] Botter et al. (2006); [m] Sánchez et al. (2007); [n] Scarcella et al. (2007); [o] Santojanni et al. (2005)

Table S6. 'Score' given to each catch of fishing sector to estimate the uncertainty associated to the data

Catch of sector	**1950-1969**	**1970-1989**	**1990-2010**
Industrial discards	1	2	3
Industrial landings	2	3	4
Artisanal discards	1	2	3
Artisanal catch	2	3	4
Subsistence catch	1	1	1
Recreational catch	1	1	2

Figure S1. Comparison between reconstructed (dotted line) and IREPA (grey line) catches for European anchovies (1) and European pilchard (2) around the coasts of Sardinia.

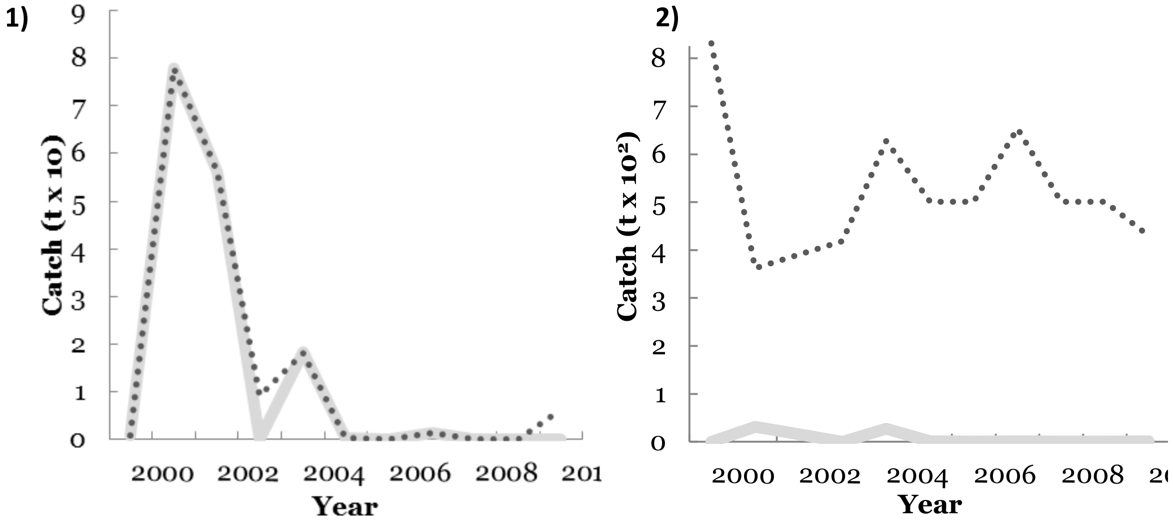
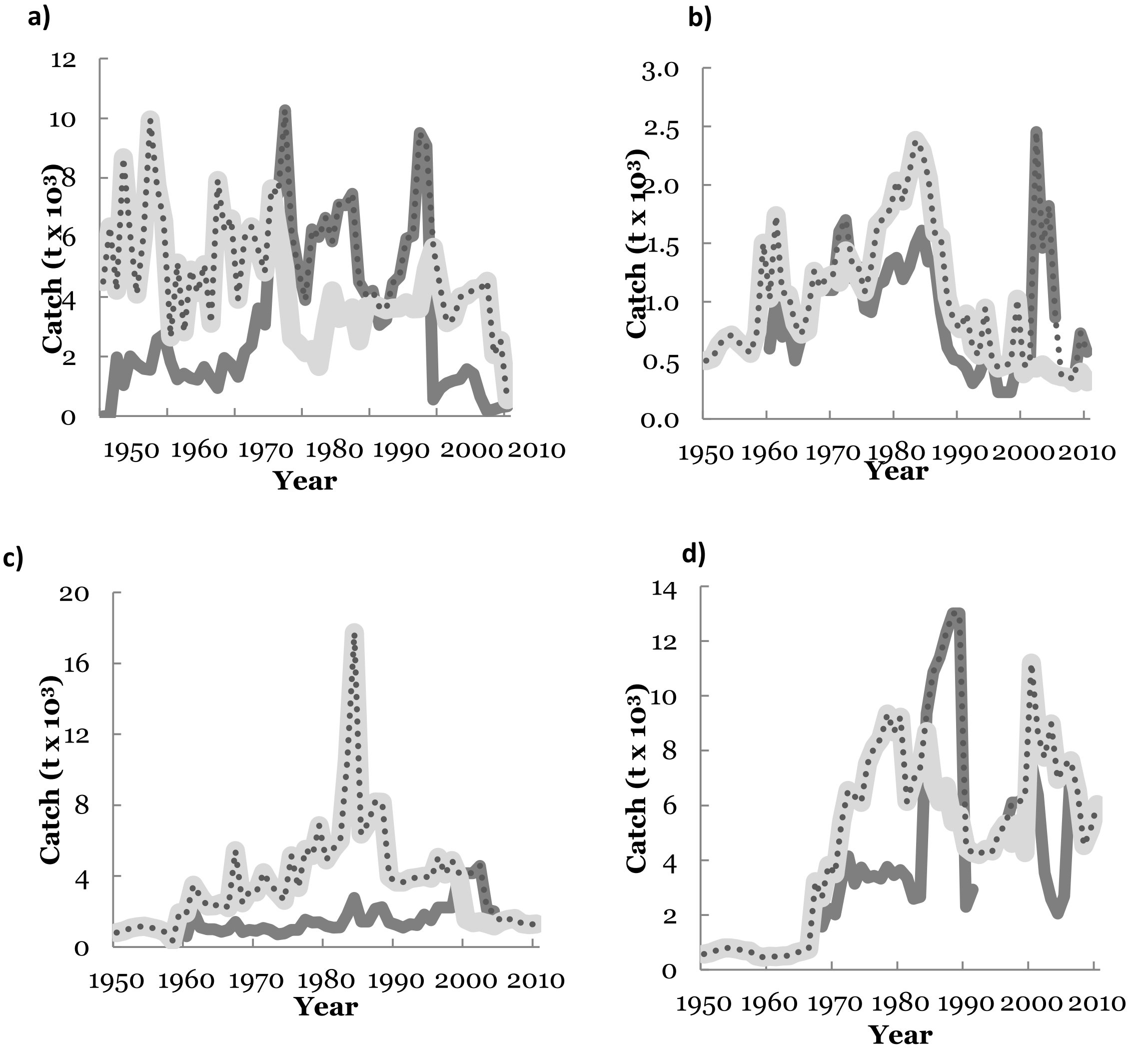


Figure S2. Comparison between ICCAT (dark line), IREPA-ISTAT (grey line) and reconstructed catches (dotted line) for Atlantic bluefin tuna (a); frigate tuna (b); Atlantic bonito (c) and swordfish (d).



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Ecosystem health of a Mediterranean semi-enclosed embayment (Amvrakikos Gulf, Greece): Assessing changes using a modeling approach

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Hindcast scenarios

ABSTRACT

Marine and coastal ecosystems are important for human wellbeing in multiple ways and yet they are subject to increasing anthropogenic stressors which pose serious threats to their health status. In this context, we used an ecosystem modeling approach to assess and quantify the health status of a semi-enclosed embayment of the Mediterranean Sea, the Amvrakikos Gulf (surface: 405 km^2; maximum depth: 60 m) (Ionian Sea). In particular, we built a food web model of the Gulf ecosystem for the 1980 and we fit it to time series from 1980 to 2013. The aim of the study was to: (1) investigate dynamics of marine resources in the last three decades considering the effect of changes in rivers run off, development of fish farming and dynamics of fisheries as the major anthropogenic drivers affecting the system; (2) assess structural and functional changes of the Gulf, using model derived indicators obtained from temporal simulations. Results indicated that the strongest drivers in the Amvrakikos food web were changes in nutrients and organic matter mostly from the loads of two local rivers. Trends in ecological indicators, which explained changes in the structure of the Gulf, highlighted a degradation of the demersal compartments of the food web and a relative stability of the pelagic ones mainly due to high eutrophication levels. By including several ecosystem drivers into the model, the present study is intended as a tool for assessing Amvrakikos ecosystem health and for developing future management policies in the Gulf.

1. Introduction

Marine ecosystems are increasingly impacted worldwide by a series of threats that include overfishing (e.g., Pauly et al., 2005), aquaculture (e.g., Naylor et al., 2000), eutrophication (e.g., Diaz and Rosenberg, 2008), habitat loss and degradation (e.g., Dobson et al., 2006), climate change (e.g., Overland et al., 2010), pollution (e.g., Islam and Tanaka, 2004) and species invasion (e.g., Libralato et al., 2015). Possible irreversible impacts and synergies among these threats are posing doubts on the long term sustainability of goods and services currently provided by marine ecosystems (Halpern et al., 2012), with the result that many national and international regulations (e.g., European Marine Strategy Framework Directive, [MSFD; 2008/56/EC]; Convention of Biological Diversity, [CBD]) are intervening to assess, control and reduce stress induced by the aforementioned threats.

Yet, while a large body of studies focus on the impact of a single factor on specific compartments of marine and coastal environments, the assessment of cumulative and cascading effects of different threats remains poorly studied as well as the trade-offs that might rise when managing them in an integrated framework (Link et al., 2010). For this reason, there has been a growing interest to develop more comprehensive tools capable of assessing the effects of anthropogenic impacts within a single common framework (Halpern et al., 2008; Libralato and Solidoro, 2009; Travers et al., 2009) in order to facilitate the setting of targets and implementation of management measures (Cury et al., 2008; Kaplan et al., 2012; Piroddi et al., 2015). The development of ecosystem models, despite requiring a large amount of multidisciplinary data to be accurate, has increased in the last decades (Heymans et al., 2014; Piroddi et al., 2015) mainly driven by a worldwide movement toward ecosystem-based management approach (Levin et al., 2009; Pikitch et al., 2004). Ecosystem modeling approaches are particularly valuable in the context of

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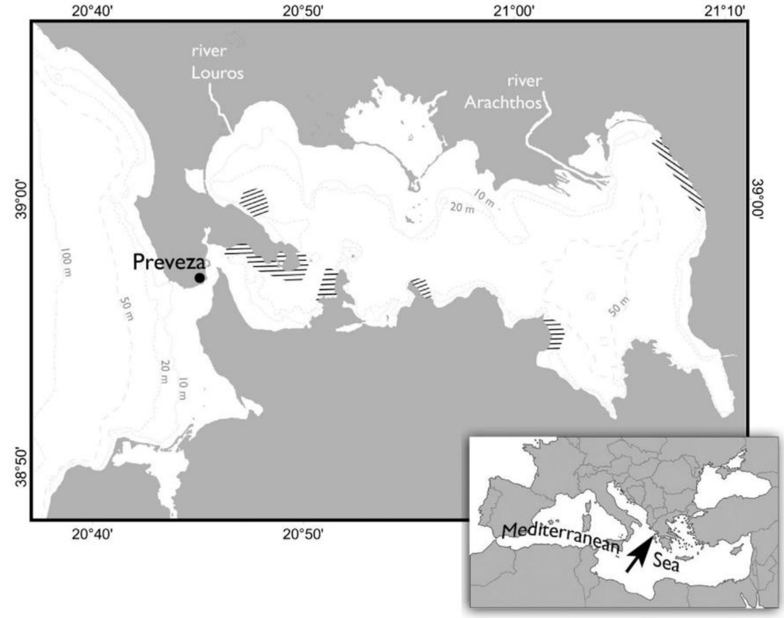

Fig. 1. The Amvrakikos Gulf map with depth profile and the location of fish farms represented by black lines.

European policies like the MSFD which requires an integrative assessment of the health status of marine and coastal ecosystems in relation to the cumulative effect of different pressures (Cardoso et al., 2010). In the following Directive, the assessment of ecosystem status and the setting of reference values and targets to achieve "Good Environmental Status" (GEnS) should be done through the use of indicators (Borja et al., 2014) which are already, at least partly, important ecosystem model outputs (Piroddi et al., 2015). Model derived indicators can in fact serve to evaluate whether an ecosystem and its services are well maintained and sustainably used so that the suitable management measures can be proposed (Piroddi et al., 2015; Shin et al., 2010).

Here we assessed the health status of the Amvrakikos Gulf (Greece, Fig. 1) which has been defined an ideal "natural laboratory" for ecosystem assessments (Bearzi et al., 2008) due to its small size, its semi-enclosed morphology (Katselis et al., 2013), its richness of charismatic megafauna (Bearzi et al., 2008) and because it provides several goods and services (EC, 2009). The Gulf is the final receptor of freshwater and nutrient loads from surrounding areas and from two important rivers, hosts several aquaculture sites (mostly fish farms active since the end of the 80s), and its resources are exploited by local small-scale fisheries. Nevertheless, despite being protected by national, European and international regulations for its diverse wildlife and wetlands (EC, 2009; Gonzalvo et al., 2014), the Gulf has undergone in the past decades through severe changes that have degraded rapidly the entire ecosystem (Katselis et al., 2013; Spyratos, 2008). It has indeed become seasonally hypoxic/anoxic (Kountoura and Zacharias, 2013) resulting in more than 50% of habitat loss on the seafloor (Ferentinos et al., 2010). Under such complex scenario, the Gulf represents a perfect case-study for applying ecosystem modeling approach and its model can be possibly of interest for other world's ecosystems facing similar pressures. The aims of our work were twofold: (1) investigate the dynamics of marine resources in the Amvrakikos Gulf from 1980 to 2013 considering the effect of rivers run off, fish farms and fisheries as major anthropogenic drivers affecting the system and (2) look at structural and functional changes of the ecosystem using model derived indicators obtained from temporal simulations.

2. Materials and methods

2.1. Study area

The Gulf of Amvrakikos (Fig. 1) is a semi-enclosed embayment of approximately 405 km^2 (excluding marshes and lagoons), situated in north-western Greece that communicates with the Ionian Sea through the Preveza Channel: a narrow (minimum width of 370 m) and shallow (<5 m at the shallowest point and ~20 m at the deepest) 3 km-long corridor. Its fjord-like hydrographic regime, because of a shallow sill, reduces deep-water exchange with the open sea; the mean depth of the Gulf is approximately 30 m (its maximum is 60 m), with a seabed mostly covered by mud or sand (Ferentinos et al., 2010). Surface salinity fluctuates widely but remains low throughout the year (17–35‰: Friligos et al., 1997) while sea-surface temperatures range between 9.0 °C and 30.6 °C (Friligos et al., 1997; Panayotidis et al., 1994). Water quality of the Gulf is influenced by the runoff of two rivers (Louros and Arachthos), located in the northern shore (Friligos et al., 1997; Kountoura and Zacharias, 2013), which is controlled by dams operating since 1953 and 1980 for Louros and Arachthos respectively (Ferentinos et al., 2010). Moreover, the Gulf is affected by fish farms, agriculture, livestock and discharges from domestic sewage from coastal towns and villages (Ferentinos et al., 2010; Gonzalvo et al., 2014). In the last 20–30 years, the deeper layers of the water column have become seasonally hypoxic/anoxic, with the western side seasonally hypoxic and the eastern seasonally anoxic (Kountoura and Zacharias, 2013), while the epipelagic layers are still characterized by abundant marine life (Bearzi et al., 2008; Gonzalvo et al., 2014; Panayotidis et al., 1994).

Commercial fisheries operating in the study area include only small-scale fisheries working mainly with set nets (i.e., trammel and gill nets). According to the Royal Fishing Law 23.3/8-4-53 trawling and purse-seining are prohibited within the Gulf all year round since 1953. Currently the active fishing fleet includes ~280 boats fishing exclusively inside the Gulf and targeting mainly European pilchard (*Sardina pilchardus*), red mullet (*Mullus barbatus*), sand steenbras (*Lithognathus mormyrus*), caramote prawn (*Penaeus kerathurus*), common cuttlefish (*Sepia officinalis*), mugilidae and Solea spp. (EC, 2009; Koutsikopoulos et al., 2008).

2.2. The food web model

A food web model was constructed for the Amvrakikos Gulf using the Ecopath with Ecosim (EwE) software version 6 (Christensen et al., 2008). In Ecopath, all principal autotroph and heterotroph species can be represented either individually or aggregated into functional groups considering their ecological roles. Ecopath, the static module of the software that permits definition of initial conditions for the dynamic module Ecosim (Christensen and Walters, 2004), is based on two main equations. In the first one, the biological production of each functional group is equal to the sum of fishing mortality, predation mortality, net migration, biomass accumulation, and other unexplained mortality as follows:

$$(P/B)i \bullet Bi = Yi + \sum_j [Bj \bullet (Q/B)j \bullet DCji] + Ei + BAi + (P/B)i \bullet Bi\,(1 - EEi) \quad (1)$$

where (P/B) is the production to biomass ratio for a certain functional group (i), Bi is the biomass of a group (i), Yi the total fishery catch of group (i), (Q/B)j is the consumption to biomass ratio for each predator (j), DCji is the proportion of the group (i) in the diet of predator (j), Ei is the net migration (emigration – immigration), BAi is the biomass accumulation for the group (i), EEi is the ecotrophic efficiency, and (1-EEi) represents mortality due to factors other than predation and fishing.

In the second equation, the consumption (Q) of each functional group (i) is equal to the sum of production (P), respiration (R), egestion (GS) and unassimilated food (GS•Q).

$$Qi = Pi + Ri + GSi \bullet Qi \quad (2)$$

The implication of these two equations is that the model is mass-balanced; under this assumption, Ecopath uses and solves a system of linear equations estimating missing parameters (see also Christensen and Walters (2004) and Pauly et al. (2000)).

In Ecosim the system of algebraic equations of Ecopath (Eq. (1)) is used to set up a system of differential equations to estimate biomass fluxes as follows:

$$dB_i/dt = g_i \sum_j Qji - \sum_j Qij + I_i - (M_i + F_i + e_i)B_i \quad (3)$$

where dB_i/dt is the biomass growth rate of group (i) during the interval dt, g_i is the net growth efficiency (production/consumption ratio), I_i is the immigration rate, M_i and F_i are natural and fishing mortality rates of group (i), e_i is emigration rate (Christensen and Walters, 2004). Consumption rates (Q_{ji}) are calculated in Ecosim based on the "foraging arena" theory where B_i's are divided into vulnerable and invulnerable fractions to account for hiding and other behavior strategies adopted by animals for balancing predation risk with foraging (Ahrens et al., 2012). In particular, Ecosim describes the interactions between each predators (j) and prey (i) by attributing a vulnerability term (v_{ij}) for each of these interactions. This vulnerability parameter sets the maximum increase in predation mortality a given predator can cause on a given prey. Low values of vulnerability (close to 1) mean that prey production determines the predation mortality ('bottom-up' control) while high values of vulnerability (e.g., 100) mean that predator biomass determines how much prey is consumed (top-down control) (Christensen and Walters, 2004). Mixed effect (vulnerability=2) is set as the default value in Ecosim. Also, in Ecosim, trophic interactions can be described as flow rates using the following formula:

$$\text{Flow rate} = a_{ij}/A_{ij} \cdot v_{ij} \cdot P_j$$

where a_{ij} is the "rate of effective search" parameter, A_{ij} the restricted area where predator *j* forages on prey *i*, v_{ij} vulnerable prey biomass and P_j the predator abundance. This equation recognizes that predators search for prey only over restricted foraging arenas and that the vulnerable prey biomass is distributed only over such areas (Christensen et al., 2008).

2.3. Model parameterization and functional groups

The Ecopath model constructed for the Amvrakikos Gulf represents an annual average of the years 1980–1981, being this the first years of available time series of catches (1980–2011) and river discharge (1981–2008). To describe both high trophic level (HTL) and low trophic level (LTL) organisms/compartments, a total of 34 functional groups were considered, including marine mammals (1), seabirds (3), sea turtle (1), fishes (15), invertebrates (6), benthos (1), zooplankton (1), bacterioplankton (1), primary producers (1), fish farms (1) and detritus (3). Biomasses (expressed as tonnes of wet weight per km^2) for benthic invertebrates, phytoplankton and zooplankton were available from scientific literature and for seabirds species also through global international databases (Birdlife www.birdlife.org and the Sea Around Us Database www.searoundus.org). Common bottlenose dolphins (*Tursiops truncatus*) biomass was available for the years 2003–2013 (Bearzi et al., 2008, Gonzalvo, unpulished data). To estimate the biomass of 1980 we used the study of Gonzalvo et al. (2014) on population abundance changes during the last 20 years based on fishers interviews. Surveys or stock assessments to estimate biomass of commercially important groups (functional groups 6–20 and 22–26 in Table S1) were not available for the area. Thus, for each of these functional groups, Catch per Unit of Effort (CPUE) estimates were used as a proxy of their relative biomass, assuming proportionality between CPUE and biomass (Myers and Worm, 2003; Watson et al., 2013). CPUEs, expressed as tonnes kW^{-1} $year^{-1}$, were calculated by dividing the reconstructed catches by the total reconstructed effort (see section below). Despite being abundant in the Gulf, no biomass estimate was available for jellyfish, thus it was estimated from the model by imposing EE equal to 0.95 under the conservative assumption that most of its production was used in the system, reducing possibilities to overestimate its abundance and effects (Christensen and Pauly, 1998; Pauly et al., 2009). In order to represent over time nutrients and organic matter loads affecting the eutrophication state of the system, we incorporated in the model fish farms and particulate organic matter (POM) as functional groups. The biomass of fish farms was represented as the total fish produced from the cages and was available from late 1980s from the Fisheries Department of Preveza Prefecture. Thanks to detailed local information on cage productivity, feed given, average feed composition and feed loss (Fisheries Department of Preveza Prefecture), we quantified organic matter and nutrient released from cages (Lupatsch and Kissil, 1998) from 1981 to 2008. Organic matter release from cages were represented by opportunely setting unassimilated fraction (including also uneaten feed) and detritus fate (to POM) for the fish farm functional group and forcing its biomass with fish farm production over time. POM initial biomass was derived from biochemical oxygen demand (BOD) estimates in water samples while net migration parameter from river and human-related discharges was used to represent

Table 1
Detailed description of the ecological indicators examined in this paper with acronyms, typology (state or trend), definitions and/or references.

Ecological Indicator	Acronym	State (S); Trend (T)	Definition and/or references
Total system throughput	TST	*S*	Sum of all the flows (consumption, export, respiration, detritus). It indicates whole ecosystem size (Christensen et al., 2008)
Total primary production/total system respiration	TPP/TR	*S*	It relates to community energetic attributes of ecosystem maturity. In the early stages of ecosystem development primary production (TPP) is expected to exceed respiration (TR) (values greater than 1). As the system matures the ratio is expected to move towards 1 (Christensen et al., 2008)
Total primary production/total biomass	TPP/TB	*S*	It relates to community energetic attributes of ecosystem maturity. As system matures, biomass accumulates, therefore TPP/TB ratio is expected to be high in developing systems and diminish as the system mature (Christensen et al., 2008)
Finn's Cycling Index	FCI	*S*	Percentage of flows recycled in the food web and path length (Finn, 1976)
Ascendancy	A	*S*	Measurement of system growth and development of network links (Monaco and Ulanowicz, 1997)
Overhead	O	*S*	Energy in reserve of an ecosystem that reflects system's strength when it is under unexpected perturbations (Ulanowicz, 1986)
System omnivory index	SOI	*S*	Weighted average of the variance of the TL of consumer's prey. It is an index of trophic specialization showing how feeding interactions are distributed between trophic levels (Libralato, 2008)
Mean Transfer Efficiency	TE	*S*	Efficiency in which energy is transferred between TLs, calculated as the geometric mean of TE for each of the integer trophic levels II to IV (Christensen et al., 2008)
Trophic levels	TL	*S*	(Christensen et al., 2008)
Trophic level of the catches	TL_C	*S*	(Christensen et al., 2008)
Primary production required	%PPR	*S, T*	Calculated as primary production required divided by the total primary production of the system to sustain the catch. Used to evaluate the sustainability of fisheries (Pauly and Christensen, 1995; Tudela et al., 2005)
Kempton's index of biodiversity	Q	*T*	Expresses biomass species diversity by considering those organisms with trophic levels 3 or higher (Kempton and Taylor, 1976)
Total pelagic versus total demersal biomass	P/D	*T*	Ratio between small pelagic species (plankton feeder group) and the piscivores species (predator and benthic groups) (Caddy, 1993, 2000)
Mean trophic level of the community	mTLco	*T*	Excluding those functional groups with TL=1 and calculated as the weighted average of the TL of all the species within the ecosystem (Shannon et al., 2014)
Mean trophic level of groups with TL between 2 and 3	mTL_{2-3}	*T*	
Mean trophic level of groups with TL > 3.25	$mTL_{3.25}$	*T*	In our case excluding marine mammals, seabirds and sea turtles (mTL3.25; Pauly and Watson, 2005)
Mean trophic level of top predators	mTL_{TP}	*T*	In our case including marine mammals and seabirds
Mean trophic level of the catches	mTLc	*T*	Weighted average of the TL of fisheries target species (Pauly et al., 1998)
Fishing in Balance index	FIB	*T*	Ratio between the energy required to sustain the fishery landings and the baseline value (the first year of the time series, Pauly et al., 2000)

annual input to the Gulf (Albanis et al., 1995; Katselis and Ramfos, 2015; Zacharias et al., 2009). Abiotic data consisted of monthly total river outflows of Louros and Arachthos (1980–2008) and was provided by the Public Power Corporation SA. Moreover, nutrient released by the rivers and by fish farm cages were used to determine nutrient inputs to the Gulf. We considered nitrogen as limiting nutrient (typical for coastal shallow ecosystems; Libralato and Solidoro, 2009) and used its estimated dynamics as forcing function for phytoplankton primary production. Bacterioplankton was included in the model to mimic main biogeochemical cycles and possible oxygen consumption due to organic matter degradation. Bacterioplankton biomass and rates, not available for the study area, were taken from similar ecosystems (Harvey et al., 2003; Libralato and Solidoro, 2009).

P/B and Q/B ratios for finfish and invertebrates were estimated using empirical equations (Christensen et al., 2008) or were taken from literature and expressed as annual rates ($year^{-1}$) (Table S1). A diet composition matrix was constructed using either field studies (e.g., stomach contents) or diet data obtained from the literature for the same species in similar ecosystems (Table S2). For some functional groups, when the information was lacking, we also integrated the outputs parameters (DC, P/B, Q/B) of previously built EwE models available for the Ionian Sea (Moutopoulos et al., 2013; Piroddi et al., 2010; Piroddi et al., 2011) and the adjacent Adriatic Sea (Coll et al., 2009b). In the case of fish farm, P/B and Q/B represented respectively the production of fish and the consumption of feed per year from the cages while the diet was opportunely set in order to represent the feed coming from outside the system (Katselis and Ramfos, 2015; Zacharias et al., 2009).

Catch data was reconstructed from a number of different sources. In particular, catch by species and total catch was available from the Preveza Department of Fisheries from 1979 to 2001 and from Koutsikopoulos et al. (2008) and local fishers interviews, from 2003 to 2007 for a fraction of the total number of fishing vessels. To estimate total catch for the 1979–2007 period we first searched in the literature for total fishing fleet size. Based on public sources of data (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009), six anchor points representing the number of fishing vessels for the years 2011, 2009, 2001, 2000, 1991 and 1980 were found. To get the overall trend of fishing fleet size for the 1979–2011 period we used the six anchor points and interpolated the estimates of the anchor points for the missing years following the same approach as described and applied in Zeller et al. (2007). We then estimated the total catch by species for 1979–2007 for the entire Amvrakikos fishing fleet using the catch/vessel ratio given by the Department of Fisheries of Preveza and applied it to the reconstructed fishing vessels time series. Fishing effort (kW) was estimated for the 1979–2011 period by taking the product of the reconstructed number of fishing vessels, kW per vessel (calculated using GT; EC, 2009), and the number of days spent fishing (Koutsikopoulos et al., 2008). Also, to account for improvements in technology not captured by kW as a measure of effort, a technological "creep factor" of 1% was applied since 1980 (Table 2), as derived from the empirical relationship by Pauly and Palomares (2010). Since no discards data were available for the Gulf, we assumed same discard ratio provided by Moutopoulos et al. (2013) for an ecosystem model of the neighboring open waters of the Ionian Sea.

Table 2
Summary statistics and network analysis indicators for the Amvrakikos Gulf food web.

Indicators		Units
Summary statistics		
Sum of all consumption	4421	t km^{-2} year^{-1}
Sum of all exports	960	t km^{-2} year^{-1}
Sum of all respiratory flows	1806	t km^{-2} year^{-1}
Sum of all flows into detritus	4605	t km^{-2} year^{-1}
Total system throughput	11792	t km^{-2} year^{-1}
Mean trophic level of the catch	2.77	
Gross efficiency (catch/net p.p.)	0.004	
Total primary production	2583	t km^{-2} year^{-1}
Total primary production/total respiration	1.43	
Proportion of primary production required to sustain fisheries (PPR%= PPR/PP*100)	8	%
Primary production required to sustain fisheries (PPR)	575	t km^{-2} year^{-1}
Total primary production/total biomass	10.43	
Total biomass (excluding detritus)	247.66	t km^{-2}
Total catch	9.53	t km^{-2} year^{-1}
Network analysis		
System Omnivory Index	0.27	
Finn's cycling index	15.85	%
Ascendancy	34.5	%
Overhead	65.5	%
Mean Transfer Efficiency	13.8	%
Pedigree Index		
Pedigree	0.57	

A detailed description of the functional groups, data to parameterize the model and associated references are listed in Tables S1, S2, S3 of Supplementary materials.

2.4. Model and data quality

In order to assess the quality of the model we reported the overall pedigree index, that ranges from 0 to 1 (see Table 1). The pedigree is calculated on the basis of the presumed quality of data entered in the model with larger weight for local experimental data and lower weight for parameters derived from other models or extrapolated from other systems. Low overall pedigrees (0.1–0.3) imply a model constructed with low-precision data and/or with data coming from areas outside the studied region, while higher values (close to 1) indicate a model constructed with locally-derived data (Christensen et al., 2008; Morissette, 2007). The highest pedigree values observed in Ecopath models ranged between 0.7 and 0.8 (Christensen et al., 2008; Morissette, 2007).

2.5. Ecosim fitting procedure

We used Ecosim to fit the model to observed time-series of data using the sum of squares (SS) deviations between predicted and observed data as a metric for assessing model performance (Christensen et al., 2008). The time-series used to fit the model were mainly biomasses, catch per unit effort (CPUE) and catches for those functional groups with available information (Table S3) while main forcings were fishing effort over time, nutrient loads and organic matter (estimated from biochemical oxygen demand [BOD] measurements) coming from fish farms, rivers run off and other diffuse sources (Fig. 2a and b). The fitting procedure followed the same methodology as described and applied in Mackinson et al. (2009), which consisted of 7 general steps:

1. Baseline model: trophic interactions with default vulnerabilities (v_{ij}=2; mixed effect), no environmental or fishery data were used to drive the model;
2. Baseline and trophic interactions: trophic interaction modifications were included while no environmental or fishery changes were used. In particular, different vulnerabilities were tested (5, 10, 15, 20, 25, 30);
3. Baseline and environment: different environmental drivers such as the limiting nutrient (in our case nitrogen) and BOD trends coming from rivers and fish farms (Fig. 2) were used to force primary production and POM concentrations. No fishery data were used to drive the model;
4. Baseline, trophic interactions and environment: no fishery data were used;
5. Fishery: Fishing effort was included as a model driver (Fig. 2). Trophic interactions were set as default and no environmental data were used;
6. Changes in trophic interactions and fishery: no environmental data was used;
7. Trophic interactions, environment and fishery were jointly included in the model as drivers.

To select the best model, at each step, the Akaike's information criterion (AIC) that takes into account the predictive accuracy (sum of squares, SS) and complexity (number of parameters, trophic interactions and environmental drivers e.g., PP) of the model, was calculated (Mackinson et al., 2009).

In addition, once the best model was chosen, to account for anoxia/hypoxia in the system, a 'mediation function' was applied (Christensen et al., 2008). In Ecosim, the mediation function allows a third variable (in our case bacterioplankton) to influence the trophic interaction between two other variables (here seabirds and marine mammals with each of their prey) by altering either the area (A_{ij}), the rate of effective search (a_{ij}) or the vulnerability

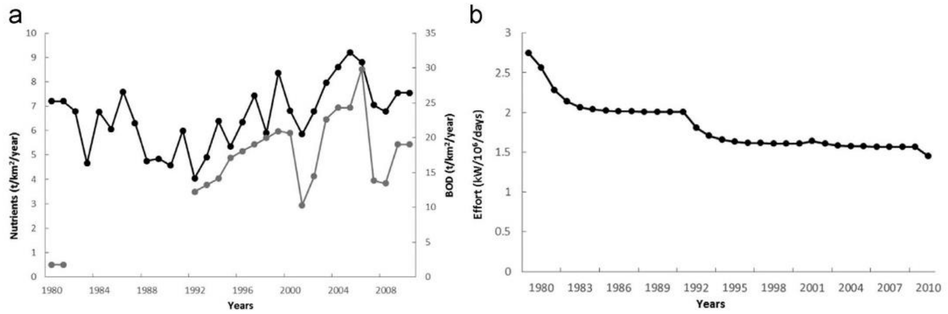

Fig. 2. a. Changes in nutrients concentration (black line) and biogeochemical oxygen demand (gray line); b. fishing effort (kW/10^{-6}/days) used as main drivers for the fitting procedure.

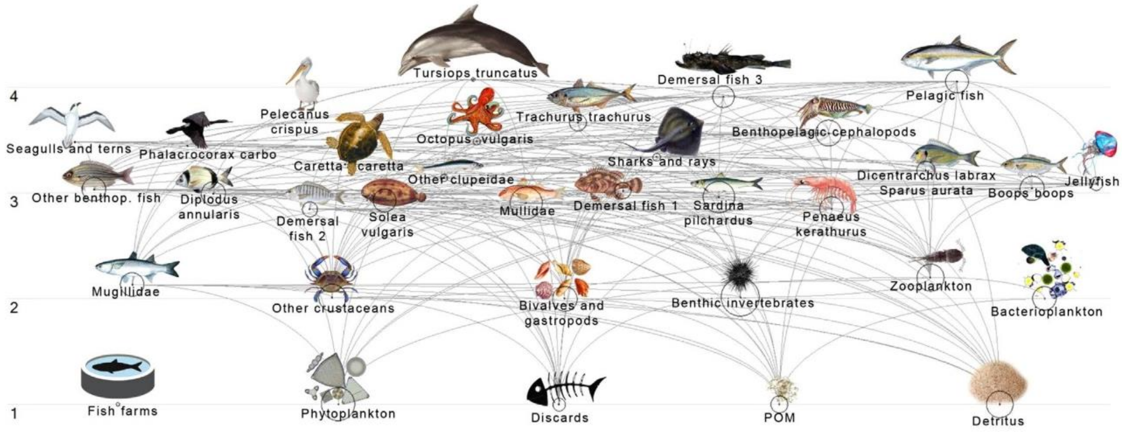

Fig. 3. Flow diagram of the Amvrakikos Gulf ecosystem (early 1980s). Each functional group is shown as a circle, with size approximately proportional to the log of its biomass. All the functional groups are represented by their trophic levels (y-axis) and linked to each other by predator-prey relationships expressed as light gray lines.

exchange rate (v_{ij}). In our case, we applied the mediation function to change both A_{ij} and v_{ij} together to assess if, in the presence of oxygen depletion in bottom layers, available preys would concentrate in a shallower stratum making them more available to predators (seabirds and marine mammals). Given that oxygen is not a modeled state variable, we used bacterioplankton dynamics as a proxy for oxygen depletion. This permits to evaluate if an increase in POM in the system through fish farms and river runoff, would affect bacterioplankton and oxygen concentrations with effects on bottlenose dolphins and seabirds abundance by increasing prey abundance at the surface due to the reduction of O_2 on the seafloor.

2.6. Model analysis

The Amvrakikos food web was represented graphically with a flow diagram that included information on trophic levels, biomasses and estimated flows (Fig. 3). Ecosystem structure and exploitation status of the Gulf were assessed through a series of indicators (Table 1) derived from network analysis and ecological studies.

3. Results

3.1. Mass-balancing

To obtain mass balance we adjusted the input parameters of those functional groups (#10) with EE values > 1. In particular, for pelagic fish, *Sardina pilchardus*, other clupeidae, other benthopelagic fish, benthopelagic cephalopods, other crustaceans, benthic invertebrates and zooplankton we adjusted the diet matrix, being the data with higher uncertainty. For example, the predation caused by pelagic fish on *Sardina pilchardus* and other clupeidae was decreased because too high (from 35% to 25% and from 0.5% to 0.2% respectively), while the consumption of benthopelagic cephalopods on crustaceans group was overestimated and was reduced by redistributing the proportions in the predator's diet. Crustacean, bivalve and gastropod biomasses were the only biomasses that had to be modified from the original input data: the values taken from closed systems (see Section 2) were indeed too low and had to be increased. Once balanced, ecotrophic efficiencies (EE) showed high values for the majority of the functional groups, indicating that total mortality in the system was mainly driven by predation and fishing. The gross food conversion efficiency (P/Q) and the respiration over assimilation (R/A) were within the expected ranges (Christensen et al., 2008). The resulting output parameters and the final diet matrix are shown in Table S1, S2 and S3 in Supplementary materials.

3.2. Model analysis

3.2.1. Trophic levels

Trophic flows, trophic levels and relative biomasses of the Amvrakikos Gulf ecosystem are represented in Fig. 3, Table 2 and Table S1. In particular, the highest trophic levels (TL) were observed for *Tursiops truncatus* (TL= 4.07), pelagic fish (mainly large pelagics, TL=4.05) and demersal fish 3 (mainly large demersals, TL=3.91). In contrast, annular seabream (*Diplodus annularis*), European sardine (*Sardina pilchardus*), European sole (*Solea vulgaris*), mullidae, demersal fish 2 (mainly sparidae species),mugilidae, other crustaceans zooplankton, benthic invertebrates, bivalves and gastropods and bacterioplankton had lower TL values ranging between 2.13 and 2.99. It should be also noted that loggerhead sea turtle (*Caretta caretta*) presented a quite low TL (3.27) due to the presence of discarded fish in its diet as it was observed in the Gulf (Zbinden et al., 2011; Gonzalvo direct observation) and in neighboring areas (White, 2004).

3.2.2. Time series fitting

The best performances in fitting observed data were obtained when trophic interactions as well as fishing and environmental variables were included all together in the fitting procedure. The best model, which was the one with the lowest AICc, explained 78% of the variance of the data (Table 3). Environmental drivers in combination with trophic interactions were able to explain the majority of the variability observed in the ecosystem (77.2%) while fishing marginally contributed with a 1.8%. Different vulnerabilities were also tested and the largest improvement was obtained with 30 trophic interactions.

The best model reflected quite well the biomass trends for the apex predators of the Amvrakikos Gulf. In particular, Ecosim was able to predict *Tursiops truncatus*, *Phalacrocorax carbo* and *Pelican crispus* abundance trends for the surveyed periods (Fig. 4). A slight improvement was found for seabirds when the mediation function was incorporated in the model, assuming an increased availability

Table 3
Model fits following the seven steps proposed by Mackinson et al. (2009) including trophic interactions, fishery and environmental drivers. Vulnerabilities are shown only for those models with the lowest Akaike Information Criterion (AICc). The "best" model (shown in italics) was the one yielding the lowest AICc.

Steps	vulnerabilities	min SS	AICc	%improved
1. Baseline	0	524.9	71.3	
2. Baseline and trophic interactions	5	524.9	81.4	−14.2
3. Baseline and environment	0	453.0	51.6	37.6
4. Baseline, trophic interactions and environment	30	211.9	16.2	77.2
5. Fishery	0	519.9	70	1.8
6. Trophic interactions and fishery	3	501.1	71.1	0.2
7. Trophic interactions, environment and fishery	*30*	*218.6*	*15.7*	*78.0*

of prey on the surface of the water column. For bottlenose dolphins, on the other hand, the trend improved when a decrease in prey and feeding area was assumed. For forage fish species like *Sardina pilchardus* the model reproduced quite well the fluctuations in CPUE observed between 1980 and 2004, while predicted trends between 2005 and 2007 were overestimated. A similar scenario was also observed for mugilidae. A good reproduction of CPUE time series data was shown for *Trachurus trachurus*, *Diplodus annularis*, mullidae and benthopelagic cephalopods. For these groups, however, the increase in biomass observed in the early 2000 s was not picked up by the model. Ecosim was not able to represent well the fluctuations observed for *Penaeus kerathurus*. As for the other commercially important groups only few data points (from 2003 to 2007) were available resulting also in a poor fit (S4 in Supplementary material).

Regarding landings, Ecosim generally underestimated observed values, had difficulties in capturing the changes in catches although trends were vaguely captured for the majority of the groups (Fig. 5).

3.2.3. Ecological indicators

Ecological state indicators calculated by Ecopath for the Amvrakikos Gulf (Table 2) revealed that the main flows in the system were flow to detritus (39%) and consumption (37%) followed by respiration (15%) and exports (8%). In addition, indicators addressing community energetics and cycling of nutrients such as the ratio between total primary production (PP) and total respiration (R) (Christensen, 1995; Odum, 1969), primary production/biomass ratio (PP/B) and the SOI (System Omnivory Index) suggested the system to be at an intermediate-low level developmental stage. The FCI (Finn's Cycling Index), the mean transfer efficiency (TE) and overhead showed relatively high values while ascendancy was quite low. Fishing indicators such as the primary production required (PPR) of the Gulf and mean the trophic level of the catches were respectively 8% and 2.77. The pedigree index of the model was 0.57.

Trends in ecological indicators calculated by Ecosim revealed changes through time in the structure of the Amvrakikos Gulf ecosystem (Fig. 6). In particular, trophic level indicators mTLco and mTL_{2-3} increased since the beginning of 1980s. Similar trend was observed also for the ratio between pelagic and demersal species. The other two trophic level indicators, $mTL_{3.25}$ and mTL_{Tp}, showed clear decrease in time, with $mTL_{3.25}$ though increasing again from middle of 2000s. Kempton's biodiversity index fluctuated in time with a certain stability and no clear trend. On the contrary, mean trophic level of the catches (mTLc), fishing in balance index and relative PPR decreased since the beginning of the studied period.

4. Discussion

A food web model was implemented for the Amvrakikos Gulf ecosystem with the aim of reproducing and quantifying main energy and matter flows in the system and dominant food–web dynamics. To do so, we integrated in the model the most important HTL and LTL organisms/compartments characterizing the ecosystem and we represented the major pressures, both from anthropogenic and environmental sources (e.g., river run off, fish farming and fishing), affecting the Gulf. Some uncertainties, which are discussed below, are still present in this model, particularly when looking at temporal changes in diet composition, discards and biomass of commercially important species. Although further research effort should increase its accuracy, we consider that the model presented here exploits at best the available resources, sheds light in many factors affecting the complex dynamics of the Amvrakikos Gulf and provides key ecosystem information that can be useful for other Mediterranean coastal enclosed areas (e.g., lagoons and gulfs/bays).

4.1. Model quality and limitations

Our Ecopath model fell within the medium-high range of the pedigree index estimated by Morissette (2007), who assessed globally the quality of 150 EwE models. The robustness of the baseline period (1980s) was mainly due to available survey data for several species/functional groups (e.g., seabirds and LTL organisms -phytoplankton, benthic invertebrates, zooplankton) of the ecosystem. Yet, data deficiencies still exist. The major gaps were related to poor quality of fisheries data (effort, catch and discards), which limited the reconstruction of the relative biomass of commercially important functional groups and the trends associated to their biomass and catch. In Greece, as well as in many other Mediterranean areas (Pauly et al., 2014), fisheries statistics are generally incomplete and have low reliability (Moutopoulos and Koutsikopoulos, 2014; Tsikliras et al., 2007) since it is not rare that fishermen deliberately misreport their catches to avoid stricter regulations or higher taxation (Bearzi et al., 2006), as it has been also observed in our study area. A recent study by Moutopoulos and Koutsikopoulos (2014) analyzing the landings as well as the fishing effort data per fishing gear reported by the Hellenic Statistical Authority over the period 1982–2010, showed abrupt changes of both recorded species and species landings per subarea, spurious correlations of landings among different species groups and misreporting of fishing gear and/or of fishing vessel characteristics. Other limiting factors were related to kW or other measures of fishing capacity (tonnage, length over all, number of boats) which are not necessarily good estimates of real fishing effort (Lleonart and Maynou, 2003): meteorological, economic and legislative conditions that hamper fishing are not considered to change over time, whereas they might be all important factors in determining exerted effort. No discard data were available for the study area. Despite the fact that further effort should be conducted to evaluate the impact of discards on commercial and non-commercial taxa, several studies have shown how discard rates in Greek small-scale fishery are relatively low and with a small impact on marine resources (Tsagarakis et al., 2013; Tzanatos et al., 2007; Vassilopoulou, 2012). Not surprisingly, therefore, fishery components in our model have the highest uncertainty. This limits the accuracy of our results, particularly in relation to CPUE trends that were used to calibrate the model. Unfortunately, this uncertainty is common to many Mediterranean areas (Coll et al., 2008; Moutopoulos et al., 2013; Piroddi et al., 2010) where stock assessments or surveys are not in place or inaccessible and where fisheries statistics are in most cases erroneously recorded (Moutopoulos and Koutsikopoulos, 2014). Despite these limitations, reconstructed CPUE trends, being the only form of available data, are

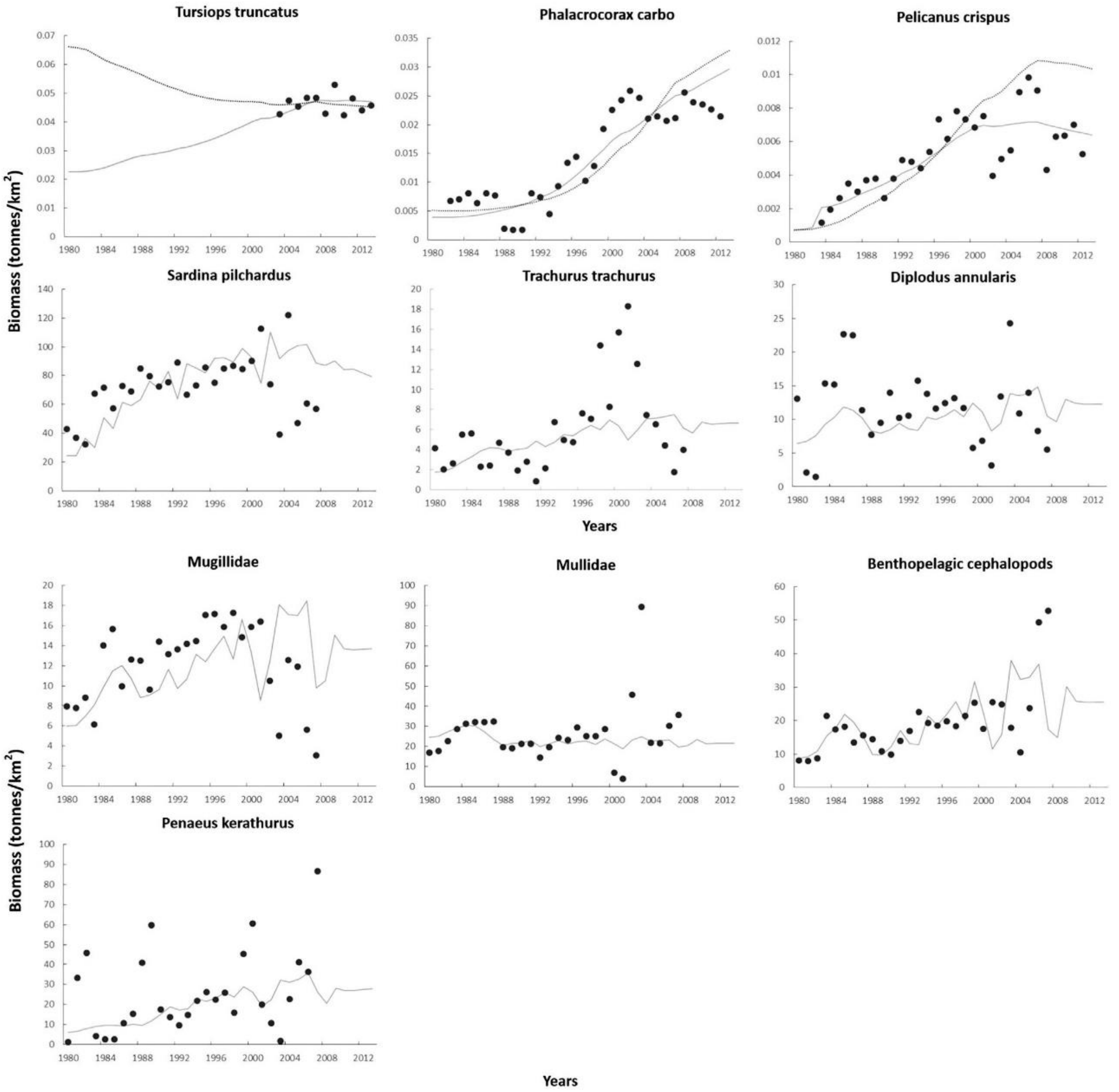

Fig. 4. Predicted (solid lines) versus observed (dots) biomass (t/km^2) for the main functional groups of the Amvrakikos ecosystem for the period 1980–2013. For the megafauna (*Tursiops truncatus, Phalacrocorax carbo, Pelicanus crispus*) the predicted model is also shown with the inclusion of mediation function (dotted line).

the most commonly used to represent relative biomass (Coll et al., 2008; Piroddi et al., 2010). Here, to limit this uncertainty, we tried to incorporate best available fisheries statistics complemented with local fishers interviews. Fishers' ecological knowledge (FEK) is gaining attention for understanding and evaluating changes in the structure and function of marine ecosystems (Bunce et al., 2008; Saenz-Arroyo et al., 2005). FEK data, obtained from fishers interviews, can be transformed into quantitative data (e.g., numerical trends) using different techniques (e.g., fuzzy logic: Ainsworth et al., 2008; Brotz et al., 2012)in order to ease their implementation in ecosystem modelling approaches (Ainsworth, 2011). Thus, we recognize that further interviews should be conducted to fill knowledge gaps and possibly move toward more realistic data, increasing model accuracy. Yet, with the data currently available, our model represents the best approximation to provide an integrated understanding of the Amvrakikos Gulf marine ecosystem.

4.2. *Model analysis*

4.2.1. *Time series fitting*

The model was able to reproduce available time series of biomass and catch data when applying nutrient, organic matter and

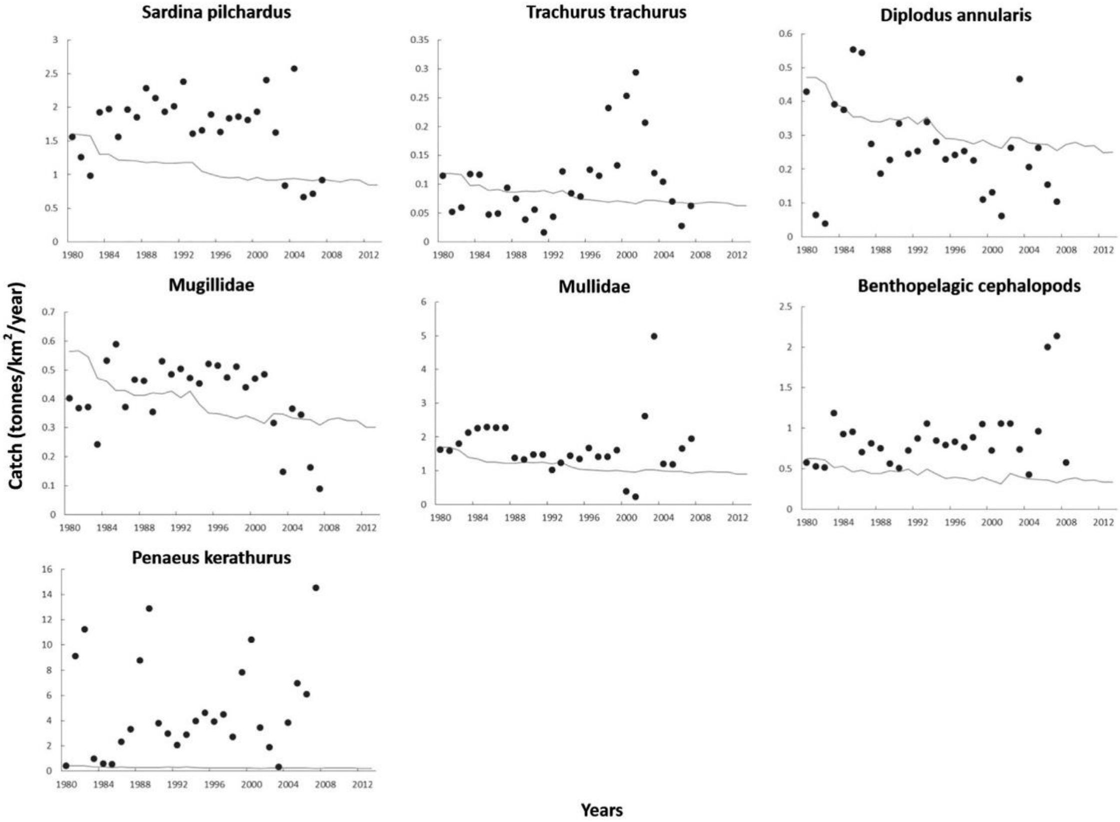

Fig. 5. Predicted (solid lines) versus observed (dots) catches (t/km^2/year) for the main commercially important functional groups of the Amvrakikos ecosystem.

fishing effort as main drivers. Changes in nutrient loads, however, seemed to be the strongest driver, explaining around 38% of the variability in the food web of the Gulf, highlighting the importance of bottom-up forces in the dynamics of this ecosystem. The explicit representation of establishment and development of fish farm from 1980 to today permitted to highlight that, during the last decades, fish farms represented a secondary contribution to nutrients and organic matter to the Gulf, whereas the two main rivers were the main drivers of the Gulf eutrophication. The strong demand for irrigation waters to the surrounding agricultural farms and the consequent runoff of minerals represented also important non-point contribution (Spyratos, 2008).

When looking at overall dynamic changes of the main functional groups of the Amvrakikos Gulf for the period 1980–2013, the model showed a relative stability of the species/functional groups at the top of the food web and fluctuations with sign of decrease for the ones at the bottom, which is in accordance with previous studies pointing at eutrophication and contaminants as the main reason for such differences (Ferentinos et al., 2010; Koutsikopoulos et al., 2008). Only 2–3 decades ago the Gulf occasionally had hypoxic conditions at depths greater than 40 m (HCMR, 1988); currently the situation has worsened and these conditions are observed in waters up to 23 m of depth (EC, 2009). This trend constitutes a serious concern not only for demersal and benthic species but also for those on top of the food web, with effects beyond trophic interactions. For instance, Gonzalvo et al. (2015) have documented epidermal lesions on the main top predator of the Gulf, the bottlenose dolphin, suggesting environmental, such as the increase of local temperature (Philandras et al., 2008) and salinity (Feidas et al., 2007), as well human-related stressors (e.g., pollution) as their likely cause.

Contaminants influencing dolphins' reproductive rates might also be the reason why this species, the only marine mammal present in the Gulf, remains currently stable (Gonzalvo, unpublished data) and not increasing since the only potential "dolphin predator" in the area is small-scale fishing fleet but evidences of by-catch were rarely observed in the Gulf. The only two species that seem to thrive in this type of ecosystem, showing an increase in population, are the *Phalacrocorax carbo* and the *Pelican crispus*. The most likely causes for such positive trend, as observed in other European wetlands (Cowx, 2013), are attributed to the legal protection granted to both species and their habitats and the presence of hot-spot areas for fish-eating birds (i.e. lagoons, fish farms) (BirdLife International, 2004; Liordos et al., 2014).

No significant results were obtained for the catches of the main commercially important groups of the ecosystem. This could be attributed, as mentioned above, to misreporting of fisheries statistics in terms of both catches and fishing fleet composition, but also to illegal, unregulated and unreported catches. Although fishery is the secondary most important component driving the system (after riverine nutrients and organic loads), as shown in this study, this poses a serious handicap for understanding the dynamics of the fishing fleet and generally of the ecosystem.

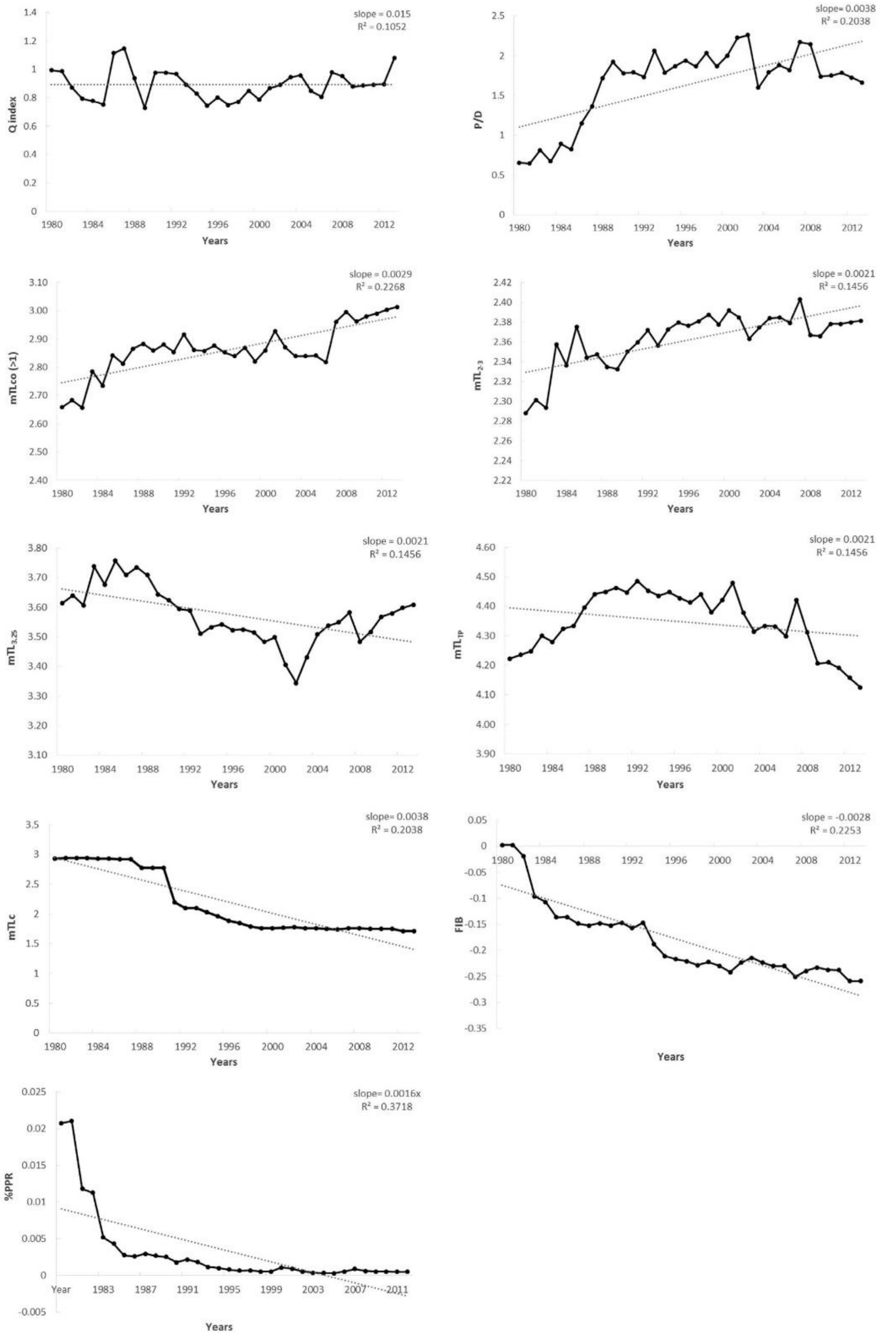

Fig. 6. Ecological and network indicators (Kempton's index of biodiversity (Q); Pelagic/Demersal ratio (P/D); Mean trophic level of the community (mTLco); Mean trophic levels of groups having trophic level between 2 and 3 (mTL_{2-3}); Mean trophic levels of groups having trophic level > 3.25 ($mTL_{3.25}$; excluding marine mammals, sea turtles and seabirds); Mean trophic level of top predators (mTL_{TP}); Mean trophic level of the catches (mTLc); Fishing in balance index (FIB); Primary production required/PP (%PPR)) calculated from Ecosim model for the period 1980–2013. The estimated trends (solid line) are shown with the value of the slope and the coefficient of variation (R^2) for the regression model.

4.2.2. Ecological indicators

The results obtained from our baseline model (year 1980), mainly regarding type of flows and cycling indices, already indicated the Amvrakikos Gulf to be an immature and perturbed system, typical of "closed" ecosystems (e.g., like estuaries, lagoons and bays) where bottom-up processes drive the system, and where possibly high levels of community stress are induced by anthropogenic and environmental forces. These results are in line with the estimates obtained for other large eutrophic ecosystems with similar historical evolutions (Ferentinos et al., 2010) and general patterns such as the Black and the Baltic Seas (Akoglu et al., 2014; Tomczak et al., 2012). These three semi-enclosed systems share, indeed, similar patterns as they have undergone in the last decades through severe ecosystem changes such as: (a) eutrophication with frequent hypoxia/anoxia events, mainly caused by the increasing concentration of human activities in the coastal zone such as industrial and agricultural waste (Akoglu et al., 2014; Readman et al., 1993; Tomczak et al., 2012), (b) local environmental changes such as the increase in the average annual air temperature (Philandras et al., 2008) and the reduction of the mean annual rainfall (Feidas et al., 2007) and (c) increasing fishery activities (Akoglu et al., 2014; Koutsikopoulos et al., 2008; Tomczak et al., 2012). Further similarities are found in their high levels of total primary production per unit of surface (t km^{-2} $year^{-1}$; Amvrakikos Gulf: 2583; Black Sea: 3483; Baltic Sea: 2434) and low levels of the mean TL of the catches (Amvrakikos Gulf: 2.78; Black Sea: 3.07; Baltic Sea: 3.3). Also, it is noteworthy not only the importance of small pelagic fish in the fisheries landings of all three areas, but also the dominance of these forage fish due to high levels of productivity in the epipelagic layers of the water column (Ferentinos et al., 2010; Oguz and Gilbert, 2007; Tomczak et al., 2012).

The high values of total primary production and eutrophication levels in Amvrakikos, which are comparable to those of most eutrophic and heavily polluted gulfs of Greece, such as Saronikos and Thermaikos Gulfs (Nikolaidis et al., 2005), are indicative of the fragile health status of the Gulf of Amvrakikos.

Trends in ecological indicators gave some explanations on changes in the structure of the Amvrakikos Gulf across the 1980–2013 period. In particular, when looking at ecosystem indicators such as the mean trophic level of the community, those groups with TL between 2 and 3, and the ratio between pelagic and demersal groups, a consistent pattern was delineated with increasing trends from the beginning of 1980. These positive trends over time reflected an increase of small pelagics and some of their predators (e.g., seabirds) and a decrease of demersal groups that might be related to the synergetic effects of nutrient enrichments and overfishing (Caddy, 1993; Libralato et al., 2004). However, since local fishery resulted to have a marginal role in the Gulf's food web and on its dynamics, a dominant effect of overfishing appears unlikely while eutrophication seems to be the only major player affecting the system.

Regarding catch related indicators, both the mean trophic level of the catches, the FIB index and PPR/PP decreased over time. Similar trend in the FIB index has been observed in another heavily degraded and highly eutrophic ecosystem as the Adriatic Sea suggesting a progressive deterioration of the ecosystem over time with a contraction of the fishery sector (Coll et al., 2009b). In particular, these trends might be a symptom of crisis in the local artisanal fishery, rather than overfishing, as observed in other areas of the Mediterranean Sea (Coll et al., 2009a; Coll et al., 2007; Piroddi et al., 2010). This crisis is also manifested by the fact that younger generations do not see any future in fisheries and that the traditionally-oriented fishing community is rapidly changing (Gonzalvo et al., 2014). Moreover, the observed P/D trend might indicate a shift in the ecosystem trophic state (i.e., eutrophication; Caddy, 1993) that mime the overfishing effects (Libralato et al., 2004). Observed changes in biomasses, catches, FIB and PPR, however, seemed not to have influenced the Kempton's Q diversity index that shows relative stability over time (Fig. 6a) suggesting rearrangement of species densities and interactions in a way to maintain system biodiversity, possibly indicating that the system as a whole is still resilient to large driver changes. A completely different question is for how long this increasingly fragile ecosystem will be showing such resilience unless some adequate management measures are implemented.

5. Conclusions

The construction of a food web model enabled us to assess and quantify changes in the structure of the Amvrakikos ecosystem and the cumulative impacts of the major factors affecting the system. Our results highlighted a general degradation of the demersal compartments of the food web and a relative stability of the pelagic ones mainly due to high eutrophication levels, which was confirmed by ecological indicators. The notorious degradation of the Gulf of Amvrakikos, particularly acute during the past 20 years, calls for action and is urgently needed if we want to preserve this increasingly fragile ecosystem. In order to produce a more accurate picture of the ecosystem dynamics of the Gulf, future initiatives should be dedicated to improve data deficiencies and to farther develop temporal simulations. Robust hind cast simulations are necessary in order to forecast ecosystem dynamics and explore different management policies and future scenarios.

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Appendix A. Suplementary Information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2015.10.007.

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S1. Input parameters (B, P/B, Q/B) and estimated outputs (trophic levels, ecotrophic efficiencies and production/consumption rates in grey cells) for the functional groups of the Amvrakikos Gulf marine ecosystem in 1980s

#	Group name	Trophic level	B (t/km²)	P/B (year)	Q/B (year)	Total Catch (t/km²/year)	EE	P/Q
1	Tursiops truncatus	4.07	0.066	0.054	22.630		0.028	0.002
2	Phalacrocorax carbo	3.44	0.005	0.205	109.450		0.095	0.002
3	Seagulls and terns	3.48	0.002	0.171	589.050		0.000	0.000
4	Pelicanus crispus	3.66	0.001	0.105	177.816		0.134	0.001
5	Caretta caretta	3.27	0.001	0.190	3.220		0.526	0.059
6	Sardina pilchardus	2.96	23.050	2.650	10.500	1.567	0.639	0.252
7	Other clupeidae	3.14	0.240	2.185	11.300	0.008	0.890	0.193
8	Trachurus trachurus	3.67	1.690	1.795	8.400	0.115	0.825	0.214
9	Diplodus annularis	2.99	6.320	0.888	7.150	0.430	0.257	0.124
10	Mugillidae	2.13	5.920	0.905	20.900	0.403	0.342	0.043
11	Other benthop. fish	3.03	5.420	0.720	7.480	0.368	0.958	0.096
12	Demersal fish 1	3.02	1.630	0.820	6.940	0.111	0.851	0.118
13	Demersal fish 2	2.85	1.220	0.940	6.730	0.083	0.698	0.140
14	Demersal fish 3	3.91	4.250	0.820	4.400	0.289	0.200	0.186
15	Pelagic fish	4.05	5.110	0.920	4.790	0.347	0.296	0.192
16	Sharks and rays	3.34	0.284	0.780	4.000	0.017	0.944	0.195
17	Solea vulgaris	2.93	4.870	0.770	7.670	0.331	0.788	0.100
18	Boops boops	3.04	6.105	0.650	6.900	0.415	0.743	0.094
19	Dicentrarchus l./Sparus a.	3.21	2.120	0.888	7.430	0.144	0.533	0.119
20	Mullidae	2.91	24.090	0.750	6.600	1.638	0.237	0.114
21	Fish farms	1.00	0.059	18.000	36.000	1.062	0.995	0.500
22	Penaeus kerathurus	2.85	5.950	1.588	6.500	0.405	0.892	0.244
23	Other crustaceans	2.01	10.940	3.500	12.000	0.200	0.989	0.292
24	Bivalves and gastropods	2.00	7.350	1.200	4.000	0.228	0.965	0.300
25	Benthopelagic cephalopds	3.56	8.520	2.000	7.500	0.579	0.964	0.267
26	Octopus vulgaris	3.49	0.230	2.000	7.000	0.016	0.600	0.286
27	Jellyfish	3.09	0.877	6.500	22.000		0.950	0.295
28	Benthic invertebrates	2.01	73.202	4.000	14.000		0.796	0.286
29	Zooplankton	2.20	10.360	20.000	70.000		0.982	0.286
30	Bacterioplankton	2.00	5.500	153.000	290.000		0.164	0.528
31	Phytoplankton	1.00	32.281	80.000	--		0.257	--
32	Discards	1.00	0.770	--	--		0.944	--
33	POM	1.00	1.757	--	--		0.756	--
34	Detritus	1.00	10.000	--	--		0.310	--

S2. Diet composition matrix for the Amvrakikos Gulf ecosystem, 1980s period. Prey are indicated by rows and predators by columns. Functional group codes are reporting according to Table S1.

Prey/predator	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	0.09	0.02	0.34	0	0	0	0	0.3	0.06	0	0	0.02	0	0.18	0.25	0.01	0	0	0.04	0	0	0	0	0	0.3	0	0	0	0	0
7	0.14	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0.005	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0.14	0	0	0	0	0	0	0	0	0	0	0	0	0.01	0.08	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0.11	0	0	0	0	0	0	0	0	0	0	0	0	0.04	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0.05	0.26	0	0.2	0	0	0	0	0	0	0	0	0	0.05	0	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0.01	0.02	0.05	0	0	0	0.1	0	0	0.01	0.05	0	0.01	0.01	0.03	0	0	0.03	0	0	0	0	0	0	0.04	0	0	0	0
12	0	0.1	0.08	0.25	0	0	0	0	0	0	0	0.01	0.01	0.01	0	0.002	0	0	0.01	0	0	0	0	0	0	0.05	0.01	0	0	0
13	0.19	0	0	0	0	0	0	0	0	0	0	0	0.01	0.01	0	0.01	0	0	0.01	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0.02	0	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0.04	0	0	0	0	0	0	0	0	0	0	0.01	0	0.005	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9E-05	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0.07	0	0	0	0	0	0	0	0	0	0	0	0	0.11	0	0.01	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0.06	0	0	0	0	0.01	0.07	0.01	0.001	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0.05	0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0	0	0.05	0	0	0	0	0	0	0	0	0	0	0
20	0.06	0	0	0	0	0	0	0	0	0	0	0	0	0.13	0	0.099	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0.03	0	0	0	0	0	0	0.01	0.04	0	0.01	0.01	0.06	0.05	0.01	0.05	0.05	0	0.04	0	0	0	0	0	0.01	0.05	0	0	0	0
23	0	0	0.1	0	0.08	0	0	0.01	0.18	0.01	0.11	0.38	0.07	0.09	0.03	0.1	0.15	0	0.18	0.01	0	0.05	0.01	0	0.05	0.1	0	0	0	0
24	0	0	0	0	0.14	0	0	0	0.09	0	0.01	0.01	0.08	0.05	0.02	0.006	0.01	0	0	0	0	0	0	0	0.02	0.1	0	0	0	0
25	0.08	0	0	0	0.07	0	0	0.07	0	0	0	0	0	0.16	0.2	0.05	0	0	0	0	0	0	0	0	0.1	0.2	0.01	0	0	0
26	0	0	0	0	0.08	0	0	0	0	0	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0	0.01	0.01	0	0	0
27	0	0	0	0	0.09	0	0	0	0.05	0	0	0	0	0	0.05	0.001	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
28	0	0	0.05	0	0.05	0	0	0	0.39	0.06	0.15	0.24	0.52	0	0	0.361	0.54	0.35	0.4	0.77	0	0.79	0	0	0	0.36	0	0	0	0
29	0	0	0	0	0	0.4	0.95	0.45	0.02	0.05	0.44	0.17	0	0	0.09	0.1	0.09	0.4	0.08	0.02	0	0	0	0	0.2	0.09	0.7	0.01	0.01	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.19	0
31	0	0	0	0	0	0.1	0.05	0	0.06	0.4	0	0.05	0	0	0	0	0	0.05	0	0	0	0	0	0	0	0	0.18	0	0.8	0
32	0	0	0.15	0	0.15	0	0	0	0	0	0	0	0	0	0	0.087	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0.08	0.28	0	0.04	0.22	0	0	0	0.08	0	0.05	0.08	0	0.07	0.49	0.5	0	0	0	0.69	0	1
34	0	0	0	0	0	0	0	0	0.03	0.2	0.08	0.02	0.02	0	0	0	0.08	0	0.05	0.02	0	0.09	0.5	0.5	0	0	0	0.3	0	0
Import	0	0.6	0.2	0.5	0.34	0.5	0	0	0	0	0.2	0	0	0	0.25	0	0	0.2	0	0.1	1	0	0	0	0.32	0	0	0	0	0
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

S 3. Main equations and/or references used for basic input parameters (Biomass (B), Production over Biomass (P/B), Consumption over Biomass (Q/B), Diet (D)) of the Amvrakikos functional groups in the 1980s. Species composition of each functional group and time series of biomass and catch used to fit the model are also given.

Functional groups	Description	Source
Tursiops truncatus		
Biomass 1980s		*(Gonzalvo et al., 2014)*
Biomass Time series	Survey data (2003-2013)	*(Bearzi et al., 2008; Gonzalvo unpublished data)*
Production/Biomass	Life history table	*(Barlow and Boveng, 1991)*
Consumption/Biomass	From modified energy requirement equation: $E = aW^{0.714}$	*(Hunter, 2005; Pauly et al., 1998)*
Diet		*(Gonzalvo unpublished data)*
Phalacrocorax carbo		
Biomass 1980s		*(Liordos et al., 2002; Liordos et al., 2014)*
Biomass Time series	Survey data (1982-2012)	*(Liordos et al., 2002; Liordos et al., 2014)*
Production/Biomass		*(Liordos and Goutner, 2008; Liordos and Goutner, 2012)*
Consumption/Biomass		*(Karpouzi, 2005; Karpouzi et al., 2007)*
Diet		*(Liordos and Goutner, 2007a, b)*
Seagulls and terns (*Sterna nilotica, Sterna sandvicensis, Sterna albifrons, Larus ridibundus*)		
Biomass 1980s		*(Karpouzi, 2005)*
Biomass Time series	--	
Production/Biomass		*(Karpouzi, 2005; Karpouzi et al., 2007)*
Consumption/Biomass		*(Karpouzi, 2005; Karpouzi et al., 2007)*
Diet		*(Karpouzi, 2005; Karpouzi et al., 2007)*
Pelicanus crispus		
Biomass 1980s		*(Crivelli et al., 2000)*
Biomass Time series	Survey data (1983-2012)	*(Crivelli et al., 2000)*
Production/Biomass		*(Catsadorakis and Crivelli, 2001; Crivelli, 1996; Crivelli et al., 1998)*
Consumption/Biomass		*(Dentressangle et al., 2008)*
Diet		*(Albanis et al., 1995a; Crivelli, 1996)*
Caretta caretta		
Biomass 1980s		*(Moutopoulos et al., 2013; Piroddi et al., 2010)*
Biomass Time series	--	
Production/Biomass		*(Rees et al., 2013)*
Consumption/Biomass		*(Rees et al., 2013; Wabnitz et al., 2010)*
Diet		*(Rees and Margaritoulis, 2006)*

Sardina pilchardus		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Somarakis et al., 2006a; Somarakis et al., 2006b)*
Consumption/Biomass		*(Somarakis et al., 2006b)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Other clupeidae (*Engraulis encrasicolus, Sardinella aurita*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series		
Production/Biomass		*(Tsikliras and Antonopoulou, 2006)*
Consumption/Biomass		*(Tsikliras and Antonopoulou, 2006)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	--	
Trachurus trachurus		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Karlou-Riga, 2000; Šantić et al., 2002)*
Consumption/Biomass		*(Karlou-Riga, 2000; Šantić et al., 2002)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Diplodus annularis		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Matić-Skoko et al., 2007)*
Consumption/Biomass		*(Froese and Pauly, 2010)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Mugillidae (Mugil cephalus, *Mugil* spp.)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Hotos, 1999; Katselis, 1996; Minos, 1996)*
Consumption/Biomass		*(Hotos, 1999; Katselis, 1996; Minos, 1996)*

Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Other Benthopelagic fish (*Dentex Dentex, Micromesistius poutassou, Oblada melanura, Pagellus bogaraveo, Pagellus erythrinus, Sarpa salpa*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Chilari et al., 2006; HCMR, 1988; Papaconstantinou et al., 1988; Stergiou and Karachle, 2006)*
Consumption/Biomass		*(Chilari et al., 2006; HCMR, 1988; Papaconstantinou et al., 1988; Stergiou and Karachle, 2006)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Demersal fish 1 (*Chelidonichthys obscurus, Citharus linguatula, Labrus spp, Scorpaena porcus, Serranus hepatus*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series		
Production/Biomass		*(Labropoulou et al., 1998; Stergiou and Karachle, 2006; Vassilopoulou, 1994)*
Consumption/Biomass		*(Labropoulou et al., 1998; Stergiou and Karachle, 2006; Vassilopoulou, 1994)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	--	
Demersal fish 2 (*Diplodus sargus, Lithognathus mormyrus, Scophthalmus maximus*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series		
Production/Biomass		*(Kallianiotis et al., 2005; Stergiou and Karachle, 2006)*
Consumption/Biomass		*(Kallianiotis et al., 2005; Stergiou and Karachle, 2006)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	--	
Demersal fish 3 (*Epinephelus aeneus, Lophius budegassa, Merluccius merluccius*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series		
Production/Biomass		*(HCMR, 1988; Stergiou and Karachle, 2006; Tsimenidis, 1984)*
Consumption/Biomass		*(HCMR, 1988; Stergiou and Karachle, 2006; Tsimenidis, 1984)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	--	
Pelagic fish (*Belone belone, Euthynnus alletteratus, Lichia amia, Pomatomus saltatrix, Sarda sarda, Scomber japonicus, Seriola dumerili*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Kozul et al., 2001; Sini, 2005; Stergiou and Karachle, 2006; Uçkun et al., 2004)*
Consumption/Biomass		*(Kozul et al., 2001; Sini, 2005; Stergiou and Karachle, 2006; Uçkun et al., 2004)*
Diet		*(Stergiou and Karpouzi, 2001)*

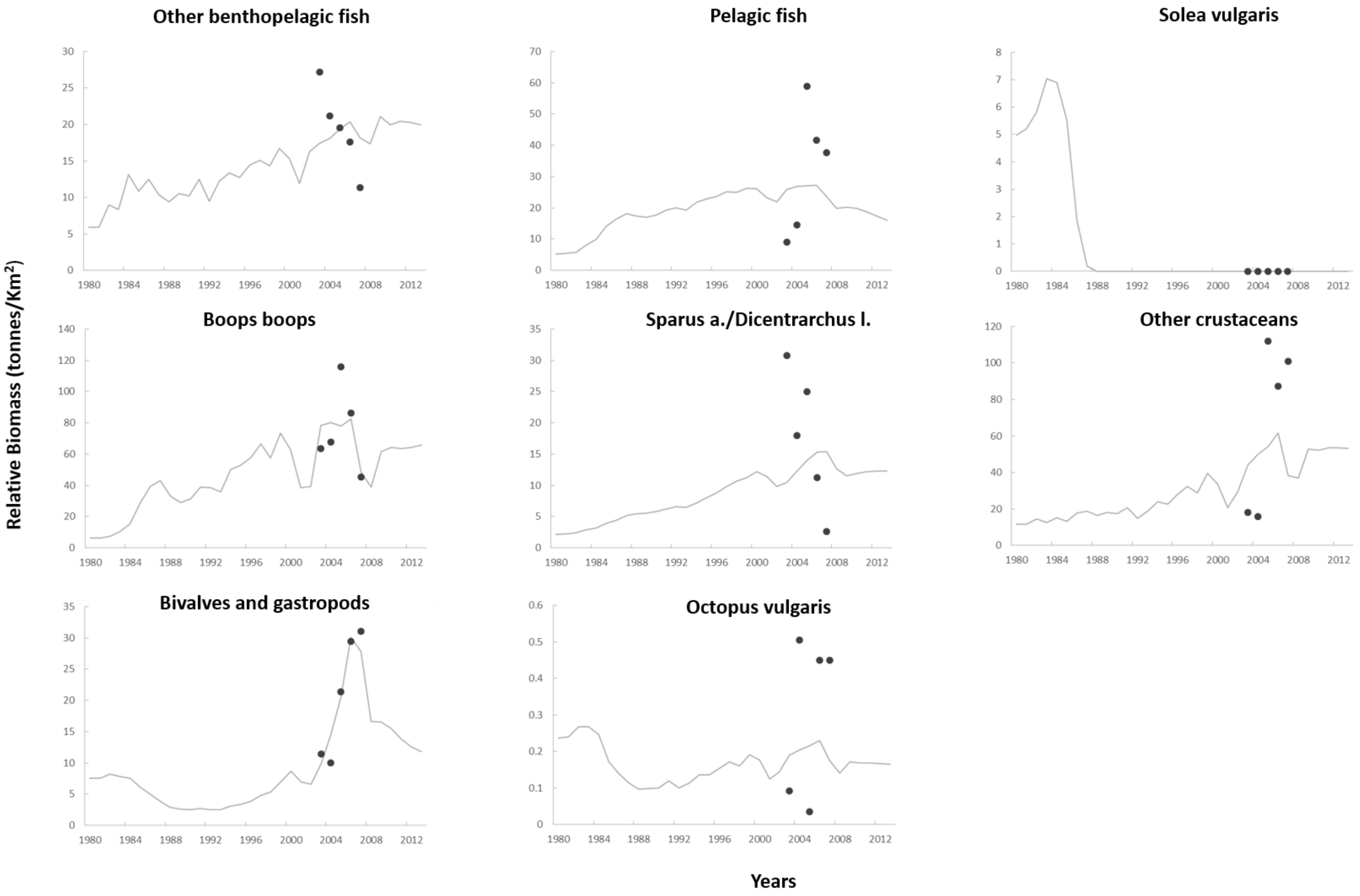
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Solea vulgaris		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Stergiou et al., 1997)*
Consumption/Biomass		*(Papaconstantinou et al., 1990)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Boops boops		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(El-Haweet et al., 2005)*
Consumption/Biomass		*(Stergiou and Karachle, 2006)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Dicentrarchus labrax/Sparus aurata		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Brando et al., 2004; Kraljević and Dulčić, 1997)*
Consumption/Biomass		*(Brando et al., 2004)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Mullidae (*Mullus barbatus, Mullus surmuletus*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Vassilopoulou et al., 2002)*
Consumption/Biomass		*(Vassilopoulou et al., 2002)*
Diet		*(Stergiou and Karpouzi, 2001)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Fish farms		
Biomass 1980s		*(Preveza Department of Fisheries; Katselis and Ramfos, 2015)*
Biomass Time series	(1988-2008)	*(Preveza Department of Fisheries; Katselis and Ramfos, 2015)*
Production/Biomass		*(Katselis and Ramfos, 2015)*
Consumption/Biomass		*(Katselis and Ramfos, 2015)*
Diet		
Catch Time series	(1988-2008)	*(Preveza Department of Fisheries; Katselis and Ramfos, 2015)*

Sharks and rays (*Raja spp., Squalus acanthias*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series		
Production/Biomass		*(Coll et al., 2009)*
Consumption/Biomass		*(Coll et al., 2009)*
Diet		*(Coll et al., 2009)*
Catch Time series	--	
Penaeus kerathurus		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Conides et al., 2008; Conides et al., 2010)*
Consumption/Biomass		*(Coll et al., 2009; Piroddi et al., 2010)*
Diet		*(Coll et al., 2009; Piroddi et al., 2010)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Other crustaceans *(Hommarus gammarus, Nephrops norvegicus, Rissoides desmaresti, others)*		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Coll et al., 2009; Piroddi et al., 2010)*
Consumption/Biomass		*(Coll et al., 2009; Piroddi et al., 2010)*
Diet		*(Coll et al., 2009; Piroddi et al., 2010)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Bivalves and gastropods		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Coll et al., 2009)*
Consumption/Biomass		*(Coll et al., 2009)*
Diet		*(Coll et al., 2009)*
Catch time series	(2003-2007)	*(Preveza Department of Fisheries; Koutsikopoulos et al., 2008; EC, 2009)*
Benthopelagic cephalopods (*Loligo vulgaris*, Loliginidae, Ommastrepidae, *Sepia officinalis*)		
Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (1980-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Coll et al., 2009)*
Consumption/Biomass		*(Coll et al., 2009)*
Diet		*(Coll et al., 2009)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Octopus vulgaris		

Biomass 1980s	CPUE	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009)*
Biomass Time series	CPUE (2003-2007)	*Catch and effort from: (Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; EC, 2009; Koutsikopoulos et al., 2008)*
Production/Biomass		*(Coll et al., 2009)*
Consumption/Biomass		*(Coll et al., 2009)*
Diet		*(Coll et al., 2009)*
Catch time series	(1980-2007)	*(Preveza Department of Fisheries; Conides et al., 2001; Conides and Papaconstantinou, 2001; Koutsikopoulos et al., 2008; EC, 2009)*
Jellyfish		
Biomass 1980s	Estimated by Ecopath	
Biomass Time series	--	
Production/Biomass		*(Coll et al., 2009)*
Consumption/Biomass		*(Coll et al., 2009)*
Diet		*(Coll et al., 2009)*
Benthic invertebrates		
Biomass 1980s		*(Nicolaidou et al., 1983; Nicolaidou and Papadopoulou, 1989; Pancucci et al., 1994; Tziavos and Vouloumanos, 1994)*
Biomass Time series	--	
Production/Biomass		*(Moutopoulos et al., 2013; Piroddi et al., 2010)*
Consumption/Biomass		*(Moutopoulos et al., 2013; Piroddi et al., 2010)*
Diet		*(Moutopoulos et al., 2013; Piroddi et al., 2010)*
Zooplankton		
Biomass 1980s		*(Kehayias and Aposporis, 2014; Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Biomass Time series	--	
Production/Biomass		*(Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Consumption/Biomass		*(Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Diet		*(Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Bacterioplankton		
Biomass 1980s		*(Harvey et al., 2003; Libralato and Solidoro, 2009)*
Biomass Time series	--	
Production/Biomass		*(Harvey et al., 2003; Libralato and Solidoro, 2009)*
Consumption/Biomass		*(Harvey et al., 2003; Libralato and Solidoro, 2009)*
Diet		*(Harvey et al., 2003; Libralato and Solidoro, 2009)*
Phytoplankton		
Biomass 1980s		*(Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Biomass Time series	--	
Production/Biomass		*(Nicolaidou et al., 1983; Panayotidis et al., 1994)*
Consumption/Biomass		
Diet		
Discards		
Biomass 1980s		*(Moutopoulos et al., 2013)*
Biomass Time series	--	

Production/Biomass		
Consumption/Biomass		
Diet		
POM		
Biomass 1980s		*(Albanis et al., 1995b; Katselis and Ramfos, 2015; Zacharias et al., 2009)*
Biomass Time series	1981-2008	*(Albanis et al., 1995b; Katselis and Ramfos, 2015; Zacharias et al., 2009)*
Production/Biomass		
Consumption/Biomass		
Diet		

S4. Predicted (solid lines) versus observed (dots) biomass (tonnes/km²) for the remaining functional groups of the Amvrakikos ecosystem



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Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity

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ABSTRACT: An ecosystem modelling approach was used to understand and assess the Mediterranean marine ecosystem structure and function as a whole. In particular, 2 food web models for the 1950s and 2000s were built to investigate: (1) the main structural and functional characteristics of the Mediterranean food web during these 2 time periods; (2) the key species/functional groups and interactions; (3) the role of fisheries and their impact; and (4) the ecosystem properties of the Mediterranean Sea in comparison with other European regional seas. Our results show that small pelagic fishes, mainly European pilchards and anchovies, prevailed in terms of biomasses and catches during both periods. Large pelagic fishes, sharks and medium pelagic fishes played a key role in the 1950s ecosystem, and have been replaced in more recent years by benthopelagic and benthic cephalopods. Fisheries showed large effects on most living groups of the ecosystem in both time periods. When comparing the Mediterranean results to those of other European regional seas modelling initiatives, the Mediterranean stood alone in relation to the type of flows (e.g. Mediterranean Sea, flow to detritus: 42%; other EU seas, consumption: 43–48%) driving the system and the cycling indices. This suggested higher levels of community stress induced by intensive fishing activities in the Mediterranean basin. This study constitutes the first attempt to build an historical and current food web model for the whole Mediterranean Sea.

KEY WORDS: Ecopath model · Food web · Ecosystem modelling · Network analysis · Fishing impact · Mediterranean Sea

INTRODUCTION

Marine ecosystem models have been progressively employed worldwide to investigate the structure and functioning of marine systems and the effects of anthropogenic pressures such as fishing, climate change and pollution on marine ecosystems (Christensen & Walters 2004, Shin et al. 2004, Fulton 2010). Understanding the mechanisms behind diverse ecological networks (e.g. trophic interactions and flows) and the roles of human activities on marine structure and function is critical when managing marine resources (Cury et al. 2003). The development of ecosystem models to explore ecosystem functions and responses to anthropogenic and/or environmental changes has been driven by the so called 'ecosystem-based management' (EBM) approach, which aims at managing the whole ecosystem rather than focusing on a single resource, helping researchers and policy makers to answer questions for responsible resource management decisions (Pikitch et al. 2004). Currently, among the most used ecological modelling

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tools for EBM in the aquatic environment is the software package 'Ecopath with Ecosim' (EwE, Christensen & Walters 2004; www.ecopath.org). EwE models have been widely used to describe the structure and functioning of marine ecosystems, evaluate the effects of anthropogenic activities and environmental changes and explore fishing management policy options (Coll et al. 2009a, Piroddi et al. 2011, Heymans et al. 2012). Here we applied the EwE approach to describe and assess the Mediterranean marine ecosystem structure and functioning as a whole.

The Mediterranean Sea is a semi-enclosed basin with unique characteristics: it is oligotrophic (Barale & Gade 2008), highly diverse in species richness (Coll et al. 2010) and yet is considered a sea 'under siege' due to multiple uses and stressors (Coll et al. 2012). Twenty-one countries in Europe, Asia and Africa surround and share this enclosed sea. Their different cultural, social and economic characteristics pose significant challenges to sustainable management of Mediterranean marine resources. As a consequence of this complexity and lack of management strategies that take this complexity into account, the Mediterranean ecosystem has degraded, and many marine species are over-exploited or depleted (Papaconstantinou & Farrugio 2000, Lleonart & Maynou 2003, Colloca et al. 2013, Tsikliras et al. 2013b, Vasilakopoulos et al. 2014). Thus, there has been an urgent need to employ EBM as a complementary management framework to address current and future threats to the Mediterranean marine ecosystems.

Several research activities have already been conducted in the region to address this issue at the basin scale. In particular, Coll et al. (2012) and Micheli et al. (2013) investigated the cumulative impacts of specific anthropogenic threats to Mediterranean marine biodiversity. Here, we applied a different approach, that is, the description of the structure and functioning of the whole Mediterranean ecosystem in terms of trophic linkages, trophic flows and biomasses, and between 2 post-World War II decades. Compared to Coll et al. (2012) and Micheli et al. (2013), who used spatial analysis and expert knowledge to assess the impacts on the ecosystem, our study quantifies the trophic interactions and effects of pressures (e.g. in this case fishing) occurring in the whole area, using the best available data to date. A recent study by Coll & Libralato (2012) highlighted that more than 40 EwE models describing local or regional Mediterranean ecosystems exist (including lagoons, marine reserves and coastal and shelf areas), but none of these past efforts focussed on the Mediterranean Sea as a whole. This is likely due to the complexity of building such an ecosystem model while being able to capture the differences in environmental and biological characteristics of the Mediterranean region, and due to difficulties regarding data mining and integration. Therefore, our study is the first attempt to comprehensively model the Mediterranean basin. Studies like this one become critically important in support of policies like the Marine Strategy Framework Directive (MSFD; 2008/56/EC), the main European Directive on marine waters that requires the assessment of all European seas at regional scales in relation to their ecosystem status and associated pressures, and the establishment of environmental targets (through the use of indicators) to achieve 'Good Environmental Status' by 2020 (Cardoso et al. 2010).

Specifically, in this study we investigated (1) the main structural and functional characteristics of the Mediterranean food web during 2 different time periods, i.e. the 1950s and 2000s; (2) the key species/functional groups and interactions for both time periods; (3) the role of fisheries and their effects; and (4) the ecosystem properties of the Mediterranean Sea in comparison with other European regional seas, namely the North Sea, Baltic Sea and Black Sea, which have already been modelled at the regional basin scale (Tomczak et al. 2012, 2013, Akoglu et al. 2014, Mackinson 2014).

MATERIALS AND METHODS

Mediterranean Sea

The Mediterranean Sea extends from 30° to 45° N and from 6° W to 36° E, and constitutes the world's largest (2 522 000 km^2) and deepest (average 1460 m, maximum 5267 m) enclosed sea. It is connected to the Atlantic Ocean via the Strait of Gibraltar in the west, to the Black Sea via the Bosporus and the Dardanelles in the north-east, and to the Red Sea via the Suez Canal in the south-east (Fig. 1). Overall, the basin is considered oligotrophic with some exceptions along coastal areas due mainly to river discharges (Barale & Gade 2008) and frontal mesoscale activity (Siokou-Frangou et al. 2010). Phosphorus, rather than nitrogen, is the limiting nutrient, especially towards the eastern basin (Krom et al. 1991). Biological productivity decreases from north to south and west to east, whereas an opposite trend is observed for temperature and salinity. In particular, the mean sea surface temperature varies between a minimum of 14–16°C (west to east) in winter and a max-

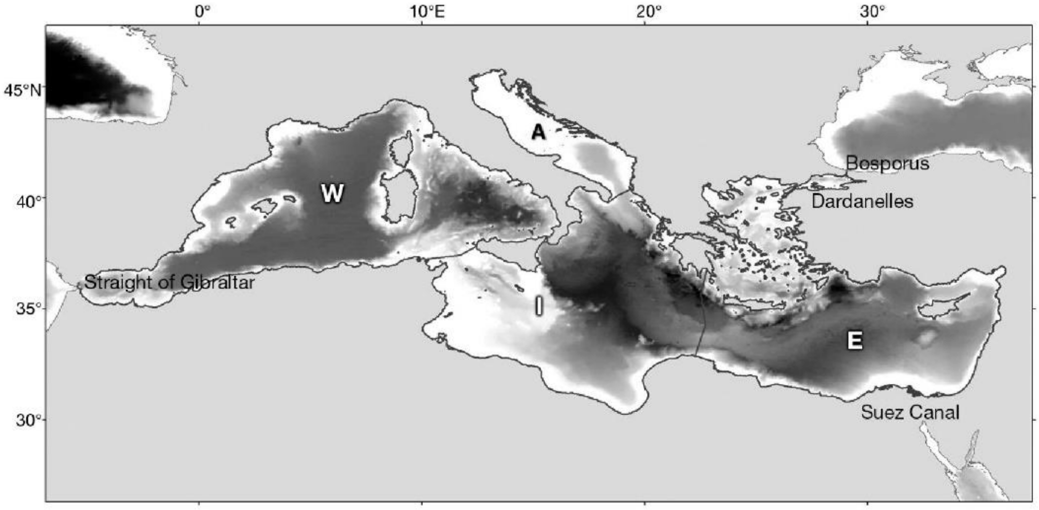


Fig. 1. Mediterranean Sea, showing depth profile (darker shading indicates greater depth) and the 4 Marine Strategy Framework Directive (MSFD) areas: Western Mediterranean Sea (W); Adriatic Sea (A); Ionian and Central Mediterranean Sea (I); Aegean and Levantine Sea (E)

imum of ca. 20–26°C (west to east) in the summer (with the exception of the shallow Adriatic Sea, where the range is between 8–10°C in winter and 26–28°C in summer) (Barale & Gade 2008). Evaporation greatly exceeds precipitation, and river runoff decreases from west to east, causing sea surface height to decrease and salinity to increase eastward (Coll et al. 2010). The Mediterranean Sea has a topographically diverse continental shelf that generally varies from south (mainly narrow and steep) to north (wider areas). In some instances, however, narrow shelves can also be found on some coasts of Turkey, in the Aegean, Ligurian and northern Alboran Seas, while extended shelves are also present on the Tunisian shelf and near the Nile Delta (Pinardi et al. 2006). Shelf waters represent 20% of the total Mediterranean surface, and the rest is open sea (Coll et al. 2010).

Mediterranean marine species richness is relatively high; to date, approximately 17 000 species have been recorded in the Mediterranean Sea, with a gradient of species richness that decreases from northwest to southeast (Bianchi & Morri 2000, Coll et al. 2010, 2012). Of these 17 000 species, at least 26% are prokaryotic (*Bacteria* and *Archaea*) and eukaryotic (protists) marine microbes. The phytoplankton community is composed predominantly of coccolithophores, dinoflagellates and Bacillariophyceae and includes more than 1500 species. Among microzooplankton, foraminiferans comprise the main group, with more than 600 species. However, the majority of species are described within the Animalia (~11 500 species), with the greatest contribution coming from the Crustacea (13.2%) and Mollusca (12.4%) (Coll et al. 2010). Among the vertebrates, 650 species of marine fishes have been recorded, of which approximately 80 are elasmobranchs and the rest are mainly actinopterygians (86%) (Coll et al. 2010). Nine species of marine mammals (5 Delphinidae, 1 Ziphiidae, 1 Physeteridae, 1 Balaenopteridae and 1 Phocidae) and 3 species of sea turtles (the green turtle *Chelonia mydas*, the loggerhead *Caretta caretta* and the leatherback *Dermochelys coriacea*) are encountered regularly in the Mediterranean Sea. Among seabirds, 15 species frequently occur in the Mediterranean Sea, including 10 gulls and terns (Charadriiformes), 4 shearwaters and storm petrels (Procellariiformes) and 1 shag (Pelecaniformes) (Coll et al. 2010).

Ecosystem modelling approach

Two food web models of the entire Mediterranean Sea were constructed using the EwE software version 6 (Christensen et al. 2008) representing annual average biomasses and trophic flows for the 1950s and the 2000s. The analysis was restricted to Ecopath, the static component of the software that describes the ecosystem and its resources at a precise period in time (Christensen & Walters 2004). In Ecopath, all principal autotroph and heterotroph species can be represented either individually or aggregated into functional groups considering their ecological roles.

The EwE model is based on 2 main equations. In the first one, the biological production of a functional group is equal to the sum of fishing mortality, predation mortality, net migration, biomass accumulation and other unexplained mortality as follows:

$$(P/B)_i \times B_i = Y_i + \sum_j B_j \times (Q/B)_j \times DC_{ji} + E_i + BA_i + (P/B)_i \times B_i (1 - EE_i) \quad (1)$$

where P/B is the production to biomass ratio for a certain functional group i, B_i is the biomass of a group i, Y_i is the total fishery catch rate of group i, $(Q/B)_j$ is the consumption to biomass ratio for each predator j, DC_{ji} is the proportion of group i in the diet of predator j, E_i is the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for the group i, EE_i is the ecotrophic efficiency, and $(1 - EE_i)$ represents mortality other than predation and fishing.

In the second equation, the consumption (Q) of a functional group (i) is equal to the sum of production (P), respiration (R) and unassimilated food ($GS \times Q$).

$$Q_i = P_i + R_i + GS_i \times Q_i \quad (2)$$

The implication of these 2 equations is that the model is mass balanced; under this assumption, Ecopath uses and solves a system of linear equations (1 for each functional group present in the system) estimating the missing parameters.

To ensure the mass balance, we applied a manual mass-balanced procedure following a top-down approach, adjusting the input parameters of those groups 'out of balance' ($EE > 1$), occurring when total energy demand placed on those groups either by predation or fishing exceeds total production. In particular, we changed those parameters associated with higher uncertainty, i.e. diet matrix, P/B and, to a lesser extent, biomass (Christensen & Walters 2004). The ecological models were considered balanced when (1) estimated EE values were <1; (2) gross food conversion efficiency (P/Q) was <0.5; and (3) respiration over assimilation (R/A) was <1 (Christensen & Walters 2004).

Parameterization and functional groups

Two food web models were constructed for the decades of 1950 and 2000, respectively. The reason for choosing these 2 time periods was related to best data collection in the case of the last decade and available catch time series (starting in the 1950s) and biogeochemical/stock assessment model outputs (e.g. biomasses for phytoplankton and fish stocks) for the first decade. To best represent the entire Mediterranean Sea ecosystem, while still considering sub-regional differences in environmental and biological characteristics, both models were divided in 4 sub-models following the 4 sub-regional divisions defined by the Marine Strategy Framework Directive (MSFD; 2008/56/EC): (1) Western Mediterranean Sea (W); (2) Adriatic Sea (A); (3) Ionian and Central Mediterranean Sea (I); (4) Aegean and Levantine Sea (E) (Fig. 1). To separate each MSFD area within the full single Mediterranean model, we assigned a habitat area which corresponds to the fraction of the total area where the functional groups occur. In particular, if a functional group occurs throughout the total Mediterranean Sea, the biomass is scaled by a factor of 1; otherwise biomass is scaled by the fraction of the Mediterranean Sea area occupied (see Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m533p047_supp.pdf).

To define functional groups, we used all available data to parameterize the model and ecological traits of species to establish the groups (see Tables S1–S4 in the Supplement).

We divided marine mammals into 'piscivorous cetaceans' (mainly dolphins), 'other cetaceans' (mainly whales) and 'pinnipeds' (monk seal *Monachus monachus*).

Fishes were divided into 'sharks', 'rays and skates', 'deep-sea fishes' (mainly mesopelagic, bathypelagic and bathydemersal), pelagic fishes and demersal fishes. Pelagic and demersal fishes were further divided in 'small' (common total length <30 cm), 'medium' (30–89 cm) and 'large' (≥90 cm) following a similar approach used by Christensen et al. (2009), which simplified the definition of the fish groups (e.g. piscivores, benthivores and herbivores) in the model parameterization but still considered fish based on their asymptotic length, feeding habitats and vertical distribution characteristics. Invertebrate species were separated into 'benthopelagic' and 'benthic cephalopods', 'bivalves and gastropods', 'crustaceans', 'jellyfishes', 'benthos' and 'zooplankton'. Primary producers were divided in 'phytoplankton' and 'seagrass'. Each MSFD area had the same functional group categories except for highly migratory species such as the 'other cetaceans' group, the 'large pelagic fishes' (e.g. tuna species and swordfish *Xiphias gladius*) and the 'sea turtles' that were allowed to move and feed in all 4 areas. 'European hake' *Merluccius merluccius*, 'European pilchard' *Sardina pilchardus* and 'European anchovy' *Engraulis encrasicolus* were considered individually due to their importance as commercial species, and thus individual groups were created to represent these species within the model. A total of 103 functional groups were described to represent the whole Mediterranean Sea model.

For each group, 5 input parameters were estimated: biomass (B), production rate per unit of biomass (P/B), consumption rate per unit of biomass (Q/B), diet composition (DC) and fisheries catch rate (Y). The biomass of each functional group, expressed as tonnes (t) of wet weight per km^2, was obtained from field surveys, estimated from empirical equations of population reconstruction or assessed by biogeochemical models. For the scope of this work, we searched mainly for data available at regional scales (either from survey campaigns or from other model outputs), and when this information was not available, local case studies were used instead (e.g. 'seagrass' biomass; see Tables S1 & S2 in the Supplement). For the 1950s model, which lacked surveyed data, the biomasses of commercially important groups (functional groups 6 to 21 in Table 1) were estimated from stock assessments (e.g. International Commission for the Conservation of Atlantic Tunas (ICCAT; https://www.iccat.int/en/pubs_CVSP.htm for the large pelagic fishes) or by applying a logistic growth model (Schaefer 1954) as in previous studies (Walters et al. 2008, Piroddi et al. 2010). In particular, this last method, also called surplus production model, expressed as:

$$N_{t+1} = N_t + rN_t(1 - N_t / k) - C_t \qquad (3)$$

allows estimating the size of a given population/stock (N) at certain time (t) knowing the historical catch time series (C_t), the intrinsic rate of population growth (r; obtained from Fishbase, Froese & Pauly 2010) and the carrying capacity (k).

'Phytoplankton' biomass was taken from the outputs of a biogeochemical model developed for the entire Mediterranean Sea (Macias et al. 2014), while 'zooplankton' was obtained from a global database available from the National Oceanic and Atmospheric Administration (www.st.nmfs.noaa.gov). For the other functional groups, information was available either through the literature (e.g. 'pinnipeds' and 'sea turtles') or reconstructed from global databases (e.g. seabird biomass from the Sea Around Us Project; www.seaaroundus.org). The P/B and Q/B ratios were estimated using empirical equations (Christensen et al. 2008) or taken from the literature and were expressed as annual rates (t km^{-2} yr^{-1}) (Tables S1 & S2 in the Supplement). A diet composition matrix was constructed using either field studies (e.g. stomach contents) or diet data obtained from the literature for the same species in similar ecosystems (Table S3 in the Supplement). For highly migratory species ('large pelagic fishes', 'other cetaceans' and 'sea turtles') and 'seabirds' groups, we accounted for a percentage of the diet being outside the marine ecosystem, assuming that those species also move outside the studied system for feeding (Coll et al. 2006, 2007, Christensen et al. 2008, Piroddi et al. 2010).

Table 1. Functional groups and fisheries included in the models together with their abbreviations

No.	Functional groups/fisheries	Abbreviation
1	Piscivorous cetaceans	PC
2	Other cetaceans	OC
3	Pinnipeds	PI
4	Seabirds	SB
5	Sea turtles	ST
6	Large pelagic fishes	LP
7	Medium pelagic fishes	MP
8	European pilchard	EP
9	European anchovy	EA
10	Other small pelagic fishes	SP
11	Large demersal fishes	LD
12	European hake	HK
13	Medium demersal fishes	MD
14	Small demersal fishes	SD
15	Deep-sea fishes	DF
16	Sharks	SK
17	Rays and skates	RS
18	Benthopelagic cephalopods	BPC
19	Benthic cephalopods	BC
20	Bivalves and gastropods	BG
21	Crustaceans	CR
22	Jellyfish	JF
23	Benthos	BE
24	Zooplankton	ZO
25	Phytoplankton	PH
26	Seagrass	SE
27	Discards	DS
28	Detritus	DE
29	Trawlers	TR
30	Dredges	DR
31	Mid-water trawlers	MT
32	Purse seiners	PS
33	Long liners	LL
34	Artisanal fisheries	AR
35	Recreational fisheries	RC

In some instances, we integrated parameters (B, DC, P/B and Q/B) from previously built EwE models for different areas of the Mediterranean Sea (Adriatic Sea: Coll et al. 2007, 2009c; Catalan Sea: Coll et al. 2006, 2008, Tecchio et al. 2013; Ionian Sea: Piroddi et al. 2010, 2011, Moutopoulos et al. 2013; Aegean Sea: Tsagarakis et al. 2010; Gulf of Lions: Bănaru et al. 2013; Tunisia: Hattab et al. 2013). In particular, the output of these models was used as a starting point for the reconstruction of those parameters for which information was lacking. Detailed descriptions of the functional groups and data used to parameterize the model are given in Tables S1–S5 in the Supplement.

The official landing data by species and by country were taken from the United Nation's Food and Agriculture Organization (FAO) database (FishStat: http://data.fao.org/database?entryId=babf3346-ff2d-4e6c-9a40-ef6a50fcd422) and available from 1950 to 2010. This time series was then complemented with data (available per country) from the Sea Around Us database (www.seaaroundus.org) to assign species to fishing fleet. We considered 6 commercial fisheries defined by gear types: bottom trawlers, bottom dredges, mid-water trawlers, purse seiners, long liners and the artisanal fisheries. Species were assigned to the following gear types by assuming the same proportion per year as observed in the Sea Around Us database (data accessed in November 2013). In the case of Italy, which is surrounded by 3 of the 4 MSFD areas, we used a detailed reconstruction of catches (Piroddi et al. 2014) available for sub-regional seas ([MFSD area 1] Ligurian; [2] Northern, Central and Southern Tyrrhenian; [3] Ionian; [4] Northern, Central and Southern Adriatic Sea; [3] Sicilian; and [4] Sardinian waters), while for Greece, which has waters both in the Ionian and in the Eastern Mediterranean Sea, we used the same proportions as calculated by Tsikliras et al. (2007, 2013a). A recreational fishery was also included in the analysis using data coming from the Sea Around Us database (in the case of Italy and Spain) and from literature reviews (Anagnopoulos et al. 1998, Gordoa et al. 2004, Pawson et al. 2007, Cisneros-Montemayor & Sumaila 2010). We estimated the percentage of discards and the species discarded using reports and scientific papers available in the literature (Megalofonou 2005, EC 2011, Vassilopoulou 2012, Tsagarakis et al. 2013) and data from previous EwE Mediterranean models available cited above. Fisheries landings and discards, expressed as annual rates (t km^{-2} yr^{-1}), for both models and for each subregion are shown in Tables S8–S11 in the Supplement. A list of functional groups and fisheries included in both models, together with their abbreviations, is given in Table 1 and in Table S5.

Pedigree index and model quality

The pedigree of the data refers to the uncertainty associated with the input values of the model. In general, higher pedigrees are associated with higher levels of data quality and with data coming from the study areas. Ecopath can take the pedigree values for all of the data entered in the model (e.g. biomass, *P/B*, *Q/B*, diets) into account and can calculate an overall pedigree index, ranging from 0 to 1. Lower pedigree values imply a model constructed with low-precision data and with data coming from areas outside the studied region, while higher values indicate a model constructed with locally-derived data (Morissette 2007, Christensen et al. 2008). Thus, to assess the quality of our input data, we calculated the overall pedigree index for both models. In addition, the pedigree was also used to guide the balancing procedure of both models, such that the lower pedigree inputs were the first to be modified while balancing the models.

Model analysis and indices

Trophic flows in terms of total production, consumption, respiration, catches and flow to detritus were estimated to represent ecosystem structure and exploitation status (Odum 1969, Ulanowicz 1986, Christensen & Pauly 1993). In particular, the following indicators were evaluated: (1) Total system throughput (TST), calculated as the sum of all flows as an indication of the whole ecosystem size. (2) Total primary production/total system respiration (TPP/TR) and total primary production/total biomass (TPP/TB), as a metric of system maturity. (3) Finn's cycling index (FCI), as the percentage of flows recycled in the food web (Finn 1976), and the predatory cycling index (PCI), as the percentage of production recycled after the removal of detritus (Christensen et al. 2008). (4) Ascendancy (A), as a measurement of system growth and development of network links (Monaco & Ulanowicz 1997). (5) Overhead (O), as the energy in reserve of an ecosystem that reflects the system's strength when it experiences unexpected perturbations (Ulanowicz 1986). (6) System omnivory index (SOI), based on the average omnivory index (OI), which is calculated as the variance of the trophic levels (TLs) of a consumer's prey groups indicating predatory specialization (Christensen & Pauly 1993). (7) Mean transfer efficiency (TE), as the efficiency in which energy is transferred between TLs. The mean TE is calculated as the geometric mean of TE for each of the integer TLs II to IV. (8) TL of each functional group expressed as:

$$TL_j = 1 + \sum_{i=1}^{n} DC_{ji} \cdot TL_i \qquad (4)$$

where *j* is the predator of prey *i*, DC_{ji} is the fraction of prey *i* in the diet of each predator *j*, and TL_i is the TL of prey *i*. By definition, TL I is attributed to primary producers and detritus, TL II to herbivores, TL III to first-order carnivores and TL IV to second-order carnivores. (9) TL of the catches (TL_C), as:

$$TL_{Ci} = \frac{\sum_{i=1}^{n} TL_i \cdot Y_i}{\sum_{i=1}^{n} Y_i} \qquad (5)$$

where Y_i refers to the landings of species (group) i. (10) Primary production required (PPR) to sustain the catch, to evaluate the sustainability of fisheries (Pauly & Christensen 1995).

To better represent trophic flows, TLs and biomasses of the Mediterranean marine ecosystem, we used 2 different graphical representations: a flow diagram and a Lindeman spine (Lindeman 1942, Ulanowicz 1995). In the Lindeman spine, primary producers and detritus (both with TL = 1) were separated to better represent the different flows going to the different compartments. To highlight differences in total biomass and mean TL of the community, we also plotted these 2 variables for each MSFD area for the 2 time periods.

Mixed trophic impact and keystone species analyses

The mixed trophic impact (MTI) analysis, expressed as:

$$MTI_{ij} = DC_{ij} - FC_{ji} \qquad (6)$$

where DC_{ij} is the diet composition term expressing how much j contributes to the diet of i, and FC_{ji} is the proportion of predation on j that is due to i as a predator, allows the quantification of the impacts that a theoretical change of a unit in the biomass of a group (including fishing activities) would have on other groups in the ecosystem (Christensen et al. 2008). It can assess both direct and indirect trophic impacts in the food web, which are either positive or negative, indicating an increase or decrease in the quantity of the affected group. Here we looked at the MTI for each MSFD area and for the 2 different time periods. In addition, and building from the MTI analysis, the keystoneness index (KS) assesses the potential roles of each functional group as keystones in the system. Normally, keystone species are species with a relative low biomass but whose biomass changes would have a disproportionately large effect on the ecosystem structure (Power et al. 1996). Here, for both time periods, we used the index proposed by Libralato et al. (2006):

$$KS_i = \log(\varepsilon_i \times 1/p_i) \qquad (7)$$

where ε_i is the overall effect expressed as the square root of the sum of m_{ij} square (with m_{ij} being the relative impact of a slight increase in biomass of impacting group i on biomass of impacted group j), and p_i is the contribution of the functional group to the total biomass of the food web.

Comparison with other European regional seas models

In an effort to support the MSFD, we compared a selection of ecological, fishing and network analysis indicators derived from the Mediterranean Sea model with those obtained from Ecopath models built for other European regional seas: the North Sea (Mackinson 2014), the Baltic Sea (Tomczak et al. 2012, 2013) and the Black Sea (Akoglu et al. 2014). This comparative analysis was done to obtain an overview, at the European scale, of similarities and differences between these exploited ecosystems. We are aware that a few limitations in confronting these models may occur due to differences in model criteria and construction (e.g. definition of certain groups, time periods), and for this reason we present model results with structural differences of the models for a better interpretation of the analysis. In addition, only those indicators more robust to model configurations (e.g. TST, mean TL of the catch, PPR to sustain fisheries, ascendancy and overhead; see Table 2 for the complete list of indicators), as previously assessed by Moloney et al. (2005) and Heymans et al. (2014), were used for the comparison.

RESULTS

Functional group input, data quality and mass balancing

Each MSFD area had 26 living groups (i.e. excluding detritus and discards), if we also consider the 3 migratory groups as part of each area. Of those 26 groups, the main mass-balancing problems were encountered among 'other small' and 'medium' pelagic fishes, 'small' and 'medium' demersal fishes, 'European pilchard' and 'anchovy', 'benthopelagic cephalopods', 'crustaceans', 'benthos' and 'zooplankton', with *EE* values >1. To obtain mass balance for these groups, we primarily adjusted the diet matrix as the data source with higher uncertainty. For instance, the predation caused by 'large pelagic fish' on 'European pilchard' and 'anchovy', 'medium' and 'other small' pelagic fishes and 'benthopelagic cephalopods' was too high and was reduced. Similarly, the consumption of 'other cetaceans', 'benthopelagic' and 'benthic cephalopods', 'large' and 'medium demersal fishes', 'sharks' and 'rays and skates' on the 'crustaceans' group was overestimated and was reduced by redistributing the proportions in the predators' diets. Biomasses of 'crustaceans' and 'bivalves and gastropods' were the only biomasses that were modified from the original input data. The biomasses of these groups were indeed too low and had to be increased. This is a common problem in prebalanced EwE models, where invertebrate biomass estimates are frequently too low to support predation mortality (Christensen et al. 2008).

Once balanced, *EE* values were high for the majority of the functional groups, indicating that total mortality in the system was mainly driven by predation and fishing. The gross food conversion efficiency (*P/Q*) and the respiration over assimilation (*R/A*) were within the expected ranges (Christensen et al. 2008). The resulting output parameters and the final diet matrix are shown for each model in Tables S1–S4 in the Supplement.

Pedigree indices were different for each time period and increased from the 1950s (0.391) to the 2000s (0.594). Individual results of the pedigree index can be found in Table S7 in the Supplement.

TLs and flows

Trophic flows, TLs and relative biomasses of the Mediterranean Sea ecosystem for the 2000s model are represented in Fig. 2 and in Table S6 (flow diagrams) in the Supplement. In the latter, flow diagrams are separated for each MSFD area. Functional groups are illustrated by their TLs ranging from 1 (primary producers) to 4.22 (marine mammals); the highest TLs were found for 'piscivorous cetaceans' and 'monk seals' (TL ≥ 4). The other marine mammal group, 'other cetaceans', showed a TL of 3.53 (mainly because of the presence of 'zooplankton' and 'benthopelagic cephalopods' in their diet). 'Seabirds', despite being considered a top predator, showed a relatively low TL due to the presence of discards (mainly small pelagic fishes, Oro & Ruiz 1997, Bozzano & Sardà 2002) in their diet. Similarly, 'sea turtles' might have a higher TL than estimated by the model, but their diet also includes discards (Tomas et al. 2001, Gómez de Segura et al. 2003, Casale et al. 2008), and thus, they presented a fairly low TL (2.68) in the model. This is an artifact of EwE that considers discards as a detritus group with TL = 1 and thus tends to lower the TL of those groups that feed considerably on discards (Christensen et al. 2008), as previously seen in other food web models of Mediter-

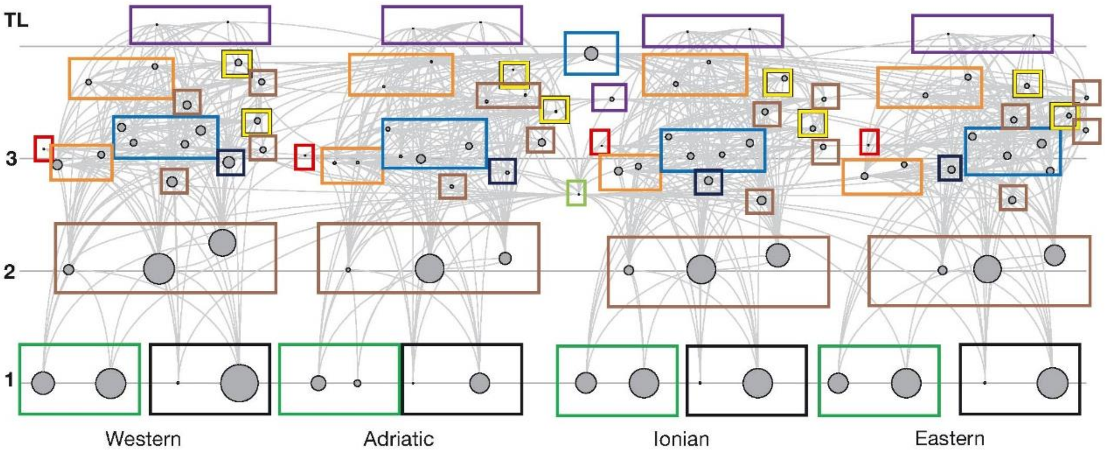


Fig. 2. Flow diagram of the Mediterranean Sea ecosystem (in the 2000s) with the Western part being at the far left followed by the Adriatic, the Ionian and the Eastern (see Fig. 1). Each functional group is shown as a circle whose size is approximately proportional to the log of its biomass. All functional groups are represented by their trophic levels (TL; *y*-axis) and linked to each other by predator–prey relationships expressed as light grey lines. Coloured boxes define the main functional groups: marine mammals (purple); pelagic fishes (blue); demersal fishes (orange); sharks/rays and skates (yellow); deep-sea fishes (dark blue); seabirds (red); invertebrates (brown); sea turtles (light green); primary producers (dark green); detritus groups (black). Individual flow diagrams of the 4 Marine Strategy Framework Directive (MSFD) areas are presented in Table S6 in the Supplement at www.int-res.com/articles/suppl/m533p047_supp.pdf

ranean areas (Coll et al. 2006, 2007, Piroddi et al. 2010). For the fish groups, 'large pelagic fishes' showed a relatively high TL (3.94), followed by 'European hake' (between 3.86 and 3.73), 'large demersal fishes' (between 3.68 and 3.56), 'sharks' (between 3.85 and 3.64) and 'rays and skates' (between 3.41 and 3.27). 'Medium' and 'other small' pelagic fishes were given a TL between 3.28 and 3.19 and between 3.14 and 2.89, respectively. 'European pilchard' and 'European anchovy' had TL values ranging between 3.25 and 3, while the lowest TLs were observed for 'medium' and 'small' demersal fishes and 'deep-sea fishes' (between 3.04 and 2.80). Of the remaining functional groups, 'benthopelagic' and 'benthic cephalopods' and 'jellyfish' reached TL >3, 'crustaceans' showed values between 2.79 and 2.63, and 'zooplankton', 'bivalves and gastropods' and 'benthos' had TL values close to 2.

Looking at the 4 MSFD areas, comparing total biomass and mean TL of the community, the Adriatic and the Western Mediterranean Sea were the areas with the highest total biomass, followed by the Ionian and Eastern Seas (Fig. 3). During the 2000s, the mean TL of the community (TLco) differed considerably whether calculated using TLco ≥1 or TLco > 1 (i.e. excluding detritus and primary producers). For TLco ≥ 1, the Adriatic was the area with highest mean TLco (1.86) followed by the Ionian (1.56), Eastern (1.5) and Western Mediterranean (1.49). For TLco > 1, the Western had the highest TLco (2.36), followed by the Eastern (2.34), Ionian (2.28) and Adriatic Seas (2.18) (Fig. 3). Several differences in TLs were also found between the 2 modelled time periods, with declines observed particularly in the Ionian and Eastern Mediterranean Sea in the 2000s compared to the 1950s (Fig. 4). However, to be able to assess changes in TL of the community in the Mediterranean Sea, a more accurate analysis is needed (such as fitting the model to time series data that will reduce the noise around the parameters; Christensen & Walters 2004).

In the Lindeman spine analysis (Fig. 5), similar patterns were observed for both time periods. Most trophic flows fell within TL I, II and III, and TL I was the pool that generated the majority of the total system throughput (1950s: 78.4 % and 2000s: 79.3 %) followed by TL II, with 20.2 % for the 1950s and 19.6 % for the 2000s. In both time periods, primary producers and TL II organisms had the highest biomasses, and comparing the 2 decades, a decline in biomasses was observed in the 2000s versus the 1950s particularly for those groups having TLs higher than III. In both systems, exports as catches were mainly concentrated within TL III.

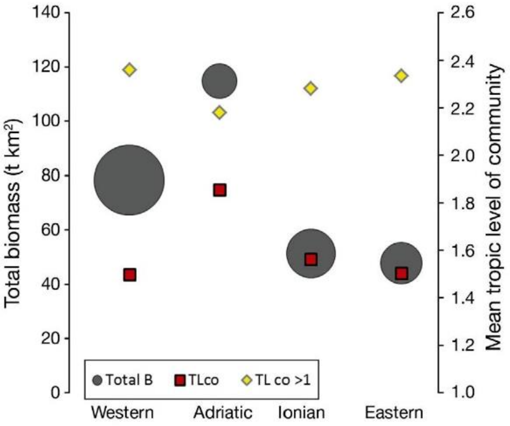
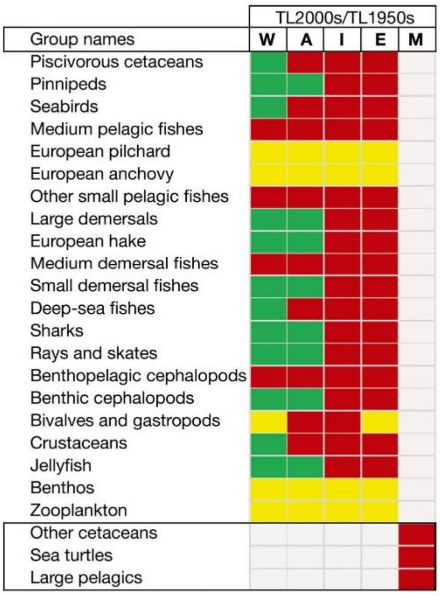


Fig. 3. Total biomass and mean trophic level of the community (TLco) with and without detritus and primary producers (TLco > 1) for each MSFD area (see Fig. 1) for the 2000s. Total biomass is shown as a circle whose size is proportional to the area of the MSFD



	TL2000s/TL1950s				
Group names	W	A	I	E	M
Piscivorous cetaceans	🟩	🟥	🟥	🟥	⬜
Pinnipeds	🟩	🟩	🟥	🟥	⬜
Seabirds	🟩	🟥	🟥	🟥	⬜
Medium pelagic fishes	🟥	🟥	🟥	🟥	⬜
European pilchard	🟨	🟨	🟨	🟨	⬜
European anchovy	🟨	🟨	🟨	🟨	⬜
Other small pelagic fishes	🟥	🟥	🟥	🟥	⬜
Large demersals	🟩	🟩	🟥	🟥	⬜
European hake	🟩	🟩	🟥	🟥	⬜
Medium demersal fishes	🟥	🟥	🟥	🟥	⬜
Small demersal fishes	🟩	🟩	🟥	🟥	⬜
Deep-sea fishes	🟩	🟥	🟥	🟥	⬜
Sharks	🟩	🟩	🟥	🟥	⬜
Rays and skates	🟩	🟩	🟥	🟥	⬜
Benthopelagic cephalopods	🟥	🟥	🟥	🟥	⬜
Benthic cephalopods	🟩	🟩	🟥	🟥	⬜
Bivalves and gastropods	🟨	🟥	🟥	🟨	⬜
Crustaceans	🟩	🟥	🟥	🟥	⬜
Jellyfish	🟩	🟩	🟥	🟥	⬜
Benthos	🟨	🟨	🟨	🟨	⬜
Zooplankton	🟨	🟨	🟨	🟨	⬜
Other cetaceans	⬜	⬜	⬜	⬜	🟥
Sea turtles	⬜	⬜	⬜	⬜	🟥
Large pelagics	⬜	⬜	⬜	⬜	🟥

Fig. 4. Changes in trophic levels (TLs) between the 1950s and the 2000s for each functional group for each Marine Strategy Framework Directive (MSFD) area (W: Western; A: Adriatic; I: Ionian/Central; E: Aegean/Levantine) and the whole Mediterranean Sea (M: Mediterranean). Green cells represent increased TLs (>0), yellow cells indicate stable TLs (=0), and red cells show decreased TLs (<0). Grey cells indicate 'not applicable'

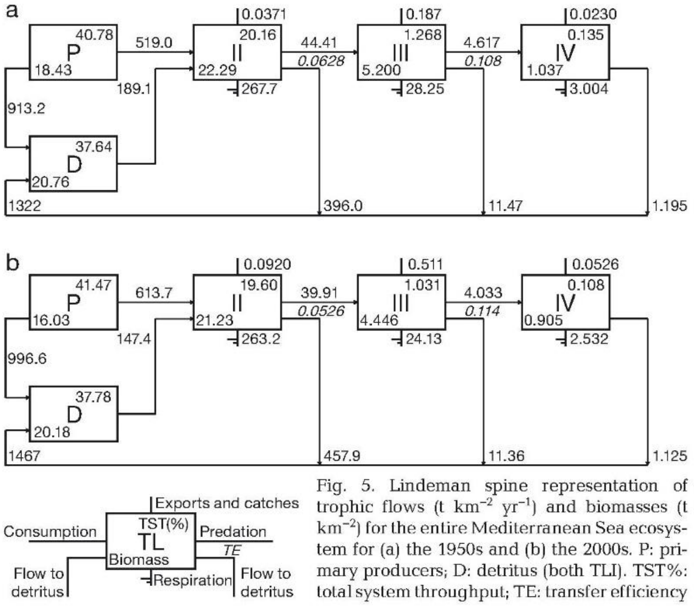


Fig. 5. Lindeman spine representation of trophic flows (t km^{-2} yr^{-1}) and biomasses (t km^{-2}) for the entire Mediterranean Sea ecosystem for (a) the 1950s and (b) the 2000s. P: primary producers; D: detritus (both TLI). TST%: total system throughput; TE: transfer efficiency

Trophic impact and keystone species

For a better interpretation of the MTI analysis, results are presented separating each MSFD area (Fig. 6). Several general patterns can be observed in all 4 areas. Among all MSFD areas, most predators had a direct negative impact on their prey through their diet preferences; functional groups negatively impacted themselves due to cannibalism/within-group competition; demersal functional groups had a greater impact (either negatively or positively) on the majority of the other groups than pelagic functional groups, and 'zooplankton' and 'phytoplankton' groups most positively affected all other groups in the system (e.g. through a bottom-up effect).

MTI analysis in both time periods revealed changes in the role of 'pinnipeds' in the West, Adriatic and Ionian Seas, with a higher impact in the food web during the 1950s and almost no impact in the 2000s. In the Eastern Mediterranean, where the species still occurred in greater numbers, the impact on the food web was greater in 2000s than in the other 3 MSFD areas but still reduced compared to the 1950s. Similar trends were observed for 'piscivorous cetaceans' in all MSFD areas, where the group had a large effect in the 1950s but because of their reduced biomass, only had a limited effect in the 2000s. For fishes, 'European anchovy' and 'European pilchard' similarly affected the Mediterranean food web with greater positive impact on top predators, pelagic fishes and fisheries (particularly mid-water trawlers and purse seiners). Interestingly, 'sharks' were negatively impacting marine mammals either through direct competition for the same resources or niche overlap. Overall, lower TL organisms, namely 'benthos', 'crustaceans' and particularly 'seagrass', positively affected the rest of the food web.

Results also revealed that the role of fisheries in the different MSFD areas has changed with time, growing in impact from 1950s to 2000s, and affecting several groups in the different food webs. In general, if only the commercially exploited functional groups were considered, results showed a greater impact of bottom trawlers, mid-water trawlers and purse seiners (Fig. 7b). More specifically, bottom trawlers and dredges had large negative impacts on targeted demersal species (mainly demersal fishes and 'molluscs') and on 'sea turtles' (incidental catches), while longline fisheries had large negative impacts on 'large pelagic fishes' (target species) and, through incidental catches, on 'sea turtles', dolphins and 'seabirds'. Mid-water trawlers and purse seiners showed negative impacts on targeted small pelagic fishes and, through direct competition for the same resources, on marine mammals and 'seabirds'. When all functional groups in the ecosystem were included in the analysis, artisanal fisheries seemed to be the fleets with greater negative impact, particularly in the Western, Ionian and Eastern Mediterranean Seas (Fig. 7a). Recreational fisheries had a negative impact on 'large pelagic fishes' and 'sharks' in the Western, Adriatic and Ionian Seas and on 'medium' and 'small' demersal and 'medium' and small pelagic fishes in the Eastern Mediterranean.

The results obtained from the keystoneness analysis (Fig. 8 and Table S6 in the Supplement) revealed that in the 1950s ecosystem, 'large pelagic fishes' had the highest overall keystoneness role followed by 'sharks' and 'medium pelagic fishes' groups, whereas in the 2000s ecosystem, 'medium pelagic fishes' were replaced by 'benthic' and 'benthopelagic cephalopods'. Interestingly lower TL groups (e.g. 'zooplankton',

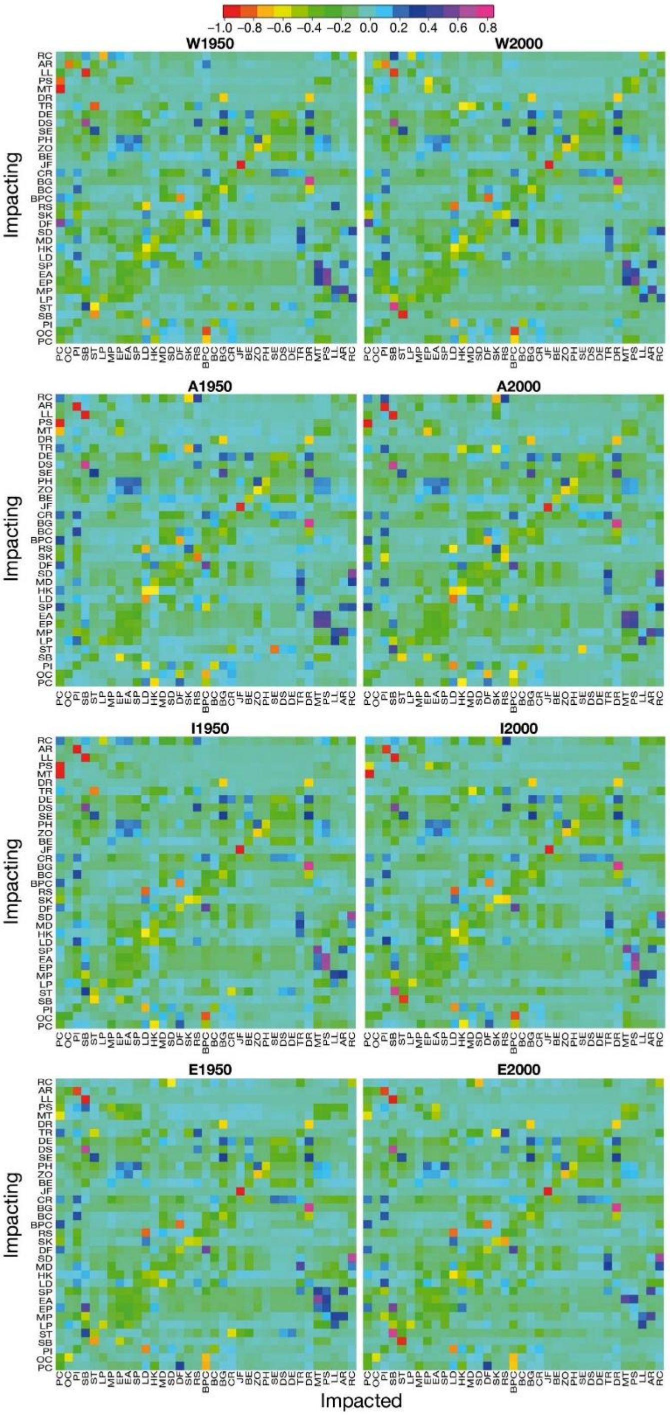


Fig. 6. Mixed trophic impact relationships between functional groups and fisheries in the 4 different Marine Strategy Framework Directive (MSFD) areas (W: Western; A: Adriatic; I: Ionian/Central; E: Aegean/Levantine). Positive values (from light blue to purple) indicate positive impacts; negative values (from light green to red) indicate negative impacts. The colors should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups. For group abbreviations, refer to Table 1

'phytoplankton' and 'benthos') were also identified in both time periods as keystone groups, probably caused by their overall low biomass and high *P/B* (characteristic of oligotrophic systems) and important role in the ecosystem. In both time periods, marine mammals, in particular 'pinnipeds' and 'piscivorous cetaceans', appeared within the least important keystone groups.

Comparison among European regional seas

The statistics and main indicators calculated from the whole Mediterranean Sea ecosystem model representing the 2000s were compared with other modelled European regional seas for the same or similar period (Table 2). The TST revealed that the main flows driving the Mediterranean Sea were flow to detritus (42%) and exports (39%) followed by consumption (15%) and respiration (5%). In the Baltic, North and Black Seas, on the other hand, consumption seemed to be the flow with the highest importance (around 43–48%) followed by flow to detritus (22–30%), respiration (20–23%; in the Black Sea, this flow constituted the second most important flow, with 29%) and exports (1–6%).

Looking at ecological indicators addressing community energetics and cycling of nutrients, under Odum's theory (Odum 1969), our results sug-

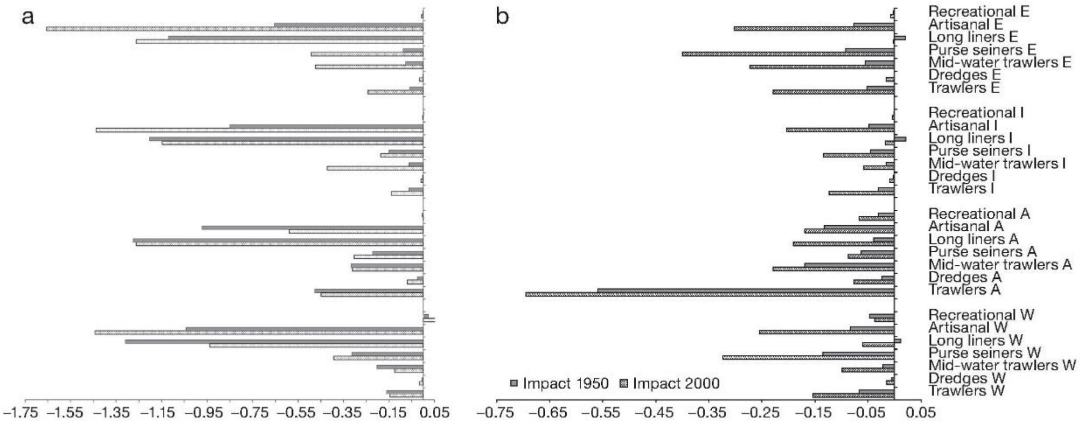


Fig. 7. Cumulative impact (either direct or through a cascade effect) of each fishing gear on (a) all functional groups of the ecosystem and (b) all commercially important species/groups of the ecosystem (see Table 1, numbers 6 to 14 and 16 to 21), in the different Marine Strategy Framework Directive (MSFD) areas (see Fig. 1) and for each studied period. The cumulative impacts were calculated from the mixed trophic impact calculations. Negative values on the *x*-axis represent negative impact to a positive change in fishery harvest

gest that the Mediterranean Sea ecosystem is at an early developmental stage. This was visible, for example, in the ratio between total primary production (PP) and total respiration (R) (Odum 1969, Christensen 1995) or in the primary production/biomass ratio (PP/*B*). On the other hand, the indicators from the other European Seas suggested that systems fell within an intermediate-low level developmental stage. For the SOI, despite the low general values, the Mediterranean Sea showed the highest value, while in relation to the 2 cycling indices, the Mediterranean basin had the highest values in PCI and the lowest in FCI. For each European regional sea, ascendancy was relatively low, whereas

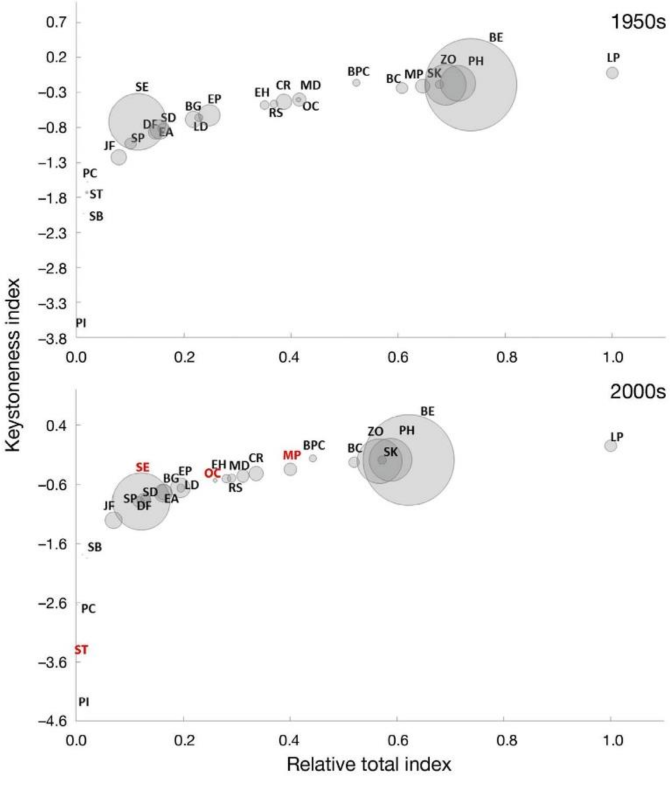


Fig. 8. Relative total impact (ε_i) versus keystoneness (KS_i) showing the role of species/groups in the ecosystem for both time periods (1950s and 2000s). The size of the circles is proportional to the species/group biomass. Functional groups that showed a decline in their keystone role in comparison to the 1950s are shown in red. For abbreviations, refer to Table 1

Table 2. Summary statistics for the Mediterranean Sea food web model in comparison with the North Sea, Baltic Sea and Black Sea

Indicators	Mediterranean Sea (this study)	North Sea (Mackinson et al. 2014)	Baltic Sea (Tomczak et al. 2012)	Black Sea (Akoglu et al. 2014)	Units
Main ecosystem features					
Area	2512000	570000	240000	150000	km^2
Studied period	2000s	1991	2000s	1995–2000	Year
Functional groups	103	68	21	10	No.
Main indicators					
Sum of all consumption	923	6157	3435	4500	$t\ km^{-2}\ yr^{-1}$
Sum of all exports	1320	105	476	490	$t\ km^{-2}\ yr^{-1}$
Sum of all respiratory flows	290	2658	1851	2990	$t\ km^{-2}\ yr^{-1}$
Sum of all flows into detritus	1467	3867	2246	2230	$t\ km^{-2}\ yr^{-1}$
Total system throughput	4000	12786	8007	10210	$t\ km^{-2}\ yr^{-1}$
Mean trophic level of the catch	3.08	3.7	3.30	3	
Gross efficiency (catch/net primary production)	0.00026	0.00226	0.0016	0.001	
Total primary production	1610	2609	2434	3483	$t\ km^{-2}\ yr^{-1}$
Total primary production/total respiration	5.55	0.98	1.26	1.16	
Primary production required to sustain fisheries (PPR, considering primary production)	1.46	5.88	52.57	28.93	%
Total primary production/total biomass	37.67	4.71	22.54	90	
Total biomass (excluding detritus)	42.74	554	108	38.7	$t\ km^{-2}$
Connectance index	0.10	0.22	0.22	2.5	
System omnivory index	0.27	0.23	0.15	0.116	
Predatory cycling index	10.96	–	0.41	–	%
Finn's cycling index	4.98	20.24	6.98	15.01	%
Mean transfer efficiency	9.2	30.2	12	7.4	%
Ascendancy	42.9	20.6	30.82	31.7	%
Overhead	57.1	79.4	69.18	68.3	%

overhead was high. The mean TE observed in the Mediterranean Sea was similar to the Baltic Sea but was lower in comparison to values calculated for the Black and North Seas. As for fishing indicators, the PPR% of the Mediterranean was 0.81%, the lowest among the other seas, while TL_c was 3.04 in the Mediterranean Sea, similar to the Black Sea and lower in comparison to the other European Seas with higher TL values (between 3.3 and 3.7).

DISCUSSION

This study constitutes the first attempt to build an historical and current food web model for the whole Mediterranean Sea with the challenging effort to integrate available spatial and temporal (in terms of comparing the 1950s and 2000s) biological data and modelling outputs in a coherent manner. We acknowledge that data gaps still exist, for example on temporal changes in diet composition, temporal estimates of discards and biomasses of non-commercially important species and deep-sea organisms. Thus, further efforts should be made to reduce this uncertainty and increase the quality of these models.

Quality of the models

As expected, the 1950s model showed a lower pedigree index, scoring in the lower range (0.164–0.676) when compared to the 150 balanced EwE models previously assessed globally by Morissette (2007). This is because the 1950s model was constructed using mainly data obtained from other modelling approaches (e.g. biogeochemical models to estimate phytoplankton biomasses and stock recruitment models to estimate biomass of fish stocks; refer to Table S5 in the Supplement for details of each functional group). Models that have tried to represent the past have always been associated with higher uncertainty, as was observed in other studies (Coll et al. 2008, 2009c, Piroddi et al. 2010, Christensen et al. 2014, Macias et al. 2014), and their outputs should be always taken with caution. To limit this uncertainty, we tried to use models for which outputs have been tested and when possible validated (Macias et al. 2014), or that have been widely utilized to assess temporal biomasses as done for fish stocks (e.g. surplus production models; Walters et al. 2008, Piroddi et al. 2011). In contrast, the 2000s model, due to its higher data quality, showed a relatively higher pedigree. This was due to the availability, in more recent years, of survey data (e.g. trawl surveys such as the MEDITS campaign) and the increase in biodiversity assessments (e.g. Coll et al. 2010) that have improved the level of knowledge in the basin. Nevertheless, data deficiencies exist, particularly in African and Arabic countries, where survey data remain either inaccessible or absent. Despite these limitations, the models developed in this study represent an important step towards an integrated understanding of the Mediterranean Sea marine ecosystem structure and function.

Biomasses, trophic flows and TLs

Results presented here show how the Mediterranean Sea is mainly dominated, in terms of biomass, by lower TL organisms, particularly 'benthos', 'zooplankton' and 'phytoplankton'. These groups dominate most of the system flows and, as observed at smaller scales in other Mediterranean food web models (Coll et al. 2006, 2007, Tsagarakis et al. 2010, Moutopoulos et al. 2013, Torres et al. 2013), constantly appear as important key species. This is probably because of the relatively low biomass at higher TLs and a relatively high mean TE overall in the food web, in line with previous studies (Pauly & Christensen 1995, Coll & Libralato 2012). This phenomenon is called the 'Mediterranean paradox' for the fact that despite the oligotrophic condition of the basin that constrains the reproduction and feeding of zooplankton, the ecosystem is capable of producing a relatively high fish abundance (Sournia 1973, Macias et al. 2014). In addition, the high TEs have been suggested as a sign of overexploitation of the Mediterranean Sea due to high production exports (Coll et al. 2009b).

Marine mammals and large pelagic fishes, on the other hand, are the top predators of the Mediterranean marine ecosystem. In particular, the Mediterranean monk seal *Monachus monachus* is the species with the highest TL followed by 'piscivorous cetaceans' and 'large pelagic fishes'. These outcomes are very interesting since the Mediterranean monk seal and several dolphin populations (e.g. the short-beaked common dolphin *Delphinus delphis*) have dramatically declined over the centuries because of a variety of anthropogenic pressures (e.g. fisheries interactions, habitat loss and pollution) and are now classified either as Critically Endangered (the Mediterranean monk seal is almost extinct), Endangered, or Vulnerable by the International Union for Conservation of Nature (IUCN) Red List of Threatened Animals (UNEP/MAP 1994, Johnson & Lavigne 1998, Reeves & Notarbartolo di Sciara 2006, Bearzi et al. 2008, Piroddi et al. 2011).

Large pelagic fishes (mainly tuna species and swordfish), the main keystone group in our modelling approach, have consistently been exploited for thousands of years in the Mediterranean Sea, and these species are also at low levels of abundance (Abdul Malak et al. 2011). This severe decline in biodiversity at the top of the food web particularly in recent decades (Briand 2000, Bearzi et al. 2008, Coll et al. 2008, 2009c, Piroddi et al. 2010, 2011, Lotze et al. 2011), as also shown in our study by their reduced biomass levels, could have induced a cascade effect throughout the food web, with effects on the complexity, connectivity and robustness of the system against further species loss (Briand 2000, Heithaus et al. 2008, Lotze et al. 2011, Piroddi et al. 2011). Defined as umbrella, sentinel, keystone or flagship species, they reflect ecosystem changes and degradation over time, as is also clear from our keystone and MTI analysis, and ensuring their survival would lead to ways of enhancing marine ecosystems and ensure sustainable human activities (Bossart 2006, Boyd et al. 2006, Trites et al. 2006, Sergio et al. 2008).

Ecological role of species and changes with time

The results of our keystone analysis for both time periods also revealed changes over time in other important keystone species. After 'large pelagic fishes', 'sharks' and 'medium pelagic fishes' have played a key role in the past ecosystem, replaced in more recent years by 'benthopelagic cephalopods'. This is not the first time that cephalopods have been identified as a keystone group in Mediterranean food webs (Coll et al. 2006, Tsagarakis et al. 2010, Bănaru et al. 2013, Hattab et al. 2013, Torres et al. 2013). This functional group, the role of which in the overall structure and functioning of marine ecosystems remains poorly understood, has an important trophic position (being both predator and prey), and because it can proliferate in highly exploited ecosystems, it constitutes a key element of present marine food webs (Pierce et al. 2008, Coll et al. 2013). As for 'sharks', particularly large predatory sharks, several studies have pointed at strong declines in species over the last centuries mainly due to intensive overexploitation (both for consumption and as discarded species; Megalofonou 2005, Ferretti et al. 2008, Maynou et al. 2011, Coll et al. 2014a). The present study suggests that these species were important in the past Mediterranean ecosystem and confirms a diminishing role within the current food web as a consequence of a reduction in their abundance.

Small and 'medium' pelagic fishes, both with high biomasses and high proportions in catches, show an important role in the Mediterranean ecosystem as structuring species of the food web (Coll et al. 2006, 2007, Piroddi et al. 2010, Tsagarakis et al. 2010). Yet, our results highlight how these organisms, despite being essential for transferring energy from lower to higher TL organisms (Cury et al. 2000, Pikitch et al. 2014), have diminished considerably between the 2 time periods and between sub-regions, causing a reduction in their ecological role.

Fishing impact and the quality of data

From the MTI analysis, bottom trawling and dredges were the fisheries with the widest impact on the food web, particularly on the demersal community. This has been observed in sub-areas of the Mediterranean Sea representing continental shelf and upper slopes (Coll et al. 2006, 2007, Bănaru et al. 2013, Hattab et al. 2013). Therefore, our results highlight the effect of bottom trawlers and dredges on marine resources and ecosystems of the Mediterranean Sea as an important issue that should be addressed if sustainable management of fisheries is to be achieved within the region (Puig et al. 2012). The impacts of artisanal fisheries on the ecosystem have also increased over time, particularly in the Ionian and Eastern Mediterranean Seas, and are probably caused by increased fishing effort in the EU, northern African and Arabic countries (Anticamara et al. 2011). This also has clear implications for the management of marine resources in the Mediterranean Sea because the artisanal fleet dominates the fishing activity in many Mediterranean countries but is poorly monitored.

Overall, our results show that over time, fisheries have exerted a negative pressure on the food web as a consequence of increased and intensive overexploitation. Yet, several interpretations of these results could be drawn: first, fisheries might not display a greater negative impact (than the one presented here) on commercially important species because of the inclusion in the analysis of developing countries (e.g. North African and Arabic countries) and developed countries together. Completely different spatiotemporal patterns/trends characterize these 2 sides of the Mediterranean Sea that might lead to a masking effect scenario. A reflection of this is visible in the increased impact of artisanal fisheries in the Ionian and Eastern Mediterranean Seas, possibly as a consequence of increased fishing effort in southern Mediterranean countries. This distortion might also be caused by discards, which we kept constant in time due to lack of information, and by Illegal, Unregulated, and Unreported IUU) activities that, despite being a serious issue in the Mediterranean Sea (Ulman et al. 2013, Coll et al. 2014b), were not included in this study due to the lack of a global estimate for the Mediterranean Sea. Also, recreational catches are not included in national fishery statistics, and only recently a European Union legislation (Council Regulation [EC] No. 1224/2009) has required the survey of recreational fishing activities. Since only few sources of information exist, which have been incorporated into the model, catches may well have been underestimated. Using fisheries statistics supplied to the FAO by individual countries could be another limiting factor. Several studies have indeed confirmed that most of these statistics largely underestimate their likely true catch by a factor of 2 or more (Zeller & Pauly 2007, Pauly et al. 2014). This could be particularly true for the Southern Mediterranean, where mechanisms to collect fisheries data are less available (FAO 2010) and for some Mediterranean countries where this factor is even higher (Pauly et al. 2014). An unrealistic scenario is also observed regarding mid-water trawling in the Eastern Mediterranean Sea, where this gear shows an impact on marine resources, despite the fact that it does not operate in most of the Eastern Mediterranean countries (Sacchi 2011). Obviously this is an error in the Sea Around Us project database, which at the time it was accessed was still under development.

These caveats represent the major weaknesses of the Mediterranean fisheries data, and some caution should be taken when interpreting the data. Currently, a database on global fisheries reconstruction from 1950 to 2010, which aims at looking at all types of fisheries removals (from reported and unreported landings to recreational landings and discards) is being constructed, including Mediterranean countries (Le Manach et al. 2011, Ulman et al. 2013, Coll et al. 2014b, Pauly et al. 2014). In the near future, this information on catch reconstructions could be integrated in modelling efforts to reduce the limitations explained above, and to capture better the fishing pressure on current and past Mediterranean marine ecosystems.

Similarities and differences among European regional seas

The relative total biomass per km^2 and per each individual sea reveals that the Adriatic and Western Mediterranean are the areas with the highest biomass followed by the Ionian and Eastern Mediterranean. This confirms a decrease gradient of richness from west to east, as observed in other studies (Bosc et al. 2004), influenced by changes in environmental parameters (e.g. productivity, temperature and salinity) that define and characterize the Mediterranean Sea. Comparing our results to other European seas illustrates that European regional seas are quite diverse. In particular, the Mediterranean Sea stands alone in relation to the type of flows that drive the system and the cycling indices that suggest higher levels of community stress induced by intensive fishing activities, as previously illustrated (Costello et al. 2010).

In regards to ecosystems development, the Mediterranean Sea appears to be in an early development stage, different from the other systems, probably because the ecosystem has been perturbed continuously over a long period of time. Indeed, when ecosystems develop, biomasses and complexity tend to increase and mature, whereas when they are disturbed, e.g. by fishing, they show the opposite trend and stay 'young' (Odum 1969).

One similarity with the other EU ecosystems is given by the TLs of the catches, which are low in the Mediterranean Sea, in the Black Sea and recently in the Baltic Sea (e.g. herrings and sprats have replaced the collapsed Eastern Baltic cod *Gadus morhua* in the landings; Tomczak et al. 2012), highlighting the importance of small pelagics in the fisheries activities of these areas. Although differences may have occurred in the way models were constructed (such as the number of functional groups and links), these outcomes are in line with other studies that pointed at differences in physical and biological features (from highly eutrophic with frequent hypoxia events to moderately eutrophic and productive or relatively oligotrophic regions; Coll et al. 2010, Tomczak et al. 2012, Mackinson 2014) as the reasons for these differences in diversity among European regional seas (Barale & Gade 2008, Narayanaswamy et al. 2013).

Concluding remarks

Overall, our study is the first to provide a basis for understanding and quantifying the structure and functioning of the whole Mediterranean Sea ecosystem, including main marine organisms, from low to high TLs, and considering fishing activity. This is also the first Ecopath model that tries to integrate subregions within a unified model to take into consideration differences in biological and environmental characteristics. The construction of 2 food web models (for the past and for current years) enabled us to assess changes in the food web and impacts (in this case fishing) affecting the system. However, further developments of spatial and temporal hind- and forecast analysis are necessary to further model the dynamics of the ecosystem (such as movements of species within and between areas and large migrations) and evaluate the exploitation status of the Mediterranean Sea and explore different management policies and future scenarios. Temporal simulations to hindcast food web dynamics have been developed in regional areas of the Mediterranean Sea such as the Catalan Sea (Coll et al. 2008), the Adriatic Sea (Coll et al. 2009c) and the Ionian Sea (Piroddi et al. 2010). Quantifying the impact of important threats (e.g. climate change and fishing pressure) on a system that is considered 'under siege' (Coll et al. 2012) becomes critically important for ensuring the sustainability of marine resources and the services they provide to humans, and the conservation of this vulnerable ecosystem. This is a step further for the regional assessment of the Mediterranean Sea ecosystem.

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S 1. Initial (light grey cells) and output (white cells) parameters of the Mediterranean marine ecosystem for the 1950s period

#	Group name	Trophic level	Habitat area (fraction)	Biomass in habitat area (t/km²)	Biomass (t/km²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic efficiency	Production / consumption
1	Piscivores cetaceans W	4.19	0.33	0.01	0.00	0.08	25.84	0.97	0.00
2	Others cetaceans	3.53	1.00	0.07	0.07	0.05	8.29	0.07	0.01
3	Pinnipeds W	4.20	0.33	0.00	0.00	0.08	13.15	0.90	0.01
4	Seabirds W	3.09	0.33	0.00	0.00	5.33	73.09	0.01	0.07
5	Sea turtles	2.68	1.00	0.02	0.02	0.19	2.78	0.14	0.07
6	Large Pelagics	3.94	1.00	0.44	0.44	0.35	2.50	0.04	0.14
7	Medium pelagics W	3.28	0.33	0.56	0.18	0.75	4.94	0.85	0.15
8	European pilchard W	3.13	0.33	0.55	0.18	0.99	8.45	1.00	0.12
9	European anchovy W	3.25	0.33	0.67	0.22	0.87	7.95	0.90	0.11
10	Other small pelagics W	3.14	0.33	0.36	0.12	0.75	6.63	0.90	0.11
11	Large demersals W	3.68	0.33	0.24	0.08	0.87	3.06	0.87	0.28
12	European hake W	3.81	0.33	0.28	0.09	0.60	2.80	0.91	0.21
13	Medium demersals W	2.94	0.33	0.79	0.26	0.70	6.40	0.92	0.11
14	Small demersals W	3.03	0.33	0.38	0.13	1.57	6.87	0.98	0.23
15	Deep fish W	2.97	0.33	0.85	0.28	0.70	3.50	0.99	0.20
16	Sharks W	3.85	0.33	0.36	0.12	0.42	3.48	0.10	0.12
17	Rays and skates W	3.34	0.33	0.28	0.09	0.80	3.67	0.83	0.22
18	Benthopelagic cephalopods W	3.69	0.33	0.32	0.11	2.00	9.00	0.96	0.22
19	Benthic cephalopods W	3.44	0.33	0.56	0.18	2.10	7.00	0.86	0.30
20	Bivalves_gastropods W	2.01	0.33	1.00	0.33	1.30	5.00	0.94	0.26
21	Crustaceans W	2.79	0.33	0.99	0.33	3.50	12.00	0.97	0.29
22	Jellyfish W	3.08	0.33	0.33	0.11	13.87	50.48	0.42	0.27
23	Benthos W	2.02	0.33	16.22	5.39	2.50	9.04	0.33	0.28
24	Zooplankton W	2.25	0.33	7.76	2.58	30.60	102.00	0.81	0.30
25	Phytoplankton W	1.00	0.33	18.40	6.11	197.00	--	0.18	--
26	Seagrass W	1.00	0.33	16.70	5.55	5.94	--	0.16	--
27	Piscivores cetaceans A	4.16	0.05	0.00	0.00	0.08	25.84	0.90	0.00
28	Pinnipeds A	4.19	0.05	0.00	0.00	0.08	13.15	0.55	0.01
29	Seabirds A	3.03	0.05	0.00	0.00	4.61	69.34	0.16	0.07
30	Medium Pelagics A	3.26	0.05	0.88	0.05	0.92	6.76	0.89	0.14
31	European pilchard A	3.00	0.05	4.32	0.23	0.80	9.19	0.31	0.09
32	European anchovy A	3.11	0.05	2.60	0.14	0.85	11.02	0.75	0.08
33	Other small pelagics A	3.02	0.05	0.53	0.03	1.00	11.29	0.48	0.09
34	Large demersals A	3.63	0.05	0.20	0.01	0.90	5.14	0.72	0.18
35	European hake A	3.86	0.05	0.28	0.01	0.40	1.85	0.79	0.22

36	Medium demersals A	2.96	0.05	0.39	0.02	1.10	5.57	0.99	0.20
37	Small demersals A	2.96	0.05	0.32	0.02	1.50	8.02	0.97	0.19
38	Deep fish A	2.88	0.05	0.61	0.03	0.70	3.50	0.98	0.20
39	Sharks A	3.79	0.05	0.10	0.01	0.50	4.00	0.26	0.13
40	Rays and skates A	3.41	0.05	0.12	0.01	0.64	4.10	0.77	0.16
41	Benthopelagic cephalopods A	3.58	0.05	0.22	0.01	2.70	9.00	0.88	0.30
42	Benthic cephalopods A	3.45	0.05	0.33	0.02	2.10	7.00	0.85	0.30
43	Bivalves_gastropods A	2.05	0.05	0.95	0.05	1.30	5.00	0.99	0.26
44	Crustaceans A	2.76	0.05	0.80	0.04	3.50	12.00	0.99	0.29
45	Jellyfish A	3.14	0.05	2.27	0.12	14.60	50.48	0.94	0.29
46	Benthos A	2.02	0.05	68.24	3.64	1.31	6.71	0.18	0.20
47	Zooplankton A	2.11	0.05	5.79	0.31	37.85	126.17	0.97	0.30
48	Phytoplankton A	1.00	0.05	15.00	0.80	140.00	--	0.33	--
49	Seagrass A	1.00	0.05	2.68	0.14	4.02	--	0.50	--

50	Piscivores cetaceans I	4.13	0.30	0.00	0.00	0.08	25.84	0.77	0.00
51	Pinnipeds I	4.16	0.30	0.00	0.00	0.08	13.15	0.35	0.01
52	Seabirds I	3.11	0.30	0.00	0.00	4.60	105.43	0.07	0.04
53	Medium Pelagics I	3.20	0.30	0.38	0.11	0.70	7.70	0.96	0.09
54	European pilchard I	3.02	0.30	0.48	0.14	0.94	8.68	0.97	0.11
55	European anchovy I	3.14	0.30	0.53	0.16	0.91	12.30	0.86	0.07
56	Other small pelagics I	3.04	0.30	0.28	0.08	0.86	8.36	0.95	0.10
57	Large demersals I	3.66	0.30	0.20	0.06	0.65	2.85	0.93	0.23
58	European hake I	3.86	0.30	0.13	0.04	0.65	3.40	0.96	0.19
59	Medium demersals I	2.89	0.30	0.65	0.20	0.90	8.13	0.82	0.11
60	Small demersals I	2.93	0.30	0.34	0.10	1.10	6.38	0.98	0.17
61	Deep fish I	2.80	0.30	0.59	0.18	0.70	3.50	0.81	0.20
62	Sharks I	3.72	0.30	0.24	0.07	0.41	4.33	0.10	0.09
63	Rays and skates I	3.27	0.30	0.24	0.07	0.60	3.00	0.76	0.20
64	Benthopelagic cephalopods I	3.53	0.30	0.17	0.05	2.70	9.00	0.93	0.30
65	Benthic cephalopods I	3.42	0.30	0.33	0.10	2.10	7.00	0.95	0.30
66	Bivalves_gastropods I	2.01	0.30	0.70	0.21	1.30	5.00	0.95	0.26
67	Crustaceans I	2.63	0.30	0.63	0.19	3.45	12.00	0.97	0.29
68	Jellyfish I	3.10	0.30	0.17	0.05	11.10	35.90	0.87	0.31
69	Benthos I	2.01	0.30	11.74	3.52	2.75	22.00	0.29	0.13
70	Zooplankton I	2.14	0.30	3.63	1.09	38.44	128.12	0.57	0.30
71	Phytoplankton I	1.00	0.30	7.60	2.28	61.80	--	0.88	--
72	Seagrass I	1.00	0.30	16.00	4.79	2.59	--	0.64	--

73	Piscivores cetaceans E	4.12	0.31	0.00	0.00	0.08	25.84	0.76	0.00
74	Pinnipeds E	4.11	0.31	0.00	0.00	0.08	13.15	0.31	0.01

75	Seabirds E	3.12	0.31	0.00	0.00	4.78	111.61	0.00	0.04
76	Medium Pelagics E	3.23	0.31	0.61	0.19	0.80	4.79	0.92	0.17
77	European pilchard E	3.02	0.31	0.48	0.15	0.95	9.49	0.99	0.10
78	European anchovy E	3.14	0.31	0.87	0.27	0.90	5.20	0.92	0.17
79	Other small pelagics E	2.89	0.31	0.48	0.15	0.95	8.23	0.91	0.12
80	Large demersals E	3.57	0.31	0.18	0.06	0.70	4.35	0.94	0.16
81	European hake E	3.79	0.31	0.28	0.09	0.60	5.26	0.92	0.11
82	Medium demersals E	2.87	0.31	0.40	0.12	1.00	9.09	0.91	0.11
83	Small demersals E	2.95	0.31	0.36	0.11	1.10	7.64	0.99	0.14
84	Deep fish E	2.90	0.31	0.42	0.13	0.70	3.50	0.94	0.20
85	Skarks E	3.70	0.31	0.20	0.06	0.50	5.16	0.10	0.10
86	Rays and skates E	3.38	0.31	0.18	0.06	0.70	4.07	0.93	0.17
87	Benthopelagic cephalopods E	3.55	0.31	0.13	0.04	2.70	9.00	0.92	0.30
88	Benthic cephalopods E	3.36	0.31	0.32	0.10	2.10	7.00	0.96	0.30
89	Bivalves_gastropods E	2.01	0.31	0.62	0.19	1.30	5.00	0.98	0.26
90	Crustaceans E	2.64	0.31	0.56	0.17	3.50	12.00	0.98	0.29
91	Jellyfish E	3.25	0.31	0.16	0.05	4.84	15.00	0.75	0.32
92	Benthos E	2.02	0.31	9.83	3.10	2.64	16.13	0.32	0.16
93	Zooplankton E	2.14	0.31	3.59	1.13	38.80	129.33	0.55	0.30
94	Phytoplankton E	1.00	0.31	8.83	2.78	70.00	--	0.66	--
95	Seagrass E	1.00	0.31	15.00	4.72	2.69	--	0.40	--
96	Discards W	1.00	0.33	0.02	0.01	--	--	0.02	--
97	Detritus W	1.00	0.33	32.01	10.63	--	--	0.04	--
98	Discards A	1.00	0.05	0.01	0.00	--	--	0.11	--
99	Detritus A	1.00	0.05	19.73	1.05	--	--	0.25	--
100	Discards I	1.00	0.30	0.01	0.00	--	--	0.27	--
101	Detritus I	1.00	0.30	14.78	4.43	--	--	0.59	--
102	Discards E	1.00	0.31	0.01	0.00	--	--	0.13	--
103	Detritus E	1.00	0.31	14.74	4.64	--	--	0.29	--

S 2. Initial and output parameters of the Mediterranean marine ecosystem for the 2000s period

#	**Group name**	**Trophic level**	**Habitat area (fraction)**	**Biomass in habitat area (t/km²)**	**Biomass (t/km²)**	**Production / biomass (/year)**	**Consumption / biomass (/year)**	**Ecotrophic efficiency**	**Production / consumption**
1	Piscivores cetaceans W	4.19	0.33	0.00	0.00	0.08	25.84	0.50	0.00
2	Others cetaceans	3.53	1.00	0.05	0.05	0.05	8.29	0.21	0.01
3	Pinnipeds W	4.22	0.33	0.00	0.00	0.08	13.15	0.41	0.01
4	Seabirds W	3.09	0.33	0.00	0.00	5.33	73.09	0.05	0.07
5	Sea turtles	2.68	1.00	0.00	0.00	0.16	2.78	0.97	0.06

6	Large Pelagics	3.94	1.00	0.40	0.40	0.39	2.50	0.15	0.16
7	Medium pelagics W	3.28	0.33	0.48	0.16	0.85	4.94	0.97	0.17
8	European pilchard W	3.13	0.33	0.39	0.13	1.20	8.45	0.97	0.14
9	European anchovy W	3.25	0.33	0.64	0.21	0.97	7.95	0.97	0.12
10	Other small pelagics W	3.14	0.33	0.32	0.11	0.99	6.63	0.88	0.15
11	Large demersals W	3.68	0.33	0.22	0.07	0.91	3.06	0.84	0.30
12	European hake W	3.82	0.33	0.24	0.08	0.70	2.80	0.87	0.25
13	Medium demersals W	2.94	0.33	0.71	0.24	0.80	6.40	0.94	0.13
14	Small demersals W	3.04	0.33	0.31	0.10	1.60	6.87	0.91	0.23
15	Deep fish W	2.97	0.33	0.87	0.29	0.70	3.50	0.96	0.20
16	Sharks W	3.85	0.33	0.35	0.11	0.50	3.48	0.09	0.14
17	Rays and skates W	3.34	0.33	0.27	0.09	0.88	3.67	0.77	0.24
18	Benthopelagic cephalopods W	3.69	0.33	0.30	0.10	2.50	8.33	0.85	0.30
19	Benthic cephalopods W	3.48	0.33	0.43	0.14	2.30	7.67	0.92	0.30
20	Bivalves_gastropods W	2.01	0.33	0.70	0.23	1.50	5.00	1.00	0.30
21	Crustaceans W	2.79	0.33	0.72	0.24	3.67	12.23	0.99	0.30
22	Jellyfish W	3.08	0.33	0.27	0.09	22.84	50.48	0.26	0.45
23	Benthos W	2.02	0.33	13.27	4.41	3.90	9.04	0.21	0.43
24	Zooplankton W	2.25	0.33	8.04	2.67	39.60	132.00	0.76	0.30
25	Phytoplankton W	1.00	0.33	20.40	6.77	185.18	--	0.23	--
26	Seagrass W	1.00	0.33	12.84	4.26	5.94	--	0.16	--

27	Piscivores cetaceans A	4.16	0.05	0.00	0.00	0.08	25.84	0.85	0.00
28	Pinnipeds A	4.21	0.05	0.00	0.00	0.08	13.15	0.55	0.01
29	Seabirds A	3.03	0.05	0.00	0.00	4.61	69.34	0.41	0.07
30	Medium Pelagics A	3.26	0.05	0.74	0.04	1.15	6.76	0.72	0.17
31	European pilchard A	3.00	0.05	3.37	0.18	0.97	9.19	0.30	0.11
32	European anchovy A	3.11	0.05	2.11	0.11	1.10	11.02	0.70	0.10
33	Other small pelagics A	3.02	0.05	0.43	0.02	1.10	11.29	0.46	0.10
34	Large demersals A	3.64	0.05	0.18	0.01	1.30	5.14	0.53	0.25
35	European hake A	3.86	0.05	0.25	0.01	0.60	2.10	0.65	0.29
36	Medium demersals A	2.96	0.05	0.28	0.02	1.54	5.57	0.94	0.28
37	Small demersals A	2.96	0.05	0.26	0.01	1.90	8.02	0.98	0.24
38	Deep fish A	2.88	0.05	0.48	0.03	0.70	3.50	0.97	0.20
39	Sharks A	3.79	0.05	0.05	0.00	0.60	4.00	0.38	0.15
40	Rays and skates A	3.42	0.05	0.10	0.01	0.74	4.10	0.44	0.18
41	Benthopelagic cephalopods A	3.56	0.05	0.17	0.01	3.30	11.00	0.98	0.30
42	Benthic cephalopods A	3.51	0.05	0.30	0.02	3.00	10.00	0.87	0.30
43	Bivalves_gastropods A	2.01	0.05	0.84	0.04	1.35	4.50	0.95	0.30

44	Crustaceans A	2.75	0.05	0.67	0.04	3.80	12.67	0.98	0.30
45	Jellyfish A	3.14	0.05	2.51	0.13	14.71	50.48	0.93	0.29
46	Benthos A	2.02	0.05	64.24	3.43	1.31	6.71	0.16	0.20
47	Zooplankton A	2.11	0.05	6.15	0.33	38.85	129.50	0.87	0.30
48	Phytoplankton A	1.00	0.05	17.73	0.95	214.00	--	0.20	--
49	Seagrass A	1.00	0.05	2.06	0.11	4.02	--	0.59	--

50	Piscivores cetaceans I	4.13	0.30	0.00	0.00	0.08	25.84	0.67	0.00
51	Pinnipeds I	4.15	0.30	0.00	0.00	0.08	13.15	0.67	0.01
52	Seabirds I	3.11	0.30	0.00	0.00	4.48	79.17	0.29	0.06
53	Medium Pelagics I	3.20	0.30	0.29	0.09	0.83	7.70	0.92	0.11
54	European pilchard I	3.02	0.30	0.39	0.12	1.00	8.68	0.99	0.12
55	European anchovy I	3.14	0.30	0.44	0.13	1.10	12.30	0.79	0.09
56	Other small pelagics I	3.04	0.30	0.26	0.08	1.10	8.36	0.91	0.13
57	Large demersals I	3.66	0.30	0.19	0.06	0.70	2.85	0.86	0.25
58	European hake I	3.86	0.30	0.12	0.04	0.70	3.40	0.95	0.21
59	Medium demersals I	2.89	0.30	0.52	0.16	1.15	8.13	0.86	0.14
60	Small demersals I	2.93	0.30	0.30	0.09	1.40	6.38	1.00	0.22
61	Deep fish I	2.80	0.30	0.51	0.15	0.70	3.50	0.97	0.20
62	Sharks I	3.71	0.30	0.24	0.07	0.58	4.33	0.09	0.13
63	Rays and skates I	3.27	0.30	0.23	0.07	0.70	3.00	0.67	0.23
64	Benthopelagic cephalopods I	3.53	0.30	0.14	0.04	3.10	10.33	0.90	0.30
65	Benthic cephalopods I	3.42	0.30	0.32	0.09	3.00	10.00	0.81	0.30
66	Bivalves_gastropods I	2.01	0.30	0.63	0.19	1.50	5.00	0.99	0.30
67	Crustaceans I	2.63	0.30	0.59	0.18	3.77	12.57	0.97	0.30
68	Jellyfish I	3.10	0.30	0.25	0.08	14.13	47.10	0.86	0.30
69	Benthos I	2.01	0.30	11.35	3.40	4.70	16.13	0.16	0.29
70	Zooplankton I	2.14	0.30	5.65	1.69	30.63	102.10	0.53	0.30
71	Phytoplankton I	1.00	0.30	14.09	4.22	173.56	--	0.21	--
72	Seagrass I	1.00	0.30	12.17	3.65	2.59	--	0.60	--

73	Piscivores cetaceans E	4.11	0.31	0.00	0.00	0.08	25.84	0.89	0.00
74	Pinnipeds E	4.10	0.31	0.00	0.00	0.08	13.15	0.62	0.01
75	Seabirds E	3.12	0.31	0.00	0.00	4.78	111.61	0.02	0.04
76	Medium Pelagics E	3.19	0.31	0.42	0.13	0.95	4.79	0.81	0.20
77	European pilchard E	3.02	0.31	0.45	0.14	1.10	9.49	0.90	0.12
78	European anchovy E	3.14	0.31	0.52	0.16	1.20	5.20	0.94	0.23
79	Other small pelagics E	2.89	0.31	0.41	0.13	1.15	8.23	0.89	0.14
80	Large demersals E	3.56	0.31	0.17	0.05	0.90	4.35	0.84	0.21
81	European hake E	3.73	0.31	0.27	0.09	0.75	4.06	0.65	0.18

82	Medium demersals E	2.84	0.31	0.35	0.11	1.18	9.09	0.90	0.13
83	Small demersals E	2.95	0.31	0.21	0.07	1.30	7.64	0.96	0.17
84	Deep fish E	2.90	0.31	0.44	0.14	0.70	5.50	0.84	0.13
85	Skarks E	3.64	0.31	0.19	0.06	0.58	5.16	0.14	0.11
86	Rays and skates E	3.38	0.31	0.17	0.05	0.78	4.07	0.89	0.19
87	Benthopelagic cephalopods E	3.54	0.31	0.11	0.03	3.10	10.33	0.94	0.30
88	Benthic cephalopods E	3.35	0.31	0.29	0.09	3.00	10.00	0.82	0.30
89	Bivalves_gastropods E	2.01	0.31	0.59	0.19	1.50	5.00	0.98	0.30
90	Crustaceans E	2.63	0.31	0.42	0.13	4.90	16.33	0.97	0.30
91	Jellyfish E	3.25	0.31	0.20	0.06	4.84	16.13	0.74	0.30
92	Benthos E	2.02	0.31	8.90	2.80	4.00	13.33	0.22	0.30
93	Zooplankton E	2.14	0.31	3.80	1.20	35.13	117.10	0.54	0.30
94	Phytoplankton E	1.00	0.31	11.61	3.66	168.99	0.00	0.20	--
95	Seagrass E	1.00	0.31	11.58	3.65	2.69	0.00	0.40	--
96	Discards W	1.00	0.33	0.04	0.01	--	--	0.02	--
97	Detritus W	1.00	0.33	32.01	10.63	--	--	0.04	--
98	Discards A	1.00	0.05	0.01	0.00	--	--	0.06	--
99	Detritus A	1.00	0.05	19.73	1.05	--	--	0.13	--
100	Discards I	1.00	0.30	0.02	0.00	--	--	0.04	--
101	Detritus I	1.00	0.30	12.78	3.83	--	--	0.08	--
102	Discards E	1.00	0.31	0.04	0.01	--	--	0.03	--
103	Detritus E	1.00	0.31	14.74	4.64	--	--	0.07	--

S3. Diet composition matrix for the Mediterranean marine ecosystem model for the 1950s period. Prey groups are indicated by rows and predators by columns. Functional group codes are reported according to Table S1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0.1	0	0	0.2	0	0.1	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	0.1	0	0	0.1	0	0.1	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0.1	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0.1	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0.2	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	0.3	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0.1	0	0.4	0	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0.1	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0.1	0	0	0	0	0	0	0	0	0.1	0	0	0	0.1	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	0.1	0	0.1	0	0	0	0	0	0	0	0.2	0.1	0.1	0.1	0	0.1	0.1	0.4	0.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0.1	0.1	0	0.4	0	0	0	0.3	0.1	0.5	0.4	0.2	0.2	0.5	0	0.3	0	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	0.3	0	0	0	0	0.5	0.9	1	0.9	0.1	0.1	0.1	0.3	0.6	0	0	0.3	0.1	0	0.2	0.7	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0.1	0	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0.1	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.2	0.1	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.1	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0.00	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
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80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0.1	0	0.1	0	0	0	0	0	0
84	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.1	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.4	0	0	0	0	0	0.1	0	0	0	0	0.1	0.1	0.1	0	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0	0	0.1	0	0.1	0.2	0	0	0.00	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	0	0.1	0.1	0.1	0.1	0	0.1	0.1	0.3	0.3	0	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
92	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0	0	0.4	0.1	0.4	0.4	0.2	0.3	0.5	0	0.3	0	0.4	0	0	0
93	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0.9	1	0.8	0.1	0.1	0.1	0.3	0.6	0	0	0.3	0.1	0	0.2	0.7	0	0.1
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.2	0	0	0	0	0.1	0	0	0	0	0	0	0.1	0	0.9
95	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0.1	0
96	0.1	0	0	0.3	0	0	0	0	0	0	0	0.1	0	0	0	0	0.2	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
97	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0.1	0	0	0	0	0.8	0.3	0.1	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.3	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0.2	0.1	0	0	0	0	0.8	0.3	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	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.3	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.2	0.1	0	0	0	0	0.8	0.4	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
102	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	0.3	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0.1	0
103	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0.2	0.1	0	0	0	0	0.8	0.4	0	0.8	0
Import	0	0.1	0	0.3	0.1	0	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0	0	0
Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

S 5. Main equations and references used for basic input parameters (Biomass (B), Production over Biomass (P/B), Consumption over Biomass, (Q/B), Diet (TL)) of the Mediterranean functional groups in the 1950 and 2000 periods. Information about species composition of each functional group is also given.

		Source			
Functional groups	**Equations**	**Western Med. Sea**	**Adriatic Sea**	**Ionian and central Med. Sea**	**Eastern and Levantine Sea**
Piscivores cetaceans: *Delphinus delphis, Stenella coeruleoalba, Tursiops truncatus*					
Biomass 1950s	Estimated by Ecopath		*(Bearzi et al. 2004)*		
Biomass 2000s		*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*
Production/Biomass	Life history table	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*
Consumption/Biomass	From modified energy requirement equation: $E = aW^{0.714}$	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*
Diet		*(Aguilar & Raga 1993, Würtz & Marrale 1993, Blanco et al. 1995, Blanco et al. 2001, Cañadas & Hammond 2008, Bearzi et al. 2009, Gómez-Campos et al. 2011)*	*(Bearzi et al. 2004, Fortuna 2006, Bearzi et al. 2009)*	*(Blanco et al. 1995, Bearzi et al. 2003, Bearzi et al. 2009, Piroddi et al. 2010)*	*(Blanco et al. 1995, Blanco et al. 2001, Bearzi et al. 2003, Bearzi et al. 2009)*
Other cetaceans: *Balaenoptera physalus, Globicephala melas, Grampus griseus, Physeter macrocephalus, Ziphius cavirostris*					
Biomass 1950s	Estimated by Ecopath				
Biomass 2000s		*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*	*(Reeves & Notarbartolo di Sciara 2006)*
Production/Biomass	Life history table	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*
Consumption/Biomass	From modified energy requirement equation: $E = aW^{0.714}$	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*
Diet		*(Würtz et al. 1992, Cañadas & Sagarminaga 2000, Drouot et al. 2004, Blanco et al. 2006, Canese et al. 2006, De Stephanis et al. 2008, Praca & Gannier 2008, Cotté et al. 2009, Rosso 2009, Bearzi et al. 2011)*	*(Santos et al. 2001, Reeves & Notarbartolo di Sciara 2006, Cotté et al. 2009)*	*(Santos et al. 2001, Reeves & Notarbartolo di Sciara 2006, Cotté et al. 2009, Bearzi et al. 2011)*	*(Santos et al. 2001, Shoham-Frider et al. 2002, Roberts 2003, Reeves & Notarbartolo di Sciara 2006, Cotté et al. 2009, Bearzi et al. 2011)*
Pinnipeds: *Monachus monachus*					
Biomass 1950s		*(Sergeant et al. 1978, UNEP/MAP 1994, Johnson & Lavigne 1998)*	*(Sergeant et al. 1978, UNEP/MAP 1994, Johnson & Lavigne 1998)*	*(Sergeant et al. 1978, UNEP/MAP 1994, Johnson & Lavigne 1998)*	*(Sergeant et al. 1978, UNEP/MAP 1994, Johnson & Lavigne 1998)*

Biomass 2000s		*(UNEP/MAP 2005, Mo et al. 2011)*	*(Gomerčić et al. 2011, Mo 2011)*	*(Panou et al. 1993, Notarbartolo di Sciara G. et al. 2009, Mo 2011)*	*(Güçlüsoy et al. 2004, Gucu et al. 2004, Notarbartolo di Sciara G. et al. 2009, Scheinin et al. 2011)*
Production/Biomass	Life history table	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*	*(Barlow & Boveng 1991)*
Consumption/Biomass	From modified energy requirement equation:E =aW$^{0.714}$	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*	*(Pauly et al. 1998, Hunter 2005)*
Diet		*(Salman et al. 2001, Karamanlidis et al. 2011, Pierce et al. 2011)*	*(Salman et al. 2001, Karamanlidis et al. 2011, Pierce et al. 2011)*	*(Salman et al. 2001, Karamanlidis et al. 2011, Pierce et al. 2011)*	*(Salman et al. 2001, Karamanlidis et al. 2011, Pierce et al. 2011)*
Seabirds: *Calonectris diomedea, Hydrobates pelagicus melitensis, Larus michahellis, Larus audouinii, Larus genei, Larus melanocephalus, Phalacrocorax aristotelis desmarestii, Puffinus yelkouan, Puffinus mauretanicus, Sterna nilotica, Sterna sandvicensis, Sterna caspia, Sterna hirundo, Sterna albifrons, Sterna bengalensis*					
Biomass 1950s		*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*
Biomass 2000s		*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*	*(Karpouzi et al. 2007, Paleczny 2012)*
Production/Biomass		*(Birdlife www.birdlife.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Birdlife www.birdlife.org; Coll et al. 2007, Coll et al. 2009)*	*(Birdlife www.birdlife.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Birdlife www.birdlife.org; Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Birdlife www.birdlife.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Birdlife www.birdlife.org; Coll et al. 2007, Coll et al. 2009)*	*(Birdlife www.birdlife.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Birdlife www.birdlife.org; Tsagarakis et al. 2010)*
Sea turtles: *Caretta caretta, Chelonia mydas*					
Biomass 1950s		*(Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Casale & Margaritoulis 2010)*	*(Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Casale & Margaritoulis 2010)*	*(Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Casale & Margaritoulis 2010)*	*(Kasparek & Baran 1989, Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Casale & Margaritoulis 2010)*
Biomass 2000s		*(Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Mingozzi et al. 2008, Bentivegna et al. 2010, Casale & Margaritoulis 2010, Lauriano et al. 2011)*	*(Groombridge 1990, Margaritoulis et al. 2003, Camiñas 2004, Mingozzi et al. 2008, Bentivegna et al. 2010, Casale & Margaritoulis 2010)*	*(Groombridge 1990, Margaritoulis & Rees 2001, Margaritoulis et al. 2003, Camiñas 2004, Mingozzi et al. 2008, Casale & Margaritoulis 2010)*	*(Groombridge, 1990; Margaritoulis et al., 2003; Camiñas, 2004; Casale and Margaritoulis, 2010)(Broderick & Godley 1996, Kasparek et al. 2001, Canbolat 2004, Yalçin-Özdilek & Yerlİ 2009)*
Production/Biomass	Z = survival rate	*(Coll et al. 2006, Coll et al. 2008, Casale et al. 2009, Wabnitz et al. 2010, Casale et al. 2011, Piovano et al. 2011)*	*(Coll et al. 2007, Casale et al. 2009, Coll et al. 2009, Casale et al. 2011, Piovano et al. 2011)*	*(Casale et al. 2009, Piroddi et al. 2010, Wabnitz et al. 2010, Casale et al. 2011, Piovano et al. 2011, Moutopoulos et al. 2013)*	*(Casale et al. 2009, Tsagarakis et al. 2010, Wabnitz et al. 2010, Casale et al. 2011, Piovano et al. 2011)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Wabnitz et al. 2010)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Wabnitz et al. 2010, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010, Wabnitz et al. 2010)*

Diet		*(Coll et al. 2006, Casale et al. 2008, Casale & Margaritoulis 2010, Wabnitz et al. 2010)*	*(Coll et al. 2007, Casale et al. 2008, Coll et al. 2009, Casale & Margaritoulis 2010)*	*(Casale & Margaritoulis 2010, Piroddi et al. 2010, Wabnitz et al. 2010, Moutopoulos et al. 2013)*	*(Casale et al. 2008, Casale & Margaritoulis 2010, Tsagarakis et al. 2010, Wabnitz et al. 2010)*
Large pelagics: *Coryphaena hippurus, Tetrapturus belone*, *Thunnus alalunga, Thunnus thynnus, Xiphias gladius*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1−N_t/k)−C_t$	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*((Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*
Biomass 2000s		*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(Fishstat www.fao.org; ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*
Production/Biomass 1950	Total mortality Z= F+M (Pauly 1980)	*(Coll et al. 2006, Coll et al. 2008, ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009, ICCAT 2010b, a, 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*	*(ICCAT 2010b, a, Piroddi et al. 2010, ICCAT 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(ICCAT 2010b, a, Tsagarakis et al. 2010, ICCAT 2011b, a, Ortiz de Zárate et al. 2011, ICCAT 2012)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
Medium pelagics: *Acanthocybium solandri, Alepes djedaba, Auxis rochei rochei, Auxis thazard thazard, Belone belone, Dicentrarchus punctatus, Euthynnus alletteratus, Katsuwonus pelamis, Lichia amia, Liza aurata, Orcynopsis unicolor, Pomatomus saltatrix, Sarda sarda, Scomber japonicus, Scomber scombrus, Scomberesox saurus saurus, Scomberomorus commerson, Seriola dumerili, Sphyraena sphyraena*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1−N_t/k)−C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Production/Biomass		*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
European pilchard: *Sardina pilchardus*					
Biomass 1950s	From a logist growth model:	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*

	$N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$				
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
European anchovy: *Engraulis encrasicolus*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
Other small pelagics: *Aphia minuta, Atherina hepsetus, Etrumeus sadina, Sardinella aurita, Spicara maena, Spicara smaris, Sprattus sprattus, Trachurus trachurus, Trachurus mediterraneus*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*

Production/Biomass		*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
1 **Large demersals:** ***Conger conger, Epinephelus aeneus, Epinephelus caninus, Epinephelus marginatus, Lophius piscatorius, Molva dypterygia, Muraena helena, Polyprion americanus***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
European hake: ***Merluccius merluccius***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*

Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
Medium demersals: ***Argyrosomus regius, Balistes capriscus, Campogramma glaycos, Cepola macrophthalma, Chelidonichthys lucerna, Chelon labrosus, Dactylopterus volitans, Dentex dentex, Dentex macrophthalmus, Dicentrarchus labrax, Epigonus telescopus, Eutrigla gurnardus, Labrus Merula, Lagocephalus sceleratus, Lepidopus caudatus,Lithognathus mormyrus, Lophius budegassa, Mugil cephalus, Naucrates ductor, Pagellus bogaraveo, Pagrus pagrus, Phycis blennoides, Platichthys flesus, Plectorhinchus mediterraneus, Sarpa salpa, Saurida undosquamis, Sciaena umbra, Scophthalmus maximus, Scophthalmus rhombus, Scorpaena scrofa, Solea solea, Sparisoma cretense, Sparus aurata, Spondyliosoma cantharus, Trisopterus luscus, Umbrina canariensis, Umbrina cirrosa, Zeus faber***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*
Small demersals: ***Atherina boyeri, Boops boops, Chelidonichthys cuculus, Dicologlossa cuneata, Diplodus annularis, Diplodus sargus sargus, Diplodus vulgaris, Gobius niger, Helicolenus dactylopterus, Lepidorhombus whiffiagonis, Merlangius merlangus, Mullus barbatus barbatus, Mullus surmuletus, Nemipterus randalli, Oblada melanura, Pagellus acarne, Pagellus erythrinus, Phycis phycis, Scorpaena porcus, Serranus cabrilla, Serranus scriba, Synodus saurus, Trachinus draco, Trisopterus minutes, Uranoscopus scaber, Xyrichtys novacula***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Stergiou & Karpouzi 2001, Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Stergiou & Karpouzi 2001, Coll et al. 2007, Coll et al. 2009)*	*(Stergiou & Karpouzi 2001, Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Stergiou & Karpouzi 2001, Tsagarakis et al. 2010)*

Deep fish: ***Alepocephalus rostratus, Argyropelecus hemigymnus, Bathypterois mediterraneus, Benthocometes robustus, Benthosema glaciale, Brama brama, Caelorhynchus caelorhynchus, Caelorhynchus mediterraneus, Cataetyx laticeps, Ceratoscopelus maderensis, Chalinura mediterranea, Chauliodus sloani, Chlorophthalmus agassizii, Coryphaenoides guentheri, Cyclothone braueri, Diaphus metopoclampus, Epigonus constanciae, Epigonus denticulatus, Epigonus telescopus, Halosaurus ovenii, Helicolenus dactylopterus, Hoplostethus mediterraneus, Hygophum benoiti, Hymenocephalus italicus, Lampanyctus crocodilus, Lepidion lepidion, Lepidopus caudatus, Lepidorhombus whiffiagonis, Micromesistius poutassou, Mora moro, Nettastoma melanorum, Nezumia aequalis, Nezumia sclerorhynchus, Notacanthus bonapartei, Notolepis rissoi, Paralepis speciosa, Polyacanthonotus rissoanus, Stomias boa, Trachyrhynchus trachyrhynchus, Trachyscorpia cristulata echinata***					
Biomass 1950s		*(Christensen et al. 2009)*	*(Christensen et al. 2009)*	*(Christensen et al. 2009)*	*(Christensen et al. 2009)*
Biomass 2000s		*(Wei et al. 2010, Tecchio et al. 2013)*	*(Wei et al. 2010)*	*(Wei et al. 2010)*	*(Wei et al. 2010)*
Production/Biomass		*(Christensen et al. 2009, Tecchio et al. 2013)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*
Consumption/Biomass		*(Christensen et al. 2009, Tecchio et al. 2013)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*
Diet		*(Christensen et al. 2009, Tecchio et al. 2013)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*	*(Christensen et al., 2009)*
Sharks: ***Alopias superciliosus, Alopias vulpinus, Carcharias taurus, Carcharodon carcharias, Centrophorus granulosus, Centrophorus granulosus, Centroscymnus coelolepis, Cetorhinus maximus, Chimaera monstrosa, Dalatias licha, Etmopterus spinax, Galeorhinus galeus, Galeus melastomus, Heptranchias perlo, Hexanchus griseus, Isurus oxyrinchus, Lamna nasus, Mustelus mustelus, Oxinotus centrina, Prionace glauca, Scyliorhinus canicula, Sharks nei, Somniosus rostratus, Squalus acanthias, Squalus blainville***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k) - C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Production/Biomass		*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Rays and skates: ***Dasyatis pastinaca, Leucoraja naevus, Gymnura altavela, Mobula mobular, Myliobatis aquila, Rays and Skates nei, Raja asterias, Raja clavata, Raja montagui, Rhinobatos rhinobatos, Rostroraja alba***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k) - C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*

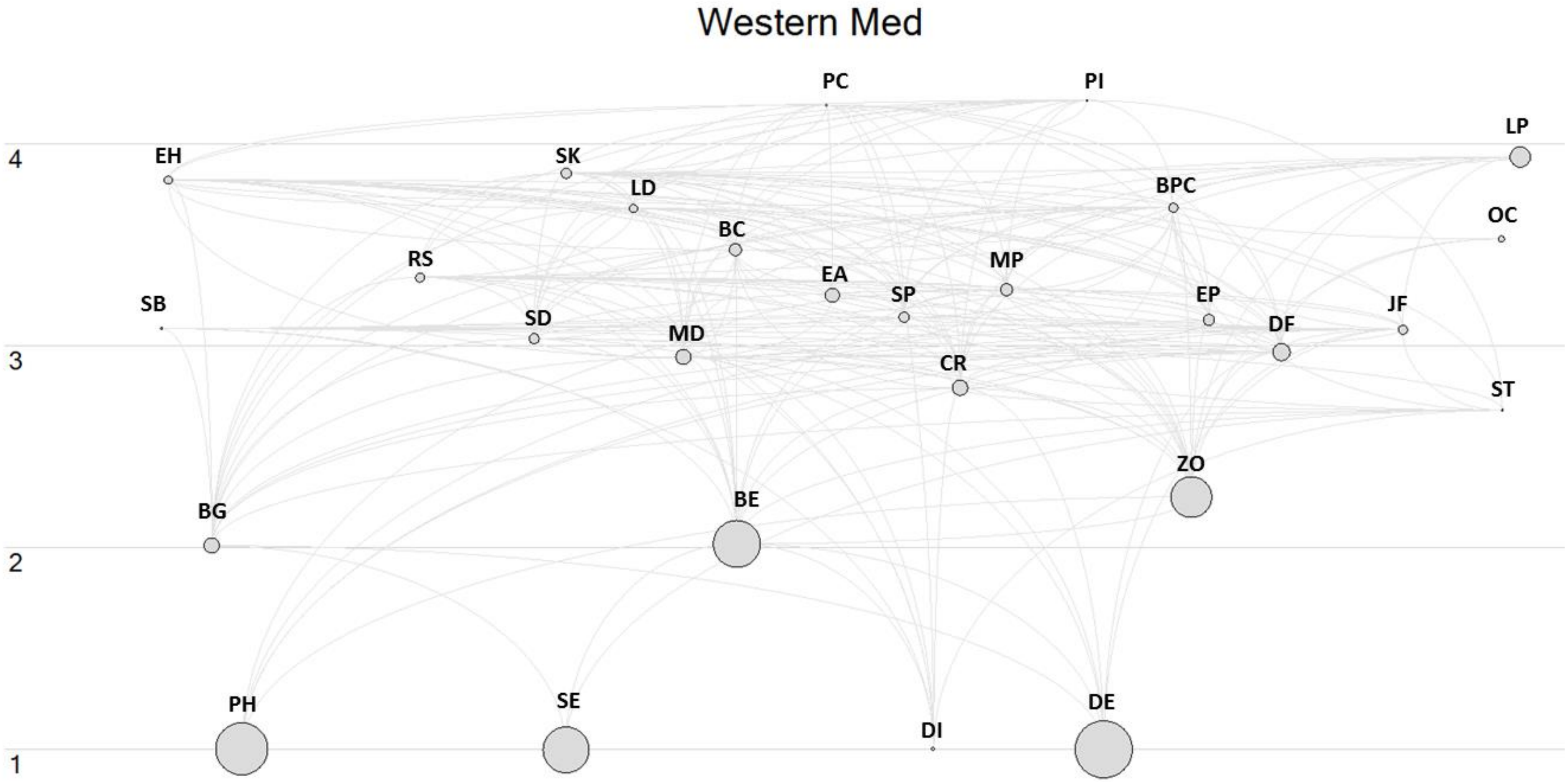
Production/Biomass		*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Benthopelagic Cephalopods: ***Alloteuthis media, Ancistroteuthis lichtensteini, Callista chione, Cerastoderma edule, Chamelea gallina, Crassostrea gigas, Donax vittatus, Eledone cirrhosa, Eledone moschata, Illex coindetii, Littorina littorea, Loligo vulgaris, Marine molluscs nei, Mytilus galloprovincialis, Octopus vulgaris, Ostrea edulis, Pecten jacobaeus, Pecten maximus, Ruditapes decussatus, Sepia officinalis, Todarodes sagittatus, Venerupis pullastra, Venus verrucosa***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Production/Biomass	Total mortality Z= F+M (Pauly, 1980)	*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Consumption/Biomass	From daily feeding rate equation FR = 0.0683 + 0.0474 W	*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Benthic Cephalopods: ***Alloteuthis media, Ancistroteuthis lichtensteini, Callista chione, Cerastoderma edule, Chamelea gallina, Crassostrea gigas, Donax vittatus, Eledone cirrhosa, Eledone moschata, Illex coindetii, Littorina littorea, Loligo vulgaris, Marine molluscs nei, Mytilus galloprovincialis, Octopus vulgaris, Ostrea edulis, Pecten jacobaeus, Pecten maximus, Ruditapes decussatus, Sepia officinalis, Todarodes sagittatus, Venerupis pullastra, Venus verrucosa***					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1-N_t/k)-C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Fishstat www.fao.org; Coll et al. 2006, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org; Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*
Production/Biomass		*(Fishstat www.fao.org; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007, Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Fishstat www.fao.org; Tsagarakis et al. 2010)*

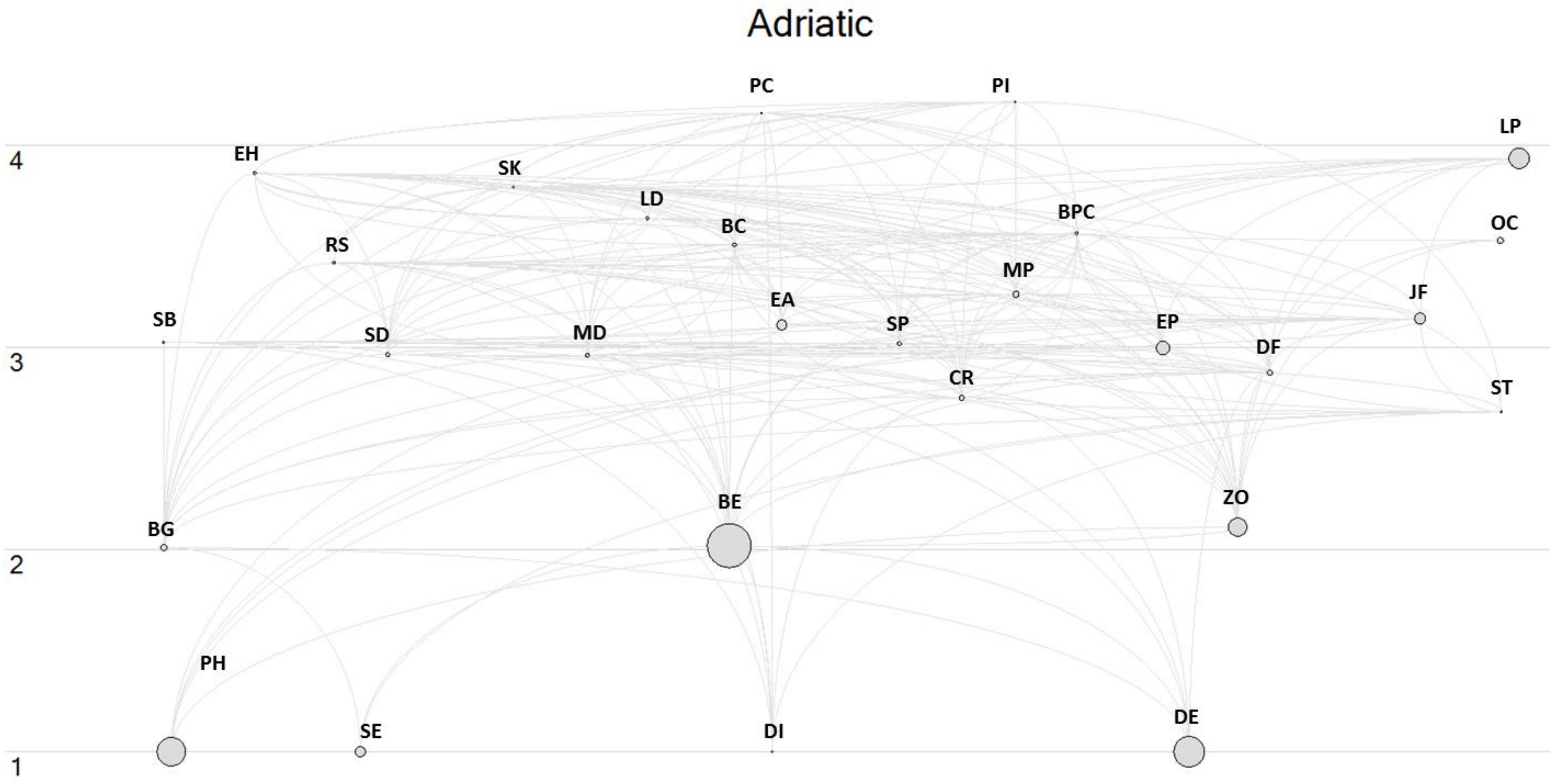
Consumption/Biomass		*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Bivalves and Gastropods: *Alloteuthis media, Ancistroteuthis lichtensteini, Callista chione, Cerastoderma edule, Chamelea gallina, Crassostrea gigas, Donax vittatus, Eledone cirrhosa, Eledone moschata, Illex coindetii, Littorina littorea, Loligo vulgaris, Marine molluscs nei, Mytilus galloprovincialis, Octopus vulgaris, Ostrea edulis, Pecten jacobaeus, Pecten maximus, Ruditapes decussatus, Sepia officinalis, Todarodes sagittatus, Venerupis pullastra, Venus verrucosa*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	*(Fishstat www.fao.org)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org)*	*(Fishstat www.fao.org)*
Biomass 2000s		*(Fishstat www.fao.org; Bănaru et al. 2013)*	*(Fishstat www.fao.org; Coll et al. 2007)*	*(Fishstat www.fao.org)*	*(Fishstat www.fao.org)*
Production/Biomass		*(Fishstat www.fao.org; Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*
Consumption/Biomass		*(Bănaru et al., 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*
Diet		*(Bănaru et al., 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Coll et al. 2007, Coll et al. 2009)*
Crustaceans: *Aristaeomorpha foliacea, Aristeus antennatus, Carcinus aestuarii, Crangon crangon, Erugosquilla massavensis, Homarus gammarus, Maja squinado, Marine crustaceans nei, Marsupenaeus japonicus, Melicertus kerathurus, Metapenaeus monoceros, Nephrops norvegicus, Palaemon serratus, Palinurus elephas, Palinurus mauritanicus, Parapenaeus longirostris, Plesionika martia, Portunus pelagicus, Scyllarides latus, Squilla mantis*					
Biomass 1950s	From a logist growth model: $N_{t+1} = N_t + rN_t(1 - N_t/k) - C_t$	*(Fishstat www.fao.org; Coll et al. 2008)*	*(Fishstat www.fao.org; Coll et al. 2009)*	*(Fishstat www.fao.org; Piroddi et al. 2010)*	*Fishstat www.fao.org*
Biomass 2000s		*(Coll et al. 2006, STECF 2010a, b, 2011a, b, 2012a, b, Bănaru et al. 2013, STECF 2013a, b)*	*(Coll et al. 2007, STECF 2010a, b, 2011a, b, 2012a, b, 2013a, b)*	*(STECF 2010a, b, Piroddi et al. 2011, STECF 2011a, b, 2012a, b, Hattab et al. 2013, Moutopoulos et al. 2013, STECF 2013a, b)*	*(STECF 2010a, b, Tsagarakis et al. 2010, STECF 2011a, b, 2012a, b, 2013a, b)*
Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Piroddi et al. 2011, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al. 2010, Hattab et al. 2013, Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Jellyfish: *Aequorea forskalea, Aurelia aurita, Pelagia noctiluca, Chrysaora hysoscella, Cotylorhiza tuberculata, Liriope tetraphylla, Mnemiopsis leidyi , Pleurobrachia rhodopis, Physalia physalis, Rhizostoma pulmo*					
Biomass 1950s		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Biomass 2000s		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*

Production/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Consumption/Biomass		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Diet		*(Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Moutopoulos et al. 2013)*	*(Tsagarakis et al. 2010)*
Benthos: cnidarians, sponges, tunicates, echinoderms, worms					
Biomass 1950s		*(Coll et al., 2008)*	*(Coll et al. 2007, Coll et al. 2009)*	*(Piroddi et al., 2010)*	*(Tsagarakis et al. 2010)*
Biomass 2000s		*(Wei et al., 2010; Coll et al. 2006, Coll et al. 2008, Bănaru et al. 2013)*	*(Wei et al., 2010; Coll et al., 2007; Wei et al., 2010)*	*(Wei et al., 2010; Piroddi et al., 2011; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Wei et al., 2010; Tsagarakis et al., 2010)*
Production/Biomass		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2011; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Consumption/Biomass		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2011; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Diet		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2010; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Zooplankton: meso and macro zooplankton (amphipods, copepods, cladocerans, euphasids, mysids, pteropods)					
Biomass 1950s		*(NOAA www.st.nmfs.noaa.gov; Coll et al., 2008)*	*(NOAA www.st.nmfs.noaa.gov; Coll et al., 2009)*	*(NOAA www.st.nmfs.noaa.gov; Piroddi et al., 2010)*	*(NOAA www.st.nmfs.noaa.gov)*
Biomass 2000s		*(Coll et al., 2006; Siokou-Frangou et al., 2010; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Siokou-Frangou et al., 2010;)*	*(Siokou-Frangou et al., 2010; Piroddi et al., 2011; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Siokou-Frangou et al., 2010; Tsagarakis et al., 2010)*
Production/Biomass		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2010; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Consumption/Biomass		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2010; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Diet		*(Coll et al., 2006; Coll et al., 2008; Bănaru et al., 2013; Tecchio et al., 2013)*	*(Coll et al., 2007; Coll et al., 2009)*	*(Piroddi et al., 2010; Hattab et al., 2013; Moutopoulos et al., 2013)*	*(Tsagarakis et al., 2010)*
Seagrass: ***Cymodocea nodosa, Posidonia oceanica, Zoostera marina, Zoostera noltii***					
Biomass 1950s		*(Ardizzone et al., 2006; Duarte et al., 2009; Giannoulaki M. et al., 2013)*	*(Guidetti et al., 2002; Duarte et al., 2009; Giannoulaki et al., 2013)*	*Duarte et al., 2009; Giannoulaki et al., 2013)*	*Duarte et al., 2009; Giannoulaki et al., 2013)*
Biomass 2000s		*(Bay, 1984; Casola et al., 1987; Duarte and Sand-Jensen, 1990; Pergent et al., 1994;*	*(Duarte and Sand-Jensen, 1990; Pergent et al., 1994;Duarte and Chiscano, 1999; Guidetti et al., 2002;*	*(Duarte and Sand-Jensen, 1990; Pergent et al., 1994;Duarte and Chiscano, 1999; Mustapha et al., 2004;Badalamenti et al.,*	*(Duarte and Sand-Jensen, 1990; Pergent et al., 1994;Duarte and Chiscano, 1999; Dural et al.,*

		Marbá et al., 1996;Cebrián et al., 1997; Duarte et al., 1998; Duarte and Chiscano, 1999; Cebrián et al., 2000; Cebrian and Duarte, 2001; Cancemi et al., 2002; Ardizzone et al., 2006; Giakoumi et al., 2013; Giannoulaki et al., 2013)	*Giakoumi et al., 2013; Giannoulaki et al., 2013)*	*2006; Borg et al., 2009; Ben Brahim et al., 2010; Costantino et al., 2010; Giakoumi et al., 2013; Giannoulaki et al., 2013; Sghaier et al., 2013)*	*2012; Giakoumi et al., 2013; Giannoulaki et al., 2013)*
Production/Biomass		*(Bay, 1984; Pergent et al., 1994; Marbá et al., 1996; Cebrián et al., 1997; Duarte et al., 1998; Duarte and Chiscano, 1999; Hemminga and Duarte, 2000; Cebrián et al., 2000; Marbà and Duarte, 2001; Cancemi et al., 2002;*	*(Peduzzi and Vukovic, 1990; Pergent et al., 1994;Duarte and Chiscano, 1999; Hemminga and Duarte, 2000)*	*(Pergent et al., 1994;Duarte and Chiscano, 1999; Hemminga and Duarte, 2000; Mustapha et al., 2004; Sghaier et al., 2013)*	*(Pergent et al., 1994;Duarte and Chiscano, 1999; Hemminga and Duarte, 2000)*
Phytoplankton: Diatoms, dinoflagellates					
Biomass 1950s		*(Macias et al., 2014)*	*(Macias et al., 2014)*	*(Macias et al., 2014)*	*(Macias et al., 2014)*
Biomass 2000s		*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010)*
Production/Biomass		*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010; Macias et al., 2014)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010; Macias et al., 2014)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010; Macias et al., 2014)*	*(EMIS emis.jrc.ec.europa.eu; Siokou-Frangou et al., 2010; Macias et al., 2014)*

S 6. Flow diagram (year 2000s) presented per each MSFD area where each functional group is shown as a circle and its size is approximately proportional to the log of its biomass. All the functional groups are represented by their trophic levels (y-axis) and linked to each other by predator-prey relationships expressed as light grey lines. For the abbreviations, please refer to Table 1.




Adriatic
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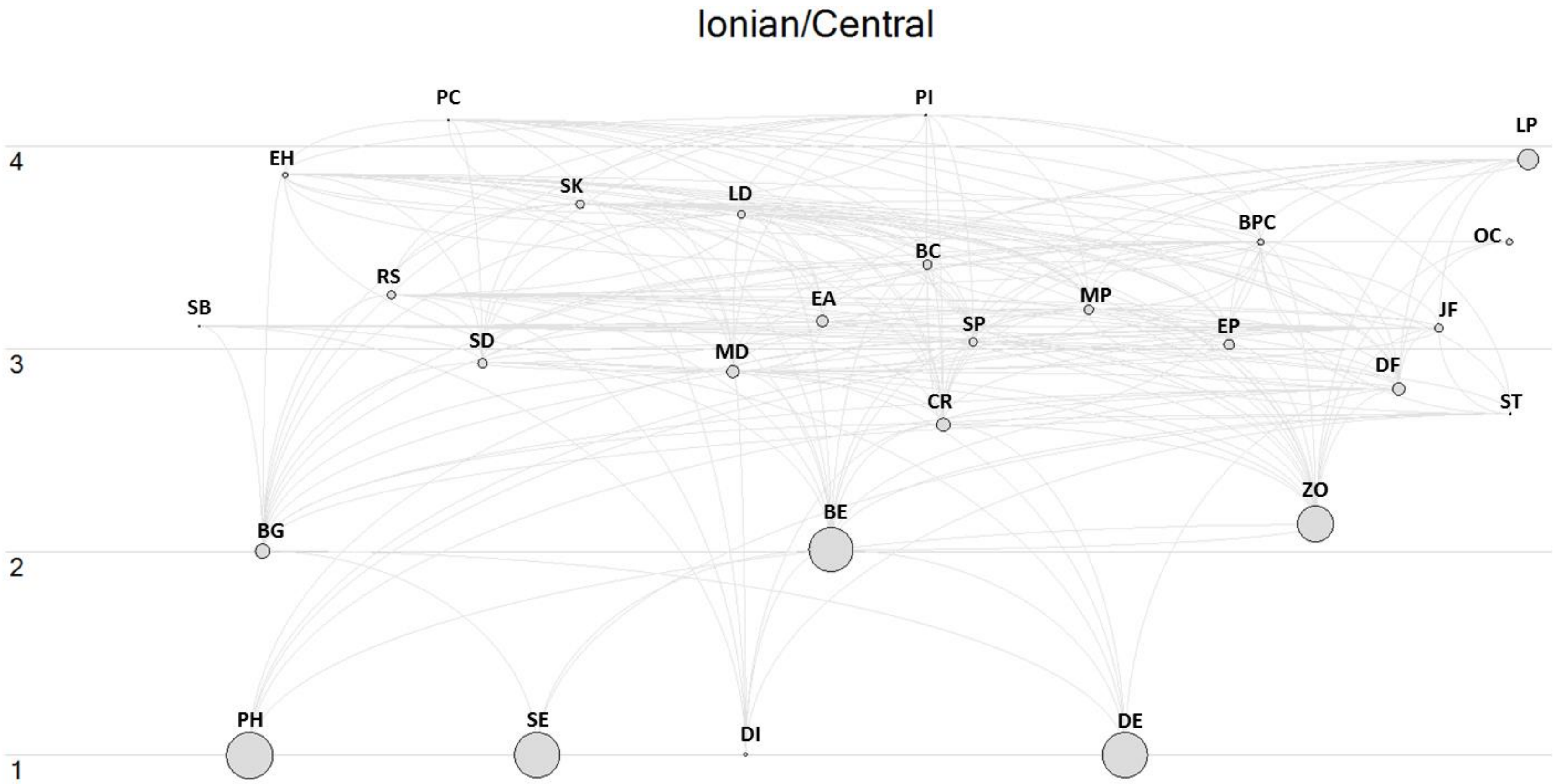
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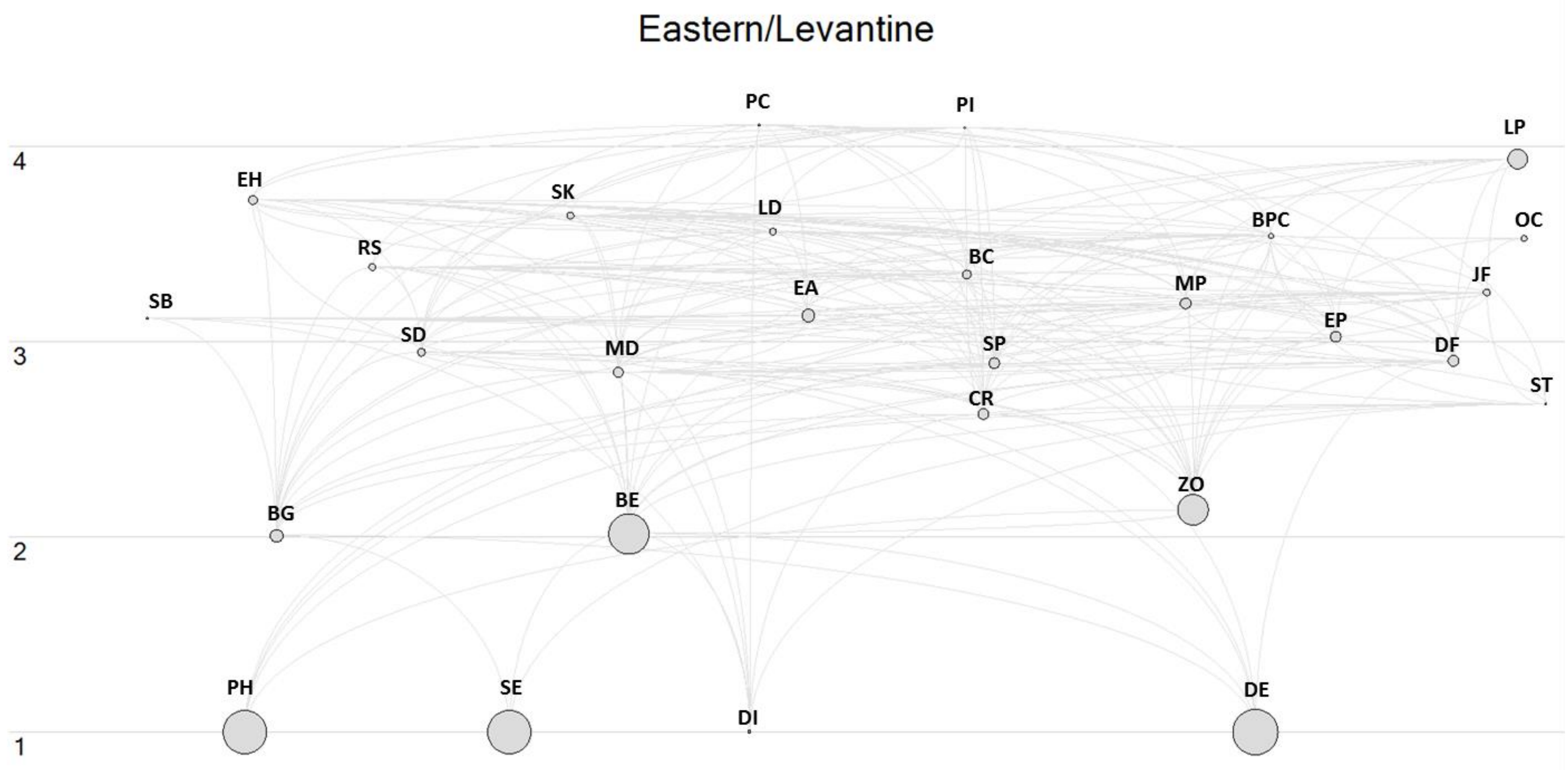
Eastern/Levantine
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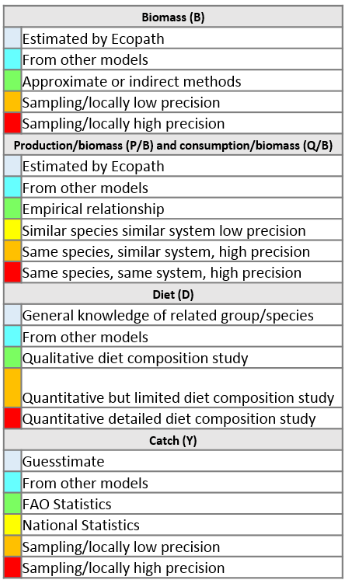
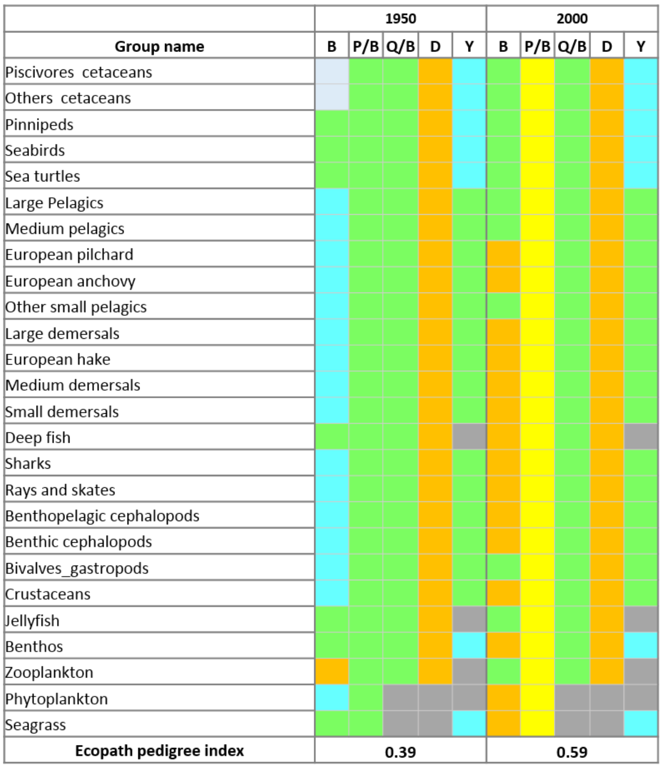
S 7. Pedigree chart of EwE basic input parameters for the Mediterranean Sea model. Definition of color codes for each parameter are given below. A quantitative description of these colors can be found as well in Christensen et al (2008).



	Biomass (B)
⬜	Estimated by Ecopath
🟦	From other models
🟩	Approximate or indirect methods
🟧	Sampling/locally low precision
🟥	Sampling/locally high precision
	Production/biomass (P/B) and consumption/biomass (Q/B)
⬜	Estimated by Ecopath
🟦	From other models
🟩	Empirical relationship
🟨	Similar species similar system low precision
🟧	Same species, similar system, high precision
🟥	Same species, same system, high precision
	Diet (D)
⬜	General knowledge of related group/species
🟦	From other models
🟩	Qualitative diet composition study
🟧	Quantitative but limited diet composition study
🟥	Quantitative detailed diet composition study
	Catch (Y)
⬜	Guesstimate
🟦	From other models
🟩	FAO Statistics
🟨	National Statistics
🟧	Sampling/locally low precision
🟥	Sampling/locally high precision



	1950					2000				
Group name	**B**	**P/B**	**Q/B**	**D**	**Y**	**B**	**P/B**	**Q/B**	**D**	**Y**
Piscivores cetaceans	⬜	🟩	🟩	🟧	🟦	🟩	🟨	🟩	🟧	🟦
Others cetaceans	⬜	🟩	🟩	🟧	🟦	🟩	🟨	🟩	🟧	🟦
Pinnipeds	🟩	🟩	🟩	🟧	🟦	🟩	🟨	🟩	🟧	🟦
Seabirds	🟩	🟩	🟩	🟧	🟦	🟩	🟨	🟩	🟧	🟦
Sea turtles	🟩	🟩	🟩	🟧	🟦	🟩	🟨	🟩	🟧	🟦
Large Pelagics	🟦	🟩	🟩	🟧	🟩	🟩	🟨	🟩	🟧	🟩
Medium pelagics	🟦	🟩	🟩	🟧	🟩	🟩	🟨	🟩	🟧	🟩
European pilchard	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
European anchovy	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Other small pelagics	🟦	🟩	🟩	🟧	🟩	🟩	🟨	🟩	🟧	🟩
Large demersals	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
European hake	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Medium demersals	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Small demersals	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Deep fish	🟩	🟩	🟩	🟧	▨	🟧	🟨	🟩	🟧	▨
Sharks	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Rays and skates	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Benthopelagic cephalopods	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Benthic cephalopods	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Bivalves_gastropods	🟦	🟩	🟩	🟧	🟩	🟩	🟨	🟩	🟧	🟩
Crustaceans	🟦	🟩	🟩	🟧	🟩	🟧	🟨	🟩	🟧	🟩
Jellyfish	🟩	🟩	🟩	🟧	▨	🟩	🟨	🟩	🟧	▨
Benthos	🟩	🟩	🟩	🟧	🟦	🟧	🟨	🟩	🟧	🟦
Zooplankton	🟧	🟩	🟩	🟧	▨	🟩	🟨	🟩	🟧	▨
Phytoplankton	🟦	🟩	▨	▨	▨	🟧	🟨	▨	▨	▨
Seagrass	🟩	🟩	▨	▨	🟦	🟧	🟨	▨	▨	🟦
Ecopath pedigree index	**0.39**					**0.59**				

S 8. Keystoneness index (KSi) and relative total impact (ε_i) from the least to the most important pecies/groups in the ecosystem and for the two time periods.

	1950				2000s		
#	**Group name**	**Keystone index**	**Relative total impact**	**#**	**Group name**	**Keystone index**	**Relative total impact**
28	Pinnipeds A	-4.163	0.000071	28	Pinnipeds A	-5.074	0.000007
51	Pinnipeds I	-3.662	0.000225	3	Pinnipeds W	-4.806	0.000014
3	Pinnipeds W	-3.608	0.000255	51	Pinnipeds I	-4.549	0.000025
74	Pinnipeds E	-3.065	0.000890	74	Pinnipeds E	-3.355	0.000388
29	Seabirds A	-2.629	0.002	27	Piscivores cetaceans A	-2.777	0.001
27	Piscivores cetaceans A	-2.451	0.004	5	Sea turtles	-2.627	0.002
73	Piscivores cetaceans E	-2.189	0.007	29	Seabirds A	-2.546	0.003
52	Seabirds I	-2.167	0.007	73	Piscivores cetaceans E	-2.473	0.003
50	Piscivores cetaceans I	-2.156	0.007	50	Piscivores cetaceans I	-2.434	0.003
4	Seabirds W	-1.753	0.018	52	Seabirds I	-2.050	0.008
5	Sea turtles	-1.727	0.019	91	Jellyfish E	-1.491	0.028
75	Seabirds E	-1.573	0.028	4	Seabirds W	-1.470	0.030
91	Jellyfish E	-1.519	0.031	68	Jellyfish I	-1.322	0.042
68	Jellyfish I	-1.443	0.037	75	Seabirds E	-1.321	0.042
10	Other small pelagics W	-1.198	0.066	1	Piscivores cetaceans W	-1.257	0.049
22	Jellyfish W	-1.148	0.074	22	Jellyfish W	-1.243	0.050
1	Piscivores cetaceans W	-1.072	0.088	38	Deep fish A	-1.038	0.081
56	Other small pelagics I	-1.005	0.103	33	Other small pelagics A	-1.023	0.083
33	Other small pelagics A	-0.999	0.104	10	Other small pelagics W	-0.956	0.097
38	Deep fish A	-0.973	0.110	37	Small demersals A	-0.924	0.105
26	Seagrass W	-0.920	0.138	26	Seagrass W	-0.907	0.118
79	Other small pelagics E	-0.908	0.128	95	Seagrass E	-0.899	0.119
9	European anchovy W	-0.904	0.129	72	Seagrass I	-0.898	0.119
72	Seagrass I	-0.903	0.142	84	Deep fish E	-0.886	0.115
95	Seagrass E	-0.899	0.143	61	Deep fish I	-0.879	0.116
61	Deep fish I	-0.887	0.135	49	Seagrass A	-0.838	0.128
84	Deep fish E	-0.877	0.138	55	European anchovy I	-0.832	0.130
37	Small demersals A	-0.856	0.144	60	Small demersals I	-0.817	0.134
49	Seagrass A	-0.850	0.146	56	Other small pelagics I	-0.816	0.135
60	Small demersals I	-0.845	0.148	83	Small demersals E	-0.806	0.137
55	European anchovy I	-0.829	0.154	14	Small demersals W	-0.801	0.139
78	European anchovy E	-0.793	0.168	9	European anchovy W	-0.796	0.141
32	European anchovy A	-0.789	0.169	34	Large demersals A	-0.783	0.145
83	Small demersals E	-0.782	0.171	79	Other small pelagics E	-0.779	0.147
45	Jellyfish A	-0.779	0.172	32	European anchovy A	-0.756	0.154
14	Small demersals W	-0.762	0.179	66	Bivalves and gastropods I	-0.746	0.158
34	Large demersals A	-0.721	0.197	45	Jellyfish A	-0.744	0.159
15	Deep fish W	-0.712	0.202	89	Bivalves and gastropods E	-0.743	0.159
20	Bivalves_gastropods W	-0.708	0.204	43	Bivalves and gastropods A	-0.740	0.160
89	Bivalves_gastropods E	-0.707	0.204	40	Rays A	-0.702	0.175
66	Bivalves_gastropods I	-0.701	0.207	20	Bivalves and gastropods W	-0.697	0.177
11	Large demersals W	-0.700	0.207	11	Large demersals W	-0.695	0.178
40	Rays and skates A	-0.665	0.224	8	European pilchard W	-0.672	0.188
77	European pilchard E	-0.638	0.239	15	Deep fish W	-0.668	0.190
54	European pilchard I	-0.637	0.239	77	European pilchard E	-0.659	0.193
80	Large demersals E	-0.615	0.251	31	European pilchard A	-0.648	0.198
43	Bivalves_gastropods A	-0.610	0.254	54	European pilchard I	-0.648	0.198
31	European pilchard A	-0.608	0.256	57	Large demersals I	-0.604	0.219
8	European pilchard W	-0.607	0.256	78	European anchovy E	-0.599	0.222
57	Large demersals I	-0.606	0.256	35	European hake A	-0.570	0.237
35	European hake A	-0.602	0.259	80	Large demersals E	-0.568	0.238
58	European hake I	-0.526	0.308	36	Medium demersals A	-0.558	0.243
90	Crustaceans E	-0.479	0.345	58	European hake I	-0.547	0.250
12	European hake W	-0.475	0.347	12	European hake W	-0.536	0.256
36	Medium demersals A	-0.473	0.348	2	Others cetaceans	-0.531	0.259
82	Medium demersals E	-0.460	0.359	82	Medium demersals E	-0.507	0.274
44	Crustaceans A	-0.445	0.372	21	Crustaceans W	-0.446	0.316
63	Rays and skates I	-0.430	0.384	17	Rays W	-0.443	0.317

21	Crustaceans W	-0.411	0.403	44	Crustaceans A	-0.433	0.325
2	Others cetaceans	-0.398	0.414	63	Rays I	-0.429	0.328
17	Rays and skates W	-0.387	0.425	7	Medium pelagics W	-0.428	0.329
67	Crustaceans I	-0.386	0.427	90	Crustaceans E	-0.421	0.334
13	Medium demersals W	-0.376	0.437	86	Rays E	-0.412	0.341
86	Rays and skates E	-0.372	0.440	30	Medium Pelagics A	-0.402	0.349
81	European hake E	-0.326	0.490	59	Medium demersals I	-0.388	0.360
7	Medium pelagics W	-0.304	0.515	13	Medium demersals W	-0.380	0.368
59	Medium demersals I	-0.301	0.519	67	Crustaceans I	-0.380	0.368
46	Benthos A	-0.259	0.610	81	European hake E	-0.366	0.379
65	Benthic cephalopods I	-0.245	0.589	76	Medium Pelagics E	-0.332	0.411
25	Phytoplankton W	-0.239	0.670	62	Sharks I	-0.265	0.478
88	Benthic cephalopods E	-0.235	0.603	25	Phytoplankton W	-0.263	0.549
41	Benthopelagic cephalopods A	-0.228	0.612	88	Benthic Cephalopods E	-0.246	0.499
42	Benthic cephalopods A	-0.226	0.615	42	Benthic Cephalopods A	-0.245	0.500
19	Benthic cephalopods W	-0.222	0.622	46	Benthos A	-0.243	0.536
87	Benthopelagic cephalopods E	-0.210	0.638	41	Benthopelagic Cephalopods A	-0.237	0.510
62	Sharks I	-0.206	0.645	93	Zooplankton E	-0.237	0.520
76	Medium Pelagics E	-0.205	0.648	53	Medium Pelagics I	-0.236	0.511
93	Zooplankton E	-0.205	0.659	85	Skarks E	-0.235	0.512
39	Sharks A	-0.199	0.654	65	Benthic Cephalopods I	-0.230	0.518
18	Benthopelagic cephalopods W	-0.198	0.657	94	Phytoplankton E	-0.205	0.588
23	Benthos W	-0.189	0.741	64	Benthopelagic Cephalopods I	-0.204	0.550
70	Zooplankton I	-0.188	0.685	70	Zooplankton I	-0.200	0.573
24	Zooplankton W	-0.184	0.709	24	Zooplankton W	-0.198	0.587
16	Sharks W	-0.179	0.687	19	Benthic Cephalopods W	-0.197	0.560
94	Phytoplankton E	-0.178	0.723	23	Benthos W	-0.191	0.616
47	Zooplankton A	-0.171	0.702	71	Phytoplankton I	-0.191	0.615
64	Benthopelagic cephalopods I	-0.169	0.702	87	Benthopelagic Cephalopods E	-0.185	0.574
30	Medium Pelagics A	-0.168	0.703	18	Benthopelagic Cephalopods W	-0.183	0.577
48	Phytoplankton A	-0.166	0.716	47	Zooplankton A	-0.177	0.589
71	Phytoplankton I	-0.165	0.737	48	Phytoplankton A	-0.174	0.600
53	Medium Pelagics I	-0.160	0.717	16	Sharks W	-0.148	0.626
85	Skarks E	-0.155	0.724	69	Benthos I	-0.146	0.670
69	Benthos I	-0.146	0.789	92	Benthos E	-0.144	0.665
92	Benthos E	-0.134	0.804	39	Sharks A	-0.117	0.672
6	Large Pelagics	-0.018	1.000	6	Large Pelagics	0.053	1.000

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S1. List of functional groups and fisheries and their abbreviations included in the Ecopath food web model and time series data sources used in the Ecosim dynamic modelling. Functional groups and fisheries categories are the same in each Marine Strategy Framework Directive (MSFD) area but their composition differ per area. This is not the case for highly migratory species (2. 'other cetaceans'; 5. 'sea turtles' and 6. 'large pelagic fish') that are common for all areas and they are allowed to move and feed in all the four sub-models [19]. NA, not available.

#	Functional groups/fisheries	Source of biomass time series	Source of catch time series
1	**Piscivorous cetaceans (PC):** *Delphinus delphis, Stenella coeruleoalba, Tursiops truncatus*	NA	
2	**Others cetaceans (OC):** *Balaenoptera physalus, Globicephala melas, Grampus griseus, Physeter macrocephalus, Ziphius cavirostris*	NA	
3	**Pinnipeds (PI):** *Monachus monachus*	[1-12]	
4	**Seabirds (SB):** *Calonectris diomedea, Hydrobates pelagicus melitensis, Larus michahellis, Larus audouinii, Larus genei, Larus melanocephalus, Phalacrocorax carbo, Puffinus yelkouan, Puffinus mauretanicus, Sterna nilotica, Sterna sandvicensis, Sterna caspia, Sterna hirundo, Sterna albifrons, Sterna bengalensis*	NA	
5	**Sea turtles (ST):** *Caretta caretta, Chelonia mydas*	[13-25]	
6	**Large Pelagics (LP):** *Coryphaena hippurus, Tetrapturus belone, Thunnus alalunga, Thunnus thynnus, Xiphias gladius*	[26]	FishSTAT (FAO); ICCAT
7	**Medium pelagics (MP):** *Acanthocybium solandri, Alepes djedaba, Auxis rochei rochei, Auxis thazard thazard, Belone belone, Dicentrarchus punctatus, Euthynnus alletteratus, Katsuwonus pelamis, Lichia amia, Liza aurata, Orcynopsis unicolor, Pomatomus saltatrix, Sarda sarda, Scomber japonicus, Scomber scombrus, Scomberesox saurus saurus, Scomberomorus commerson, Seriola dumerili, Sphyraena sphyraena*	NA	FishSTAT (FAO)
8	**European pilchard (EP):** *Sardina pilchardus*	[27-43]	FishSTAT (FAO)
9	**European anchovy /EA):** *Engraulis encrasicolus*	[27, 28, 32-44]	FishSTAT (FAO)
10	**Other small pelagics (SP):** *Aphia minuta, Atherina hepsetus, Etrumeus sadina, Sardinella aurita, Spicara maena, Spicara smaris, Sprattus sprattus, Trachurus trachurus, Trachurus mediterraneus*	NA	FishSTAT (FAO)
11	**Large demersals (LD):** *Conger conger, Epinephelus aeneus, Epinephelus caninus, Epinephelus marginatus, Lophius piscatorius, Molva dypterygia, Muraena helena, Polyprion americanus*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
12	**European hake (HK):** *Merluccius merluccius*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)

13	**Medium demersals (MD):** *Argyrosomus regius, Balistes capriscus, Campogramma glaycos, Cepola macrophthalma, Chelidonichthys lucerna, Chelon labrosus, Dactylopterus volitans, Dentex dentex, Dentex macrophthalmus, Dicentrarchus labrax, Epigonus telescopus, Eutrigla gurnardus, Labrus Merula, Lagocephalus sceleratus, Lepidopus caudatus,Lithognathus mormyrus, Lophius budegassa, Mugil cephalus, Naucrates ductor, Pagellus bogaraveo, Pagrus pagrus, Phycis blennoides, Platichthys flesus, Plectorhinchus mediterraneus, Sarpa salpa, Saurida undosquamis, Sciaena umbra, Scophthalmus maximus, Scophthalmus rhombus, Scorpaena scrofa, Solea solea, Sparisoma cretense, Sparus aurata, Spondyliosoma cantharus, Trisopterus luscus, Umbrina canariensis, Umbrina cirrosa, Zeus faber*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
14	**Small demersals (SD):** *Atherina boyeri, Boops boops, Chelidonichthys cuculus, Dicologlossa cuneata, Diplodus annularis, Diplodus sargus sargus, Diplodus vulgaris, Gobius niger, Helicolenus dactylopterus, Lepidorhombus whiffiagonis, Merlangius merlangus, Mullus barbatus barbatus, Mullus surmuletus, Nemipterus randalli, Oblada melanura, Pagellus acarne, Pagellus erythrinus, Phycis phycis, Scorpaena porcus, Serranus cabrilla, Serranus scriba, Synodus saurus, Trachinus draco, Trisopterus minutes, Uranoscopus scaber, Xyrichtys novacula*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
15	**Deep sea fish (DF):** *Alepocephalus rostratus, Argyropelecus hemigymnus, Bathypterois mediterraneus, Benthocometes robustus, Benthosema glaciale, Brama brama, Caelorhynchus caelorhynchus, Caelorhynchus mediterraneus, Cataetyx laticeps, Ceratoscopelus maderensis, Chalinura mediterranea, Chauliodus sloani, Chlorophthalmus agassizii, Coryphaenoides guentheri, Cyclothone braueri, Diaphus metopoclampus, Epigonus constanciae, Epigonus denticulatus, Epigonus telescopus, Halosaurus ovenii, Helicolenus dactylopterus, Hoplostethus mediterraneus, Hygophum benoiti, Hymenocephalus italicus, Lampanyctus crocodilus, Lepidion lepidion, Lepidopus caudatus, Lepidorhombus whiffiagonis, Micromesistius poutassou, Mora moro, Nettastoma melanorum, Nezumia aequalis, Nezumia sclerorhynchus, Notacanthus bonapartei, Notolepis rissoi, Paralepis speciosa, Polyacanthonotus rissoanus, Stomias boa, Trachyrhynchus trachyrhynchus, Trachyscorpia cristulata echinata*	[45]	
16	**Sharks (SK):** Alopias superciliosus, Alopias vulpinus, Carcharias taurus, Carcharodon carcharias, Centrophorus granulosus, Centrophorus granulosus, Centroscymnus coelolepis, Cetorhinus maximus, Chimaera monstrosa, Dalatias licha, Etmopterus spinax, Galeorhinus galeus, Galeus melastomus, Heptranchias perlo,	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)

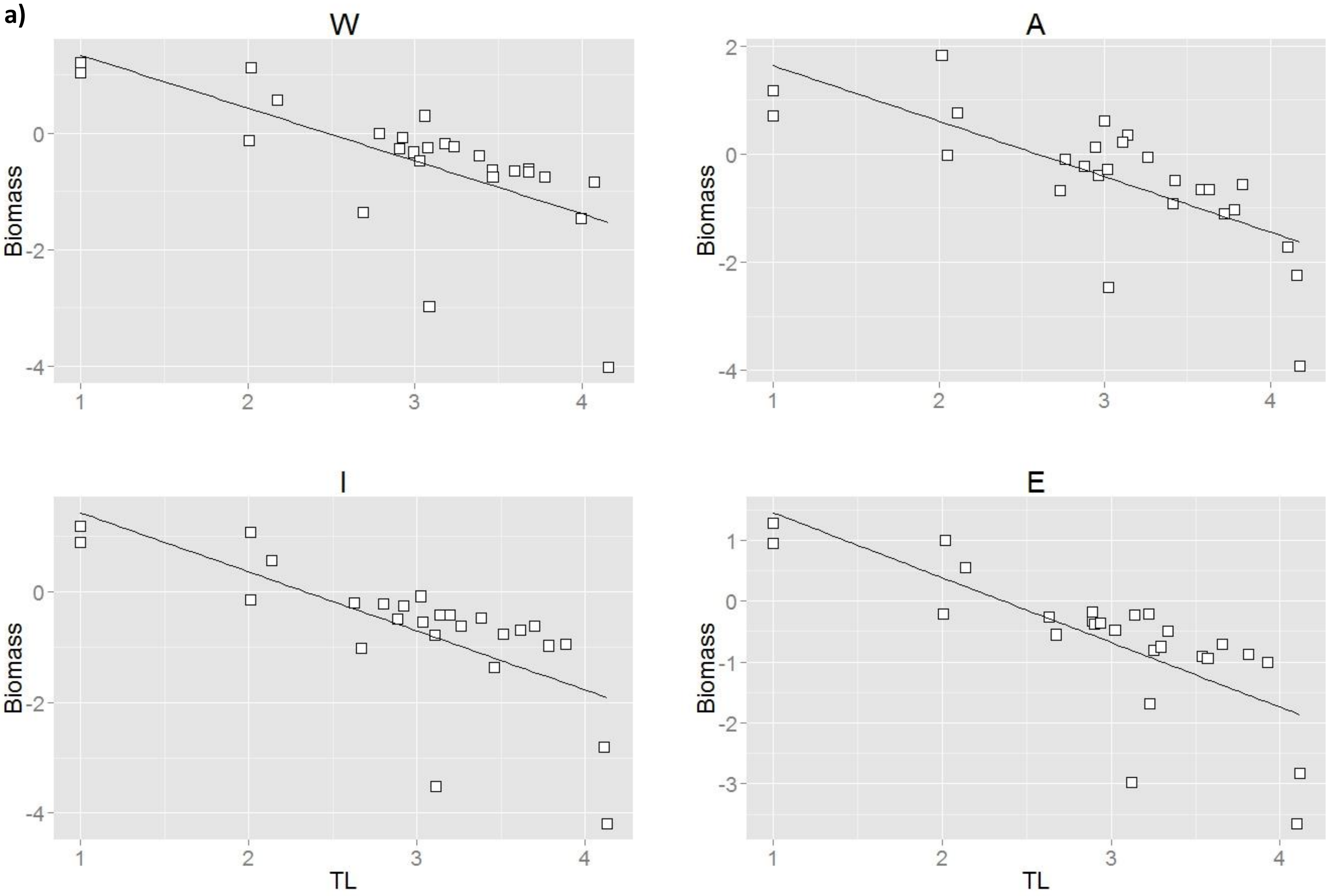
	Hexanchus griseus, Isurus oxyrinchus, Lamna nasus, Mustelus mustelus, Oxinotus centrina, Prionace glauca, Scyliorhinus canicula, Sharks nei, Somniosus rostratus, Squalus acanthias, Squalus blainville		
17	**Rays and skates (RS):** *Dasyatis pastinaca, Leucoraja naevus, Gymnura altavela, Mobula mobular, Myliobatis aquila, Rays and Skates nei, Raja asterias, Raja clavata, Raja montagui, Rhinobatos rhinobatos, Rostroraja alba*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
18	**Benthopelagic cephalopods (BPC):** *Alloteuthis media, Ancistroteuthis lichtensteini, Illex coindetii, Loligo vulgaris, Marine molluscs nei, Ostrea edulis, Sepia officinalis, Todarodes sagittatus*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
19	**Benthic cephalopods (BC)**: *Eledone cirrhosa, Eledone moschata, Marine molluscs nei, Octopus vulgaris*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
20	**Bivalves_gastropods (BG):** *Callista chione, Cerastoderma edule, Chamelea gallina, Crassostrea gigas, Donax vittatus, Littorina littorea, Marine molluscs nei, Mytilus galloprovincialis, Ostrea edulis, Pecten jacobaeus, Pecten maximus, Ruditapes decussatus, Venerupis pullastra, Venus verrucosa*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
21	**Crustaceans (CR):** *Aristaeomorpha foliacea, Aristeus antennatus, Carcinus aestuarii, Crangon crangon, Erugosquilla massavensis, Homarus gammarus, Maja squinado, Marine crustaceans nei, Marsupenaeus japonicus, Melicertus kerathurus, Metapenaeus monoceros, Nephrops norvegicus, Palaemon serratus, Palinurus elephas, Palinurus mauritanicus, Parapenaeus longirostris, Plesionika martia, Portunus pelagicus, Scyllarides latus, Squilla mantis*	International Bottom Trawl Survey in the Mediterranean (Medits database)	FishSTAT (FAO)
22	**Jellyfish (JF):** *Aequorea forskalea, Aurelia aurita, Pelagia noctiluca, Chrysaora hysoscella, Cotylorhiza tuberculata, Liriope tetraphylla, Mnemiopsis leidyi , Pleurobrachia rhodopis, Physalia physalis, Rhizostoma pulmo*	NA	
23	**Benthos (BE):** nematodes, copepods (and naupliar stages), polychaetes, oligochaetes, isopods, cumaceans, amphipods, acarians, ostracods, oligochaetes, tanaidaceans, cnidarians, kinorhynchs, turbellarians, gastrotriches, nemerteans, bivalves, priapulids (including larvae), cladocerans, decapods (larvae) and echinoderms	[45]	
24	**Zooplankton (ZO):** meso and macro zooplankton (amphipods, copepods, cladocerans, euphasids, mysids, pteropods)	NA	
25	**Phytoplankton (PH):** diatoms, dinoflagellates	NA	
26	**Seagrass (SE):** *Cymodocea nodosa, Posidonia oceanica, Zoostera marina, Zoostera noltii*	NA	
27	**Detritus (DE)**		

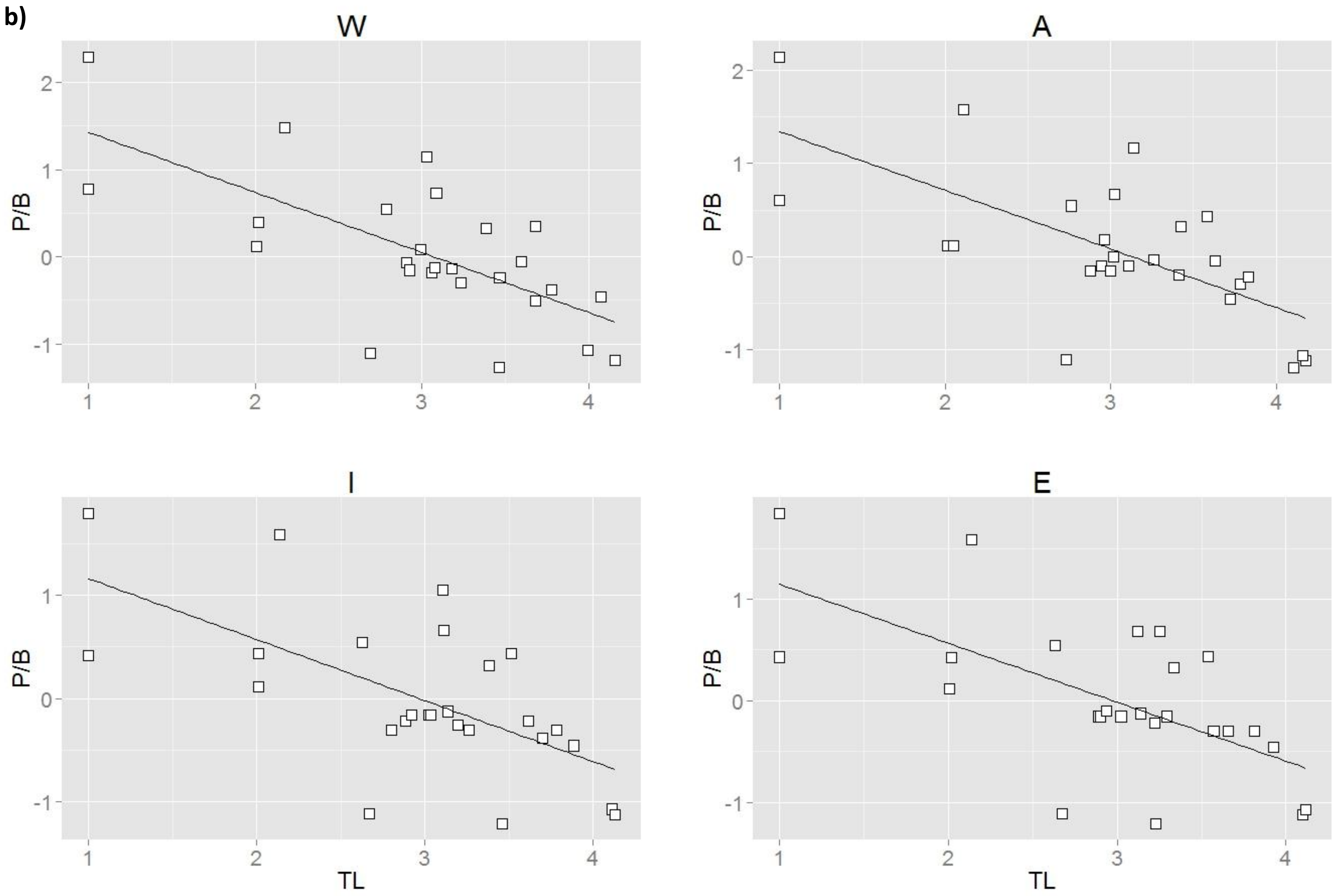
28	**Discards (DI)**		
29	**Trawlers (TR)**		
30	**Purse seiners (PS)**		
31	**Long liners (LL)**		
32	**Artisanal fisheries (AR)**		
33	**Recreational fisheries (RC)**		

S2 Refer to S1 in Annex 4

S3 Refer to S3 in Annex 4

S4. PREBAL for each Mediterranean sub-area (Western [W]; Adriatic [A]; Ionian [I]; Eastern and Levantine [E] plotting (a) biomass estimates (t/km^2), (b) production/biomass ratio (per year), and (c) consumption/biomass (per year) on a log scale vs trophic level, from lowest to highest trophic level, of each species/functional group.

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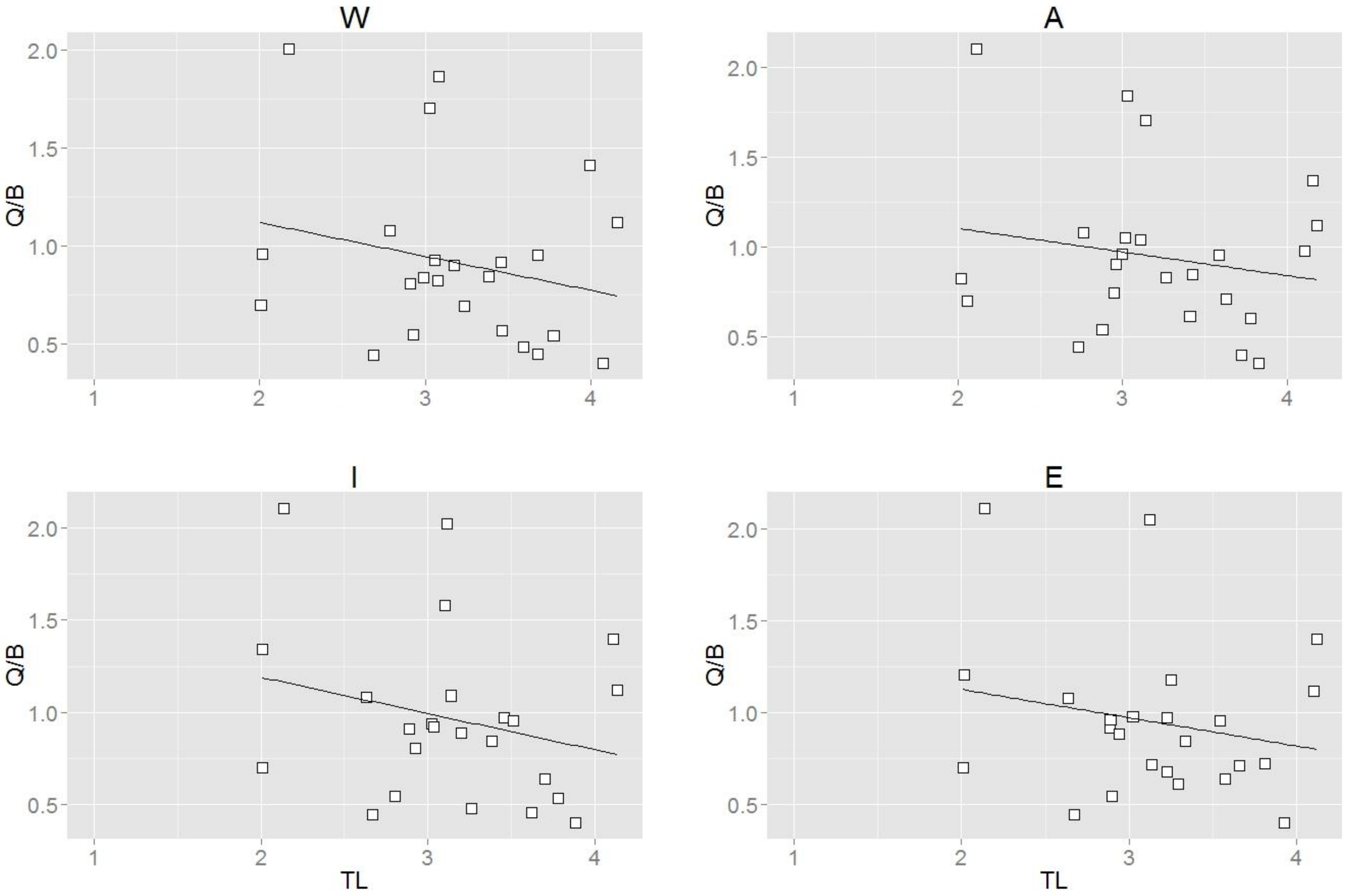
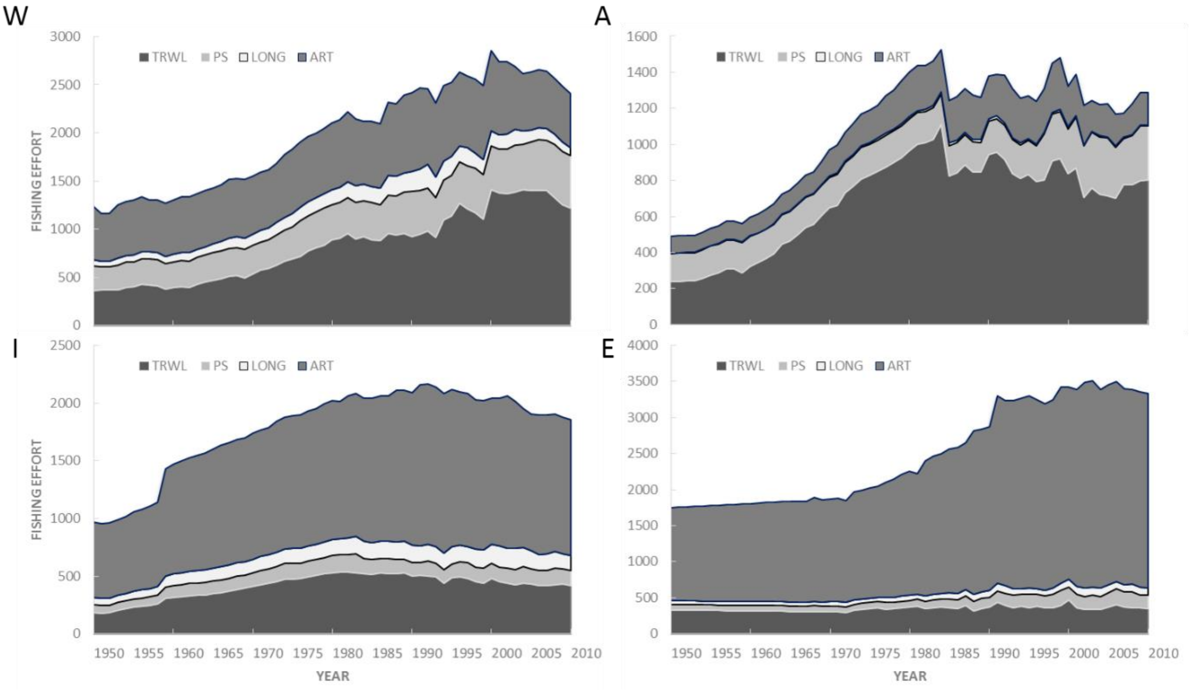


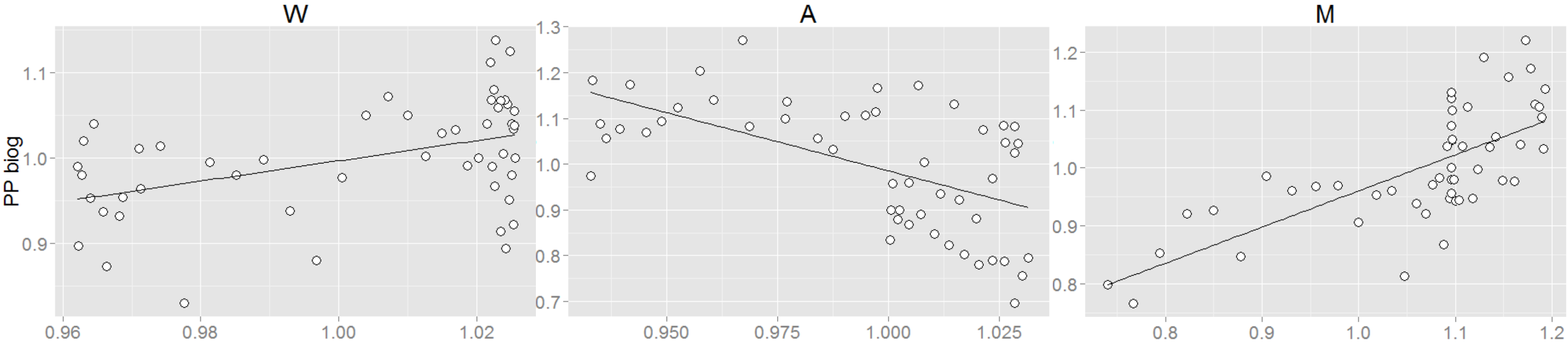
S5. Reconstructed fishing effort (kW·days^{-1}) for the main fishing fleets (trawlers: TRWL; purse seiners: PS; long liners: LONG; artisanals: ART) of the four Mediterranean sub-areas (Western: W; Adriatic: A; Ionian: I; Eastern and Levantine: E).

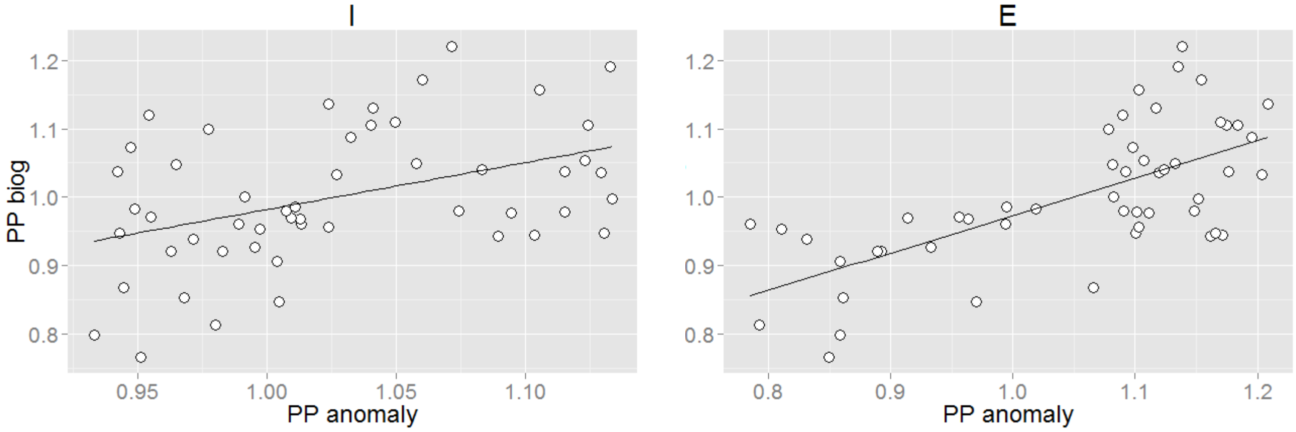


S6. Technological coefficients of fishing vessels by gear type used in the analyses (Sources: [27-29]).

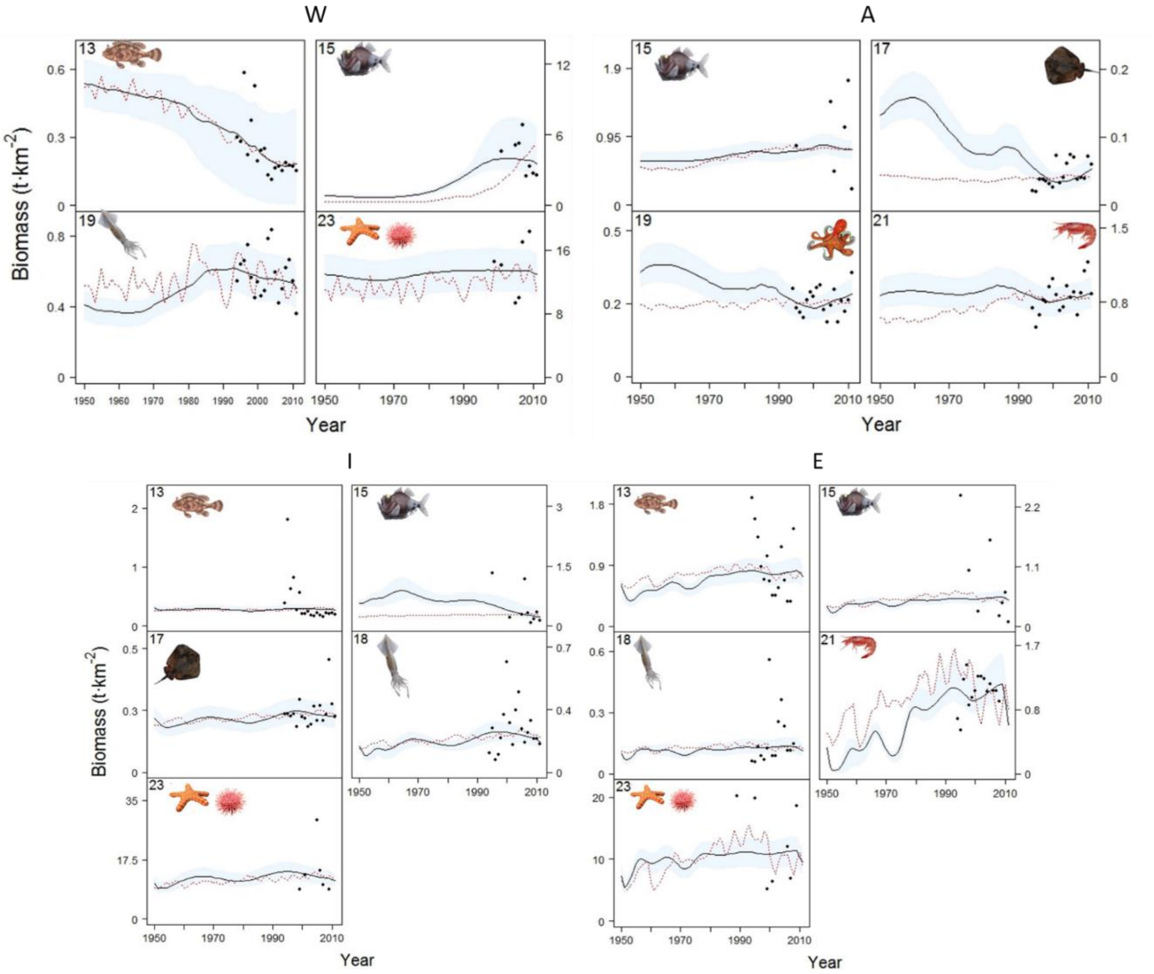
	Technological coefficient		
Vessel type	**1950-1979**	**1980-1995**	**1996-2010**
Trawlers	0.5	1	1.8
Purse seiners	0.5	1	1.8
Artisanal	0.5	1	1.3
Longliners	0.5	1	2.8

S7. Graphical presentation of the Spearman correlation analysis. Scatter plots show, for the four sub-areas (Western: W; Adriatic: A; Ionian: I; Eastern and Levantine: E) and for the additional Mediterranean Sea as whole (Mediterranean: M), values of PP from the biogeochemical model (PP biog) versus PP anomaly. Both time series were divided by their mean to be able to compare the two trends.

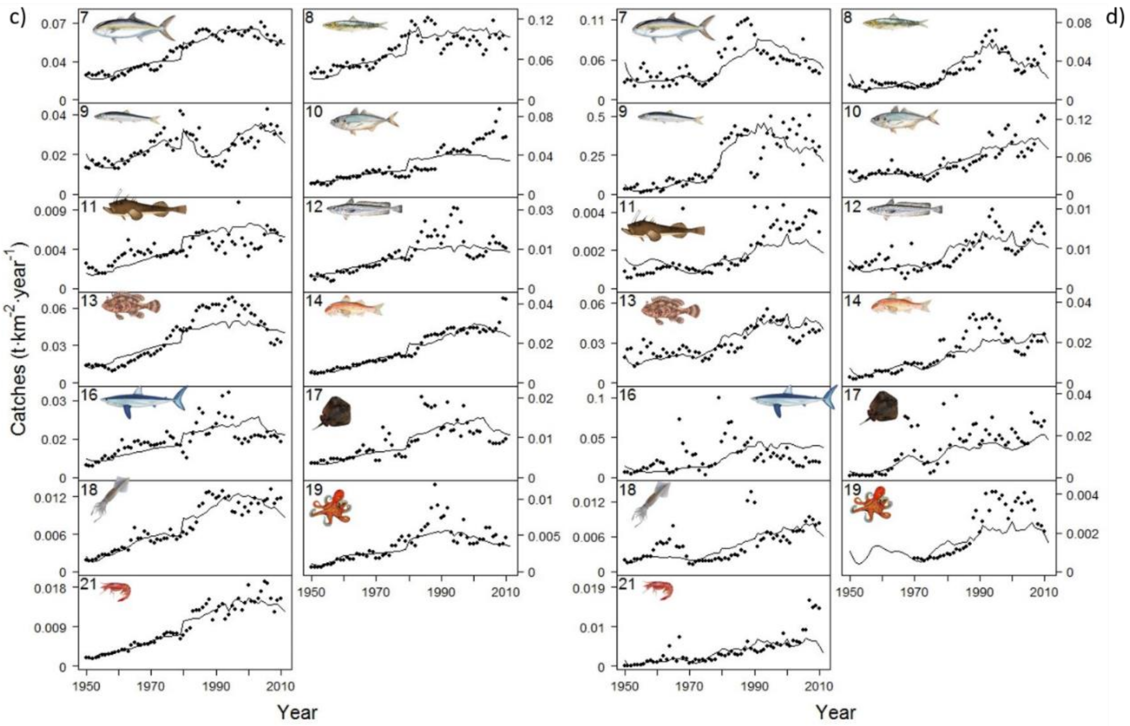




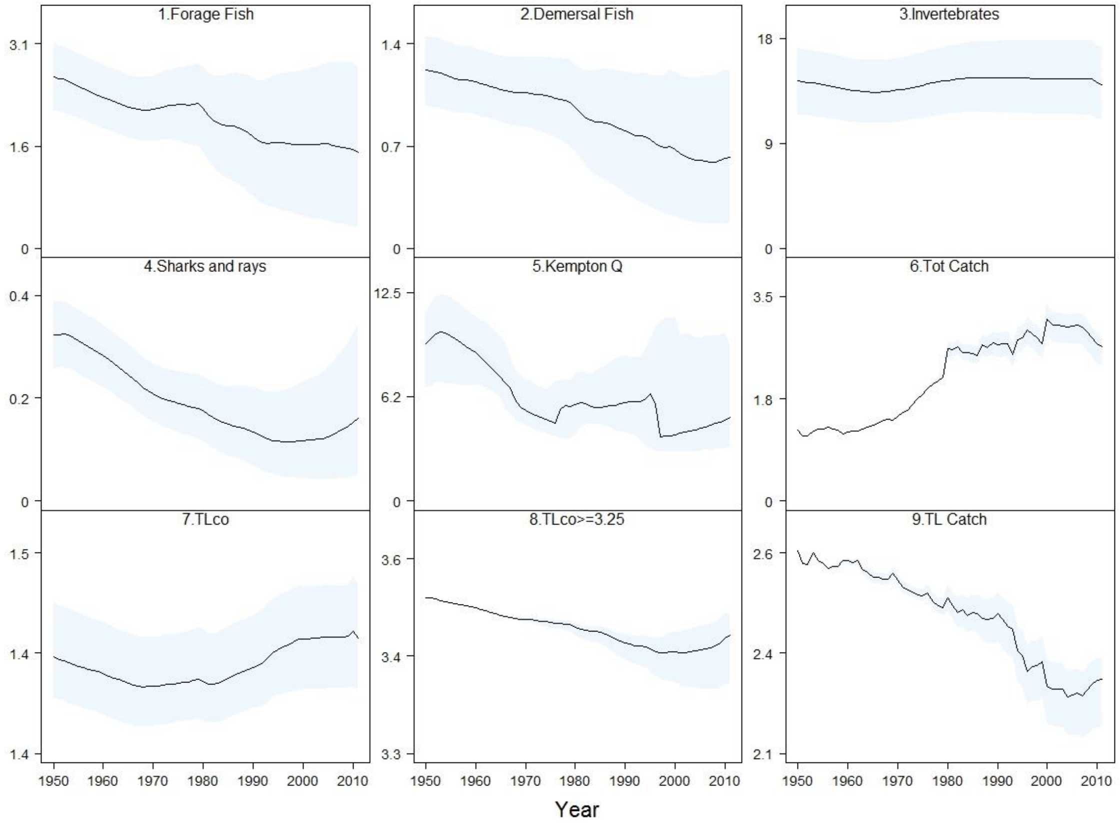
S8. Representation of modelling fitting for the remaining functional groups occurring in the Western (W), Adriatic (A), Ionian (I) and Eastern/Levantine (E) Seas for the period 1950-2011. Predicted biomass (t·km^{-2}) is shown as solid black lines while observed data is represented as black dots. Functional groups codes correspond to those given in Fig 2. The predicted model results (dashed red line) using the modelled biogeochemical PP is also shown. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.



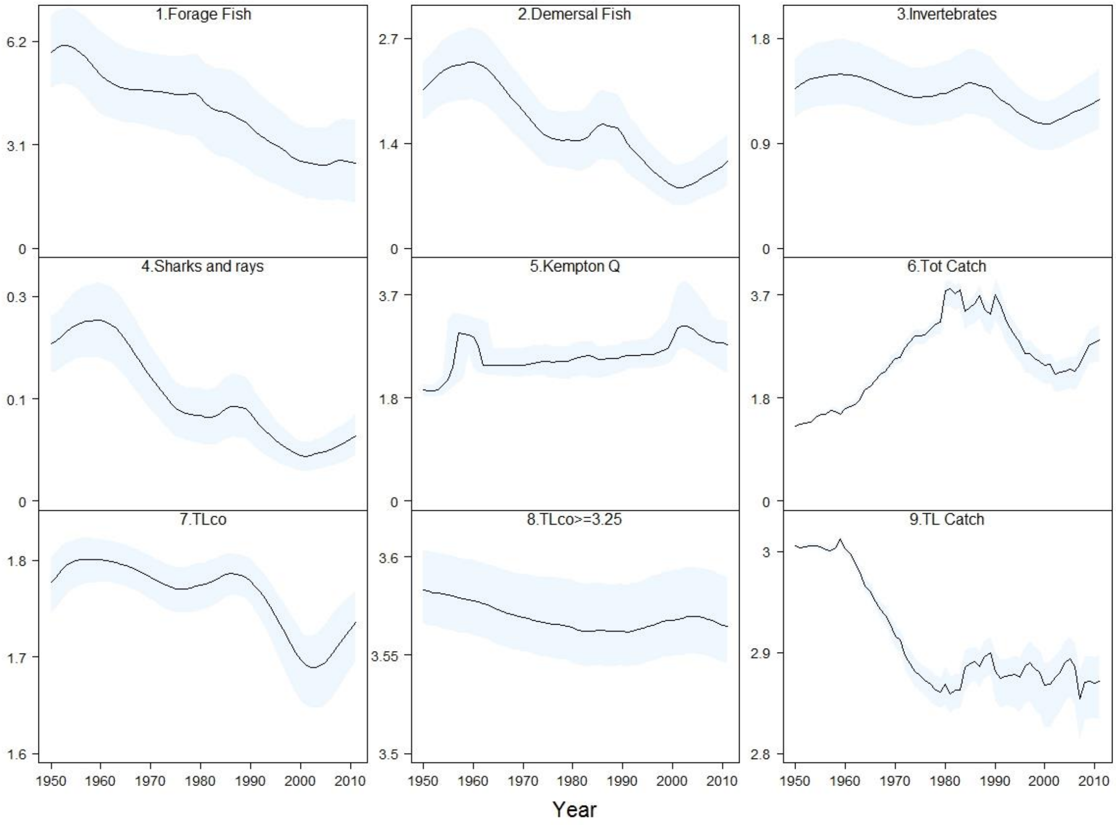
S9. Predicted (solid lines) versus observed (dots) catches (t·km^{-2}·year^{-1}) for main commercially important functional groups of the Ionian (c) and Eastern (d) Mediterranean ecosystems (1950-2011).



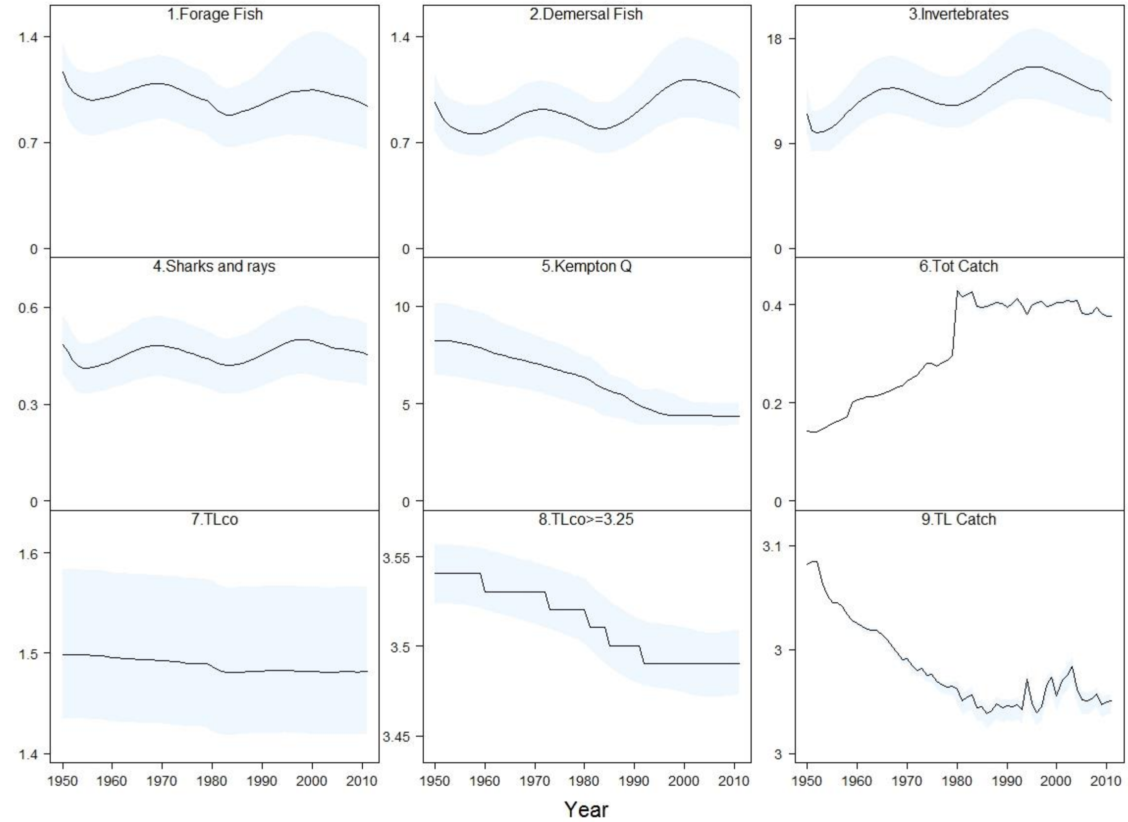
S10. Ecological indicators (1. Forage fish biomass (t·km^{-2}); 2. Demersal fish biomass (t·km^{-2}); 3. Invertebrates biomass (t·km^{-2}); 4. Sharks/rays and skate biomass (t·km^{-2}); 5. Kempton's index of biodiversity; 6. Tot Catch: Total Catch (t· km^{-2}·year^{-1}); 7. mTLco: Mean trophic level of the community; 8. mTL>3.25: Mean trophic levels of groups having trophic level >3.25 (excluding marine mammals, sea turtles and seabirds); 9 mTLC: Mean trophic level of the catches) estimated from results of the Ecosim model for the period 1950-2011 for the Western Mediterranean Sea. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.



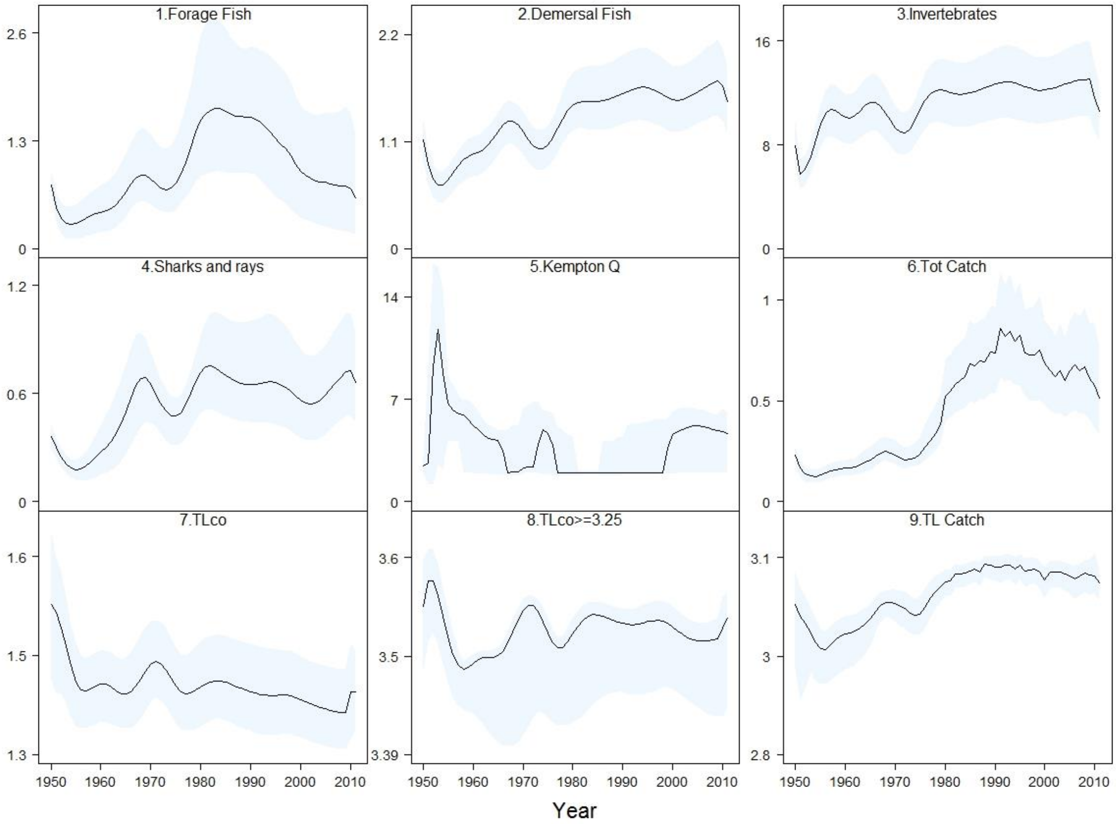
S11. Ecological indicators (1. Forage fish biomass (t·km^{-2}); 2. Demersal fish biomass (t·km^{-2}); 3. Invertebrates biomass (t·km^{-2}); 4. Sharks/rays and skate biomass (t·km^{-2}); 5. Kempton's index of biodiversity; 6. Tot Catch: Total Catch (t· km^{-2}·year^{-1}); 7. mTLco: Mean trophic level of the community; 8. mTL>3.25: Mean trophic levels of groups having trophic level >3.25 (excluding marine mammals, sea turtles and seabirds); 9 mTLC: Mean trophic level of the catches) estimated from results of the Ecosim model for the period 1950-2011 for the Adriatic Sea. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.



S12. Ecological indicators (1. Forage fish biomass (t·km^{-2}); 2. Demersal fish biomass (t·km^{-2}); 3. Invertebrates biomass (t·km^{-2}); 4. Sharks/rays and skate biomass (t·km^{-2}); 5. Kempton's index of biodiversity; 6. Tot Catch: Total Catch (t· km^{-2}·year^{-1}); 7. mTLco: Mean trophic level of the community; 8. mTL>3.25: Mean trophic levels of groups having trophic level >3.25 (excluding marine mammals, sea turtles and seabirds); 9 mTLC: Mean trophic level of the catches) estimated from results of the Ecosim model for the period 1950-2011 for the Ionian Sea. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.



S13. Ecological indicators (1. Forage fish biomass ($t \cdot km^{-2}$); 2. Demersal fish biomass ($t \cdot km^{-2}$); 3. Invertebrates biomass ($t \cdot km^{-2}$); 4. Sharks/rays and skate biomass ($t \cdot km^{-2}$); 5. Kempton's index of biodiversity; 6. Tot Catch: Total Catch ($t \cdot km^{-2} \cdot year^{-1}$); 7. mTLco: Mean trophic level of the community; 8. mTL>3.25: Mean trophic levels of groups having trophic level >3.25 (excluding marine mammals, sea turtles and seabirds); 9 mTLC: Mean trophic level of the catches) estimated from results of the Ecosim model for the period 1950-2011 for the Eastern Mediterranean Sea. Blue shadow represents the 95% percentile and 5% percentile obtained through the Monte Carlo routine.



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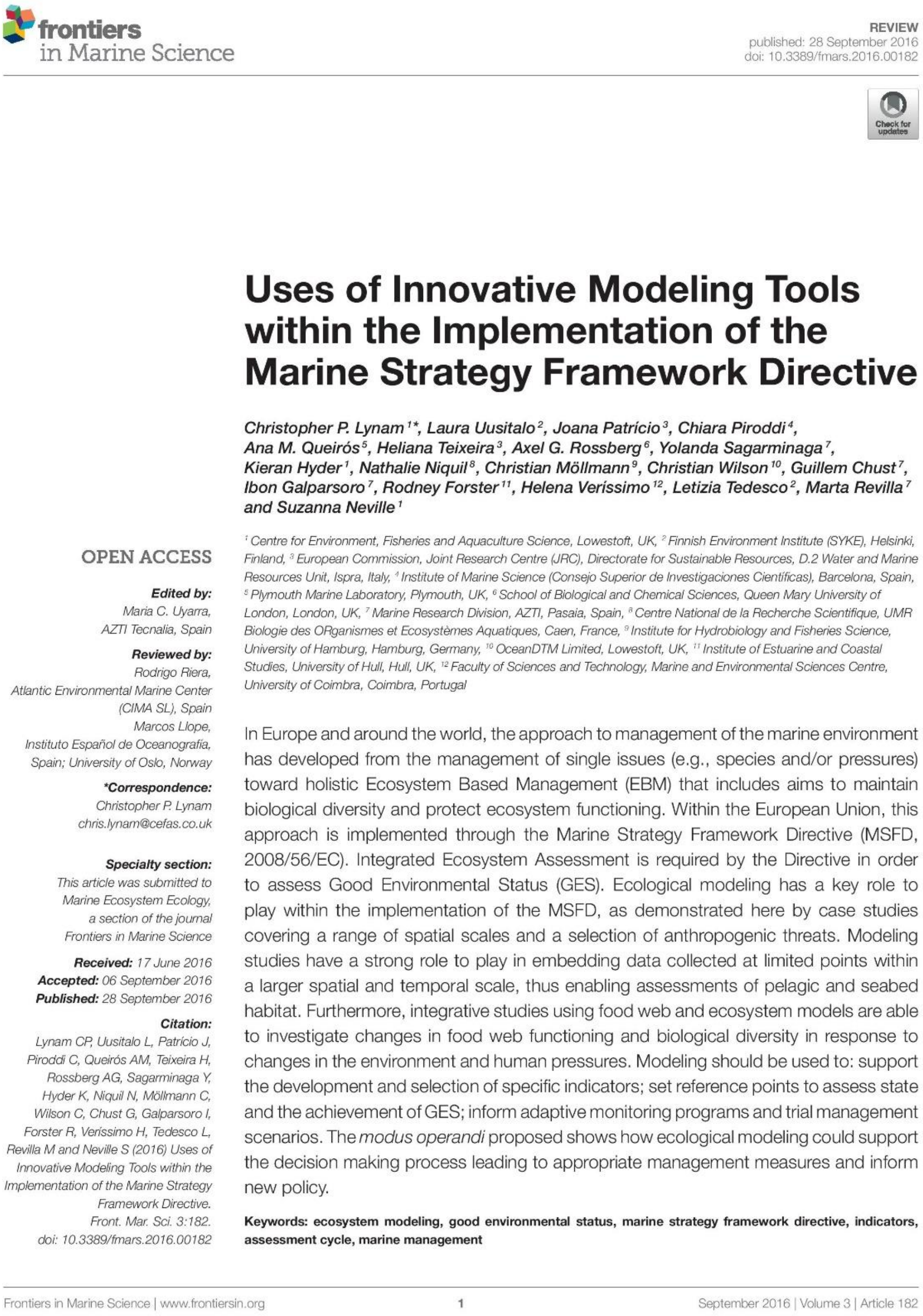

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Uses of Innovative Modeling Tools within the Implementation of the Marine Strategy Framework Directive

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In Europe and around the world, the approach to management of the marine environment has developed from the management of single issues (e.g., species and/or pressures) toward holistic Ecosystem Based Management (EBM) that includes aims to maintain biological diversity and protect ecosystem functioning. Within the European Union, this approach is implemented through the Marine Strategy Framework Directive (MSFD, 2008/56/EC). Integrated Ecosystem Assessment is required by the Directive in order to assess Good Environmental Status (GES). Ecological modeling has a key role to play within the implementation of the MSFD, as demonstrated here by case studies covering a range of spatial scales and a selection of anthropogenic threats. Modeling studies have a strong role to play in embedding data collected at limited points within a larger spatial and temporal scale, thus enabling assessments of pelagic and seabed habitat. Furthermore, integrative studies using food web and ecosystem models are able to investigate changes in food web functioning and biological diversity in response to changes in the environment and human pressures. Modeling should be used to: support the development and selection of specific indicators; set reference points to assess state and the achievement of GES; inform adaptive monitoring programs and trial management scenarios. The *modus operandi* proposed shows how ecological modeling could support the decision making process leading to appropriate management measures and inform new policy.

Keywords: ecosystem modeling, good environmental status, marine strategy framework directive, indicators, assessment cycle, marine management

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Ecosystem services sustainability in the Mediterranean Sea: assessment of status and trends using multiple modelling approaches

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Mediterranean ecosystems support important processes and functions that bring direct benefits to human society. Yet, marine ecosystem services are usually overlooked due to the challenges in identifying and quantifying them. This paper proposes the application of several biophysical and ecosystem modelling approaches to assess spatially and temporally the sustainable use and supply of selected marine ecosystem services. Such services include food provision, water purification, coastal protection, lifecycle maintenance and recreation, focusing on the Mediterranean region. Overall, our study found a higher number of decreasing than increasing trends in the natural capacity of the ecosystems to provide marine and coastal services, while in contrast the opposite was observed to be true for the realised flow of services to humans. Such a study paves the way towards an effective support for Blue Growth and the European maritime policies, although little attention is paid to the quantification of marine ecosystem services in this context. We identify a key challenge of integrating biophysical and socio-economic models as a necessary step to further this research.

Ecosystem services (ES) are the contribution of natural ecosystems to human well-being, for instance in the form of food provision, protection from flood events or inspiration for science and arts. Since ecosystems play a basic role for human societies[1,2], ES have been commonly used to raise awareness of biodiversity conservation and broader ecosystem health[3]. In particular, the ES concept has been created to promote a rational and balanced measure of the use of natural resources taking into account both public and private benefits. Thus, assessing ES becomes important for fostering the sustainable management of the environment across its different functions and across multiple planning sectors.

In addition, evaluating ES spatially and temporally is essential for highlighting where the benefits for maritime economic sectors (and more generally for society) are, and how they might have changed in time. These are necessary steps needed to support and guide current regulations like the EU Maritime Spatial Planning Directive (Directive 2014/89/EU) and the Marine Strategy Framework Directive (Directive 2008/56/EC), although these regulations do not explicitly tackle ES. Only with this knowledge base can policy-makers have the necessary tools to make appropriate management decisions in order to guide proper sustainable Blue Growth in which all marine and maritime sectors can contribute to welfare, innovation and growth.

Despite the recent interest in assessing marine and coastal ES, so far most studies have described static systems, and thus static ES, with the result that currently spatial and/or temporal approaches that evaluate marine ES are still uncommon[4,5] (e.g. only a few studies can be found and mostly at a local scale[6,7]). Data availability, knowledge gaps and uncertainty seem to be the major limiting factors.

Marine and coastal ES can be evaluated spatially and temporally through (a) the analysis or extrapolation of primary data like field sampling, surveys or high resolution remote sensing; (b) the use of seabed habitat maps and land use maps as a proxy for ES supply based on look-up tables or scoring factors; or (c) the use of selected models either ecological, socio-economic, bio-economic or specific for ES. The present study follows the third option, in particular using ecosystem models to describe the main processes/functions and quantify the delivery of marine ES. Such models have considerably evolved in the last decade driven by a worldwide movement towards

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An indicator framework for assessing ecosystem services in support of the EU Biodiversity Strategy to 2020

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ABSTRACT

In the EU, the mapping and assessment of ecosystems and their services, abbreviated to MAES, is seen as a key action for the advancement of biodiversity objectives, and also to inform the development and implementation of related policies on water, climate, agriculture, forest, marine and regional planning. In this study, we present the development of an analytical framework which ensures that consistent approaches are used throughout the EU. It is framed by a broad set of key policy questions and structured around a conceptual framework that links human societies and their well-being with the environment. Next, this framework is tested through four thematic pilot studies, including stakeholders and experts working at different scales and governance levels, which contributed indicators to assess the state of ecosystem services. Indicators were scored according to different criteria and assorted per ecosystem type and ecosystem services using the common international classification of ecosystem services (CICES) as typology. We concluded that there is potential to

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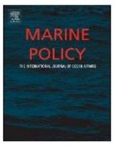

Capabilities of Baltic Sea models to assess environmental status for marine biodiversity

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ABSTRACT

To date there has been no evaluation of the capabilities of the Baltic Sea ecosystem models to provide information as outlined by the Marine Strategy Framework Directive. This work aims to fill in this knowledge gap by exploring the modelling potential of nine Baltic Sea ecosystem models to support this specific European policy and, in particular, models' capabilities to inform on marine biodiversity. Several links are found between the Model-Derived Indicators and some of the relevant biodiversity-related descriptors (i.e. biological diversity and food webs), and pressures (i.e. interference with hydrological processes, nutrient and organic matter enrichment and marine acidification). However several gaps remain, in particular in the limited representation of habitats other than the pelagic that the models are able to address for descriptor sea-floor integrity and inability to assess descriptor non-indigenous species. The general outcome is that the Baltic Sea models considered do not adequately cover all the requested needs of the MSFD, but can potentially do so to a certain extent, while for some descriptors/criteria/indicators/pressures new indicators and/or modelling techniques need to be developed in order to satisfactorily address the requirement of the MSFD and assess the environmental status of the Baltic Sea.

1. Introduction

The Directive 2008/56/EC, known as the Marine Strategy Framework Directive (MSFD), establishes a framework for community action in the field of marine environmental policy [1]. It was formally adopted by the European Union in July 2008. The MSFD outlines a legislative framework for an ecosystem-based approach to the management of human activities that supports the sustainable use of marine goods and services. The overarching goal of the Directive is to achieve Good Environmental Status (GEnS)[1] by 2020 across the European marine environment. The Directive defines GEnS as 'the environmental status of marine waters where these provide ecologically diverse and dynamic oceans and seas which are intrinsically clean, healthy and productive, and the use of the marine environment is at a level that is sustainable, thus safeguarding the potential for use and activities by current and future generations'. With the aim to support its implementation, the MSFD sets out in Annex I 11 qualitative *descriptors*[2] (D1-D11, Table 1), either state or pressure *descriptors*. Later, a Commission decision defines also 29 related *criteria* and 56 related *indicators* [4] that are used in the assessment of the status of the seas. An example of *criteria* and *indicators* defined for biological diversity (D1) is shown in Table 2.

With the aim to facilitate the implemention of the MSFD, Borja et al. [5] proposed an operational definition of GEnS, i.e. 'GEnS is achieved when physicochemical and hydrographical conditions are maintained at a level that main structuring components of the ecosystem are present, allowing the functionality of the system to provide resistance and resilience against deleterious effects of human pressures/activities/impacts, maintaining and delivering

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[1] Following the recommendation of Mee et al. [2] the acronym GEnS for Good Environmental Status is used here to discern from Good Ecological Status (GEcS) defined by the Water Framework Directive [3].

[2] *Descriptors/criteria/indicators/pressures* are here identified in italics when strictly referring to those defined by the Marine Strategy Framework Directive.

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Relationships among fisheries exploitation, environmental conditions, and ecological indicators across a series of marine ecosystems

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Partial least squares path modeling

ABSTRACT

Understanding how external pressures impact ecosystem structure and functioning is essential for ecosystem-based approaches to fisheries management. We quantified the relative effects of fisheries exploitation and environmental conditions on ecological indicators derived from two different data sources, fisheries catch data (catch-based) and fisheries independent survey data (survey-based) for 12 marine ecosystems using a partial least squares path modeling approach (PLS-PM). We linked these ecological indicators to the total biomass of the ecosystem. Although the effects of exploitation and environmental conditions differed across the ecosystems, some general results can be drawn from the comparative approach. Interestingly, the PLS-PM analyses showed that survey-based indicators were less tightly associated with each other than the catch-based ones. The analyses also showed that the effects of environmental conditions on the ecological indicators were predominantly significant, and tended to be negative, suggesting that in the recent period, indicators accounted for changes in environmental conditions and the changes were more likely to be adverse. Total biomass was associated with fisheries exploitation and environmental conditions; however its association with the ecological indicators was weak across the ecosystems. Knowledge of the relative influence of exploitation and environmental pressures on the dynamics within exploited ecosystems will help us to move towards ecosystem-based approaches to fisheries management. PLS-PM proved to be a useful approach to quantify the relative effects of fisheries exploitation and environmental conditions and suggest it could be used more widely in fisheries oceanography.

1. Introduction

There are two main mechanisms controlling the trophodynamics of marine ecosystems: (1) bottom–up control from plankton species that are directly influenced by ocean climate (e.g., Richardson and

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Fishing impact in Mediterranean ecosystems: an EcoTroph modeling approach

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ABSTRACT

The EcoTroph modeling approach was applied to five Mediterranean marine ecosystems to characterize their food webs and investigate their responses to several simulated fishing scenarios. First, EcoTroph was used to synthesize the outputs of five pre-existing heterogeneous Ecopath models in a common framework, and thus to compare different ecosystems through their trophic spectra of biomass, catch, and fishing mortalities. This approach contributes to our understanding of ecosystem functioning, from both ecological and fisheries perspectives. Then, we assessed the sensitivity of each ecosystem to fishery, using EcoTroph simulations. For the five ecosystems considered, we simulated the effects of increasing or decreasing fishing mortalities on both the biomass and the catch per trophic class. Our results emphasize that the Mediterranean Sea is strongly affected by the depletion of high trophic level organisms. Results also show that fisheries impacts, at the trophic level scale, differ between ecosystems according to their trophic structure and exploitation patterns. A top-down compensation effect is observed in some simulations where a fishing-induced decrease in the biomass of predators impacts their prey, leading to an increase in the biomass at lower trophic levels. The results of this comparative analysis highlight that ecosystems where top-down controls are observed are less sensitive to variations in fishing mortality in terms of total ecosystem biomass. This suggests that the magnitude of top-down control present in a system can affect its stability.

1. Introduction

Depletion of fishery resources and degradation of marine ecosystems are observed worldwide (Pitcher and Cheung, 2013; Worm et al., 2009). Fisheries can directly and indirectly affect the whole food web and overfishing is a primary threat to ecosystem structure (e.g., species diversity, trophic levels) and dynamics (e.g., stability, resilience) (Daskalov, 2002; Pauly et al., 2002; Travers and Shin, 2010). Thus, it is imperative to properly assess the ecosystem effects of fishing (Cury et al., 2008).

The use of trophic models, such as Ecopath with Ecosim (Christensen and Walters, 2004; Walters et al., 1999), OSMOSE (Shin and Cury, 2001, 2004) and Atlantis (Fulton et al., 2004), is an effective way to describe the trophic structure and functioning of marine ecosystems. These models can provide a comprehensive image of an ecosystem and allow the full complexities of the food web to be considered.

EcoTroph is a more recent trophic model which represents marine ecosystems and assesses fisheries impacts by treating the distribution of biomass or related quantities as a function of continuous trophic levels (TLs) (Gascuel, 2005; Gascuel and Pauly, 2009). An EcoTroph representation of an ecosystem consists of various ecosystem parameters, such as biomass, production, catch or fishing mortality, displayed along trophic spectra (Gascuel, 2005). Unlike the trophic pyramids of Lindeman (1942), where the biomass of each component of ecosystems was shoehorned into a few integer TLs, EcoTroph is based on fractional

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