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Capturing the big picture of Mediterranean marine biodiversity with an end-to-end model of climate and fishing impacts

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Abstract

The Mediterranean Sea is one of the main hotspots of marine biodiversity in the world. The combined pressures of fishing activity and climate change have also made it a hotspot of global change amidst increasing concern about the worsening status of exploited marine species. To anticipate the impacts of global changes in the Mediterranean Sea, more integrated modelling approaches are needed, which can then help policymakers prioritize management actions and formulate strategies to mitigate impacts and adapt to changes. The aim of this study was to develop a holistic model of marine biodiversity in the Mediterranean Sea with an explicit representation of the spatial, multispecies dynamics of exploited resources subject to the combined influence of climate variability and fishing pressure. To this end, we used the individual-based OSMOSE model (Object-oriented Simulator of Marine ecOSystEms), including 100 marine species (fish, cephalopods and crustaceans) representing about 95% of the total declared catch, at a high spatial resolution (400 km^2) and a large spatial scale (the entire Mediterranean basin) – the first time such a resolution and scale have been modelled. We then combined OSMOSE with the NEMOMED 12 physical model and the Eco3M-S biogeochemical low trophic level model to build the end-to-end model, OSMOSE-MED. We fitted OSMOSE-MED model with observed or estimated biomass and commercial catch data using a likelihood approach and an evolutionary optimization algorithm. The outputs of OSMOSE-MED were then verified against observed biomass and catch data, and compared with independent datasets (MEDITS data, diet composition and trophic levels). The model results – at different hierarchical levels, from individuals to the scale of the ecosystem – were consistent with current knowledge of the structure, functioning and dynamics of the ecosystems in the Mediterranean Sea. While the model could be further improved in future iterations, all the modelling steps – the comprehensive representation of key ecological processes and feedback, the selective parameterization of the model, and the comparison with observed data in the validation process – strengthened the predictive performance of OSMOSE-MED and thus its relevance as an impact model to explore the future of marine biodiversity under scenarios of global change. It is a promising tool to support ecosystem-based fishery management in the Mediterranean Sea.

Keywords: Ecosystem model, Ecosystem Approach to Fisheries Management, OSMOSE model, NEMOMED model, Eco3M-S model, Global change

1 Introduction

The Mediterranean Sea is the largest semi-enclosed sea in Europe and is one of the main reservoirs of biodiversity in the world (Coll et al., 2010). It is home to 4–18% of identified marine species, which is considerable given it makes up only 0.82% of the global ocean surface (Coll et al., 2010). It is also a hotspot of global changes caused by human activity (Coll et al., 2012, 2010; Giorgi, 2006; Giorgi and Lionello, 2008; Micheli et al., 2013a; Ramírez et al., 2018; Stock et al., 2018). Overfishing, pollution from land-based sources, degradation or loss of critical habitats, species introductions and climate change are all widespread in the Mediterranean Sea; impacts that may operate in synergy, leading to profound modifications in the structure, stability and functioning of marine ecosystems (Albouy et al., 2014; Coll et al., 2012; Lotze et al., 2006). Fishing is considered one of the highest threats to biodiversity in the region: the exploitation rate is steeply increasing due to poor fishing selectivity, and fish stocks are shrinking (Colloca et al., 2017; Vasilakopoulos et al., 2014). As a consequence, more than 90% of the assessed stocks were categorized as overfished in 2017 (GFCM, 2017a; STECF, 2017). However, while fish stocks are declining on the continental shelf (especially long-lived species such as European hake *Merluccius merluccius*), a few short-lived species such as shrimp, cephalopods, and other fish species (e.g. red mullet *Mullus barbatus*), have shown trends of increasing biomass (GFCM, 2017a; Maynou et al., 2011). Deep-water rose shrimp *Parapenaeus longirostris* is the most emblematic example: its biomass has increased all over the Mediterranean Sea in the last decade due to the increasing temperature and decreasing predatory pressure (e.g. by European hake) (Colloca et al., 2014; Ligas et al., 2011; Sbrana et al., 2019).

In the absence of strong management plans, the deteriorating status of fisheries in the Mediterranean is likely to worsen, particularly in a context of climate change (Cheung et al., 2018; FAO, 2018). The Mediterranean Sea has been identified as one of the most vulnerable regions in future climate change projections (Cramer et al., 2018; Giorgi, 2006; Hoegh-Guldberg et al., 2014). The effects of climate change on marine ecosystems are already clearly observable, with impacts reported on species from low trophic levels (e.g. macrophytes and phytoplankton) to high (e.g. predatory fish), and from individuals to the scale of entire ecosystems (Calvo et al., 2011; Durrieu de Madron et al., 2011; Lejeusne et al., 2010; Marbà et al., 2015; Tzanatos et al., 2014). These impacts are expected to affect biodiversity, commercial fisheries, food webs and ecosystem functioning (Albouy et al., 2014; AllEnvi, 2016; Bosello et al., 2015; Hattab et al., 2014; Jordà et al., 2012; Marbà et al., 2015; Pecl et al., 2017; Piroddi et al., 2017).

Anthropogenic pressures on Mediterranean ecosystems are projected to increase in the future, especially those related to climate change, habitat degradation and resource exploitation (Butchart et al., 2010; Calvo et al., 2011; Coll et al., 2010). Considering the range of human and natural pressures and the likelihood that these act in synergy on marine ecosystems, there is an urgent need for more holistic and integrative approaches to quantify, anticipate, mitigate and manage human impacts on natural environments (Colloca et al., 2017; Hilborn, 2011; Link, 2010). In response, Ecosystem-Based Management (EBM) and, more specifically, the Ecosystem Approach to Fisheries Management (EAFM) emerged in the early 1990s to consider all anthropogenic activities that might affect the sustainability of goods and services provided by ecosystems (Pikitch et al., 2004). In the European Union, these approaches are integrated in the Common Fisheries Policy (CFP, 2013) and the European Marine Strategy Framework Directive (MSFD; European Commission, 2008), which requires that all member states take the necessary measures to achieve or maintain ‘Good Environmental Status’ for marine ecosystems, with the explicit regulatory objective that ‘biodiversity be maintained’ by 2020 at the latest (European Commission, 2008). The requirements of the MSFD necessitate the development of suitable tools to evaluate the status of marine ecosystems and their response to human activity, as well as the sustainable management and harvesting of commercial species. This makes it essential to develop our ability to predict the future impacts of various policy interventions and strategic management plans for restoring marine ecosystems and biodiversity while ensuring the sustained provision of marine fishery products to human societies.

In order to project plausible biodiversity scenarios at the scale of the whole Mediterranean Sea that can inform decision-making in the region, the aim of this study was to develop a model able to explicitly represent the spatial, multispecies dynamics of marine resources subject to the combined influences of climate change and fishing pressure. End-to-End models (E2E), which represent the entire food web, from plankton to top predators, as well as their abiotic environment, are promising tools for assessing the effects of climate change and fishing on ecosystem dynamics (Fulton, 2010; Grimm et al., 2017; Nicholson et al., 2019; Piroddi et al., 2017, 2015b; Rose et al., 2010; Travers et al., 2007). But while there has been state-of-the-art modelling of food webs and multispecies communities within Mediterranean ecosystems, there remains a gap in modelling the biodiversity dynamics at the scale of the entire Mediterranean Sea: modelling that accounts for the complexity of species introductions, multispecies interactions and spatial dynamics in a context of global change. While trophic modelling of coastal marine ecosystems in specific areas of the Mediterranean has greatly improved, no model has yet shown species assemblages at the whole Mediterranean scale, with explicit modelling of the spatial, trait-based, lifecycle dynamics and interactions of multiple exploited species.

To address this, we used the individual-based ecosystem model OSMOSE (Object-oriented Simulator of Marine ecOSystEms) for the first time at a large spatial scale (the entire Mediterranean basin), a high spatial resolution (400 km^2), and for as many as 100 marine species (fish, cephalopods and crustaceans) representing about 95% of total declared catches in the Mediterranean Sea. Our end-to-end modelling approach combined the OSMOSE model (representing high trophic level species) with the physical model NEMOMED 12 and the biogeochemical model Eco3M-S (representing low trophic levels). The resulting end-to-end model, OSMOSE-MED, was calibrated to represent the Mediterranean Sea during the 2006–2013 period. We then evaluated its ability to represent key indicators of the Mediterranean: for example, biomass, catches and trophic levels from the scale of the individual to the community. The methodology, results and challenges are discussed below.

2 Materials and methods

The individual-based OSMOSE model considers a large proportion of the fishable food web and simulates trophic interactions between several target and non-target marine species – mainly fish species. In order to model the effects of environmental heterogeneity and variability, which could affect the entire food web through bottom-up control, OSMOSE was forced (i.e. through offline one-way coupling) by the NEMOMED 12 / Eco3M-S low trophic levels (LTL) model. The resulting end-to-end model, OSMOSE-MED, represented the whole food web, from primary and secondary producers to the main top predators.

2.1 The low trophic level (LTL) model NEMOMED 12 / Eco3M-S

Eco3M-S is a biogeochemical model that simulates the lower trophic levels of marine ecosystems (phyto- and zooplankton), and the biogeochemical cycles of carbon and other key elements such as phosphorus and nitrogen in the Mediterranean Sea (Auger et al., 2011; Ulses et al., 2016). Independently of our study, Eco3M-S has been coupled with NEMOMED12, a high-resolution (≈1/12°) hydrodynamic model adapted to the Mediterranean region (see Beuvier et al., 2012 for more details on the structure and parameterization of NEMOMED 12) (Kessouri, 2015; Kessouri et al., 2017).

NEMOMED12 is a regional circulation model. It is an updated version of the OPAMED 8 and NEMOMED 8 models used by Ben Rais Lasram et al. (2010), Hattab et al. (2014), Albouy et al. (2014, 2013, 2012) and more recently by Halouani et al. (2016) as input for niche/habitat models at local or regional scales in the Mediterranean Sea. The area of NEMOMED 12 covers the whole Mediterranean Sea and part of the Atlantic Ocean (from 11 °W to 7.5 °W) to take into account inter-ocean exchanges (Beuvier et al., 2012a; Beuvier et al., 2012b). It does not cover the Black Sea. Based on NEMO's standard ORCA tripolar grid at 1/12° (≈7 km), NEMOMED 12 resolution varies in latitude and longitude, but allows the explicit resolution of most mesoscale features. It is an eddy-resolving model that covers the majority of the Mediterranean Sea (Beuvier et al., 2012a). It has a time step of 12 minutes and is daily forced by atmospheric ARPERA data, which is obtained by performing dynamical downscaling of European Centre for Medium-Range Weather Forecasts (ECMWF) products over the European-Mediterranean region (Beuvier et al., 2012a; Herrmann and Somot, 2008).

The coupling of NEMOMED 12 and the biogeochemical Eco3M-S model was done offline (one-way coupling). The Eco3M-S model represents several element cycles such as carbon (C), nitrogen (N), phosphorus (P) and silica (Si) in order to reproduce the different limitations and co-limitations observed in the Mediterranean Sea and the dynamics of different plankton groups. Seven plankton functional types (representing the main types), and the range of the plankton size spectrum in the Mediterranean Sea were modelled. The resulting structure of the trophic web base included three size-classes of phytoplankton (pico-, nano- and micro-phytoplankton), three size-classes of zooplankton (nano-, micro- and meso-zooplankton), and heterotrophic bacteria as decomposers (Table 1). The representation of the phytoplankton dynamics was derived from the Eco3M model presented in Baklouti et al. (2006). Of the primary producers, nanophytoplankton dominated the biomass of phytoplankton communities for most of the year, while microphytoplankton occasionally contributed to a large part of primary production during the spring period in the northwestern Mediterranean (Auger et al., 2011; Ulses et al., 2016). The structure of Eco3M-S reflects major grazing links such as nanozooplankton preying on small phytoplankton and bacteria, microzooplankton consuming microphytoplankton, and mesozooplankton, mainly composed of copepods, grazing on the largest categories of plankton (i.e. microphyto- and microzooplankton). Bacteria (i.e. heterotrophic picoplankton) are responsible for the remineralization of dissolved organic matter. The representation of the heterotrophic processes was based on the models developed by Anderson and Pondaven (2003) and Raick et al. (2005). All features, formulations and parameterization of biogeochemical processes integrated in the mechanistic Eco3M-S model are described in detail in Auger et al. (2011), Kessouri (2015) and Ulses et al. (2016).

Table 1 Parameters of the seven low trophic level compartments used to build the trophic links with OSMOSE. Other parameters used to run ECO3M-S are documented in Auger et al. (2011), Ulses et al., (2016) and Kessouri et al., (2017).

Main Plankton Functional Types (PFTs)	Main species / groups	Min size (μm)	Max size (μm)	Trophic level
Picophytoplankton	*Synechococcus spp.*	0.7	2	1
Nanophytoplankton	Dinoflagellates	2	20	1
Microphytoplankton	Diatoms	20	200	1
Nanozooplankton	Bacterivorous flagellates and small ciliates	5	20	2
Microzooplankton	Ciliates and large flagellates	20	200	2
Mesozooplankton	Copepods and amphipods	200	-	2
Benthos[a]	Based on benthos groups included in the Ecopath model of Piroddi et al. (2017)	2000	50000	2.4

[a]Benthos is considered an LTL group, but is not an output of the Eco3M-S model. This group is included as a 'black box' in the HTL model OSMOSE.

2.2 The high trophic level (HTL) model OSMOSE

The OSMOSE model has been used to assess the impacts of both fishing and climate change scenarios on marine food web functioning and species resilience in different types of ecosystems such as upwelling (Southern Benguela and Humboldt), temperate (Canadian west coast and Jiaozhou Bay), Mediterranean (Gulf of Gabès and Gulf of Lion) and subtropical ecosystems (West Florida shelf) (Fu et al., 2013; Grüss et al., 2015; Halouani et al., 2016; Marzloff et al., 2009; Travers et al., 2009; Xing et al., 2017). OSMOSE is a size-based multispecies trophic model that focuses on high trophic levels, mainly fish species. It is spatially explicit and represents the whole lifecycle of several interacting marine species. It models the major processes of the lifecycle step by step, from eggs to adult fish: i.e. growth, predation, reproduction, natural and starvation mortality, as well as fishing mortality. As it is constrained by computing limitations (of time and memory), rather than being truly individual-based, OSMOSE is based on 'super-individuals' that serve as proxies for fish schools, defined as a group of individuals sharing the same age, length, diet and spatial position and interacting with other schools in a two-dimensional grid. Species interact through predation in a spatial and dynamic way (Shin and Cury, 2004). The model is forced by species-specific spatial distribution maps that can vary interannually, seasonally, or depending on ontogenetic stages. OSMOSE allows the emergence of complex trophic interactions from two basic assumptions of the predation process: for a given individual (a school), prey consumption depends on the spatio-temporal co-occurrence of the predator and its prey (in the horizontal and vertical dimensions) and is conditioned by size compatibility between a predator and its prey. Thus, unlike other trophic models such as Ecopath with Ecosim (Christensen and Walters, 2004), species dynamics and trophic structures are not modelled from pre-established trophic interactions between species: each fish can potentially be a predator or prey, regardless of its taxonomy, but depending on size compatibility (Shin et al., 2004; Shin and Cury, 2001). A maximum and a minimum predator/prey size ratio are thus defined to govern predator–prey interactions (Travers et al., 2009). To integrate a vertical dimension in the food web, accessibility coefficients are defined in the form of a prey–predator accessibility matrix that reflects possible mismatches or overlap between species' vertical distributions and/or potential refugia, allowing a certain proportion of a fish school to remain inaccessible to predation. At each time step, a predation efficiency rate can be calculated for each fish school (i.e. the food biomass ingested within a time step over the maximum ingestion rate), from which growth, starvation and reproduction rates are determined. In OSMOSE, the functions defining growth and mortality are deterministic. The main source of stochasticity comes from the species' movement within their habitat and the order at which schools interact (through predation). Model details and equations are provided in Appendix A and on https://documentation.osmose-model.org/.

2.3 Parameterization of OSMOSE-MED

OSMOSE-MED covers the whole Mediterranean basin, from the Strait of Gibraltar to the Levant basin and from the Northern Adriatic Sea to the Southern Ionian Sea (Figure 1). This area extends from approximately 26.9°N to 46.3°N in latitude and from approximately 5.6°W to 36.1°E in longitude. The Marmara Sea and the Black Sea were not included in the model. The OSMOSE-MED model was built on a regular grid divided into 20x20 km cells (for a total of 6229 cells). Grid resolution was a compromise between the fine-scale ecology of the modelled species and computing time limitations. The time step was set according to the spatial resolution: we adopted a time resolution of 15 days within which species were assumed to have access to the first layer of surrounding cells when foraging for prey.

A 15-day climatology was constructed from the 2006–2013 outputs of the biogeochemical model Eco3M-S and used to force the HTL model (offline coupling). The forcing model outputs thus reflected an average year in the period 2006–2013, characterized by seasonal and spatial variability of climate and plankton state variables. The coupling between NEMOMED 12/Eco3M-S and OSMOSE was realized through the predation process. At each time step and location, the biomass of the 6 plankton groups was used as potential prey fields forcing the HTL model. As within OSMOSE, predation on plankton groups was modelled as an opportunistic size-based process (Travers-Trolet et al., 2014) controlled by a minimum and a maximum predation size ratio parameter. While benthic organisms (mainly invertebrates, crustaceans and polychaetes) are part of the diet of several HTL species included in OSMOSE-MED, they were not explicitly modelled in either ECO3M-S or in OSMOSE. We thus created an additional 'benthos compartment' for which no lifecycle or dynamics were modelled, but a few parameters were provided (size range and trophic level, see Table 1), as well as a biomass level (derived from Piroddi et al., 2017) that was considered uniform over the Mediterranean Sea.

Regarding HTL species, 100 fish, cephalopod and crustacean species were explicitly modelled in OSMOSE-MED: 85 fish species, 5 cephalopods and 10 crustaceans (Appendix B). The selection of the 86 fish species was strongly dependent on data availability both for model parameterization (biological parameters and life history traits, for example) and for comparing the output to observations (species biomass data, for example). Data search and mining for the parameterization of the modelled species' lifecycles represented a significant time investment. Of the 635 fish species included in the FishMed database (Albouy et al., 2015), we were able to find the life history parameters (i.e. growth, reproduction and mortality) required to parameterize the OSMOSE model for only 86 fish species in our search of the scientific literature. Cephalopod and crustacean species were selected for their high commercial value, high contribution to total biomass and data availability. Additionally, they play an important role in food web dynamics (Peristeraki et al., 2005; Roberts, 2003) and represent key components in several Ecopath models applied to ecosystems in the Mediterranean Sea (e.g. Bănaru et al., 2013; Corrales et al., 2017; Hattab et al., 2013; Piroddi et al., 2017). All these species represented on average around 95% of declared fishery catches in the Mediterranean in the 2006–2013 period (FAO, 2006; 2017). The biological parameters linked to growth (Von Bertalanffy parameters, length–weight relationship parameters), mortality (maximum age, natural mortality not explicitly represented in OSMOSE, age/size at recruitment), reproduction (size at maturity, relative fecundity) and predation (minimum and maximum predation size ratios), along with their sources, are detailed in Appendix B and C. As much as possible, the data was specific to Mediterranean ecosystems and was derived from or used as a resource for fishery stock assessment working groups in the Mediterranean Sea.

Within each time step (15 days), the following events were modelled to occur successively in OSMOSE-MED (Figure 1). First, each school was uniformly distributed in space according to a unique distribution map specified for each species (see 2.4). In this application of OSMOSE, due to the lack of observation data, we did not account for any seasonal or ontogenetic variation in fish distribution. As the maps did not change from one time step to the next, schools could move to an adjacent cell or remain in the same cell following a random walk process (Shin et al., 2004; Travers-Trolet et al., 2014). Second, mortality (predation mortality, additional natural mortality and fishing mortality) were applied to schools. The order at which schools interact as well as the order of mortality events was randomly drawn within each time step. Third, food intake, subsequent to predation events, modulated the growth (weight and size) of species and their starvation level. Finally, reproduction occurred for fish with a length greater than that at sexual maturity, allowing the introduction of new schools of age 0 (eggs) in the system (Appendix A).

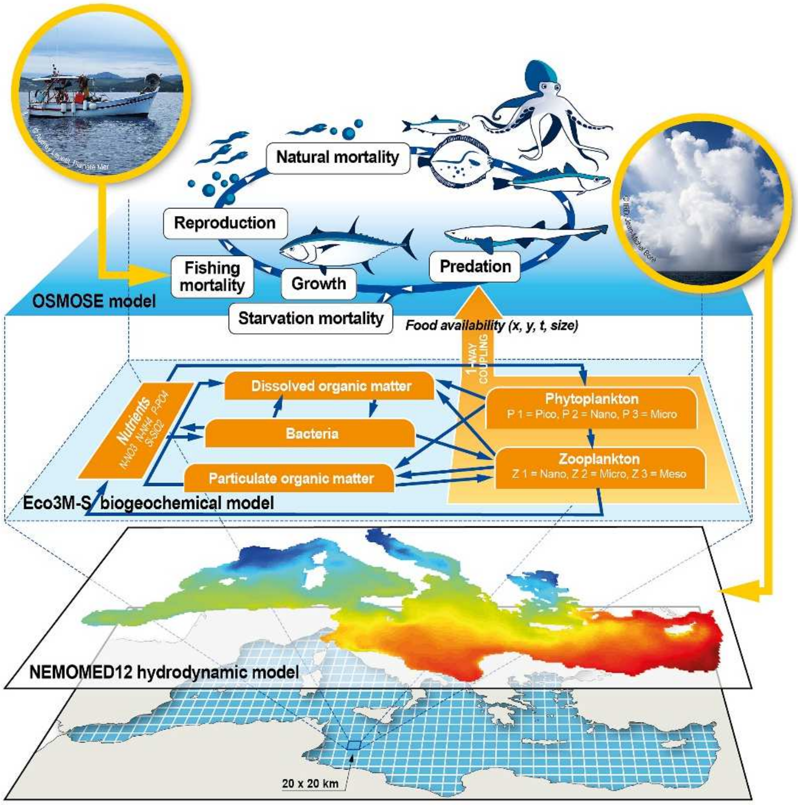

Figure 1 Conceptual representation of the OSMOSE-MED end-to-end model applied to the whole Mediterranean Sea. The high trophic level OSMOSE model is forced (one-way coupling) by the biogeochemical Eco3M-S model through the predation by high trophic levels (i.e. fish, cephalopods and crustaceans) on low trophic levels (i.e. phyto- and zooplankton). Eco3M-S is forced by the NEMOMED 12 hydrodynamic model. Impacts of climate variability and fishing mortality can be explicitly taken into account.

2.4 Modelling high trophic level species distribution

We used a niche modelling approach based on environmental data to generate species distribution maps in the Mediterranean Sea; these maps were then used as input in OSMOSE. Species occurrence was compiled and merged from multiple sources: the Ocean Biogeographic Information System (OBIS: www.iobis.org), the Global Biodiversity Information Facility (GBIF: www.gbif.org), the Food and Agriculture Organization's Geonetwork portal (www.fao.org/geonetwork) and the atlas of Fishes of the Northern Atlantic and Mediterranean in the FishMed database (Albouy et al., 2015) (Appendix D). Values of environmental predictor variables for climate data were extracted from the World Ocean Atlas 2013 version 2 (https://www.nodc.noaa.gov/OC5/woa13/woa13data.html). To take into account the vertical distribution of species in the water column, six environmental metrics were derived from monthly temperature and salinity climatologies: mean sea surface temperature and salinity (0–50 m depth), mean vertical temperature and salinity (0–200m depth) and mean sea bottom temperature and salinity (50 m – maximum bathymetry depth). These metrics were used to model bioclimatic envelopes for each species. The use of environmental variables assumed that current species ranges are mainly driven by the abiotic environment, which is a reasonable hypothesis for marine species as water temperature is commonly considered as the main driver of fish geographic ranges (Ben Rais Lasram et al., 2010; Ben Rais Lasram and Mouillot, 2009; Cheung et al., 2009; Sabatés et al., 2006).

Current distribution was modelled using eight climate suitability models (generalized linear models, generalized additive models, classification tree analysis, boosted regression trees, random forests, multivariate adaptive regression splines, artificial neural networks and flexible discriminant analysis) embedded in the BIOMOD2 R package (Thuiller et al., 2009).

As OBIS and GBIF databases provide occurrence data only at world scale (Hattab et al., 2014), to build reliable species distribution models, pseudo-absences (PAs) were generated in order to better characterize the environmental conditions experienced by species within their current ranges (Hattab et al., 2014, 2013b). These PAs were selected randomly, outside the suitable area of the surface range envelope model. The number of simulated PAs was double the occurrence data; they were equally weighted to the presence points during the fitting process.

In order to assess the accuracy of our final distribution maps, the True Skill Statistic (TSS, Allouche et al., 2006) was used to measure the performance of each model. This represents a combined measure of model sensitivity (i.e. the proportion of correctly predicted presences) and specificity (i.e. the proportion of correctly predicted absences).

For each species, the consensus distribution was obtained with an ensemble forecast approach. Results were weighted according to the TSS criterion (Allouche et al., 2006), i.e. weights were calculated on the basis of model accuracy in independent situations (Thuiller et al., 2009). To derive a consensus prediction, only the best model outputs (i.e. models with a TSS > 0.6) were kept (Appendix D). To transform the probabilistic consensus distribution into a presence/absence distribution, we preserved the occurrence probabilities for pixels above the sensitivity–specificity sum maximization threshold (i.e. the threshold that maximized the TSS criterion), and set to zero the occurrence probability for pixels under the threshold (Barbet-Massin et al., 2009). Spatial distribution maps are available in Appendix D.

2.5 Calibration of the OSMOSE-MED end-to-end model

An evolutionary algorithm (EA), inspired by the process of Darwinian evolution and developed to calibrate complex stochastic models, was used to calibrate OSMOSE-MED (Duboz et al., 2010; Oliveros-Ramos and Shin, 2016). By estimating certain unknown parameters (i.e. larval mortality rates of HTL species, availability coefficients of LTL species to all HTL species, and fishing mortality for exploited species), the calibration process aimed to constrain predicted biomass and catch of HTL species in OSMOSE-MED within realistic ranges. The model was compared to observed data using a maximum likelihood approach (Oliveros-Ramos et al., 2017). A log-normal distribution was assumed for biomass and catch errors.

The aim of the EA is to optimize an objective function over a given search parameter space: in our case, a penalized negative log-likelihood function (Oliveros-Ramos et al., 2017). A population of ‘individuals’, where each individual is a set of parameters (called the genotype) in the search space, was first created. Different unknown combinations of parameters were tested in order to minimize the objective function. Computation of the phenotype (i.e. outputs produced by a run of OSMOSE-MED with a given set of parameters) and of the fitness (i.e. goodness-of-fit from the minimization of the negative log-likelihood function) was done in a second step. At each generation (i.e. iteration of the optimization process), the algorithm calculated an ‘optimal parent’, which resulted from the recombination of the parameter sets that provided the best solution for each objective (partial likelihoods for species biomass and catch) (Oliveros-Ramos and Shin, 2016). The optimal parent was then used to produce a new set of parameter combinations (by recombination/mutation) which constituted the next generation. The EA was run until the convergence of the objective function or was stopped after a given number of generations (Duboz et al., 2010; Oliveros-Ramos et al., 2017; Oliveros-Ramos and Shin, 2016).

A steady-state calibration of the OSMOSE-MED model was performed using the mean of reported and reconstructed catches averaged over the period 2006–2013 (called hereafter the ‘reference state period’) as target data. For tuna and other large pelagic species (e.g. the swordfish *Xiphias gladius*), catch data was extracted from the International Commission of the Conservation of Atlantic Tuna (ICCAT) statistics database. For all other exploited species, reported fishery landings were provided by the UN Food and Agriculture Organization General Fisheries Commission for the Mediterranean (FAO-GFCM) database (http://www.fao.org/gfcm/data/capture-production-statistics) and reconstructed catches were obtained from the Sea Around Us (SAU) project (Zeller and Pauly, 2015). The latter were used in order to reduce data gaps and take into account discarded bycatch and illegal, unreported and unregulated fishing in the Mediterranean Sea, where actual catches are often underestimated (European Commission, 2003; Moutopoulos and Koutsikopoulos, 2014).

Cumulated biomass from stock assessments in different geographical sub-areas (GSA) of the Mediterranean Sea were used when available and realistic (i.e. when cumulated available biomass by species was higher than the average of FAO/SAU catches: for example, for *Merluccius merluccius, Sardina pilchardus* or *Engraulis encrasicolus*), and averaged over the reference state period (Appendix C). Biomass estimates of *Thunnus thynnus* and *Thunnus alalunga* were based on expert knowledge (Fromentin J.M. and Winker H., pers. comm.). For all other species for which biomass estimates were not available, we applied strong penalties to the objective function when output biomass from OSMOSE-MED did not lie within plausible ranges. Specifically, we considered FAO reported catches as a minimum threshold for species biomass and the maximum biomass threshold was derived from mean FAO/SAU catches and a fishery exploitation rate of 15%, which is assumed to be a very low exploitation rate in the context of Mediterranean fisheries (Vasilakopoulos et al., 2014).

The model was run for 100 years for each set of parameters to make sure that OSMOSE-MED reached a steady state, and only the last 30 years were analyzed by the EA. The calibration process allowed a set of parameters to be estimated for each species represented in OSMOSE-MED: the coefficients of plankton accessibility of the 7 LTL groups considered in the model (7 parameters), larval mortality rates of the 100 HTL species (100 parameters), and fishing mortality rates for species for which catch data was available (87 parameters). Following the methodology described in Oliveros-Ramos et al. (2017), a sequential multi-phase calibration was applied to estimate the 194 unknown parameters (Oliveros Ramos, 2014), with three successive calibration phases (detailed in Table 2).

The optimization process used the ‘calibrar’ and OSMOSE R packages (Oliveros-Ramos et al., 2017; Oliveros-Ramos and Shin, 2016) available from the CRAN website (https://cran.r-project.org/web/packages/calibrar). The calculation was performed using DATARMOR, the French Research Institute of Marine Exploitation (IFREMER) high-performance computing facility at the ‘Pôle de Calcul et de Données Marines’ (https://wwz.ifremer.fr/pcdm/Equipement), in which 36 compute nodes representing 1008 cores (2.4Ghz) and around 4 TB of RAM were mobilized to perform the calibration, which involved several iterative trials over more than one year.

Table 2 Order in which the parameters were estimated in the multi-phase calibration of the OSMOSE-MED model, using the evolutionary optimization algorithm included in the ‘calibrar’ R package.

Phase	Parameters	Number of estimated parameters	Number of generations
1	Coefficients of plankton accessibility	7	100
2	Previous parameters + larval mortalities	107 (including previous 7)	200
3	Previous parameters + fishing mortalities	194 (including previous 107)	600

Due to the inherent stochasticity of OSMOSE, 10 replicated simulations (i.e. with an identical set of parameters) were averaged to analyze the outputs of the last 10 years.

2.6 Evaluation of OSMOSE-MED outputs with independent data

In order to evaluate the ability of OSMOSE-MED to predict the spatial distribution of the entire biomass in a realistic way, we compared the model output to observed data that was not used either for the calibration of OSMOSE-MED, or its parameterization, or for the climate niche modelling used to generate the species distribution maps. The ranking of geographical sub-areas (GSAs), based on cumulated biomass estimates by species (in kg.km^{-2}) from the MEDITS survey (International bottom trawl survey in the Mediterranean, Bertrand et al., 2002) in 2006–2013 was compared to the ranking predicted in OSMOSE-MED (see Appendix F for the correspondence between GSA numbers, names and sizes). To evaluate the consistency of the OSMOSE-MED model at the community level, the mean trophic level (mTL) of each species was calculated and compared with three different sources: the FishMed database, which contains ecological and biological traits for 635 Mediterranean fish species (Albouy et al., 2015), the Ecopath model built at the scale of the Mediterranean basin by Piroddi et al. (2017, 2015a), and a review of feeding habits and trophic levels of 148 Mediterranean fish species (Karachle and Stergiou, 2017; Stergiou and Karpouzi, 2002).

An important step in the validation of the model lay in comparing simulated species diets to observations and to current knowledge of the trophic functioning of the Mediterranean ecosystem. In OSMOSE, the diet composition of a species is not determined *a priori* in model input, but emerges from the assumption of an opportunistic predation process, based on predator–prey size constraints and spatio-temporal co-occurrence. To check whether this size-based predation rule led to realistic and consistent dietary features, we focused on the diet composition of four of the most important species in terms of catch volume or value in the Mediterranean, namely the European anchovy, the European pilchard, the red mullet and the European hake. We compared the adult diets modelled by OSMOSE-MED to the diets derived from the mass-balanced Ecopath model of the Mediterranean Sea (Piroddi et al., 2015a), as the functional groups in the latter were mostly parameterized to represent adults. The diet matrix used for parameterizing Ecopath was compiled from the available literature and mainly based on empirical data (Piroddi et al., 2017, 2015a), it is thus a convenient way to access observed diets and current knowledge on major trophic interactions, at least for well-studied species.

3 Results and discussion

3.1 Calibration

Our OSMOSE-MED model reached a steady state after around 50 years of simulation. The evolutionary algorithm converged and stabilized after 500 generations. Both negative log-likelihoods and global AIC improved during each phase, but regarding the global evolution of the likelihoods, larval mortality parameters seemed to play the most important role in the calibration process.

Accessibility coefficients of LTL groups to HTL organisms ranged between around 10^{-9} and 10^{-1} (Appendix E). The smallest values were obtained for small-size plankton groups (except for picophytoplankton), which could be expected in view of their high biomass and low predation rates by HTL organisms (Jackson and Lenz, 2016; Morote et al., 2010; Pepin and Penney, 2000). In contrast, higher coefficients were found for mesozooplankton and benthos groups, for which around 1% and 0.5% were respectively available to predation by HTL. These coefficients were in the same order of magnitude as in other modelled ecosystems (e.g. Grüss et al., 2015; Marzloff et al., 2009; Travers-Trolet et al., 2014).

Estimated larval mortality rates (M_0) ranged between 0.14 $year^{-1}$ for the caramote prawn (*Penaeus kerathurus*) and 10.60 $year^{-1}$ for the small-spotted catshark (*Scyliorhinus canicula*) (Appendix E). The larval mortality rate found for *P. kerathurus* was probably an underestimate, since compared to the value (M_0 =1.58 $year^{-1}$) estimated by Halouani et al. (2016b) with the

OSMOSE-GoG model, the biomass estimated by our model lies outside a valid interval. The majority of larval mortality lay between 1.49 and 5.29 $year^{-1}$ (mean = 3.69 ± 2.70 $year^{-1}$; Appendix E). A low larval mortality rate estimated by the evolutionary algorithm for a particular species does not necessarily mean that the total natural mortality is small, but may reflect that most of the sources of mortality (predation by the other modelled species, for example) are simulated explicitly in the model (Travers-Trolet et al., 2014).

As fishing mortality rates (F) estimated by stock assessments were not available for all exploited species, we chose to estimate these parameters by comparing the model output to observed and reconstructed catches during the third phase of the calibration process. Most of the fishing mortality rates were within the range of 0.23 to 0.8 $year^{-1}$, and the global fishing mortality rate was on average 0.60 ± 0.48 $year^{-1}$ (Appendix E).

3.2 Comparing OSMOSE-MED predictions to observations and current knowledge

3.2.1 Species biomass

In our model, the estimated biomass, averaged over the last ten years of simulation and over ten replicates, generally fell in acceptable intervals (i.e. above FAO reported catch and below a theoretical maximum biomass considering an exploitation rate of 15% for the averaged FAO-SAU catches) (Figure 2). For species for which stock assessments were available – for instance, the European pilchard (*Sardina pilchardus*), the European anchovy (*Engraulis encrasicolus*) and the European hake (*Merluccius merluccius*) – the total biomass predicted by OSMOSE-MED was slightly higher or very close to previously estimated biomass (Figure 2). Given that most available stock assessments were for European waters, the higher estimated biomass for species such as *Sardina pilchardus*, *Parapenaeus longirostris* and *Mullus barbatus barbatus* may actually reflect a biomass volume present in the southern Mediterranean or in unassessed areas of the Mediterranean Sea. Overall, the European anchovy and the European pilchard (around 1.8 million tons of biomass) represented around 50% of the total cumulative biomass of the system (excluding plankton). The prevalence, in terms of biomass, of pelagic fish was also found in an Ecopath model of the Mediterranean Sea (Piroddi et al., 2015a). For species such as *Crangon crangon, Atherina boyeri* and *Etrumeus teres*, due to their highly variable population dynamics (high fecundity, short lifespan, high biomass turnover rate), biomass was particularly difficult to calibrate and was overestimated by OSMOSE-MED. Additionally, for non-native species (e.g. *Etrumeus teres*), more research is needed on their biology and ecology in their new expansion areas in order to obtain robust life history trait estimates and improve model predictions (Dimarchopoulou et al., 2017; Katsanevakis et al., 2014, 2012). The lack of stock assessments or difficulty in accessing these assessments constitute real barriers to the development, parameterization and calibration of ecosystem models in the region (Coll et al., 2013; Katsanevakis et al., 2015; Piroddi et al., 2015a). Around 25% of landed biomass and less than 10% of exploited stocks are currently assessed, and this on an irregular basis (Tsikliras et al., 2015). Moreover, the monitoring of fish stocks is hindered by the lack of biological or ecological observational data for far too many species, with approximately 80% of landings coming from stocks that are data deficient (Dimarchopoulou et al., 2017; Le Quesne et al., 2013).

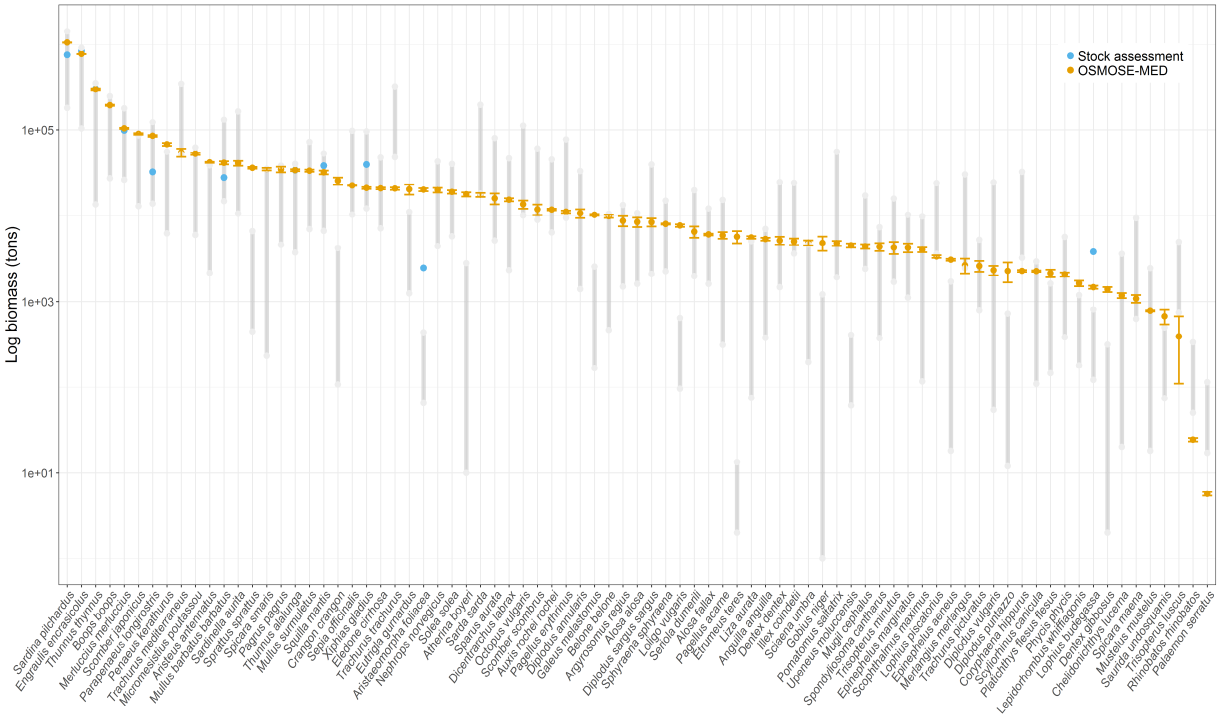

Figure 2 Average biomass of exploited species (87 species out of the 100 modelled) predicted by OSMOSE-MED (in orange) in log scale and associated standard deviation. Cumulative biomass from stock assessments (in blue) (only cumulative biomass higher than the FAO reported catch is shown). The grey bars show the minimum biomass (the FAO reported catch) and the theoretical maximum biomass, considering an exploitation rate of 15% and the average between the FAO and Sea Around Us catch.

The model accurately predicted the spatial distribution of the overall biomass, at least for the northern part of the Mediterranean where the MEDITS surveys were conducted, as suggested by the significant Spearman's rank correlation coefficient value of 0.71 between MEDITS and OSMOSE-MED biomass ranking. Differences that exist between the rankings of certain GSAs can be explained in two ways. For instance, around the island of Corsica, OSMOSE-MED predicted less relative biomass (ranked 15 out of a total of 16 GSAs) than was estimated by MEDITS (ranked 8). This is partly due to the very narrow continental shelf around Corsica and to the resolution of our model (20×20 km²), which may be too coarse to represent the dynamics in this area, with the result that the climate niche models and distribution maps input in OSMOSE-MED did not resolve precisely enough the spatial distribution of species closely associated to the Corsican continental shelf. Developing OSMOSE-MED at a finer resolution was attempted in the early stages of model configuration, but the computing cost for the calibration process was judged too high (at least two to three times the computing time required for a 10×10 km² resolution). In contrast, for GSAs that ranked higher in OSMOSE-MED than in MEDITS (i.e. below the 1:1 line in Figure 3), these differences could be explained by the fact that MEDITS is a demersal trawl survey with low catchability of small pelagic fish. While data from the trawl survey is useful in assessing the spatial and temporal trends of pelagic species in the Mediterranean (Brind'Amour et al., 2016), some biases may exist, such as the survey's potential significant underestimation of the biomass of some small pelagic fish.

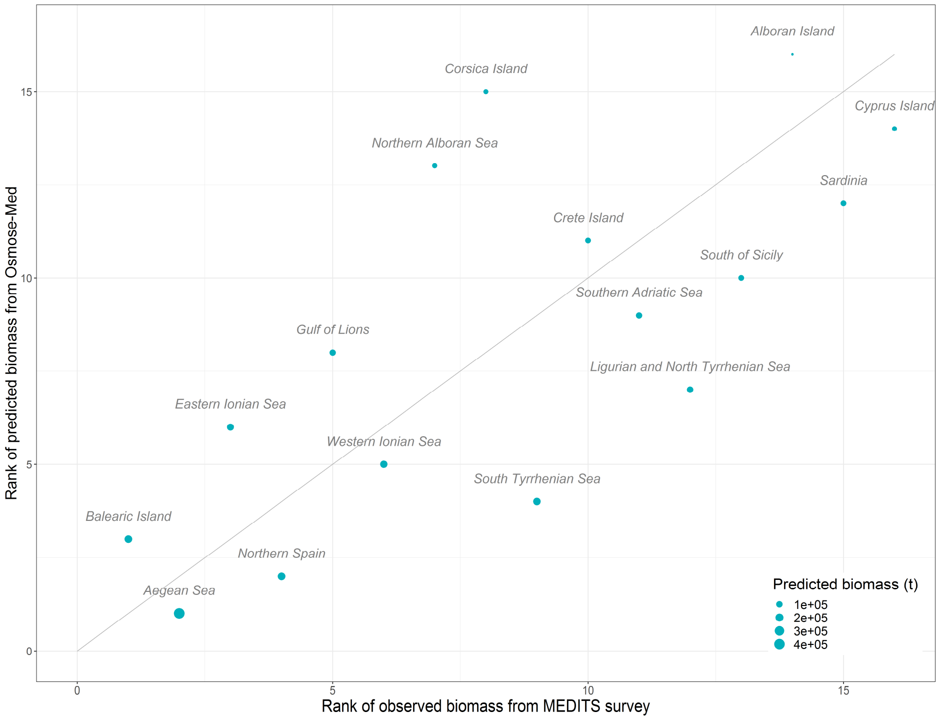

Figure 3 Comparison of predicted and observed ranking of total biomass by geographical sub-areas (GSAs). Observed total biomass data is from the MEDITS survey (2006–2013). Circle size is proportional to the total predicted biomass in the GSA. Solid line is the 1:1 relationship.

3.2.2 Species catches

Catches predicted by OSMOSE-MED were globally consistent with reported/reconstructed catch data in the Mediterranean Sea (Figure 4 and Figure 5). Our model predicted a total catch of around 802,470 t at the scale of the whole basin, which compares well to the 681,243 t recorded by the FAO and the 952,930 t reconstructed by the Sea Around Us (817,087 t on average). The European pilchard and the European anchovy represented almost 30% of the total catch in OSMOSE-MED and around 40% in reported or reconstructed catches over the 2006–2013 period (FAO, 2016; Pauly and Zeller, 2016). According to Stergiou et al. (2015), small pelagic species, mainly European anchovy and European pilchard, dominate the landings across the entire Mediterranean, making up 34% of cumulative landings in the western Mediterranean, 41% in the central area, and 25% in the east. The Spearman's correlation coefficient between the rank of the average FAO-SAU catch by species and that estimated by OSMOSE-MED was 0.79 (Figure 5). The main difference between predicted and average reported/reconstructed catches came from the model's under- or overestimation of species biomass. For instance, the common prawn (*Palaemon serratus*) seemed to be underestimated in terms of predicted biomass and catch. For species for which stock assessment biomass estimates were available, the OSMOSE-MED model predicted the catches relatively well. For instance, the OSMOSE-MED estimated catch for the European anchovy was around 118,480 t, while the FAO reported catch was 103,650 t and the SAU reconstructed catch was 169,870 t over the 2006–2013 period.

In the current version of OSMOSE (Version 3 update 2), fishing effort is homogeneous in space. Catch outputs could be improved with spatialization of the fishing effort – this is being implemented in the latest version in development. However, data on fishing effort and distribution is either unavailable or difficult to access in some Mediterranean regions (Katsanevakis et al., 2015). One solution might be to use data from the new Global Fishing Watch database, which collects data from an automatic identification system (AIS) of fishing fleets around the world (Kroodsma et al., 2018). An index of the fishing effort in the Mediterranean Sea could then be calculated by evaluating the fishing time by vessel characteristics (Kroodsma et al., 2018). However, as most of the fishing boats in the Mediterranean fleet are less than 10 m and AIS is only compulsory for large European vessels, effort would remain underestimated (Ferrà et al., 2018). Fitting an ecosystem model based on catch data is a difficult task in the Mediterranean due to the poor quality of fishery statistics (Pauly et al., 2014; Piroddi et al., 2017). A significant quantity of catches is still not recorded and some stocks are data deficient. The large difference (almost twice) between reported and reconstructed catches highlighted by Pauly and Zeller (2016) illustrates this issue. As suggested by Piroddi et al. (2017), better and improved availability of catch data for modelling studies could help to estimate more realistic fishing trends and mortalities in space and time. The new MedFish4Ever initiative, launched by the European Commission in 2017 to rebuild a sustainable fisheries sector, could play a key role in the improvement of such data, at least in the northern Mediterranean (https://ec.europa.eu/fisheries/inseparable/en/medfish4ever).

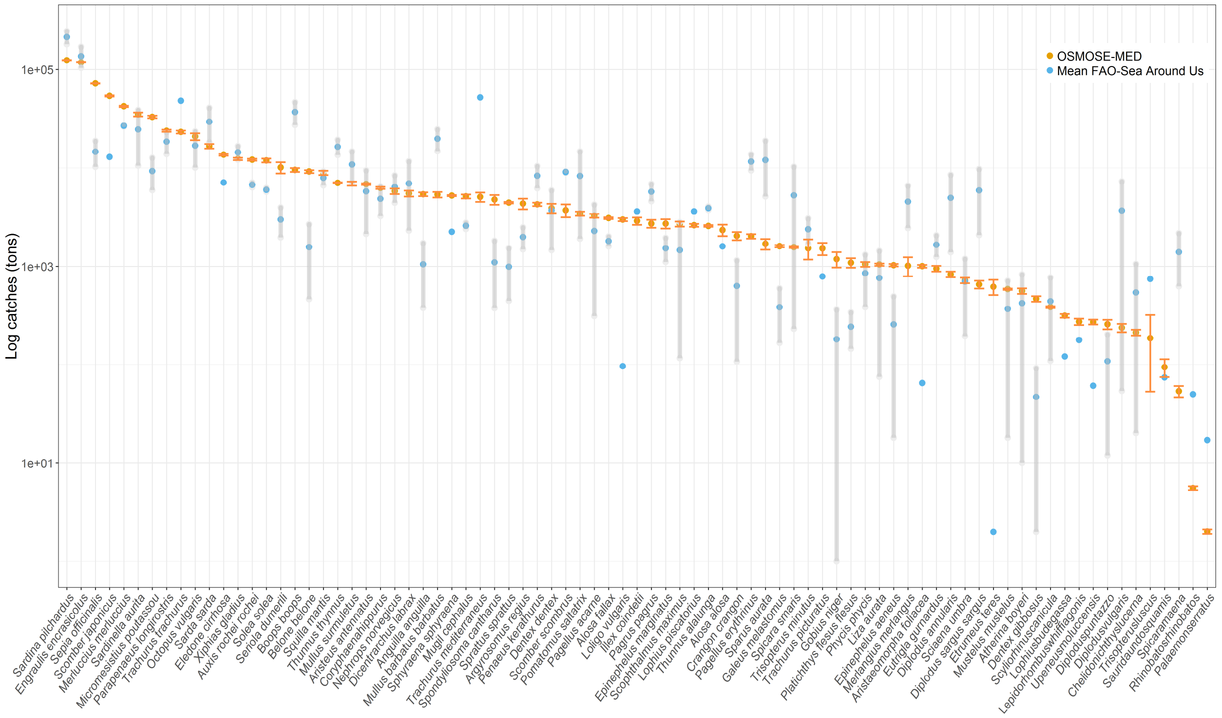

Figure 4 For the 2006–2013 period, average catches predicted by OSMOSE-MED of all exploited species (in orange) in log scale and associated standard deviation. Average FAO–SAU catch data, which served as target data during the calibration process, in blue. Grey bars show the minimum (FAO reported) catch and the maximum (SAU reconstructed) catch.

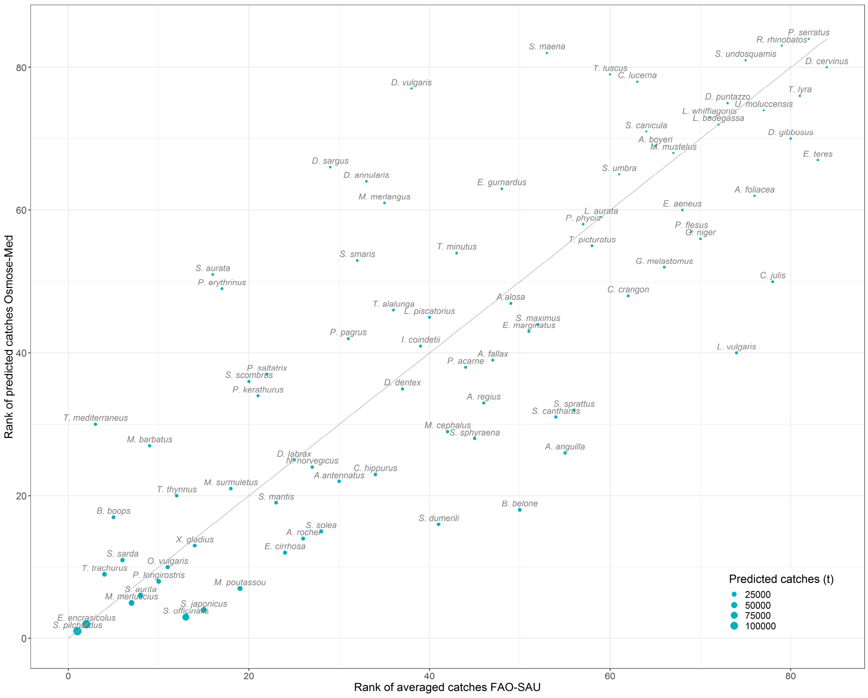

Figure 5 Comparison of predicted and observed ranking of catches by species. Reported/reconstructed catches are the averages of FAO-SAU catches (2006–2013). Circle size is proportional to the predicted catches. Predictions and data for the 2006-2013 period. Solid line is the 1:1 relationship.

3.2.3 Species trophic levels

In general, the trophic levels predicted by OSMOSE-MED were consistent with the results obtained by other studies in the Mediterranean (Figure 6). A significant majority (69%) of the OSMOSE-MED mTLs were close to previously estimated mTLs (by less than 0.3). Of the 81 species that had several mTL data sources, OSMOSE-MED mTLs stood within the range of previously estimated mTLs for 58 species (72% of the species). Trophic levels from OSMOSE-MED were generally higher than those of the Ecopath model and generally lower than those of FishMed, which were mainly from the Fishbase database (Albouy et al., 2015). The significant Spearman's correlation coefficients between the OSMOSE-MED trophic levels and the FishMed, Ecopath and Karachle and Stergiou (2017) trophic levels were 0.67, 0.51 and 0.68, respectively. In OSMOSE-MED, the swordfish *Xiphias gladius* had the highest trophic level (mTL = 4.64 ± 0.002) and the European pilchard had the lowest (mTL = 3.11 ± 0.0003). Large pelagic fish species such as the swordfish, dolphinfish (*Coryphaena hippurus*), bluefin and albacore tuna (*Thunnus thynnus* and *Thunnus alalunga)*, and Atlantic bonito (*Sarda sarda*), shark species such as the common guitarfish (*Rhinobatos rhinobatos*), common smooth-hound (*Mustelus mustelus*) and small-spotted catshark (*Scyliorhinus canicula*), and demersal species such as the European hake (*Merluccius merluccius*) were all identified as top predators by the

OSMOSE-MED model (i.e. mTL > 4.15). These results are consistent with other trophic models for the Mediterranean, which have identified large pelagic fish and shark species (except for common guitarfish) at the top of the food web (Albouy et al., 2010; Coll et al., 2007; Corrales et al., 2015; Halouani et al., 2016; Hattab et al., 2013a).

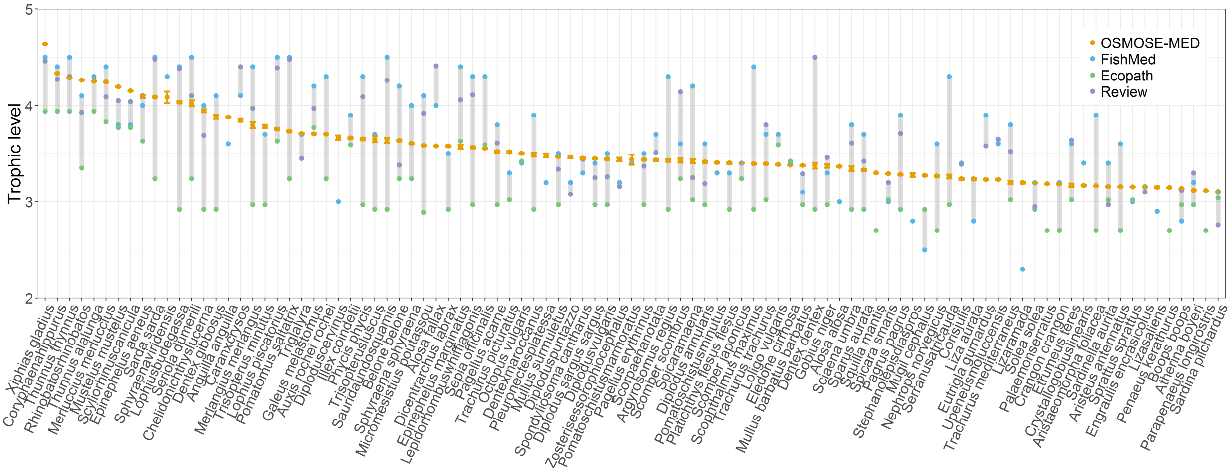

Figure 6 Mean species trophic levels predicted by OSMOSE-MED (in orange), the FishMed database (Albouy et al., 2015) (in blue), the Mediterranean Ecopath model (Piroddi et al.,2017, 2015a) (in green) and Karachle and Stergiou (2017) (in purple).

3.2.4 Species diets

In regard to the prey composition of the diet of the four species under scrutiny, OSMOSE-MED and the Mediterranean Ecopath model were more or less in agreement (Figure 7). For the European anchovy and the European pilchard, the simulated diets were similar and largely dominated by zooplankton, a pattern in line with other observations (Karachle and Stergiou, 2017; Stergiou and Karpouzi, 2002). In OSMOSE-MED, the European pilchard consumed less phytoplankton (4.5%, mainly diatoms) than in the Ecopath model (10%), but the result remains qualitatively realistic (i.e. the main prey is zooplankton followed by phytoplankton). The dominance of zooplankton in the diet of pilchards could be explained in two ways. First, the availability coefficients of phytoplankton to HTL organisms were estimated to be very low by the model calibration (ranging between 10^{-1} and 10^{-7}), which does not allow the European pilchard to feed more on these groups. Secondly, it has been shown that European pilchard populations living in lower productivity regions, as is the case for the Mediterranean, would preferentially capture larger individual prey via particulate feeding and would consume more zooplankton than populations in the Northwest Atlantic (Costalago et al., 2015). Regarding red mullet (*Mullus barbatus barbatus*), the main difference between the two models lies in the higher proportion of zooplankton prey predicted by OSMOSE-MED. This discrepancy is due to the fact that some of the crustaceans eaten in the Ecopath model were either included in the benthos group in the simulated diet of the red mullet in OSMOSE-MED or explicitly modelled at the species level, as is the case for *P. longirostris* and *P. kerathurus*. For the European hake, most of its prey simulated by OSMOSE-MED was grouped in more aggregated trophic boxes in Ecopath. For instance, Ecopath classified shrimps in the functional group ‘crustaceans’, octopus in ‘benthic cephalopods’, and some species such as *Mullus surmuletus* or *Boops boops* in ‘small demersals’. However, the proportional contribution of some prey such as the European pilchard and European anchovy differed more significantly between the two models. For example, the European pilchard represented 5.7% of the diet of the European hake in OSMOSE-MED and 12.5% in Ecopath. This may be explained by the fact that the hake diet varies greatly depending on prey availability and abundance, both in the Mediterranean and in the Atlantic Ocean (Carrozzi et al., 2019; Cartes et al., 2009; Velasco and Olaso, 1998). Carrozzi et al. (2018) found, for instance, that in the central Mediterranean, the European pilchard represented 3.78% and the European anchovy 1.32% of the hake diet.

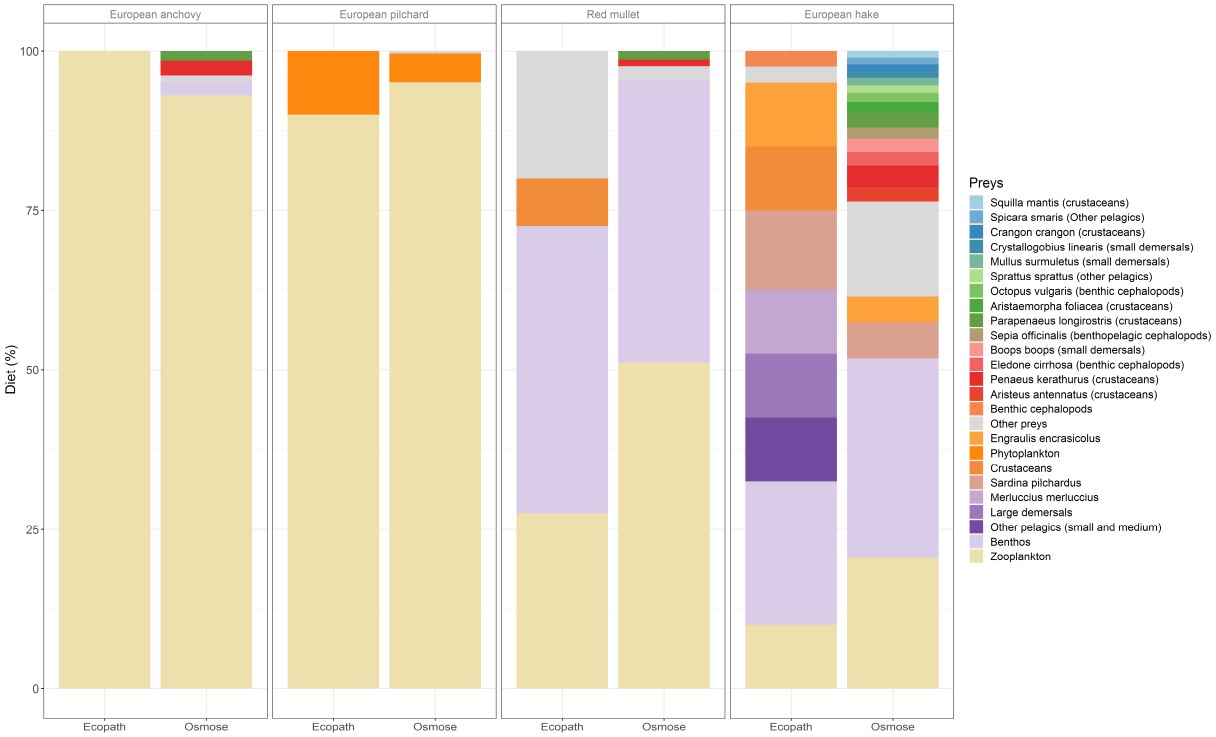

Figure 7 Diets simulated by OSMOSE-MED and the Mediterranean Ecopath model for four species (two small pelagic fish species (European anchovy and European pilchard) and two dermersal fish species (red mullet and European hake). Functional groups used in the Ecopath model in which OSMOSE-MED species are grouped are indicated in parentheses. In both cases, diets are expressed as a percentage of overall prey by mass.

3.2.5 Emerging spatial patterns

The total biomass (all HTL species combined) was mainly distributed on the continental shelf and in areas where primary and secondary production were higher (Figure 8), in line with findings from previous studies (Durrieu de Madron et al., 2011; Bosc et al. 2004). The higher biomass found in highly productive areas (the Gulf of Lion, the Catalan Sea or the South Levantine Sea, fed respectively by the Rhône, Ebro and Nile rivers, which enhance primary productivity through nutrient discharge and hence play a major role in local food webs) suggested that primary production, through bottom-up control, was one of the main drivers of the biomass distribution of HTL organisms in the Mediterranean Sea. Numerous Ecopath models built at more local scales in the region confirm this hypothesis (Coll et al., 2007, 2006; Coll and Libralato, 2012; Halouani et al., 2016; Hattab et al., 2013a). The control of marine productivity, from plankton to fish, principally mediated through bottom-up processes that can be traced back to the characteristics of riverine discharges, has also been demonstrated by Macias et al. (2014). This renders the Mediterranean Sea vulnerable to sources of potential impacts on primary production such as climate change and marine pollution (Cheung et al., 2011; Jochum et al., 2012; Macias et al., 2015; Moullec et al., 2016) and highlights the need for integrating physicochemical oceanographic drivers with the dynamics of HTL organisms in a single modelling framework in order to take into account possible bottom-up control and improve our ability to predict future ecosystem changes (Piroddi et al., 2017; Rose et al., 2010; Travers-Trolet et al., 2014). It should also be noted that since fishing effort was spatially uniform in our model, we could not precisely assess the direct role of fishing in the spatial distribution of the HTL biomass, but only its impacts on species biomass, composition and interactions, which were indirectly reflected by the biomass distribution across the Mediterranean Sea.

A low gradient of biomass was observed from northwestern to southeastern regions, in line with previously observed gradients of production and biodiversity (Coll et al., 2010; Mouillot et al., 2011). The OSMOSE-MED model showed the western Mediterranean Sea accounting for 35% of total biomass, the Adriatic Sea 9%, the Ionian and central Mediterranean Seas 31%, and the Aegean and Levantine Seas 25%. The total biomass in the Adriatic Sea may be an underestimation in view of the results of a Mediterranean Ecopath model (Piroddi et al., 2015a), which found that the Adriatic Sea had the highest total biomass, followed by the western Mediterranean Sea and the Ionian and Eastern Seas. This is partly due to the Eco3M-S biogeochemical model's underestimation of the concentration of phytoplankton in this area (Kessouri, 2015). In OSMOSE-MED, the Eastern basin appeared highly oligotrophic, with low biomass values, with the exception of the Gulf of Gabès and the waters surrounding the Nile plume, two regions that have been characterized by high productivity (Hattab et al., 2013a).

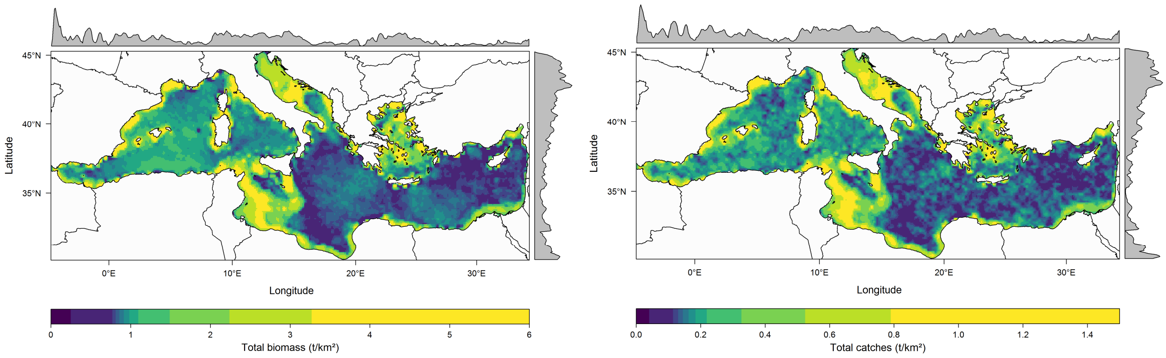

Figure 8 Spatial distribution of the simulated total biomass (left) and catches (right) (all HTL species combined) expressed in t.km^{-2}. Graphs on the top and right respectively represent the meridionally and zonally averaged distribution of biomass and catches.

The spatial distribution of catches, resulting from uniformly distributed fishing effort, generally followed the spatial distribution of biomass, with relatively fewer catches in the high seas (Figure 8). As with biomass, the model predicted a low gradient of catch from the north to the south and from the west to the east, in line with the pattern of productivity in the Mediterranean (Bosc et al., 2004; Ignatiades et al., 2009). The Iberian shelf waters, the Balearic Sea, the Gulf of Lion, the North Tyrrhenian Sea, the Adriatic Sea, the waters south of Sicily, the Gulf of Gabès and the north Aegean Sea were all identified as exploitation hotspots concentrating most of the catches at the scale of the Mediterranean. Most of these have been identified as highly impacted areas (Micheli et al., 2013a), in particular by demersal fishing activity and climate-induced change, and coincide with the areas of conservation concern identified by Coll et al. (2012).

The distribution of the mean body size of the fish community revealed a clear gradient from the northwestern to the southeastern regions (Figure 9). Despite the fact that small pelagic fish species were mainly concentrated in the northwestern region, the mean body size weighted by abundance values was higher in the northern part of the basin. Some authors have argued that high salinity, high temperature, low productivity or a combination of all these factors are responsible for 'Levantine nanism' (dwarfism), a phenomenon that results in small body sizes for all species in general (Por, 1989; Sharir et al., 2011; Sonin et al., 2007). In OSMOSE, growth in size is linked to predation success. If predation success is lower than a critical predation efficiency threshold corresponding to maintenance requirements, fish can starve, and the growth rate is reduced (Shin and Cury, 2001). Thus, the oligotrophic conditions in the eastern Mediterranean could lead to reduced growth rates and smaller size for some species, as indicated in the OSMOSE-MED model. The spatial distribution of mean size also showed large individuals in the Western high seas, where catches were lower (Figure 9). The large mean body size in this area is likely explained by the greater local abundance of large fish species (e.g. *Thunnus thynnus* and *Xiphias gladius*) in the Western high seas. On the other hand, the small body size found in certain areas (e.g. around the Balearic Islands, the Northern Adriatic Sea and Cyprus) could be the result of heavy fishing, which preferentially harvests larger-bodied individuals (either of a given species, or of species with larger mean size) and also induces the natural selection of slow-growing individuals (Jørgensen et al., 2007; Law, 2000; Shin et al., 2005).

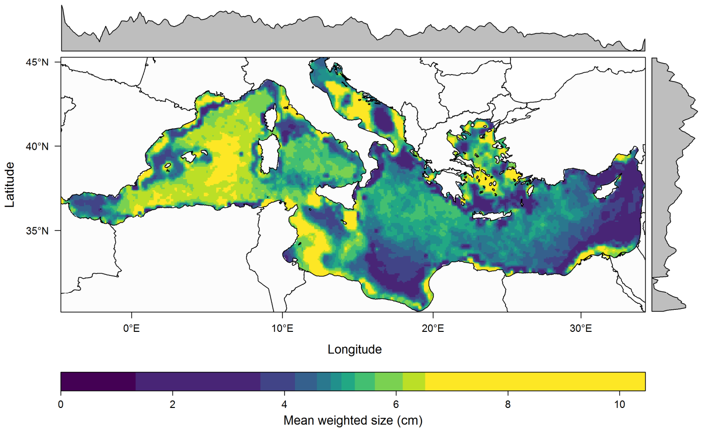

Figure 9 Spatial distribution of mean body size (mean size weighted by species abundance) expressed in cm. Graphs at the top and right represent the meridionally and zonally averaged weighted size.

4 Conclusion and perspectives

4.1 A unique large-scale end-to-end model

While numerous trophic modelling studies have been carried out on the Mediterranean Sea, most are at a local scale (Bănaru et al., 2013; Coll et al., 2007; Corrales et al., 2017b, 2017a; Halouani et al., 2016; Hattab et al., 2013a), with a few rare examples at the basin scale (Albouy et al., 2014; Piroddi et al., 2017, 2015a). This study was the first attempt to use an end-to-end trophic approach at the scale of the entire Mediterranean Sea, with explicit spatial, life-trait-based modelling of the whole lifecycle of the dynamics of 100 interacting species. The OSMOSE-MED integrated end-to-end model coupled a physical model (NEMOMED 12), a low trophic level model (Eco3M-S) and a high trophic level model (OSMOSE) to represent the ecosystem dynamics and the trophic structure of the entire Mediterranean. The OSMOSE model, originally developed by Shin and Cury (2004, 2001), has never been applied to such a large number of species in interaction and at such a broad spatial scale. As noted by Fu et al. (2017), no more than 10 to 15 key species are typically included in an OSMOSE model. This restricted number of species may be explained by: (i) the extensive data required concerning species' life histories to properly parameterize a model, (ii) the computing capacity required to fit the model to observations, and (iii) a desire to focus on major species and interactions to simplify the complexity of the system. We decided to take the modelling approach to the next step to allow much more comprehensive, explicit modelling of a large number of marine species. Our ultimate goal was to build a tool representing the diversity of species and their interactions in a realistic way at a basin-wide scale, in order to better address the future repercussions of climate change (e.g. species distribution shifts and plankton production changes) combined with other anthropogenic drivers on biodiversity (e.g. fishing). By modelling the spatial dynamics of the community across the whole Mediterranean as well as in geographical sub-areas, we can predict the potential cascading effects of these changes on food webs and ecosystem services.

To our knowledge, OSMOSE-MED is the most complete model built at the scale of the entire Mediterranean in terms of species and process representativeness. We used existing biological and ecological data from various databases and also took advantage of the high-performance computing (HPC) platform DATARMOR, which allowed the calibration of such a complex model. As for most end-to-end models, one challenge lies in searching through and integrating a large amount of data from various sources – databases, scientific and 'grey' literature, output from other models (de Mora et al., 2016; Fulton, 2010). While OSMOSE-MED integrated the best ecological knowledge available for the Mediterranean, certain gaps should be noted, mainly concerning fish species in the southern part of the basin (Dimarchopoulou et al., 2017). According to some estimates, there is no biological information for as many as 43% of Mediterranean fish species (Dimarchopoulou et al., 2017). This lack of biological and ecological data, as well as the variable quality of commercial fisheries data, especially in the southern and eastern Mediterranean Sea, hinder reliable stock assessments. A crucial challenge is to increase the number of assessed stocks: first, to ensure their sustainable exploitation, and second, to allow the development of integrated ecosystem models that would help to design more effective ecosystem-based fisheries management in the Mediterranean basin (Coll et al., 2013; Piroddi et al., 2017, 2015a; Cardinale and Scarcella, 2017; Colloca et al., 2013). Another challenge is that the region generally suffers from problems with data ownership, reliability and accessibility (Katsanevakis et al., 2015).

The model also represents a significant advance in complex ecosystem modelling. The most critical and time-consuming step, given the stochasticity and the complexity of the model, was to maintain the coexistence of all HTL species to provide a realistic representation of biodiversity. In an OSMOSE model, the number of trophic links, the connectance, and the importance of feedback controls can be very large and can make the calibration procedure complicated and time-consuming (Halouani et al., 2016; Marzloff et al., 2009; Travers-Trolet et al., 2014). We exploited the capacities of the evolutionary optimization algorithm in order to find a set of estimated parameters within a 195-dimensional search space that reproduced state variables and indicators close to observations (Oliveros-Ramos et al., 2017; Oliveros-Ramos and Shin, 2016). This is the first time the 'calibrar' R package has been used to configure such a complex model (a large number of parameters in a stochastic model with many nonlinearities), and it proved its ability to solve complicated minimization problems (Oliveros-Ramos and Shin, 2016). Due to computing time and the need for continuous iterative trials and feedback between model parameterization and observations, the calibration of OSMOSE-MED took more than a year and required high-performance computing facilities. The development of OSMOSE-MED is an important step forward for both OSMOSE and calibrar user communities, and more broadly for the field of ecosystem modelling, as proof of concept that the complex representation of species dynamics and interactions can be achieved and can produce realistic spatial and lifecycle dynamics of multiple species subject to climate and anthropogenic impacts.

4.2 Limitations of the model

Ecosystem models, despite their increasing complexity, granularity and representativeness remain idealized or simplified conceptual representations of very complex systems (Gunawardena, 2014). These simplifications result in certain limitations in our model:

- *Benthos compartment:* strong benthic–pelagic coupling exists in the Mediterranean Sea, as highlighted in several Ecopath models of the region (Bănaru et al., 2013; Coll et al., 2007; Corrales et al., 2015; Hattab et al., 2013a). Moreover, many species included in OSMOSE-MED have omnivorous and carnivorous diets partly based on benthic organisms such as polychaetes, amphipods or crustaceans. To account for this, we added to the model a benthos 'black box' with a constant biomass and uniform spatial distribution. Given its importance in the Mediterranean, this trophic compartment would merit improved representation: for example, by considering multiple functional groups with common biological and ecological characteristics (e.g. meiofauna, bivalves, echinoderms) (Grüss et al., 2016). As the data to do this is lacking for both the parameterization and calibration of the model, an intermediate complexity approach could be adopted to model these more refined benthic compartments as ‘background taxa’ for which only predation, mean growth rate and spatial distribution are modelled. This new category of ‘intermediate complexity’ species would deal with limited datasets and allow more species of interest to be included while keeping the model reasonably complex: this has recently been coded in OSMOSE (Fu et al., 2017).

- *Ontogenetic habitat shifts*: Numerous species included in OSMOSE-MED exhibit clear ontogenetic habitat shifts in the Mediterranean (Cartes et al., 2009; Druon et al., 2016, 2015; Giannoulaki et al., 2013b, 2013a; Macpherson, 1998). These range shifts can play a critical role in population dynamics and ecosystem functioning (MacCall, 1990; Macpherson and Duarte, 1991; Methratta and Link, 2007). For instance, Caddy (1990) hypothesized that the sustainability of the majority of Mediterranean fisheries depends on spawners refuging on continental slopes. For most major commercial species (including hake, monkfish and shrimp), the continental slope and canyons, less accessible to fishing fleets, are used as spawning areas, while the continental shelf and the coastal strip, which are more intensively fished, are preferred zones for nurseries (Würtz, 2012). Thus, including different spatial distribution maps (i.e. spawning and nursery grounds) for certain key species such as small pelagic fish (e.g. European anchovy, European pilchard and European mackerel) and demersal fish (e.g. European hake and red mullet) could potentially improve the spatial representation of food webs and population dynamics, as well as their vulnerability to fishing. Habitat suitability models by stage or size class that relate abundance information from surveys to environmental variables could be used for this purpose (Druon et al., 2015; Giannoulaki et al., 2013a).

- *Biological and ecological processes*: OSMOSE does not model many processes relating to the lifecycle of species which depend on highly sophisticated regulatory mechanisms that modulate physiological organism responses (e.g. diel and seasonal rhythms, sexual maturation and mating, resting phases, behavioral and ontogenetic plasticity, migratory patterns or variable prey selectivity according to net energy gained). In order to improve the ability to represent complex marine systems, the metabolic requirements of species should be considered in future modelling studies (Carozza et al., 2019; Jørgensen et al., 2016). In our approach, the representation of growth and fecundity could be replaced by a bioenergetics model that mechanistically represents the energetic trade-off between growth and reproduction and describes plasticity in bioenergetic rates in response to food abundance, oxygen and temperature.

- *Spatialized fishing effort/mortality*: While OSMOSE-MED assumed a uniform spatial distribution of fishing effort, this is not realistic since fishing effort is mainly distributed along coasts and the continental shelf (Kroodsma et al., 2018; Leleu et al., 2014; Maynou et al., 2011; Ramírez et al., 2018), although the lower biomass in the open sea counterbalances this potential source of bias (Figure 8). In addition, fisheries targeting large pelagic fish such as tuna or swordfish often operate in the open sea, due to the distribution pattern of the target species (Druon et al., 2016). Fishing effort metadata, reported at the scale of species and geographical sub-area, available in the Data Collection Reference Framework (GFCM, 2018) could be used to improve the differential pressures exerted by fishing across the Mediterranean. Another option to spatialize fishing effort/mortality would be to model as many exploited populations of a species as the number of evaluated stocks. This would require knowing the true number of stocks in the Mediterranean and the possible connectivity between them (Fiorentino et al., 2014; Ragonese et al., 2016).

- *Uncertainty*: Marine ecosystems are structurally complex, spatially and temporally variable, and difficult and costly to observe, all of which can potentially lead to considerable uncertainty in model predictions (Cheung et al., 2016; Hill et al., 2007; Payne et al., 2016). There are many sources of uncertainty in ecosystem models, from structural (model) uncertainty, and initialization and internal variability uncertainty to parametric uncertainty (Payne et al., 2016). Assessing these different types of uncertainty would allow building confidence intervals around the OSMOSE-MED predictions and increase its relevance for making projections and supporting policymaking in the Mediterranean Sea (Gal et al., 2014; Hill et al., 2007; Hyder et al., 2015; Payne et al., 2016). Uncertainty due to the sources of input data (i.e. parametric uncertainty) could be tested as a first step. While most of the data used for parameterizing the model came from the study area, some parameters for data-poor species (e.g. relative fecundity and growth parameters) were obtained from ecosystems outside the Mediterranean region, and these can differ considerably according to the ecosystem (Halouani et al., 2016). A sensitivity analysis on such parameters could be carried out following the methodology employed in Lehuta et al. (2010) or Ortega-Cisneros et al. (2017).

4.3 Potential uses of OSMOSE-MED

This integrated ecosystem model of Mediterranean marine biodiversity can provide valuable scientific support to fishery management strategy in light of the combined effects of fishing and climate change (Moullec et al., 2019).

For example, the model can provide insights on climate change impacts on operational fisheries reference levels, such as Maximum Sustainable Yield (MSY) and multi-species MSY at the Mediterranean scale (Lehuta et al., 2016). It could also guide spatial conservation planning priorities, such as the implementation of marine protected area networks (Lehuta et al., 2016; Liquete et al., 2016; Micheli et al., 2013b) as required by the Marine Strategy Framework Directive (MSFD) (European Commission, 2008). Many MSFD indicators regarding biodiversity and food webs can be directly derived from OSMOSE-MED, making it a relevant tool to aid the policy objective of achieving ‘Good Environmental Status’ for all European seas by 2020 (Cardoso et al., 2010; Piroddi et al., 2015b). Evidence provided by the model can also inform decision-making in the framework of the EU’s Blue Growth strategy to support sustainable growth in the marine and maritime sectors (European Commission, 2017), as well as the mid-term strategy (2017–2020) of the General Fisheries Commission for the Mediterranean (GFCM), developed to support the achievement of UN Sustainable Development Goal 14 (GFCM, 2017b). Lastly, the model can be used as a tool to communicate with stakeholders, including managers and non-scientist end users of Mediterranean ecosystems, to help incorporate scientific evidence into environmental decision-making (Cartwright et al., 2016; Jönsson et al., 2015; Rose et al., 2010).

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Author contributions

F.M. developed the model and acquired, analyzed and interpreted the data. L.V., P.V., N.B., F.G. and Y-J.S. helped in developing the model. Y-J.S. helped in data analysis and interpretation. C.U. provided data on primary and secondary production (from the biogeochemical model). P.V. and N.B. helped with the OSMOSE programming code and use of the DATARMOR HPC cluster. P.C., A.E., C.F., M.G., A.J., A.L., E.L.D., P.M., P.P., M.T.S., I.T.

and M.V. provided data from the MEDITS survey. F.M. drafted the manuscript with contributions and revisions from all the authors.

Competing interests

The authors declare no competing financial interests.

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