



**HAL**  
open science

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

Fabien Moullec, Laure Velez, Philippe Verley, Nicolas Barrier, Caroline Ulses, Pierluigi Carbonara, Antonio Esteban, Cristina Follesa, Michele Gristina, Angelique Jadaud, et al.

### ► To cite this version:

Fabien Moullec, Laure Velez, Philippe Verley, Nicolas Barrier, Caroline Ulses, et al.. Capturing the big picture of Mediterranean marine biodiversity with an end-to-end model of climate and fishing impacts. *Progress in Oceanography*, 2019, 178, pp.102179. 10.1016/j.pocean.2019.102179 . hal-02307206

**HAL Id: hal-02307206**

**<https://hal.umontpellier.fr/hal-02307206>**

Submitted on 20 Dec 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

1 Manuscript to submit for publication in the journal "Progress in Oceanography"

2

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

6

7 **Fabien Moullec<sup>a,\*</sup>, Laure Velez<sup>a</sup>, Philippe Verley<sup>b</sup>, Nicolas Barrier<sup>c</sup>, Caroline Ulses<sup>d</sup>, Pierluigi**  
8 **Carbonara<sup>e</sup>, Antonio Esteban<sup>f</sup>, Cristina Follesa<sup>g</sup>, Michele Gristina<sup>h</sup>, Angélique Jadaud<sup>c</sup>,**  
9 **Alessandro Ligas<sup>i</sup>, Eduardo López Díaz<sup>j</sup>, Porzia Maiorano<sup>k</sup>, Panagiota Peristeraki<sup>l,m</sup>, Maria**  
10 **Teresa Spedicato<sup>e</sup>, Ioannis Thasitis<sup>n</sup>, Maria Valls<sup>o</sup>, François Guilhaumon<sup>a</sup> and Yunne-Jai**  
11 **Shin<sup>a,p</sup>**

12 <sup>(a)</sup> Marine Biodiversity Exploitation and Conservation (MARBEC), Université de Montpellier, IRD, CNRS,  
13 Ifremer, Montpellier, France

14 <sup>(b)</sup> Botanique et Bioinformatique de l'Architecture des Plantes (AMAP) IRD, CIRAD, Boulevard de la  
15 Lironde, 34398 Montpellier Cedex 5, France

16 <sup>(c)</sup> Marine Biodiversity Exploitation and Conservation (MARBEC), Université de Montpellier, IRD, CNRS,  
17 Ifremer, Sète, France

18 <sup>(d)</sup> Laboratoire d'Aérodynamique, Université de Toulouse, CNRS, UPS, Toulouse, France

19 <sup>(e)</sup> COISPA Tecnologia and Ricerca, Stazione Sperimentale per lo Studio delle Risorse del Mare, Bari,  
20 Italy

21 <sup>(f)</sup> Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Murcia, Murcia, Spain

22 <sup>(g)</sup> Dipartimento di Biologia Animale ed Ecologia, Università di Cagliari, Cagliari, Italy

23 <sup>(h)</sup> Institute for the Coastal Marine Environment (CNR), Mazara del Vallo, Italy

24 <sup>(i)</sup> Consorzio per il Centro Interuniversitario di Biologia Marina ed Ecologia Applicata 'G. Bacci', viale N.  
25 Sauro 4, I-57128 Livorno, Italy

26 <sup>(j)</sup> Instituto Español de Oceanografía (IEO), Centro Oceanográfico de Málaga, Fuengirola, Málaga, Spain

27 <sup>(k)</sup> Department of Biology, University of Bari, Bari, Italy

28 <sup>(l)</sup> Hellenic Center for Marine Research, Iraklion, Crete, Greece

29 <sup>(m)</sup> University of Crete, Biology Department, Stavrakia, Heraklion, Crete

30 <sup>(n)</sup> Department of Fisheries and Marine Research, Ministry of Agriculture, Natural Resources and  
31 Environment, Nicosia, Cyprus

32 <sup>(o)</sup> Instituto Español de Oceanografía (IEO), Centre Oceanogràfic de les Balears s/n, 07015 Palma, Spain

33 <sup>(p)</sup> Marine Research (MA-RE) Institute and Department of Biological Sciences, University of Cape Town,  
34 Private Bag X3, Rondebosch 7701, South Africa

35

36 \*Corresponding author, E-mail: fabien.moullec@ird.fr  
37 E-mail addresses: laure.velez@umontpellier.fr (L. Velez), philippe.verley@ird.fr (P. Verley),  
38 nicolas.barrier@ird.fr (N. Barrier), caroline.ulsés@aero.obs-mip.fr (C. Ulsés), carbonara@coispa.it (P.  
39 Carbonara), antonio.esteban@ieo.es (A. Esteban), follesac@unica.it (C. Follesa),  
40 michele.gristina@iamc.cnr.it (M. Gristina), angelique.jadaud@ifremer.fr (A. Jadaud), ligas@cibm.it (A.  
41 Ligas), eduardo.lopez@ieo.es (E. López Díaz), porzia.maiorano@uniba.it (P. Maiorano),  
42 notap@her.hcmr.gr (P. Peristeraki), spedicato@coispa.it (M.T. Spedicato), ithasitis@dfmr.moa.gov.cy (I.  
43 Thasitis), maria.valls@ieo.es (M. Valls), francois.guilhaumon@ird.fr (F. Guilhaumon), yunne-  
44 jai.shin@ird.fr (Y.J. Shin)

45

## 46 **Abstract**

47 The Mediterranean Sea is one of the main hotspots of marine biodiversity in the world. The  
48 combined pressures of fishing activity and climate change have also made it a hotspot of global  
49 change amidst increasing concern about the worsening status of exploited marine species. To  
50 anticipate the impacts of global changes in the Mediterranean Sea, more integrated modelling  
51 approaches are needed, which can then help policymakers prioritize management actions and  
52 formulate strategies to mitigate impacts and adapt to changes. The aim of this study was to  
53 develop a holistic model of marine biodiversity in the Mediterranean Sea with an explicit  
54 representation of the spatial, multispecies dynamics of exploited resources subject to the  
55 combined influence of climate variability and fishing pressure. To this end, we used the  
56 individual-based OSMOSE model (Object-oriented Simulator of Marine ecOSystEms), including  
57 100 marine species (fish, cephalopods and crustaceans) representing about 95% of the total  
58 declared catch, at a high spatial resolution (400 km<sup>2</sup>) and a large spatial scale (the entire  
59 Mediterranean basin) – the first time such a resolution and scale have been modelled. We then  
60 combined OSMOSE with the NEMOMED 12 physical model and the Eco3M-S biogeochemical  
61 low trophic level model to build the end-to-end model, OSMOSE-MED. We fitted OSMOSE-MED  
62 model with observed or estimated biomass and commercial catch data using a likelihood  
63 approach and an evolutionary optimization algorithm. The outputs of OSMOSE-MED were then  
64 verified against observed biomass and catch data, and compared with independent datasets  
65 (MEDITS data, diet composition and trophic levels). The model results – at different hierarchical  
66 levels, from individuals to the scale of the ecosystem – were consistent with current knowledge  
67 of the structure, functioning and dynamics of the ecosystems in the Mediterranean Sea. While  
68 the model could be further improved in future iterations, all the modelling steps – the  
69 comprehensive representation of key ecological processes and feedback, the selective  
70 parameterization of the model, and the comparison with observed data in the validation process  
71 – strengthened the predictive performance of OSMOSE-MED and thus its relevance as an

72 impact model to explore the future of marine biodiversity under scenarios of global change. It is  
73 a promising tool to support ecosystem-based fishery management in the Mediterranean Sea.

74  
75 **Keywords:** Ecosystem model, Ecosystem Approach to Fisheries Management, OSMOSE  
76 model, NEMOMED model, Eco3M-S model, Global change

77

## 78 **1 Introduction**

79 The Mediterranean Sea is the largest semi-enclosed sea in Europe and is one of the main  
80 reservoirs of biodiversity in the world (Coll et al., 2010). It is home to 4–18% of identified marine  
81 species, which is considerable given it makes up only 0.82% of the global ocean surface (Coll et  
82 al., 2010). It is also a hotspot of global changes caused by human activity (Coll et al., 2012,  
83 2010; Giorgi, 2006; Giorgi and Lionello, 2008; Micheli et al., 2013a; Ramírez et al., 2018; Stock  
84 et al., 2018). Overfishing, pollution from land-based sources, degradation or loss of critical  
85 habitats, species introductions and climate change are all widespread in the Mediterranean Sea;  
86 impacts that may operate in synergy, leading to profound modifications in the structure, stability  
87 and functioning of marine ecosystems (Albouy et al., 2014; Coll et al., 2012; Lotze et al., 2006).  
88 Fishing is considered one of the highest threats to biodiversity in the region: the exploitation rate  
89 is steeply increasing due to poor fishing selectivity, and fish stocks are shrinking (Colloca et al.,  
90 2017; Vasilakopoulos et al., 2014). As a consequence, more than 90% of the assessed stocks  
91 were categorized as overfished in 2017 (GFCM, 2017a; STECF, 2017). However, while fish  
92 stocks are declining on the continental shelf (especially long-lived species such as European  
93 hake *Merluccius merluccius*), a few short-lived species such as shrimp, cephalopods, and other  
94 fish species (e.g. red mullet *Mullus barbatus*), have shown trends of increasing biomass (GFCM,  
95 2017a; Maynou et al., 2011). Deep-water rose shrimp *Parapenaeus longirostris* is the most  
96 emblematic example: its biomass has increased all over the Mediterranean Sea in the last  
97 decade due to the increasing temperature and decreasing predatory pressure (e.g. by European  
98 hake) (Colloca et al., 2014; Ligas et al., 2011; Sbrana et al., 2019).

99 In the absence of strong management plans, the deteriorating status of fisheries in the  
100 Mediterranean is likely to worsen, particularly in a context of climate change (Cheung et al.,  
101 2018; FAO, 2018). The Mediterranean Sea has been identified as one of the most vulnerable  
102 regions in future climate change projections (Cramer et al., 2018; Giorgi, 2006; Hoegh-Guldberg  
103 et al., 2014). The effects of climate change on marine ecosystems are already clearly  
104 observable, with impacts reported on species from low trophic levels (e.g. macrophytes and

105 phytoplankton) to high (e.g. predatory fish), and from individuals to the scale of entire  
106 ecosystems (Calvo et al., 2011; Durrieu de Madron et al., 2011; Lejeusne et al., 2010; Marbà et  
107 al., 2015; Tzanatos et al., 2014). These impacts are expected to affect biodiversity, commercial  
108 fisheries, food webs and ecosystem functioning (Albouy et al., 2014; AllEnvi, 2016; Bosello et  
109 al., 2015; Hattab et al., 2014; Jordà et al., 2012; Marbà et al., 2015; Pecl et al., 2017; Piroddi et  
110 al., 2017).

111 Anthropogenic pressures on Mediterranean ecosystems are projected to increase in the future,  
112 especially those related to climate change, habitat degradation and resource exploitation  
113 (Butchart et al., 2010; Calvo et al., 2011; Coll et al., 2010). Considering the range of human and  
114 natural pressures and the likelihood that these act in synergy on marine ecosystems, there is an  
115 urgent need for more holistic and integrative approaches to quantify, anticipate, mitigate and  
116 manage human impacts on natural environments (Colloca et al., 2017; Hilborn, 2011; Link,  
117 2010). In response, Ecosystem-Based Management (EBM) and, more specifically, the  
118 Ecosystem Approach to Fisheries Management (EAFM) emerged in the early 1990s to consider  
119 all anthropogenic activities that might affect the sustainability of goods and services provided by  
120 ecosystems (Pikitch et al., 2004). In the European Union, these approaches are integrated in the  
121 Common Fisheries Policy (CFP, 2013) and the European Marine Strategy Framework Directive  
122 (MSFD; European Commission, 2008), which requires that all member states take the necessary  
123 measures to achieve or maintain 'Good Environmental Status' for marine ecosystems, with the  
124 explicit regulatory objective that 'biodiversity be maintained' by 2020 at the latest (European  
125 Commission, 2008). The requirements of the MSFD necessitate the development of suitable  
126 tools to evaluate the status of marine ecosystems and their response to human activity, as well  
127 as the sustainable management and harvesting of commercial species. This makes it essential  
128 to develop our ability to predict the future impacts of various policy interventions and strategic  
129 management plans for restoring marine ecosystems and biodiversity while ensuring the  
130 sustained provision of marine fishery products to human societies.

131 In order to project plausible biodiversity scenarios at the scale of the whole Mediterranean Sea  
132 that can inform decision-making in the region, the aim of this study was to develop a model able  
133 to explicitly represent the spatial, multispecies dynamics of marine resources subject to the  
134 combined influences of climate change and fishing pressure. End-to-End models (E2E), which  
135 represent the entire food web, from plankton to top predators, as well as their abiotic  
136 environment, are promising tools for assessing the effects of climate change and fishing on  
137 ecosystem dynamics (Fulton, 2010; Grimm et al., 2017; Nicholson et al., 2019; Piroddi et al.,

138 2017, 2015b; Rose et al., 2010; Travers et al., 2007). But while there has been state-of-the-art  
139 modelling of food webs and multispecies communities within Mediterranean ecosystems, there  
140 remains a gap in modelling the biodiversity dynamics at the scale of the entire Mediterranean  
141 Sea: modelling that accounts for the complexity of species introductions, multispecies  
142 interactions and spatial dynamics in a context of global change. While trophic modelling of  
143 coastal marine ecosystems in specific areas of the Mediterranean has greatly improved, no  
144 model has yet shown species assemblages at the whole Mediterranean scale, with explicit  
145 modelling of the spatial, trait-based, lifecycle dynamics and interactions of multiple exploited  
146 species.

147 To address this, we used the individual-based ecosystem model OSMOSE (Object-oriented  
148 Simulator of Marine ecOSystEms) for the first time at a large spatial scale (the entire  
149 Mediterranean basin), a high spatial resolution (400 km<sup>2</sup>), and for as many as 100 marine  
150 species (fish, cephalopods and crustaceans) representing about 95% of total declared catches  
151 in the Mediterranean Sea. Our end-to-end modelling approach combined the OSMOSE model  
152 (representing high trophic level species) with the physical model NEMOMED 12 and the  
153 biogeochemical model Eco3M-S (representing low trophic levels). The resulting end-to-end  
154 model, OSMOSE-MED, was calibrated to represent the Mediterranean Sea during the 2006–  
155 2013 period. We then evaluated its ability to represent key indicators of the Mediterranean: for  
156 example, biomass, catches and trophic levels from the scale of the individual to the community.  
157 The methodology, results and challenges are discussed below.

## 158 **2 Materials and methods**

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

### 166 **2.1 The low trophic level (LTL) model NEMOMED 12 / Eco3M-S**

167 Eco3M-S is a biogeochemical model that simulates the lower trophic levels of marine  
168 ecosystems (phyto- and zooplankton), and the biogeochemical cycles of carbon and other key  
169 elements such as phosphorus and nitrogen in the Mediterranean Sea (Auger et al., 2011; Ulses

170 et al., 2016). Independently of our study, Eco3M-S has been coupled with NEMOMED12, a high-  
171 resolution ( $\approx 1/12^\circ$ ) hydrodynamic model adapted to the Mediterranean region (see Beuvier et al.,  
172 2012 for more details on the structure and parameterization of NEMOMED 12) (Kessouri, 2015;  
173 Kessouri et al., 2017).

174 NEMOMED12 is a regional circulation model. It is an updated version of the OPAMED 8 and  
175 NEMOMED 8 models used by Ben Rais Lasram et al. (2010), Hattab et al. (2014), Albouy et al.  
176 (2014, 2013, 2012) and more recently by Halouani et al. (2016) as input for niche/habitat models  
177 at local or regional scales in the Mediterranean Sea. The area of NEMOMED 12 covers the  
178 whole Mediterranean Sea and part of the Atlantic Ocean (from  $11^\circ\text{W}$  to  $7.5^\circ\text{W}$ ) to take into  
179 account inter-ocean exchanges (Beuvier et al., 2012a; Beuvier et al., 2012b). It does not cover  
180 the Black Sea. Based on NEMO's standard ORCA tripolar grid at  $1/12^\circ$  ( $\approx 7$  km), NEMOMED 12  
181 resolution varies in latitude and longitude, but allows the explicit resolution of most mesoscale  
182 features. It is an eddy-resolving model that covers the majority of the Mediterranean Sea  
183 (Beuvier et al., 2012a). It has a time step of 12 minutes and is daily forced by atmospheric  
184 ARPERA data, which is obtained by performing dynamical downscaling of European Centre for  
185 Medium-Range Weather Forecasts (ECMWF) products over the European-Mediterranean region  
186 (Beuvier et al., 2012a; Herrmann and Somot, 2008).

187 The coupling of NEMOMED 12 and the biogeochemical Eco3M-S model was done offline (one-  
188 way coupling). The Eco3M-S model represents several element cycles such as carbon (C),  
189 nitrogen (N), phosphorus (P) and silica (Si) in order to reproduce the different limitations and co-  
190 limitations observed in the Mediterranean Sea and the dynamics of different plankton groups.  
191 Seven plankton functional types (representing the main types), and the range of the plankton  
192 size spectrum in the Mediterranean Sea were modelled. The resulting structure of the trophic  
193 web base included three size-classes of phytoplankton (pico-, nano- and micro-phytoplankton),  
194 three size-classes of zooplankton (nano-, micro- and meso-zooplankton), and heterotrophic  
195 bacteria as decomposers (Table 1). The representation of the phytoplankton dynamics was  
196 derived from the Eco3M model presented in Baklouti et al. (2006). Of the primary producers,  
197 nanophytoplankton dominated the biomass of phytoplankton communities for most of the year,  
198 while microphytoplankton occasionally contributed to a large part of primary production during  
199 the spring period in the northwestern Mediterranean (Auger et al., 2011; Ulses et al., 2016). The  
200 structure of Eco3M-S reflects major grazing links such as nanozooplankton preying on small  
201 phytoplankton and bacteria, microzooplankton consuming microphytoplankton, and  
202 mesozooplankton, mainly composed of copepods, grazing on the largest categories of plankton

203 (i.e. microphyto- and microzooplankton). Bacteria (i.e. heterotrophic picoplankton) are  
 204 responsible for the remineralization of dissolved organic matter. The representation of the  
 205 heterotrophic processes was based on the models developed by Anderson and Pondaven  
 206 (2003) and Raick et al. (2005). All features, formulations and parameterization of  
 207 biogeochemical processes integrated in the mechanistic Eco3M-S model are described in detail  
 208 in Auger et al. (2011), Kessouri (2015) and Ulses et al. (2016).

209 *Table 1 Parameters of the seven low trophic level compartments used to build the trophic links with OSMOSE. Other*  
 210 *parameters used to run ECO3M-S are documented in Auger et al. (2011), Ulses et al., (2016) and Kessouri et al.,*  
 211 *(2017).*

Main Plankton				
Functional Types (PFTs)	Main species / groups	Min size (µm)	Max size (µm)	Trophic level
Picophytoplankton	<i>Synechococcus spp.</i>	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 <sup>a</sup>	Based on benthos groups included in the Ecopath model of Piroddi et al. (2017)	2000	50000	2.4

212 <sup>a</sup>Benthos is considered an LTL group, but is not an output of the Eco3M-S model. This group is included as a 'black  
 213 box' in the HTL model OSMOSE.

## 214 **2.2 The high trophic level (HTL) model OSMOSE**

215 The OSMOSE model has been used to assess the impacts of both fishing and climate change  
 216 scenarios on marine food web functioning and species resilience in different types of  
 217 ecosystems such as upwelling (Southern Benguela and Humboldt), temperate (Canadian west  
 218 coast and Jiaozhou Bay), Mediterranean (Gulf of Gabès and Gulf of Lion) and subtropical  
 219 ecosystems (West Florida shelf) (Fu et al., 2013; Grüss et al., 2015; Halouani et al., 2016;  
 220 Marzloff et al., 2009; Travers et al., 2009; Xing et al., 2017). OSMOSE is a size-based  
 221 multispecies trophic model that focuses on high trophic levels, mainly fish species. It is spatially  
 222 explicit and represents the whole lifecycle of several interacting marine species. It models the  
 223 major processes of the lifecycle step by step, from eggs to adult fish: i.e. growth, predation,  
 224 reproduction, natural and starvation mortality, as well as fishing mortality. As it is constrained by  
 225 computing limitations (of time and memory), rather than being truly individual-based, OSMOSE  
 226 is based on 'super-individuals' that serve as proxies for fish schools, defined as a group of  
 227 individuals sharing the same age, length, diet and spatial position and interacting with other  
 228 schools in a two-dimensional grid. Species interact through predation in a spatial and dynamic



229 way (Shin and Cury, 2004). The model is forced by species-specific spatial distribution maps  
230 that can vary interannually, seasonally, or depending on ontogenetic stages. OSMOSE allows  
231 the emergence of complex trophic interactions from two basic assumptions of the predation  
232 process: for a given individual (a school), prey consumption depends on the spatio-temporal co-  
233 occurrence of the predator and its prey (in the horizontal and vertical dimensions) and is  
234 conditioned by size compatibility between a predator and its prey. Thus, unlike other trophic  
235 models such as Ecopath with Ecosim (Christensen and Walters, 2004), species dynamics and  
236 trophic structures are not modelled from pre-established trophic interactions between species:  
237 each fish can potentially be a predator or prey, regardless of its taxonomy, but depending on  
238 size compatibility (Shin et al., 2004; Shin and Cury, 2001). A maximum and a minimum  
239 predator/prey size ratio are thus defined to govern predator–prey interactions (Travers et al.,  
240 2009). To integrate a vertical dimension in the food web, accessibility coefficients are defined in  
241 the form of a prey–predator accessibility matrix that reflects possible mismatches or overlap  
242 between species’ vertical distributions and/or potential refugia, allowing a certain proportion of a  
243 fish school to remain inaccessible to predation. At each time step, a predation efficiency rate can  
244 be calculated for each fish school (i.e. the food biomass ingested within a time step over the  
245 maximum ingestion rate), from which growth, starvation and reproduction rates are determined.  
246 In OSMOSE, the functions defining growth and mortality are deterministic. The main source of  
247 stochasticity comes from the species’ movement within their habitat and the order at which  
248 schools interact (through predation). Model details and equations are provided in Appendix A  
249 and on <https://documentation.osmose-model.org/>.

### 250 **2.3 Parameterization of OSMOSE-MED**

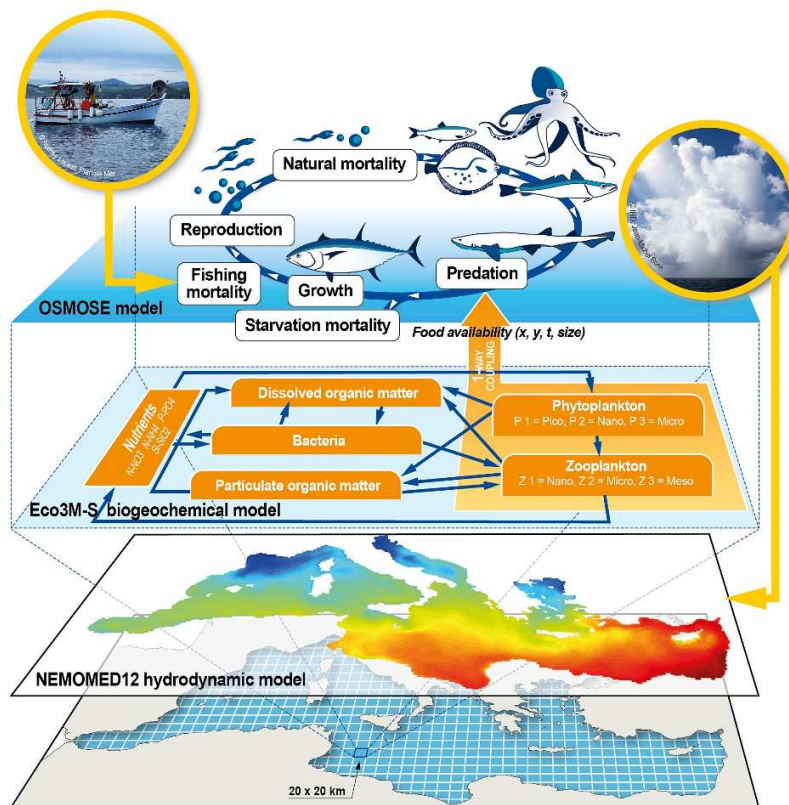
251 OSMOSE-MED covers the whole Mediterranean basin, from the Strait of Gibraltar to the Levant  
252 basin and from the Northern Adriatic Sea to the Southern Ionian Sea (Figure 1). This area  
253 extends from approximately 26.9°N to 46.3°N in latitude and from approximately 5.6°W to  
254 36.1°E in longitude. The Marmara Sea and the Black Sea were not included in the model. The  
255 OSMOSE-MED model was built on a regular grid divided into 20x20 km cells (for a total of 6229  
256 cells). Grid resolution was a compromise between the fine-scale ecology of the modelled  
257 species and computing time limitations. The time step was set according to the spatial  
258 resolution: we adopted a time resolution of 15 days within which species were assumed to have  
259 access to the first layer of surrounding cells when foraging for prey.

260 A 15-day climatology was constructed from the 2006–2013 outputs of the biogeochemical model  
261 Eco3M-S and used to force the HTL model (offline coupling). The forcing model outputs thus

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

274 Regarding HTL species, 100 fish, cephalopod and crustacean species were explicitly modelled  
275 in OSMOSE-MED: 85 fish species, 5 cephalopods and 10 crustaceans (Appendix B). The  
276 selection of the 86 fish species was strongly dependent on data availability both for model  
277 parameterization (biological parameters and life history traits, for example) and for comparing  
278 the output to observations (species biomass data, for example). Data search and mining for the  
279 parameterization of the modelled species’ lifecycles represented a significant time investment.  
280 Of the 635 fish species included in the FishMed database (Albouy et al., 2015), we were able to  
281 find the life history parameters (i.e. growth, reproduction and mortality) required to parameterize  
282 the OSMOSE model for only 86 fish species in our search of the scientific literature. Cephalopod  
283 and crustacean species were selected for their high commercial value, high contribution to total  
284 biomass and data availability. Additionally, they play an important role in food web dynamics  
285 (Peristeraki et al., 2005; Roberts, 2003) and represent key components in several Ecopath  
286 models applied to ecosystems in the Mediterranean Sea (e.g. Bănaru et al., 2013; Corrales et  
287 al., 2017; Hattab et al., 2013; Piroddi et al., 2017). All these species represented on average  
288 around 95% of declared fishery catches in the Mediterranean in the 2006–2013 period (FAO,  
289 2006; 2017). The biological parameters linked to growth (Von Bertalanffy parameters, length–  
290 weight relationship parameters), mortality (maximum age, natural mortality not explicitly  
291 represented in OSMOSE, age/size at recruitment), reproduction (size at maturity, relative  
292 fecundity) and predation (minimum and maximum predation size ratios), along with their  
293 sources, are detailed in Appendix B and C. As much as possible, the data was specific to  
294 Mediterranean ecosystems and was derived from or used as a resource for fishery stock  
295 assessment working groups in the Mediterranean Sea.

296 Within each time step (15 days), the following events were modelled to occur successively in  
 297 OSMOSE-MED (Figure 1). First, each school was uniformly distributed in space according to a  
 298 unique distribution map specified for each species (see 2.4). In this application of OSMOSE, due  
 299 to the lack of observation data, we did not account for any seasonal or ontogenetic variation in  
 300 fish distribution. As the maps did not change from one time step to the next, schools could move  
 301 to an adjacent cell or remain in the same cell following a random walk process (Shin et al., 2004;  
 302 Travers-Trolet et al., 2014). Second, mortality (predation mortality, additional natural mortality  
 303 and fishing mortality) were applied to schools. The order at which schools interact as well as the  
 304 order of mortality events was randomly drawn within each time step. Third, food intake,  
 305 subsequent to predation events, modulated the growth (weight and size) of species and their  
 306 starvation level. Finally, reproduction occurred for fish with a length greater than that at sexual  
 307 maturity, allowing the introduction of new schools of age 0 (eggs) in the system (Appendix A).  
 308



309  
 310 *Figure 1 Conceptual representation of the OSMOSE-MED end-to-end model applied to the whole Mediterranean Sea.*  
 311 *The high trophic level OSMOSE model is forced (one-way coupling) by the biogeochemical Eco3M-S model through*  
 312 *the predation by high trophic levels (i.e. fish, cephalopods and crustaceans) on low trophic levels (i.e. phyto- and*  
 313 *zooplankton). Eco3M-S is forced by the NEMOMED 12 hydrodynamic model. Impacts of climate variability and fishing*  
 314 *mortality can be explicitly taken into account.*

## 315 **2.4 Modelling high trophic level species distribution**

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

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

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

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

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

### 357 **2.5 Calibration of the OSMOSE-MED end-to-end model**

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

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

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

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

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

413 The optimization process used the ‘calibrar’ and OSMOSE R packages (Oliveros-Ramos et al.,  
 414 2017; Oliveros-Ramos and Shin, 2016) available from the CRAN website ([https://cran.r-](https://cran.r-project.org/web/packages/calibrar)  
 415 [project.org/web/packages/calibrar](https://cran.r-project.org/web/packages/calibrar)). The calculation was performed using DATARMOR, the  
 416 French Research Institute of Marine Exploitation (IFREMER) high-performance computing  
 417 facility at the ‘Pôle de Calcul et de Données Marines’ (<https://wwz.ifremer.fr/pcdm/Equipement>),  
 418 in which 36 compute nodes representing 1008 cores (2.4Ghz) and around 4 TB of RAM were  
 419 mobilized to perform the calibration, which involved several iterative trials over more than one  
 420 year.

421 *Table 2 Order in which the parameters were estimated in the multi-phase calibration of the OSMOSE-MED model,*  
 422 *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

423  
 424 Due to the inherent stochasticity of OSMOSE, 10 replicated simulations (i.e. with an identical set  
 425 of parameters) were averaged to analyze the outputs of the last 10 years.

## 426 **2.6 Evaluation of OSMOSE-MED outputs with independent data**

427 In order to evaluate the ability of OSMOSE-MED to predict the spatial distribution of the entire  
 428 biomass in a realistic way, we compared the model output to observed data that was not used  
 429 either for the calibration of OSMOSE-MED, or its parameterization, or for the climate niche  
 430 modelling used to generate the species distribution maps. The ranking of geographical sub-  
 431 areas (GSAs), based on cumulated biomass estimates by species (in kg.km<sup>-2</sup>) from the MEDITS  
 432 survey (International bottom trawl survey in the Mediterranean, Bertrand et al., 2002) in 2006–  
 433 2013 was compared to the ranking predicted in OSMOSE-MED (see Appendix F for the  
 434 correspondence between GSA numbers, names and sizes). To evaluate the consistency of the  
 435 OSMOSE-MED model at the community level, the mean trophic level (mTL) of each species was  
 436 calculated and compared with three different sources: the FishMed database, which contains  
 437 ecological and biological traits for 635 Mediterranean fish species (Albouy et al., 2015), the  
 438 Ecopath model built at the scale of the Mediterranean basin by Piroddi et al. (2017, 2015a), and  
 439 a review of feeding habits and trophic levels of 148 Mediterranean fish species (Karachle and  
 440 Stergiou, 2017; Stergiou and Karpouzi, 2002).

441 An important step in the validation of the model lay in comparing simulated species diets to  
 442 observations and to current knowledge of the trophic functioning of the Mediterranean

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

### 455 **3 Results and discussion**

#### 456 **3.1 Calibration**

457

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

463 Accessibility coefficients of LTL groups to HTL organisms ranged between around  $10^{-9}$  and  $10^{-1}$   
464 (Appendix E). The smallest values were obtained for small-size plankton groups (except for  
465 picophytoplankton), which could be expected in view of their high biomass and low predation  
466 rates by HTL organisms (Jackson and Lenz, 2016; Morote et al., 2010; Pepin and Penney,  
467 2000). In contrast, higher coefficients were found for mesozooplankton and benthos groups, for  
468 which around 1% and 0.5% were respectively available to predation by HTL. These coefficients  
469 were in the same order of magnitude as in other modelled ecosystems (e.g. Grüss et al., 2015;  
470 Marzloff et al., 2009; Travers-Trolet et al., 2014).

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



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

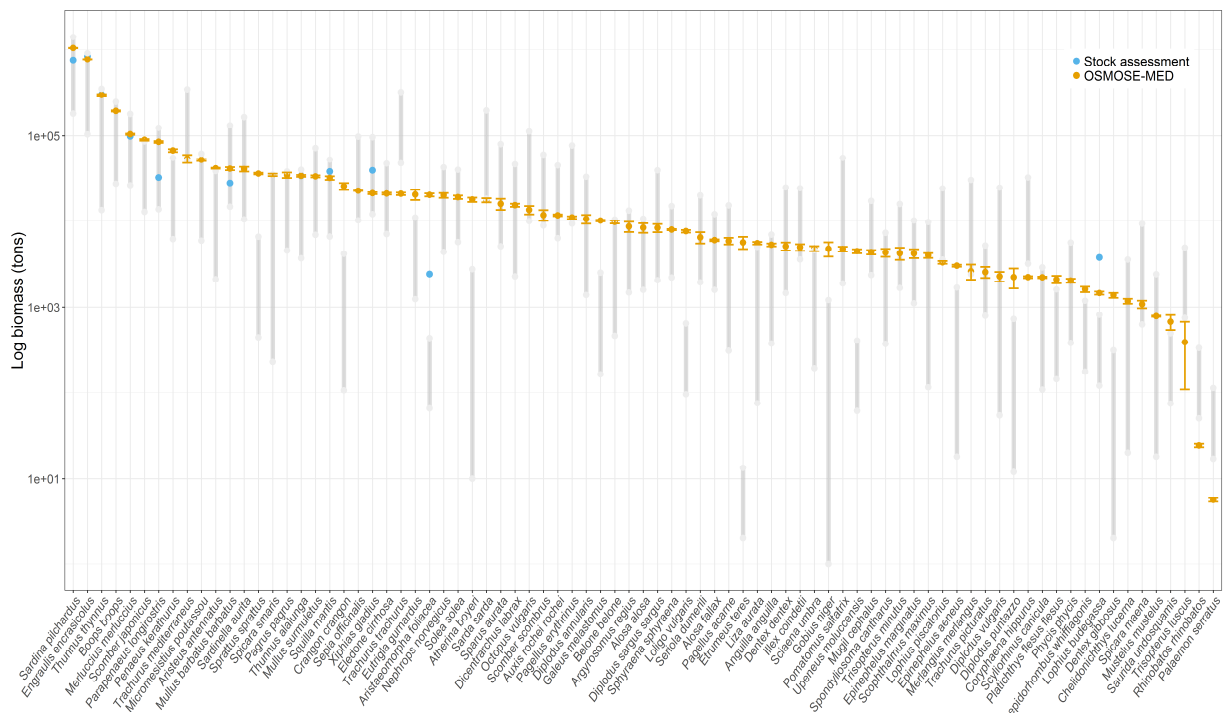
481 As fishing mortality rates ( $F$ ) estimated by stock assessments were not available for all exploited  
482 species, we chose to estimate these parameters by comparing the model output to observed  
483 and reconstructed catches during the third phase of the calibration process. Most of the fishing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

## 486 **3.2 Comparing OSMOSE-MED predictions to observations and current knowledge**

### 487 **3.2.1 Species biomass**

488 In our model, the estimated biomass, averaged over the last ten years of simulation and over ten  
489 replicates, generally fell in acceptable intervals (i.e. above FAO reported catch and below a  
490 theoretical maximum biomass considering an exploitation rate of 15% for the averaged FAO-  
491 SAU catches) (Figure 2). For species for which stock assessments were available – for instance,  
492 the European pilchard (*Sardina pilchardus*), the European anchovy (*Engraulis encrasicolus*) and  
493 the European hake (*Merluccius merluccius*) – the total biomass predicted by OSMOSE-MED  
494 was slightly higher or very close to previously estimated biomass (Figure 2). Given that most  
495 available stock assessments were for European waters, the higher estimated biomass for  
496 species such as *Sardina pilchardus*, *Parapenaeus longirostris* and *Mullus barbatus barbatus*  
497 may actually reflect a biomass volume present in the southern Mediterranean or in unassessed  
498 areas of the Mediterranean Sea. Overall, the European anchovy and the European pilchard  
499 (around 1.8 million tons of biomass) represented around 50% of the total cumulative biomass of  
500 the system (excluding plankton). The prevalence, in terms of biomass, of pelagic fish was also  
501 found in an Ecopath model of the Mediterranean Sea (Piroddi et al., 2015a). For species such as  
502 *Crangon crangon*, *Atherina boyeri* and *Etrumeus teres*, due to their highly variable population  
503 dynamics (high fecundity, short lifespan, high biomass turnover rate), biomass was particularly  
504 difficult to calibrate and was overestimated by OSMOSE-MED. Additionally, for non-native  
505 species (e.g. *Etrumeus teres*), more research is needed on their biology and ecology in their  
506 new expansion areas in order to obtain robust life history trait estimates and improve model  
507 predictions (Dimarchopoulou et al., 2017; Katsanevakis et al., 2014, 2012). The lack of stock

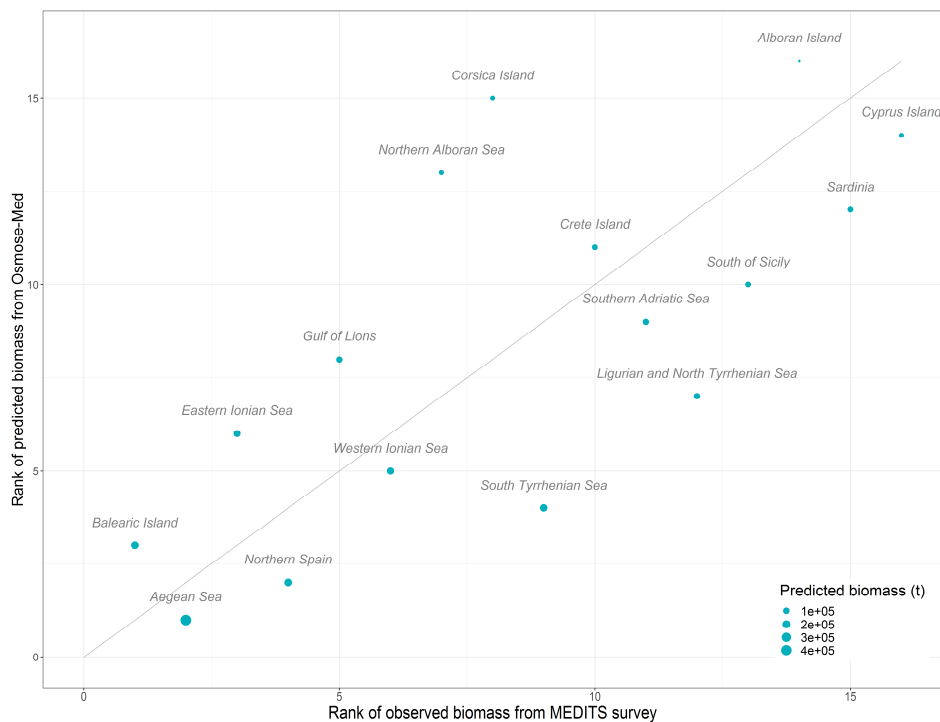
508 assessments or difficulty in accessing these assessments constitute real barriers to the  
 509 development, parameterization and calibration of ecosystem models in the region (Coll et al.,  
 510 2013; Katsanevakis et al., 2015; Piroddi et al., 2015a). Around 25% of landed biomass and less  
 511 than 10% of exploited stocks are currently assessed, and this on an irregular basis (Tsilkliras et  
 512 al., 2015). Moreover, the monitoring of fish stocks is hindered by the lack of biological or  
 513 ecological observational data for far too many species, with approximately 80% of landings  
 514 coming from stocks that are data deficient (Dimarchopoulou et al., 2017; Le Quesne et al.,  
 515 2013).



516  
 517 *Figure 2 Average biomass of exploited species (87 species out of the 100 modelled) predicted by OSMOSE-MED (in*  
 518 *orange) in log scale and associated standard deviation. Cumulative biomass from stock assessments (in blue) (only*  
 519 *cumulative biomass higher than the FAO reported catch is shown). The grey bars show the minimum biomass (the*  
 520 *FAO reported catch) and the theoretical maximum biomass, considering an exploitation rate of 15% and the average*  
 521 *between the FAO and Sea Around Us catch.*

522 The model accurately predicted the spatial distribution of the overall biomass, at least for the  
 523 northern part of the Mediterranean where the MEDITS surveys were conducted, as suggested  
 524 by the significant Spearman's rank correlation coefficient value of 0.71 between MEDITS and  
 525 OSMOSE-MED biomass ranking. Differences that exist between the rankings of certain GSAs  
 526 can be explained in two ways. For instance, around the island of Corsica, OSMOSE-MED  
 527 predicted less relative biomass (ranked 15 out of a total of 16 GSAs) than was estimated by  
 528 MEDITS (ranked 8). This is partly due to the very narrow continental shelf around Corsica and to

529 the resolution of our model (20×20 km<sup>2</sup>), which may be too coarse to represent the dynamics in  
 530 this area, with the result that the climate niche models and distribution maps input in OSMOSE-  
 531 MED did not resolve precisely enough the spatial distribution of species closely associated to the  
 532 Corsican continental shelf. Developing OSMOSE-MED at a finer resolution was attempted in the  
 533 early stages of model configuration, but the computing cost for the calibration process was  
 534 judged too high (at least two to three times the computing time required for a 10×10 km<sup>2</sup>  
 535 resolution). In contrast, for GSAs that ranked higher in OSMOSE-MED than in MEDITS (i.e.  
 536 below the 1:1 line in Figure 3), these differences could be explained by the fact that MEDITS is a  
 537 demersal trawl survey with low catchability of small pelagic fish. While data from the trawl survey  
 538 is useful in assessing the spatial and temporal trends of pelagic species in the Mediterranean  
 539 (Brind'Amour et al., 2016), some biases may exist, such as the survey's potential significant  
 540 underestimation of the biomass of some small pelagic fish.  
 541



542  
 543 *Figure 3 Comparison of predicted and observed ranking of total biomass by geographical sub-areas (GSAs).*  
 544 *Observed total biomass data is from the MEDITS survey (2006–2013). Circle size is proportional to the total predicted*  
 545 *biomass in the GSA. Solid line is the 1:1 relationship.*

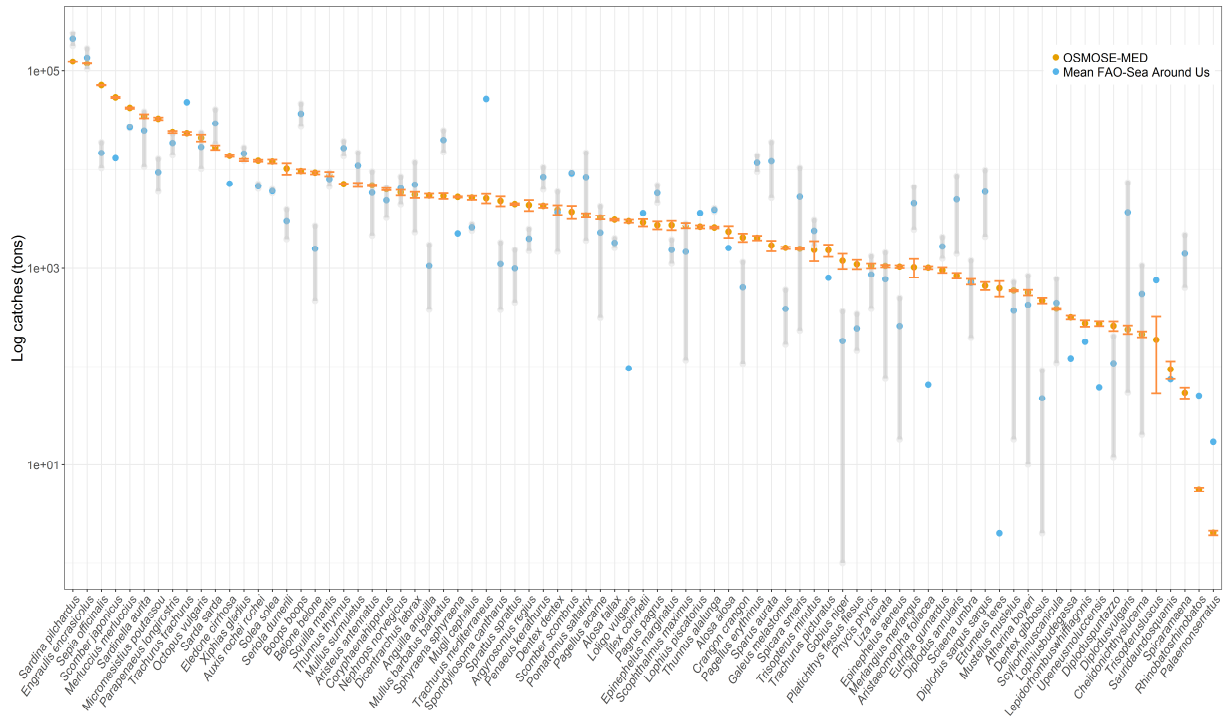
546 **3.2.2 Species catches**

547 Catches predicted by OSMOSE-MED were globally consistent with reported/reconstructed catch  
 548 data in the Mediterranean Sea (Figure 4 and Figure 5). Our model predicted a total catch of  
 549 around 802,470 t at the scale of the whole basin, which compares well to the 681,243 t recorded

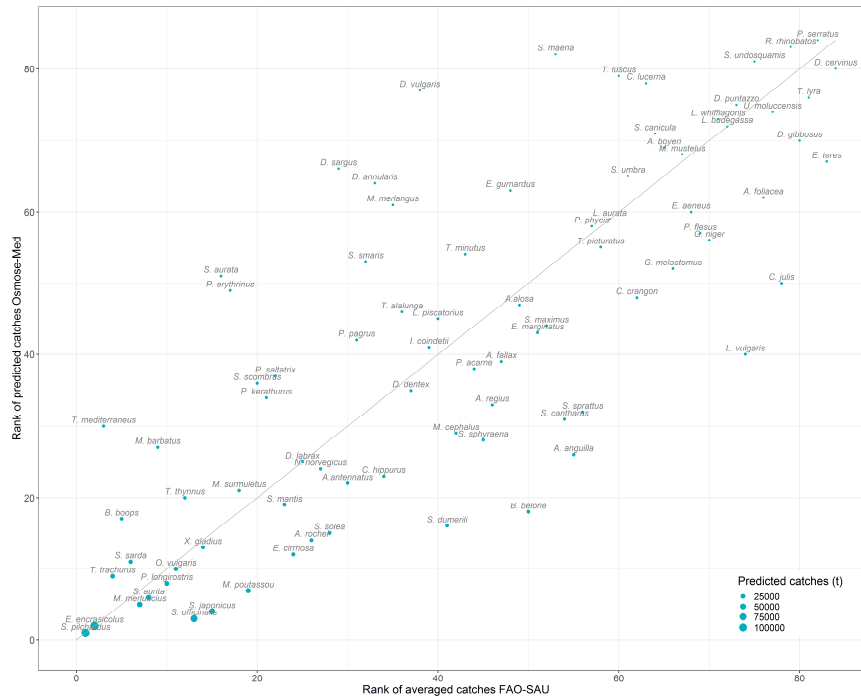
550 by the FAO and the 952,930 t reconstructed by the Sea Around Us (817,087 t on average). The  
551 European pilchard and the European anchovy represented almost 30% of the total catch in  
552 OSMOSE-MED and around 40% in reported or reconstructed catches over the 2006–2013  
553 period (FAO, 2016; Pauly and Zeller, 2016). According to Stergiou et al. (2015), small pelagic  
554 species, mainly European anchovy and European pilchard, dominate the landings across the  
555 entire Mediterranean, making up 34% of cumulative landings in the western Mediterranean, 41%  
556 in the central area, and 25% in the east. The Spearman's correlation coefficient between the  
557 rank of the average FAO-SAU catch by species and that estimated by OSMOSE-MED was 0.79  
558 (Figure 5). The main difference between predicted and average reported/reconstructed catches  
559 came from the model's under- or overestimation of species biomass. For instance, the common  
560 prawn (*Palaemon serratus*) seemed to be underestimated in terms of predicted biomass and  
561 catch. For species for which stock assessment biomass estimates were available, the  
562 OSMOSE-MED model predicted the catches relatively well. For instance, the OSMOSE-MED  
563 estimated catch for the European anchovy was around 118,480 t, while the FAO reported catch  
564 was 103,650 t and the SAU reconstructed catch was 169,870 t over the 2006–2013 period.

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

583 fisheries sector, could play a key role in the improvement of such data, at least in the northern  
 584 Mediterranean (<https://ec.europa.eu/fisheries/inseparable/en/medfish4ever>).  
 585



586  
 587 *Figure 4 For the 2006–2013 period, average catches predicted by OSMOSE-MED of all exploited species (in orange)*  
 588 *in log scale and associated standard deviation. Average FAO–SAU catch data, which served as target data during the*  
 589 *calibration process, in blue. Grey bars show the minimum (FAO reported) catch and the maximum (SAU*  
 590 *reconstructed) catch.*



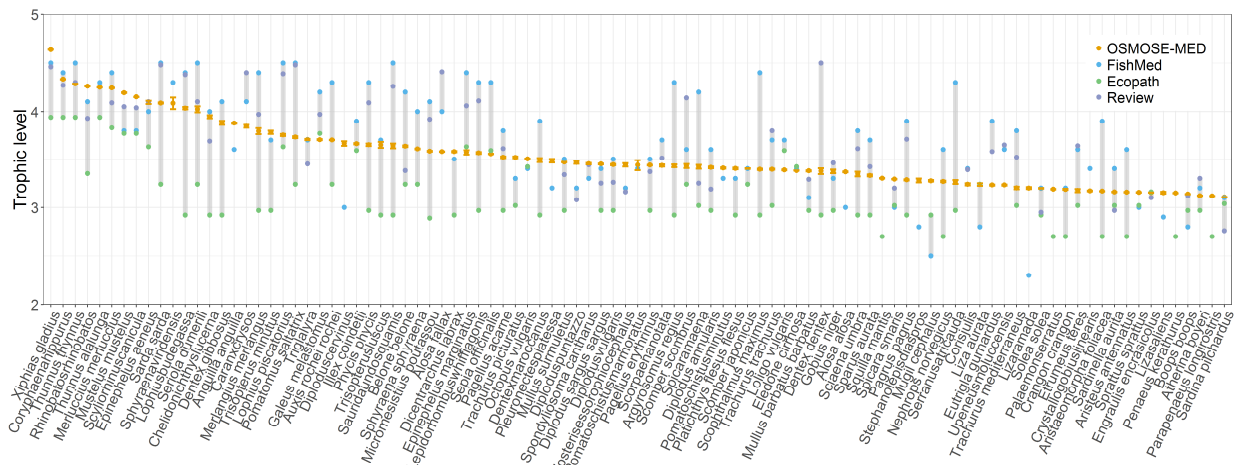
591

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

595 **3.2.3 Species trophic levels**

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

612 OSMOSE-MED model (i.e. mTL > 4.15). These results are consistent with other trophic models  
 613 for the Mediterranean, which have identified large pelagic fish and shark species (except for  
 614 common guitarfish) at the top of the food web (Albouy et al., 2010; Coll et al., 2007; Corrales et  
 615 al., 2015; Halouani et al., 2016; Hattab et al., 2013a).  
 616

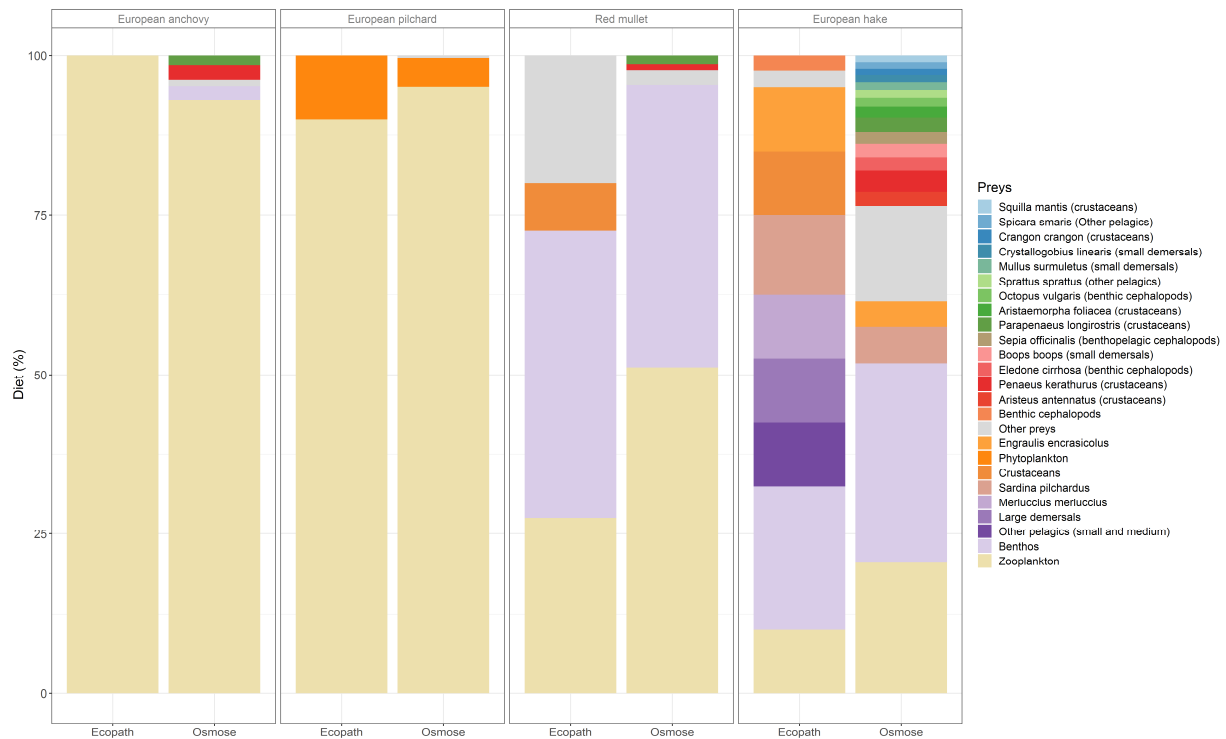


617  
 618 *Figure 6 Mean species trophic levels predicted by OSMOSE-MED (in orange), the FishMed database (Albouy et al.,*  
 619 *2015) (in blue), the Mediterranean Ecopath model (Piroddi et al., 2017, 2015a) (in green) and Karachle and Stergiou*  
 620 *(2017) (in purple).*

### 621 **3.2.4 Species diets**

622  
 623 In regard to the prey composition of the diet of the four species under scrutiny, OSMOSE-MED  
 624 and the Mediterranean Ecopath model were more or less in agreement (Figure 7). For the  
 625 European anchovy and the European pilchard, the simulated diets were similar and largely  
 626 dominated by zooplankton, a pattern in line with other observations (Karachle and Stergiou,  
 627 2017; Stergiou and Karpouzi, 2002). In OSMOSE-MED, the European pilchard consumed less  
 628 phytoplankton (4.5%, mainly diatoms) than in the Ecopath model (10%), but the result remains  
 629 qualitatively realistic (i.e. the main prey is zooplankton followed by phytoplankton). The  
 630 dominance of zooplankton in the diet of pilchards could be explained in two ways. First, the  
 631 availability coefficients of phytoplankton to HTL organisms were estimated to be very low by the  
 632 model calibration (ranging between  $10^{-1}$  and  $10^{-7}$ ), which does not allow the European pilchard to  
 633 feed more on these groups. Secondly, it has been shown that European pilchard populations  
 634 living in lower productivity regions, as is the case for the Mediterranean, would preferentially  
 635 capture larger individual prey via particulate feeding and would consume more zooplankton than  
 636 populations in the Northwest Atlantic (Costalago et al., 2015). Regarding red mullet (*Mullus*  
 637 *barbatus barbatus*), the main difference between the two models lies in the higher proportion of

638 zooplankton prey predicted by OSMOSE-MED. This discrepancy is due to the fact that some of  
 639 the crustaceans eaten in the Ecopath model were either included in the benthos group in the  
 640 simulated diet of the red mullet in OSMOSE-MED or explicitly modelled at the species level, as  
 641 is the case for *P. longirostris* and *P. kerathurus*. For the European hake, most of its prey  
 642 simulated by OSMOSE-MED was grouped in more aggregated trophic boxes in Ecopath. For  
 643 instance, Ecopath classified shrimps in the functional group 'crustaceans', octopus in 'benthic  
 644 cephalopods', and some species such as *Mullus surmuletus* or *Boops boops* in 'small  
 645 demersals'. However, the proportional contribution of some prey such as the European pilchard  
 646 and European anchovy differed more significantly between the two models. For example, the  
 647 European pilchard represented 5.7% of the diet of the European hake in OSMOSE-MED and  
 648 12.5% in Ecopath. This may be explained by the fact that the hake diet varies greatly depending  
 649 on prey availability and abundance, both in the Mediterranean and in the Atlantic Ocean  
 650 (Carrozzi et al., 2019; Cartes et al., 2009; Velasco and Olaso, 1998). Carrozzi et al. (2018)  
 651 found, for instance, that in the central Mediterranean, the European pilchard represented 3.78%  
 652 and the European anchovy 1.32% of the hake diet.



653  
 654 *Figure 7 Diets simulated by OSMOSE-MED and the Mediterranean Ecopath model for four species (two small pelagic*  
 655 *fish species (European anchovy and European pilchard) and two demersal fish species (red mullet and European*  
 656 *hake). Functional groups used in the Ecopath model in which OSMOSE-MED species are grouped are indicated in*  
 657 *parentheses. In both cases, diets are expressed as a percentage of overall prey by mass.*

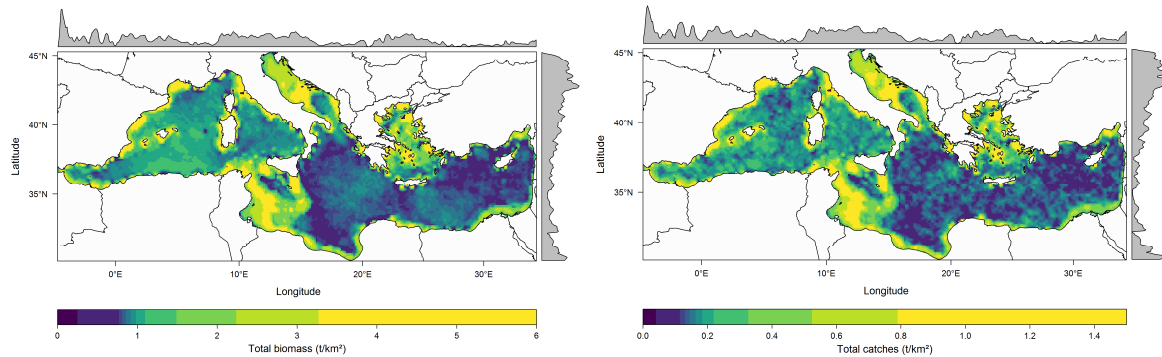


658 **3.2.5 Emerging spatial patterns**

659 The total biomass (all HTL species combined) was mainly distributed on the continental shelf  
660 and in areas where primary and secondary production were higher (Figure 8), in line with  
661 findings from previous studies (Durrieu de Madron et al., 2011; Bosc et al. 2004). The higher  
662 biomass found in highly productive areas (the Gulf of Lion, the Catalan Sea or the South  
663 Levantine Sea, fed respectively by the Rhône, Ebro and Nile rivers, which enhance primary  
664 productivity through nutrient discharge and hence play a major role in local food webs)  
665 suggested that primary production, through bottom-up control, was one of the main drivers of the  
666 biomass distribution of HTL organisms in the Mediterranean Sea. Numerous Ecopath models  
667 built at more local scales in the region confirm this hypothesis (Coll et al., 2007, 2006; Coll and  
668 Libralato, 2012; Halouani et al., 2016; Hattab et al., 2013a). The control of marine productivity,  
669 from plankton to fish, principally mediated through bottom-up processes that can be traced back  
670 to the characteristics of riverine discharges, has also been demonstrated by Macias et al.  
671 (2014). This renders the Mediterranean Sea vulnerable to sources of potential impacts on  
672 primary production such as climate change and marine pollution (Cheung et al., 2011; Jochum  
673 et al., 2012; Macias et al., 2015; Moullec et al., 2016) and highlights the need for integrating  
674 physicochemical oceanographic drivers with the dynamics of HTL organisms in a single  
675 modelling framework in order to take into account possible bottom-up control and improve our  
676 ability to predict future ecosystem changes (Piroddi et al., 2017; Rose et al., 2010; Travers-  
677 Trolet et al., 2014). It should also be noted that since fishing effort was spatially uniform in our  
678 model, we could not precisely assess the direct role of fishing in the spatial distribution of the  
679 HTL biomass, but only its impacts on species biomass, composition and interactions, which  
680 were indirectly reflected by the biomass distribution across the Mediterranean Sea.

681 A low gradient of biomass was observed from northwestern to southeastern regions, in line with  
682 previously observed gradients of production and biodiversity (Coll et al., 2010; Mouillot et al.,  
683 2011). The OSMOSE-MED model showed the western Mediterranean Sea accounting for 35%  
684 of total biomass, the Adriatic Sea 9%, the Ionian and central Mediterranean Seas 31%, and the  
685 Aegean and Levantine Seas 25%. The total biomass in the Adriatic Sea may be an  
686 underestimation in view of the results of a Mediterranean Ecopath model (Piroddi et al., 2015a),  
687 which found that the Adriatic Sea had the highest total biomass, followed by the western  
688 Mediterranean Sea and the Ionian and Eastern Seas. This is partly due to the Eco3M-S  
689 biogeochemical model's underestimation of the concentration of phytoplankton in this area  
690 (Kessouri, 2015). In OSMOSE-MED, the Eastern basin appeared highly oligotrophic, with low

691 biomass values, with the exception of the Gulf of Gabès and the waters surrounding the Nile  
692 plume, two regions that have been characterized by high productivity (Hattab et al., 2013a).

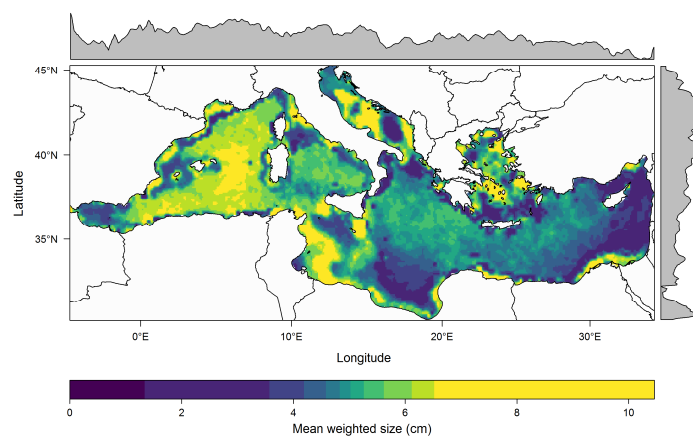


693  
694 *Figure 8 Spatial distribution of the simulated total biomass (left) and catches (right) (all HTL species combined)*  
695 *expressed in t.km<sup>-2</sup>. Graphs on the top and right respectively represent the meridionally and zonally averaged*  
696 *distribution of biomass and catches.*

697 The spatial distribution of catches, resulting from uniformly distributed fishing effort, generally  
698 followed the spatial distribution of biomass, with relatively fewer catches in the high seas (Figure  
699 8). As with biomass, the model predicted a low gradient of catch from the north to the south and  
700 from the west to the east, in line with the pattern of productivity in the Mediterranean (Bosc et al.,  
701 2004; Ignatiades et al., 2009). The Iberian shelf waters, the Balearic Sea, the Gulf of Lion, the  
702 North Tyrrhenian Sea, the Adriatic Sea, the waters south of Sicily, the Gulf of Gabès and the  
703 north Aegean Sea were all identified as exploitation hotspots concentrating most of the catches  
704 at the scale of the Mediterranean. Most of these have been identified as highly impacted areas  
705 (Micheli et al., 2013a), in particular by demersal fishing activity and climate-induced change, and  
706 coincide with the areas of conservation concern identified by Coll et al. (2012).

707 The distribution of the mean body size of the fish community revealed a clear gradient from the  
708 northwestern to the southeastern regions (Figure 9). Despite the fact that small pelagic fish  
709 species were mainly concentrated in the northwestern region, the mean body size weighted by  
710 abundance values was higher in the northern part of the basin. Some authors have argued that  
711 high salinity, high temperature, low productivity or a combination of all these factors are  
712 responsible for 'Levantine nanism' (dwarfism), a phenomenon that results in small body sizes for  
713 all species in general (Por, 1989; Sharir et al., 2011; Sonin et al., 2007). In OSMOSE, growth in  
714 size is linked to predation success. If predation success is lower than a critical predation  
715 efficiency threshold corresponding to maintenance requirements, fish can starve, and the growth  
716 rate is reduced (Shin and Cury, 2001). Thus, the oligotrophic conditions in the eastern  
717 Mediterranean could lead to reduced growth rates and smaller size for some species, as

718 indicated in the OSMOSE-MED model. The spatial distribution of mean size also showed large  
719 individuals in the Western high seas, where catches were lower (Figure 9). The large mean body  
720 size in this area is likely explained by the greater local abundance of large fish species (e.g.  
721 *Thunnus thynnus* and *Xiphias gladius*) in the Western high seas. On the other hand, the small  
722 body size found in certain areas (e.g. around the Balearic Islands, the Northern Adriatic Sea and  
723 Cyprus) could be the result of heavy fishing, which preferentially harvests larger-bodied  
724 individuals (either of a given species, or of species with larger mean size) and also induces the  
725 natural selection of slow-growing individuals (Jørgensen et al., 2007; Law, 2000; Shin et al.,  
726 2005).



727  
728 *Figure 9 Spatial distribution of mean body size (mean size weighted by species abundance) expressed in cm. Graphs*  
729 *at the top and right represent the meridionally and zonally averaged weighted size.*

## 730 4 Conclusion and perspectives

### 731 4.1 A unique large-scale end-to-end model

732 While numerous trophic modelling studies have been carried out on the Mediterranean Sea,  
733 most are at a local scale (Bănanu et al., 2013; Coll et al., 2007; Corrales et al., 2017b, 2017a;  
734 Halouani et al., 2016; Hattab et al., 2013a), with a few rare examples at the basin scale (Albouy  
735 et al., 2014; Piroddi et al., 2017, 2015a). This study was the first attempt to use an end-to-end  
736 trophic approach at the scale of the entire Mediterranean Sea, with explicit spatial, life-trait-  
737 based modelling of the whole lifecycle of the dynamics of 100 interacting species. The  
738 OSMOSE-MED integrated end-to-end model coupled a physical model (NEMOMED 12), a low  
739 trophic level model (Eco3M-S) and a high trophic level model (OSMOSE) to represent the  
740 ecosystem dynamics and the trophic structure of the entire Mediterranean. The OSMOSE  
741 model, originally developed by Shin and Cury (2004, 2001), has never been applied to such a

742 large number of species in interaction and at such a broad spatial scale. As noted by Fu et al.  
743 (2017), no more than 10 to 15 key species are typically included in an OSMOSE model. This  
744 restricted number of species may be explained by: (i) the extensive data required concerning  
745 species' life histories to properly parameterize a model, (ii) the computing capacity required to fit  
746 the model to observations, and (iii) a desire to focus on major species and interactions to  
747 simplify the complexity of the system. We decided to take the modelling approach to the next  
748 step to allow much more comprehensive, explicit modelling of a large number of marine species.  
749 Our ultimate goal was to build a tool representing the diversity of species and their interactions in  
750 a realistic way at a basin-wide scale, in order to better address the future repercussions of  
751 climate change (e.g. species distribution shifts and plankton production changes) combined with  
752 other anthropogenic drivers on biodiversity (e.g. fishing). By modelling the spatial dynamics of  
753 the community across the whole Mediterranean as well as in geographical sub-areas, we can  
754 predict the potential cascading effects of these changes on food webs and ecosystem services.

755 To our knowledge, OSMOSE-MED is the most complete model built at the scale of the entire  
756 Mediterranean in terms of species and process representativeness. We used existing biological  
757 and ecological data from various databases and also took advantage of the high-performance  
758 computing (HPC) platform DATARMOR, which allowed the calibration of such a complex model.  
759 As for most end-to-end models, one challenge lies in searching through and integrating a large  
760 amount of data from various sources – databases, scientific and 'grey' literature, output from  
761 other models (de Mora et al., 2016; Fulton, 2010). While OSMOSE-MED integrated the best  
762 ecological knowledge available for the Mediterranean, certain gaps should be noted, mainly  
763 concerning fish species in the southern part of the basin (Dimarchopoulou et al., 2017).  
764 According to some estimates, there is no biological information for as many as 43% of  
765 Mediterranean fish species (Dimarchopoulou et al., 2017). This lack of biological and ecological  
766 data, as well as the variable quality of commercial fisheries data, especially in the southern and  
767 eastern Mediterranean Sea, hinder reliable stock assessments. A crucial challenge is to  
768 increase the number of assessed stocks: first, to ensure their sustainable exploitation, and  
769 second, to allow the development of integrated ecosystem models that would help to design  
770 more effective ecosystem-based fisheries management in the Mediterranean basin (Coll et al.,  
771 2013; Piroddi et al., 2017, 2015a; Cardinale and Scarcella, 2017; Colloca et al., 2013). Another  
772 challenge is that the region generally suffers from problems with data ownership, reliability and  
773 accessibility (Katsanevakis et al., 2015).

774 The model also represents a significant advance in complex ecosystem modelling. The most  
775 critical and time-consuming step, given the stochasticity and the complexity of the model, was to  
776 maintain the coexistence of all HTL species to provide a realistic representation of biodiversity.  
777 In an OSMOSE model, the number of trophic links, the connectance, and the importance of  
778 feedback controls can be very large and can make the calibration procedure complicated and  
779 time-consuming (Halouani et al., 2016; Marzloff et al., 2009; Travers-Trolet et al., 2014). We  
780 exploited the capacities of the evolutionary optimization algorithm in order to find a set of  
781 estimated parameters within a 195-dimensional search space that reproduced state variables  
782 and indicators close to observations (Oliveros-Ramos et al., 2017; Oliveros-Ramos and Shin,  
783 2016). This is the first time the ‘calibrar’ R package has been used to configure such a complex  
784 model (a large number of parameters in a stochastic model with many nonlinearities), and it  
785 proved its ability to solve complicated minimization problems (Oliveros-Ramos and Shin, 2016).  
786 Due to computing time and the need for continuous iterative trials and feedback between model  
787 parameterization and observations, the calibration of OSMOSE-MED took more than a year and  
788 required high-performance computing facilities. The development of OSMOSE-MED is an  
789 important step forward for both OSMOSE and calibrar user communities, and more broadly for  
790 the field of ecosystem modelling, as proof of concept that the complex representation of species  
791 dynamics and interactions can be achieved and can produce realistic spatial and lifecycle  
792 dynamics of multiple species subject to climate and anthropogenic impacts.

#### 793 **4.2 Limitations of the model**

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

797 - *Benthos compartment*: strong benthic–pelagic coupling exists in the Mediterranean Sea, as  
798 highlighted in several Ecopath models of the region (Bănaru et al., 2013; Coll et al., 2007;  
799 Corrales et al., 2015; Hattab et al., 2013a). Moreover, many species included in OSMOSE-MED  
800 have omnivorous and carnivorous diets partly based on benthic organisms such as polychaetes,  
801 amphipods or crustaceans. To account for this, we added to the model a benthos ‘black box’  
802 with a constant biomass and uniform spatial distribution. Given its importance in the  
803 Mediterranean, this trophic compartment would merit improved representation: for example, by  
804 considering multiple functional groups with common biological and ecological characteristics  
805 (e.g. meiofauna, bivalves, echinoderms) (Grüss et al., 2016). As the data to do this is lacking for  
806 both the parameterization and calibration of the model, an intermediate complexity approach

807 could be adopted to model these more refined benthic compartments as 'background taxa' for  
808 which only predation, mean growth rate and spatial distribution are modelled. This new category  
809 of 'intermediate complexity' species would deal with limited datasets and allow more species of  
810 interest to be included while keeping the model reasonably complex: this has recently been  
811 coded in OSMOSE (Fu et al., 2017).

812 - *Ontogenetic habitat shifts*: Numerous species included in OSMOSE-MED exhibit clear  
813 ontogenetic habitat shifts in the Mediterranean (Cartes et al., 2009; Druon et al., 2016, 2015;  
814 Giannoulaki et al., 2013b, 2013a; Macpherson, 1998). These range shifts can play a critical role  
815 in population dynamics and ecosystem functioning (MacCall, 1990; Macpherson and Duarte,  
816 1991; Methratta and Link, 2007). For instance, Caddy (1990) hypothesized that the sustainability  
817 of the majority of Mediterranean fisheries depends on spawners refuging on continental slopes.  
818 For most major commercial species (including hake, monkfish and shrimp), the continental slope  
819 and canyons, less accessible to fishing fleets, are used as spawning areas, while the continental  
820 shelf and the coastal strip, which are more intensively fished, are preferred zones for nurseries  
821 (Würtz, 2012). Thus, including different spatial distribution maps (i.e. spawning and nursery  
822 grounds) for certain key species such as small pelagic fish (e.g. European anchovy, European  
823 pilchard and European mackerel) and demersal fish (e.g. European hake and red mullet) could  
824 potentially improve the spatial representation of food webs and population dynamics, as well as  
825 their vulnerability to fishing. Habitat suitability models by stage or size class that relate  
826 abundance information from surveys to environmental variables could be used for this purpose  
827 (Druon et al., 2015; Giannoulaki et al., 2013a).

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

838 - *Spatialized fishing effort/mortality*: While OSMOSE-MED assumed a uniform spatial distribution  
839 of fishing effort, this is not realistic since fishing effort is mainly distributed along coasts and the

840 continental shelf (Kroodsmas et al., 2018; Leleu et al., 2014; Maynou et al., 2011; Ramírez et al.,  
841 2018), although the lower biomass in the open sea counterbalances this potential source of bias  
842 (Figure 8). In addition, fisheries targeting large pelagic fish such as tuna or swordfish often  
843 operate in the open sea, due to the distribution pattern of the target species (Druon et al., 2016).  
844 Fishing effort metadata, reported at the scale of species and geographical sub-area, available in  
845 the Data Collection Reference Framework (GFCM, 2018) could be used to improve the  
846 differential pressures exerted by fishing across the Mediterranean. Another option to spatialize  
847 fishing effort/mortality would be to model as many exploited populations of a species as the  
848 number of evaluated stocks. This would require knowing the true number of stocks in the  
849 Mediterranean and the possible connectivity between them (Fiorentino et al., 2014; Ragonese et  
850 al., 2016).

851 - *Uncertainty*: Marine ecosystems are structurally complex, spatially and temporally variable, and  
852 difficult and costly to observe, all of which can potentially lead to considerable uncertainty in  
853 model predictions (Cheung et al., 2016; Hill et al., 2007; Payne et al., 2016). There are many  
854 sources of uncertainty in ecosystem models, from structural (model) uncertainty, and  
855 initialization and internal variability uncertainty to parametric uncertainty (Payne et al., 2016).  
856 Assessing these different types of uncertainty would allow building confidence intervals around  
857 the OSMOSE-MED predictions and increase its relevance for making projections and supporting  
858 policymaking in the Mediterranean Sea (Gal et al., 2014; Hill et al., 2007; Hyder et al., 2015;  
859 Payne et al., 2016). Uncertainty due to the sources of input data (i.e. parametric uncertainty)  
860 could be tested as a first step. While most of the data used for parameterizing the model came  
861 from the study area, some parameters for data-poor species (e.g. relative fecundity and growth  
862 parameters) were obtained from ecosystems outside the Mediterranean region, and these can  
863 differ considerably according to the ecosystem (Halouani et al., 2016). A sensitivity analysis on  
864 such parameters could be carried out following the methodology employed in Lehuta et al.  
865 (2010) or Ortega-Cisneros et al. (2017).

#### 866 **4.3 Potential uses of OSMOSE-MED**

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

870 For example, the model can provide insights on climate change impacts on operational fisheries  
871 reference levels, such as Maximum Sustainable Yield (MSY) and multi-species MSY at the  
872 Mediterranean scale (Lehuta et al., 2016). It could also guide spatial conservation planning

873 priorities, such as the implementation of marine protected area networks (Lehuta et al., 2016;  
874 Liqueste et al., 2016; Micheli et al., 2013b) as required by the Marine Strategy Framework  
875 Directive (MSFD) (European Commission, 2008). Many MSFD indicators regarding biodiversity  
876 and food webs can be directly derived from OSMOSE-MED, making it a relevant tool to aid the  
877 policy objective of achieving 'Good Environmental Status' for all European seas by 2020  
878 (Cardoso et al., 2010; Piroddi et al., 2015b). Evidence provided by the model can also inform  
879 decision-making in the framework of the EU's Blue Growth strategy to support sustainable  
880 growth in the marine and maritime sectors (European Commission, 2017), as well as the mid-  
881 term strategy (2017–2020) of the General Fisheries Commission for the Mediterranean (GFCM),  
882 developed to support the achievement of UN Sustainable Development Goal 14 (GFCM, 2017b).  
883 Lastly, the model can be used as a tool to communicate with stakeholders, including managers  
884 and non-scientist end users of Mediterranean ecosystems, to help incorporate scientific  
885 evidence into environmental decision-making (Cartwright et al., 2016; Jönsson et al., 2015; Rose  
886 et al., 2010).

887

## 888 **Acknowledgements**

889 The authors would like to thank the Pôle de Calcul et de Données Marines (PCDM) for providing  
890 access to their DATARMOR computing resources (<http://www.ifremer.fr/pcdm>). We are also  
891 grateful to the participants of the MEDITS survey, conducted within the Data Collection  
892 Framework (DCF) since 1994. Sabine Drira's help was very valuable in developing the species  
893 distribution models. Fabien Moullec was funded by a PhD grant from the French Ministry of  
894 Higher Education, Research and Innovation. This work was partially funded by the  
895 Mediterranean Centre for Environment and Biodiversity Laboratory of Excellence (LabEx  
896 CeMEB) *USBIO* project (Uncertainty in Scenarios of Biodiversity), an Agence Nationale de  
897 Recherche (ANR) 'Investissements d'avenir' program (ANR-10-LABX-04-01), and the SOMBEE  
898 project of the joint BiodivERsA and Belmont Forum "BiodivScen 2018" call (ANR-18-EBI4-0003-  
899 01).

900

## 901 **Author contributions**

902 F.M. developed the model and acquired, analyzed and interpreted the data. L.V., P.V., N.B.,  
903 F.G. and Y-J.S. helped in developing the model. Y-J.S. helped in data analysis and  
904 interpretation. C.U. provided data on primary and secondary production (from the  
905 biogeochemical model). P.V. and N.B. helped with the OSMOSE programming code and use of  
906 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.



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

909

## 910 **Competing interests**

911 The authors declare no competing financial interests.

912

## 913 **References**

- 914 Albouy, C., Ben Rais Lasram, F., Velez, L., Guilhaumon, F., Meynard, C.N., Boyer, S.,  
915 Benestan, L., Mouquet, N., Douzery, E., Aznar, R., Troussellier, M., Somot, S., Leprieur,  
916 F., Le Loc'h, F., Mouillot, D., 2015. FishMed: traits, phylogeny, current and projected  
917 species distribution of Mediterranean fishes, and environmental data. *Ecology* 96, 2312–  
918 2313. <https://doi.org/10.1890/14-2279.1>
- 919 Albouy, C., Guilhaumon, F., Araújo, M.B., Mouillot, D., Leprieur, F., 2012. Combining projected  
920 changes in species richness and composition reveals climate change impacts on coastal  
921 Mediterranean fish assemblages. *Glob. Change Biol.* 18, 2995–3003.  
922 <https://doi.org/10.1111/j.1365-2486.2012.02772.x>
- 923 Albouy, C., Guilhaumon, F., Leprieur, F., Ben Rais Lasram, F., Somot, S., Aznar, R., Velez, L.,  
924 Le Loc'h, F., Mouillot, D., 2013. Projected climate change and the changing  
925 biogeography of coastal Mediterranean fishes. *J. Biogeogr.* 40, 534–547.  
926 <https://doi.org/10.1111/jbi.12013>
- 927 Albouy, C., Mouillot, D., Rocklin, D., Culioli, J., Le Loc'h, F., 2010. Simulation of the combined  
928 effects of artisanal and recreational fisheries on a Mediterranean MPA ecosystem using  
929 a trophic model. *Mar. Ecol. Prog. Ser.* 412, 207–221. <https://doi.org/10.3354/meps08679>
- 930 Albouy, C., Velez, L., Coll, M., Colloca, F., Le Loc'h, F., Mouillot, D., Gravel, D., 2014. From  
931 projected species distribution to food-web structure under climate change. *Glob. Change*  
932 *Biol.* 20, 730–741. <https://doi.org/10.1111/gcb.12467>
- 933 AllEnvi, 2016. Alliance nationale de recherche pour l'environnement (France). The  
934 Mediterranean region under climate change: a scientific update. IRD editions, Marseille.
- 935 Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution  
936 models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–  
937 1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- 938 Anderson, T.R., Pondaven, P., 2003. Non-redfield carbon and nitrogen cycling in the Sargasso  
939 Sea: pelagic imbalances and export flux. *Deep Sea Res. Part Oceanogr. Res. Pap.* 50,  
940 573–591. [https://doi.org/10.1016/S0967-0637\(03\)00034-7](https://doi.org/10.1016/S0967-0637(03)00034-7)
- 941 Auger, P.A., Diaz, F., Ulses, C., Estournel, C., Neveux, J., Joux, F., Pujo-Pay, M., Naudin, J.J.,  
942 2011. Functioning of the planktonic ecosystem on the Gulf of Lions shelf (NW  
943 Mediterranean) during spring and its impact on the carbon deposition: a field data and 3-  
944 D modelling combined approach. *Biogeosciences* 8, 3231–3261.  
945 <https://doi.org/10.5194/bg-8-3231-2011>
- 946 Baklouti, M., Faure, V., Pawlowski, L., Sciandra, A., 2006. Investigation and sensitivity analysis  
947 of a mechanistic phytoplankton model implemented in a new modular numerical tool  
948 (Eco3M) dedicated to biogeochemical modelling. *Prog. Oceanogr.* 71, 34–58.  
949 <https://doi.org/10.1016/j.pocean.2006.05.003>
- 950 Bănar, D., Mellon-Duval, C., Roos, D., Bigot, J.-L., Souplet, A., Jadaud, A., Beaubrun, P.,  
951 Fromentin, J.-M., 2013. Trophic structure in the Gulf of Lions marine ecosystem (north-  
952 western Mediterranean Sea) and fishing impacts. *J. Mar. Syst.* 111, 45–68.  
953 <https://doi.org/10.1016/j.jmarsys.2012.09.010>

- 954 Barbet-Massin, M., Walther, B.A., Thuiller, W., Rahbek, C., Jiguet, F., 2009. Potential impacts of  
955 climate change on the winter distribution of Afro-Palaeartic migrant passerines. *Biol.*  
956 *Lett.* rsbl.2008.0715. <https://doi.org/10.1098/rsbl.2008.0715>
- 957 Ben Rais Lasram, F., Guilhaumon, F., Albouy, C., Somot, S., Thuiller, W., Mouillot, D., 2010.  
958 The Mediterranean Sea as a 'cul-de-sac' for endemic fishes facing climate change. *Glob.*  
959 *Change Biol.* 16, 3233–3245. <https://doi.org/10.1111/j.1365-2486.2010.02224.x>
- 960 Ben Rais Lasram, F., Mouillot, D., 2009. Increasing southern invasion enhances congruence  
961 between endemic and exotic Mediterranean fish fauna. *Biol. Invasions* 11, 697.  
962 <https://doi.org/10.1007/s10530-008-9284-4>
- 963 Bertrand, J.A., Sola, L.G. de, Papaconstantinou, C., Relini, G., Souplet, A., 2002. The general  
964 specifications of the MEDITS surveys. *Sci. Mar.* 66, 9–17.  
965 <https://doi.org/10.3989/scimar.2002.66s29>
- 966 Beuvier, J., Béranger, K., Lebeaupin Brossier, C., Somot, S., Sevault, F., Drillet, Y., Bourdallé-  
967 Badie, R., Ferry, N., Lyard, F., 2012. Spreading of the Western Mediterranean Deep  
968 Water after winter 2005: Time scales and deep cyclone transport. *J. Geophys. Res.*  
969 *Oceans* 117, C07022. <https://doi.org/10.1029/2011JC007679>
- 970 Beuvier, Jonathan, Brossier, C.L., Béranger, K., Arsouze, T., Bourdallé-Badie, R., Deltel, C.,  
971 Drillet, Y., Drobinski, P., Ferry, N., Lyard, F., Sevault, F., Somot, S., 2012. MED12,  
972 Oceanic component for the modeling of the regional Mediterranean earth system.  
973 *Mercator Ocean Quarterly Newsletter*, 46. <hal-01138958>.
- 974 Bosc, E., Bricaud, A., Antoine, D., 2004. Seasonal and interannual variability in algal biomass  
975 and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS  
976 observations. *Glob. Biogeochem. Cycles* 18. <https://doi.org/10.1029/2003GB002034>
- 977 Bosello, F., Delpiazzo, E., Eboli, F., 2015. Acidification in the Mediterranean Sea: impacts and  
978 adaptation strategies. *Rev. Environ. Energy Econ.* Re3 Forthcom.
- 979 Brind'Amour, A., Rochet, M.-J., Ordines, F., Hosack, G.R., Berthelé, O., Mérigot, B., Carbonara,  
980 P., Follesa, M.C., Jadaud, A., Lefkaditou, E., Maiorano, P., Peristeraki, P., Mannini, A.,  
981 Rabiller, M., Spedicato, M.T., Tserpes, G., Trenkel, V.M., 2016. Environmental drivers  
982 explain regional variation of changes in fish and invertebrate functional groups across the  
983 Mediterranean Sea from 1994 to 2012. *Mar. Ecol. Prog. Ser.* 562, 19–35.  
984 <https://doi.org/10.3354/meps11912>
- 985 Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A.,  
986 Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson,  
987 J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A.,  
988 Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F.,  
989 Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Hernández Morcillo,  
990 M., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear,  
991 D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C.,  
992 Watson, R., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–  
993 1168. <https://doi.org/10.1126/science.1187512>
- 994 Caddy, J.F., 1990. Options for the regulation of Mediterranean demersal fisheries. *Nat. Resour.*  
995 *Model.* 4, 427–475. <https://doi.org/10.1111/j.1939-7445.1990.tb00219.x>
- 996 Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J., Pelejero, C., 2011.  
997 Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan  
998 Sea. *Clim. Res.* 50, 1–29. <https://doi.org/10.3354/cr01040>
- 999 Cardinale, M., Scarcella, G., 2017. Mediterranean Sea: A Failure of the European Fisheries  
1000 Management System. *Front. Mar. Sci.* 4. <https://doi.org/10.3389/fmars.2017.00072>
- 1001 Cardoso, A.C., Cochrane, S., Doerner, H., Ferreira, J.G., Galgani, F., Hagebro, C., Hanke, G.,  
1002 Hoepffner, N., Keizer, P.D., Law, R., Olenin, S., Piet, G.J., Rice, J., Rogers, S.I.,  
1003 Swartenbroux, F., Tasker, M.L., Van de Bund, W., Piha, H., European Commission, Joint  
1004 Research Centre, International Council for the Exploration of the Sea (ICES), 2010.

1005 Scientific support to the European Commission Marine Strategy Framework Directive:  
1006 management group report, EUR 24336 EN – 2010. Publications Office, Luxembourg.

1007 Carozza, D.A., Bianchi, D., Galbraith, E.D., 2019. Metabolic impacts of climate change on  
1008 marine ecosystems: Implications for fish communities and fisheries. *Glob. Ecol.*  
1009 *Biogeogr.* 28, 158–169. <https://doi.org/10.1111/geb.12832>

1010 Carrozzi, V., Di Lorenzo, M., Massi, D., Titone, A., Ardizzone, G., Colloca, F., 2019. Prey  
1011 preferences and ontogenetic diet shift of European hake *Merluccius merluccius*  
1012 (Linnaeus, 1758) in the central Mediterranean Sea. *Reg. Stud. Mar. Sci.* 25, 100440.  
1013 <https://doi.org/10.1016/j.rsma.2018.100440>

1014 Cartes, J.E., Hidalgo, M., Papiol, V., Massutí, E., Moranta, J., 2009. Changes in the diet and  
1015 feeding of the hake *Merluccius merluccius* at the shelf-break of the Balearic Islands:  
1016 Influence of the mesopelagic-boundary community. *Deep Sea Res. Part Oceanogr. Res.*  
1017 *Pap.* 56, 344–365. <https://doi.org/10.1016/j.dsr.2008.09.009>

1018 Cartwright, S.J., Bowgen, K.M., Collop, C., Hyder, K., Nabe-Nielsen, J., Stafford, R., Stillman,  
1019 R.A., Thorpe, R.B., Sibly, R.M., 2016. Communicating complex ecological models to non-  
1020 scientist end users. *Ecol. Model.* 338, 51–59.  
1021 <https://doi.org/10.1016/j.ecolmodel.2016.07.012>

1022 Cheung, W.W.L., Dunne, J., Sarmiento, J.L., Pauly, D., 2011. Integrating ecophysiology and  
1023 plankton dynamics into projected maximum fisheries catch potential under climate  
1024 change in the Northeast Atlantic. *ICES J. Mar. Sci.* 68, 1008–1018.  
1025 <https://doi.org/10.1093/icesjms/fsr012>

1026 Cheung, W.W.L., Jones, M.C., Reygondeau, G., Frölicher, T.L., 2018. Opportunities for climate-  
1027 risk reduction through effective fisheries management. *Glob. Change Biol.* 24, 5149–  
1028 5163. <https://doi.org/10.1111/gcb.14390>

1029 Cheung, W.W.L., Jones, M.C., Reygondeau, G., Stock, C.A., Lam, V.W.Y., Frölicher, T.L., 2016.  
1030 Structural uncertainty in projecting global fisheries catches under climate change. *Ecol.*  
1031 *Model.* 325, 57–66. <https://doi.org/10.1016/j.ecolmodel.2015.12.018>

1032 Cheung, W.W.L., Lam, V.W.Y., Sarmiento, J.L., Kearney, K., Watson, R., Pauly, D., 2009.  
1033 Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.*  
1034 10, 235–251. <https://doi.org/10.1111/j.1467-2979.2008.00315.x>

1035 Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations.  
1036 *Ecol. Model., Placing Fisheries in their Ecosystem Context* 172, 109–139.  
1037 <https://doi.org/10.1016/j.ecolmodel.2003.09.003>

1038 Coll, M., Cury, P., Azzurro, E., Bariche, M., Bayadas, G., Bellido, J.M., Chaboud, C., Claudet, J.,  
1039 El-Sayed, A.-F., Gascuel, D., Knittweis, L., Pipitone, C., Samuel-Rhoads, Y., Taleb, S.,  
1040 Tudela, S., Valls, A., Workshop Participants, 2013. The scientific strategy needed to  
1041 promote a regional ecosystem-based approach to fisheries in the Mediterranean and  
1042 Black Seas. *Rev. Fish Biol. Fish.* 23, 415–434. [https://doi.org/10.1007/s11160-013-9305-  
1044 y](https://doi.org/10.1007/s11160-013-9305-<br/>1043 y)

1044 Coll, M., Libralato, S., 2012. Contributions of food web modelling to the ecosystem approach to  
1045 marine resource management in the Mediterranean Sea. *Fish Fish.* 13, 60–88.  
1046 <https://doi.org/10.1111/j.1467-2979.2011.00420.x>

1047 Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and  
1048 fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *J. Mar. Syst.* 59,  
1049 63–96. <https://doi.org/10.1016/j.jmarsys.2005.09.001>

1050 Coll, M., Piroddi, C., Albouy, C., Ben Rais Lasram, F., Cheung, W.W.L., Christensen, V.,  
1051 Karpouzi, V.S., Guilhaumon, F., Mouillot, D., Paleczny, M., Palomares, M.L., Steenbeek,  
1052 J., Trujillo, P., Watson, R., Pauly, D., 2012. The Mediterranean Sea under siege: spatial  
1053 overlap between marine biodiversity, cumulative threats and marine reserves. *Glob. Ecol.*  
1054 *Biogeogr.* 21, 465–480. <https://doi.org/10.1111/j.1466-8238.2011.00697.x>

- 1055 Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Ballesteros,  
1056 E., Bianchi, C.N., Corbera, J., Dailianis, T., Danovaro, R., Estrada, M., Froggia, C., Galil,  
1057 B.S., Gasol, J.M., Gertwagen, R., Gil, J., Guilhaumon, F., Kesner-Reyes, K., Kitsos, M.-  
1058 S., Koukouras, A., Lampadariou, N., Laxamana, E., Cuadra, C.M.L.-F. de la, Lotze, H.K.,  
1059 Martin, D., Mouillot, D., Oro, D., Raicevich, S., Rius-Barile, J., Saiz-Salinas, J.I., Vicente,  
1060 C.S., Somot, S., Templado, J., Turon, X., Vafidis, D., Villanueva, R., Voultsiadou, E.,  
1061 2010. The Biodiversity of the Mediterranean Sea: Estimates, Patterns, and Threats.  
1062 PLOS ONE 5, e11842. <https://doi.org/10.1371/journal.pone.0011842>
- 1063 Coll, M., Santojanni, A., Palomera, I., Tudela, S., Arneri, E., 2007. An ecological model of the  
1064 Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts.  
1065 J. Mar. Syst. 67, 119–154. <https://doi.org/10.1016/j.jmarsys.2006.10.002>
- 1066 Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M.,  
1067 Fiorentino, F., 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological  
1068 sustainability. Fish Fish. 14, 89–109. <https://doi.org/10.1111/j.1467-2979.2011.00453.x>
- 1069 Colloca, F., Mastrantonio, G., Lasinio, G.J., Ligas, A., Sartor, P., 2014. *Parapenaeus longirostris*  
1070 (Lucas, 1846) an early warning indicator species of global warming in the central  
1071 Mediterranean Sea. J. Mar. Syst., The wrapping up of the IDEADOS project:  
1072 International Workshop on Environment, Ecosystems and Demersal Resources, and  
1073 Fisheries 138, 29–39. <https://doi.org/10.1016/j.jmarsys.2013.10.007>
- 1074 Colloca, F., Scarcella, G., Libralato, S., 2017. Recent Trends and Impacts of Fisheries  
1075 Exploitation on Mediterranean Stocks and Ecosystems. Front. Mar. Sci. 4.  
1076 <https://doi.org/10.3389/fmars.2017.00244>
- 1077 Corrales, X., Coll, M., Ofir, E., Piroddi, C., Goren, M., Edelist, D., Heymans, J.J., Steenbeek, J.,  
1078 Christensen, V., Gal, G., 2017a. Hindcasting the dynamics of an Eastern Mediterranean  
1079 marine ecosystem under the impacts of multiple stressors. Mar. Ecol. Prog. Ser. 580,  
1080 17–36. <https://doi.org/10.3354/meps12271>
- 1081 Corrales, X., Coll, M., Tecchio, S., Bellido, J.M., Fernández, Á.M., Palomera, I., 2015.  
1082 Ecosystem structure and fishing impacts in the northwestern Mediterranean Sea using a  
1083 food web model within a comparative approach. J. Mar. Syst. 148, 183–199.  
1084 <https://doi.org/10.1016/j.jmarsys.2015.03.006>
- 1085 Corrales, X., Ofir, E., Coll, M., Goren, M., Edelist, D., Heymans, J.J., Gal, G., 2017b. Modeling  
1086 the role and impact of alien species and fisheries on the Israeli marine continental shelf  
1087 ecosystem. J. Mar. Syst. 170, 88–102. <https://doi.org/10.1016/j.jmarsys.2017.02.004>
- 1088 Costalago, D., Garrido, S., Palomera, I., 2015. Comparison of the feeding apparatus and diet of  
1089 European sardines *Sardina pilchardus* of Atlantic and Mediterranean waters: ecological  
1090 implications. J. Fish Biol. 86, 1348–1362. <https://doi.org/10.1111/jfb.12645>
- 1091 Cramer, W., Guiot, J., Fader, M., Garrabou, J., Gattuso, J.-P., Iglesias, A., Lange, M.A., Lionello,  
1092 P., Llasat, M.C., Paz, S., Peñuelas, J., Snoussi, M., Toreti, A., Tsimplis, M.N., Xoplaki,  
1093 E., 2018. Climate change and interconnected risks to sustainable development in the  
1094 Mediterranean. Nat. Clim. Change 8, 972. <https://doi.org/10.1038/s41558-018-0299-2>
- 1095 de Mora, L., Butenschön, M., Allen, J.I., 2016. The assessment of a global marine ecosystem  
1096 model on the basis of emergent properties and ecosystem function: a case study with  
1097 ERSEM. Geosci. Model Dev. 9, 59–76. <https://doi.org/10.5194/gmd-9-59-2016>
- 1098 Dimarchopoulou, D., Stergiou, K.I., Tsikliras, A.C., 2017. Gap analysis on the biology of  
1099 Mediterranean marine fishes. PLOS ONE 12, e0175949.  
1100 <https://doi.org/10.1371/journal.pone.0175949>
- 1101 Druon, J.-N., Fiorentino, F., Murenu, M., Knittweis, L., Colloca, F., Osio, C., Mérigot, B.,  
1102 Garofalo, G., Mannini, A., Jadaud, A., Sbrana, M., Scarcella, G., Tserpes, G., Peristeraki,  
1103 P., Carlucci, R., Heikkonen, J., 2015. Modelling of European hake nurseries in the  
1104 Mediterranean Sea: An ecological niche approach. Prog. Oceanogr. 130, 188–204.  
1105 <https://doi.org/10.1016/j.pocean.2014.11.005>

1106 Druon, J.-N., Fromentin, J.-M., Hanke, A.R., Arrizabalaga, H., Damalas, D., Tičina, V., Quílez-  
1107 Badia, G., Ramirez, K., Arregui, I., Tserpes, G., Reglero, P., Deflorio, M., Oray, I., Saadet  
1108 Karakulak, F., Megalofonou, P., Ceyhan, T., Grubišić, L., MacKenzie, B.R., Lamkin, J.,  
1109 Afonso, P., Addis, P., 2016. Habitat suitability of the Atlantic bluefin tuna by size class:  
1110 An ecological niche approach. *Prog. Oceanogr.* 142, 30–46.  
1111 <https://doi.org/10.1016/j.pocean.2016.01.002>

1112 Duboz, R., Versmisse, D., Travers, M., Ramat, E., Shin, Y.-J., 2010. Application of an  
1113 evolutionary algorithm to the inverse parameter estimation of an individual-based model.  
1114 *Ecol. Model.* 221, 840–849. <https://doi.org/10.1016/j.ecolmodel.2009.11.023>

1115 Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D’Ortenzio, F., Estournel,  
1116 C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P.,  
1117 Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S., Bensoussan,  
1118 N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F., Chami, M.,  
1119 Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-Poulichet, F.,  
1120 Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P., Gaertner, J.C.,  
1121 Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C., Guidi, L., Guizien,  
1122 K., Heimbürger, L.-E., Jacquet, S.H.M., Jeffrey, W.H., Joux, F., Le Hir, P., Leblanc, K.,  
1123 Lefèvre, D., Lejeusne, C., Lemé, R., Loÿe-Pilot, M.-D., Mallet, M., Méjanelle, L., Mélin, F.,  
1124 Mellon, C., Mérigot, B., Merle, P.-L., Migon, C., Miller, W.L., Mortier, L., Mostajir, B.,  
1125 Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A., Poggiale, J.-C., Prieur, L.,  
1126 Pujon-Pay, M., Pulido-Villena, Raimbault, P., Rees, A.P., Ridame, C., Rontani, J.-F., Ruiz  
1127 Pino, D., Sicre, M.A., Taillandier, V., Tamburini, C., Tanaka, T., Taupier-Letage, I.,  
1128 Tedetti, M., Testor, P., Thébault, H., Thouvenin, B., Touratier, F., Tronczynski, J., Ulses,  
1129 C., Van Wambeke, F., Vantrepotte, V., Vaz, S., Verney, R., 2011. Marine ecosystems’  
1130 responses to climatic and anthropogenic forcings in the Mediterranean. *Prog. Oceanogr.*  
1131 91, 97–166. <https://doi.org/10.1016/j.pocean.2011.02.003>

1132 European Commission, 2017. Report on the Blue Growth Strategy. Towards more sustainable  
1133 growth and jobs in the blue economy. Commission staff working document. Brussels,  
1134 31.3.2017 SWD (2017) 128 final.

1135 European Commission, 2008. Directive 2008/56/EC of the European Parliament and of the  
1136 Council establishing a framework for community action in the field of marine  
1137 environmental policy (Marine Strategy Framework Directive) *Off. J. Eur. Union*, L164  
1138 (2008), pp. 19–40.

1139 European Commission, 2003. Proposal for a Council regulation concerning measures for the  
1140 sustainable exploitation of fishery resources in the Mediterranean Sea and amending  
1141 regulations (EC) No 2847/93 and (EC) No 973/2001. Commission of the European  
1142 Communities. Brussels, 9 October 2003, COM (2003) 589 final, 2003/0229 (CNS), 39 pp.

1143 FAO, 2018. Impacts of climate change on fisheries and aquaculture. Synthesis of current  
1144 knowledge, adaptation and mitigation options. FAO fisheries and aquaculture technical  
1145 paper 627. FAO, Rome, Italy. 654p.

1146 FAO, 2016. Fisheries and aquaculture software. FAO, Fisheries and aquaculture software  
1147 FishStatJ - software for fishery statistical time series. FAO Fisheries and Aquaculture  
1148 Department, Rome (2016). <http://www.fao.org/fishery/>.

1149 FAO, 2006. Fisheries and aquaculture software. FishStat Plus - Universal software for fishery  
1150 statistical time series. In: FAO Fisheries and Aquaculture Department [online]. Rome.  
1151 Updated 28 November 2013. [Cited 4 July 2017].  
1152 <http://www.fao.org/fishery/statistics/software/fishstat/en>.

1153 Ferrà, C., Tasseti, A.N., Grati, F., Pellini, G., Polidori, P., Scarcella, G., Fabi, G., 2018. Mapping  
1154 change in bottom trawling activity in the Mediterranean Sea through AIS data. *Mar.*  
1155 *Policy* 94, 275–281. <https://doi.org/10.1016/j.marpol.2017.12.013>

1156 Fiorentino, F., Massuti, E., Tinti, F., Somarakis, S., Garofalo, G., Russo, T., Facchini, M.T.,  
1157 Carbonara, P., Kapiris, K., Tugores, P., Cannas, R., Tsigenopoulos, C., Patti, B., Colloca,  
1158 F., Sbrana, M., Mifsud, R., Valavanis, V., Spedicato, M.T., 2014. Stock units:  
1159 Identification of distinct biological units (stock units) for different fish and shellfish species  
1160 and among different GFCM-GSA. STOCKMED Deliverable 03: FINAL REPORT (1st and  
1161 2nd parts), 460 pp.

1162 Fu, C., Olsen, N., Taylor, N., Grüss, A., Batten, S., Liu, H., Verley, P., Shin, Y.-J., 2017. Spatial  
1163 and temporal dynamics of predator-prey species interactions off western Canada. ICES  
1164 J. Mar. Sci. 74, 2107–2119. <https://doi.org/10.1093/icesjms/fsx056>

1165 Fu, C., Perry, R.I., Shin, Y.-J., Schweigert, J., Liu, H., 2013. An ecosystem modelling framework  
1166 for incorporating climate regime shifts into fisheries management. Prog. Oceanogr., Strait  
1167 of Georgia Ecosystem Research Initiative (ERI) 115, 53–64.  
1168 <https://doi.org/10.1016/j.pocean.2013.03.003>

1169 Fulton, E.A., 2010. Approaches to end-to-end ecosystem models. J. Mar. Syst., Contributions  
1170 from Advances in Marine Ecosystem Modelling Research II 23–26 June 2008, Plymouth,  
1171 UK 81, 171–183. <https://doi.org/10.1016/j.jmarsys.2009.12.012>

1172 Gal, G., Makler-Pick, V., Shachar, N., 2014. Dealing with uncertainty in ecosystem model  
1173 scenarios: Application of the single-model ensemble approach. Environ. Model. Softw.  
1174 61, 360–370. <https://doi.org/10.1016/j.envsoft.2014.05.015>

1175 GFCM, 2018. GFCM Data Collection Reference Framework (DCRF). Version: 2018.1. 121p.

1176 GFCM, 2017a. Working Group on Stock Assessment of Demersal Species (WGSAD). FAO  
1177 headquarters, Rome, Italy, 13–18 November 2017. Final Report. 70p.

1178 GFCM, 2017b. Mid-term strategy (2017-2020) towards the sustainability of Mediterranean and  
1179 Black Sea fisheries (Mid-term strategy). FAO-GFCM 2017. Rome.

1180 Giannoulaki, M., Belluscio, A., Colloca, F., Fraschetti, S., Scardi, M., Smith, C., Panayotidis, P.,  
1181 Valavanis, V., Spedicato, M.T., 2013a. Mediterranean Sensitive Habitats (2013). Edited  
1182 by Giannoulaki M., A. Belluscio, F. Colloca, S. Fraschetti, M. Scardi, C. Smith, P.  
1183 Panayotidis, V. Valavanis M.T. Spedicato. DG MARE Specific Contract SI2.600741, Final  
1184 Report, 557 p.

1185 Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., Felice, A.D., Leonori, I.,  
1186 Bigot, J.L., Tičina, V., Pyrounaki, M.M., Tsagarakis, K., Machias, A., Somarakis, S.,  
1187 Schismenou, E., Quinci, E., Basilone, G., Cuttitta, A., Campanella, F., Miquel, J., Oñate,  
1188 D., Roos, D., Valavanis, V., 2013b. Characterizing the potential habitat of European  
1189 anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. Fish.  
1190 Oceanogr. 22, 69–89. <https://doi.org/10.1111/fog.12005>

1191 Giorgi, F., 2006. Climate change hot-spots. Geophys. Res. Lett. 33, L08707.  
1192 <https://doi.org/10.1029/2006GL025734>

1193 Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob.  
1194 Planet. Change, Mediterranean climate: trends, variability and change 63, 90–104.  
1195 <https://doi.org/10.1016/j.gloplacha.2007.09.005>

1196 Grimm, V., Ayllón, D., Railsback, S.F., 2017. Next-Generation Individual-Based Models Integrate  
1197 Biodiversity and Ecosystems: Yes We Can, and Yes We Must. Ecosystems 20, 229–236.  
1198 <https://doi.org/10.1007/s10021-016-0071-2>

1199 Grüss, A., Schirripa, M.J., Chagaris, D., Drexler, M., Simons, J., Verley, P., Shin, Y.-J.,  
1200 Karnauskas, M., Oliveros-Ramos, R., Ainsworth, C.H., 2015. Evaluation of the trophic  
1201 structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. J.  
1202 Mar. Syst. 144, 30–47. <https://doi.org/10.1016/j.jmarsys.2014.11.004>

1203 Grüss, A., Schirripa, M.J., Chagaris, D., Velez, L., Shin, Y.-J., Verley, P., Oliveros-Ramos, R.,  
1204 Ainsworth, C.H., 2016. Estimating natural mortality rates and simulating fishing scenarios  
1205 for Gulf of Mexico red grouper (*Epinephelus morio*) using the ecosystem model

1206 OSMOSE-WFS. J. Mar. Syst. 154, 264–279.  
1207 <https://doi.org/10.1016/j.jmarsys.2015.10.014>

1208 Gunawardena, J., 2014. Models in biology: 'accurate descriptions of our pathetic thinking.' BMC  
1209 Biol. 12, 29. <https://doi.org/10.1186/1741-7007-12-29>

1210 Halouani, G., Ben Rais Lasram, F., Shin, Y.-J., Velez, L., Verley, P., Hattab, T., Oliveros-Ramos,  
1211 R., Diaz, F., Ménard, F., Baklouti, M., Guyennon, A., Romdhane, M.S., Le Loc'h, F.,  
1212 2016. Modelling food web structure using an end-to-end approach in the coastal  
1213 ecosystem of the Gulf of Gabes (Tunisia). Ecol. Model. 339, 45–57.  
1214 <https://doi.org/10.1016/j.ecolmodel.2016.08.008>

1215 Hattab, T., Albouy, C., Ben Rais Lasram, F., Somot, S., Le Loc'h, F., Leprieur, F., 2014.  
1216 Towards a better understanding of potential impacts of climate change on marine  
1217 species distribution: a multiscale modelling approach. Glob. Ecol. Biogeogr. 23, 1417–  
1218 1429. <https://doi.org/10.1111/geb.12217>

1219 Hattab, T., Ben Rais Lasram, F., Albouy, C., Romdhane, M.S., Jarboui, O., Halouani, G., Cury,  
1220 P., Le Loc'h, F., 2013a. An ecosystem model of an exploited southern Mediterranean  
1221 shelf region (Gulf of Gabes, Tunisia) and a comparison with other Mediterranean  
1222 ecosystem model properties. J. Mar. Syst. 128, 159–174.  
1223 <https://doi.org/10.1016/j.jmarsys.2013.04.017>

1224 Hattab, T., Ben Rais Lasram, F., Albouy, C., Sammari, C., Romdhane, M.S., Cury, P., Leprieur,  
1225 F., Loc'h, F.L., 2013b. The Use of a Predictive Habitat Model and a Fuzzy Logic  
1226 Approach for Marine Management and Planning. PLOS ONE 8, e76430.  
1227 <https://doi.org/10.1371/journal.pone.0076430>

1228 Herrmann, M.J., Somot, S., 2008. Relevance of ERA40 dynamical downscaling for modeling  
1229 deep convection in the Mediterranean Sea. Geophys. Res. Lett. 35, L04607.  
1230 <https://doi.org/10.1029/2007GL032442>

1231 Hilborn, R., 2011. Future directions in ecosystem based fisheries management: A personal  
1232 perspective. Fish. Res. 108, 235–239. <https://doi.org/10.1016/j.fishres.2010.12.030>

1233 Hill, S.L., Watters, G.M., Punt, A.E., McAllister, M.K., Quéré, C.L., Turner, J., 2007. Model  
1234 uncertainty in the ecosystem approach to fisheries. Fish Fish. 8, 315–336.  
1235 <https://doi.org/10.1111/j.1467-2979.2007.00257.x>

1236 Hoegh-Guldberg, O., Cai, R., Poloczanska, E.S., Brewer, P.G., Sundby, S., Hilmi, K., Fabry,  
1237 V.J., Jung, S., 2014. The Ocean – Chapter 30. In: Climate Change 2014: Impacts,  
1238 Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II  
1239 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change  
1240 [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M.  
1241 Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S.  
1242 MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press,  
1243 Cambridge, United Kingdom and New York, NY, USA, pp. 1655-1731.

1244 Hyder, K., Rossberg, A.G., Allen, J.I., Austen, M.C., Barciela, R.M., Bannister, H.J., Blackwell,  
1245 P.G., Blanchard, J.L., Burrows, M.T., Defriez, E., Dorrington, T., Edwards, K.P., Garcia-  
1246 Carreras, B., Heath, M.R., Hembury, D.J., Heymans, J.J., Holt, J., Houle, J.E., Jennings,  
1247 S., Mackinson, S., Malcolm, S.J., McPike, R., Mee, L., Mills, D.K., Montgomery, C.,  
1248 Pearson, D., Pinnegar, J.K., Pollicino, M., Popova, E.E., Rae, L., Rogers, S.I., Speirs, D.,  
1249 Spence, M.A., Thorpe, R., Turner, R.K., van der Molen, J., Yool, A., Paterson, D.M.,  
1250 2015. Making modelling count - increasing the contribution of shelf-seas community and  
1251 ecosystem models to policy development and management. Mar. Policy 61, 291–302.  
1252 <https://doi.org/10.1016/j.marpol.2015.07.015>

1253 Ignatiades, L., Gotsis-Skretas, O., Pagou, K., Krasakopoulou, E., 2009. Diversification of  
1254 phytoplankton community structure and related parameters along a large-scale  
1255 longitudinal east–west transect of the Mediterranean Sea. J. Plankton Res. 31, 411–428.  
1256 <https://doi.org/10.1093/plankt/fbn124>

- 1257 Jackson, J.M., Lenz, P.H., 2016. Predator-prey interactions in the plankton: larval fish feeding on  
1258 evasive copepods. *Sci. Rep.* 6, 33585. <https://doi.org/10.1038/srep33585>
- 1259 Jochum, M., Schneider, F.D., Crowe, T.P., Brose, U., O’Gorman, E.J., 2012. Climate-induced  
1260 changes in bottom-up and top-down processes independently alter a marine ecosystem.  
1261 *Philos. Trans. R. Soc. B Biol. Sci.* 367, 2962–2970.  
1262 <https://doi.org/10.1098/rstb.2012.0237>
- 1263 Jönsson, A.M., Anderbrant, O., Holmér, J., Johansson, J., Schurgers, G., Svensson, G.P.,  
1264 Smith, H.G., 2015. Enhanced science–stakeholder communication to improve ecosystem  
1265 model performances for climate change impact assessments. *Ambio* 44, 249–255.  
1266 <https://doi.org/10.1007/s13280-014-0553-4>
- 1267 Jordà, G., Marbà, N., Duarte, C.M., 2012. Mediterranean seagrass vulnerable to regional climate  
1268 warming. *Nat. Clim. Change* 2, 821–824. <https://doi.org/10.1038/nclimate1533>
- 1269 Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B.,  
1270 Gårdmark, A.G., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka,  
1271 A., Dieckmann, U., Heino, M., Rijnsdorp, A.D., 2007. Ecology: Managing Evolving Fish  
1272 Stocks. *Science* 318, 1247–1248. <https://doi.org/10.1126/science.1148089>
- 1273 Jørgensen, C., Enberg, K., Mangel, M., 2016. Modelling and interpreting fish bioenergetics: a  
1274 role for behaviour, life-history traits and survival trade-offs. *J. Fish Biol.* 88, 389–402.  
1275 <https://doi.org/10.1111/jfb.12834>
- 1276 Karachle, P.K., Stergiou, K.I., 2017. An update on the feeding habits of fish in the Mediterranean  
1277 Sea (2002–2015). *Mediterr. Mar. Sci.* 18, 43–52. <https://doi.org/10.12681/mms.1968>
- 1278 Katsanevakis, S., Bogucarskis, K., Gatto, F., Vandekerkhove, J., Deriu, I., Cardoso, A.C., 2012.  
1279 Building the European Alien Species Information Network (EASIN): a novel approach for  
1280 the exploration of distributed alien species data. *BiolInvasions Rec.* 1, 235–245.  
1281 <https://doi.org/10.3391/bir.2012.1.4.01>
- 1282 Katsanevakis, S., Levin, N., Coll, M., Giakoumi, S., Shkedi, D., Mackelworth, P., Levy, R.,  
1283 Velegrakis, A., Koutsoubas, D., Caric, H., Brokovich, E., Öztürk, B., Kark, S., 2015.  
1284 Marine conservation challenges in an era of economic crisis and geopolitical instability:  
1285 The case of the Mediterranean Sea. *Mar. Policy* 51, 31–39.  
1286 <https://doi.org/10.1016/j.marpol.2014.07.013>
- 1287 Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E., Öztürk, B.,  
1288 Grabowski, M., Golani, D., Cardoso, A.C., 2014. Impacts of invasive alien marine species  
1289 on ecosystem services and biodiversity: a pan-European review. *Aquat. Invasions* 9,  
1290 391–423. <https://doi.org/10.3391/ai.2014.9.4.01>
- 1291 Kessouri, F., 2015. Cycles biogéochimiques de la mer Méditerranée : processus et bilans, PhD  
1292 thesis, Univ. Toulouse III Paul Sabatier, Toulouse, France.
- 1293 Kessouri, F., Ulses, C., Estournel, C., Marsaleix, P., Severin, T., Pujo-Pay, M., Caparros, J.,  
1294 Raimbault, P., Pasqueron de Fommervault, O., D’Ortenzio, F., Taillandier, V., Testor, P.,  
1295 Conan, P., 2017. Nitrogen and Phosphorus Budgets in the Northwestern Mediterranean  
1296 Deep Convection Region. *J. Geophys. Res. Oceans* 122, 9429–9454.  
1297 <https://doi.org/10.1002/2016JC012665>
- 1298 Kroodsmas, D.A., Mayorga, J., Hochberg, T., Miller, N.A., Boerder, K., Ferretti, F., Wilson, A.,  
1299 Bergman, B., White, T.D., Block, B.A., Woods, P., Sullivan, B., Costello, C., Worm, B.,  
1300 2018. Tracking the global footprint of fisheries. *Science* 359, 904–908.  
1301 <https://doi.org/10.1126/science.aao5646>
- 1302 Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668.  
1303 <https://doi.org/10.1006/jmsc.2000.0731>
- 1304 Le Quesne, W., Brown, M., De oliveira, J., Casey, J., O’Brien, C., 2013. Data-deficient fisheries  
1305 in EU waters. Directorate-General for internal policies. Policy department B: Structural ad  
1306 cohesion policies. IP/B/PECH/IC/2012-118. PE 495.865. June 2013. 74p.



1307 Lehuta, S., Girardin, R., Mahévas, S., Travers-Trolet, M., Vermard, Y., 2016. Reconciling  
1308 complex system models and fisheries advice: Practical examples and leads. *Aquat.*  
1309 *Living Resour.* 29, 208. <https://doi.org/10.1051/alr/2016022>

1310 Lehuta, S., Mahévas, S., Petitgas, P., Pelletier, D., 2010. Combining sensitivity and uncertainty  
1311 analysis to evaluate the impact of management measures with ISIS–Fish: marine  
1312 protected areas for the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery. *ICES J.*  
1313 *Mar. Sci.* 67, 1063–1075. <https://doi.org/10.1093/icesjms/fsq002>

1314 Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C.F., Pérez, T., 2010.  
1315 Climate change effects on a miniature ocean: the highly diverse, highly impacted  
1316 Mediterranean Sea. *Trends Ecol. Evol.* 25, 250–260.  
1317 <https://doi.org/10.1016/j.tree.2009.10.009>

1318 Leleu, K., Pelletier, D., Charbonnel, E., Letourneur, Y., Alban, F., Bachel, F., Boudouresque,  
1319 C.F., 2014. Métiers, effort and catches of a Mediterranean small-scale coastal fishery:  
1320 The case of the Côte Bleue Marine Park. *Fish. Res.* 154, 93–101.  
1321 <https://doi.org/10.1016/j.fishres.2014.02.006>

1322 Ligas, A., Sartor, P., Colloca, F., 2011. Trends in population dynamics and fishery of  
1323 *Parapenaeus longirostris* and *Nephrops norvegicus* in the Tyrrhenian Sea (NW  
1324 Mediterranean): the relative importance of fishery and environmental variables. *Mar.*  
1325 *Ecol.* 32, 25–35. <https://doi.org/10.1111/j.1439-0485.2011.00440.x>

1326 Link, J.S., 2010. Ecosystem-based fisheries management: confronting tradeoffs. Cambridge  
1327 University Press, Cambridge ; New York.

1328 Liquete, C., Piroddi, C., Macías, D., Druon, J.-N., Zulian, G., 2016. Ecosystem services  
1329 sustainability in the Mediterranean Sea: assessment of status and trends using multiple  
1330 modelling approaches. *Sci. Rep.* 6. <https://doi.org/10.1038/srep34162>

1331 Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell,  
1332 S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B.C., 2006. Depletion, Degradation, and  
1333 Recovery Potential of Estuaries and Coastal Seas. *Science* 312, 1806–1809.  
1334 <https://doi.org/10.1126/science.1128035>

1335 MacCall, A.D., 1990. Dynamic geography of marine fish populations, Books in recruitment  
1336 fishery oceanography. Washington Sea Grant Program: Distributed by University of  
1337 Washington Press, Seattle.

1338 Macias, D., Garcia-Gorriz, E., Piroddi, C., Stips, A., 2014. Biogeochemical control of marine  
1339 productivity in the Mediterranean Sea during the last 50 years. *Glob. Biogeochem.*  
1340 *Cycles* 28, 897–907. <https://doi.org/10.1002/2014GB004846>

1341 Macias, D.M., Garcia-Gorriz, E., Stips, A., 2015. Productivity changes in the Mediterranean Sea  
1342 for the twenty-first century in response to changes in the regional atmospheric forcing.  
1343 *Front. Mar. Sci.* 2. <https://doi.org/10.3389/fmars.2015.00079>

1344 Macpherson, E., 1998. Ontogenetic shifts in habitat use and aggregation in juvenile sparid  
1345 fishes. *J. Exp. Mar. Biol. Ecol.* 220, 127–150. [https://doi.org/10.1016/S0022-0981\(97\)00086-5](https://doi.org/10.1016/S0022-0981(97)00086-5)

1347 Macpherson, E., Duarte, C.M., 1991. Bathymetric trends in demersal fish size: is there a general  
1348 relationship? *Mar. Ecol. Prog. Ser.* 71, 103–112.

1349 Marbà, N., Jorda, G., Agusti, S., Girard, C., Duarte, C.M., 2015. Footprints of climate change on  
1350 Mediterranean Sea biota. *Front. Mar. Sci.* 2. <https://doi.org/10.3389/fmars.2015.00056>

1351 Marzloff, M., Shin, Y.-J., Tam, J., Travers, M., Bertrand, A., 2009. Trophic structure of the  
1352 Peruvian marine ecosystem in 2000–2006: Insights on the effects of management  
1353 scenarios for the hake fishery using the IBM trophic model *Osmose*. *J. Mar. Syst.* 75,  
1354 290–304. <https://doi.org/10.1016/j.jmarsys.2008.10.009>

1355 Maynou, F., Recasens, L., Lombarte, A., 2011. Fishing tactics dynamics of a Mediterranean  
1356 small-scale coastal fishery. *Aquat. Living Resour.* 24, 149–159.  
1357 <https://doi.org/10.1051/alr/2011131>

1358 Methratta, E.T., Link, J.S., 2007. Ontogenetic variation in habitat associations for four flatfish  
1359 species in the Gulf of Maine-Georges Bank region. *J. Fish Biol.* 70, 1669–1688.  
1360 <https://doi.org/10.1111/j.1095-8649.2007.01428.x>

1361 Micheli, F., Halpern, B.S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., Lewison, R.,  
1362 Nykjaer, L., Rosenberg, A.A., 2013a. Cumulative Human Impacts on Mediterranean and  
1363 Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PLOS*  
1364 *ONE* 8, e79889. <https://doi.org/10.1371/journal.pone.0079889>

1365 Micheli, F., Levin, N., Giakoumi, S., Katsanevakis, S., Abdulla, A., Coll, M., Fraschetti, S., Kark,  
1366 S., Koutsoubas, D., Mackelworth, P., Maiorano, L., Possingham, H.P., 2013b. Setting  
1367 Priorities for Regional Conservation Planning in the Mediterranean Sea. *PLOS ONE* 8,  
1368 e59038. <https://doi.org/10.1371/journal.pone.0059038>

1369 Morote, E., Olivar, M.P., Villate, F., Uriarte, I., 2010. A comparison of anchovy (*Engraulis*  
1370 *encrasicolus*) and sardine (*Sardina pilchardus*) larvae feeding in the Northwest  
1371 Mediterranean: influence of prey availability and ontogeny. *ICES J. Mar. Sci.* 67, 897–  
1372 908. <https://doi.org/10.1093/icesjms/fsp302>

1373 Mouillot, D., Albouy, C., Guilhaumon, F., Ben Rais Lasram, F., Coll, M., Devictor, V., Meynard,  
1374 C.N., Pauly, D., Tomasini, J.A., Troussellier, M., Velez, L., Watson, R., Douzery, E.J.P.,  
1375 Mouquet, N., 2011. Protected and Threatened Components of Fish Biodiversity in the  
1376 Mediterranean Sea. *Curr. Biol.* 21, 1044–1050. <https://doi.org/10.1016/j.cub.2011.05.005>

1377 Moullec, F., Barrier, N., Drira, S., Guilhaumon, F., Marsaleix, P., Somot, S., Ulses, C., Velez, L.,  
1378 Shin, Y.-J., 2019. An End-to-End model reveals losers and winners in a warming  
1379 Mediterranean Sea. *Front. Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00345>

1380 Moullec, F., Benedetti, F., Saraux, C., Van Beveren, E., Shin, Y.-J., 2016. Climate change  
1381 induces bottom-up changes in the food webs of the Mediterranean Sea. In: Thiébaud S.,  
1382 Moatti J.P. (eds.). *The Mediterranean region under climate change – A scientific update.*  
1383 Allenvi / IRD Editions, Marseille. pp: 219-228.

1384 Moutopoulos, D.K., Koutsikopoulos, C., 2014. Fishing strange data in national fisheries statistics  
1385 of Greece. *Mar. Policy* 48, 114–122. <https://doi.org/10.1016/j.marpol.2014.03.017>

1386 Nicholson, E., Fulton, E.A., Brooks, T.M., Blanchard, R., Leadley, P., Metzger, J.P., Mokany, K.,  
1387 Stevenson, S., Wintle, B.A., Woolley, S.N.C., Barnes, M., Watson, J.E.M., Ferrier, S.,  
1388 2019. Scenarios and Models to Support Global Conservation Targets. *Trends Ecol. Evol.*  
1389 34, 57–68. <https://doi.org/10.1016/j.tree.2018.10.006>

1390 Oliveros Ramos, R., 2014. End-to-end modelling for an ecosystem approach to fisheries in the  
1391 Northern Humboldt Current Ecosystem. *Inst. MAR PERU - IMARPE.*

1392 Oliveros-Ramos, R., Shin, Y.-J., 2016. Calibrar: an R package for fitting complex ecological  
1393 models. *ArXiv160303141 Math Q-Bio Stat.*

1394 Oliveros-Ramos, R., Verley, P., Echevin, V., Shin, Y.-J., 2017. A sequential approach to  
1395 calibrate ecosystem models with multiple time series data. *Prog. Oceanogr.* 151, 227–  
1396 244. <https://doi.org/10.1016/j.pocean.2017.01.002>

1397 Ortega-Cisneros, K., Cochrane, K., Fulton, E.A., 2017. An Atlantis model of the southern  
1398 Benguela upwelling system: Validation, sensitivity analysis and insights into ecosystem  
1399 functioning. *Ecol. Model.* 355, 49–63. <https://doi.org/10.1016/j.ecolmodel.2017.04.009>

1400 Pauly, D., Ullman, A., Piroddi, C., Bultel, E., Coll, M., 2014. ‘Reported’ versus ‘likely’ fisheries  
1401 catches of four Mediterranean countries. *Sci. Mar.* 78, 11–17.  
1402 <https://doi.org/10.3989/scimar.04020.17A>

1403 Pauly, D., Zeller, D., 2016. Catch reconstructions reveal that global marine fisheries catches are  
1404 higher than reported and declining. *Nat. Commun.* 7, 10244.  
1405 <https://doi.org/10.1038/ncomms10244>

1406 Payne, M.R., Barange, M., Cheung, W.W.L., MacKenzie, B.R., Batchelder, H.P., Cormon, X.,  
1407 Eddy, T.D., Fernandes, J.A., Hollowed, A.B., Jones, M.C., Link, J.S., Neubauer, P., Ortiz,  
1408 I., Queirós, A.M., Paula, J.R., 2016. Uncertainties in projecting climate-change impacts in

1409 marine ecosystems. ICES J. Mar. Sci. 73, 1272–1282.  
1410 <https://doi.org/10.1093/icesjms/fsv231>

1411 Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T.D.,  
1412 Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia,  
1413 R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S.,  
1414 Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J.,  
1415 Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R.,  
1416 Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J.M., Tuanmu, M.-N., Vergés, A.,  
1417 Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity  
1418 redistribution under climate change: Impacts on ecosystems and human well-being.  
1419 Science 355, eaai9214. <https://doi.org/10.1126/science.aai9214>

1420 Pepin, P., Penney, R., 2000. Feeding by a larval fish community: impact on zooplankton. Mar.  
1421 Ecol. Prog. Ser. 204, 199–212. <https://doi.org/10.3354/meps204199>

1422 Peristeraki, P., Tserpes, G., Lefkaditou, E., 2005. What cephalopod remains from *Xiphias*  
1423 *gladius* stomachs can imply about predator-prey interactions in the Mediterranean Sea?  
1424 J. Fish Biol. 67, 549–554. <https://doi.org/10.1111/j.0022-1112.2005.00742.x>

1425 Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P.,  
1426 Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel,  
1427 M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-Based Fishery  
1428 Management. Science 305, 346–347. <https://doi.org/10.1126/science.1098222>

1429 Piroddi, C., Coll, M., Liqueste, C., Macias, D., Greer, K., Buszowski, J., Steenbeek, J., Danovaro,  
1430 R., Christensen, V., 2017. Historical changes of the Mediterranean Sea ecosystem:  
1431 modelling the role and impact of primary productivity and fisheries changes over time.  
1432 Sci. Rep. 7, 44491. <https://doi.org/10.1038/srep44491>

1433 Piroddi, C., Coll, M., Steenbeek, J., Macias Moy, D., Christensen, V., 2015a. Modelling the  
1434 Mediterranean marine ecosystem as a whole: addressing the challenge of complexity.  
1435 Mar. Ecol. Prog. Ser. 533, 47–65. <https://doi.org/10.3354/meps11387>

1436 Piroddi, C., Teixeira, H., Lynam, C.P., Smith, C., Alvarez, M.C., Mazik, K., Andonegi, E.,  
1437 Churilova, T., Tedesco, L., Chifflet, M., Chust, G., Galparsoro, I., Garcia, A.C., Kämäri,  
1438 M., Kryvenko, O., Lassalle, G., Neville, S., Niquil, N., Papadopoulou, N., Rossberg, A.G.,  
1439 Suslin, V., Uyarra, M.C., 2015b. Using ecological models to assess ecosystem status in  
1440 support of the European Marine Strategy Framework Directive. Ecol. Indic. 58, 175–191.  
1441 <https://doi.org/10.1016/j.ecolind.2015.05.037>

1442 Por, D., 1989. The legacy of Tethys. Kluwer Academic Publishers, Dordrecht, p 41–64.

1443 Ragonese, S., Cannizaro, G., Norrito, P., Jereb, P., 2016. Watch your stock! A warning about  
1444 the endorsement of the “Stock concept” adopted by the STOCKMED project for the  
1445 Mediterranean groundfish fisheries. NTR-ITPP, sr72: 20 pp.

1446 Raick, C., Delhez, E.J.M., Soetaert, K., Grégoire, M., 2005. Study of the seasonal cycle of the  
1447 biogeochemical processes in the Ligurian Sea using a 1D interdisciplinary model. J. Mar.  
1448 Syst. 55, 177–203. <https://doi.org/10.1016/j.jmarsys.2004.09.005>

1449 Ramírez, F., Coll, M., Navarro, J., Bustamante, J., Green, A.J., 2018. Spatial congruence  
1450 between multiple stressors in the Mediterranean Sea may reduce its resilience to climate  
1451 impacts. Sci. Rep. 8, 14871. <https://doi.org/10.1038/s41598-018-33237-w>

1452 Roberts, S.M., 2003. Examination of the stomach contents from a Mediterranean sperm whale  
1453 found south of Crete, Greece. J. Mar. Biol. Assoc. U. K. 83, 667–670.  
1454 <https://doi.org/10.1017/S0025315403007628h>

1455 Rose, K.A., Allen, J.I., Artioli, Y., Barange, M., Blackford, J., Carlotti, F., Cropp, R., Daewel, U.,  
1456 Edwards, K., Flynn, K., Hill, S.L., HilleRisLambers, R., Huse, G., Mackinson, S., Megrey,  
1457 B., Moll, A., Rivkin, R., Salihoglu, B., Schrum, C., Shannon, L., Shin, Y.-J., Smith, S.L.,  
1458 Smith, C., Solidoro, C., St. John, M., Zhou, M., 2010. End-To-End Models for the

1459 Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps. *Mar. Coast. Fish.*  
1460 2, 115–130. <https://doi.org/10.1577/C09-059.1>

1461 Sabatés, A., Martín, P., Lloret, J., Raya, V., 2006. Sea warming and fish distribution: the case of  
1462 the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. *Glob. Change*  
1463 *Biol.* 12, 2209–2219. <https://doi.org/10.1111/j.1365-2486.2006.01246.x>

1464 Sbrana, M., Zupa, W., Ligas, A., Capezzuto, F., Chatzisprou, A., Follesa, M.C., Gancitano, V.,  
1465 Guijarro, B., Isajlovic, I., Jadaud, A., Markovic, O., Micallef, R., Peristeraki, P., Piccinetti,  
1466 C., Thasitis, I., Carbonara, P., 2019. Spatiotemporal abundance pattern of deep-water  
1467 rose shrimp, *Parapenaeus longirostris*, and Norway lobster, *Nephrops norvegicus*, in  
1468 European Mediterranean waters. *Sci. Mar.* <https://doi.org/10.3989/scimar.04858.27A>

1469 Sharir, Y., Kerem, D., Gol din, P., Spanier, E., 2011. Small size in the common bottlenose  
1470 dolphin -*Tursiops truncatus* in the eastern Mediterranean: a possible case of Levantine  
1471 nanism. *Mar. Ecol. Prog. Ser.* 438, 241–251. <https://doi.org/10.3354/meps09282>

1472 Shin, Y.-J., Cury, P., 2004. Using an individual-based model of fish assemblages to study the  
1473 response of size spectra to changes in fishing. *Can. J. Fish. Aquat. Sci.* 61, 414–431.  
1474 <https://doi.org/10.1139/f03-154>

1475 Shin, Y.-J., Cury, P., 2001. Exploring fish community dynamics through size-dependent trophic  
1476 interactions using a spatialized individual-based model. *Aquat. Living Resour.* 14, 65–80.  
1477 [https://doi.org/10.1016/S0990-7440\(01\)01106-8](https://doi.org/10.1016/S0990-7440(01)01106-8)

1478 Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J.G., Gislason, H., 2005. Using size-based  
1479 indicators to evaluate the ecosystem effects of fishing. *ICES J. Mar. Sci.* 62, 384–396.  
1480 <https://doi.org/10.1016/j.icesjms.2005.01.004>

1481 Shin, Y.-J., Shannon, L.J., Cury, P.M., 2004. Simulations of fishing effects on the southern  
1482 Benguela fish community using an individual-based model: learning from a comparison  
1483 with ECOSIM. *Afr. J. Mar. Sci.* 26, 95–114. <https://doi.org/10.2989/18142320409504052>

1484 Sonin, O., Spanier, E., Levi, D., Patti, B., Rizzo, P., Andreoli, M.G., 2007. Nanism (dwarfism) in  
1485 fish: a comparison between red mullet *Mullus barbatus* from the southeastern and the  
1486 central Mediterranean. *Mar. Ecol. Prog. Ser.* 343, 221–228.  
1487 <https://doi.org/10.3354/meps06917>

1488 STECF, 2017. Reports of the Scientific, Technical and Economic Committee for Fisheries  
1489 (STECF)-56th Plenary meeting Report (PLEN-17-03). 2017. Publications office of the  
1490 European union, Luxembourg, ISSN 1831-9424, 162 pp.

1491 Stergiou, K.I., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish.  
1492 *Rev. Fish Biol. Fish.* 11, 217–254. <https://doi.org/10.1023/A:1020556722822>

1493 Stergiou, K.I., Somarakis, S., Triantafyllou, G., Tsiaras, K.P., Giannoulaki, M., Petihakis, G.,  
1494 Machias, A., Tsikliras, A.C., 2016. Trends in productivity and biomass yields in the  
1495 Mediterranean Sea Large Marine Ecosystem during climate change. *Environ. Dev.*,  
1496 Thematic Issue - Ecosystem Based Management of Large Marine Ecosystems 17, 57–  
1497 74. <https://doi.org/10.1016/j.envdev.2015.09.001>

1498 Stock, A., Crowder, L.B., Halpern, B.S., Micheli, F., 2018. Uncertainty analysis and robust areas  
1499 of high and low modeled human impact on the global oceans. *Conserv. Biol.* 32, 1368–  
1500 1379. <https://doi.org/10.1111/cobi.13141>

1501 Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD – a platform for ensemble  
1502 forecasting of species distributions. *Ecography* 32, 369–373.  
1503 <https://doi.org/10.1111/j.1600-0587.2008.05742.x>

1504 Travers, M., Shin, Y.-J., Jennings, S., Cury, P., 2007. Towards end-to-end models for  
1505 investigating the effects of climate and fishing in marine ecosystems. *Prog. Oceanogr.*  
1506 75, 751–770. <https://doi.org/10.1016/j.pocean.2007.08.001>

1507 Travers, M., Shin, Y.-J., Jennings, S., Machu, E., Huggett, J.A., Field, J.G., Cury, P.M., 2009.  
1508 Two-way coupling versus one-way forcing of plankton and fish models to predict  
1509 ecosystem changes in the Benguela. *Ecol. Model.*, Selected Papers from the Sixth

1510 European Conference on Ecological Modelling - ECEM '07, on Challenges for ecological  
1511 modelling in a changing world: Global Changes, Sustainability and Ecosystem Based  
1512 Management, November 27-30, 2007, Trieste, Italy 220, 3089–3099.  
1513 <https://doi.org/10.1016/j.ecolmodel.2009.08.016>

1514 Travers-Trolet, M., Shin, Y.-J., Field, J.G., 2014. An end-to-end coupled model ROMS-  
1515 N2P2Z2D2-OSMOSE of the southern Benguela foodweb: parameterisation, calibration  
1516 and pattern-oriented validation. *Afr. J. Mar. Sci.* 36, 11–29.  
1517 <https://doi.org/10.2989/1814232X.2014.883326>

1518 Tsikliras, A.C., Dinouli, A., Tsiros, V.-Z., Tsalkou, E., 2015. The Mediterranean and Black Sea  
1519 Fisheries at Risk from Overexploitation. *PLOS ONE* 10, e0121188.  
1520 <https://doi.org/10.1371/journal.pone.0121188>

1521 Tzanatos, E., Raitsos, D.E., Triantafyllou, G., Somarakis, S., Tsonis, A.A., 2014. Indications of a  
1522 climate effect on Mediterranean fisheries. *Clim. Change* 122, 41–54.  
1523 <https://doi.org/10.1007/s10584-013-0972-4>

1524 Ulses, C., Auger, P.-A., Soetaert, K., Marsaleix, P., Diaz, F., Coppola, L., Herrmann, M.J.,  
1525 Kessouri, F., Estournel, C., 2016. Budget of organic carbon in the North-Western  
1526 Mediterranean open sea over the period 2004–2008 using 3-D coupled physical-  
1527 biogeochemical modeling. *J. Geophys. Res. Oceans* 121, 7026–7055.  
1528 <https://doi.org/10.1002/2016JC011818>

1529 Vasilakopoulos, P., Maravelias, C.D., Tserpes, G., 2014. The Alarming Decline of Mediterranean  
1530 Fish Stocks. *Curr. Biol.* 24, 1643–1648. <https://doi.org/10.1016/j.cub.2014.05.070>

1531 Velasco, F., Olaso, I., 1998. European hake *Merluccius merluccius* (L., 1758) feeding in the  
1532 Cantabrian Sea: seasonal, bathymetric and length variations. *Fish. Res.* 38, 33–44.  
1533 [https://doi.org/10.1016/S0165-7836\(98\)00111-8](https://doi.org/10.1016/S0165-7836(98)00111-8)

1534 Whitehead, P., Bauchot, L., Hureau, J., Nielsen, J., Tortonese, E., 1986. Fishes of the North-  
1535 Eastern Atlantic and the Mediterranean, Vols. 1–3. UNESCO, Paris.

1536 Würtz, M., 2012. Mediterranean submarine canyons: ecology and governance. Gland,  
1537 Switzerland and Malaga. Spain: IUCN. 216p. IUCN.

1538 Xing, L., Zhang, C., Chen, Y., Shin, Y.-J., Verley, P., Yu, H., Ren, Y., 2017. An individual-based  
1539 model for simulating the ecosystem dynamics of Jiaozhou Bay, China. *Ecol. Model.* 360,  
1540 120–131. <https://doi.org/10.1016/j.ecolmodel.2017.06.010>

1541 Zeller, D., Pauly, D., 2015. Reconstructing marine fisheries catch data. In: D. Pauly and D. Zeller  
1542 (eds). *Catch reconstruction: concepts, methods and data sources*. Online Publication.  
1543 *Sea Around Us* ([www.seaaroundus.org](http://www.seaaroundus.org)). University of British Columbia.  
1544