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

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

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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 km²) 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 km²), 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°W to 7.5°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 $1/12^\circ$ (≈ 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 ^a	Based on benthos groups included in the Ecopath model of Piroddi et al. (2017)	2000	50000	2.4

212 ^aBenthos 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**

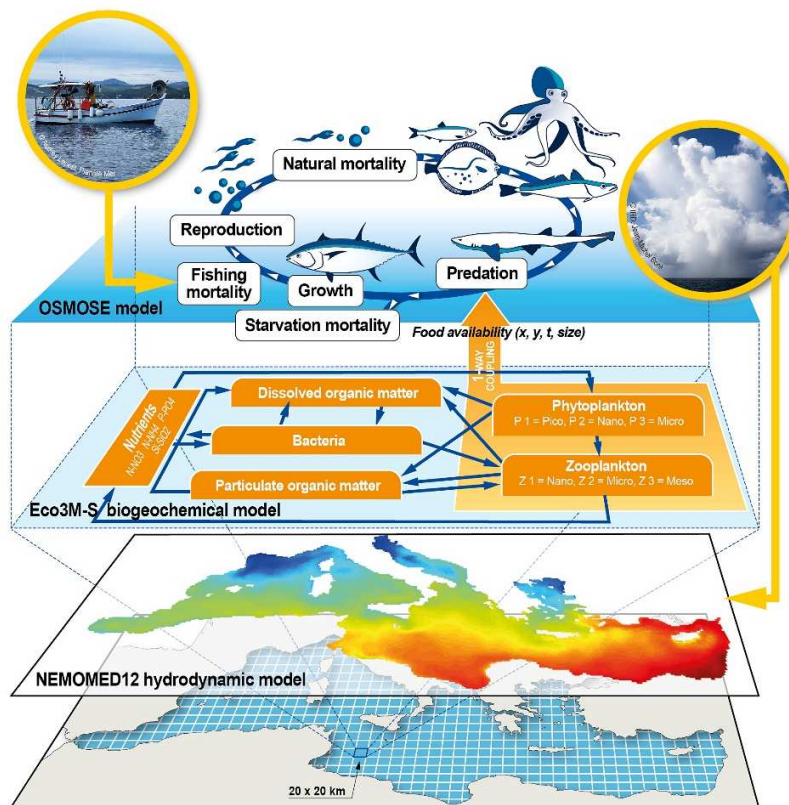
251 OSMOSE-MED covers the whole Mediterranean basin, from the Strait of Gibraltar to the Levant
252 basin and from the Northern Adriatic Sea to the Southern Ionian Sea (Figure 1). This area
253 extends from approximately 26.9°N to 46.3°N in latitude and from approximately 5.6°W to
254 36.1°E in longitude. 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), the Global Biodiversity Information Facility (GBIF:
320 www.gbif.org), the Food and Agriculture Organization's Geonetwork portal
321 (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⁻²) 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 year^{-1} for the caramote prawn
472 (*Penaeus kerathurus*) and 10.60 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 ± 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).

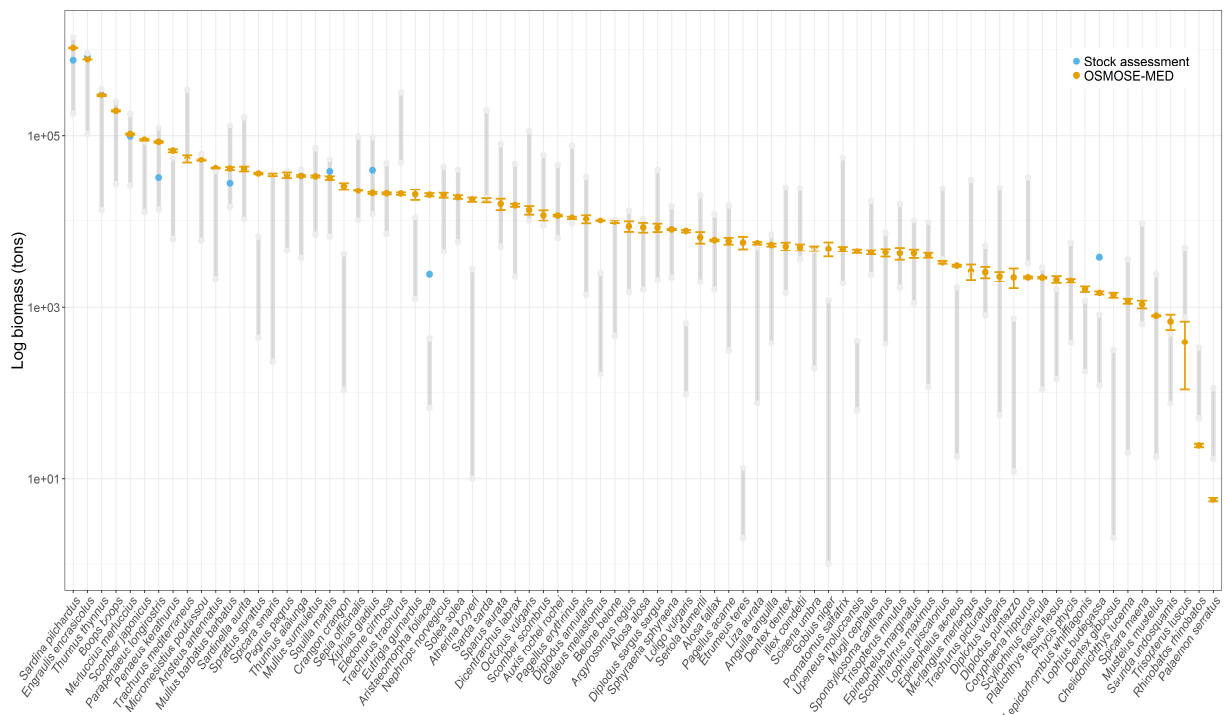
481 As fishing mortality rates (F) estimated by stock assessments were not available for all exploited
482 species, we chose to estimate these parameters by comparing the model output to observed
483 and reconstructed catches during the third phase of the calibration process. Most of the fishing
484 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 ± 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

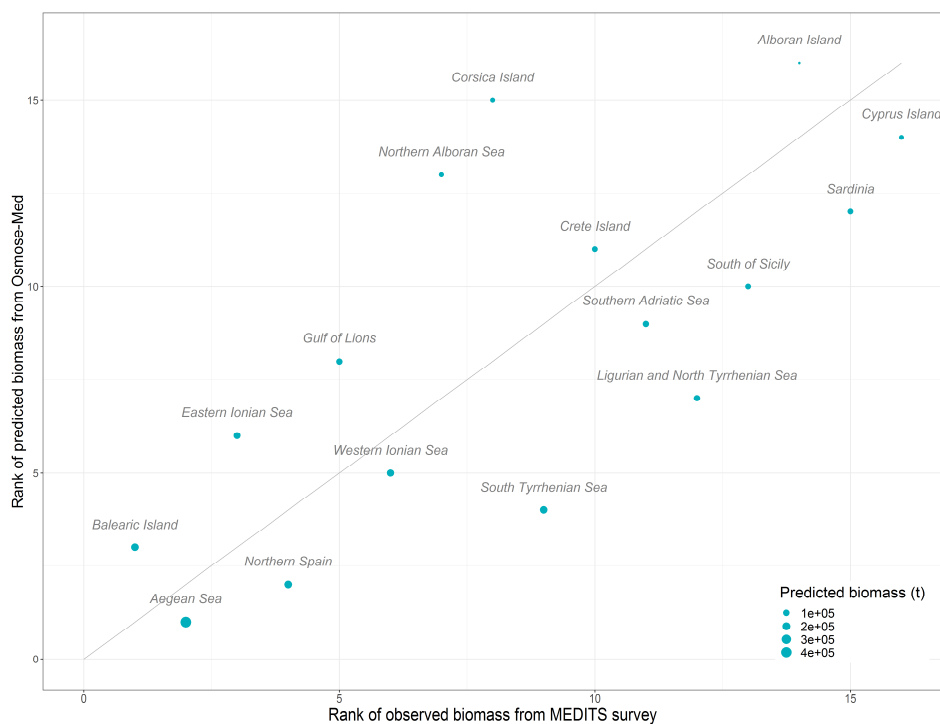
508 assessments or difficulty in accessing these assessments constitute real barriers to the
 509 development, parameterization and calibration of ecosystem models in the region (Coll et al.,
 510 2013; Katsanevakis et al., 2015; Piroddi et al., 2015a). Around 25% of landed biomass and less
 511 than 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 km²), 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 km²
 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.*

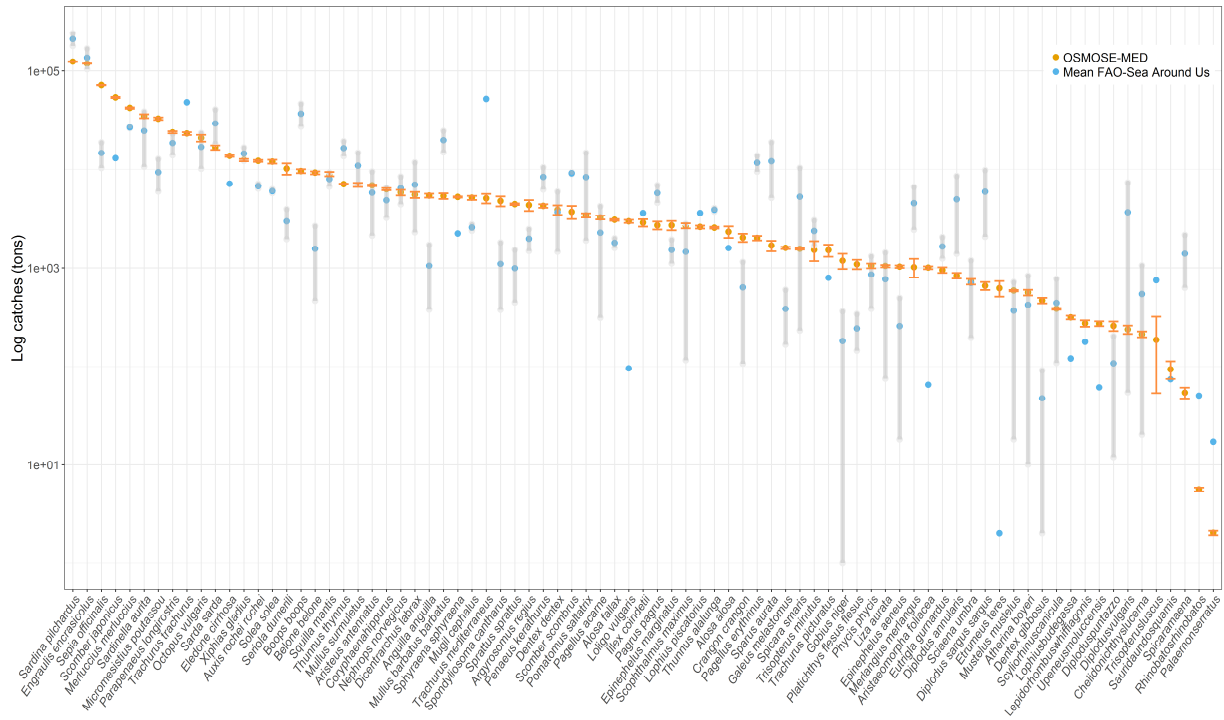
546 **3.2.2 Species catches**

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

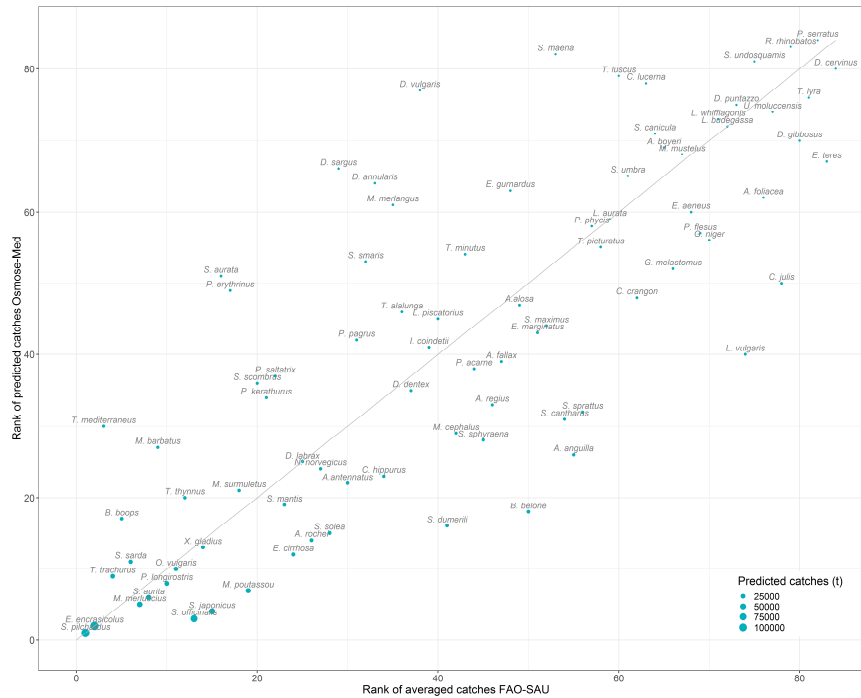
550 by the FAO and the 952,930 t reconstructed by the Sea Around Us (817,087 t on average). The
551 European pilchard and the European anchovy represented almost 30% of the total catch in
552 OSMOSE-MED and around 40% in reported or reconstructed catches over the 2006–2013
553 period (FAO, 2016; Pauly 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.*



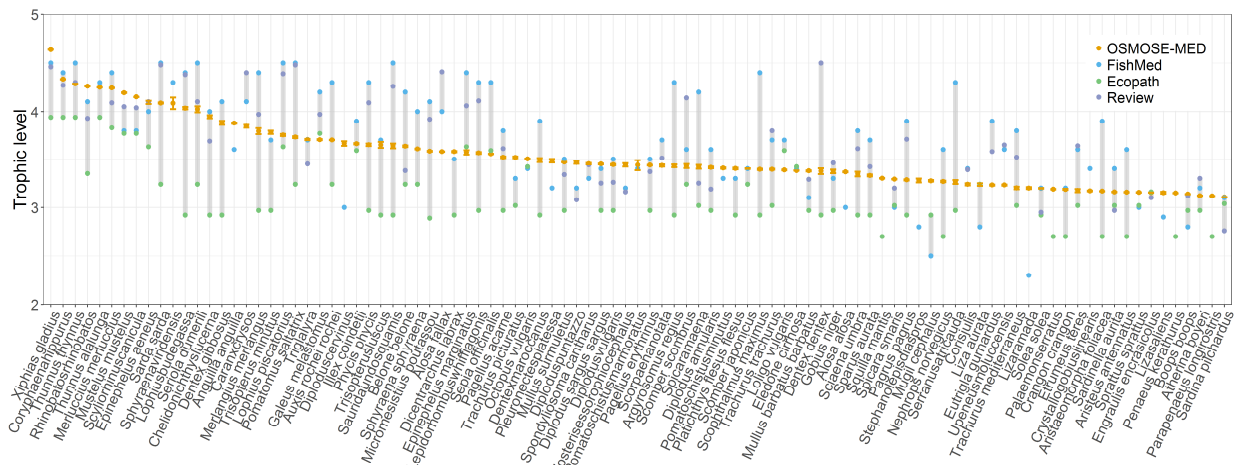
591

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 ± 0.002) and the European pilchard had the lowest (mTL = 3.11 ± 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

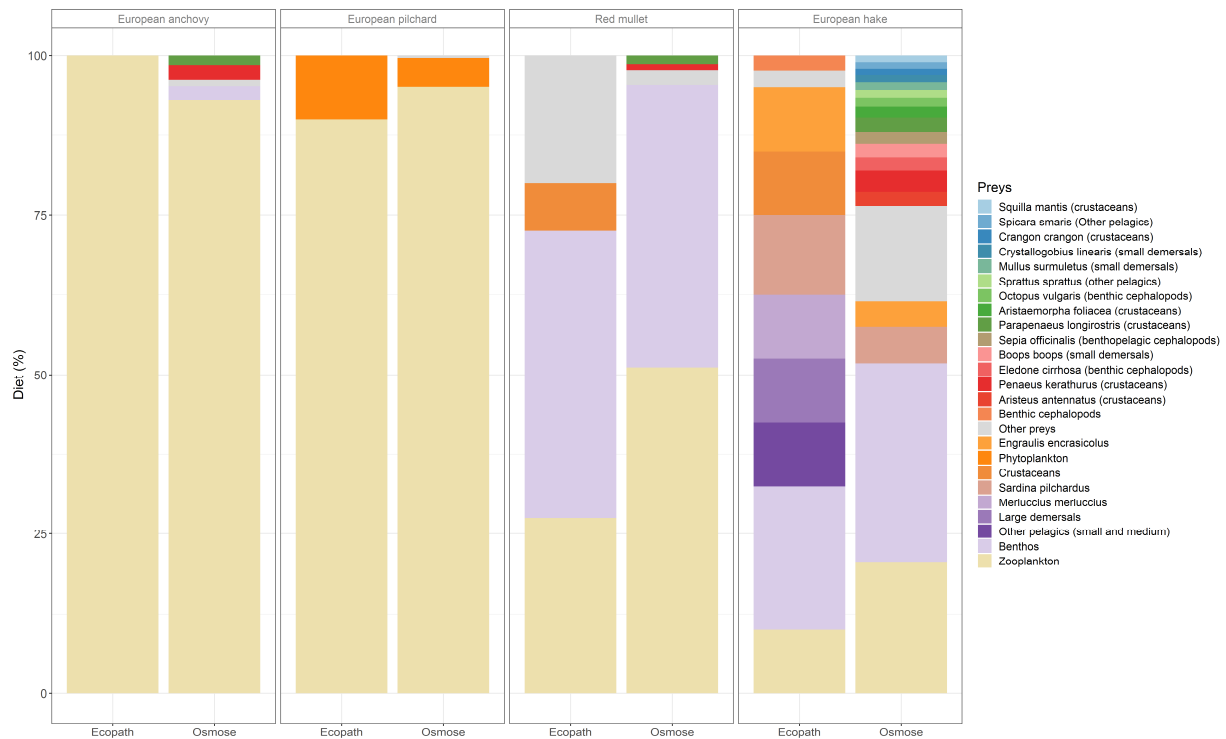


617
 618 *Figure 6 Mean species trophic levels predicted by OSMOSE-MED (in orange), the FishMed database (Albouy et al.,*
 619 *2015) (in blue), the Mediterranean Ecopath model (Piroddi et al., 2017, 2015a) (in green) and Karachle and Stergiou*
 620 *(2017) (in purple).*

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.



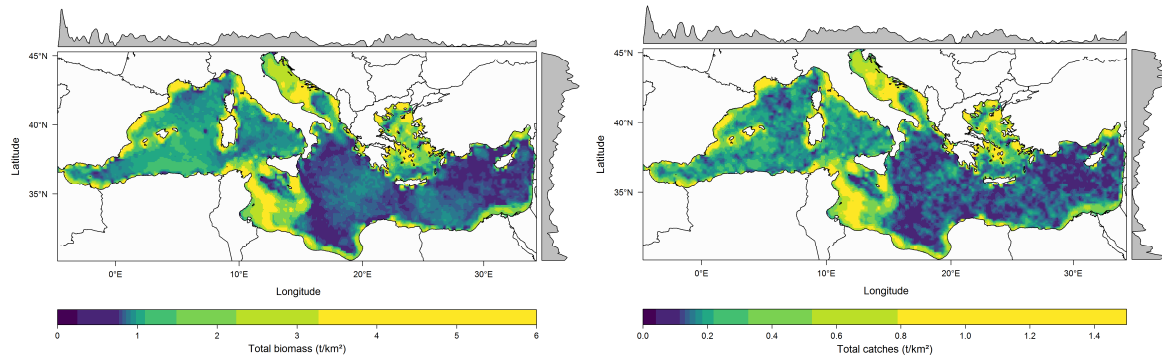
653
 654 *Figure 7 Diets simulated by OSMOSE-MED and the Mediterranean Ecopath model for four species (two small pelagic*
 655 *fish species (European anchovy and European pilchard) and two demersal fish species (red mullet and European*
 656 *hake). Functional groups used in the Ecopath model in which 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).

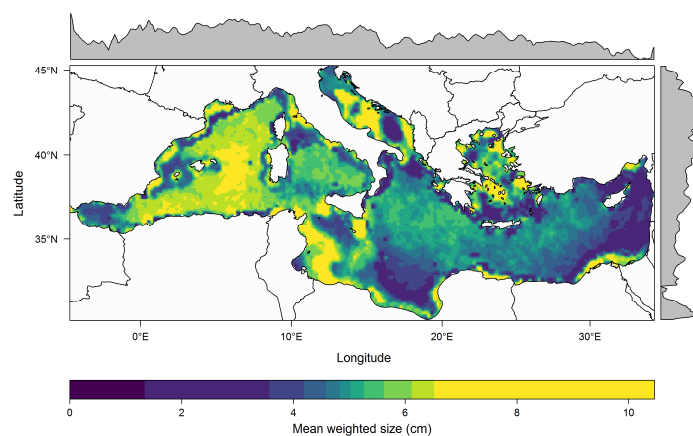


693
694 *Figure 8 Spatial distribution of the simulated total biomass (left) and catches (right) (all HTL species combined)*
695 *expressed in t.km⁻². Graphs on the top and right respectively represent the meridionally and zonally averaged*
696 *distribution of biomass and catches.*

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 (Bănaru 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

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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

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