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# Ecosystem modelling in the Northwestern Mediterranean Sea: structure and functioning of a complex system

Thomas SEYER(1,2), Daniela BĂNARU(2), Sandrine VAZ(3), Tarek HATTAB(3), Céline  
LABRUNE(4), Shawn BOOTH(2), Sabine CHARMASSON(1)

(1) IRSN, Institut de Radioprotection et de Sûreté Nucléaire, PSE-ENV/SRTE/LRTA,  
BP3, F-13115 Saint Paul Lez Durance

(2) Aix-Marseille Université, Université de Toulon, CNRS, IRD, MIO UM110, Mediterranean  
Institute of Oceanography, Marseille, France

(3) MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, Sète, France

(4) CNRS, Sorbonne Université, LECOB, UMR 8222, Observatoire Océanologique, F-66650  
Banyuls-sur-Mer, France

Email: [thomas.seyer@irsn.fr](mailto:thomas.seyer@irsn.fr)

## ABSTRACT

Ecopath mass-balanced models are widely-used tools to address various challenges in the understanding and protection of ecosystems. To track the continuing improvements in data and the evolving environment (climate change, anthropic pressure), new models are regularly being developed. In this study, we built a Gulf of Lion Ecopath model, focused on the continental shelf, featuring enhanced representation of benthic invertebrates and a realistic assessment of catches, and which takes into account the significant changes observed after 2008 – 2009 in the trophic structure of this ecosystem as well as related changes in fisheries activities. The model is composed of 68 functional groups, including 6 primary producers, discards and detritus, 27 invertebrate groups, 31 fish groups, dolphins and seabirds. New datasets were taken into account for biomasses, as well as for diets. P/B and Q/B parameters were calculated to include the most recent and geographically closest data. Model results highlight a food web diagram, ranging over 5 trophic levels and placing *Prionace glauca*, *Squalus acanthias* and dolphins as top predators. The mixed trophic impact analysis showed that the groups with the highest accumulated negative impacts are, in decreasing order, benthic trawls, nets and carnivorous echinoderms. The groups with the highest accumulated positive impacts are, in decreasing order, detritus, microphytoplankton and nanoplankton. The flux analysis shows that a major part of the flows occurs at trophic level 2 with 35.1% of the model total throughput and 43.8% of the total biomass. The catches have a mean trophic level of 3.47, higher than in previous studies, reflecting the evolution of changes the fisheries activities.

**Keywords:** Ecopath; Trophic structure; Modelling; Mediterranean; Gulf of Lion

## 1. INTRODUCTION

In the current context of climatic change and ever-growing anthropic pressure, it is essential to understand the structure and the functioning of marine ecosystems in order to predict how they will react to ongoing disturbances.

As both a hotspot of biodiversity, with 17 000 species (Coll *et al.*, 2010) and a center of human activities for centuries (*Large Marine Ecosystems Hub*, [www.lmehub.net](http://www.lmehub.net)), the Mediterranean Sea is a place of

44 particular interest for such studies. Many of its ecosystems are already impacted (Calvo *et al.*, 2011;  
45 Durrieu de Madron *et al.*, 2011; Micheli *et al.*, 2013; Fortibuoni, 2017) and the Gulf of Lion (GoL), in  
46 the Northwestern Mediterranean Sea, is no exception. A regime shift has been observed in its ecosystem  
47 since 2008, resulting mainly in important changes of condition and individual sizes of small  
48 planktivorous fishes (Van Beveren *et al.*, 2014; Saraux *et al.*, 2019; Feuilloley *et al.*, 2020) and most  
49 demersal fishes (Bensebaini *et al.*, 2022).

50 Historically-used single-species models have proven insufficient to accurately explain the processes  
51 influencing the biomass of a species (Cochrane, 2002). Ecosystem-based modelling is a response to this  
52 complexity and has been increasingly developed over the past decades. Ecopath with Ecosim (EwE,  
53 Ecopath.org) is today among the most widely-used software in this field. Since its introduction, it has  
54 been continuously improved, starting from a static ecosystem snapshot to become a dynamic and  
55 spatialized simulation (Polovina, 1984; Christensen and Pauly, 1992; Walters, Christensen and Pauly,  
56 1997; Walters, Pauly and Christensen, 1999; Heymans *et al.*, 2016). Its many uses include studies on  
57 the impact of fishing and fisheries management, the effectiveness of MPAs, habitat loss and degradation,  
58 understanding food webs and the dissemination of pollution (Coll and Libralato, 2012). Regarding this  
59 last aspect, the representation of biological groups interacting strongly with sediment is of paramount  
60 importance for the comprehension of some continental shelf marine areas (Cresson *et al.*, 2020) as well  
61 as for the modeling of the fate of contaminants in food webs (Hammerschmidt *et al.*, 2004; Ono *et al.*,  
62 2015; Tateda *et al.*, 2020).

63 Bănaru *et al.* (2013) developed an Ecopath model for the Gulf of Lion (NW Mediterranean Sea) and  
64 pointed out the lack of data for benthic invertebrate groups, the need for improved diet and biomass data  
65 and catch estimates. Their model covered the period 2000 - 2009; however an important shift in the GoL  
66 species composition and size occurred at the end of this period (Van Beveren *et al.*, 2014; Saraux *et al.*,  
67 2019) and may have led to changes in the structure and functioning of this system as well as fishing  
68 activities.

69 The aim of the present work is to investigate the current trophic functioning of the GoL after the changes  
70 observed from 2008 by developing a new Ecopath model that also includes the most accurate  
71 representation of sediment-dependent biological groups.

## 72 **2. MATERIALS AND METHODS**

### 73 **2.1. Study area**

74

75 The GOLEM (Gulf of Lion Ecopath Model) model area is located in the Gulf of Lion (GoL) between 0  
76 to 200 m depth, for a total area of 12172 km<sup>2</sup>. The 200 m isobath is located at the limit between the  
77 continental shelf and the canyons of the continental slope (**Fig. 1**). This model represents an average of  
78 the ecosystem situation between 2010 and 2014. The main environmental phenomena in this area are  
79 strong continental winds from the north-west (Tramontane) and north (Mistral) producing coastal  
80 upwellings (Millot, 1999; Agostini and Bakun, 2002), the mesoscale circulation of the western  
81 Mediterranean and the freshwater input from the Rhone River, which is the largest source of freshwater  
82 in the Mediterranean Sea (Margat, 1992; Petrenko *et al.*, 2005). The Rhone River is an important source  
83 of dissolved and particulate organic carbon (Lefevre *et al.*, 1997; Gaudy *et al.*, 2003; Harmelin-Vivien  
84 *et al.*, 2008). These phenomena lead to high primary and secondary production that supports a major  
85 part of the food web flows (Bănaru *et al.*, 2013, 2019; Cresson *et al.*, 2014). The sea floor features sandy  
86 and muddy substrates (Durrieu De Madron *et al.*, 2000) and few *Posidonia oceanica* meadows (Telesca  
87 *et al.*, 2015).

88

## 89 2.2. Ecopath software and balancing

90

91 The Ecopath software version 6.6.5 has been used to build the GOLEM model and ensure its mass and  
92 energy balance (Christensen *et al.*, 2008; Christensen and Walters, 2004; www.ecopath.org). The main  
93 equation driving Ecopath models is:

$$94 P_i = \sum B_j * M_{2ij} + Y_i + E_i + BA_i + P_i * (1 - EE_i)$$

95 with P the production of the functional group i,  $M_{2ij}$  the predation caused on i by a predator j and  $B_j$  its  
96 associated biomass, Y and E the export terms, the first for the fisheries and the latter for the other types  
97 of export, BA the biomass accumulation in the system and EE the ecotrophic efficiency (i. e. the  
98 proportion of the production of group i that is explained by the model, either by its exports or its  
99 predation). Thus,  $(1 - EE_i)$  represents other mortality, or mortality not explained in the system.

100 The first equation can be re-expressed as follows:

$$101 B_i * (P/B)_i = \sum B_j * (Q/B)_j * DC_{ij} + Y_i + E_i + BA_i + B_i * (P/B)_i + (1 - EE_i)$$

102 where  $(P/B)_i$  represents the production per biomass unit and, under steady state, is equivalent to Z, the  
103 total mortality (Allen, 1971),  $(Q/B)_j$  is the consumption per biomass unit and  $DC_{ij}$  is the portion of i in  
104 the diet of predator j (in weight or volume units).

105 For each functional group, Ecopath requires three among the following parameters: B, P/B, Q/B and  
106 EE. It also takes as input the diet of each group, their captures and discards, the assimilation rate (ratio  
107 of unassimilated/consumed food) and net migration rate (here considered as an 'import' part of the diet).

108 After all the input data were entered in the Ecopath software, but prior to balancing the model, special  
109 attention was paid to the P/Q ratio, as expected values range from 0.1 to 0.3 (Darwall *et al.*, 2010;  
110 Heymans *et al.*, 2016). Groups with too high P/Q values were corrected by recalculating the most  
111 uncertain between the P/B and Q/B. This was done by varying the parameters used to estimate P/B and  
112 Q/B (see section 2.4.3) within the range given by the literature.

113 When balancing the model, to adjust the values, the Automatic Mass Balance Procedure (Kavanagh *et al.*,  
114 2004) was used by removing the P/B or biomass (preferably the P/B, considered the most uncertain)  
115 data and setting the EE to 0.95, except for *Prionace glauca*, as a top predator, with  $EE = 0.1$  and  
116 planktonic groups, with  $EE = 0.99$ .

117 The model was considered balanced when all the EE, respiration/assimilation and net efficiency were  
118 less than 1 and the respiration/biomass was within expected values (Heymans *et al.*, 2016).

119

## 120 2.3. Functional groups

121

122 The species to be included in the model were selected mainly from the MEDITS database (Jadaud and  
123 Certain, 1994) in order to represent 99% of their estimated biomass indices. Then, others were included  
124 due to the large volume of capture in the area (total number of species representing 97% of the cumulated  
125 captures recorded in the SIH (Halieutics Information System, <http://sih.ifremer.fr>) fisheries database).  
126 Finally, some essential groups not represented in these data sets have been added, such as the planktonic  
127 and benthic groups, Posidonia and macrophytes. Then the diet for each species was completed from the  
128 literature (details below).

129 To form the functional groups, the species were grouped in two ways: the invertebrates were grouped  
130 according to the major taxa (brachyurids, echinids, etc.) with subdivisions based on the diet (e.g.  
131 carnivorous and detritivorous worms). Vertebrates (except birds and marine mammals) were grouped  
132 using hierarchical clustering based on their diet (**Appendix 1**). This clustering was carried out with  
133 STATISTICA software (version 12, Dell Inc.) using Ward's method and Euclidian distances.

134 This approach led to the constitution of 68 functional pelagic, demersal and benthic groups, the species  
135 composition of which is detailed in **Table 1**. They include 31 groups of fishes, 27 invertebrates, 6  
136 primary producers, a group of sea birds and a group of dolphins. Among them, 19 have been kept  
137 monospecific, either for commercial reasons (*Homarus gammarus*, *Mullus barbatus*) or for conservation  
138 interest (sharks and rays).

## 139 **2.4. Data sources and processing**

140

### 141 **2.4.1. Biomasses**

142 The main source of information on fish and invertebrates biomass used in this work comes from the  
143 MEDITS set of annual scientific bottom trawling campaigns (Jadaud and Certain, 1994) (**Appendix 2**).  
144 Their sampling scope has broadened over the years and includes all captured supra- and epibenthic  
145 invertebrate species since 2012.

146 The MEDITS data set has been processed to produce an average estimate of biomass (in t.km<sup>-2</sup>) for the  
147 period 2010-2014 and between 0 and 200 m depth while keeping information about the spatial  
148 heterogeneity of the species. The calculations were first carried out according to three depth strata (10-  
149 50 m, 50-100 m, 100-200 m) before being rescaled to the entire area. Given the geomorphology of the  
150 gulf (influence of the Rhône River in the east, mesoscale gyre in the west), it was decided to apply a  
151 correction factor to render the horizontal heterogeneity of the species distribution. For each species, its  
152 longitudinal extent was calculated and if it was less than 1.2° (over the 2.035° extent of the GoL), the  
153 biomass was corrected by the ratio of the longitudinal extent of the species to the longitudinal extent of  
154 the GoL. The value of 1.2° was considered suitable because species below this threshold would either  
155 be rare or restricted to part of the gulf, so their total weight value had to be lowered to avoid  
156 overestimation by multiplication by the area of the depth strata. No correction was applied to species  
157 present at a single station as it was impossible to determine whether it was highly localized, particularly  
158 rare or difficult to sample. The groups that contain at least one species concerned by this correction are  
159 the following: cnidarians, depositivorous molluscs, filter feeder molluscs, pagurids, *Homarus*  
160 *gammarus*, filter feeder echinoderms, holothurians, invertivorous fishes, wormivorous fishes, mullet  
161 and piscivorous flat fishes.

162 For *Engraulis encrasicolus*, *Sardina pilchardus*, *Sprattus sprattus*, *Trachurus Trachurus*, *T.*  
163 *mediterraneus*, *Scomber scomber* and *S. colias*, the datasets from the annual Mediterranean acoustic  
164 survey PELMED (Bourdeix and Hattab, (1985) were used. The GFCM (General Fisheries Commission  
165 for the Mediterranean) biomass data estimated by the stock assessment committees for this area were  
166 used for *Merluccius merluccius* and *Mullus barbatus*. In order to obtain densities per km<sup>2</sup>, the PELMED  
167 data, delivered in total weight, were divided by the surface surveyed by the GFCM, i.e. 11400 km<sup>2</sup>

168 Benthic endofauna data were provided by Labrune (pers. comm.) and estimated from Bonifácio *et al.*,  
169 (2018). They are based on REDIT2010 and APPEALMED cruises (Labrune and Amouroux, 2010;  
170 Labrune, 2018). These data were used for the following groups: cnidarians, sessile suspension feeders,  
171 depositivorous molluscs, filter feeder molluscs, carnivorous molluscs, depositivorous worms, filter  
172 feeder worms, carnivorous worms, sipuncula, suprabenthic and benthic invertebrates, pagurids and  
173 carnivorous echinoderms.

174 Among the species included to reach 97% of the total captures, some lacked biomass estimates. These  
175 missing values were completed from the literature (see **Appendix 2**).

176 To estimate the biomass of the detritus group, the particulate organic carbon (POC) inventory from  
177 Many *et al.* (2021) was used (average between 2011 and 2014, in t C). Their value was converted to wet  
178 weight (ww) with a 10x factor (Dalsgaard and Pauly, 1997) and divided by the GoL area.

179 The import term was calculated using data from the Rhone sediment observatory (Thollet *et al.*, 2018).  
180 The daily liquid discharge and daily concentration of particulate organic carbon (POC) from 2010 to  
181 2014 were used to determine an average annual import of POC (t C) from the Rhone River to the GoL.  
182 According to Many *et al.* (2021), the Rhone river accounted for 97% of the POC riverine input in the  
183 GoL over the period 2011 to 2014 (consistent with the 97.4% calculated from Higuera *et al.* (2014),  
184 over 2008-2009). In order to account for the inputs of the other rivers, an increase corresponding to 3%  
185 was applied. Again, a factor of 10 was applied to convert the carbon mass to wet weight, for a final POC  
186 import of 98.05 t/km<sup>2</sup>/y.

187

## 188 **2.4.2. Catches**

189 The landings data recorded from the GoL were provided by the Halieutics Information System (SIH).  
190 The raw data were averaged over 2010-2014, by species and fishing gear type, and over the entire GoL  
191 fishing area. Gear types were then regrouped into: benthic trawls, pelagic trawls, nets, seines, long lines,  
192 recreational fishing and other. The 2010-2014 averages of the reported Spanish catches  
193 (<https://www.fao.org/faostat>) in the study area were added. As the gear used were not specified, they  
194 were distributed by species in the 7 functional fleet groups according their relative importance in the  
195 French catches.

196 The organization of fisheries in the GoL, with a high proportion of small boats (< 10 m) and a small  
197 number of auction sale halls, makes it difficult to accurately assess the catches, as part of them are sold  
198 directly in small harbours, fish markets and/or are undeclared (CRPMEM PACA, 2016). To account for  
199 that, a correction factor was applied, based on the R3 report of SIH (Demaneche *et al.*, 2009) for the  
200 available species.

201 To improve the representativeness of the catches, discards and recreational fishing were considered.  
202 Discards were taken into account only for *Merluccius merluccius*, *Sardina pilchardus* and *Trachurus*  
203 *mediterraneus*, based on estimates by OBSMER (2009) and Bourjea *et al.* (2019). Recreational fishing  
204 is widespread in this region and SIH data probably represents only a small fraction of this activity. It  
205 was estimated by Levrel (2012) to amount to 4814 tonnes of fish for the Mediterranean French coast. In  
206 this work, we added together both sources raising this estimate to 4855 tonnes. This value was split  
207 between the species pointed out by Font and Lloret, (2014); Kayal *et al.* (2020); Lloret and Font (2013)  
208 according to their relative weight per unit effort. Some adjustments have been made to represent the  
209 environmental characteristics of the GoL. Several of these surveys took place in the rocky western part  
210 of the GoL whereas sandy coasts are the main type of substrate in the study area, which leads to  
211 unrealistic catch values. Levrel, (2012) also estimated recreational captures of the cephalopods for  
212 France at 704 t. It was decided, for lack of a better estimator, to attribute 33.2% to the French  
213 Mediterranean coast (the same proportion as for fish). The 233.7 t were then divided between octopus  
214 and squid, proportionally to their respective biomasses.

215

## 216 **2.4.3. Production/biomass (P/B) and consumption/biomass (Q/B) ratios**

217 These two ratios (in y<sup>-1</sup>) were calculated for each species using different methods depending on whether  
218 they belonged to the invertebrates or vertebrates, according to the indications of Heymans *et al.* (2016).

219 For invertebrates, the artificial neural network model of Brey (2001, 2012) was used to determine the  
220 P/B. For each taxon, it takes as inputs the body mass (J), the depth (here, we have chosen the maximum  
221 depth from MEDITS data), the temperature (set at 13.5°C, the annual average at 50 m depth estimated  
222 from SOMLIT (Service d'Observation en Milieu Littoral, www.somlit.fr) time series in the GoL) and  
223 five other parameters depending on the mobility, life style and diet of the species.

224 In order to obtain the body mass in joules for each species, the average body mass in grams was  
225 calculated from the entire MEDITS data sets (1994-2019), then converted using Brey's conversion  
226 factor calculator (Brey, 2010). The most accurate taxon for the given species was selected among those  
227 available and only marine species were included in the computation. For gastropods and bivalvia, the  
228 'with shell' conversion factor was chosen, to remain consistent with the MEDITS data.

229 The Q/B ratio of invertebrates was calculated based on the following empirical relation (Cammen, 1979;  
230 Brey, 2001):

$$231 \text{Log (Q)} = -0.42 + 0.742 * \text{log (BM)}$$

232 where BM is the body mass (mg DW) and Q the consumption (mg DW d<sup>-1</sup>). The average dry weight of  
233 each species was obtained as explained above, from the MEDITS dataset and the Brey conversion factor  
234 calculator.

235 For vertebrates, the P/B was estimated as follows:

$$236 \text{P/B} = \text{Z} = \text{F} + \text{M}$$

237 with Z the total mortality (y<sup>-1</sup>), F the fisheries mortality (y<sup>-1</sup>) and M the natural mortality (y<sup>-1</sup>). F is the  
238 ratio between the catches of a species and its biomass. M was calculated using Pauly's empirical  
239 equation (Pauly, 1980):

$$240 \text{Log (M)} = -0.0066 - 0.279 * \text{log (L}\infty) + 0.6543 * \text{log (K)} + 0.4634 * \text{log (T)}$$

241 with L $\infty$  the length at infinity (cm), K the von Bertalanffy growth parameter (y<sup>-1</sup>) and T the mean annual  
242 temperature (°C), in this case 15.7°C (from SOMLIT, surface temperature). K and L $\infty$  were found in  
243 the literature (see **Appendix 2**).

244 Similarly, vertebrates Q/B was estimated using the Palomares and Pauly (1998) empirical equation:

$$245 \text{Log (Q/B)} = 7.964 - 0.204 * \text{log (W}\infty) - 1.1965 * \text{T}' + 0.083 * \text{A} + 0.532 * \text{h} + 0.398 * \text{d}$$

246 with W $\infty$  the weight at infinity (g), T' expressed as 1000/(T + 273.1), A the aspect ratio of the tail (from  
247 www.fishbase.org) and h and d the herbivory and detritivory parameters, respectively. The latter were  
248 set to 1 if the species had the corresponding feeding habit and 0 otherwise. W $\infty$  was calculated using the  
249 weight/length relation provided on www.fishbase.org and L $\infty$ .

250

#### 251 **2.4.4. Diet and data quality**

252 The diet for each species was obtained from the literature (see **Table 3 and Appendix 2**). When multiple  
253 data sources were found, the closest geographically was chosen. For multispecies groups, the diets were  
254 calculated in proportion to the biomass of each species making up the group.

255 As advised by Heymans (2016), the integrated pedigree routine was used to assess the input data and  
256 the overall model quality. For each input parameter (biomass, P/B, Q/B, diet and catches), a score was  
257 assigned to the source according to the Ecopath default rating scale. The routine is then able to produce  
258 an overall score for the model, ranging from 0 to 1, with 1 being the best quality.

259

## 260 2.5. Network analysis

261 As indicated by Heymans *et al.* (2016), to compare this model with the model of Bănaru *et al.* (2013)  
262 and other models, we used the four indices below, as they are less sensitive to differences in the model  
263 construction. These indices are: the Total System Throughput (TST, t/km<sup>2</sup>/y), the total net primary  
264 production on the TST (PP/TST), the sum of all consumptions on the TST (Q/TST) and the sum of all  
265 exports on the TST (Ex/TST) (**Table 6**).

266 The following indicators are used to describe the modelled ecosystem. The Trophic Level (TL), for each  
267 group, represents the weighted average of the trophic level of its preys, with the primary producers and  
268 detritus TL set to 1.

$$269 TL_i = 1 + \sum_{j=1} DC_{ij} TL_j$$

270 with  $DC_{ij}$  the fraction of prey  $j$  in the diet of  $i$  and  $TL_j$ , the trophic level of prey  $j$ .

271 The Omnivory Index (OI) gives an indication on the specialization of a predator's diet, tending towards  
272 zero when the group feeds on a single trophic level and higher when the group is unspecialized (Pauly  
273 *et al.*, 1993). It is calculated as follows:

$$274 OI_i = \sum_{j=1} (TL_j - (TL_i - 1))^2 \cdot DC_{ij}$$

275 The Mixed Trophic Impact (MTI), as adapted by Ulanowicz and Puccia, (1990), is the representation of  
276 the theoretical impact, positive or negative, of a small variation in the biomass of one group on all the  
277 others in the modelled ecosystem. It accounts both for direct (predation) and indirect (competition)  
278 interaction.

279 Valls *et al.* (2015) define a keystone species as “a predator species which disproportionately influences  
280 the food-web structure of its community”. The Keystoness (KS) of each group was calculated following  
281 their method:

$$282 KS_i = \varepsilon_i \times \text{drank}(B_i) \quad \varepsilon_i = \sqrt{\sum_{j=1} m_{ij}^2}$$

283 with  $\text{drank}(B_i)$  the rank in a decreasing ranking of the biomass of group  $i$ ,  $\varepsilon_i$  the overall trophic impact  
284 of  $i$  and  $m_{ij}$  the net MTI. The Valls *et al.* (2015) method was preferred to the other two available in the  
285 Network Analysis plugin (Power *et al.*, 1996; Libralato, Christensen and Pauly, 2006) because it gives  
286 balanced weighting to trophic impact and biomass in the calculation of the KS, unlike the others. The  
287 fluxes and biomasses of each discrete trophic level can be summarized in a ‘Lindeman spine plot’, a  
288 diagram presenting the food chain in a linear form, consisting of TL boxes and fluxes entering or leaving  
289 each of them. This plot also includes transfer efficiency, total throughput and flux to detritus for each  
290 TL.

291

## 292 3. RESULTS

293

### 294 3.1. General outputs

295 The output parameters of the model are presented in **Table 4**. Invertebrates represent 68.2% of the total  
296 biomass (detritus groups excluded) against 23.4% for vertebrates. The most important group in term of  
297 biomass is the mesozooplankton with 8.7%, the three small pelagics together account for 10.9% (S.

298 *pilchardus*, *S. sprattus* and *E. encrasicolus*) while dolphins and sea birds represent only a minute part  
299 of the biomass (< 0.01% ).

300 The highest Omnivory Indexes (OI) are found, in decreasing order, for sea birds (1.55), *Dicentrarchus*  
301 *labrax* (1.13) and *Homarus gammarus* (0.88). The lowest non-zero OI values concern filter feeder  
302 worms and depositivorous molluscs. The overall omnivory of the system is low, at 0.21, and only eight  
303 groups are above 0.5, indicating that the groups have a rather selective diet towards a limited range of  
304 trophic levels.

305 Eighteen groups show a higher fishing mortality than predation mortality (e.g. octopus, crustivorous  
306 fishes 2, *Scomber scombrus*, etc.) (**Table 4**). The 3 most fished groups are *Sparus aurata*, *Merluccius*  
307 *merluccius*, and *Engraulis encrasicolus*. Despite its importance in the catches, *E. encrasicolus* has  
308 fishing mortality that is lower than its predation mortality.

309 For *Sardina pilchardus* and *Engraulis encrasicolus*, the main consumers were squid and tuna,  
310 respectively.

311 The most consumed groups are nanoplankton, detritus, picoplankton, microphytoplankton and  
312 mesozooplankton, with 32.8, 19.8, 16, 7.3 and 5.7% of the total consumption, respectively.  
313 Consumption of vertebrates represents only 0.63% of the total consumption. Among fishes,  
314 wormivorous fishes are the most consumed, with 26.2%, followed by *E. encrasicolus*, *S. pilchardus* and  
315 *S. sprattus* with 17.2, 16.9 and 16.7%, respectively. On the consumer side, zooplankton groups are  
316 responsible for 54.5% of the total consumption, other invertebrates 38.4% and the vertebrates 7%.

317 The model has an overall pedigree of 0.631 (1 being the best quality possible), which places it at the  
318 high end of the range given in the review by Coll  ter *et al.* (2015) who carried out a survey of 433 EwE  
319 models of which only 34 provided a pedigree, the latter ranging from 0.137 to 0.743.

320

## 321 **3.2. Network analysis and flows**

322 The balanced model includes five trophic levels (**Table 4**), with *Prionace glauca*, *Squalus acanthias*  
323 and dolphin exhibiting the highest trophic levels i.e. 5.2, 5.0 and 5.0, respectively. Thirteen other groups  
324 have TL > 4, including anglerfish, rays and *Conger conger*. The resulting trophic network diagram is  
325 shown in **Figure 2**.

326 The Lindeman spine plot (**Figure 3**) shows that the majority of the fluxes towards detritus, from lower  
327 TL and respiration occurs in TL II. It hosts 35.1% of the total system throughput and 43.8% of the total  
328 biomass (excluding detritus). However, this is not the case for the export and catches flow, dominated  
329 by fisheries, which is greater for TL III and IV, showing a preference in catches for intermediate TL. It  
330 is confirmed by the mean trophic level of the catches of 3.47 (**Table 5**). The total transfer efficiency  
331 reaches 18.2%, which is higher than the average of 10% proposed by Pauly & Christensen (1995) for  
332 aquatic systems, or the 15.7% reported by Tecchio *et al.* (2013), but slightly lower than the value of  
333 19.7% mentioned by B  naru *et al.* (2013).

334

## 335 **3.3. Trophic impact and keystone**

336 The mixed trophic impact matrix (**Figure 4**) shows that the mesozooplankton group plays an important  
337 role in the food web, with a relatively high direct negative impact on its prey (pico, nano and  
338 microzooplankton) and on itself (through competition) and a positive impact on its predators (4 groups  
339 of small pelagic planktonophagous fishes). It also has multiple smaller impacts throughout the food  
340 chain. Both suprabenthic/benthic invertebrates and decapod groups have a widespread impact, being

341 preyed upon by many higher TL groups. This also applies to the four groups of small pelagic fishes, but  
342 with a more limited impact on other vertebrates, since few invertebrates feed on them (except  
343 cephalopods). One can note the negative indirect impact of *E. encrasicolus* on *M. barbatus*, via  
344 promotion of *M. merluccius*, which is a predator of *M. barbatus*. In the same way, detritus has a negative  
345 impact on the microphytobenthos by favoring the sipuncula and the depositivorous molluscs.  
346 Crustivorous fishes 2 have a strong direct negative impact on jellyfish, of which they are the only  
347 predator in this model. Finally, fisheries have a strong negative impact on many fishes at high and  
348 intermediate TL. The highest negative impact is exerted by benthic trawls on *Squalus acanthias*,  
349 *Scyliorhinus canicula* and anglerfish, by nets on *Palinurus elephas* and by long lines on *Prionace*  
350 *glauca*. Overall, the groups with the highest negative impact (summed MTIs) are, in decreasing order,  
351 benthic trawls (-4.1), nets (-2.8) and carnivorous equinoderms (-1.6). On the other hand, the three groups  
352 with the highest accumulated positive impacts are, in decreasing order, detritus (4.7),  
353 microphytoplankton (2.3) and nanoplankton (2.1).

354 Regarding the Valls keystone index (Valls *et al.*, 2015), the three groups with the highest keystone index are  
355 the crustivorous fishes 2, squid and *Conger conger* (**Figure 5**). The plot of the keystone index according  
356 to Power *et al.* (1996) against the relative total impact is also given to allow comparison with the work  
357 of Bănaru *et al.* (2013). This index gives a higher value to species with low biomass. In this case, the  
358 three keystone groups are marine birds, dolphin and *C. conger*.

359

## 360 **4. DISCUSSION**

### 361 **4.1. Exploitation of the GoL**

362 According to Patterson (1992), a value of the exploitation rate ( $E = F / Z$ ) greater than 0.4 leads to a  
363 decline of the stock, i. e. overexploitation. On this basis, according to the GOLEM indices (**Table 4**),  
364 10 groups suffer from overexploitation by fisheries: octopus, *Palinurus elephas*, crustivorous fishes 2,  
365 mullet, *Sparus aurata*, carnivorous demersal fishes, anglerfish, *Dicentrarchus labrax*, *Merluccius*  
366 *merluccius* and *Conger conger*.

367 According to the GFCM stock assessment data available for the period 2010 – 2014  
368 (<https://www.fao.org/gfcm/data/safs>), *M. merluccius* is indeed considered to be overfished. On the  
369 other hand, the low modelled exploitation rate of *Engraulis encrasicolus* and *Sardina pilchardus* (0.06  
370 and 0.03, respectively) is in agreement with the GFCM data which assessed their fishing mortality as  
371 low. This is most likely due to the ecosystem shift of 2008 that resulted in unfavorable environmental  
372 conditions for these two species, leading to low abundance of commercial size fish. This, coupled  
373 with an increase in the biomass of *Sprattus sprattus*, which has a low commercial interest and which  
374 is captured along with *E. encrasicolus* and *S. pilchardus*, has led to a reduction in fishing effort on the  
375 small pelagics. This has also led to the diversification of the fisheries activity towards demersal  
376 species (GFCM stock assessment report for *M. merluccius*, 2013), increasing the fishing mortality of  
377 *M. merluccius*.

378 Although no information is available for the period 2010 – 2014, recent observations (Certain, pers.  
379 comm.) have revealed that anglerfish are also overfished in the GoL area. Given the model results, it  
380 seems reasonable to assume that it was indeed the case during the modelled period and that it could  
381 be a consequence of the diversification of the fisheries activities, as for *M. merluccius*. Overall, these  
382 facts show the consistency of the GOLEM model with the functioning of the GoL ecosystem and its  
383 ability to reflect the consequences of the 2008 shift.

384

## 385 **4.2. Comparison between models**

386 Comparison of Ecopath models is often difficult as many of the indicators produced are structure-  
387 dependent (Pinnegar *et al.*, 2005) and it is rather rare that models share enough traits (especially for area  
388 and species aggregation) to overcome this. However, Heymans *et al.* (2014, 2016) proposed several  
389 indices normalized to the total system throughput (TST, sum of the flows in the system) that are more  
390 robust with regard to the system construction (**Table 5 and 6**). We proposed here a comparison between  
391 6 Ecopath models (Sánchez and Olaso, 2004 (F); Coll *et al.*, 2006 (A), 2007b (D); Tsagarakis *et al.*,  
392 2010 (E); Bănaru *et al.*, 2013 (C)), 5 in the Mediterranean and one from the Cantabrian Sea (N-E  
393 Atlantic).

394 Before dealing with the comparison of the output parameters of these 6 models, as two of them have  
395 been developed on the GoL, a presentation of the differences in the structure of these two models is first  
396 given.

### 397 **4.2.1. Differences between the two GoL models**

398 Bănaru *et al.* (2013) achieved a first representation of the ecosystem of the GoL, giving an overview of  
399 its functioning and the impact of the fisheries. However, the limited availability of the data at that time  
400 did not allow for a good description of certain groups, especially among the invertebrates. The increased  
401 research effort on these species over the last decade, notably in terms of biomass and diet, made possible  
402 the creation of a new model, with a better resolution of functional group, radically changing the structure  
403 of the trophic network.

404 Previously divided into 7 groups, the benthic invertebrates are represented by 22 groups in the present  
405 work. These improvements enable us to better characterize the interactions between important  
406 compartments, such as holothurians and detritivorous worms with detritus. The flows in the system were  
407 consequently impacted, as shown in the Lindeman diagram (**Figure 3**), with a flow from detritus to  
408 trophic level II 2.5 times greater in the present model (606 t km<sup>-2</sup> y<sup>-1</sup>) than in the previous one (265 t  
409 km<sup>-2</sup> y<sup>-1</sup>), the latter being probably underestimated (an influence from the modelled area is also  
410 possible). The additional sharpness in the trophic network description provides better insight into species  
411 interactions, as can be seen in the mixed trophic impact matrix (**Figure 4**). For example, one may note  
412 the strong negative impact exerted on sipuncula and echinids by carnivorous mollusks, not visible on  
413 Bănaru *et al.* (2013) matrix.

414 In addition to the use of recent data, the catches estimate has been improved by the addition of catches  
415 from recreational fishing. Far from being negligible, they represent about 16% of the total estimated  
416 catches, improving the representation of the fisheries activity and its impact on the GoL food web.

417

### 418 **4.2.2. Flow indices, pedigree and omnivory index**

419 One of the most noticeable differences between the GOLEM model and the C model is on the TST. The  
420 higher TST value in GOLEM can be explained by the fact that the model focuses on the continental  
421 shelf (from 0 to 200 m), where most of the biological activity occurs, whereas the Bănaru *et al.* (2013)  
422 model incorporated an additional area (from 0 to 2500 m), mainly characterized by greater depth and  
423 therefore lower biological activity. This results in a dilution of the flows by the modelled area. The larger  
424 number of functional groups in GOLEM may also influence the TST, making explicit the flows that  
425 occurred within previously larger functional groups.

426 The difference in total biomass is also explained by the “dilution” phenomenon. It is further supported  
427 by the fact that the total net primary production (PP) and consumption (Q) calculated by Bănaru *et al.*  
428 (2013) are lower (**Table 5**) while the PP/TST and Q/TST ratios (**Table 6**) are quite similar, highlighting  
429 similarities between the biologically active parts of these two systems.

430 By analyzing the PP/TST, it may be noted that the Mediterranean models have a rather narrow range  
431 of values, between 0.23 and 0.35, which are lower than the Atlantic model (F) (other authors found  
432 similar high values in the Atlantic: 0.41 for Araujo *et al.* (2005); 0.43 for Damsiri *et al.* (2022)). This  
433 range may be even narrower, since the lowest value of model A does not include the 0-50 m zone, where  
434 high primary production often occurs. This rather low range of values of PP/TST may be related to the  
435 oligotrophic nature of the Mediterranean, characterized by low primary production compared to the  
436 Atlantic Ocean (Liénart *et al.*, 2017).

437 Overall, the E model from the North Aegean Sea shows strong similarities with GOLEM for PP/TST,  
438 Q/TST and Ex/TST but lower values for TST and total biomass. This highlights the similarities between  
439 the two systems, although Tsagarakis *et al.* (2010) pointed out differences in productivity between the  
440 western and eastern Mediterranean systems. The low values of TST and total biomass in model E could  
441 be explain by a smaller number of functional groups (40) and the exclusion of the 0 – 20 m zone,  
442 respectively. It is supported by the presence of *Posidonia* meadows in the area, known to have a high  
443 biomass per area (Boudouresque *et al.*, 2006). This resemblance is consistent with the similar nature of  
444 the two modelled areas, i. e. Mediterranean oligotrophic coastal areas, with productivity supported by  
445 large continental shelves and riverine inputs (Tsagarakis *et al.*, 2010). Both areas show sandy to muddy  
446 sediments, however the North Aegean Sea shows more *Posidonia* meadows, their distribution being  
447 limited in the GoL by the freshwater inputs of the Rhone River.

448 The slightly lower pedigree of the GOLEM model compared to model C is likely due to the increased  
449 number of the invertebrate groups for which data on diet, P/B and Q/B are scarce compared to  
450 vertebrates. Yet, it should be kept in mind that the splitting of these groups is a major step towards a  
451 better representation of the GoL ecosystem, made possible by the recent efforts to study invertebrate  
452 biomass.

453 Despite the structural differences, the omnivory index of the GOLEM and Bănaru *et al.* (2013) system  
454 are equal (0.21). Models A, D and E show slightly smaller indexes, and model F shows a less specialized  
455 food web with 0.27. As for PP/TST, the Mediterranean models show a small range of values at rather  
456 low level, compared to the Atlantic one. This is probably related to the oligotrophy of the Mediterranean  
457 food webs.

458

### 459 **4.2.3. Trophic levels and captures**

460 The TLs from GOLEM are in relatively good agreement with the C model, except for a few groups  
461 including cephalopods, lobster, herbivorous fishes, *T. mediterraneus* and *C. conger*. Regarding  
462 herbivorous fishes, the species considered are not exactly the same. For the remaining groups, the main  
463 explanation is the better resolution in the constitution of the functional groups (especially for the  
464 invertebrates) allowing the TL to more accurately reflect the diet.

465 The average trophic level of catches in GOLEM (3.47) is higher than in model A and C (3.12 and 3.24  
466 or 3.35, depending on the fishery scenario, respectively). Even if the structure of the model might have  
467 impacted this value, it is very likely that it reflects the recent collapse in the GoL of sardine fishery (and  
468 anchovy to a lesser extent), species characterized by a low TL. Over the period 2007-2008, *S. pilchardus*  
469 represented 39% of the total catches (Bănaru *et al.*, 2013) against 4.6% over 2010 – 2014 (this study).  
470 Coll *et al.* (2006) reported a similar trend, with sardines being the largest part of the catches in 1994 and  
471 decreasing by 70% in 2003. In addition, concerning the other side of the TL spectra, this work attempted  
472 to achieve a better estimate of the fisheries by integrating corrections accounting for recreational fishing  
473 and IUUs (illegal, unreported and regulated catches). These catches concerned relatively high TL  
474 species (e.g. 3.08 for *S. aurata*, 3.97 for *S. scombrus*, 3.9 for *D. labrax*) which increased the average TL  
475 of the catches.

476 The exports and catches terms in the Lindeman diagrams also reflect these two facts: the sum, although  
477 comparable, is lower in Bănaru *et al.* (2013) (2.11 against 2.39 t km<sup>-2</sup> y<sup>-1</sup> in this study), explained by the  
478 addition of recreational catches and the decrease in landings of small pelagic fishes. It also appears in  
479 the distribution of exports and catches between trophic levels, with a lower value for TL III but higher  
480 for TL IV and V in the present study.

481 Bănaru *et al.* (2013) pointed out that while *E. encrasicaulus* and *S. pilchardus* were the most important  
482 landings, their mortality was mainly due to natural causes (predation and other causes). It seems that  
483 this is still the case in the current model, but their importance in the landings has strongly decreased (see  
484 **section 4.1**).

485 Compared with E model, the average TL of the catches are identical and the total catches are close (2.43  
486 t km<sup>-2</sup> y<sup>-1</sup> for GOLEM against 2.35 for the northern Aegean Sea), adding to the similarities between the  
487 two systems.

488

### 489 **4.3. System maturity and keystone**

490 Based on Christensen (1995) and the ecosystem maturity theory of Odum (1969), a comparison of  
491 attributes between the GOLEM model and the C model is proposed in **Table 7**. Odum defined two  
492 stages of ecosystem maturity: young, associated with high production, growth and quantity, and  
493 mature, characterized by stability and quality over quantity. Christensen retained 12 of the 24 Odum  
494 attributes and, for simplicity, we retained 7 of them, for which Christensen (1995) did not find a  
495 correlation with the number of groups in the models.

496 Five of them (in bold, **Table 7**) indicate the C model is the most mature ecosystem, according to  
497 Odum's theory. As the latter was qualified by Bănaru *et al.* (2013) as "at a rather low development  
498 stage", the current GoL ecosystem appears at an even lower stage. The difference in the modelled  
499 domains (down to 2500 m depth; GOLEM: 200 m depth) seems an unlikely explanation as the  
500 majority of the biological activity occurs on the continental shelf (0-200 m). This decrease in the  
501 maturity of the ecosystem could be explained by a general degradation of the system and/or as one of  
502 the consequences of the 2008 shift. For example, the B/P attribute is an index for the average size of  
503 the organisms and a decrease in the size of sardine, anchovy and sprat has been indeed noted in the  
504 GoL during this period (Van Beveren *et al.*, 2014; Saraux *et al.*, 2019).

505 The 3 species/groups with the highest KS, according to the Valls index are, in decreasing order, squids,  
506 *C. conger* and cuttlefish. Crustivorous fishes 2 are in the top 3 keystone species with the index of Valls  
507 *et al.* (2015) and are in fourth position with the index of Power *et al.* (1995), its mixed trophic impact  
508 (MTI) being high enough to compensate for the advantage given to low biomass by the Power index.  
509 **Figure 4** shows, that this group MTI comes mainly from its impact on jellyfish, which have a very low  
510 biomass and of which crustivorous fishes 2 are the only predators. Thus, the MTI of this group is  
511 probably overestimated.

512

## 513 **5. CONCLUSION**

514

515 Ecopath models are a widely-used solution to address various challenges such as fisheries management  
516 or ecosystem characterization. Nevertheless, in order to track the ongoing evolution of the environment  
517 (climate change, anthropic pressures, etc.) and to better face these challenges, they should be regularly  
518 enhanced.

519 In this work, we built a new model of the GoL based on the most recent data for diet, biomass  
520 (integrating the shift observed in the GoL around 2008), P/B and Q/B, improved resolution of functional  
521 groups and fisheries corrections. This represents a new step towards a better representation and  
522 understanding of the GoL ecosystem.

523 Key results include:

524 - a diagram of the trophic network on five trophic levels, with *Prionace glauca*, dolphin and *Squalus*  
525 *acanthias* the 3 top predators. They differ from earlier studies because *P. glauca* and *S. acanthias* were  
526 not included previously.

527 - various functional traits of the trophic network, such as the most consumed and the most consuming  
528 groups, the omnivory index of the system and the distribution of fluxes between trophic levels. Squid,  
529 *C. conger* and cuttlefish are given as keystone species according to the most recent index.

530 - a mixed trophic impact matrix allowing to understand the impact of each group on the rest of the  
531 network and highlighting the negative impact of fisheries on fished groups, in particular benthic trawls  
532 on *S. acanthias*, *S. canicula* and anglerfish, nets on *P. elephas* and long lines on *P. glauca*.

533 Despite the existing difficulties to compare models with different structures, the comparison between  
534 different Mediterranean models #highlights some similarities, such as the narrow range of PP/TST or  
535 the omnivory index. The North Aegean Sea model and GOLEM seem to have strong similarities,  
536 explained by the resemblance between their modelled areas and ecosystems.

537 Finally, this study provides both insights for a better understanding of the local ecosystem and a basic  
538 tool for potential management initiatives.

539 The project of which the present work is a part aims to take advantage of this new Ecopath model, in  
540 particular the representation of invertebrates and their interaction with the detritus compartment, in order  
541 to build a complete spatialized and dynamic model able to track the fate of radionuclides and other  
542 contaminants in the environment.

543

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563

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## Table des figures et tableaux

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- 794 • **Figure 1** Location and bathymetry of the study area in the Gulf of Lion north-western  
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- 796 • **Table 1** Description of the functional groups of GOLEM model.
- 797 • **Table 2** Input parameters of the GOLEM model by functional group:  $B_i$  = initial estimated  
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- 800 • **Table 3** Diet composition matrix of the GOLEM model.
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802 the model are indicated in bold. TL = trophic level,  $B_f$  = final biomass ( $t\ km^{-2}$ ),  $EE$  =  
803 ecotrophic efficiency,  $F$  = fishing mortality ( $y^{-1}$ ),  $M_2$  = predation mortality ( $y^{-1}$ ),  $M_0$  =  
804 natural mortality ( $y^{-1}$ ),  $F/Z$  = exploitation rate,  $Q$  = consumption ( $t\ km^{-2}\ y^{-1}$ ),  $FD$  = flow to  
805 detritus ( $t\ km^{-2}\ y^{-1}$ ),  $P/Q$  = production/consumption,  $NE$  = net efficiency,  $OI$  = Omnivory  
806 Index.
- 807 • **Figure 2** Trophic diagram of the GOLEM model. The ordinate axis represents the trophic  
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820 = primary production,  $Q$  = consumption
- 821 • **Table 7** Odum's attributes (1969) as calculated by Christensen (1995). For each attribute,  
822 values in bold indicate the most mature model.  $PP/R$  = total primary production/total  
823 respiration,  $PP/B$  = total primary production/total biomass (\*excluding detritus),  $B/TST$  =  
824 biomass (\*)/total throughput, total respiration/total biomass(\*),  $B/P$  = total biomass(\*)/ total  
825 production,  $B/(R+Exp)$  = total biomass/(total respiration+total export)

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**Table 1** Description of the functional groups GOLEM model.

Functional group	Species/groups included
1 Picoplankton	Cyanobacteria, autotrophic and heterotrophic pico-eucaryotes
2 Nanoplankton	Bacteria, protist, autotrophic and heterotrophic nano-eucaryotes
3 Microphytoplankton	Diatoms, dinobionts
4 Microphytobenthos	spp.
5 Posidonia	<i>Posidonia oceanica</i>
6 Benthic macrophytes and epibionts	spp.
7 Microzooplankton	Eggs and nauplii of copepods, small cladocerans, pteropods, euphausiids, and mysids
8 Mesozooplankton	Copepods, cladocerans, pteropods, euphausiids, mysids, amphipods, ostracods, fish and invertebrate eggs and larvae
9 Macrozooplankton	Krill, fish and invertebrate eggs and larvae, pteropods, euphausiids, mysids, amphipods and non-jellyfish gelatinous zooplankton
10 Jellyfishes	35.9% <i>Pelgia noctiluca</i> , 64.4% <i>Rhizostoma pulmo</i>
11 Cnidarians	13.6% <i>Pteroeides spinosum</i> , 34.9% <i>Veretillum</i> spp, 6.3% <i>Funiculina quadrangularis</i> , 31% Alcyoniidae, 2.3% <i>Nemertesia antennina</i> , 4.5% <i>Nemertesia ramosa</i> , 7.3% Actinaria ( <i>Adamsia palliata</i> , <i>Calliactis parasitica</i> )
12 Sessile suspension feeders	Bryozoa, Tunicata and Porifera
13 Depositivorous molluscs	<i>Cerastoderma edule</i> , <i>Ruditapes</i> spp, <i>Calliostoma granulatum</i> , <i>Littorina littorea</i> , <i>Tritia mutabilis</i> , <i>Turritella communis</i>
14 Filter feeder molluscs	<i>Atrina pectinata</i> , <i>Acanthocardia echinata</i> , <i>Glossus humanus</i> , <i>Mytilus galloprovincialis</i> , Ostreidae, <i>Tellina</i> spp
15 Carnivorous Molluscs	<i>Bolinus brandaris</i> , <i>Buccinum undatum</i> , <i>Galeodea echinophora</i> , <i>Galeodea rugosa</i> , <i>Scaphander lignarius</i>
16 Octopuses	51.3% <i>Octopus vulgaris</i> , 2.2% <i>Octopus salutii</i> , 35.4% <i>Eledone cirrhosa</i> , 11.1% <i>Eledone moschata</i>
17 Cuttlefishes	32.6% <i>Sepia officinalis</i> , 8.3% <i>Sepia elegans</i> , 50.3% <i>Sepia orbignyana</i> , 8.8% <i>Sepietta oweniana</i>
18 Squids	10.3% <i>Alloteuthis</i> spp, 58.3% <i>Illex coindetii</i> , 20.5% <i>Loligo</i> spp, 10.9% <i>Todaropsis eblanae</i>
19 Detritivorous worms	Maldanidae, enteropneusta
20 Filter feeding worms	<i>Serpula</i> spp.
21 Carnivorous worms	<i>Aphrodita aculeata</i> , nemerteans
22 Sipuncula	spp.
23 Suprabenthic and benthic crustaceans	Mysids, amphipods, isopods, cumaceans, benthic copepods, euphausiids,
24 Pagurids	10.5% <i>Pagurus excavatus</i> , 71.3% <i>Pagurus prideaux</i> , 18.2% <i>Dardanus arrosor</i>
25 Shrimps - decapods	<i>Natantia</i> , <i>Palaemon serratus</i> , <i>Parapenaeus longirostris</i>
26 Other Malacostraca	46.6% <i>Squilla mantis</i> , 53.4% <i>Nephrops norvegicus</i>
27 Brachyurids	<i>Carcinus aestuarii</i> , <i>Liocarcinus depurator</i> , <i>Macropipus tuberculatus</i> , <i>Medorippe lanata</i> , <i>Necora puber</i>
28 Palinurus elephas	
29 Homarus gammarus	
30 Filter feeder echinoderms	<1% <i>Ophiolithrix</i> spp, 7.7% <i>Antedon</i> spp, 88.6% <i>Leptometra</i> spp, 3.7% <i>Ocnus planci</i>
31 Carnivorous echinoderms	38.4% <i>Anseropoda placenta</i> , 39.2% <i>Astropecten irregularis pentacanthus</i> , 16.4% <i>Echinaster sepositus</i> , 5.9% <i>Ophiura ophiura</i>
32 Holothurians	18.8% <i>Leptopentacta elongata</i> , 81.2% <i>Parastichopus regalis</i>
33 Echinids	<1% <i>Brissopsis lyrifera</i> , 7.1% <i>Cidaris cidaris</i> , 9.8% <i>Gracilechinus acutus</i> , 81.3% <i>Paracentrotus lividus</i> , 1.7% <i>Spatangus purpureus</i>
34 Herbivorous fishes	99% <i>Sarpa salpa</i> , 1% <i>Diplodus annularis</i>
35 Sardina pilchardus	
36 Engraulis encrasicolus	
37 Sprattus sprattus	
38 Planctonophagous pelagic	63.4% <i>Sardinella aurita</i> , 3.2% <i>Spicara smari</i> , 33.3% Atherinidae
39 Planctonophagous demersal	1.7% <i>Spicara flexuosa</i> , 5.2% <i>Cepala macrophtalma</i> , 21.3% <i>Boops boop</i> , 1.2% <i>Argentina sphyraena</i> , 1.7% <i>Micromesistius poutassou</i> , 68.9% <i>Scomber colias</i>
40 Invertivorous fishes	42.3% <i>Trisopterus capelanus</i> , <1% <i>Trisopterus luscus</i> , 1.4% <i>Gobius niger</i> , 36.1% <i>Diplodus cervinus</i> , <1% <i>Blennius ocellaris</i> , 5.8% <i>Lepidotrigla cavillone</i> , 1.6% <i>Lepidotrigla dieuzeidei</i> , 1% <i>Scorpeana notata</i> , 4.1% <i>Lepidorhombus boscii</i> , 7% <i>Serranus hepatus</i>
41 Crustivorous fishes 1	7.2% <i>Chelidonichthys lucerna</i> , 8.5% <i>Trachinus draco</i> , 67.6% <i>Eutrigla gurnadus</i> , 16.8% <i>Serranus cabrilla</i>
42 Crustivorous fishes 2	8.6% <i>Trigla lyra</i> , 12.7% <i>Mullus surmuletus</i> , 21.8% <i>Chelidonichthys cuculus</i> , 2% <i>Phycis blennoides</i> , 27.2% <i>Pagellus acarne</i> , 17.9% <i>Pagellus erythrinus</i> , 4.4% <i>Spondyliosoma cantharus</i> , 3.8% <i>Capros aper</i> , 1.5% <i>Macroramphosus scolopax</i>
43 Wormivorous fishes	1% <i>Deltentosteus quadrimaculatus</i> , <1% <i>Lesueurigobius friesii</i> , <1% <i>Callionymus maculatus</i> , 98.6% <i>Diplodus sargus</i>
44 Mulets	25% <i>Mugil cephalus</i> , <1% <i>Liza aurata</i> , <1% <i>Liza ramda</i> , <1% <i>Oedalechilus labeo</i> , 74.8% <i>Chelon labrosus</i>
45 Lagoon flat fish	13.4% <i>Microchirus variegatus</i> , 53.2% <i>Solea solea</i> , 33.3% <i>Pegusa lascaris</i>
46 Scomber scombrus	
47 Trachurus mediterraneus	
48 Trachurus trachurus	
49 Mullus barbatus	
50 Sparus aurata	
51 Diplodus vulgaris	
52 Coris julis	
53 Carnivorous demersal fishes 1	6.25% <i>Seriola dumerili</i> , <1% <i>Dentex dentex</i> , 4.9% <i>Scorpeana scrofa</i> , 2.5% <i>Scorpeana elongata</i> , 8.7% <i>Uranoscopus scaber</i> , 3% <i>Torpedo marmorata</i> , 14.9% <i>Torpedo nobiliana</i> , 6.25% Muraenidae, 6.7% <i>Pagellus bogaraveo</i> , 1.6% <i>Pagrus pagrus</i> , 6.25% <i>Limanda limanda</i> , 6.25% <i>Lithognathus mormyrus</i> , 8.4% <i>Scopthalmus maximus</i> , 3.8% <i>Scopthalmus rhombus</i> , 13.8% <i>Zeus faber</i> , 6.25% <i>Sarda sarda</i>
54 Piscivorous flat fishes	2% <i>Lepidorhombus whiffiagonis</i> , 26.8% <i>Arnoglossus laterna</i> , 71.2% <i>Citharus linguatula</i>
55 Piscivorous fishes	<i>Sphyraena</i> spp., <i>Xiphias gladius</i> , <i>Lepidopus caudatus</i>
56 Thunas	<i>Thunnus thynnus</i> , <i>Thunnus alalunga</i> , <i>Katsuwonus pelamis</i>
57 Anglerfish	64.3% <i>Lophius budegassa</i> , 35.7% <i>Lophius piscatorius</i>
58 Dicentrarchus labrax	
59 Merluccius merluccius	
60 Conger conger	
61 Squalus acanthias	
62 Scyliorhinus canicula	
63 Prionace glauca	
64 Rays	16.7% <i>Leucoraja naevus</i> , 29.6% <i>Pteroplatytrigon violacea</i> , 8% <i>Raja asterias</i> , 26.4% <i>Raja clavata</i> , 2.6% <i>Raja montagui</i> , 16.7% <i>Rostroraja alba</i>
65 Dolphins	<i>Tursiops truncatus</i>
66 Sea birds	<i>Larus michaellis</i> , <i>Calonectris diomedea diomedea</i> , <i>Puffinus yelkouan yelkouan</i> , <i>Puffinus yelkouan mauretanicus</i> , <i>Sterna hirundo</i> , <i>Morus bassanus</i>

830 Table 2 Input parameters of the GOLEM model by functional group:  $B_i$  =initial estimated biomass,  $P/B$   
831 = production/biomass,  $Q/B$  = consumption/biomass,  $EE$  = ecotrophic efficiency,  $U/Q$  = unassimilated  
832 food/consumption.

	Functionnal groups	Bi (t km-2)	(t P/B (y-1))	Q/B (y-1)	EE	U/Q	Total landings (t km-1 y-1)
1	Picoplankton	3,537	200			0	0
2	Nanoplankton	6,026	97,29			0	0
3	Microphytoplankton	3,537	84,29			0	0
4	Microphytobenthos	0,742	100			0	0
5	Posidonia	4,819	1,18			0	0
6	Benthic macrophytes and epibionts	3,24	12,46			0	0
7	Microzooplankton	0,76	120	145,00		0,4	0
8	Mesozooplankton	9,07	39	80,00		0,4	0
9	Macrozooplankton	2,25	18	38,00		0,2	0
10	Jellyfishes	0,0002	14,6	50,48		0,2	0
11	Cnidarians	1,966	0,13	15,37		0,2	0
12	Sessile suspension feeders	0,048	3,20	3,80		0,2	9,34E-04
13	Depositivorous molluscs	0,851	7,00	31,28		0,2	0,03
14	Filter feeder molluscs	3,103	7,90	16,74		0,4	0,16
15	Carnivorous Molluscs	0,24	5,30	19,21		0,2	0,02
16	Octopuses	0,083	2,01	8,07		0,2	0,18
17	Cuttlefishes	0,011	2,70	13,21		0,2	0,01
18	Squids	0,032	2,96	14,20		0,2	0,04
19	Detritivorous worms	7,519	10,83	18,75		0,4	3,91E-05
20	Filter feeding worms	0,873	35,99	32,52		0,3	4,50E-06
21	Carnivorous worms	2,865	3,85	14,20		0,2	1,49E-05
22	Sipuncula	1,136	0,13	4,30		0,6	0
23	Suprabenthic and benthic crustaceans	1,559	11	25,00		0,3	0
24	Pagurids	0,061	1,82	16,09		0,3	2,51E-04
25	Shrimps - decapods	0,001	9,80	11,00		0,2	7,89E-04
26	Other Malacostraca	0,005	2,92	12,18		0,3	5,23E-03
27	Brachyurids	0,008	2,87	16,59		0,3	2,62E-03
28	Palinurus elephas	0,001	1,79	6,31		0,2	6,99E-04
29	Homarus gammarus	0,001	1,78	5,70		0,2	3,74E-04
30	Filter feeder echinoderms	0,304	3,69	28,06		0,2	0
31	Carnivorous echinoderms	0,515	3,18	18,04		0,2	0
32	Holothurians	0,139	1,58	15,61		0,3	4,33E-05
33	Echinids	1,906	2,40	11,80		0,2	2,23E-02
34	Herbivorous fishes	0,262	1,45	22,14		0,3	0,08
35	Sardina pilchardus	5,039	0,95	9,94		0,3	0,12
36	Engraulis encrasicolus	2,724	1,12	8,24		0,3	0,20
37	Sprattus sprattus	3,578	0,68	11,88		0,3	1,19E-06
38	Planctonophagous pelagic fishes	0,029	0,95	7,41		0,3	0,01
39	Planctonophagous demersal fishes	0,219	0,94	6,09		0,3	0,10
40	Invertivorous fishes	0,146	0,91	8,03		0,2	0,16
41	Crustivorous fishes 1	0,049	0,53	5,33		0,2	0,03
42	Crustivorous fishes 2	0,117	1,16	6,52		0,2	0,11
43	Wormivorous fishes	0,042	1,05	11,05		0,2	0,03
44	Mulets	0,278	0,50	3,68		0,2	0,16
45	Lagoon flat fish	0,057	1,04	5,29		0,2	0,06
46	Scomber scombrus	0,227	1,29	7,29		0,2	0,16
47	Trachurus mediterraneus	0,531	0,64	6,24		0,2	0,00
48	Trachurus trachurus	0,698	0,55	7,37		0,2	0,05
49	Mullus barbatus	0,095	0,98	5,89		0,2	0,03
50	Sparus aurata	0,169	1,00	4,90		0,2	0,39
51	Diplodus vulgaris	0,008	1,16	11,00		0,2	0,01
52	Coris julis	0,101	0,40	6,58		0,2	0,01
53	Carnivorous demersal fishes	0,095	0,59	3,50		0,2	0,09
54	Piscivorous flat fishes	0,013	0,49	6,68		0,2	0,01
55	Piscivorous fishes	0,324	0,27	3,49		0,2	0,01
56	Thunas	0,657	0,17	3,27		0,2	0,02
57	Anglerfish	0,070	0,69	5,70		0,2	0,07
58	Dicentrachus labrax	0,118	1,13	3,54		0,2	0,21
59	Merluccius merluccius	0,376	0,94	3,07		0,2	0,21
60	Conger conger	0,007	0,91	4,15		0,2	0,04
61	Squalus acanthias	0,006	0,25	2,88		0,2	9,65E-05
62	Scyliorhinus canicula	0,045	0,46	3,87		0,2	2,64E-03
63	Prionace glauca		0,30	2,80	0,1	0,2	6,22E-04
64	Rays	0,140	0,48	3,12		0,2	0,01
65	Dolphins	0,008	0,02	6,12		0,2	0
66	Marine birds	0,003	0,60	66,00		0,2	0
67	Discards	0,298				0,2	0
68	Detritus	64,700				0	0



836 Table 4 Main output parameters of the GOLEM model. Biomass parameters estimated by the model  
 837 are indicated by bold characters. TL = trophic level, Bf = final biomass (t km<sup>-2</sup>), EE = ecotrophic  
 838 efficiency, F = fishing mortality (y<sup>-1</sup>), M2 = predation mortality (y<sup>-1</sup>), M0 = natural mortality (y<sup>-1</sup>),  
 839 F/Z = exploitation rate, Q = consumption (t km<sup>-2</sup> y<sup>-1</sup>), FD = flow to detritus (t km<sup>-2</sup> y<sup>-1</sup>), P/Q =  
 840 production/consumption, NE = net efficiency, OI = Omnivory Index.

Functional group	TL	Bf	Bf/B0	EE	F	M2	M0	F/Z	Q	FD	P/Q	NE	OI
1 Picoplankton	1,00	3,54	1,00	0,70	0	139,08	60,92	0,00		215,48			0
2 Nanoplankton	1,00	6,03	1,00	0,99	0	166,85	1,69	0,00		10,16			0
3 Microphytoplankton	1,00	3,54	1,00	0,76	0	63,669	20,62	0,00		72,94			0
4 Microphytobenthos	1,00	0,74	1,00	0,88	0	87,931	12,07	0,00		8,96			0
5 Posidonia	1,00	4,82	1,00	0,89	0	1,046	0,13	0,00		0,65			0
6 Benthic macrophytes and	1,00	3,24	1,00	0,99	0	12,294	0,17	0,00		0,54			0
7 Microzooplankton	2,00	<b>0,90</b>	1,18	0,99	0,00	118,84	1,16	0,00	359,60	141,29	0,30	0,49	0
8 Mesozooplankton	2,05	9,07	1,00	0,50	0,00	19,41	19,59	0,00	1179,10	637,55	0,30	0,49	0,05
9 Macrozooplankton	2,72	2,25	1,00	0,46	0,00	8,26	9,74	0,00	135,00	48,91	0,30	0,38	0,22
10 Jellyfishes	2,82	0,00	1,00	0,30	0,00	4,41	10,19	0,00	0,01	0,00	0,29	0,36	0,53
11 Cnidarians	2,45	2,49	1,26	1,00	0,00	4,50	0,00	0,00	38,19	7,65	0,29	0,37	0,28
12 Sessile suspension feeders	2,05	<b>3,64</b>	75,77	0,98	0,00	3,12	0,08	0,00	38,92	8,07	0,30	0,37	0,04
13 Depositivorous molluscs	2,00	<b>5,08</b>	5,97	0,95	0,01	6,65	0,35	0,00	158,91	33,56	0,22	0,28	0,00
14 Filter feeder molluscs	2,05	<b>3,42</b>	1,10	1,00	0,05	7,83	0,02	0,01	90,50	36,28	0,30	0,50	0,05
15 Carnivorous Molluscs	3,02	<b>1,69</b>	7,02	0,99	0,01	5,23	0,05	0,00	32,38	6,56	0,28	0,34	0,18
16 Octopuses	4,22	<b>0,15</b>	1,85	1,00	1,17	0,84	0,00	0,58	1,24	0,25	0,25	0,31	0,10
17 Cuttlefishes	4,22	<b>0,30</b>	26,04	1,00	0,04	3,74	0,02	0,01	3,95	0,79	0,29	0,36	0,16
18 Squids	4,29	<b>0,24</b>	7,63	1,00	0,15	2,80	0,01	0,05	3,46	0,69	0,21	0,26	0,18
19 Detritivorous worms	2,00	7,52	1,00	0,78	0,00	8,44	2,39	0,00	270,68	123,52	0,30	0,49	0,00
20 Filter feeding worms	2,00	0,87	1,00	0,55	0,00	5,54	4,46	0,00	29,68	12,79	0,29	0,42	0,00
21 Carnivorous worms	3,11	2,87	1,00	1,00	0,00	5,55	0,01	0,00	54,45	10,92	0,29	0,37	0,09
22 Sipuncula	2,00	1,14	1,00	0,95	0,00	0,45	0,02	0,00	4,88	2,96	0,11	0,27	0,00
23 Suprabenthic and benthic c	2,06	<b>4,63</b>	2,97	0,97	0,00	14,62	0,38	0,00	236,27	72,63	0,29	0,42	0,08
24 Pagurids	2,90	0,06	1,00	0,98	0,00	4,89	0,11	0,00	1,04	0,32	0,29	0,42	0,33
25 Shrimps - decapods	3,20	2,27	2493,39	1,00	0,00	9,79	0,01	0,00	74,94	15,00	0,30	0,37	0,27
26 Other Malacostraca	3,63	<b>0,05</b>	9,51	0,97	0,11	2,71	0,10	0,04	0,60	0,18	0,24	0,34	0,78
27 Brachyurids	3,32	<b>2,12</b>	271,77	1,00	0,00	4,20	0,00	0,00	35,16	10,55	0,25	0,36	0,59
28 Palinurus elephas	3,22	0,00	1,00	0,56	1,00	0,00	0,79	0,56	0,00	0,00	0,28	0,36	0,35
29 Homarus gammarus	3,13	0,00	1,00	0,27	0,44	0,05	1,30	0,25	0,00	0,00	0,30	0,37	0,88
30 Filter feeder echinoderms	2,02	0,30	1,00	0,95	0,00	4,71	0,25	0,00	8,52	1,78	0,18	0,22	0,02
31 Carnivorous echinoderms	3,26	<b>2,47</b>	4,80	1,00	0,00	5,30	0,00	0,00	44,62	8,93	0,29	0,37	0,26
32 Holothurians	2,00	0,14	1,00	0,73	0,00	1,16	0,42	0,00	2,17	0,71	0,10	0,14	0,00
33 Echinids	2,07	<b>4,21</b>	2,21	1,00	0,01	3,53	0,00	0,00	49,62	9,93	0,30	0,38	0,09
34 Herbivorous fishes	2,00	0,26	1,00	0,19	0,20	0,08	1,17	0,14	5,79	2,04	0,07	0,09	0,00
35 Sardina pilchardus	2,95	5,04	1,00	0,71	0,03	0,65	0,28	0,03	50,08	16,43	0,10	0,14	0,11
36 Engraulis encrasicolus	3,15	2,72	1,00	0,95	0,08	1,22	0,06845116	0,06	22,43	6,92	0,17	0,24	0,06
37 Sprattus sprattus	3,10	3,58	1,00	0,95	0,00	0,90	0,05	0,00	42,51	12,92	0,08	0,11	0,03
38 Planctonophagous pelagic	3,08	<b>0,33</b>	11,42	0,95	0,04	0,86	0,05	0,04	2,44	0,75	0,13	0,18	0,09
39 Planctonophagous demersal	3,61	<b>0,87</b>	3,96	0,98	0,08	0,83	0,02	0,09	5,29	1,61	0,15	0,22	0,37
40 Invertivorous fishes	3,97	<b>1,96</b>	13,46	1,00	0,05	0,86	0,00	0,05	15,75	3,15	0,11	0,14	0,41
41 Crustivorous fishes 1	4,13	<b>0,45</b>	9,27	0,99	0,01	0,68	0,00	0,02	2,41	0,48	0,13	0,16	0,46
42 Crustivorous fishes 2	3,38	0,12	1,00	0,95	0,73	0,71	0,08	0,48	0,76	0,16	0,23	0,29	0,32
43 Wormivorous fishes	3,19	<b>3,58</b>	85,57	0,95	0,01	1,42	0,07	0,01	39,54	8,18	0,14	0,17	0,29
44 Mulets	2,50	0,28	1,00	0,88	0,38	0,06	0,06	0,76	1,02	0,22	0,14	0,17	0,42
45 Lagoon flat fish	3,29	<b>0,15</b>	2,60	0,95	0,38	0,61	0,05	0,36	0,78	0,16	0,20	0,25	0,77
46 Scomber scombrus	3,97	<b>0,23</b>	1,00	0,52	0,49	0,19	0,62	0,38	1,65	0,47	0,18	0,22	0,05
47 Trachurus mediterraneus	3,68	0,53	1,00	0,08	0,00	0,05	0,59	0,00	3,31	0,97	0,10	0,13	0,25
48 Trachurus trachurus	3,83	0,70	1,00	0,73	0,07	0,33	0,15	0,13	5,14	1,13	0,07	0,09	0,05
49 Mullus barbatus	3,57	0,10	1,00	0,95	0,36	1,15	0,08	0,23	0,56	0,12	0,27	0,34	0,37
50 Sparus aurata	3,08	<b>0,33</b>	1,92	0,95	0,94	0,01	0,05	0,94	1,59	0,33	0,20	0,26	0,56
51 Diplodus vulgaris	3,21	<b>0,03</b>	3,87	0,96	0,15	0,96	0,04	0,13	0,35	0,07	0,11	0,13	0,10
52 Coris julis	3,58	0,10	1,00	0,96	0,08	0,31	0,02	0,19	0,66	0,13	0,06	0,08	0,23
53 Carnivorous demersal fishes	4,32	<b>0,12</b>	1,29	0,95	0,60	0,40	0,05	0,57	0,43	0,09	0,30	0,37	0,44
54 Piscivorous flat fishes	4,33	<b>1,02</b>	75,88	0,84	0,01	0,54	0,10	0,01	6,79	1,46	0,10	0,12	0,12
55 Piscivorous fishes	4,28	0,32	1,00	0,36	0,02	0,07	0,17	0,09	1,13	0,28	0,08	0,10	0,24
56 Thunas	4,19	0,66	1,00	0,18	0,03	0,00	0,14	0,18	2,15	0,52	0,05	0,06	0,29
57 Anglerfish	4,77	0,07	1,00	0,95	1,07	0,00	0,06	0,95	0,40	0,08	0,20	0,25	0,19
58 Dicentrarchus labrax	3,91	<b>0,14</b>	1,15	0,95	1,08	0,01	0,05	0,95	0,53	0,11	0,29	0,36	1,13
59 Merluccius merluccius	4,19	0,38	1,00	0,89	0,55	0,28	0,11	0,59	1,18	0,28	0,30	0,37	0,05
60 Conger conger	4,42	<b>0,08</b>	11,78	0,96	0,50	0,38	0,04	0,55	0,33	0,07	0,22	0,27	0,32
61 Squalus acanthias	4,95	0,01	1,00	0,19	0,05	0,00	0,20	0,19	0,02	0,00	0,09	0,11	0,14
62 Scyliorhinus canicula	4,34	0,04	1,00	0,13	0,06	0,00	0,40	0,13	0,17	0,05	0,12	0,15	0,07
63 Prionace glauca	5,19	0,02	NA	0,10	0,03	0,00	0,27	0,10	0,06	0,02	0,11	0,13	0,09
64 Rays	4,43	0,14	1,00	0,14	0,07	0,00	0,41	0,14	0,44	0,14	0,15	0,19	0,31
65 Dolphins	4,95	0,01	1,00	0,00	0,00	0,00	0,02	0,00	0,05	0,01	0,00	0,00	0,19
66 Sea birds	3,84	0,00	1,00	0,00	0,00	0,00	0,60	0,00	0,20	0,04	0,01	0,01	1,55
67 Discards	1,00	0,30	1,00	0,98					0	0,00		0	0
68 Detritus	1,00	64,70	1,00	0,37					1559,99	0,00		0	0,32

841

842 Table 5 Ecological indicators related to community energetics, structure, flows and information  
 843 theory.

	Value	Units
<i>Statistics and flows</i>		
Sum of all consumption	3069,81	t km <sup>-2</sup> y <sup>-1</sup>
Sum of all exports	1053,91	t km <sup>-2</sup> y <sup>-1</sup>
Sum of all respiratory flows	1187,96	t km <sup>-2</sup> y <sup>-1</sup>
Sum of all flows into detritus	1658,06	t km <sup>-2</sup> y <sup>-1</sup>
Total system throughput	6969,74	t km <sup>-2</sup> y <sup>-1</sup>
Sum of all production	3002,08	t km <sup>-2</sup> y <sup>-1</sup>
Mean trophic level of the catch	3,47	
Gross efficiency (catch/net p.p.)	0,001	
Calculated total net primary production	2141,38	t km <sup>-2</sup> y <sup>-1</sup>
Total primary production/total respiration	1,80	
Net system production	953,42	t km <sup>-2</sup> y <sup>-1</sup>
Total primary production/total biomass	20,57	
Total biomass/total throughput	0,01	t km <sup>-2</sup> y <sup>-1</sup>
Total biomass (excluding detritus)	104,11	t km <sup>-2</sup>
Total catch	2,43	t km <sup>-2</sup> y <sup>-1</sup>
Connectance Index	0,16	
System Omnivory Index	0,21	
Ecopath pedigree	0,64	
Measure of fit. t*	6,63	
Shannon diversity index	3,46	
<i>Network flow indices</i>		
Throughput cycled (excluding detritus)	15,8	t km <sup>-2</sup> y <sup>-1</sup>
Predatory cycling index	0,432	% of throughput without detritus
Throughput cycled (including detritus)	312,4	t km <sup>-2</sup> y <sup>-1</sup>
Finn's cycling index	4,48	% of total throughput
Finn's mean path length	3,11	
<i>Information indices</i>		
Ascendency	28,79	%
Overhead	71,21	%
Capacity (total)	38073	Flowbits

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847 Table 6 Comparison between GOLEM model and models from the literature based on total  
 848 throughput (TST) normalized parameters (Heymans, 2014) and three other useful indices. PP =  
 849 primary production, Q = consumption

	Area	modelled period	n° of functional groups	PP / TST	Q / TST	Export / TST	TST (t/Km <sup>2</sup> /y)	Total biomass (excluding detritus, t/Km <sup>2</sup> )	Modelled area (Km <sup>2</sup> )	Depth range (m)	Omnivory index	Reference
A	Catalan Sea (N-W Mediterranean)	1994	40	0,23	0,51	0,04	1657	58,99	4500	50 - 400	0,19	Coll et al (2006)
B	Gulf of Lion	2010-2014	68	0,31	0,44	0,15	6969,74	104,11	12172	0 - 200	0,21	GOLEM
C	Gulf of Lion	2000-2009	40	0,35	0,49	0,08	2995	68,9	20403	0 - 2500	0,21	Banaru (2013)
D	Adriatic Sea (central Mediterranean)	1990s	40	0,3	0,34	0,19	3844	130,3	55500	10 - 230	0,19	Coll et al (2007)
E	Aegean Sea (N-E Mediterranean)	2003-2006	40	0,27	0,44	0,14	1976	33,04	8374	20 - 300	0,18	Tsagarakis et al (2010)
F	Cantabrian Sea (N-E Atlantic)	1994	28	0,48	0,24	0,31	10143	174,86	16000	NS	0,27	Sanchez & Olaso (2004)

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852 Table 7 Odum's attributes (1969) as calculated by Christensen (1995). For each attribute, values in  
 853 bold indicate the most mature model. PP/R = total primary production/total respiration, PP/B = total  
 854 primary production/total biomass (\*excluding detritus), B/TST = biomass (\*)/total throughput, total  
 855 respiration/total biomass(\*), B/P = total biomass(\*)/ total production, B/(R+Exp) = total  
 856 biomass/(total respiration+total export)

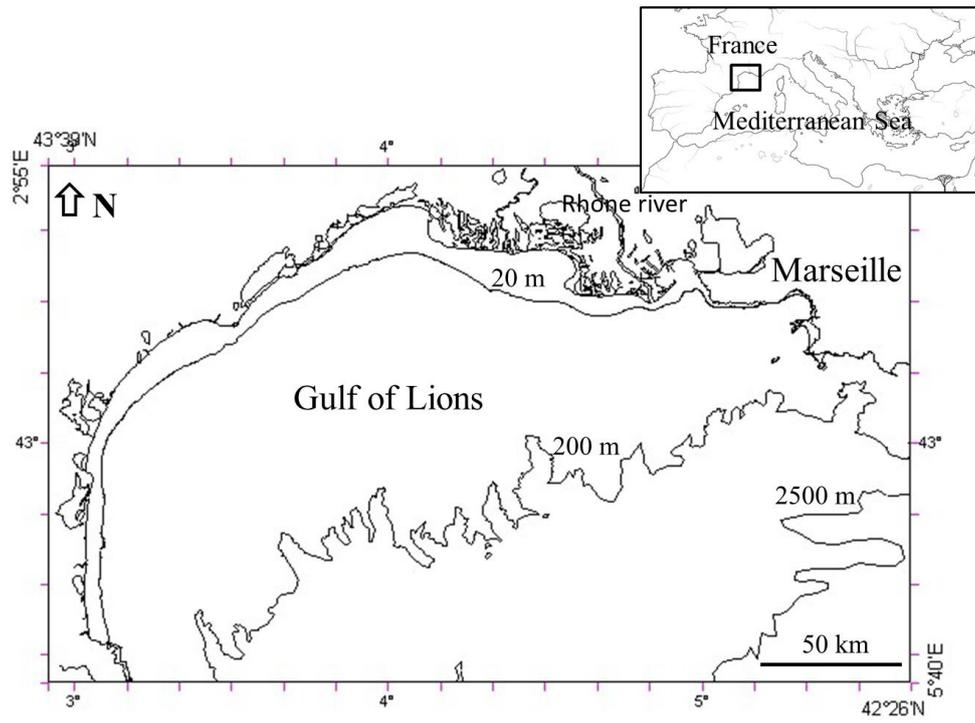
	PP/R	PP/B	B/TST	R/B	B/P	Residence time of energy B/(R+Exp)	Finn's mean path length	Connectance Index	System Omnivory Index
GOLEM	<b>1,8</b>	20,57	0,015	<b>11,41</b>	0,035	0,046	3,11	0,16	0,21
Banaru (2013)	2,09	<b>15,1</b>	<b>0,023</b>	7,24	<b>0,044</b>	<b>0,092</b>	<b>3,99</b>	0,15	0,21

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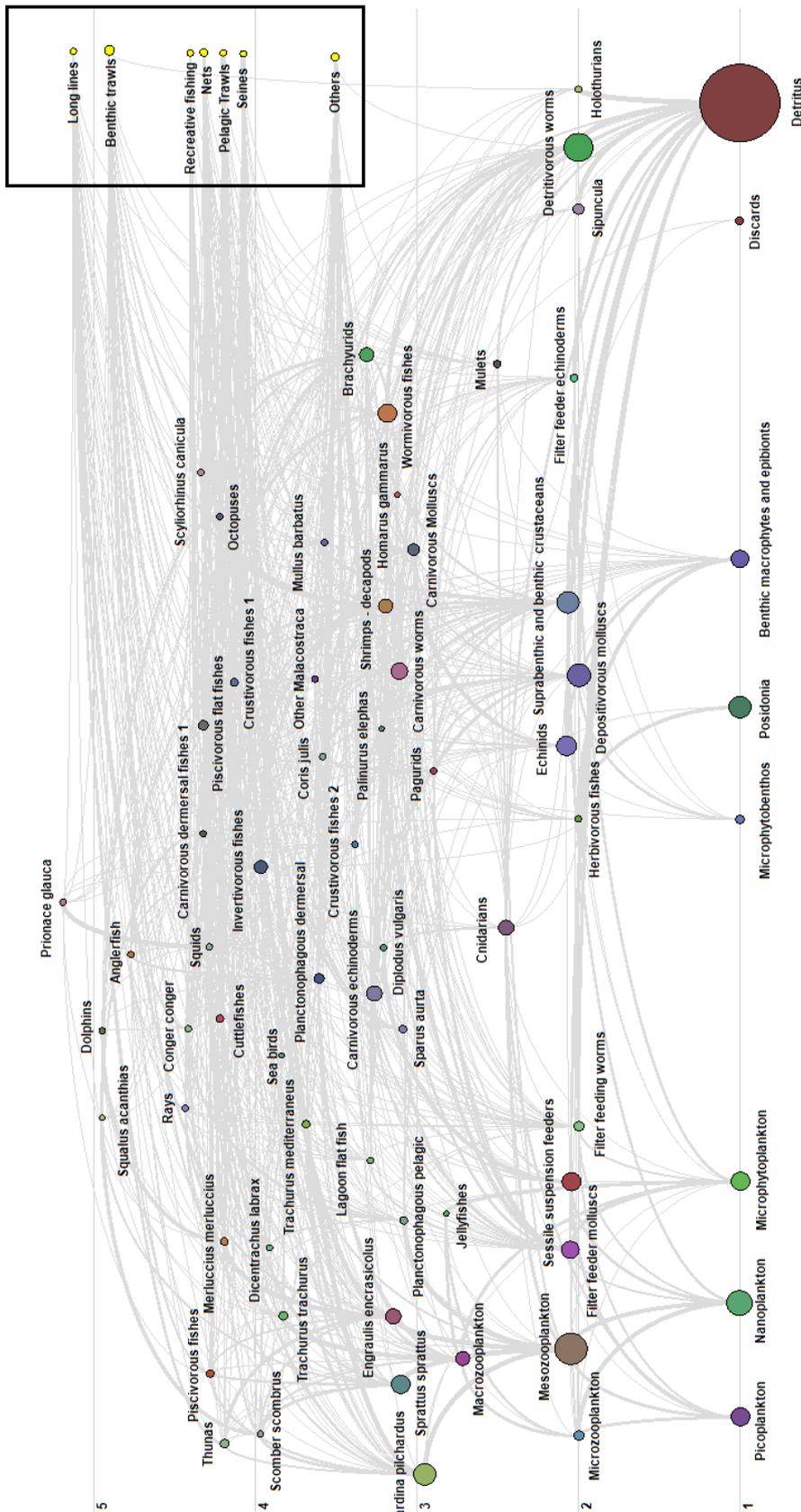
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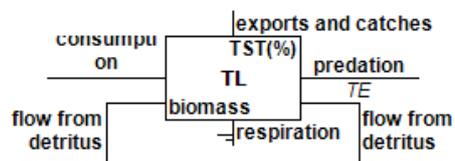
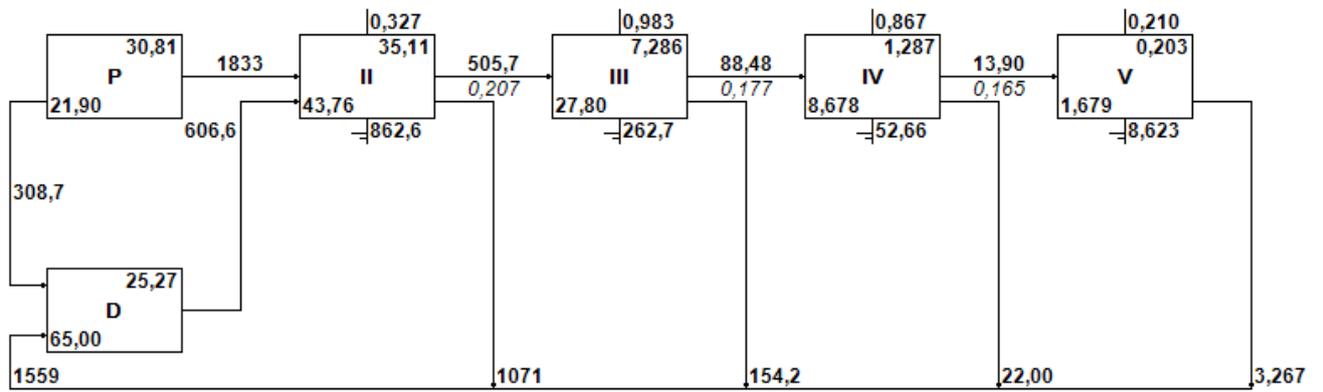
862 **Figure 1** Location and bathymetry of the study area in the Gulf of Lion north-western Mediterranean  
863 Sea.

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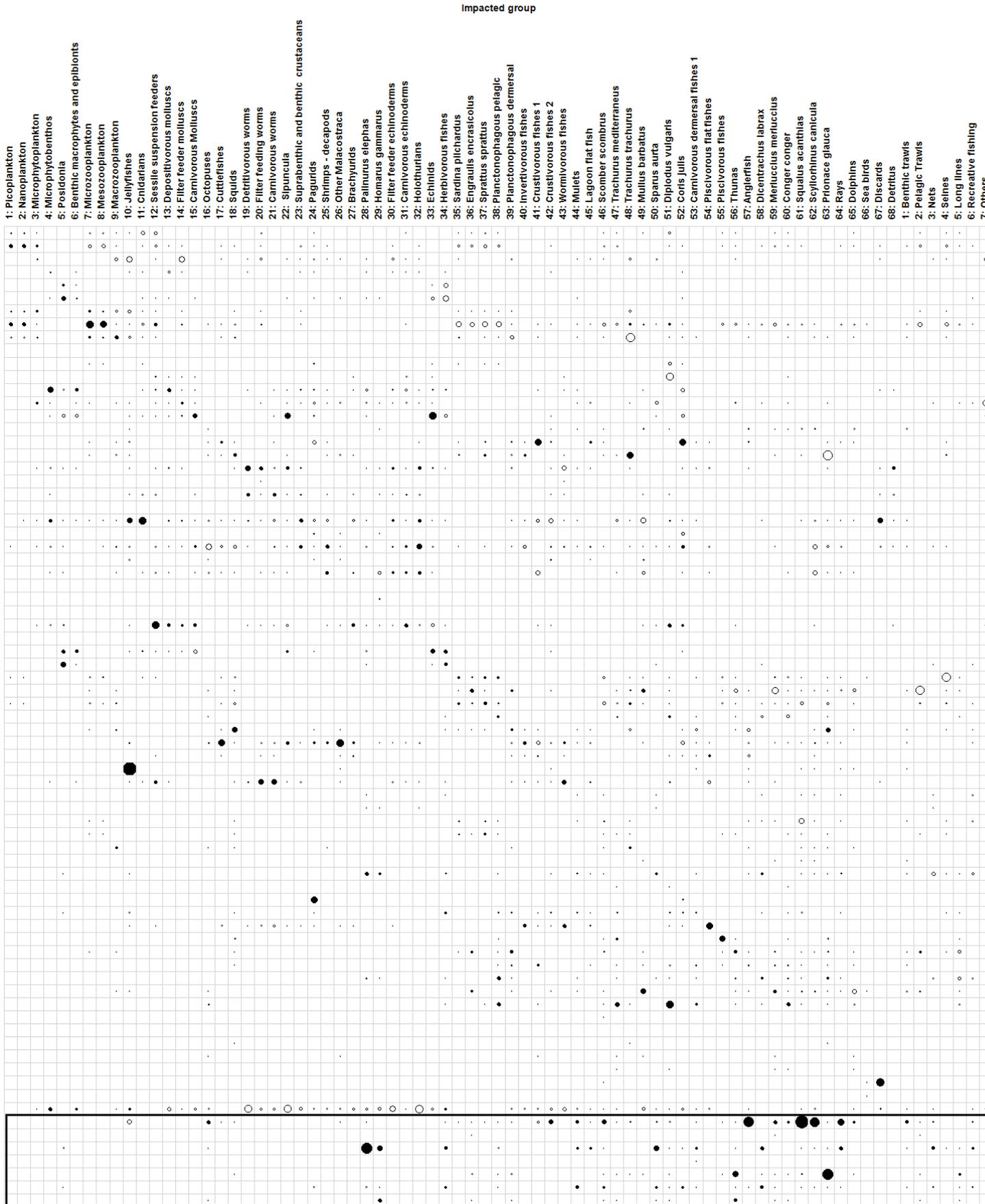
866 **Figure 2** Trophic diagram of the GOLEM model. The ordinate axis represents the trophic level. Black  
 867 rectangle highlights the fisheries. The dot size is proportional to the group biomass and the link  
 868 width to flow between the two groups.



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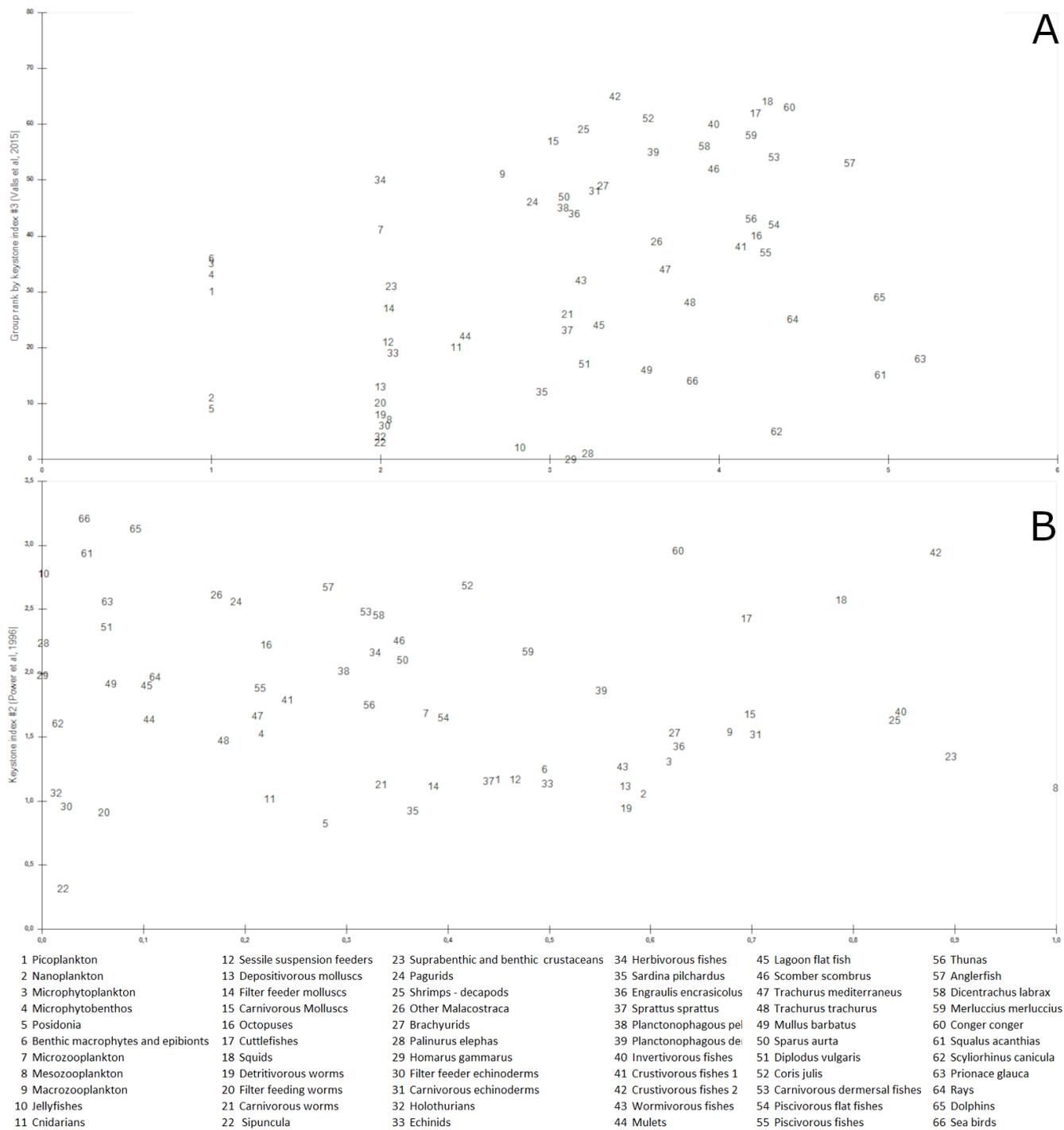
870 **Figure 3** Lindeman spine diagram of GOLEM model: P: primary producers, D: detritus, TST: total  
 871 system throughput and TE: trophic efficiency

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874 **Figure 4** Mixed trophic impact matrix. Black rectangle highlights the fisheries impact on other groups.

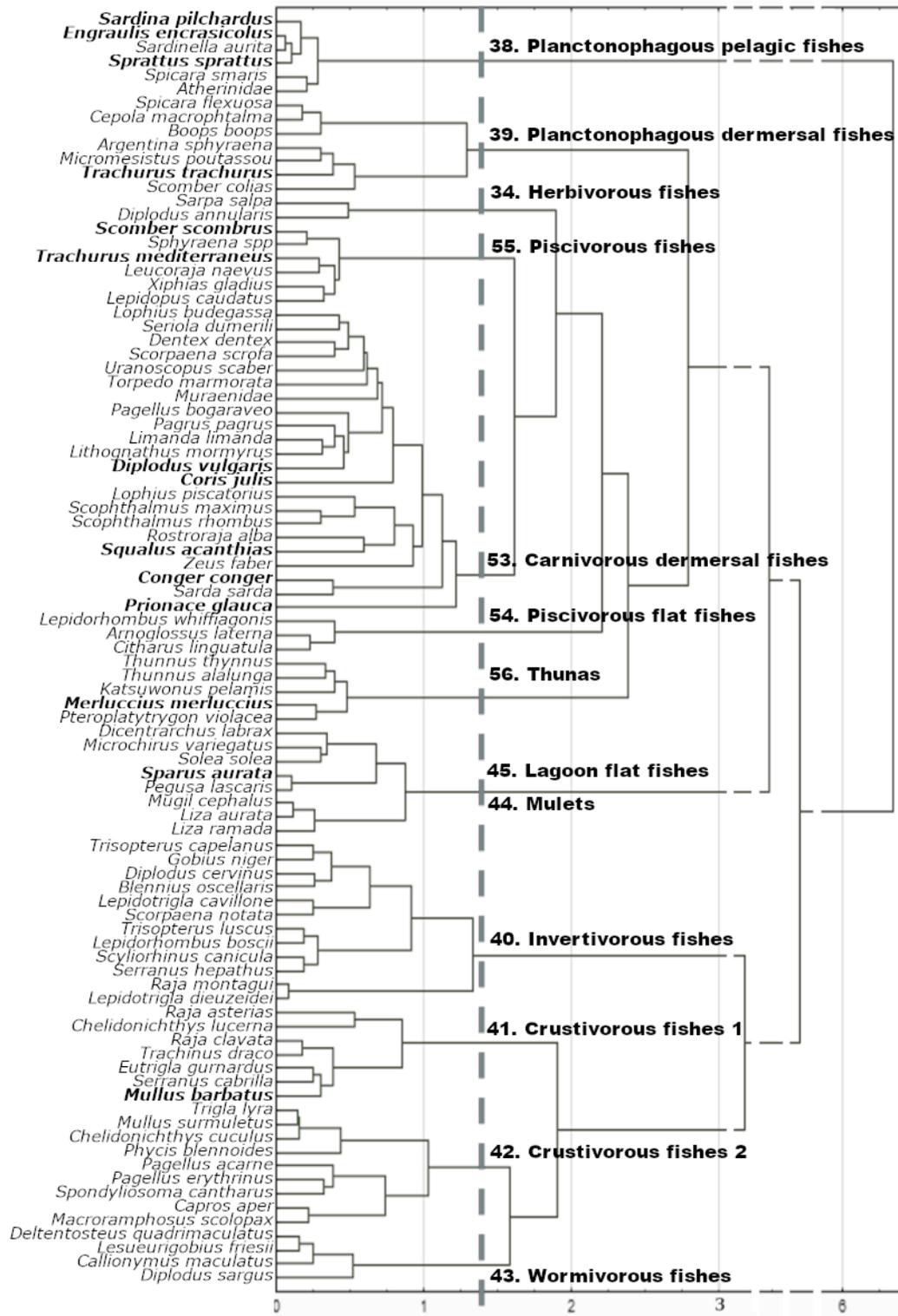


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876 **Figure 5** Keystoness plots. A) Valls keystone index against trophic levels. B) Power keystone index  
877 against the relative total impact.

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880

881 **Appendix 1** Cluster analysis using Ward method and mean distance between classes, representing  
 882 the diet similarity between the 91 analyzed fish species. The number and the name of the groups in  
 883 the model were indicated and species represented separately were indicated in bold characters.

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• Functional group	• Data sources and references
•	•
• 1. Picozooplankton	•
• Biomass	• Hunt et al., 2017; Lefevre et al., 1997; Marty et al., 2008
• P/B	• Landry et al., 2021; Lefevre et al., 1997; Schwinghamer et al., 1986
•	•
• 2. Nanozooplankton	•
• Biomass	• Christaki et al., 2009; Hunt et al., 2017; Lefevre et al., 1997; Marty et al., 2008
• P/B	• Gaudy et al., 2003; Lefevre et al., 1997
•	•
• 3. Microphytoplankton	•
• Biomass	• Christaki et al., 2009; Harmelin-Vivien et al., 2008; Hunt et al., 2017; Lefevre et al., 1997; Marty et al., 2008
• P/B	• Gaudy et al., 2003; Lefevre et al., 1997
•	•
• 4. Microphytobenthos	•
• Biomass	• Plante-Cuny & Bodoy, 1987; Riaux-Gobin et al., 1998
• P/B	• Plante-Cuny & Bodoy, 1987; Schwinghamer et al., 1986; van der Heijden et al., 2020
•	•
• 5. Posidonie	•
• Biomass, P/B	• Boudouresque et al., 2006
•	•
• 6. Benthic macrophytes + epibiontes	•
• Biomass	• Bănaru et al., 2013
• P/B	•
•	•
• 7. Microzooplankton	•

- Biomass
- P/B, Q/B
- Diet
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- 8. Mesozooplankton
- Biomass
- P/B, Q/B
- Diet
- 
- 9. Macrozooplankton
- Biomass
- P/B, Q/B
- Diet
- 
- 10. Jellyfishes
- Biomass
- P/B, Q/B
- Diet
- 
- 11. Cnidarians (benthic)
- Biomass
- P/B
- Diet
- 
- 12. Sessile Suspension Feeders
- Biomass
- P/B, Q/B
- Diet
- 
- www.somlit.fr ; Carlotti, pers. comm. ; Christaki et al., 2009; Gaudy et al., 2003; Vaqué et al., 1997
- Gaudy et al., 2003; Le Borgne, 1982; Pinnegar, 2000; Plounevez & Champalbert, 2000
- Chen, 2019
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- www.somlit.fr, Carlotti, pers. comm.
- Gaudy et al., 2003; Pinnegar, 2000; Plounevez & Champalbert, 2000
- C.-T. Chen, 2019
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- www.somlit.fr, Carlotti, pers. comm.
- Labat & Cuzin-Roudy, 1996; Pinnegar, 2000; Velsch, 1997
- C.-T. Chen, 2019
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- Medits
- Coll et al., 2007
- Pérez-Ruzafa et al., 2002; Tilves et al., 2018
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- C. Labrune pers. comm., Bonifácio et al., 2018
- Munari et al., 2013
- Coma et al., 1995; Sebens & Koehl, 1984
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- C. Labrune pers. comm., Bonifácio et al., 2018
- Ortiz et al., 2013; Wong et al., 2011
- Cook et al., 2018; Petersen, 2007; Ribes et al., 1999
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- 13. Depositivorous Molluscs
  - Biomass
  - P/B, Q/B
  - Diet
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Doris.fffesm.fr T. mutabilis, Ferro & Cretella, 1993; Imrie et al., 1990; Kang et al., 1999; Watanabe et al., 2009; Yonge, 1946
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- 14. Filter Feeder Molluscs
  - Biomass
  - P/B
  - Q/B
  - Diet
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- C. Labrune pers. comm., Bonifácio et al., 2018
- Loo & Rosenberg, 1996
- T. Brey see Materials & methods
- Dupuy et al., 2000; Gosling, 2003; Prato et al., 2010
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- 15. Carnivorous Molluscs
  - Biomass
  - P/B, Q/B
  - Diet
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Eilertsen & Malaquias, 2013; Himmelman & Hamel, 1993; Hughes, 1986; Riedel, 1995; Scolding et al., 2007; Vasconcelos et al., 2012
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- 16. Octopuses
  - Biomass
  - P/B, Q/B
  - Diet
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- Medits
- T. Brey see Materials & methods
- Kaci, 2012; Quetglas et al., 2005
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- 17. Cuttlefishes
  - Biomass
  - P/B, Q/B
  - Diet
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- Medits
- T. Brey see Materials & methods
- Alves et al., 2006; Bergström, 1985; Kaci, 2012
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- 18. Squids
  - Biomass
  - P/B, Q/B
- Medits
- T. Brey see Materials & methods

- Diet
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- 19. Detritivorous worms
- Biomass
- P/B, Q/B
- Diet
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- 20. Filter feeders worms
- Biomass
- P/B, Q/B
- Diet
- 
- 21. Carnivorous worms
- Biomass
- P/B, Q/B
- Diet
- 
- 22. Sipuncula
- Biomass
- P/B
- Q/B
- Diet
- 
- 23. Suprabenthic and benthic invertebrates
- Biomass
- P/B, Q/B
- Diet
- 
- 24. Pagurids
- Biomass
- P/B, Q/B
- Diet
- Coelho et al., 1997; Hastie et al., 2013; Kaci, 2012; Roscian, 2016
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Jumars et al., 2015
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Jumars et al., 2015
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Jumars et al., 2015; Mettam, 1980
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- C. Labrune pers. comm., Bonifácio et al., 2018
- Han, 2019
- Lovvorn et al., 2015
- Cutler, 1994
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Arrontes, 1990; Bozzano, 2002; Domingues et al., 2000
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Kunze & Anderson, 1979; Ramsay et al., 1996

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- 25. Decapods
- Biomass
- P/B, Q/B
- Diet
- 
- 26. Other Malacostracas
- Biomass
- P/B, Q/B
- Diet
- 
- 27. Brachyurids
- Biomass
- P/B, Q/B
- Diet
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- 28. Palinurus elephas
- Biomass
- P/B, Q/B
- Diet
- 
- 29. Homarus gammarus
- Biomass
- P/B, Q/B
- Diet
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- 30. Filter Feeder Echinoderms
- Biomass
- P/B, Q/B
- Diet
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- Medits
- Viegas et al., 2007
- Cartes, 1995; Guerao & Ribera, 1996
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- T. Brey see Materials & methods
- Baden et al., 1990; Mili et al., 2013
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- Abello, 1989; R. B. Chen et al., 2004; Freire, 1996
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- T. Brey see Materials & methods
- Goñi et al., 2001
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- Sainte-Marie & Chabot, 2002
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- T. Brey see Materials & methods
- La Touche & West, 1980; Massin, 1982; Warner, 1982
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- 31. Carnivorous Echinoderms
- Biomass
- P/B, Q/B
- Diet
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- 32. Holothurians
- Biomass
- P/B, Q/B
- Diet
- 
- 33. Echinids
- Biomass
- P/B, Q/B
- Diet
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- 34. Herbivorous fishes
- Biomass
- K and L<sub>∞</sub>
- Diet
- 
- 35. *Sardina pilchardus*
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 36. *Engraulis encrasicolus*
- Biomass
- K and L<sub>∞</sub>
- Diet
- 
- 37. *Sprattus sprattus*
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- C. Labrune pers. comm., Bonifácio et al., 2018
- T. Brey see Materials & methods
- Baeta & Ramón, 2013; Guillou, 1987; Vasserot, 1961; Warner, 1982
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- T. Brey see Materials & methods
- Fankboner, 1981; Ramón et al., 2019
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- T. Brey see Materials & methods
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- Dufour et al., 1995, Fishbase.org, Medits
- Campillo, 1992; Criscoli et al., 2006
- Cresson et al., 2014; Havelange et al., 1997
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- PELMED
- Van Beveren et al., 2014
- C.-T. Chen, 2019
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- PELMED
- Bigot et al., 2014
- C.-T. Chen, 2019
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- Biomass
- K and  $L_{\infty}$
- Diet
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- 38. Pelagic planktonophagous fishes
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 39. Demersal planktonophagous fishes
- Biomass
- K and  $L_{\infty}$
- Diet
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- 40. Invertivorous
- Biomass
- K and  $L_{\infty}$
- Diet
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- 41. Crustivorous fishes 1
- Biomass
- K and  $L_{\infty}$
- PELMED
- Kasapoğlu, 2018
- C.-T. Chen, 2019
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- Medits, PELMED 2009
- Delaunay, 2017; Dulčić et al., 2003; Tsikliras et al., 2005
- C.-T. Chen, 2019; Cresson et al., 2014; Danilova, 1991
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- Medits, PELMED 2009
- Campillo, 1992; Çiçek et al., 2007; Dulčić et al., 2008; Ferri et al., 2017; Velasco et al., 2011
- Bourgogne, 2014; C.-T. Chen, 2019; Le Luherne, 2012; Sever, 2019; Sever et al., 2013
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- Dufour et al., 1995, Medits
- Baştusta et al., 2017; Campillo, 1992; Delaunay, 2017; Derbal & Kara, 2013; Dulčić et al., 2007; Filiz, 2009; Merayo & Villegas, 1994; Ragonese & Bianchini, 1998; Scarcella et al., 2011
- Bilecenoglu, 2009; Cresson et al., 2014; Derbal & Kara, 2006; Dobroslavić, 2015; Joyeux et al., 1991; Kabasakal, 1999; Labarta, 1976; Labropoulou & Machias, 1998; Labropoulou & Papadopoulou-Smith, 1999; M. S. Morte et al., 2001; S. Morte et al., 1999
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- Medits
- Buz & Baştusta, 2015; Ismen et al., 2004; McCarthy et al., 2018; Rachedi & Tania Dahel, 2019

- Diet
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- 42. Crustivorous fishes 2
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 43. Wormivorous fishes
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 44. Mulets
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 45. Lagoon flat fishes
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 46. Scomber scombrus
- Biomass
- K and L<sub>∞</sub>
- Diet
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- 47. Trachurus mediterraneus
- Castriota et al., 2012; Cresson et al., 2014; Montanini et al., 2010; Šantić et al., 2016
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- Campillo, 1992; Matić-Skoko et al., 2012
- S. Blanco et al., 2003
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- Campillo, 1992; Félix et al., 2011
- Cresson et al., 2014; Darnaude, 2005
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- PELMED 2009
- Campillo, 1992
- Le Luherne, 2012
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- Biomass
- K and  $L_{\infty}$
- Diet
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- 48. *Trachurus trachurus*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 49. *Mullus barbatus*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 50. *Sparus aurata*
- Biomass
- P/B, Q/B
- Diet
- 
- 51. *Diplodus vulgaris*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 52. *Coris julis*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 53. Demersal carnivorous fishes
- Biomass
- K and  $L_{\infty}$
- PELMED 2009
- Karlou-Riga, 2000
- Le Luherne, 2012
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- PELMED 2009
- Campillo, 1992
- Le Luherne, 2012
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- Jadaud et al., 2018 average 2010-2014, calculated from weight at age and abundance at age
- Jadaud et al., 2018
- Bautista-Vega, 2007
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- Vaudo, 2002
- Palomares et al., 1993
- Rosecchi, 1987
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- Medits
- Campillo, 1992
- Cresson et al., 2014; Sala & Ballesteros, 1997
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- Francour, 1997
- Gordo et al., 2000
- Sinopoli et al., 2017
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- Medits
- Akyol, 2001; Boufersaoui et al., 2018; Campillo, 1992; Duman & Basusta, 2013; Félix et al.,

- 2011; Kaya & Bařusta, 2016; Kozul et al., 2001; Matić-Skoko et al., 2011; Morales-Nin & Moranta, 1997; S. I. Rizkalla & Bakhoun, 2009; Valeiras, Macías, et al., 2008; Vassilopoulou & Papaconstantinou, 1992
- Diet
  - Abdel-Aziz, 1994; Campo et al., 2006; Capapé et al., 2007; Capezzuto et al., 2021; Cresson et al., 2014; Matallanas et al., 1995; Morales-Nin & Moranta, 1997; Morato et al., 2001; Papaconstantinou & Caragitsou, 1989; S. Rizkalla & Philips, 2008; Sallami, 2014; Šantić et al., 2010; Schückel et al., 2012; Stergiou & Fourtouni, 1991; Vinagre et al., 2011
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- 54. Piscivorous flat fishes
  - Biomass
  - K and  $L_{\infty}$
  - Diet
    - Medits
    - Félix et al., 2011; Teixeira et al., 2010; Tičina & Matić-Skoko, 2012
    - de Juan et al., 2007; Fanelli et al., 2009; S. Morte et al., 1999
  -
- 55. Piscivorous fishes
  - Biomass
  - K and  $L_{\infty}$
  - Diet
    - Medits, Tserpes, 2010
    - Demestre et al., 1993; Rim et al., 2009; Valeiras, de la Serna, et al., 2008
    - Cresson et al., 2014; Demestre et al., 1993; Romeo et al., 2009; Salman, 2004; Torre et al., 2019
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- 56. Thunas
  - Biomass
  - K and  $L_{\infty}$
  - Diet
    - Estimate
    - Campillo, 1992
    - Imbert et al., 2007; Van Beveren et al., 2017; Varela et al., 2019
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- 57. Anglerfishes
  - Biomass
  - K and  $L_{\infty}$
  - Diet
    - Medits
    - García-Rodríguez et al., 2005; Landa et al., 2001
    - N. López et al., 2016; N. L. López, 2014

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- 58. *Dicentrarchus labrax*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 59. *Merluccius merluccius*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 60. *Conger conger*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 61. *Squalus acanthias*
- Biomass
- K and  $L_{\infty}$
- Diet
- 
- 62. *Scyliorhinus canicula*
- Biomass
- K and  $L_{\infty}$
- Diet
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- 63. *Prionace glauca*
- P/B, Q/B
- Diet
- 
- 64. Rays
- Biomass
- 
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- Vaudo, 2002
- R. López et al., 2015
- Cresson et al., 2014; Pasquaud et al., 2008
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- Kitchell et al., 2002
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