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

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

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

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

2. MATERIALS AND METHODS

2.1. Study area

The GOLEM (Gulf of Lion Ecopath Model) model area is located in the Gulf of Lion (GoL) between 0 to 200 m depth, for a total area of 12172 km². The 200 m isobath is located at the limit between the continental shelf and the canyons of the continental slope (**Fig. 1**). This model represents an average of the ecosystem situation between 2010 and 2014. The main environmental phenomena in this area are strong continental winds from the north-west (Tramontane) and north (Mistral) producing coastal upwellings (Millot, 1999; Agostini and Bakun, 2002), the mesoscale circulation of the western Mediterranean and the freshwater input from the Rhone River, which is the largest source of freshwater in the Mediterranean Sea (Margat, 1992; Petrenko *et al.*, 2005). The Rhone River is an important source of dissolved and particulate organic carbon (Lefevre *et al.*, 1997; Gaudy *et al.*, 2003; Harmelin-Vivien *et al.*, 2008). These phenomena lead to high primary and secondary production that supports a major part of the food web flows (Bănaru *et al.*, 2013, 2019; Cresson *et al.*, 2014). The sea floor features sandy and muddy substrates (Durrieu De Madron *et al.*, 2000) and few *Posidonia oceanica* meadows (Telesca *et al.*, 2015).

2.2. Ecopath software and balancing

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

$$P_i = \sum B_j * M2_{ij} + Y_i + E_i + BA_i + P_i * (1 - EE_i)$$

with P the production of the functional group i, $M2_{ij}$ the predation caused on i by a predator j and B_j its associated biomass, Y and E the export terms, the first for the fisheries and the latter for the other types of export, BA the biomass accumulation in the system and EE the ecotrophic efficiency (i. e. the proportion of the production of group i that is explained by the model, either by its exports or its predation). Thus, (1 – EEi) represents other mortality, or mortality not explained in the system.

The first equation can be re-expressed as follows:

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

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

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

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

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

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

2.3. Functional groups

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

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

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

2.4. Data sources and processing

2.4.1. Biomasses

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

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

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

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

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

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

The import term was calculated using data from the Rhone sediment observatory (Thollet *et al.*, 2018). The daily liquid discharge and daily concentration of particulate organic carbon (POC)from 2010 to 2014 were used to determine an average annual import of POC (t C) from the Rhone River to the GoL. According to Many *et al.* (2021), the Rhone river accounted for 97% of the POC riverine input in the GoL over the period 2011 to 2014 (consistent with the 97.4% calculated from Higueras *et al.* (2014), over 2008-2009). In order to account for the inputs of the other rivers, an increase corresponding to 3% was applied. Again, a factor of 10 was applied to convert the carbon mass to wet weight, for a final POC import of 98.05 t/km²/y.

2.4.2. Catches

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

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

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

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

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

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

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

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

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

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

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

$$P/B = Z = F + M$$

with Z the total mortality (y^{-1}), F the fisheries mortality (y^{-1}) and M the natural mortality (y^{-1}). F is the ratio between the catches of a species and its biomass. M was calculated using Pauly's empirical equation (Pauly, 1980):

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

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

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

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

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

2.4.4. Diet and data quality

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

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

2.5. Network analysis

As indicated by Heymans *et al.* (2016), to compare this model with the model of Bănaru *et al.* (2013) and other models, we used the four indices below, as they are less sensitive to differences in the model construction. These indices are: the Total System Throughput (TST, t/km²/y), the total net primary production on the TST (PP/TST), the sum of all consumptions on the TST (Q/TST) and the sum of all exports on the TST (Ex/TST) (**Table 6**).

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

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

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

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

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

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

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

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

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

3. RESULTS

3.1. General outputs

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

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

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

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

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

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

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

3.2. Network analysis and flows

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

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

3.3. Trophic impact and keystoneness

The mixed trophic impact matrix (**Figure 4**) shows that the mesozooplankton group plays an important role in the food web, with a relatively high direct negative impact on its prey (pico, nano and microzooplankton) and on itself (through competition) and a positive impact on its predators (4 groups of small pelagic planktonophagous fishes). It also has multiple smaller impacts throughout the food chain. Both suprabenthic/benthic invertebrates and decapod groups have a widespread impact, being preyed upon by many higher TL groups. This also applies to the four groups of small pelagic fishes, but with a more limited impact on other vertebrates, since few invertebrates feed on them (except cephalopods). One can note the negative indirect impact of *E. encrasicolus on M. barbatus*, via promotion of *M. merluccius*, which is a predator of *M. barbatus*. In the same way, detritus has a negative impact on the microphytobenthos by favoring the sipuncula and the depositivorous molluscs. Crustivorous fishes 2 have a strong direct negative impact on jellyfish, of which they are the only predator in this model. Finally, fisheries have a strong negative impact on many fishes at high and intermediate TL. The highest negative impact is exerted by benthic trawls on *Squalus acanthias*, *Scyliorhinus canicula* and anglerfish, by nets on *Palinurus elephas* and by long lines on *Prionace glauca.* Overall, the groups with the highest negative impact (summed MTIs) are, in decreasing order, benthic trawls (-4.1), nets (-2.8) and carnivorous equinoderms (-1.6). On the other hand, the three groups with the highest accumulated positive impacts are, in decreasing order, detritus (4.7), microphytoplankton (2.3) and nanoplankton (2.1).

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

4. DISCUSSION

4.1. Exploitation of the GoL

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

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

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

4.2. Comparison between models

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

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

4.2.1. Differences between the two GoL models

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

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

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

4.2.2. Flow indices, pedigree and omnivory index

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

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

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

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

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

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

4.2.3. Trophic levels and captures

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

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

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

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

Compared with E model, the average TL of the catches are identical and the total catches are close (2.43 t km^{-2} y^{-1} for GOLEM against 2.35 for the northern Aegean Sea), adding to the similarities between the two systems.

4.3. System maturity and keystoneness

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

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

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

5. CONCLUSION

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

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

Key results include:

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

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

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

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

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

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

6. ACKNOWLEDGEMENTS

This work was funded by the Institut de Radioprotection et de Sûreté Nucléaire (IRSN) and by the French *Investissement d'Avenir* program run by the National Research Agency (CNRS) (AMORAD project, grant ANR-11- RSNR-0002). T. Seyer’s thesis is co-funded by the Provence-Alpes-Côte d’Azur Region and IRSN (2020-03395). T. Seyer was hosted for 1 year at the Mediterranean Institute of Oceanography in order to build this model based on their most recent data on the GoL food web.

This work was also carried out in the framework of collaboration with the consortium of CONTAMPUMP (ANR-19-CE34-0001) and WINDSERV (ANR-10-IEED-06-34) projects. D. Bănaru benefited from leave within the ANR CONTAMPUMP.

The REDIT2010 and APPEALMED data used in this work are from samples collected on board the NO Tethys II. The REDIT2010 data are part of P. Bonifácio’s doctoral thesis which was funded by the Agence de l'Eau Corse-Méditerranée (convention n°2010 0871), LECOB (UMR CNRS – UPMC), EPOC (UMR CNRS – Université Bordeaux 1) and the Agence des Aires Marines Protégées (Marché N° 2009-AAMP-16; Lot N°9; ASCONIT/GIS Posidonie). The APPEAL project was funded by France Energies Marines and the National Research Agency within the framework of Investissements d’Avenir (ANR-10-IEED-0006-25). The authors would like to thank L. Lescure and J-M. Amouroux for sorting and identifying macrofauna, as well as the captains and crew members of N.O. Thetys and Nereis II for technical assistance during sampling for these projects.

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Table des figures et tableaux

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

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

	Functionnal groups	Bi (t km-2)	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 dermersal 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 aurta	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 dermersal 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

Tab le 3 Diet composition matrix of the GOLEM model.

Prey \ predator	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
1 Picoplankton	0,30	0,30			0,25	0,33		0,03						0,17																
2 Nanoplankton	0,60	0,60				0,37		0,17						0,17			0,20													
3 Microphytoplankton	0,10	0,05	0,30	0,40	0,06	0,09	0,03	0,49						0,17			0,10							0,19					0,10	
4 Microphytobenthos							0,24									0,05	0,10	0,05						0,00			0,06			
5 Posidonia																											0,06	0,40		
6 Benthic macrophytes and							0,08										0,02	0,08	0,01	0,06	0,02	0,03	0,06				0,30	0,60		
7 Microzooplankton		0,05	0,30	0,23	0,02	0,05		0,05												0,00				0,02						
8 Mesozooplankton			0,40	0,07	0,36														0,02										0,89	0,86
9 Macrozooplankton				0,30							0,05	0,04							0,06										0,01	0,14
10 Jellyfishes																														
11 Cnidarians					0,00												0,03		0,03				0,02				0,03	0,00		
12 Sessile suspension feeders																		0,01			0,00	0,01			0,16		0,02	0,00		
13 Depositivorous molluscs					0,02				0,12	0,00	0,00				0,10			0,18	0,11	0,04	0,03	0,25	0,05		0,30					
14 Filter feeder molluscs					0,00				0,16	0,00	0,01				0,05			0,21	0,09	0,10	0,08	0,21	0,15		0,18					
15 Carnivorous Molluscs					0,00				0,05	0,00	0,00							0,07	0,04	0,01	0,01	0,10	0,02		0,07					
16 Octopuses										0,00	0,00	0,01								0,02		0,00								
17 Cuttlefishes										0,03	0,04	0,05								0,02										
18 Squids												0,01																		
19 Detritivorous worms					0,00				0,07	0,03	0,00	0,00			0,47			0,06	0,09	0,10	0,10	0,01	0,04	0,00	0,01					
20 Filter feeding worms					0,00				0,01	0,00	0,00	0,00			0,01			0,01	0,01	0,01	0,01	0,00	0,00	0,00	0,00					
21 Carnivorous worms					0,00				0,03	0,01	0,00	0,00			0,03			0,02	0,03	0,04	0,04	0,00	0,02	0,00	0,00					
22 Sipuncula									0,01										0,00											
23 Suprabenthic and benthic c					0,02				0,06	0,00	0,02	0,00			0,30		0,02	0,21	0,36	0,04	0,24	0,04	0,02	0,00	0,11		0,01			
24 Pagurids					0,00					0,00									0,00	0,04		0,01	0,04							
25 Shrimps - decapods					0,00					0,58	0,49	0,27							0,03	0,12	0,15	0,14	0,00							
26 Other Malacostraca																				0,02										
27 Brachyurids					0,00					0,24	0,05	0,01							0,01	0,04	0,03		0,26		0,08					
28 Palinurus elephas																														
29 Homarus gammarus																							0,01							
30 Filter feeder echinoderms															0,01			0,00	0,01	0,01	0,01		0,00		0,01					
31 Carnivorous echinoderms															0,04			0,01	0,04	0,10	0,14		0,01		0,05					
32 Holothurians																		0,00	0,00		0,00									
33 Echinids									0,40									0,00	0,01	0,02	0,02	0,15	0,01							
34 Herbivorous fishes																														
35 Sardina pilchardus										0,02	0,08	0,20																		
36 Engraulis encrasicolus										0,01	0,04	0,02								0,04										
37 Sprattus sprattus										0,03	0,09	0,23																		
38 Planctonophagous pelagic											0,00	0,00																		
39 Planctonophagous dermers											0,04	0,00																		
40 Invertivorous fishes										0,03		0,11								0,04								0,00		
41 Crustivorous fishes 1											0,05																			
42 Crustivorous fishes 2										0,00	0,01	0,00								0,03										
43 Wormivorous fishes																														
44 Mulets																														
45 Lagoon flat fish										0,00	0,01	0,00								0,01										
46 Scomber scombrus																														
47 Trachurus mediterraneus																														
48 Trachurus trachurus												0,05																		
49 Mullus barbatus										0,01										0,03										
50 Sparus aurta																														
51 Diplodus vulgaris																														
52 Coris julis											0,01																			
53 Carnivorous dermersal fish																														
54 Piscivorous flat fishes											0,01	0,00																		
55 Piscivorous fishes										0,00																				
56 Thunas																														
57 Anglerfish																														
58 Dicentrachus labrax																														
59 Merluccius merluccius																														
60 Conger conger																														
61 Squalus acanthias																														
62 Scyliorhinus canicula																														
63 Prionace glauca																														
64 Rays																														
65 Dolphins																														
66 Sea birds																														
67 Discards																	0,00													
68 Detritus					0,27	0,17	0,65	0,26	0,10				1,00	0,50		0,95	0,53	0,10	0,06	0,06	0,13	0,05	0,28	0,78	0,02	1,00	0,52			
Import																														
Sum	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0

Prey \ predator	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
1 Picoplankton																														
2 Nanoplankton																														
3 Microphytoplankton		0,03																												
4 Microphytobenthos																														
5 Posidonia																														
6 Benthic macrophytes and		0,00		0,03		0,01	0,06	0,07								0,00	0,00													
7 Microzooplankton																														
8 Mesozooplankton	0,92	0,83	0,12			0,02		0,12			0,16	0,02																		
9 Macrozooplankton	0,08	0,07	0,41	0,00	0,00	0,00				0,18	0,04	0,72					0,01		0,07	0,01	0,02									0,01
10 Jellyfishes						0,00																								
11 Cnidarians				0,00		0,00									0,19		0,00													
12 Sessile suspension feeders				0,00		0,01	0,07								0,57	0,00	0,00													
13 Depositivorous molluscs		0,00	0,00	0,02	0,00	0,05	0,00		0,01				0,01	0,03	0,04	0,37	0,02				0,00									0,01
14 Filter feeder molluscs			0,00	0,02	0,00	0,02	0,01		0,15					0,31		0,00	0,02	0,00			0,00							0,00		0,01
15 Carnivorous Molluscs		0,00	0,00	0,01		0,02	0,00		0,00				0,00		0,02	0,37	0,00				0,00							0,00		0,01
16 Octopuses						0,00											0,00		0,02		0,00			0,10	0,23	0,01		0,06	0,12	
17 Cuttlefishes				0,04	0,01	0,00											0,02		0,02									0,08		
18 Squids			0,07	0,00	0,00	0,00											0,02		0,11	0,02	0,00						0,83	0,02	0,02	0,01
19 Detritivorous worms		0,04	0,23	0,04		0,03	0,57		0,14	0,00	0,04		0,12	0,05	0,07	0,00	0,02	0,00						0,00		0,00		0,01		
20 Filter feeding worms		0,00	0,03	0,01		0,00	0,07		0,02	0,00	0,00		0,01	0,01	0,01	0,00	0,00	0,00								0,00		0,00		
21 Carnivorous worms		0,02	0,09	0,02		0,01	0,22		0,06	0,00	0,02		0,05	0,02	0,03	0,00	0,01	0,00								0,00		0,00		
22 Sipuncula				0,01					0,01							0,01														
23 Suprabenthic and benthic c			0,01	0,06	0,24	0,47	0,00	0,11	0,04	0,02	0,17		0,42	0,09		0,00	0,03	0,01			0,00	0,08	0,02					0,05		0,02
24 Pagurids				0,00		0,00			0,00							0,24	0,00	0,00										0,00		
25 Shrimps - decapods			0,03	0,43	0,16	0,07	0,00		0,01	0,01	0,10	0,23	0,07				0,04	0,30	0,03		0,08		0,02			0,44		0,13		
26 Other Malacostraca				0,01	0,00												0,00	0,00			0,00							0,01		
27 Brachyurids			0,00	0,11	0,37	0,06	0,00		0,00				0,28				0,03	0,03					0,01	0,05		0,43		0,09	0,02	
28 Palinurus elephas																														
29 Homarus gammarus																														
30 Filter feeder echinoderms			0,00	0,00		0,01	0,00		0,00				0,00		0,00		0,00				0,00									
31 Carnivorous echinoderms			0,00	0,00		0,09	0,00		0,04				0,02		0,04		0,00													
32 Holothurians						0,00	0,00		0,02																					
33 Echinids				0,03		0,10									0,04		0,01				0,01									
34 Herbivorous fishes																	0,03							0,02						
35 Sardina pilchardus			0,00	0,02	0,00					0,29	0,16	0,01					0,05	0,00	0,25	0,18		0,10		0,19				0,07	0,04	0,04
36 Engraulis encrasicolus			0,00	0,01	0,00					0,16	0,09	0,01					0,01		0,14	0,47		0,05	0,77					0,20	0,08	0,01
37 Sprattus sprattus			0,01	0,01	0,00					0,34	0,22	0,01					0,01		0,26	0,04		0,10			0,14		0,05	0,04		
38 Planctonophagous pelagic				0,00													0,09		0,03		0,00	0,18		0,31				0,00		
39 Planctonophagous dermers			0,00		0,00												0,20		0,01	0,11	0,27		0,07	0,02				0,03	0,09	
40 Invertivorous fishes			0,00	0,01	0,09	0,00			0,00								0,06	0,10			0,15			0,00		0,12	0,02	0,06		
41 Crustivorous fishes 1																	0,07				0,17			0,05				0,03		0,02
42 Crustivorous fishes 2					0,00												0,05		0,00		0,00						0,03		0,07	0,02
43 Wormivorous fishes				0,09	0,05	0,01											0,04	0,50			0,08		0,06		0,01			0,02		
44 Mulets				0,00													0,02													
45 Lagoon flat fish																	0,02	0,00			0,02			0,01				0,01		
46 Scomber scombrus																			0,01	0,01					0,45					0,03
47 Trachurus mediterraneus																	0,01		0,01					0,04				0,00		
48 Trachurus trachurus					0,00												0,01		0,02		0,00			0,02				0,01	0,04	
49 Mullus barbatus			0,00														0,01						0,06					0,02		
50 Sparus aurta																	0,01													
51 Diplodus vulgaris																	0,01							0,08						
52 Coris julis																	0,01													
53 Carnivorous dermersal fish																	0,03				0,02			0,06	0,13		0,04			
54 Piscivorous flat fishes					0,07													0,05	0,00		0,05									
55 Piscivorous fishes																			0,02		0,01						0,02			
56 Thunas																														
57 Anglerfish																														
58 Dicentrachus labrax																	0,00													
59 Merluccius merluccius																	0,02		0,01		0,08		0,01	0,02	0,05			0,05	0,41	0,04
60 Conger conger																	0,01				0,02			0,03					0,12	
61 Squalus acanthias																														
62 Scyliorhinus canicula																														
63 Prionace glauca																														
64 Rays																	0,00													
65 Dolphins																														
66 Sea birds																														
67 Discards																														0,06
68 Detritus				0,00			0,00	0,19																						
Import								0,50	0,50					0,50						0,17		0,50								0,73
Sum	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0	1,0

Table 4 Main output parameters of the GOLEM model. Biomass parameters estimated by the model are indicated by bold characters. TL = trophic level, Bf = final biomass (t km−2), EE = ecotrophic efficiency, F = fishing mortality (y−1), M2 = predation mortality (y−1), M0 = natural mortality (y−1), F/Z = exploitation rate, Q = consumption (t km−2 y−1), FD = flow to detritus (t km−2 y−1), P/Q = 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	**0,90**	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	**3,64**	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	**5,08**	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	**3,42**	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	**1,69**	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	**0,15**	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	**0,30**	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	**0,24**	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 cı	2,06	**4,63**	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	**0,05**	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	**2,12**	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	**2,47**	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	**4,21**	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	**0,33**	11,42	0,95	0,04	0,86	0,05	0,04	2,44	0,75	0,13	0,18	0,09
39	Planctonophagous dermersa	3,61	**0,87**	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	**1,96**	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	**0,45**	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	**3,58**	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	**0,15**	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	0,23	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 aurta	3,08	**0,33**	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	**0,03**	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 dermersal fishe	4,32	**0,12**	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	**1,02**	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	Dicentrachus labrax	3,91	**0,14**	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	**0,08**	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

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

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

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

	Area	modelled period	n° of functional groups	PP / TST	Q / TST	Export / TST	TST (t/Km²/y)	Total biomass (excluding detritus, t/Km²)	Modelled area (Km²)	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)

Table 7 Odum's attributes (1969) as calculated by Christensen (1995). For each attribute, values in bold indicate the most mature model. PP/R = total primary production/total respiration, PP/B = total primary production/total biomass (*excluding detritus), B/TST = biomass (*)/total troughput, total repsiration/total biomass(*), B/P = total biomass(*)/ total production, B/(R+Exp) = total 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	**1,8**	20,57	0,015	**11,41**	0,035	0,046	3,11	0,16	0,21
Banaru (2013)	2,09	**15,1**	**0,023**	7,24	**0,044**	**0,092**	**3,99**	0,15	0,21

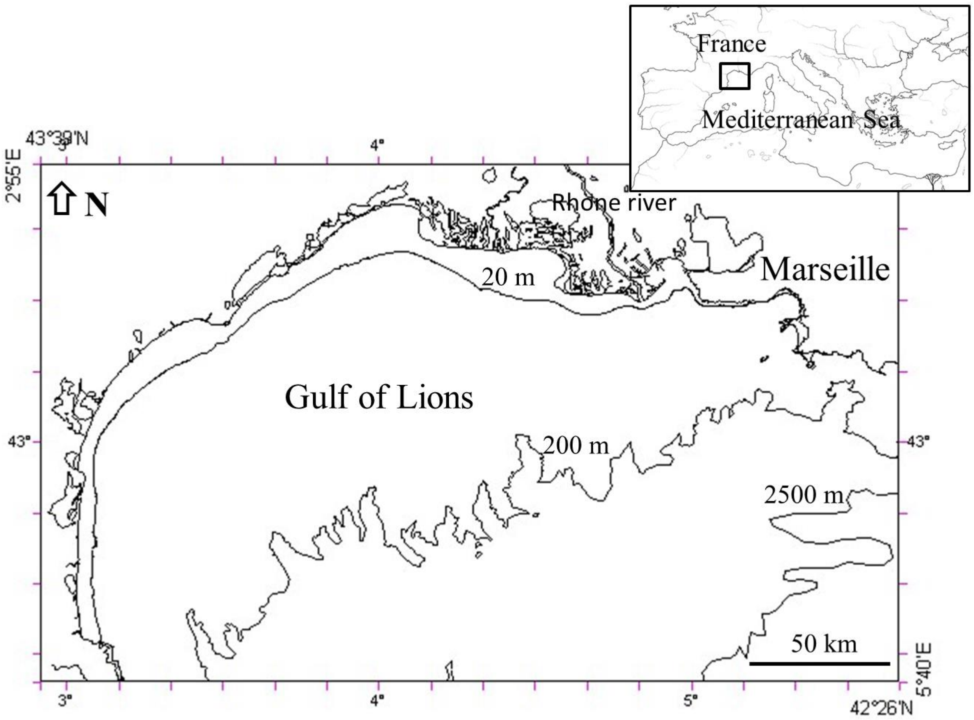


Figure 1 Location and bathymetry of the study area in the Gulf of Lion north-western Mediterranean Sea.

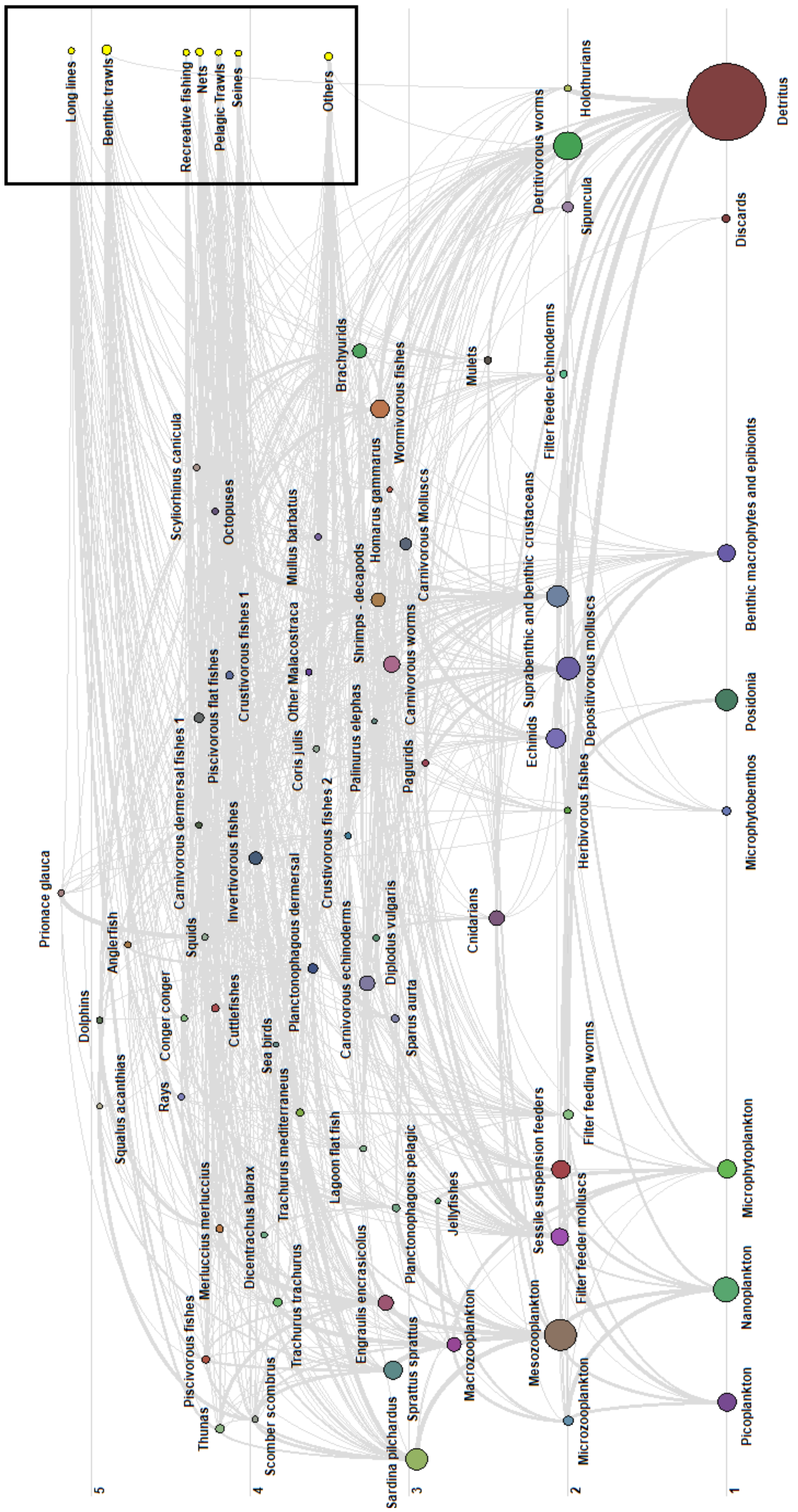


Figure 2 Trophic diagram of the GOLEM model. The ordinate axis represents the trophic level. Black rectangle highlights the fisheries. The dot size is proportional to the group biomass and the link width to flow between the two groups.

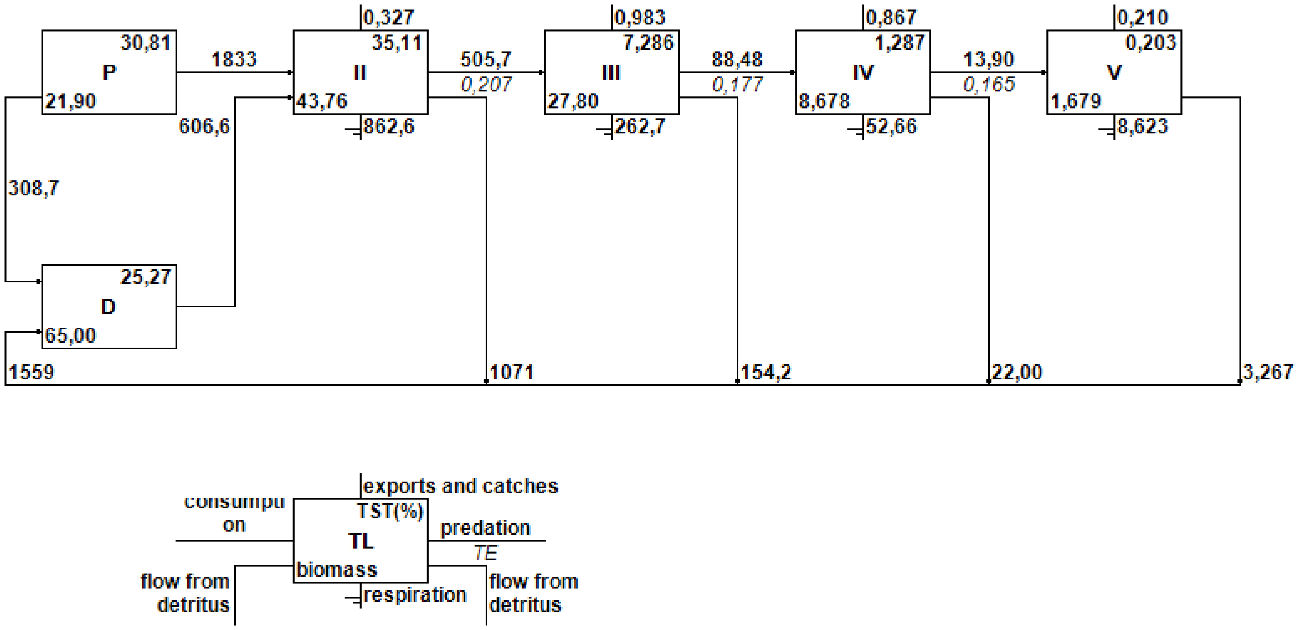


Figure 3 Lindeman spine diagram of GOLEM model: P: primary producers, D: detritus, TST: total system throughput and TE: trophic efficiency

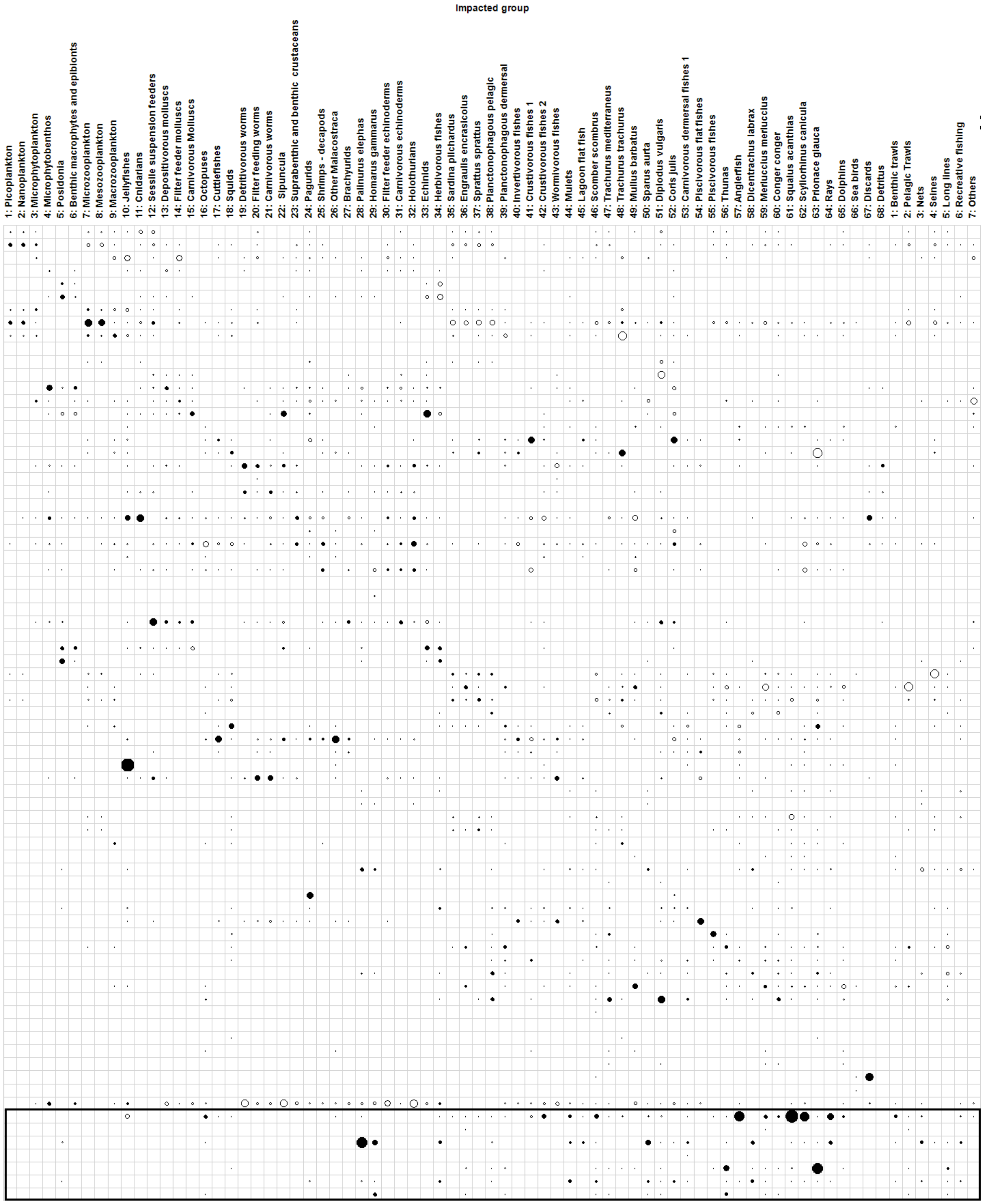


Figure 4 Mixed trophic impact matrix. Black rectangle highlights the fisheries impact on other groups.

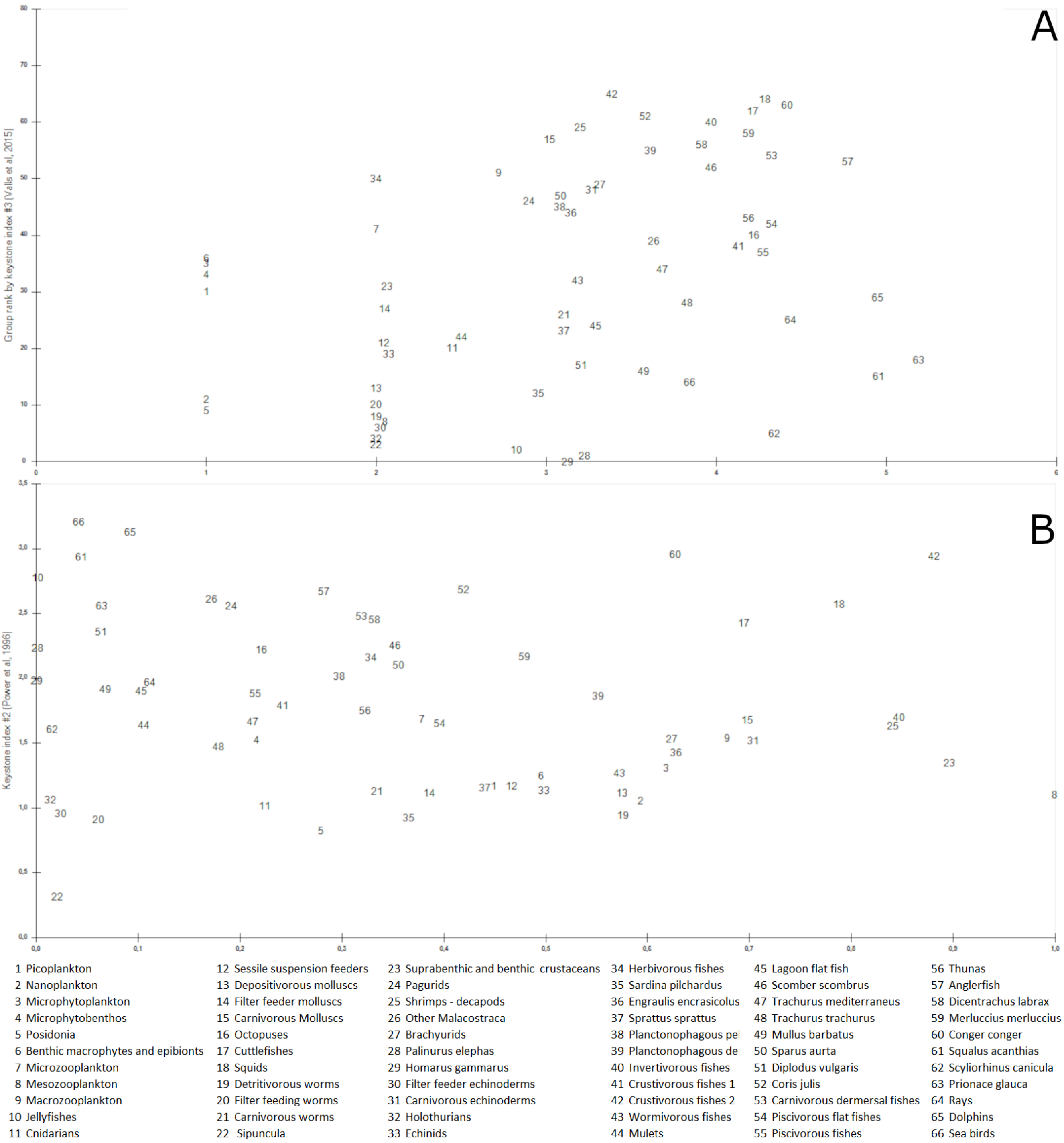
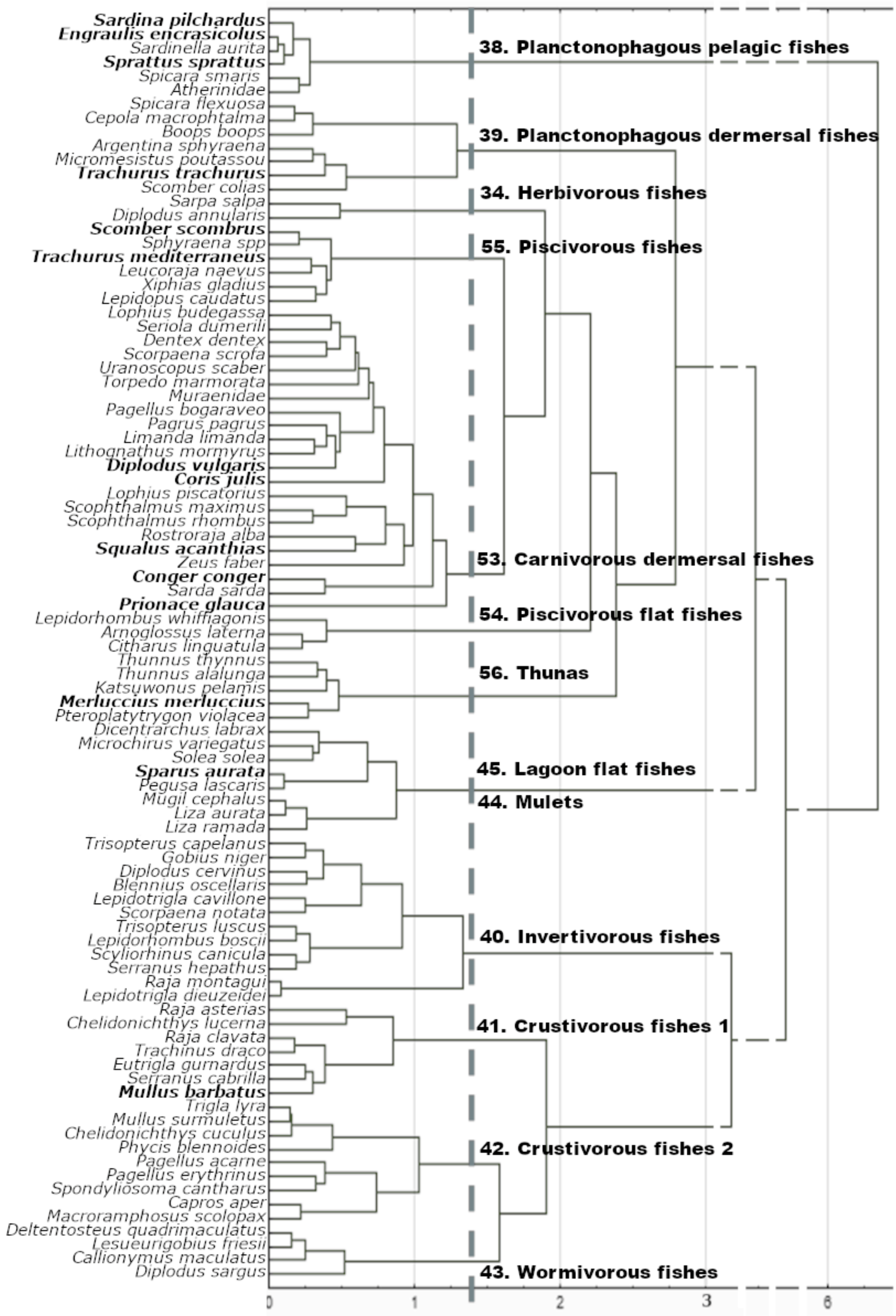


Figure 5 Keystoness plots. A) Valls keystone index against trophic levels. B) Power keystone index against the relative total impact.



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

Appendix 2

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	• www.somlit.fr ; Carlotti, pers. comm. ; Christaki et al., 2009; Gaudy et al., 2003; Vaqué et al., 1997
• P/B, Q/B	• Gaudy et al., 2003; Le Borgne, 1982; Pinnegar, 2000; Plounevez & Champalbert, 2000
• Diet	• Chen, 2019
•	•
• 8. Mesozooplankton	•
• Biomass	• www.somlit.fr, Carlotti, pers. comm.
• P/B, Q/B	• Gaudy et al., 2003; Pinnegar, 2000; Plounevez & Champalbert, 2000
• Diet	• C.-T. Chen, 2019
•	•
• 9. Macrozooplankton	•
• Biomass	• www.somlit.fr, Carlotti, pers. comm.
• P/B, Q/B	• Labat & Cuzin-Roudy, 1996; Pinnegar, 2000; Velsch, 1997
• Diet	• C.-T. Chen, 2019
•	•
• 10. Jellyfishes	•
• Biomass	• Medits
• P/B, Q/B	• Coll et al., 2007
• Diet	• Pérez-Ruzafa et al., 2002; Tilves et al., 2018
•	•
• 11. Cnidarians (benthic)	•
• Biomass	• C. Labrune pers. comm., Bonifácio et al., 2018
• P/B	• Munari et al., 2013
• Diet	• Coma et al., 1995; Sebens & Koehl, 1984
•	•
• 12. Sessile Suspension Feeders	•
• Biomass	• C. Labrune pers. comm., Bonifácio et al., 2018
• P/B, Q/B	• Ortiz et al., 2013; Wong et al., 2011
• Diet	• Cook et al., 2018; Petersen, 2007; Ribes et al., 1999
•	•

13. Depositivorous Molluscs	
Biomass	C. Labrune pers. comm., Bonifácio et al., 2018
P/B, Q/B	T. Brey see Materials & methods
Diet	Doris.ffessm.fr T. mutabilis, Ferro & Cretella, 1993; Imrie et al., 1990; Kang et al., 1999; Watanabe et al., 2009; Yonge, 1946
14. Filter Feeder Molluscs	
Biomass	C. Labrune pers. comm., Bonifácio et al., 2018
P/B	Loo & Rosenberg, 1996
Q/B	T. Brey see Materials & methods
Diet	Dupuy et al., 2000; Gosling, 2003; Prato et al., 2010
15. Carnivorous Molluscs	
Biomass	C. Labrune pers. comm., Bonifácio et al., 2018
P/B, Q/B	T. Brey see Materials & methods
Diet	Eilertsen & Malaquias, 2013; Himmelman & Hamel, 1993; Hughes, 1986; Riedel, 1995; Scolding et al., 2007; Vasconcelos et al., 2012
16. Octopuses	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Kaci, 2012; Quetglas et al., 2005
17. Cuttlefishes	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Alves et al., 2006; Bergström, 1985; Kaci, 2012
18. Squids	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods

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

25. Decapods	
Biomass	Medits
P/B, Q/B	Viegas et al., 2007
Diet	Cartes, 1995; Guerao & Ribera, 1996
26. Other Malacostracas	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Baden et al., 1990; Mili et al., 2013
27. Brachyurids	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Abello, 1989; R. B. Chen et al., 2004; Freire, 1996 doris.ffessm.fr N. puber
28. Palinurus elephas	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Goñi et al., 2001
29. Homarus gammarus	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Sainte-Marie & Chabot, 2002
30. Filter Feeder Echinoderms	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	La Touche & West, 1980; Massin, 1982; Warner, 1982

31. Carnivorous Echinoderms	
Biomass	C. Labrune pers. comm., Bonifácio et al., 2018
P/B, Q/B	T. Brey see Materials & methods
Diet	Baeta & Ramón, 2013; Guillou, 1987; Vasserot, 1961; Warner, 1982
32. Holothurians	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	Fankboner, 1981; Ramón et al., 2019
33. Echinids	
Biomass	Medits
P/B, Q/B	T. Brey see Materials & methods
Diet	doris.ffessm.fr C. cidaris, Bay-Nouailhat 2008, web voir file, Barberá et al., 2011; Hollertz & Duchêne, 2001; Verlaque & Nédelec, 1983
34. Herbivorous fishes	
Biomass	Dufour et al., 1995, Fishbase.org, Medits
K and L∞	Campillo, 1992; Criscoli et al., 2006
Diet	Cresson et al., 2014; Havelange et al., 1997
35. Sardina pilchardus	
Biomass	PELMED
K and L∞	Van Beveren et al., 2014
Diet	C.-T. Chen, 2019
36. Engraulis encrasicolus	
Biomass	PELMED
K and L∞	Bigot et al., 2014
Diet	C.-T. Chen, 2019
37. Sprattus sprattus	

• Biomass	• PELMED
• K and L∞	• Kasapoğlu, 2018
• Diet	• C.-T. Chen, 2019
•	•
• 38. Pelagic planktonophagous fishes	•
• Biomass	• Medits, PELMED 2009
• K and L∞	• Delaunay, 2017; Dulčić et al., 2003; Tsikliras et al., 2005
• Diet	• C.-T. Chen, 2019; Cresson et al., 2014; Danilova, 1991
•	•
• 39. Demersal planktonophagous fishes	•
• Biomass	• Medits, PELMED 2009
• K and L∞	• Campillo, 1992; Çiçek et al., 2007; Dulčić et al., 2008; Ferri et al., 2017; Velasco et al., 2011
• Diet	• Bourgogne, 2014; C.-T. Chen, 2019; Le Luherne, 2012; Sever, 2019; Sever et al., 2013
•	•
• 40. Invertivorous	•
• Biomass	• Dufour et al., 1995, Medits
• K and L∞	• Başusta 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
• Diet	• 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
•	•
• 41. Crustivorous fishes 1	•
• Biomass	• Medits
• K and L∞	• Buz & Başusta, 2015; Ismen et al., 2004; McCarthy et al., 2018; Rachedi & Tania Dahel, 2019

Diet	Castriota et al., 2012; Cresson et al., 2014; Montanini et al., 2010; Šantić et al., 2016
42. Crustivorous fishes 2	
Biomass	Medits
K and L∞	Borges, 2000; Boughamou et al., 2015; Busalacchi et al., 2014; Campillo, 1992; Vagenas et al., 2020
Diet	Bautista-Vega, 2007; Caragitsou & Papaconstantinou, 1994; Carpentieri et al., 2016; Cresson et al., 2014; Dulčić et al., 2006; Macpherson, 1978; Montanini et al., 2017
43. Wormivorous fishes	
Biomass	Medits, Dufour et al., 1995
K and L∞	Erguden et al., 2016; Hussein et al., 2011; Metin et al., 2011; Nash, 1982
Diet	Bell & Harmelin-Vivien, 1983; Cresson et al., 2014; Gibson & Ezzi, 1979, 1987
44. Mulets	
Biomass	Dufour et al., 1995, Fishbase.org, Medits
K and L∞	Campillo, 1992; Matić-Skoko et al., 2012
Diet	S. Blanco et al., 2003
45. Lagoon flat fishes	
Biomass	Medits
K and L∞	Campillo, 1992; Félix et al., 2011
Diet	Cresson et al., 2014; Darnaude, 2005
46. Scomber scombrus	
Biomass	PELMED 2009
K and L∞	Campillo, 1992
Diet	Le Luherne, 2012
47. Trachurus mediterraneus	

• Biomass	• PELMED 2009
• K and L∞	• Karlou-Riga, 2000
• Diet	• Le Luherne, 2012
•	•
• 48. Trachurus trachurus	•
• Biomass	• PELMED 2009
• K and L∞	• Campillo, 1992
• Diet	• Le Luherne, 2012
•	•
• 49. Mullus barbatus	•
• Biomass	• Jadaud et al., 2018average 2010-2014, calculated from weight at age and abundance at age
• K and L∞	• Jadaud et al., 2018
• Diet	• Bautista-Vega, 2007
•	•
• 50. Sparus aurata	•
• Biomass	• Vaudo, 2002
• P/B, Q/B	• Palomares et al., 1993
• Diet	• Rosecchi, 1987
•	•
• 51. Diplodus vulgaris	•
• Biomass	• Medits
• K and L∞	• Campillo, 1992
• Diet	• Cresson et al., 2014; Sala & Ballesteros, 1997
•	•
• 52. Coris julis	•
• Biomass	• Francour, 1997
• K and L∞	• Gordoa et al., 2000
• Diet	• Sinopoli et al., 2017
•	•
• 53. Demersal carnivorous fishes	•
• Biomass	• Medits
• K and L∞	• Akyol, 2001; Boufersaoui et al., 2018; Campillo, 1992; Duman & Basusta, 2013; Félix et al.,

	2011; Kaya & Başusta, 2016; Kozul et al., 2001; Matić-Skoko et al., 2011; Morales-Nin & Moranta, 1997; S. I. Rizkalla & Bakhoum, 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
54. Piscivorous flat fishes	
Biomass	Medits
K and L∞	Félix et al., 2011; Teixeira et al., 2010; Tičina & Matić-Skoko, 2012
Diet	de Juan et al., 2007; Fanelli et al., 2009; S. Morte et al., 1999
55. Piscivorous fishes	
Biomass	Medits, Tserpes, 2010
K and L∞	Demestre et al., 1993; Rim et al., 2009; Valeiras, de la Serna, et al., 2008
Diet	Cresson et al., 2014; Demestre et al., 1993; Romeo et al., 2009; Salman, 2004; Torre et al., 2019
56. Thunas	
Biomass	Estimate
K and L∞	Campillo, 1992
Diet	Imbert et al., 2007; Van Beveren et al., 2017; Varela et al., 2019
57. Anglerfishes	
Biomass	Medits
K and L∞	García-Rodríguez et al., 2005; Landa et al., 2001
Diet	N. López et al., 2016; N. L. López, 2014

58. Dicentrarchus labrax	
Biomass	Vaudo, 2002
K and L∞	R. López et al., 2015
Diet	Cresson et al., 2014; Pasquaud et al., 2008
59. Merluccius merluccius	
Biomass	Jadaud et al., 2011
K and L∞	Jadaud et al., 2011
Diet	Merquiol, 2015
60. Conger conger	
Biomass	Medits
K and L∞	Matić-Skoko et al., 2012
Diet	Sallami et al., 2015
61. Squalus acanthias	
Biomass	Medits
K and L∞	Avsar, 2001
Diet	Henderson et al., 2002
62. Scyliorhinus canicula	
Biomass	Medits
K and L∞	Ozcan & Basusta, 2018
Diet	Mialet et al., 2017
63. Prionace glauca	
P/B, Q/B	Kitchell et al., 2002
Diet	Clarke et al., 1996
64. Rays	
Biomass	Medits

K and L∞	Campillo, 1992; Delaunay, 2017; Gallagher et al., 2004; Serra-Pereira et al., 2005; Yıgın & Ismen, 2010
P/B, Q/B	R. asterias: Coll et al., 2013
Diet	Barría et al., 2015; Farias et al., 2006; Lipej et al., 2013; Šantić et al., 2012; Sviben et al., 2019; Valls et al., 2011; Yıgın & Ismen, 2010
65. Dolphins	
Biomass, P/B, Q/B	Bănaru et al., 2013
Diet	Astruc, 2005; C. Blanco et al., 2001
66. Marine birds	
Biomass, P/B, Q/B, diet	Bănaru et al., 2013

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