
Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts

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Abstract:

The Gulf of Lions ecosystem was described using the Ecopath mass-balance model to characterise its structure and functioning and to examine the effects of the multispecific fisheries operating in this area. The model is composed of 40 compartments, including 1 group of seabirds, 2 groups of cetaceans, 18 groups of fish, 12 groups of invertebrates, 5 groups of primary producers, detritus and discards. Input data were based on several recurrent scientific surveys, two alternative datasets for fishing data, stock assessment outputs, stomach content analyses and published information. Results showed that the functional groups were organised into five trophic levels with the highest one represented by dolphins, anglerfish, Atlantic bluefin tuna, European hake and European conger. European pilchard and European anchovy dominated in terms of fish biomass and catch. Other fish with high biomass such as Atlantic mackerel and blue whiting were highly important in the food web. Seabirds, dolphins and cuttlefish–squids represented keystone species. Important coupled pelagic–demersal–benthic interactions were described. The 7 different fisheries analysed were operating at mean trophic levels situated between 2.6 for small artisanal boats, and 4.1 for purse seines (> 24 m) targeting large pelagic fish, indicating an intensively exploited ecosystem. Large trawlers (24–40 m) had the highest impact on most of the groups considered; while purse seines (12–24 m) targeting small pelagic fish had the lowest impact. Preliminary results highlighted the importance of data sources for further ecosystem and fisheries analyses and management scenarios.

Highlights

► We characterize the structure and the functioning of the food web in the Gulf of Lion. ► European pilchard and European anchovy represented key link groups and high landings. ► We showed coupling between compartments and top-down control by demersal predators. ► Indices showed that the Gulf of Lion's ecosystem was highly exploited by fisheries. ► Large trawls had the most negative impact and small purse seines had the lowest one.

Keywords: Gulf of Lions ; Ecopath with Ecosim ; Food web ; Fishing impacts

1. Introduction

The Gulf of Lions is an important feeding area for fish, birds and mammals, for both resident and migratory species. It represents a highly productive system because of the Rhone River inputs, coastal upwelling activity, bottom morphology and water circulation (Lefevre et al., 1997; Agostini and Bakun 2002; Petrenko et al., 2005; Hu et al., 2009). In this area many species of commercial interest have been intensively exploited on the continental shelf and upper slope for decades by the French and Spanish fleets using multispecific artisanal gear such as trawlers, purse seines, gillnets and other gear (Farrugio et al., 1993; Lleonart and Maynou, 2003; Sacchi, 2008). Throughout the Mediterranean Sea, marine resources have been exploited since ancient times (Margalef, 1985), although in the last decades the development of fishing technologies and the increasing demand for marine resources have generated a stronger and more amplified pressure on marine resources. Current analyses suggest that most demersal and pelagic stocks are fully exploited or overexploited (Aldebert and Recasens, 1996; Sardà, 1998; Papaconstantinou and Farrugio, 2000; Bas et al., 2003; FAO, 2009).

Fishing is known to be one of the major human disturbances in coastal marine ecosystems (Jennings and Kaiser, 1998; Jackson et al., 2001). It has various kinds of direct and indirect impact, in addition to those induced by oceanographic features and other anthropogenic and natural disturbances (Hall, 1999; Christensen et al., 2003). According to Food and Agriculture Organisation (FAO 1995, 2002) “the achievement of real marine ecosystem-based management of fisheries implies the regulation of the use of the living resources based on the understanding of the structure and dynamics of the ecosystem of which the resource is a part”. This requires an improvement in our understanding of the structure and functioning of exploited ecosystems and of the changes induced in them by human and environmental factors.

In the north-western Mediterranean Sea coupled physical and biogeochemical models were made (Baklouti et al., 2006). In these models the highest trophic level was represented by mesozooplankton (Eisenhauer et al., 2009).

This work is the first ecosystem modelling approach in the Gulf of Lions ecosystem, taking into account the entire food web from primary producers to top predators, and covering a large area from the coast up to 2500 m. The objective was to analyse the structure and the functioning of the food web and to estimate the relative impact of the different fishing gear. To do so, we used the Ecopath with Ecosim (EwE) software that has been widely used in many places over the world to quantitatively describe marine and aquatic ecosystems and to

assess fishing impact (Pauly et al., 2000; Christensen and Walters, 2004). Ecosystem modelling has been proposed as a management tool for marine fisheries (Plagányi, 2007) and also in Mediterranean Sea (Cochrane and De Young, 2008), where EwE models were previously made in different areas (Libralato et al., 2002; Pinnegar and Polunin, 2004; Coll et al., 2006, 2007; Tsagarakis et al., 2010; Coll and Libralato, 2011).

2. Materials and methods

2.1 Study area

The Ecopath model represents an average annual situation over the last decade (2000 - 2009) of the Gulf of Lions ecosystem covering a total area of 20400 km² and with a bathymetry between 0 and 2500 m. The Gulf of Lions is located in the north-western Mediterranean Sea (42°26.3'N, 3°9.9'E; 43°12.6'N, 5°27.5'E) (Fig. 1). The continental slope constitutes a long open boundary to the southeast of the Gulf. Along this boundary, the main mesoscale circulation feature is a strong geostrophic current, the Northern Current, which generally flows along the continental slope of the Gulf of Lions (Millot, 1999). The dominant forcing drivers in the area are the strong north-western (tramontane) and northern (mistral) winds which induce strong coastal upwelling activity (Millot, 1999, Agostini and Bakun, 2002), the western Mediterranean mesoscale circulation, and the fresh water input from the Rhone River (Petrenko et al., 2005). These drivers generate important primary and secondary production and the Rhone River is an important source of dissolved and particulate organic matter in this system (Lefevre et al., 1997; Gaudy et al., 2003; Harmelin et al., 2008). The Gulf of Lions shows a decreasing trend in nutrient concentration and production from east to west and from the continental shelf to deeper waters. The substrate is characterised by muddy and sandy bottoms. The area presents a high diversity of organisms and many aspects of their ecology and biology have been investigated over the past decades (Beaubrun, 1995; Labruno et al., 2007; Hermand et al., 2008; Mellon-Duval et al., 2009).

2.2 The Ecopath model

The Ecopath and Ecosim (EwE) modelling approach version 6 (Christensen and Walters, 2004; Christensen et al., 2008; Link, 2009; www.ecopath.org) was used to ensure the energy balance of the model of the Gulf of Lions' marine system. Ecopath has been widely used for constructing, parametrisation and analysis of food web models of aquatic and terrestrial

ecosystems. It led to generalisations on the structure and functioning of many marine ecosystems and has been used in fisheries assessments.

EwE divides the production (P) of each component or functional group (i) of the ecosystem into: (1) predation mortality (M_{2ij}) caused by the biomass of the predators (B_j), (2) exports from the system both from fishing activity (Y_i) and (3) other exports (E_i), (4) biomass accumulation in the ecosystem (BA_i) and (5) baseline mortality or other mortality ($1-EE_i$), where EE is the ecotrophic efficiency of the group within the system, or the proportion of the production of (i) that is exported out of the ecosystem (i.e. by fishing activity) and consumed by predators within it.

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

This equation can be re-expressed as:

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

where $(P/B)_i$ indicates the production of (i) per unit of biomass and is equivalent to total mortality, or Z, under steady-state conditions (Allen, 1971); $(Q/B)_i$ is the consumption of (i) per unit of biomass; and DC_{ij} indicates the proportion of (i) that is in the diet of predator (j) in terms of volume or weight units. EwE parameterizes the model by describing a system of linear equations for all the functional groups of the model, where for each equation three of the basic parameters: B_i , $(P/B)_i$, $(Q/B)_i$ or EE_i have to be known for each group (i). The energy balance of each trophic group (i) is given by the basic equation:

$$\text{consumption (i)} = \text{production (i)} + \text{respiration (i)} + \text{unassimilated food (i)}$$

When the system equations are solved they provide a snapshot of the trophic flow within the system. Units of the model are expressed in $t \text{ km}^{-2} \text{ y}^{-1}$ wet weight organic matter for flows and $t \text{ km}^{-2}$ for biomasses.

Input parameters of the Gulf of Lions model were : B (biomass), P/B (production/biomass ratio), Q/B (consumption/biomass ratio), EE (ecotrophic efficiency) for some groups, U/Q (assimilation rate estimated from the ratio unassimilated/consumed food), catch and discards, diet composition and net migration rate (estimated as “imports” in the diet).

The Automatic Mass Balance Procedure (Kavanagh et al., 2004) was used after having modified some data with higher uncertainty in terms of biomass. These changes concerned some invertebrates (benthic primary producers, zooplankton, cuttlefish-squids and echinoderms) and fish species (other planctonophagous fish, blue whiting, Atlantic horse mackerel and European conger). For the majority of these groups initial biomass was assessed by the swept area method applied to experimental trawl survey data. In these cases the alternative input of EE taken from other studies in similar areas in the literature was used to estimate the biomass of species/groups from the food demands of the upper levels and

fisheries. Anyway this is a weak point of the model because such parameter is context-dependent, functional group-dependent, but also dependent of the structure of the model (Christensen et al., 2005; Plagányi, 2007), the effect of this parameter is top-down (Steele, 2009) and it is a parameter that can not be estimated from the field.

The model was considered balanced when: (1) realistic estimates of the missing parameters were obtained ($EE < 1$), (2) values of production/consumption ratios (P/Q , or gross efficiency of food conversion) for functional groups were between 0.10 and 0.35 with the exception of fast growing groups with higher values and top predators with lower values, (3) values of respiration/biomass ratios (R/B) were consistent with the group's activities with high values for small organisms and top predators, (4) values of respiration/food assimilation ratios (R/A) were < 1 and values for top predators were higher, (5) values of net efficiency of food conversion were < 1 for all the functional groups (Christensen et al., 2005).

The “pedigree” of input data was recorded, identifying whether it was taken from a model of a similar system, or based on a rough or precise estimate from local data. These values were then used to assess model quality (Pauly et al., 2000; Christensen and Walters, 2004; Christensen et al., 2005).

2.3 Functional groups and data sources

The model is composed of 40 functional groups, including 5 groups of primary producers, detritus and discards, 12 groups of invertebrates, 18 groups of fish, 1 group of seabirds and 2 groups of cetaceans (Table 1, Appendix 1). It includes more than 99% of the exploited fish and invertebrate species in the Gulf of Lions.

All functional groups of the model were described in term of species composition and percentages of biomass in Table 1. Twelve fish species, the most important in term of landings in this area, were considered as individual functional groups in the model (Table 1). Other 29 fish species that are important for the fisheries and the food web were grouped. Cluster analysis using Ward method and mean distance between classes, based on the similarity of their diet produced 5 groups of fish (Appendix 2). The main preys of fish from each of these groups were: mesozooplankton, plants, fish, benthic crustaceans and other benthic invertebrates. Initially we had also other group of fish feeding on macrozooplankton, including blue whiting and Mediterranean horse mackerel which was finally separated as they have different biomasses and ecological role in the system. The group of fish feeding on fish, initially composed of pelagic and benthic-demersal species, was also separated for the same reasons into two groups. The pelagic fish group feeding on fish is composed of chub mackerel

and swordfish, while the benthic-demersal group includes raies, small-spotted catshark, East Atlantic red gurnard and two flat fish species.

Initial inputs and the diet composition matrix of the model are shown in Tables 2 and 3.

Definition of the groups was based on similarities in their ecological and biological features (feeding, habitat) and on the importance of the species in terms of fisheries.

Two size groups of pelagic primary producers were considered in the model: pico-nano and microphytoplankton, as in the pelagic compartment predation is known to be mostly size-dependent (Shin and Cury, 2004). Pelagic invertebrates were grouped according to size, as consumption is also often conditioned by size and sampling in this compartment is also generally focused on size. Gelatinous organisms were considered separately from the other macrozooplankton organisms because they have a different trophic role (Javidpour et al., 2009).

Some authors have chosen not to represent in their models the area between 0 and 10 meters or 50 meters because of the lack of knowledge and data on benthic primary producers and invertebrates (Coll et al., 2006, 2007; Tsagarakis et al., 2010). A preliminary analysis of the spatial distribution of the main commercial fish species in the Gulf of Lions showed that 60% of their biomass is located in the 0 - 50 meter area (Banaru, pers. comm., estimated from “International bottom trawl survey in the Mediterranean” (MEDITS) and “Pelagique Méditerranée” (PELMED) indices of biomass by species and by bathymetric strata).

Therefore, this area represents a very important feeding ground for most of the functional groups and we decided to include it in our study.

Benthic primary producers such as *Posidonia oceanica*, benthic macrophytes and microphyto benthos were included in the model. These groups represent important food sources in the area situated between 0 and 30 m.

Benthic and demersal invertebrates were grouped, based on published prey types of fish. The main commercial fish species were considered separately because better information about their different input parameters was available. This separation will further help in studying the impact of fisheries on the functioning the Gulf of Lions ecosystem. In addition to these 29 key commercial species, a hierarchical classification of the fish species according to their prey was performed to detect the other fish species/groups that have to be included in the model. Seabirds, dolphins and whales were also considered as functional groups in the model.

An annual average model was described, in which biomass, diet and species composition in different seasons were averaged according to available data and time series (Appendix 1).

When available, published and unpublished sources concerning the Gulf of Lions were used

to generate input parameters, but it was necessary to draw some parameters from the literature more widely in some cases.

Biomass (t km^{-2}) was estimated using satellite and literature data for the phytoplankton groups. For pelagic and benthic vertebrates and invertebrates, we used information from scientific surveys, especially recurrent aerial, acoustic and bottom trawl surveys that have been carried out by the French Research Institute for Exploration of the Sea (IFREMER) in the Gulf of Lions for several years/decades, as well as published information and results from the General Fisheries Commission for the Mediterranean (GFCM) stock assessment working groups for exploited fish populations (Appendix 1). Biomass of fish and invertebrates was estimated for each bathymetric stratum (0-2500 m). Mean biomass for the Gulf of Lions was estimated taking in account the weight of each stratum in the total surface area (Bertrand et al., 1998). Limited information was available for some groups, such as the benthic primary producers, and input parameters (P/B and Q/B) and the alternative EwE input were used to estimate the biomass of these groups from the food demands of the upper levels. Estimated biomass of birds and mammals was based on the number of resident and migratory species and individuals from the studied area (Appendix 1).

Detritus biomass was estimated from primary production using an empirical equation (Pauly et al., 1993). The microbial food web was not directly considered in the model, but it was indirectly considered within the box of detritus compartment (Calbet et al., 2002). We chose this parameterization because (1) inputs for the microbial food-web are scarce and difficult to estimate, (2) their flows could overshadow other trophic flows in the system (Christensen et al., 2005), and (3) previous models built for the Mediterranean Sea did not directly include the dynamic of the microbial food-web (see Pinnegar, 2000; Coll et al., 2006, 2007; Tsagarakis et al., 2010).

Production/biomass ratios (P/B) (y^{-1}) and consumption/biomass ratios (Q/B) (y^{-1}) were taken from the literature or obtained from the application of empirical equations (Palomares and Pauly, 1998; Christensen et al., 2005) using length and weight data (data sources in Appendix 1). The P/B values of the phytoplankton and zooplankton groups were estimated using in-situ data from published results (Appendix 1). Assimilation rates were compiled from published information. Input parameters (P/B, Q/B and sometimes EE) for the invertebrates were taken from models built in similar areas (data sources in Appendix 1). For fish, birds and mammals these parameters were estimated using empirical equations (Nilsson and Nilsson, 1976; Innes et al., 1987; Trites et al., 1997; Palomares and Pauly, 1998; Christensen et al., 2005). In the absence of information, steady state conditions were assumed with biomass accumulation (BA) = 0. Migratory patterns of some species (Atlantic bluefin tuna, some mammals, birds and

fish) were taken into account by “modelling” a proportion of the diet of these groups as “imports” to the system. For example Atlantic bluefin tuna living 6 months by year in the studied area was feeding 50% in the system and other 50% of his diet was coming from “imports”.

Diets were estimated using published information on stomach content analyses for fish, birds and mammals and stable isotope analyses for most of the invertebrate groups. Diets of invertebrates, birds and mammals originated from the studied area. Data on fish diets concerned the Gulf of Lions (33%), the Mediterranean Sea (80%), and the north-eastern Atlantic (20%) (Appendix 1). The weight of species’ diet in the functional group’s diet was proportional to their percentage of biomass in the group. The input parameters (P/B, Q/B and U/Q) of the mixed groups were estimated by weighting the inputs by the relative biomass of each species following default procedures (Christensen et al., 2005; Coll et al., 2006, 2007). Seven multi-species artisanal fleets operating in this area were included in the model: trawls (12-24m) and purse seine (<12m), trawls (24-40m), purse seine (12-24m), purse seine (>24m), gillnet (<12m <3 nautical miles), gillnet (<12m, 12-18m >3 nautical miles), other small gear (<12m, <3 nautical miles) (Demaneche et al., 2009). Trawls are operating in both bottom and mid-waters; large purse seines > 24m are targeting large pelagic fish while smaller purse seines 12 – 24m are targeting small pelagic fish.

Input concerning landings ($t\ km^{-2}\ y^{-1}$) was mostly based on two data sources compiled by IFREMER: (i) the R3 report that compiled observed landings of all fishing gears operating in the area in 2007-2008 and (ii) the IFREMER database (2002-2009) called “Harmonie” which is based on auction sales reports of French catches operated in the Gulf of Lions (Demaneche et al., 2009; Fisheries Information System, IFREMER). These data sources were completed by data on Spanish catches made in the Gulf of Lions for the 30 most important species/groups (B. Guijarro from IEO, pers. comm.). Landings registered in the R3 report for the Atlantic bluefin tuna (mostly juveniles) and European hake were likely underestimated (Fromentin, Jadaud and Mellon-Duval, pers. comm.). These values were corrected from the survey of the French purse seiners fleet operating in the Mediterranean Sea for the Atlantic bluefin tuna (Fromentin, pers. comm, mean values of landings 2001-2006) and stock assessment commissions (GFCM, mean values of landings 1998-2008) for the European hake. Discard data ($t\ km^{-2}\ y^{-1}$) concerned only some pelagic fish species (sardine and horse mackerel) and were based on a preliminary IFREMER report (IFREMER, 2009). In the Gulf of Lions very small individuals of all species are usually sold on markets and other discards are probably low (Farrugio, pers. comm.). Anyway this study does not include illegal, unreported and unregulated (IUU) fishing estimations such data were not available.

Two different Ecopath models were balanced using either the R3 or the Harmonie data (both completed by Spanish data) to compare the sensitivity of EwE parameters to different sources of landings.

2.4 Model analysis

Ecological indices were used to analyse fishing impacts based on trophic flow analysis, thermodynamic concepts, information theory and trophodynamic indicators (Christensen and Walters, 2004; Christensen et al., 2005; Cury et al., 2005).

Total trophic flows within the ecosystem in terms of consumption, production, respiration, exports and imports and flow to detritus ($t\ km^{-2}\ y^{-1}$) were quantified. The sum of all these flows, the Total System Throughput (TST), can be seen as an indirect indicator of the size of the ecosystem (Christensen and Pauly, 1993).

The Trophic Levels (TL) of the functional groups were also calculated. The TL was first defined as an integer identifying the position of organisms within food webs (Lindeman, 1942) and it was later modified to make it fractional (Odum and Heald, 1975). Following an established convention, a TL of 1 is attributed to primary producers and detritus, a TL of 2 to herbivores and detritivores, a TL of 3 to first order carnivores and a TL of 4 to second order carnivores. Thus, the TL can be formulated as follows: $TL_j = 1 + \sum DC_{ij} * TL_i$, where j is the predator of prey i, DC_{ji} is the fraction of prey i in the diet of predator j and TL_i is the trophic level of prey i. Trophic flows and TL can be represented in terms of a flow diagram by functional group.

From trophic flows and TLs, the Transfer Efficiency (TE) can be calculated, which summarizes all the inefficiencies of the food web (due to respiration, excretion, egestion and other natural mortality) present at each step of the trophic chain. Linderman spine is produced for aggregation of flows with the same number of steps (trophic links) (Lindeman, 1942). Detritus and primary producers were represented separated and linked. The TE is obtained by calculating the ratio between the production of a given TL and the preceding TL (Lalli and Parsons, 1993; Pauly and Christensen, 1995). Flows, TLs and TE were visualized in the form of a Lindeman Spine (Lindeman, 1942; Ulanowicz, 1986; Wulff et al., 1989; Libralato et al., 2002).

The Mixed Trophic Impact (MTI) analysis (Ulanowicz and Puccia, 1990), quantifies direct and indirect trophic interactions among functional groups. It provides a quantification of the positive or negative impact that a hypothetical increase in the biomass of a group would produce on the other groups in the ecosystem, including the fishery.

The net MTI (m_{ij}) was also used to estimate the overall impact ε_i on functional group j ,

$$\varepsilon_i = \sqrt{\sum_{j=1}^n m_{ij}^2}$$

where in m_{ij} the impact on the group itself is not considered. By plotting the overall impact (or relative total impact) ε_i versus the keystoneity (KS_i), we can identify keystone groups (groups that play an important role in the food-web with relatively low biomass) and the dominant groups (groups that play an important role and have a relative large biomass) in the ecosystem, as proposed by Libralato et al. (2006).

$KS_i = \log[\varepsilon_i(1-p_i)]$, where p_i is the relative biomass of the group, excluding detritus biomass.

The indicated keystone and dominant groups are system specific and may differ if the ecosystem is disturbed (Libralato et al., 2006; Coll et al., 2009; Coll and Libralato, 2011), thus this indicator is sensitive to changes in the food-web.

The exploitation rate (F/Z) is the ratio of the fishery-induced mortality (F) relative to total mortality (Z) and was used to assess the exploitation status of each functional group. The Primary Production Required (PPR) to sustain the fishery, the average Trophic Level of the Catch (TL_c), partitioning of mortalities, the Gross Efficiency of the fishery ($GE_f = \text{catch}/\text{primary production}$) and the relative consumption of total production, were analysed to place the fisheries within the ecosystem context (Cury et al., 2005). The PPR from the primary production and detritus (flows from $TL=1$), typically measured as $t \text{ km}^{-2} \text{ y}^{-1}$, is obtained by back-calculating the flows, expressed in primary production and detritus equivalents, for all pathways from the caught species down to the primary producers and detritus (Pauly and Christensen, 1995). It is formulated as: $PPR = 1/9 * \sum [Y_i * (1/TE)^{TL_i-1}]$, where Y_i is the catch of a given group (i), TE is the mean transfer efficiency, TL_i is the trophic level of group (i) and factor $1/9$ is taken as the average conversion coefficient from wet weight to g C. This index can be expressed per unit of catch relative to the primary production and detritus of the ecosystem (%PPR). The TL_c reflects the overall strategy of a fishery and is calculated by weighting the proportions of each type of organism from the catch and its TL (Pauly et al., 1998).

Odum's ecological indicators related to the ecosystem development theory (Margalef, 1968; Odum, 1969; Christensen, 1995) were also analysed. These indicators included: (a) various coefficients of flows and biomasses (total primary production/ total respiration, total production / total biomass and total biomass / total system throughputs); (b) the Finn's cycling index (which describes the fraction of the throughput that is recycled) and predatory cycling index; (c) the System Omnivory Index (SOI, which measures the distribution of the trophic interactions among trophic levels); and (d) the Ascendency, which is related to the average

mutual information in a system scaled by the TST (Finn, 1976; Ulanowicz, 1986; Christensen et al., 2005). The average mutual information describes the uncertainty about where a unit of energy will flow next if we know its location (Ulanowicz and Norden, 1990).

Several models were previously built in the Mediterranean (Catalan, Adriatic and Aegean Seas) (Coll et al., 2006; Coll et al., 2007; Tsagarakis et al., 2010) and Atlantic (Cantabrian Sea) (Sánchez and Olaso, 2004). Even if similitudes exist between these models and the Gulf of Lions' model, the comparison was not possible because they cover different bathymetric areas, have differences in the model structure, the definition of some groups and parameters.

3. Results

3.1 Output parameters

Resulting output parameters of the model are shown in Table 4. Excluding detritus, 21% of the biomass was allocated to the phytoplankton groups, 11% to zooplankton, 10% to benthic primary producers, 26% to demersal and benthic invertebrates groups, 16% to small pelagic fish and 15% to other fish groups. The biomass of birds and mammals represented less than 1% in the system. The biomass was almost equally distributed between pelagic and benthodemersal compartments.

EE of the phytoplankton groups, as well as detritus and discards, were rather low and flows to detritus from these groups were high. Fish presented generally high EE values, except for Atlantic mackerel, Mediterranean horse mackerel, fish (feeding on fish) (Table 4). For some species or groups ecotrophic efficiencies (EE) were initially higher than 1 (i.e. gelatinous zooplankton, cuttlefish-squid, octopus, other planktonophagous fish, blue whiting, Atlantic horse mackerel, European conger and fish feeding on benthic crustaceans). In this case EE values come from the literature from other model in close areas.

Phytoplankton groups and worms showed the highest flows to detritus, followed by zooplankton groups, European pilchard and benthic crustaceans (Table 4).

Production/consumption ratios (P/Q) and net food conversion efficiencies were within the expected range (Christensen and Walters, 2004). These values were very low (or null) for marine mammals and birds, around 0.1 to 0.4 for most of the fish and large invertebrates while exceeding 0.45 for zooplankton (Table 4). Omnivory index was highest for juvenile Atlantic bluefin tuna and seabirds and lowest for European anchovy and other planktonophagous fish (Table 4).

3.2 Trophic levels and trophic flows

Functional groups were organised into five trophic levels (Fig. 2). The trophic level of the groups ranged from 1 for primary producers up to 4.83 for dolphins. Invertebrates had trophic levels between 2.05 for microzooplankton and 3.88 for cuttlefish and squid, while the trophic levels of fish were around 3 for small pelagic fish species and higher for predator species such as anglerfish (4.45), European conger (4.16), juvenile Atlantic bluefin tuna and European hake (4.14) (Table 4).

There is high coupling through consumption between the pelagic, the demersal and the benthic compartments (Fig. 3). From this perspective, phyto and zooplankton are consumed by demersal and benthic invertebrates ($88 \text{ t km}^{-2} \text{ y}^{-1}$), which are consumed by demersal invertebrates and fish ($2.5 \text{ t km}^{-2} \text{ y}^{-1}$). Small pelagic fish are consumed by demersal and benthic predator fish ($3.2 \text{ t km}^{-2} \text{ y}^{-1}$) and small benthic fish are consumed by demersal fish ($0.6 \text{ t km}^{-2} \text{ y}^{-1}$). Demersal predators thus play an important top-down control role in the food web, while the highest flows in term of biomass are due to bottom-up control in relation to the phytoplankton productivity.

The main flows ($\text{t km}^{-2} \text{ y}^{-1}$) between trophic levels are schematically represented through the Lindeman flow diagram, where primary producers and detritus were separated to clarify the representation (Fig. 4). High flows to the detritus originated from the primary producers and TL 2. Different export values by catches were obtained according to data sources, i.e. R3 report and auction sales database, and were lower in the second case. Catch flows are highest at the TL 3 ($1.140 \text{ t km}^{-2} \text{ y}^{-1}$). The highest predation flows are within TL 1, 2 and 3, while flows in the upper TLs were very low. The average transfer efficiency ($\text{TE} = 19\%$) and the fraction of the total flows (that is either exported or transferred to other trophic levels through consumption) were high. Values of TE for flows between the 2rd and 3rd were also high and these values decreased progressively between the 2rd-3rd and the 4th-5th trophic levels.

3.3 Consumption

The most consumed groups in the food web were phytoplankton (53%), zooplankton (21%), detritus (12%) and worms (9%) (Fig. 5a). The consumption of biomass of all the other groups (including fish) represented less than 5%. Among fish, the most consumed in the food web were the European pilchard (32%), the group of other planctonophagous fish (19%), the blue whiting (16%), the European anchovy (15%), the Atlantic mackerel (7%), and the group of

fish (feeding on benthic crustaceans) (5%) (Fig. 5b). The consumption of all the other fish species represented less than 4% (Table 4).

The biomass produced by the exploited fish species was mainly consumed by fish (77%) or exploited by fisheries (18%). The consumption of fish by cephalopods (5%) and other groups thus remained secondary.

3.4 Mortality

For most of the invertebrates and fish, especially worms, gastropods, cuttlefish and squids, benthic crustaceans, other planktonophagous fish, blue whiting, poor cod, fish feeding on benthic crustaceans and fish feeding on polychaetes, mortality was mainly due to predation. However, fishing was the main cause of mortality for some species, such as octopus, the group of fish feeding on plants, Atlantic bluefin tuna, European hake, Atlantic horse mackerel, anglerfish, European conger and gilthead seabream (Table 4).

Interestingly, for the European pilchard and European anchovy which include the highest landings in this area, the mortality was firstly due to natural causes (M_0), followed by predation and to a lesser extent by fishing. Among the most important consumers of the European pilchard were the European hake (37%), cuttlefish-squid (35%) and Atlantic bluefin tuna (13%). For the European anchovy the main consumers were Atlantic bluefin tuna (32%), Atlantic mackerel (19%) and European hake (12%).

3.5 Summary statistics

Results from the ecological model in terms of aggregated summary statistics, network flows and information indices are shown in (Table 5). The total consumption and the flow to detritus dominated the Total System Throughput ($TST \text{ t km}^{-2} \text{ y}^{-1}$) and would represent 36.9% and 37.1% of the total flows, respectively. Indices related to Odum (1969) theory and the maturity of the system like total primary production/total biomass, connectance index, Finn's cycling index, omnivory index, ascendancy and overhead showed a rather low developmental stage of the Gulf of Lions system (Table 5). Applying EwE on the two sources of landings data modified the total catches (2.131-1.274), the mean trophic level of catches (3.24-3.35), the gross efficiency (0.002-0.001) and the primary production required to sustain the fisheries reported to the total primary production (13.58-10.28).

3.6 Mixing trophic impact

Interactions within the ecosystem, analyzed using the Mixed Trophic Impact (MTI) routine, are shown in Fig. 6. These analyses describe increases or decreases in the biomass of a group that are to be expected if hypothetical changes in the biomass of another group occur. Direct impact resulting from trophic interactions can be underlined but also indirect impact due to prey availability and niche overlapping as well as to cascade effects. For example, European pilchard had a direct positive effect on their predators (such as cuttlefish-squid and hake) and a direct negative impact on their main prey (mesozooplankton). It had also an indirect negative impact on their competitors such as European anchovy and other planktonophagous fish. Through a cascade effect European pilchard negatively impacted the Atlantic mackerel and Mediterranean horse mackerel which prey on macrozooplankton and which was a competitor of the European pilchard for the mesozooplankton. Main beneficial predators were Atlantic mackerel and fish (feeding on benthic crustaceans). Numerous functional groups in the model were impacted by groups at the base of the food web such as detritus, phytoplankton, zooplankton, worms and benthic crustaceans. European pilchard, European anchovy, and blue whiting also showed a strong impact on numerous functional groups of higher and lower TLs.

3.7 Relative total impact and keystone index

Sea birds, dolphins and cuttlefish-squids had the highest keystone index and very low biomass and were considered as keystone species. Fish such as Atlantic mackerel, fish feeding on benthic crustaceans, European pilchard and blue whiting, as well as some invertebrates (mesozooplankton, benthic crustaceans, echinoderms and bivalves – gastropods) had a very important role in the food web (Fig. 7). These groups had high biomass and were considered as dominant species/groups in the ecosystem. Forage groups, such as small pelagic fish, had high impact on many other groups of higher and lower trophic level in the Gulf of Lions.

3.8 Fisheries and their impact on the functional groups

European pilchard and European anchovy represented the main species caught and landed in the Gulf of Lions, representing 39% and 11% respectively (Fig. 8). Other fish species such as: Atlantic mackerel, fish feeding on benthic crustaceans, European hake, poor cod, Atlantic bluefin tuna and fish feeding on polychaetes, as well as some invertebrates (bivalves-gastropods and octopuses) showed high values in landings (Fig. 8; Appendix 3).

The detail of landings by gear and by species from the R3 report is presented in Appendix 3. Data on landings from auction sales are indicated for comparison in Appendix 4, but only in R report the detailed values by species were available. The highest landing were made by large trawls (24-40 m) targeting mainly European pilchard and lowest ones by purse seine (> 24m) and gillnets (<12m, 12-18m, >3nm) targeting Atlantic bluefin tuna. Total landings in R3 report were 67% higher than in the auction sales database. Spanish catches represented 3.1% of the total R3 catches.

Fisheries were operating at mean trophic levels situated between 2.6 for other small gears, 3.2 to 3.8 for gillnets, 3.3 to 3.4 for trawls, 3.0 for small purse seine (12-24 m) and 4.1 for large purse seine (24-40 m).

Large trawls (24-40 m) had the highest landing rates and the most strongly negative impact on the majority of the groups as it is a multispecific gear, while small purse seine (12-24 m) had low landing rates and the lowest impact as it targeted mainly the European pilchard (Fig. 9). In general, negatively impacted species were targeted species, while main prey (phyto and zooplankton, benthic crustaceans, other planctonophagous fish, blue whiting, fish feeding on benthic crustaceans) and competitors (gelatinous organisms) were generally positively impacted by cascade effects.

4. Discussion

The present paper describe the structure and the functioning of the Gulf of Lions's marine system and estimate the relative impact of the different fishing gear operating in this area. This is the first ecosystem model, including high trophic levels, conceived for this area. Similar Ecopath models were constructed in different areas in the Mediterranean sea: Catalan, Adriatic and Aegean seas (Coll et al., 2006, 2007; Tsagarakis et al., 2010). However it is rather difficult to compare these models as they were not always constructed on the same areas, for the same periods, with the same compartments and parameters. This model includes coastal area (0-50 m) with higher biomasses and goes up to deep waters (2500 m) with lower biomasses that the rest of the continental shelf and slope that was generally considered in the other models in the Méditerrananean sea (Coll et al., 2006, 2007; Tsagarakis et al., 2010). Only the Cantabrian Sea' Ecopath model considered a similar large area (0-2000 m) (Sánchez and Oloso, 2004).

The Ecopath model of the Gulf of Lions has more photoplankton and zooplankton groups that the other models and this may affect the trophic level. However TLs in this model were in accordance with previous results for the Mediterranean and Cantabrian Seas (Stergiou and Karpouzi, 2002; Sánchez and Oloso, 2004; Coll et al., 2006, 2007; Tsagarakis et al., 2010).

Most of the species and groups of species showed similar trophic levels between the gulf of Lions and the Catalan and Adriatic Sea. There were some differences for the horse mackerels, mackerels and dolphins which showed lower values than in our study. More differences appeared with the results from the Aegean Sea where sardine and anchovy had higher trophic levels than in the gulf of Lions, while horse mackerels, seabirds and dolphins showed lower trophic levels.

Coupling between the pelagic and demersal-benthic compartments was also noticed in other systems (Coll et al., 2006, 2007; Tsagarakis et al., 2010).

The highest predation flows were within TL 1, 2 and 3, while flows in the upper TLs were almost insignificant, similarly to other systems (Coll et al., 2006, 2007; Tsagarakis et al., 2010).

The average transfer efficiency was higher than in other marine systems (Coll et al., 2006, 2007; Tsagarakis et al., 2010), probably because for some groups EE was fixed to high values. Other explanations could be that low trophic level production or biomass is underestimated, or that this is real and this high TE% is produced by large impact of removing production of the system due to fishing. Values of TE for flows through TL 2 and TL 3 were high, both suggesting good coupling between zooplanktivores and detritivores and their predators (Baird et al., 1991).

Other authors highlighted the importance of small pelagic fish species, particularly European pilchard and European anchovy as forage species within the Mediterranean foodwebs (Coll et al., 2006, 2007; Tsagarakis et al., 2010). These species represent key link groups in terms of consumption and flows between pelagic primary producers and consumers from both the pelagic and the demersal compartments.

Gelatinous organisms seemed to be less important in the Gulf of Lions than in the Catalan, Adriatic and Aegean seas (Coll et al., 2006, 2007; Tsagarakis et al., 2010) because their biomass was probably underestimated and thus their importance may be underestimated. Pauly et al. (2009) also reported these problems in jellyfish parametrization.

Mortality values were in agreement with the range of values from stock assessment (Lleonart, 1990; Jadaud, pers. comm.; Roos, pers. comm.), where most of the groups showed high predation mortality.

Fishing is an important pressure component in the Gulf of Lions food-web as it is responsible for a high rate of “consumption” of the fish compartment, similarly to the case in other Mediterranean ecosystems (Coll et al., 2006, 2007). Results related to fisheries like mean trophic level of the catch, gross efficiency, primary production required to sustain fishery/total primary production and total catch were different in the two models using the two

different fisheries databases and highlights the importance of these data for an eventual modelling support to the management of these resources.

The mean trophic level of the catches was rather low, similarly to other models applied in the Mediterranean sea (Coll et al., 2006, 2007; Tsagarakis et al., 2010), but it was higher than in the Black sea (Banaru et al., 2010b) and lower than in the Cantabrian Sea (Sánchez and Olaso, 2004).

Atlantic mackerel had in the Gulf of Lions the highest role as a dominant group, just like in the Cantabrian sea system (Sánchez and Olaso, 2004). Sea birds and dolphins were keystone species like in other Mediterranean ecosystems (Coll et al., 2007). Small pelagic fish, had high impact on many other groups in the Gulf of Lions, like in other marine ecosystems (Coll et al., 2006, 2007), highlighting the importance of these groups as forage species in the ecosystem and possible wasp-waist predator-prey interactions (Cury et al., 2000).

4.1 Improvements and limits of the data sources

The pedigree index score of 0.67 implied a moderate quality of the data sources (Morissette, 2007), similar to other studies for the Mediterranean and Cantabrian seas (Sánchez and Olaso, 2004; Coll et al., 2006, 2007; Tsagarakis et al., 2010). However, in order to develop future Ecosim and Ecospace scenarios, based on Ecopath, some input data need to be reviewed or improved.

Phytoplankton biomass was estimated using satellite data on surface chlorophyll and a model estimating the euphotic depth. Values obtained were similar to those of previously published data. We might also compare them with results from a coupled physical and biochemical model in the Gulf of Lion - Symphonie Eco3M (Diaz and Campbell, pers. data), in order to see whether results are similar.

Zooplankton data were obtained from published in situ sampling campaigns (1998-1999). One may wonder whether the sampled period is representative or not for the entire modelled period, acknowledging that zooplankton presents large annual variations in terms of biomass, production and species composition. Results for these parameters might also be compared with the same coupled physical and biochemical model in the gulf of Lion - Symphonie Eco3M (Diaz and Campbell, pers. data).

At the same time, the Ecopath model may provide data on the consumption of phyto- and zooplankton by the organisms from the upper trophic levels. Future end-to-end models might be constructed by forcing/coupling Ecopath with Ecosim and Ecospace (high trophic level

models) with the coupled physical and biochemical models (low trophic level models) existing for this area.

For the benthic primary producers more studies concerning the area covered in the Gulf of Lions need to be undertaken. Available data on benthic invertebrates in terms of biomass by taxonomic and trophic group concerned mainly the coastal area (0 -100m), but data for between 100 and 2500m were rather poor. Data on diet, and only for the coastal area (0 - 100m), were deduced from stable isotope analyses performed on some species and then extrapolated to taxonomic groups. Further data regarding species composition, spatial distribution, biomass and diet are necessary for all benthic invertebrates. Production/biomass and consumption/biomass reports were taken from other models from similar areas. Some studies showed wide variability in the values from these reports for the same species in different systems, and even wider among the same taxonomic group in different areas (Arias-Gonzales, 1984). Knowledge about each species' diet, productivity and consumption is necessary when grouping species, in order to achieve a better estimation of group's parameters.

Biomass of most fish and invertebrate species were estimated only in summer time (PELMED, MEDITS surveys) and should be completed with data concerning the other seasons. Migrations of some of fish species should also be better quantified.

For some species or groups, ecotrophic efficiencies (EE) were initially higher than 1 indicating that the initial biomass was probably underestimated. Their biomass had been estimated from the literature or assessed by experimental trawl surveys, which is not appropriate for all these species, as shown by the report between final biomass estimated by the model and initial biomass (Tables 2 and 4). Most of these groups are pelagic and demersal and their habitat is mainly located in the coastal area (<10m) which is not covered by the scientific surveys. Therefore, input parameters (P/B and Q/B) and the alternative input of EE taken from the literature were used to estimate the biomass of these groups using the food demands of the upper levels and fisheries landings. This method led to an increase in their biomass but also in the demand on other functional groups (zooplankton, echinoderms and fish), that are prey of the previous groups, and these biomasses were also raised (Table 4). More studies are necessary and other methods should also be implemented (virtual population analysis, acoustic methods, etc.) in order to improve these data.

We noted that the same difficulty of estimating the biomass of some demersal and benthic fish and invertebrates has been already stressed by other authors who modified initial estimated biomass of some functional groups (see Pinnegar, 2000; Sánchez and Olaso, 2004; Coll et al., 2006, 2007; Tsagarakis et al., 2010).

Production and consumption parameters calculated using empiric equations (fish, birds and mammals) need to be validated with in situ measures on the studied species. The diet of some species (octopus, cuttlefish and squid, European pilchard, other small planktivorous fish species, Atlantic bluefin tuna, horse mackerels, mackerels, blue whiting, anglerfish, European conger) should be studied in the Gulf of Lions, as feeding behaviour may differ according to areas and to available food resources.

Bird and mammal abundance observations were made mainly in summer. These data need to be completed during all seasons and knowledge on their daily/seasonal behaviour; diet and migration patterns should also be improved.

The biomass of detritus originating from primary producers and estimated with an empiric equation was probably overestimated. Comparing this parameter with outputs from the other models (Symphonie-Eco3M) may improve the results. The lack of knowledge on the migration patterns of organisms and biomass accumulation in the system, probably increased the flows to detritus of the biomass non-consumed and non-exploited in the system.

There were wide differences in some species landings registered in the two data sources used in this study (Appendix 4). Auction sales databases underestimate catches because they included mainly data on catches from large boats (purse seine, trawls, some gillnets). On the other hand, the differences between auction sales databases and the detailed R3 report based on observed landings (Demaneche et al., 2009) were so wide for some species that we wonder whether they corresponded to reality, knowing that the number of observations was sometimes very low. The bottom trawling and mid-water trawling are merged in the analysis of gears impacts due to data availability. This is a limitation because these fleets likely target very different commercial species thus it is impeding to properly assess the role and impact of these two distinct fleets. In order to improve the Ecopath results and to build future Ecosim scenarios, improvements in landings databases are thus required. A big challenge, particularly in the Mediterranean Sea, is not only to include better catch, discards and effort data but also to assess and estimate Illegal Unreported Unregulated (IUU) fisheries considered one, if not the major, threat for marine biodiversity in the Mediterranean Sea.

Grouping of species according to diet should also be carefully analysed. For example in our study we first grouped blue whiting and Mediterranean horse mackerel, both consumers of macrozooplankton. Consumption in this group was high mainly because of the predation on the blue whiting but the biomass was mainly accounted for by the Mediterranean horse mackerel. The biomass of the blue whiting assessed by experimental trawl survey is highly underestimated because this species is mainly located in the water column on the continental slope and this area is difficult to sample. To balance the model, we had to raise the biomass of

the group, but this resulted in cascade effects on the prey of the Mediterranean horse mackerel and the biomass of other functional groups was also raised. Finally we chose to treat separately the two species in this group. This is an example of the effect of grouping species. We have to keep in mind that the structure of this model is mainly based on functional groups constituted of many species, some of them, such as benthic invertebrates with ecological and biological traits that are still poorly known in this area, taken from other areas or estimated using empirical equations.

Previous models were confronted with similar difficulties concerning data sources and limits. It is important to highlight these limits and to try to improve the quality of data as in the future these models might probably be used as a basis for management decisions.

Although some deficiencies in available biological and landings data sources have been identified, the model quality was satisfactory (as indicated by the pedigree index of 0.67).

The model is good enough to provide results on the structure and functioning of the ecosystem in the Gulf of Lions, on key species, flows and fishing impacts.

5. Conclusion

Ecosystem modelling can increase our understanding of fisheries impact on the whole food webs and not solely on targeted species. There is little consensus concerning the conceptual and analytical tools that should be used to study trophic interactions in ecosystems (Walters et al., 1997). The last two decades have seen a tremendous growth in the number and type of multispecies models designed for the study of fisheries impact (reviewed in Hollowed et al., 2000; Whipple et al., 2000), each having certain benefits and limitations. The mass-balance approach incorporated in the Ecopath software has been the most popular and is widely used to represent marine food webs and to address issues relevant to fisheries management (Pauly et al., 2000).

The present model constitutes the first mass-balance model to characterise the structure and the functioning of the food web in the Gulf of Lions and to quantify fisheries impact. It represents an important effort to synthesize the best available data on all the functional compartments of this ecosystem. The main results indicated that:

- Functional groups were organised in five trophic levels, with anglerfish, European conger, juvenile Atlantic bluefin tuna and European hake, as top predators.
- European pilchard and European anchovy represented the most important species in term of landings but also key link groups in the food web in term of consumption and flows between pelagic primary producers and consumers. Other fish species with high

biomasses, such as Atlantic mackerel, fish (feeding on benthic crustaceans) and blue whiting had a high impact in the food web. Sea birds, dolphins and cuttlefish-squids represented keystone species.

- There was high coupling between the pelagic, the demersal and the benthic compartments. Demersal predators like hake thus played an important top-down control role, while the highest flows in term of biomass were due to a bottom-up control in relation to the phytoplankton productivity.

- Large trawls (24-40 m) had the most negative impact on the entire ecosystem and on the majority of the groups in the food web, while small purse seines (12-24 m) had the lowest impact.

- Indices calculated by the model and the percentage of fish production exploited by fisheries showed that the Gulf of Lions ecosystem was highly exploited.

The advantages of having an Ecopath model for the Gulf of Lions is to give a global image of the ecosystem, to identify important elements of its structure, interactions between groups and species and also to highlight incomplete and missing data on some groups in order to orientate future studies and improve these data and model analysis.

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<http://oceancolor.gsfc.nasa.gov>

www.ecopath.org

www.fishbase.org

Figures captions

Figure 1. Study area situated in the Gulf of Lions (north-western Mediterranean Sea).

Figure 2. Structure of the pelagic, demersal and benthic food web. The links between the different compartments show the trophic flows. Continuous arrows indicate main flows and dotted arrows indicate less important flows.

Figure 3. Representation of coupling (flows of biomass between pelagic - demersal and benthic - demersal compartments) through consumption. Flows to detritus were not considered and flows to/from other groups not involved into coupling between compartments were not represented. Numbers between brackets represent groups numbers (cf. Table 1). Demersal fish play a highly important top down control in the system and in coupling processes. The arrows are proportional to the consumption trophic flows.

Figure 4. Lindeman spine of the Gulf of Lions's EwE model: flows between trophic levels (model based on R3 report). P = primary producers, D = detritus, 2-5 = trophic levels (TL).

Figure 5. Consumption of the biomass produced by the functional groups in the food web: a) consumption of all groups b) consumption of fish.

Figure 6. Graphic representation of the mixed trophic impact of each functional group on the other groups.

Figure 7. Relative total impact versus keystone index (KS_i) (Libralato et al., 2006) showing the role of species/groups in the ecosystem. The size of the circles is proportional to their biomass. Groups such as seabirds and dolphins with high keystone index and low biomass were considered as keystone species, while groups with high relative total impact, keystone index and biomass such as Atlantic mackerel were considered as dominant species.

Figure 8. Composition of total annual landings in the Gulf of Lions in 2007-2008 (based on data from R3 report).

Figure 9. Graphic representation of the cumulate impact of the fishing gears on the Gulf of Lions' system induced by direct or cascade effect. The cumulate impact of a gear is the sum of its impacts on all model groups (excepting the other gears) and is based on the results from the MTI method. Excepting purse seine 12-24 m, all the gear had negative values of the total impact.

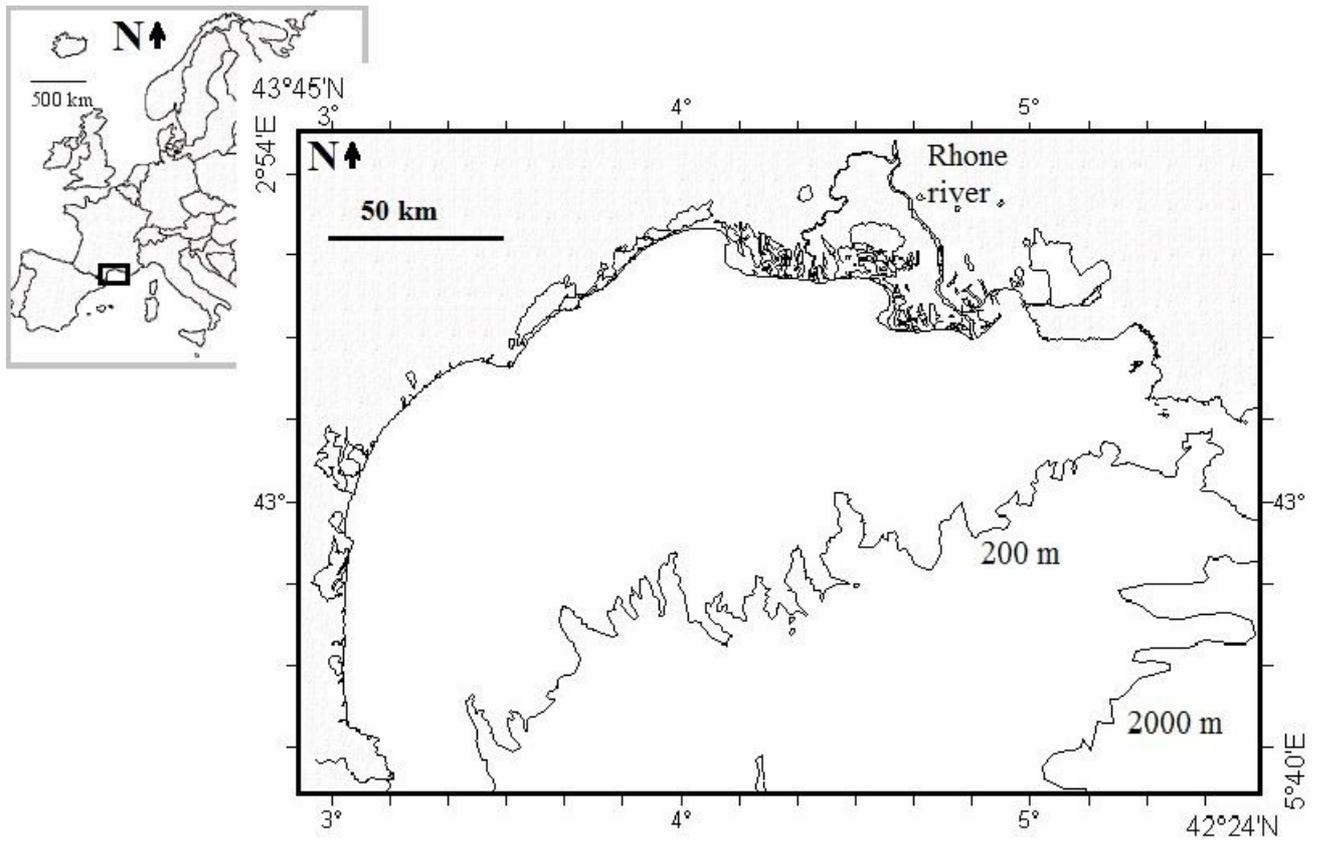


Figure 1.

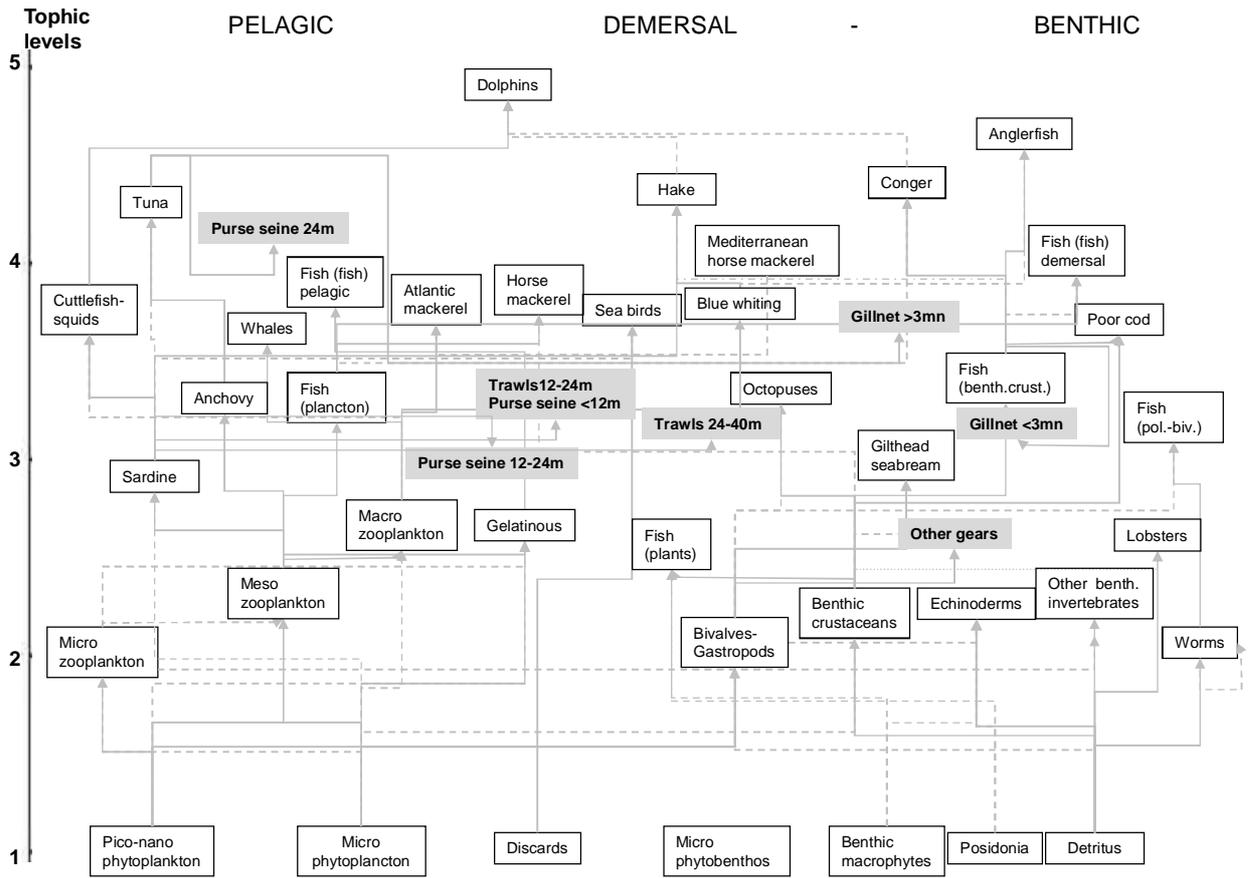


Figure 2.

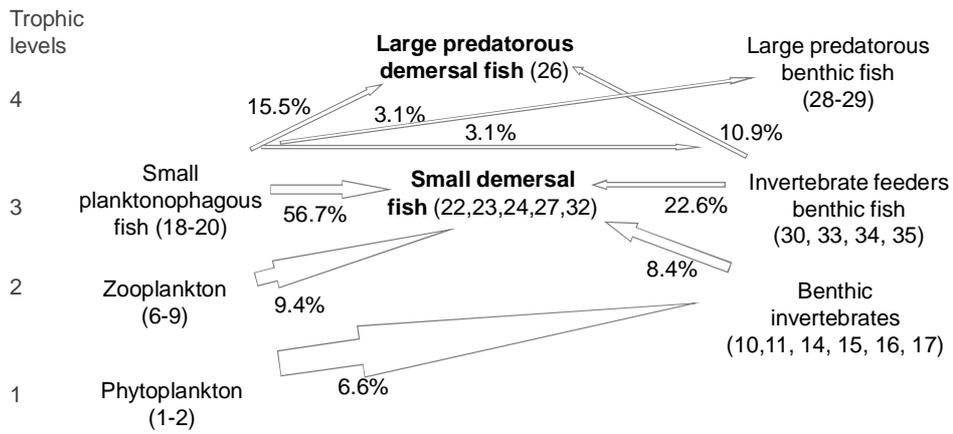


Figure 3.

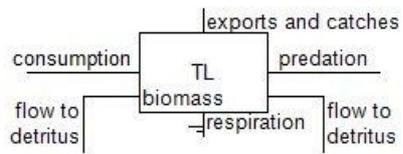
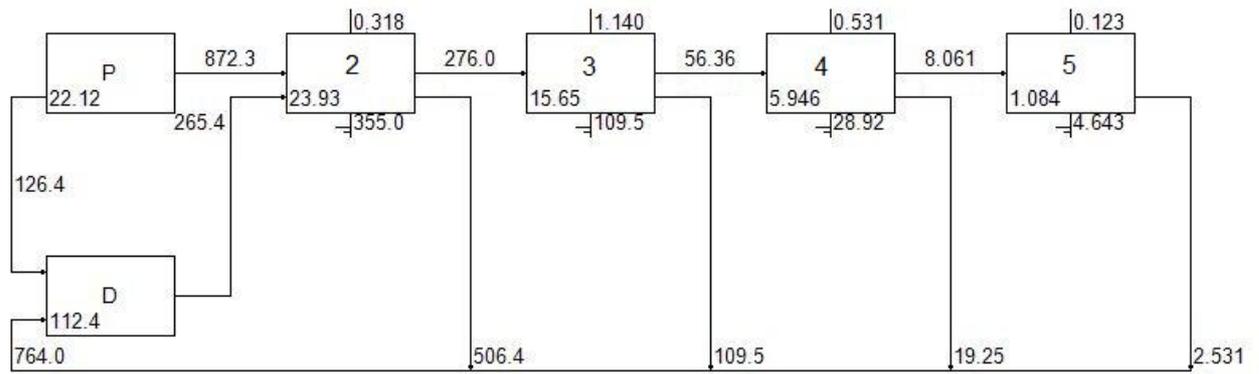
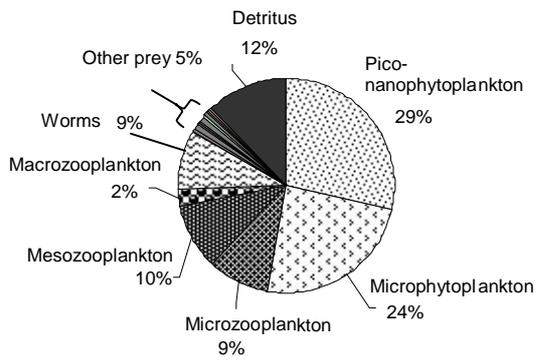
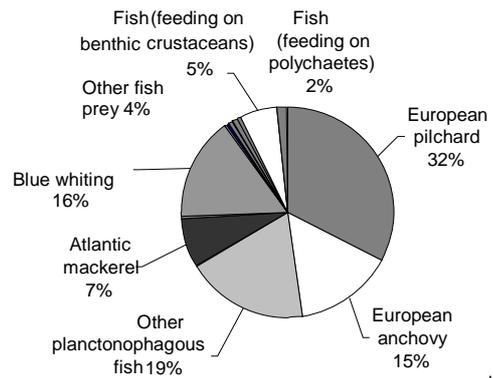


Figure 4.



a



b

Figures 5a, 5b.

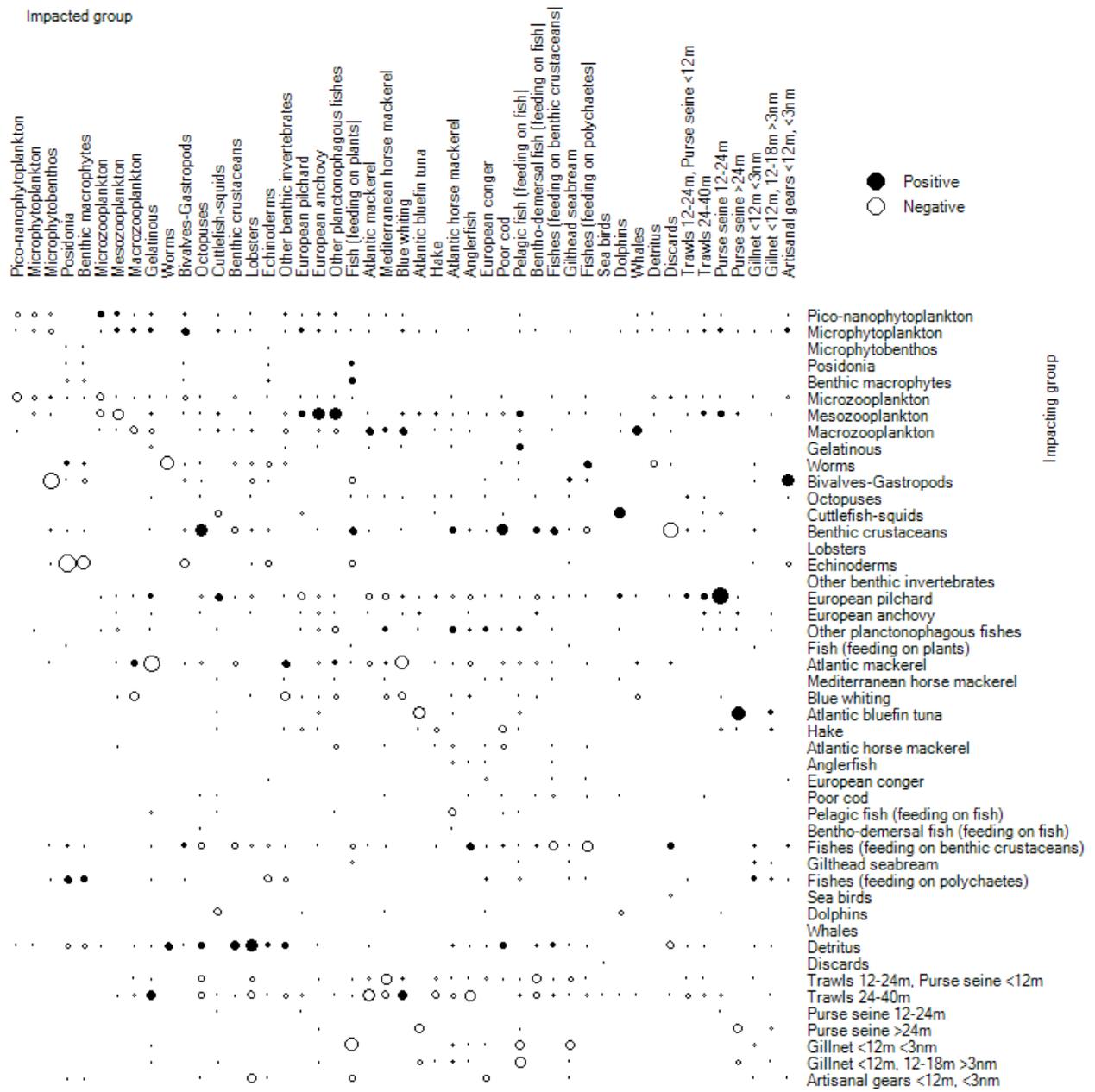


Figure 6.

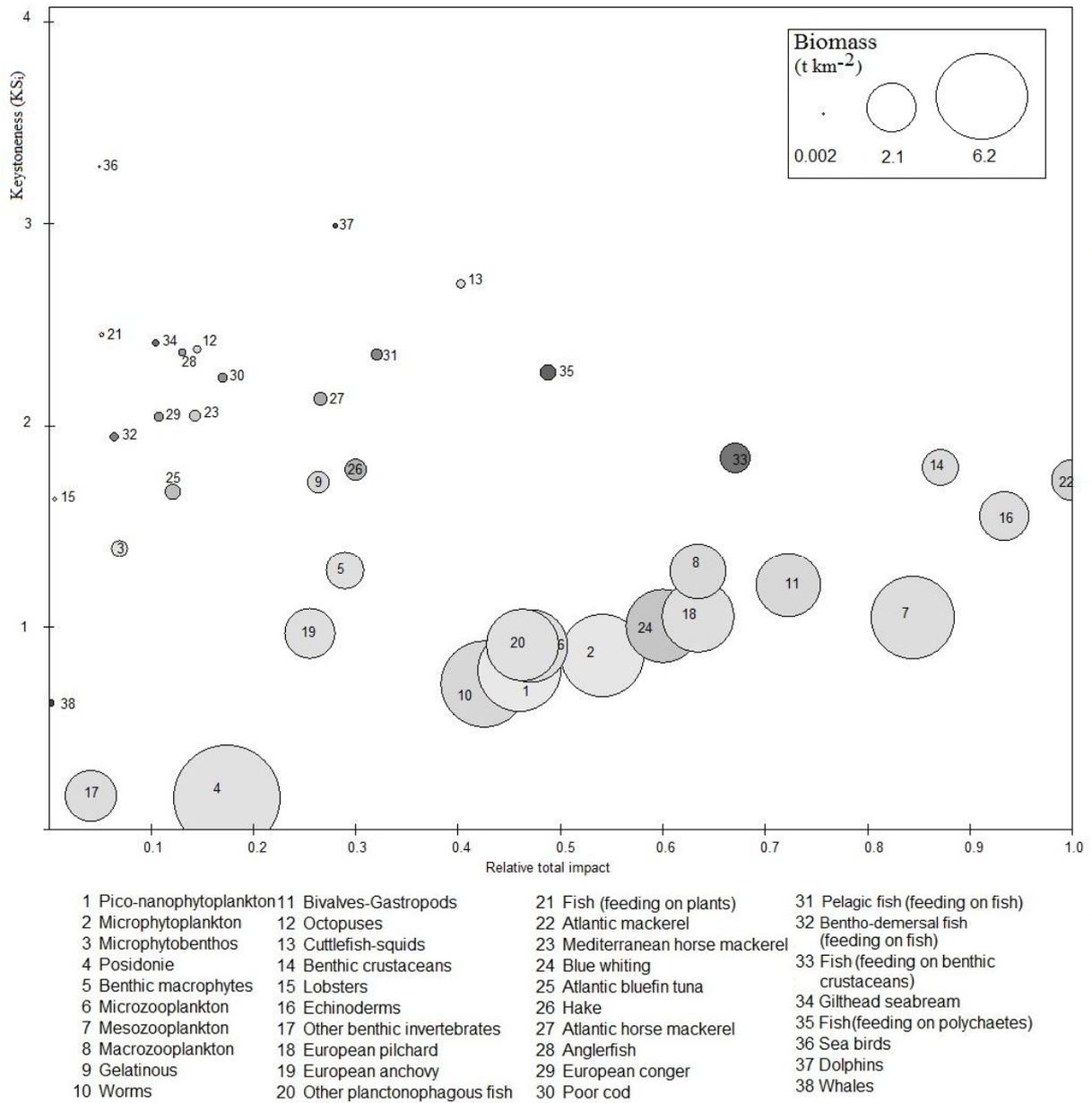


Figure 7.

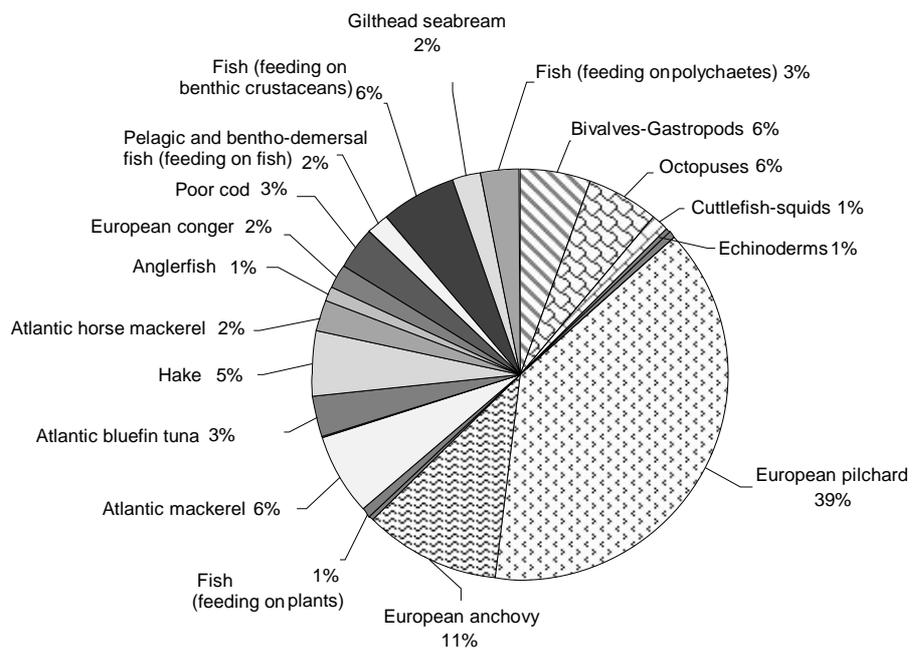


Figure 8.

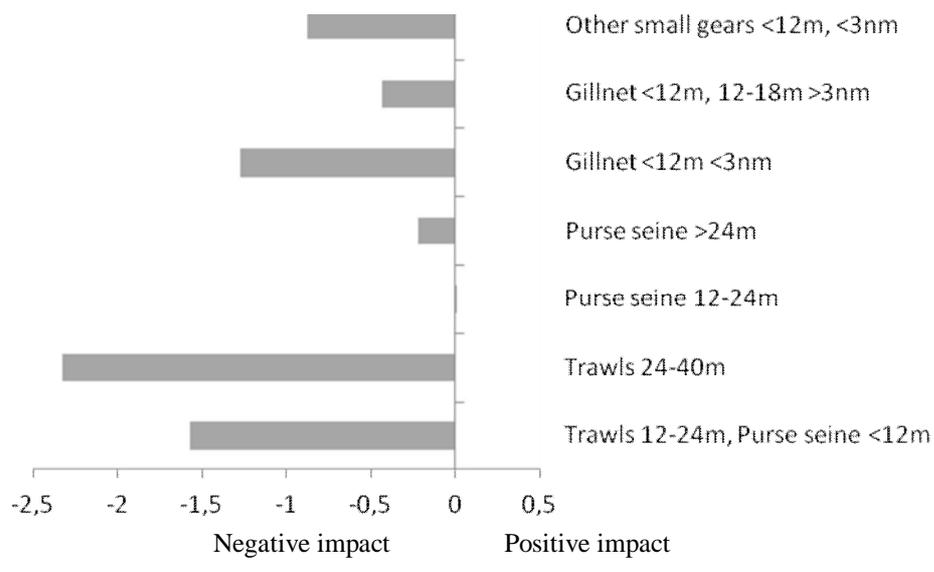


Figure 9.

Table 1. Description of the functional groups of the Gulf of Lions' Ecopath model.

Functional group	Common and latin names of species/groups and their percentages	
1	Pico-nanophytoplankton	autotrophe bacteria, pico-eucaryotes (<i>Synechococcus</i>), autotrophe nanophytoplankton (<i>Mesodinium</i>)
2	Microphytoplankton	diatoms, dinoflagellates
3	Microphytobenthos	spp.
4	Posidonia	<i>Posidonia oceanica</i> leaf (blade and sheath)
5	Benthic macrophytes and epibionts	spp.
6	Nano-microzooplankton	ciliats, eggs and nauplii of copepods, small cladocerans, pteropods, euphausiids, mysids
7	Mesozooplankton	copepods, cladocerans, pteropods, euphausiids, mysids, amphipods, ostracods, fish and invertebrate eggs and larvae
8	Macrozooplankton	krill, fish and invertebrate eggs and larvae, pteropods, euphausiids, mysids, amphipods
9	Gelatinous zooplankton	siphonophorae, tunicate (salpida, doliolida, appendicularia), hydromedusae, ctenophora, chaetognatha
10	Worms	nematods and annelids
11	Bivalves and gastropods	spp.
12	Octopuses	<i>Octopus</i> spp., <i>Eledone cirrhosa</i> , <i>E. moschata</i>
13	Cuttlefish and squids	<i>Sepia</i> spp., <i>Sepietta</i> spp., <i>Sepiolo</i> spp., <i>Ilex coindettii</i> , <i>Loligo</i> spp., <i>Todarodes</i> spp., <i>Allotheuthis</i> spp., <i>Histioteuthis</i> spp.
14	Suprabenthic and benthic crustaceans	mysids, amphipods, isopods, cumaceans, benthic copepods, euphausiids, pagurids, shrimps, brachyurids
15	Lobsters	<i>Nephrops norvegicus</i> , <i>Palinurus</i> spp., <i>Homarus vulgaris</i>
16	Echinoderms	echinids, asterids, ophiurids, crinoids, holothurians
17	Other benthic invertebrates	cnidarians, sponges, tunicats, siponcles, etc
18	European pilchard	<i>Sardina pilchardus</i> (W., 1972)
19	European anchovy	<i>Engraulis encrasicolus</i> (L., 1758)
20	Other planctonophagous Fish	28% round sardinella- <i>Sardinella aurita</i> V., 1847; 20% European sprat- <i>Sprattus sprattus</i> (L., 1758); 50% picarel- <i>Spicara</i> spp.; 2% red bandfish- <i>Cepola macrophthalma</i> (L., 1758); <1% big-scale sand smelt- <i>Atherina boyeri</i> R., 1810
21	Fish (feeding on plants)	90% bogue- <i>Boops boops</i> (L., 1758); 10% salema- <i>Sarpa salpa</i> (L., 1758)
22	Atlantic mackerel	<i>Scomber scombrus</i> L., 1758
23	Mediterranean horse mackerel	<i>Trachurus mediterraneus</i> (S., 1868)
24	Blue whiting	<i>Micromesistius poutassou</i> (R., 1827)
25	Atlantic bluefin tuna	<i>Thunnus thynnus</i> (L., 1758)
26	European hake	<i>Merluccius merluccius</i> (L., 1758)
27	Atlantic horse mackerel	<i>Trachurus trachurus</i> (L., 1758)
28	Anglerfish	67% <i>Lophius budegassa</i> S., 1807; 33% <i>L. piscatorius</i> L., 1758
29	European conger	<i>Conger conger</i> (L., 1758)
30	Poor cod	<i>Trisopterus minutus</i> (L., 1758)
31	Pelagic fish (feeding on fish)	72% Chub mackerel- <i>Scomber japonicus</i> H., 1782; 28% swordfish- <i>Xiphias gladius</i> L., 1758
32	Benthic-demersal fish (feeding on fish)	44% small-spotted catshark- <i>Scyliorhinus canicula</i> (L., 1758); 43% raies- <i>Raja</i> spp.; 9% East Atlantic red gurnard- <i>Aspitrigla cuculus</i> (L., 1758); 2% megrim- <i>Lepidorhombus whiffiagonis</i> (W., 1792); 2% brill- <i>Scophthalmus rhombus</i> (L., 1758)
33	Fish (feeding on benthic crustaceans)	45% European seabass- <i>Dicentrarchus labrax</i> (L., 1758); 22% gurnards- <i>Trigla</i> spp., <i>Lepidotrigla</i> spp., <i>Eutripla gurnardus</i> (L.,

		1758); 10% scorpion fish- <i>Scorpaena</i> spp., <i>Helicolenus dactylopterus dactylopterus</i> (D., 1809); 9% red mullets- <i>Mullus barbatus barbatus</i> L., 1758, <i>M. surmuletus</i> L., 1758; 8% axillary seabream- <i>Pagellus acarne</i> (R., 1827); 2% fourspotted megrim- <i>Lepidorhombus boschii</i> (R., 1810); 2% greater forkbeard <i>Phycis blennoides</i> (B., 1768); 2% gobies- <i>Gobius</i> spp.; <1% mullets- <i>Mugil</i> spp., <i>Liza</i> spp.
34	Gilthead seabream	<i>Sparus aurata</i> L., 1758
35	Fish (feeding on polychaetes, bivalve and gastropods)	85% soles- <i>Solea</i> spp.; 9% common pandora- <i>Pagellus erythrinus</i> (L., 1758); 4% striped seabream- <i>Lithognathus mormyrus</i> (L., 1758); 2% sars- <i>Diplodus</i> spp.; < 1% Mediterranean rainbow wrasse- <i>Coris julis</i> (L., 1758)
36	Sea birds	90.9% gulls- <i>Larus michahellis</i> ; shearwaters : 6.4% <i>Calonectris diomedea diomedea</i> , 0.1% <i>Puffinus yelkouan yelkouan</i> , 0.5% <i>P. yelkouan mauretanicus</i> ; 1.2% terns- <i>Sterna hirundo</i> ; 0.9% Northern Gannet- <i>Morus bassanus</i>
37	Dolphins	12.4% bottlenose dolphin- <i>Tursiops truncatus</i> , 17.3% striped dolphin- <i>Stenella coeruleoalba</i> , 3.4% Risso's dolphin- <i>Grampus griseus</i> ; 5.1% sperm whale- <i>Physeter macrocephalus</i> ; 61.8% pilot whale- <i>Globicephala melas</i>
38	Whales	fin whale- <i>Balaenoptera physalus</i>
39	Detritus	and associated heterotrophe bacteria
40	Discards	20% of total landings of <i>Sardina pilchardus</i> , 60% of total landings of <i>Trachurus</i> spp.

Table 2. Input parameters of the Gulf of Lions's Ecopath model by functional group: B_i = initial estimated biomass, P/B = production/biomass, Q/B = consumption/biomass, EE = ecotrophic efficiency, U/Q = unassimilated food/consumption.

Functional group	B_i (tons km ⁻²)	P/B (y ⁻¹)	Q/B (y ⁻¹)	EE	U/Q	Total landings (R3 report)
1 Pico-nanophytoplankton	5.70	97.29				
2 Microphytoplankton	5.70	84.29				
3 Microphytobenthos	0.21	4.82				
4 Posidonie	0.22	0.55		0.10		
5 Benthic macrophytes	0.16	1.08		0.75		
6 Microzooplankton	2.02	42.52	120.00	0.66	0.40	
7 Mesozooplankton	2.04	39.00	80.00	0.66	0.40	
8 Macrozooplankton	0.74	18.00	38.00	0.66	0.20	
9 Gelatinous	0.04	18.00	38.00	0.20	0.20	
10 Worms	6.18	5.61	30.00		0.60	
11 Bivalves-Gastropods	3.40	1.06	4.00		0.40	0.104
12 Octopuses	0.04	3.00	8.50		0.20	0.116
13 Cuttlefish-squids	0.02	3.20	9.10	0.95	0.20	0.024
14 Benthic crustaceans	1.06	8.46	25.00		0.30	0.004
15 Lobsters	0.01	1.20	4.56		0.20	0.005
16 Echinoderms	0.34	0.26	2.47	0.43	0.30	0.011
17 Other benthic invertebrates	2.16	1.02	4.00		0.40	
18 European pilchard	4.27	0.92	8.45		0.30	0.884
19 European anchovy	2.08	0.87	7.95		0.30	0.202
20 Other planctonophagous fish	0.28	0.84	9.95	0.50	0.30	0.005
21 Fish (feeding on plants)	0.01	1.03	7.56		0.30	0.013
22 Atlantic mackerel	1.41	0.89	7.05		0.20	0.122
23 Mediterranean horse mackerel	0.10	0.97	6.91		0.20	0.009
24 Blue whiting	0.03	0.47	4.87	0.98	0.20	0.064
25 Atlantic bluefin tuna	0.20	0.48	4.11		0.20	0.111
26 Hake age	0.38	0.61	2.15		0.20	0.078
27 Atlantic horse mackerel	0.08	1.18	6.91	0.84	0.20	0.024
28 Anglerfish	0.04	0.69	5.70		0.20	0.043
29 European conger	0.01	0.91	4.15	0.86	0.20	0.061
30 Poor cod	0.08	2.19	6.39		0.20	0.032
31 Pelagic fish (feeding on fish)	0.11	0.73	7.04		0.20	0.002
32 Benthic-demersal fish (feeding on fish)	0.06	0.63	3.61		0.20	0.030
33 Fish (feeding on benthic crustaceans)	0.17	2.06	6.22		0.20	0.044
34 Gilthead seabream	0.03	1.69	4.85		0.20	0.058
35 Fish (feeding on polychaetes)	0.08	2.10	7.79		0.20	0.064
36 Sea birds	0.002	0.60	66.00		0.20	
37 Dolphins	0.022	0.02	6.12		0.20	
38 Whales	0.044	0.01	4.04		0.20	
39 Detritus	112.2					
40 Discards	0.17					

Table 3. Diet composition matrix of the Gulf of Lions' EwE model

Prey \ predator	6	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	37	38			
1 Pico-nanophytoplankton	0,55	0,40	0,10	0,15	0,10	0,30			0,11			0,20																								
2 Microphytoplankton	0,25	0,35	0,25	0,20	0,10	0,40			0,11			0,20	0,18																							
3 Microphytobenthos						0,05					0,05																									
4 Posidonia											0,10					0,20																				
5 Benthic macrophytes						0,01					0,15					0,33																				
6 Microzooplankton	0,05	0,15	0,25	0,15					0,03			0,20																								
7 Mesozooplankton		0,05	0,30	0,30					0,03			0,05	0,76	1,00	0,99		0,10		0,11							0,02										
8 Macrozooplankton			0,05	0,10				0,22		0,20		0,00	0,02	0,00	0,01		0,39	0,34	0,85	0,02							0,02					0,01		0,50		
9 Gelatinous																											0,28									
10 Worms				0,10	0,02				0,05							0,02		0,01							0,02		0,03	0,04	0,07	0,64						
11 Bivalves-Gastropods							0,10		0,02	0,05	0,20													0,06			0,01	0,34	0,13	0,02						
12 Octopuses																							0,01			0,01		0,03						0,01		
13 Cuttlefish-squids							0,01	0,01										0,03		0,02		0,01			0,01	0,04	0,02					0,01	0,57			
14 Benthic crustaceans							0,81	0,07	0,01	0,25						0,45	0,18	0,05				0,03	0,33	0,02	0,07	0,49	0,09	0,27	0,71	0,09	0,07	0,02				
15 Lobsters																																				
16 Echinoderms																												0,03		0,06						
17 Other benthic invertebrates																		0,02	0,01		0,02		0,01										0,03			
18 European pilchard							0,05	0,61										0,02	0,15	0,46	0,03					0,13						0,04	0,01			
19 European anchovy							0,01	0,07									0,02	0,06	0,31	0,12	0,05					0,07	0,17	0,02				0,01	0,01			
20 Other planctonophagous fishes																		0,27	0,04		0,09	0,41	0,09	0,25		0,33	0,02									
21 Fish (feeding on plants)																																				
22 Atlantic mackerel																																	0,03			
23 Mediterranean horse mackerel																																		0,01		
24 Blue whiting																0,19				0,04	0,00	0,26	0,10				0,08									
25 Atlantic bluefin tuna																				0,02		0,01											0,04	0,07		
26 Hake																																				
27 Atlantic horse mackerel																											0,06	0,03								
28 Anglerfish																																				
29 European conger																								0,02	0,02										0,03	
30 Poor cod																									0,01		0,06	0,03								
31 Pelagic fish (feeding on fish)																																				
32 Benthic-demersal fish (feeding on fish)																																				
33 Fishes (feeding on benthic crustaceans)							0,01	0,01												0,17		0,18	0,14	0,50	0,36	0,45		0,36	0,08		0,01	0,03	0,02			
34 Gilthead seabream																																				
35 Fishes (feeding on polychaetes)							0,01	0,01																												0,02
36 Sea birds																																				
37 Dolphins																																				
38 Whales																																				
39 Detritus	0,15	0,05	0,05	0,10	0,70	0,22			0,64	0,50	0,50	0,35	0,04																							
40 Discards																																			0,06	0,01
41 Import																																				
42 Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table 4. Main output parameters of the Gulf of Lions' Ecopath model. In bold characters were indicated biomass parameters estimated by the model. 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 groups	TL	Bf	EE	F	M2	M0	F/Z	Q	FD	P/Q	NE	OI
1 Pico-nanophytoplankton	1.00	5.70	0.93	0.00	90.27	7.02	0.00		30.02			0.00
2 Microphytoplankton	1.00	5.70	0.74	0.00	62.35	21.94	0.00		93.80			0.00
3 Microphytobenthos	1.00	0.21	0.90	0.00	4.32	0.50	0.00		0.11			0.00
4 Posidonie	1.00	9.35	0.10	0.00	0.05	0.49	0.00		2.30			0.00
5 Benthic macrophytes	1.00	1.16	0.75	0.00	0.81	0.27	0.00		0.16			0.00
6 Microzooplankton	2.05	4.43	0.66	0.00	28.06	14.46	0.00	523.54	207.38	0.35	0.59	0.05
7 Mesozooplankton	2.22	5.73	0.66	0.00	25.74	13.26	0.00	449.42	194.34	0.49	0.81	0.19
8 Macrozooplankton	2.71	2.56	0.66	0.00	11.88	6.12	0.00	97.03	35.08	0.47	0.59	0.36
9 Gelatinous	2.69	0.38	0.20	0.00	3.60	14.40	0.00	13.79	8.37	0.47	0.59	0.42
10 Worms	2.11	6.18	0.62	0.00	3.46	2.15	0.00	185.28	124.46	0.19	0.47	0.11
11 Bivalves-Gastropods	2.02	3.40	0.55	0.03	0.55	0.48	0.03	13.59	7.06	0.27	0.44	0.02
12 Octopuses	3.23	0.05	0.93	2.50	0.30	0.20	0.83	0.40	0.09	0.35	0.44	0.09
13 Cuttlefish-squids	3.88	0.06	0.98	0.39	2.75	0.05	0.12	0.56	0.11	0.35	0.44	0.07
14 Benthic crustaceans	2.16	1.06	0.74	0.00	6.23	2.22	0.00	26.48	10.29	0.34	0.48	0.15
15 Lobsters	2.68	0.01	0.38	0.45	0.00	0.75	0.38	0.05	0.02	0.26	0.33	0.51
16 Echinoderms	2.20	1.98	0.43	0.01	0.11	0.15	0.02	4.92	1.77	0.11	0.15	0.17
Other benthic												
17 invertebrates	2.27	2.16	0.13	0.00	0.13	0.89	0.00	8.63	5.37	0.26	0.43	0.22
18 European pilchard	2.96	4.27	0.48	0.21	0.24	0.48	0.22	36.03	12.86	0.11	0.16	0.27
19 European anchovy	3.22	2.08	0.55	0.10	0.38	0.39	0.11	16.56	5.79	0.11	0.16	0.00
Other planctono												
20 -phagous fish	3.22	4.30	0.50	0.00	0.42	0.42	0.00	40.62	14.63	0.08	0.12	0.00
21 Fish (feeding on plants)	2.54	0.01	0.91	0.93	0.01	0.09	0.91	0.11	0.03	0.14	0.19	0.33
22 Atlantic mackerel	3.75	1.41	0.10	0.09	0.00	0.80	0.10	9.94	3.11	0.13	0.16	0.26
Mediterranean horse												
23 mackerel	4.01	0.10	0.10	0.09	0.01	0.87	0.10	0.67	0.22	0.14	0.18	0.15
24 Blue whiting	3.67	4.50	0.98	0.00	0.46	0.01	0.00	21.98	4.43	0.10	0.12	0.04
25 Atlantic bluefin tuna	4.14	0.20	0.68	0.33	0.00	0.15	0.68	0.81	0.10	0.12	0.15	1.25
26 Hake	4.14	0.38	0.63	0.30	0.09	0.23	0.48	0.81	0.25	0.28	0.36	0.11
27 Atlantic horse mackerel	3.90	0.15	0.84	0.52	0.47	0.19	0.44	0.99	0.23	0.17	0.21	0.29
28 Anglerfish	4.45	0.04	0.81	0.56	0.00	0.13	0.81	0.25	0.05	0.12	0.15	0.08
29 European conger	4.16	0.07	0.86	0.58	0.20	0.13	0.64	0.31	0.07	0.22	0.27	0.21
30 Poor cod	3.76	0.08	0.88	0.81	1.11	0.26	0.37	0.48	0.12	0.34	0.43	0.38
Pelagic fish												
31 (feeding on fish)	3.98	0.11	0.02	0.02	0.00	0.72	0.02	0.82	0.23	0.10	0.13	0.19
Bentho-demersal fish												
32 (feeding on fish)	3.98	0.06	0.85	0.54	0.00	0.10	0.85		0.05	0.18	0.22	0.32
Fish (feeding on benthic												
33 crustaceans)	3.33	0.73	0.95	0.16	1.81	0.10	0.08	4.61	0.98	0.33	0.41	0.17
34 Gilthead seabream	3.06	0.03	0.84	1.42	0.00	0.27	0.84	0.15	0.02	0.35	0.44	0.53
Fish (feeding												
35 on polychaetes)	3.13	0.20	0.96	0.29	1.74	0.08	0.14	1.58	0.33	0.27	0.34	0.03
36 Sea birds	3.74	0.00	0.00	0.00	0.00	0.60	0.00	0.13	0.01	0.01	0.01	1.42
37 Dolphins	4.83	0.02	0.00	0.00	0.00	0.02	0.00	0.13	0.03	0.00	0.00	0.80
38 Whales	3.71	0.04	0.00	0.00	0.00	0.01	0.00	0.18	0.02	0.00	0.00	0.92
39 Detritus	1.00	112	0.35					872.16	0.00		0.00	0.30
40 Discards	1.00	0.17	0.36					0.00	0.11		0.00	0.00

Table 5. Ecological indicators related to community energetics, structure, flows and information theory. R3 model used data on landings from R3 observed landings report, while H model used data from auction sales database. In bold characters were indicated the differences between the results of the two models.

<i>Statistics and flows</i>	Value R3 model	Value H model	Units
Sum of all consumption	1480.1	1480.1	tons km ⁻² y ⁻¹
Sum of all exports	251.7	251.7	tons km ⁻² y ⁻¹
Sum of all respiratory flows	498.7	498.7	tons km ⁻² y ⁻¹
Sum of all flows into detritus	764.6.3	764.6.3	tons km ⁻² y ⁻¹
Total system throughput	2995.0	2995.0	tons km ⁻² y ⁻¹
Sum of all production	1572.8	1572.8	tons km ⁻² y ⁻¹
Mean trophic level of the catch	3.24	3.35	
Gross efficiency (catch/net p.p.)	0.002	0.001	
Calculated total net primary production	1042.4	1042.4	tons km ⁻² y ⁻¹
Total primary production/total respiration	2.09	2.09	
Net system production	543.7	543.7	tons km ⁻² y ⁻¹
Total primary production/total biomass	15.1	15.1	
Total biomass/total throughput	0.023	0.023	
Total biomass (excluding detritus)	68.9	68.9	t km ⁻²
Primary production required to sustain fishery/ total primary production	13.58	10.28	%
Total transfer efficiency	19.70	19.70	%
Total catches	2.131	1.274	
Connectance Index	0.150	0.150	
Ecopath Pedigree index (0-1)	0.67	0.67	
<i>Network flow indices</i>			
Throughput cycled (excluding detritus)	73.52	73.52	tons km ⁻² y ⁻¹
Predatory cycling index	4.29	4.29	% of throughput without detritus
Throughput cycled (including detritus)	355.6	355.6	tons km ⁻² y ⁻¹
Finn's cycling index	11.87	11.87	% of total throughput
Finn's mean path length	3.99	3.99	
System Omnivory Index	0.21	0.21	
<i>Information indices</i>			
Ascendency	17.4	17.4	%
Overhead	82.6	82.6	%
Capacity (total)	13809	13809	flowbits

Appendix 1. Input data and references by functional group for the Gulf of Lions' EwE model. P/B= production/biomass ratio (y^{-1}), Q/B=consumption/biomass ratio (y^{-1}), U/B=unassimilated food, EE= ecotrophic efficiency.

Functional group	Sources and references
1. Pico-nanophytoplankton	
Biomass	http://oceancolor.gsfc.nasa.gov ; 50% microphytoplankton and 50% pico-nanophytoplankton estimated by Lefevre <i>et al.</i> , 1997; Rossi <i>et al.</i> , 2006; Harmelin <i>et al.</i> , 2008; Marty <i>et al.</i> , 2008; Christaki <i>et al.</i> , 2009;
P/B	Lefevre <i>et al.</i> , 1997; Gaudy <i>et al.</i> , 2003; http://oceancolor.gsfc.nasa.gov ;
2. Microphytoplankton	
Biomass	http://oceancolor.gsfc.nasa.gov ; 50% microphytoplankton and 50% pico-nanophytoplankton estimated by Lefevre <i>et al.</i> , 1997; Rossi <i>et al.</i> , 2006; Harmelin <i>et al.</i> , 2008; Marty <i>et al.</i> , 2008; Christachi <i>et al.</i> , 2009;
P/B	Lefevre <i>et al.</i> , 1997; Gaudy <i>et al.</i> , 2003; http://oceancolor.gsfc.nasa.gov ;
3. Microphytobenthos	
Biomass	Plante-Cuny and Bodoy, 1987; Riaux-Gobin <i>et al.</i> , 1998;
P/B	Plante-Cuny and Bodoy, 1987;
4. Posidonie	
P/B	Pergent-Martini <i>et al.</i> , 1994; Pergent <i>et al.</i> , 1997;
EE	Pergent <i>et al.</i> , 1997; Romero, 2004; Boudouresque <i>et al.</i> , 2006;
5. Benthic macrophytes	
P/B	McClanahan <i>et al.</i> , 1997; Sala and Boudouresque, 1997;
EE	Boudouresque (pers. comm.);
6. Nano-microzooplankton	
Biomass	Vaqué <i>et al.</i> , 1997; Gaudy <i>et al.</i> , 2003; Christaki <i>et al.</i> , 2009; Banaru <i>et al.</i> , pers. comm.;
Biomass	Plounevez and Champalbert, 2000; Gaudy <i>et al.</i> , 2003;
P/B	Plounevez and Champalbert, 2000; Gaudy <i>et al.</i> , 2003;
Q/B	Pinnegar, 2000;
U/B	Christensen and Pauly, 1991;
Trophic data	Champalbert, 1996; Christaki <i>et al.</i> , 2009; Decembrini <i>et al.</i> , 2009; Banaru <i>et al.</i> , pers. comm.;
7. Mesozooplankton	
Biomass	Furnestin, 1960; Razouls and Kouwenberg, 1993; Plounevez and Champalbert, 2000; Gaudy <i>et al.</i> , 2003; Banaru <i>et al.</i> , pers. comm.;
Biomass	Plounevez and Champalbert, 2000; Gaudy <i>et al.</i> , 2003;
P/B	Plounevez and Champalbert, 2000; Gaudy <i>et al.</i> , 2003;
Q/B	Pinnegar, 2000;
U/B	Christensen and Pauly, 1991;
Trophic data	Champalbert, 1996; Saiz <i>et al.</i> , 2007; Christaki <i>et al.</i> , 2009; Decembrini <i>et al.</i> , 2009; Banaru <i>et al.</i> , pers. comm.;
8. Macrozooplankton	
Biomass	Furnestin, 1960; Razouls and Kouwenberg, 1993; Velsch, 1997;
Biomass	Boucher and Thiriot, 1972; Kulka and Corey, 1982; Velsch, 1997; Cartes <i>et al.</i> , 2008;
P/B	Labat and Cuzin-Roudy, 1996; Velsch, 1997;
Q/B	Pinnegar, 2000;
U/B	Christensen and Pauly, 1991;
Trophic data	Bamstedt and Karlson, 1998; Sabatés <i>et al.</i> , 2007; Saiz <i>et al.</i> , 2007; Morote <i>et al.</i> , 2008; Eiane and Tande, 2009; Vadstein, 2009; Banaru <i>et al.</i> , pers. comm.;
9. Gelatinous zooplankton	
Biomass	Boucher and Thiriot, 1972; Bertrand <i>et al.</i> , 1998; Cartes <i>et al.</i> , 2008; French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009);
P/B	Pinnegar, 2000; Coll <i>et al.</i> , 2006, 2007;
Q/B	Pinnegar, 2000; Coll <i>et al.</i> , 2006, 2007;

U/B	Christensen and Pauly, 1991;
Trophic data	Graham and Kroutil, 2001;
10. Worms	
Biomass	De Bovée et al., 1990; Ratsimbazafy et al., 1994; Stora et al., 1999; Labrune et al., 2007; Hermand et al., 2008; Sorbe, pers. comm.;
P/B	Ropert, 1999; Sanchez and Olaso, 2004;
Q/B	Pinnegar, 2000;
U/B	Christensen and Pauly, 1991;
Trophic data	Bozzano et Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Banaru, 2008;
11. Bivalves and gastropods	
Biomass	De Bovée et al., 1990; Stora et al., 1999; Labrune et al., 2007; Hermand et al., 2008; Sorbe, pers. comm.;
P/B	Dauvin, 1985; Pinnegar, 2000;
Q/B	Pinnegar, 2000; Coll et al., 2006, 2007;
U/B	Christensen and Pauly, 1991;
Trophic data	Sala et al., 1998; Ruitton et al., 2000; Bozzano et Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Sala and Boudouresque, 1997; Banaru, 2008; Cartes et al., 2008;
12. Octopuses	
Biomass (mean-maximum)	Bertrand et al., 1998; French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009);
P/B	Sanchez and Olaso, 2004;
Q/B	Pinnegar, 2000; Coll et al., 2006, 2007;
U/B	Christensen and Pauly, 1991;
Trophic data	Dieng et al., 2000;
13. Cuttlefish and squids	
Biomass (mean-maximum)	Bertrand et al., 1998; French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009);
P/B	Sanchez and Olaso, 2004;
Q/B	Sanchez and Olaso, 2004; Coll et al., 2006;
U/B	Christensen and Pauly, 1991;
Trophic data	Coelho et al., 1997; Alves et al., 2006;
14. Suprabenthic and benthic crustaceans	
Biomass	De Bovée et al., 1990; Stora et al., 1999; Labrune et al., 2007; Hermand et al., 2008; Sorbe, pers. comm.;
P/B	Coll et al., 2006, 2007; Cartes and Sorbe, 1999;
Q/B	Maynou and Cartes, 1998; Sanchez and Olaso, 2004;
U/B	Christensen and Pauly, 1991;
Trophic data	Cartes, 1998; Sala et al., 1998; Bozzano et Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Banaru, 2008; Cartes et al., 2008;
15. Lobsters	
Biomass (mean-maximum)	Bertrand et al., 1998; French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009);
P/B	Coll et al., 2006;
Q/B	Coll et al., 2006, 2007;
U/B	Christensen and Pauly, 1991;
Trophic data	Sala et al., 1998; Ruitton et al., 2000; Bozzano et Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Banaru, 2008; Cartes et al., 2008;
16. Echinoderms	
Biomass	De Bovée et al., 1990; Stora et al., 1999; Labrune et al., 2007; Hermand et al., 2008;

	Sorbe, pers. comm.;
P/B	Pinnegar, 2000;
Q/B	Pinnegar, 2000;
U/B	Christensen and Pauly, 1991;
Trophic data	Sala et al., 1998; Ruitton et al., 2000; Bozzano et Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Sala and Boudouresque., 1997; Banaru, 2008; Cartes et al., 2008;
17. Other benthic invertebrates	
Biomass	De Bovée et al., 1990; Stora et al., 1999; Labrune et al., 2007; Hermand et al., 2008; Sorbe, pers. comm.;
P/B	Coll et al., 2006, 2007;
Q/B	Sanchez and Olaso, 2004; Coll et al., 2006;
U/B	Christensen and Pauly, 1991;
Trophic data	Sala et al., 1998; Ruitton et al., 2000; Bozzano and Sarda, 2002; Darnaude et al., 2004a, b; Boudouresque et al., 2006; Carlier et al., 2007; Banaru, 2008; Cartes et al., 2008;
18. European pilchard	
Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009);
P/B	Farrugio et al., 1991; Christensen et al., 2005; Roos, pers.comm. - GFCM;
Q/B	Farrugio et al., 1991; Palomares and Pauly, 1998; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Lee, 1961; Garrido et al., 2008;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);
19. European anchovy	
Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009);
P/B	Campillo, 1992; Christensen et al., 2005; Roos, pers.comm. - GFCM;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Plounevez and Champalbert, 2000;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);
20. Other planctonophagous fish	
Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009); French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Farrugio et al., 1991; Avsar, 1995; Christensen et al., 2005; GFCM, 2010;
Q/B	Farrugio et al., 1991; Avsar, 1995; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Bell and Harmelin, 1983; Danilova, 1991; Stergiou, 1993; Oven et al., 1997; Bowman et al., 2000;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009);
21. Fish (feeding on plants)	
Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005; www.fishbase.org;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Bell and Harmelin, 1983; Pergent et al., 1994; Rico-Raimondino, 1995; Havelange et al., 1997;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

22. Atlantic mackerel

Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009);
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Olaso et al., 2005;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

23. Mediterranean horse mackerel

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Santic et al., 2003;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

24. Blue whiting

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Geistdoerfer, 1983;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009);

25. Atlantic bluefin tuna

Biomass (mean)	J.-M. Fromentin, pers. comm. estimated from VPA and aerial surveys
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Contino, 2004; Bearzi et al., 2006; fishermen from the Gulf of Lions, pers. comm.;
Landings	J.-M. Fromentin, pers. comm.;

26. European hake

Biomass	Annual mean biomass (1998-2008) estimated by virtual population analysis (GFCM);
P/B	Christensen et al., 2005; Mellon et al., 2009; virtual population analysis parameters
Q/B	Campillo, 1992; Palomares and Pauly, 1998; virtual population analysis parameters;
U/B	Christensen and Pauly, 1991;
Trophic data	Mellon et al., in prep.;
Landings	Annual mean landings database (1998-2008) from French and Spanish sources used by GFCM for virtual population analysis;

27. Atlantic horse mackerel

Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009);
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Santic et al., 2005;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

28. Anglerfish

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Presciado et al., 2006;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

29. European conger

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Bell and Harmelin, 1983; Cau and Manconi, 1984;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

30. Poor cod

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Farrugio <i>et al.</i> , 1991; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Santic et al., 2009;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

31. Pelagic fish (feeding on fish)

Biomass (mean-maximum)	French Mediterranean pelagic acoustic surveys - IFREMER database PELMED (1993-2009); Imbert et al., 2007; Banaru et al., 2010a;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Sever et al., 2006; Imbert et al., 2007;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

32. Benthodemersal fish (feeding on fish)

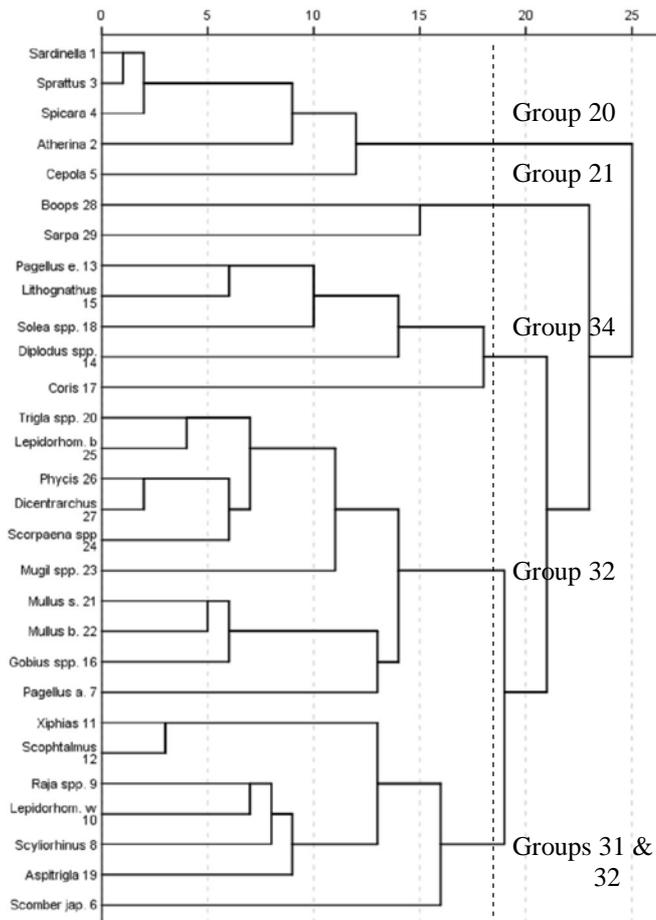
Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;
Trophic data	Moreno-Amich, 1992; Olaso et al., 1998; Morte et al., 1999; Demirhan et al., 2005; Banaru et al., 2009;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);

33. Fish (feeding on benthic crustaceans)

Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998; Vaudo, 2002;
P/B	Farrugio et al., 1991; Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org ;
U/B	Christensen and Pauly, 1991;

Trophic data	Mcperson, 1978; Bell and Harmelin, 1983; Costa, 1988; Pisarevskaya and Aksenova, 1991; Morte et al., 1999; Bautista et al., 2008; Pasquaud et al., 2008; Fehri-Bedoui, 2009;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);
34. Gilthead seabream	
Biomass (mean-maximum)	Vaudo, 2002;
P/B	Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Rosecchi, 1987;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);
35. Fish (feeding on polychaetes, bivalves and gastropods)	
Biomass (mean-maximum)	French Mediterranean bottom trawl surveys - IFREMER database MEDITS (1994-2009); Bertrand et al., 1998; Vaudo, 2002;
P/B	Farrugio et al., 1991; Campillo, 1992; Christensen et al., 2005;
Q/B	Campillo, 1992; Palomares and Pauly, 1998; www.fishbase.org;
U/B	Christensen and Pauly, 1991;
Trophic data	Bell and Harmelin, 1983; Rosecchi, 1987; Rosecchi and Nouaze, 1987; Darnaude et al., 2004b; Kallianiotis et al., 2005;
Landings	FIS "Fisheries Information System"- IFREMER data on landings from auction sales Database (2002-2009); Demaneche et al., 2009 (landings 2007-2008);
36. Sea birds	
Biomass	Cadiou et al., 2004; Beaubrun, pers. comm.;
P/B	Cadiou et al., 2004; Beaubrun, pers. comm.;
Q/B	Nilsson et al., 1976; Cadiou et al., 2004; Beaubrun, pers. comm.;
U/B	Christensen and Pauly, 1991;
Trophic data	Thezenas, 1993; Gonzales-Solis et al., 1997; Conéjéro, 1998; Cramm et al., 1998; Arcos, 1999; Louzao et al., 2009; Beaubrun, pers. comm.;
37. Dolphins (Odontocetes)	
Biomass	Roussel et al., 2000; Ripoll et al., 2001; Beaubrun, pers. comm.;
P/B	Ripoll et al., 2001; Beaubrun, pers. comm.;
Q/B	Innes et al., 1987; Beaubrun, 1995; Trites et al., 1997;
U/B	Christensen and Pauly, 1991;
Trophic data	Astruc, 2005; Beaubrun, pers. comm.;
38. Whale (Mysticetes)	
Biomass	Beaubrun, 1995; Roussel et al., 2000;
P/B	Roussel et al., 2000; Beaubrun, pers. comm.;
Q/B	Innes et al., 1987; Beaubrun, 1995; Trites et al., 1997;
U/B	Christensen and Pauly, 1991;
Trophic data	Astruc, 2005; Ruchonnet et al., 2006; Beaubrun, pers. comm.;
39. Detritus	
Biomass	estimated from primary production (Pauly et al., 1993; Dalsgaard and Pauly, 1997; Tanaka and Rassoulzadegan, 2002); detritus import from inputs of particulate organic matter by the Rhône river (Harmelin et al., 2010);
40. Discards	
Biomass	SIH IFREMER data on landings from auction sales database (2002-2009); Demaneche et al., 2009 (landings 2007); IFREMER, 2009.

Appendix 2. Cluster analysis using Ward method and mean distance between classes, representing the diet similarity between the 29 analysed fish species. Complete names of the species were indicated in Table 1.



Appendix 3. Landings in the Gulf of Lions by French and Spanish fishing gear and by species (R3 report 2007-2008). G1 = Trawls 12-24 m, Purse seine < 12 m; G2 = Trawls 24-40 m; G3 = Purse seine 12-24 m; G4 = Purse seine > 24 m; G5 = Gillnet <12m, <3nm; G6 = Gillnet < 12 m, 12-18 m, > 3nm; G7 = other small gears < 12 m, <3nm. Total R3 = sum of catches by gear from R3 report. Total H = total catches from Harmonie auction sales database (mean annual values over the period 2002-2009).

	Functional group	G1	G2	G3	G4	G5	G6	G7	Total R3	Total H
11	Bivalves-Gastropods	0.002	0.001			0.007		0.094	0.104	0.016
12	Octopuses	0.046	0.056			0.004		0.010	0.116	0.078
13	Cuttlefish-squids	0.011	0.013						0.024	0.024
14	Benthic crustaceans	0.001						0.003	0.004	0.001
15	Lobsters	0.001	0.002					0.002	0.005	0.004
16	Echinoderms							0.011	0.011	
18	European pilchard	0.132	0.554	0.196		0.001		0.001	0.884	0.481
19	European anchovy	0.001	0.198	0.003					0.202	0.183
20	Other planctonophagous fish	0.001	0.001				0.003		0.005	0.003
21	Fish (feeding on plants)					0.009		0.004	0.013	0.008
22	Atlantic mackerel	0.025	0.092	0.004			0.001		0.122	0.046
23	Mediterranean horse mackerel	0.005	0.004						0.009	0.011
25	Atlantic bluefin tuna				0.043		0.021		0.064	0.064
26	Hake age	0.029	0.063			0.003	0.010	0.006	0.111	0.111
27	Atlantic horse mackerel	0.022	0.048	0.001		0.005	0.002		0.078	0.045
28	Anglerfish	0.004	0.017			0.002	0.001		0.024	0.020
29	European conger	0.012	0.01			0.004		0.017	0.043	0.015
30	Poor cod	0.015	0.046						0.061	0.032
31	Pelagic fish (feeding on fish)					0.001	0.001		0.002	0.000
32	Benthopelagic fish (feeding on fish)	0.014	0.015			0.001			0.030	0.026
33	Fish (feeding on benthic crustaceans)	0.030	0.028	0.003		0.036	0.006	0.014	0.117	0.068
34	Gilthead seabream	0.009	0.007			0.020	0.003	0.005	0.044	0.017
35	Fish (feeding on polychaetes)	0.013	0.013			0.020	0.007	0.005	0.058	0.021
	Sum	0.373	1.168	0.207	0.043	0.113	0.055	0.172	2.131	1.274

Appendix 4. Differences between the two landings data sources (report R3 and Harmonie auction sales) in 2007.

Functional group	Landings (tons km ⁻²)		
	R3(2007)	H(2007)	R3/H
11 Bivalves-Gastropods	0.104	-	
12 Octopuses	0.108	0.081	1.3
13 Cuttlefish-squids	0.022	-	
14 Benthic crustaceans	0.004	-	
15 Lobsters	0.002	-	
16 Echinoderms	0.011	-	
18 European pilchard	0.729	0.654	1.1
19 European anchovy	0.201	0.203	1.0
20 Other planctonophagous fish	0.005	-	
21 Fish (feeding on plants)	0.013	0.001	10.8
22 Atlantic mackerel	0.121	0.081	1.5
23 Mediterranean horse mackerel	0.002	-	
26 Hake	0.101	0.083	1.2
27 Atlantic horse mackerel	0.046	0.030	1.5
28 Anglerfish	0.020	0.011	1.9
29 European conger	0.041	0.015	2.7
30 Poor cod	0.059	0.036	1.6
31 Pelagic fish (feeding on fish)	0.002	-	
32 Benthic-demersal fish (feeding on fish)	0.030	0.012	2.5
33 Fish (feeding on benthic crustaceans)	0.109	0.037	2.9
34 Gilthead seabream	0.044	0.012	3.7
35 Fish (feeding on polychaetes)	0.058	0.021	2.8