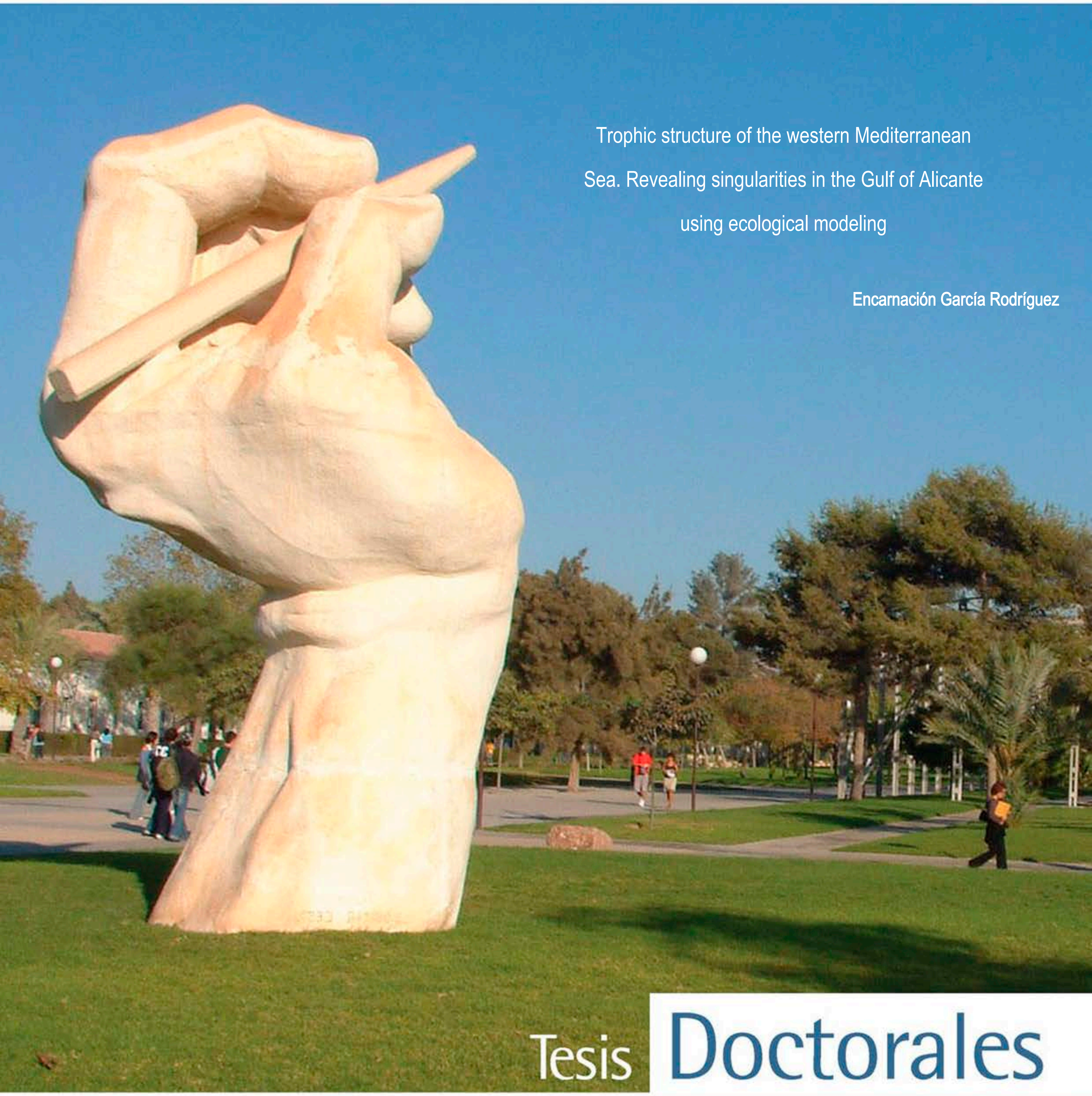

Trophic structure of the western Mediterranean Sea. Revealing singularities in the Gulf of Alicante using ecological modeling

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Tesis presentada para aspirar al grado de DOCTORA por la
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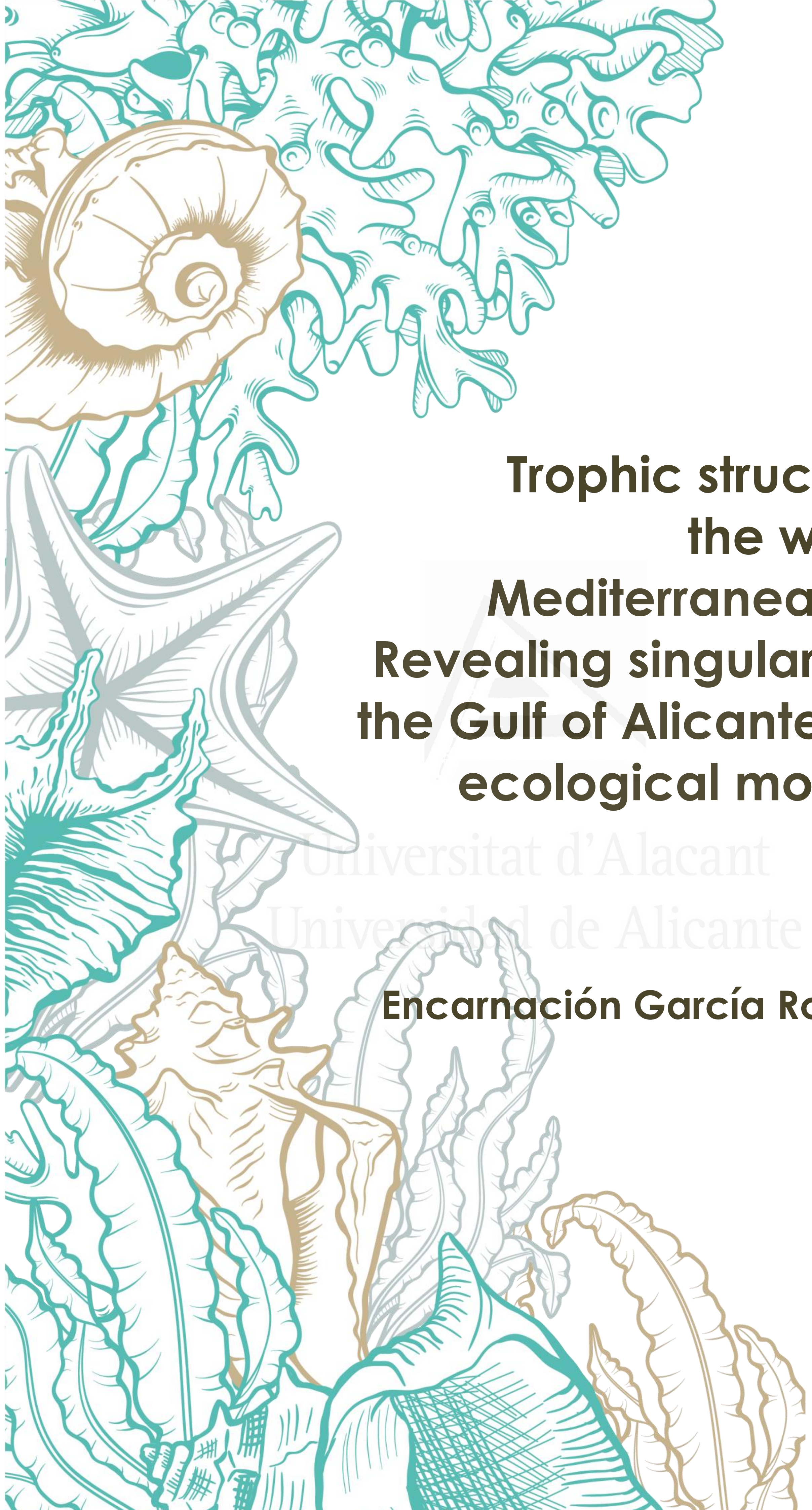
A mis padres

El sueño del héroe, es ser grande en todas partes y pequeño al lado de sus padres

(Victor Hugo)



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Summary

In the last years, many studies have addressed the understanding of different mechanisms and interactions around which the species within the marine ecosystem are subject. Additionally, ecosystem modeling has been demonstrated to be paramount in the understanding of the impact of fisheries on the whole food webs and not only on target species.

This PhD thesis aims to update the existing knowledge related to trophic webs concerning the Northern Spain-GSA6 and more specifically in the implementation of an ecological model in a particular ecosystem belonging this area, the Gulf of Alicante (GoA, onwards). For this reason, we hypothesize that exist certain features in the marine ecosystem located in the GoA, differing it from neighbour ecosystems due to its oceanographic and biological singularities.

With this motivation, we studied the dietary preferences of 61 western Mediterranean species of fish belonging to different trophic levels. Most of them were collected in the Northern Spain-GSA6 waters during the annual bottom trawl survey MEDITS for the period 2011-2018, with a total of 16,588 stomach contents analyzed.

Therefore, the first step in this study was to determine the adequacy of the sample size for each species to describe the species diet through the estimation of cumulative prey curves. Thus, cumulative prey curves methodology was applied to determine if the number of stomachs analyzed was adequate to represent the trophic spectrum of each predator studied. Further, a mathematical approach was applied using Clench´s function for the first time in a study of Mediterranean fish species.

Then the major trophic guilds exploiting similar food resources were identified focusing on how the environmental drivers of habitat type, latitude and depth affected the different trophic guild structures, using four main indicators, namely the Shannon diversity index, biomass, mean trophic level and fish community composition. Main findings highlighted how those environmental factors investigated drove fish composition structure. Regarding the three variables investigated, depth had the greatest impact on the fish community structure, particularly affecting diversity and fish community composition. Latitudinal gradient only seemed to affect fish community composition, showing consistency along a latitudinal north-south axis. Habitat type was found to be significant in the fish community structure. Mean trophic level was the only indicator that was not affected significantly by environmental variables.

In addition, we investigated the particular case of seven key Gadiformes fishes to explore ontogenetic shifts in diet, trophic interactions (both inter- and intra-specific) and feeding strategies. These species were: silvery pout (*Gadiculus argenteus*), bigeye rockling

(*Gaidropsarus biscayensis*), Spanish ling (*Molva macrophthalma*), European hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), greater forkbeard (*Phycis blennoides*) and poor cood (*Trisopterus minutus*).

The results concerning the seven Gadiforms studied showed that all species investigated underwent ontogenetic dietary shifts, increasing their trophic level with size, except for *Gaidropsarus biscayensis* and *Trisopterus minutus*. The species hold different trophic positions, from opportunistic to highly specialized piscivore behavior. These insights revealed four different feeding strategies among the co-occurring species and size classes along the study area, as well as the degree of dietary overlap, shedding light on ecological patterns within the fish assemblage.

Finally, a food web model was built to characterize the ecosystem of the Gulf of Alicante and investigate its singularities concerning neighboring ecosystems, namely, Gulf of Cadiz model (GoC), located to the south of GoA and north western Mediterranean model (NWM), located to the north of GoA. This mass-balance model was implemented following the approach incorporated in the Ecopath software, which has been the most widely used in representing marine food webs, addressing issues relevant to fisheries management. The study area modeled for the year 2011 covered a total area of 7,085 km^2 including the continental shelf and upper slope with depths from 50 to 800 m. In total, 45 functional groups including all components of the food web (i.e. fish, marine mammals, seabirds, invertebrates, primary producers and detritus) were selected to build the model. The approach conducted in the Gulf of Alicante revealed the peculiar organization of this ecosystem in contrast to results reported in neighboring ecosystems where main differences found with regard to the compared models are related to the low primary production in the GoA. Despite the high values of ecotrophic efficiencies and mortality rates, the Gulf of Alicante evidenced the lowest fishing pressure of all three compared models, pointing out a moderate overexploitation level.

Moreover, results suggest that GoA is a very stable and mature ecosystem, where efficiency has been achieved through the use of detritus. Thus, it is a mature but nutrient-poor system, suggesting the existence of a delicate balance between the supply of nutrients and the exploitation of detritus.

These findings suggest that the GoA presents a higher level of complexity of internal flows, which is correlated with stability and maturity. This indicates that the system looks more like a web-like than a chain-like structure, in contrast with the linearity detected in the food web of NWM and GoC ecosystems. Hence, a higher development stage *sensu* Odum is evidenced in the GoA, which remains efficient and stable in its poor conditions, but also very delicate and vulnerable because it depends on the efficient and circular use of its biomass.

Resumen

En los últimos años, han sido muchos los estudios que han pretendido abordar el conocimiento de los diferentes mecanismos e interacciones que determinan el comportamiento y la presencia de las diferentes especies en los ecosistemas marinos. En este sentido, la modelización ecosistémica ha demostrado ser fundamental a la hora de explicar el efecto de la pesca, no únicamente sobre sus especies objetivo, sino también en el conjunto de las especies que conforman dicho ecosistema sometido a explotación.

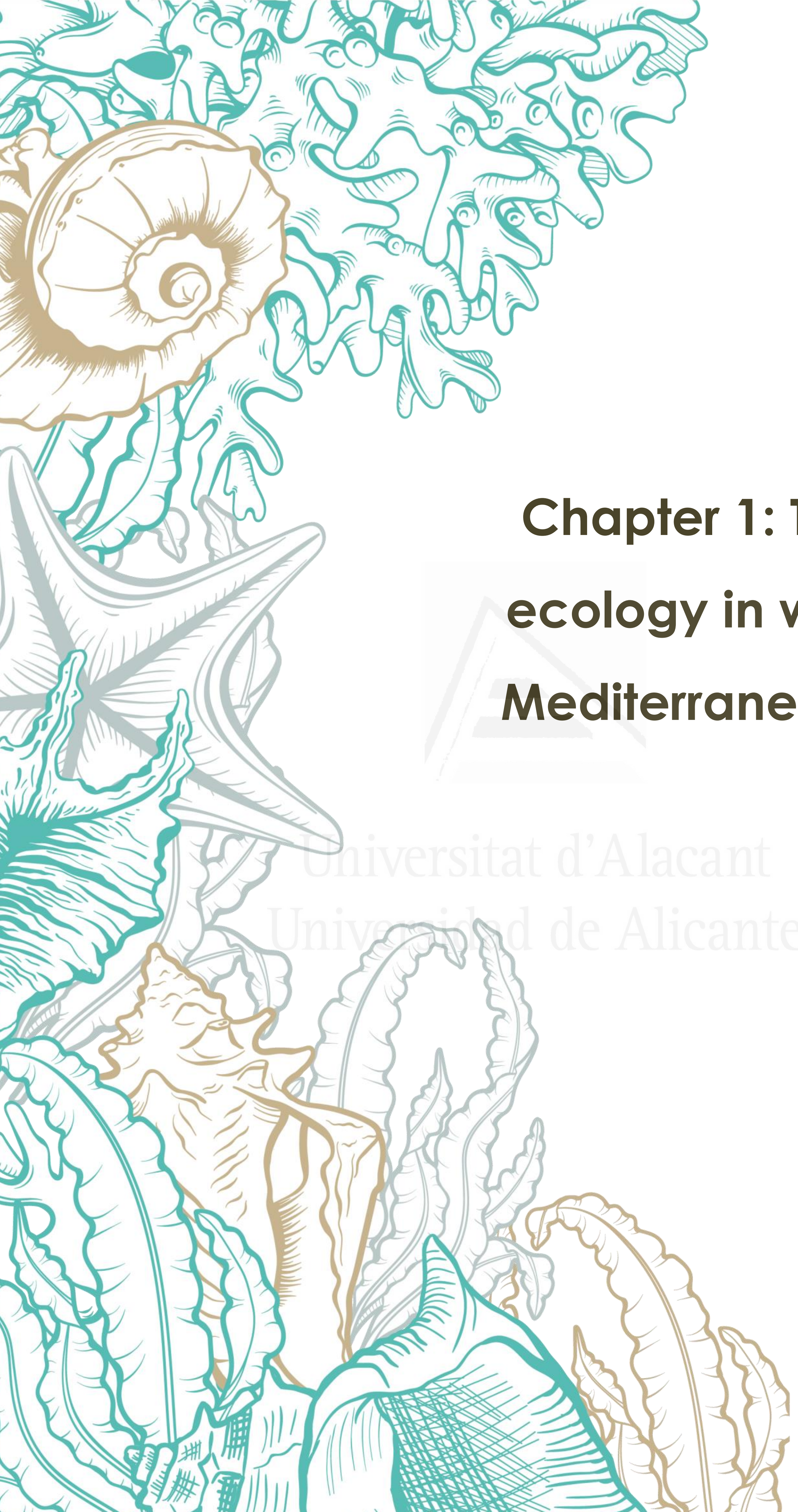
Desde su concepción, esta tesis tuvo como objetivo la actualización de los estudios existentes relacionados con las redes tróficas que caracterizan la zona de estudio, la costa este del Mediterráneo español (denominada como GSA6 por la Comisión General de Pesquerías del Mediterráneo, CGPM). Además de la actualización y ampliación del conocimiento de la ecología trófica del área de estudio, se ha construido un modelo de redes tróficas mediante el empleo del software Ecopath para la zona del Golfo de Alicante (GoA), un ecosistema marino incluido dentro de la zona de estudio. Así pues, a lo largo de la tesis se ha podido articular y comprobar una hipótesis que siempre visitaba nuestro pensamiento: que existen ciertas características en el ecosistema marino del GoA que lo diferencian de sus ecosistemas vecinos, debido en gran medida a sus singularidades tanto oceanográficas como biológicas y ecológicas. Con esta motivación, se estudiaron los hábitos alimenticios de 61 especies de peces existentes en la zona de estudio pertenecientes a diferentes niveles tróficos. La mayoría de las muestras fueron analizadas durante las prospecciones anuales llevadas a cabo durante las campañas oceanográficas de arrastre de fondo denominadas MEDITS en la zona de estudio. El estudio comprendió el periodo 2011-2018, durante el cual se analizaron un total de 16588 contenidos estomacales.

En el **captítulo II**, el primer paso consistió en determinar la idoneidad del tamaño mínimo muestral necesario para describir la dieta de cada una de las especies. Este proceso se hizo mediante el uso de curvas de acumulación de presas. Así pues, se aplicó la metodología de curvas de presas acumuladas para determinar si el número de estómagos analizados era suficiente para representar el espectro trófico de cada uno de los depredadores estudiados. Es más, para dar una mayor consistencia y robustez a este método, se aplicó una aproximación matemática mediante el uso de la función de Clench. Es importante resaltar que éste es el primer estudio en el que se aplica dicha aproximación matemática en especies marinas en el Mediterráneo.

En el **capítulo III**, una vez descritas las dietas de cada una de las especies analizadas, se identificaron los principales grupos de especies que explotan recursos tróficos similares. Seguidamente, el estudio se centró en cómo los factores ambientales tales como el tipo de hábitat, la latitud y la profundidad, afectaron a la estructura y organización de estos grupos tróficos. Para ello se utilizaron cuatro indicadores principales; el índice de diversidad de Shannon, la biomasa, el nivel trófico promedio y la composición específica de la comunidad de peces. Los principales hallazgos destacaron cómo los factores ambientales estudiados condicionaron la estructura de la composición específica de la comunidad íctica. Con respecto a las tres variables investigadas, la profundidad pareció afectar particularmente a la diversidad y la composición de la comunidad de peces. En el caso del gradiente latitudinal, éste sólo pareció afectar a la composición de la comunidad de peces, mostrando consistencia a lo largo de un eje latitudinal norte-sur. Además, se encontró que el tipo de hábitat es significativo en la estructura de la comunidad de peces, mientras que el nivel trófico promedio fue el único indicador que no se vio afectado significativamente por las variables ambientales investigadas.

Por otro lado, en el **capítulo IV**, investigamos el caso particular de siete especies pertenecientes al orden de los Gadiformes con el propósito de explorar aspectos importantes de la ecología trófica tales como los cambios ontogenéticos en su dieta, las interacciones tróficas (tanto inter- como intra-específicas), así como sus estrategias de alimentación. Las especies estudiadas fueron: marujito (*Gadiculus argenteus*), barbada (*Gaidropsarus biscayensis*), maruca azul (*Molva macrophthalma*), merluza europea (*Merluccius merluccius*), bacaladilla (*Micromesistius poutassou*), brótola de fango (*Phycis blennoides*) y la faneca (*Trisopterus minutus*). Los resultados mostraron que las siete especies estudiadas experimentaron cambios en su estrategia trófica ligados al desarrollo ontogenético. En consecuencia, se observó un aumento en el nivel trófico de la especie con el crecimiento, exceptuando el caso de *Gaidropsarus biscayensis* y *Trisopterus minutus*. Del mismo modo, se comprobó cómo las especies son capaces de ocupar diferentes nichos tróficos, desarrollando desde estrategias oportunistas hasta los comportamientos piscívoros más altamente especializados. De esta forma se pudieron distinguir cuatro estrategias de alimentación dentro de las especies coexistentes así como entre las diferentes clases de talla seleccionadas a lo largo del área de estudio. Igualmente resultó interesante el estudio del grado de solapamiento de las diferentes estrategias tróficas, arrojando luz sobre los patrones ecológicos existentes dentro de la comunidad de peces.

Finalmente, en el **capítulo V** se desarrolló un modelo trófico para caracterizar el ecosistema del Golfo de Alicante e investigar sus singularidades con respecto a sus ecosistemas vecinos. Es decir, el modelo ecosistémico localizado en el Golfo de Cádiz (GoC), al suroeste de GoA y el modelo del Mediterráneo Noroccidental (NWM), ubicado al norte de GoA. Este modelo de balance de masas se ha implementado siguiendo el enfoque incorporado en el software Ecopath, uno de los modelos más utilizados a la hora de representar las redes tróficas marinas, abordando cuestiones relevantes para la gestión pesquera. El área de estudio modelada para el año 2011 abarcó una superficie total de 7085 km^2, incluyendo la plataforma continental y el talud superior, cubriendo profundidades a partir de los 50 m hasta los 800 m. Para construir el modelo, se seleccionaron un total de 45 grupos funcionales que incluyeron todos los componentes de la red trófica (peces, mamíferos marinos, aves marinas, invertebrados, productores primarios y grupos de detrito). La aproximación realizada en el Golfo de Alicante reveló la peculiar organización de este ecosistema. Esto contrasta con los resultados obtenidos en los ecosistemas vecinos comparados, poniendo de manifiesto que las principales diferencias encontradas están relacionadas con la baja producción primaria existente en el GoA. A pesar de los altos valores tanto de eficiencias ecotróficas como de tasas de mortalidad, los resultados del Golfo de Alicante evidenciaron una menor presión pesquera, lo cual apunta a un nivel de sobreexplotación moderado en el Golfo de Alicante. Por tanto, estos resultados sugieren que GoA es un ecosistema estable y maduro, donde la eficiencia se logra principalmente a partir de un uso eficiente de los detritos. Por tanto, podría decirse que el GoA se caracteriza por tratarse de un sistema maduro pero pobre en nutrientes, lo que sugiere la existencia de un delicado equilibrio entre el aporte de nutrientes y la explotación del detrito. Por consiguiente, el Golfo de Alicante presenta un mayor nivel de complejidad de los flujos internos, lo cual se correlaciona con una situación de estabilidad y madurez. Esto indica que el sistema se parece más a una red, en contraste con la mayor linealidad detectada en la red trófica de los ecosistemas vecinos del NWM y GoC. De ahí la evidencia, según Odum, que el GoA se encuentre en una etapa de desarrollo superior, donde se mantiene eficiente y estable dentro de sus pobres condiciones, pero al mismo tiempo delicado y vulnerable, ya que depende del uso eficiente y circular de su biomasa.



Chapter 1: Trophic ecology in western Mediterranean Sea

1. Background

In the marine environment, many impacts are affecting at a physical-chemical level (e.g., increase in temperature, acidification, changes in ocean circulation, increased stratification, changes in wave intensity) and at the biological level (e.g., massive mortality, changes in species distribution, decrease in primary production, decrease in CO_2 absorption capacity, decline of structuring species), with a continuous loss of marine biodiversity. Consequently, all these disruptions will be noticed in a very marked way in marine ecosystems. Under this context, fisheries science was born from the management needs resulting from the increasing exploitation of marine living resources. The growing demand for food and the industrial development of fishing technologies has led fishing to represent one of the greatest pressures on marine ecosystems (Costello et al., 2010) since any kind of fishery can perturb the marine ecosystem and its trophic structure. In this regard, population dynamics within the community must be well-studied to identify the factors driving these changes. From an ecological point of view, those interactions determined by intrinsic and extrinsic relationships between the different components within marine ecosystems have to be acknowledged, understood, and quantified (Cury et al., 2003).

1.1. Food web as a basis for an Ecosystem Approach to Fisheries

The ecosystem approach to fisheries (EAF) seeks to strengthen the conventional fisheries management to reinforce them and contribute to their sustainable development (García et al., 2003; Levin et al., 2009). This approach is based on the FAO Code of Conduct for Responsible Fisheries (FAO, 1995) and therefore emphasizes a management procedure that maintains the health of the marine ecosystems, along with appropriate human use of the marine environments for the benefit of future generations.

This entails considering not only the resource exploited but also the ecosystem (including ecological interdependencies between species and their relationships with the environment) and socio-economic aspects linked to the human activity. Under this scenario comes up the EU Marine Strategy Framework Directive (MSFD: 2008/56/EC), requiring that each Member State takes the necessary measures to achieve or maintain the “Good Environmental Status” (GES) of marine waters. The MSFD takes into account topics such as biodiversity, contaminants, marine litter, commercially exploited fish and marine food webs.

In this sense, trophic web description of “who eats whom” in an ecosystem has been a well-documented tool to achieve a fisheries ecosystem approach (Pauly et al., 1998, 2000), providing the knowledge of trophodynamic interactions and food web structure. Hence, trophodynamics studies of marine resources are considered key for the understanding of ecological communities' processes, i.e. predation and competition have been recognized as being of great importance in fish population dynamics (Bax, 1998; Trites, 2003).

For this reason, food webs have been extensively studied in marine and freshwater ecosystems along the world. Traditional stomach content analysis have been complemented with indirect techniques, such as stable isotopes (Fry and Sherr, 1984; Peterson and Fry, 1987) and lipid biomarkers in order to identify both, diet composition and trophic position of the main species occurring in the ecosystem. In addition, there are two particular issues in this kind of studies that are worth highlighting: the ontogenetic shifts and the niche complementarity (Ebeling and Hixon, 1991). On the one hand, ontogenetic variation in diet is considered as a mechanism to avoid, or at least minimize, intra-specific competition by allowing exploitation of different food resources at each developmental stage (Marrin, 1983; Castro and Hernández-García, 1995). It is associated with an increase in inferred trophic levels of the species, allowing them to occupy several niches or sub-niches simultaneously, thus contributing to segregation between size classes (Pauly et al., 2001). Concerning to the niche complementary hypothesis, which assumes that a particular species, which overlaps with others (or other size categories) in a given niche dimension, would separate along another dimension, thus maintaining resource partitioning. Furthermore, describing and comparing these relationships, using indices reflecting niche overlap or niche breadth can help to explain feeding behaviors that range from generalist to specialist in nature (Silva et al., 2014). Therefore, trophic and spatial segregation is explored as a mechanism to manage the resource partitioning within and amongst species co-occurring in a broad geographic area.

Moving to ecosystems located on the western Mediterranean, more precisely on the Eastern Spanish coast, it is remarkable that most of the reported studies related to trophic interactions and diet compositions are conducted at local spatial scales such as the Catalan Sea (e.g. Macpherson, 1977; 1978a; 1978b; 1980a; 1980b; Carrassón and Matallanas, 2002; Cartes et al., 2002; Fanelli and Cartes, 2010; López et al., 2016) and the Gulf of Valencia (Morte et al., 2001; 2002; Jaramillo et al., 2011).

1.2. Ecosystem approach through Ecopath modeling

Multiple connections where organisms take food from different trophic levels exist in the marine food webs, which characterize the position of organisms within food webs (Lindeman, 1942). Due to the high level of requirements needed as a basis when you build an ecological model, it is important to collect all this information to provide a more precise representation of the modeled ecosystem.

In the last years, more attention has been paid to the implementation of ecosystem models capable to include interactions between the biotic and abiotic components. Consequently, the processes involved in these interactions (e.g. impacts of fishing) can be addressed through ecosystem modeling. In such a context, ecosystem models are considered efficient management tools developed and used by scientists for fisheries managers and stakeholders to provide an approximation to the marine ecosystems.

Ecopath with Ecosim (EwE) modeling approach is a clear example (Polovina, 1984; Christensen and Pauly, 1992; Walters et al., 1997; 2000). This mass balance model provides a static description of an ecosystem at a given time period, estimating the flows amongst different food web components (Christensen and Walters, 2004). It is possible to aggregate these components in functional groups or let them as single-species groups, ontogenetic phases of a species (or multi-stanza groups), or species groups representing similar ecological guilds in the ecosystem, i.e. have similar growth rates, consumption rates, diets, habitats, and predators (Christensen et al., 2008; Heymans et al., 2016).

The Ecopath model is based on two master equations, the first of which splits the production term for each functional group *i* into its components:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + M0_i \qquad (1)$$

where, P_i is the total production rate of group *i*, Y_i is the total fisheries catch rate, B_i the biomass, $M2_i$ is the total predation rate, E_i the net migration rate (emigration -immigration), BA_i the biomass accumulation rate and $M0_i$ is the so-called "other mortality", which includes mortality caused by diseases, starvation, etc., or being consumed by predators not included in the model ($M0_i = P_i \cdot (1- EE_i)$, where EE_i is the ecotrophic efficiency of group *i*).

The second master equation describes the energy balance within each functional group:

$$Q_i = P_i + R_i + U_i \qquad (2)$$

where, Q_i stands for consumption, P_i for the total production rate, R_i for respiration, and U_i for unassimilated food. The Ecopath model uses a linear system of equations to estimate one parameter per equation and functional group, either B, P/B, Q/B or EE (a detailed description of the model's foundations is given in Christensen et al., 2008; Christensen and Walters, 2004). This approach is one of the most used modeling frameworks for addressing ecosystem approaches, leading to its implementation worldwide by a growing body of scientists (e.g. Colleter et al., 2015; Villasante et al., 2016). Furthermore, it has been widely used in the Mediterranean Sea and nearby Atlantic waters (Fig 1.1.2.1) (e.g. 1: Torres et al., 2013; 2: Corrales et al. 2015; 3: Coll et al., 2006; 4: Tecchio et al., 2013; 5: Vilas et al., 2020; 6: Banaru et al., 2013; 7: Valls et al., 2012; 8: Prato et al., 2016; 9: Pinnegar and Polunin, 2004; 10: Albouy et al., 2010; 11: Diaz et al., 2008).

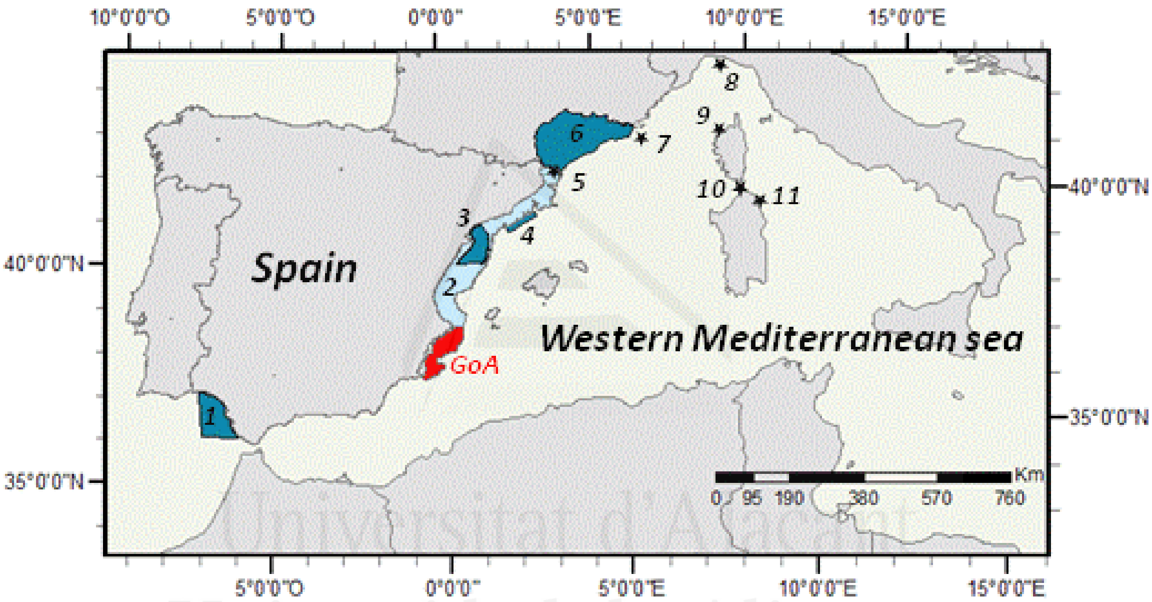


Fig. 1.1.2.1 Ecopath models implemented in western Mediterranean Sea and nearby Atlantic waters. 1: Gulf of Cadiz; 2: Northwestern Mediterranean model; 3: Catalan Sea model; 4: Catalan deep sea model; 5: Cap de Creus AMP model; 6: Guf of Lion model; 7: Port-Cross APM model; 8: Portofino model; 9: Bay of Calvi model; 10: Bonnifacio model; 11: Aranci bay model.

2. Mediterranean Sea environments

The Mediterranean is one of the largest marginal seas on the planet, located in the temperate zone of the northern hemisphere, cartographically it is located between the meridians 6ºW and 35ºE and the parallels 30º N and 45ºN. It is a long and narrow sea, showing about 3,800 km long and 900 km wide. Its total extension is about 2.5 million km^2 and reservoirs about 4.5 million km^3 of water. So it is renewed every 100-150 years, thanks to the peculiar system of currents of this sea.

Morphologically, the Mediterranean is made up of two large basins, the western one has a total area of about 860,000 km^2 while the eastern one, is about 1,682,000 km^2. The western basin communicates with the Atlantic Ocean through the Strait of Gibraltar, with a fairly irregular orography of its bottoms and coasts and with limiting values of about 300 m of minimum depth and 14 km between its nearest coasts. In this basin are included the Alboran, Balearic, Ligurian and Tyrrhenian seas. The eastern basin communicates with the Black Sea through the Bosphorus, scarcely 40 m deep, while the communication with the Red Sea, the Suez Canal, is artificial and recently opened in 1869. The two basins are connected through the Strait of Sicily, with an average depth of about 460 m, and the Strait of Messina, only 3 km wide and about 100 m deep. The reduced physical communication between the two basins makes it difficult to mix their deeper water masses, together with the different geographical location, climate and topography of their bottoms, giving rise to their own oceanographic and biogeographic characteristics (Fig. 1.2.1).

The geographical situation and complex topography on the coast make the Mediterranean Sea a region with strong contrasts, as well as very heterogeneous at the regional and local levels. Hence, between north and south, and between west and east, there are notable climatic differences. The great evaporation originated as a consequence of the insolation and prevailing winds, together with the insufficient supply of water from the rivers and rains, makes the Mediterranean function as a negative estuary (Estrada, 1996). This chronic deficit tends to be offset by the entry of Atlantic water through the Strait of Gibraltar. The constant inflow of Atlantic surface water into the Mediterranean to compensate for the aforementioned deficit, which would produce a progressive increase in its salinity, is offset by an outflow to the Atlantic of more saline deep Mediterranean water.

Circulation in the Mediterranean has a marked thermohaline character due to the differences in temperature and salinity that are created between superficial and deep waters. During its dispersion through the Mediterranean from west to east and from south to north, Atlantic water will transform into Mediterranean water.

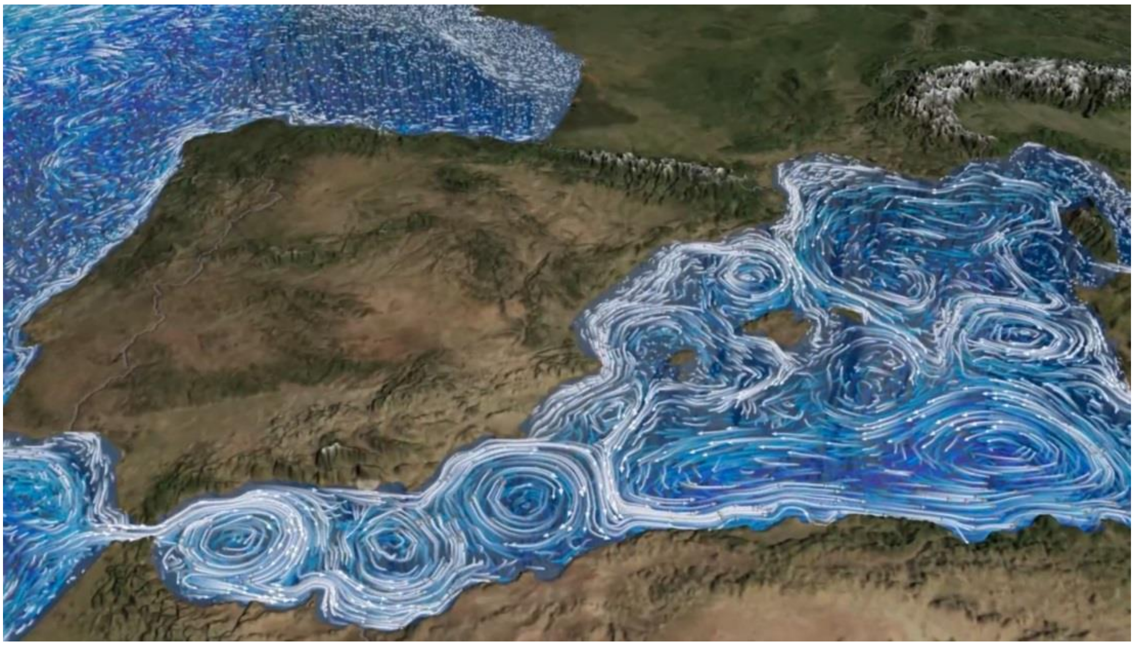


Fig. 1.2.1 western Mediterranean Eddies. Source: NASA Scientific Visualization Studio.

The current biota of the Mediterranean Sea is made up of a mixture of relic species from the ancient Tethys, species from the Atlantic (from boreal, temperate, subtropical and tropical regions). They are endemic, cosmopolitan and species from the Red Sea and from other seas introduced by human activity, some of which have become invasive. Such is the case of the Alboran Sea and the north coast of Africa, where it is notable the influence of the incoming Atlantic water so that Atlantic species with all kinds of affinities are abundant. The central sector of this basin is the warmest and is populated mainly by Mediterranean species while in the northern sector of the basin, subtropical species are significantly reduced and those of temperate-cold waters start increasing their abundance. Finally, in the eastern Mediterranean, there is a significant reduction in species with temperate-cold water affinities, increasing the subtropical Atlantic species and the presence of Indo-Pacific species introduced through the Suez Canal.

The high complexity is reflected in a great diversity of habitats and species. The Mediterranean is considered one of the 25 hot spots in the world in terms of marine biodiversity (Tortonese 1985; Boudouresque 2004; Coll et al., 2010). Paradoxically, the Mediterranean is an oligotrophic sea; this means poor in nutrients, a poverty that is reflected in the high transparency of its waters. This low productivity is accompanied by a low population density in most of its species. The chronic poverty of the Mediterranean is mainly because the incoming Atlantic waters are shallow and therefore poor in nutrients (Sánchez-Leal et al., 2017), while the outgoing Mediterranean waters are deep and therefore enriched in nutrients by bacterial action.

2.1 Western Mediterranean

In the western Mediterranean, two permanent currents influence our coasts: the north current, which transports Atlantic water with a long period of circulation in the Mediterranean and the Algerian current, formed by recently incorporated water. The incoming Atlantic water tends to flow close to the Andalusian coast. Immediately, two large, more or less stable, anticyclonic gyres appear, occupying the entire basin (Minas et al., 1984; Lohrenz et al., 1988). The current is diverted to the southeast by the Almería-Oran and leaves the Alboran basin attached to the African coast, following the continental margin. It is known as the Algerian current and from it, as it flows eastward, eddies can be released and divert Atlantic water to the north, reaching the Balearic Islands. On the other hand, the north or Liguro-Provençal current flows along the Catalan and Valencian coast coming from the Ligurian Sea and following the edge of the platform. In the Gulf of Valencia, this current continues towards the Ibiza channel, where appears a bifurcation to the northeast, the Balearic current which flows parallel to the west coast of the islands. The main flow crosses the channel and continues along the Spanish Mediterranean coast to the south to Almería, where it meets the incoming Atlantic waters. The interaction between these two bodies of water with different characteristics originates the Almería-Oran Front. Close to the slope, the intermediate and deep Mediterranean water, each at its depth, flows southwards. Hence, the Catalan coast would represent the coldest sector; from Cape la Nao to Cape Gata the warmest sector; and from here to the Strait of Gibraltar the sector most influenced by Atlantic water.

2.2 Gulf of Alicante

In the Gulf of Alicante (GoA), located in the western Mediterranean Sea, the oceanographic conditions reveal how it is still under the influence of the Atlantic flow when leaving the Alboran Sea and is linked to the existence of an anticyclone circulation between Cape Palos and Cape La Nao. These processes highlight the presence of two anticyclonic gyres, one outside and another inside the continental shelf (Gil, 1992). Similarly, there is a thermohaline front located to the north of Cape La Nao that separates the GoA from the Catalan Sea. Furthermore, the Alicante continental shelf average width from Cape La Nao to Cape Palos is 32 km, with a minimum and a maximum of 23 km and 40 km, with a dominance of sandy and muddy bottoms (Diaz del Rio et al., 1986). The slope has a uniform relief presenting a width between 30 and 52 km, with two canyons; the one from Alicante, gently sloping, and the other in Benidorm, narrower and rough with a head that originates at the foot of the continental slope at a depth of 650 m (Diaz del Rio, 1991) (Fig.1.2.2.1). Furthermore, the influence of river inputs, which is significantly low in the GoA (e.g. Segura River), may be associated with a low productivity in this area. All these features may influence the biological communities (García-Rodríguez et al., 2011) in the area and affect the functioning of the whole food web. The Gulf of Alicante supports a multifleet fishery, primarily operated by trawlers and artisanal boats, which exploits a wide range of species using diverse types of fishing gear.

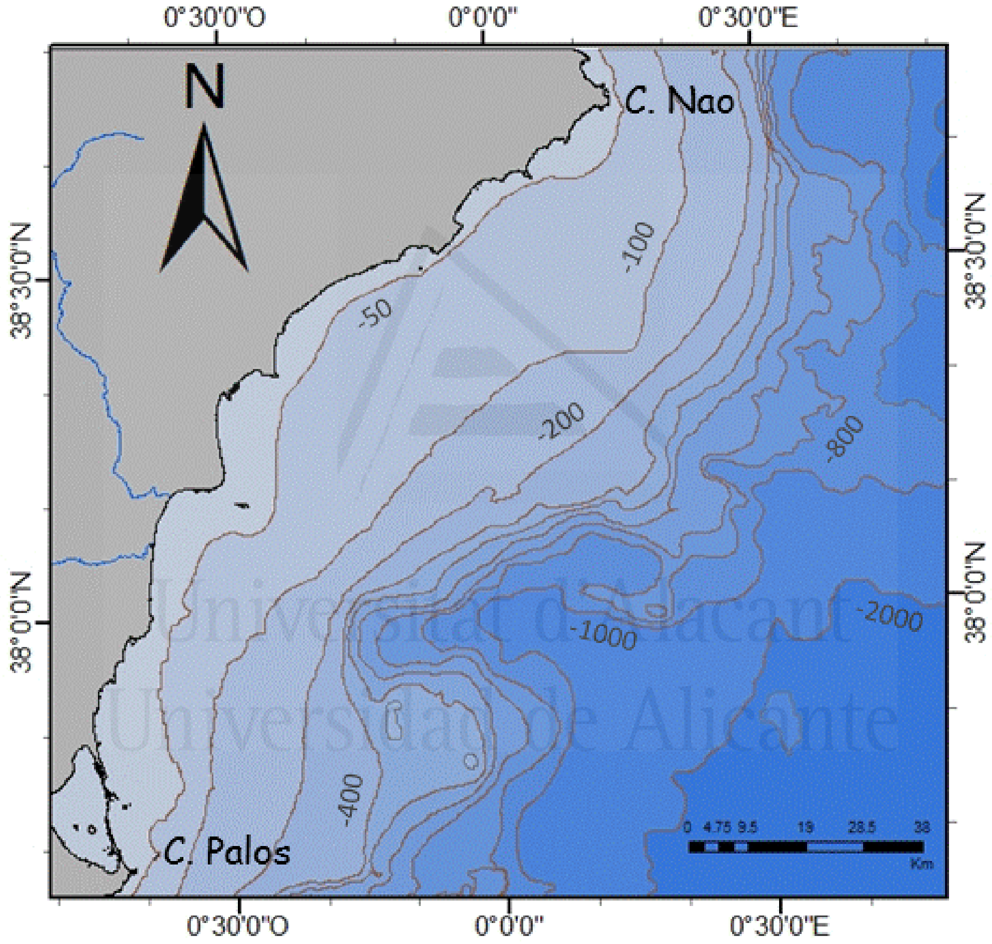


Fig. 1.2.2.1 Map of the Gulf of Alicante including the studied area with isobaths ranging from 50 m to 800 m depth.

3. Material and Methods

3.1 Study area

The trophic study was conducted along the continental shelf and slope of the eastern coast of the Iberian Peninsula, located in the western Mediterranean Sea, from Cape Palos to Cape Creus, one of the fourth sub-regional divisions defined by the Marine Strategy Framework Directive (MSFD; 2008/56/EC) (38°44'2.44"N – 0º44'33"W; 37°38'10"N – 0º36'27"E). This area includes particularly productive zones due to a combined effect of the Northern Current and run-off from the Ebro River (Estrada, 1996). This particular region is considered as an important fishing ground in the Mediterranean Sea, showing significant marine biodiversity and species of great economic value (Navarro et al., 2015).

3.2 Sampling procedure

Most of our samples were taken on board the scientific bottom trawl survey MEDITS (MEDiterranean International Trawl Survey) conducted in the Geographic Sub-Area 06 (GSA6) as defined by the General Fisheries Commission of the Mediterranean (GFCM) for the period 2011-2018. This survey takes place yearly during approximately 26 days from May to June and aims to evaluate the demersal resources in the area. The standard sampling device used is a bottom trawl (GOC 73) designed for experimental fishing, in which the gear has a 40 mm mesh size and the codend a 20 mm mesh size (Fig. 1.3.2.1).

Fig. 1.3.2.1 R/V Miguel Oliver fishing during the Medits surveys in Spanish Mediterranean waters.

A total of 910 hauls were performed at depths ranging from 40 to 730 m, where the duration of each haul varied depending on depth: 30 minutes up to 200 m and 60 minutes below 200 m (Fig. 1.3.2.2). The trophic ecology of 61 fish species occurring over the shelf and upper slope were studied through stomach content analysis (See Table A1 in Chapter 2), where the content of 16,588 stomachs was quantitatively analyzed. After each fishing haul, a maximum of ten individuals of each target species was randomly sampled and quantitative diet estimates were obtained by measuring the stomach content volume using a trophometer (Fig. 1.3.2.3). This is considered a practical device suitable for use on board oceanographic vessels because it enables the examination of a large number of stomachs in a relatively short period (Olaso, 1990).

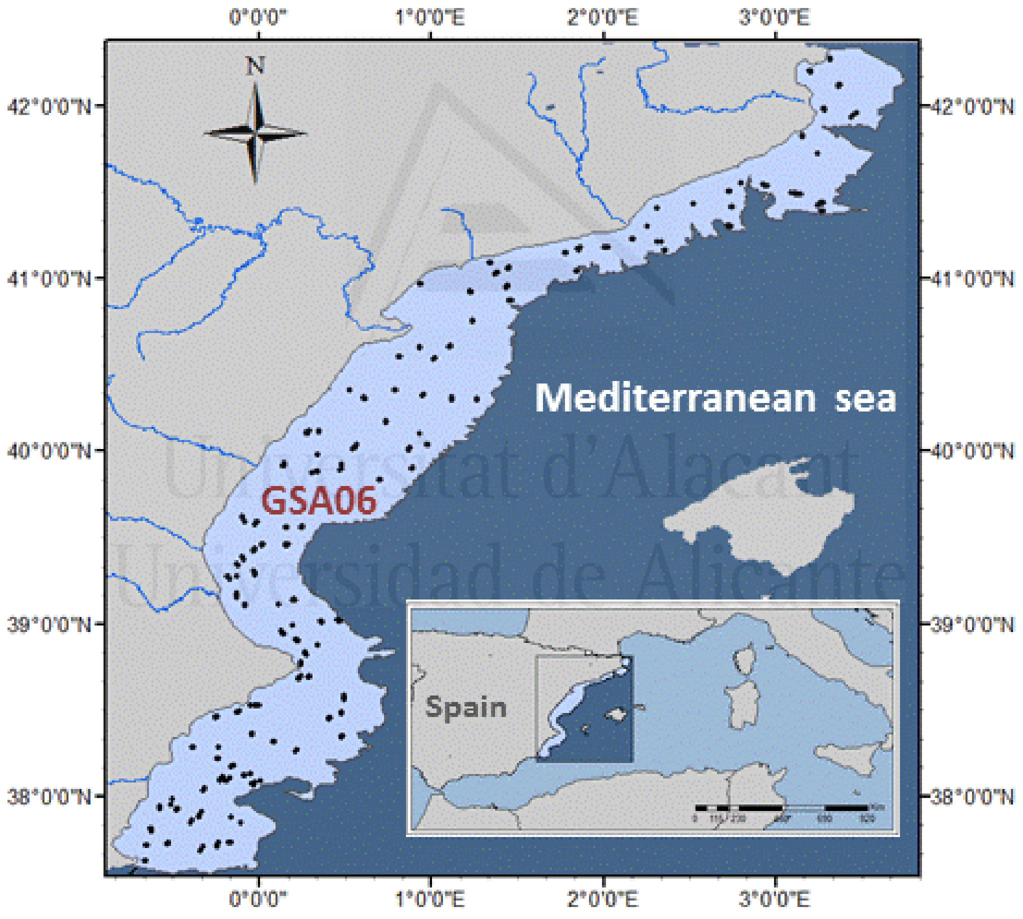


Fig. 1.3.2.2 Study area with the sampling locations, all of them between the isobaths of 40 and 800 m. Dots indicate the position of the fishing hauls during 2011-2018.

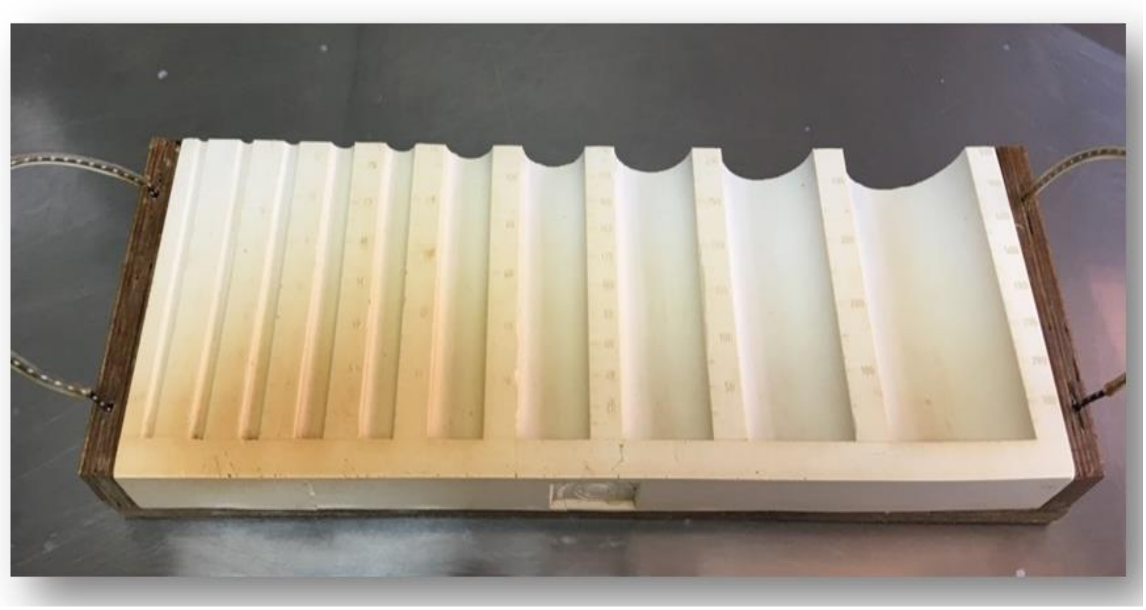


Fig. 1.3.2.3 Trophometer used on board for stomach sampling.

For all the specimens examined, data on sex and total length (cm) were recorded according to MEDITS guidelines (Bertrand et al., 2002). Once the stomach was opened, the content was separated into different food items that were later identified to the lowest possible taxonomic level under a stereoscopic microscope. The presence of skeletal and other hard body parts (e.g. fish otoliths, cephalopods beaks, gnathopods and claws from crustaceans and setae from worms) were also recorded (Fig. 1.3.2.4).

Specimens that had regurgitated stomachs were replaced by others of a similar size class. The degree of digestion of all identified prey items was also recorded; the content was rated as fresh, partially digested, or fully digested.

Additionally and regarding some pelagic species, namely, *Scomber colias*, *Scomber scombrus*, *Trachurus trachurus*, *Trachurus mediterraneus* and *Trachurus picturatus*, the trophic study was conducted monthly due to the seasonal variation of their preys along the year. For this reason, samples were caught on board the commercial fleet operating off the coasts of the Gulf of Alicante from 2011 to 2018.

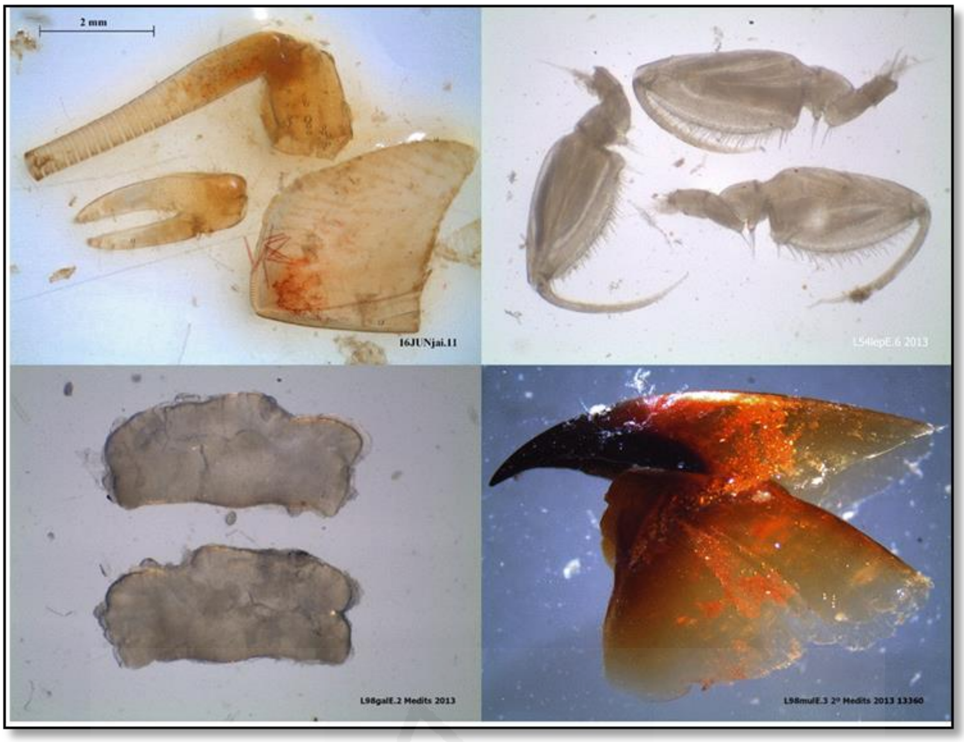


Fig. 1.3.2.4 Some hard structures found in the stomach contents analyzed.

3.3 Trophic indices

Stomach content analysis has been widely used in ecological researches to describe the diet and feeding habits of fish and other marine organisms (Hyslop, 1980). For this reason, common dietary indices are used to describe diet compositions; those indices are the ‘frequency of occurrence index’ (F%), expressed as the percentage of stomachs with a specific type of prey concerning the total number of stomachs containing food; the ‘volumetric index’ (V%), estimated to quantify the percentage contribution of each prey to the whole content in volume and the ‘geometric index of importance’ (GII%) computed as $GII\% = (\Sigma V_i)_j/n$, where V_i represents the value of the i´th Relative Measures of Prey Quantity (RMPQ´s) for the prey category *j* and *n* is the number of RMPQ´s used in the equation (Assis, 1996).

In addition, ‘niche breadth’ was also estimated through the Levin’s Standardized Index (Levins, 1968). This index ranges from 0 to 1, where values close to zero indicate a specialized diet while those close to one represent more generalized feeding habits. This index is computed as:

$$B_i = 1/n-1(1/ \Sigma_j p^2_{ij} - 1) \qquad (3)$$

where B_i represents Levin’s Standardized Index; p_{ij} is the proportion of prey *j* in the diet of predator *i* and *n* is the total number of prey categories.

The trophic niche overlap among the different species analyzed was estimated by the 'Simplified Morisita Index' (Morisita, 1959), which compares pairs of species ranging between 0 (no prey overlap) to 1 (full prey overlap) as follows:

$$C_{ik} = (2\ \Sigma\ p_{ij}p_{ik}) / (\Sigma\ p^2_{ij} + \Sigma\ p^2_{ik}) \qquad (4)$$

where C_{ik} represents the Simplified Morisita Index for predators *i* and *k* and p_{ij} and p_{kj} are the proportions of predators *i* and *k* with prey *j* in their stomachs.

The 'Trophic Level' (TL) was calculated using the formula developed by Christensen and Pauly (1992):

$$TL = 1 + (\Sigma\ DC_{ij})\ (NT_j) \qquad (5)$$

where DC_{ij} is the proportion of prey *j* in the diet of the predator *i* and NT_j is the trophic level of prey *j*. Prey TLs were determined empirically using local information or when this was not possible, from literature close to the modeled area. In this study, the TL of each of the defined size categories was first calculated by weighting its average biomass obtained during the MEDITS surveys for the period 2011-2018.

Finally, the Jaccard index (S_{ij}) was used to measure co-occurrence, as an expression of association between species (Jaccard, 1901):

$$S_{ij} = a / (a + b + c) \qquad (6)$$

where *a* is the number of occasions on which both species/length ranges are present, and *b* and *c* are the number of occasions on which only one of the two species/length ranges is present. This index was calculated as the percentage of occasions that both species/length ranges appeared together in the same haul. In this study, only those hauls where at least one of the species/length ranges of each pair was present were considered.

3.4 Ecosystem and ecological indicators

Once the Ecopath model is balanced, several indicators can be estimated to describe the structure and functioning of the studied ecosystem, e.g. Total System Throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), considered as an overall measure of the "ecological size" of the system and Total Flow to Detritus (TFD, $t \cdot km^{-2} \cdot year^{-1}$) (Ulanowicz, 1986); Total Production (TP, $t \cdot km^{-2} \cdot year^{-1}$); Total Biomass excluding detritus (TB, $t \cdot km^{-2}$); the ratios Total Primary Production/Total Respiration (Pp/R) and total Primary Production/Total Biomass (Pp/B, $t \cdot km^{-2} \cdot year^{-1}$).

Furthermore, there are other indicators of food web complexity such as The System Omnivory Index (SOI) (Christensen and Walters, 2004); The Finn's Cycling Index (FCI, %), defined as the percentage of all flows that are recycled in the trophic network (Finn, 1976).

Also, it is important to estimate the Transfer Efficiency (TE) from primary producers and from detritus, which is the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem or transferred to higher trophic levels through consumption (Lindeman, 1942). In addition, indicators giving information regarding fishing intensity and impacts in the ecosystem, such as the mean trophic level of the catch (mTLc), calculated as the weighted average of the TL of caught species; the mean trophic level of the community (mTLco), which is estimated as the weighted average of the TL for functional groups with a TL>2 (Christensen, 1996); the Primary Production Required to sustain the fishery (%PPR, considering Pp); the Primary Production Required to sustain the fishery (%PPR, considering Pp + detritus) (Pauly and Christensen 1995); and the loss in production index (Lindex), which represents the loss in secondary production due to fishing and the probability of an ecosystem being sustainably fished (P_{sust}) used to identify the ecosystem effects of fishing (Libralato et al., 2008).

The ECOIND plug-in (Coll and Steenbeek, 2017) is used to calculate standardized ecological indicators in order to stablish proper comparison between models built with similar ecological criteria. We have used four of these indicators to compare results in GoA with neighboring models.

Biomass-based indicators: based on the abundance of organisms in the food web, e.g. the ratio of Invertebrates biomass and Fish biomass; biomass of demersal (Demersal B) and Pelagic (Pelagic B) organism and their ratio (Demersal B/Pelagic B).

Catch-based indicators: based on the catch and discard species in the ecosystem, e.g. the catch of fish (Fish C); invertebrates (Invertebrates C) and their ratio (Invertebrates C/Fish C); demersal (Demersal C); Pelagic (Pelagic C); catch of organisms and their ratio (Demersal C/Pelagic C).

Trophic-level based indicators: indicators based on the trophic level concept, e.g. Tropic level of the catch (TLc) (Christensen, 1996; Pauly et al., 1998); the Marine Trophic Index (MTI, or TLc including organisms with TL ≤ 3.25) (Pauly et al., 2005); TL of the community including all organisms (TL co); TLco including organisms with TL ≤ 2 (TLco 2); TLco including organisms with TL ≤ 3.25 (TLco 3.25), and TLco including organisms with TL ≤ 4 (Tlco 4).

Species-based indicators: indicators specifically based on species traits and conservation status, e.g. The Intrinsic Vulnerability Index of the catch (IVIc) is a weighted mean of the vulnerability of exploited fish species (Cheung et al., 2007); the biomass of endangered species in the community (UICN species B) and in the catch (IUCN species C) using the IUCN (International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015).

3.5 Minimum sampling size

The software EstimateS 9.1 was used, for the first time in a study of Mediterranean fish species, to estimate cumulative prey curves in order to determine the adequacy of the sample size for each species in representing the species diet.

We applied cumulative prey curves to determine if the number of stomachs analyzed was adequate to represent the trophic spectrum of each predator studied. The software EstimateS 9.1 (Colwell, 2013) was used to perform species accumulation curves, which were plots of the cumulative number of prey taxa against the cumulative number of samples examined. To avoid biased estimates, the sample order was randomized 100 times following Colwell and Codington (1994).

The curve is a function of effort that increases monotonically until an asymptote is reached (Chao and Chiu, 2016). The y-value of that asymptote is the maximum number of prey that could be achieved. To evaluate sample quality, a function able to describe the cumulative curve is requested.

The cumulative curve for each species was fitted to logarithmic ($y = \log a^x$) and Clench´s functions (Clench, 1979) (Fig. 1, Annex 1).

4. Hypothesis and aims

This PhD thesis aims to focus on the understanding of the trophic structure and functioning of the Northern Spain-GSA6 food web, providing an ecosystem approach comparison in the axe north-south along the Mediterranean Spanish coast through the modeling of the Gulf of Alicante, as a singular ecosystem located in this area. Hence, we hypothesize that exist certain features in this particular marine ecosystem, which makes it different from neighboring ecosystems due to the combination of its oceanographic and biological singularities, especially the low productivity.

4.1 General objectives

- To characterize the food-web and trophic interactions within the fish community in Northern Spain and update the existing studies taking into account the interaction between species as well as its ontogenetic shifts.

- To obtain insights into the ecosystem structure and functioning by means of a mass balance approach using Ecopath software which allow the comparison with neighboring models.

Some specific objetives to reach the general objectives are the following:

- To apply in marine trophic studies, a mathematical approach based on cumulative prey curves for determining the adequate number of samples required to report the diet compositions of the species investigated.

- To explore ecological relationships such as ontogenetic variation in diet or trophic and spatial segregation in Gadiformes species as a mechanism to manage the resource partitioning within and amongst them.

- To identify in the fish community the major trophic guilds exploiting similar food resources and how the environmental drivers such as habitat type, latitude and depth affect its structure.

- To investigate changes in feeding patterns for each species between Gulf of Alicante and the rest of Mediterranean Northern Spain.

- To obtain ecological indicators with the aim to explore the fishing impacts on the ecosystem studied.

Chapter 2: Revealing environmental forcing in the different trophic guilds of fish communities off the western Mediterranean Sea

Revealing environmental forcing in the different trophic guilds of fish communities off the western Mediterranean Sea[1]

Abstract

The dietary preferences of 61 western Mediterranean species of fish belonging to different trophic levels were studied. Specimens were collected during the annual bottom trawl survey MEDITS for the period 2011-2018, with a total of 16,588 stomach contents analyzed, providing a highly valuable raw dataset for advanced studies in trophic ecology. The software EstimateS 9.1 was used, for the first time in a study of Mediterranean fish species, to estimate cumulative prey curves in order to determine the adequacy of the sample size for each species in representing the species diet. The main findings revealed the existence of nine well-identified feeding strategies, or trophic guilds, based on food preferences. Indicators, namely the Shannon diversity index, biomass estimated from standard surveys, mean trophic level and fish community composition, were used to categorize the structure of the fish community in western Mediterranean marine food webs. In addition, the effects of latitude, depth and habitat type on fish community structure were investigated. Results show all these environmental factors investigated drove fish composition structure. Regarding the three variables investigated, depth had the greatest impact on the fish community structure, particularly affecting diversity and fish community composition. Latitudinal gradient only seemed to affect fish community composition, showing consistency along a latitudinal north-south axis. Habitat type was found to be significant in fish community structure. Mean trophic level was the only indicator that was not affected significantly by environmental variables. The present study shows the relevance of environmental forcing in fish community structure. These findings highlight the need of ecosystem studies, since information about the trophic networks in the study area is still scarce, jeopardizing the development of ecosystem models. The present work aims to fill this gap for the effective implementation of an ecosystem approach to fisheries management in the western Mediterranean Sea.

Keywords: dietary preferences, food web, feeding strategies, fish community structure, habitat types, environmental forcing, cumulative prey curves, mean trophic level, diversity index, diet overlapping.

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2.1 Introduction

The study of marine food webs has not only become a useful tool to identify the relevance of species relationships and food resource partitioning, but is also a way to explore different levels of producers or consumers (Polis and Strong, 1996). Food web studies play an essential role in explaining disruptions such as overfishing (e.g. Coll et al., 2014), alien species (Streftaris and Zenetos, 2006; Corrales et al., 2017) and habitat destruction in marine ecosystems (Muntadas et al., 2013). In this regard, one of the most threatened areas is the continental shelf, an area that hosts most of the exploited species and is distinctively characterized by a high biological production (Coll et al., 2008; 2014).

The EU Marine Strategy Framework Directive (MSFD: 2008/56/EC) requires that each Member State takes the necessary measures to achieve or maintain Good Environmental Status of marine waters. The MSFD takes into account topics such as biodiversity, contaminants, marine litter, commercially exploited fish and marine food webs. Likewise, the Spanish inventory of Habitat and Marine species (MAPAMA, 2013) can help to identify singular habitats as well as to determine habitat-related species. Similarly, other variables to explore along with habitat type are, for instance, geographical variation in fish community structure along the north-south coast and bathymetric ranges (Ferreira et al., 2004).

Even though the western Mediterranean Sea is one of the most studied seas, most of the reported research is focused at local spatial scales over short periods of time as in studies of the Catalan Sea (Macpherson, 1980a; 1980b; Carrascón and Matallanas, 2002; López et al., 2016) and the Gulf of Valencia (Morte et al., 2001; 2002; Jaramiño et al., 2011). To better understand latitudinal and depth patterns, trophic ecology research covering a broader study area is needed, such as that for the Spanish western Mediterranean Sea, i.e. Geographical Sub-Area 6 (GSA06) as defined by the General Fisheries Commission of the Mediterranean (GFCM).

Our study was conducted along the continental shelf and slope of the eastern coast of the Iberian Peninsula, located in the western Mediterranean Sea, from Cape Palos to Cape Creus (Fig. 2.1.1). This area includes zones that have high biological productivity due to the combined effects of the Northern Current and run-off from the Ebro River (Estrada, 1996). This region is an important fishing ground in the Mediterranean Sea, showing significant marine biodiversity and species of great economic value (Navarro et al., 2015).

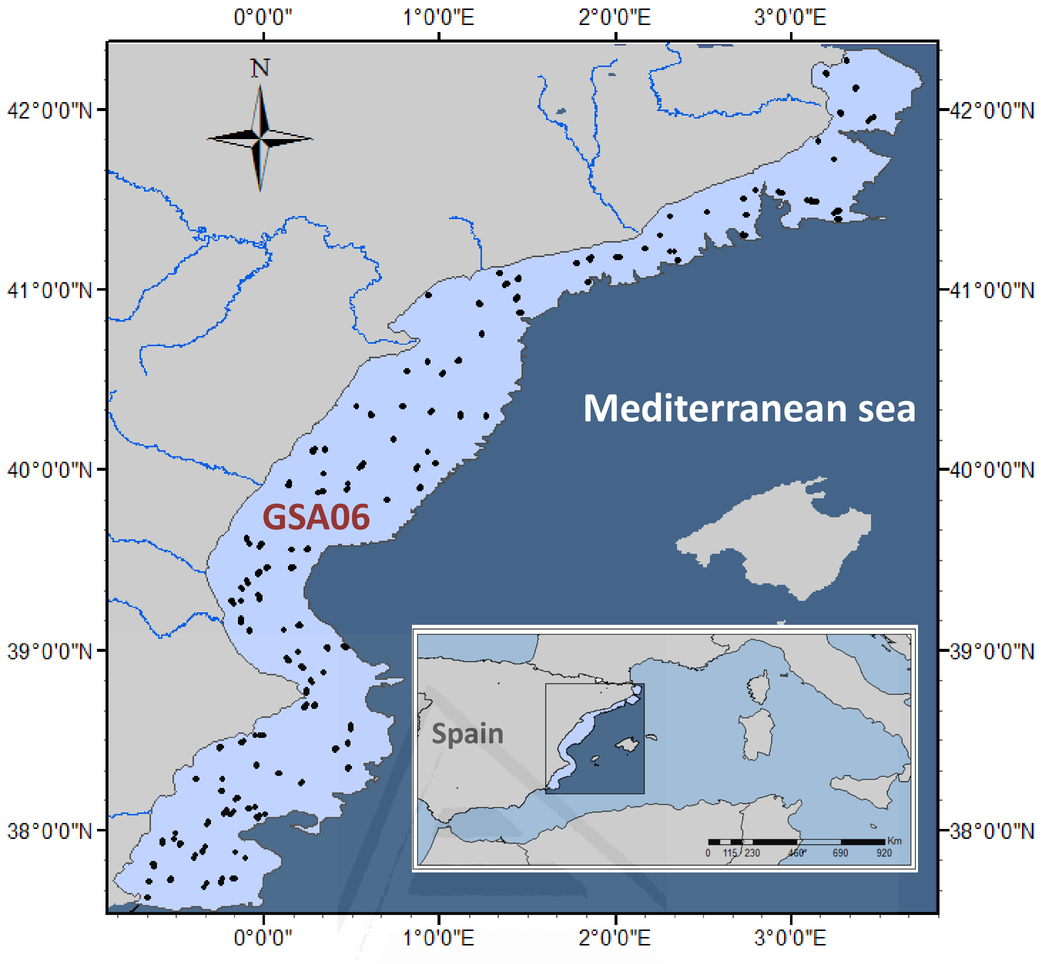

Fig. 2.1.1 Map of the study area showing the sampling locations between the isobaths of 40 and 800 m. Dots indicate the position of the fishing hauls analyzed.

A well-recognized problem related to trophic studies has been accurately determining the minimum sample size for each species sampled. To address this problem, we applied, for the first time in marine trophic ecology studies, a mathematical approach based on cumulative prey curves for determining the adequate number of samples required to determine the diet of the species studied (Modde and Ross, 1983; Ferry and Caillet, 1996). In the study area, we propose that cumulative prey curve studies provide useful information for implementing future and improved ecosystem-based models along the western Mediterranean. Ecosystem-based models are widely used to investigate ecological and fishery connections and they are recognized as effective assessment tools in the evaluation of the trophic structure of marine communities (e.g. Christensen and Walters, 2002; Coll et al., 2007; Torres et al., 2013). Despite the importance of ecosystem studies, information about the trophic networks in the study area is still scarce, thus limiting the development of ecosystem models. The present work aims to fill this gap.

This study provides an important and updated contribution to existing knowledge addressing the trophic ecology of 61 species. First, we investigated the diet compositions of the most representative fish species coexisting in the western Mediterranean Sea, applying the cumulative prey curve methodology. We then identified the major trophic guilds exploiting similar food resources, considering a trophic guild as a specific set of species that are clustered following similar feeding strategy (Kornan and Kropil, 2014). Finally, we investigated how the environmental drivers of habitat type, latitude and depth affected the different trophic guild structures, using four main indicators, namely the Shannon diversity index, biomass, mean trophic level and fish community composition.

2.2 Material and methods

Stomach sampling

The most representative species of each trophic level, according to its biomass, were selected for our study to improve our understanding of the main components of the trophic web in the study area. Thus, the trophic ecology of 61 fish species occurring over the shelf and upper slope were studied through stomach content analysis. Samples were collected and analyzed during the 'MEDITS' bottom trawl surveys conducted continuously between 2011 and 2018 (Bertrand et al., 2002). This survey takes place yearly from May to June and aims to evaluate the demersal resources in the area. The standard sampling device used is a bottom trawl (GOC 73) designed for experimental fishing, in which the gear has a 40 mm mesh size and the codend a 20 mm mesh size.

A total of 910 hauls were performed at depths ranging from 40 to 730 m, where the duration of each haul varied depending on depth: 30 minutes up to 200 m and 60 minutes below 200 m (Table A.2.1).

The content of 13,342 full stomachs was quantitatively analyzed. After each fishing haul, a maximum of ten individuals of each target species was randomly sampled and quantitative diet estimates obtained by measuring the stomach content volume using a trophometer. This is considered a practical device suitable for use on board oceanographic vessels because it enables the examination of a large number of stomachs in a relatively short period of time (Olaso, 1990).

For all the specimens examined, data on sex and total length (cm) were recorded according to MEDITS guidelines (Bertrand et al., 2002). Once the stomach was opened, the content was separated into different food items that were later identified to the lowest possible taxonomic level under a stereoscopic microscope. The presence of skeletal and other hard body parts (e.g. fish otoliths, cephalopods beaks, gnathopods and claws from crustaceans and setae from worms) were also recorded.

Specimens that had regurgitated stomachs were replaced by others of a similar size class.

Table 2.1 Acronyms used for the major prey groups and nine trophic guilds identified

Acronym	Group name
Major Prey Groups	
SP	Small Plankton
LP	Large Plankton
GP	Gelatinous Plankton
PO	Polychaeta
PE	Peracarids
BI	Benthic invertebrates
NA	Natantia
RE	Reptantia
BC	Benthic Cephalopods
BT	Benthopelagic Cephalopods
PF	Pelagic Fishes
FF	Flatfishes
GA	Gadoids
IF	Ichthyophagous Demersal Fishes
GO	Gobids
TR	Triglids
HA	European Hake
MU	Mullets
SF	Sparids-Serranids-Scorpenids Fishes
BF	Benthopelagic Fishes
Trophic Guilds	
PP	Pelagic Piscivores
PG	Planktophagous Specialized on Gelatinous Plankton
PC	Planktophagous Specialized on Copepods
PB	Pelagic, Benthopelagic Fishes and Natantian Feeders
GB	Gadoids and Benthopelagic Fish Feeders
AE	Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders
BR	Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta
PN	Peracarid and Natantian Feeders
DF	Decapod Feeders

The degree of digestion of all identified prey items was also recorded; the content was rated as fresh, partially digested or fully digested. A total of 346 prey items were identified and grouped into 20 categories according to both taxonomic and feeding behavior criteria (see acronyms in Table 2.1).

Cumulative prey curves

We applied cumulative prey curves to determine if the number of stomachs analyzed was adequate to represent the trophic spectrum of each predator studied. The software EstimateS 9.1 (Colwell, 2013) was used to perform species accumulation curves, which were plots of the cumulative number of prey taxa against the cumulative number of samples examined. To avoid biased estimates, sample order was randomized 100 times following Colwell and Codington (1994). All the identified prey items (N = 346) were grouped into 207 major categories to guarantee the wide range of prey items needed to build a robust curve.

The curve is a function of effort that increases monotonically until an asymptote is reached (Chao and Chiu, 2016). The y-value of that asymptote is the maximum number of prey that could be achieved. To evaluate sample quality, a function able to describe the cumulative curve is requested. Therefore, an asymptotic approach was provided to reach the asymptote estimation of the species accumulation curve using non-parametric estimators ACE and Chao 1 (Table A.2.2). The value of the asymptote of the cumulative curve represents the maximum number of prey that would be reached if the sample size were infinite (Colwell and Coddington, 1994).

The cumulative curve for each species was fitted to logarithmic ($y = \log a^x$) and Clench´s functions (Clench, 1979):

$$Sn = a * n / (1 + b * n) \qquad (1)$$

where the asymptote is a/b and the slope of the tangent line to the Clench equation is calculated as:

$$a / (1 + b * n)^2 \qquad (2)$$

Coefficient r^2 values of both functions were compared by using a paired t-test.

In this study, sample size for each of the species was considered to be sufficient when the value of the slope of the tangent line to the curve was ≤ 0.05. All models produced were fitted using the quasi-Newton method provided by the package Statistica 7 (StatSoft 2004).

Diet compositions and feeding strategies

Three dietary indices were used to describe diet compositions. According to Hyslop (1980), the frequency of occurrence index (F%), expressed as the percentage of stomachs with a specific type of prey in relation to the total number of stomachs containing food, was calculated. The volumetric index (V%) was also estimated to quantify the percentage contribution of each prey to the whole content in volume. Finally, the geometric index of importance (GII%) was computed as: $GII\% = (\Sigma V_i)_j/n$, where V_i represents the value of the i´th Relative Measures of Prey Quantity (RMPQ´s) for the prey category *j* and *n* is the number of RMPQ´s used in the equation (Assis, 1996).

Likewise, Levin’s index (B_i) was calculated to investigate the trophic niche breadth of each of the 61 fish species selected for this study. This index is computed as $B_i = 1 / (n – 1) (1 / \Sigma_j p^2_{ij} –$

1), where B_i represents Levin's standardized index; p_{ij} is the proportion of prey *j* in the diet of predator *i* and n is the total number of prey categories. This index ranges from 0 to 1, where lower values indicate a specialist diet while higher values indicate a generalist diet (Levins, 1968).

The actual trophic level (TL) was also estimated to describe the food web position for each of the 61 species studied. This was useful in providing relevant information as an indicator of the state of the marine ecosystem studied. TL is computed as $TL = 1+ (\Sigma DC_{ij}) (NT_j)$, where DC_{ij} is the proportion of prey *j* in the diet of the predator *i* and NT_j is the trophic level of prey *j* (Christensen and Pauly, 1992). In the case of prey TLs, values were taken from specialized literature (Cortes, 1999; Ebert and Bizzarro, 2007; Jacobsen and Bennett, 2013; Karachle and Stergiou, 2017; Rosas-Luis et al., 2014).

Environment effects on trophic guild structures

To define the different trophic guilds represented by a set of species exploiting similar food resources, quantitative information on diet composition was grouped by using clustering analysis. For each of the resulting groups, indices already mentioned (F%, V%, GII%, B_i and TL) and the Shannon diversity index ($H = - \Sigma p_j \log p_j$, where p_j is the proportion of each trophic guild within the fish community) were estimated to describe the resulting trophic guilds. In addition, mean trophic level (MTL) was estimated by weighting the relative biomass of each species within the groups. To do so, the necessary abundance indices for these computations were obtained from MEDITS surveys. To identify potential food competition among groups, the degree of overlap in diet was calculated using the Simplified Morisita Index (Morisita, 1959), which compares pairs of groups ranging between 0 (i.e. no prey overlapping) and 1 (i.e. prey overlapping) and is computed as $C_{ik} = (2 \Sigma p_{ij}p_{ik}) / (\Sigma p^2_{ij} + \Sigma p^2_{ik})$, where C_{ik} represents the Simplified Morisita Index for predators *i* and *k* and p_{ij} and p_{kj} are the proportions of predators *i* and *k* with prey *j* in their stomachs.

We then explored how different environment conditions affect the resulting trophic guilds. We investigated how these communities (characterized by Shannon, biomass, mean trophic level and fish community composition) change depending on different environments (characterized by latitude, depth and habitat type). First, two geographical areas were tested (north and south) delimited by parallel 38º 22.82´N according to MEDITS guidelines (Bertrand et al., 2002). Secondly, four bathymetric depth strata (50-100 m, 101-200 m, 201-500 m and 501-800 m) were considered. Finally, we analyzed changes in fish community structure by the eight different habitat types identified and defined by the Spanish inventory of marine habitats (MAPAMA, 2013) (Table 2.2).

Table 2.2 Codes and description for the different habitat types.

CODE		DESCRIPTION	MAIN SPECIES	DEPTH RANGE (m)
MAE	I	maërl and biogenic bottoms	*Rhodophyceae, Molgula appendiculata, Sphaerechinus granularis*	45-65
AF_AE	II	sandy and muddy circalittoral bottoms consisting mainly in Ascidians and Echinoderms	*Polycarpa* spp., *Botryllus* spp., *Parastichopus regalis*	45-70
AF_PE	III	sandy and muddy circalittoral bottoms consisting mainly in Pennatulacea	*Alcyonium palmatum, Pennatula rubra, Trachythyone* spp.	45-80
FS_EC	IV	sedimentary and detritic bottoms consisting mainly in Echinoderms	*Echinus* spp., *Parastichopus regalis, Alcyonium palmatum*	82-267
FS_PE	V	sedimentary and detritic bottoms consisting mainly in Pennatulacea and Alcyoniidae	*Alcyonium palmatum, Pennatula rubra, Venus nux*	82-177
FS_CP	VI	sedimentary and detritic bottoms consisting mainly on Crinozoa and Parastichopus	*Antedon mediterranea, Parastichopus regalis, Ophiura ophiura*	72-230
FS_FU	VII	bottoms consisting mainly in Funiculina quadrangularis	*Funiculina quadrangularis, Alcyonium palmatum*	68-338
BAT	VIII	bathyal bottoms	*Aporrhais serresianus, Brissopsis* spp., *Alcyonium palmatum*	218-735

Statistical analyses

With the goal of investigating different standardized diet compositions among species, clustering ordination analyses and non-metric multidimensional scaling (MDS) were conducted. A Bray–Curtis similarity index and a square-root transformed for standardized data were performed, preserving abundance information but reducing the contribution of the most abundant species to the general pattern. Similarity values among clusters that were ≥ 40% of the maximum overall similarity distance were considered to indicate major divisions and therefore, used to distinguish trophic guilds within the food web studied.

To explore differences in fish community composition according to depth, latitude and habitat types, an analysis of similarities (ANOSIM) was conducted. To this end, biomass relative values of previously identified trophic guilds were estimated.

An independent sample t-test was used (Student´s t-test) to determine whether there were significant differences in mean trophic level, Shannon diversity index and total biomass between the two geographical areas. Finally, one-way ANOVA, post-hoc Tukey and Dunnett T3 tests, depending on the homogeneity of variances, were used to detect differences according to depth and habitat type.

A significance level of 0.05 was set for all statistical analyses. All multivariate analyses were conducted in PRIMER 6 (Clarke and Gorley, 2006) and SPSS Statistics 17.0 software (SPSS, 2008).

2.3 Results

Sample size accurate determination

The paired-sample t-tests showed significant differences in goodness of fit r^2 between the logarithmic function and Clench´s function (t = 7.706, $p < 0.001$). The better fit of cumulative prey curves for the entire dataset was obtained using Clench´s function (mean ± SD = 0.986 ± 0.012) rather than using the logarithmic function (mean ± SD = 0.960 ± 0.023). Goodness of fit r^2 values with Clench´s equation ranged from 1.00 for some species, such as *Conger conger* or *Scorpaena porcus*, to 0.93 for *Scomber colias* (Table A.2.2). According to Clench (1979), 48 of the 61 studied species (i.e. 78%) showed the slope of the tangent line to the curve ≤ 0.05. Therefore, the achieved sample size was considered adequate to accurately characterize their diet composition. The remaining 13 species did not reach the asymptotic threshold. Nevertheless, these species were included in the study, not for a detailed description but to provide a broad overview of their feeding habits. The non-parametric estimator ACE proved to be the most appropriate to estimate sampling coverage. The highest values were obtained for *Scyliorhinus canicula* and *C. conger* with a potential number of prey of 95 and 98, respectively. Conversely, *Spicara smaris* and *Molva macrophthalma* showed the lowest values of prey items (14 and 17, respectively).

Diet compositions and feeding strategies

A summary of prey species per predator is presented in Table A.2.3 with a total of 16,588 stomachs examined. Of the 13,342 full stomachs analyzed, a total of 346 prey taxa were identified and grouped into 20 major categories (Table A.2.4). Overall, the most relevant prey groups in the diet of the 61 fish species were Reptantia (V = 19.3±22.7%; F = 27.8±27.0%; GII = 23.6±24.4%; mean±SD), represented mainly by *Goneplax rhomboides* (V = 4.9%) and *Liocarcinus* spp. (V = 4.5%) as well as Natantia (V = 17.8±18.8%; F = 25.9±20.9%; GII = 21.8%±19.2%) composed mainly of *Alpheus glaber* (V = 5.3%) and *Solenocera membranacea* (V = 2.2%).

The main predators of Reptantia were *Arnoglossus imperialis, Chelidonichthys lastoviza, Scorpaena porcus* and *Serranus hepatus*. The first two species preyed mainly on *Liocarcinus* spp. (V = 48.5% and V = 31.8% respectively), while the latter species, *S. porcus* and *S. hepatus*, preyed primarily on *G. rhomboides* (V = 38.0% and V = 26.5% respectively).

The species group Natantia “prawns & shrimps” was the second most consumed group, *Trisopterus minutus* and *Phycis blennoides* being the main predators of *A. glaber* (V = 44.1% and V = 34.1% respectively) while *Leucoraja naevus* and *Raja* spp. showed preferences for *S. membranacea* (V = 42.2% and V = 20.1% respectively).

For all species, a wide niche breadth (B_i) ranging from 0.01 to 0.56 was observed, where the highest values showed that *Capros aper* (B_i = 0.56) fed mainly on copepods and euphausiids (V = 17% and V = 16.5% respectively); *Pagellus acarne* (B_i = 0.50) focused its diet on mysids (V = 18.2%) and polychaeta (V = 15.2%) and *Citharus linguatula* (B_i = 0.50) preyed mainly on teleosts (V = 72%) and *A. glaber* (V = 8.9%). Finally, *Scorpaena elongata* (B_i = 0.45) showed a remarkable presence of teleosts in its diet (V = 52.7%) followed by reptantian decapods (V = 21.5%). For these species a more generalist diet was assigned due to the diverse range of prey items consumed (Table A.2.4). On the other hand, results showed the lowest values of Levin’s index for *M. dypterygia* (B_i = 0.01), with a preference for *Gadiculus argenteus* (V = 30.6%); *Scomber scombrus* (B_i = 0.05) focused its diet on *Sardina pilchardus* (V = 49.1%) while *S. smaris* (B_i = 0.05) consumed primarily copepods (V = 88.2%).

Trophic level (TL) ranged from 3.02 to 4.76 with *S. smaris* showing the lowest value and therefore the lowest position in the food web and *Lophius piscatorius* was ranked as the top predator (Table A.2.4).

Resulting trophic guilds

The hierarchical classification analysis based on diet composition initially identified seven trophic guilds, each a homogeneous group. With the aim of conducting a more in-depth study, the most numerous guild were split into three sub-groups taking into account both feeding and behavior, resulting in a total of nine trophic groups (Fig. 2.3.1). These categories are codified and summarized in Table 2.1. Generally, the results identified a total of nine feeding strategies for the 61 species studied. For the first trophic guild (Pelagic Piscivores, PP), the most consumed prey groups were pelagic fishes (V = 79.5%; F = 33.9%; GII = 56.7%), in particular *S. pilchardus* (V = 37.2%). In the second group (Planktophagous Specialized on Gelatinous Plankton, PG), the presence of gelatinous zooplankton is noteworthy (V = 74.2%; F = 56.9%; GII = 65.6%) with *Pyrosoma atlanticum* as the most common prey (V = 69.3%). Small plankton (V = 45.5%; F = 77.3%; GII = 61.4%) dominate the diet of the third group (Planktophagous Specialized on Copepods, PC), preying mainly on copepods (V = 42.2%). In the diet of the fourth group (Pelagic, Benthopelagic Fishes and Natantian Feeders, PB), the pelagic fishes prey group (V = 18.0%; F = 11.2%; GII = 14.6%) is important, where *Engraulis* *encrasicolus* dominate (V = 8.6%), followed by *Micromesistius poutassou* (V = 3.9%) and *M. merluccius* (V = 2.2%).

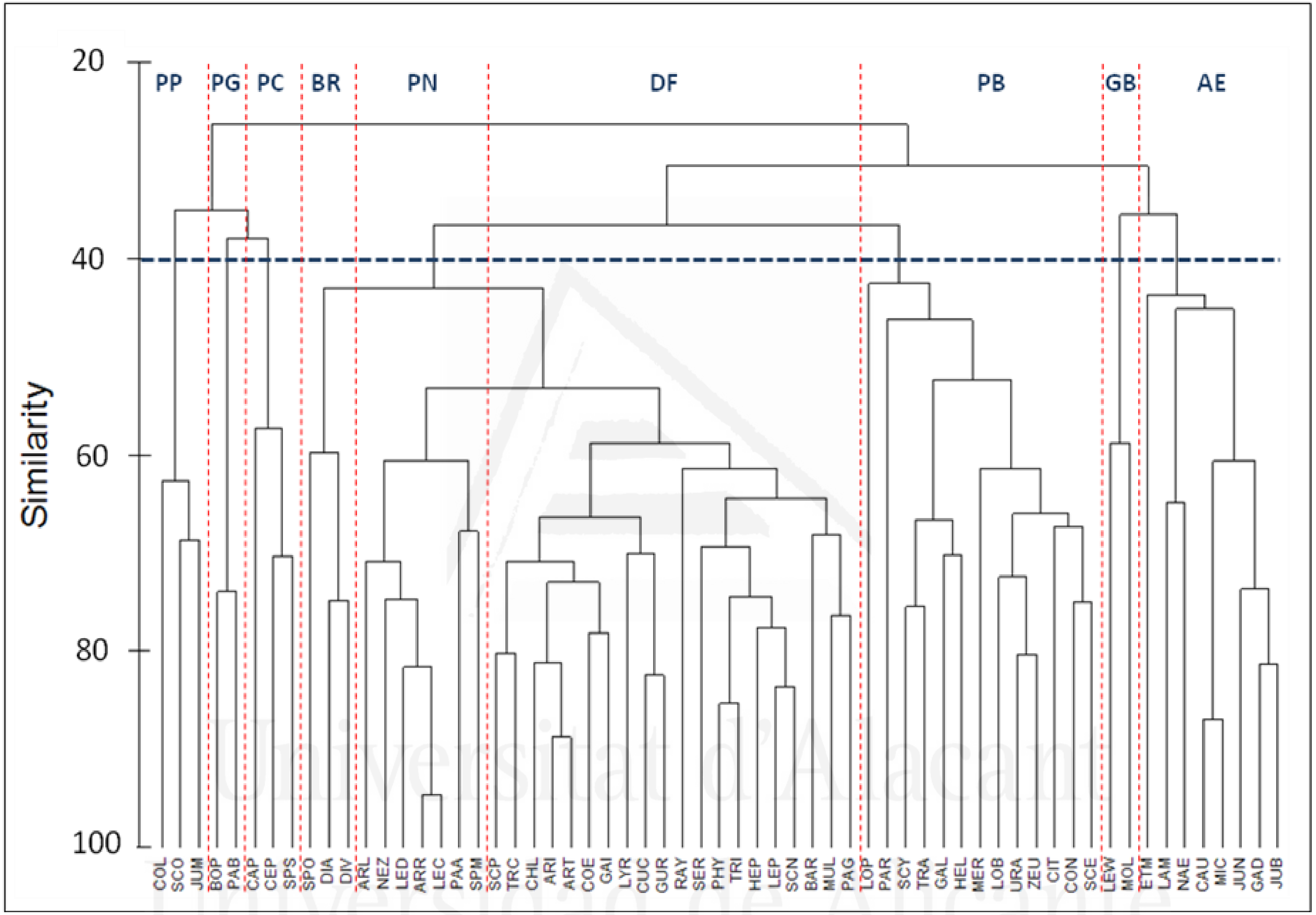

Fig. 2.3.1 Dendrogram using group average clustering from Bray-Curtis similarities based on stomach content analysis grouping the studied species into nine trophic guilds. PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders.

Table 2.3 Volumetric Index (V%), Frequency Index (F%), Geometric Index of Importance (GII%), Niche breadth (B_i) and Mean trophic level (MTL) estimated for the nine trophic guilds (TG). Dashes represent no consumption. Acronyms are referenced in Table 2.1.

TG	Bi	MTL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
PP	0.03	4.08	V%	0.3	8.5	2.2	0.2	2.8	0.0	1.2	1.0	0.6	0.4	79.5	-	0.0	0.2	0.7	-	-	2.2	-	0.2
			F%	6.2	67.7	54.5	2.6	35.0	1.2	4.5	4.0	1.9	0.8	33.9	-	0.3	0.1	0.9	-	-	5.1	-	0.4
			GII%	3.2	38.1	28.3	1.4	18.9	0.6	2.8	2.5	1.3	0.6	56.7	-	0.2	0.2	0.8	-	-	3.7	-	0.3
PG	0.04	3.35	V%	0.2	3.6	74.2	1.7	1.2	4.6	3.8	0.0	3.8	0.1	0.3	3.7	-	-	-	-	-	-	-	2.8
			F%	5.2	18.4	56.9	12.9	21.6	14.4	4.2	0.9	1.6	0.2	0.5	1.2	-	-	-	-	-	-	-	8.2
			GII%	2.7	11.0	65.6	7.3	11.4	9.5	4.0	0.5	2.7	0.2	0.4	2.5	-	-	-	-	-	-	-	5.5
PC	0.12	3.39	V%	45.5	26.2	0.8	7.1	17.5	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	77.3	26.2	4.9	3.8	27.6	-	2.4	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	61.4	26.2	2.8	5.5	22.5	-	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-
PB	0.45	4.15	V%	0.8	8.0	0.5	1.1	0.4	0.2	14.5	9.2	3.9	5.4	18.0	2.4	10.0	5.7	1.3	0.7	2.5	0.6	1.7	12.9
			F%	0.2	21.3	1.1	3.8	8.0	0.4	30.9	21.0	6.5	2.4	11.2	2.1	16.3	2.0	6.9	0.5	1.9	0.2	1.4	10.7
			GII%	0.5	14.7	0.8	2.5	4.2	0.3	22.7	15.1	5.2	3.9	14.6	2.3	13.2	3.9	4.1	0.6	2.2	0.4	1.5	11.8
GB	0.03	4.58	V%	-	0.3	-	-	1.0	-	7.5	0.4	0.2	-	-	-	78.0	-	-	-	-	-	-	12.7
			F%	-	3.2	-	-	6.4	-	7.7	1.3	1.9	-	-	-	78.2	-	-	-	-	-	-	9.6
			GII%	-	1.8	-	-	3.7	-	7.6	0.8	1.0	-	-	-	78.1	-	-	-	-	-	-	11.1
AE	0.09	3.68	V%	2.3	45.8	0.3	0.0	0.7	-	10.6	0.2	0.2	0.4	0.5	0.0	1.2	-	0.2	-	0.1	-	-	37.6
			F%	3.8	51.4	1.1	0.5	7.4	-	21.7	0.6	0.8	2.9	0.5	0.1	1.3	-	0.6	-	0.2	-	-	38.3
			GII%	3.1	48.6	0.7	0.2	4.1	-	16.2	0.4	0.5	1.6	0.5	0.0	1.2	-	0.4	-	0.1	-	-	38.0
BR	0.19	3.50	V%	3.7	0.4	0.7	26.6	4.0	24.1	3.2	28.6	0.6	0.4	0.7	1.3	-	-	5.7	-	-	-	-	-
			F%	2.7	2.5	3.5	46.5	31.9	38.4	4.2	27.0	2.1	0.2	1.2	0.6	-	-	1.5	-	-	-	-	-
			GII%	3.2	1.4	2.1	36.6	17.9	31.2	3.7	27.8	1.4	0.3	0.9	0.9	-	-	3.6	-	-	-	-	-
PN	0.13	3.51	V%	1.3	8.4	2.3	7.6	48.9	4.6	16.5	4.8	2.6	-	1.1	0.2	0.1	-	1.7	-	-	-	-	-
			F%	9.4	3.5	1.2	10.3	80.0	3.4	21.6	16.0	0.9	-	0.2	0.2	0.1	-	2.7	-	-	-	-	-
			GII%	5.4	5.9	1.7	8.9	64.4	4.0	19.0	10.4	1.7	-	0.6	0.2	0.1	-	2.2	-	-	-	-	-
DF	0.13	3.63	V%	0.0	1.4	0.0	8.1	4.4	2.7	46.1	26.6	2.6	0.6	0.6	0.2	2.3	0.5	1.7	0.1	0.5	0.4	0.1	1.3
			F%	2.6	5.2	0.2	12.3	41.5	5.1	43.8	52.8	2.4	0.1	0.4	0.8	4.4	0.4	3.7	0.2	0.3	0.0	0.2	1.4
			GII%	1.3	3.3	0.1	10.2	23.0	3.9	44.9	39.7	2.5	0.4	0.5	0.5	3.4	0.4	2.7	0.1	0.4	0.2	0.1	1.3

For the fifth group (Gadoids and Benthopelagic Fish Feeders, GB), gadoids were the most consumed prey group (V = 78.0%; F = 78.2%; GII = 78.1%), with *M. poutassou* and *G. argenteus* (V = 31.6%; and V = 26.3%, respectively) being the most representative prey. In the sixth group (Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders, AE), large plankton (V = 45.8%; F = 51.4%; GII = 48.6%), mostly composed of euphausiids (V = 44.6%) and benthopelagic fishes (V = 37.6%; F = 38.3%; GII = 38.0%), led by *Ceratoscopelus maderensis* (V = 12.4%), were the main prey. In the BR sub-group (Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta), Reptantia were the most consumed prey (V = 28.6%; F = 27%; GII = 27.8%) highlighted by the contribution of *G. rhomboides* (V = 7.6%), followed by Polychaeta (V = 26.6%; F = 46.5%; GII = 36.6%) represented by sabellids (V = 73.6%) and benthic invertebrates (V = 24.1%; F = 38.4%; GII = 31.2%), in particular opistobranch molluscs (V = 21.2%). For the PN sub-group (Peracarid and Natantian Feeders), the most consumed preys were Peracarids (V = 48.9%; F = 80%; GII = 64.4%) indicating the presence of amphipods (V = 7.4%) and mysids (V = 6.1%). For the last sub-group identified (Decapod Feeders, DF), Natantia was the most significant group (V = 46.1%; F = 43.8%; GII = 44.9%) with *A. glaber* as the most common prey (V = 21.7%) (Table 2.3).

Overall, the main prey groups consumed by the whole fish community were Natantia (V = 18.8%) and large plankton (V = 17.6%) together with benthopelagic fishes (V = 14.8%). The resulting MTL for this community was 3.81.

3.4. Dietary overlapping and trophic position

For the evaluation of the niche breadth and dietary overlap, measurements of ecological indices were quantified among the nine trophic guilds (Fig. 2.3.2).

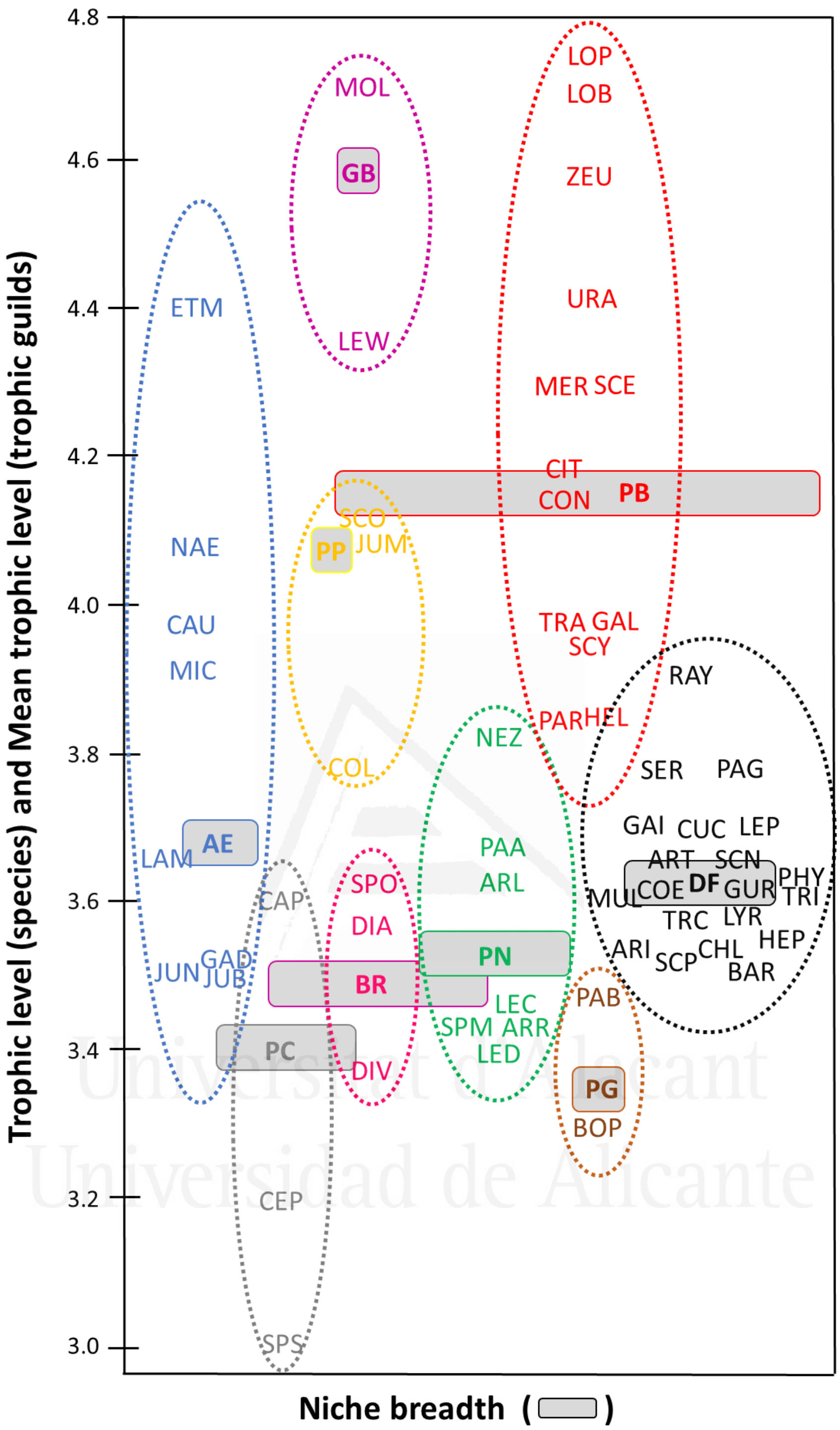

Fig. 2.3.2 Scheme with 61 species studied and the nine trophic guilds (bordered with dotted lines) showing the trophic position (TL and MTL) and the niche breadth (box size). PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantian and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders. Acronyms of species are referenced in Table A.2.1.

Regarding diet breadth, Levin’s index ranged from 0.03 for the specialist guilds GB and PP, to 0.45 for the generalist guild PB (Table 2.3).

The Morisita-Horn index (C_H) showed the lowest niche overlap values ($C_H = 0.00$) for PP-GB. Conversely, the highest values of dietary overlap (0.50) corresponded to DF-PB, which concurred in the consumption of *M. merluccius*, *A. glaber* and *Illex coindetii* (Table 2.4).

The mean trophic level (MTL) calculated in this study showed the lowest value (MTL = 3.35) for the group consisting of PG, contrasting with GB, which ranked the highest in the food web (MTL = 4.58).

Table 2.4 Estimated dietary Overlap index (CH; Simplified Morisita) between the nine trophic guilds studied. Extreme values are shown in bold. Acronyms are referenced in Table 2.1.

	PP	PG	PC	PB	GB	AE	BR	PN	DF
PP	1.00								
PG	0.04	1.00							
PC	0.06	0.05	1.00						
PB	**0.41**	0.06	0.15	1.00					
GB	**0.00**	**0.01**	**0.01**	0.29	1.00				
AE	0.09	0.07	**0.40**	**0.44**	0.13	1.00			
BR	**0.03**	0.06	0.17	0.23	**0.01**	**0.02**	1.00		
PN	0.07	0.09	**0.41**	0.21	0.04	0.18	0.29	1.00	
DF	**0.03**	0.05	0.10	**0.50**	0.12	0.19	**0.48**	**0.41**	1.00

Trophic guilds *versus* environment forcing

In this study, significant differences in fish community composition existed among depth strata (R = 0.224, p = 0.001), geographical areas (R = 0.024, p = 0.001) and habitat types (R = 0.356, p = 0.001) (Fig. 2.3.3).

Changes in MTL were significant by depth stratum ($F_{3,510} = 9.39$; $p < 0.001$), also showing significant differences between the first and the remaining strata ($p < 0.005$). Significant differences were also found between the third and fourth strata ($p = 0.02$). On the other hand, results showed no significant differences between habitat types ($F_{7,690} = 1.637$; $p = 0.122$). The t-test also showed no significant differences among the latitudinal areas defined ($p = 0.109$) (Fig. 2.3.4).

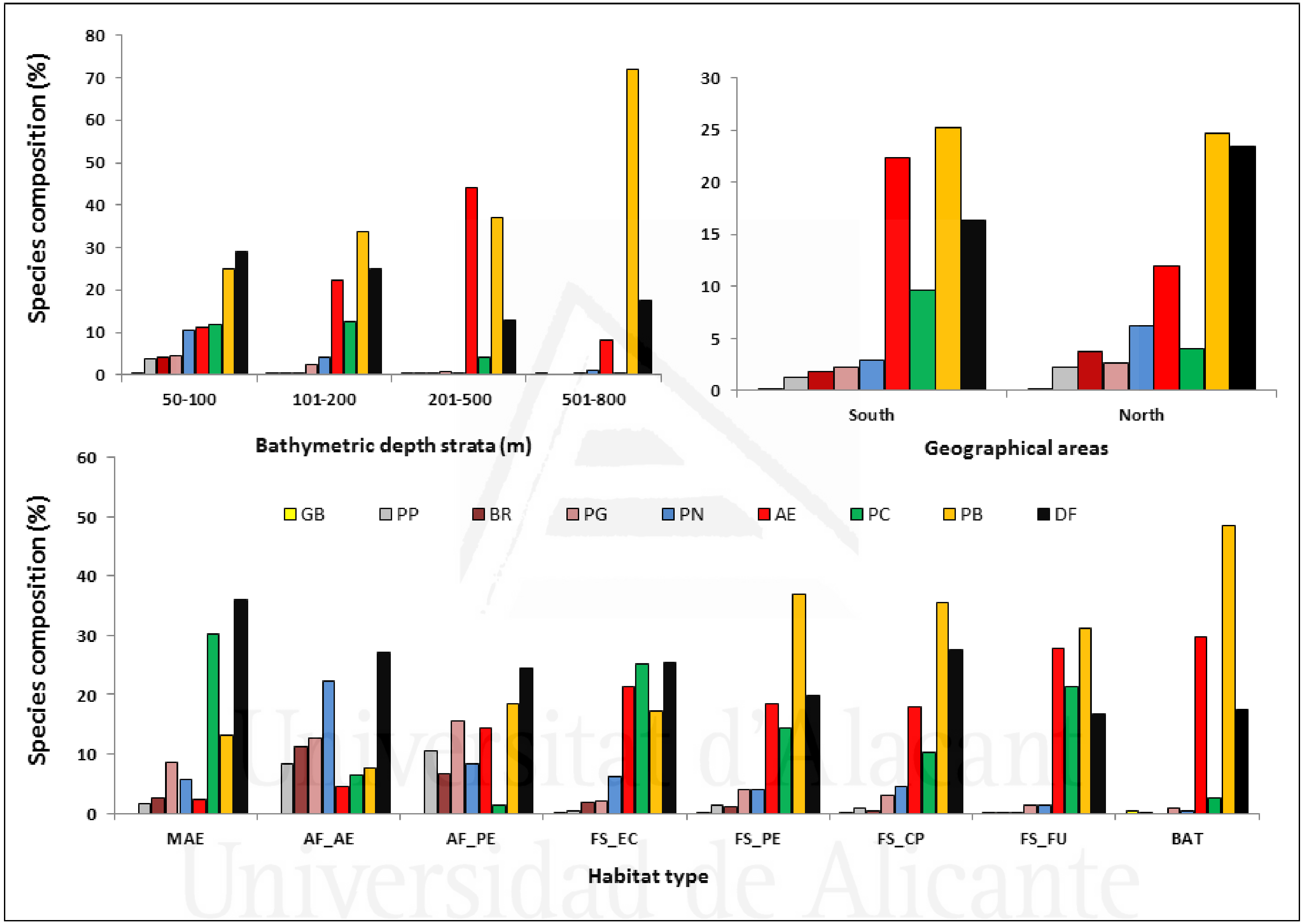

Fig. 2.3.3 Trophic guilds identified according to the different environmental drivers: bathymetric strata, geographical area and habitat type. PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders. Acronyms for habitat types are referenced in Table 2.2.

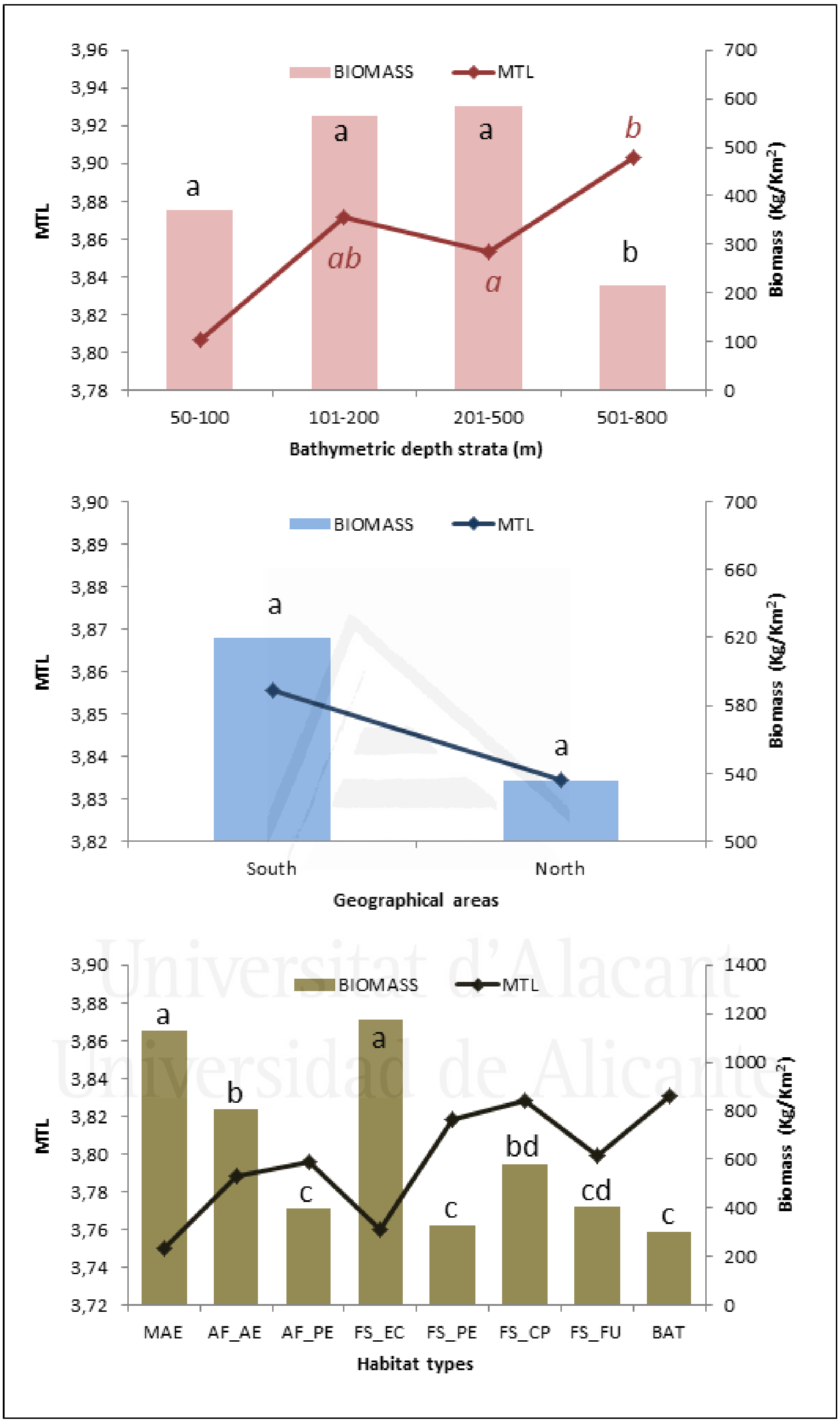

Fig. 2.3.4 Variation of fish community biomass and Mean Trophic Level indicators related to bathymetric strata, geographical area and habitat type. Acronyms are referenced in Table 2.2. Columns with no letters in common are significantly different.

Fish community diversity was investigated by habitat and depth stratum ($F_{7,697} = 44.71$; $p < 0.001$ and $F_{3,564} = 88.85$; $p < 0.001$ respectively). Regarding habitat, significant differences between three groups were found: 1) Sandy and muddy circalittoral bottoms and maerl, 2) Sedimentary and detrital bottoms and 3) Bathyal bottoms. Additionally, a decreasing trend of diversity with depth was apparent, showing significant differences among depth strata. No significant differences were found across geographical areas (Fig. 2.3.5).

Depth stratum and habitat type were tested to investigate shifts in fish community biomass, showing significant differences in both factors ($F_{3,744} = 8.372$; $p < 0.001$ and $F_{7,672} = 21.604$; $p < 0.001$, respectively). A post hoc test found that the deepest stratum showed significant differences from shallower strata ($p < 0.001$). For habitat types (see acronyms in Table 2), a post hoc test showed no significant differences between habitats I and IV. Similar results were also found between habitats II and VI as well as between habitats III, V, VII and VIII ($p > 0.05$) (Fig. 5). The t-test did not show significant differences in fish community biomass between geographical areas ($p = 0.129$).

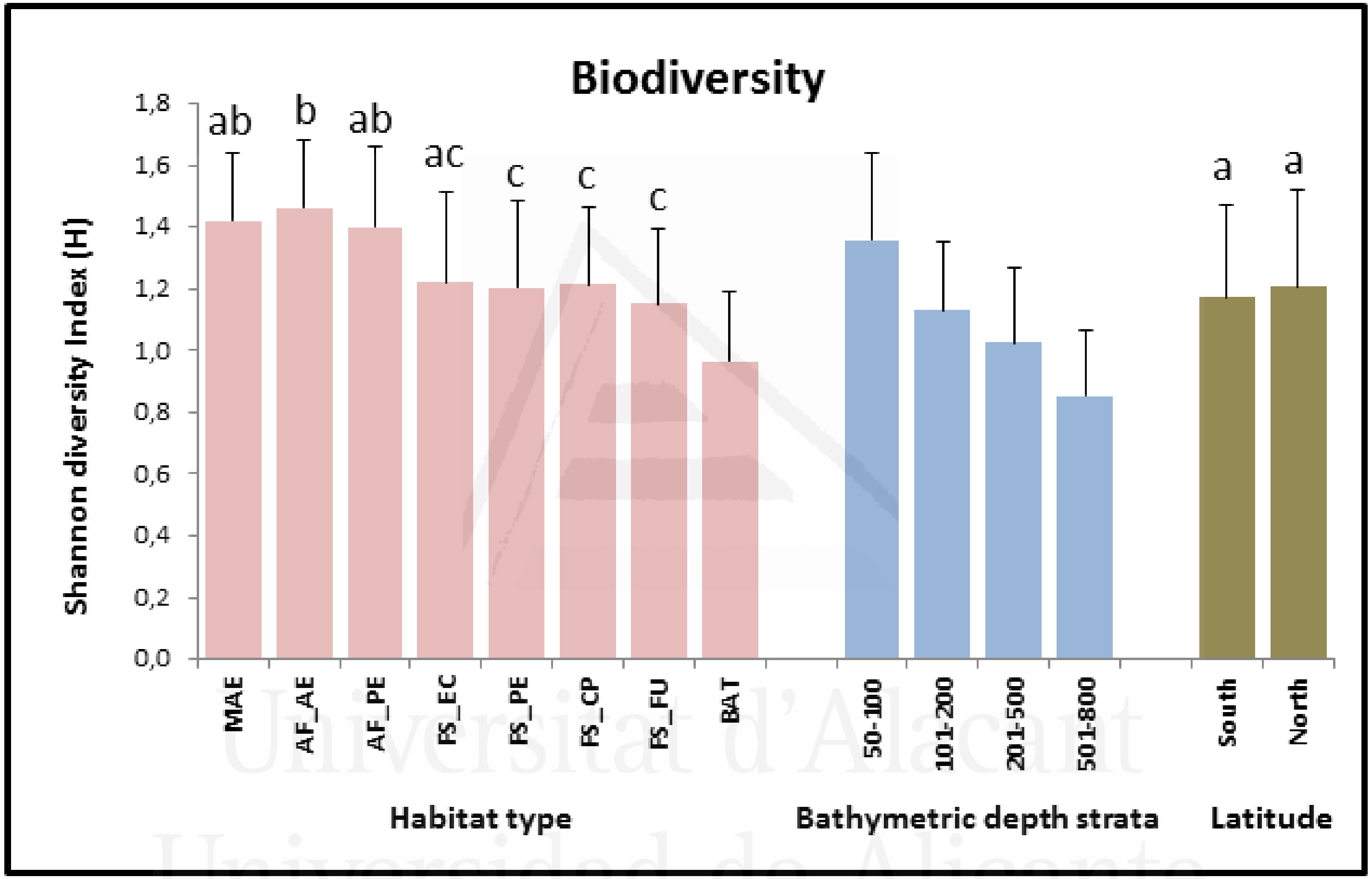

Fig. 2.3.5 Fish community biodiversity calculated by habitat type, bathymetric strata and latitude based on the Shannon diversity index. Acronyms are referenced in Table 2.2. Columns with no letters in common are significantly different. Error bars mean Standard Deviation.

2.4 Discussion

In this study, we present results on diet compositions and feeding strategies of 61 fish species in the Spanish western Mediterranean Sea, providing a recent and valuable dataset for future studies on trophic ecology in this region. Secondly, we identify trophic guilds and demonstrate how these fish communities vary depending on environmental forcing such as depth, latitude and habitat type.

The feeding patterns of the western Mediterranean marine trophic web described here shed new light on the complex trophic relationships existing between the fish species studied. To ensure the robustness of the results, sufficiently large sample sizes should be analysed when studying diet composition (Mulas et al., 2014; Bernal et al., 2015). Cumulative prey curves are a powerful technique for determining the adequacy of sample size for diet characterization. The present study not only aimed to estimate the asymptotic value provided by the cumulative curves, but also applied a mathematical method consisting of the calculation of the slope on a fitted function. Previously, Jimenez-Valverde and Hortal (2003) successfully applied this technique using Clench´s function in a study based on arachnids. Indeed, Ferry and Cailliet (1996) reviewed over 200 papers primarily comparing fish diets across species, sites and sample dates, concluding that none of the studies they reviewed provided estimates of any precision. Clench´s function has been demonstrated to be a good fit in most cases of the faunistic or floristic inventories in which it was tested (Soberón and Llorente, 1993; Leon-Cortés et al., 1998; Moreno and Halffter, 2001). This information on the adequacy of samples is lacking for all of the marine food web studies performed previously in the study area and reviewed herein.

In a marine trophic research context, some recent studies in nearby areas have implemented the analysis of cumulative prey curves (López-López, 2017; Valls, 2017). However, the innovation of our study was the best fitting of these curves with both logarithmic and Clench´s functions, which enabled a proper minimum sample size for each species to be determined mathematically. Among the analyses performed, it was found that Clench´s function proved to be suitable for most of the species. The present study was the first to apply this mathematical approach to marine trophic ecology studies. Based on our results, we recommend this method to assess if the number of samples collected is sufficient to describe the diet of the species studied.

The present study included an extensive collection of samples and a large number of analyses. For example, 48 of the species studied were collected in sufficient numbers to determine their diets validly, but the remaining 13 species are also important in the ecosystem. Consequently, further investigations will be required in the future to address the diets of these species. Nevertheless, their inclusion in this work is fundamental to the complete ecological trophic study in the area concerned.

The present study for the whole group of species analyzed enabled us to calculate their trophic levels and thus, to place them in different trophic niches, identifying their roles within the trophic web. The trophic level values estimated basically concur with those reported by Stergiou and Karpouzi (2002) and Karache and Stergiou (2017) in the Mediterranean. Examining trophic strategies exploiting different resources and environments sheds light on how the relationships between existing trophic guilds function in the study area. Through the analysis of diet composition, nine trophic guilds were identified; six of them occupied the lowest position within the fish community studied, including “Planktophagous Specialized on Gelatinous Plankton” (PG), “Planktophagous Specialized on Copepods” (PC), “Benthic Invertebrate Feeders Specialized on Reptantian and Polychaeta” (BR), “Peracarid and Natantian Feeders” (PN), “Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders” (AE) and “Decapod Feeders” (DF). The first two groups (PG and PC) are characterized by planktophagous habits showing the lowest mean trophic levels. Examples of species belonging to these groups are *Pagellus bogaraveo* and *Cepola macrophthalma*. In the case of *P. bogaraveo*, results presented by Morato et al. (2001) in Azores are slightly different. These authors reported that fishes were an important element in the diet of this species, while gelatinous plankton was relatively rare. The consumption of fish in the Azores compared to that in the western Mediterranean may be a result of the high productivity of seamounts and the aggregation of fish around them (Morato et al., 2001). Findings reported by Sever et al. (2010) in Aegean Sea waters are in accordance with the planktivorous behavior of *C. macrophtalma* described here.

On the other hand, the remaining four groups (BR, PN, AE and DF), whose distinctive feature is the high consumption of crustaceans and benthic invertebrates, ranked slightly higher, occupying intermediate levels in the energy flows within the food web. Sparids, mullets, triglids, scorpaenids, rays and some flatfishes formed these groups.

All of them share a relatively narrow niche breadth, inherent in specialist species. This becomes evident in the case of PG, the most specialized of these six groups. In an intermediate position, between the groups named above and the top of the food web, “Pelagic Piscivores” can be found, characterized by piscivore habits and “Pelagic, Benthopelagic Fishes and Natantian Feeders”, whose diet is mainly composed of decapod crustaceans as well as fishes. Thus, this is a species characterized by a diet based on an elevated consumption of teleosts. Examples of species belonging to these groups are mackerels, anglerfishes, hake, conger and benthic sharks. The last group, “Gadoids and Benthopelagic Fish Feeders” (GB) is characterized by a diet highly specialized on piscivore species such as *Lepidorhombus whiffiagonis*, in accordance with findings reported by Morte et al. (1999), and *M. macrophthalma.* This group is at the top of the food web, reaching the highest trophic level values. Regarding the niche breadth and in contrast to PB, considered the most generalistic group, GB is the most specialized with a high consumption of gadoids.

Regarding niche overlap, trophic guilds located in the lowest trophic positions (PG and PC) showed low overlap due to the development of different feeding strategies, thus exploiting diverse trophic niches. This is in line with general knowledge of the existence of strongly selective feeding strategies in oligotrophic regions, where competition pressure for scarce food resources is expected (Van Noord et al., 2013).

At an upper-intermediate level, AE presents a low overlap with the other three groups (BR, PN and DF). In contrast, these three trophic guilds show a high overlap. Indeed, they show the most common feeding strategy within the food web, characterized by a notable percentage of crustaceans in their diet, especially decapods, in agreement with previous findings reported by Rodriguez-Marín (2004) in the Cantabrian Sea and Moreno-Amich (1992; 1996), Colloca et al. (1994) and Morte et al. (1999) in the western Mediterranean.

At a higher level in the trophic web, where the distinctive feature is the high consumption of teleosts, both “Pelagic Piscivores” and “Pelagic, Benthopelagic Fishes and Natantian Feeders” presented a considerable overlap due to the relevance of small pelagic fishes and euphausiids as common preys in their diets.

At the top of the trophic web, “Gadoids and Benthopelagic Fish Feeders” were found to share feeding strategies with “Pelagic, Benthopelagic Fishes and Natantian Feeders” in terms of consumption of benthopelagic fishes, especially gadoids, and natantian decapods. On the contrary, the minor overlap existing between “Gadoids and Benthopelagic Fish Feeders” and “Pelagic Piscivores” was caused by the lack of small pelagic fishes in the diet of GB, the dominant prey for PP.

Overall, those groups that play an important role in the fish community as a whole are: natantian, pelagic peracarids, euphausiids and benthopelagic fishes, which is consistent with the wide spectrum of feeding guilds and food resource partitioning suggested in previous studies performed in the western Mediterranean (Polunin et al., 2001; Madurell et al., 2008; Fanelli et al., 2009; 2010; Valls et al., 2014).

In this paper, the structure of the fish community has been described through the analysis of indicators including diversity, biomass, MTL and fish community composition. Three environment variables, latitude, depth, and habitat type, were investigated to explore how they affect variations in the indicators for fish community structure.

Results showed that changes in fish community composition along latitude, depth and habitat type were significant.

With respect to latitude, the southern geographical area was characterized by a higher percentage of pelagic crustacean feeders as well as a lower percentage of demersal crustacean feeders in its fish community composition. This is in agreement with Floeter et al. (2004), who reported changes in trophic structure and spatial patterns along the latitudinal gradient. In addition, planktophagous species were more abundant in the southern geographical area, in agreement with Cartes et al. (2002) who reported a progressive north-south increase in these species. This environmental attribute was shown to play a decisive role in structuring the fish community, inducing changes in fish composition across the whole fish community. Opposite, we did not find changes in MTL, biomass and diversity in the fish community across latitudinal gradient. According to depth, changes in MTL were detected, in particular between the first and the rest of the stratum and between the third and fourth stratum, caused by the low trophic position of the species occupying shallower depths compared to those species occupying the deepest bottoms. This relationship between depth and trophic level was reported by Rex in gastropods (Rex, 1977). Concerning to biomass, the deepest stratum shows differences from other strata, in line with the usual distribution of biomass in the ocean (Abad et al., 2007). Regarding to diversity and fish composition, the relationship between depth and them was evident.

With respect to habitat type, maerl and biogenic bottoms (MAE), Sandy and muddy circalittoral bottoms consisting mainly of ascidians and echinoderms (AF_AE) and sedimentary and detritic bottoms consisting mainly of echinoderms (FS_EC), were the three habitats able to withstand the highest carrying capacity of fish biomass within the ecosystem studied. This finding is in agreement with those studies that highlight the important role of habitat in the production of fish species. Some of the most important demersal resources of the coastal shelf are dependent on macro-benthic habitat type (Ordinas and Massuti, 2009), and high levels of biomass and biodiversity are found associated with *Peyssonnelia* beds (Ballesteros, 1994). By contrast, in the present study, the lowest carrying capacity of fish biomass was found on habitats dominated by *Funniculina quadrangularis* and *Pennatulacea* spp. (FS_FU, AF_PE and FS_PE) and especially “Bathyal bottoms” (BAT). Besides, the habitat characteristics of shallow waters present higher diversity compared to deeper ones (Navarro et al., 2015).

Findings highlighted differences across habitat type in fish community biomass, diversity and fish composition. In contrast, we did not find changes in MTL in the fish community across habitat type.

To conclude, considering the three environmental drivers investigated, depth was found to be the most influential factor in the fish community structure studied, particularly affecting both diversity and fish community composition. However, the latitudinal gradient only seemed to affect fish community composition showing consistency along a longitudinal north-south axis.

Finally, this is the only study presenting information based on stomach content analysis for this study area that includes robust estimations on minimum sample size for a large number of representative species between 2011 and 2018. Despite the fact that a considerable amount of information has been published describing the feeding habits of single or groups of commercial species in the Mediterranean (e.g. Macpherson, 1980a; 1980b; Carrasón and Matallanas, 2002; López et al., 2016), there are only a few studies on the whole trophic web in the western Mediterranean (Macpherson, 1981; Fanelli and Cartes, 2010; Valls, 2017). It is therefore relevant to highlight the importance of this study in the context of the ecosystem approach to fisheries management where information on diet is often ecosystem-specific (Hanson and Chouinard, 2002), and when implementing ecosystem models or similar studies related to marine food webs.

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2.7 Supplementary material

Table A.2.1 Information of the sample size analyzed, number of prey items identified, predator length ranges (mm) and depths (m) reported for all the species studied. (*) anal length.

PREDATOR	**Species code**	**Nº full stomachs**	**Nº preys**	**Min size**	**Max size**	**Mean length (mean ± SD)**	**Min depth**	**Max depth**	**Mean depth (mean ± SD)**
Arnoglossus imperialis	ARI	36	19	75	164	121 ± 17	47	279	117 ± 65
Arnoglossus laterna	ARL	144	30	59	121	91 ± 11	36	279	75 ± 27
Arnoglossus rueppelii	ARR	92	20	90	148	116 ± 12	102	273	146 ± 46
Arnoglossus thori	ART	138	32	66	124	93 ± 10	45	122	69 ± 22
Boops boops	BOP	150	27	108	265	174 ± 28	36	142	88 ± 30
Capros aper	CAP	78	15	55	117	77 ± 17	77	282	181 ± 90
Cepola macrophtalma	CEP	117	16	167	600	344 ± 93	41	129	87 ± 17
Chelidonichthys cuculus	CUC	282	50	104	295	168 ± 34	42	269	114 ± 38
Chelidonichthys lastoviza	CHL	227	50	94	305	174 ± 32	40	125	55 ± 17
Citharus linguatula	CIT	200	38	71	250	167 ± 33	35	272	79 ± 30
*Coelorinchus caelorhincus**	COE	204	21	24	105	51 ± 17	238	542	388 ± 82
Conger conger	CON	368	79	242	955	471 ± 104	35	732	171 ± 168
Diplodus annularis	DIA	234	46	108	223	160 ± 20	35	128	47 ± 10
Diplodus vulgaris	DIV	132	40	140	304	211 ± 30	40	124	58 ± 14
Etmopterus spinax	ETM	59	22	110	426	222 ± 86	380	724	545 ± 104
Eutrigla gurnardus	GUR	293	51	75	361	164 ± 39	47	331	102 ± 29
Gadiculus argenteus	GAD	234	25	70	133	103 ± 10	206	586	314 ± 81
Gaidropsarus biscayensis	GAI	102	24	40	180	83 ± 29	88	630	337 ± 123
Galeus melastomus	GAL	372	73	135	615	441 ± 139	270	732	528 ± 126
Helicolenus dactylopterus	HEL	304	60	73	305	145 ± 42	106	650	279 ± 124
Lampanyctus crocodilus	LAM	118	21	76	215	135 ± 23	411	724	568 ± 87
Lepidopus caudatus	CAU	154	21	222	880	358 ± 91	83	717	289 ± 106
Lepidorhombus boscii	LEP	298	45	81	370	212 ± 53	42	594	242 ± 127
Lepidorhombus whiffiagonis	LEW	34	18	118	367	241 ± 66	140	337	233 ± 49
Lepidotrigla cavillone	LEC	265	27	83	198	113 ± 12	45	155	80 ± 25
Lepidotrigla dieuzeidei	LED	181	27	70	142	110 ± 11	56	273	147 ± 48

Table A.2.1 (Continued)

PREDATOR	Species code	Nº full stomachs	Nº preys	Min size	Max size	Mean length (mean ± SD)	Min depth	Max depth	Mean depth (mean ± SD)
Leucoraja naevus	NAE	39	17	154	535	351 ± 74	91	272	143 ± 51
Lophius budegassa	LOB	419	65	44	930	248 ± 82	37	594	132 ± 85
Lophius piscatorius	LOP	87	37	64	1050	282 ± 166	42	590	117 ± 108
Merluccius merluccius	MER	907	61	87	460	187 ± 66	36	590	93 ± 47
Micromesistius poutassou	MIC	558	38	89	371	229 ± 56	85	610	307 ± 97
Molva macrophthalma	MOL	122	15	83	740	184 ± 96	122	605	269 ± 103
Mullus barbatus	BAR	247	29	104	270	176 ± 28	35	221	84 ± 39
Mullus surmuletus	MUL	303	50	70	332	206 ± 41	36	522	117 ± 92
*Nezumia aequalis**	NEZ	89	18	22	54	36 ± 7	510	724	626 ± 70
Pagellus acarne	PAA	148	43	118	254	181 ± 28	36	273	60 ± 27
Pagellus bogaraveo	PAB	275	50	100	465	176 ± 41	47	722	227 ± 146
Pagellus erytrinus	PAG	255	44	114	471	232 ± 48	37	142	58 ± 16
Pagrus pagrus	PAR	87	33	135	379	218 ± 55	44	130	62 ± 19
Phycis blennoides	PHY	275	49	85	393	208 ± 61	92	588	292 ± 143
Raja sp.	RAY	356	71	135	865	359 ± 136	42	522	149 ± 72
Scomber colias	COL	578	36	217	381	296 ± 32	38	85	58 ± 11
Scomber scombrus	SCO	291	30	121	367	247 ± 47	48	126	89 ± 22
Scorpaena elongata	SCE	201	55	78	465	183 ± 67	43	335	131 ± 49
Scorpaena notata	SCN	231	38	64	205	107 ± 22	38	143	81 ± 32
Scorpaena porcus	SCP	35	13	97	299	174 ± 36	38	94	50 ± 10
Scyliorhinus canicula	SCY	488	79	92	605	402 ± 70	41	586	171 ± 110
Serranus cabrilla	SER	235	54	91	251	160 ± 29	38	143	82 ± 20
Serranus hepatus	HEP	276	33	67	136	99 ± 12	41	143	93 ± 26
Spicara maena	SPM	244	34	96	241	148 ± 25	38	140	70 ± 19
Spicara smaris	SPS	91	11	103	193	136 ± 19	45	122	73 ± 21
Spondyliosoma cantharus	SPO	152	32	151	353	217 ± 45	38	146	74 ± 21
Trachinus draco	TRA	203	43	122	366	243 ± 46	41	148	84 ± 29
Trachurus mediterraneus	JUM	164	41	110	353	243 ± 42	37	105	59 ± 21
Trachurus picturatus	JUN	35	15	126	330	221 ± 50	48	515	124 ± 81

Table A.2.1 (Continued)

PREDATOR	Species code	Nº full stomachs	Nº preys	Min size	Max size	Mean length (mean ± SD)	Min depth	Max depth	Mean depth (mean ± SD)
Trachurus trachurus	JUB	133	25	131	336	202 ± 43	47	589	135 ± 104
*Trachyrhinchus scabrus**	TRC	48	20	27	135	97 ± 18	459	604	555 ± 35
Trigla lyra	LYR	286	47	55	300	177 ± 29	52	586	224 ± 83
Trisopterus minutus	TRI	309	43	78	272	167 ± 29	48	287	113 ± 57
Uranoscopus scaber	URA	116	38	42	316	228 ± 45	40	141	77 ± 21
Zeus faber	ZEU	243	40	70	528	247 ± 109	38	556	135 ± 59

Table A.2.2 Sample size, number of prey items identified, potential number of preys estimated (asymptote) and fitting of cumulative prey curves to Clench function (r^2) estimated for all fish size categories studied. (*) species with slope > 0.05.

			CLENCH			ACE	CHAO 1		
PREDATOR	**Nº Full stomachs**	**Nº Preys**	**Asymptote**	**Slope**	**r^2**		**Chao 1**	**95% Lower Bound**	**95% Upper Bound**
Arnoglossus imperialis	36	19	30	0.191*	1.00	29	33	21.9	85.8
Arnoglossus laterna	144	30	35	0.034	0.99	38	35	31.0	52.8
Arnoglossus rueppelii	92	20	24	0.043	0.99	26	24	20.6	41.9
Arnoglossus thori	138	32	38	0.043	0.98	44	38	33.5	59.3
Boops boops	150	27	33	0.037	0.99	44	45	31.5	101.8
Capros aper	78	15	16	0.019	0.99	18	16	15.1	25.7
Cepola macrophtalma	117	16	18	0.019	0.97	28	24	17.3	58.5
Chelidonichthys cuculus	282	50	56	0.024	0.98	69	65	54.3	103.5
Chelidonichthys lastoviza	227	50	57	0.029	0.99	56	55	51.1	73.4
Citharus linguatula	200	38	48	0.039	0.99	44	41	38.5	52.5
Coelorinchus caelorhincus	204	21	22	0.006	0.98	23	23	21.2	36.1
Conger conger	368	79	101	0.048	1.00	98	98	85.9	132.9
Diplodus annularis	234	46	55	0.038	0.98	83	109	65.2	254.6
Diplodus vulgaris	132	40	49	0.057*	0.99	49	47	42.3	65.0
Etmopterus spinax	59	22	31	0.113*	1.00	37	25	85.6	12.7
Eutrigla gurnardus	293	51	60	0.031	0.98	68	68	56.1	110.8
Gadiculus argenteus	234	25	29	0.017	0.97	34	31	26.2	52.1
Gaidropsarus biscayensis	102	24	29	0.041	1.00	29	28	24.6	46.0
Galeus melastomus	372	73	87	0.036	0.99	88	92	79.5	128.8
Helicolenus dactylopterus	304	60	74	0.040	0.99	85	72	64.1	96.7
Lampanyctus crocodilus	118	21	28	0.043	0.99	30	30	22.9	65.7
Lepidopus caudatus	154	21	26	0.028	0.98	34	30	22.9	65.9
Lepidorhombus boscii	298	45	50	0.019	0.99	62	64	50.2	117.8
Lepidorhombus whiffiagonis	34	18	33	0.237*	1.00	42	33	21.5	81.6
Lepidotrigla cavillone	265	27	29	0.009	0.99	29	28	27.1	35.5
Lepidotrigla dieuzeidei	181	27	33	0.028	0.99	29	29	27.2	39.5
Leucoraja naevus	39	17	23	0.108*	0.99	33	32	20.9	84.8
Lophius budegassa	419	65	78	0.028	0.98	82	86	72.0	129.8
Lophius piscatorius	87	37	66	0.186*	1.00	54	50	41.3	79.7
Merluccius merluccius	907	61	69	0.009	0.97	81	72	64.6	96.9

Table A.2.2 (Continued)

			CLENCH			ACE	CHAO 1		
PREDATOR	**Nº Full stomachs**	**Nº Preys**	**Asymptote**	**Slope**	r^2		**Chao 1**	**95% Lower Bound**	**95% Upper Bound**
Micromesistius poutassou	558	38	42	0.009	0.97	51	49	40.7	82.1
Molva macrophthalma	122	15	20	0.032	0.98	17	16	15.0	25.6
Mullus barbatus	247	29	31	0.013	0.95	36	33	29.6	47.9
Mullus surmuletus	303	50	55	0.020	0.98	69	80	58.2	162.4
Nezumia aequalis	89	18	20	0.026	0.99	19	18	18.0	22.8
Pagellus acarne	148	43	60	0.087*	0.98	87	86	56.2	181.5
Pagellus bogaraveo	275	50	69	0.050	0.99	88	85	63.4	147.7
Pagellus erytrinus	255	44	54	0.036	0.99	61	65	50.1	116.6
Pagrus pagrus	87	33	50	0.133*	0.99	69	60	41.2	122.0
Phycis blennoides	275	49	53	0.023	0.96	77	68	55.1	111.3
Raja sp.	356	71	83	0.034	0.98	90	85	75.8	113.7
Scomber colias	578	36	36	0.003	0.93	44	41	37.0	63.6
Scomber scombrus	291	30	31	0.007	0.99	36	32	30.2	42.5
Scorpaena elongata	201	55	72	0.068*	1.00	70	70	59.8	102.8
Scorpaena notata	231	38	46	0.032	0.98	54	49	41.1	78.5
Scorpaena porcus	35	13	19	0.115*	1.00	21	15	13.4	29.8
Scyliorhinus canicula	488	79	91	0.024	0.99	95	95	84.2	125.6
Serranus cabrilla	235	54	64	0.040	1.00	62	65	56.9	95.9
Serranus hepatus	276	33	38	0.017	0.99	39	42	34.9	77.9
Spicara maena	244	34	45	0.035	0.99	53	79	46.1	205.3
Spicara smaris	91	11	15	0.035	0.99	14	12	11.1	21.7
Spondyliosoma cantharus	152	32	41	0.048	0.99	36	35	32.4	47.3
Trachinus draco	203	43	55	0.049	0.99	54	47	44.0	60.7
Trachurus mediterraneus	164	41	49	0.047	0.98	52	49	43.0	72.5
Trachurus picturatus	35	15	26	0.181*	0.99	21	20	15.8	47.1
Trachurus trachurus	133	25	33	0.047	1.00	31	28	25.4	40.3
Trachyrhinchus scabrus	48	20	29	0.133*	1.00	28	27	21.4	53.5
Trigla lyra	286	47	53	0.020	0.99	53	59	49.7	101.2
Trisopterus minutus	309	43	48	0.020	0.98	59	54	46.1	83.6
Uranoscopus scaber	116	38	57	0.112*	0.99	76	72	48.8	145.5
Zeus faber	243	40	51	0.038	0.99	50	54	43.4	95.5

Table A.2.3 Diet compositions of the 61 studied species expressed in volume (V%). Species codes: ARI, *Arnoglossus imperialis*; ARL, *A. laterna*; ARR, *A. rueppelii*; ART, *A. thori*; BOP, *Boops boops*; CAP, *Capros aper*; CEP, *Cepola macrophtalma*; CUC, *Chelidonichthys cuculus*; GUR, *E. gurnardus*; CHL, *C. lastoviza*; CIT, *Citharus linguatula*; COE, *Coelorinchus caelorhincus*; CON, *Conger conger*; DIA, *Diplodus annularis*; DIV, *D. vulgaris*; ETM, *Etmopterus spinax*; GAD, *Gadiculus argenteus*; GAI, *Gaidropsarus biscayensis*; GAL, *Galeus melastomus*; HEL, *Helicolenus dactylopterus*; LAM, *Lampanyctus crocodilus*; CAU, *Lepidopus caudatus*; LEP, *Lepidorhombus boscii*; LEW, *L. whiffiagonis*; LEC, *Lepidotrigla cavillone*; LED, *L. dieuzeidei*; NAE, *Leucoraja naevus*; LOB, *Lophius budegassa*; LOP, *L. piscatorius*; MER, *Merluccius merluccius*; MIC, *Micromesistius poutassou*; MOL, *Molva macrophthalma*; BAR, *Mullus barbatus*; MUL, *M. surmuletus*; NEZ, Nezumia aequalis; PAA, *Pagellus acarne*; PAB, *P. bogaraveo*; PAG, *P. erytrinus*; PAR, *Pagrus pagrus*; PHY, *Phycis blennoides*; RAY, *Raja* sp.; COL, *Scomber colias*; SCO, *S. scombrus*; SCE, *Scorpaena elongata*; SCN, *S. notata*; SCP, *S. porcus*; SCY, *Scyliorhinus canicula*; SER, Serranus cabrilla; HEP, *S. hepatus*; SPM, *Spicara maena*; SPS, *S. smaris*; SPO, *Spondyliosoma cantharus*; TRA, *Trachinus draco*; JUM, *Trachurus mediterraneus*; JUN, *T. picturatus*; JUB, *T. trachurus*; TRC, *Trachyrhinchus scabrus*; LYR, *Trigla lyra*; TRI, *Trisopterus minutus*; URA, *Uranoscopus scaber*; ZEU, *Zeus faber*.

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Porifera	**0.011**														
Cnidaria	**0.018**				**0.000**	**0.001**			**0.000**	**0.001**	**0.033**				
Actiniaria	0.011														
Diphyidae					0.000	0.001			0.000	0.001	0.033				
Siphonophorae					0.000										
Plumularioidea	0.007														
Polychaeta	**0.253**	**0.000**	**0.001**	**0.003**	**0.000**	**0.001**	**0.000**	**0.013**		**0.003**			**0.014**	**0.003**	**0.006**
Eunice spp.					0.000										
Eunicidae					0.000										
Sabellidae	0.001														
Errantia unidentified															0.000
Polychaeta unidentified	0.253	0.000	0.001	0.003	0.000	0.001	0.000	0.013		0.003			0.014	0.003	0.005
Nemertea	**0.001**														
Echinodermata	**0.046**						**0.001**								
Asteroidea unidentified	0.004														
Echinacea	0.009														
Leptopentacta tergestina	0.003														
Ophiuridae	0.030						0.001								
Crustacea	**0.376**	**0.114**	**0.744**	**0.828**	**0.399**	**0.806**	**0.608**	**0.932**	**0.729**	**0.140**	**0.722**	**0.813**	**0.980**	**0.959**	**0.817**
Amphipoda	**0.049**		**0.009**	**0.025**	**0.028**	**0.009**	**0.010**	**0.011**	**0.005**	**0.010**	**0.084**	**0.002**	**0.109**	**0.044**	**0.005**
Brachyscelus spp.					0.016	0.002	0.006								
Hyperiidea			0.001		0.001	0.001	0.001		0.003	0.006	0.008				
Phronima sedentaria					0.010			0.001		0.001	0.025			0.004	0.001
Phrosina semilunata					0.001	0.005			0.001	0.000					
Vibilia spp.			0.001		0.000		0.000		0.001	0.001	0.051				
Ampelisca spp.						0.000				0.000			0.019	0.005	0.000
Epimeria spp.							0.002	0.001					0.001		
Eusirus spp.						0.000		0.001					0.001		
Gammaridae										0.000					
Gitana spp.						0.000									
Hippomedon spp.															0.000
Ichnopus spp.							0.000								
Iphimedia spp.						0.000									
Leucothoe spp.													0.000		0.003
Lysianassa spp.													0.003		
Lysianassidae	0.008		0.002			0.000		0.000						0.002	
Maera spp.								0.001							0.000
Monoculodes spp.				0.001		0.000						0.001	0.011	0.000	
Nicippe spp.							0.000						0.000		0.000
Rhachotropis spp.					0.000		0.000								0.000
Stegocephaloides spp.						0.000									
Westwoodilla spp.			0.000	0.000		0.001		0.000					0.042	0.003	0.000

Table A.2.3 (Continued)

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Phtisica spp.						0.000									
Pseudoprotella spp.								0.000							
Caprellids unidentified	0.004			0.000				0.005					0.002		
Amphipods unidentified	0.037		0.006	0.023	0.000	0.000	0.001	0.003	0.001	0.001	0.000	0.001	0.030	0.030	0.000
Isopoda	**0.011**		**0.012**	**0.000**	**0.001**	**0.001**	**0.024**	**0.001**	**0.000**	**0.003**	**0.000**	**0.004**	**0.004**	**0.002**	**0.004**
Cirolanidae					0.000										
Gnathia spp.	0.001														
Gnathiidae						0.000	0.000								
Idotea spp.	0.001						0.000			0.000					
Synisoma spp.								0.000							
Isopods unidentified	0.009		0.012	0.000	0.001	0.001	0.024	0.000	0.000	0.003	0.000	0.004	0.004	0.002	0.004
Cumacea	**0.000**						**0.000**						**0.003**	**0.000**	
Lophogastrida				**0.066**	**0.000**	**0.062**	**0.006**			**0.000**		**0.004**	**0.290**	**0.472**	**0.006**
Lophogaster typicus				0.066	0.000	0.062	0.006			0.000		0.004	0.290	0.472	0.006
Mysida	**0.001**		**0.012**	**0.029**	**0.000**	**0.087**	**0.002**	**0.023**	**0.004**	**0.038**		**0.001**	**0.152**	**0.087**	**0.014**
Tanaidacea	**0.000**												**0.002**		
Copepoda			**0.060**	**0.015**		**0.000**		**0.000**	**0.042**	**0.004**	**0.003**		**0.001**	**0.000**	
Ostracoda	**0.000**				**0.000**		**0.000**			**0.000**					
Euphausiacea		**0.011**	**0.512**	**0.027**	**0.062**	**0.006**	**0.162**	**0.005**	**0.673**		**0.611**	**0.036**		**0.006**	**0.007**
Euphausia krohnii			0.112				0.010		0.208						
Meganyctiphanes norvegica		0.011	0.027		0.048		0.055		0.234		0.393				0.005
Nematoscelis spp.		0.000	0.007		0.002		0.000								
Euphausiacids unidentified		0.000	0.366	0.027	0.012	0.006	0.096	0.005	0.230		0.218	0.036		0.006	0.002
Scalpelliformes	**0.014**														
Scalpellum scalpellum	0.013														
Scalpelliformes unidentified	0.001														
Decapoda	**0.299**	**0.103**	**0.069**	**0.653**	**0.300**	**0.619**	**0.388**	**0.889**	**0.004**	**0.078**	**0.019**	**0.758**	**0.411**	**0.336**	**0.767**
Acanthephyra spp.					0.003										
Aegaeon spp.														0.016	0.002
Alpheus glaber				0.095	0.002	0.122	0.084	0.341		0.000				0.021	0.141
Aristeus antennatus					0.022							0.040			
Athanas spp.						0.000	0.000	0.004							
Chlorotocus crassicornis					0.001	0.041	0.001	0.028				0.023	0.010	0.004	0.087
Crangonidae						0.002				0.001			0.007		
Deosergestes henseni		0.005										0.023			
Eusergestes arcticus		0.001		0.040	0.019	0.004	0.001				0.016	0.422			0.002
Gennadas elegans			0.003		0.001							0.046			
Pasiphaea multidentata					0.031							0.040			
Pasiphaea sivado		0.039	0.000		0.080		0.005					0.008			
Pasiphaea spp.		0.030	0.005		0.031					0.000		0.001			
Philocheras spp.						0.014		0.000		0.000			0.027	0.003	0.001
Plesionika spp.							0.005								
Plesionika acanthonotus					0.002					0.003					
Plesionika edwardsii				0.025			0.027								0.007
Plesionika giglioli				0.013											0.011
Plesionika heterocarpus						0.006	0.039								0.008
Plesionika martia					0.007										
Plesionika narval							0.010								
Pontophilus spp.						0.007							0.010	0.005	0.001
Processa spp.			0.017	0.017	0.001	0.013	0.006	0.027		0.003			0.006	0.136	0.042
Sergia robusta		0.001			0.016							0.050			
Solenocera membranacea					0.010		0.001						0.094	0.060	0.121
Atelecyclus rotundatus								0.006							
Calocaris macandreae			0.001	0.320	0.028		0.023	0.007				0.002			0.024
Ebalia spp.								0.001							
Eurynome spp.	0.011														
Galathea spp.	0.118			0.002		0.000	0.000	0.003					0.001		
Geryon longipes					0.005										
Goneplax rhomboides	0.067			0.105		0.133	0.068	0.265					0.058	0.011	0.113
Inachus spp.	0.008							0.000							

Table A.2.3 (Continued)

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Liocarcinus spp.	0.026					0.187	0.005	0.018					0.056	0.013	0.046
Macropipus tuberculatus					0.003		0.007								0.010
Macropodia spp.	*0.013*														
Monodaeus couchii				0.011	0.003		0.015	0.008							0.003
Munida spp.	0.004			0.008	0.000	0.032	0.021								0.071
Nephrops norvegicus					0.003		0.011								0.023
Paguridae	0.005					0.000		0.004					0.002		
Pagurus spp.	0.002														
Polycheles typhlops					0.009										
Portunidae							0.001			0.000					0.002
Scyllarus spp.					0.001	0.002				0.002			0.009	0.008	0.000
Thalassinidea							0.001								
Upogebia spp.					0.002		0.004	0.006		0.003					0.000
Decapod larvae						0.000			0.001	0.053	0.003		0.001	0.001	
Nephrops larvae										0.002					
Natantia unidentified	0.000	0.028	0.041	0.009	0.012	0.033	0.028	0.122		0.011		0.105	0.091	0.051	0.038
Brachyura unidentified	0.045			0.004	0.001	0.011	0.010	0.042	0.000	0.000			0.009	0.002	0.003
Decapoda unidentified			0.003	0.003	0.007	0.012	0.017	0.009	0.003				0.031	0.006	0.010
Stomapoda					**0.005**	**0.018**	**0.011**			**0.001**					**0.013**
Rissoides desmaresti					0.004	0.018	0.009								0.013
Squila mantis					0.001										
Stomatopod larvae										0.000					
Stomatopoda unidentified							0.002			0.001					
Crustacea unidentified	0.000		0.070	0.012	0.002	0.003	0.005	0.002	0.002	0.006	0.005	0.008	0.008	0.012	0.001
Cephalopods	**0.019**	**0.499**			**0.204**	**0.024**	**0.035**		**0.004**	**0.005**				**0.032**	**0.011**
Sepiida	**0.000**	**0.007**			**0.033**	**0.024**	**0.002**		**0.004**	**0.005**				**0.032**	**0.011**
Rondeletiola minor						0.001			0.004	0.005					0.000
Sepietta oweniana					0.001	0.003								0.032	
Sepiolid unidentified	0.000	0.007			0.032	0.020	0.002		0.001						0.011
Oegopsida	**0.014**	**0.425**			**0.125**		**0.033**								
Abralia veranyi		0.004			0.013										
Abraliopsis pfefferi					0.001										
Ancistroteuthis lichtensteinii					0.006										
Chiroteuthis veranii					0.002										
Histioteuthis bonnellii					0.002										
Histioteuthis reversa		0.028			0.024		0.028								
Histioteuthis spp.		0.126			0.011										
Illex coindetii	0.014	0.007			0.017										
Todarodes sagittatus		0.203													
Teuthida unidentified		0.056			0.050		0.005								
Cephalopod eggs	0.004														
Cephalopods unidentified		0.066			0.046		0.000								0.000
Other Mollusca	**0.112**					**0.001**	**0.002**	**0.001**	**0.000**	**0.000**					
Pteropoda	**0.000**					**0.000**	**0.002**	**0.001**	**0.000**	**0.000**					
Cavolinia spp.	0.000					0.000	0.002	0.001	0.000	0.000					
Bivalvia	**0.076**					**0.000**		**0.000**							
Arcidae	0.001														
Pteria hirundo	0.000														
Bivalvia unidentified	0.075					0.000		0.000							
Gastropoda	**0.037**					**0.000**				**0.000**					
Calyptraea chinensis	0.028														
Turritella spp.	0.000					0.000									
Heterobranchia	0.006														
Gastropoda unidentified	0.002					0.000				0.000					
Tunicata	**0.026**		**0.001**		**0.007**		**0.038**		**0.003**	**0.000**	**0.064**	**0.002**			
Ascidiacea	0.019														
Pyrosoma atlanticum	0.004						0.031		0.003		0.064	0.002			
Tunicata unidentified	0.002		0.001		0.007		0.007			0.000					
Teleosts	**0.105**	**0.387**	**0.246**	**0.169**	**0.380**	**0.167**	**0.311**	**0.054**	**0.262**	**0.851**	**0.180**	**0.185**	**0.005**	**0.006**	**0.166**
Clupleiformes										**0.409**					

Table A.2.3 (Continued)

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Engraulis encrasicolus										0.113					
Sardina pilchardus										0.297					
Argentiniformes					**0.002**	**0.003**	**0.027**								
Argentina sphyraena					0.002	0.003	0.027								
Myctophiformes		**0.079**	**0.018**		**0.115**	**0.053**	**0.003**		**0.168**			**0.072**			
Benthosema glaciale									0.033						
Ceratoscopelus maderensis			0.003		0.021	0.041			0.128						
Diaphus spp.												0.008			
Hygophum spp.					0.001										
Lampanyctus crocodilus		0.052	0.009		0.058		0.003					0.024			
Notoscopelus elongatus		0.005			0.015	0.003			0.007						
Myctophum punctatum		0.022			0.019	0.008									
Myctophids unidentified			0.007		0.001	0.000						0.041			
Stomiiformes		**0.022**	**0.160**		**0.028**		**0.061**		**0.082**		**0.068**				
Argyropelecus hemigymnus					0.001										
Chauliodus sloani		0.014			0.020		0.023								
Maurolicus mullueri			0.016		0.000		0.009		0.082		0.068				
Stomias boa		0.009			0.007		0.028								
Vinciguerria spp.			0.003												
Cyclothone spp.			0.142		0.000										
Gadiformes		**0.002**	**0.007**	**0.157**	**0.034**	**0.015**	**0.074**		**0.007**	**0.004**					**0.129**
Gadiculus argenteus			0.007		0.005	0.004	0.015								0.000
Merluccius merluccius		0.002													
Micromesistius poutassou					0.008		0.034		0.007						0.007
Molva dypterygia										0.004					0.001
Gaidropsarus biscayensis				0.157			0.019								0.063
Phycis blennoides					0.019	0.000									0.032
Trisopterus minutus					0.001	0.010	0.006								0.026
Perciformes		**0.000**			**0.011**	**0.052**	**0.013**	**0.046**	**0.003**	**0.395**			**0.001**	**0.006**	**0.018**
Ammodytes tobianus										0.319					
Aphia minuta										0.004					
Blennius ocellaris										0.000					
Callionymus spp.					0.000	0.049	0.003	0.011		0.005					0.009
Capros aper					0.002										
Cepola macrophthalma						0.001									
Crystallogobius linearis									0.002						
Deltentosteus spp.							0.009								0.002
Epigonus spp.					0.002										
Gobidae		0.000				0.002	0.001			0.003			0.001		0.002
Lepidopus caudatus					0.006										
Lesueurogobius spp.								0.035	0.002					0.006	
Mullus spp.										0.005					
Synchiropus phaeton															0.004
Trachurus spp.										0.058					
Aulopiformes		**0.044**			**0.051**		**0.005**				**0.083**	**0.073**			
Arctozenus risso					0.036		0.005				0.061				
Evermannella balbo												0.073			
Lestidiops spp.					0.001										
Paralepididae		0.044			0.013		0.000				0.023				
Scorpaeniformes							**0.003**								
Helicolenus dactylopterus							0.003								
Pleuronectiformes					**0.000**	**0.010**		**0.001**	**0.000**						
Arnoglossus spp.						0.004									
Symphurus spp.						0.003									
Pleuronectiformes unidentified					0.000	0.003		0.001	0.000						
Anguilliformes					**0.000**		**0.006**								
Conger conger							0.003								
Gnathophis mystax							0.003								
Ophichthus rufus					0.000										
Teleost larvae			0.000	0.004		0.001			0.001	0.035	0.001				

Table A.2.3 (Continued)

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Teleost eggs	0.095		0.000		0.046				0.000						
Teleosts unidentified	0.010	0.240	0.061	0.008	0.093	0.034	0.119	0.007	0.001	0.008	0.027	0.039	0.004		0.019
Elasmobranchs					**0.009**		**0.005**								
Galeus melastomus							0.005								
Elasmobranchs unidentified					0.009										
Other	**0.034**		**0.007**		**0.000**										
Cnidaria						**0.000**		**0.000**			**0.009**	**0.007**	**0.002**		**0.000**
Actiniaria								0.000			0.005	0.000	0.000		
Diphyidae						0.000					0.004	0.005			0.000
Plumularioidea												0.001			
Pennatulidae												0.001			
Cnidaria unidentified													0.002		
Polychaeta		**0.000**		**0.052**		**0.000**		**0.076**	**0.003**	**0.088**	**0.152**	**0.027**	**0.145**	**0.055**	**0.001**
Aphroditidae				0.019										0.042	
Eunice spp.								0.000					0.005		
Eunicidae								0.000					0.001		
Glycera spp.													0.000		
Phyllodocidae													0.001		
Syllidae								0.000							
Sternaspis scutata				0.002									0.000		
Errantia unidentified		0.000		0.002				0.003					0.001		0.000
Sedentaria unidentified													0.003		
Polychaeta unidentified				0.028		0.000		0.072	0.003	0.088	0.152	0.027	0.133	0.012	0.001
Sipuncula								**0.000**			**0.001**	**0.001**	**0.010**		
Nemertea													**0.001**		
Echinodermata		**0.000**		**0.136**				**0.034**		**0.006**	**0.047**	**0.046**	**0.009**	**0.009**	
Asteroidea unidentified													0.003		
Echinacea												0.000		0.001	
Irregularia		0.000													
Holothuroidea unidentified													0.002	0.009	
Ophiuridae				0.136				0.034		0.006	0.043	0.033	0.005		
Leptometra spp.											0.004	0.013			
Crustacea	**0.221**	**0.048**	**0.009**	**0.743**	**0.099**	**0.466**	**0.010**	**0.809**	**0.649**	**0.900**	**0.445**	**0.095**	**0.648**	**0.484**	**0.901**
Amphipoda				**0.082**	**0.001**	**0.001**	**0.000**	**0.031**	**0.004**	**0.515**	**0.140**	**0.022**	**0.001**	**0.000**	**0.006**
Brachyscelus spp.					0.001	0.000		0.000							0.000
Hyperia spp.											0.001				
Hyperiidea					0.000	0.000		0.001		0.001	0.000	0.002			
Phronima sedentaria				0.001	0.000	0.000		0.000			0.026	0.001			0.004
Phrosina semilunata												0.002			
Vibilia spp.					0.000	0.000		0.000		0.002	0.001	0.006			
Abludomelita spp.								0.000							
Ampelisca spp.				0.000	0.000			0.003	0.002		0.000		0.000		0.000
Amphilochoides spp.								0.000							
Aoridae spp.								0.001							
Apherusa spp.								0.000							
Bathymedon spp.				0.001											
Cheirocratus spp.								0.000							
Epimeria spp.				0.034				0.000			0.001	0.000	0.001		0.000
Eusirus spp.								0.000							0.000
Gammaridae								0.002							
Gammaropsis spp.								0.000							
Harpinia spp.								0.000				0.000			
Ichnopus spp.								0.001							
Idunella spp.								0.000							0.000
Lembos spp.								0.000							
Lepidepecreum spp.								0.000							
Leptocheirus spp.								0.000				0.000			
Leucothoe spp.								0.000							
Lysianassa spp.					0.000			0.003							0.000
Lysianassidae				0.004				0.002	0.001	0.005		0.001			0.000

Table A.2.3 (Continued)

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Maera spp.								0.000							
Monoculodes spp.				0.001				0.000				0.000			
Nicippe spp.				0.024				0.000							
Oedicerotidae				0.000				0.000							
Orchomene spp.								0.001							
Orchomenella spp.								0.000							
Peltocoxa spp.												0.000			
Phoxocephalus spp.											0.000				
Pseudotiron spp.								0.000							
Rhachotropis spp.				0.000						0.007					0.000
Scopelocheirus spp.								0.002							
Socarne spp.								0.000							
Syrrhoites spp.								0.000							
Tryphosites spp.				0.002				0.007							
Urothoe spp.								0.000							
Westwoodilla spp.				0.003			0.000	0.001			0.000				
Parvipalpus spp.								0.000							
Photis spp.											0.000				
Phtisica spp.				0.001				0.000							
Caprellids unidentified				0.000							0.005	0.002			0.000
Amphipods unidentified				0.010	0.000	0.000		0.004	0.001	0.500	0.105	0.008	0.001	0.000	0.001
Isopoda		**0.000**		**0.002**	**0.000**	**0.001**	**0.000**	**0.015**	**0.085**	**0.021**		**0.009**			**0.010**
Gnathiidae												0.000			
Isopods unidentified		0.000		0.002	0.000	0.001	0.000	0.015	0.085	0.021		0.009			0.010
Cumacea				**0.000**				**0.001**		**0.001**	**0.000**	**0.000**			
Lophogastrida			**0.000**	**0.101**	**0.001**	**0.000**		**0.011**	**0.002**						**0.004**
Lophogaster typicus			0.000	0.101	0.001	0.000		0.011	0.002						0.004
Mysida	**0.023**			**0.005**	**0.001**	**0.000**	**0.001**	**0.006**	**0.001**	**0.171**	**0.182**	**0.000**	**0.000**		**0.005**
Tanaidacea											**0.000**	**0.000**			**0.000**
Peracarids unidentified										0.005					
Copepoda				**0.000**	**0.000**			**0.000**		**0.007**	**0.001**	**0.004**			**0.000**
Ostracoda										**0.004**		**0.000**			**0.000**
Euphausiacea		**0.000**		**0.036**	**0.042**	**0.289**	**0.003**		**0.000**	**0.015**	**0.003**	**0.031**	**0.017**		**0.033**
Euphausia krohnii				0.001		0.001									
Meganyctiphanes norvegica				0.029	0.001	0.048						0.001			0.025
Nematoscelis spp.					0.000	0.003							0.017		
Nyctiphanes couchii					0.007	0.013									
Euphausiacids unidentified		0.000		0.007	0.034	0.223	0.003		0.000	0.015	0.003	0.031			0.008
Scalpelliformes												**0.000**			
Scalpellum scalpellum												0.000			
Decapoda	**0.195**	**0.038**	**0.002**	**0.515**	**0.052**	**0.174**	**0.006**	**0.734**	**0.557**	**0.135**	**0.117**	**0.027**	**0.628**	**0.484**	**0.813**
Aegaeon spp.				0.033	0.002			0.003							0.002
Alpheus glaber	0.006	0.003	0.000	0.025	0.004			0.120	0.004		0.006	0.001	0.188		0.341
Athanas spp.								0.002							
Chlorotocus crassicornis		0.001			0.013			0.046	0.032				0.010		0.072
Crangonidae					0.000			0.000			0.000				
Deosergestes henseni						0.001									
Eusergestes arcticus						0.009	0.002					0.003			
Gennadas elegans							0.002								
Hymenopenaeus debilis		0.001													
Ligur ensiferus				0.003											
Parapenaeus longirostris															
Pasiphaea multidentata						0.032									
Pasiphaea sivado					0.001	0.068						0.002			0.005
Pasiphaea spp.					0.002	0.012									0.002
Philocheras spp.				0.002	0.000			0.002		0.005	0.001		0.000		0.000
Plesionika acanthonotus															0.001
Plesionika edwardsii		0.001													
Plesionika giglioli					0.001	0.001									
Plesionika heterocarpus	0.081	0.002			0.000							0.009			

Table A.2.3 (Continued)

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Plesionika martia							0.001								
Plesionika narval		0.000													
Pontophilus spp.				0.001	0.000			0.001							
Processa spp.	0.012	0.000	0.000	0.003	0.004	0.001		0.150	0.031				0.005		0.042
Sergia robusta						0.024									
Table A.2.3 (Continued)															
Atelecyclus rotundatus				0.017				0.006							
Calcinus spp.														0.001	
Calocaris macandreae				0.004		0.000				0.060					0.061
Ctenodrilus spp.				0.000											
Ebalia spp.				0.001							0.001				
Eurynome spp.				0.002											
Galathea spp.				0.001				0.006			0.002		0.000	0.003	0.000
Goneplax rhomboides		0.001		0.202				0.024			0.000		0.111	0.152	0.078
Inachus spp.		0.000												0.000	
Liocarcinus spp.		0.000		0.100	0.001			0.141			0.003		0.131	0.132	0.018
Macropipus tuberculatus				0.026										0.047	0.001
Macropodia spp.				0.010										0.001	
Monodaeus couchii				0.032				0.003		0.010					0.008
Munida spp.	0.010			0.027				0.006					0.005	0.004	0.012
Nephrops norvegicus						0.001									
Paguridae				0.007					0.000		0.006		0.003	0.006	0.000
Pagurus spp.				0.003									0.001	0.015	
Palinurus elephas								0.003							
Portunidae					0.000			0.023					0.019	0.007	
Scyllarus spp.				0.001	0.000			0.002					0.001		0.001
Upogebia spp.					0.000			0.012			0.009		0.005		0.001
Decapod larvae								0.001			0.002	0.000			
Natantia unidentified	0.083	0.009	0.000	0.002	0.010	0.023		0.068	0.068	0.053	0.047	0.012	0.040	0.022	0.055
Brachyura unidentified				0.013	0.000			0.035		0.007	0.033	0.001	0.043	0.088	0.004
Decapoda unidentified	0.002	0.001		0.001	0.003	0.002		0.016			0.000	0.001	0.038	0.000	0.009
Stomapoda		**0.010**	**0.007**		**0.000**									**0.000**	**0.027**
Rissoides desmaresti		0.005	0.001		0.000										0.027
Squila mantis		0.005	0.006												
Stomatopoda unidentified														0.000	
Crustacea unidentified	0.002	0.000		0.002	0.002	0.001		0.010		0.032	0.002	0.002	0.001		0.002
Cephalopods	**0.005**	**0.025**	**0.139**	**0.009**	**0.057**	**0.007**		**0.034**			**0.035**	**0.054**	**0.080**	**0.067**	**0.007**
Sepiida	**0.005**	**0.009**	**0.110**	**0.008**	**0.022**			**0.025**			**0.034**	**0.013**	**0.061**		**0.000**
Heteroteuthis dispar												0.003			
Rondeletiola minor					0.001			0.006					0.008		
Sepia elegans		0.000			0.013										
Sepia officinalis			0.109												
Sepia orbignyana		0.004											0.025		
Sepia spp.		0.003						0.001							
Sepietta oweniana		0.002			0.005			0.011					0.027		
Sepiolid unidentified	0.005	0.000	0.001	0.008	0.003			0.007			0.034	0.010	0.001		0.000
Myopsida		**0.003**						**0.009**							
Alloteuthis spp.		0.003						0.009							
Oegopsida		**0.012**			**0.034**	**0.007**						**0.006**			**0.003**
Abralia veranyi						0.004									
Illex coindetii		0.012			0.034										0.003
Teuthida unidentified						0.003						0.006			
Octopoda			**0.029**											**0.067**	
Eledone spp.			0.029											0.067	
Cephalopod eggs					0.000										
Cephalopods unidentified		0.001	0.001	0.001	0.000						0.002	0.036	0.020		0.003
Other Mollusca				**0.017**				**0.013**		**0.000**	**0.078**	**0.003**	**0.010**	**0.000**	
Pteropoda				**0.003**							**0.000**	**0.002**			
Cavolinia spp.				0.003							0.000	0.002			
Bivalvia				**0.005**				**0.013**		**0.000**	**0.029**	**0.000**	**0.004**		

Table A.2.3 (Continued)

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Bivalvia unidentified				0.005				0.013		0.000	0.029	0.000	0.004		
Gastropoda				**0.010**				**0.000**			**0.049**		**0.006**	**0.000**	
Calyptraea chinensis														0.000	
Heterobranchia				0.009							0.049		0.003		
Gastropoda unidentified				0.001				0.000					0.004		
Tunicata											**0.076**	**0.572**		**0.000**	
Ascidiacea												0.009			
Pyrosoma atlanticum											0.034	0.463			
Tunicata unidentified											0.043	0.100		0.000	
Cephalochordata								**0.001**							
Branchiostoma lanceolatum								0.001							
Teleosts	**0.775**	**0.926**	**0.827**	**0.042**	**0.845**	**0.526**	**0.990**	**0.033**	**0.348**		**0.155**	**0.190**	**0.094**	**0.381**	**0.089**
Clupleiformes		**0.016**			**0.388**	**0.009**					**0.012**	**0.008**		**0.287**	
Engraulis encrasicolus		0.004			0.284									0.136	
Sardina pilchardus		0.012			0.102	0.009					0.012	0.008		0.151	
Sprattus sprattus					0.002										
Argentiniformes	**0.029**	**0.000**			**0.001**		**0.006**								
Argentina sphyraena		0.000			0.001										
Glossanodon leioglossus	0.029						0.006								
Myctophiformes					**0.012**	**0.421**	**0.010**					**0.044**			**0.004**
Benthosema glaciale						0.041						0.004			
Ceratoscopelus maderensis					0.001	0.182						0.035			0.004
Lampanyctus crocodilus					0.011	0.165						0.001			
Notoscopelus elongatus					0.000	0.012	0.010					0.003			
Myctophum punctatum						0.005									
Myctophids unidentified					0.000	0.015						0.002			
Stomiiformes				**0.023**	**0.002**	**0.048**						**0.018**			**0.003**
Argyropelecus hemigymnus												0.002			
Maurolicus mullueri				0.023	0.001	0.006						0.004			0.003
Stomias boa					0.001	0.030						0.012			
Cyclothone spp.						0.011						0.000			
Gonostoma denudatum						0.000									
Gadiformes	**0.376**	**0.219**	**0.207**	**0.010**	**0.167**	**0.019**	**0.888**	**0.003**	**0.074**				**0.004**		**0.062**
Gadiculus argenteus	0.191	0.003	0.000		0.001		0.306								
Merluccius merluccius		0.062	0.185		0.038				0.039						0.011
Micromesistius poutassou	0.134	0.016	0.004		0.108	0.008	0.427		0.035						
Molva macrophthalma		0.001													
Gaidropsarus biscayensis		0.006	0.003	0.010	0.004		0.014	0.003					0.004		0.046
Phycis blennoides		0.097	0.014		0.006	0.011	0.044								0.000
Trisopterus minutus	0.050	0.034	0.001		0.012	0.000	0.096								0.005
Perciformes	**0.214**	**0.274**	**0.292**	**0.005**	**0.201**			**0.014**	**0.074**		**0.017**		**0.045**	**0.061**	
Boops boops		0.021			0.145										
Callionymus spp.		0.006	0.001	0.005	0.001			0.003			0.003		0.000		
Capros aper	0.214	0.001													
Cepola macrophthalma		0.030			0.006			0.009	0.008						
Crystallogobius linearis														0.003	
Deltentosteus spp.		0.005			0.000				0.066				0.017		
Diplodus spp.		0.005	0.017											0.030	
Gobidae		0.028	0.000		0.002			0.001					0.008		
Lesueurogobius spp.		0.002	0.000		0.001						0.014		0.011		
Mullus spp.		0.016	0.068		0.001								0.009		
Pagellus erythrinus		0.017													
Serranus cabrilla					0.000										
Serranus hepatus		0.005													
Spicara smaris					0.004										
Spicara maena		0.022	0.031		0.014										
Spicara spp.		0.003													
Trachinus draco		0.092	0.090		0.001										
Trachurus spp.		0.021	0.001		0.026									0.029	
Uranoscopus scaber			0.083												

Table A.2.3 (Continued)

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Aulopiformes					**0.010**	**0.008**						**0.009**			**0.014**
Lestidiops spp.						0.008									0.014
Paralepididae					0.010							0.009			
Scorpaeniformes		**0.013**	**0.010**		**0.000**										
Chelidonichthys spp.		0.002													
Lepidotrigla spp.		0.001													
Scorpaena notata		0.002													
Scorpaena porcus			0.010												
Triglidae		0.008			0.000										
Pleuronectiformes		**0.107**	**0.142**	**0.001**							**0.002**		**0.002**		
Arnoglossus spp.		0.013	0.003										0.002		
Citharus linguatula		0.082	0.011												
Lepidorhombus spp.		0.002													
Solea spp.			0.127												
Symphurus spp.		0.007	0.001												
Pleuronectiformes unidentified		0.003		0.001							0.002				
Anguilliformes		**0.097**	**0.059**					**0.004**	**0.137**				**0.018**	**0.014**	
Conger conger		0.076	0.045					0.004					0.018		
Gnathophis mystax		0.005													
Ophichthus rufus		0.016	0.014						0.137					0.014	
Syngnathiformes		**0.000**													
Macroramphosus scolopax		0.000													
Ophidiiformes		**0.090**	**0.060**										**0.004**		
Ophidion barbatum		0.090	0.060										0.004		
Teleost larvae	0.003			0.000		0.001					0.023			0.002	
Teleost eggs												0.000			
Teleosts unidentified	0.152	0.109	0.056	0.003	0.064	0.020	0.086	0.013	0.063		0.100	0.111	0.020	0.015	0.007
Elasmobranchs			**0.025**												**0.001**
Scylliorhynus															0.001
Elasmobranchs unidentified			0.025												
Other											**0.002**	**0.001**			

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Porifera																**0.003**
Cnidaria						**0.199**			**0.086**				**0.321**		**0.000**	**0.042**
Actiniaria													0.000			0.008
Scyphozoa						0.148							0.115			
Diphyidae						0.022			0.086				0.204		0.000	
Epizoanthidae																0.003
Plumularioidea						0.029										0.019
Pennatulidae																0.012
Cnidaria unidentified													0.002			
Polychaeta	**0.002**	**0.007**	**0.042**	**0.052**	**0.187**	**0.015**	**0.113**		**0.006**	**0.003**	**0.004**	**0.159**	**0.001**	**0.000**	**0.003**	**0.213**
Aphroditidae														0.000		
Sabellidae				0.001		0.004										0.004
Sternaspis scutata					0.009											
Errantia unidentified									0.003			0.009	0.001			
Sedentaria unidentified																0.021
Polychaeta unidentified	0.002	0.007	0.042	0.051	0.178	0.011	0.113		0.003	0.003	0.004	0.150	0.000	0.000	0.003	0.187
Sipuncula													**0.000**			**0.012**
Nemertea						**0.007**										
Echinodermata										**0.000**						**0.050**
Astropecten irregularis																0.003
Holothuroidea unidentified																0.012
Ophiuridae										0.000						0.009
Leptometra spp.																0.026
Crustacea	**0.963**	**0.923**	**0.956**	**0.915**	**0.741**	**0.085**	**0.860**	**0.339**	**0.826**	**0.969**	**0.248**	**0.815**	**0.120**	**0.342**	**0.736**	**0.381**
	0.056	**0.130**	**0.067**	**0.160**	**0.037**	**0.033**	**0.290**		**0.029**	**0.053**		**0.025**	**0.028**	**0.000**	**0.005**	**0.020**

Table A.2.3 (Continued)

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Anchylomera spp.													0.000			
Brachyscelus spp.							0.004						0.019			
Hemityphis spp.													0.000			
Hyperia spp.													0.000			
Hyperiidea						0.018	0.101		0.001				0.005			
Hyperionyx spp.													0.000			
Leptocotis spp.													0.000			
Phronima sedentaria						0.010							0.000			
Phrosina semilunata							0.004						0.002	0.000		
Platyscelidae													0.000			
Streetsia spp.													0.000			
Vibilia spp.						0.003	0.010		0.017	0.000		0.000	0.001		0.000	
Ampelisca spp.	0.023	0.058	0.019	0.117	0.017					0.003		0.002	0.000		0.001	0.000
Bathymedon spp.												0.000				
Cheirocratus spp.										0.001					0.000	
Epimeria spp.										0.001		0.000			0.001	
Eusirus spp.	0.004				0.000					0.000						
Gammaridae													0.000			
Harpinia spp.					0.001											
Ichnopus spp.										0.002					0.000	
Lembos spp.												0.000				
Leptocheirus spp.					0.000					0.000						
Leucothoe spp.					0.000					0.000						
Lysianassa spp.										0.004					0.000	
Lysianassidae		0.003					0.002		0.002	0.000		0.000	0.000			
Maera spp.					0.000					0.001		0.002			0.000	
Monoculodes spp.		0.001	0.008	0.002						0.001		0.000			0.000	
Nicippe spp.					0.000							0.004				
Orchomene spp.										0.000						
Rhachotropis spp.										0.001		0.001				
Stegocephaloides spp.															0.000	
Syrrhoe spp.												0.000				
Tryphosites spp.												0.001				
Westwoodilla spp.		0.007		0.002	0.001					0.000		0.001			0.000	0.000
Caprellids unidentified	0.007	0.011	0.003	0.004	0.000	0.000	0.133		0.000	0.000						0.005
Amphipods unidentified	0.022	0.051	0.037	0.036	0.018	0.001	0.036		0.009	0.040		0.012	0.000	0.000	0.003	0.015
Isopoda	**0.012**	**0.000**	**0.001**	**0.002**	**0.000**	**0.006**	**0.014**		**0.000**	**0.002**	**0.001**	**0.081**	**0.001**	**0.002**	**0.000**	**0.007**
Gnathiidae				0.001			0.001		0.000				0.000			
Idotea spp.				0.000						0.001						
Synisoma spp.										0.000						
Isopods unidentified	0.012	0.000	0.001	0.001	0.000	0.006	0.013			0.001	0.001	0.081	0.001	0.002	0.000	0.007
Cumacea		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**			**0.001**	**0.000**			**0.000**			**0.000**
Lophogastrida	**0.117**	**0.034**	**0.419**	**0.006**	**0.004**					**0.018**				**0.000**	**0.044**	**0.001**
Lophogaster typicus	0.117	0.034	0.419	0.006	0.004					0.018				0.000	0.044	0.001
Mysida	**0.000**	**0.151**	**0.076**	**0.032**	**0.015**	**0.003**	**0.030**		**0.029**	**0.040**	**0.031**	**0.012**	**0.054**	**0.000**	**0.031**	**0.002**
Tanaidacea					**0.000**							**0.001**				
Copepoda		**0.088**	**0.001**	**0.001**	**0.000**	**0.002**	**0.170**		**0.504**			**0.006**	**0.004**			**0.000**
Ostracoda									**0.000**			**0.000**	**0.000**			**0.000**
Euphausiacea				**0.007**		**0.000**	**0.165**	**0.224**	**0.167**		**0.042**	**0.021**	**0.007**	**0.001**	**0.001**	
Meganyctiphanes norvegica							0.024	0.006						0.001	0.000	
Nematoscelis spp.							0.018				0.004					
Nyctiphanes couchii												0.001				
Euphausiacids unidentified				0.007		0.000	0.122	0.218	0.167		0.039	0.020	0.007	0.000	0.001	
Decapoda	**0.778**	**0.515**	**0.392**	**0.609**	**0.679**	**0.039**	**0.042**	**0.115**	**0.017**	**0.841**	**0.171**	**0.569**	**0.014**	**0.326**	**0.652**	**0.328**
Acanthephyra spp.																
Aegaeon spp.		0.014		0.004						0.084			0.000	0.001		
Alpheus glaber		0.096			0.232	0.001					0.089	0.031		0.063	0.021	0.019
Athanas spp.		0.004			0.003					0.002						
Chlorotocus crassicornis		0.021			0.010					0.006	0.003			0.006	0.039	
Crangonidae			0.014	0.003			0.024			0.003	0.001			0.001	0.001	0.006

Table A.2.3 (Continued)

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Eusergestes arcticus								0.000						0.000		
Hippolytidae	0.008									0.007			0.000			
Pasiphaea sivado								0.099								
Pasiphaea spp.								0.004						0.001		
Philocheras spp.	0.003	0.053	0.029	0.013	0.002					0.016	0.005	0.000			0.012	
Plesionika acanthonotus													0.000			
Plesionika heterocarpus			0.020		0.003									0.004	0.008	
Pontophilus spp.	0.011	0.074	0.017	0.007						0.009					0.005	
Processa spp.	0.064	0.017	0.119	0.043	0.117					0.006	0.013	0.004		0.008	0.003	0.001
Sergia robusta														0.000		
Solenocera membranacea					0.038					0.004	0.008			0.013	0.001	
Atelecyclus rotundatus										0.006		0.000			0.001	
Calocaris macandreae				0.005							0.004	0.469		0.002		
Ctenodrilus spp.										0.005						
Ebalia spp.										0.000					0.000	
Ergasticus clouei										0.001						
Ethusa spp.										0.016						
Galathea spp.	0.036	0.008	0.010	0.169	0.000					0.116				0.000	0.003	0.012
Geryon longipes														0.027		
Goneplax rhomboides	0.143	0.090	0.113	0.043	0.049					0.035	0.013	0.003		0.082	0.073	0.095
Inachus spp.				0.001						0.006						
Jaxea nocturna														0.000		
Liocarcinus spp.	0.485	0.060	0.020	0.189	0.010					0.318				0.031	0.286	0.005
Macropipus tuberculatus														0.005	0.024	
Macropodia spp.										0.019					0.001	
Majidae										0.001						
Medoripe lanata										0.013						0.018
Monodaeus couchii		0.006	0.010							0.011		0.024		0.007		
Munida spp.														0.014	0.118	
Nephrops norvegicus														0.030		
Paguridae	0.012	0.002	0.000	0.091						0.006						0.004
Pagurus spp.										0.008				0.001		
Palicus spp.										0.008						
Portunidae				0.001	0.001					0.019				0.003		
Scyllarus spp.										0.003					0.002	0.007
Thalassinidea																0.008
Upogebia spp.					0.000					0.013						
Decapod larvae	0.003	0.003		0.001	0.000	0.000		0.000	0.017	0.001			0.011			
Ethusidae larvae													0.000			
Nephrops larvae													0.002			
Palinuridae larvae													0.000			
Geryon eggs														0.005		
Natantia unidentified	0.006	0.051	0.041	0.013	0.146	0.036	0.008	0.011		0.008	0.025	0.017	0.000	0.010	0.018	0.023
Brachyura unidentified	0.007	0.007		0.014	0.024					0.090	0.000	0.016	0.000	0.011	0.021	0.126
Decapoda unidentified		0.008		0.011	0.044	0.002	0.010			0.003	0.010	0.005	0.001	0.001	0.014	0.004
Stomapoda										**0.004**			**0.004**	**0.012**		**0.023**
Rissoides desmaresti										0.004				0.008		0.015
Squila mantis														0.004		
Stomatopod larvae													0.004			
Stomatopoda unidentified													0.000	0.000		0.008
Crustacea unidentified	0.004		0.099	0.005	0.002	0.150		0.079	0.009	0.004	0.099	0.008		0.003		0.004
Cephalopods					**0.034**		**0.002**		**0.017**	**0.028**		**0.006**	**0.038**	**0.101**	**0.001**	**0.034**
Sepiida					**0.034**				**0.016**	**0.005**		**0.000**	**0.013**	**0.101**		**0.034**
Rondeletiola minor										0.001	0.005				0.039	
Rossia macrosoma														0.005		
Sepia orbignyana														0.004		
Sepia spp.														0.002		
Sepietta oweniana						0.034				0.009			0.000	0.002	0.031	
Sepiolid unidentified										0.006				0.001	0.031	
Myopsida											**0.022**			**0.001**		

Table A.2.3 (Continued)

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Alloteuthis spp.											0.022			0.001		
Oegopsida							**0.002**					**0.006**	**0.001**			**0.002**
Histioteuthis bonnellii													0.001			
Illex coindetii												0.006				
Teuthida unidentified							0.002									
Octopoda														**0.022**		
Eledone spp.														0.022		
Cephalopods unidentified										0.001	0.000		0.000	0.001	0.000	0.001
Other Mollusca	**0.004**			**0.000**	**0.071**	**0.000**				**0.000**			**0.001**		**0.001**	**0.097**
Pteropoda						**0.000**							**0.001**			
Limacina spp.													0.000			
Cavolinia spp.						0.000							0.001			
Bivalvia				**0.000**	**0.071**					**0.000**			**0.000**		**0.001**	**0.009**
Bivalvia unidentified				0.000	0.071					0.000			0.000		0.001	0.009
Gastropoda	**0.004**				**0.000**										**0.000**	**0.088**
Umbraculum umbraculum																0.013
Heterobranchia																0.070
Gastropoda unidentified	0.004				0.000										0.000	0.005
Tunicata						**0.594**	**0.004**		**0.035**				**0.005**		**0.001**	**0.015**
Ascidiacea						0.005										0.011
Pyrosoma atlanticum						0.571	0.004								0.001	0.004
Tunicata unidentified						0.017			0.035				0.005			
Teleosts	**0.030**	**0.070**	**0.002**	**0.032**	**0.001**	**0.044**	**0.023**	**0.659**	**0.047**	**0.011**	**0.720**	**0.026**	**0.546**	**0.617**	**0.157**	**0.122**
Clupleiformes								**0.009**			**0.115**		**0.363**	**0.020**		
Engraulis encrasicolus											0.004		0.026	0.006		
Sardina pilchardus								0.009			0.111		0.337	0.014		
Argentiniformes								**0.002**						**0.009**		
Argentina sphyraena								0.002								
Glossanodon leioglossus														0.009		
Myctophiformes								**0.156**						**0.001**	**0.002**	
Benthosema glaciale								0.009								
Ceratoscopelus maderensis								0.079								
Lampanyctus crocodilus								0.009								
Notoscopelus elongatus								0.050						0.001		
Myctophum punctatum								0.003							0.002	
Myctophids unidentified								0.005								
Stomiiformes								**0.255**						**0.002**		
Maurolicus mullueri								0.245								
Stomias boa														0.002		
Cyclothone spp.								0.010								
Gadiformes		**0.035**						**0.002**			**0.171**	**0.026**		**0.052**	**0.012**	
Gadiculus argenteus											0.016			0.006	0.002	
Merluccius merluccius											0.030			0.002		
Micromesistius poutassou								0.002			0.024			0.007		
Gaidropsarus biscayensis		0.035										0.026		0.019	0.003	
Phycis blennoides														0.016		
Trisopterus minutus											0.101			0.002	0.007	
Perciformes	**0.030**	**0.031**		**0.028**				**0.003**		**0.000**	**0.238**		**0.053**	**0.255**	**0.095**	**0.038**
Blennius ocellaris															0.001	0.003
Callionymus spp.		0.023						0.003			0.009			0.005	0.023	
Cepola macrophthalma											0.059			0.022	0.061	
Crystallogobius linearis	0.030			0.004										0.000		
Deltentosteus spp.											0.023			0.002	0.002	
Gobidae		0.007		0.018						0.000	0.065			0.064	0.005	0.017
Lesueurogobius spp.		0.001		0.006							0.081			0.006	0.002	0.019
Mullus spp.													0.045			
Serranus cabrilla														0.016		
Serranus hepatus														0.019		
Spicara smaris														0.064		
Spicara maena														0.048		

Table A.2.3 (Continued)

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Synchiropus phaeton														0.001		
Trachurus spp.													0.008	0.007		
Aulopiformes								**0.161**								
Arctozenus risso								0.065								
Paralepididae								0.096								
Scorpaeniformes											**0.014**			**0.013**	**0.024**	
Chelidonichthys spp.											0.014			0.011	0.001	
Helicolenus dactylopterus														0.001	0.021	
Triglidae															0.001	
Pleuronectiformes						**0.003**				**0.001**	**0.027**			**0.015**	**0.012**	**0.009**
Arnoglossus spp.										0.001	0.002					
Citharus linguatula											0.005			0.003		
Symphurus spp.														0.007	0.005	
Pleuronectiformes						0.003					0.019			0.005	0.007	0.009
Anguilliformes														**0.051**		
Conger conger														0.037		
Ophichthus rufus														0.015		
Notacanthiformes														**0.006**		
Notacanthus bonaparte														0.006		
Ophidiiformes														**0.021**		
Ophidion barbatum														0.021		
Teleost larvae				0.002			0.006		0.042	0.003	0.002		0.116	0.003		
Teleost eggs													0.000	0.004		0.012
Teleosts unidentified		0.003	0.002	0.002	0.001	0.041	0.018	0.071	0.005	0.006	0.153		0.014	0.165	0.013	0.064
Elasmobranchs														**0.002**		
Scylliorhynus														0.001		
Elasmobranchs unidentified														0.001		
Other						**0.022**										**0.064**

Table A.2.4 Volumetric Index (V%), Frequency Index (F%), Geometric Index of Importance (GII%), Niche breadth (B_i) and Mean trophic level (MTL) estimated for the 61 species studied along the Spanish western Mediterranean Sea. Dashes represent no consumption. Acronyms are referenced in Table 2.1.

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
A. imperialis	0.16	3.6	V%	-	0.3	-	0.2	18.5	0.4	9.2	68.3	-	-	-	-	-	-	3.0	-	-	-	-	-
			F%	-	8.3	-	2.8	55.6	2.8	19.4	75.0	-	-	-	-	-	-	5.6	-	-	-	-	-
			GII%	-	4.3	-	1.5	37.0	1.6	14.3	71.7	-	-	-	-	-	-	4.3	-	-	-	-	-
A. laterna	0.42	3.6	V%	8.9	0.3	-	0.7	31.8	-	33.6	17.8	-	-	-	-	3.7	-	3.3	-	-	-	-	-
			F%	24.3	3.5	-	3.5	61.8	-	39.6	31.3	-	-	-	-	0.7	-	4.9	-	-	-	-	-
			GII%	16.6	1.9	-	2.1	46.8	-	36.6	24.5	-	-	-	-	2.2	-	4.1	-	-	-	-	-
A. rueppelii	0.30	3.5	V%	0.1	0.2	-	4.2	56.3	-	23.9	15.3	-	-	-	-	-	-	-	-	-	-	-	-
			F%	1.1	1.1	-	10.9	70.7	-	23.9	21.7	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.6	0.6	-	7.5	63.5	-	23.9	18.5	-	-	-	-	-	-	-	-	-	-	-	-
A. thori	0.20	3.7	V%	0.1	1.1	-	5.3	22.7	0.0	8.6	59.2	-	-	-	-	-	-	3.1	-	-	-	-	-
			F%	1.4	5.8	-	21.0	59.4	0.7	15.9	71.0	-	-	-	-	-	-	2.9	-	-	-	-	-
			GII%	0.8	3.5	-	13.1	41.0	0.4	12.3	65.1	-	-	-	-	-	-	3.0	-	-	-	-	-
B. boops	0.08	3.3	V%	0.2	3.4	77.6	1.5	1.0	4.3	4.0	-	3.5	-	-	4.5	-	-	-	-	-	-	-	-
			F%	9.3	23.3	73.3	6.7	6.7	10.0	4.0	0.7	0.7	-	-	3.3	-	-	-	-	-	-	-	-
			GII%	4.8	13.4	75.5	4.1	3.8	7.2	4.0	-	2.1	-	-	3.9	-	-	-	-	-	-	-	-
C. aper	0.56	3.6	V%	25.8	22.0	0.5	14.0	32.5	-	5.2	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	47.4	35.9	1.3	7.7	56.4	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	36.6	28.9	0.9	10.9	44.5	-	6.4	-	-	-	-	-	-	-	-	-	-	-	-	-
C. macrophtalma	0.38	3.2	V%	55.4	27.3	12.1	0.6	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	85.5	31.6	11.1	2.6	25.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	70.5	29.5	11.6	1.6	15.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. cuculus	0.16	3.7	V%	-	0.1	0.1	0.3	8.1	0.1	11.1	54.3	10.1	-	-	1.3	1.3	-	3.6	0.2	-	-	2.3	6.9
			F%	-	2.1	0.7	5.0	50.7	1.1	30.1	61.7	9.6	-	-	3.9	3.2	-	10.6	1.1	-	-	2.5	1.1
			GII%	-	1.1	0.4	2.6	29.4	0.6	20.6	58.0	9.9	-	-	2.6	2.3	-	7.1	0.7	-	-	2.4	4.0
C. lastoviza	0.11	3.6	V%	-	0.4	-	0.3	11.5	0.0	14.4	70.8	1.7	-	-	0.6	-	-	0.2	-	-	-	-	-
			F%	-	4.8	-	6.6	67.4	1.8	38.3	81.5	4.0	-	-	1.3	-	-	1.3	-	-	-	-	-
			GII%	-	2.6	-	3.5	39.4	0.9	26.4	76.1	2.8	-	-	1.0	-	-	0.7	-	-	-	-	-

Table A. 2.4 (Continued)

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
C. linguatula	0.50	4.2	V%	-	4.5	-	0.4	3.2	-	15.5	1.8	2.8	-	14.7	3.4	17.9	-	22.7	1.8	3.8	-	-	7.5
			F%	-	6.5	-	1.0	29.0	-	34.0	2.5	2.0	-	5.0	5.0	11.0	-	22.5	1.5	1.5	-	-	3.5
			GII%	-	5.5	-	0.7	16.1	-	24.7	2.2	2.4	-	9.8	4.2	14.5	-	22.6	1.6	2.7	-	-	5.5
C. caelorhincus	0.26	3.6	V%	0.7	2.4	-	15.9	13.6	-	6.0	58.8	-	-	-	-	2.6	-	-	-	-	-	-	-
			F%	27.5	1.0	-	47.5	69.1	-	9.3	46.6	-	-	-	-	1.0	-	-	-	-	-	-	-
			GII%	14.1	1.7	-	31.7	41.3	-	7.7	52.7	-	-	-	-	1.8	-	-	-	-	-	-	-
C. conger	0.43	4.1	V%	0.4	0.4	-	0.0	0.2	0.0	10.8	23.1	3.7	0.1	12.4	2.1	6.8	5.3	10.8	1.6	0.3	-	11.6	10.4
			F%	0.3	3.0	-	0.5	3.5	0.0	41.3	53.5	3.5	0.3	4.1	1.4	9.0	2.4	10.9	0.5	0.5	-	2.4	8.7
			GII%	0.3	1.7	-	0.3	1.9	0.0	26.1	38.3	3.6	0.2	8.3	1.7	7.9	3.9	10.8	1.1	0.4	-	7.0	9.5
D. annularis	0.39	3.6	V%	1.3	-	0.4	24.1	3.3	21.7	5.3	32.1	0.1	-	-	2.2	-	-	9.6	-	-	-	-	-
			F%	2.1	-	0.4	36.3	29.1	32.9	6.4	33.8	0.4	-	-	1.3	-	-	3.4	-	-	-	-	-
			GII%	1.7	-	0.4	30.2	16.2	27.3	5.9	32.9	0.2	-	-	1.7	-	-	6.5	-	-	-	-	-
D. vulgaris	0.37	3.4	V%	9.8	1.0	0.6	26.2	6.4	22.9	0.0	31.0	0.5	1.5	-	-	-	-	-	-	-	-	-	-
			F%	6.1	2.3	1.5	47.7	49.2	50.8	0.8	42.4	2.3	0.8	-	-	-	-	-	-	-	-	-	-
			GII%	7.9	1.7	1.1	37.0	27.8	36.8	0.4	36.7	1.4	1.1	-	-	-	-	-	-	-	-	-	-
E. spinax	0.26	4.4	V%	-	1.1	-	0.0	-	0.0	10.3	-	5.5	44.4	-	-	-	-	0.0	-	0.5	-	-	38.2
			F%	-	8.5	-	1.7	-	0.0	30.5	-	8.5	44.1	-	-	-	-	1.7	-	1.7	-	-	40.7
			GII%	-	4.8	-	0.9	-	0.0	20.4	-	7.0	44.2	-	-	-	-	0.9	-	1.1	-	-	39.4
E. gurnardus	0.25	3.6	V%	0.0	1.4	0.1	0.1	15.4	0.1	24.7	39.2	2.4	-	-	1.3	1.8	-	6.4	-	-	-	-	7.1
			F%	1.0	4.8	0.3	2.4	57.0	1.4	42.3	52.6	4.8	-	-	3.4	8.2	-	9.2	-	-	-	-	7.2
			GII%	0.5	3.1	0.2	1.3	36.2	0.7	33.5	45.9	3.6	-	-	2.4	5.0	-	7.8	-	-	-	-	7.1
G. argenteus	0.19	3.5	V%	6.7	57.1	0.1	0.1	3.5	-	7.6	0.1	-	-	-	-	1.0	-	-	-	-	-	-	23.9
			F%	12.8	65.8	0.4	0.4	19.2	-	9.0	0.4	-	-	-	-	0.9	-	-	-	-	-	-	20.5
			GII%	9.7	61.5	0.3	0.3	11.4	-	8.3	0.3	-	-	-	-	0.9	-	-	-	-	-	-	22.2
G. biscayensis	0.40	3.7	V%	1.5	3.2	-	0.3	12.2	-	20.3	46.0	-	-	-	-	16.5	-	-	-	-	-	-	-
			F%	18.6	8.8	-	1.0	39.2	-	17.6	37.3	-	-	-	-	7.8	-	-	-	-	-	-	-
			GII%	10.1	6.0	-	0.7	25.7	-	19.0	41.6	-	-	-	-	12.2	-	-	-	-	-	-	-
G. melastomus	0.36	4.0	V%	4.6	9.1	0.8	0.0	0.1	-	24.5	6.1	7.9	12.5	-	0.1	4.7	2.1	0.0	-	-	-	-	27.5
			F%	0.5	60.8	4.8	1.3	2.2	-	44.1	24.5	23.4	19.1	-	0.3	5.1	4.3	0.3	-	-	-	-	34.4
			GII%	2.6	34.9	2.8	0.7	1.1	-	34.3	15.3	15.6	15.8	-	0.2	4.9	3.2	0.1	-	-	-	-	31.0

Table A. 2.4 (Continued)

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
H. dactylopterus	0.39	3.9	V%	0.0	17.2	3.8	0.0	3.6	0.1	21.7	18.4	0.2	3.3	-	-	11.9	1.3	2.0	-	-	-	0.5	15.8
			F%	0.7	21.4	6.9	0.7	25.0	1.3	31.9	38.8	1.0	0.7	-	-	6.6	1.0	4.6	-	-	-	0.3	6.3
			GII%	0.3	19.3	5.3	0.3	14.3	0.7	26.8	28.6	0.6	2.0	-	-	9.2	1.2	3.3	-	-	-	0.4	11.0
L. crocodilus	0.12	3.7	V%	-	3.6	0.2	-	1.1	-	76.4	0.2	-	-	-	-	-	-	-	-	-	-	-	18.5
			F%	-	16.9	0.8	-	5.9	-	68.6	0.8	-	-	-	-	-	-	-	-	-	-	-	13.6
			GII%	-	10.3	0.5	-	3.5	-	72.5	0.5	-	-	-	-	-	-	-	-	-	-	-	16.0
L. caudatus	0.18	3.9	V%	-	22.4	-	-	-	-	11.5	-	-	0.2	1.1	-	0.2	-	0.4	-	-	-	-	64.3
			F%	-	50.0	-	-	-	-	11.7	-	-	1.3	0.6	-	1.3	-	0.6	-	-	-	-	63.0
			GII%	-	36.2	-	-	-	-	11.6	-	-	0.7	0.9	-	0.7	-	0.5	-	-	-	-	63.6
L. boscii	0.24	3.7	V%	-	0.8	-	0.6	2.9	-	46.7	31.3	1.1	-	-	-	14.5	0.1	2.0	-	-	-	-	-
			F%	-	4.4	-	1.3	18.1	-	53.7	53.0	1.3	-	-	-	17.1	0.7	3.7	-	-	-	-	-
			GII%	-	2.6	-	1.0	10.5	-	50.2	42.2	1.2	-	-	-	15.8	0.4	2.8	-	-	-	-	-
L. whiffiagonis	0.31	4.4	V%	-	0.3	-	-	2.4	-	18.7	1.0	0.5	-	-	-	46.8	-	-	-	-	-	-	30.3
			F%	-	2.9	-	-	14.7	0.0	29.4	5.9	8.8	-	-	-	23.5	-	-	-	-	-	-	11.8
			GII%	-	1.6	-	-	8.5	-	24.1	3.5	4.6	-	-	-	35.2	-	-	-	-	-	-	21.1
L. cavillone	0.24	3.5	V%	0.1	0.1	-	1.4	56.6	-	26.6	14.7	-	-	-	-	-	-	0.5	-	-	-	-	-
			F%	2.6	1.9	-	1.9	86.8	-	32.5	23.4	-	-	-	-	-	-	3.0	-	-	-	-	-
			GII%	1.4	1.0	-	1.7	71.7	-	29.5	19.0	-	-	-	-	-	-	1.8	-	-	-	-	-
L. dieuzeidei	0.16	3.4	V%	1.7	3.3	-	3.3	85.6	-	25.4	8.8	1.7	-	-	-	-	-	1.1	-	-	-	-	-
			F%	0.8	2.2	-	1.8	73.3	-	27.9	6.2	2.4	-	-	-	-	-	0.8	-	-	-	-	-
			GII%	-	0.0	-	0.3	9.2	-	55.7	0.0	-	-	-	-	4.3	-	8.0	-	4.8	-	-	17.7
L. naevus	0.22	4.1	V%	-	2.6	-	7.7	51.3	-	69.2	2.6	-	-	-	-	5.1	-	5.1	-	5.1	-	-	12.8
			F%	-	1.3	-	4.0	30.2	-	62.4	1.3	-	-	-	-	4.7	-	6.6	-	5.0	-	-	15.3
			GII%	-	0.0	-	0.0	0.0	0.0	3.7	1.1	1.3	1.2	6.9	12.1	17.7	19.2	4.6	1.3	7.1	1.8	5.9	16.1
L. budegassa	0.41	4.7	V%	-	0.5	-	0.2	1.2	0.2	21.0	4.3	2.6	0.5	4.3	10.7	31.5	4.8	14.3	1.7	4.5	1.0	3.3	17.2
			F%	-	0.2	-	0.1	0.6	0.1	12.3	2.7	2.0	0.8	5.6	11.4	24.6	12.0	9.5	1.5	5.8	1.4	4.6	16.6
			GII%	-	-	-	-	0.0	-	0.2	0.7	13.9	-	0.1	15.2	2.4	25.9	0.3	-	19.8	7.3	6.2	8.0
L. piscatorius	0.42	4.8	V%	-	-	-	-	1.1	-	10.3	3.4	13.8	-	1.1	8.0	16.1	17.2	12.6	-	1.1	3.4	8.0	16.1
			F%	-	-	-	-	0.6	-	5.3	2.1	13.9	-	0.6	11.6	9.2	21.6	6.4	-	10.5	5.4	7.1	12.0
			GII%	0.0	4.4	-	-	0.1	-	5.2	0.2	2.2	3.4	60.9	-	14.0	0.1	0.5	0.0	4.1	0.1	1.5	3.4

Table A.2.4 (Continued)

PREDATOR	**B_i**	**TL**	**DI**	**SP**	**LP**	**GP**	**PO**	**PE**	**BI**	**NA**	**RE**	**BC**	**BT**	**PF**	**FF**	**GA**	**IF**	**GO**	**TR**	**HA**	**MU**	**SF**	**BF**
M. merluccius	0.10	4.3	V%	0.1	27.5	-	-	6.1	-	24.9	1.8	2.8	0.1	33.0	-	17.9	0.1	2.9	0.1	2.0	0.1	0.4	2.2
			F%	0.1	15.9	-	-	3.1	-	15.0	1.0	2.5	1.8	46.9	-	15.9	0.1	1.7	0.1	3.0	0.1	1.0	2.8
			GII%	-	29.1	0.0	0.0	0.1	-	17.3	0.1	-	0.8	1.0	-	2.0	-	-	-	-	-	-	49.6
M. poutassou	0.20	3.9	V%	-	55.2	0.2	0.2	1.8	-	22.0	0.4	-	1.8	0.9	-	1.8	-	-	-	-	-	-	53.6
			F%	-	42.2	0.1	0.1	1.0	-	19.7	0.2	-	1.3	0.9	-	1.9	-	-	-	-	-	-	51.6
			GII%	-	0.3	-	-	0.1	-	0.6	-	-	-	-	-	97.3	-	-	-	-	-	-	1.7
M. macrophthalma	0.01	4.7	V%	-	3.3	-	-	4.1	-	1.6	-	-	-	-	-	93.4	-	-	-	-	-	-	9.0
			F%	-	1.8	-	-	2.1	-	1.1	-	-	-	-	-	95.4	-	-	-	-	-	-	5.4
			GII%	0.0	0.1	-	18.7	5.7	7.1	59.2	9.1	-	-	-	-	-	-	-	-	-	-	-	-
M. barbatus	0.25	3.5	V%	0.4	1.6	-	34.4	52.6	12.6	57.5	26.3	-	-	-	-	-	-	-	-	-	-	-	-
			F%	0.2	0.9	-	26.6	29.2	9.8	58.3	17.7	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.1	0.2	-	7.6	6.4	4.7	47.3	27.0	3.4	-	-	-	0.4	0.6	0.7	-	-	-	-	1.6
M. surmuletus	0.20	3.6	V%	1.3	3.0	-	23.8	52.1	15.2	55.4	53.5	2.6	-	-	-	0.7	0.7	1.3	-	-	-	-	2.3
			F%	0.7	1.6	-	15.7	29.3	9.9	51.4	40.2	3.0	-	-	-	0.5	0.6	1.0	-	-	-	-	1.9
			GII%	1.1	1.8	-	8.8	73.6	0.7	6.0	8.0	-	-	-	-	-	-	-	-	-	-	-	-
N. aequalis	0.13	3.8	V%	25.8	3.4	-	21.3	94.4	3.4	7.9	18.0	-	-	-	-	-	-	-	-	-	-	-	-
			F%	13.5	2.6	-	15.1	84.0	2.0	6.9	13.0	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.1	5.7	8.0	15.3	29.6	13.1	6.1	5.5	3.5	-	5.1	1.0	-	-	7.1	-	-	-	-	-
P. acarne	0.50	3.7	V%	6.1	6.8	6.1	32.4	69.6	16.2	8.8	15.5	1.4	-	1.4	1.4	-	-	9.5	-	-	-	-	-
			F%	3.1	6.2	7.0	23.9	49.6	14.6	7.4	10.5	2.4	-	3.2	1.2	-	-	8.3	-	-	-	-	-
			GII%	0.4	4.5	56.8	2.8	2.1	5.7	2.7	0.1	5.3	0.6	1.8	-	-	-	-	-	-	-	-	17.2
P. bogaraveo	0.16	3.5	V%	2.9	15.6	48.0	16.4	29.8	16.7	4.4	1.1	2.2	0.4	0.7	-	-	-	-	-	-	-	-	12.7
			F%	1.7	10.1	52.4	9.6	15.9	11.2	3.5	0.6	3.7	0.5	1.3	-	-	-	-	-	-	-	-	15.0
			GII%	-	1.7	-	15.5	0.2	2.2	28.7	34.2	8.0	-	-	0.3	0.6	2.3	4.5	-	-	1.2	-	0.5
P. erytrinus	0.27	3.7	V%	-	3.5	-	35.3	5.5	7.8	25.1	47.8	3.5	-	-	2.4	0.4	2.4	7.8	-	-	0.4	-	0.4
			F%	-	2.6	-	25.4	2.8	5.0	26.9	41.0	5.8	-	-	1.3	0.5	2.3	6.2	-	-	0.8	-	0.5
			GII%	-	0.2	0.0	5.5	0.0	0.9	2.6	45.8	7.1	-	33.0	-	-	-	0.3	-	-	-	3.1	1.5
P. pagrus	0.19	3.9	V%	-	1.1	1.1	24.1	3.4	5.7	9.2	73.6	4.6	-	13.8	-	-	-	2.3	-	-	-	2.3	1.1
			F%	-	0.7	0.6	14.8	1.7	3.3	5.9	59.7	5.8	-	23.4	-	-	-	1.3	-	-	-	2.7	1.3
			GII%	-	2.6	-	7.7	51.3	-	69.2	2.6	-	-	-	-	5.1	-	5.1	-	5.1	-	-	12.8

Table A.2.4 (Continued)

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
P. blennoides	0.10	3.6	V%	0.0	3.8	0.0	0.1	2.2	-	62.7	21.5	0.4	0.3	-	-	5.5	0.1	0.0	-	1.2	-	-	2.2
			F%	1.1	13.8	0.4	3.6	32.4	-	68.0	53.8	1.1	0.4	-	-	13.1	0.7	0.7	-	0.7	-	-	2.2
			GII%	0.5	8.8	0.2	1.9	17.3	-	65.4	37.6	0.7	0.3	-	-	9.3	0.4	0.4	-	1.0	-	-	2.2
Raja spp	0.21	3.9	V%	0.0	0.1	0.2	0.5	5.6	0.2	33.0	30.4	1.2	7.3	3.3	1.0	4.7	0.2	-	0.6	3.5	3.2	-	5.1
			F%	4.7	4.4	1.7	9.2	58.9	0.8	75.3	37.8	1.9	1.4	1.9	0.8	4.7	0.8	-	0.6	1.9	0.3	-	5.8
			GII%	2.4	2.3	0.9	4.8	32.2	0.5	54.1	34.1	1.6	4.3	2.6	0.9	4.7	0.5	-	0.6	2.7	1.7	-	5.5
S. colias	0.23	3.8	V%	0.4	17.4	32.4	0.1	5.8	0.2	0.1	0.0	0.0	0.6	38.3	-	-	-	-	-	-	4.7	-	-
			F%	7.3	82.7	72.5	3.3	45.8	1.9	3.3	0.7	1.0	0.9	22.5	-	-	-	-	-	-	6.6	-	-
			GII%	3.8	50.0	52.4	1.7	25.8	1.1	1.7	0.4	0.5	0.7	30.4	-	-	-	-	-	-	5.6	-	-
S. scombrus	0.05	4.1	V%	-	5.0	3.2	-	0.2	-	0.0	1.8	0.9	0.9	82.5	-	0.1	-	-	-	-	4.7	-	0.6
			F%	-	35.1	48.5	-	5.5	-	2.4	8.6	4.5	1.0	58.4	-	1.0	-	-	-	-	4.8	-	1.4
			GII%	-	20.1	25.8	-	2.8	-	1.2	5.2	2.7	1.0	70.5	-	0.6	-	-	-	-	4.7	-	1.0
S. elongata	0.45	4.3	V%	-	0.1	-	0.0	0.1	0.0	10.2	20.0	8.3	-	13.7	3.2	9.9	2.8	3.6	0.6	8.0	16.3	1.3	1.9
			F%	-	1.0	-	1.5	5.5	0.5	37.8	36.8	9.0	-	1.5	2.5	17.9	1.5	11.9	1.5	5.5	0.5	4.5	2.5
			GII%	-	0.5	-	0.8	2.8	0.3	24.0	28.4	8.6	-	7.6	2.9	13.9	2.1	7.8	1.1	6.8	8.4	2.9	2.2
S. notata	0.18	3.7	V%	-	-	-	0.5	1.5	0.0	47.0	39.3	4.8	-	-	-	4.6	1.6	0.3	0.2	-	-	-	-
			F%	-	-	-	3.5	19.0	0.4	48.9	53.2	0.9	-	-	-	2.6	1.3	2.2	1.3	-	-	-	-
			GII%	-	-	-	2.0	10.3	0.2	47.9	46.3	2.9	-	-	-	3.6	1.4	1.2	0.8	-	-	-	-
S. porcus	0.15	3.5	V%	-	2.5	-	-	0.1	-	15.9	81.5	-	-	-	-	-	-	-	-	-	-	-	-
			F%	-	2.9	-	-	5.7	-	40.0	80.0	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	-	2.7	-	-	2.9	-	28.0	80.7	-	-	-	-	-	-	-	-	-	-	-	-
S. canicula	0.42	4	V%	-	12.8	0.3	2.8	0.5	0.4	19.0	14.9	3.4	6.3	18.3	0.1	7.2	4.1	0.0	1.2	0.0	-	-	8.8
			F%	-	50.6	0.6	22.1	10.2	0.8	52.5	26.6	12.9	3.5	5.5	0.6	7.2	2.7	0.6	0.4	0.4	-	-	11.1
			GII%	-	31.7	0.4	12.5	5.4	0.6	35.7	20.8	8.1	4.9	11.9	0.4	7.2	3.4	0.3	0.8	0.2	-	-	9.9
S. cabrilla	0.27	3.8	V%	0.0	0.6	-	1.2	2.0	0.1	19.0	42.7	5.4	-	13.8	-	6.3	0.2	8.8	-	-	-	-	-
			F%	0.4	5.1	-	5.1	21.7	1.3	31.5	63.8	3.4	-	4.7	-	8.1	0.4	9.8	-	-	-	-	-
			GII%	0.2	2.8	-	3.1	11.9	0.7	25.2	53.3	4.4	-	9.3	-	7.2	0.3	9.3	-	-	-	-	-
S. hepatus	0.18	3.6	V%	0.0	0.7	-	1.3	3.4	0.0	52.7	36.4	-	-	-	0.2	-	-	5.3	-	-	-	-	-
			F%	0.7	2.9	-	5.4	33.0	0.4	38.8	55.1	-	-	-	0.7	-	-	4.3	-	-	-	-	-
			GII%	0.4	1.8	-	3.4	18.2	0.2	45.7	45.7	-	-	-	0.4	-	-	4.8	-	-	-	-	-

Table A.2.4 (Continued)

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
S. maena	0.25	3.5	V%	2.0	12.6	1.1	6.9	53.3	3.3	16.6	1.0	3.2	-	-	-	-	-	-	-	-	-	-	-
			F%	12.7	4.5	2.0	11.1	83.6	4.9	8.2	1.6	2.0	-	-	-	-	-	-	-	-	-	-	-
			GII%	7.4	8.5	1.6	9.0	68.5	4.1	12.4	1.3	2.6	-	-	-	-	-	-	-	-	-	-	-
S. smaris	0.05	3	V%	90.4	5.7	-	0.2	2.8	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	92.3	11.0	-	2.2	5.5	-	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	91.3	8.4	-	1.2	4.1	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
S. cantharus	0.21	3.6	V%	0.0	0.7	2.8	41.4	1.5	40.2	0.4	2.7	3.9	-	6.4	-	-	-	-	-	-	-	-	-
			F%	0.7	6.6	9.9	61.2	21.1	36.2	3.9	3.3	4.6	-	3.9	-	-	-	-	-	-	-	-	-
			GII%	0.3	3.6	6.3	51.3	11.3	38.2	2.2	3.0	4.2	-	5.2	-	-	-	-	-	-	-	-	-
T. draco	0.35	4	V%	-	7.7	3.0	0.8	1.2	0.0	7.2	16.9	6.1	-	38.1	-	8.1	-	0.2	-	-	-	-	10.7
			F%	-	6.9	1.0	3.4	11.3	1.0	25.1	58.6	3.9	-	10.3	-	5.9	-	2.0	-	-	-	-	10.3
			GII%	-	7.3	2.0	2.1	6.3	0.5	16.2	37.8	5.0	-	24.2	-	7.0	-	1.1	-	-	-	-	10.5
T. mediterraneus	0.05	4.1	V%	0.4	10.2	0.1	0.3	4.4	0.0	1.9	0.6	0.5	-	79.5	-	-	0.4	1.2	-	-	0.5	-	-
			F%	13.4	72.6	1.8	4.9	49.4	0.6	12.2	7.3	0.6	-	30.5	-	-	0.6	5.5	-	-	0.6	-	-
			GII%	6.9	41.4	1.0	2.6	26.9	0.3	7.1	4.0	0.5	-	55.0	-	-	0.5	3.4	-	-	0.6	-	-
T. picturatus	0.17	3.5	V%	0.3	70.4	9.8	-	0.1	-	1.6	-	-	-	-	-	-	-	-	-	-	-	-	17.9
			F%	2.9	68.6	22.9	-	5.7	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-	11.4
			GII%	1.6	69.5	16.3	-	2.9	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	14.6
T. trachurus	0.10	3.4	V%	4.2	68.1	0.4	-	0.4	-	-	0.4	0.4	-	-	0.0	0.7	-	0.3	-	-	-	-	25.1
			F%	15.0	71.4	2.3	-	11.3	-	-	2.3	2.3	-	-	0.8	0.8	-	3.0	-	-	-	-	12.8
			GII%	9.6	69.7	1.3	-	5.9	-	-	1.3	1.3	-	-	0.4	0.7	-	1.7	-	-	-	-	18.9
T. scabrus	0.08	3.6	V%	0.1	2.3	0.9	0.8	3.4	-	9.8	78.4	-	-	-	-	-	-	-	-	-	-	-	4.2
			F%	10.4	2.1	2.1	8.3	43.8	-	18.8	91.7	-	-	-	-	-	-	-	-	-	-	-	4.2
			GII%	5.3	2.2	1.5	4.6	23.6	-	14.3	85.0	-	-	-	-	-	-	-	-	-	-	-	4.2
T. lyra	0.25	3.6	V%	0.0	4.0	-	5.2	18.9	15.0	6.9	44.8	1.1	-	-	0.1	1.0	-	0.6	-	-	-	-	2.4
			F%	1.4	9.4	-	16.1	61.2	38.1	10.8	57.3	2.1	-	-	0.3	1.0	-	3.1	-	-	-	-	0.3
			GII%	0.7	6.7	-	10.6	40.1	26.6	8.8	51.1	1.6	-	-	0.2	1.0	-	1.9	-	-	-	-	1.4

Table A.2.4 (Continued)

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
T. minutus	0.10	3.6	V%	-	3.2	-	0.1	1.9	-	66.1	18.6	2.8	-	0.6	0.0	3.8	-	2.2	-	0.6	-	-	0.2
			F%	-	13.3	-	1.3	18.1	-	78.3	39.8	2.9	-	0.3	0.3	6.1	-	3.6	-	1.0	-	-	0.3
			GII%	-	8.2	-	0.7	10.0	-	72.2	29.2	2.9	-	0.5	0.2	5.0	-	2.9	-	0.8	-	-	0.3
U. scaber	0.39	4.4	V%	-	-	-	-	0.0	-	8.6	0.4	3.9	0.2	27.2	4.3	27.2	-	5.1	2.0	7.0	-	5.0	9.0
			F%	-	-	-	-	1.7	-	31.9	2.6	7.8	0.9	17.2	6.9	27.6	-	18.1	1.7	1.7	-	0.9	3.4
			GII%	-	-	-	-	0.9	-	20.3	1.5	5.8	0.5	22.2	5.6	27.4	-	11.6	1.8	4.4	-	2.9	6.2
Z. faber	0.26	4.6	V%	-	0.9	-	-	0.1	-	0.7	0.1	0.1	0.2	24.0	2.2	33.4	-	1.5	0.1	9.3	-	6.7	20.5
			F%	-	8.2	-	-	6.2	-	0.4	0.4	0.8	0.8	8.6	0.4	55.1	-	9.5	0.4	7.0	-	2.9	21.4
			GII%	-	4.6	-	-	3.1	-	0.6	0.3	0.5	0.5	16.3	1.3	44.3	-	5.5	0.3	8.2	-	4.8	21.0

Chapter 3: Ontogenic shifts and feeding strategies of 7 key species of Gadiformes in the western Mediterranean Sea

Ontogenetic shifts and feeding strategies of 7 key species of Gadiformes in the western Mediterranean Sea[2]

Abstract

The trophic ecology of 7 key species of Gadiformes, the silvery pout (*Gadiculus argenteus*), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*), European hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), Mediterranean ling (*Molva macrophthalma*), greater forkbeard (*Phycis blennoides*), and poor cod (*Trisopterus minutus*), in the western Mediterranean Sea was explored. A total of 3192 fish stomachs were examined during 2011–2017 to investigate ontogenetic shifts in diet, trophic interactions (both interspecific and intraspecific), and feeding strategies. The results from applying multivariate statistical techniques indicate that all investigated species, except the Mediterranean bigeye rockling and poor cod, underwent ontogenetic dietary shifts, increasing their trophic level with size. The studied species hold different trophic positions, from opportunistic (e.g., the Mediterranean bigeye rockling, with a trophic level of 3.51) to highly specialized piscivore behavior (e.g., the Mediterranean ling, with a trophic level of 4.47). These insights reveal 4 different feeding strategies among the co-occurring species.

3.1 Introduction

One of the most important aspects of analysis of trophic interactions is the study of trophic levels, understood as a hierarchical way of classifying organisms according to their feeding relationships within an ecosystem, contributing to knowledge about the ecological role of a species (Cochran et al., 2019). This knowledge is critical in investigating predator–prey interactions and is necessary for an ecosystem-based approach to fisheries management (Christensen, 1996; García et al., 2003). Additionally, feeding patterns offer useful insights about the long-term stability of marine ecosystems (Trites, 2003; McDonald- Madden et al., 2016).

In general, fish change their diets with size to optimize their energetic return (Scharf et al., 2000; Juanes et al., 2002). In addition, ontogenetic shifts can be considered a mechanism to avoid, or at least minimize, intraspecific competition by allowing exploitation of different food resources at each developmental stage (Marrin, 1983; Castro and Hernández-García, 1995). More broadly, fish species have a wide range of strategies, on both intraspecific and

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interspecific levels, that result in and maintain resource partitioning (Madurell et al., 2008; Fanelli et al., 2009, 2013). Such strategies include not only food selection but also habitat selection and temporal segregation (Schoener, 1974). Hence, resource partitioning occurs when fish species are segregated into at least 1 of 3 niche dimensions. As a result, niche overlap is avoided and resource competition is minimized among fish species. This hypothesis is known as niche complementarity (Ebeling and Hixon, 1991) and assumes that a particular species, which overlaps with others in a given niche dimension, would separate along another dimension, maintaining resource partitioning. Describing and comparing these relationships, by using indices that reflect niche overlap or niche breadth, can help to explain feeding behaviors that range from generalist to specialist in nature (Silva et al., 2014).

This study aimed to investigate niche complementarity and co-occurrence of 7 fish species of Gadiformes in the western Mediterranean Sea off the coast of Spain. In particular, we analyzed ontogenetic shifts in diet, trophic interactions (both interspecific and intraspecific), feeding strategies, and the degree of dietary overlap among the studied species, to ascertain the ecological patterns of dietary interrelationships within the fish assemblage.

The selected gadiform species can inhabit depths greater than 1000 m (Fanelli et al., 2013) and play an important role in the middle of the food web (i.e., in both bottom-up and top-down controls) within marine ecosystems (Libralato et al., 2006), indicating that they feed on different trophic levels (Miller et al., 2010). They are prey for many other fish species (e.g., Preciado et al., 2008; Rodríguez-Cabello et al., 2014), and they occupy different substrates, ranging from sandy to rocky (Cohen et al., 1990).

In the Mediterranean Sea, the biology and behavior of many species of Gadiformes are well-documented (Morte et al., 2001, 2002), and they are important commercially and ecologically. For example, the European hake (Merluccius merluccius) is one of the most common representatives of this group, considering the amount of landings, and is currently experiencing overexploitation, with fishing mortality rates around 1.8–8.1 times higher than the assumed reference level of fishing mortality that would provide maximum sustainable yield (Colloca et al., 2013).

In the western Mediterranean Sea, studies of fish feeding habits usually focus on a few species and omit trophic interactions, information about which is essential for an effective implementation of an ecosystem approach to fisheries management (García et al., 2003). For instance, off the coast of Spain, Macpherson (1978a) studied age- related seasonal feeding habits of blue whiting (*Micromesistius poutassou*) in the Gulf of Valencia and of silvery pout (*Gadiculus argenteus*) in the Catalan Sea. He also investigated the diet of the Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) and Mediterranean ling (*Molva macrophthalma*)

(Macpherson, 1978b, 1981). Bozzano et al. (1997) reported seasonal feeding habits of European hake in the Gulf of Lion off the coast of France, and Morte et al. (2001, 2002) analyzed the diet of poor cod (*Trisopterus minutus*) and greater forkbeard (*Phycis blennoides*) in the Gulf of Valencia. Unfortunately, none of these studies have investigated further interactions between species and fish assemblage.

Studies that address a broader geographic area and include ontogenetic shifts in diets of gadiform species, therefore, are scarce for the Mediterranean Sea off the coast of Spain, and it is necessary to fill this gap in knowledge as well as update current information. Additionally, the fish assemblage in the western Mediterranean Sea is currently facing problems of not only overfishing and biodiversity loss but also environmental pressures, such as the massive urbanization of coastlines, with increases in water pollution and decreases in sediments from principal rivers (e.g., Coll et al., 2010).

Catch quality is decreasing, resulting in landings with a higher proportion of low-value species and a higher ratio of small to large fish. Furthermore, in the case of some of the most damaging and commonly used gear, namely bottom trawls, discard rates of low-value species are high (Bellido et al.[3]; Paradinas et al., 2016). Under this scenario of overfishing and environmental pressures, a declining trend in the landed biomass of the commercial species of Gadiformes investigated in our study has been observed in the area (MAGRAMA[4]; MAPAMA[5]; MAPA[6]). Consequently, more local and updated data on intraspecific and interspecific interactions are needed to develop ecosystem models for an ecosystem-based approach to fisheries management (Christensen and Walters, 2004; Gascuel, 2005).

3.2 Material and methods

Study area and sampling procedure

We carried out our study in the Mediterranean Sea off the coast of Spain from Cape Palos to Cape Creus (Fig. 3.2.1). According to the General Fisheries Commission for the Mediterranean, this area is also known as geographical subarea 06 (GSA-06), and it extends along 808 km of coastline, with a total area of 30,119 km2 and depths of 40–800 m. The study area is

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[3] Bellido, J. M., A. Carbonell, M. T. García, and M. González. 2014. The obligation to land all catches—consequences for the Mediterranean: in-depth analysis, 46 p. Policy Dep. B: Struct. Cohes. Policies, Dir. Gen. Intern. Policies, Eur. Parliam., Brussels, Belgium. [Available from website.]

[4] MAGRAMA (Ministerio de Agricultura, Alimentación y Medio Ambiente). 2013–2015. Estadísticas pesqueras: Noviembre [2013–2015]. Minist. Agric. Aliment. Medio Ambiente, Madrid, Spain. [Available from website.]

[5] MAPAMA (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente). 2016–2017. Estadísticas pesqueras: Noviembre [2016–2017]. Minist. Agric. Pesca Aliment. Medio Ambiente, Madrid, Spain. [Available from website.]

[6] MAPA (Ministerio de Agricultura, Pesca y Alimentación). 2018– 2020. Estadísticas pesqueras: Noviembre [2018–2020]. Minist. Agric. Pesca Aliment., Madrid, Spain. [Available from website.]

characterized by high biodiversity (García-Rodríguez et al., 2011) and oligotrophic conditions. Nevertheless, within the study area, certain zones (e.g., Ebro Delta) are exceptions because of their moderate levels of primary production (Estrada, 1996). The main fishery resources in this area are demersal and benthic organisms, such as fish species (Osteichthyes and Chondrichthyes) and invertebrates (mollusks and crustaceans). Some of the fish species, such as the bogue (*Boops boops*) or blotched picarel (*Spicara maena*), are heavily discarded, or they are used as bait, although they are an increasing component of landings, mainly in the bottom-trawl fishery (Bellido et al.1). Most of these species, including the European hake and blue whiting, both of the order Gadiformes, are fully exploited or overexploited (Coll et al., 2008; Cardinale, 2012, 2013; Coll et al., 2014; FAO, 2018).

Stomach samples were collected from fish caught during bottom-trawl surveys conducted as part of the Mediterranean International Trawl Survey (MEDITS) program in GSA-06 in 2011–2017 (Bertrand et al., 2002). The surveys of this program take place yearly from May through June for the purpose of evaluating the demersal resources throughout the study area. The standard MEDITS sampling gear is a bottom trawl called the GOC 73, which has a net with a mesh size of 40 mm and a codend with a mesh size of 20 mm. This gear is specifically designed for experimental fishing. A total of 604 trawl tows were carried out during daylight, from 0800 to 1800, at depths of 40–730 m.

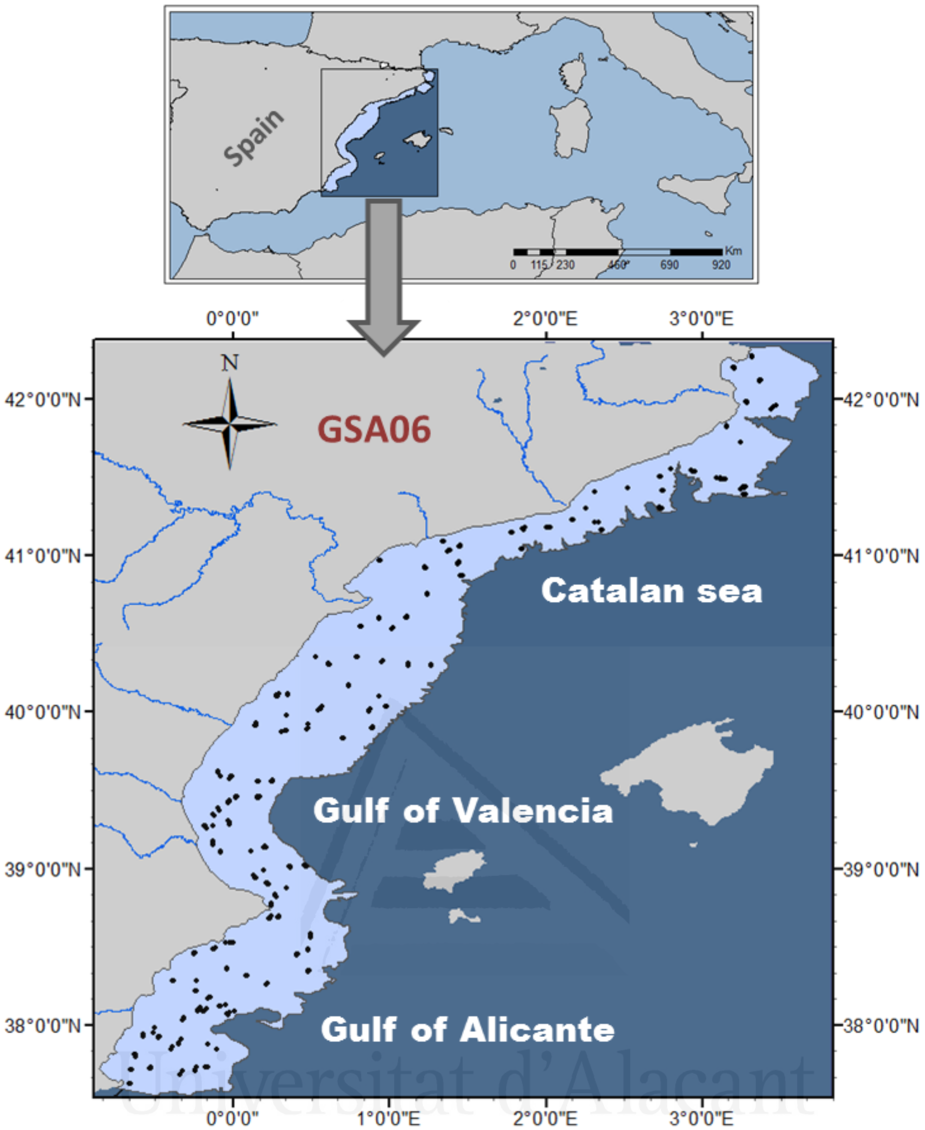

Fig. 3.2.1 Map showing the locations where 7 species of Gadiformes were sampled between 2011 and 2017 in the Mediterranean Sea off the coast of Spain from Cape Palos to Cape Creus, in the geographical subarea 06 (GSA-06) defined by the General Fisheries Commission for the Mediterranean. Dots indicate the positions of the trawl tows conducted during surveys. The light gray shaded area indicates the area between isobaths of 40 and 800 m where specimens were caught.

For this investigation, we selected the species of the order Gadiformes that were most abundant in the study area: the silvery pout, Mediterranean bigeye rockling, Mediterranean ling, European hake, blue whiting, greater forkbeard, and poor cod. During the survey cruises in the study period, the contents of 3192 stomachs were analyzed on board vessels (for details for these 7 species, see Table 3.1). After each trawl tow, 10 individuals of each of the studied species were randomly sampled from the haul. For all specimens examined, total length (TL) in millimeters, sex, and maturity stage were recorded according to MEDITS guidelines (Bertrand et al., 2002). Later, diet was assessed quantitatively by measuring the volume of stomach contents with a trophometer, a calibrated device that consists of several semicylinders of different sizes (Olaso, 1990). The use of this instrument is helpful on board oceanographic vessels because it allows a large number of stomachs to be examined in a relatively short period.

Once a stomach was opened, its contents were analyzed under a binocular microscope (Leica MZ6[7], Leica Microsystems, Wetzlar, Germany). Prey found in stomachs (prey items) were identified to the lowest possible taxon by using published guides (Zariquiey, 1968; Lombarte et al., 2006) and our own reference collection. The degrees of digestion of all prey items identified were also noted, as fresh, partially digested, or fully digested. The stomachs that contained any items presumably consumed in the net during fishing operations (i.e., stomachs from individuals of anglerfish species) were excluded from the analyses. The presence of skeletal remains and other hard body parts was also recorded. Stomach samples from specimens that had regurgitated the contents of their stomachs were replaced with samples from individuals of a similar size class (García-Rodríguez et al., 2020). Following Robb (1992), the color and size of the gall bladder of European hake were used to determine if a specimen had an empty stomach or had regurgitated during the fishing operation.

Table 3.1 Summary information related to the 7 most abundant species of Gadiformes sampled in the western Mediterranean Sea between 2011 and 2017. For each species, the scientific and common names, depth range (in meters), number of stomachs for which contents were examined, and size range (total lengths in millimeters) are provided.

Scientific Name	Common name	Depth range	No. of stomachs	Size range
Gadiculus argenteus	silvery pout	109-647	263	60-133
Gaidropsarus biscayensis	bigeye rockling	59-634	116	40-180
Molva macrophthalma	Spanish ling	86-634	164	83-740
Merluccius merluccius	European hake	34-722	1254	87-549
Micromesistius poutassou	blue whiting	76-722	786	89-377
Phycis blennoides	greater forkbeard	53-728	286	85-393
Trisopterus minutus	poor cod	36-352	323	78-272

Dietary indices

Three conventional dietary indices were calculated to provide quantitative information on diet compositions of the gadiform species investigated. A raw data set including prey species for each predator species is included in Supplementary Table A.3.1. The first index used was frequency of occurrence (%FO), defined as the number of stomachs containing a prey item

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[7] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA

compared with the total number of stomachs examined. The second index was the number index (%N), defined as the number of individuals of a prey item compared with the total number of individual prey ingested. The third index calculated was the volume index (%V), which represents the volume of a prey item compared with the total volume of ingested prey (Hyslop, 1980). Finally, the geometric index of importance (%GII), which incorporates both %FO and %V, was used to avoid redundancy in the combination of mathematically dependent measures instead of other traditional indices (Tirasin and Jørgensen, 1999). It was computed as follows (Assis, 1996):

$$GII\%_j = \left(\sum_{i=1}^{n} V_i\right)_j / n, \qquad (1)$$

where Vi = the value of the ith relative measure of prey quantity for the prey group j (in this case, Vi=%FO+%V), and
n = the number of the relative measures of prey quantity used in the analysis (in this case, n=2, %FO and %V).
Therefore, in this study, the %GII was calculated as (%V+%FO)/2. Values for all indices are given as percentages.

Ontogenetic shifts in diet

Before identifying when ontogenetic shifts occur and establishing trophic groups based on different size classes, 10 major prey groups were identified according to taxonomic criteria and, in the case of fish species, habitat type criteria: small plankton; large plankton; Polychaeta; Cephalopoda; crab, lobster, and mantis shrimp species; shrimp species; Peracarida; demersal fish species; pelagic fish species; and benthopelagic fish species.

To investigate variation in a predator's diet according to size, trends in the volume index values of the most representative prey groups, mentioned in the previous paragraph, were plotted against fish length of predators to define the different categories that combine species and size class. We first compared both quantitative and qualitative methods. Results indicate similar outcomes for some species, such as the European hake or blue whiting, and outcomes were less realistic for those species with a small number of samples. Therefore, we decided to use a qualitative method based on a graphic technique that allows easy identification of the size at which the trend in the trophic strategy changed for each species studied. In the quantitative method, the number of size classes was estimated following the Sturges procedure (Scherrer, 1984), and in the qualitative method, the lengths were represented continuously at every millimeter along the x-axis of graphs.

This graphic technique allows qualitative identification of the size at which a trophic shift occurred. We used this size for each gadiform species studied to divide size classes into large and small categories (sizes varied depending on the species; Table 3.2). In addition, size at first maturity was plotted with the aim of linking it with the size at which a trophic shift occurred. Sizes at first maturity for all the studied species were based on previously published data from studies in nearby areas (Biagi et al., 1992; Benghali et al., 2014; European Parliament and Council, 2019; Ismen et al., 2019).

Trophic indices to describe feeding strategies

To describe the degree of dietary diversity of a given spe- cies, we used niche breadth in accordance with Levins's standardized index (Levins, 1968). This index ranges from 0 to 1, with values close to 0 indicating a specialized diet and those close to 1 indicating more generalized feeding habits. This index was computed as follows:

$$B_i = 1/n\text{-}1(1/ \Sigma_j\, p^2_{ij} - 1), \qquad (2)$$

where B_i = Levins's standardized index;

p_{ij} = the proportion of prey *j* in the diet of predator *i*; and

N = the total number of prey groups.

The trophic niche overlap among the different studied species was estimated by using the simplified Morisita index (Morisita, 1959), which compares pairs of species with values ranging between 0.00 (no prey overlap) to 1.00 (full prey overlap) as follows:

$$C_{ik} = (2\ \Sigma\ p_{ij}p_{ik}) \,/\, (\Sigma\ p^2_{ij} + \Sigma\ p^2_{ik}), \qquad (3)$$

where C_{ik} = the simplified Morisita index for predators i and k, and

p_{ij} and p_{kj} = the proportions of predators i and k with prey j in their stomachs.

The trophic level (T) was calculated by using the fol- lowing formula developed by Christensen and Pauly (1992):

$$T = 1 + (\Sigma\ DC_{ij})\ (NT_j), \qquad (4)$$

where DC_{ij} = the proportion of prey j in the diet of the predator i, and

NT_j = the trophic level of prey j.

Trophic levels of prey were determined empirically by using local information or, when this information was not available, by using the modeled area (Cortés, 1999; Ebert and Bizzarro, 2007; Fanelli et al., 2011; Jacobsen and Bennett, 2013; Corrales et al., 2015; for details on the species of prey for which these cited references were sources of local information on trophic levels, see Supplementary Table A.3.2). In this study, the trophic level of each of the defined categories based on species and size class was first calculated by weighting its average biomass obtained during the surveys of the MEDITS program conducted in 2011–2017.

Co-occurrence measures

To analyze patterns of species associations related to food resource partitioning, we studied interspecific and intraspecific co-occurrence. Therefore, for the entire study period, we accounted for the abundance of all species and size classes estimated during surveys. The abundance of Mediterranean bigeye rockling was underestimated because of the low selectivity of the gear used to catch this small species. Therefore, this species was not included in the co-occurrence analysis. The Jaccard index (S_{ij}) was used to measure co-occurrence, as an expression of association between species (Jaccard, 1901):

$$S_{ij} = a / (a + b + c), \qquad (5)$$

where a = the number of occasions in which both species or size classes are present;

b = the number of occasions in which only one of the species is present; and

c = the number of occasions in which only the other species is present.

This index was calculated as the percentage of occasions that both species or size classes appeared in the same haul. In this study, the only hauls that were considered were those in which at least one of the species or size classes of each pair was present.

Statistical analyses

All data were standardized by using square-root transfor- mation, and a Bray–Curtis similarity matrix was calculated. One-way analyses of similarity were performed to identify significant differences ($P<0.05$) in trophic strategies between pairs of size classes (i.e., intraspecific competition). We used the software PRIMER 6 (PRIMER-e, Quest Research Ltd., Aukland, New Zealand) (Clarke and Gorley, 2006) to estimate global R as a scaled measure of the separation between groups of samples, with values ranging from 0 (no differences) to 1 (completely different) (Clarke, 1993).

Similarity percentage analysis was applied to determine which prey groups contributed most to the dissimilarity in diet composition between such pairs. According to these results, new species-and-size categories were considered for further analyses. Finally, clustering methods and multidimensional scaling were used to analyze prey affinities and to discern feeding strategies that possibly were different between the studied species among size classes. All calculations were done by using PRIMER 6.

3.3 Results

Diet composition and ontogenetic variation

Overall, for all studied species as a group, the most common prey groups in terms of %V were large plankton; crab, lobster, and mantis shrimp species; shrimp species; and benthopelagic fish species. Large plankton, represented mainly by euphausiids, was the most common prey (mostly for silvery pout and blue whiting). In the case of decapod species, the red snapping shrimp (*Alpheus glaber*), green shrimp (*Chlorotocus crassicornis*), and angular crab (*Goneplax rhomboides*), all members of Pleocyemata, were the most abundant prey (mostly for Mediterranean bigeye rockling, poor cod, and greater forkbeard). Finally, benthopelagic fish species were primarily represented by blue whiting and myctophids as prey for studied species (mostly for Mediterranean ling and blue whiting) (Table 3.3). The raw data set provided in Supplementary Table A.3.1 documents in detail the different prey items found in stomachs and identified to the lowest taxonomic level in this study.

Regarding the ontogenetic variation in diet, for each of the studied species, the graph indicates trends in trophic strategies for 2 prey groups that were the opposite of the other, and this observation of different trends enabled us to establish a cutoff between the 2 size classes: the size at which a trophic shift occurred (Fig. 3.3.1). Only in the case of the silvery pout did the selected cutoff between size classes seem to be related to size at first maturity. For the Mediterranean bigeye rockling, no data are available on size at first maturity in the study area.

Table 3.2 Dietary indices for each prey group identified in the stomach contents of specimens of 7 species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. The number of trawl tows, sample size, range of total lengths (TLs), niche breadth, depth range, trophic level, and number of prey items also are provided for each of the 12 categories that combine species and size class (small [S] and large [L]). The dietary indices used in analyses include frequency of occurrence (%FO), the number of stomachs that contained a prey group compared with the total number of stomachs examined; the number index (%N), the number of individuals of a prey group compared with the total number of ingested prey; the volume index (%V), the volume of a prey group compared with the total volume of all prey ingested by a predator category; and the geo- metric index of importance (%GII), which incorporates both %FO and %V. A dash indicates that no consumption of that prey group was recorded for that species. The species studied include the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI).

Information type or prey group	Index	GAD$_S$	GAD$_L$	GAI	MOL$_S$	MOL$_L$	MER$_S$	MER$_L$	MIC$_S$	MIC$_L$	PHY$_S$	PHY$_L$	TRI
No. of trawl tows		16	29	45	26	20	90	154	25	36	13	56	45
Sample size		44	219	116	107	57	405	849	172	614	75	211	323
Length range (mm)		60-92	93-133	40-180	83-165	166-740	87-149	150-549	89-169	170-377	85-149	150-393	78-272
Niche breadth		0.51	0.39	0.34	0.14	0.30	0.60	0.45	0.24	0.28	0.64	0.17	0.14
Depth range (m)		109-647	131-647	59-634	122-327	86-634	34-342	34-722	76-611	137-722	53-728	176-728	36-352
Trophic level		3.47	3.57	3.93	4.36	4.49	3.95	4.24	3.98	4.21	3.99	3.99	3.94
No. of prey items		9	33	27	8	13	47	65	28	38	25	58	43
Small Plankton	**F%**	18.8	11.9	17.7	–	–	–	–	–	–	1.5	1.0	–
	V%	14.3	5.4	3.0	–	–	–	–	–	–	0.0	0.0	–
	N%	79.9	60.7	30.2	–	–	–	–	–	–	0.4	0.2	–
	GII%	16.5	8.7	10.3	–	–	–	–	–	–	0.7	0.5	–

Table 3.2 (Continued)

Information type or prey group	**Index**	**GAD_S**	**GAD_L**	**GAI**	**MOL_S**	**MOL_L**	**MER_S**	**MER_L**	**MIC_S**	**MIC_L**	**PHY_S**	**PHY_L**	**TRI**
Large Plankton	**F%**	46.9	51.5	7.8	2.6	4.6	40.6	19.4	87.28	46.8	13.0	13.6	9.9
	V%	48.8	47.2	1.6	0.1	1.5	29.0	8.1	59.9	26.5	11.6	4.4	2.7
	N%	10.8	29.6	4.0	2.2	5.5	83.1	69.0	98.1	58.3	13.2	8.4	11.9
	GII%	47.8	49.4	4.7	1.3	3.0	34.8	13.8	73.5	36.7	12.3	9.0	6.3
Polychaeta	**F%**	–	0.5	1.0	–	–	–	–	–	0.2	8.7	1.9	1.2
	V%	–	0.3	1.8	–	–	–	–	–	2.8	2.6	0.1	0.4
	N%	–	0.0	0.4	–	–	–	–	–	0.0	2.1	0.6	0.5
	GII%	–	0.4	1.4	–	–	–	–	–	1.5	5.7	1.0	0.8
Cephalopoda	**F%**	–	–	–	–	–	2.0	3.3	–	2.7	–	1.9	2.8
	V%	–	–	–	–	–	2.3	3.7	–	1.2	–	1.1	2.8
	N%	–	–	–	–	–	0.3	0.9	–	0.5	–	0.4	1.0
	GII%	–	–	–	–	–	2.1	3.5	–	2.0	–	1.5	2.8
Crab, lobster, and Mantis shrimp species	**F%**	–	0.5	38.2	–	–	1.7	1.6	–	0.5	52.2	54.4	33.4
	V%	–	0.2	51.5	–	–	1.5	1.1	–	0.1	35.4	23.3	19.2
	N%	–	0.0	17.4	–	–	0.3	0.5	–	0.1	22.5	22.1	21.9
	GII%	–	0.3	44.9	–	–	1.6	1.4	–	0.3	43.8	38.9	26.3
Shrimp species	**F%**	3.1	9.4	18.6	–	6.8	25.5	25.0	1.7	27.5	18.8	82.5	65.9
	V%	2.1	16.0	12.8	–	4.7	20.3	16.8	2.4	18.9	18.2	63.8	65.5
	N%	0.3	1.1	8.5	–	13.7	6.5	8.6	0.1	10.4	7.5	51.0	51.4
	GII%	2.6	12.7	15.7	–	5.7	22.9	20.9	2.0	23.2	18.5	73.2	65.7

Table 3.2 (Continued)

Information type or prey group	**Index**	**GAD$_S$**	**GAD$_L$**	**GAI**	**MOL$_S$**	**MOL$_L$**	**MER$_S$**	**MER$_L$**	**MIC$_S$**	**MIC$_L$**	**PHY$_S$**	**PHY$_L$**	**TRI**
Peracarida	**F%**	21.9	18.8	37.3	3.9	4.5	12.4	3.1	1.7	1.8	55.1	22.8	14.2
	V%	24.6	12.0	17.5	0.1	0.4	3.4	1.1	0.3	1.2	32.1	1.4	3.8
	N%	5.0	4.0	36.4	3.3	17.8	4.0	1.2	0.2	0.5	54.3	12.4	9.1
	GII%	23.2	15.4	27.4	2.0	2.5	7.9	2.1	1.0	1.5	43.6	12.1	9.0
Demersal fish species	**F%**	–	–	7.8	16.9	31.8	15.8	6.9	3.4	0.2	–	17.5	6.2
	V%	–	–	11.9	17.3	38.0	16.0	4.8	0.6	2.1	–	4.7	3.9
	N%	–	–	3.1	27.2	27.4	2.7	2.0	0.2	0.0	–	4.3	3.2
	GII%	–	–	9.9	17.1	34.9	15.9	5.8	2.0	1.2	–	11.1	5.1
Pelagic fish species	**F%**	–	–	–	–	–	10.4	42.1	1.7	0.7	–	–	0.3
	V%	–	–	–	–	–	14.5	44.4	7.1	2.2	–	–	0.7
	N%	–	–	–	–	–	1.6	12.2	0.2	0.2	–	–	0.2
	GII%	–	–	–	–	–	12.5	43.2	4.4	1.5	–	–	0.5
Benthopelagic fish species	**F%**	9.4	13.9	–	41.6	43.2	9.7	18.9	15.4	64.8	–	3.9	1.2
	V%	10.2	18.8	–	82.5	55.4	13.0	19.9	29.8	45.0	–	1.3	1.0
	N%	4.0	4.4	–	67.4	35.6	1.5	5.6	1.2	29.9	–	0.8	0.7
	GII%	9.8	16.3	–	62.0	49.3	11.4	19.4	22.6	54.9	–	2.6	1.1

Table 3.3 Volume index (%V) values for prey groups identified in the stomach contents of specimens of 7 key species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. The %V value for a prey group represents the volume of that prey item compared with the total volume of all prey ingested by specimens of that species. The 7 species are the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rock- ling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI). A dash indicates that no consumption of that prey group was recorded for that species. An asterisk indicates the prey group with the highest %V value for each species. Information on niche breadth and the number of prey items is also reported.

	GAD	**GAI**	**MOL**	**MER**	**MIC**	**PHY**	**TRI**
Niche breadth	0.34	0.34	0.17	0.38	0.26	0.16	0.14
No. of prey items	33	27	15	74	49	60	43
Prey group							
Small Plankton	6.2	3.0	–	0.0	–	0.0	–
Large Plankton	51.6*	1.6	0.9	12.0	40.3*	4.9	2.7
Polychaeta	0.3	1.8	–	–	1.9	0.4	0.4
Cephalopoda	–	–	–	3.7	0.8	1.0	2.8
Crab, lobster, and mantis shrimp species	0.1	51.5*	–	0.8	0.1	24.4	19.2
Shrimp species	12.4	12.8	2.5	14.4	13.2	60.6*	65.5*
Peracarida	11.1	17.5	0.3	1.0	0.9	2.8	3.8
Demersal fish species	–	11.9	22.6	6.6	1.7	4.3	3.9
Pelagic fish species	–	–	–	40.8*	3.6	–	0.7
Benthopelagic fish species	18.3	–	73.8*	20.6	37.4	1.6	1.0

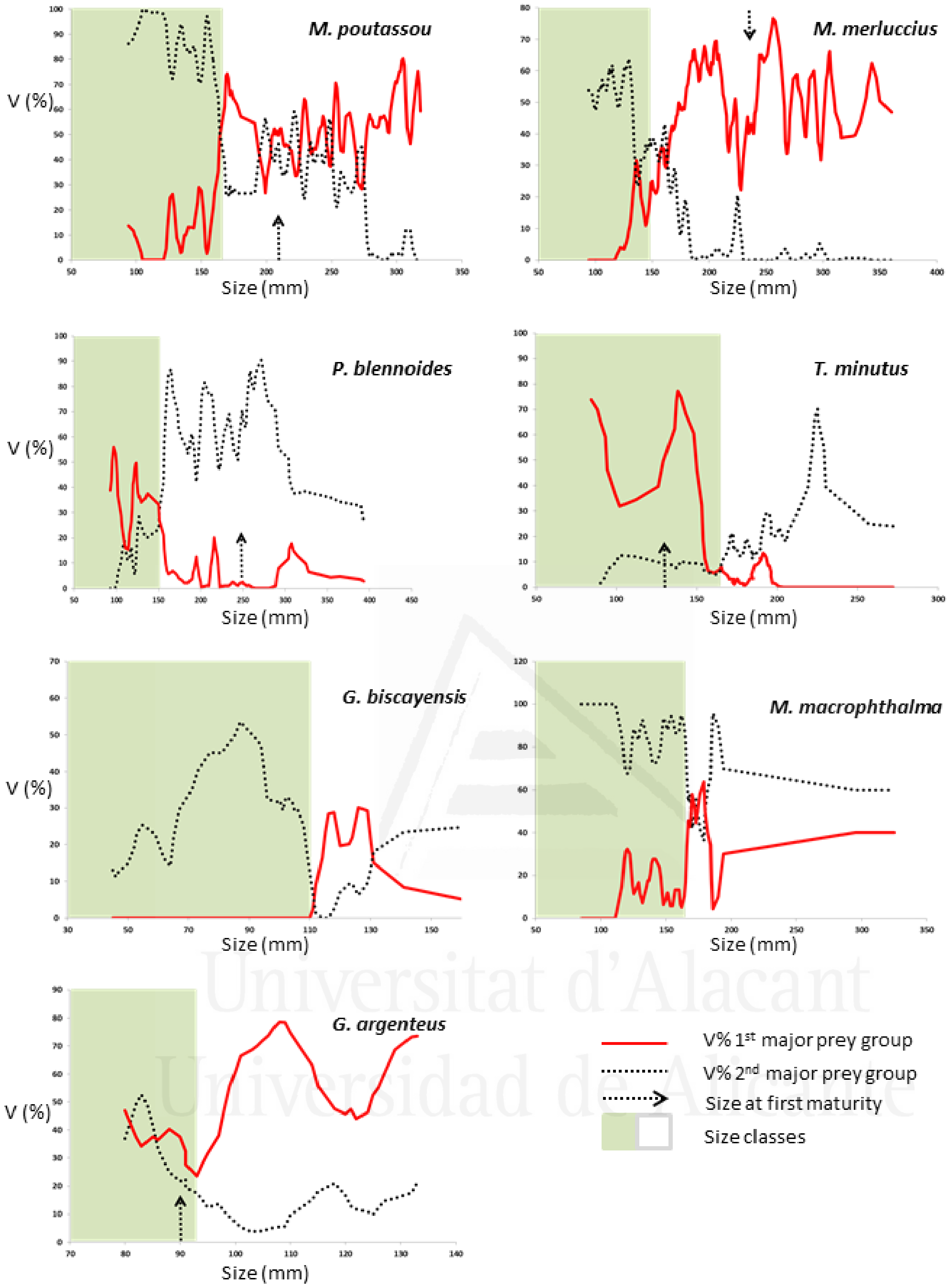

Fig. 3.3.1 Trends in volume index (%V) values for the first and second major prey groups in relation to sizes of speci- mens of 7 species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. These graphs were used in a qualitative method to identify the size at which the trophic strategy changed for each species studied. This size is considered the cutoff between small (green shaded area) and large size classes for each species. Sizes are given as total lengths. Arrows indicate the size at first maturity for each species, except for the Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) and Mediterrenean ling (*Molva macrophtalma*) because this information was not available for these species. The other species studied include the blue whiting (*Micromesistius poutassou*), European hake (*Merluccius merluccius*), greater forkbeard (*Phycis blennoides*), poor cod (*Trisopterus minutus*), and silvery pout (*Gadiculus argenteus*).

The results obtained for species and size classes indicate that silvery pout fed mainly on large plankton (%GII=51.2%, %V=51.6%, %FO=50.9%), with *Euphausia krohnii* as the most predominant prey species. The diet of Mediterranean bigeye rockling was based primarily on crab, lobster, and mantis shrimp species (%GII=44.9%, %V=51.5%, %FO=38.2%) and species of Peracarida (%GII=27.4%, %V=17.5%, %FO=37.3%), represented mainly by *Calocaris macandreae* and *Lophogaster typicus*, respectively. Benthopelagic fish species (%GII=57.0%, %V=73.8%, %FO=40.2%) composed the major prey group for Mediterranean ling, for which the most commonly consumed prey was another species of Gadiformes, the silvery pout. Pelagic fish spe- cies (%GII=29.0%, %V=40.8%, %FO=17.2%) and large plankton (%GII=15.1%, %V=12.0%, %FO=18.3%) were the main prey groups for European hake, with European anchovy (*Engraulis encrasicolus*) and euphausiids being the most important of the consumed prey, respectively. Blue whiting fed mainly on large plankton (%GII=39.3%, %V=40.3%, %FO=38.3%) and benthopelagic fish species (%GII=36.5%, %V=37.4%, %FO=35.6%), of which euphausiids and the myctophid horned lanternfish (*Ceratoscopelus maderensis*) were the main prey, respectively. Similar prey items were also found in the diet of both greater fork- beard and poor cod: prey species were primarily shrimp species (%GII=61.8%, %V=60.6%, and %FO=62.9% and %GII=65.7%, %V=65.5%, and %FO=65.6%, respectively), with red snapping shrimp as the most-represented prey.

Results of the one-way analyses of similarity indicate that there were significant differences in trophic composition between size classes ($P \leq 0.05$) for all species studied except for the Mediterranean bigeye rockling and poor cod (Suppl. Table A.3.3). Moreover, results of the similarity percentage analysis for the 5 species that had ontogenetic shifts identify the contribution of each prey item to the mean Bray–Curtis dissimilarity for each species. The average dissimilarity between size classes ranged from 41% for Mediterranean ling to 75% for European hake. These differences were a result of the distinct contribution of major prey groups to the stomach contents in specimens examined for each species (Suppl. Table A.3.4). The major prey groups contributing the most to the ontogenetic shifts in the diet of silvery pout were large plankton and Peracarida, and for Mediterranean ling, the major prey groups were teleosts, such as demersal and benthopelagic fish species. Pelagic fish, large plankton, and shrimp species accounted for more than 60% of the diet of European hake. Species of large plankton and benthopelagic fish species contributed most to the diet of blue whiting (accounting for approximately 34% and 32% of the diet of this species, respectively); greater forkbeard fed mainly on shrimp species and species of Peracarida (Suppl. Table A.3.4).

Trophic ecology

The trophic niche breadth index (B_i) was highest for European hake, Mediterrean bigeye rockling, and silvery pout (Table 3.3). Conversely, poor cod had the lowest B_i value, with a strong preference for red snapping shrimp (%V=44.1%), despite the high number of prey items (52) identified in its diet.

Niche breadth across the 12 categories that are based on species and size class was lowest (B_i=0.136) for the small size class of Mediterranean ling; whereas, the small size class of greater forkbeard ranked the highest (B_i=0.636). Simplified Morisita index values ranged from 0.00 (pair of the small size class of Mediterranean ling and the small size class of greater forkbeard) to 1.00 (pair of the large size class of greater forkbeard and poor cod) (Table 3.4). Overall, niche overlap was highest between the small size class of greater forkbeard and poor cod, whose diet had a high proportion of shrimp species, represented principally by red snapping shrimp. The lowest values were found between the small size class of Mediterranean ling and poor cod as well as greater forkbeard.

The lowest and highest trophic levels were inferred for silvery pout (trophic level=3.51) and the large size class of Mediterranean ling (trophic level=4.49), respectively.

Within this range, only Mediterranean ling and the large size classes of European hake and blue whiting were determined to be at a trophic level ≥4, representative of top predators (Table 3.2). For all species, with the exception of the greater forkbeard, which had no changes in trophic level with size, the large size classes were at a higher trophic level. The greatest increases in trophic level linked to an ontogenetic shift occurred in European hake (from 3.95 to 4.24) and blue whiting (from 3.98 to 4.21).

Table 3.4 Simplified Morisita index values, which indicate trophic niche overlap between pairs of 12 categories of gadiform species for which stomach contents from specimens caught in the western Mediterranean Sea from 2011 through 2017 were examined. Categories combine species and size class (small [S] and large [L]; length ranges for size classes are provided in Table 3.2). Asterisks indicate extreme index values, defined as those ≥0.9 and <0.1. The species studied were the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater fork- beard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI).

Category	**GAD$_S$**	**GAD$_L$**	**GAI**	**MOL$_S$**	**MOL$_L$**	**MER$_S$**	**MER$_L$**	**MIC$_S$**	**MIC$_L$**	**PHY$_S$**	**PHY$_L$**	**TRI**
GAD$_S$	1.00											
GAD$_L$	0.92*	1.00										
GAI	0.18	0.17	1.00									
MOL$_S$	0.16	0.31	0.04*	1.00								
MOL$_L$	0.17	0.31	0.13	0.90*	1.00							
MER$_S$	0.64	0.80	0.24	0.30	0.46	1.00						
MER$_L$	0.22	0.36	0.12	0.35	0.38	0.67	1.00					
MIC$_S$	0.83	0.91*	0.04*	0.42	0.39	0.71	0.39	1.00				
MIC$_L$	0.57	0.79	0.11	0.73	0.71	0.72	0.53	0.78	1.00			
PHY$_S$	0.46	0.43	0.88	0.00*	0.03*	0.37	0.17	0.21	0.24	1.00		
PHY$_L$	0.10	0.33	0.53	0.03*	0.12	0.47	0.32	0.10	0.36	0.56	1.00	
TRI	0.09*	0.32	0.49	0.03*	0.11	0.47	0.33	0.08*	0.35	0.54	1.00*	1.00

Feeding strategies

Four groups of predators were identified on the basis of different feeding strategies (Fig. 3.3.2). The first group consisted of species with strong preferences for decapods, such as the Mediterranean bigeye rockling, poor cod, and greater forkbeard. The red snapping shrimp was the dominant prey species for the large size class of greater forkbeard (%V=35.3%) and for poor cod (%V=44.1%), and *Calocaris macandreae* (%V=32.0%) and angular crab (%V=15.6%) were the main prey species for Mediterranean bigeye rockling and the small size class of greater forkbeard. The second group was composed of both size classes of Mediterranean ling, with silvery pout as the dominant prey (with %V values of 52.4% and 24.3% for the small and large size classes, respectively).

The third group identified was composed of both size classes of silvery pout, which had a high preference for large plankton, although in the case of small silvery pout, species of Peracarida were also consumed. In both size classes, euphausiids were the most common prey item (with %V values of 46.8% and 36.8% for the small and large size classes, respectively).

The last group was represented by both size classes of blue whiting and European hake. The small size classes of both of these species preyed mostly on large plankton, with euphausiids as the most prevalent prey (with %V values of 51.3% and 24.3%, respectively). Benthopelagic fish species, namely the horned lanternfish (%V=19.3%) and the jewel lanternfish (Lampanyctus crocodilus) (%V=17.9%), were the main prey for the large size class of blue whiting. Pelagic fish species, such as the European anchovy (*Engraulis encrasicolus*) (%V=30.3%) and European pilchard (*Sardina pilchardus*) (%V=9.9%), were the species most widely consumed by the large size class of European hake.

Co-occurrence and trophic overlap

The highest percentages of co-occurrence were found for the associations of European hake with poor cod (75.8%) and blue whiting with greater forkbeard (64.1%) (Fig.3.3.3). Conversely, the lowest values of co-occurrence were observed for Mediterranean ling with poor cod (11.3%) and European hake with Mediterranean ling (14.1%). These results, together with analysis of trophic levels, indicate a high niche overlap between silvery pout and blue whiting and a low degree of overlap between Mediterranean ling and poor cod.

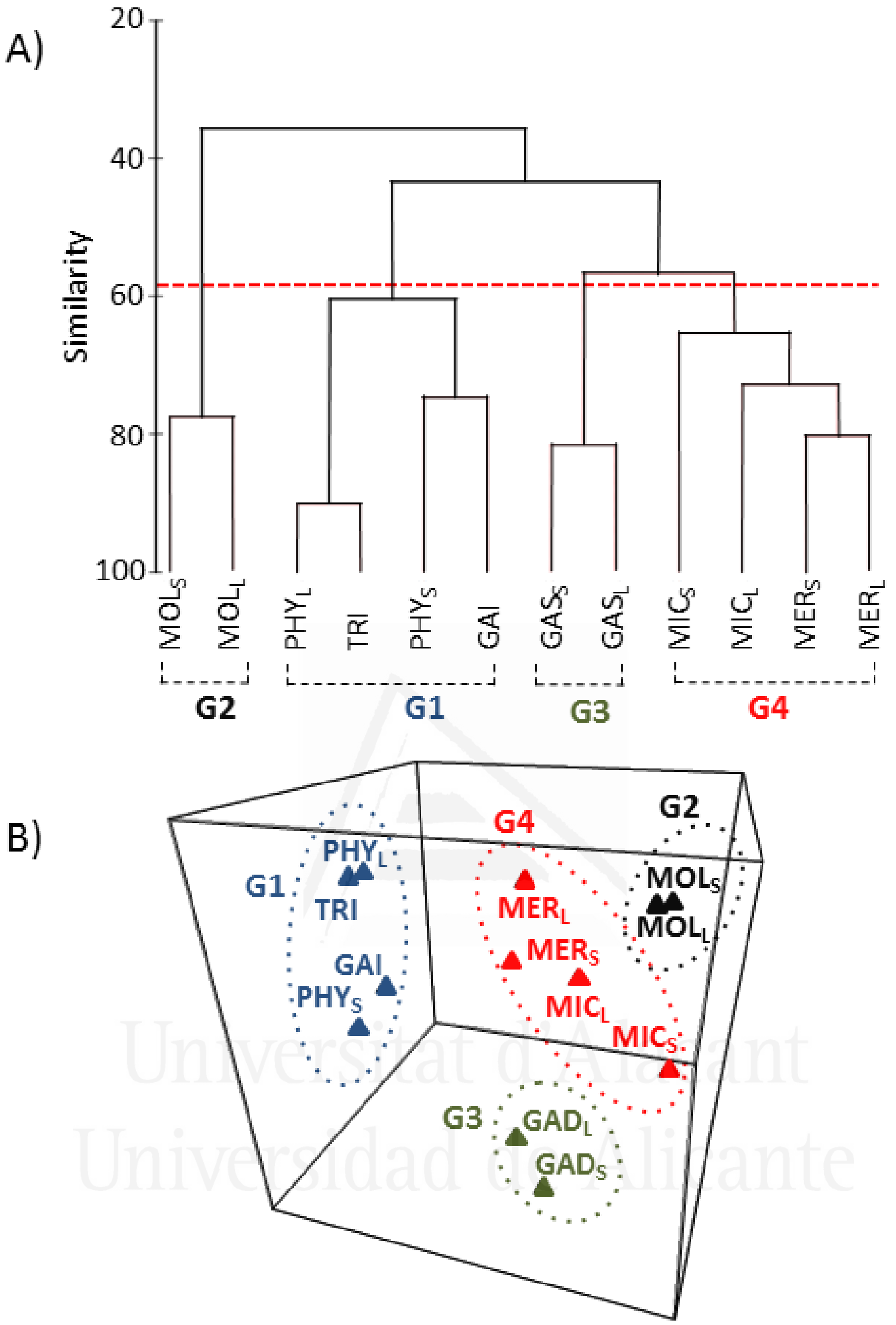

Fig. 3.3.2 Multidimensional scaling ordination of stomach contents of specimens of 7 species of Gadiformes caught in the western Mediterranean Sea from 2011 through 2017. In the (a) 2-dimensional and (b) 3-dimensional plots, dashed lines indicate or dotted lines surround predator groups (G1, G2, G3, and G4) identified by using cluster analysis based on feeding strategies. Results are given for 12 categories that combine species and size class (small [S] and large [L]; length ranges for size classes are provided in Table 3.2). The horizontal dashed line in panel A indicates the threshold similarity for group selection. The species studied include the Mediterrenean ling (*Molva macrophtalma*) (MOL), greater forkbeard (*Phycis blennoides*) (PHY), poor cod (*Trisopterus minutus*) (TRI), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), silvery pout (*Gadiculus argenteus*) (GAD), blue whiting (*Micromesistius poutassou*) (MIC), and European hake (*Merluccius merluccius*) (MER).

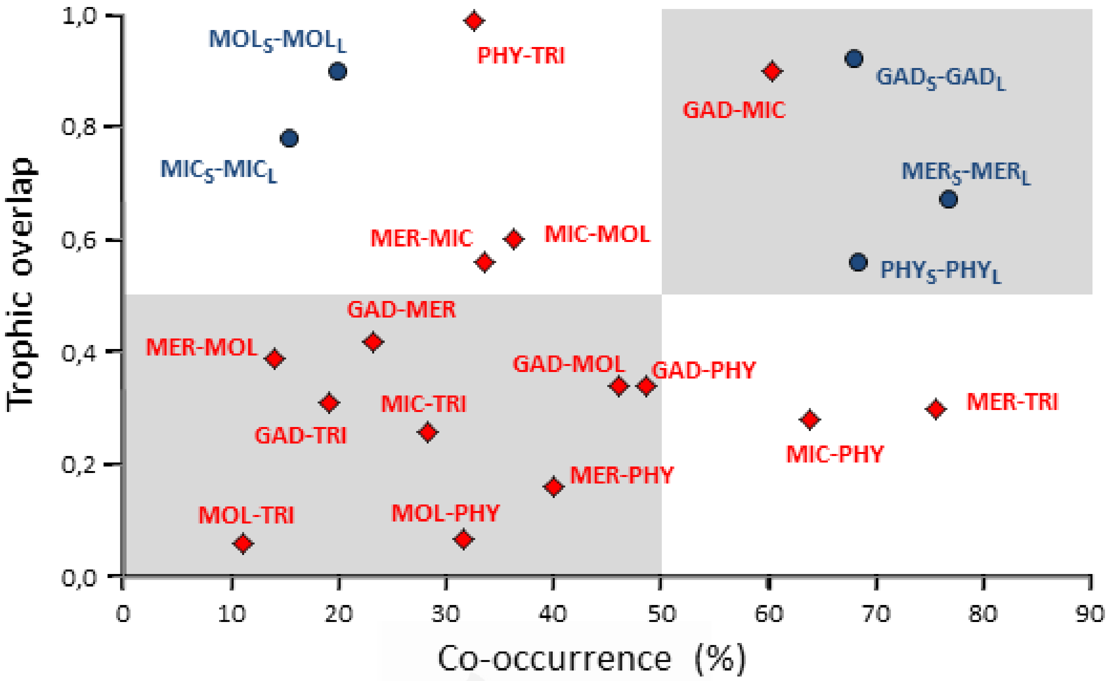

Fig. 3.3.3 Trophic overlap and percentage of co-occurrence for the seven gadiform species studied. Acronyms used are referenced in Table 1. Size classes are split into small (S) and large (L). Diamonds and gray circles indicate inter-specific and intra-specific interactions, respectively. Dark gray area means niche overlap; light gray area means high niche overlap.

All species had an intraspecific trophic overlap greater than 0.50. Greater forkbeard had the lowest value (0.56), and silvery pout had the highest value (0.92). On the other hand, low co-occurrence was found for both blue whiting and Mediterranean ling (0.16 and 0.20, respectively), and high values of co-occurrence were found for European hake, greater forkbeard, and silvery pout (0.77, 0.69, and 0.68, respectively).

3.4 Discussion

Our comprehensive study of feeding habits and trophic relationships among 7 fish species of the order Gadiformes that are important to fisheries in the western Mediterranean Sea explored ecological patterns such as those of ontogenetic variation in diet or trophic and spatial segregation of species. The results of this work can inform efforts to improve management of resource partitioning within and among these species in a broad geographic area (i.e., the entire GSA-06).

Our data indicate that the species studied are structured into 4 major guilds based on their feeding habits. The first group comprises the Mediterranean bigeye rockling, poor cod, and greater forkbeard. These species occupy medium-high positions within the food web. Their diets have previously been reported to consist of decapods and other small crustaceans, for example, for poor cod or greater forkbeard in the Catalan Sea (Macpherson, 1978b), in the

Gulf of Valencia (Morte et al., 2001, 2002), and in the Adriatic Sea (Dulčić and Dulčić, 2004). However, for Mediterranean bigeye rockling, our results differ from those of Macpherson (1978b), who identified *Eusergestes arcticus* and northern krill (*Meganyctiphanes norvegica*) as the predominant prey. Our results indicate that *Calocaris macandrae* was the primary prey species of Mediterranean bigeye rockling, and it is worth noting that this species was also found to be cannibalistic. These differences may be related to the 38-year gap between the 2 studies or are possibly a result of the fact that our sampling did not explore seasonal dietary changes; we restricted our study to the spring, when the MEDITS is carried out. This high degree of predation on decapod crustaceans by greater forkbeard and poor cod is indicative of a narrow trophic niche breadth compared with that of the Mediterranean bigeye rockling, which was found to have more generalist feeding habits. Moreover, and in agreement with results reported by Morte et al. (2002), an ontogenetic shift occurred in the diet of greater forkbeard in our study, but our findings differ from those of Morte et al. (2001) for poor cod in that no ontogenetic dietary shift was found.

The second group consists of both size classes of Mediterranean ling, and this species had the highest trophic levels among the 7 species studied. The diet of this species is primarily composed of benthopelagic and demersal fishes, such as the silvery pout and poor cod. This evidence indicates that the Mediterranean ling occupies a narrow trophic niche, a finding that is in agreement with the results previously reported by Macpherson (1981) for the same study area.

A third trophically distinct group is composed of both size classes of silvery pout, which is the only species primarily exploiting resources at the base of the food web, playing an important role in the energy flow from the lowest levels to the top of the food web. The majority of the diet of the silvery pout consists of a variety of small crustaceans, such as euphausiids and shrimp species, confirming the feeding habit observations previously reported by Macpherson (1978a) for silvery pout in the western Mediterranean. Therefore, these results indicate that the silvery pout consumes a broad range of prey items, a diet characteristic of a generalist feeder. We also found ontogenetic variation for this species, with it becoming a more specialized predator as its trophic level increased. This result contrasts with the findings reported by Macpherson (1978a), who observed no clear link between diet and size for the silvery pout.

The last of the 4 feeding guilds we identified is represented by both size classes of European hake and blue whiting, which occupy a position high in the food web. As has been observed for Mediterranean ling, both the European hake and blue whiting seem to be primarily piscivorous, although their diets in addition include shrimp species (Pasiphaea spp.) and large plankton, particularly euphausiids (e.g., northern krill). For European hake, our findings are consistent with those of other studies from the western Mediterranean Sea (Bozzano et al., 1997; Cartes et al., 2009). However, slight differences were found when comparing the diets of fish sampled in waters of the north Atlantic Ocean and the eastern Mediterranean Sea, where crustaceans were relatively less important and mackerels play the role reserved for sardines in our study area (Guichet, 1995; Velasco and Olaso, 1998; Philips, 2012). Regarding blue whiting, our results agree with those reported by Olaso and Rodríguez-Marín[8], Velasco et al.[9], and Gutiérrez-Zabala et al.[10] for this species in the Cantabrian Sea off the northern coast of Spain, but they contrast with the findings of Preciado et al. (2002) for blue whiting in the south of Galicia in the northwest of Spain and of Torres et al. (2013) for this species in the Gulf of Cadiz off the southern coasts of Portugal and Spain. In these latter 2 papers, a higher dependency on crustaceans, particularly euphausiids, was reported.

As far as differences in diet compositions between the European hake and blue whiting in our study are concerned, the European hake was found to prey mainly on pelagic fish species (i.e., sardines and European anchovy), as well as on benthopelagic (e.g., blue whiting) and demersal (e.g., poor cod) fish species, and the blue whiting was found to feed mainly on benthopelagic fish species (e.g., the horned lanternfish and jewel lanternfish). This ability of European hake to prey on different groups resulted in the European hake occupying the broadest trophic niche of all the species studied. Hence, in relation to ontogenetic shifts in diet, both species are characterized by a decreasing consumption of euphausiids and an increasing proportion of fish species with size. All of these results agree with those reported by Bozzano et al. (1997) for work in the Gulf of Lion and by Cartes et al. (2009) for a study in the Balearic Islands, a small archipelago off the northeastern coast of Spain.

Results for examination of niche breadth indicate a pattern that relates size class to niche breadth. The small size classes had a broader trophic niche than that of the large size classes, for all species studied except the Mediterranean ling, with ontogenetic growth leading to greater specialization in these species. In contrast, the Mediterranean ling is a specialist piscivorous species, the larger size of the specimens of which, in comparison to the size of individuals of other species studied, allowed it to have access to a greater number of potential

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[8] Olaso, I., and E. Rodríguez-Marín. 1995. Alimentación de veinte especies de peces demersales pertenecientes a la división VIIIc del ICES. Otoño 1991. Inst. Esp. Oceanogr., Inf. Téc. 157, 56 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

[9] Velasco, F., I. Olaso, and F. de la Gándara. 1996. Alimentación de veintidós especies de peces demersales de la división VIIIc del ICES. Otoños de 1992 y 1993. Inst. Esp. Oceanogr., Inf. Téc. 164, 62 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

[10] Gutiérrez-Zabala, J. L., F. Velasco, and I. Olaso. 2001. Alimentación de veintiuna especies de peces demersales de la división VIIIc del CIEM. Otoños de 1994 y 1995. Inst. Esp. Oceanogr., Datos Resúm. 16, 61 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

prey in its diet. Therefore, its trophic niche increased with the ontogenetic development of specimens. Our findings for the Mediterranean ling indicate a relationship between size class and trophic level, with the trophic level being lower in the small size classes and increasing after the ontogenetic shift. This difference in the trophic level between size classes was greater for those species located higher in the trophic web (e.g., the European hake, blue whiting, and Mediterranean ling).

We found that the studied species of Gadiformes exploit food resources at different trophic levels of the food web, indicating ontogenetic shifts in diet and resource parti- tioning. The silvery pout, for example, plays a role closer to that of a primary consumer, with the specimens that composed the small size class being those with the lowest tro- phic level. Fish species that play a similar role within the food web include species of Gobius, Mullus, Symphodus, and Diplodus, according to Karachle and Stergiou (2017). An intermediate trophic position is occupied by the poor cod, greater forkbeard, Mediterranean bigeye rockling, and the small size classes of blue whiting and European hake, as well as of the blackmouth catshark (*Galeus melastomus*) and species of Serranus, Pagellus, and Chelidonichthys (Karachle and Stergiou, 2017). Large specimens of European hake and blue whiting have a position in the upper part of the food web, along with species of Raja and Scorpaena (Karachle and Stergiou, 2017). Finally, the Mediterranean ling, primarily a piscivorous species, is in the highest trophic level, similar to other piscivorous species such as the common dentex (*Dentex dentex*), greater amberjack (*Seriola dumerili*), bluefin tuna (*Thunnus thynnus*), and John dory (*Zeus faber*) (Karachle and Stergiou, 2017).

If an ecosystem is structured in accordance with the hypothesis of niche complementarity (Ebeling and Hixon, 1991), on the basis of the distribution and diet of the species involved, the structure should have consistently low niche overlap such that the coexistence of similar species occurs because of differences in resource use (Pianka, 1973; Schoener, 1974). We investigated the dietary overlap of coexisting species for which a partitioning of trophic resources was found among species and size classes. This finding indicates that the 7 species studied occupy different trophic positions, ranging from a generalized feeding behavior to specialized piscivorous habits. These results might complement those reported by Macpherson (1978a) and Morte et al. (2001, 2002), who investigated changes with season and depth, respectively, in the diets of blue whiting, silvery pout, poor cod, and greater forkbeard. They related availability of prey to diet depending on the season. Moreover, differences in the patterns of species distribution reduce niche overlap even further.

Only 3 pairs of species had a co-occurrence greater than 50%, with the pairs of blue whiting and greater forkbeard and of European hake and poor cod having by far the highest values of spatial overlap but correspondingly low values of trophic overlap. This distributional and trophic strategy minimizes interspecific competition. Cases in point are the Mediterranean ling and blue whiting, which may avoid intraspecific competition through this mechanism. Only the species pair of silvery pout and blue whiting had high values for both indices, indicating strong competition for resources between these 2 species.

For 5 of the 7 species, excluding the Mediterranean bigeye rockling and poor cod, ontogenetic shifts in diet were found, shifts that allowed them to occupy several niches or subniches simultaneously (Deselle et al., 1978; Keast, 1978). These ontogenetic shifts were associated with an increase in inferred trophic levels for all the species, contributing to increasing segregation between size classes (Pauly et al., 2001). Although the size classes described in this study are related to shifts in trophic strategies, intraspecific trophic overlap was observed for those 5 species that had ontogenetic shifts in their diets, and the intraspecific overlap was generally higher than the interspecific overlap. This result is in line with that of Bergstad (1991), who found that the effects of competitive interactions are more likely to occur between size classes of the same species than between different species.

Of those 5 species, the greater forkbeard, European hake, and silvery pout had high co-occurrence that involved strong competition for food resources, resulting in high intraspecific trophic overlap. An important aspect of this kind of competition is cannibalism, which was found in European hake, and this result is in agreement with findings reported by Macpherson (1979), Bozzano (1997), and Cartes et al. (2009) for studies in the western Mediterranean Sea, as well as in nearby regions of the Atlantic Ocean (Torres et al., 2013; López-López et al., 2015).

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3.6 Supplementary material

Table A.3.1 Diet composition for the 7 gadiform species studied, based on the volume index (%V) for each prey item identified to the lowest taxonomic level possible and prey category found in the stomach contents of specimens caught in the western Mediterranean Sea during 2011–2017.

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Teleosts	**17.34**	**17.61**	**84.49**	**52.62**	**99.08**	**9.04**	**7.36**
Scyliorhinidae						0.11	
Scyliorhinus canicula						0.11	
Clupeiformes			**38.76**	**0.92**			**0.54**
Engraulis encrasicolus			28.40				
Sardina pilchardus			10.19	0.92			0.54
Sprattus sprattus			0.18				
Argentiniformes			0.09		**0.62**		
Argentina sphyraena			0.09				
Glossanodon leioglossus					0.62		
Myctophiformes	**1.50**		**1.21**	**42.14**	**1.02**	**0.36**	**0.17**
Benthosema glaciale				4.13			
Ceratoscopelus maderensis			0.11	18.20		0.36	
Lampanyctus crocodilus	1.36		1.07	16.55			
Notoscopelus elongatus			0.03	1.23	1.02		0.17
Myctophum punctatum				0.52			
Unidentified myctophids	0.14		0.00	1.51			
Stomiiformes	**9.29**		**0.20**	**4.79**		**0.27**	
Maurolicus muelleri	2.48		0.06	0.62		0.27	
Stomias boa boa			0.13	3.04			
Vinciguerria sp.	0.42						
Cyclothone sp.	6.39			1.11			
Gonostoma denudatum				0.03			
Gadiformes	**1.14**	**16.39**	**16.73**	**1.90**	**89.29**	**6.15**	**3.83**
Gadiculus argenteus	1.14		0.05		31.98		

Table A.3.1 (Continued)

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Merluccius merluccius			3.77			1.11	0.51
Micromesistius poutassou			10.82	0.77	44.62		
Gaidropsarus biscayensis		16.39	0.38		1.47	4.54	3.32
Phycis blennoides			0.55	1.09	1.23	0.03	
Trisopterus minutus			1.16	0.04	9.99	0.47	
Perciformes			**21.10**	**0.77**		**1.43**	**1.95**
Cepola macrophthalma			0.59				
Boops boops			14.45				
Serranus cabrilla			0.01				
Mullus sp.			0.09				
Trachinus draco			0.06				
Deltentosteus quadrimaculatus			0.01				
Gobiidae			0.21				0.44
Lesueurigobius sp.			0.10				0.49
Callionymus sp.			0.11				1.02
Aulopiformes			**5.46**	**0.77**		**1.43**	
Lestidiops sp.				0.77		1.43	
Paralepididae			1.03				
Spicara smaris			0.43				
Spicara maena			1.37				
Trachurus sp.			2.63				
Scorpaeniformes			**0.04**				
Trigla lyra			0.04				
Pleuronectiformes							**0.03**
Arnoglossus sp.							0.03
Teleost larvae	0.01	0.39		0.07			
Unidentified teleosts	5.40	0.83	6.35	2.03	8.15	0.72	0.84
Mollusca			**5.65**	**0.75**		**0.69**	**2.84**
Cephalopoda			**5.65**	**0.75**		**0.69**	**2.83**
Abralia veranyi				0.42			
Illex coindetii			3.43			0.32	
Rondeletiola minor			0.08				

Table A.3.1 (Continued)

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Sepia elegans			1.32				
Sepietta oweniana			0.53				0.71
Unidentified sepiolids			0.29			0.03	1.92
Unidentified teuthids				0.28			
Unidentified cephalopods			0.01	0.05		0.34	0.20
Pteropoda							0.01
Crustacea	**82.46**	**82.04**	**9.86**	**46.62**	**0.92**	**90.14**	**89.71**
Decapoda	**10.26**	**62.82**	**5.24**	**17.41**	**0.47**	**81.13**	**83.56**
Alpheus glaber		9.86	0.41			34.08	44.10
Athanas sp.							0.03
Chlorotocus crassicornis			1.29			7.15	6.32
Crangonidae			0.00				
Gennadas elegans	0.55				0.24		
Pasiphaea sp.	0.07		0.29	11.15		0.69	
Philocheras sp.			0.04			0.05	0.20
Plesionika acanthonotus						0.07	
Plesionika edwardsii		2.62					
Plesionika gigliolii		1.38	0.14	0.15			
Plesionika heterocarpus			0.02				
Aegaeon sp.			0.21			0.20	
Pontophilus sp.			0.04				0.03
Processa sp.	2.66	1.81	0.36	0.14		4.17	4.29
Eusergestes arcticus		4.15		0.95	0.23		
Deosergestes henseni				0.06			
Robustosergia robusta				2.37			
Solenocera membranacea			1.04			9.93	1.02
Calocaris macandreae	0.16	28.28		0.01		6.09	0.04
Galathea sp.						0.04	0.03
Goneplax rhomboides		10.92				7.75	4.36
Jaxea sp.							0.08
Liocarcinus sp.			0.10			1.80	10.87
Macropipus tuberculatus						0.13	0.12

Table A.3.1 (Continued)

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Portunidae			0.01				0.03
Monodaeus couchii		1.18				0.80	0.16
Munida sp.		0.87				1.17	0.59
Nephrops norvegicus				0.11			
Paguridae						0.02	
Scyllarus sp.			0.01			0.14	
Upogebia sp.			0.01			0.14	0.10
Unidentified carideans	6.41	0.96	0.95	2.31		5.46	5.84
Unidentified brachyurans		0.46	0.02			0.39	0.76
Unidentified decapods	0.41	0.33	0.31	0.16		0.87	4.59
Stomatopoda			**0.04**			**2.67**	**0.22**
Rissoides pallidus			0.04			2.67	0.22
Peracarida	**3.21**	**13.55**	**0.23**	**0.22**	**0.14**	**2.78**	**2.28**
Amphipoda	**1.11**	**3.25**	**0.11**	**0.10**	**0.04**	**0.76**	**0.80**
Caprellidae		0.03				0.02	
Ampelisca sp.			0.00			0.02	
Epimeria sp.						0.02	0.03
Eusirus sp.						0.02	
Idunella sp.						0.02	
Lysianassa sp.			0.00			0.02	0.12
Lysianassidae	0.25					0.02	
Moerella sp.							0.05
Monoculodes sp.		0.44					
Rhachotropis sp.						0.04	0.03
Scopelocheirus sp.							0.11
Tryphosites sp.							0.02
Westwoodilla sp.	0.27	0.44			0.04		
Brachyscelus sp.			0.05	0.04		0.04	
Hyperiidea	0.14		0.01	0.01			
Phronima sedentaria			0.02	0.01		0.40	0.38
Vibilia sp.	0.08		0.02	0.03			0.02
Unidentified amphipods	0.37	2.34	0.01	0.01		0.12	0.03

Table A.3.1 (Continued)

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Isopoda	1.07	0.44	0.00	0.10	0.03	1.04	0.32
Lophogastrida		**6.83**	**0.06**	**0.01**		**0.45**	**0.93**
Lophogaster typicus		6.83	0.06	0.01		0.45	0.93
Mysida	1.03	3.04	0.05	0.00	0.06	0.52	0.23
Tanaidacea						0.02	
Copepoda	9.48	1.56	0.00			0.02	
Ostracoda						0.02	
Euphausiacea	**53.18**	**2.84**	**4.19**	**28.89**	**0.31**	**3.31**	**2.74**
Euphausia krohnii	17.69			0.05			
Meganyctiphanes norvegica	4.28		0.06	4.85		2.54	2.11
Nematoscelis sp.	1.14		0.01	0.35			
Nyctiphanes couchii			0.71	1.30			
Unidentified euphausiaceans	30.07	2.84	3.41	22.34	0.31	0.76	0.62
Unidentified crustaceans	6.34	1.27	0.16	0.09		0.21	0.92
Annelida	**0.20**	**0.35**		**0.01**		**0.12**	**0.09**
Hydrozoa				**0.01**		**0.02**	
Diphyidae				0.01		0.02	

Table A.3.2 Summary of the composition taxa and species identified in the stomach contents of specimens of 7 gadiform species caught in the western Mediterranean Sea during 2011–2017. Trophic levels (TL) of prey items and groups and the references used as sources of this information on trophic levels are provided.

Prey items	TL	Reference
CEPHALOPODA		
Abralia veranyi	3.20	Cortés (1999)
Eggs	1.00	
Illex coindetii	3.85	Rosas-Luis et al. (2014)
Rondeletiola minor	3.20	Cortés (1999)
Sepia elegans	3.20	Cortés (1999)
Sepietta oweniana	3.20	Cortés (1999)
Sepiolidae	3.20	Cortés (1999)
Teuthida	3.85	Rosas-Luis et al. (2014)
Undefined cephalopoda	3.20	Cortés (1999)
CRAB, LOBSTER, AND MANTIS SHRIMP SPECIES		
Brachyura	2.88	Corrales et al. (2015)
Calocaris macandreae	2.88	Corrales et al. (2015)
Galathea sp.	2.88	Corrales et al. (2015)
Goneplax rhomboides	2.88	Corrales et al. (2015)
Jaxea nocturna	2.88	Corrales et al. (2015)
Liocarcinus sp.	2.88	Corrales et al. (2015)
Macropipus tuberculatus	2.88	Corrales et al. (2015)
Monodaeus couchii	2.88	Corrales et al. (2015)
Munida sp.	2.88	Corrales et al. (2015)
Paguridae	2.88	Corrales et al. (2015)
Portunidae	2.88	Corrales et al. (2015)
Unidentified crabs	2.88	Corrales et al. (2015)
Upogebia sp.	2.88	Corrales et al. (2015)
Nephrops norvegicus	2.88	Corrales et al. (2015)
Rissoides sp.	2.88	Corrales et al. (2015)
Scyllarus sp.	2.88	Corrales et al. (2015)
BENTHOPELAGIC FISH SPECIES		
Argentina sphyraena	3.44	Pinnegar et al. (2002)
Benthosema glaciale	3.24	Cortés (1999)
Cepola macrophthalma	3.18	This study
Ceratoscopelus maderensis	3.24	Cortés (1999)
Cyclothone sp.	3.20	Fanelli et al. (2011)
Gadiculus argenteus	3.32	This study
Glossanodon leioglossus	3.44	Froese and Pauly (2019)
Gonostoma sp.	3.24	Cortés (1999)
Lampanyctus crocodilus	3.65	This study
Lestidiops sp.	3.24	Cortés (1999)
Maurolicus muelleri	3.24	Cortés (1999)
Merluccius merluccius	3.89	This study
Micromesistius poutassou	3.58	This study
Myctophidae	3.24	Cortés (1999)
Myctophum punctatum	3.60	Fanelli et al. (2011)
Notoscopelus elongatus	3.24	Cortés (1999)

Table A.3.2 (Continued)

Prey items	TL	Reference
BENTHOPELAGIC FISH SPECIES		
Paralepididae	3.24	Cortés (1999)
Stomias boa boa	4.60	Fanelli et al. (2011)
Vinciguerria sp.	3.24	Cortés (1999)
DEMERSAL FISH SPECIES		
Arnoglossus sp.	3.57	This study
Callionymus sp.	3.09	Karachle and Stergiou (2017)
Deltentosteus quadrimaculatus	3.24	Karachle and Stergiou (2017)
Gaidropsarus biscayensis	3.69	This study
Gobiidae	3.32	Karachle and Stergiou (2017)
Lesueurigobius friesii	3.23	Froese and Pauly (2021)
Mullus sp.	3.52	This study
Phycis blennoides	3.46	This study
Scyliorhinus canicula	3.80	This study
Serranus cabrilla	3.77	This study
Spicara maena	3.46	This study
Trachinus draco	3.94	This study
Triglidae	3.48	This study
Trisopterus minutus	3.59	This study
Arnoglossus sp.	3.57	This study
PELAGIC FISH SPECIES		
Boops boops	3.29	This study
Engraulis encrasicolus	3.02	Corrales et al. (2015)
Sardina pilchardus	2.91	Corrales et al. (2015)
Spicara smaris	3.02	This study
Sprattus sprattus	3.02	Corrales et al. (2015)
Trachurus sp.	4.10	This study
PERACARIDA		
Ampelisca sp.	3.18	Ebert and Bizzarro (2007)
Undefined amphipods	3.18	Ebert and Bizzarro (2007)
Caprellidae	3.18	Ebert and Bizzarro (2007)
Epimeria cornigera	3.18	Ebert and Bizzarro (2007)
Eusirus longipes	3.18	Ebert and Bizzarro (2007)
Idunella sp.	3.18	Ebert and Bizzarro (2007)
Isopoda	3.18	Ebert and Bizzarro (2007)
Lophogaster typicus	2.25	Ebert and Bizzarro (2007)
Lysianassa sp.	3.18	Ebert and Bizzarro (2007)
Lysianassidae	3.18	Ebert and Bizzarro (2007)
Moerella sp.	3.18	Ebert and Bizzarro (2007)
Monoculodes sp.	3.18	Ebert and Bizzarro (2007)
Mysida	2.25	Ebert and Bizzarro (2007)
Rhachotropis sp.	3.18	Ebert and Bizzarro (2007)
Scopelocheirus sp.	3.18	Ebert and Bizzarro (2007)
Tanaidacea	2.40	Ebert and Bizzarro (2007)
Tryphosites sp.	3.18	Ebert and Bizzarro (2007)
Westwoodilla sp.	3.18	Ebert and Bizzarro (2007)

Table A.3.2 (Continued)

Prey items	TL	Reference
SMALL PLANKTON		
Copepoda	3.00	Fanelli et al. (2011)
Ostracoda	2.20	Fanelli et al. (2011)
Pelagic eggs	1.00	
LARGE PLANKTON		
Brachyscelus crusculum	3.18	Ebert and Bizzarro (2007)
Diphyidae	2.10	Cortés (1999)
Euphausia krohnii	2.25	Cortés (1999)
Euphausiacea	2.25	Cortés (1999)
Euthecosomata	2.10	Cortés (1999)
Fish larvae	3.00	
Hyperiidea	3.18	Ebert and Bizzarro (2007)
Meganyctiphanes norvegica	3.50	Fanelli et al. (2011)
Nematoscelis megalops	3.50	Fanelli et al. (2011)
Nyctiphanes couchii	3.50	Fanelli et al. (2011)
Phronima sedentaria	3.40	Fanelli et al. (2011)
Tunicata	2.10	Jacobsen and Bennett (2013)
Vibilia sp.	2.00	Fanelli et al. (2011)
POLYCHAETA		
Polychaeta	2.05	Corrales et al. (2015)
SHRIMP SPECIES		
Alpheus glaber	2.94	Corrales et al. (2015)
Athanas sp.	2.94	Corrales et al. (2015)
Chlorotocus crassicornis	2.94	Corrales et al. (2015)
Crangonidae	2.94	Corrales et al. (2015)
Deosergestes henseni	3.60	Fanelli et al. (2011)
Eusergestes arcticus	3.60	Fanelli et al. (2011)
Gennadas elegans	3.60	Fanelli et al. (2011)
Pasiphaea multidentata	3.70	Fanelli et al. (2011)
Pasiphaea sivado	3.70	Fanelli et al. (2011)
Philocheras sp.	2.94	Corrales et al. (2015)
Plesionika acanthonotus	2.94	Corrales et al. (2015)
Plesionika edwardsii	2.94	Corrales et al. (2015)
Plesionika gigliolii	2.94	Corrales et al. (2015)
Plesionika heterocarpus	2.77	Fanelli and Cartes (2008)
Pontocaris sp.	2.94	Corrales et al. (2015)
Pontophilus sp.	2.94	Corrales et al. (2015)
Processa sp.	2.94	Corrales et al. (2015)
Sergia robusta	3.60	Fanelli et al. (2011)
Solenocera membranacea	2.94	Corrales et al. (2015)
Unidentified shrimps	2.94	Corrales et al. (2015)

References

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Fanelli, E., and J. E. Cartes. 2008. Spatio-temporal changes in gut contents and stable isotopes in two deep Mediterraneanpandalids: influence on the reproductive cycle. Mar. Ecol. Prog. Ser. 355:219–233. Crossref

Froese, R. and D. Pauly (eds.). 2019 FishBase, vers. 11/2019. [World Wide Web electronic publication.] [Available fromwebsite, accessed November 2019.]

Table A.3.3 Results of analysis of similarity by size class (small [S] and large [L]) for the 7 gadiform species studied to detect intraspecific food habit differences. The number of stomachs examined (n), length range (total lengths in millimeters), and Global R, a comparative measure of the degree of separation between size classes, are provided. An asterisk (*) indicates a probability below the significance level of 0.05. Specimens of the species were caught in the western Mediterranean Sea during 2011–2017.

	Size class	n	Length range	Global R	*P*
G. argenteus	S	44	60-92	0.146	0.012*
	L	219	93-133		
G. biscayensis	S	86	40-110	0.138	0.097
	L	30	111-180		
M. macrophthalma	S	107	83-165	0.124	0.016*
	L	57	166-740		
M. merluccius	S	405	87-149	0.161	0.001*
	L	849	150-549		
M. poutassou	S	172	89-169	0.112	0.006*
	L	614	170-377		
P. blennoides	S	75	85-149	0.478	0.001*
	L	211	150-393		
T. minutus	S	169	78-169	0.002	0.351
	L	154	170-272		

Table A.3.4 Results of the similarity percentage analysis of the stomach contents from specimens of species of Gadiformes caught in the western Mediterranean Sea during 2011–2017, based on the average dissimilarity between size classes (small [S] and large [L]) to determine which prey groups contributed the most to the dissimilarity in diet composition. Of the 7 studied species, 2 of the species did not have shifts in diet according to size and are not included in this table.

Species	**Av. Diss**	**Prey group**	**Av. Abund S**	**Av. Abund L**	**Av. Diss**	**Diss/SD**	**Contrib%**	**Cum%**
Gadiculus argenteus	63.43	LARGE PLANKTON	0.53	0.60	17.72	1.23	27.94	27.94
		PERACARIDA	0.27	0.21	13.57	0.95	21.40	49.34
Molva macrophthalma	41.66	DEMERSAL FISH SPECIES	0.27	0.44	19.44	1.12	46.67	46.67
		BENTHOPELAGIC FISH SPECIES	0.88	0.60	17.70	0.95	42.49	89.15
Merluccius merluccius	75.12	PELAGIC FISHES	0.19	0.50	18.26	1.11	24.31	24.31
		LARGE PLANKTON	0.35	0.12	14.02	0.92	18.66	42.97
		SHRIMP SPECIES	0.28	0.25	13.20	0.98	17.57	60.54
Micromesistius poutassou	60.2	LARGE PLANKTON	0.67	0.36	20.34	1.31	33.78	33.78
		BENTHOPELAGIC FISH SPECIES	0.36	0.58	19.24	1.30	31.97	65.75
Phycis blennoides	62.02	SHRIMP SPECIES	0.31	0.75	18.45	1.54	29.74	29.74
		PERACARIDA	0.45	0.06	14.38	1.18	23.19	52.93

Chapter 4: A food-web comparative modeling approach highlights ecosystem singularities of the Gulf of Alicante (western Mediterranean Sea)

A food-web comparative modeling approach highlights ecosystem singularities of the Gulf of Alicante (western Mediterranean Sea)[11]

Abstract

A food-web comparative modeling approach using Ecopath with Ecosim (EwE) was built to characterize the ecosystem of the Gulf of Alicante (GoA) and investigate its singularities. The GoA differs from neighboring ecosystems of the western Mediterranean Sea because of its different oceanographic characteristics. We developed a model of the study area representing early 2010s, covering a total area of 7085 km2, and including the continental shelf and upper slope with depths from 50 to 800 m. In total, 45 functional groups considering all components of the food web (fish, marine mammals, seabirds, invertebrates, primary producers, and detritus) were selected to build the ecological model. The fishery was represented by the four main fleets operating in the area (i.e., bottom trawl, purse seine, longlines, and small-scale fisheries) and we included official landing data and estimated percentage of discarded species. Results were then compared with available outputs of available models representing adjacent ecosystems such as the Gulf of Cadiz (in the Atlantic side) and the north western Mediterranean Sea (north of the study area). The study revealed that the major differences found between models were due to the lower primary production in the GoA. This led to lower catches and higher importance of the demersal compartment, where the most biomass was associated to the detritus. The main trophic flows in the GoA were originated at the basis of the food web, likely related to bottom-up flow control. Interactions between pelagic and demersal groups were weaker than in neighboring areas. Despite the high values of ecotrophic efficiencies and mortality rates, results showed a lower fishing pressure than in neighboring areas, suggesting a moderate exploitation level of marine resources in the GoA. This study fills a knowledge gap in the area and sets the baseline to develop future studies to test scenarios of change and management options.

Keywords: Ecopath model, Ecosystem-based approach to fisheries management (EAFM), ecological indicators, trophic interactions, fishing impacts, comparative modeling approach

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4.1 Introduction

The declining trend of several marine resources is being observed worldwide and the main drivers behind are climate change and anthropogenic pressures such as overfishing and industrial and agricultural activity (Diaz et al., 2019; Halpern et al., 2019).

Overall, it is recognized that the impacts and interactions between species and fisheries have induced the seeking of alternative ways to better manage marine resources. The conventional management of marine resources has been based on the assessment of single-species, which has resulted incomplete (Pitcher and Cochrane, 2002). Therefore, an Ecosystem Approach to Fisheries (EAF) has been suggested worldwide as a common starting point for the appropriate management of marine resources (Garcia et al., 2003).

In this context, ecosystem models can be useful tools to contribute to fisheries management by providing relevant information to describe the trophic structure and functioning of marine ecosystems and the ecosystem impacts caused by human activities (Link, 2011; Christensen and Walters, 2011). Within the variety of ecosystem models available, Ecopath with Ecosim (EwE) (Polovina, 1984; Christensen and Pauly, 1992; 1993) is one of the most frequently used modelling frameworks for ecosystem approaches, leading to its applications worldwide by a growing body of scientists (e.g. Coll et al. 2015a; Colléter et al., 2015).

This approach has been also frequently used in the Mediterranean Sea (e.g., Tsagarakis et al., 2010; Coll and Libralato 2012; Corrales et al., 2015, 2017), a hotspot of biodiversity largely threatened by multiple stressors (Coll et al., 2010, 2012). The biodiversity of the Mediterranean Sea depends strongly on the heterogeneity of habitats. In particular, habitat disruption has become a problem, leading to biodiversity loss and a decreasing trend in commercial stocks and catches of main target species in recent years (Ballesteros, 2006; Coll et al., 2010; Bellido et al., 2014; Fernandes et al., 2017; FAO, 2018).

Focusing on the western Mediterranean and adjacent Atlantic waters, different food-web models have been developed, such as the South Catalan Sea model (CSM) (Coll et al., 2006); the deep-sea ecosystem model in the NW Mediterranean (DSM) (Tecchio et al., 2013); the Gulf of Lion model (GoL) (Banaru et al., 2013); the Northwestern Mediterranean model (NWM) (Corrales et al. 2015) covering the geographical sub-areas (GSAs) 6 and 7 of the General Fisheries Commission for the Mediterranean (GFCM, FAO); or the Gulf of Cadiz model (GoC) in the adjacent Atlantic (Torres et al., 2013). In addition to these models, there are also two EwE models in the region developed to study trophic structure and energy fluxes in an aquaculture system (Forestal et al., 2012; Bayle-Sempere et al., 2013), one to study the Fisheries Restricted

Area (FRA) area in the GoL (Vilas et al., 2021) and several to study smaller coastal protected and adjacent areas (Corrales et al., 2020; Vilas et al., 2020).

Even though the Mediterranean Sea is generally considered an oligotrophic sea (Estrada, 1996), the Northern part of the western Mediterranean basin presents a cyclonic circulation with some relative productive regions (Estrada and Margalef, 1988). These are the cases of the Gulf of Lion (GoL), where the strong prevailing NW winds during winter result in local upwelling processes (Minas, 1968), and to a lesser extent the Catalano-Balearic basin with a permanent southwestward current which flows from the Ligurian Sea to the Catalan Sea and follows the continental slope at the north of Cape La Nao (Millot, 1987). In this region, this current splits, and one branch flows eastward along the south of the Balearic Islands (Castellón et al. 1990) forming the thermohaline front that separates the central waters of the Catalan Sea from modified Atlantic waters (Font et al. 1988), configuring the Gulf of Alicante (GoA) as a transition area to Gulf of Vera and Alboran Sea (Almeria-Oran front), with a marked Atlantic influence.

The case of the Gulf of Alicante (GoA) seems to be specific because it is still under the influence of the Atlantic flow when leaving the Alboran Sea and is linked to the existence of an anticyclone circulation between Cape Palos and Cape La Nao. These features highlight the presence of two anticyclonic eddies, one very marked outside and another inside the continental shelf (Gil, 1992). Similarly, the thermohaline front located to the north of Cape La Nao that separates the GoA and the Catalan Sea could give certain singularity to the composition and dynamics of the marine ecosystems associated with the GoA. However, to date, there are no food-web modelling studies conducted in this area and thus our understanding of the functioning of the marine ecosystem of the GoA is still limited.

Despite the lack of information regarding the structure and functioning of the GoA, the hypothesis derived from the oceanographic conditions is that this ecosystem presents elements of singularity concerning those found north of Cape La Nao. Hence, the aim of the present study is to describe the trophic structure and functional integrity of the GoA marine ecosystem for the first time using a food-web modeling approach. Particularly, and following previous initiatives, we develop a food-web model for the first time that allows us to analyze various aspects of the structure and functioning of the ecosystem, including trophic interactions and the effects of fishing. Afterwards, we compare our results with other existing models located north to the Cape La Nao (Northwestern Mediterranean) and southeastwards Cape Palos (in the Atlantic Gulf of Cadiz). To develop the comparison, we first use robust ecosystem indicators to model comparisons (Heymans et al. 2014; Moloney et al. 2005). Secondly, we also use the ECOIND plug-in (Coll and Steenbeek, 2017) to complement the ecological indicators and obtain further insights into the GoA marine ecosystem properties. One of the interesting aspects of the approach presented here is that it opens the possibility to compare these indicators with those proposed for the EU Marine Strategy Framework Directive (MSFD: EU-COM, 2008) in future studies. The MSFD aims to monitor food-web status and trends in order to collect information needed to assess the current situation and implement the necessary preventive measures to ensure a Good Environmental Status (GES). Our study is a first step forward in this direction in the Gulf of Alicante, complementing available modelling experiences of the western Mediterranean Sea. It also sets the baseline to develop scenarios of climate change and management options in the area.

4.2 Material and methods

Study area

The study was conducted in the Gulf of Alicante (GoA), which is located in the western Mediterranean Sea, one of the fourth sub-regional divisions defined by the Marine Strategy Framework Directive (MSFD; 2008/56/EC) (38°44'2.44"N – 0º44'33"W; 37°38'10"N – 0º36'27"E) (Fig. 4.2.1). The study area includes several important harbors where diverse commercial and recreational activities are carried out. It covers a total area of 7,085 km2 including the continental shelf and upper slope. It covers a depth range between 50 and 800 m. The Alicante continental shelf average width from Cape La Nao to Cape Palos is 32 km, with a minimum and a maximum of 23 km and 40 km, with a dominance of sandy and muddy bottoms (Diaz del Rio et al., 1986). The slope has a uniform relief with a width between 30 and 52 km. There are two major canyons: the one from Alicante is gently sloping and the other in Benidorm is narrower and rough with a head that originates at the foot of the continental slope at a depth of 650 m (Diaz del Rio, 1991).

Ecopath mass-balanced model

A trophic model was developed to provide a static description of the GoA ecosystem in early 2010s, when the best data regarding biomass of the demersal community were available in terms of stability along the time series. The model was constructed using the Ecopath with Ecosim (EwE) software version 6.6 (Christensen et al., 2008) and we followed the best practices and applied the PREBAL approach (Heymans et al. 2016; Link 2010).

Several functional groups were defined and required information for biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and diet. In addition, estimates of catches and discards for fished groups were compiled.

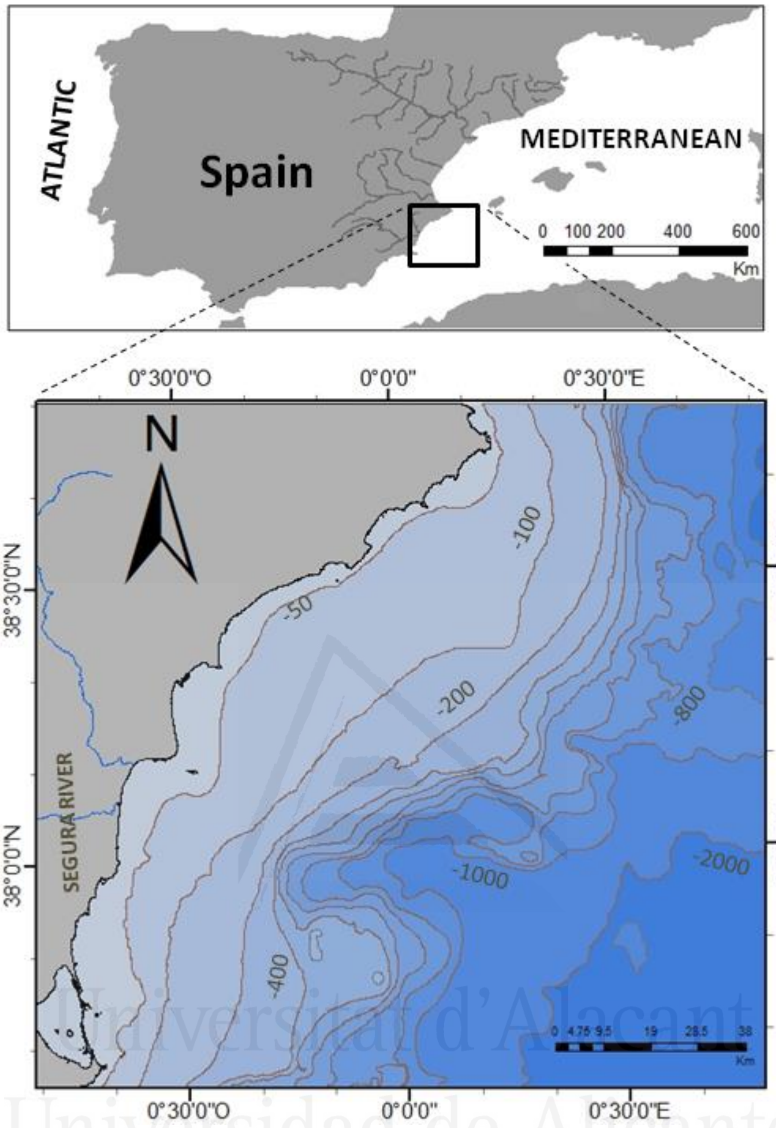

Fig. 4.2.1 Map of the Northwestern Mediterranean Sea including the Gulf of Alicante.

The Ecopath modeling framework, based on the pioneering work of Polovina (1984), estimates the flows amongst different food-web components (Christensen and Walters 2004). These components, also called functional groups, can be single-species, ontogenetic phases of a species (or multi-stanza groups), or species groups representing similar ecological guilds in the ecosystem (i.e., have similar growth rates, consumption rates, diets, habitats, and predators) (Christensen et al., 2008; Heymans et al., 2016).

The Ecopath model is based on two master equations, the first of which splits the production term for each functional group *i* into its components:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + M0_i \qquad (1)$$

where P_i is the total production rate of group *i*, Y_i is the total fisheries catch rate, B_i is the biomass, $M2_i$ is the total predation rate, E_i is the net migration rate (emigration -immigration), BA_i is the biomass accumulation rate, and $M0_i$ is the so-called "other mortality," which includes mortality caused by diseases, starvation, etc..., or being consumed by predators not included in the model ($M0_i = P_i \bullet (1- EE_i)$), where EE_i is the ecotrophic efficiency of group *i*).

The second master equation describes the energy balance within each functional group:

$$Q_i = P_i + R_i + U_i \qquad (2)$$

where Q_i stands for consumption, P_i for the total production rate, R_i for respiration, and U_i for unassimilated food. The Ecopath model uses a linear system of equations to estimate one parameter per equation and functional group, either B, P/B, Q/B, or EE (a detailed description of the model's foundations is given in Christensen et al., 2008; Christensen and Walters, 2004).

Input data

The selection of the functional groups represents a compromise between the biological and ecological characteristics of the modeled species. As a result, we identified 45 functional groups consisting of 23 fish groups, one group of marine mammals, one group of seabirds, 16 invertebrate groups, two primary producers, and two groups of detritus (Tables 4.1 and A.4.1).

Table 4.1 Modified input parameters and outputs obtained from the Gulf of Alicante (GoA) model in 2011. Bf = final biomass; P/B = production/biomass ratio; Q/B = consumption/biomass ratio; EE = ecotrophic efficiency; P/Q = production/consumption ratio; R/B = respiration/biomass ratio; R/A = respiration/assimilation ratio; P/R = production/respiration ratio; NE = net efficiency; F = fishing mortality (years^{-1}); M2= predation mortality (years^{-1}); M0 = other natural mortality (years^{-1}); F/Z = exploitation rate; OI = omnivory index; FD = flow to detritus (t·km^{-2}·years^{-1}); TL = trophic level.

Functional group	**Bf**	**P/B**	**Q/B**	**EE**	**TL**	**P/Q**	**R/B**	**R/A**	**P/R**	**NE**	**F**	**M2**	**MO**	**F/Z**	**OI**	**FD**
1. Dolphins	0.010	0.03	12.32	0.00	4.07	0.002	9.83	0.997	0.003	0.003	0.00	0.00	0.03	0.000	0.58	0.02
2. Seabirds	0.003	4.47	70.89	0.00	3.01	0.063	52.24	0.921	0.086	0.079	0.00	0.00	4.47	0.000	0.76	0.05
3. Large pelagic fishes	0.095	0.20	1.45	0.28	3.63	0.139	0.96	0.826	0.211	0.174	0.06	0.00	0.15	0.281	1.02	0.04
4. Benthic sharks	0.068	0.65	5.30	0.58	3.43	0.123	3.58	0.846	0.182	0.154	0.30	0.08	0.27	0.459	0.70	0.09
5. Rays and skates	0.006	1.20	4.36	0.72	4.00	0.276	2.29	0.655	0.526	0.345	0.85	0.01	0.34	0.709	0.20	0.01
6. Demersal ichthyophagous fishes	0.038	1.56	5.48	0.99	3.96	0.285	2.82	0.643	0.554	0.357	0.88	0.67	0.02	0.560	0.35	0.04
7. Pelagic ichthyophagous fishes	0.096	1.42	4.65	0.47	3.97	0.305	2.30	0.619	0.615	0.381	0.61	0.05	0.75	0.432	1.40	0.16
8. Anglerfishes	0.034	1.16	3.90	0.72	4.15	0.297	1.96	0.629	0.590	0.371	0.83	0.00	0.32	0.719	0.74	0.04
9. Juvenile hake	0.032	1.53	10.83	0.85	3.64	0.141	7.14	0.824	0.214	0.176	0.00	1.30	0.23	0.000	0.18	0.08
10. Adult hake	0.112	1.48	4.58	0.13	3.85	0.323	2.18	0.596	0.678	0.404	0.00	0.19	1.29	0.000	0.44	0.25
11. Mullets	0.031	1.85	6.36	0.99	3.46	0.292	3.23	0.636	0.574	0.364	1.25	0.58	0.02	0.674	0.21	0.04
12. Blue whiting	0.196	0.83	6.07	0.99	3.71	0.136	4.03	0.830	0.205	0.170	0.48	0.33	0.01	0.586	0.11	0.24
13. Sardine	2.848	0.81	9.56	0.88	2.17	0.084	6.84	0.894	0.118	0.106	0.11	0.60	0.10	0.136	0.19	5.72
14. Anchovy	0.293	1.05	9.87	0.96	3.26	0.107	6.84	0.867	0.154	0.133	0.30	0.71	0.04	0.285	0.10	0.59

Table 4.1 (Continued)

Functional group	Bf	P/B	Q/B	EE	TL	P/Q	R/B	R/A	P/R	NE	F	M2	MO	F/Z	OI	FD
15. Small pelagics	0.230	2.59	8.98	0.92	3.08	0.288	4.60	0.640	0.563	0.360	1.81	0.56	0.22	0.699	0.04	0.46
16. Flatfishes	0.036	0.87	8.40	0.96	3.50	0.104	5.84	0.870	0.149	0.130	0.30	0.53	0.04	0.347	0.41	0.06
17. Benthopelagic fishes	0.186	1.17	10.11	0.95	3.28	0.115	6.92	0.856	0.169	0.144	0.41	0.70	0.06	0.351	0.10	0.39
18. Mesopelagic fishes	0.368	1.33	10.26	0.99	3.12	0.130	6.88	0.838	0.193	0.162	0.00	1.31	0.02	0.002	0.28	0.76
19. Mackerels	0.125	0.70	5.95	0.88	3.52	0.118	4.06	0.853	0.172	0.147	0.34	0.27	0.08	0.490	0.12	0.16
20. Horse mackerels	0.276	0.79	7.02	0.90	3.41	0.112	4.83	0.860	0.163	0.140	0.34	0.36	0.08	0.437	0.10	0.41
21. Gobiids	0.127	1.05	10.57	0.97	3.11	0.099	7.41	0.876	0.141	0.124	0.05	0.96	0.03	0.051	0.23	0.27
22. Gelatinous plankton feeders	0.153	1.67	6.55	0.98	3.66	0.255	3.57	0.682	0.467	0.318	0.29	1.34	0.03	0.176	0.10	0.21
23. Sparids	0.006	2.64	6.64	0.99	3.43	0.398	2.67	0.502	0.990	0.498	1.95	0.66	0.03	0.737	0.21	0.01
24. Suprabenthos feeders	0.030	1.06	7.00	0.98	3.40	0.151	4.54	0.811	0.233	0.189	0.38	0.66	0.02	0.356	0.17	0.04
25. Natantia feeders	0.086	1.33	6.78	0.95	3.57	0.196	4.09	0.755	0.325	0.245	0.79	0.47	0.06	0.596	0.39	0.12
26. Benthopelagic cephalopods	0.042	3.20	9.10	0.96	3.66	0.352	4.08	0.560	0.784	0.440	1.52	1.56	0.12	0.475	0.57	0.08
27. Benthic cephalopods	0.014	3.10	8.80	1.00	3.74	0.352	3.94	0.560	0.787	0.440	1.19	1.91	0.00	0.385	0.43	0.03
28. Octopuses	0.070	3.00	8.50	0.85	3.42	0.353	3.80	0.559	0.789	0.441	2.31	0.23	0.46	0.769	0.66	0.15
29. Blue and red shrimp	0.011	2.11	20.57	0.94	3.34	0.103	14.35	0.872	0.147	0.128	1.17	0.82	0.12	0.553	0.16	0.04
30. Deep water rose shrimp	0.013	2.40	24.12	0.29	2.96	0.099	16.89	0.876	0.142	0.124	0.67	0.02	1.71	0.277	0.15	0.09

Table 4.1 (Continued)

Functional group	Bf	P/B	Q/B	EE	TL	P/Q	R/B	R/A	P/R	NE	F	M2	MO	F/Z	OI	FD
31. Norway lobster	0.029	5.16	19.84	0.20	2.94	0.260	10.71	0.675	0.481	0.325	0.57	0.48	4.10	0.111	0.50	0.23
32. Crabs	0.396	1.93	7.07	0.99	2.92	0.273	3.73	0.659	0.518	0.341	0.14	1.78	0.01	0.070	0.32	0.56
33. Other shrimps	0.731	1.89	8.49	0.94	2.98	0.222	4.90	0.722	0.385	0.278	0.02	1.76	0.11	0.012	0.42	1.32
34. Suprabenthos	0.616	7.87	52.10	0.90	2.13	0.151	28.60	0.784	0.275	0.216	0.00	7.04	0.83	0.000	0.12	10.14
35. Worms	6.180	5.61	30.00	0.30	2.03	0.187	12.39	0.688	0.453	0.312	0.00	1.70	3.91	0.000	0.03	98.33
36. Echinoderms	0.849	0.24	2.75	0.98	2.02	0.086	1.83	0.886	0.129	0.114	0.01	0.22	0.00	0.041	0.02	0.59
37. Bivalves and gastropods	2.118	1.63	6.78	0.13	2.10	0.240	2.44	0.600	0.667	0.400	0.00	0.22	1.41	0.000	0.10	8.74
38. Other benthic invertebrates	1.244	1.04	4.00	0.21	2.29	0.260	1.76	0.629	0.591	0.371	0.01	0.21	0.82	0.008	0.26	2.51
39. Microzooplankton	3.705	32.32	120.0	0.41	2.02	0.269	63.68	0.663	0.507	0.337	0.00	13.32	18.99	0.000	0.02	159.3
40. Meso- and macrozooplankton	0.682	14.97	49.82	0.99	2.63	0.300	19.90	0.571	0.752	0.429	0.00	14.83	0.14	0.000	0.28	10.3
41. Gelatinous plankton	0.247	12.89	49.38	0.38	2.75	0.261	26.61	0.674	0.484	0.326	0.00	4.91	7.99	0.000	0.26	4.41
42. Phytoplankton	6.220	146.2	–	0.38	1.00	–	–	–	–	–	0.00	56.20	89.95	0.000	–	559.5
43. Benthic macrophytes	0.405	1.08	–	0.95	1.00	–	–	–	–	–	0.00	1.03	0.05	0.000	–	0.02
44. Discards	0.106	–	–	0.86	1.00	–	–	–	–	–	–	–	–	–	–	0.03
45. Detritus	75.6	–	–	0.41	1.00	–	–	–	–	–	–	–	–	–	0.29	–

One of the consumers, *Merluccius merluccius*, was split into a multi-stanza group to ensure consistency between ontogenetic groups, capturing diet shifts and/or different exploitation patterns (Christensen and Walters 2004; Heymans et al., 2016), i.e. adult hake (i.e. ≥ 15 cm) and juvenile hake (i.e. < 15 cm). The fishery in the model is represented by the four main fleets targeting the modeled species: bottom trawl, purse seine, longlines, and small-scale fisheries. Both the official landing data and the estimated percentage of discarded species were taken from the IEO Database (Table A.4.2).

Most biomass data (Table 4.1) were estimated from a series of scientific bottom trawl surveys (MEDITS) by the swept area method taking into account the weight of each stratum in the total surface area (Bertrand et al., 1998).

Phytoplankton biomass was estimated using satellite imagery data (https://neo.sci.gsfc.nasa.gov). Also, the biomass of detritus was estimated using the empirical equation by Pauly et al. (1993):

$$\text{Log } D = -2.41 + 0.954 \cdot \text{Log } Pp + 0.863 \cdot \text{Log } E \qquad (3)$$

where D is detritus biomass (gr $C \cdot m^{-2}$), Pp is primary production (gr $C \cdot m^{-2} \cdot yr^{-1}$), and E the depth of the light penetration (m).

The P/B and Q/B ratios were estimated through empirical equations (Palomares and Pauly, 1998; Christensen et al., 2005) obtained from literature or using assumptions from other models and corrected following Optiz (1996) (Tables A.4.3 and A.4.4).

The diet data matrix was constructed based on either field studies in GSA6 (i.e., stomach contents) (García-Rodríguez et al., 2020, 2021) or diet data obtained from the literature for the same species in similar ecosystems in cases where information was not available for the studied area (Table A.4.5).

To build the diet composition matrix, a statistical analysis was previously performed to determine which of these species showed differences in their dietary preferences between the Gulf of Alicante and the rest of the GSA6. Further differences between diets were explored with non-parametric analysis of similarities (ANOSIM) that are based on multi-dimensional scaling (MDS) of the Bray–Curtis dissimilarity index. In the case of those species showing differences in their dietary patterns, the specific diets of the Gulf of Alicante were used. For the rest of the species that did not show differences, the diet characterized in GSA6 was used.

Migratory patterns of mammals, seabirds, and large pelagic fishes were included in the ecosystem by modeling a proportion of their diet composition as an import (following Coll et al., 2006; Christensen et al., 2008). 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).

For the mass-balancing model, it is required to maintain the laws of thermodynamics following the rules described by Darwall et al. (2010). Therefore, once the model has been balanced and all the Ecotrophic Efficiencies (EE) were <1; Gross food conversion efficiency (GE) presented, in general, values between 0.1 and 0.3; Net efficiency (NE) presented a default value of 0.2; Respiration/Assimilation Biomass ratio <1; Production/Respiration ratio <1. In addition, it was useful to check the PREBAL diagnostics, including estimates of biomasses, biomass ratios, vital rates, and vital rates ratios (Link, 2010). More information about the balancing procedure is provided in the Supplementary Material (A.4.1).

Pedigree index

To check the uncertainty and quality of input data sources, the pedigree index was applied (Christensen et al., 2008). We used the default value of uncertainty or confidence intervals assigned to each parameter for each functional group to estimate an overall index of model quality. This index varies between 0 (low quality) and 1 (high quality), enabling a comparison between models.

Ecosystem structure and functioning

The Ecopath model implemented provides a snapshot of the interactions of the Gulf of Alicante ecosystem in early 2010 and can be used to calculate several ecological indicators. In this study, we selected ecological indicators related to functional groups and trophic interactions, to the theory of ecosystem maturity (sensu Odum, 1969; Christensen, 1995) that were robust to model comparisons (Heymans et al. 2014; Moloney et al., 2005) and using the ECOIND plug-in (Coll and Steenbeek, 2017).

Functional groups and trophic interactions

The indicators that allow analysis of each functional group to investigate their roles within the GoA ecosystem (Table 1) were atural mortality rate (M) that can be split into non-predation natural mortality rate (M0) and the predation natural mortality rate (M2). The trophic level (TL) per functional group was also calculated, which identifies the trophic position of organisms within food webs by identifying the source of energy for each organism. Following an established convention, fractional TLs are calculated by assigning producers (and often also detritus) to TL= 1 and consumers to a TL= 1 plus the average TL of their prey, weighted by their proportion in weight in the predator's diet (Christensen, 1996). The TL is computed as TL = 1+

(Σ DC_{ij}) (NT_j), where DC_{ij} is the proportion of prey *j* in the diet of the predator *i* and NT_j is the trophic level of prey *j* (Christensen and Pauly, 1992). Besides, the Omnivory Index (OI) was included, highlighting the trophic specialization of each group and is computed as the variance of the TL of their prey *i* (Christensen et al., 2008) (Table 4.1).

The Mixed Trophic Impact analysis (MTI) quantifies the trophic impact that a hypothetical change in the biomass of a functional group would have on each group including fisheries (Ulanowicz and Puccia, 1990). Thus, it is possible to investigate the total effect of one functional group on all the others in a given model, allowing the estimation of keystoneness (KS) for the functional groups. A keystone species is defined as one whose impact on the community or ecosystem is high and disproportionately large relative to its abundance (Power et al., 1996).

The KS index attempts to reconcile the importance of a species concerning its biomass and the relative importance in the ecosystem. There are currently three formulations of the KS in EwE that formulate the biomass ratio differently (Power et al. 1996; Libralato et al., 2006; Valls et al., 2015). We selected the Valls Keystone Index, which tries to reach a compromise between the biomass and impact components of the indicator (Valls et al., 2015). The index is calculated as $KS = IC \cdot BC$, where IC is the impact component and BC is the biomass component. The IC represents the overall effect of group i on all other groups in the food web excluding the impact on i itself and the impacts on dead groups and fleets (Libralato et al., 2006). The BC is defined as the rank of the group according to their biomass values in descending order (Valls et al., 2015).

Ecosystem indicators:

Several indicators allowed us to analyze the ecosystem again criteria describing the stage of maturity, efficiency, health, and development. Several indicators were used to describe the structure and functioning of GoA ecosystem: Total System Throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), considered as an overall measure of the "ecological size" of the system and the sum of all trophic flows within the system; Total Consumption (TQ, $t \cdot km^{-2} \cdot year^{-1}$); Exports (E, $t \cdot km^{-2} \cdot year^{-1}$); Total Respiration (TR, $t \cdot km^{-2} \cdot year^{-1}$) and Total Flow to Detritus (TFD, $t \cdot km^{-2} \cdot year^{-1}$) (Ulanowicz, 1986); Total Production (TP, $t \cdot km^{-2} \cdot year^{-1}$); Net Production (NP, $t \cdot km^{-2} \cdot year^{-1}$); Total Biomass excluding detritus (TB, $t \cdot km^{-2}$); the ratios Primary production/TST (Pp/TST); TFD/TST; TQ/TST; TR/TST; E/TST; Pp/P; Total Primary Production/Total Respiration (Pp/R) and total Primary Production/Total Biomass (Pp/B, $t \cdot km^{-2} \cdot year^{-1}$).

Other indicators of food-web complexity were estimated: the System Omnivory Index (SOI), defined as the average of the OIs of each consumer group, weighted by the logarithm of their consumption (Christensen and Walters, 2004); and the Finn's Cycling Index (FCI, %), defined as the percentage of all flows that are recycled in the trophic network (Finn, 1976). FCI is an index used to measure the recycling and development of an ecosystem, although it is also linked to stress and its stability (Odum, 1969). Thus, ecosystems, where recycling is considerable, are stable and have a greater capacity to resist disturbances (Christensen, 1995). Finally, Finn's mean Path Length (MPL) represents the number of functional groups that a flow connects within the ecosystem (Finn, 1976).

We calculated the Transfer Efficiency (TE) from primary producers and from detritus, which is the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem or transferred to higher trophic levels through consumption (Lindeman, 1942).

Ecological indicators: ECOIND

In addition, the ECOIND plug-in (Coll and Steenbeek, 2017) was used to calculate standardized ecological indicators. This plug-in uses additional species traits and adds new capabilities to EwE facilitating its applications into biodiversity and conservation-based frameworks. ECOIND allows calculation of the following type of indicators:

- Biomass-based indicators: based on the abundance of organisms in the food web. These indicators include total biomass (Total B) of species in the ecosystem; biomass of commercial species (Commercial B); biomass of fish (Fish B); invertebrates (Invertebrates B) and the ratio of the two latter (Invertebrates/Fish B); biomass of demersal (Demersal B) and Pelagic (Pelagic B) organisms and their ratio (Demersal/Pelagic B) and the Kempton's biodiversity index (Q). The Q index is proportional to the inverse slope of the species-abundance curve and is a proxy of ecosystem biodiversity (Ainsworth and Pitcher, 2006).
- Catch-based indicators: based on the catch and discard species in the ecosystem. These indicators include total catch (Total C) and the catch of fish (Fish C); invertebrates (Invertebrates C) and their ratio (Invertebrates/Fish C); demersal (Demersal C); Pelagic (Pelagic C); catch of organisms and their ratio (Demersal/Pelagic C); catch of predatory organisms (Predatory C), defined as organisms with trophic level (TL) ≥ 4, and total discarded catch (Discards).
- Trophic-level based indicators: since fishing selectively removes organisms from the food web, the trophic and size structure of the ecosystem may be altered. Therefore, these six indicators based on the trophic level concept and can be used to understand this effect (Shannon et al., 2014). These indicators include Tropic level (TL) of the catch (TL catch) (Christensen, 1996; Pauly et al., 1998); the Marine Trophic Index (MTI, or TLc including organisms with TL ≤ 3.25) (Pauly et al., 2005); TL of the community including all organisms (TL

co); TLco including organisms with TL ≤ 2 (TLco 2); TLco including organisms with TL ≤ 3.25 (TLco 3.25), and TLco including organisms with TL ≤ 4 (Tlco 4).

- Species-based indicators: includes eight indicators specifically based on species traits and conservation status: The Intrinsic Vulnerability Index of the catch (IVIc) is a weighted mean of the vulnerability of exploited fish species (Cheung et al., 2007); the biomass (B) of endemic species in the community (Endemics B) and in the catch (C) (Endemics C) provide a measure of how abundant endemic species are in the ecosystem (Coll et al., 2012, 2016, 2015b); the biomass of endangered species in the community (UICN species B) and in the catch (IUCN species C) using the IUCN (International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015).

Role of fishing activities

We selected those indicators that can give information regarding fishing intensity and impacts in the ecosystem: the mean trophic level of the catch (mTLc), calculated as the weighted average of the TL of caught species and the mean trophic level of the community (mTLco), which was estimated as the weighted average of the TL for functional groups with a TL>2 (Christensen, 1996); the Primary Production Required to sustain the fishery (%PPR, considering Pp); and the Primary Production Required to sustain the fishery (%PPR, considering Pp + detritus) (Pauly and Christensen 1995), the loss in production index (Lindex), which represents the loss in secondary production due to fishing, and the probability of an ecosystem being sustainably fished (Psust), which can be used to determine the ecosystem effects of fishing (Libralato et al., 2008).

Finally, the fishing mortality 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 ecological group.

Comparative analysis with other adjacent ecosystems

To test our original hypothesis, we contrasted results obtained from our GoA model with other models previously implemented in the Mediterranean Sea as the Northwestern Mediterranean model (NWM) (Corrales et al., 2015) and in the Atlantic area as the Gulf of Cadiz model (GoC) (Torres et al., 2013). A similar methodology was used to build the three models, which are similar in terms of ecological structure (Heymans et al., 2016) and cover similar bathymetric range along the Spanish Mediterranean Coast including the Gulf of Cadiz in the Atlantic side.

4.3 Results

Quality and uncertainty of the model

The Pedigree index calculated by the model was 0.55. The majority of sources of uncertainty were associated with the biomass estimations for several groups, in particular for the invertebrate groups (Table 4.2). However, most of the diet composition data for predators representing the food web in the study area as well as data regarding landings and discards were all collected at local level and therefore showed a low degree of uncertainty.

Description by functional group

Overall, ecotrophic efficiencies were high (EE>0.95), mainly for those groups specially predated and exploited in the system, such as fish and invertebrate groups (e.g., Demersal ichthyophagous fishes, Mullets and Crabs), pointing out that total mortality in the system was mainly driven by predation and fishing. On the other hand, those groups without predation mortality or exploitation such as top predators showed lower EE (e.g., Dolphins, Seabirds and Large pelagic fishes) (Table 4.1).

Trophic levels ranged from TL = 1 for primary producers and detritus group, to TL = 4.15 for Anglerfishes and 4.07 for Dolphins. Within the fish community, Sardine and Small pelagics showed the lowest values (2.17 and 3.08, respectively) due to the dominant presence of phytoplankton and zooplankton groups in their diet. In the case of Cephalopods, TLs ranged between 3.74 for Benthic cephalopods to 3.42 for Octopuses. For crustaceans, natantia presented higher trophic levels (e.g., Blue and red shrimp, 3.34) than reptantia (Crabs, 2.92) (Table 4.1).

The partition of natural mortality (M) beyond planktonic groups showed higher values of mortality caused by predation (M2) for Benthic cephalopods, Crabs, Other shrimps, Worms, Benthopelagic cephalopods, Gelatinous plankton feeders and Mesopelagic fishes. Concerning non-predation natural mortality (M0) and also beyond planktonic groups, Seabirds, Norway lobster, Worms and Deep water rose shrimp showed the highest values (Table 4.1).

Table 4.2 Summary statistics and ecosystem indicators for the Gulf of Alicante in comparison with models of nearby areas. GoA= Gulf of Alicante; NWM= Northwestern Mediterranean Model; GoC = Gulf of Cadiz. All units are provided in the table.

Ecosystem Information	**GoA**	**NWM**	**GoC**	**Units**
Years modelled	2011	1999-2003	2009	
Depth range	50-800	0-1000	15-800	m
Area modelled	7,085	45,547	7,224	km^2
Number of functional groups	45	54	43	
Number of primary producers	2	4	1	
Ecopath Pedigree index	0.55	0.62	0.63	
Ecosystem Indicators				
Sum of all Consumptions (TQ)	789.04	897.27	1946.9	t·km^{-2}·year^{-1}
Sum of all Exports (E)	511.93	1088.08	2233.7	t·km^{-2}·year^{-1}
Sum of all Respiratory Flows (TR)	398.19	279.55	955.1	t·km^{-2}·year^{-1}
Sum of all Flows to Detritus (TFD)	866.77	1493.14	2599.2	t·km^{-2}·year^{-1}
Total System Throughput (TST)	2565.93	3758.03	7734.9	t·km^{-2}·year^{-1}
Sum of all Production (TP)	1095.33	1599.93	3704.4	t·km^{-2}·year^{-1}
Calculated Total Net Primary Production (NPp)	909.47	1366.1	3187.7	t·km^{-2}·year^{-1}
Total Primary Production/Total Respiration (Pp/R)	2.28	4.89	3.3	
Net System Production (NT)	511.27	1086.55	2231.6	t·km^{-2}·year^{-1}
Total Primary Production/Total Biomass (Pp/B)	31.30	32	39.8	
System Omnivory Index (SOI)	0.26	0.19	0.18	
Total Biomass (excluding detritus) (TB)	29.06	42.69	80.02	t·km^{-2}
Mean Trophic Level of the community (mTLco)	1.18	1.38	1.61	
mTLco (excluding TL=1)	2.32	2.48	2.55	

Table 4.2 (Continued)

Fishery Indicators	**GoA**	**NWM**	**GoC**	**Units**
Total Catches (TC)	1.94	4.18	4.55	$t \cdot km^{-2} \cdot year^{-1}$
Mean Trophic Level of the Catch (mTLc)	3.16	3.13	3.32	
Gross Efficiency of the fishery (GE)	0.002	0.003	0.001	
Primary Production Required to sustain the fishery (PpR, considering Pp)	16.28	12.08	12.97	%
Primary Production Required to sustain the fishery (PpR, considering Pp + detritus)	22.67	17.36	16.45	%
Psust	66.2	28.4	22.8	%
Recycling Indicators				
Finn's cycling index (of total throughput) (FCI)	9.33	9.12	3	% of TST
Finn's mean Path Lenght (MPL)	2.82	2.75	2.43	
Predatory cycling index (PCI)	2.04	0.56	8	% of TST without detritus
Mean Transfer Efficiency (mTE)	13.9	14.3	14.3	%
TE From primary producers	14.8	15.4	15.5	%
TE From detritus	12.9	13.3	18.6	%

Mixed trophic impact and Keystoness

The results of the mixed trophic impact routine (MTI) showed that all groups had a negative impact on themselves due to within-group competition, especially for Worms, Microzooplankton, Gelatinous plankton, Large pelagic fishes, Gelatinous plankton feeders, and Phytoplankton (Fig. 4.3.1). An increase of Adult hake would have a negative impact on Juvenile hake due to cannibalism. In addition, an increase of Microzooplankton could have an indirect negative impact on Bivalves and gastropods and Sardine due to competition for preys. Numerous functional groups in the model were positively impacted by the groups at the base of the food web such as Phytoplankton, Micro-, Meso- Macrozooplankton, Suprabenthos and Other benthic invertebrates.

Regarding the fishing activity, the bottom trawling fleet had the highest impact on most ecosystem compartments and the largest impacts on some demersal groups, primarily Anglerfishes, Deep water rose shrimp, Rays and skates, Benthic sharks, Octopuses, Blue and red shrimp, Adult hake and, to a lesser extent Norway lobster, Blue whiting and Mullets. The purse seine fishery showed important negative impacts on their target species (small pelagics) and Demersal ichthyophagous fishes possibly due to the removal of prey. There was a slight negative impact on Dolphins because they compete for their prey. The small scale fishery had a negative impact on Sparids and, to a lesser extent, on Octopuses, Pelagic ichthyophagous fishes and Mullets. The longline fishery presented large negative impacts on its main target species (Large pelagic fishes).

With respect to the interactions between fleets, bottom trawls produced the highest negative impact on small-scale fisheries. Bottom trawl, longlines, and purse seine revealed strong competition between themselves while small-scale fisheries did not.

The keystoneness index analysis using Valls Keystone Index identified top predators such as Adult hake, Dolphins, Anglerfishes and Octopuses as potential keystone species in the GoA ecosystem (Fig. 4.3.2).

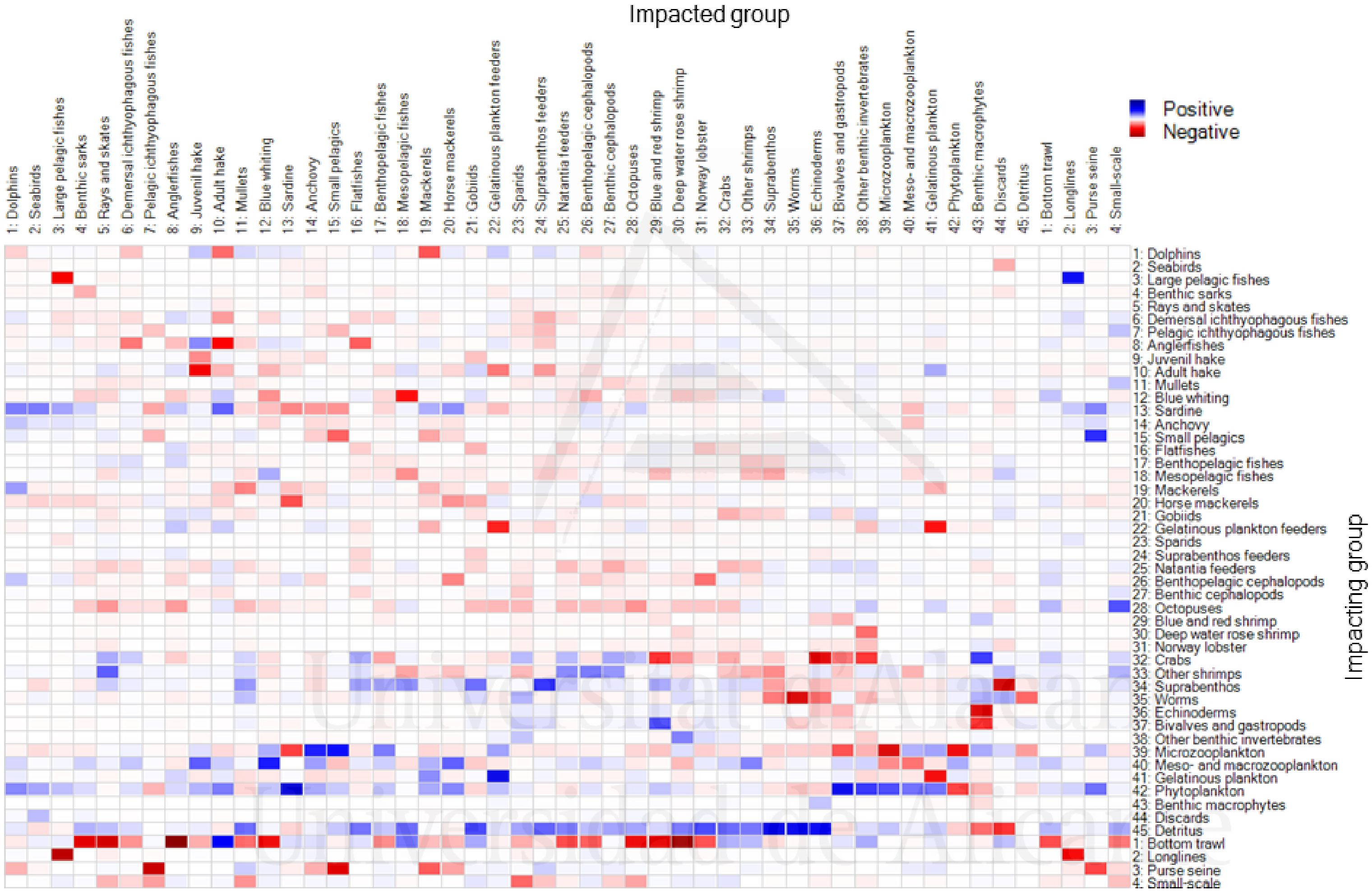

Fig. 4.3.1 Mixed trophic Impact (MTI) analysis of the GoA model. Negative (red) and positive (blue) impacts are represented.

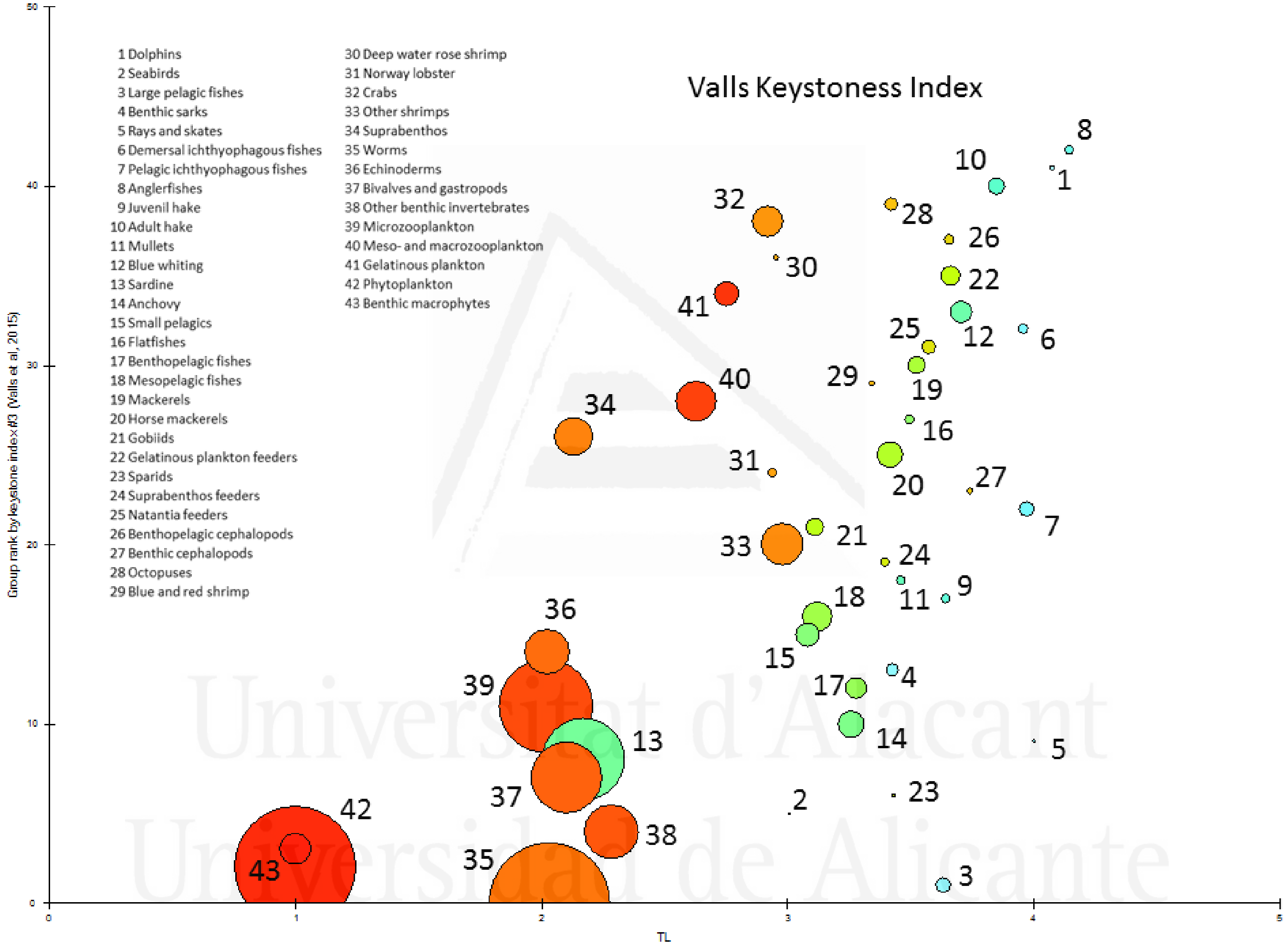

Fig. 4.3.2 Functional groups plotted against keystone index of Valls and trophic level. The numbers identify the functional groups of the model (see Table 1). Circle size is proportional to the biomass of the functional group.

Trophic flows and ecosystem indicators

The flow diagram representing the main links between functional groups and the flow of energy illustrated that main trophic flows originated from the trophic groups located at the base of the trophic web (*Detritus* and *Phytoplankton*), which transfer their energy to groups with higher TLs (Fig. 4.3.3). Among fish groups, small pelagics such as *Sardine* were the most important component in terms of flows to detritus.

Of the Total System Throughput (TST%), 30.8% of the flows were consumed in the ecosystem, 33.8% became part of the detritus, 15.5% were attributed to respiration, and of the remaining 20% considered as export outside the ecosystem, 99% was due to detritus. Thus, the ecosystem was dominated mainly by detritus flow and consumption.

The mean transfer efficiency (mTE) obtained from primary producers up the food web (14.9%) was higher than the mTE of the detritus food web (13.0%), which highlighted that the GoA ecosystem was more limited by primary producers than by detritus (Table 4.2).

The total biomass supported by the ecosystem was estimated at 104.8 t*km^{-2}, which corresponded to 48.3%, 13.8%, and 37.9% of the demersal, pelagic, and planktonic domains, respectively. The dominance of *Phytoplankton* (21.3%), *Worms* (21.2%), *Microzooplankton* (12.7%) and *Sardine* (9.8%) was remarkable. In addition, 93.9% of the total production came from *Phytoplankton* (83.0%) and *Microzooplankton* (10.9%), while *Microzooplankton* (56.4%) and *Worms* (23.5%) concentrated the 79.8% of the total consumption. In the case of flow to detritus, it was dominated by *Phytoplankton* (64.6 %), *Microzooplankton* (18.4 %) and *Worms* (11.4 %).

The Pp/R ratio, close to unity in mature ecosystems, was high in the GoA, which indicates that there was a higher production (2.28 times more) of energy in the ecosystem. In the case of the Pp/B, the GoA presented a high value (31.3), reflecting a low level of biomass accumulation within the system compared to its productivity. The system omnivory index, also correlated with system maturity, showed an intermediate value (0.26) when compared with other Mediterranean regions, highlighting a certain level of food chain complexity of the system. In this context, it is noteworthy to mention the low values of the functional groups *Microzooplankton* (0.02), *Echinoderms* (0.02), *Worms* (0.03) and *Sardine* (0.19), whilst those found with a more diverse diet were *Pelagic ichthyophagous fishes* (1.4), *Large pelagic fishes* (1.02) and *Seabirds* (0.76). The importance of cycling through Finn´s cycling index and the mean Path Length revealed differences between the GoA and GoC ecosystems (Table 4.2).

ECOIND analysis

Concerning the Demersal/Pelagics Biomass-based indicator (1.35), the dominance of the demersal compartment in the GoA model was highlighted (Table 4.3), which is in line with results from the GoC (1.57), and in contrast with those obtained from the NWM (0.42). In the same line were the results of the ratio Invertebrates/Fish Biomass-based indicator. Similarly, this ratio showed a high proportion of the invertebrate compartment in the GoA (3.09) and GoC areas (1.67), in contrast with the NWM results (0.29), with low relevance of invertebrates. In turn, the biomass of fish species was much lower in GoA (5.47 t·km^{-2}) if compared with the values obtained for NWM (10.59 t·km-^{2}) and GoC (16.27 t·km^{-2}) (Table 4.3).

Regarding Catch-based indicators, total catch in GoA (1.84 t·km^{-2}) was lower than that obtained in NWM (4.14 t·km^{-2}) and GoC (4.55 t·km^{-2}). In the case of the pelagic fraction, the lowest catches were observed in GoA (1.16 t·km^{-2}). In this case, the Demersal/Pelagics Catch-based indicator showed intermediate values (0.55 t·km^{-2}) between NWM and GoC (0.30 and 0.80 t·km^{-2} respectively). Likewise, Trophic-based indicators analyzed showed intermediate values for the GoA model (3.16) between NWM and GoC (0.11 and 3.32, respectively) (Table 4.3).

With respect to Species-based indicators, the 'Intrinsic vulnerability index of the catch' (IVIc) in the GoA showed the lower values in comparison with the other two models. Similar results were obtained for the 'biomass of endangered species in the community using the IUCN' (International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015) (IUCN species B) and in the 'catch of endangered species in the community using the IUCN' (IUCN species C) (Table 4.3).

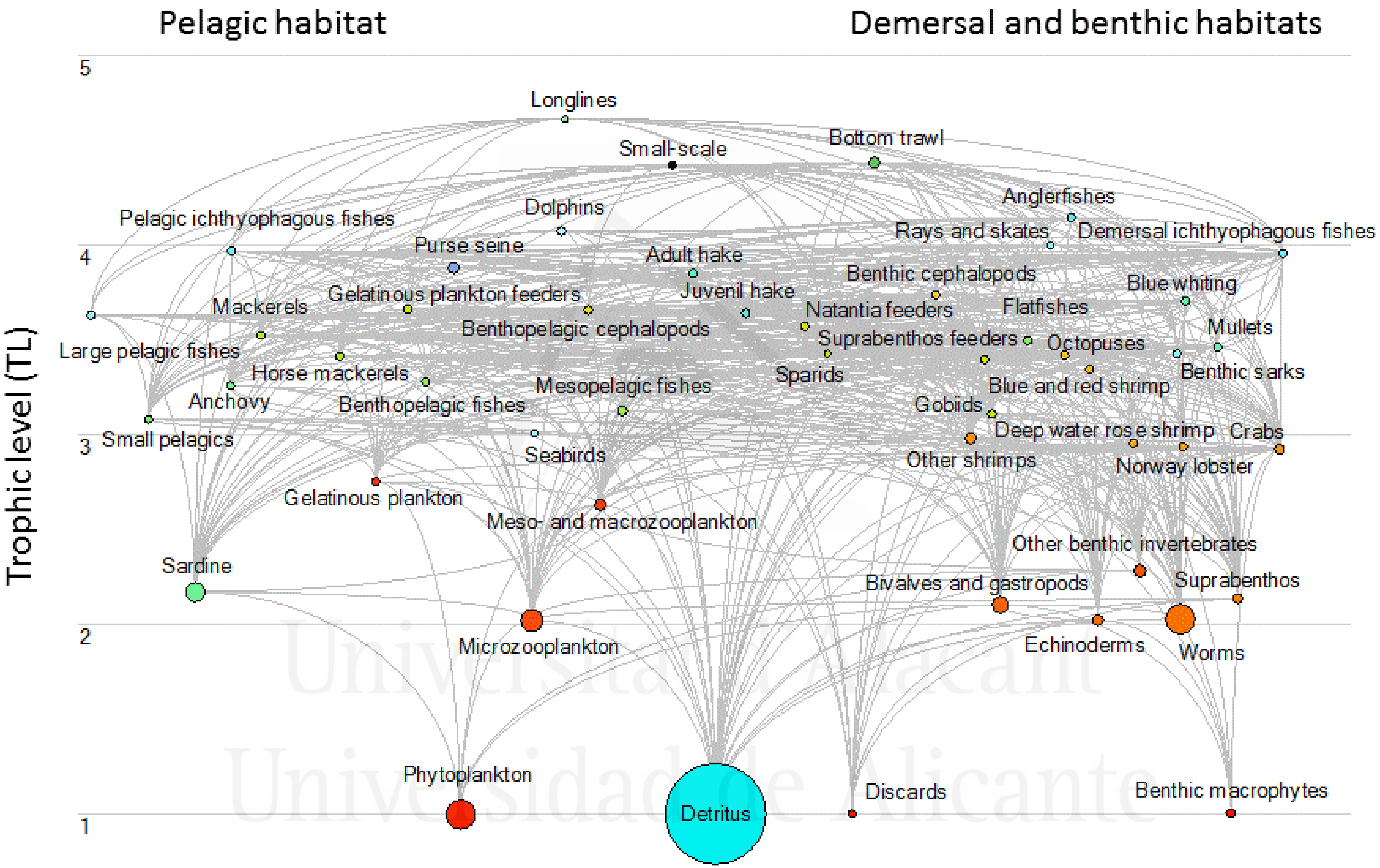

Fig. 4.3.3 Flow diagram defining the structure of the Gulf of Alicante Ecopath model. The scale on the left corresponds to the trophic level and circles are scaled to the group's biomass.

Table 4.3 Ecological indicators comparing across the Gulf of Alicante (GoA) (results from this study), the Northwestern Mediterranean (NWM) (Corrales et al. 2015) and the Gulf of Cadiz (GoC) (Torres et al. 2013).

Indicator	Description	NWM (1999-2003)	GoC (2009)	GoA (2011)	Units
A. Biomass-based					
Total B	Total biomass (B)	130.48	152.10	104.76	t·km^{-2}
Commercial B	Biomass (B) of commercial species	16.64	29.26	9.23	t·km^{-2}
Fish B	Biomass (B) of fish species	10.59	16.27	5.47	t·km^{-2}
Invertebrates B	Biomass (B) of invertebrate species	3.05	27.24	16.89	t·km^{-2}
Invertebrates/Fish B	Biomass (B) of invertebrates over fish	0.29	1.67	3.09	
Demersal B	Biomass (B) of demersal species	4.10	19.63	12.38	t·km^{-2}
Pelagic B	Biomass (B) of pelagic species	9.65	12.50	9.15	t·km^{-2}
Demersal/Pelagic B	Biomass (B) of demersal over pelagic species	0.42	1.57	1.35	
Predatory B	Biomass (B) of predatory organisms with trophic level ≤ 4	0.86	0.49	0.05	t·km^{-2}
Kempton's Q	Kempton's biodiversity index (Q)	8.05	5.49	6.39	
B. Catch-based					
Total C	Total Catch (C)	4.14	4.55	1.84	t·km^{-2}
Fish C	Catch (C) of all fish species	3.60	3.23	1.47	t·km^{-2}
Invertebrate C	Catch (C) of all invertebrate species	0.53	1.32	0.32	t·km^{-2}
Invertebrates/Fish C	Catch (C) of invertebrates over fish	0.15	0.41	0.22	
Demersal C	Catch (C) of demersal species	0.95	2.02	0.63	t·km^{-2}
Pelagic C	Catch (C) of pelagic species	3.18	2.53	1.16	t·km^{-2}
Demersal/pelagic C	Catch (C) of demersal over pelagic species	0.30	0.80	0.55	
Predatory C	Catch (C) of predatory organisms with trophic level 4	0.20	0.28	0.03	t·km^{-2}
Discards	Total discarded catch	0.86	1.13	0.19	t·km^{-2}

Table 4.3 (Continued)

Indicator	Description	NWM (1999-2003)	GoC (2009)	GoA (2011)	Units
C. Trophic-based					
TL catch	Tropic level (TL) of the catch	3.11	3.32	3.16	
MTI	Marine trophic index, trophic level (TL) of the catch (including organisms with TL ≤ 3.25)	3.64	3.68	3.55	
TL co.	Trophic level (TL) of the community (including all organisms)	1.39	1.61	1.28	
TL co. 2	Trophic level (TL) of the community (including organisms with TL ≤ 2)	2.49	2.55	2.32	
TL co. 3.25	Trophic level (TL) of the community (including organisms with TL ≤ 3.25)	3.63	3.71	3.54	
TL co. 4	Trophic level (TL) of the community (including organisms with TL ≤ 4)	4.13	4.18	4.11	
D. Species-based					
Intrinsic Vul. Index	Intrinsic Vulnerability Index of the catch	35.94	38.31	38.62	
Endemics B	Biomass (B) of endemic species in the community	0.08	0.00	0.00	$t{\cdot}km^{-2}$
Endemics C	Endemic species in the catch (C)	0.05	0.00	0.00	$t{\cdot}km^{-2}$
IUCN species B	Biomass (B) of IUCN-endangered species in the community	0.42	0.60	0.13	$t{\cdot}km^{-2}$
IUCN species C	IUCN-endangered species in the catch (C)	0.10	0.12	0.07	$t{\cdot}km^{-2}$

Fishing impacts

Octopuses, Sparids, Small pelagics, Benthopelagic cephalopods and Mullets presented the highest values of fishing mortality (F). Despite the high exploitation rates (F/Z), just a few groups (Sparids or Octopuses) exceeded the recommended rates (0.5) for overexploited demersal stocks (Mertz and Myers, 1998; Rochet and Trenkel, 2003) while Small pelagics, Mackerel, Horse mackerel and Pelagic ichthyophagous fishes exceeded the 0.4 recommended rate for overexploited pelagics stocks (Patterson, 1992) (Table 4.1).

The primary production required to sustain the fishery (%PPR) in the GoA during 2011 was 16.28%, taking into account only the primary producers. When considering both the primary producers and detritus, the value was 22.67%, suggesting the importance of detritivorous organisms within the catch. These values were the highest of all three compared models (Table 4.2). In turn, the probability of the GoA being sustainably exploited (P_{sust}) using the estimated Loss in production index (L_{index}) score was low (66%), but higher than values obtained for NWM and GoC ecosystems (28% and 23%, respectively) (Table 4.2).

4.4 Discussion

From a trophodynamic point of view, marine ecosystems off the Eastern Iberian coast have been poorly studied and there is still a need to fulfill that knowledge gap, particularly in the meso-scale. The underlying hypothesis of our study was that the singular characteristics of the Gulf of Alicante would cause an organization of the ecosystem that would differentiate it from neighboring ecosystems. These features should be reflected in a different food-web structure and functioning; thereby the Ecopath model presented here is the first attempt to test this hypothesis. The addition of the GoA model to the list of published studies available from the western Mediterranean Sea (e.g., Coll et al., 2006; Torres et al., 2013; Corrales et al., 2015) allows the possibility of further comparing these meso-scale marine ecosystems, testing the variability and similarities in the ecosystem structure along the north-south axes on the east coast of the Iberian Peninsula (western Mediterranean), including the Gulf of Cádiz in the Atlantic coast. With this study we cover an existing knowledge gap in terms of ecosystem modeling, with relevance to trophic ecology and the fisheries management. This study will also be relevant in the context of the MSFD and the new steps to follow towards the achievement of a Good Environmental Status (GES) within European Seas.

Our model was primarily based on data collected from local studies giving a pedigree index value of 0.55, in line with those obtained for nearby Ecopath models. This value places the model at the mid-upper end of the range reviewed for a large number of models worldwide (Morissette, 2007) and suggests that the inputs used in this model were of relatively high quality. This is especially true for the trophic data used in this model (García et al., 2020, García et al., 2021). However, the continuous incorporation of new empirical data from the region into the model can improve these results in the future. For example, estimations of

IUUs and recreational fleet data may be used in the future for a better understanding of the real impacts of fishing activity in the area.

Results from the trophic model (GoA) showed that the main differences found in comparison with neighboring areas are related to the lower primary production of the system (mainly influenced by local oceanographic conditions), which determines the higher importance of the demersal compartment, where most biomass was associated to the detritus food web, and lower catches.

Ecosystem structure and functioning of the Gulf of Alicante

High values of ecotrophic efficiencies and mortality rates suggested that the ecosystem is highly constrained by predation and fishing mortalities. The case of exploited fishes and invertebrate groups for which the EE were almost 1 is remarkable. The phytoplankton group also showed relatively high values in agreement with the oligotrophic nature of this ecosystem. These results contrast with those reported by Coll et al. (2006) and Corrales et al. (2015), who found in their models located northwards of GoA lower values of EE for some functional groups, suited to more productive ecosystems (Estrada, 1996; Agostini and Bakun, 2002).

Concerning the trophic levels, they were overall consistent with values published for those species in the Mediterranean Sea (Karachle and Stergiou, 2017) and other ecological models of nearby areas (Coll et al., 2006; Corrales et al., 2015; Torres et al., 2013). The low values of TL of Seabirds (TL=3.01), which are considered top predators, were in agreement with previously reported values as a consequence of the high percentage of discards in their diet, which is assumed to be parameterized as a detritus group and therefore, resulting in underestimated trophic levels (Coll et al., 2006).

The mixed trophic impact analysis highlighted the importance of groups located at the base of the food web such as Phytoplankton, Micro-, Meso- Macrozooplankton, Suprabenthos, Other benthic invertebrates, highlighting the importance of bottom-up flow control interactions occurring in the ecosystem. All of these findings, together with the important role of the detritus as a source of food, are consistent with those observed in the NWM and GoC models. However, we did not find a notable interaction between the pelagic and the demersal groups, which is in contrast with important bentho-pelagic coupling observed in other Mediterranean ecosystems (Agnetta et al., 2019; Ricci et al., 2019). This could be related to the higher productivity and high fishing pressure reported in these areas (Coll et al., 2006, Torres et al., 2013, Corrales et al., 2015).

The keystoneness index highlighted the importance of top predators in the ecosystem. Indeed, Dolphins and Octopuses were selected as keystone groups in other Mediterranean models (e.g. Southern Catalan Sea, Coll et al., 2006; 2013; Northeastern Ionian Sea, Piroddi et al., 2010; Carlucci et al., 2020).

Trophic flows and ecosystem statistics of the Gulf of Alicante

The main trophic flows in the GoA were originated from the functional groups located at the lower levels of the trophic network. Likewise, a large percentage of primary production flowed to the detritus, highlighting its role within the ecosystem, which evidenced the importance of this compartment. Similarly, the levels of primary production were shown to be lower than those obtained in the NWM and GoC models, which consequently resulted in a smaller size of the entire system in terms of flows (Ulanowicz, 1986). These results agreed with the TST values obtained for the three models compared, where the GoA has, by far, a different size in terms of total energy flow.

Regarding the transfer efficiencies (TEs), the highest values were observed for TLs II-IV, which can be related to the low productivity of the ecosystem (Shannon et al., 2003; Coll et al., 2006). This suggests a good coupling between preys and their predators, showing more efficient use of energy if compared to the average value of 10% estimated by Pauly and Christensen (1995) for marine ecosystems. The ecosystem then may be food limited (Shannon et al., 2003), in line with findings reported in the other three models. According to the attributes of maturity sensu Odum (1969), the Pp/R ratio in the GoA was the lowest value of the three compared models, especially in the case of NWM. Also, the Pp/B ratio, which is supposed to decrease in developing ecosystems, presented a high value in the GoA, in line with the results of NWM, but lower than GoC, where higher values of Pp/B ratio reflected a low level of biomass accumulation within the system.

In addition, the proportion of throughput cycled within the ecosystem (%FCI) was higher than in the other two models, which may be related to lower levels of stress, just as could be the case of NWM and GoC (e.g., higher fishing pressure). Likewise, food-web complexity indices such as the System Omnivory Index and Finn´s mean Path Length showed higher values than those obtained for compared models.

These results suggest that the GoA presents a higher level of complexity of internal flows, which is correlated with stability and maturity. This indicates that the system looks more like a web-like than a chain-like structure (Christensen, 1995), in contrast with the linearity detected in the food web of NWM and GoC ecosystems. Hence, the GoA may be in a higher development stage sensu Odum (1969), which remains efficient and stable, but is also delicate and vulnerable because it depends on the efficient and circular use of its biomass and it is primary production limited. These features may be partially related to the relatively lower fishing activity carried out in the area (see next section).

The impact of fishing activities in the Gulf of Alicante

The GoA showed lower values of catch per unit of surface compared to neighboring areas (Table 4.2) but high values of fishing mortality for most of the commercial groups in 2011 (Octopuses, Sparids, Small pelagics and Benthopelagic cephalopods) (Table 4.1). These results were in line with results obtained in available independent stock assessments (GCFM, 2012a, 2012b) and with results reported by nearby models. Regarding exploitation rates (F/Z), taking into account the recommended rates for overexploited demersal (0.5) and pelagics (0.4) stocks (Mertz and Myers, 1998; Rochet and Trenkel, 2003; Patterson, 1992), the three ecosystems compared presented high values for demersal and pelagic target species. In the case of the GoA, both, demersal and pelagic functional groups presented high exploitation rate values, namely for Rays and skates, Anglerfishes, Mullets, Octopuses, Small pelagics, Mackerels, Horse mackerels and Pelagic ichthyophagous fishes. In the NWM, exploitation rates were remarkable for Atlantic bluefin tuna and Adult sardine too, while in the GoC, Common octopus, Anglerfishes and Mackerels had values above the recommended rates.

The primary production required to sustain the fishery (%PPR) in the GoA during 2011 was the highest of all three compared models but was within the range of values from temperate shelves recorded by Pauly and Christensen (1995). However, the probability of the ecosystem being sustainably exploited (Psust), based on the estimated loss in production index (Libralato et al., 2008), pointed out a moderate exploitation, lower than those achieved in NWM or GoC ecosystems. This is mainly due to a lower total amount of catches and an intermediate Trophic Level of the catch (see next section).

Similarly, the 'Intrinsic vulnerability index of the catch' (IVIc) (Cheung et al., 2007), the 'Biomass of IUCN-endangered species in the community' (IUCN species B), and the 'Biomass of IUCN-endangered species in the community' (IUCN species C) showed lower values for the GoA, pointing out again to the lower fishing pressure in the area with the consequent decrease of the proportion of endangered species captured.

The Gulf of Alicante and its neighboring systems

Total catches in the GoA were lower than in ecosystems compared, consistent with the lowest biomasses, especially in the case of fish biomass, and hence in accordance with the low levels of primary production in the area (Estrada, 1996). In this regard, our results revealed the importance of the demersal versus pelagic compartment in the GoA ecosystem, exhibiting a high recycling efficiency. As a result of this, the mean trophic level of the catch in the GoA was slightly higher than in the NWM but lower than the GoC, probably due to the larger proportion of demersal species, with an overall high trophic level reported in the landings of these ecosystems. Despite a low value of mTLc, it is considered as a sign of a distinguished characteristic of Mediterranean exploited ecosystems (Pauly et al., 1998; Bas et al., 1985). In the case of the three ecosystems studied, it seemed to be related with 'Demersal/Pelagic biomasses ratio'. Indeed, the ratios 'D/P biomasses' used as standardized ecological indicators (Pennino and Bellido, 2012; Coll and Steenbeek, 2017), evidenced to be opposite to those described in the NWM, where the pelagic compartment plays a stronger role (Coll et al., 2006; Corrales et al., 2015). Consequently, small pelagics catches northwards in the GoA ecosystem were almost three times higher. This may be associated with the influence of river inputs, which were significantly low in the GoA (e.g., Segura River), impacting the low productivity of the area, in contrast with the highest values of river discharges (e.g., Ebro) in the Catalan sea (Estrada, 1996).

Conclusions

The comparisons undertaken in this study revealed common features between the three ecosystems considered. However, the GoA ecosystem did show differences in structural features with the two other models located north and south of the study area. This information allows us to link these features to some observed patterns and ecosystem properties, such as low productivity and low catches. According to our results, the GoA should be defined as a detritus-based system, bottom-up controlled, and dominated by the demersal compartment. Despite being an exploited ecosystem, the GoA presents a higher development stage than compared neighboring models likely due to lower fisheries pressure. The approach presented here contributes to our understanding of Mediterranean marine ecosystems functioning, from both ecological and fisheries perspectives, providing a comprehensive image of an ecosystem by following a comparative approach of nearby areas. This study represents a baseline from where to develop simulations of different exploitation scenarios taking into account climate change and alternative management options.

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4.6 Supplementary material

Balancing procedure

Model balancing was carried out manually following a top-down strategy (Fig. A.4.1). For all modeled groups, Ecotrophic efficiencies were the missing parameter and were estimated by EwE while Biomass, (P/B) and (Q/B) were inputs to the model. One exception concerned the “Pelagic ichthyophagous fishes” group due to the absence of reliable biomass estimations. In this case, we used an input value of 0.47 for EE, following recommendations from Christensen et al. (2005), and we let the model estimate the biomass. In the same way, P/B values for Norway lobster, Bivalves and gastropods and other benthic invertebrates (F.G. 31, 37 and 38, respectively) were estimated by the model. When attempting to balance the model, many of the Ecotrophic Efficiencies were greater than 1 meaning that more of the group was being consumed than produced, and thus had to be reduced. For that reason, inconsistent values were slightly modified following the criteria given by Christensen et al. (2008).

Biomasses were the first parameters modified during model balancing due to they were obtained from scientific surveys, where the sampling method, specifically, the swept-area method (i.e., estimation of biomass per area sampled by trawling), has been reported to underestimate biomass of the sampled species (Sánchez and Olaso, 2004, Tsagarakis et al., 2010, Torres et al., 2013). Thus, their biomass input values were based on a guesstimate to reach the mass balanced ecosystem model requirements. The biomasses of these groups were indeed too low and had to be increased (e.g. F.G. 37. F.G. 18, F.G. 21, F.G. 33, F.G.38, F.G.16 and F.G. 15). This is a common problem in prebalanced EwE models, where invertebrate biomass estimates are frequently too low to support predation mortality (Christensen et al. 2008). In the same way, P/B values were modified according to these criteria. Also and to complete the final mass balance model, we adjusted the diet matrix as a data source with some uncertainty, especially for those groups for which diet information was not from the modeled area.

The resulting input data were tested through ecological and fishery principles used in conjunction with PREBAL diagnostics to identify issues of model structure and data quality before network model balancing. Hence, following Link (2010), a set of diagnostics, i.e. biomasses, biomass ratios, vital rates, vital rate ratios, total production, and total removals (and slopes thereof) across the taxa and trophic levels could be tested through graphical representation. Regarding biomasses, results showed that Worms (F.G 35), Phytoplankton (F.G. 42), Microzooplankton (F.G. 39), Sardine (F.G. 13), Bivalves and gastropods (F.G. 37) could potentially be overestimated (Fig.1) while Flatfishes (F.G 16), Mullets (F.G 11), Sparids (F.G 23), Benthic sharks (F.G 4), Octopuses (F.G 28), Blue and red shrimp (F.G 29) and Norway lobster (F.G 31) could be underestimated. As we mentioned at the beginning of the balancing procedure, the biomass estimations determined with the survey could generate this kind of uncertainty, therefore, some adjustments were necessary to balance the model.

In addition, in the GoA model, the P/B ratios were low for all groups in general, except for Phytoplankton (F.G. 42) and Microzooplankton (F.G. 39). In the case of P/Q ratios, the highest values were detected for Microzooplankton (F.G. 39), Suprabenthos (F.G. 34), Meso- and macrozooplankton (F.G. 40), Gelatinous plankton (F.G. 41) and Seabirds (F.G. 2).

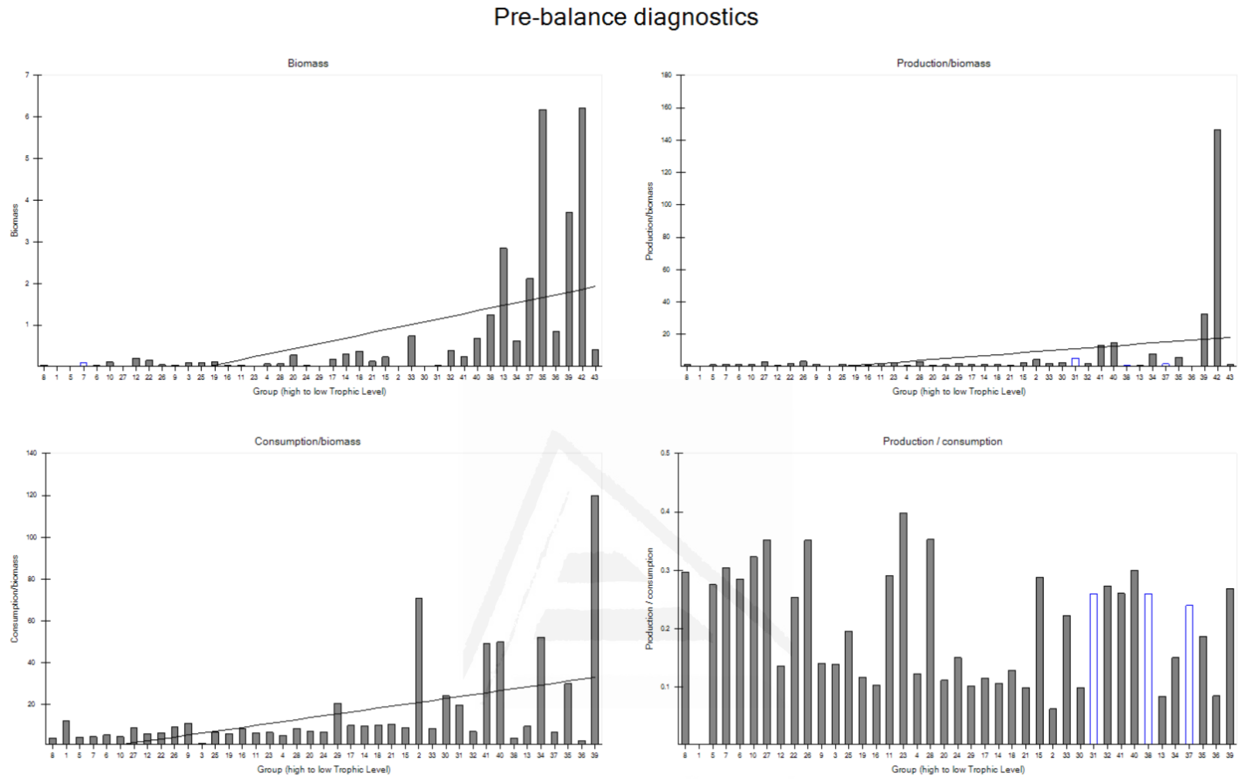

Fig. A.4.1 Results of the PREBAL analysis regarding the trends of Biomass, Production/Biomass, Consumption/Biomass and Production/Consumption along the functional groups arranged by trophic level.

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Table A.4.1 Species composition by functional group.

Functional group	Species composition. Description
1.Dolphins	*Stenella coeruleoalba*, *Tursiops truncatus*
2.Seabirds	*Alca torda, Chroicocephalus ridibundus, Larus audouinii, L. fuscus, L. melanocephalus, L. michahellis, Morus bassanus, Phalacrocorax aristotelis, Puffinus mauretanicus, P. yelkouan, Stercorarius skua*
3.Large pelagic fishes	*Thunnus thynnus, Xiphias gladius*
4.Benthic sharks	*Etmopterus spinax, Galeus melastomus, Scyliorhinus canicula*
5.Rays and Skates	*Raja asterias, Raja brachyura, Raja clavata, Raja montagui, Torpedo marmorata*
6.Demersal ichthyophagous fishes	*Conger conger, Helicolenus dactylopterus, Lepidopus caudatus, Molva dypterygia, Pagrus pagrus, Scorpaena elongata, Scorpaena scrofa, Trachinus draco, Uranoscopus scaber, Zeus faber*
7.Pelagic ichthyophagous fishes	*Auxis rochei rochei, Euthynnus alletteratus, Lichia amia, Sarda sarda, Seriola dumerili, Sphyraena sphyraena*
8.Anglerfishes	*Lophius budegassa, L. piscatorius*
9.Juvenile hake	*Merluccius merluccius* < 15 cm
10.Adult hake	*Merluccius merluccius* ≥ 15 cm
11.Mullets	*Mullus barbatus, M. surmuletus*
12.Blue whiting	*Micromesistius poutassou*
13.Sardine	*Sardina pilchardus*
14.Anchovy	*Engraulis encrasicolus*
15.Small pelagics	*Sardinella aurita, Spicara smaris*
16.Flatfishes	*Arnoglossus imperialis, A. laterna, A. rueppelii, A. thori, Citharus linguatula, Lepidorhombus boscii, L. whiffiagonis, Microchirus variegatus, Solea solea*
17.Benthopelagic fishes	*Argentina sphyraena, Capros aper, Cepola macrophthalma, Gadiculus argenteus argenteus, Glossanodon leioglossus, Macroramphosus scolopax*
18.Mesopelagic fishes	*Ceratoscopelus maderensis, Hymenocephalus italicus, Lampanyctus crocodilus, Maurolicus muelleri, Myctophum punctatum, Notoscopelus elongatus, Stomias boa boa*
19.Mackerels	*Scomber colias, S. scombrus*
20.Horse mackerels	*Trachurus mediterraneus, T. picturatus, T. trachurus*
21.Gobiids	*Aphia minuta, Blennius ocellaris, Callionymus maculatus, Crystallogobius linearis, Deltentosteus quadrimaculatus, Gobius niger, Lesueurigobius friesii, Synchiropus phaeton*
22.Gelatinous plankton feeders	*Boops boops, Pagellus bogaraveo*
23.Sparids	*Diplodus annularis, D. vulgaris, Spondyliosoma cantharus*
24.Suprabenthos feeders	*Lepidotrigla cavillone, Lepidotrigla dieuzeidei, Nezumia aequalis, Pagellus acarne, Spicara maena*
25.Natantia feeders	*Chelidonichthys cuculus, Chelidonichthys lastoviza, Chelidonichthys obscurus, Coelorinchus caelorhincus, Eutrigla gurnardus, Gaidropsarus biscayensis, Pagellus erythrinus, Phycis blennoides, Scorpaena notata, Scorpaena porcus, Serranus cabrilla, Serranus hepatus, Trachyrincus scabrus, Trigla lyra, Trisopterus minutus*
26.Benthopelagic cephalopods	*Abralia veranyi, Alloteuthis media, Alloteuthis subulata, Illex coindetii, Loligo vulgaris, Todarodes sagittatus*
27.Benthic cephalopods	*Callistoctopus macropus, Octopus salutii, Pteroctopus tetracirrhus, Rossia macrosoma, Scaeurgus unicirrhus, Sepia elegans, Sepia officinalis, Sepia orbignyana, Sepietta oweniana*
28.Octopuses	*Eledone cirrhosa, Eledone moschata, Octopus vulgaris*
29.Blue and red shrimp	*Aristeus antennatus*
30.Deep water rose shrimp	*Parapenaeus longirostris*
31.Norway lobster	*Nephrops norvegicus*

Table A.4.1 (Continued)

Functional group	**Species composition. Description**
32.Crabs	*Atelecyclus rotundatus, Calocaris macandreae, Dardanus arrosor, Ebalia* spp.*, Ethusa mascarone, Eurynome aspera, Galathea* spp.*, Geryon longipes, Goneplax rhomboides, Inachus* spp.*, Liocarcinus* spp.*, Macropipus tuberculatus, Macropodia* spp.*, Medorippe lanata, Monodaeus couchii, Munida* spp.*, Pagurus* spp.*, Palinurus* spp.*, Parthenope* spp.*, Pisa armata, Polycheles typhlops, Rissoides desmaresti, Scyllarus* spp.*, Squilla mantis, Upogebia* spp.
33.Other shrimps	*Aegaeon* spp.*, Alpheus glaber, Athanas* spp.*, Chlorotocus crassicornis, Eusergestes arcticus, Gennadas elegans, Pasiphaea multidentata, P. sivado, Philocheras* spp.*, Plesionika acanthonotus, P. antigai, Plesionika edwardsii, P. gigliolii, P. heterocarpus, P. martia, P. narval, Pontophilus* spp.*, Processa* spp.*, Sergia robusta, Solenocera membranacea*
34.Suprabenthos	Amphipods, cumaceans, isopods, mysids
35.Worms	Nematods, annelids
36.Echinoderms	*Antedon mediterranea, Astropecten aranciacus, A. irregularis, Cidaris cidaris, Echinaster sepositus, Gracilechinus acutus, Echinus melo, Holothuroidea, Luidia* spp.*, Marthasterias glacialis, Ophidiaster ophidianus, Ophiura ophiura, Parastichopus regalis, Spatangus purpureus, Sphaerechinus granularis, Tethyaster subinermis*
37.Bivalves and gastropods	*Acanthocardia* spp.*, Aporrhais serresianus, Bolma rugosa, Atrina fragilis, Bolinus brandaris, Calliostoma granulatum, Bivetiella cancellata, Galeodea echinophora, Cuspidaria cuspidata, Neopycnodonte cochlear, Nucula* spp.*,* Opistobranchia*, Pteria hirundo, Scaphander lignarius, Tellina* spp.*, Turritella* spp.*, Venus* spp.*, Xenophora crispa*
38. Other benthic invertebrates	Porifera, Cnidaria*, Scalpellum scalpellum, Veretillum cynomorium, Funiculina quadrangularis, Pennatula rubra, Aplidium conicum, Diazona violacea,* Ascidiidae, *Ascidiella aspersa, Ascidiella scabra, Ascidia mentula, Phallusia mammillata, Polycarpa pomaria, Botryllus schlosseri, Microcosmus* spp.*, Molgula* spp., Hydrozoa, *Geodia* spp.*, Epizoanthus* spp.*, Alcyonium palmatum, Pteroeides spinosum, Suberites domuncula, Halocynthia papillosa, Microcosmus sabatieri, Ircinia oros, Microcosmus vulgaris, Molgula appendiculata, Polycarpa mamillaris, Ascidiella* spp.
39.Microzooplankton	Copepoda, Ostracoda*, Branquiostoma, Acrania,* Planktonic eggs
40.Meso- and macro-zooplankton	Hyperiidea, Euphausiacea, Crustacean larvae, Fish larvae, Pteropoda
41.Gelatinous plankton	Cnidaria, Diphyidae, Salpida, Hydrozoa, Scyphozoa, *Pyrosoma atlanticum, Cymbulia peronii*

Table A.4.2 Landings ($t \cdot km^{-2} \cdot year^{-1}$) by functional group and fleet.

Functional group	Bottom trawl	Longlines	Purse seine	Small-scale	Total
1. Dolphins	-	-	-	-	-
2. Seabirds	-	-	-	-	-
3. Large pelagic fishes	0.000	0.005	-	0.000	0.005
4. Benthic sharks	0.007	0.000	-	0.001	0.008
5. Rays and skates	0.004	0.000	-	0.001	0.005
6. Demersal ichthyophagous fishes	0.025	0.001	0.000	0.005	0.031
7. Pelagic ichthyophagous fishes	0.002	0.000	0.045	0.011	0.059
8. Anglerfishes	0.027	-	-	-	0.027
9. Juvenile hake	-	-	-	-	-
10. Adult hake	0.097	0.001	-	0.006	0.104
11. Mullets	0.027	0.000	-	0.011	0.038
12. Blue whiting	0.094	-	-	0.000	0.094
13. Sardine	0.006	-	0.298	0.003	0.308
14. Anchovy	0.012	-	0.075	0.000	0.087
15. Small pelagics	0.003	0.000	0.410	0.000	0.413
16. Flatfishes	0.009	-	-	0.001	0.010
17. Benthopelagic fishes	0.001	-	-	-	0.001
18. Mesopelagic fishes	-	-	-	-	-
19. Mackerels	0.005	0.000	0.031	0.000	0.037
20. Horse mackerels	0.038	0.000	0.041	0.001	0.081
21. Gobiids	0.001	-	-	0.000	0.001
22. Gelatinous plankton feeders	0.014	0.000	0.009	0.001	0.023
23. Sparids	0.006	0.000	0.001	-	0.007
24. Suprabenthos feeders	0.003	-	-	0.001	0.004
25. Natantia feeders	0.056	0.000	0.000	0.007	0.064
26. Benthopelagic cephalopods	0.063	-	0.000	0.000	0.063
27. Benthic cephalopods	0.011	0.000	-	0.005	0.017
28. Octopuses	0.126	0.000	-	0.033	0.159
29. Blue and red shrimp	0.012	-	-	-	0.012
30. Deep water rose shrimp	0.009	-	-	-	0.009
31. Norway lobster	0.016	-	-	-	0.016
32. Crabs	0.051	0.000	-	0.001	0.052
33. Other shrimps	0.008	-	-	0.009	0.017
34. Suprabenthos	-	-	-	-	-
35. Worms	-	-	-	-	-
36. Echinoderms	0.000	-	-	-	0.000
37. Bivalves and gastropods	0.000	-	-	0.000	0.000
38. Other benthic invertebrates	-	-	-	-	-
39. Microzooplankton	-	-	-	-	-
40. Meso- and macrozooplankton	-	-	-	-	-
41. Gelatinous plankton	-	-	-	-	-
42. Phytoplankton	-	-	-	-	-
43. Benthic macrophytes	-	-	-	-	-
44. Discards	-	-	-	-	-
45. Detritus	-	-	-	-	-
Sum landings	0.734	0.009	0.910	0.098	1.750
Sum discards	0.178	0.000	0.006	0.011	0.195

Table A.4.3 Main equations and references used to estimate basic input parameters of the Gulf of Alicante model for 2011. Biomass ($t{\cdot}km^{-2}$); P/B = production/biomass ($year^{-1}$); Q/B = consumption/biomass ($year^{-1}$); P/Q = production/consumption ratio.

Functional group		Value	Sources and References
1.Dolphins	Biomass	0.001	Based on abundance estimates for Gulf of Alicante waters (Arcos, pers. comm). Toothed whales that stay in the study area a 95% of
	P/B	0.03	Coll et al., 2006
	Q/B	12.32	Innes et al., 1987 & Trites et al., 1997
	Diet		Astruc, 2005
2.Seabirds	Biomass	0.003	Based on population estimates in the study area from SEO/Birdlife, 2014. Seabirds that stay in the study area a 60% of the total time
	P/B	4.47	Pinnegar, 2000. Data corrected following Optiz, 1996
	Q/B	70.89	Nilsson and Nilsson, 1976
	Diet		Data compiled out of Oro, 1996; Oro et al., 1997; Granadeiro et al., 1998; Arcos, 2001
3.Large pelagic fishes	Biomass	0.095	ICCAT, 2012. Large pelagic fishes that stay in the study area a 50% of the total time
	P/B	0.20	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	1.45	From the empirical equation of Pauly et al., 1990
	Diet		Compiled out of Stergiou and Karpouzi, 2001; Carmona-Antoñanzas et al., 2006
4.Benthic sharks	Biomass	0.068	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.65	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.30	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
5.Rays and Skates	Biomass	0.006	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.19	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.36	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *T. marmorata* (Romanelli et al., 2006)
6.Demersal ichthyophagous fishes	Biomass	0.038	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.56	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.48	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
7.Pelagic ichthyophagous fishes	Biomass	0.096	Estimated by the model
	P/B	1.42	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.65	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Allam et al., 1999; Andaloro and Pipitone, 1997; Falautano et al., 2007; Fletcher et al., 2013; Hajjej et al., 2018
8.Anglerfishes	Biomass	0.034	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.16	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	3.90	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
9.Juvenile hake	Biomass	0.032	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.53	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.83	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020

Table A.4.3 (Continued)

Functional group		**Value**	**Sources and References**
10.Adult hake	Biomass	0.112	Estimated from EwE as multistanza group (lead by Juvenil hake)
	P/B	1.48	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.58	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
11.Mullets	Biomass	0.031	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.85	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.36	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
12.Blue whiting	Biomass	0.196	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.83	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.07	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
13.Sardine	Biomass	2.848	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	0.81	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	9.56	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Stergiou and Karpouzi, 2001
14.Anchovy	Biomass	0.293	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	1.05	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	9.87	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Tudela and Palomera, 1997; Costalago et al., 2012
15.Small pelagics	Biomass	0.23	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	2.59	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	8.98	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *S. aurita*, compiled out of Tsikliras et al., 2005
16.Flatfishes	Biomass	0.036	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.87	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	8.40	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *S. solea* and *M. variegatus*, compiled out of Stergiou and Karpouzi, 2001
	Diet		García-Rodríguez et al., 2020, except for *S. solea* and *M. variegatus*, compiled out of Stergiou and Karpouzi, 2001
17.Benthopelagic fishes	Biomass	0.186	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.17	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.11	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *A. sphyraena*, *G. leioglossus*, *M. scolopax*, compiled out of Sever et al., 2013; Carpentieri et al., 2016
18.Mesopelagic fishes	Biomass	0.368	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.33	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.26	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *C. maderensis*, *H. italicus*, *M. muelleri*, *M. punctatum*, *N. elongatus*, *S. boa boa* , compiled out of Sutton and Hopkins, 1996; Stergiou and Karpouzi, 2001; www.fishbase.org

Table A.4.3 (Continued)

Functional group		Value	Sources and References
19.Mackerels	Biomass	0.125	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	0.70	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.95	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
20.Horse mackerels	Biomass	0.276	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 and acoustic surveys MEDIAS using Landing factor (IEO database)
	P/B	0.79	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	7.02	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
21.Gobiids	Biomass	0.127	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.05	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.57	From the empirical equation of Pauly et al., 1990
	Diet		www.fishbase.org
22.Gelatinous plankton feeders	Biomass	0.153	Based on abundance estimates from bottom trawl surveys MEDITS and acoustic surveys MEDIAS in 2011 (IEO database)
	P/B	1.67	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.55	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
23.Sparids	Biomass	0.006	Based on abundance estimates from bottom trawl surveys MEDITS in 2011-2017 (IEO database)
	P/B	2.64	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.64	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020 and data compiled tergiou and out of Stergiou and Karpouzi, 2001; www.fishbase.org
24.Suprabenthos feeders	Biomass	0.030	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.06	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	7.00	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
25.Natantia feeders	Biomass	0.086	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.33	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.78	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
26.Benthopelagic cephalopods	Biomass	0.042	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.20	Sánchez y Olaso, 2004
	Q/B	9.10	Sánchez y Olaso, 2004; Coll et al., 2006
	Diet		Data compiled out of Quetglas et al., 1999; Pierce et al., 2010; Valls et al., 2015; Martinez-Baena et al., 2016; Valls et al., 2017
27.Benthic cephalopods	Biomass	0.014	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.1	Sánchez y Olaso, 2004
	Q/B	8.8	Sánchez y Olaso, 2004; Coll et al., 2006
	Diet		Data compiled out of Bernardino and Guerra, 1990; Quetglas et al., 2005; 2009; Mendes Alves et al., 2006; Giordano et al., 2010; ICES, 2015

Table A.4.3 (Continued)

Functional group		Value	Sources and References
28.Octopuses	Biomass	0.070	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.00	Sánchez y Olaso, 2004
	Q/B	8.50	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Data compiled out of Quetglas et al., 1998; Krstulovic, 2009; Regueira, 2017
29.Blue and red shrimp	Biomass	0.011	Based on stock assessment of Esteban et al., 2011
	P/B	2.11	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	20.57	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Cartes and Sarda, 1989
30.Deep water rose shrimp	Biomass	0.013	Based on stock assessment of Perez Gil et al., 2018
	P/B	2.40	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	24.12	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Nouar et al., 2011
31.Norway lobster	Biomass	0.029	Based on stock assessment of Esteban et al., 2018
	P/B	5.16	Estimated by the model
	Q/B	19.84	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Cristo and Cartes, 1998
32.Crabs	Biomass	0.396	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.93	Corrales, 2013
	Q/B	7.07	Corrales, 2013
	Diet		Data compiled out of Abello and Cartes, 1987; Abello, 1989; Cartes, 1993; Mili et al., 2013
33.Other shrimps	Biomass	0.731	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.89	Z=F+M; M = Multi-Parameter P/B-Model (Brey, 2001)
	Q/B	8.49	Corrales, 2013
	Diet		Data compiled out of Cartes, 1993; Fanelli and Cartes, 2004
34.Suprabenthos	Biomass	0.616	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	7.87	Cartes & Maynou, 1998
	Q/B	52.1	Cartes & Maynou, 2001
	Diet		Data compiled out of Cartes et al., 2001
35.Worms	Biomass	6.180	Based on estimated data of Banarú, 2013
	P/B	5.61	Ropert, 1999; Sanchez and Olaso, 2004
	Q/B	30.00	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Data compiled out of Fauchald and Jumars, 1979
36.Echinoderms	Biomass	0.849	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.24	Z=F+M; M = Multi-Parameter P/B-Model (Brey, 2001)
	Q/B	2.75	Albouy et al., 2010; Hattab et al., 2013. Data corrected following Opitz, 1996
	Diet		Data compiled out of Millar, 1971; Rodríguez, 1972; Coulon and Jangoux, 1993; De Juan et al., 2007

Table A.4.3 (Continued)

Functional group		Value	Sources and References
37.Bivalves and gastropods	Biomass	2.118	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.63	Estimated by the model
	Q/B	6.78	Pinnegar, 2000; Coll et al., 2006; 2007
	Diet		Based on data compiled out of Perron and Turner, 1978; Lalli and Gilmer, 1989
38.Other benthic invertebrates	Biomass	1.244	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.04	Estimated by the model
	Q/B	4.00	Sanchez and Olaso, 2004; Coll et al., 2006
	Diet		Based on data compiled out of Millar, 1971; Rodríguez, 1972; Coulon and Jangoux, 1993; De Juan et al., 2007
39.Microzooplankton	Biomass	3.705	Based on estimated data of Corrales, 2013
	P/B	32.32	Based on data of Plounevez and Champalbert, 2000; Gaudy et al., 2003
	Q/B	120.00	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Calbet et al., 2002
40.Meso- and macrozooplankton	Biomass	0.682	Based on data estimated by Coll et al., 2006
	P/B	14.97	Based on estimated data by Labat and Cuzin-Roudy, 1996
	Q/B	49.82	Baamstedt and Karlson, 1998
	Diet		Baamstedt and Karlson, 1998
41.Gelatinous plankton	Biomass	0.247	Based on data estimated by Coll et al., 2006
	P/B	12.89	Based on data compiled by Malej, 1989. Data corrected following Opitz, 1996
	Q/B	49.38	Malej (1989). Data corrected following Opitz, 1996
	Diet		Data compiled out of Graham and Kroutil, 2001; Örek, 2000
42.Phytoplankton	Biomass	6.22	From Chl-a via satellite (https://neo.sci.gsfc.nasa.gov); conversion factors from Jorgensen et al., 1991; Dalsgaard and Pauly, 1997
	P/B	146.146	Primary production from via satellite data (https://neo.sci.gsfc.nasa.gov)
43.Benthic macrophytes	Biomass	0.405	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.08	Data compiled out of McClanahan et Sala, 1997; Sala and Boudouresque, 1997
44.Discards	Biomass	0.195	From IEO on board observer programme database
45.Detritus	Biomass	75.6	From the empirical equation of Pauly et al., 1993

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Table A.4.4 References of data used for parameterizing the Gulf of Alicante model. Linf: asymptotic length (cm); K: von Bertalanffy growth constant (year); a: intercept; b: allometric constant.

Functional groups	***L_{inf}***		***k***	***Reference***	***a***	***b***	***Reference***
3.Large pelagic fishes							
Thunnus thynnus	315	Fishbase	0.09	Fishbase	0.0196	3.01	Fishbase
Xiphias gladius	237	Mejuto and Serna, 1993	0.12	Fishbase	0.000001	3.55	Fishbase
4.Benthic sharks							
Etmopterus spinax	87.4	MEDITS survey	0.20	Fishbase	0.0030	3.13	Fishbase
Galeus melastomus	48.4	IEO Database	0.42	Darna et al., 2018	0.0025	3.02	Fishbase
Scyliorhinus canicula	76.8	IEO Database	0.20	Fishbase	0.0016	3.16	Fishbase
5.Rays and Skates							
Raja asterias	93.2	MEDITS survey	0.45	MEDITS survey	0.0018	3.27	MEDITS survey
Raja brachyura	91.1	MEDITS survey	0.10	MEDITS survey	0.0028	3.23	MEDITS survey
Raja clavata	93.7	MEDITS survey	0.10	MEDITS survey	0.0024	3.20	MEDITS survey
Raja montagui	76.8	MEDITS survey	0.20	MEDITS survey	0.0002	3.89	MEDITS survey
Torpedo marmorata	61.1	IEO Database	0.19	Duman and Basusta, 2013	0.0273	2.91	MEDITS survey
6.Demersal ichthyophagous fishes							
Conger conger	160.0	IEO Database	0.07	Fishbase	0.0006	3.21	MEDITS survey
Helicolenus dactylopterus	36.8	IEO Database	0.10	Fishbase	0.0127	3.04	MEDITS survey
Pagrus pagrus	47.4	IEO Database	1.90	Fishbase	0.0282	2.80	MEDITS survey
Trachinus draco	41.1	IEO Database	0.08	Fishbase	0.0074	2.93	MEDITS survey
Scorpaena elongata	54.7	MEDITS survey	0.11	Fishbase	0.0249	2.89	MEDITS survey
Uranoscopus scaber	36.3	MEDITS survey	0.20	Fishbase	0.0106	3.15	MEDITS survey
Molva dypterygia	94.7	IEO Database	0.11	Fishbase	0.0009	3.26	MEDITS survey
Zeus faber	64.2	IEO Database	0.30	Fishbase	0.0186	2.88	MEDITS survey
Scorpaena scrofa	50.0	MEDITS survey	0.08	Fishbase	0.0220	2.94	MEDITS survey
Lepidopus caudatus	126.3	IEO Database	0.14	Fishbase	0.0003	3.19	MEDITS survey
7.Pelagic ichthyophagous fishes							
Sarda sarda	85.3	IEO Database	0.72	Fishbase	0.0095	3.10	IEO Database
Euthynnus alletteratus	128.4	Fishbase	0.13	Fishbase	0.0213	2.92	IEO Database
Auxis rochei rochei	52.6	Fishbase	0.70	Fishbase	0.0101	3.13	IEO Database
Lichia amia	121.1	IEO Database	0.22	Smith, 2008	0.0086	2.97	IEO Database
Seriola dumerili	184.2	Fishbase	0.19	Fishbase	0.0273	2.74	IEO Database
Sphyraena sphyraena	118.9	IEO Database	0.12	Fishbase	0.0648	2.32	IEO Database

Table A.4.4 (Continued)

Functional groups	L_{inf}		k	Reference	a	b	Reference
8.Anglerfishes							
Lophius piscatorius	153.7	IEO Database	0.34	IEO Database	0.0206	2.89	IEO Database
Lophius budegassa	103.2	IEO Database	0.19	Data call 2019	0.0563	2.60	IEO Database
9.Juvenile hake							
Merluccius merluccius	15.0	Data call 2019	0.18	Data call 2019	0.0055	3.07	Data call 2019
10.Adult hake							
Merluccius merluccius	115.8	MEDITS survey	0.18	MEDITS survey	0.0068	3.04	MEDITS survey
11.Mullets							
Mullus barbatus	36.3	Data call 2019	0.34	Data call 2019	0.0076	3.13	Data call 2019
Mullus surmuletus	37.9	Data call 2019	0.16	Data call 2019	0.0091	3.09	Data call 2019
12.Blue whiting							
Micromesistius poutassou	44.2	IEO Database	0.16	Data call 2018	0.0043	3.15	Data call 2018
13.Sardine							
Sardina pilchardus	23.7	Data call 2018	0.31	Data call 2018	0.0038	3.25	Data call 2018
14.Anchovy							
Engraulis encrasicolus	20.0	Data call 2018	0.32	Data call 2018	0.0050	3.34	Data call 2018
15.Small pelagics							
Sardinella aurita	34.7	IEO Database	0.44	Fishbase	0.0068	2.99	MEDITS survey
Spicara smaris	23.7	IEO Database	0.40	IEO Database	0.0245	2.62	MEDITS survey
16.Flatfishes							
Solea solea	45.8	MEDITS survey	0.36	Fishbase	0.0014	3.52	MEDITS survey
Microchirus variegatus	18.9	MEDITS survey	0.39	Fishbase	0.1759	1.92	MEDITS survey
Citharus lingutaula	32.6	IEO Database	0.25	Fishbase	0.0030	3.30	MEDITS survey
Lepidorhombus whiffiagonis	51.6	IEO Database	0.16	Fishbase	0.0064	2.99	MEDITS survey
lepidorhombus boscii	41.1	IEO Database	0.11	Fishbase	0.0643	2.27	MEDITS survey
Arnoglossus imperialis	17.4	MEDITS survey	0.25	Fishbase	0.0045	3.17	MEDITS survey
Arnoglossus laterna	16.3	MEDITS survey	0.55	Fishbase	0.0025	3.45	MEDITS survey
Arnoglossus thori	14.2	MEDITS survey	0.33	Fishbase	0.0064	3.17	MEDITS survey
Arnoglossus rueppelii	15.8	MEDITS survey	0.33	Fishbase	0.0051	3.01	MEDITS survey
17.Benthopelagic fishes							
Argentina sphyraena	22.6	MEDITS survey	0.28	Fishbase	0.0047	3.05	MEDITS survey
Glossanodon leioglossus	16.3	MEDITS survey	0.44	Fishbase	0.0022	3.32	MEDITS survey
Capros aper	16.8	MEDITS survey	0.42	Fishbase	0.0282	2.81	MEDITS survey

Table A.4.4 (Continued)

Functional groups	L_{inf}		k	Reference	a	b	Reference
17.Benthopelagic fishes							
Cepola macrophthalma	69.5	IEO Database	0.21	Fishbase	0.0119	2.22	MEDITS survey
Gadiculus argenteus argenteus	18.4	MEDITS survey	0.19	Fishbase	0.0562	2.11	MEDITS survey
Macroramphosus scolopax	20.0	MEDITS survey	0.36	Fishbase	0.0040	3.15	MEDITS survey
18.Mesopelagic fishes							
Stomias boa boa	28.6	MEDITS survey	0.28	Fishbase	0.0051	2.98	MEDITS survey
Maurolicus muelleri	7.6	MEDITS survey	0.88	Fishbase	0.0016	3.96	MEDITS survey
Myctophum punctatum	10.2	MEDITS survey	0.17	Fishbase	0.0080	3.00	MEDITS survey
Notoscopelus elongatus	14.4	MEDITS survey	0.89	Fishbase	0.0135	3.00	MEDITS survey
Ceratoscopelus maderensis	11.3	MEDITS survey	0.40	Fishbase	0.0135	3.00	MEDITS survey
Lampanyctus crocodilus	23.4	MEDITS survey	0.89	Fishbase	0.0051	2.98	MEDITS survey
Hymenocephalus italicus	5.5	MEDITS survey	0.23	Fishbase	0.1277	2.80	MEDITS survey
19.Mackerels							
Scomber colias	47.4	IEO Database	0.15	Data call 2019	0.0024	3.40	Data call 2019
Scomber scombrus	41.6	IEO Database	0.50	Data call 2019	0.0042	3.21	Data call 2019
20.Horse mackerels							
Trachurus picturatus	39.5	MEDITS survey	0.25	Fishbase	0.0089	2.96	MEDITS survey
Trachurus mediterraneus	41.1	MEDITS survey	0.22	Data call 2019	0.0138	2.76	Data call 2019
Trachurus trachurus	44.2	IEO Database	0.17	Data call 2019	0.0099	2.96	Data call 2019
21.Gobiids							
Crystallogobius linearis	4.9	MEDITS survey	0.97	Fishbase	0.0096	3.45	MEDITS survey
Deltentosteus quadrimaculatus	14.2	MEDITS survey	0.37	Fishbase	0.0074	3.05	MEDITS survey
Callionymus maculatus	14.2	MEDITS survey	0.58	Fishbase	0.0156	2.49	MEDITS survey
Aphia minuta	5.3	MEDITS survey	2.23	Fishbase	0.0096	3.45	MEDITS survey
Lesueurigobius friesi	8.4	MEDITS survey	0.70	Fishbase	0.0392	2.13	MEDITS survey
Blennius ocellaris	20.0	MEDITS survey	0.38	Fishbase	0.0168	2.91	MEDITS survey
Synchiropus phaeton	23.2	MEDITS survey	0.58	Fishbase	0.0615	2.11	MEDITS survey
Gobius niger	20.0	IEO Database	0.30	Fishbase	0.0089	3.09	MEDITS survey
22.Gelatinous plankton feeders							
Boops boops	36.8	IEO Database	0.17	Fishbase	0.0082	3.00	MEDITS survey
Pagellus bogaraveo	49.5	IEO Database	0.09	Fishbase	0.0130	2.99	MEDITS survey

Table A.4.4 (Continued)

Functional groups	L_{inf}		k	Reference	a	b	Reference
23.Sparids							
Diplodus annularis	25.3	MEDITS survey	0.46	Fishbase	0.0115	3.17	MEDITS survey
Diplodus vulgaris	35.8	IEO Database	0.39	Fishbase	0.0149	3.01	MEDITS survey
Spondyliosoma cantharus	48.4	IEO Database	0.18	Fishbase	0.0015	3.71	MEDITS survey
24.Suprabenthos feeders							
Spicara maena	24.2	MEDITS survey	0.17	Fishbase	0.0062	3.20	MEDITS survey
Lepidotrigla dieuzeidei	16.8	IEO Database	0.42	Fishbase	0.0078	3.12	MEDITS survey
Lepidotrigla cavillone	18.9	IEO Database	0.56	Fishbase	0.0058	3.26	MEDITS survey
Nezumia aequalis	6.8	MEDITS survey	0.16	Fishbase	0.1279	2.82	MEDITS survey
Pagellus acarne	31.6	MEDITS survey	0.37	Fishbase	0.0066	3.21	MEDITS survey
25.Natantia feeders							
Chelidonichthys lastoviza	31.6	MEDITS survey	0.28	Fishbase	0.0178	2.82	MEDITS survey
Eutrigla gurnardus	32.6	MEDITS survey	0.22	Fishbase	0.0029	3.49	MEDITS survey
Chelidonichthys cuculus	32.1	MEDITS survey	0.35	Fishbase	0.0051	3.20	MEDITS survey
Chelidonichthys obscurus	24.7	MEDITS survey	0.18	Fishbase	0.0067	3.08	MEDITS survey
Coelorinchus caelorhincus	12.6	MEDITS survey	0.12	Fishbase	0.0925	3.14	MEDITS survey
Gaidropsarus biscayensis	15.8	MEDITS survey	0.31	Fishbase	0.0040	3.20	MEDITS survey
Pagellus Erythrinus	54.2	MEDITS survey	0.14	Fishbase	0.0219	2.82	MEDITS survey
Phycis blennoides	67.4	IEO Database	0.22	Fishbase	0.0069	2.97	MEDITS survey
Scorpaena notata	18.9	MEDITS survey	0.22	Fishbase	0.0169	3.04	MEDITS survey
Scorpaena porcus	31.6	MEDITS survey	0.18	Fishbase	0.0183	3.02	MEDITS survey
Serranus cabrilla	28.4	IEO Database	0.30	Fishbase	0.0092	3.07	MEDITS survey
Serranus hepatus	20.0	MEDITS survey	0.25	Fishbase	0.0091	3.24	MEDITS survey
Trachyrincus scabrus	20.0	MEDITS survey	0.17	Fishbase	0.0410	3.06	MEDITS survey
Trigla lyra	35.8	MEDITS survey	0.17	Fishbase	0.0082	2.96	MEDITS survey
Trisopterus minutus	30.5	IEO Database	0.39	Fishbase	0.0075	3.06	MEDITS survey

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Table A.4.5 Diet composition matrix for the Gulf of Alicante model.

	Prey / Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Dolphins																				
2	Seabirds																				
3	Large pelagic fishes																				
4	Benthic sarks				0.009	0.009	0.003		0.004												
5	Rays and skates							0.000													
6	Demersal ichthyophagous	0.050		0.003	0.002	0.003	0.007	0.001	0.098		0.001	0.003					0.000				
7	Pelagic ichthyophagous fishes							0.010													
8	Anglerfishes					0.000	0.000														
9	Juvenil hake	0.010		0.002			0.012	0.000	0.009	0.024	0.042						0.006				
10	Adult hake	0.050			0.000	0.028	0.013		0.078												
11	Mullets					0.007	0.000	0.000	0.026		0.001									0.017	0.000
12	Blue whiting			0.015	0.005	0.001	0.064		0.016	0.020	0.057		0.003				0.009			0.000	0.001
13	Sardine	0.210	0.250	0.281	0.141	0.019	0.111	0.043	0.116	0.251	0.442		0.020				0.042			0.352	0.380
14	Anchovy	0.100	0.040	0.072	0.056	0.013	0.049	0.032	0.004	0.057	0.026						0.001			0.031	0.012
15	Small pelagics	0.090	0.010	0.032		0.036	0.017	0.153	0.003	0.008	0.036									0.001	0.007
16	Flatfishes				0.001	0.003	0.008		0.069								0.006				0.000
17	Benthopelagic fishes			0.002	0.028	0.070	0.080	0.002	0.066	0.005	0.030	0.008	0.008				0.019	0.002		0.000	0.003
18	Mesopelagic fishes			0.006	0.031	0.000	0.053	0.021		0.023	0.015		0.208					0.009	0.013	0.000	0.008
19	Mackerels	0.200					0.013	0.005			0.010									0.000	
20	Horse mackerels	0.040		0.002			0.018	0.003	0.072		0.031									0.010	0.007
21	Gobiids			0.000	0.000	0.013	0.020	0.000	0.040	0.043	0.002	0.003					0.057				0.011
22	Gelatinous plankton feeders				0.046		0.029	0.026	0.160		0.168									0.000	
23	Sparids					0.020	0.002	0.001	0.004												
24	Suprabenthos feeders					0.024	0.020	0.007	0.044		0.011										
25	Natantia feeders			0.000	0.010	0.026	0.028	0.002	0.027	0.000	0.009	0.002	0.002				0.022				
26	Benthopelagic cephalopods	0.100		0.032	0.014	0.046	0.013	0.008	0.013		0.017	0.004	0.008				0.004			0.006	
27	Benthic cephalopods	0.010		0.000	0.006	0.009	0.005	0.004	0.009	0.001	0.002	0.012					0.005			0.000	0.001
28	Octopuses	0.020			0.018		0.020		0.004		0.000										
29	Blue and red shrimp				0.002														0.001		
30	Deep water rose shrimp				0.001	0.001		0.000													
31	Norway lobster				0.001		0.005						0.001				0.009				
32	Crabs			0.022	0.092	0.249	0.144	0.009	0.011	0.007	0.002	0.175	0.000				0.203	0.004	0.001	0.001	0.005
33	Other shrimps			0.011	0.090	0.340	0.094	0.049	0.032	0.111	0.046	0.178	0.073			0.008	0.157	0.050	0.035	0.001	0.016
34	Suprabenthos				0.004	0.062	0.018	0.013	0.000	0.011	0.001	0.217	0.001			0.042	0.188	0.220	0.255	0.056	0.084
35	Worms				0.118	0.004	0.030		0.000			0.286	0.000			0.002	0.159	0.083	0.140	0.001	0.002
36	Echinoderms				0.000		0.003		0.000			0.016						0.000			
37	Bivalves and gastropods				0.001	0.001	0.000	0.006				0.043					0.004	0.001		0.000	0.000
38	Other benthic invertebrates				0.002							0.000						0.000		0.000	
39	Microzooplankton				0.004	0.000	0.000	0.000		0.050		0.000	0.100	0.095	0.595	0.866	0.013	0.354	0.164	0.004	0.059
40	Meso- and macrozooplankton			0.022	0.128	0.001	0.078	0.005	0.000	0.389	0.053	0.052	0.577	0.045	0.400	0.080	0.022	0.271	0.256	0.201	0.401
41	Gelatinous plankton				0.003	0.001	0.014						0.000			0.001		0.005	0.002	0.319	0.002
42	Phytoplankton													0.860							
43	Benthic macrophytes																				
44	Discards	0.010	0.100		0.019	0.001	0.000	0.000	0.005												
45	Detritus	0.035			0.167	0.014	0.028	0.000	0.091						0.005	0.001	0.076		0.133		
	Import	0.075	0.600	0.500				0.600													
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Table A.4.5 (Continued)

	Prey / Predator	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
1	Dolphins																					
2	Seabirds																					
3	Large pelagic fishes																					
4	Benthic sarks					0.000	0.001															
5	Rays and skates																					
6	Demersal ichthyophagous					0.004	0.001	0.003														
7	Pelagic ichthyophagous fishes						0.001															
8	Anglerfishes																					
9	Juvenil hake					0.004	0.000	0.019														
10	Adult hake						0.000	0.009	0.001													
11	Mullets					0.001																
12	Blue whiting					0.001	0.003															
13	Sardine		0.000		0.037	0.007	0.121	0.025	0.139													
14	Anchovy					0.005	0.061	0.033	0.024				0.004									
15	Small pelagics						0.001	0.016														
16	Flatfishes		0.001	0.010	0.007	0.003		0.015														
17	Benthopelagic fishes		0.000			0.010	0.004	0.032	0.021	0.026			0.007									
18	Mesopelagic fishes		0.001			0.004	0.072	0.022		0.026				0.011								
19	Mackerels																					
20	Horse mackerels			0.003			0.115															
21	Gobiids			0.044	0.053	0.022	0.018	0.039	0.033													
22	Gelatinous plankton feeders						0.006		0.083				0.004									
23	Sparids						0.002	0.008														
24	Suprabenthos feeders						0.000															
25	Natantia feeders					0.009		0.018	0.007													
26	Benthopelagic cephalopods		0.000	0.009		0.001	0.006		0.013													
27	Benthic cephalopods		0.001	0.002	0.004	0.008	0.006	0.006	0.003			0.000		0.000								
28	Octopuses			0.005	0.004			0.003	0.002													
29	Blue and red shrimp							0.000					0.002									
30	Deep water rose shrimp																					
31	Norway lobster						0.016		0.003													
32	Crabs	0.071	0.000	0.275	0.069	0.228	0.015	0.234	0.224	0.115		0.053	0.010	0.000								
33	Other shrimps	0.080	0.039	0.016	0.106	0.302	0.291	0.293	0.066	0.095		0.106	0.009	0.008								
34	Suprabenthos	0.350	0.041	0.048	0.375	0.112	0.015	0.045	0.040	0.223	0.136	0.087	0.193	0.190								
35	Worms	0.299	0.015	0.259	0.126	0.143	0.006	0.056	0.119	0.098	0.282	0.225	0.304	0.153		0.030		0.100				
36	Echinoderms	0.004	0.000	0.043	0.034	0.011		0.011	0.015	0.086		0.022	0.042	0.001								
37	Bivalves and gastropods	0.038	0.000	0.098	0.056	0.002	0.005	0.014	0.040	0.296		0.049	0.057	0.008			0.020					
38	Other benthic invertebrates		0.042	0.091	0.007	0.000	0.000				0.213	0.058	0.040	0.000								
39	Microzooplankton	0.063	0.002	0.061	0.003	0.000	0.006			0.007	0.232			0.050	0.130				0.200	0.020	0.570	0.640
40	Meso- and		0.034	0.027	0.062	0.045	0.087	0.015	0.000	0.029		0.087	0.090	0.311					0.050		0.030	0.050
41	Gelatinous plankton		0.801	0.007	0.058	0.000	0.007						0.004									0.010
42	Phytoplankton																	0.640	0.400	0.680	0.300	0.200
43	Benthic macrophytes		0.020		0.001		0.001						0.006				0.100	0.010				
44	Discards						0.013		0.017			0.016	0.002		0.003		0.001					
45	Detritus	0.095	0.002	0.003	0.000	0.080	0.118	0.084	0.150		0.136	0.296	0.226	0.268	0.867	0.970	0.879	0.250	0.350	0.300	0.100	0.100
	Import																					
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

Chapter 5: General Discussion

General discussion

The increasing need to understand and quantify ecosystems behavior and properties has come to the forefront of environmental management planning, particularly in the field of the ecosystem approach to fisheries (García et al., 2003). Therefore, the work presented in this thesis pursues the identification of feeding patterns and trophic interactions of the main predators occurring over the shelf and upper slope of the Northern Spain through stomach content analysis methodology. This represents a step forward, contributing to the collection of the necessary input data required for the implementation of the increasingly use of ecosystem models.

Some of the uncertainties surrounding trophic studies are due precisely to the fact that there is a lack of methodologies capable of establishing the adequate number of samples required to determine the diet of the species studied in an ecosystem (Modde and Ross, 1983; Ferry and Caillet, 1996). Therefore, our implementation of a mathematical approach based on cumulative prey curves revealed to be a robust approach to cover this limitation in this kind of studies.

Furthermore, the mathematical method consisting in the calculation of the slope on a fitted function using Clench´s function (Clench, 1979) was really successful for most of our species. To date, Clench´s function has been demonstrated being a good fit in most cases of the faunistic or floristic inventories in which it was tested (Soberón and Llorente, 1993; Leon-Cortés et al., 1998; Moreno and Halffter, 2001). Thus, our implementation of this methodology with a robust mathematical approach fullfiled a gap of knowledge of the previous marine food web studies in the study area.

The first chapter of this thesis studied the trophic ecology of 61 fish species occurring over the shelf and upper slope through the study of stomach content analysis. Main findings revealed the existence of different feeding strategies, identifying the major trophic guilds exploiting similar food resources (Kornan and Kropil, 2014). Subsequently, the three environmental drivers investigated, namely latitude, habitat type and depth affecting the resulting trophic guilds revealed that latitudinal gradient only seemed to affect fish community composition, showing that the southern geographical area was characterized by a higher percentage of pelagic crustacean feeders as well as a lower percentage of demersal crustacean feeders. These results showed consistency along a latitudinal north-south axis, in agreement with Floeter et al. (2004), who reported changes in trophic structure and spatial patterns along the latitudinal gradient. In addition, planktophagous species were more abundant in the southern geographical area, in agreement with Cartes et al. (2002) who reported a progressive north-south increase in the abundance of these species. Conversely, latitude did not seem to affect mean trophic level (MTL), biomass and diversity.

Habitat type was found significant in relation to fish community structure, biomass and diversity, but not for MTL. In fact, maërl and biogenic bottoms, sandy and muddy circalittoral bottoms (consisting mainly of ascidians and echinoderms) and sedimentary and detritic bottoms (consisting mainly of echinoderms), were the three habitats able to bear the highest carrying capacity of fish biomass. These results highlight the important role of the type of habitat in the production of fish species, in agreement with Ordinas and Massuti (2009), who reported that some of the most important demersal resources of the coastal shelf in the fishing grounds off the Balearic Islands are dependent on macro-benthic habitat type, associated with a high level of biomass and biodiversity.

According to depth, changes in MTL were detected, in particular between the first and the rest of the strata and between the third and fourth strata, caused by the low trophic position of the species occupying shallower waters compared to those species occupying the deepest bottoms. Concerning to biomass, the deepest stratum shows differences from other strata, in line with the usual distribution of biomass in the ocean (Abad et al., 2007). Regarding to diversity and fish composition, the relationship between depth and them was evident.

This thesis extended the study to ontogenetic shifts and trophic ecology of seven commercial gadiforms species: silvery pout (*Gadiculus argenteus*), bigeye rockling (*Gaidropsarus biscayensis*), Spanish ling (*Molva macrophthalma*), European hake (*Merluccius* merluccius), blue whiting (*Micromesistius poutassou*), greater forkbeard (*Phycis blennoides*) and poor cood (*Trisopterus minutus*).

Dietary overlap analysis of co-existing species revealed a partitioning of trophic resources among species and size classes. This suggests that the seven species occupy different trophic positions, ranging from a generalized feeding behavior to specialized piscivorous habits, resulting in differing trophic niches. These results might complement those reported by Macpherson (1978a) and Morte (2001; 2002) who investigated seasonal and bathymetric changes, respectively, in the diets of blue whiting, silvery pout, poor cod and greater forkbeard. They related availability of prey to diet depending on the season. In particular, five of the seven species of gadiforms investigated, with the exception of bigeye rockling (*Gaidropsarus biscayensis*) and poor cod (*Trisopterus minutus*), showed ontogenetic shifts in diet, allowing them to occupy several niches or sub-niches simultaneously. With the only exception of *G. argenteus* and *M. poutassou*, the studied species showed mechanisms aimed at avoiding an excessive niche overlap, diversifying their strategies and thus minimizing competition for trophic and spatial resources. An example of these mechanisms is the case of

M. poutassou-P. blennoides and *M. merluccius-T. minutus*. Both pairs of species exhibited by far the highest values of spatial overlap, which the species in turn compensated with low values of trophic overlap. In contrast, *P. blennoides-T. minutus, M. poutassou-M. macrophthalma* and *M. merluccius-M. poutassou*, showed high values of trophic niche overlap, which in turn compensated with low values of spatial co-occurrence. In this way, with the only exception above mentioned, the studied gadiform species seem to be organized following the hypothesis of niche complementarity (Ebeling and Hixon, 1991). According to this statement, if an ecosystem is structured under this hypothesis, it should show consistently low overlap so such that the coexistence of similar species occurs due to differences in resource use (Pianka, 1973; Schoener, 1974).

Regarding niche breadth, there does appear to be a pattern that relates size class to niche breadth. Therefore, the small sizes presented a broader trophic niche than that of the large classes, with the exception of Spanish ling (*Molva macropththalma*), a specialist piscivorous species, where the larger size of the specimens allows it to have access to a greater number of potential prey in its diet, thus increasing its trophic niche with the ontogenetic development of the specimens. Our results showed a relationship between the size class and its trophic level (TL), with the TL being lower in the small sizes and increasing with the ontogenetic shift. This difference in the trophic level between size classes was greater for those species located higher in the trophic web (e.g., hake, blue whiting and Spanish ling).

Once the trophic web was described for the Northern Spain-GSA6, a statistical analysis was previously performed to determine which of these species showed differences in their dietary preferences between the Gulf of Alicante and the rest of the GSA6. Further differences between diets were explored with non-parametric analysis of similarities (ANOSIM), based on multi-dimensional scaling (MDS) of the Bray–Curtis dissimilarity index. Consequently, diet matrix of those species with specific feeding patterns in the Gulf of Alicante was used as input data for the implementation of the ecological model. For the rest of the species which did not show differences, the diet characterized for the entire GSA6 was used.

Then, a mass-balance model Ecopath of the marine ecosystem in the GoA was created with the aim of giving a description of trophic relationships and dynamics of this ecosystem functioning. Main findigs revealed that the Gulf of Alicante ecosystem showed differences in structural features with the two models compared located north; Northwestern Mediterranean model (NWM) (Corrales et al. 2015) and south; Gulf of Cadiz model (GoC) (Torres et al., 2013) of the study area, which could be explained by its singular oceanographic and biological characteristics. The comparison between existing models in neighboring areas showed that main differences found may indeed be related to the primary production, which revealed to reach the lowest values in the GoA.

Despite the high values of ecotrophic efficiencies and mortality rates, the Gulf of Alicante evidenced the lowest fishing pressure of all three compared models, pointing out a moderate overexploitation level. Thus, highlighting the importance of the demersal compartment, where most biomasses were associated to the detritus. Since the ecosystem is stable and based on detritus, it may highly depend on the biomass of the system itself. Thus, this ecosystem remains efficient and stable in its poor conditions, but at the same time delicate and vulnerable because it depends on the efficient and circular use of its own biomass. Therefore, excessive biomass withdrawals by fishing, above their sustainability, could affect the contribution of detritus and hence the stability of the system. This is of particular interest because could explain the stability of the small pelagic fisheries with respect to the decline seen further north, where the NWM is more influenced by continental contributions from the Ebro and Rodano rivers, which have notably decreased in the last century. As the GoA ecosystem is more based on recycled nutrients rather than on new nutrients from continental contributions, the GoA seems to be a poorer but more stable ecosystem based on oceanic conditions, leaded by its primary production. These results are in line with those reported by Estrada (1996) who related an apparently high yield of Mediterranean fisheries with relatively low primary production values, also known as “paradox of the Mediterranean”.

The analysis of main Ecopath ecosystem indicators suggests that the GoA presents a higher level of complexity of internal flows, which is correlated with stability and maturity above mentioned. This indicates that the system looks more a web-like than a chain-like structure (Christensen, 1995), in contrast with the linearity detected in the food web of NWM and GoC ecosystems.

Concerning to the demersal versus pelagic compartment in the GoA ecosystem, our results revealed the importance of a high recycling efficiency. As a result of this, the mean trophic level of the catch in GoA is slightly higher than NWM but lower than GoC, probably due to the larger proportion of demersal species, with an overall high trophic level reported in the landings of these ecosystems. This could be possible be explained because demersal compartment is more efficient in using those recycled nutrients.

Consequently, the findings obtained in this thesis represent a great advance in the field of trophic ecology and modeling in the study area, aiming to update previuos studies and describe the structure and functioning of the main trophic components within the food web in the Northern Spain-GSA6. In turn, the ecological model implemented in the Gulf of Alicante, a singular ecosystem constrained by its environmental features, makes the difference with nearby ecosystems. Thus, the approach presented here contributes to our understanding of Mediterranean ecosystem functioning, from both ecological and fisheries perspective providing a comprehensive image of an ecosystem by following a comparative approach of nearby modeled areas. Hence, this study represents a baseline from where to develop simulation of different exploitation scenarios taking into account climate change and management options.

Discusión general

La creciente necesidad de comprender y cuantificar las propiedades de los ecosistemas así como el de las especies que los integran, ha pasado a ocupar un lugar destacado en la planificación de la gestión ambiental. Este hecho ha cobrado importancia de forma muy particular en lo referente al enfoque ecosistémico de la pesca (García et al., 2003).

El trabajo presentado en la presente tesis persigue la descripción de los posibles patrones de alimentación de las principales especies que habitan tanto en la plataforma como en el talud superior de la costa este del Mediterráneo español (GSA6). Para ello, se procedió mediante el análisis de contenidos estomacales a la identificación de los diferentes tipos de interacciones tróficas que ocurren entre ellas. Por consiguiente, esto representa un importante avance científico, contribuyendo a la recopilación de los datos de entrada necesarios para la implementación de modelos tróficos, cada vez más usados en la gestión pesquera actual debido a la creciente tendencia a abordar su aproximación desde un punto de vista global o ecosistémico.

Mucha es la incertidumbre que rodea a los estudios tróficos. Uno de los motivos principales es precisamente la falta de metodología capaz de establecer el número adecuado de muestras necesario para determinar la dieta de las especies estudiadas en un ecosistema (Modde y Ross, 1983; Ferry y Caillet, 1996). Por lo tanto, el presente estudio no sólo tuvo como objetivo estimar el valor asintótico proporcionado por las curvas de acumulación de presas, sino que también propuso una aproximación matemática consistente en el cálculo de la pendiente de una recta tangente a una determinada función ajustada. En el presente estudio se investigó la adecuidad del ajuste de dos funciones matemáticas (función logarítmica y función de Clench), a la curva de acumulación de presas. El análisis de los datos reveló que la función de Clench (Clench, 1979) se ajustó mejor a la curva de acumulación en la práctica totalidad de los casos estudiados. De hecho, estos resultados coincidieron con los estudios realizados por Soberón y Llorente (1993), Leon-Cortés et al. (1998) y Moreno y Halffter (2001), quienes encontraron que esta función se ajustaba bien en la mayoría de los estudios de inventarios faunísticos o florísticos en los que se probó. Aun así, la implementación de esta metodología ligada a un enfoque matemático en los estudios de redes tróficas marinas realizados anteriormente en el área de estudio ha sido omitida. Consecuentemente, esta metodología reveló ser una aproximación robusta para cubrir dicha limitación en este tipo de estudios de forma que funcionó con éxito en la mayoría de las especies investigadas en nuestra zona de estudio.

La primera fase de esta tesis consistió en estudiar la ecología trófica de 61 especies de peces que se encuentran en la plataforma y el talud superior de la GSA6 mediante el análisis de su contenido estomacal. Los principales hallazgos revelaron la existencia de diferentes estrategias de alimentación, identificando los principales grupos tróficos que explotaron recursos similares (Kornan y Kropil, 2014). El objetivo final del estudio fue el de analizar cómo la estructura de la comunidad de peces se ve afectada por tres importantes factores ambientales (tipo de hábitat, gradiente latitudinal y profundidad). Con este fin, previamente se seleccionaron cuatro indicadores empleados como descriptores de la estructura de la comunidad de peces (índice de diversidad de Shannon, biomasa, nivel trófico promedio y composición específica de la comunidad de peces). De este modo, se analizó a través de estas cuatro características que definen una comunidad de peces, cómo ésta se adaptaba a la variabilidad ambiental presente dentro de los tres factores investigados. Los resultados revelaron que los tres factores estudiados afectaron en mayor o menor grado a los cuatro indicadores escogidos para describir la comunidad de peces caracterizada en la zona de estudio.

Así, el análisis de los descriptores de la comunidad en función del tipo de hábitat, mostró la existencia de cambios significativos tanto en la composición específica, la biomasa como en la diversidad de la comunidad de peces, aunque no en el nivel trófico promedio. De hecho, los fondos de maërl y biogénicos (1), fondos circalitorales arenosos y fangosos constituidos principalmente por ascidias y equinodermos (2) y los fondos sedimentarios y detríticos constituidos principalmente por equinodermos (3), fueron los tres hábitats con mayor idoneidad a la hora de soportar la mayor capacidad de carga de biomasa de peces. Estos resultados destacan el importante papel del tipo de hábitat en la producción de biomasa de peces. Esto se encuentra en consonancia con los estudios realizados por Ordinas y Massutí (2009), quienes informaron que algunos de los recursos demersales más importantes de la plataforma costera dependen del tipo de hábitat macro-bentónico, a su vez asociado a un alto nivel de biomasa y biodiversidad.

En el caso del gradiente latitudinal, éste sólo parece afectar a la composición de la comunidad de peces. Así mismo, el área geográfica sur se caracterizó por un mayor porcentaje de consumidores de crustáceos pelágicos, en detrimento de los consumidores de crustáceos demersales. Estos resultados mostraron consistencia a lo largo de un eje latitudinal norte-sur, de acuerdo con los indicios aportados por Floeter et al. (2004), quienes reportaron cambios en la estructura trófica y patrones espaciales a lo largo del gradiente latitudinal. Así mismo, las especies planctófagas fueron más abundantes en la zona geográfica sur, de acuerdo con Cartes et al. (2002), quienes informaron de un aumento progresivo en el eje norte-sur en cuanto a la abundancia de estas especies. Por el contrario, la latitud no pareció afectar ni al nivel trófico promedio, a la biomasa o a la diversidad.

Con respecto a la profundidad, éste fue el único de los tres factores ambientales estudiados que afectó a los cuatro descriptores seleccionados para definir la comunidad de peces. De este modo, cambios en la profundidad afectaron a los valores de nivel trófico promedio, mostrando diferencias entre el primer y el resto de los estratos y entre el tercer y cuarto estrato. Esto puede explicarse debido a la baja posición trófica de las especies que habitan a menor profundidad en comparación con aquellas que ocupan los fondos más profundos. En cuanto a la biomasa, el estrato más profundo mostró diferencias con otros estratos, en consonancia con la distribución habitual de la biomasa en el océano (Abad et al., 2007). Por último, tanto la diversidad como la composición específica de la comunidad íctica mostraron una relación directa con la profundidad. En el caso de la diversidad, se apreció un claro descenso de sus valores con el aumento de la profundidad.

Una segunda parte de esta tesis se dedicó al estudio de los cambios ontogenéticos y la ecología trófica de siete especies comerciales pertenecientes al orden Gadiformes. Las especies seleccionadas para este estudio fueron: marujito (*Gadiculus argenteus*), barbada (*Gaidropsarus biscayensis*), maruca azul (*Molva macrophthalma*), merluza europea (*Merluccius merluccius*), bacaladilla (*Micromesistius poutassou*), brótola de fango (*Phycis blennoides*) y faneca (*Trisopterus minutus*). El estudio de solapamiento trófico de las especies coexistentes mostró una división de los recursos tróficos tanto entre las siete especies estudiadas como entre sus correspondientes clases de talla establecidas. Los resultados sugieren que las siete especies ocupan diferentes posiciones tróficas, que varían desde un patrón de alimentación generalista hasta un patrón caracterizado por hábitos piscívoros altamente especializados. Esta característica ecológica nos lleva a situarlas en nichos tróficos bien diferenciados. Estos resultados complementarían a aquellos reportados por Macpherson (1978a) y Morte (2001; 2002) quienes investigaron los cambios estacionales y batimétricos en las dietas de *M. poutassou*, G. *biscayensis*, *T. minutus* y *P. blennoides*, relacionando la disponibilidad de presas en la dieta con la estacionalidad. En particular, cinco de las siete especies de gadiformes investigadas, con la excepción de *G. biscayensis* y *T. minutus*, mostraron cambios ontogenéticos en la dieta, lo que les permitió ocupar varios nichos o subnichos simultáneamente. Con la única excepción de *G. argenteus* and *M. poutassou*, las especies estudiadas evidenciaron mecanismos dirigidos a evitar un excesivo solapamiento de nicho, diversificando sus estrategias y minimizando de este modo la competencia por los recursos tróficos y espaciales. Un ejemplo de estos mecanismos es el caso de las parejas *M. poutassou*-*P. blennoides* y *M. merluccius*-*T. minutus*. Ambas parejas de especies exhibieron con diferencia los valores más altos de solapamiento espacial, que las especies compensaron a su vez con valores bajos de solapamiento trófico. Por el contrario, las parejas *P. blennoides*-*T. minutus*, *M. poutassou*-*M. macrophthalma* y *M. merluccius*- *M. poutassou*, mostraron valores altos de solapamiento de nicho trófico, que compensaron a su vez con valores bajos de co-ocurrencia espacial. De este modo, con la única excepción arriba mencionada, las especies de gadiformes estudiadas parecen organizarse siguiendo la hipótesis de complementariedad de nicho (Ebeling y Hixon, 1991). Según este principio, si un ecosistema se estructura en acordancia con esta hipótesis, éste mostraría consistentemente bajo solapamiento de forma que la coexistencia de especies similares ocurriría debido a las diferencias en el uso de los recursos disponibles (Pianka, 1973; Schoener, 1974).

En relación a la amplitud del nicho trófico, parece haber un patrón que relaciona la clase de talla con la amplitud del nicho. Por tanto, pudo observarse como las clases pequeñas presentaron un nicho trófico más amplio que el de las clases grandes. No obstante, se da la excepción de *M*. *macropththalma*, una especie con comportamiento piscívoro altamente especializado, donde el mayor tamaño de los ejemplares le permite tener acceso a un mayor número de presas potenciales en su dieta, aumentando así su nicho trófico con el desarrollo ontogenético de los ejemplares. Por otra parte, los resultados mostraron una relación entre la clase de talla y el nivel trófico, de forma que los ejemplares de clases de talla más pequeñas presentaron un nivel trófico más bajo, aumentando éste con el desarrollo ontogenético de la especie. Esta diferencia en lo referente al nivel trófico entre clases de talla fue mayor para aquellas especies posicionadas en niveles superiores de la red trófica (por ejemplo, *M*. *merluccius*, *M*. *poutassou* y *M*. *macropththalma*).

Una vez descrita la red trófica para la zona de estudio (GSA6), se realizó un análisis estadístico para determinar qué especies mostraban diferencias en sus preferencias tróficas entre el Golfo de Alicante y el resto de la GSA6. Para ello, se exploraron dichas diferencias entre dietas mediante un análisis no paramétrico de similaridad (ANOSIM), basado en el escalamiento multidimensional (MDS) del índice de disimilaridad de Bray-Curtis (Clarke and Gorley, 2006). Con los resultados obtenidos se construyó la matriz de dietas, compuesta por aquellas especies con patrones de alimentación específicos para el Golfo de Alicante, que fueron utilizados como datos de entrada para la implementación del modelo ecológico planteado en dicha zona. Para el resto de especies que no presentaron diferencias, se utilizó la dieta caracterizada para dichas especies en toda la GSA6. Una vez determinada la matriz de dietas, se estimaron el resto de datos de entrada necesarios para construir el modelo ecológico.

Seguidamente, una vez recopilada toda la información necesaria, se construyó un modelo de equilibrio de masas Ecopath para el ecosistema marino ubicado en el Golfo de Alicante. El objetivo fue el de ofrecer una descripción de las relaciones tróficas y la dinámica del funcionamiento de este ecosistema y realizar un análisis comparativo con ecosistemas vecinos para ver sus posibles similaridades o diferencias. Los principales hallazgos revelaron que el ecosistema del Golfo de Alicante presenta diferencias en cuanto a las características estructurales con respecto a los dos modelos con los que ha sido comparado. Estos modelos se encuentran ubicados al norte; Modelo del Noroeste del Mediterráneo (NWM) (Corrales et al. 2015) y al sur; Modelo Golfo de Cádiz (GoC) (Torres et al., 2013) de la zona de estudio. La existencia de estas diferencias podría ser debida a las singulares características oceanográficas y biológicas imperantes en la zona. La comparación llevada a cabo con los modelos existentes en áreas vecinas mostró que las principales diferencias encontradas podrían estar relacionadas con la producción primaria, que mostró los valores más bajos precisamente en el Golfo de Alicante.

Cuando exploramos algunos de los indicadores que nos ofrece este modelo, vemos que a pesar de los elevados valores tanto de eficiencia ecotrófica como de tasa de mortalidad por pesca, el Golfo de Alicante mostró una menor presión pesquera si comparamos con los otros dos modelos mencionados anteriormente. Esto nos induce a pensar que el nivel de explotación del ecosistema puede ser considerado como moderado. Otra característica reseñable es la importancia del compartimento demersal, donde la mayoría de la biomasa se asoció a los grupos de detrito. De esta forma, al ser un sistema basado en el detrito, éste puede depender en gran medida de la biomasa generada por el propio sistema, lo cual se puede relacionar con un cierto grado de estabilidad.

Consecuentemente, este ecosistema se mantiene eficiente y estable en sus pobres condiciones en cuanto al aporte de nutrientes, pero al mismo tiempo delicado y vulnerable porque depende del uso eficiente y circular de su propia biomasa. Por tanto, si se diera el caso de un exceso en la extracción de biomasa por pesca por encima de su sostenibilidad, esto podría afectar al aporte de detrito y por tanto a la estabilidad del propio sistema. Esta característica resulta de especial interés, ya que podría explicar la estabilidad de las pesquerías de pequeños pelágicos en relación al declive observado más al norte, donde el ecosistema localizado en el NWM, al estar más influenciado por las aportaciones continentales de los ríos Ebro y Ródano, ha visto mermadas sus capturas notablemente durante el último siglo.

Tal como se ha mencionado anteriormente, el Golfo de Alicante se caracteriza por tratarse de un ecosistema con bajos valores de producción primaria (Estrada, 1996), de modo que basa su dinámica en nutrientes reciclados más que en nuevos aportes procedentes de las contribuciones continentales. De este modo, hablamos de un sistema pobre en nutrientes pero al mismo tiempo más estable, guiado por su propia producción primaria. Estos resultados están en línea con los reportados por Estrada (1996), quien relacionó un rendimiento aparentemente alto de las pesquerías mediterráneas con valores de producción primaria relativamente bajos, fenómeno conocido como “paradoja del Mediterráneo”.

El análisis de los principales indicadores del ecosistema que nos ofrece el modelo Ecopath sugiere que el Golfo de Alicante presenta un mayor nivel de complejidad de los flujos internos, lo cual se correlaciona con la estabilidad y madurez antes mencionadas. Esta cualidad del sistema permite que éste se organice como una red más que como una estructura de cadena (Christensen, 1995). Esto contrasta con la linealidad detectada en la red trófica de los ecosistemas descritos en el NWM y en el GoC. Con respecto al compartimento demersal versus pelágico, en el ecosistema del Golfo de Alicante, nuestros resultados revelaron la importancia de la elevada eficiencia del reciclaje. Como resultado de esto, el nivel trófico promedio de la captura en el Golfo de Alicante muestra valores ligeramente más altos que los estimados en el NWM pero más bajos que los del GoC. Esto probablemente se debe a la mayor proporción de especies demersales que aparecen en las capturas tanto del Golfo de Alicante como en el de Cádiz, lo que implica que los desembarcos presenten un nivel trófico promedio más alto. La mayor eficiencia del compartimento demersal en el uso de los nutrientes reciclados podría explicar estas diferencias.

En definitiva, los hallazgos obtenidos en esta tesis representan un gran avance en el campo de la ecología trófica y la modelización ecosistémica en el área de estudio. De este modo, se pudo cumplir el objetivo de describir la estructura y funcionamiento de los principales componentes tróficos dentro de la red trófica de la GSA6. A su vez, el modelo ecológico implementado en el Golfo de Alicante, reveló que se trata de un ecosistema singular condicionado por sus particulares características ambientales, lo que marcó la diferencia con respecto a los ecosistemas cercanos con los que fue comparado. En consecuencia, el estudio presentado en esta tesis contribuye a la comprensión del funcionamiento de un ecosistema mediterráneo, desde una perspectiva tanto ecológica como pesquera. El marco comparativo utilizando áreas modeladas ubicadas en ecosistemas cercanos nos ha proporcionado una imagen integral de lo que ocurre a lo largo del eje latitudinal norte-sur en la costa mediterránea española. Por tanto, este estudio representa una línea de base desde la que desarrollar la simulación de diferentes escenarios de explotación teniendo en cuenta factores tan importantes como el cambio climático y las diferentes oportunidades de gestión.

Chapter 6: Conclusions

Conclusions

1. The innovation of the study was the best fitting of cumulative prey curves through Clench´s functions, which enabled to establish the minimum sample size for each species by means of a mathematical procedure.

2. The diet compositions and feeding strategies of 61 fish species coexisting in the western Mediterranean Sea provided an updated and valuable dataset for future studies related to trophic ecology in this region.

3. The analysis of the nine trophic guilds identified along the Northern Spain area revealed that the three factors explored, namely, latitude, habitat type and depth, affected to a greater or lesser degree the four indicators chosen (fish community composition, biomass, diversity of fish community and mean trophic level) to describe the fish community characterized in the study area.

4. Latitudinal gradient only seemed to affect fish community composition, showing consistency along a latitudinal north-south axis. On the contrary, latitude did not seem to affect mean trophic level, biomass and diversity.

5. The analysis of the community descriptors based on the type of habitat, showed the existence of significant changes, both in the fish community composition, the biomass and in the diversity of the fish community, although not in the mean trophic level.

6. Depth was the only one of the three environmental factors studied that affected the four descriptors selected to define the fish community, particularly affecting diversity and fish community composition.

7. Gadiformes species seem to exploit food resources at different trophic levels of the food web, showing ontogenetic shifts in diet and resource partitioning, occupying different trophic positions that range from a generalized feeding behavior to specialized piscivorous habits.

8. Five of the seven species of Gadiforms investigated, except for bigeye rockling (*Gaidropsarus biscayensis*) and poor cod (*Trisopterus minutus*), showed ontogenetic shifts in diet, allowing them to occupy several niches or sub-niches simultaneously.

9. Regarding niche breadth in Gadiforms, there does appear to be a pattern that relates size class to niche breadth. Therefore, the smaller sizes presented broader trophic niches than those presented by the largest specimens, except for Spanish ling (*Molva macrophthalma*). In this

case, the larger size of the specimens allows it to have access to a greater number of potential prey in its diet, thus increasing its trophic niche with ontogenetic development.

10. The effects of competitive interactions in Gadiforms are more likely between size groups of the same species than between different species.

11. The Gulf of Alicante ecosystem showed differences in structural features with the two models compared located north and south of the study area, which could be explained by its singular oceanographic, biological and ecological characteristics.

12. The main differences found concerning the compared models were due to the low primary production in the GoA, which involves lower catches and higher importance of the demersal compartment where most biomasses were associated to the detritus.

13. Main trophic flows were originated at the base of the food web, likely related to bottom-up predator-prey interactions.

14. Trophic levels ranged from TL = 1 for primary producers and detritus groups, to TL = 4.15 for anglerfishes and 4.07 for dolphins.

15. Interactions between pelagic and demersal groups were week, and only noticeable between *Adult hake* and *Sardine*.

16. Valls keystones index highlighted the importance of top predators' influence, such as anglerfishes, dolphins, adult hake and octopuses.

17. Despite the high values of ecotrophic efficiencies and mortality rates, results showed a lower fishing pressure if compared with the other neighboring areas.

18. Fishing pressure indicators point out a moderate level of overexploitation, so it may be necessary to reduce total catches in the Gulf of Alicante.

19. The analysis of the trophic impact matrix showed that bottom trawling fleet had the highest impact on most ecosystem compartments and the largest impacts on some demersal groups, mainly on anglerfishes, deep water rose shrimp, rays and skates, benthic sharks, octopuses, blue and red shrimp and adult hake.

20. The Purse Seine fishery showed important negative impacts on their target species (small pelagics) and demersal ichthyophagous fishes due to the removal of prey.

21. Bottom trawl, longlines and purse seine revealed strong competition between themselves while small scale fisheries did not.

22. The primary production required to sustain the fishery (%PPR) in the GoA during 2011 was 16.3%, the highest of the three compared models.

23. The probability of the GoA being sustainable exploited was low (66%) but much higher than values obtained for NWM and GoC ecosystems (28% and 23%, respectively).

24. In terms of flow to detritus, it was dominated by *Phytoplankton*, *Microzooplankton* and *Worms*. Among fish groups, small pelagics, such as *Sardine*, was the most important component.

25. Demersal/Pelagics biomass-based indicator highlighted the dominance of the demersal compartment in the GoA model.

26. The GoA showed high values of fishing mortality for most of the commercial modeled groups (*Octopuses*, *Sparids*, *Small pelagics* and *Benthopelagic cephalopods*), in line with results obtained in independent information on stock assessment conventions.

27. The GoA presents a high level of complexity of internal flows, supported by a high value of Sytem Omnivory index, pointing out that the system looks more a web-like than a chain-like structure, in turn, correlated with stability and maturity.

Conclusiones

1. Este estudio introduce el ajuste de las curvas de presas acumuladas mediante el uso de la función de Clench, siendo la primera vez que se utiliza en Ciencias Marinas, lo que se considera una aportación muy novedosa en este ámbito. Esta metodología ha permitido establecer el tamaño mínimo de muestra necesario para caracterizar la dieta de cada una de las especies estudiadas a través de un procedimiento matemático.

2. La descripción de la dieta y las estrategias de alimentación de 61 especies de peces que coexisten en el Mar Mediterráneo Occidental proporcionaron un conjunto de datos actualizado y valioso para futuros estudios relacionados con la ecología trófica en esta extensa región.

3. El análisis de los diferentes grupos tróficos identificados a lo largo del área estudiada reveló que los tres factores ambientales explorados tales como la latitud, el tipo de hábitat y la profundidad, afectaron en mayor o menor medida a los cuatro indicadores (composición específica, biomasa, diversidad de la comunidad y nivel trófico promedio) seleccionados para describir la comunidad de peces caracterizada en el área de estudio.

4. El gradiente latitudinal sólo pareció afectar a la composición específica de la comunidad de peces, mostrando consistencia a lo largo de un eje latitudinal norte-sur. Por el contrario, la latitud no pareció afectar al nivel trófico promedio, a la biomasa o a la diversidad.

5. El análisis de los descriptores de la comunidad en función del tipo de hábitat, mostró la existencia de cambios significativos tanto en la composición específica, en la biomasa como en la diversidad de la comunidad de peces. Por el contrario, tales cambios no fueron detectados para el nivel trófico promedio.

6. La profundidad fue el único de los tres factores ambientales estudiados que afectó a los cuatro descriptores seleccionados para definir la comunidad de peces, afectando de forma particular a la diversidad y a la composición específica de la comunidad de peces.

7. Los resultados sugieren que las siete especies de Gadiformes investigadas ocupan diferentes posiciones tróficas, que varían desde un patrón de alimentación generalista hasta un patrón caracterizado por hábitos piscívoros altamente especializados.

8. Cinco de las siete especies de Gadiformes investigadas, con excepción de *Gaidropsarus biscayensis* y *Trisopterus minutus*, mostraron cambios ontogenéticos en la dieta, lo que les permitió ocupar varios nichos o subnichos simultáneamente.

9. En relación a la amplitud del nicho trófico en Gadiformes, parece existir un patrón que relaciona la clase de talla con la amplitud de nicho. Por consiguiente, las tallas pequeñas presentaron un nicho trófico más amplio que las grandes, a excepción de *Molva macrophthalma*, donde el mayor tamaño de los ejemplares le permite tener acceso a un mayor número de presas potenciales en su dieta, aumentando así su nicho trófico con el desarrollo ontogenético.

10. Las especies de Gadiformes estudiadas presentan una mayor competencia entre grupos de talla dentro de la misma especie (relación intra-específica) que entre especies distintas (relación inter-específica).

11. El ecosistema descrito para el Golfo de Alicante mostró diferencias en cuanto a las características estructurales con respecto a los dos modelos con los que se comparó, uno ubicado al norte y otro al sur del mismo, lo que podría explicarse por sus singulares características biológicas y ecológicas.

12. Las principales diferencias encontradas con respecto a los modelos comparados están relacionadas con la baja producción primaria encontrada en el Golfo de Alicante, lo que se traduce en una menor proporción de capturas y una mayor importancia del compartimento demersal, donde la mayoría de las biomasas se encuentra asociada al detrito.

13. Los principales flujos tróficos estimados por el modelo se originaron en la base de la red trófica, lo que estaría relacionado con la interacción predador-presa que tiene lugar desde la base de la red trófica hacia arriba (“bottom-up”).

14. Los niveles tróficos estimados variaron desde un nivel trófico igual a 1 para los productores primarios y grupos de detritus, hasta un nivel trófico de 4,15 para los rapes o de 4,07 para los delfines.

15. No se apreciaron interacciones substanciales entre los grupos funcionales de especies pelágicas y demersales, tan sólo la interacción puntual entre la merluza adulta y la sardina.

16. El índice de especies clave sugerido por Valls y colaboradores destacó la influencia en la red trófica de los principales predadores, tales como los rapes, delfines, la merluza adulta y los pulpos.

17. A pesar de los elevados valores de eficiencia ecotrófica y tasas de mortalidad pesquera estimadas, el Golfo de Alicante mostró la menor presión pesquera de los tres modelos comparados.

18. Los indicadores de presión pesquera apuntan a un nivel de sobreexplotación moderado, por lo que sería recomendable reducir las capturas totales en el Golfo de Alicante.

19. El análisis de la matriz trófica de impacto mostró que la flota de arrastre de fondo tuvo el mayor impacto en la mayoría de los compartimentos del ecosistema y los mayores impactos en algunos grupos demersales, principalmente en los rapes, gamba blanca, rayas, tiburones bentónicos, pulpos, gamba roja y merluza adulta.

20. La flota de cerco también mostró importantes impactos negativos en sus especies objetivo (pequeños pelágicos) y peces ictiófagos demersales, debido al efecto en cascada que produjo la extracción de sus presas principales.

21. Tanto la flota de arrastre de fondo, como la de palangre y la de cerco, mostraron una fuerte competencia entre ellas, al contrario de lo que ocurrió con la flota artesanal.

22. La producción primaria requerida para sostener la pesquería estimada para el Golfo de Alicante durante 2011 fue del 16,3%, presentando el mayor valor de los tres ecosistemas comparados.

23. La probabilidad de que el ecosistema del Golfo de Alicante sea explotado de manera sostenible (Psust) fue baja (66%) pero mucho más alta que la obtenida en los modelos de los ecosistemas comparados, NWM y GoC (28% y 23%, respectivamente).

24. El flujo al detrito está dominado por *fitoplancton*, *microzooplancton* y *anélidos*. Dentro de los grupos de peces, la *sardina* fue el grupo más importante.

25. El indicador basado en el ratio biomasa demersal/biomasa pelágica, destacó el predominio del compartimento demersal en el modelo GoA.

26. El Golfo de Alicante mostró valores elevados de mortalidad por pesca para la mayoría de los grupos comerciales modelados (pulpos, espáridos, pequeños pelágicos y cefalópodos bentopelágicos), en consonancia con los resultados obtenidos en informes locales oficiales de evaluación de stocks pesqueros.

27. El Golfo de Alicante presenta un alto nivel de complejidad de los flujos internos, lo cual se ve apoyado por el elevado valor del Índice del Omnivoría del Sistema (IOS), permitiendo que el sistema se organice como una red más que como una estructura de cadena.

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ANNEX I. Cumulative Prey Curves

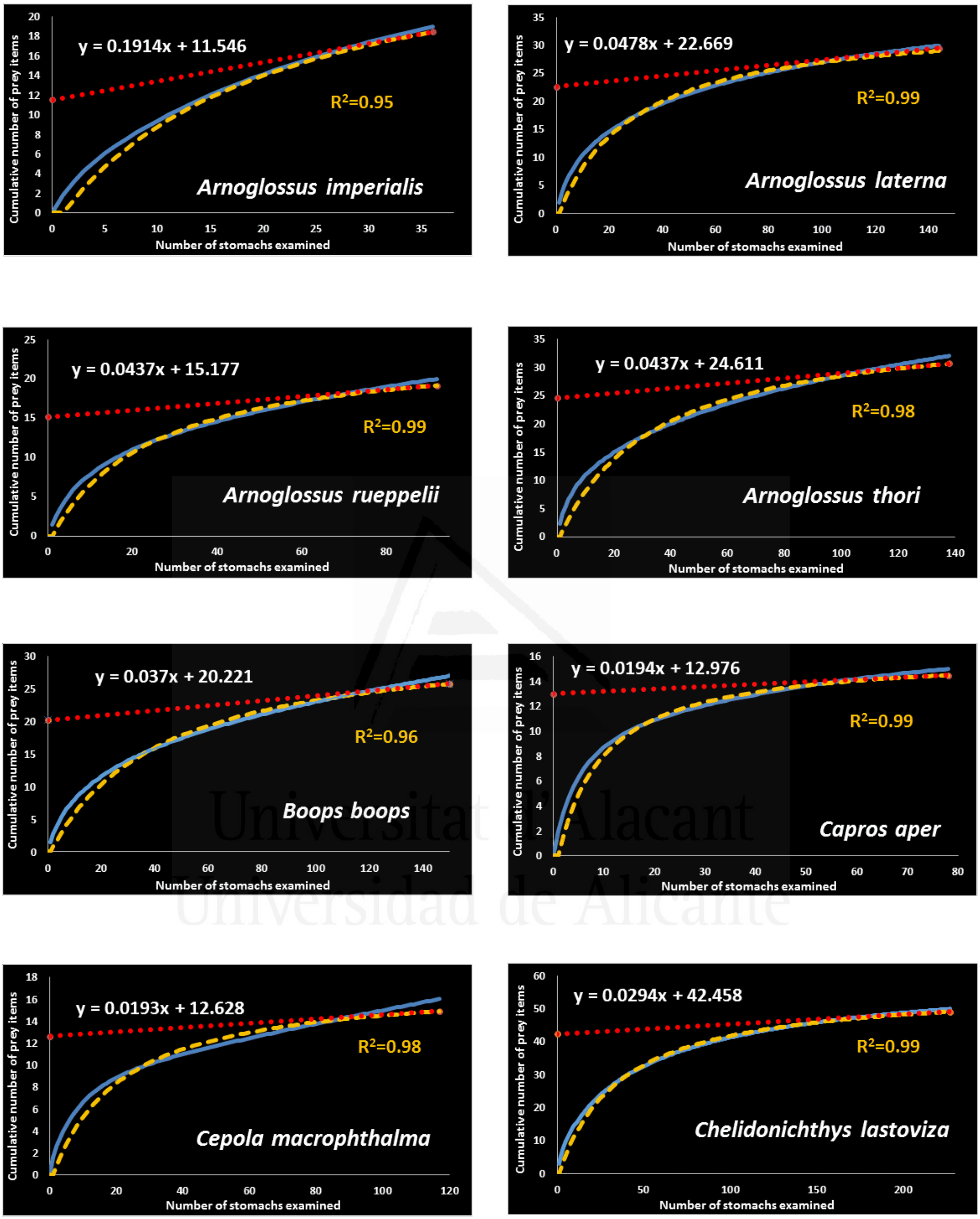
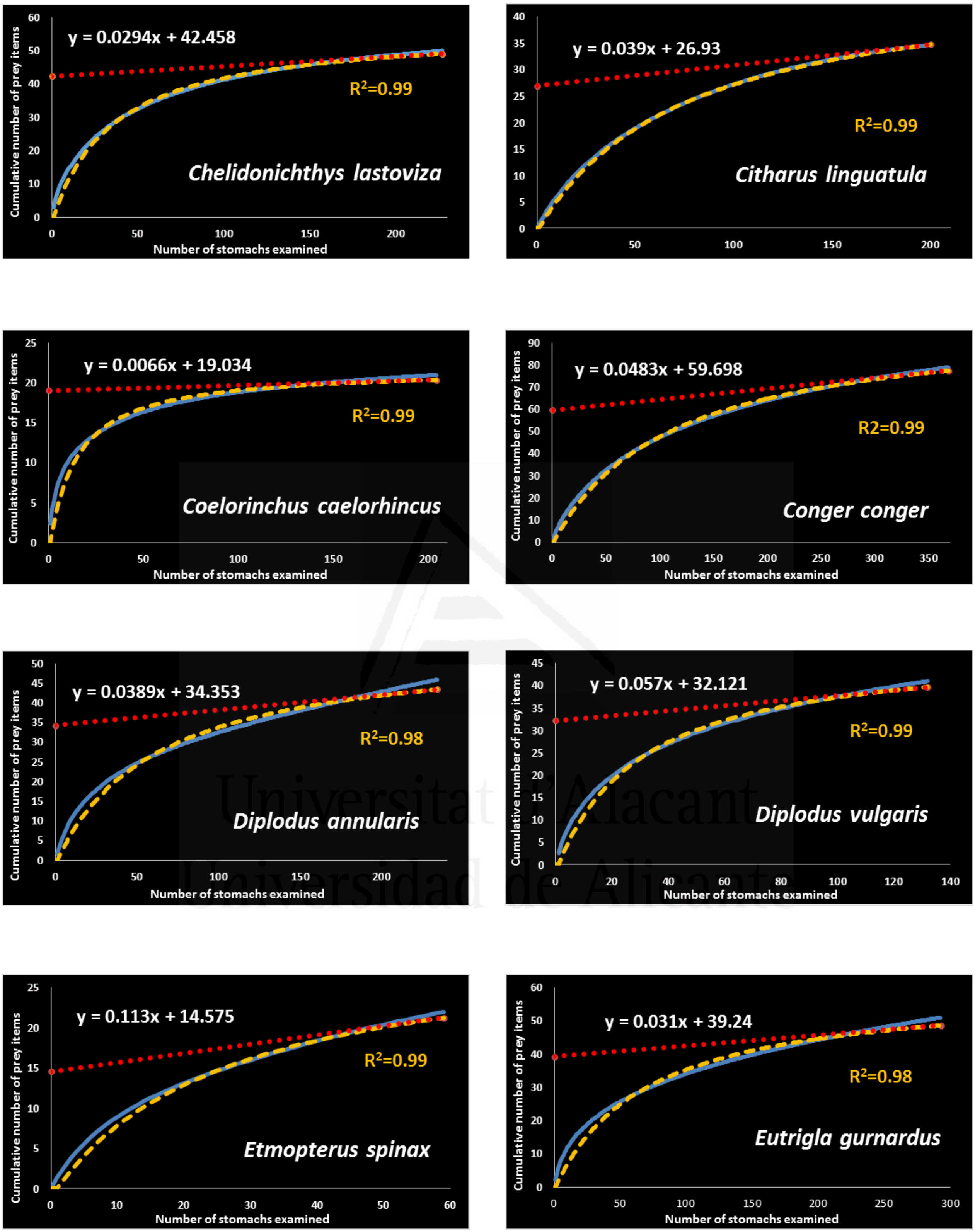


Fig. 1 Cummulative prey curves (blue line) for the 61 fish species analyzed, fitted to Clench`s function (dashed yellow line). Asymptote to Clench`s function (dotted red line).



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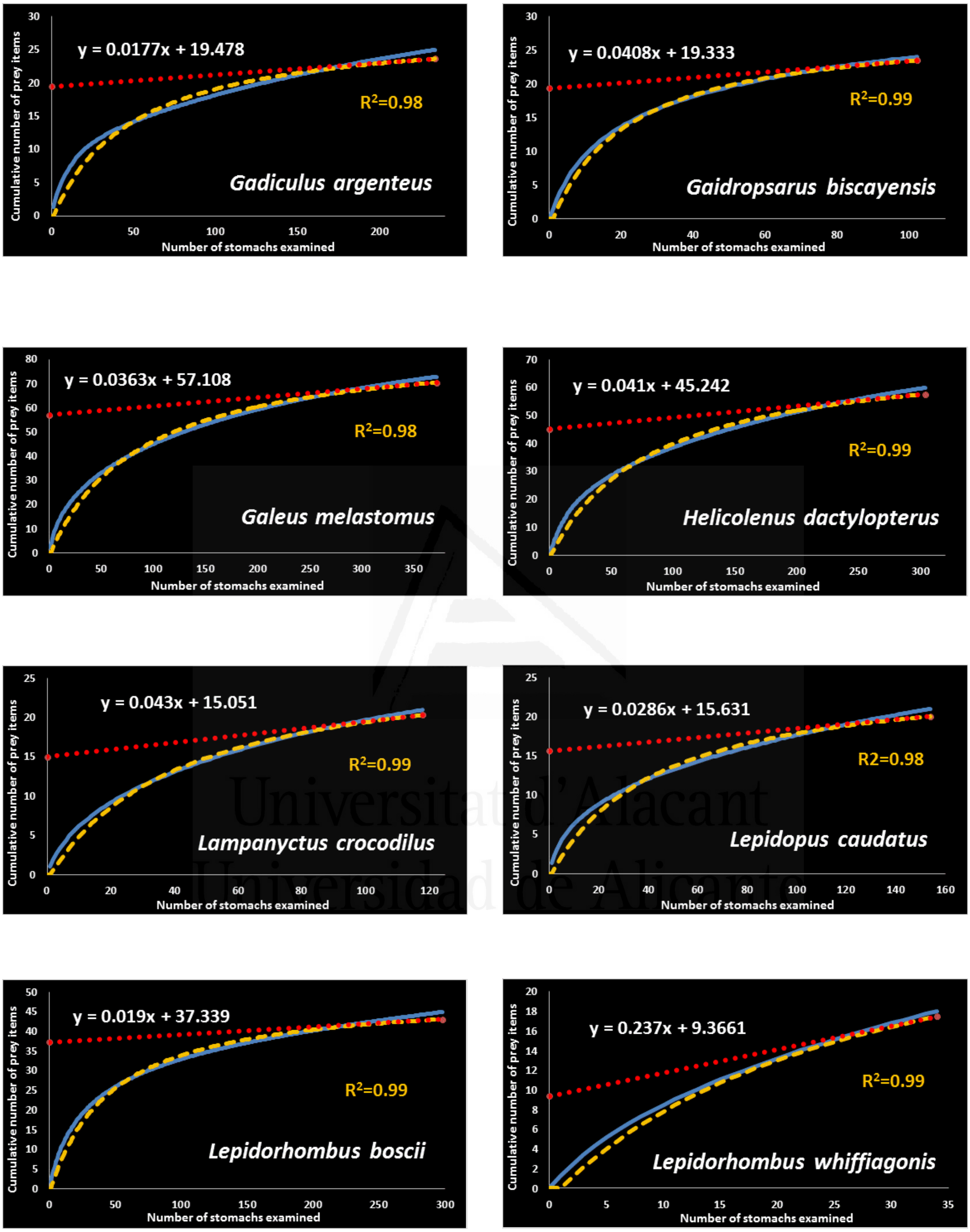

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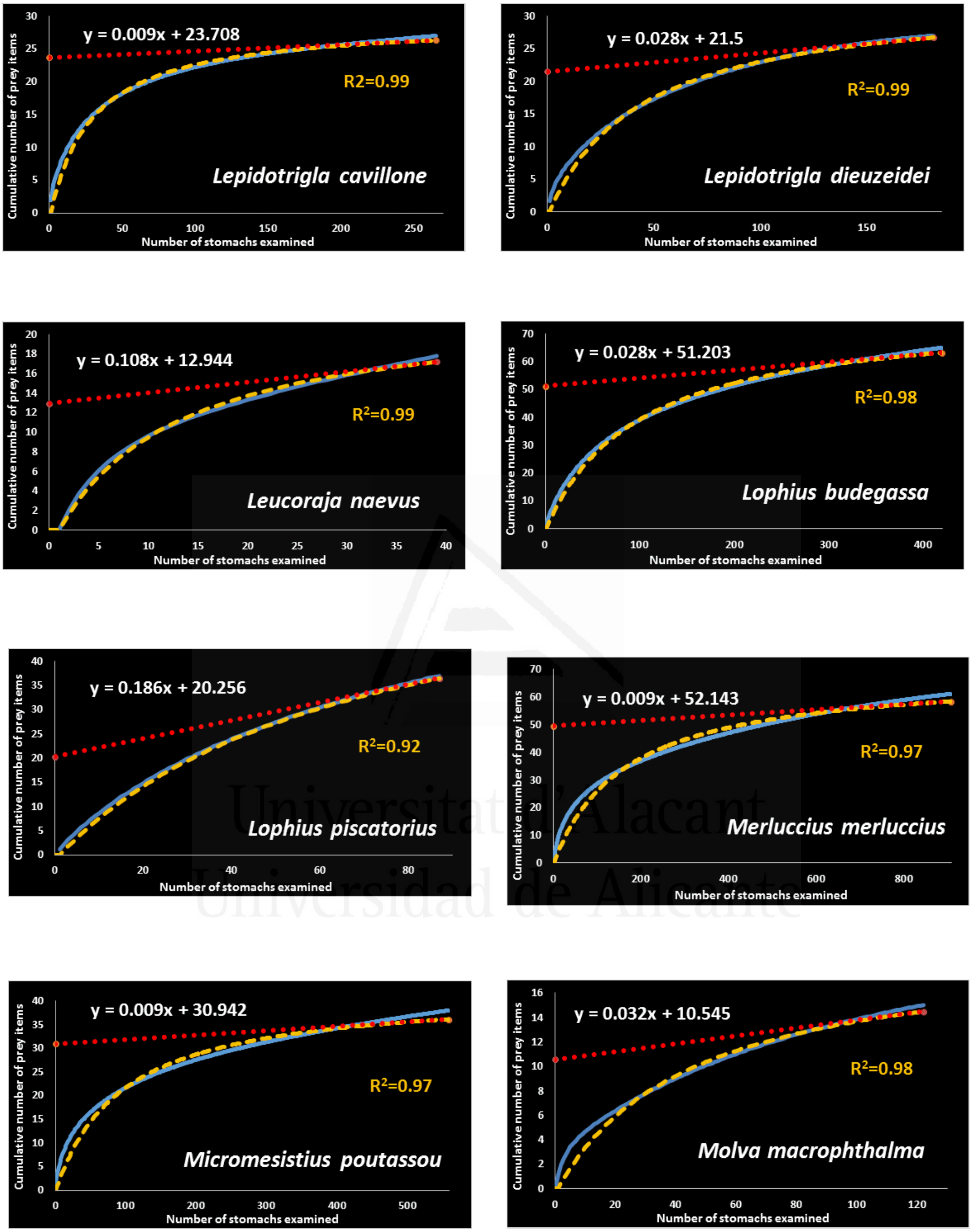

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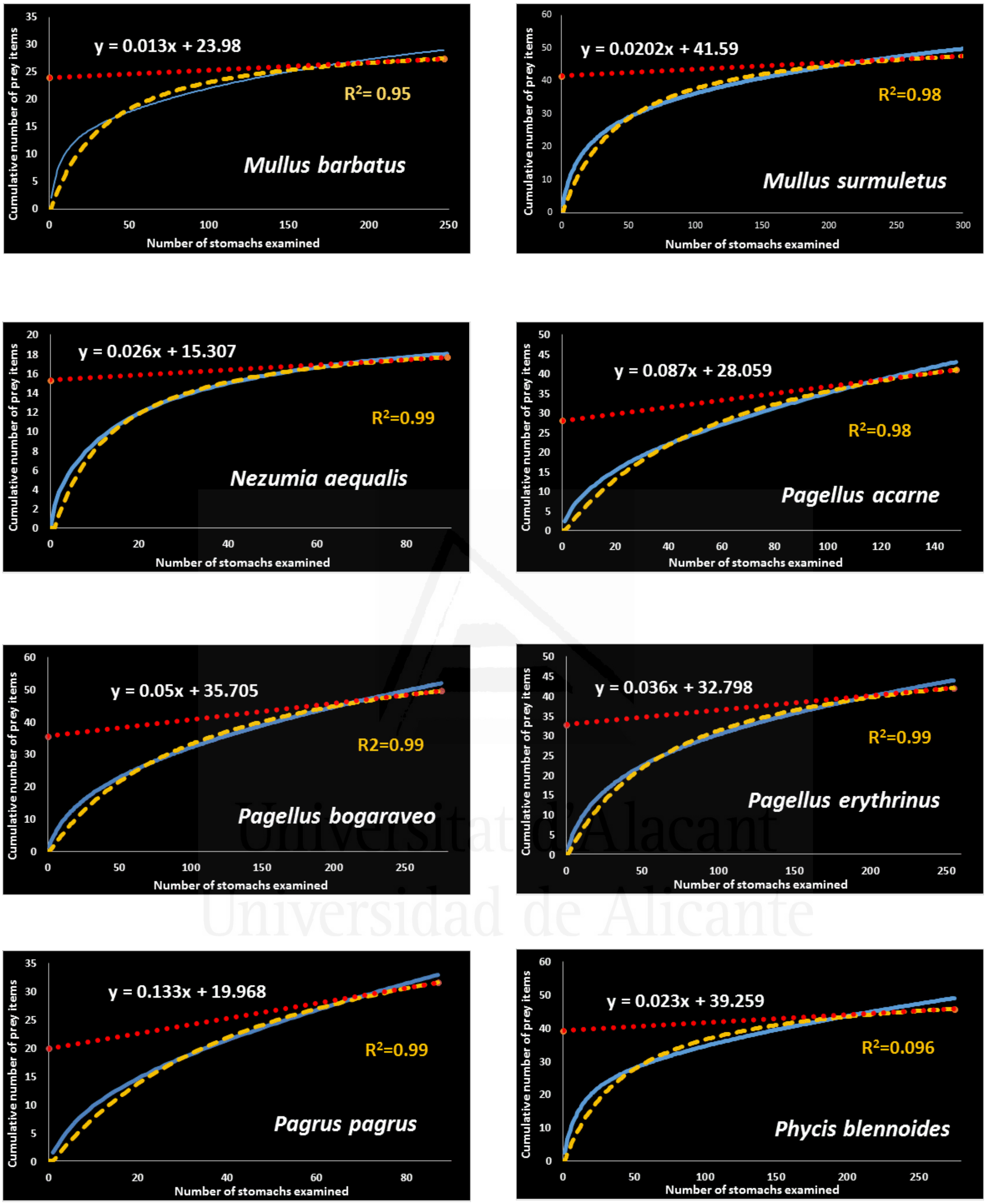

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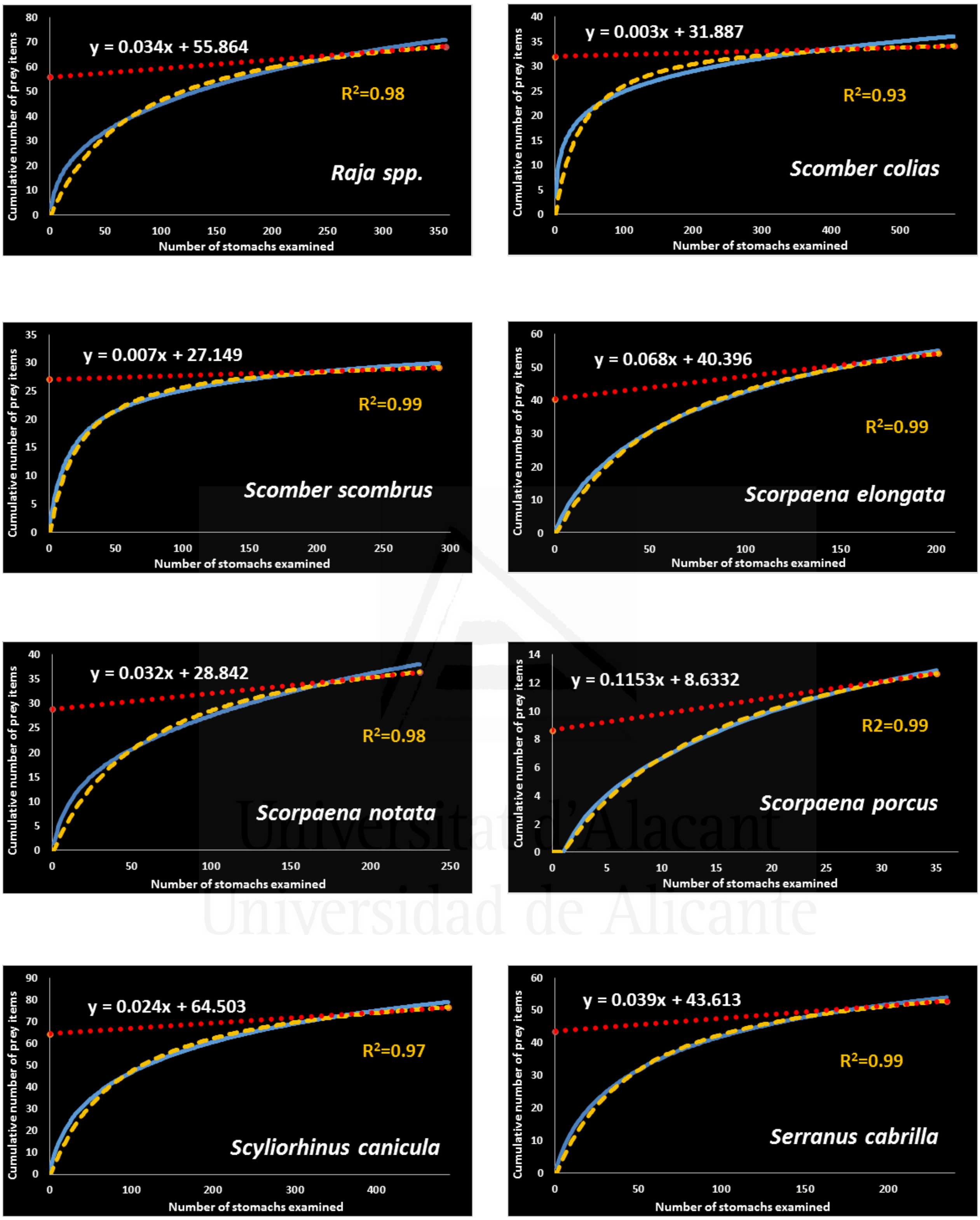

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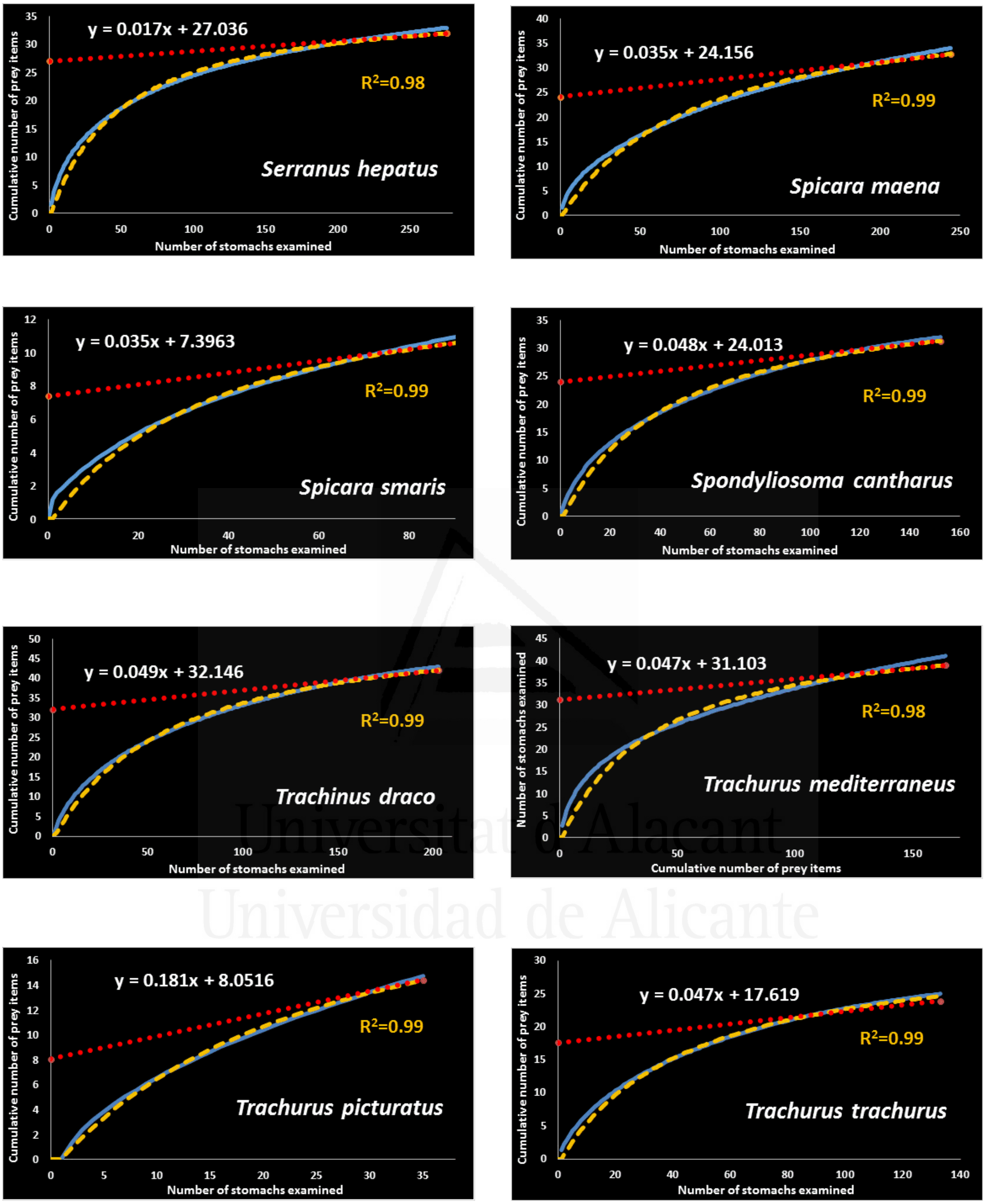

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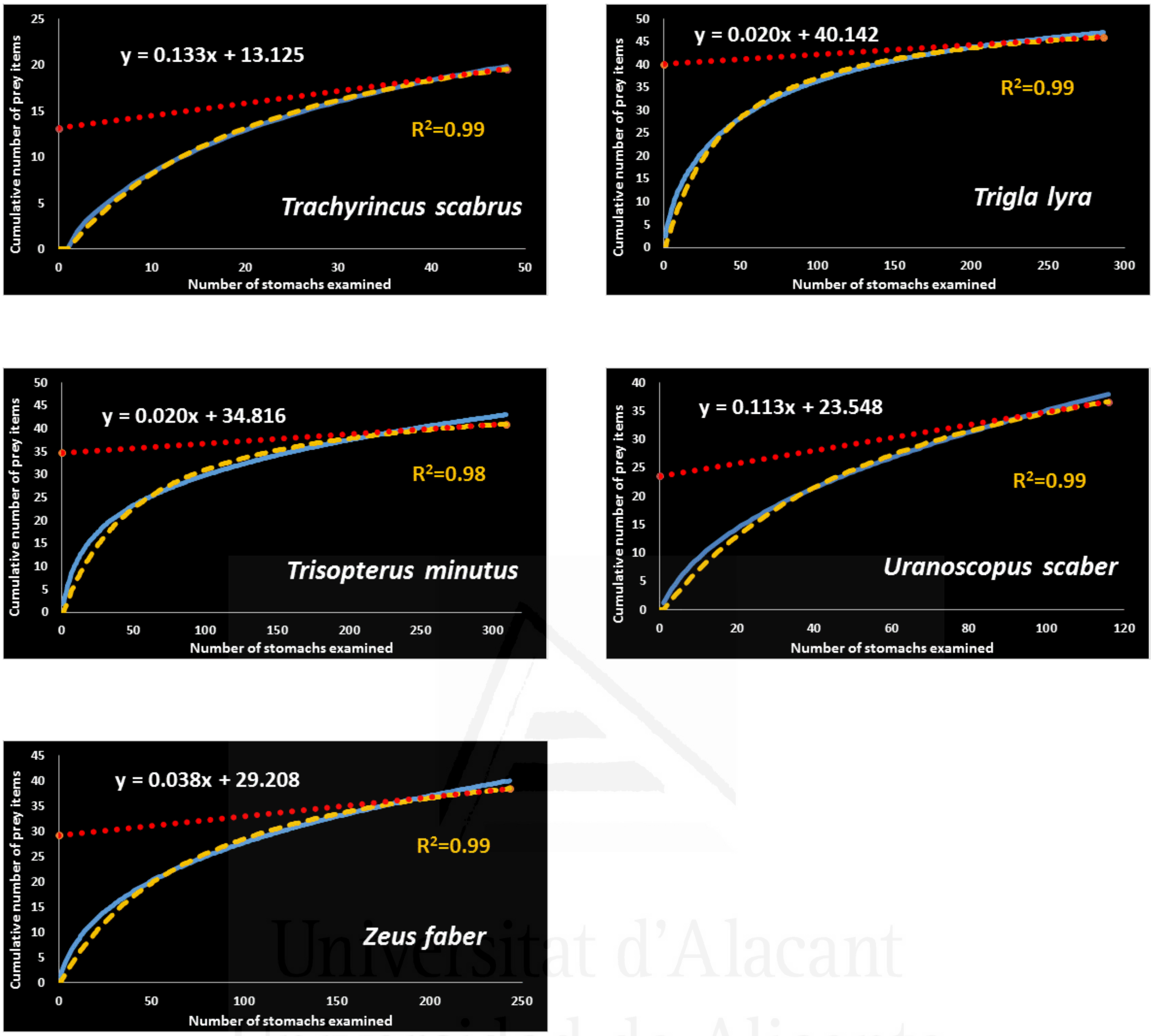

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ANNEX II. Papers published in peer-reviewed journals

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Revealing environmental forcing in the different trophic guilds of fish communities off the Western Mediterranean Sea

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ABSTRACT

The dietary preferences of 61 Western Mediterranean species of fish belonging to different trophic levels were studied. Specimens were collected during the annual bottom trawl survey MEDITS for the period 2011–2018, with a total of 16,588 stomach contents analyzed, providing a highly valuable raw dataset for advanced studies in trophic ecology. The software EstimateS 9.1 was used, for the first time in a study of Mediterranean fish species, to estimate cumulative prey curves in order to determine the adequacy of the sample size for each species in representing the species diet. The main findings revealed the existence of nine well-identified feeding strategies, or trophic guilds, based on food preferences. Indicators, namely the Shannon diversity index, biomass estimated from standard surveys, mean trophic level and fish community composition, were used to categorize the structure of the fish community in Western Mediterranean marine food webs. In addition, the effects of latitude, depth and habitat type on fish community structure were investigated. Results show all these environmental factors investigated drove fish composition structure. Regarding the three variables investigated, depth had the greatest impact on the fish community structure, particularly affecting diversity and fish community composition. Latitudinal gradient only seemed to affect fish community composition, showing consistency along a latitudinal north-south axis. Habitat type was found to be significant in fish community structure. Mean trophic level was the only indicator that was not affected significantly by environmental variables. The present study shows the relevance of environmental forcing in fish community structure. These findings highlight the need of ecosystem studies, since information about the trophic networks in the study area is still scarce, jeopardizing the development of ecosystem models. The present work aims to fill this gap for the effective implementation of an ecosystem approach to fisheries management in the Western Mediterranean Sea.

1. Introduction

The study of marine food webs has not only become a useful tool to identify the relevance of species relationships and food resource partitioning, but is also a way to explore different levels of producers or consumers (Polis and Strong, 1996). Food web studies play an essential role in explaining disruptions such as overfishing (e.g. Coll et al., 2014a, 2014b), alien species (Streftaris and Zenetos, 2006; Corrales et al., 2017) and habitat destruction in marine ecosystems (Muntadas et al., 2014). In this regard, one of the most threatened areas is the continental shelf, an area that hosts most of the exploited species and is distinctively characterized by a high biological production (Coll et al., 2008, 2014a, 2014b).

The EU Marine Strategy Framework Directive (European Commission, 2008) requires that each Member State takes the necessary measures to achieve or maintain Good Environmental Status of marine waters. The MSFD takes into account topics such as biodiversity, contaminants, marine litter, commercially exploited fish and marine food webs. Likewise, the Spanish inventory of Habitat and Marine species (Mapama, 2013) can help to identify singular habitats as well as to determine habitat-related species. Similarly, other variables to explore along with habitat type are, for instance, geographical variation in fish community structure along the north-south coast and bathymetric ranges (Ferreira et al., 2004).

Even though the western Mediterranean Sea is one of the most studied seas, most of the reported research is focused at local spatial scales over short periods of time as in studies of the Catalan Sea (Macpherson, 1980a, 1980b; Carrassón and Matallanas, 2002; López

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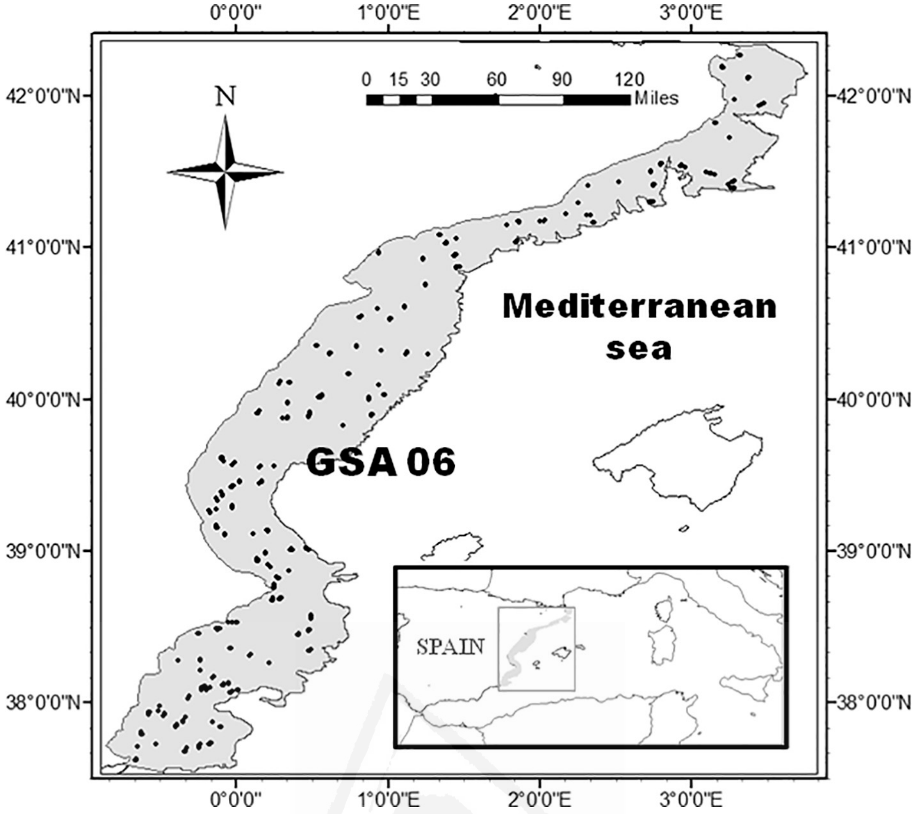

Fig. 1. Map of the study area showing the sampling locations between the isobaths of 40 and 800 m. Dots indicate the position of the fishing hauls analyzed.

et al., 2016) and the Gulf of Valencia (Morte et al., 2001, 2002; Jaramillo et al., 2011). To better understand latitudinal and depth patterns, trophic ecology research covering a broader study area is needed, such as that for the Spanish Western Mediterranean Sea, i.e. Geographical Sub-Area 6 (GSA06) as defined by the General Fisheries Commission of the Mediterranean (CFCM).

Our study was conducted along the continental shelf and slope of the eastern coast of the Iberian Peninsula, located in the Western Mediterranean Sea, from Cape Palos to Cape Creus (Fig. 1). This area includes zones that have high biological productivity due to the combined effects of the Northern Current and run-off from the Ebro River (Estrada, 1996). This region is an important fishing ground in the Mediterranean Sea, showing significant marine biodiversity and species of great economic value (Navarro et al., 2015).

A well-recognized problem related to trophic studies has been accurately determining the minimum sample size for each species sampled. To address this problem, we applied, for the first time in marine trophic ecology studies, a mathematical approach based on cumulative prey curves for determining the adequate number of samples required to determine the diet of the species studied (Modde and Ros, 1983; Ferry and Cailliet, 1996). In the study area, we propose that cumulative prey curve studies provide useful information for implementing future and improved ecosystem-based models along the Western Mediterranean. Ecosystem-based models are widely used to investigate ecological and fishery connections and they are recognized as effective assessment tools in the evaluation of the trophic structure of marine communities (e.g. Christensen and Walters, 2002; Coll et al., 2007; Torres et al., 2013). Despite the importance of ecosystem studies, information about the trophic networks in the study area is still scarce, thus limiting the development of ecosystem models. The present work aims to fill this gap.

This study provides an important and updated contribution to existing knowledge addressing the trophic ecology of 61 species. First, we investigated the diet compositions of the most representative fish species coexisting in the Western Mediterranean Sea, applying the cumulative prey curve methodology. We then identified the major trophic guilds exploiting similar food resources, considering a trophic guild as a specific set of species that are clustered following similar feeding strategy (Koran and Kropil, 2014). Finally, we investigated how the environmental drivers of habitat type, latitude and depth affected the different trophic guild structures, using four main indicators, namely the Shannon diversity index, biomass, mean trophic level and fish community composition.

2. Material and methods

2.1. Stomach sampling

The most representative species of each trophic level, according to its biomass, were selected for our study to improve our understanding of the main components of the trophic web in the study area. Thus, the trophic ecology of 61 fish species occurring over the shelf and upper slope were studied through stomach content analysis. Samples were collected and analyzed during the 'MEDITS' bottom trawl surveys conducted continuously between 2011 and 2018 (Bertrand et al., 2002). This survey takes place yearly from May to June and aims to evaluate the demersal resources in the area. The standard sampling device used is a bottom trawl (GOC 73) designed for experimental fishing, in which the gear has a 40 mm mesh size and the codend a 20 mm mesh size.

A total of 910 hauls were performed at depths ranging from 40 to 730 m, where the duration of each haul varied depending on depth: 30 min up to 200 m and 60 min below 200 m (Table A.1).

The content of 13,342 full stomachs was quantitatively analyzed. After each fishing haul, a maximum of ten individuals of each target species was randomly sampled and quantitative diet estimates obtained by measuring the stomach content volume using a trophometer. This is considered a practical device suitable for use on board oceanographic

Table 1
Acronyms used for the major prey groups and nine trophic guilds identified.

Acronym	Group name
Major prey groups	
SP	Small Plankton
LP	Large Plankton
GP	Gelatinous Plankton
PO	Polychaeta
PE	Peracarids
BI	Benthic invertebrates
NA	Natantia
RE	Reptantia
BC	Benthic Cephalopods
BT	Benthopelagic Cephalopods
PF	Pelagic Fishes
FF	Flatfishes
GA	Gadoids
IF	Icthyophagous Demersal Fishes
GO	Gobids
TR	Triglids
HA	European Hake
MU	Mullets
SF	Sparids-Serranids-Scorpenids Fishes
BF	Benthopelagic Fishes
Trophic guilds	
PP	Pelagic Piscivores
PG	Planktophagous Specialized on Gelatinous Plankton
PC	Planktophagous Specialized on Copepods
PB	Pelagic, Benthopelagic Fishes and Natantian Feeders
GB	Gadoids and Benthopelagic Fish Feeders
AE	Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders
BR	Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta
PN	Peracarid and Natantian Feeders
DF	Decapod Feeders

vessels because it enables the examination of a large number of stomachs in a relatively short period of time (Olaso, 1990).

For all the specimens examined, data on sex and total length (cm) were recorded according to MEDITS guidelines (Bertrand et al., 2002). Once the stomach was opened, the content was separated into different food items that were later identified to the lowest possible taxonomic level under a stereoscopic microscope. The presence of skeletal and other hard body parts (e.g. fish otoliths, cephalopods beaks, gnathopods and claws from crustaceans and setae from worms) were also recorded.

Specimens that had regurgitated stomachs were replaced by others of a similar size class.

The degree of digestion of all identified prey items was also recorded; the content was rated as fresh, partially digested or fully digested. A total of 346 prey items were identified and grouped into 20 categories according to both taxonomic and feeding behavior criteria (see acronyms in Table 1).

2.2. *Cumulative prey curves*

We applied cumulative prey curves to determine if the number of stomachs analyzed was adequate to represent the trophic spectrum of each predator studied. The software EstimateS 9.1 (Colwell, 2013) was used to perform species accumulation curves, which were plots of the cumulative number of prey taxa against the cumulative number of samples examined. To avoid biased estimates, sample order was randomized 100 times following Colwell and Coddington (1994). All the identified prey items ($N = 346$) were grouped into 207 major categories to guarantee the wide range of prey items needed to build a robust curve.

The curve is a function of effort that increases monotonically until an asymptote is reached (Chao and Chiu, 2016). The y-value of that asymptote is the maximum number of prey that could be achieved. To evaluate sample quality, a function able to describe the cumulative curve is requested. Therefore, an asymptotic approach was provided to reach the asymptote estimation of the species accumulation curve using non-parametric estimators ACE and Chao 1 (Table A.2). The value of the asymptote of the cumulative curve represents the maximum number of prey that would be reached if the sample size were infinite (Colwell and Coddington, 1994).

The cumulative curve for each species was fitted to logarithmic ($y = \log a^x$) and Clench's functions (Clench, 1979) (Eq. (1)):

$$Sn = a * n/(1 + b * n) \tag{1}$$

where the asymptote is a/b and the slope of the tangent line to the Clench equation (Eq. (2)) is calculated as:

$$a/(1 + b * n)^2 \tag{2}$$

Coefficient r^2 values of both functions were compared by using a paired t-test.

In this study, sample size for each of the species was considered to be sufficient when the value of the slope of the tangent line to the curve was ≤ 0.05. All models produced were fitted using the quasi-Newton method provided by the package Statistica 7 (StatSoft, 2004).

2.3. *Diet compositions and feeding strategies*

Three dietary indices were used to describe diet compositions. According to Hyslop (1980), the frequency of occurrence index (F%), expressed as the percentage of stomachs with a specific type of prey in relation to the total number of stomachs containing food, was calculated. The volumetric index (V%) was also estimated to quantify the percentage contribution of each prey to the whole content in volume. Finally, the geometric index of importance (GII%) was computed as: $GII\% = (\Sigma V_i)_j/\sqrt{n}$, where V_i represents the value of the i'th Relative Measures of Prey Quantity (RMPQ's) for the prey category *j* and *n* is the number of RMPQ's used in the equation (Assis, 1996).

Likewise, Levin's index (B_i) was calculated to investigate the trophic niche breadth of each of the 61 fish species selected for this study. This index is computed as $B_i = 1/(n-1)\ (1/\Sigma_j\ p_{ij}^2 - 1)$, where B_i represents Levin's standardized index; p_{ij} is the proportion of prey j in the diet of predator i and n is the total number of prey categories. This index ranges from 0 to 1, where lower values indicate a specialist diet while higher values indicate a generalist diet (Levins, 1968).

The actual trophic level (TL) was also estimated to describe the food web position for each of the 61 species studied. This was useful in providing relevant information as an indicator of the state of the marine ecosystem studied. TL is computed as $TL = 1 + (\Sigma\ DC_{ij})\ (NT_j)$, where DC_{ij} is the proportion of prey *j* in the diet of the predator *i* and NT_j is the trophic level of prey *j* (Christensen and Pauly, 1992). In the case of prey TLs, values were taken from specialized literature (Cortés, 1999; Ebert and Bizzarro, 2007; Jacobsen and Bennett, 2013; Karachle and Stergiou, 2017; Rosas-Luis et al., 2014).

2.4. *Environment effects on trophic guild structures*

To define the different trophic guilds represented by a set of species exploiting similar food resources, quantitative information on diet composition was grouped by using clustering analysis. For each of the resulting groups, indices already mentioned (F%, V%, GII%, B_i and TL) and the Shannon diversity index ($H = -\Sigma\ p_j\ \log p_j$, where p_j is the proportion of each trophic guild within the fish community) were estimated to describe the resulting trophic guilds. In addition, mean trophic level (MTL) was estimated by weighting the relative biomass of each species within the groups. To do so, the necessary abundance indices for these computations were obtained from MEDITS surveys. To identify potential food competition among groups, the degree of overlap in diet was calculated using the Simplified Morisita Index (Morisita, 1959), which compares pairs of groups ranging between 0

Table 2
Codes and description for the different habitat types.

Code		Description	Main species	Depth range (m)
MAE	I	maerl and biogenic bottoms	*Rhodophyceae, Molgula appendiculata, Sphaerechinus granularis*	45–65
AF_AE	II	sandy and muddy circalittoral bottoms consisting mainly in Ascidians and Echinoderms	*Polycarpa* spp., *Botryllus* spp., *Parastichopus regalis*	45–70
AF_PE	III	sandy and muddy circalittoral bottoms consisting mainly in Pennatulacea	*Alcyonium palmatum, Pennatula rubra, Trachythyone* spp.	45–80
FS_EC	IV	sedimentary and detritic bottoms consisting mainly in Echinoderms	*Echinus* spp., *Parastichopus regalis, Alcyonium palmatum*	82–267
FS_PE	V	sedimentary and detritic bottoms consisting mainly in Pennatulacea and Alcyoniidae	*Alcyonium palmatum, Pennatula rubra, Venus nux*	82–177
FS_CP	VI	sedimentary and detritic bottoms consisting mainly on Crinozoa and Parastichopus	*Antedon mediterranea, Parastichopus regalis, Ophiura ophiura*	72–230
FS_FU	VII	bottoms consisting mainly in *Funiculina quadrangularis*	*Funiculina quadrangularis, Alcyonium palmatum*	68–338
BAT	VIII	bathyal bottoms	*Aporrhais serresianus, Brissopsis* spp., *Alcyonium palmatum*	218–735

(i.e. no prey overlapping) and 1 (i.e. prey overlapping) and is computed as $C_{ik} = (2\,\Sigma\, p_{ij}p_{ik})/(\Sigma\, p_{ij}^2 + \Sigma\, p^2_{ik})$, where C_{ik} represents the Simplified Morisita Index for predators i and k and p_{ij} and p_{kj} are the proportions of predators i and k with prey j in their stomachs.

We then explored how different environment conditions affect the resulting trophic guilds. We investigated how these communities (characterized by Shannon, biomass, mean trophic level and fish community composition) change depending on different environments (characterized by latitude, depth and habitat type). First, two geographical areas were tested (north and south) delimited by parallel 38° 22.82′N according to MEDITS guidelines (Bertrand et al., 2002). Secondly, four bathymetric depth strata (50–100 m, 101–200 m, 201–500 m and 501–800 m) were considered. Finally, we analyzed changes in fish community structure by the eight different habitat types identified and defined by the Spanish inventory of marine habitats (Mapama, 2013) (Table 2).

2.5. Statistical analyses

With the goal of investigating different standardized diet compositions among species, clustering ordination analyses and non-metric multidimensional scaling (MDS) were conducted. A Bray–Curtis similarity index and a square-root transformed for standardized data were performed, preserving abundance information but reducing the contribution of the most abundant species to the general pattern. Similarity values among clusters that were ≥ 40% of the maximum overall similarity distance were considered to indicate major divisions and therefore, used to distinguish trophic guilds within the food web studied.

To explore differences in fish community composition according to depth, latitude and habitat types, an analysis of similarities (ANOSIM) was conducted. To this end, biomass relative values of previously identified trophic guilds were estimated.

An independent sample *t*-test was used (Student's t-test) to determine whether there were significant differences in mean trophic level, Shannon diversity index and total biomass between the two geographical areas. Finally, one-way ANOVA, post-hoc Tukey and Dunnett T3 tests, depending on the homogeneity of variances, were used to detect differences according to depth and habitat type.

A significance level of 0.05 was set for all statistical analyses. All multivariate analyses were conducted in PRIMER 6 (Clarke and Gorley, 2006) and SPSS Statistics 17.0 software (SPSS Inc, 2008).

3. Results

3.1. Sample size accurate determination

The paired-sample *t*-tests showed significant differences in goodness of fit r^2 between the logarithmic function and Clench's function ($t = 7.706$, $p < .001$). The better fit of cumulative prey curves for the entire dataset was obtained using Clench's function (mean ± SD = 0.986 ± 0.012) rather than using the logarithmic function (mean ± SD = 0.960 ± 0.023). Goodness of fit r^2 values with Clench's equation ranged from 1.00 for some species, such as *Conger conger* or *Scorpaena porcus*, to 0.93 for *Scomber colias* (Table A.2). According to Clench (1979), 48 of the 61 studied species (i.e. 78%) showed the slope of the tangent line to the curve ≤0.05. Therefore, the achieved sample size was considered adequate to accurately characterize their diet composition. The remaining 13 species did not reach the asymptotic threshold. Nevertheless, these species were included in the study, not for a detailed description but to provide a broad overview of their feeding habits. The non-parametric estimator ACE proved to be the most appropriate to estimate sampling coverage. The highest values were obtained for *Scyliorhinus canicula* and *C. conger* with a potential number of prey of 95 and 98, respectively. Conversely, *Spicara smaris* and *Molva dypterygia* showed the lowest values of prey items (14 and 17, respectively).

3.2. Diet compositions and feeding strategies

A summary of prey species per predator is presented in Table A.3 with a total of 16,588 stomachs examined. Of the 13,342 full stomachs analyzed, a total of 346 prey taxa were identified and grouped into 20 major categories (Table A.4). Overall, the most relevant prey groups in the diet of the 61 fish species were Reptantia (V = 19.3 ± 22.7%; F = 27.8 ± 27.0%; GII = 23.6 ± 24.4%; mean ± SD), represented mainly by *Goneplax rhomboides* (V = 4.9%) and *Liocarcinus* spp. (V = 4.5%) as well as Natantia (V = 17.8 ± 18.8%; F = 25.9 ± 20.9%; GII = 21.8% ± 19.2%) composed mainly of *Alpheus glaber* (V = 5.3%) and *Solenocera membranacea* (V = 2.2%).

The main predators of Reptantia were *Arnoglossus imperialis, Chelidonichthys lastoviza, Scorpaena porcus* and *Serranus hepatus*. The first two species preyed mainly on *Liocarcinus* spp. (V = 48.5% and V = 31.8% respectively), while the latter species, *S. porcus* and *S. hepatus*, preyed primarily on *G. rhomboides* (V = 38.0% and V = 26.5% respectively).

The species group Natantia “prawns & shrimps” was the second most consumed group, *Trisopterus minutus* and *Phycis blennoides* being the main predators of *A. glaber* (V = 44.1% and V = 34.1% respectively) while *Leucoraja naevus* and *Raja* spp. showed preferences for *S. membranacea* (V = 42.2% and V = 20.1% respectively).

For all species, a wide niche breadth (B_i) ranging from 0.01 to 0.56 was observed, where the highest values showed that *Capros aper* (B_i = 0.56) fed mainly on copepods and euphausiids (V = 17% and V = 16.5% respectively); *Pagellus acarne* (B_i = 0.50) focused its diet on mysids (V = 18.2%) and polychaeta (V = 15.2%) and *Citharus linguatula* (B_i = 0.50) preyed mainly on teleosts (V = 72%) and *A. glaber* (V = 8.9%). Finally, *Scorpaena elongata* (B_i = 0.45) showed a remarkable presence of teleosts in its diet (V = 52.7%) followed by reptantian decapods (V = 21.5%). For these species a more generalist diet was assigned due to the diverse range of prey items consumed (Table A.4). On the other hand, results showed the lowest values of Levin's index for *M. dypterygia* (B_i = 0.01), with a preference for *Gadiculus argenteus* (V = 30.6%); *Scomber scombrus* (B_i = 0.05) focused its diet on *Sardina pilchardus* (V = 49.1%) while *S. smaris* (B_i = 0.05) consumed primarily copepods (V = 88.2%).

Trophic level (TL) ranged from 3.02 to 4.76 with *S. smaris* showing the lowest value and therefore the lowest position in the food web and *Lophius piscatorius* was ranked as the top predator (Table A.4).

3.3. Resulting trophic guilds

The hierarchical classification analysis based on diet composition initially identified seven trophic guilds, each a homogeneous group. With the aim of conducting a more in-depth study, the most numerous guild were split into three sub-groups taking into account both feeding and behavior, resulting in a total of nine trophic groups (Fig. 2). These categories are codified and summarized in Table 1. Generally, the results identified a total of nine feeding strategies for the 61 species studied. For the first trophic guild (Pelagic Piscivores, PP), the most consumed prey groups were pelagic fishes (V = 79.5%; F = 33.9%; GII = 56.7%), in particular *S. pilchardus* (V = 37.2%). In the second group (Planktophagous Specialized on Gelatinous Plankton, PG), the presence of gelatinous zooplankton is noteworthy (V = 74.2%; F = 56.9%; GII = 65.6%) with *Pyrosoma atlanticum* as the most common prey (V = 69.3%). Small plankton (V = 45.5%; F = 77.3%; GII = 61.4%) dominate the diet of the third group (Planktophagous Specialized on Copepods, PC), preying mainly on copepods (V = 42.2%). In the diet of the fourth group (Pelagic, Benthopelagic Fishes and Natantian Feeders, PB), the pelagic fishes prey group (V = 18.0%; F = 11.2%; GII = 14.6%) is important, where *Engraulis encrasicolus* dominate (V = 8.6%), followed by *Micromesistius poutassou* (V = 3.9%) and *M. merluccius* (V = 2.2%).

For the fifth group (Gadoids and Benthopelagic Fish Feeders, GB), gadoids were the most consumed prey group (V = 78.0%; F = 78.2%; GII = 78.1%), with *M. poutassou* and *G. argenteus* (V = 31.6%; and V = 26.3%, respectively) being the most representative prey. In the sixth group (Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders, AE), large plankton (V = 45.8%; F = 51.4%; GII = 48.6%), mostly composed of euphausiids (V = 44.6%) and benthopelagic fishes (V = 37.6%; F = 38.3%; GII = 38.0%), led by *Ceratoscopelus maderensis* (V = 12.4%), were the main prey. In the BR sub-group (Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta), Reptantia were the most consumed prey (V = 28.6%; F = 27%; GII = 27.8%) highlighted by the contribution of *G. rhomboides* (V = 7.6%), followed by Polychaeta (V = 26.6%; F = 46.5%; GII = 36.6%) represented by sabellids (V = 73.6%) and benthic invertebrates (V = 24.1%; F = 38.4%; GII = 31.2%), in particular opistobranch molluscs (V = 21.2%). For the PN sub-group (Peracarid and Natantian Feeders), the most consumed preys were Peracarids (V = 48.9%; F = 80%; GII = 64.4%) indicating the presence of amphipods (V = 7.4%) and mysids (V = 6.1%). For the last sub-group identified (Decapod Feeders, DF), Natantia was the most significant group (V = 46.1%; F = 43.8%; GII = 44.9%) with *A. glaber* as the most common prey (V = 21.7%) (Table 3).

Overall, the main prey groups consumed by the whole fish community were Natantia (V = 18.8%) and large plankton (V = 17.6%) together with benthopelagic fishes (V = 14.8%). The resulting MTL for this community was 3.81.

3.4. Dietary overlapping and trophic position

For the evaluation of the niche breadth and dietary overlap, measurements of ecological indices were quantified among the nine trophic guilds (Fig. 3).

Regarding diet breadth, Levin's index ranged from 0.03 for the specialist guilds GB and PP, to 0.45 for the generalist guild PB (Table 3).

The Morisita-Horn index (C_H) showed the lowest niche overlap values (C_H = 0.00) for PP-GB. Conversely, the highest values of dietary overlap (0.50) corresponded to DF-PB, which concurred in the consumption of *M. merluccius, A. glaber* and *Illex coindetii* (Table 4).

The mean trophic level (MTL) calculated in this study showed the lowest value (MTL = 3.35) for the group consisting of PG, contrasting with GB, which ranked the highest in the food web (MTL = 4.58).

3.5. Trophic guilds versus environment forcing

In this study, significant differences in fish community composition existed among depth strata ($R = 0.224$, $p = .001$), geographical areas ($R = 0.024$, $p = .001$) and habitat types ($R = 0.356$, $p = .001$) (Fig. 4).

Changes in MTL were significant by depth stratum ($F_{3,510} = 9.39$; $p < .001$), also showing significant differences between the first and the remaining strata ($p < .005$). Significant differences were also found between the third and fourth strata ($p = .02$). On the other hand, results showed no significant differences between habitat types ($F_{7,690} = 1.637$; $p = .122$). The *t*-test also showed no significant differences among the latitudinal areas defined ($p = .109$) (Fig. 5).

Fish community diversity was investigated by habitat and depth stratum ($F_{7,697} = 44.71$; $p < .001$ and $F_{3,564} = 88.85$; $p < .001$ respectively). Regarding habitat, significant differences between three groups were found: 1) Sandy and muddy circalittoral bottoms and maerl, 2) Sedimentary and detrital bottoms and 3) Bathyal bottoms. Additionally, a decreasing trend of diversity with depth was apparent, showing significant differences among depth strata. No significant differences were found across geographical areas (Fig. 6).

Depth stratum and habitat type were tested to investigate shifts in

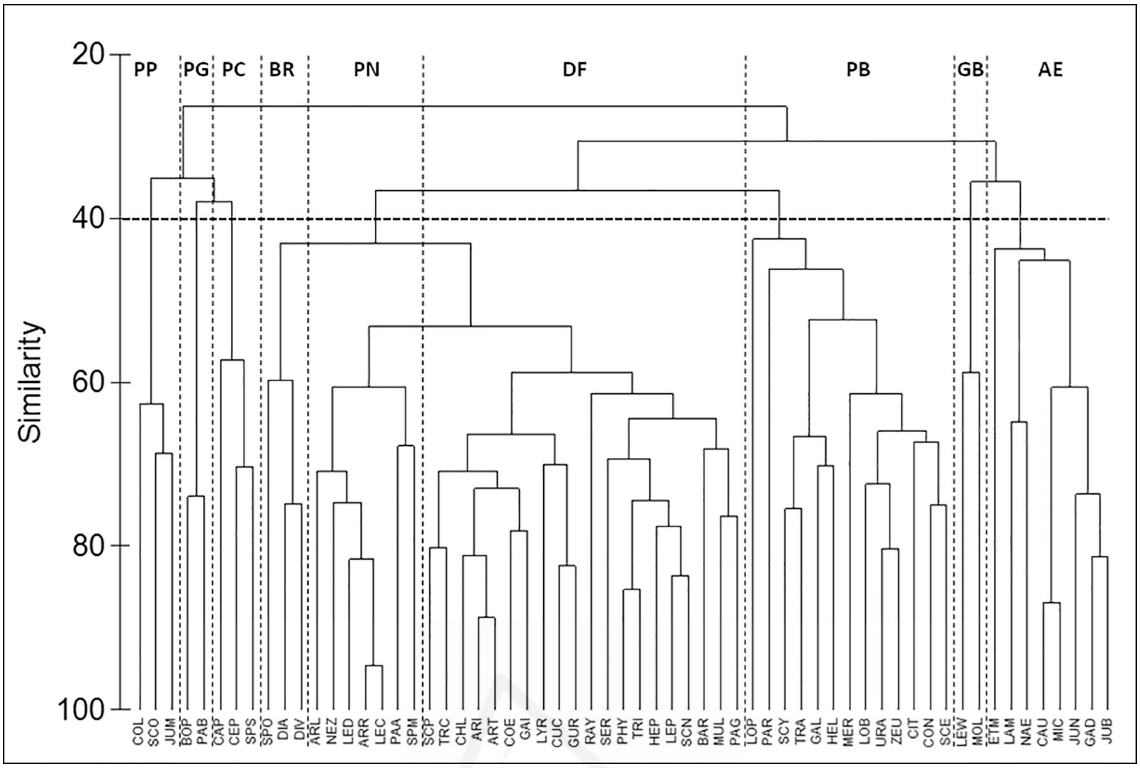

Fig. 2. Dendrogram using group average clustering from Bray-Curtis similarities based on stomach content analysis grouping the studied species into nine trophic guilds. PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders.

fish community biomass, showing significant differences in both factors ($F_{3,744} = 8.372$; $p < .001$ and $F_{7,672} = 21.604$; $p < .001$, respectively). A post hoc test found that the deepest stratum showed significant differences from shallower strata ($p < .001$). For habitat types (see acronyms in Table 2), a post hoc test showed no significant differences between habitats I and IV. Similar results were also found between habitats II and VI as well as between habitats III, V, VII and VIII ($p > .05$) (Fig. 5). The *t*-test did not show significant differences in

Table 3

Volumetric Index (V%), Frequency Index (F%), Geometric Index of Importance (GII%), Niche breadth (Bi) and Mean trophic level (MTL) estimated for the nine trophic guilds (TG). Dashes represent no consumption. Acronyms are referenced in Table 1.

TG	Bi	MTL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
PP	0.03	4.08	V%	0.3	8.5	2.2	0.2	2.8	0.0	1.2	1.0	0.6	0.4	79.5	–	0.0	0.2	0.7	–	–	2.2	–	0.2
			F%	6.2	67.7	54.5	2.6	35.0	1.2	4.5	4.0	1.9	0.8	33.9	–	0.3	0.1	0.9	–	–	5.1	–	0.4
			GII%	3.2	38.1	28.3	1.4	18.9	0.6	2.8	2.5	1.3	0.6	56.7	–	0.2	0.2	0.8	–	–	3.7	–	0.3
PG	0.04	3.35	V%	0.2	3.6	74.2	1.7	1.2	4.6	3.8	0.0	3.8	0.1	0.3	3.7	–	–	–	–	–	–	–	2.8
			F%	5.2	18.4	56.9	12.9	21.6	14.4	4.2	0.9	1.6	0.2	0.5	1.2	–	–	–	–	–	–	–	8.2
			GII%	2.7	11.0	65.6	7.3	11.4	9.5	4.0	0.5	2.7	0.2	0.4	2.5	–	–	–	–	–	–	–	5.5
PC	0.12	3.39	V%	45.5	26.2	0.8	7.1	17.5	–	2.9	–	–	–	–	–	–	–	–	–	–	–	–	–
			F%	77.3	26.2	4.9	3.8	27.6	–	2.4	–	–	–	–	–	–	–	–	–	–	–	–	–
			GII%	61.4	26.2	2.8	5.5	22.5	–	2.7	–	–	–	–	–	–	–	–	–	–	–	–	–
PB	0.45	4.15	V%	0.8	8.0	0.5	1.1	0.4	0.2	14.5	9.2	3.9	5.4	18.0	2.4	10.0	5.7	1.3	0.7	2.5	0.6	1.7	12.9
			F%	0.2	21.3	1.1	3.8	8.0	0.4	30.9	21.0	6.5	2.4	11.2	2.1	16.3	2.0	6.9	0.5	1.9	0.2	1.4	10.7
			GII%	0.5	14.7	0.8	2.5	4.2	0.3	22.7	15.1	5.2	3.9	14.6	2.3	13.2	3.9	4.1	0.6	2.2	0.4	1.5	11.8
GB	0.03	4.58	V%	–	0.3	–	–	1.0	–	7.5	0.4	0.2	–	–	–	78.0	–	–	–	–	–	–	12.7
			F%	–	3.2	–	–	6.4	–	7.7	1.3	1.9	–	–	–	78.2	–	–	–	–	–	–	9.6
			GII%	–	1.8	–	–	3.7	–	7.6	0.8	1.0	–	–	–	78.1	–	–	–	–	–	–	11.1
AE	0.09	3.68	V%	2.3	45.8	0.3	0.0	0.7	–	10.6	0.2	0.2	0.4	0.5	0.0	1.2	–	0.2	–	0.1	–	–	37.6
			F%	3.8	51.4	1.1	0.5	7.4	–	21.7	0.6	0.8	2.9	0.5	0.1	1.3	–	0.6	–	0.2	–	–	38.3
			GII%	3.1	48.6	0.7	0.2	4.1	–	16.2	0.4	0.5	1.6	0.5	0.0	1.2	–	0.4	–	0.1	–	–	38.0
BR	0.19	3.50	V%	3.7	0.4	0.7	26.6	4.0	24.1	3.2	28.6	0.6	0.4	0.7	1.3	–	–	5.7	–	–	–	–	–
			F%	2.7	2.5	3.5	46.5	31.9	38.4	4.2	27.0	2.1	0.2	1.2	0.6	–	–	1.5	–	–	–	–	–
			GII%	3.2	1.4	2.1	36.6	17.9	31.2	3.7	27.8	1.4	0.3	0.9	0.9	–	–	3.6	–	–	–	–	–
PN	0.13	3.51	V%	1.3	8.4	2.3	7.6	48.9	4.6	16.5	4.8	2.6	–	1.1	0.2	0.1	–	1.7	–	–	–	–	–
			F%	9.4	3.5	1.2	10.3	80.0	3.4	21.6	16.0	0.9	–	0.2	0.2	0.1	–	2.7	–	–	–	–	–
			GII%	5.4	5.9	1.7	8.9	64.4	4.0	19.0	10.4	1.7	–	0.6	0.2	0.1	–	2.2	–	–	–	–	–
DF	0.13	3.63	V%	0.0	1.4	0.0	8.1	4.4	2.7	46.1	26.6	2.6	0.6	0.6	0.2	2.3	0.5	1.7	0.1	0.5	0.4	0.1	1.3
			F%	2.6	5.2	0.2	12.3	41.5	5.1	43.8	52.8	2.4	0.1	0.4	0.8	4.4	0.4	3.7	0.2	0.3	0.0	0.2	1.4
			GII%	1.3	3.3	0.1	10.2	23.0	3.9	44.9	39.7	2.5	0.4	0.5	0.5	3.4	0.4	2.7	0.1	0.4	0.2	0.1	1.3

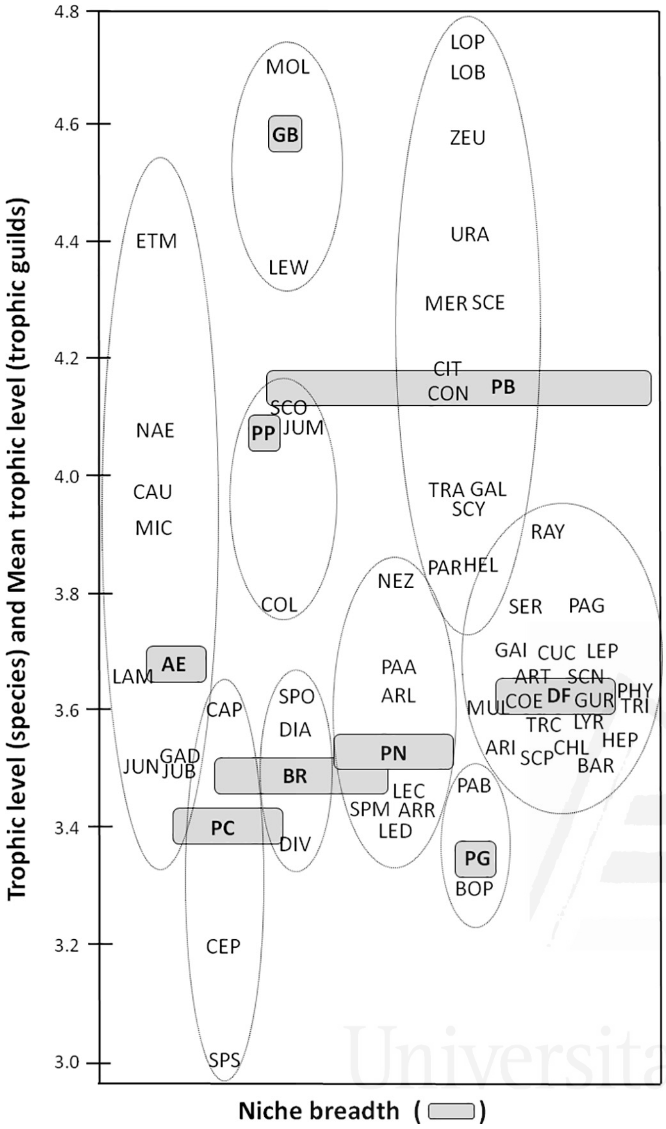

Fig. 3. Scheme with 61 species studied and the nine trophic guilds (bordered with dotted lines) showing the trophic position (TL and MTL) and the niche breadth (box size). PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantian and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders. Acronyms of species are referenced in Table A.1.

Table 4

Estimated dietary Overlap index (C_H; Simplified Morisita) between the nine trophic guilds studied. Extreme values are shown in bold. Acronyms are referenced in Table 1.

	PP	PG	PC	PB	GB	AE	BR	PN	DF
PP	1.00								
PG	0.04	1.00							
PC	0.06	0.05	1.00						
PB	**0.41**	0.06	0.15	1.00					
GB	**0.00**	**0.01**	**0.01**	0.29	1.00				
AE	0.09	0.07	**0.40**	**0.44**	0.13	1.00			
BR	**0.03**	0.06	0.17	0.23	**0.01**	**0.02**	1.00		
PN	0.07	0.09	**0.41**	0.21	0.04	0.18	0.29	1.00	
DF	**0.03**	0.05	0.10	**0.50**	0.12	0.19	**0.48**	**0.41**	1.00

fish community biomass between geographical areas (p = .129).

4. Discussion

In this study, we present results on diet compositions and feeding strategies of 61 fish species in the Spanish Western Mediterranean Sea, providing a recent and valuable dataset for future studies on trophic ecology in this region. Secondly, we identify trophic guilds and demonstrate how these fish communities vary depending on environmental forcing such as depth, latitude and habitat type.

The feeding patterns of the Western Mediterranean marine trophic web described here shed new light on the complex trophic relationships existing between the fish species studied. To ensure the robustness of the results, sufficiently large sample sizes should be analyzed when studying diet composition (Mulas et al., 2015; Bernal et al., 2015). Cumulative prey curves are a powerful technique for determining the adequacy of sample size for diet characterization. The present study not only aimed to estimate the asymptotic value provided by the cumulative curves, but also applied a mathematical method consisting of the calculation of the slope on a fitted function. Previously, Jiménez-Valverde and Hortal (2003) successfully applied this technique using Clench's function in a study based on arachnids. Indeed, Ferry and Cailliet (1996) reviewed over 200 papers primarily comparing fish diets across species, sites and sample dates, concluding that none of the studies they reviewed provided estimates of any precision. Clench's function has been demonstrated to be a good fit in most cases of the faunistic or floristic inventories in which it was tested (Soberón and Llorente, 1993; León-Cortés et al., 1998; Moreno and Halffter, 2001). This information on the adequacy of samples is lacking for all of the marine food web studies performed previously in the study area and reviewed herein.

In a marine trophic research context, some recent studies in nearby areas have implemented the analysis of cumulative prey curves (López-López, 2017; Valls, 2017). However, the innovation of our study was the best fitting of these curves with both logarithmic and Clench's functions, which enabled a proper minimum sample size for each species to be determined mathematically. Among the analyses performed, it was found that Clench's function proved to be suitable for most of the species. The present study was the first to apply this mathematical approach to marine trophic ecology studies. Based on our results, we recommend this method to assess if the number of samples collected is sufficient to describe the diet of the species studied.

The present study included an extensive collection of samples and a large number of analyses. For example, 48 of the species studied were collected in sufficient numbers to determine their diets validly, but the remaining 13 species are also important in the ecosystem. Consequently, further investigations will be required in the future to address the diets of these species. Nevertheless, their inclusion in this work is fundamental to the complete ecological trophic study in the area concerned.

The present study for the whole group of species analyzed enabled us to calculate their trophic levels and thus, to place them in different trophic niches, identifying their roles within the trophic web. The trophic level values estimated basically concur with those reported by Stergiou and Karpouzi (2002) and Karachle and Stergiou (2017) in the Mediterranean. Examining trophic strategies exploiting different resources and environments sheds light on how the relationships between existing trophic guilds function in the study area. Through the analysis of diet composition, nine trophic guilds were identified; six of them occupied the lowest position within the fish community studied, including "Planktophagous Specialized on Gelatinous Plankton" (PG), "Planktophagous Specialized on Copepods" (PC), "Benthic Invertebrate Feeders Specialized on Reptantian and Polychaeta" (BR), "Peracarid and Natantian Feeders" (PN), "Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders" (AE) and "Decapod Feeders" (DF). The first two groups (PG and PC) are characterized by planktophagous habits

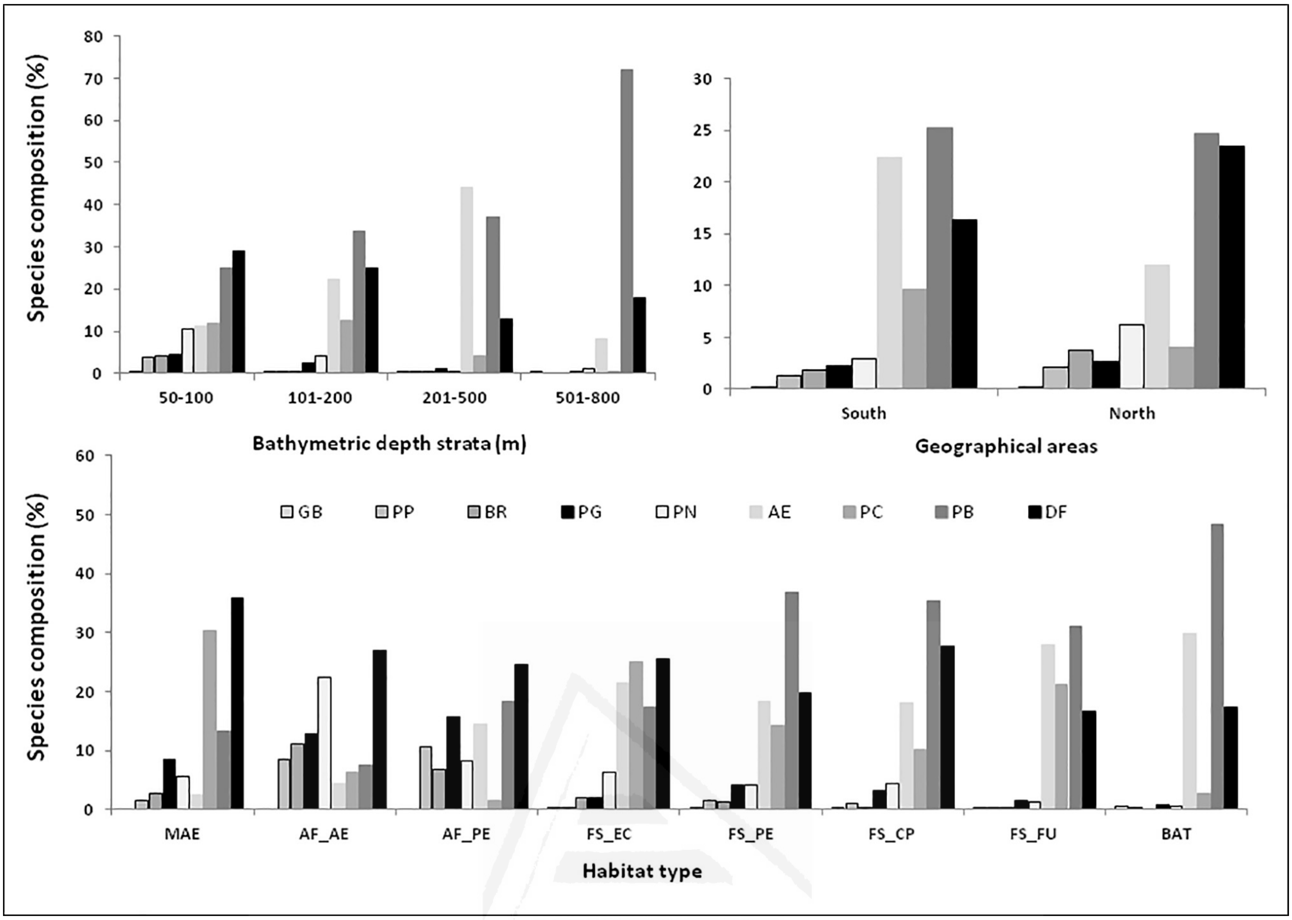

Fig. 4. Trophic guilds identified according to the different environmental drivers: bathymetric strata, geographical area and habitat type. PP: Pelagic Piscivores; PG: Planktophagous Specialized on Gelatinous Plankton; PC: Planktophagous Specialized on Copepods; PB: Pelagic, Benthopelagic Fishes and Natantian Feeders; GB: Gadoids and Benthopelagic Fish Feeders; AE: Pelagic Amphipods, Euphausiids and Benthopelagic Fish Feeders; BR: Benthic Invertebrate Feeders Specialized on Reptantia and Polychaeta; PN: Peracarid and Natantian Feeders; DF: Decapod Feeders. Acronyms for habitat types are referenced in Table 2.

showing the lowest mean trophic levels. Examples of species belonging to these groups are *Pagellus bogaraveo* and *Cepola macrophthalma*. In the case of *P. bogaraveo*, results presented by Morato et al. (2001) in Azores are slightly different. These authors reported that fishes were an important element in the diet of this species, while gelatinous plankton was relatively rare. The consumption of fish in the Azores compared to that in the Western Mediterranean may be a result of the high productivity of seamounts and the aggregation of fish around them (Morato et al., 2001). Findings reported by Sever et al. (2010) in Aegean Sea waters are in accordance with the planktivorous behavior of *C. macrophtalma* described here.

On the other hand, the remaining four groups (BR, PN, AE and DF), whose distinctive feature is the high consumption of crustaceans and benthic invertebrates, ranked slightly higher, occupying intermediate levels in the energy flows within the food web. Sparids, mullets, triglids, scorpaenids, rays and some flatfishes formed these groups.

All of them share a relatively narrow niche breadth, inherent in specialist species. This becomes evident in the case of PG, the most specialized of these six groups. In an intermediate position, between the groups named above and the top of the food web, "Pelagic Piscivores" can be found, characterized by piscivore habits and "Pelagic, Benthopelagic Fishes and Natantian Feeders", whose diet is mainly composed of decapod crustaceans as well as fishes. Thus, this is a species characterized by a diet based on an elevated consumption of teleosts. Examples of species belonging to these groups are mackerels, anglerfishes, hake, conger and benthic sharks. The last group, "Gadoids and Benthopelagic Fish Feeders" (GB) is characterized by a diet highly specialized on piscivore species such as *Lepidorhombus whiffiagonis*, in accordance with findings reported by Morte et al. (1999), and *M. dypterygia*. This group is at the top of the food web, reaching the highest trophic level values. Regarding the niche breadth and in contrast to PB, considered the most generalistic group, GB is the most specialized with a high consumption of gadoids.

Regarding niche overlap, trophic guilds located in the lowest trophic positions (PG and PC) showed low overlap due to the development of different feeding strategies, thus exploiting diverse trophic niches. This is in line with general knowledge of the existence of strongly selective feeding strategies in oligotrophic regions, where competition pressure for scarce food resources is expected (Van Noord et al., 2013).

At an upper-intermediate level, AE presents a low overlap with the other three groups (BR, PN and DF). In contrast, these three trophic guilds show a high overlap. Indeed, they show the most common feeding strategy within the food web, characterized by a notable percentage of crustaceans in their diet, especially decapods, in agreement with previous findings reported by Rodríguez-Marín (2004) in the Cantabrian Sea and Moreno-Amich (1992, 1996), Colloca et al. (1994) and Morte et al. (1999) in the Western Mediterranean.

At a higher level in the trophic web, where the distinctive feature is the high consumption of teleosts, both "Pelagic Piscivores" and "Pelagic, Benthopelagic Fishes and Natantian Feeders" presented a considerable overlap due to the relevance of small pelagic fishes and euphausiids as common preys in their diets.

At the top of the trophic web, "Gadoids and Benthopelagic Fish

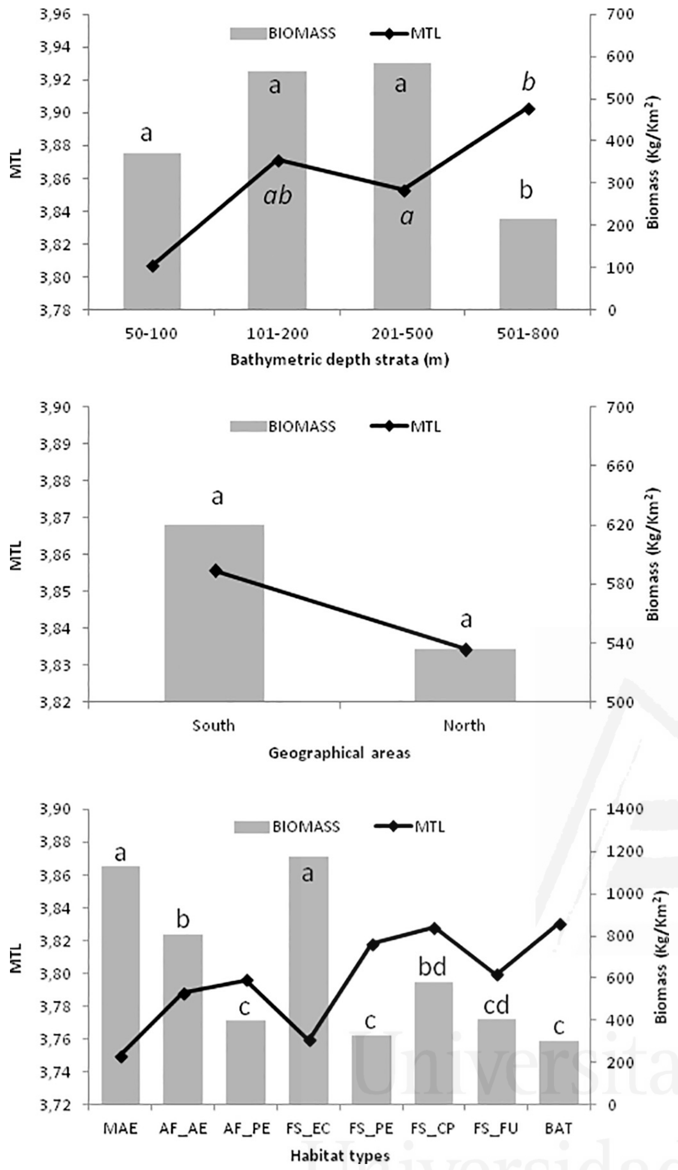

Fig. 5. Variation of fish community biomass and Mean Trophic Level indicators related to bathymetric strata, geographical area and habitat type. Acronyms are referenced in Table 2. Columns with no letters in common are significantly different.

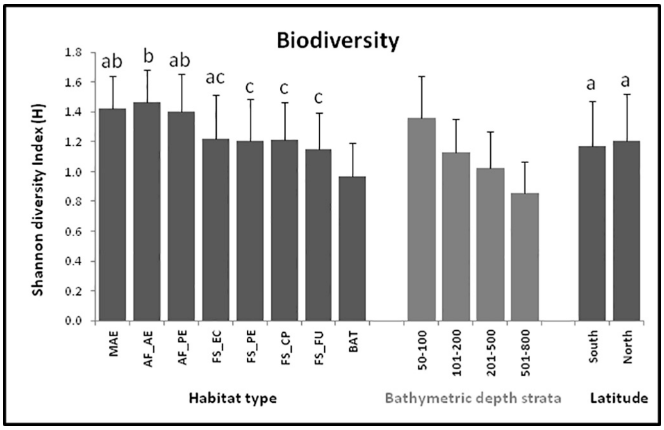

Fig. 6. Fish community biodiversity calculated by habitat type, bathymetric strata and latitude based on the Shannon diversity index. Acronyms are referenced in Table 2. Columns with no letters in common are significantly different. Error bars mean Standard Deviation.

Feeders" were found to share feeding strategies with "Pelagic, Benthopelagic Fishes and Natantian Feeders" in terms of consumption of benthopelagic fishes, especially gadoids, and natantian decapods. On the contrary, the minor overlap existing between "Gadoids and Benthopelagic Fish Feeders" and "Pelagic Piscivores" was caused by the lack of small pelagic fishes in the diet of GB, the dominant prey for PP.

Overall, those groups that play an important role in the fish community as a whole are: natantian, pelagic peracarids, euphausiids and benthopelagic fishes, which is consistent with the wide spectrum of feeding guilds and food resource partitioning suggested in previous studies performed in the Western Mediterranean (Polunin et al., 2001; Madurell et al., 2008; Fanelli et al., 2009; Fanelli and Cartes, 2010; Valls et al., 2014).

In this paper, the structure of the fish community has been described through the analysis of indicators including diversity, biomass, MTL and fish community composition. Three environment variables, latitude, depth, and habitat type, were investigated to explore how they affect variations in the indicators for fish community structure.

Results showed that changes in fish community composition along latitude, depth and habitat type were significant.

With respect to latitude, the southern geographical area was characterized by a higher percentage of pelagic crustacean feeders as well as a lower percentage of demersal crustacean feeders in its fish community composition. This is in agreement with Floeter et al. (2004), who reported changes in trophic structure and spatial patterns along the latitudinal gradient. In addition, planktophagous species were more abundant in the southern geographical area, in agreement with Cartes et al. (2002) who reported a progressive north-south increase in these species. This environmental attribute was shown to play a decisive role in structuring the fish community, inducing changes in fish composition across the whole fish community. Opposite, we did not find changes in MTL, biomass and diversity in the fish community across latitudinal gradient. According to depth, changes in MTL were detected, in particular between the first and the rest of the stratum and between the third and fourth stratum, caused by the low trophic position of the species occupying shallower depths compared to those species occupying the deepest bottoms. This relationship between depth and trophic level was reported by Rex in gastropods (Rex, 1977). Concerning to biomass, the deepest stratum shows differences from other strata, in line with the usual distribution of biomass in the ocean (Abad et al., 2007). Regarding to diversity and fish composition, the relationship between depth and them was evident.

With respect to habitat type, maerl and biogenic bottoms (MAE), Sandy and muddy circalittoral bottoms consisting mainly of ascidians and echinoderms (AF_AE) and sedimentary and detritic bottoms consisting mainly of echinoderms (FS_EC), were the three habitats able to withstand the highest carrying capacity of fish biomass within the ecosystem studied. This finding is in agreement with those studies that highlight the important role of habitat in the production of fish species. Some of the most important demersal resources of the coastal shelf are dependent on macro-benthic habitat type (Ordinas and Massutí, 2009), and high levels of biomass and biodiversity are found associated with *Peyssonnelia* beds (Ballesteros, 1994). By contrast, in the present study, the lowest carrying capacity of fish biomass was found on habitats dominated by *Funniculina quadrangularis* and *Pennatulacea* spp. (FS_FU, AF_PE and FS_PE) and especially "Bathyal bottoms" (BAT). Besides, the habitat characteristics of shallow waters present higher diversity compared to deeper ones (Navarro et al., 2015).

Findings highlighted differences across habitat type in fish community biomass, diversity and fish composition. In contrast, we did not find changes in MTL in the fish community across habitat type.

To conclude, considering the three environmental drivers investigated, depth was found to be the most influential factor in the fish community structure studied, particularly affecting both diversity and fish community composition. However, the latitudinal gradient only seemed to affect fish community composition showing consistency along a longitudinal north-south axis.

Finally, this is the only study presenting information based on stomach content analysis for this study area that includes robust estimations on minimum sample size for a large number of representative species between 2011 and 2018. Despite the fact that a considerable amount of information has been published describing the feeding habits of single or groups of commercial species in the Mediterranean (e.g. Macpherson, 1980a, 1980b; Carrassón and Matallanas, 2002; López et al., 2016), there are only a few studies on the whole trophic web in the Western Mediterranean (Macpherson, 1981; Fanelli and Cartes, 2010; Valls, 2017). It is therefore relevant to highlight the importance of this study in the context of the ecosystem approach to fisheries management where information on diet is often ecosystem-specific (Hanson and Chouinard, 2002), and when implementing ecosystem models or similar studies related to marine food webs.

Declaration of Competing Interest

None.

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Author declaration template

We wish to confirm that there are no known conflicts of interest associated with this publication and there has been no significant financial support for this work that could have influenced its outcome.

We confirm that the manuscript has been read and approved by all named authors and that there are no other persons who satisfied the criteria for authorship but are not listed.

We further confirm that the order of authors listed in the manuscript has been approved by all of us.

We confirm that we have given due consideration to the protection of intellectual property associated with this work and that there are no impediments to publication, including the timing of publication, with respect to intellectual property. In so doing we confirm that we have followed the regulations of our institutions concerning intellectual property.

We further confirm that any aspect of the work covered in this manuscript that has involved either experimental animal has been conducted with the ethical approval of all relevant bodies and that such approvals are acknowledged within the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.seares.2020.101958.

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PREDATOR	**Species code**	**Nº full stomachs**	**Nº preys**	**Min size**	**Max size**	**Mean length (mean ± SD)**	**Min depth**	**Max depth**	**Mean depth (mean ± SD)**
Arnoglossus imperialis	ARI	36	19	75	164	121 ± 17	47	279	117 ± 65
Arnoglossus laterna	ARL	144	30	59	121	91 ± 11	36	279	75 ± 27
Arnoglossus rueppelii	ARR	92	20	90	148	116 ± 12	102	273	146 ± 46
Arnoglossus thori	ART	138	32	66	124	93 ± 10	45	122	69 ± 22
Boops boops	BOP	150	27	108	265	174 ± 28	36	142	88 ± 30
Capros aper	CAP	78	15	55	117	77 ± 17	77	282	181 ± 90
Cepola macrophtalma	CEP	117	16	167	600	344 ± 93	41	129	87 ± 17
Chelidonichthys cuculus	CUC	282	50	104	295	168 ± 34	42	269	114 ± 38
Chelidonichthys gurnardus	GUR	293	51	75	361	164 ± 39	47	331	102 ± 29
Chelidonichthys lastoviza	CHL	227	50	94	305	174 ± 32	40	125	55 ± 17
Citharus linguatula	CIT	200	38	71	250	167 ± 33	35	272	79 ± 30
*Coelorinchus caelorhincus**	COE	204	21	24	105	51 ± 17	238	542	388 ± 82
Conger conger	CON	368	79	242	955	471 ± 104	35	732	171 ± 168
Diplodus annularis	DIA	234	46	108	223	160 ± 20	35	128	47 ± 10
Diplodus vulgaris	DIV	132	40	140	304	211 ± 30	40	124	58 ± 14
Etmopterus spinax	ETM	59	22	110	426	222 ± 86	380	724	545 ± 104
Gadiculus argenteus	GAD	234	25	70	133	103 ± 10	206	586	314 ± 81
Gaidropsarus biscayensis	GAI	102	24	40	180	83 ± 29	88	630	337 ± 123
Galeus melastomus	GAL	372	73	135	615	441 ± 139	270	732	528 ± 126
Helicolenus dactylopterus	HEL	304	60	73	305	145 ± 42	106	650	279 ± 124
Lampanyctus crocodilus	LAM	118	21	76	215	135 ± 23	411	724	568 ± 87
Lepidopus caudatus	CAU	154	21	222	880	358 ± 91	83	717	289 ± 106
Lepidorhombus boscii	LEP	298	45	81	370	212 ± 53	42	594	242 ± 127
Lepidorhombus whiffiagonis	LEW	34	18	118	367	241 ± 66	140	337	233 ± 49
Lepidotrigla cavillone	LEC	265	27	83	198	113 ± 12	45	155	80 ± 25
Lepidotrigla dieuzeidei	LED	181	27	70	142	110 ± 11	56	273	147 ± 48
Leucoraja naevus	NAE	39	17	154	535	351 ± 74	91	272	143 ± 51
Lophius budegassa	LOB	419	65	44	930	248 ± 82	37	594	132 ± 85
Lophius piscatorius	LOP	87	37	64	1050	282 ± 166	42	590	117 ± 108
Merluccius merluccius	MER	907	61	87	460	187 ± 66	36	590	93 ± 47
Micromesistius poutassou	MIC	558	38	89	371	229 ± 56	85	610	307 ± 97
Molva dypterygia	MOL	122	15	83	740	184 ± 96	122	605	269 ± 103
Mullus barbatus	BAR	247	29	104	270	176 ± 28	35	221	84 ± 39

Mullus surmuletus	MUL	303	50	70	332	206 ± 41	36	522	117 ± 92
*Nezumia aequalis**	NEZ	89	18	22	54	36 ± 7	510	724	626 ± 70
Pagellus acarne	PAA	148	43	118	254	181 ± 28	36	273	60 ± 27
Pagellus bogaraveo	PAB	275	50	100	465	176 ± 41	47	722	227 ± 146
Pagellus erytrinus	PAG	255	44	114	471	232 ± 48	37	142	58 ± 16
Pagrus pagrus	PAR	87	33	135	379	218 ± 55	44	130	62 ± 19
Phycis blennoides	PHY	275	49	85	393	208 ± 61	92	588	292 ± 143
Raja sp.	RAY	356	71	135	865	359 ± 136	42	522	149 ± 72
Scomber colias	COL	578	36	217	381	296 ± 32	38	85	58 ± 11
Scomber scombrus	SCO	291	30	121	367	247 ± 47	48	126	89 ± 22
Scorpaena elongata	SCE	201	55	78	465	183 ± 67	43	335	131 ± 49
Scorpaena notata	SCN	231	38	64	205	107 ± 22	38	143	81 ± 32
Scorpaena porcus	SCP	35	13	97	299	174 ± 36	38	94	50 ± 10
Scyliorhinus canicula	SCY	488	79	92	605	402 ± 70	41	586	171 ± 110
Serranus cabrilla	SER	235	54	91	251	160 ± 29	38	143	82 ± 20
Serranus hepatus	HEP	276	33	67	136	99 ± 12	41	143	93 ± 26
Spicara maena	SPM	244	34	96	241	148 ± 25	38	140	70 ± 19
Spicara smaris	SPS	91	11	103	193	136 ± 19	45	122	73 ± 21
Spondyliosoma cantharus	SPO	152	32	151	353	217 ± 45	38	146	74 ± 21
Trachinus draco	TRA	203	43	122	366	243 ± 46	41	148	84 ± 29
Trachurus mediterraneus	JUM	164	41	110	353	243 ± 42	37	105	59 ± 21
Trachurus picturatus	JUN	35	15	126	330	221 ± 50	48	515	124 ± 81
Trachurus trachurus	JUB	133	25	131	336	202 ± 43	47	589	135 ± 104
*Trachyrhinchus scabrus**	TRC	48	20	27	135	97 ± 18	459	604	555 ± 35
Trigla lyra	LYR	286	47	55	300	177 ± 29	52	586	224 ± 83
Trisopterus minutus	TRI	309	43	78	272	167 ± 29	48	287	113 ± 57
Uranoscopus scaber	URA	116	38	42	316	228 ± 45	40	141	77 ± 21
Zeus faber	ZEU	243	40	70	528	247 ± 109	38	556	135 ± 59

Table A.1. Information of the sample size analyzed, number of prey items identified, predator length ranges (mm) and depths (m) reported for all the species studied. (*) anal length.

PREDATOR	**Nº Full stomachs**	**Nº Preys**	**CLENCH**			**ACE**	**CHAO 1**		
			Asymptote	**Slope**	r^2		**Chao 1**	**95% Lower Bound**	**95% Upper Bound**
Arnoglossus imperialis	36	19	30	0.191*	1.00	29	33	21.9	85.8
Arnoglossus laterna	144	30	35	0.034	0.99	38	35	31.0	52.8
Arnoglossus rueppelii	92	20	24	0.043	0.99	26	24	20.6	41.9
Arnoglossus thori	138	32	38	0.043	0.98	44	38	33.5	59.3
Boops boops	150	27	33	0.037	0.99	44	45	31.5	101.8
Capros aper	78	15	16	0.019	0.99	18	16	15.1	25.7
Cepola macrophtalma	117	16	18	0.019	0.97	28	24	17.3	58.5
Chelidonichthys cuculus	282	50	56	0.024	0.98	69	65	54.3	103.5
Chelidonichthys gurnardus	293	51	60	0.031	0.98	68	68	56.1	110.8
Chelidonichthys lastoviza	227	50	57	0.029	0.99	56	55	51.1	73.4
Citharus linguatula	200	38	48	0.039	0.99	44	41	38.5	52.5
Coelorinchus caelorhincus	204	21	22	0.006	0.98	23	23	21.2	36.1
Conger conger	368	79	101	0.048	1.00	98	98	85.9	132.9
Diplodus annularis	234	46	55	0.038	0.98	83	109	65.2	254.6
Diplodus vulgaris	132	40	49	0.057*	0.99	49	47	42.3	65.0
Etmopterus spinax	59	22	31	0.113*	1.00	37	25	85.6	12.7
Gadiculus argenteus	234	25	29	0.017	0.97	34	31	26.2	52.1
Gaidropsarus biscayensis	102	24	29	0.041	1.00	29	28	24.6	46.0
Galeus melastomus	372	73	87	0.036	0.99	88	92	79.5	128.8
Helicolenus dactylopterus	304	60	74	0.040	0.99	85	72	64.1	96.7
Lampanyctus crocodilus	118	21	28	0.043	0.99	30	30	22.9	65.7
Lepidopus caudatus	154	21	26	0.028	0.98	34	30	22.9	65.9
Lepidorhombus boscii	298	45	50	0.019	0.99	62	64	50.2	117.8
Lepidorhombus whiffiagonis	34	18	33	0.237*	1.00	42	33	21.5	81.6
Lepidotrigla cavillone	265	27	29	0.009	0.99	29	28	27.1	35.5
Lepidotrigla dieuzeidei	181	27	33	0.028	0.99	29	29	27.2	39.5
Leucoraja naevus	39	17	23	0.108*	0.99	33	32	20.9	84.8
Lophius budegassa	419	65	78	0.028	0.98	82	86	72.0	129.8
Lophius piscatorius	87	37	66	0.186*	1.00	54	50	41.3	79.7
Merluccius merluccius	907	61	69	0.009	0.97	81	72	64.6	96.9
Micromesistius poutassou	558	38	42	0.009	0.97	51	49	40.7	82.1

Molva dypterygia	122	15	20	0.032	0.98	17	16	15.0	25.6
Mullus barbatus	247	29	31	0.013	0.95	36	33	29.6	47.9
Mullus surmuletus	303	50	55	0.020	0.98	69	80	58.2	162.4
Nezumia aequalis	89	18	20	0.026	0.99	19	18	18.0	22.8
Pagellus acarne	148	43	60	0.087*	0.98	87	86	56.2	181.5
Pagellus bogaraveo	275	50	69	0.050	0.99	88	85	63.4	147.7
Pagellus erytrinus	255	44	54	0.036	0.99	61	65	50.1	116.6
Pagrus pagrus	87	33	50	0.133*	0.99	69	60	41.2	122.0
Phycis blennoides	275	49	53	0.023	0.96	77	68	55.1	111.3
Raja sp.	356	71	83	0.034	0.98	90	85	75.8	113.7
Scomber colias	578	36	36	0.003	0.93	44	41	37.0	63.6
Scomber scombrus	291	30	31	0.007	0.99	36	32	30.2	42.5
Scorpaena elongata	201	55	72	0.068*	1.00	70	70	59.8	102.8
Scorpaena notata	231	38	46	0.032	0.98	54	49	41.1	78.5
Scorpaena porcus	35	13	19	0.115*	1.00	21	15	13.4	29.8
Scyliorhinus canicula	488	79	91	0.024	0.99	95	95	84.2	125.6
Serranus cabrilla	235	54	64	0.040	1.00	62	65	56.9	95.9
Serranus hepatus	276	33	38	0.017	0.99	39	42	34.9	77.9
Spicara maena	244	34	45	0.035	0.99	53	79	46.1	205.3
Spicara smaris	91	11	15	0.035	0.99	14	12	11.1	21.7
Spondyliosoma cantharus	152	32	41	0.048	0.99	36	35	32.4	47.3
Trachinus draco	203	43	55	0.049	0.99	54	47	44.0	60.7
Trachurus mediterraneus	164	41	49	0.047	0.98	52	49	43.0	72.5
Trachurus picturatus	35	15	26	0.181*	0.99	21	20	15.8	47.1
Trachurus trachurus	133	25	33	0.047	1.00	31	28	25.4	40.3
Trachyrhinchus scabrus	48	20	29	0.133*	1.00	28	27	21.4	53.5
Trigla lyra	286	47	53	0.020	0.99	53	59	49.7	101.2
Trisopterus minutus	309	43	48	0.020	0.98	59	54	46.1	83.6
Uranoscopus scaber	116	38	57	0.112*	0.99	76	72	48.8	145.5
Zeus faber	243	40	51	0.038	0.99	50	54	43.4	95.5

Table A.2. Sample size, number of prey items identified, potential number of preys estimated (asymptote) and fitting of cumulative prey curves to Clench function (r^2) estimated for all fish size categories studied. (*) species with slope > 0.05.

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Porifera																**0.003**
Cnidaria						**0.199**			**0.086**				**0.321**		**0.000**	**0.042**
Actiniaria													0.000			0.008
Scyphozoa						0.148							0.115			
Diphyidae						0.022			0.086				0.204		0.000	
Epizoanthidae																0.003
Plumularioidea						0.029										0.019
Pennatulidae																0.012
Cnidaria unidentified													0.002			
Polychaeta	**0.002**	**0.007**	**0.042**	**0.052**	**0.187**	**0.015**	**0.113**		**0.006**	**0.003**	**0.004**	**0.159**	**0.001**	**0.000**	**0.003**	**0.213**
Aphroditidae														0.000		
Sabellidae				0.001		0.004										0.004
Sternaspis scutata					0.009											
Errantia unidentified									0.003			0.009	0.001			
Sedentaria unidentified																0.021
Polychaeta unidentified	0.002	0.007	0.042	0.051	0.178	0.011	0.113		0.003	0.003	0.004	0.150	0.000	0.000	0.003	0.187
Sipuncula													**0.000**			**0.012**
Bryozoa						**0.007**										
Echinodermata										**0.000**						**0.050**
Astropecten irregularis																0.003
Holothuroidea unidentified																0.012
Ophiuridae										0.000						0.009
Leptometra spp.																0.026
Crustacea	**0.963**	**0.923**	**0.956**	**0.915**	**0.741**	**0.085**	**0.860**	**0.339**	**0.826**	**0.969**	**0.248**	**0.815**	**0.120**	**0.342**	**0.736**	**0.381**
Amphipoda	**0.056**	**0.130**	**0.067**	**0.160**	**0.037**	**0.033**	**0.290**		**0.029**	**0.053**		**0.025**	**0.028**	**0.000**	**0.005**	**0.020**
Anchylomera spp.													0.000			
Brachyscelus spp.							0.004						0.019			
Hemityphis spp.													0.000			
Hyperia spp.													0.000			
Hyperiidea						0.018	0.101		0.001				0.005			
Hyperionyx spp.													0.000			
Leptocotis spp.													0.000			
Phronima sedentaria						0.010							0.000			
Phrosina semilunata							0.004						0.002	0.000		
Platyscelidae													0.000			
Streetsia spp.													0.000			
Vibilia spp.						0.003	0.010		0.017	0.000		0.000	0.001		0.000	
Ampelisca spp.	0.023	0.058	0.019	0.117	0.017					0.003		0.002	0.000		0.001	0.000
Bathymedon spp.												0.000				
Cheirocratus spp.										0.001					0.000	
Epimeria spp.										0.001		0.000			0.001	
Eusirus spp.	0.004				0.000					0.000						
Gammaridae													0.000			
Harpinia spp.					0.001											
Ichnopus spp.										0.002					0.000	
Lembos spp.												0.000				
Leptocheirus spp.					0.000					0.000						
Leucothoe spp.					0.000					0.000						
Lysianassa spp.										0.004					0.000	
Lysianassidae		0.003					0.002		0.002	0.000		0.000	0.000			
Maera spp.					0.000					0.001		0.002			0.000	
Monoculodes spp.		0.001	0.008	0.002						0.001		0.000			0.000	
Nicippe spp.					0.000							0.004				
Orchomene spp.										0.000						
Rhachotropis spp.										0.001		0.001				
Stegocephaloides spp.															0.000	
Syrrhoe spp.												0.000				
Tryphosites spp.												0.001				
Westwoodilla spp.		0.007		0.002	0.001					0.000		0.001			0.000	0.000
Caprellids unidentified	0.007	0.011	0.003	0.004	0.000	0.000	0.133		0.000	0.000						0.005
Amphipods unidentified	0.022	0.051	0.037	0.036	0.018	0.001	0.036		0.009	0.040		0.012	0.000	0.000	0.003	0.015
Isopoda	**0.012**	**0.000**	**0.001**	**0.002**	**0.000**	**0.006**	**0.014**		**0.000**	**0.002**	**0.001**	**0.081**	**0.001**	**0.002**	**0.000**	**0.007**
Gnathiidae				0.001			0.001		0.000				0.000			
Idotea spp.				0.000						0.001						
Synisoma spp.										0.000						
Isopods unidentified	0.012	0.000	0.001	0.001	0.000	0.006	0.013			0.001	0.001	0.081	0.001	0.002	0.000	0.007

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC	DIA
Cumacea		**0.000**	**0.000**	**0.000**	**0.000**	**0.000**			**0.001**	**0.000**			**0.000**			**0.000**
Lophogastrida	**0.117**	**0.034**	**0.419**	**0.006**	**0.004**					**0.018**				**0.000**	**0.044**	**0.001**
Lophogaster typicus	0.117	0.034	0.419	0.006	0.004					0.018				0.000	0.044	0.001
Mysida	**0.000**	**0.151**	**0.076**	**0.032**	**0.015**	**0.003**	**0.030**		**0.029**	**0.040**	**0.031**	**0.012**	**0.054**	**0.000**	**0.031**	**0.002**
Tanaidacea					**0.000**							**0.001**				
Copepoda		**0.088**	**0.001**	**0.001**	**0.000**	**0.002**	**0.170**		**0.504**			**0.006**	**0.004**			**0.000**
Ostracoda									**0.000**			**0.000**	**0.000**			**0.000**
Euphausiacea				**0.007**		**0.000**	**0.165**	**0.224**	**0.167**		**0.042**	**0.021**	**0.007**	**0.001**	**0.001**	
Meganyctiphanes norvegica							0.024	0.006						0.001	0.000	
Nematoscelis spp.							0.018				0.004					
Nyctiphanes couchii												0.001				
Euphausiacids unidentified				0.007		0.000	0.122	0.218	0.167		0.039	0.020	0.007	0.000	0.001	
Decapoda	**0.778**	**0.515**	**0.392**	**0.609**	**0.679**	**0.039**	**0.042**	**0.115**	**0.017**	**0.841**	**0.171**	**0.569**	**0.014**	**0.326**	**0.652**	**0.328**
Acanthephyra spp.																
Aegaeon spp.		0.014		0.004						0.084			0.000	0.001		
Alpheus glaber		0.096			0.232	0.001					0.089	0.031		0.063	0.021	0.019
Athanas spp.		0.004			0.003					0.002						
Chlorotocus crassicornis		0.021			0.010					0.006	0.003			0.006	0.039	
Crangonidae			0.014	0.003			0.024			0.003	0.001			0.001	0.001	0.006
Eusergestes arcticus								0.000						0.000		
Hippolytidae	0.008									0.007			0.000			
Pasiphaea sivado								0.099								
Pasiphaea spp.								0.004						0.001		
Philocheras spp.	0.003	0.053	0.029	0.013	0.002					0.016	0.005	0.000			0.012	
Plesionika acanthonotus													0.000			
Plesionika heterocarpus			0.020		0.003									0.004	0.008	
Pontophilus spp.	0.011	0.074	0.017	0.007						0.009					0.005	
Processa spp.	0.064	0.017	0.119	0.043	0.117					0.006	0.013	0.004		0.008	0.003	0.001
Sergia robusta														0.000		
Solenocera membranacea					0.038					0.004	0.008			0.013	0.001	
Atelecyclus rotundatus										0.006		0.000			0.001	
Calocaris macandreae				0.005							0.004	0.469		0.002		
Ctenodrilus spp.										0.005						
Ebalia spp.										0.000					0.000	
Ergasticus clouei										0.001						
Ethusa spp.										0.016						
Galathea spp.	0.036	0.008	0.010	0.169	0.000					0.116				0.000	0.003	0.012
Geryon longipes														0.027		
Goneplax rhomboides	0.143	0.090	0.113	0.043	0.049					0.035	0.013	0.003		0.082	0.073	0.095
Inachus spp.				0.001						0.006						
Jaxea nocturna														0.000		
Liocarcinus spp.	0.485	0.060	0.020	0.189	0.010					0.318				0.031	0.286	0.005
Macropipus tuberculatus														0.005	0.024	
Macropodia spp.										0.019					0.001	
Majidae										0.001						
Medoripe lanata										0.013						0.018
Monodaeus couchii		0.006	0.010							0.011		0.024		0.007		
Munida spp.														0.014	0.118	
Nephrops norvegicus														0.030		
Paguridae	0.012	0.002	0.000	0.091						0.006						0.004
Pagurus spp.										0.008				0.001		
Palicus spp.										0.008						
Portunidae				0.001	0.001					0.019				0.003		
Scyllarus spp.										0.003					0.002	0.007
Thalassinidea																0.008
Upogebia spp.					0.000					0.013						
Decapod larvae	0.003	0.003		0.001	0.000	0.000		0.000	0.017	0.001			0.011			
Ethusidae larvae													0.000			
Nephrops larvae													0.002			
Palinuridae larvae													0.000			
Geryon eggs														0.005		
Natantia unidentified	0.006	0.051	0.041	0.013	0.146	0.036	0.008	0.011		0.008	0.025	0.017	0.000	0.010	0.018	0.023
Brachyura unidentified	0.007	0.007		0.014	0.024					0.090	0.000	0.016	0.000	0.011	0.021	0.126
Decapoda unidentified		0.008		0.011	0.044	0.002	0.010			0.003	0.010	0.005	0.001	0.001	0.014	0.004
Stomapoda										**0.004**			**0.004**	**0.012**		**0.023**
Rissoides desmaresti										0.004				0.008		0.015

		ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC
Squila mantis														0.004		
Stomatopod larvae													0.004			
Stomatopoda unidentified													0.000	0.000		0.008
Crustacea unidentified		0.004		0.099	0.005	0.002	0.150		0.079	0.009	0.004	0.099	0.008		0.003	
Cephalopods						**0.034**		**0.002**		**0.017**	**0.028**		**0.006**	**0.038**	**0.101**	**0.001**
Sepiida						**0.034**				**0.016**	**0.005**		**0.000**	**0.013**	**0.101**	
Rondeletiola minor										0.001	0.005				0.039	
Rossia macrosoma														0.005		
Sepia orbignyana														0.004		
Sepia spp.														0.002		
Sepietta oweniana						0.034				0.009			0.000	0.002	0.031	
Sepiolid unidentified										0.006				0.001	0.031	
Myopsida											**0.022**			**0.001**		
Alloteuthis spp.											0.022			0.001		
Oegopsida								**0.002**					**0.006**	**0.001**		
Histioteuthis bonnellii														0.001		
Illex coindetii													0.006			
Teuthida unidentified								0.002								
Octopoda														**0.022**		
Eledone spp.														0.022		
Cephalopods unidentified										0.001	0.000		0.000	0.001	0.000	0.001
Other Mollusca	**0.004**			**0.000**	**0.071**	**0.000**				**0.000**			**0.001**		**0.001**	**0.097**
Pteropoda						**0.000**							**0.001**			
Limacina spp.													0.000			
Cavolinia spp.						0.000							0.001			
Bivalvia				**0.000**	**0.071**					**0.000**			**0.000**		**0.001**	**0.009**
Bivalvia unidentified				0.000	0.071					0.000			0.000		0.001	0.009
Gastropoda	**0.004**				**0.000**										**0.000**	**0.088**
Umbraculum umbraculum																0.013
Heterobranchia																0.070
Gastropoda unidentified	0.004				0.000										0.000	0.005
Tunicata						**0.594**	**0.004**		**0.035**				**0.005**		**0.001**	**0.015**
Ascidiacea						0.005										0.011
Pyrosoma atlanticum						0.571	0.004								0.001	0.004
Tunicata unidentified						0.017			0.035				0.005			
Teleosts	**0.030**	**0.070**	**0.002**	**0.032**	**0.001**	**0.044**	**0.023**	**0.659**	**0.047**	**0.011**	**0.720**	**0.026**	**0.546**	**0.617**	**0.157**	**0.122**
Clupleiformes								**0.009**			**0.115**		**0.363**	**0.020**		
Engraulis encrasicolus											0.004		0.026	0.006		
Sardina pilchardus								0.009			0.111		0.337	0.014		
Argentiniformes								**0.002**						**0.009**		
Argentina sphyraena								0.002								
Glossanodon leioglossus														0.009		
Myctophiformes								**0.156**						**0.001**	**0.002**	
Benthosema glaciale								0.009								
Ceratoscopelus maderensis								0.079								
Lampanyctus crocodilus								0.009								
Notoscopelus elongatus								0.050						0.001		
Myctophum punctatum								0.003							0.002	
Myctophids unidentified								0.005								
Stomiiformes								**0.255**						**0.002**		
Maurolicus mullueri								0.245								
Stomias boa														0.002		
Cyclothone spp.								0.010								
Gadiformes		**0.035**						**0.002**			**0.171**	**0.026**		**0.052**	**0.012**	
Gadiculus argenteus											0.016			0.006	0.002	
Merluccius merluccius											0.030			0.002		
Micromesistius poutassou								0.002			0.024			0.007		
Gaidropsarus biscayensis		0.035										0.026		0.019	0.003	
Phycis blennoides														0.016		
Trisopterus minutus											0.101			0.002	0.007	
Perciformes	**0.030**	**0.031**		**0.028**				**0.003**		**0.000**	**0.238**		**0.053**	**0.255**	**0.095**	**0.038**
Blennius ocellaris															0.001	0.003
Callionymus spp.		0.023						0.003			0.009			0.005	0.023	
Cepola macrophthalma											0.059			0.022	0.061	
Crystallogobius linearis	0.030			0.004										0.000		
Deltentosteus spp.											0.023			0.002	0.002	

	ARI	ARL	ARR	ART	BAR	BOP	CAP	CAU	CEP	CHL	CIT	COE	COL	CON	CUC
Gobidae	0.007		0.018						0.000	0.065			0.064	0.005	0.017
Lesueurogobius spp.	0.001		0.006							0.081			0.006	0.002	0.019
Mullus spp.												0.045			
Serranus cabrilla													0.016		
Serranus hepatus													0.019		
Spicara smaris													0.064		
Spicara maena													0.048		
Synchiropus phaeton													0.001		
Trachurus spp.												0.008	0.007		
Aulopiformes							**0.161**								
Arctozenus risso							0.065								
Paralepididae							0.096								
Scorpaeniformes										**0.014**			**0.013**	**0.024**	
Chelidonichthys spp.										0.014			0.011	0.001	
Helicolenus dactylopterus													0.001	0.021	
Triglidae														0.001	
Pleuronectiformes					**0.003**				**0.001**	**0.027**			**0.015**	**0.012**	**0.009**
Arnoglossus spp.									0.001	0.002					
Citharus linguatula										0.005			0.003		
Symphurus spp.													0.007	0.005	
Pleuronectiformes					0.003					0.019			0.005	0.007	0.009
Anguilliformes													**0.051**		
Conger conger													0.037		
Ophichthus rufus													0.015		
Notacanthiformes													**0.006**		
Notacanthus bonaparte													0.006		
Ophidiiformes													**0.021**		
Ophidion barbatum													0.021		
Teleost larvae			0.002			0.006		0.042	0.003	0.002		0.116	0.003		
Teleost eggs												0.000	0.004		0.012
Teleosts unidentified	0.003	0.002	0.002	0.001	0.041	0.018	0.071	0.005	0.006	0.153		0.014	0.165	0.013	0.064
Elasmobranchs													**0.002**		
Scylliorhynus													0.001		
Elasmobranchs unidentified													0.001		
Other					**0.022**										**0.064**

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Porifera	**0.011**														
Cnidaria	**0.018**				**0.000**	**0.001**			**0.000**	**0.001**	**0.033**				
Actiniaria	0.011														
Diphyidae					0.000	0.001			0.000	0.001	0.033				
Siphonophorae					0.000										
Plumularioidea	0.007														
Polychaeta	**0.253**	**0.000**	**0.001**	**0.003**	**0.000**	**0.001**	**0.000**	**0.013**		**0.003**			**0.014**	**0.003**	**0.006**
Eunice spp.					0.000										
Eunicidae					0.000										
Sabellidae	0.001														
Errantia unidentified															0.000
Polychaeta unidentified	0.253	0.000	0.001	0.003	0.000	0.001	0.000	0.013		0.003			0.014	0.003	0.005
Nemertea	**0.001**														
Echinodermata	**0.046**						**0.001**								
Asteroidea unidentified	0.004														
Echinacea	0.009														
Leptopentacta tergestina	0.003														
Ophiuridae	0.030						0.001								
Crustacea	**0.376**	**0.114**	**0.744**	**0.828**	**0.399**	**0.806**	**0.608**	**0.932**	**0.729**	**0.140**	**0.722**	**0.813**	**0.980**	**0.959**	**0.817**
Amphipoda	**0.049**		**0.009**	**0.025**	**0.028**	**0.009**	**0.010**	**0.011**	**0.005**	**0.010**	**0.084**	**0.002**	**0.109**	**0.044**	**0.005**
Brachyscelus spp.					0.016	0.002	0.006								
Hyperiidea			0.001		0.001	0.001	0.001		0.003	0.006	0.008				
Phronima sedentaria					0.010			0.001		0.001	0.025			0.004	0.001
Phrosina semilunata					0.001	0.005			0.001	0.000					
Vibilia spp.			0.001		0.000		0.000		0.001	0.001	0.051				
Ampelisca spp.						0.000				0.000			0.019	0.005	0.000
Epimeria spp.							0.002	0.001					0.001		
Eusirus spp.						0.000		0.001					0.001		

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Gammaridae										0.000					
Gitana spp.						0.000									
Hippomedon spp.															0.000
Ichnopus spp.							0.000								
Iphimedia spp.						0.000									
Leucothoe spp.													0.000		0.003
Lysianassa spp.													0.003		
Lysianassidae	0.008		0.002			0.000		0.000						0.002	
Maera spp.								0.001							0.000
Monoculodes spp.				0.001		0.000						0.001	0.011	0.000	
Nicippe spp.							0.000						0.000		0.000
Rhachotropis spp.					0.000		0.000								0.000
Stegocephaloides spp.						0.000									
Westwoodilla spp.			0.000	0.000		0.001		0.000					0.042	0.003	0.000
Phtisica spp.						0.000									
Pseudoprotella spp.								0.000							
Caprellids unidentified	0.004			0.000				0.005					0.002		
Amphipods unidentified	0.037		0.006	0.023	0.000	0.000	0.001	0.003	0.001	0.001	0.000	0.001	0.030	0.030	0.000
Isopoda	**0.011**		**0.012**	**0.000**	**0.001**	**0.001**	**0.024**	**0.001**	**0.000**	**0.003**	**0.000**	**0.004**	**0.004**	**0.002**	**0.004**
Cirolanidae					0.000										
Gnathia spp.	0.001														
Gnathiidae						0.000	0.000								
Idotea spp.	0.001						0.000			0.000					
Synisoma spp.								0.000							
Isopods unidentified	0.009		0.012	0.000	0.001	0.001	0.024	0.000	0.000	0.003	0.000	0.004	0.004	0.002	0.004
Cumacea	**0.000**						**0.000**						**0.003**	**0.000**	
Lophogastrida				**0.066**	**0.000**	**0.062**	**0.006**			**0.000**		**0.004**	**0.290**	**0.472**	**0.006**
Lophogaster typicus				0.066	0.000	0.062	0.006			0.000		0.004	0.290	0.472	0.006
Mysida	**0.001**		**0.012**	**0.029**	**0.000**	**0.087**	**0.002**	**0.023**	**0.004**	**0.038**		**0.001**	**0.152**	**0.087**	**0.014**
Tanaidacea	**0.000**												**0.002**		
Copepoda			**0.060**	**0.015**		**0.000**		**0.000**	**0.042**	**0.004**	**0.003**		**0.001**	**0.000**	
Ostracoda	**0.000**				**0.000**		**0.000**			**0.000**					
Euphausiacea		**0.011**	**0.512**	**0.027**	**0.062**	**0.006**	**0.162**	**0.005**	**0.673**		**0.611**	**0.036**		**0.006**	**0.007**
Euphausia krohnii			0.112				0.010		0.208						
Meganyctiphanes norvegica		0.011	0.027		0.048		0.055		0.234		0.393				0.005
Nematoscelis spp.		0.000	0.007		0.002		0.000								
Euphausiacids unidentified		0.000	0.366	0.027	0.012	0.006	0.096	0.005	0.230		0.218	0.036		0.006	0.002
Scalpelliformes	**0.014**														
Scalpellum scalpellum	0.013														
Scalpelliformes unidentified	0.001														
Decapoda	**0.299**	**0.103**	**0.069**	**0.653**	**0.300**	**0.619**	**0.388**	**0.889**	**0.004**	**0.078**	**0.019**	**0.758**	**0.411**	**0.336**	**0.767**
Acanthephyra spp.					0.003										
Aegaeon spp.														0.016	0.002
Alpheus glaber				0.095	0.002	0.122	0.084	0.341		0.000				0.021	0.141
Aristeus antennatus					0.022							0.040			
Athanas spp.						0.000	0.000	0.004							
Chlorotocus crassicornis					0.001	0.041	0.001	0.028				0.023	0.010	0.004	0.087
Crangonidae						0.002				0.001			0.007		
Deosergestes henseni		0.005										0.023			
Eusergestes arcticus		0.001		0.040	0.019	0.004	0.001				0.016	0.422			0.002
Gennadas elegans			0.003		0.001							0.046			
Pasiphaea multidentata					0.031							0.040			
Pasiphaea sivado		0.039	0.000		0.080		0.005					0.008			
Pasiphaea spp.		0.030	0.005		0.031					0.000		0.001			
Philocheras spp.						0.014		0.000		0.000			0.027	0.003	0.001
Plesionika spp.							0.005								
Plesionika acanthonotus					0.002					0.003					
Plesionika edwardsii				0.025			0.027								0.007
Plesionika giglioli				0.013											0.011
Plesionika heterocarpus						0.006	0.039								0.008
Plesionika martia					0.007										
Plesionika narval							0.010								
Pontophilus spp.						0.007							0.010	0.005	0.001
Processa spp.			0.017	0.017	0.001	0.013	0.006	0.027		0.003			0.006	0.136	0.042
Sergia robusta		0.001			0.016							0.050			
Solenocera membranacea					0.010		0.001						0.094	0.060	0.121

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Atelecyclus rotundatus								0.006							
Calocaris macandreae			0.001	0.320	0.028		0.023	0.007				0.002			0.024
Ebalia spp.								0.001							
Eurynome spp.	0.011														
Galathea spp.	0.118			0.002		0.000	0.000	0.003					0.001		
Geryon longipes					0.005										
Goneplax rhomboides	0.067			0.105		0.133	0.068	0.265					0.058	0.011	0.113
Inachus spp.	0.008							0.000							
Liocarcinus spp.	0.026					0.187	0.005	0.018					0.056	0.013	0.046
Macropipus tuberculatus					0.003		0.007								0.010
Macropodia spp.	0.013														
Monodaeus couchii				0.011	0.003		0.015	0.008							0.003
Munida spp.	0.004			0.008	0.000	0.032	0.021								0.071
Nephrops norvegicus					0.003		0.011								0.023
Paguridae	0.005					0.000		0.004					0.002		
Pagurus spp.	0.002														
Polycheles typhlops					0.009										
Portunidae							0.001			0.000					0.002
Scyllarus spp.					0.001	0.002				0.002			0.009	0.008	0.000
Thalassinidea							0.001								
Upogebia spp.					0.002		0.004	0.006		0.003					0.000
Decapod larvae						0.000			0.001	0.053	0.003		0.001	0.001	
Nephrops larvae										0.002					
Natantia unidentified	0.000	0.028	0.041	0.009	0.012	0.033	0.028	0.122		0.011		0.105	0.091	0.051	0.038
Brachyura unidentified	0.045			0.004	0.001	0.011	0.010	0.042	0.000	0.000			0.009	0.002	0.003
Decapoda unidentified			0.003	0.003	0.007	0.012	0.017	0.009	0.003				0.031	0.006	0.010
Stomapoda					**0.005**	**0.018**	**0.011**			**0.001**					**0.013**
Rissoides desmaresti					0.004	0.018	0.009								0.013
Squila mantis					0.001										
Stomatopod larvae										0.000					
Stomatopoda unidentified							0.002			0.001					
Crustacea unidentified	0.000		0.070	0.012	0.002	0.003	0.005	0.002	0.002	0.006	0.005	0.008	0.008	0.012	0.001
Cephalopods	**0.019**	**0.499**			**0.204**	**0.024**	**0.035**		**0.004**	**0.005**				**0.032**	**0.011**
Sepiida	**0.000**	**0.007**			**0.033**	**0.024**	**0.002**		**0.004**	**0.005**				**0.032**	**0.011**
Rondeletiola minor						0.001			0.004	0.005					0.000
Sepietta oweniana					0.001	0.003								0.032	
Sepiolid unidentified	0.000	0.007			0.032	0.020	0.002		0.001						0.011
Oegopsida	**0.014**	**0.425**			**0.125**		**0.033**								
Abralia veranyi		0.004			0.013										
Abraliopsis pfefferi					0.001										
Ancistroteuthis lichtensteinii					0.006										
Chiroteuthis veranii					0.002										
Histioteuthis bonnellii					0.002										
Histioteuthis reversa		0.028			0.024		0.028								
Histioteuthis spp.		0.126			0.011										
Illex coindetii	0.014	0.007			0.017										
Todarodes sagittatus		0.203													
Teuthida unidentified		0.056			0.050		0.005								
Cephalopod eggs	0.004														
Cephalopods unidentified		0.066			0.046		0.000								0.000
Other Mollusca	**0.112**					**0.001**	**0.002**	**0.001**	**0.000**	**0.000**					
Pteropoda	**0.000**					**0.000**	**0.002**	**0.001**	**0.000**	**0.000**					
Cavolinia spp.	0.000					0.000	0.002	0.001	0.000	0.000					
Bivalvia	**0.076**					**0.000**		**0.000**							
Arcidae	0.001														
Pteria hirundo	0.000														
Bivalvia unidentified	0.075					0.000		0.000							
Gastropoda	**0.037**					**0.000**				**0.000**					
Calyptraea chinensis	0.028														
Turritella spp.	0.000					0.000									
Heterobranchia	0.006														
Gastropoda unidentified	0.002					0.000				0.000					
Tunicata	**0.026**		**0.001**		**0.007**		**0.038**		**0.003**	**0.000**	**0.064**	**0.002**			
Ascidiacea	0.019														
Pyrosoma atlanticum	0.004						0.031		0.003		0.064	0.002			
Tunicata unidentified	0.002		0.001		0.007		0.007			0.000					

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Teleosts	**0.105**	**0.387**	**0.246**	**0.169**	**0.380**	**0.167**	**0.311**	**0.054**	**0.262**	**0.851**	**0.180**	**0.185**	**0.005**	**0.006**	**0.166**
Clupleiformes										**0.409**					
Engraulis encrasicolus										0.113					
Sardina pilchardus										0.297					
Argentiniformes					**0.002**	**0.003**	**0.027**								
Argentina sphyraena					0.002	0.003	0.027								
Myctophiformes		**0.079**	**0.018**		**0.115**	**0.053**	**0.003**		**0.168**			**0.072**			
Benthosema glaciale									0.033						
Ceratoscopelus maderensis			0.003		0.021	0.041			0.128						
Diaphus spp.												0.008			
Hygophum spp.					0.001										
Lampanyctus crocodilus		0.052	0.009		0.058		0.003					0.024			
Notoscopelus elongatus		0.005			0.015	0.003			0.007						
Myctophum punctatum		0.022			0.019	0.008									
Myctophids unidentified			0.007		0.001	0.000						0.041			
Stomiiformes		**0.022**	**0.160**		**0.028**		**0.061**		**0.082**		**0.068**				
Argyropelecus hemigymnus					0.001										
Chauliodus sloani		0.014			0.020		0.023								
Maurolicus mullueri			0.016		0.000		0.009		0.082		0.068				
Stomias boa		0.009			0.007		0.028								
Vinciguerria spp.			0.003												
Cyclothone spp.			0.142		0.000										
Gadiformes		**0.002**	**0.007**	**0.157**	**0.034**	**0.015**	**0.074**		**0.007**	**0.004**					**0.129**
Gadiculus argenteus			0.007		0.005	0.004	0.015								0.000
Merluccius merluccius		0.002													
Micromesistius poutassou					0.008		0.034		0.007						0.007
Molva dypterygia										0.004					0.001
Gaidropsarus biscayensis				0.157			0.019								0.063
Phycis blennoides					0.019	0.000									0.032
Trisopterus minutus					0.001	0.010	0.006								0.026
Perciformes		**0.000**			**0.011**	**0.052**	**0.013**	**0.046**	**0.003**	**0.395**			**0.001**	**0.006**	**0.018**
Ammodytes tobianus										0.319					
Aphia minuta										0.004					
Blennius ocellaris										0.000					
Callionymus spp.					0.000	0.049	0.003	0.011		0.005					0.009
Capros aper					0.002										
Cepola macrophthalma						0.001									
Crystallogobius linearis									0.002						
Deltentosteus spp.							0.009								0.002
Epigonus spp.					0.002										
Gobidae		0.000				0.002	0.001			0.003			0.001		0.002
Lepidopus caudatus					0.006										
Lesueurogobius spp.								0.035	0.002					0.006	
Mullus spp.										0.005					
Synchiropus phaeton															0.004
Trachurus spp.										0.058					
Aulopiformes		**0.044**			**0.051**		**0.005**				**0.083**	**0.073**			
Arctozenus risso					0.036		0.005				0.061				
Evermannella balbo												0.073			
Lestidiops spp.					0.001										
Paralepididae		0.044			0.013		0.000				0.023				
Scorpaeniformes							**0.003**								
Helicolenus dactylopterus							0.003								
Pleuronectiformes					**0.000**	**0.010**		**0.001**	**0.000**						
Arnoglossus spp.						0.004									
Symphurus spp.						0.003									
Pleuronectiformes					0.000	0.003		0.001	0.000						
Anguilliformes					**0.000**		**0.006**								
Conger conger							0.003								
Gnathophis mystax							0.003								
Ophichthus rufus					0.000										
Teleost larvae			0.000	0.004		0.001			0.001	0.035	0.001				
Teleost eggs	0.095		0.000		0.046				0.000						
Teleosts unidentified	0.010	0.240	0.061	0.008	0.093	0.034	0.119	0.007	0.001	0.008	0.027	0.039	0.004		0.019
Elasmobranchs					**0.009**		**0.005**								
Galeus melastomus							0.005								

	DIV	ETM	GAD	GAI	GAL	GUR	HEL	HEP	JUB	JUM	JUN	LAM	LEC	LED	LEP
Elasmobranchs unidentified					0.009										
Other	**0.034**		**0.007**		**0.000**										

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Cnidaria						**0.000**		**0.000**			**0.009**	**0.007**	**0.002**		**0.000**
Actiniaria								0.000			0.005	0.000	0.000		
Diphyidae						0.000					0.004	0.005			0.000
Plumularioidea												0.001			
Pennatulidae												0.001			
Cnidaria unidentified													0.002		
Polychaeta		**0.000**		**0.052**		**0.000**		**0.076**	**0.003**	**0.088**	**0.152**	**0.027**	**0.145**	**0.055**	**0.001**
Aphroditidae				0.019										0.042	
Eunice spp.								0.000					0.005		
Eunicidae								0.000					0.001		
Glycera spp.													0.000		
Phyllodocidae													0.001		
Syllidae								0.000							
Sternaspis scutata				0.002									0.000		
Errantia unidentified		0.000		0.002				0.003					0.001		0.000
Sedentaria unidentified													0.003		
Polychaeta unidentified				0.028		0.000		0.072	0.003	0.088	0.152	0.027	0.133	0.012	0.001
Sipuncula								**0.000**			**0.001**	**0.001**	**0.010**		
Nemertea													**0.001**		
Echinodermata		**0.000**		**0.136**				**0.034**		**0.006**	**0.047**	**0.046**	**0.009**	**0.009**	
Asteroidea unidentified													0.003		
Echinacea												0.000		0.001	
Irregularia		0.000													
Holothuroidea unidentified													0.002	0.009	
Ophiuridae				0.136				0.034		0.006	0.043	0.033	0.005		
Leptometra spp.											0.004	0.013			
Crustacea	**0.221**	**0.048**	**0.009**	**0.743**	**0.099**	**0.466**	**0.010**	**0.809**	**0.649**	**0.900**	**0.445**	**0.095**	**0.648**	**0.484**	**0.901**
Amphipoda				**0.082**	**0.001**	**0.001**	**0.000**	**0.031**	**0.004**	**0.515**	**0.140**	**0.022**	**0.001**	**0.000**	**0.006**
Brachyscelus spp.					0.001	0.000		0.000							0.000
Hyperia spp.											0.001				
Hyperiidea					0.000	0.000		0.001		0.001	0.000	0.002			
Phronima sedentaria				0.001	0.000	0.000		0.000			0.026	0.001			0.004
Phrosina semilunata												0.002			
Vibilia spp.					0.000	0.000		0.000		0.002	0.001	0.006			
Abludomelita spp.								0.000							
Ampelisca spp.				0.000	0.000			0.003	0.002		0.000		0.000		0.000
Amphilochoides spp.								0.000							
Aoridae spp.								0.001							
Apherusa spp.								0.000							
Bathymedon spp.				0.001											
Cheirocratus spp.								0.000							
Epimeria spp.				0.034				0.000			0.001	0.000	0.001		0.000
Eusirus spp.								0.000							0.000
Gammaridae								0.002							
Gammaropsis spp.								0.000							
Harpinia spp.								0.000				0.000			
Ichnopus spp.								0.001							
Idunella spp.								0.000							0.000
Lembos spp.								0.000							
Lepidepecreum spp.								0.000							
Leptocheirus spp.								0.000				0.000			
Leucothoe spp.								0.000							
Lysianassa spp.					0.000			0.003							0.000
Lysianassidae				0.004				0.002	0.001	0.005		0.001			0.000
Maera spp.								0.000							
Monoculodes spp.				0.001				0.000				0.000			
Nicippe spp.				0.024				0.000							
Oedicerotidae				0.000				0.000							

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Orchomene spp.								0.001							
Orchomenella spp.								0.000							
Peltocoxa spp.												0.000			
Phoxocephalus spp.											0.000				
Pseudotiron spp.								0.000							
Rhachotropis spp.				0.000						0.007					0.000
Scopelocheirus spp.								0.002							
Socarne spp.								0.000							
Syrrhoites spp.								0.000							
Tryphosites spp.				0.002				0.007							
Urothoe spp.								0.000							
Westwoodilla spp.				0.003			0.000	0.001			0.000				
Parvipalpus spp.								0.000							
Photis spp.											0.000				
Phtisica spp.				0.001				0.000							
Caprellids unidentified				0.000							0.005	0.002			0.000
Amphipods unidentified				0.010	0.000	0.000		0.004	0.001	0.500	0.105	0.008	0.001	0.000	0.001
Isopoda		**0.000**		**0.002**	**0.000**	**0.001**	**0.000**	**0.015**	**0.085**	**0.021**		**0.009**			**0.010**
Gnathiidae												0.000			
Isopods unidentified		0.000		0.002	0.000	0.001	0.000	0.015	0.085	0.021		0.009			0.010
Cumacea				**0.000**				**0.001**		**0.001**	**0.000**	**0.000**			
Lophogastrida			**0.000**	**0.101**	**0.001**	**0.000**		**0.011**	**0.002**						**0.004**
Lophogaster typicus			0.000	0.101	0.001	0.000		0.011	0.002						0.004
Mysida	**0.023**			**0.005**	**0.001**	**0.000**	**0.001**	**0.006**	**0.001**	**0.171**	**0.182**	**0.000**	**0.000**		**0.005**
Tanaidacea											**0.000**	**0.000**			**0.000**
Peracarids unidentified										0.005					
Copepoda				**0.000**	**0.000**			**0.000**		**0.007**	**0.001**	**0.004**			**0.000**
Ostracoda										**0.004**		**0.000**			**0.000**
Euphausiacea		**0.000**		**0.036**	**0.042**	**0.289**	**0.003**		**0.000**	**0.015**	**0.003**	**0.031**	**0.017**		**0.033**
Euphausia krohnii				0.001		0.001									
Meganyctiphanes norvegica				0.029	0.001	0.048						0.001			0.025
Nematoscelis spp.					0.000	0.003							0.017		
Nyctiphanes couchii					0.007	0.013									
Euphausiacids unidentified		0.000		0.007	0.034	0.223	0.003		0.000	0.015	0.003	0.031			0.008
Scalpelliformes												**0.000**			
Scalpellum scalpellum												0.000			
Decapoda	**0.195**	**0.038**	**0.002**	**0.515**	**0.052**	**0.174**	**0.006**	**0.734**	**0.557**	**0.135**	**0.117**	**0.027**	**0.628**	**0.484**	**0.813**
Aegaeon spp.				0.033	0.002			0.003							0.002
Alpheus glaber	0.006	0.003	0.000	0.025	0.004			0.120	0.004		0.006	0.001	0.188		0.341
Athanas spp.								0.002							
Chlorotocus crassicornis		0.001			0.013			0.046	0.032				0.010		0.072
Crangonidae					0.000			0.000			0.000				
Deosergestes henseni						0.001									
Eusergestes arcticus						0.009	0.002					0.003			
Gennadas elegans							0.002								
Hymenopenaeus debilis		0.001													
Ligur ensiferus				0.003											
Parapenaeus longirostris															
Pasiphaea multidentata						0.032									
Pasiphaea sivado					0.001	0.068						0.002			0.005
Pasiphaea spp.					0.002	0.012									0.002
Philocheras spp.				0.002	0.000			0.002		0.005	0.001		0.000		0.000
Plesionika acanthonotus															0.001
Plesionika edwardsii		0.001													
Plesionika giglioli					0.001	0.001									
Plesionika heterocarpus	0.081	0.002			0.000							0.009			
Plesionika martia							0.001								
Plesionika narval		0.000													
Pontophilus spp.				0.001	0.000			0.001							
Processa spp.	0.012	0.000	0.000	0.003	0.004	0.001		0.150	0.031				0.005		0.042
Sergia robusta						0.024									
Solenocera membranacea	0.002	0.018	0.002		0.010			0.065	0.422		0.006		0.025	0.005	0.099
Atelecyclus rotundatus				0.017				0.006							
Calcinus spp.														0.001	
Calocaris macandreae				0.004		0.000				0.060					0.061
Ctenodrilus spp.				0.000											

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Ebalia spp.				0.001							0.001				
Eurynome spp.				0.002											
Galathea spp.				0.001				0.006			0.002		0.000	0.003	0.000
Goneplax rhomboides		0.001		0.202				0.024			0.000		0.111	0.152	0.078
Inachus spp.		0.000												0.000	
Liocarcinus spp.		0.000		0.100	0.001			0.141			0.003		0.131	0.132	0.018
Macropipus tuberculatus				0.026										0.047	0.001
Macropodia spp.				0.010										0.001	
Monodaeus couchii				0.032				0.003		0.010					0.008
Munida spp.	0.010			0.027				0.006					0.005	0.004	0.012
Nephrops norvegicus						0.001									
Paguridae				0.007					0.000		0.006		0.003	0.006	0.000
Pagurus spp.				0.003									0.001	0.015	
Palinurus elephas								0.003							
Portunidae					0.000			0.023					0.019	0.007	
Scyllarus spp.				0.001	0.000			0.002					0.001		0.001
Upogebia spp.					0.000			0.012			0.009		0.005		0.001
Decapod larvae								0.001			0.002	0.000			
Natantia unidentified	0.083	0.009	0.000	0.002	0.010	0.023		0.068	0.068	0.053	0.047	0.012	0.040	0.022	0.055
Brachyura unidentified				0.013	0.000			0.035		0.007	0.033	0.001	0.043	0.088	0.004
Decapoda unidentified	0.002	0.001		0.001	0.003	0.002		0.016			0.000	0.001	0.038	0.000	0.009
Stomapoda		**0.010**	**0.007**		**0.000**									**0.000**	**0.027**
Rissoides desmaresti		0.005	0.001		0.000										0.027
Squila mantis		0.005	0.006												
Stomatopoda unidentified														0.000	
Crustacea unidentified	0.002	0.000		0.002	0.002	0.001		0.010		0.032	0.002	0.002	0.001		0.002
Cephalopods	**0.005**	**0.025**	**0.139**	**0.009**	**0.057**	**0.007**		**0.034**			**0.035**	**0.054**	**0.080**	**0.067**	**0.007**
Sepiida	**0.005**	**0.009**	**0.110**	**0.008**	**0.022**			**0.025**			**0.034**	**0.013**	**0.061**		**0.000**
Heteroteuthis dispar												0.003			
Rondeletiola minor					0.001			0.006					0.008		
Sepia elegans		0.000			0.013										
Sepia officinalis			0.109												
Sepia orbignyana		0.004											0.025		
Sepia spp.		0.003						0.001							
Sepietta oweniana		0.002			0.005			0.011					0.027		
Sepiolid unidentified	0.005	0.000	0.001	0.008	0.003			0.007			0.034	0.010	0.001		0.000
Myopsida		**0.003**						**0.009**							
Alloteuthis spp.		0.003						0.009							
Oegopsida		**0.012**			**0.034**	**0.007**						**0.006**			**0.003**
Abralia veranyi						0.004									
Illex coindetii		0.012			0.034										0.003
Teuthida unidentified						0.003						0.006			
Octopoda			**0.029**											**0.067**	
Eledone spp.			0.029											0.067	
Cephalopod eggs					0.000										
Cephalopods unidentified		0.001	0.001	0.001	0.000						0.002	0.036	0.020		0.003
Other Mollusca				**0.017**				**0.013**		**0.000**	**0.078**	**0.003**	**0.010**	**0.000**	
Pteropoda				**0.003**							**0.000**	**0.002**			
Cavolinia spp.				0.003							0.000	0.002			
Bivalvia				**0.005**				**0.013**		**0.000**	**0.029**	**0.000**	**0.004**		
Bivalvia unidentified				0.005				0.013		0.000	0.029	0.000	0.004		
Gastropoda				**0.010**				**0.000**			**0.049**		**0.006**	**0.000**	
Calyptraea chinensis														0.000	
Heterobranchia				0.009							0.049		0.003		
Gastropoda unidentified				0.001				0.000					0.004		
Tunicata											**0.076**	**0.572**		**0.000**	
Ascidiacea												0.009			
Pyrosoma atlanticum											0.034	0.463			
Tunicata unidentified											0.043	0.100		0.000	
Cephalochordata								**0.001**							
Branchiostoma lanceolatum								0.001							
Teleosts	**0.775**	**0.926**	**0.827**	**0.042**	**0.845**	**0.526**	**0.990**	**0.033**	**0.348**		**0.155**	**0.190**	**0.094**	**0.381**	**0.089**
Clupleiformes		**0.016**			**0.388**	**0.009**					**0.012**	**0.008**		**0.287**	
Engraulis encrasicolus		0.004			0.284									0.136	
Sardina pilchardus		0.012			0.102	0.009					0.012	0.008		0.151	
Sprattus sprattus					0.002										

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Argentiniformes	**0.029**	**0.000**			**0.001**		**0.006**								
Argentina sphyraena		0.000			0.001										
Glossanodon leioglossus	0.029						0.006								
Myctophiformes					**0.012**	**0.421**	**0.010**					**0.044**			**0.004**
Benthosema glaciale						0.041						0.004			
Ceratoscopelus maderensis					0.001	0.182						0.035			0.004
Lampanyctus crocodilus					0.011	0.165						0.001			
Notoscopelus elongatus					0.000	0.012	0.010					0.003			
Myctophum punctatum						0.005									
Myctophids unidentified					0.000	0.015						0.002			
Stomiiformes				**0.023**	**0.002**	**0.048**						**0.018**			**0.003**
Argyropelecus hemigymnus												0.002			
Maurolicus mullueri				0.023	0.001	0.006						0.004			0.003
Stomias boa					0.001	0.030						0.012			
Cyclothone spp.						0.011						0.000			
Gonostoma denudatum						0.000									
Gadiformes	**0.376**	**0.219**	**0.207**	**0.010**	**0.167**	**0.019**	**0.888**	**0.003**	**0.074**				**0.004**		**0.062**
Gadiculus argenteus	0.191	0.003	0.000		0.001		0.306								
Merluccius merluccius		0.062	0.185		0.038				0.039						0.011
Micromesistius poutassou	0.134	0.016	0.004		0.108	0.008	0.427		0.035						
Molva dypterygia		0.001													
Gaidropsarus biscayensis		0.006	0.003	0.010	0.004		0.014	0.003					0.004		0.046
Phycis blennoides		0.097	0.014		0.006	0.011	0.044								0.000
Trisopterus minutus	0.050	0.034	0.001		0.012	0.000	0.096								0.005
Perciformes	**0.214**	**0.274**	**0.292**	**0.005**	**0.201**			**0.014**	**0.074**		**0.017**		**0.045**	**0.061**	
Boops boops		0.021			0.145										
Callionymus spp.		0.006	0.001	0.005	0.001			0.003			0.003		0.000		
Capros aper	0.214	0.001													
Cepola macrophthalma		0.030			0.006			0.009	0.008						
Crystallogobius linearis														0.003	
Deltentosteus spp.		0.005			0.000				0.066				0.017		
Diplodus spp.		0.005	0.017											0.030	
Gobidae		0.028	0.000		0.002			0.001					0.008		
Lesueurogobius spp.		0.002	0.000		0.001						0.014		0.011		
Mullus spp.		0.016	0.068		0.001								0.009		
Pagellus erythrinus		0.017													
Serranus cabrilla					0.000										
Serranus hepatus		0.005													
Spicara smaris					0.004										
Spicara maena		0.022	0.031		0.014										
Spicara spp.		0.003													
Trachinus draco		0.092	0.090		0.001										
Trachurus spp.		0.021	0.001		0.026									0.029	
Uranoscopus scaber			0.083												
Aulopiformes					**0.010**	**0.008**						**0.009**			**0.014**
Lestidiops spp.						0.008									0.014
Paralepididae					0.010							0.009			
Scorpaeniformes		**0.013**	**0.010**		**0.000**										
Chelidonichthys spp.		0.002													
Lepidotrigla spp.		0.001													
Scorpaena notata		0.002													
Scorpaena porcus			0.010												
Triglidae		0.008			0.000										
Pleuronectiformes		**0.107**	**0.142**	**0.001**							**0.002**		**0.002**		
Arnoglossus spp.		0.013	0.003										0.002		
Citharus linguatula		0.082	0.011												
Lepidorhombus spp.		0.002													
Solea spp.			0.127												
Symphurus spp.		0.007	0.001												
Pleuronectiformes		0.003		0.001							0.002				
Anguilliformes		**0.097**	**0.059**					**0.004**	**0.137**				**0.018**	**0.014**	
Conger conger		0.076	0.045					0.004					0.018		
Gnathophis mystax		0.005													
Ophichthus rufus		0.016	0.014						0.137					0.014	
Syngnathiformes		**0.000**													
Macroramphosus scolopax		0.000													

	LEW	LOB	LOP	LYR	MER	MIC	MOL	MUL	NAE	NEZ	PAA	PAB	PAG	PAR	PHY
Ophidiiformes		**0.090**	**0.060**										**0.004**		
Ophidion barbatum		0.090	0.060										0.004		
Teleost larvae	0.003			0.000		0.001					0.023			0.002	
Teleost eggs												0.000			
Teleosts unidentified	0.152	0.109	0.056	0.003	0.064	0.020	0.086	0.013	0.063		0.100	0.111	0.020	0.015	0.007
Elasmobranchs			**0.025**												**0.001**
Scylliorhynus															0.001
Elasmobranchs unidentified			0.025												
Other											**0.002**	**0.001**			

	RAY	SCE	SCN	SCO	SCP	SCY	SER	SPM	SPO	SPS	TRA	TRC	TRI	URA	ZEU
Porifera															
Cnidaria	**0.000**			**0.028**				**0.034**	**0.407**						
Actiniaria									0.235						
Scyphozoa				0.003					0.012						
Diphyidae	0.000			0.025				0.003	0.000						
Epizoanthidae								0.013	0.002						
Plumularioidea								0.015	0.038						
Veretillum spp.									0.007						
Pennatulidae								0.003	0.032						
Alcyonium palmatum									0.080						
Alcyonacea unidentified									0.000						
Polychaeta	**0.005**	**0.000**	**0.005**			**0.028**	**0.012**	**0.068**	**0.414**	**0.002**	**0.008**	**0.008**	**0.001**		
Aphrodita aculeata						0.001									
Aphroditidae	0.000					0.001									
Eunicidae						0.000									
Glyceridae						0.000									
Sabellidae								0.010	0.302						
Sternaspis scutata						0.001									
Terebellidae									0.004						
Errantia unidentified	0.000					0.000	0.007		0.002						
Sedentaria unidentified						0.001		0.004							
Polychaeta unidentified	0.004	0.000	0.005			0.022	0.005	0.054	0.107	0.002	0.008	0.008	0.001		
Sipuncula						**0.000**									
Nemertea						**0.003**		**0.000**							
Bryozoa									**0.001**						
Echinodermata						**0.000**	**0.001**								
Ophiuridae						0.000	0.001								
Crustacea	**0.690**	**0.304**	**0.878**	**0.060**	**0.975**	**0.471**	**0.641**	**0.727**	**0.052**	**0.965**	**0.330**	**0.918**	**0.897**	**0.090**	**0.018**
Amphipoda	**0.003**	**0.000**	**0.009**	**0.003**	**0.001**	**0.004**	**0.004**	**0.063**	**0.020**	**0.005**	**0.002**	**0.013**	**0.008**		**0.000**
Brachyscelus spp.						0.001									0.000
Hemityphis spp.				0.000											
Hyperiidea	0.000			0.000		0.000	0.001	0.000	0.001						
Hyperionyx spp.				0.000											
Phronima sedentaria				0.000		0.001							0.004		
Phrosina semilunata				0.000							0.001				
Platyscelidae				0.001											
Vibilia spp.	0.000			0.000		0.000		0.001	0.005		0.000		0.000		0.000
Ampelisca spp.	0.000		0.000			0.000	0.001	0.000			0.000				
Bathymedon spp.	0.000														
Epimeria spp.							0.000		0.000				0.000		
Eusirus spp.												0.001			
Hippomedon spp.	0.000					0.000									
Ichnopus spp.						0.000									
Leucothoe spp.												0.000			
Lysianassa spp.													0.001		
Lysianassidae	0.000		0.001		0.001		0.001								
Maera spp.												0.001	0.000		
Monoculodes spp.	0.000								0.000						
Nicippe spp.	0.000											0.005			
Rhachotropis spp.													0.000		
Scopelocheirus spp.						0.000							0.001		

	RAY	SCE	SCN	SCO	SCP	SCY	SER	SPM	SPO	SPS	TRA	TRC	TRI	URA	ZEU
Tryphosites spp.	0.000												0.000		
Westwoodilla spp.	0.000						0.000	0.000							
Phtisica spp.							0.000								
Caprellids unidentified		0.000					0.000	0.026	0.012						
Amphipods unidentified	0.002	0.000	0.008	0.001		0.000	0.001	0.035	0.001	0.005		0.006	0.000		0.000
Isopoda	**0.028**	**0.000**	**0.001**	**0.000**		**0.002**	**0.004**	**0.002**	**0.001**	**0.004**	**0.000**	**0.020**	**0.003**	**0.000**	**0.000**
Gnathiidae	0.000														
Idotea spp.				0.000											
Isopods unidentified	0.028	0.000	0.001	0.000		0.002	0.004	0.002	0.001	0.004	0.000	0.020	0.003	0.000	0.000
Cumacea															
Lophogastrida	**0.018**	**0.001**	**0.002**			**0.002**	**0.001**						**0.009**		
Lophogaster typicus	0.018	0.001	0.002			0.002	0.001						0.009		
Mysida	**0.005**	**0.000**	**0.003**	**0.000**		**0.000**	**0.011**	**0.463**	**0.001**	**0.019**	**0.012**	**0.001**	**0.002**		**0.000**
Tanaidacea												**0.000**			
Copepoda	**0.000**						**0.000**	**0.020**	**0.000**	**0.882**		**0.000**			
Ostracoda								**0.000**				**0.001**			
Euphausiacea	**0.001**	**0.001**		**0.034**		**0.123**	**0.003**	**0.001**	**0.001**	**0.037**	**0.075**		**0.027**		**0.009**
Euphausia krohnii						0.009									
Meganyctiphanes norvegica						0.071							0.021		
Nematoscelis spp.						0.000									0.001
Nyctiphanes couchii						0.000					0.005				
Euphausiacids unidentified	0.001	0.001		0.034		0.042	0.003	0.001	0.001	0.037	0.070		0.006		0.008
Decapoda	**0.599**	**0.243**	**0.834**	**0.006**	**0.601**	**0.316**	**0.597**	**0.175**	**0.030**	**0.019**	**0.234**	**0.883**	**0.836**	**0.090**	**0.008**
Aegaeon spp.	0.000		0.003				0.012				0.001				
Alpheus glaber	0.015	0.016	0.278		0.135	0.059	0.087	0.071			0.048	0.040	0.441	0.008	
Athanas spp.			0.004										0.000		
Balssia gasti									0.001						
Chlorotocus crassicornis	0.053	0.013	0.002			0.019	0.008	0.070			0.012		0.063	0.001	
Crangonidae	0.002		0.001			0.000	0.001								
Deosergestes henseni												0.004			
Eusergestes arcticus						0.000			0.001			0.003			
Hippolytidae							0.000								
Ilia spp.	0.000														
Parapenaeus longirostris	0.003					0.001									
Pasiphaea sivado						0.010									
Pasiphaea spp.	0.001					0.001						0.045			
Philocheras spp.	0.000		0.001			0.000	0.003	0.002					0.002		
Plesionika acanthonotus		0.002													
Plesionika giglioli						0.001									
Plesionika heterocarpus	0.001	0.003				0.011	0.017								
Plesionika martia	0.001														
Plesionika narval	0.000	0.021													0.007
Pontophilus spp.	0.000					0.001	0.002						0.000		
Processa spp.	0.015	0.004	0.099		0.024	0.008	0.005	0.007			0.003		0.043	0.004	
Solenocera membranacea	0.192	0.013	0.023			0.040	0.015				0.000		0.010	0.052	
Atelecyclus rotundatus	0.047										0.002				
Calappa granulata	0.004														
Calocaris macandreae	0.000	0.000				0.013					0.001	0.764	0.000		
Ctenodrilus spp.														0.000	
Dardanus arrosor	0.001						0.009								
Ebalia spp.			0.001												
Ethusa spp.					0.001										
Galathea spp.	0.000	0.001	0.010		0.000		0.020	0.002	0.000		0.000		0.000		
Goneplax rhomboides	0.023	0.040	0.153		0.380	0.004	0.159	0.002			0.078	0.002	0.044		
Inachus spp.					0.005		0.003								
Jaxea nocturna							0.002						0.001		
Liocarcinus spp.	0.069	0.028	0.086		0.016	0.024	0.084				0.063		0.109	0.001	
Macropipus tuberculatus	0.021	0.030				0.001					0.003		0.001		
Macropodia spp.			0.004				0.005		0.000						
Medoripe lanata	0.001														
Monodaeus couchii	0.002	0.000	0.018		0.000		0.028					0.011	0.002		
Munida spp.	0.037	0.035	0.006			0.047	0.020				0.001		0.006		0.001
Nephrops norvegicus						0.001									
Paguridae	0.002		0.000				0.003	0.004	0.003			0.001			
Pagurus spp.	0.001					0.014	0.007		0.024		0.002				
Palicus spp.		0.001													

	RAY	SCE	SCN	SCO	SCP	SCY	SER	SPM	SPO	SPS	TRA	TRC	TRI	URA	ZEU
Pilumnus spinifer							0.003								
Portunidae	0.017		0.004			0.003	0.004				0.001		0.000		
Scyllarus spp.	0.003		0.007		0.016	0.001									
Thalassinidea						0.001									
Upogebia spp.	0.000		0.027			0.007	0.014				0.002		0.001	0.002	
Decapod larvae				0.003			0.000	0.000		0.010					
Ethusidae larvae				0.000											
Palinuridae larvae				0.001											
Natantia unidentified	0.035	0.030	0.045	0.000		0.027	0.036	0.012	0.002	0.009	0.005	0.005	0.058	0.020	
Brachyura unidentified	0.049	0.005	0.043		0.024	0.006	0.038	0.002			0.004	0.000	0.008		
Decapoda unidentified	0.003	0.002	0.018	0.002		0.016	0.011	0.002			0.006	0.006	0.046	0.001	
Stomapoda	**0.036**	**0.058**	**0.023**	**0.016**	**0.373**	**0.018**	**0.020**				**0.007**		**0.002**		
Pseudosquillopsis cerisii	0.001														
Rissoides desmaresti	0.022		0.023			0.016	0.020				0.005		0.002		
Squila mantis	0.013	0.056			0.373	0.002									
Stomatopoda unidentified		0.002		0.016							0.001				
Crustacea unidentified	0.001	0.000	0.006	0.001		0.006	0.000	0.004			0.001		0.009	0.000	0.000
Cephalopods	**0.084**	**0.083**	**0.048**	**0.018**		**0.096**	**0.054**	**0.032**	**0.039**		**0.048**		**0.028**	**0.041**	**0.003**
Sepiida	**0.003**	**0.022**	**0.048**	**0.004**		**0.021**	**0.054**		**0.010**		**0.043**		**0.026**	**0.013**	**0.001**
Rondeletiola minor	0.001					0.005	0.005								0.001
Sepia elegans						0.001								0.008	
Sepia officinalis						0.000									
Sepietta oweniana		0.009	0.048			0.008	0.043				0.023		0.007	0.005	
Sepiolid unidentified	0.002	0.013		0.004		0.007	0.006		0.010		0.020		0.019		
Myopsida	**0.013**	**0.033**				**0.000**					**0.005**			**0.023**	
Alloteuthis spp.		0.033				0.000					0.005			0.023	
Loligo vulgaris	0.013														
Oegopsida	**0.053**			**0.009**		**0.063**								**0.002**	**0.002**
Abralia veranyi						0.001									
Histioteuthis bonnellii						0.000									
Histioteuthis spp.						0.027									
Illex coindetii	0.044			0.007		0.033								0.002	0.002
Teuthida unidentified	0.008			0.002		0.002									
Octopoda		**0.023**						**0.008**	**0.025**					**0.002**	
Eledone spp.		0.023												0.002	
Octopus vulgaris								0.008	0.025						
Cephalopod eggs								0.024							
Cephalopods unidentified	0.016	0.003		0.006		0.012			0.004				0.002	0.001	0.000
Other Mollusca	**0.002**	**0.000**	**0.000**	**0.004**		**0.001**	**0.000**	**0.002**	**0.004**	**0.001**	**0.000**		**0.000**		
Pteropoda				**0.004**					**0.000**	**0.001**			**0.000**		
Cavolinia spp.				0.004					0.000	0.001			0.000		
Bivalvia	**0.002**	**0.000**					**0.000**	**0.000**	**0.000**		**0.000**				
Bivalvia unidentified	0.002	0.000					0.000	0.000	0.000		0.000				
Gastropoda			**0.000**			**0.001**		**0.002**	**0.004**						
Heterobranchia								0.002	0.004						
Gastropoda unidentified			0.000			0.001									
Tunicata	**0.002**			**0.004**		**0.003**		**0.007**	**0.018**		**0.030**	**0.009**			
Ascidiacea									0.002						
Pyrosoma atlanticum	0.002							0.005	0.011		0.030				
Tunicata unidentified				0.004		0.003		0.003	0.004			0.009			
Teleosts	**0.217**	**0.613**	**0.067**	**0.886**	**0.025**	**0.380**	**0.293**	**0.123**	**0.064**	**0.031**	**0.571**	**0.065**	**0.074**	**0.851**	**0.978**
Clupleiformes	**0.013**			**0.659**		**0.157**	**0.109**		**0.033**		**0.322**		**0.005**	**0.229**	**0.025**
Engraulis encrasicolus	0.013			0.168		0.105	0.053				0.312			0.181	0.009
Sardina pilchardus				0.491		0.052	0.056		0.033		0.010		0.005	0.048	0.015
Argentiniformes	**0.033**														**0.035**
Argentina sphyraena	0.010														0.034
Glossanodon leioglossus	0.024														0.000
Myctophiformes	**0.000**			**0.001**		**0.012**					**0.080**	**0.042**	**0.002**		**0.011**
Benthosema glaciale						0.001									0.000
Ceratoscopelus maderensis	0.000					0.004					0.066				0.000
Lampanyctus crocodilus						0.000									
Notoscopelus elongatus				0.001		0.004							0.002		0.000
Myctophum punctatum						0.000					0.012	0.042			0.002
Myctophids unidentified						0.002					0.002				0.008
Stomiiformes						**0.002**									**0.006**
Maurolicus mullueri						0.000									0.006

	RAY	SCE	SCN	SCO	SCP	SCY	SER	SPM	SPO	SPS	TRA	TRC	TRI	URA	ZEU
Stomias boa						0.002									
Gadiformes	**0.071**	**0.134**	**0.027**	**0.001**		**0.065**	**0.051**				**0.070**		**0.038**	**0.314**	**0.402**
Coelorinchus caelorhincus						0.003									
Gadiculus argenteus	0.003	0.019				0.004									0.052
Merluccius merluccius	0.025	0.060				0.000							0.005	0.065	0.088
Micromesistius poutassou	0.005	0.015		0.001		0.039	0.006				0.065		0.000		0.189
Molva dypterygia			0.007				0.002								
Gaidropsarus biscayensis	0.003	0.017	0.020				0.003						0.033	0.001	0.003
Phycis blennoides		0.004				0.011								0.028	0.019
Trisopterus minutus	0.035	0.020				0.009	0.040				0.005			0.220	0.052
Perciformes	**0.045**	**0.258**	**0.001**	**0.166**		**0.043**	**0.069**		**0.026**		**0.026**		**0.019**	**0.155**	**0.401**
Ammodytes tobianus	0.001														
Blennius ocellaris							0.004								
Boops boops		0.093		0.006							0.011				0.115
Callionymus spp.		0.013	0.001				0.015				0.001		0.010	0.012	0.002
Capros aper	0.005														0.002
Cepola macrophthalma	0.006	0.004		0.004		0.016					0.014			0.041	0.121
Deltentosteus spp.		0.002												0.003	0.001
Diplodus spp.														0.046	
Gobidae		0.005	0.001				0.012						0.004	0.025	0.006
Lepidopus caudatus						0.027									
Lesueurogobius spp.		0.007				0.000	0.039						0.005	0.007	0.005
Mullus spp.	0.022	0.122		0.044											
Pagellus erythrinus															0.001
Scomber spp.				0.008										0.020	
Serranus hepatus		0.003													
Spicara smaris	0.012			0.021											0.010
Spicara maena															0.062
Spicara spp.		0.009													0.039
Trachurus spp.				0.083					0.026						0.037
Aulopiformes						**0.016**									**0.019**
Chlorophthalmus agassizi															0.019
Lestidiops spp.						0.001									
Paralepididae						0.015									
Scorpaeniformes	**0.004**	**0.011**													
Chelidonichthys spp.															0.001
Helicolenus dactylopterus		0.007													
Lepidotrigla spp.	0.004													0.018	
Triglidae		0.005	0.001			0.011									
Pleuronectiformes	**0.007**	**0.024**				**0.001**							**0.000**	**0.040**	**0.021**
Arnoglossus spp.													0.000	0.029	
Citharus linguatula														0.006	0.021
Lepidorhombus spp.	0.007														
Monochirus hispidus						0.000									
Symphurus spp.	0.001	0.021				0.000								0.004	
Pleuronectiformes		0.004													
Anguilliformes		**0.015**				**0.023**									
Conger conger		0.007				0.001									
Nettastoma melanurum		0.008													
Ophichthus rufus						0.022									
Lophiiformes	**0.001**	**0.013**													
Lophius spp.	0.001	0.013													
Syngnathiformes		**0.002**													
Macroramphosus scolopax		0.002													
Ophidiiformes	**0.002**					**0.004**								**0.042**	
Ophidion barbatum	0.002					0.004								0.042	
Teleost larvae	0.000			0.007	0.025	0.001	0.002	0.002		0.009	0.000				0.000
Teleost eggs										0.022					
Teleosts unidentified	0.041	0.155	0.038	0.052		0.056	0.062	0.121	0.005		0.072	0.023	0.008	0.072	0.058
Elasmobranchs	**0.000**					**0.008**									
Scylliorhynus	0.000														
Elasmobranchs unidentified						0.008									
Other								**0.007**	**0.001**						

Table A.3. Diet compositions of the 61 studied species expressed in volume (V%). **Species codes: ARI**, *Arnoglossus imperialis;* **ARL**, *A. laterna;* **ARR**, *A. rueppelii;* **ART**, *A. thori;* **BOP**, *Boops boops;* **CAP**, *Capros aper;* **CEP**, *Cepola macrophtalma;* **CUC**, *Chelidonichthys cuculus;* **GUR**, *C. gurnardus;* **CHL**, *C. lastoviza;* **CIT**, *Citharus linguatula;* **COE**, *Coelorinchus caelorhincus;* **CON**, *Conger conger;* **DIA**, *Diplodus annularis;* **DIV**, *D. vulgaris;* **ETM**, *Etmopterus spinax;* **GAD**, *Gadiculus argenteus;* **GAI**, *Gaidropsarus biscayensis;* **GAL**, *Galeus melastomus;* **HEL**, *Helicolenus dactylopterus;* **LAM**, *Lampanyctus crocodilus;* **CAU**, *Lepidopus caudatus;* **LEP**, *Lepidorhombus boscii;* **LEW**, *L. whiffiagonis;* **LEC**, *Lepidotrigla cavillone;* **LED**, *L. dieuzeidei;* **NAE**, *Leucoraja naevus;* **LOB**, *Lophius budegassa;* **LOP**, *L. piscatorius;* **MER**, *Merluccius merluccius;* **MIC**, *Micromesistius poutassou;* **MOL**, *Molva dypterygia;* **BAR**, *Mullus barbatus;* **MUL**, *M. surmuletus;* **NEZ**, *Nezumia aequalis;* **PAA**, *Pagellus acarne;* **PAB**, *P. bogaraveo;* **PAG**, *P. erytrinus;* **PAR**, *Pagrus pagrus;* **PHY**, *Phycis blennoides;* **RAY**, *Raja sp.;* **COL**, *Scomber colias;* **SCO**, *S. scombrus;* **SCE**, *Scorpaena elongata;* **SCN**, *S. notata;* **SCP**, *S. porcus;* **SCY**, *Scyliorhinus canicula;* **SER**, *Serranus cabrilla;* **HEP**, *S. hepatus;* **SPM**, *Spicara maena;* **SPS**, *S. smaris;* **SPO**, *Spondyliosoma cantharus;* **TRA**, *Trachinus draco;* **JUM**, *Trachurus mediterraneus;* **JUN**, *T. picturatus;* **JUB**, *T. trachurus;* **TRC**, *Trachyrhinchus scabrus;* **LYR**, *Trigla lyra;* **TRI**, *Trisopterus minutus;* **URA**, *Uranoscopus scaber;* **ZEU**, *Zeus faber.*

PREDATOR	B_i	TL	DI	SP	LP	GP	PO	PE	BI	NA	RE	BC	BT	PF	FF	GA	IF	GO	TR	HA	MU	SF	BF
A. imperialis	0.16	3.6	V%	-	0.3	-	0.2	18.5	0.4	9.2	68.3	-	-	-	-	-	-	3.0	-	-	-	-	-
			F%	-	8.3	-	2.8	55.6	2.8	19.4	75.0	-	-	-	-	-	-	5.6	-	-	-	-	-
			GII%	-	4.3	-	1.5	37.0	1.6	14.3	71.7	-	-	-	-	-	-	4.3	-	-	-	-	-
A. laterna	0.42	3.6	V%	8.9	0.3	-	0.7	31.8	-	33.6	17.8	-	-	-	-	3.7	-	3.3	-	-	-	-	-
			F%	24.3	3.5	-	3.5	61.8	-	39.6	31.3	-	-	-	-	0.7	-	4.9	-	-	-	-	-
			GII%	16.6	1.9	-	2.1	46.8	-	36.6	24.5	-	-	-	-	2.2	-	4.1	-	-	-	-	-
A. rueppelii	0.30	3.5	V%	0.1	0.2	-	4.2	56.3	-	23.9	15.3	-	-	-	-	-	-	-	-	-	-	-	-
			F%	1.1	1.1	-	10.9	70.7	-	23.9	21.7	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.6	0.6	-	7.5	63.5	-	23.9	18.5	-	-	-	-	-	-	-	-	-	-	-	-
A. thori	0.20	3.7	V%	0.1	1.1	-	5.3	22.7	0.0	8.6	59.2	-	-	-	-	-	-	3.1	-	-	-	-	-
			F%	1.4	5.8	-	21.0	59.4	0.7	15.9	71.0	-	-	-	-	-	-	2.9	-	-	-	-	-
			GII%	0.8	3.5	-	13.1	41.0	0.4	12.3	65.1	-	-	-	-	-	-	3.0	-	-	-	-	-
B. boops	0.08	3.3	V%	0.2	3.4	77.6	1.5	1.0	4.3	4.0	-	3.5	-	-	4.5	-	-	-	-	-	-	-	-
			F%	9.3	23.3	73.3	6.7	6.7	10.0	4.0	0.7	0.7	-	-	3.3	-	-	-	-	-	-	-	-
			GII%	4.8	13.4	75.5	4.1	3.8	7.2	4.0	-	2.1	-	-	3.9	-	-	-	-	-	-	-	-
C. aper	0.56	3.6	V%	25.8	22.0	0.5	14.0	32.5	-	5.2	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	47.4	35.9	1.3	7.7	56.4	-	7.7	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	36.6	28.9	0.9	10.9	44.5	-	6.4	-	-	-	-	-	-	-	-	-	-	-	-	-
C. macrophtalma	0.38	3.2	V%	55.4	27.3	12.1	0.6	4.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	85.5	31.6	11.1	2.6	25.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	70.5	29.5	11.6	1.6	15.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
C. cuculus	0.16	3.7	V%	-	0.1	0.1	0.3	8.1	0.1	11.1	54.3	10.1	-	-	1.3	1.3	-	3.6	0.2	-	-	2.3	6.9
			F%	-	2.1	0.7	5.0	50.7	1.1	30.1	61.7	9.6	-	-	3.9	3.2	-	10.6	1.1	-	-	2.5	1.1
			GII%	-	1.1	0.4	2.6	29.4	0.6	20.6	58.0	9.9	-	-	2.6	2.3	-	7.1	0.7	-	-	2.4	4.0
C. gurnardus	0.25	3.6	V%	0.0	1.4	0.1	0.1	15.4	0.1	24.7	39.2	2.4	-	-	1.3	1.8	-	6.4	-	-	-	-	7.1
			F%	1.0	4.8	0.3	2.4	57.0	1.4	42.3	52.6	4.8	-	-	3.4	8.2	-	9.2	-	-	-	-	7.2
			GII%	0.5	3.1	0.2	1.3	36.2	0.7	33.5	45.9	3.6	-	-	2.4	5.0	-	7.8	-	-	-	-	7.1
C. lastoviza	0.11	3.6	V%	-	0.4	-	0.3	11.5	0.0	14.4	70.8	1.7	-	-	0.6	-	-	0.2	-	-	-	-	-
			F%	-	4.8	-	6.6	67.4	1.8	38.3	81.5	4.0	-	-	1.3	-	-	1.3	-	-	-	-	-
			GII%	-	2.6	-	3.5	39.4	0.9	26.4	76.1	2.8	-	-	1.0	-	-	0.7	-	-	-	-	-
C. linguatula	0.50	4.2	V%	-	4.5	-	0.4	3.2	-	15.5	1.8	2.8	-	14.7	3.4	17.9	-	22.7	1.8	3.8	-	-	7.5
			F%	-	6.5	-	1.0	29.0	-	34.0	2.5	2.0	-	5.0	5.0	11.0	-	22.5	1.5	1.5	-	-	3.5
			GII%	-	5.5	-	0.7	16.1	-	24.7	2.2	2.4	-	9.8	4.2	14.5	-	22.6	1.6	2.7	-	-	5.5
C. caelorhincus	0.26	3.6	V%	0.7	2.4	-	15.9	13.6	-	6.0	58.8	-	-	-	-	2.6	-	-	-	-	-	-	-
			F%	27.5	1.0	-	47.5	69.1	-	9.3	46.6	-	-	-	-	1.0	-	-	-	-	-	-	-
			GII%	14.1	1.7	-	31.7	41.3	-	7.7	52.7	-	-	-	-	1.8	-	-	-	-	-	-	-
C. conger	0.43	4.1	V%	0.4	0.4	-	0.0	0.2	0.0	10.8	23.1	3.7	0.1	12.4	2.1	6.8	5.3	10.8	1.6	0.3	-	11.6	10.4
			F%	0.3	3.0	-	0.5	3.5	0.0	41.3	53.5	3.5	0.3	4.1	1.4	9.0	2.4	10.9	0.5	0.5	-	2.4	8.7

			GII%	0.3	1.7	-	0.3	1.9	0.0	26.1	38.3	3.6	0.2	8.3	1.7	7.9	3.9	10.8	1.1	0.4	-	7.0	9.5
D. annularis	0.39	3.6	V%	1.3	-	0.4	24.1	3.3	21.7	5.3	32.1	0.1	-	-	2.2	-	-	9.6	-	-	-	-	-
			F%	2.1	-	0.4	36.3	29.1	32.9	6.4	33.8	0.4	-	-	1.3	-	-	3.4	-	-	-	-	-
			GII%	1.7	-	0.4	30.2	16.2	27.3	5.9	32.9	0.2	-	-	1.7	-	-	6.5	-	-	-	-	-
D. vulgaris	0.37	3.4	V%	9.8	1.0	0.6	26.2	6.4	22.9	0.0	31.0	0.5	1.5	-	-	-	-	-	-	-	-	-	-
			F%	6.1	2.3	1.5	47.7	49.2	50.8	0.8	42.4	2.3	0.8	-	-	-	-	-	-	-	-	-	-
			GII%	7.9	1.7	1.1	37.0	27.8	36.8	0.4	36.7	1.4	1.1	-	-	-	-	-	-	-	-	-	-
E. spinax	0.26	4.4	V%	-	1.1	-	0.0	-	0.0	10.3	-	5.5	44.4	-	-	-	-	0.0	-	0.5	-	-	38.2
			F%	-	8.5	-	1.7	-	0.0	30.5	-	8.5	44.1	-	-	-	-	1.7	-	1.7	-	-	40.7
			GII%	-	4.8	-	0.9	-	0.0	20.4	-	7.0	44.2	-	-	-	-	0.9	-	1.1	-	-	39.4
G. argenteus	0.19	3.5	V%	6.7	57.1	0.1	0.1	3.5	-	7.6	0.1	-	-	-	-	1.0	-	-	-	-	-	-	23.9
			F%	12.8	65.8	0.4	0.4	19.2	-	9.0	0.4	-	-	-	-	0.9	-	-	-	-	-	-	20.5
			GII%	9.7	61.5	0.3	0.3	11.4	-	8.3	0.3	-	-	-	-	0.9	-	-	-	-	-	-	22.2
G. biscayensis	0.40	3.7	V%	1.5	3.2	-	0.3	12.2	-	20.3	46.0	-	-	-	-	16.5	-	-	-	-	-	-	-
			F%	18.6	8.8	-	1.0	39.2	-	17.6	37.3	-	-	-	-	7.8	-	-	-	-	-	-	-
			GII%	10.1	6.0	-	0.7	25.7	-	19.0	41.6	-	-	-	-	12.2	-	-	-	-	-	-	-
G. melastomus	0.36	4.0	V%	4.6	9.1	0.8	0.0	0.1	-	24.5	6.1	7.9	12.5	-	0.1	4.7	2.1	0.0	-	-	-	-	27.5
			F%	0.5	60.8	4.8	1.3	2.2	-	44.1	24.5	23.4	19.1	-	0.3	5.1	4.3	0.3	-	-	-	-	34.4
			GII%	2.6	34.9	2.8	0.7	1.1	-	34.3	15.3	15.6	15.8	-	0.2	4.9	3.2	0.1	-	-	-	-	31.0
H. dactylopterus	0.39	3.9	V%	0.0	17.2	3.8	0.0	3.6	0.1	21.7	18.4	0.2	3.3	-	-	11.9	1.3	2.0	-	-	-	0.5	15.8
			F%	0.7	21.4	6.9	0.7	25.0	1.3	31.9	38.8	1.0	0.7	-	-	6.6	1.0	4.6	-	-	-	0.3	6.3
			GII%	0.3	19.3	5.3	0.3	14.3	0.7	26.8	28.6	0.6	2.0	-	-	9.2	1.2	3.3	-	-	-	0.4	11.0
L. crocodilus	0.12	3.7	V%	-	3.6	0.2	-	1.1	-	76.4	0.2	-	-	-	-	-	-	-	-	-	-	-	18.5
			F%	-	16.9	0.8	-	5.9	-	68.6	0.8	-	-	-	-	-	-	-	-	-	-	-	13.6
			GII%	-	10.3	0.5	-	3.5	-	72.5	0.5	-	-	-	-	-	-	-	-	-	-	-	16.0
L. caudatus	0.18	3.9	V%	-	22.4	-	-	-	-	11.5	-	-	0.2	1.1	-	0.2	-	0.4	-	-	-	-	64.3
			F%	-	50.0	-	-	-	-	11.7	-	-	1.3	0.6	-	1.3	-	0.6	-	-	-	-	63.0
			GII%	-	36.2	-	-	-	-	11.6	-	-	0.7	0.9	-	0.7	-	0.5	-	-	-	-	63.6
L. boscii	0.24	3.7	V%	-	0.8	-	0.6	2.9	-	46.7	31.3	1.1	-	-	-	14.5	0.1	2.0	-	-	-	-	-
			F%	-	4.4	-	1.3	18.1	-	53.7	53.0	1.3	-	-	-	17.1	0.7	3.7	-	-	-	-	-
			GII%	-	2.6	-	1.0	10.5	-	50.2	42.2	1.2	-	-	-	15.8	0.4	2.8	-	-	-	-	-
L. whiffiagonis	0.31	4.4	V%	-	0.3	-	-	2.4	-	18.7	1.0	0.5	-	-	-	46.8	-	-	-	-	-	-	30.3
			F%	-	2.9	-	-	14.7	0.0	29.4	5.9	8.8	-	-	-	23.5	-	-	-	-	-	-	11.8
			GII%	-	1.6	-	-	8.5	-	24.1	3.5	4.6	-	-	-	35.2	-	-	-	-	-	-	21.1
L. cavillone	0.24	3.5	V%	0.1	0.1	-	1.4	56.6	-	26.6	14.7	-	-	-	-	-	-	0.5	-	-	-	-	-
			F%	2.6	1.9	-	1.9	86.8	-	32.5	23.4	-	-	-	-	-	-	3.0	-	-	-	-	-
			GII%	1.4	1.0	-	1.7	71.7	-	29.5	19.0	-	-	-	-	-	-	1.8	-	-	-	-	-
L. dieuzeidei	0.16	3.4	V%	1.7	3.3	-	3.3	85.6	-	25.4	8.8	1.7	-	-	-	-	-	1.1	-	-	-	-	-
			F%	0.8	2.2	-	1.8	73.3	-	27.9	6.2	2.4	-	-	-	-	-	0.8	-	-	-	-	-

			GII%	-	0.0	-	0.3	9.2	-	55.7	0.0	-	-	-	-	4.3	-	8.0	-	4.8	-	-	17.7
L. naevus	0.22	4.1	V%	-	2.6	-	7.7	51.3	-	69.2	2.6	-	-	-	-	5.1	-	5.1	-	5.1	-	-	12.8
			F%	-	1.3	-	4.0	30.2	-	62.4	1.3	-	-	-	-	4.7	-	6.6	-	5.0	-	-	15.3
			GII%	-	0.0	-	0.0	0.0	0.0	3.7	1.1	1.3	1.2	6.9	12.1	17.7	19.2	4.6	1.3	7.1	1.8	5.9	16.1
L. budegassa	0.41	4.7	V%	-	0.5	-	0.2	1.2	0.2	21.0	4.3	2.6	0.5	4.3	10.7	31.5	4.8	14.3	1.7	4.5	1.0	3.3	17.2
			F%	-	0.2	-	0.1	0.6	0.1	12.3	2.7	2.0	0.8	5.6	11.4	24.6	12.0	9.5	1.5	5.8	1.4	4.6	16.6
			GII%	-	-	-	-	0.0	-	0.2	0.7	13.9	-	0.1	15.2	2.4	25.9	0.3	-	19.8	7.3	6.2	8.0
L. piscatorius	0.42	4.8	V%	-	-	-	-	1.1	-	10.3	3.4	13.8	-	1.1	8.0	16.1	17.2	12.6	-	1.1	3.4	8.0	16.1
			F%	-	-	-	-	0.6	-	5.3	2.1	13.9	-	0.6	11.6	9.2	21.6	6.4	-	10.5	5.4	7.1	12.0
			GII%	0.0	4.4	-	-	0.1	-	5.2	0.2	2.2	3.4	60.9	-	14.0	0.1	0.5	0.0	4.1	0.1	1.5	3.4
M. merluccius	0.10	4.3	V%	0.1	27.5	-	-	6.1	-	24.9	1.8	2.8	0.1	33.0	-	17.9	0.1	2.9	0.1	2.0	0.1	0.4	2.2
			F%	0.1	15.9	-	-	3.1	-	15.0	1.0	2.5	1.8	46.9	-	15.9	0.1	1.7	0.1	3.0	0.1	1.0	2.8
			GII%	-	29.1	0.0	0.0	0.1	-	17.3	0.1	-	0.8	1.0	-	2.0	-	-	-	-	-	-	49.6
M. poutassou	0.20	3.9	V%	-	55.2	0.2	0.2	1.8	-	22.0	0.4	-	1.8	0.9	-	1.8	-	-	-	-	-	-	53.6
			F%	-	42.2	0.1	0.1	1.0	-	19.7	0.2	-	1.3	0.9	-	1.9	-	-	-	-	-	-	51.6
			GII%	-	0.3	-	-	0.1	-	0.6	-	-	-	-	-	97.3	-	-	-	-	-	-	1.7
M. dypterygia	0.01	4.7	V%	-	3.3	-	-	4.1	-	1.6	-	-	-	-	-	93.4	-	-	-	-	-	-	9.0
			F%	-	1.8	-	-	2.1	-	1.1	-	-	-	-	-	95.4	-	-	-	-	-	-	5.4
			GII%	0.0	0.1	-	18.7	5.7	7.1	59.2	9.1	-	-	-	-	-	-	-	-	-	-	-	-
M. barbatus	0.25	3.5	V%	0.4	1.6	-	34.4	52.6	12.6	57.5	26.3	-	-	-	-	-	-	-	-	-	-	-	-
			F%	0.2	0.9	-	26.6	29.2	9.8	58.3	17.7	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.1	0.2	-	7.6	6.4	4.7	47.3	27.0	3.4	-	-	-	0.4	0.6	0.7	-	-	-	-	1.6
M. surmuletus	0.20	3.6	V%	1.3	3.0	-	23.8	52.1	15.2	55.4	53.5	2.6	-	-	-	0.7	0.7	1.3	-	-	-	-	2.3
			F%	0.7	1.6	-	15.7	29.3	9.9	51.4	40.2	3.0	-	-	-	0.5	0.6	1.0	-	-	-	-	1.9
			GII%	1.1	1.8	-	8.8	73.6	0.7	6.0	8.0	-	-	-	-	-	-	-	-	-	-	-	-
N. aequalis	0.13	3.8	V%	25.8	3.4	-	21.3	94.4	3.4	7.9	18.0	-	-	-	-	-	-	-	-	-	-	-	-
			F%	13.5	2.6	-	15.1	84.0	2.0	6.9	13.0	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	0.1	5.7	8.0	15.3	29.6	13.1	6.1	5.5	3.5	-	5.1	1.0	-	-	7.1	-	-	-	-	-
P. acarne	0.50	3.7	V%	6.1	6.8	6.1	32.4	69.6	16.2	8.8	15.5	1.4	-	1.4	1.4	-	-	9.5	-	-	-	-	-
			F%	3.1	6.2	7.0	23.9	49.6	14.6	7.4	10.5	2.4	-	3.2	1.2	-	-	8.3	-	-	-	-	-
			GII%	0.4	4.5	56.8	2.8	2.1	5.7	2.7	0.1	5.3	0.6	1.8	-	-	-	-	-	-	-	-	17.2
P. bogaraveo	0.16	3.5	V%	2.9	15.6	48.0	16.4	29.8	16.7	4.4	1.1	2.2	0.4	0.7	-	-	-	-	-	-	-	-	12.7
			F%	1.7	10.1	52.4	9.6	15.9	11.2	3.5	0.6	3.7	0.5	1.3	-	-	-	-	-	-	-	-	15.0
			GII%	-	1.7	-	15.5	0.2	2.2	28.7	34.2	8.0	-	-	0.3	0.6	2.3	4.5	-	-	1.2	-	0.5
P. erytrinus	0.27	3.7	V%	-	3.5	-	35.3	5.5	7.8	25.1	47.8	3.5	-	-	2.4	0.4	2.4	7.8	-	-	0.4	-	0.4
			F%	-	2.6	-	25.4	2.8	5.0	26.9	41.0	5.8	-	-	1.3	0.5	2.3	6.2	-	-	0.8	-	0.5
			GII%	-	0.2	0.0	5.5	0.0	0.9	2.6	45.8	7.1	-	33.0	-	-	-	0.3	-	-	-	3.1	1.5
P. pagrus	0.19	3.9	V%	-	1.1	1.1	24.1	3.4	5.7	9.2	73.6	4.6	-	13.8	-	-	-	2.3	-	-	-	2.3	1.1
			F%	-	0.7	0.6	14.8	1.7	3.3	5.9	59.7	5.8	-	23.4	-	-	-	1.3	-	-	-	2.7	1.3
			GII%	-	2.6	-	7.7	51.3	-	69.2	2.6	-	-	-	-	5.1	-	5.1	-	5.1	-	-	12.8

P. blennoides	0.10	3.6	V%	0.0	3.8	0.0	0.1	2.2	-	62.7	21.5	0.4	0.3	-	-	5.5	0.1	0.0	-	1.2	-	-	2.2
			F%	1.1	13.8	0.4	3.6	32.4	-	68.0	53.8	1.1	0.4	-	-	13.1	0.7	0.7	-	0.7	-	-	2.2
			GII%	0.5	8.8	0.2	1.9	17.3	-	65.4	37.6	0.7	0.3	-	-	9.3	0.4	0.4	-	1.0	-	-	2.2
Raja spp	0.21	3.9	V%	0.0	0.1	0.2	0.5	5.6	0.2	33.0	30.4	1.2	7.3	3.3	1.0	4.7	0.2	-	0.6	3.5	3.2	-	5.1
			F%	4.7	4.4	1.7	9.2	58.9	0.8	75.3	37.8	1.9	1.4	1.9	0.8	4.7	0.8	-	0.6	1.9	0.3	-	5.8
			GII%	2.4	2.3	0.9	4.8	32.2	0.5	54.1	34.1	1.6	4.3	2.6	0.9	4.7	0.5	-	0.6	2.7	1.7	-	5.5
S. colias	0.23	3.8	V%	0.4	17.4	32.4	0.1	5.8	0.2	0.1	0.0	0.0	0.6	38.3	-	-	-	-	-	-	4.7	-	-
			F%	7.3	82.7	72.5	3.3	45.8	1.9	3.3	0.7	1.0	0.9	22.5	-	-	-	-	-	-	6.6	-	-
			GII%	3.8	50.0	52.4	1.7	25.8	1.1	1.7	0.4	0.5	0.7	30.4	-	-	-	-	-	-	5.6	-	-
S. scombrus	0.05	4.1	V%	-	5.0	3.2	-	0.2	-	0.0	1.8	0.9	0.9	82.5	-	0.1	-	-	-	-	4.7	-	0.6
			F%	-	35.1	48.5	-	5.5	-	2.4	8.6	4.5	1.0	58.4	-	1.0	-	-	-	-	4.8	-	1.4
			GII%	-	20.1	25.8	-	2.8	-	1.2	5.2	2.7	1.0	70.5	-	0.6	-	-	-	-	4.7	-	1.0
S. elongata	0.45	4.3	V%	-	0.1	-	0.0	0.1	0.0	10.2	20.0	8.3	-	13.7	3.2	9.9	2.8	3.6	0.6	8.0	16.3	1.3	1.9
			F%	-	1.0	-	1.5	5.5	0.5	37.8	36.8	9.0	-	1.5	2.5	17.9	1.5	11.9	1.5	5.5	0.5	4.5	2.5
			GII%	-	0.5	-	0.8	2.8	0.3	24.0	28.4	8.6	-	7.6	2.9	13.9	2.1	7.8	1.1	6.8	8.4	2.9	2.2
S. notata	0.18	3.7	V%	-	-	-	0.5	1.5	0.0	47.0	39.3	4.8	-	-	-	4.6	1.6	0.3	0.2	-	-	-	-
			F%	-	-	-	3.5	19.0	0.4	48.9	53.2	0.9	-	-	-	2.6	1.3	2.2	1.3	-	-	-	-
			GII%	-	-	-	2.0	10.3	0.2	47.9	46.3	2.9	-	-	-	3.6	1.4	1.2	0.8	-	-	-	-
S. porcus	0.15	3.5	V%	-	2.5	-	-	0.1	-	15.9	81.5	-	-	-	-	-	-	-	-	-	-	-	-
			F%	-	2.9	-	-	5.7	-	40.0	80.0	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	-	2.7	-	-	2.9	-	28.0	80.7	-	-	-	-	-	-	-	-	-	-	-	-
S. canicula	0.42	4	V%	-	12.8	0.3	2.8	0.5	0.4	19.0	14.9	3.4	6.3	18.3	0.1	7.2	4.1	0.0	1.2	0.0	-	-	8.8
			F%	-	50.6	0.6	22.1	10.2	0.8	52.5	26.6	12.9	3.5	5.5	0.6	7.2	2.7	0.6	0.4	0.4	-	-	11.1
			GII%	-	31.7	0.4	12.5	5.4	0.6	35.7	20.8	8.1	4.9	11.9	0.4	7.2	3.4	0.3	0.8	0.2	-	-	9.9
S. cabrilla	0.27	3.8	V%	0.0	0.6	-	1.2	2.0	0.1	19.0	42.7	5.4	-	13.8	-	6.3	0.2	8.8	-	-	-	-	-
			F%	0.4	5.1	-	5.1	21.7	1.3	31.5	63.8	3.4	-	4.7	-	8.1	0.4	9.8	-	-	-	-	-
			GII%	0.2	2.8	-	3.1	11.9	0.7	25.2	53.3	4.4	-	9.3	-	7.2	0.3	9.3	-	-	-	-	-
S. hepatus	0.18	3.6	V%	0.0	0.7	-	1.3	3.4	0.0	52.7	36.4	-	-	-	0.2	-	-	5.3	-	-	-	-	-
			F%	0.7	2.9	-	5.4	33.0	0.4	38.8	55.1	-	-	-	0.7	-	-	4.3	-	-	-	-	-
			GII%	0.4	1.8	-	3.4	18.2	0.2	45.7	45.7	-	-	-	0.4	-	-	4.8	-	-	-	-	-
S. maena	0.25	3.5	V%	2.0	12.6	1.1	6.9	53.3	3.3	16.6	1.0	3.2	-	-	-	-	-	-	-	-	-	-	-
			F%	12.7	4.5	2.0	11.1	83.6	4.9	8.2	1.6	2.0	-	-	-	-	-	-	-	-	-	-	-
			GII%	7.4	8.5	1.6	9.0	68.5	4.1	12.4	1.3	2.6	-	-	-	-	-	-	-	-	-	-	-
S. smaris	0.05	3	V%	90.4	5.7	-	0.2	2.8	-	0.9	-	-	-	-	-	-	-	-	-	-	-	-	-
			F%	92.3	11.0	-	2.2	5.5	-	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-
			GII%	91.3	8.4	-	1.2	4.1	-	1.0	-	-	-	-	-	-	-	-	-	-	-	-	-
S. cantharus	0.21	3.6	V%	0.0	0.7	2.8	41.4	1.5	40.2	0.4	2.7	3.9	-	6.4	-	-	-	-	-	-	-	-	-
			F%	0.7	6.6	9.9	61.2	21.1	36.2	3.9	3.3	4.6	-	3.9	-	-	-	-	-	-	-	-	-
			GII%	0.3	3.6	6.3	51.3	11.3	38.2	2.2	3.0	4.2	-	5.2	-	-	-	-	-	-	-	-	-

T. draco	0.35	4	V%	-	7.7	3.0	0.8	1.2	0.0	7.2	16.9	6.1	-	38.1	-	8.1	-	0.2	-	-	-	-	10.7
			F%	-	6.9	1.0	3.4	11.3	1.0	25.1	58.6	3.9	-	10.3	-	5.9	-	2.0	-	-	-	-	10.3
			GII%	-	7.3	2.0	2.1	6.3	0.5	16.2	37.8	5.0	-	24.2	-	7.0	-	1.1	-	-	-	-	10.5
T. mediterraneus	0.05	4.1	V%	0.4	10.2	0.1	0.3	4.4	0.0	1.9	0.6	0.5	-	79.5	-	-	0.4	1.2	-	-	0.5	-	-
			F%	13.4	72.6	1.8	4.9	49.4	0.6	12.2	7.3	0.6	-	30.5	-	-	0.6	5.5	-	-	0.6	-	-
			GII%	6.9	41.4	1.0	2.6	26.9	0.3	7.1	4.0	0.5	-	55.0	-	-	0.5	3.4	-	-	0.6	-	-
T. picturatus	0.17	3.5	V%	0.3	70.4	9.8	-	0.1	-	1.6	-	-	-	-	-	-	-	-	-	-	-	-	17.9
			F%	2.9	68.6	22.9	-	5.7	-	2.9	-	-	-	-	-	-	-	-	-	-	-	-	11.4
			GII%	1.6	69.5	16.3	-	2.9	-	2.2	-	-	-	-	-	-	-	-	-	-	-	-	14.6
T. trachurus	0.10	3.4	V%	4.2	68.1	0.4	-	0.4	-	-	0.4	0.4	-	-	0.0	0.7	-	0.3	-	-	-	-	25.1
			F%	15.0	71.4	2.3	-	11.3	-	-	2.3	2.3	-	-	0.8	0.8	-	3.0	-	-	-	-	12.8
			GII%	9.6	69.7	1.3	-	5.9	-	-	1.3	1.3	-	-	0.4	0.7	-	1.7	-	-	-	-	18.9
T. scabrus	0.08	3.6	V%	0.1	2.3	0.9	0.8	3.4	-	9.8	78.4	-	-	-	-	-	-	-	-	-	-	-	4.2
			F%	10.4	2.1	2.1	8.3	43.8	-	18.8	91.7	-	-	-	-	-	-	-	-	-	-	-	4.2
			GII%	5.3	2.2	1.5	4.6	23.6	-	14.3	85.0	-	-	-	-	-	-	-	-	-	-	-	4.2
T. lyra	0.25	3.6	V%	0.0	4.0	-	5.2	18.9	15.0	6.9	44.8	1.1	-	-	0.1	1.0	-	0.6	-	-	-	-	2.4
			F%	1.4	9.4	-	16.1	61.2	38.1	10.8	57.3	2.1	-	-	0.3	1.0	-	3.1	-	-	-	-	0.3
			GII%	0.7	6.7	-	10.6	40.1	26.6	8.8	51.1	1.6	-	-	0.2	1.0	-	1.9	-	-	-	-	1.4
T. minutus	0.10	3.6	V%	-	3.2	-	0.1	1.9	-	66.1	18.6	2.8	-	0.6	0.0	3.8	-	2.2	-	0.6	-	-	0.2
			F%	-	13.3	-	1.3	18.1	-	78.3	39.8	2.9	-	0.3	0.3	6.1	-	3.6	-	1.0	-	-	0.3
			GII%	-	8.2	-	0.7	10.0	-	72.2	29.2	2.9	-	0.5	0.2	5.0	-	2.9	-	0.8	-	-	0.3
U. scaber	0.39	4.4	V%	-	-	-	-	0.0	-	8.6	0.4	3.9	0.2	27.2	4.3	27.2	-	5.1	2.0	7.0	-	5.0	9.0
			F%	-	-	-	-	1.7	-	31.9	2.6	7.8	0.9	17.2	6.9	27.6	-	18.1	1.7	1.7	-	0.9	3.4
			GII%	-	-	-	-	0.9	-	20.3	1.5	5.8	0.5	22.2	5.6	27.4	-	11.6	1.8	4.4	-	2.9	6.2
Z. faber	0.26	4.6	V%	-	0.9	-	-	0.1	-	0.7	0.1	0.1	0.2	24.0	2.2	33.4	-	1.5	0.1	9.3	-	6.7	20.5
			F%	-	8.2	-	-	6.2	-	0.4	0.4	0.8	0.8	8.6	0.4	55.1	-	9.5	0.4	7.0	-	2.9	21.4
			GII%	-	4.6	-	-	3.1	-	0.6	0.3	0.5	0.5	16.3	1.3	44.3	-	5.5	0.3	8.2	-	4.8	21.0

Table A.4. Volumetric Index (V%), Frequency Index (F%), Geometric Index of Importance (GII%), Niche breadth (B_i) and Mean trophic level (MTL) estimated for the 61 species studied along the Spanish Western Mediterranean Sea. Dashes represent no consumption. Acronyms are referenced in Table 1.

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Ontogenetic shifts and feeding strategies of 7 key species of Gadiformes in the western Mediterranean Sea

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Abstract—The trophic ecology of 7 key species of Gadiformes, the silvery pout (*Gadiculus argenteus*), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*), European hake (*Merluccius merluccius*), blue whiting (*Micromesistius poutassou*), Mediterranean ling (*Molva macrophthalma*), greater forkbeard (*Phycis blennoides*), and poor cod (*Trisopterus minutus*), in the western Mediterranean Sea was explored. A total of 3192 fish stomachs were examined during 2011–2017 to investigate ontogenetic shifts in diet, trophic interactions (both interspecific and intraspecific), and feeding strategies. The results from applying multivariate statistical techniques indicate that all investigated species, except the Mediterranean bigeye rockling and poor cod, underwent ontogenetic dietary shifts, increasing their trophic level with size. The studied species hold different trophic positions, from opportunistic (e.g., the Mediterranean bigeye rockling, with a trophic level of 3.51) to highly specialized piscivore behavior (e.g., the Mediterranean ling, with a trophic level of 4.47). These insights reveal 4 different feeding strategies among the co-occurring species and size classes in the study area, as well as the degree of dietary overlap. Such information on ecological patterns within a fish assemblage, including species interactions, is often requested by those who aim to implement ecosystem management. Therefore, these findings can be used to improve management of sustainable fisheries in this region.

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One of the most important aspects of analysis of trophic interactions is the study of trophic levels, understood as a hierarchical way of classifying organisms according to their feeding relationships within an ecosystem, contributing to knowledge about the ecological role of a species (Cochran et al., 2019). This knowledge is critical in investigating predator–prey interactions and is necessary for an ecosystem-based approach to fisheries management (Christensen, 1996; García et al., 2003). Additionally, feeding patterns offer useful insights about the long-term stability of marine ecosystems (Trites, 2003; McDonald-Madden et al., 2016).

In general, fish change their diets with size to optimize their energetic return (Scharf et al., 2000; Juanes et al., 2002). In addition, ontogenetic shifts can be considered a mechanism to avoid, or at least minimize, intraspecific competition by allowing exploitation of different food resources at each developmental stage (Marrin, 1983; Castro and Hernández-García, 1995). More broadly, fish species have a wide range of strategies, on both intraspecific and interspecific levels, that result in and maintain resource partitioning (Madurell et al., 2008; Fanelli et al., 2009, 2013). Such strategies include not only food selection but also habitat selection and temporal segregation (Schoener, 1974). Hence, resource partitioning occurs when fish species are segregated into at least 1 of 3 niche dimensions. As a result, niche overlap is avoided and resource competition is minimized among fish species. This hypothesis is known as niche complementarity (Ebeling and Hixon, 1991) and assumes that a particular species, which overlaps with others in a given niche dimension, would separate along another dimension, maintaining resource partitioning. Describing and comparing these relationships, by using indices that reflect niche overlap or niche breadth, can help to explain feeding behaviors that range from generalist to specialist in nature (Silva et al., 2014).

This study aimed to investigate niche complementarity and co-occurrence of 7 fish species of Gadiformes in the western Mediterranean Sea off the coast of Spain. In particular, we analyzed ontogenetic shifts in diet, trophic interactions (both interspecific and intraspecific), feeding strategies, and the degree of dietary overlap among the studied species, to ascertain the ecological patterns of dietary interrelationships within the fish assemblage.

The selected gadiform species can inhabit depths greater than 1000 m (Fanelli et al., 2013) and play an important role in the middle of the food web (i.e., in both bottom-up and top-down controls) within marine ecosystems (Libralato et al., 2006), indicating that they feed on different trophic levels (Miller et al., 2010). They are prey for many other fish species (e.g., Preciado et al., 2008; Rodríguez-Cabello et al., 2014), and they occupy different substrates, ranging from sandy to rocky (Cohen et al., 1990).

In the Mediterranean Sea, the biology and behavior of many species of Gadiformes are well-documented (Morte et al., 2001, 2002), and they are important commercially and ecologically. For example, the European hake (*Merluccius merluccius*) is one of the most common representatives of this group, considering the amount of landings, and is currently experiencing overexploitation, with fishing mortality rates around 1.8–8.1 times higher than the assumed reference level of fishing mortality that would provide maximum sustainable yield (Colloca et al., 2013).

In the western Mediterranean Sea, studies of fish feeding habits usually focus on a few species and omit trophic interactions, information about which is essential for an effective implementation of an ecosystem approach to fisheries management (García et al., 2003). For instance, off the coast of Spain, Macpherson (1978a) studied age-related seasonal feeding habits of blue whiting (*Micromesistius poutassou*) in the Gulf of Valencia and of silvery pout (*Gadiculus argenteus*) in the Catalan Sea. He also investigated the diet of the Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) and Mediterranean ling (*Molva macrophthalma*) (Macpherson, 1978b, 1981). Bozzano et al. (1997) reported seasonal feeding habits of European hake in the Gulf of Lion off the coast of France, and Morte et al. (2001, 2002) analyzed the diet of poor cod (*Trisopterus minutus*) and greater forkbeard (*Phycis blennoides*) in the Gulf of Valencia. Unfortunately, none of these studies have investigated further interactions between species and fish assemblage.

Studies that address a broader geographic area and include ontogenetic shifts in diets of gadiform species, therefore, are scarce for the Mediterranean Sea off the coast of Spain, and it is necessary to fill this gap in knowledge as well as update current information. Additionally, the fish assemblage in the western Mediterranean Sea is currently facing problems of not only overfishing and biodiversity loss but also environmental pressures, such as the massive urbanization of coastlines, with increases in water pollution and decreases in sediments from principal rivers (e.g., Coll et al., 2010). Catch quality is decreasing, resulting in landings with a higher proportion of low-value species and a higher ratio of small to large fish. Furthermore, in the case of some of the most damaging and commonly used gear, namely bottom trawls, discard rates of low-value species are high (Bellido et al.[1]; Paradinas et al., 2016). Under this scenario of overfishing and environmental pressures, a declining trend in the landed biomass of the commercial species of Gadiformes investigated in our study has been observed in the area (MAGRAMA[2]; MAPAMA[3]; MAPA[4]). Consequently, more local and updated data on intraspecific and interspecific interactions are needed to develop ecosystem models for an ecosystem-based approach to fisheries management (Christensen and Walters, 2004; Gascuel, 2005).

Material and methods

Study area and sampling procedure

We carried out our study in the Mediterranean Sea off the coast of Spain from Cape Palos to Cape Creus (Fig. 1). According to the General Fisheries Commission for the Mediterranean, this area is also known as geographical subarea 06 (GSA-06), and it extends along 808 km of coastline, with a total area of 30,119 km^2 and depths of 40–800 m. The study area is characterized by high biodiversity (García-Rodríguez et al., 2011) and oligotrophic conditions. Nevertheless, within the study area, certain zones (e.g., Ebro Delta) are exceptions because of their moderate levels of primary production (Estrada, 1996). The main fishery resources in this area are demersal and benthic organisms, such as fish species (Osteichthyes and Chondrichthyes) and invertebrates (mollusks and crustaceans). Some of the fish species, such as the bogue (*Boops boops*) or blotched picarel (*Spicara maena*), are heavily discarded, or they are used as bait, although they are an increasing component of landings, mainly in the bottom-trawl fishery (Bellido et al.[1]). Most of these species, including the European hake and blue whiting, both of the order Gadiformes, are fully exploited or overexploited (Coll et al., 2008; Cardinale, 2012, 2013; Coll et al., 2014; FAO, 2018).

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[1] Bellido, J. M., A. Carbonell, M. T. García, and M. González. 2014. The obligation to land all catches—consequences for the Mediterranean: in-depth analysis, 46 p. Policy Dep. B: Struct. Cohes. Policies, Dir.-Gen. Intern. Policies, Eur. Parliam., Brussels, Belgium. [Available from website.]

[2] MAGRAMA (Ministerio de Agricultura, Alimentación y Medio Ambiente). 2013–2015. Estadísticas pesqueras: Noviembre [2013–2015]. Minist. Agric. Aliment. Medio Ambiente, Madrid, Spain. [Available from website.]

[3] MAPAMA (Ministerio de Agricultura y Pesca, Alimentación y Medio Ambiente). 2016–2017. Estadísticas pesqueras: Noviembre [2016–2017]. Minist. Agric. Pesca Aliment. Medio Ambiente, Madrid, Spain. [Available from website.]

[4] MAPA (Ministerio de Agricultura, Pesca y Alimentación). 2018–2020. Estadísticas pesqueras: Noviembre [2018–2020]. Minist. Agric. Pesca Aliment., Madrid, Spain. [Available from website.]

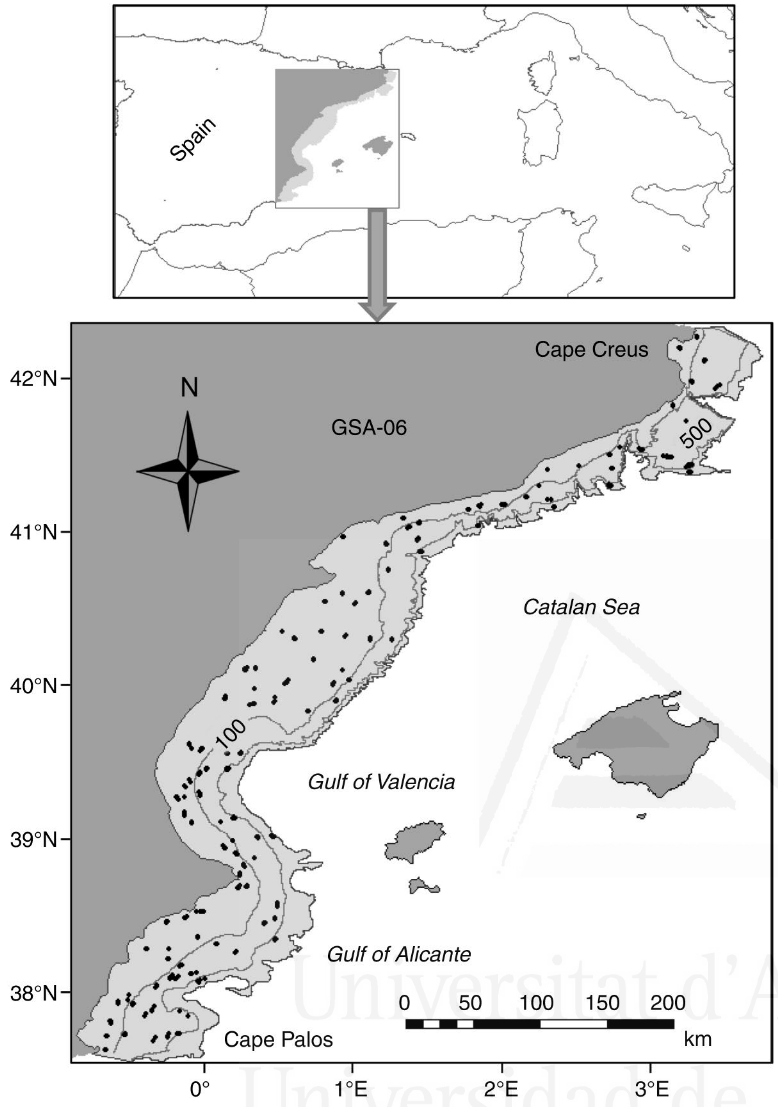

Figure 1

Map showing the locations where 7 species of Gadiformes were sampled between 2011 and 2017 in the Mediterranean Sea off the coast of Spain from Cape Palos to Cape Creus, in the geographical subarea 06 (GSA-06) defined by the General Fisheries Commission for the Mediterranean. Dots indicate the positions of the trawl tows conducted during surveys. The light gray shaded area indicates the area between isobaths of 40 and 800 m where specimens were caught.

Stomach samples were collected from fish caught during bottom-trawl surveys conducted as part of the Mediterranean International Trawl Survey (MEDITS) program in GSA-06 in 2011–2017 (Bertrand et al., 2002). The surveys of this program take place yearly from May through June for the purpose of evaluating the demersal resources throughout the study area. The standard MEDITS sampling gear is a bottom trawl called the GOC 73, which has a net with a mesh size of 40 mm and a codend with a mesh size of 20 mm. This gear is specifically designed for experimental fishing. A total of 604 trawl tows were carried out during daylight, from 0800 to 1800, at depths of 40–730 m.

For this investigation, we selected the species of the order Gadiformes that were most abundant in the study area: the silvery pout, Mediterranean bigeye rockling, Mediterranean ling, European hake, blue whiting, greater forkbeard, and poor cod. During the survey cruises in the study period, the contents of 3192 stomachs were analyzed on board vessels (for details for these 7 species, see Table 1). After each trawl tow, 10 individuals of each of the studied species were randomly sampled from the haul. For all specimens examined, total length (TL) in millimeters, sex, and maturity stage were recorded according to MEDITS guidelines (Bertrand et al., 2002). Later, diet was assessed quantitatively by measuring the volume of stomach contents with a trophometer, a calibrated device that consists of several semicylinders of different sizes (Olaso, 1990). The use of this instrument is helpful on board oceanographic vessels because it allows a large number of stomachs to be examined in a relatively short period.

Once a stomach was opened, its contents were analyzed under a binocular microscope (Leica MZ6[5], Leica Microsystems, Wetzlar, Germany). Prey found in stomachs (prey items) were identified to the lowest possible taxon by using published guides (Zariquiey, 1968; Lombarte et al., 2006) and our own reference collection. The degrees of digestion of all prey items identified were also noted, as fresh, partially digested, or fully digested. The stomachs that contained any items presumably consumed in the net during fishing operations (i.e., stomachs from individuals of anglerfish species) were excluded from the analyses. The presence of skeletal remains and other hard body parts was also recorded. Stomach samples from specimens that had regurgitated the contents of their stomachs were replaced with samples from individuals of a similar size class (García-Rodríguez et al., 2020). Following Robb (1992), the color and size of the gall bladder of European hake were used to determine if a specimen had an empty stomach or had regurgitated during the fishing operation.

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[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Summary information related to the 7 most abundant species of Gadiformes sampled in the western Mediterranean Sea between 2011 and 2017. For each species, the scientific and common names, depth range (in meters), number of stomachs for which contents were examined, and size range (total lengths in millimeters) are provided.

Scientific name	Common name	Depth range	No. of stomachs	Size range
Gadiculus argenteus	Silvery pout	109–647	263	60–133
Gaidropsarus biscayensis	Mediterranean bigeye rockling	59–634	116	40–180
Molva macrophthalma	Mediterranean ling	86–634	164	83–740
Merluccius merluccius	European hake	34–722	1254	87–549
Micromesistius poutassou	Blue whiting	76–722	786	89–377
Phycis blennoides	Greater forkbeard	53–728	286	85–393
Trisopterus minutus	Poor cod	36–352	323	78–272

Dietary indices

Three conventional dietary indices were calculated to provide quantitative information on diet compositions of the gadiform species investigated. A raw data set including prey species for each predator species is included in Supplementary Table 1. The first index used was frequency of occurrence (%FO), defined as the number of stomachs containing a prey item compared with the total number of stomachs examined. The second index was the number index (%N), defined as the number of individuals of a prey item compared with the total number of individual prey ingested. The third index calculated was the volume index (%V), which represents the volume of a prey item compared with the total volume of ingested prey (Hyslop, 1980). Finally, the geometric index of importance (%GII), which incorporates both %FO and %V, was used to avoid redundancy in the combination of mathematically dependent measures instead of other traditional indices (Tirasin and Jørgensen, 1999). It was computed as follows (Assis, 1996):

$$\%GII_j = \left(\sum_{i=1}^{n} V_i\right)_j / n, \tag{1}$$

where V_i = the value of the ith relative measure of prey quantity for the prey group j (in this case, $V_i = \%FO + \%V$), and

n = the number of the relative measures of prey quantity used in the analysis (in this case, $n=2$, %FO and %V).

Therefore, in this study, the %GII was calculated as $(\%V+\%FO)/2$. Values for all indices are given as percentages.

Ontogenetic shifts in diet

Before identifying when ontogenetic shifts occur and establishing trophic groups based on different size classes, 10 major prey groups were identified according to taxonomic criteria and, in the case of fish species, habitat type criteria: small plankton; large plankton; Polychaeta; Cephalopoda; crab, lobster, and mantis shrimp species; shrimp species; Peracarida; demersal fish species; pelagic fish species; and benthopelagic fish species.

To investigate variation in a predator's diet according to size, trends in the volume index values of the most representative prey groups, mentioned in the previous paragraph, were plotted against fish length of predators to define the different categories that combine species and size class. We first compared both quantitative and qualitative methods. Results indicate similar outcomes for some species, such as the European hake or blue whiting, and outcomes were less realistic for those species with a small number of samples. Therefore, we decided to use a qualitative method based on a graphic technique that allows easy identification of the size at which the trend in the trophic strategy changed for each species studied. In the quantitative method, the number of size classes was estimated following the Sturges procedure (Scherrer, 1984), and in the qualitative method, the lengths were represented continuously at every millimeter along the x-axis of graphs.

This graphic technique allows qualitative identification of the size at which a trophic shift occurred. We used this size for each gadiform species studied to divide size classes into *large* and *small* categories (sizes varied depending on the species; Table 2). In addition, size at first maturity was plotted with the aim of linking it with the size at which a trophic shift occurred. Sizes at first maturity for all the studied species were based on previously published data from studies in nearby areas (Biagi et al., 1992; Benghali et al., 2014; European Parliament and Council, 2019; Ismen et al., 2019).

Trophic indices to describe feeding strategies

To describe the degree of dietary diversity of a given species, we used niche breadth in accordance with Levins's

Table 2

Dietary indices for each prey group identified in the stomach contents of specimens of 7 species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. The number of trawl tows, sample size, range of total lengths (TLs), niche breadth, depth range, trophic level, and number of prey items also are provided for each of the 12 categories that combine species and size class (small [S] and large [L]). The dietary indices used in analyses include frequency of occurrence (%FO), the number of stomachs that contained a prey group compared with the total number of stomachs examined; the number index (%N), the number of individuals of a prey group compared with the total number of ingested prey; the volume index (%V), the volume of a prey group compared with the total volume of all prey ingested by a predator category; and the geometric index of importance (%GII), which incorporates both %FO and %V. A dash indicates that no consumption of that prey group was recorded for that species. The species studied include the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI).

Information type or prey group	Index	GAD_S	GAD_L	GAI	MOL_S	MOL_L	MER_S	MER_L	MIC_S	MIC_L	PHY_S	PHY_L	TRI
No. of trawl tows		16	29	45	26	20	90	154	25	36	13	56	45
Sample size		44	219	116	107	57	405	849	172	614	75	211	323
Length range (mm)		60–92	93–133	40–180	83–165	166–740	87–149	150–549	89–169	170–377	85–149	150–393	78–272
Niche breadth		0.51	0.39	0.34	0.14	0.30	0.60	0.45	0.24	0.28	0.64	0.17	0.14
Depth range (m)		109–647	131–647	59–634	122–327	86–634	34–342	34–722	76–611	137–722	53–728	176–728	36–352
Trophic level		3.47	3.57	3.93	4.36	4.49	3.95	4.24	3.98	4.21	3.99	3.99	3.94
No. of prey items		9	33	27	8	13	47	65	28	38	25	58	43
Small plankton	%FO	18.8	11.9	17.7	–	–	–	–	–	–	1.5	1.0	–
	%V	14.3	5.4	3.0	–	–	–	–	–	–	0.0	0.0	–
	%N	79.9	60.7	30.2	–	–	–	–	–	–	0.4	0.2	–
	%GII	16.5	8.7	10.3	–	–	–	–	–	–	0.7	0.5	–
Large plankton	%FO	46.9	51.5	7.8	2.6	4.6	40.6	19.4	87.28	46.8	13.0	13.6	9.9
	%V	48.8	47.2	1.6	0.1	1.5	29.0	8.1	59.9	26.5	11.6	4.4	2.7
	%N	10.8	29.6	4.0	2.2	5.5	83.1	69.0	98.1	58.3	13.2	8.4	11.9
	%GII	47.8	49.4	4.7	1.3	3.0	34.8	13.8	73.5	36.7	12.3	9.0	6.3
Polychaeta	%FO	–	0.5	1.0	–	–	–	–	–	0.2	8.7	1.9	1.2
	%V	–	0.3	1.8	–	–	–	–	–	2.8	2.6	0.1	0.4
	%N	–	0.0	0.4	–	–	–	–	–	0.0	2.1	0.6	0.5
	%GII	–	0.4	1.4	–	–	–	–	–	1.5	5.7	1.0	0.8
Cephalopoda	%FO	–	–	–	–	–	2.0	3.3	–	2.7	–	1.9	2.8
	%V	–	–	–	–	–	2.3	3.7	–	1.2	–	1.1	2.8
	%N	–	–	–	–	–	0.3	0.9	–	0.5	–	0.4	1.0
	%GII	–	–	–	–	–	2.1	3.5	–	2.0	–	1.5	2.8

(*Continued on next page*)

Table 2 (*Continued*)

Information type or prey group	Index	GAD_S	GAD_L	GAI	MOL_S	MOL_L	MER_S	MER_L	MIC_S	MIC_L	PHY_S	PHY_L	TRI
Crab, lobster, and mantis shrimp species	%FO	–	0.5	38.2	–	–	1.7	1.6	–	0.5	52.2	54.4	33.4
	%V	–	0.2	51.5	–	–	1.5	1.1	–	0.1	35.4	23.3	19.2
	%N	–	0.0	17.4	–	–	0.3	0.5	–	0.1	22.5	22.1	21.9
	%GII	–	0.3	44.9	–	–	1.6	1.4	–	0.3	43.8	38.9	26.3
Shrimp species	%FO	3.1	9.4	18.6	–	6.8	25.5	25.0	1.7	27.5	18.8	82.5	65.9
	%V	2.1	16.0	12.8	–	4.7	20.3	16.8	2.4	18.9	18.2	63.8	65.5
	%N	0.3	1.1	8.5	–	13.7	6.5	8.6	0.1	10.4	7.5	51.0	51.4
	%GII	2.6	12.7	15.7	–	5.7	22.9	20.9	2.0	23.2	18.5	73.2	65.7
Peracarida	%FO	21.9	18.8	37.3	3.9	4.5	12.4	3.1	1.7	1.8	55.1	22.8	14.2
	%V	24.6	12.0	17.5	0.1	0.4	3.4	1.1	0.3	1.2	32.1	1.4	3.8
	%N	5.0	4.0	36.4	3.3	17.8	4.0	1.2	0.2	0.5	54.3	12.4	9.1
	%GII	23.2	15.4	27.4	2.0	2.5	7.9	2.1	1.0	1.5	43.6	12.1	9.0
Demersal fish species	%FO	–	–	7.8	16.9	31.8	15.8	6.9	3.4	0.2	–	17.5	6.2
	%V	–	–	11.9	17.3	38.0	16.0	4.8	0.6	2.1	–	4.7	3.9
	%N	–	–	3.1	27.2	27.4	2.7	2.0	0.2	0.0	–	4.3	3.2
	%GII	–	–	9.9	17.1	34.9	15.9	5.8	2.0	1.2	–	11.1	5.1
Pelagic fish species	%FO	–	–	–	–	–	10.4	42.1	1.7	0.7	–	–	0.3
	%V	–	–	–	–	–	14.5	44.4	7.1	2.2	–	–	0.7
	%N	–	–	–	–	–	1.6	12.2	0.2	0.2	–	–	0.2
	%GII	–	–	–	–	–	12.5	43.2	4.4	1.5	–	–	0.5
Benthopelagic fish species	%FO	9.4	13.9	–	41.6	43.2	9.7	18.9	15.4	64.8	–	3.9	1.2
	%V	10.2	18.8	–	82.5	55.4	13.0	19.9	29.8	45.0	–	1.3	1.0
	%N	4.0	4.4	–	67.4	35.6	1.5	5.6	1.2	29.9	–	0.8	0.7
	%GII	9.8	16.3	–	62.0	49.3	11.4	19.4	22.6	54.9	–	2.6	1.1

standardized index (Levins, 1968). This index ranges from 0 to 1, with values close to 0 indicating a specialized diet and those close to 1 indicating more generalized feeding habits. This index was computed as follows:

$$B_{\mathrm{i}} = \frac{1}{\mathrm{N}-1} \times \frac{1}{\sum_{\mathrm{j}} p_{\mathrm{ij}}^{2} - 1}, \tag{2}$$

where B_{i} = Levins's standardized index;
p_{ij} = the proportion of prey j in the diet of predator i; and
N = the total number of prey groups.

The trophic niche overlap among the different studied species was estimated by using the simplified Morisita index (Morisita, 1959), which compares pairs of species with values ranging between 0.00 (no prey overlap) to 1.00 (full prey overlap) as follows:

$$C_{\mathrm{jk}} = \frac{2\sum p_{\mathrm{ij}} p_{\mathrm{jk}}}{\sum p_{\mathrm{ij}}^{2} + \sum p_{\mathrm{ik}}^{2}}, \tag{3}$$

where C_{ik} = the simplified Morisita index for predators i and k, and
p_{ij} and p_{kj} = the proportions of predators i and k with prey j in their stomachs.

The trophic level (T) was calculated by using the following formula developed by Christensen and Pauly (1992):

$$T = 1 + (\Sigma\, DC_{\mathrm{ij}})(NT_{\mathrm{j}}), \tag{4}$$

where DC_{ij} = the proportion of prey j in the diet of the predator i, and
NT_{j} = the trophic level of prey j.

Trophic levels of prey were determined empirically by using local information or, when this information was not available, by using the modeled area (Cortés, 1999; Ebert and Bizzarro, 2007; Fanelli et al., 2011; Jacobsen and Bennett, 2013; Corrales et al., 2015; for details on the species of prey for which these cited references were sources of local information on trophic levels, see Supplementary Table 2). In this study, the trophic level of each of the defined categories based on species and size class was first calculated by weighting its average biomass obtained during the surveys of the MEDITS program conducted in 2011–2017.

Co-occurrence measures

To analyze patterns of species associations related to food resource partitioning, we studied interspecific and intraspecific co-occurrence. Therefore, for the entire study period, we accounted for the abundance of all species and size classes estimated during surveys. The abundance of Mediterranean bigeye rockling was underestimated because of the low selectivity of the gear used to catch this small species. Therefore, this species was not included in the co-occurrence analysis. The Jaccard index (S_{ij}) was used to measure co-occurrence, as an expression of association between species (Jaccard, 1901):

$$S_{\mathrm{ij}} = a\,/\,(a + b + c), \tag{5}$$

where a = the number of occasions in which both species or size classes are present;
b = the number of occasions in which only one of the species is present; and
c = the number of occasions in which only the other species is present.

This index was calculated as the percentage of occasions that both species or size classes appeared in the same haul. In this study, the only hauls that were considered were those in which at least one of the species or size classes of each pair was present.

Statistical analyses

All data were standardized by using square-root transformation, and a Bray–Curtis similarity matrix was calculated. One-way analyses of similarity were performed to identify significant differences ($P<0.05$) in trophic strategies between pairs of size classes (i.e., intraspecific competition). We used the software PRIMER 6 (PRIMER-e, Quest Research Ltd., Aukland, New Zealand) (Clarke and Gorley, 2006) to estimate global R as a scaled measure of the separation between groups of samples, with values ranging from 0 (no differences) to 1 (completely different) (Clarke, 1993).

Similarity percentage analysis was applied to determine which prey groups contributed most to the dissimilarity in diet composition between such pairs. According to these results, new species-and-size categories were considered for further analyses. Finally, clustering methods and multidimensional scaling were used to analyze prey affinities and to discern feeding strategies that possibly were different between the studied species among size classes. All calculations were done by using PRIMER 6.

Results

Diet composition and ontogenetic variation

Overall, for all studied species as a group, the most common prey groups in terms of %V were large plankton; crab, lobster, and mantis shrimp species; shrimp species; and benthopelagic fish species. Large plankton, represented mainly by euphausiids, was the most common prey (mostly for silvery pout and blue whiting). In the case of decapod species, the red snapping shrimp (*Alpheus glaber*), green shrimp (*Chlorotocus crassicornis*), and angular crab (*Goneplax rhomboides*), all members of Pleocyemata, were the most abundant prey (mostly for Mediterranean bigeye rockling, poor cod, and greater forkbeard). Finally, benthopelagic fish species were primarily represented by blue whiting and myctophids as prey for studied species (mostly for Mediterranean ling and blue whiting) (Table 3). The raw data set

Table 3

Volume index (%V) values for prey groups identified in the stomach contents of specimens of 7 key species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. The %V value for a prey group represents the volume of that prey item compared with the total volume of all prey ingested by specimens of that species. The 7 species are the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI). A dash indicates that no consumption of that prey group was recorded for that species. An asterisk indicates the prey group with the highest %V value for each species. Information on niche breadth and the number of prey items is also reported.

	%V						
Information type	GAD	GAI	MOL	MER	MIC	PHY	TRI
Niche breadth	0.34	0.34	0.17	0.38	0.26	0.16	0.14
No. of prey items	33	27	15	74	49	60	43
Prey group							
Small plankton	6.2	3.0	–	0.0	–	0.0	–
Large plankton	51.6*	1.6	0.9	12.0	40.3*	4.9	2.7
Polychaeta	0.3	1.8	–	–	1.9	0.4	0.4
Cephalopoda	–	–	–	3.7	0.8	1.0	2.8
Crab, lobster, and mantis shrimp species	0.1	51.5*	–	0.8	0.1	24.4	19.2
Shrimp species	12.4	12.8	2.5	14.4	13.2	60.6*	65.5*
Peracarida	11.1	17.5	0.3	1.0	0.9	2.8	3.8
Demersal fish species	–	11.9	22.6	6.6	1.7	4.3	3.9
Pelagic fish species	–	–	–	40.8*	3.6	–	0.7
Benthopelagic fish species	18.3	–	73.8*	20.6	37.4	1.6	1.0

provided in Supplementary Table 1 documents in detail the different prey items found in stomachs and identified to the lowest taxonomic level in this study.

Regarding the ontogenetic variation in diet, for each of the studied species, the graph indicates trends in trophic strategies for 2 prey groups that were the opposite of the other, and this observation of different trends enabled us to establish a cutoff between the 2 size classes: the size at which a trophic shift occurred (Fig. 2). Only in the case of the silvery pout did the selected cutoff between size classes seem to be related to size at first maturity. For the Mediterranean bigeye rockling, no data are available on size at first maturity in the study area.

The results obtained for species and size classes indicate that silvery pout fed mainly on large plankton (%GII=51.2%, %V=51.6%, %FO=50.9%), with *Euphausia krohnii* as the most predominant prey species. The diet of Mediterranean bigeye rockling was based primarily on crab, lobster, and mantis shrimp species (%GII=44.9%, %V=51.5%, %FO=38.2%) and species of Peracarida (%GII=27.4%, %V=17.5%, %FO=37.3%), represented mainly by *Calocaris macandreae* and *Lophogaster typicus*, respectively. Benthopelagic fish species (%GII=57.0%, %V=73.8%, %FO=40.2%) composed the major prey group for Mediterranean ling, for which the most commonly consumed prey was another species of Gadiformes, the silvery pout. Pelagic fish species (%GII=29.0%, %V=40.8%, %FO=17.2%) and large plankton (%GII=15.1%, %V=12.0%, %FO=18.3%) were the main prey groups for European hake, with European anchovy (*Engraulis encrasicolus*) and euphausiids being the most important of the consumed prey, respectively. Blue whiting fed mainly on large plankton (%GII=39.3%, %V=40.3%, %FO=38.3%) and benthopelagic fish species (%GII=36.5%, %V=37.4%, %FO=35.6%), of which euphausiids and the myctophid horned lanternfish (*Ceratoscopelus maderensis*) were the main prey, respectively. Similar prey items were also found in the diet of both greater forkbeard and poor cod: prey species were primarily shrimp species (%GII=61.8%, %V=60.6%, and %FO=62.9% and %GII=65.7%, %V=65.5%, and %FO=65.6%, respectively), with red snapping shrimp as the most-represented prey.

Results of the one-way analyses of similarity indicate that there were significant differences in trophic composition between size classes ($P \leq 0.05$) for all species studied except for the Mediterranean bigeye rockling and poor cod (Suppl. Table 3). Moreover, results of the similarity percentage analysis for the 5 species that had ontogenetic shifts identify the contribution of each prey item to the mean Bray–Curtis dissimilarity for each species. The average dissimilarity between size classes ranged from 41% for Mediterranean ling to 75% for European hake. These differences were a result of the distinct contribution of major prey groups to the stomach contents in specimens examined for each species (Suppl. Table 4). The major prey groups contributing the most to the ontogenetic shifts in the diet of silvery pout were large plankton and Peracarida, and for Mediterranean ling, the major prey groups were teleosts, such as demersal and benthopelagic fish species. Pelagic fish, large plankton, and shrimp species

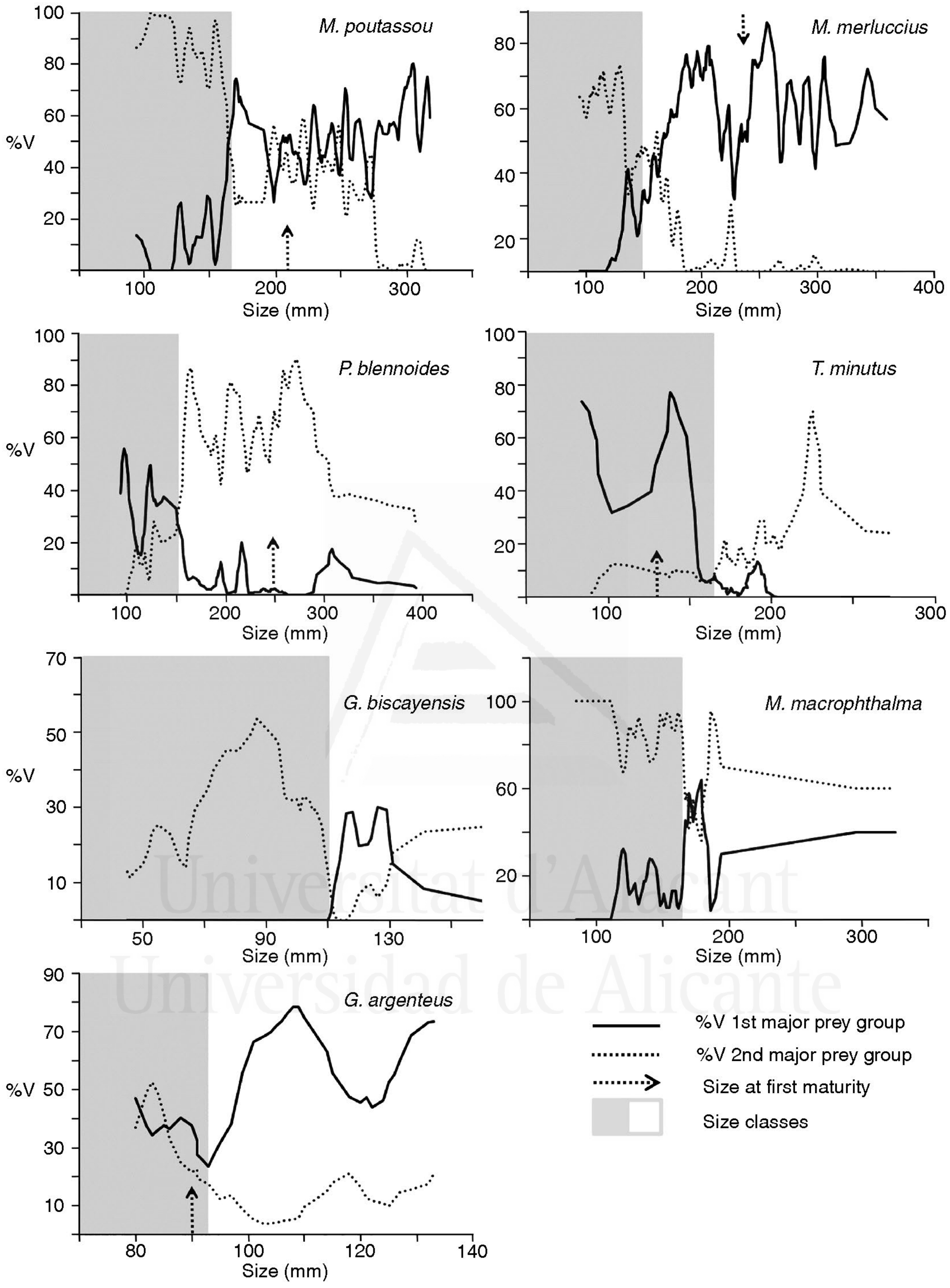

Figure 2

Trends in volume index (%V) values for the first and second major prey groups in relation to sizes of specimens of 7 species of Gadiformes caught in the western Mediterranean Sea during 2011–2017. These graphs were used in a qualitative method to identify the size at which the trophic strategy changed for each species studied. This size is considered the cutoff between small (gray shaded area) and large size classes for each species. Sizes are given as total lengths. Arrows indicate the size at first maturity for each species, except for the Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) and Mediterrenean ling (*Molva macrophtalma*) because this information was not available for these species. The other species studied include the blue whiting (*Micromesistius poutassou*), European hake (*Merluccius merluccius*), greater forkbeard (*Phycis blennoides*), poor cod (*Trisopterus minutus*), and silvery pout (*Gadiculus argenteus*).

accounted for more than 60% of the diet of European hake. Species of large plankton and benthopelagic fish species contributed most to the diet of blue whiting (accounting for approximately 34% and 32% of the diet of this species, respectively); greater forkbeard fed mainly on shrimp species and species of Peracarida (Suppl. Table 4).

Trophic ecology

The trophic niche breadth index (B_i) was highest for European hake, Mediterrean bigeye rockling, and silvery pout (Table 3). Conversely, poor cod had the lowest B_i value, with a strong preference for red snapping shrimp (%V=44.1%), despite the high number of prey items (52) identified in its diet.

Niche breadth across the 12 categories that are based on species and size class was lowest (B_i=0.136) for the small size class of Mediterranean ling; whereas, the small size class of greater forkbeard ranked the highest (B_i=0.636).

Simplified Morisita index values ranged from 0.00 (pair of the small size class of Mediterranean ling and –the small size class of greater forkbeard) to 1.00 (pair of the large size class of greater forkbeard and poor cod) (Table 4). Overall, niche overlap was highest between the small size class of greater forkbeard and poor cod, whose diet had a high proportion of shrimp species, represented principally by red snapping shrimp. The lowest values were found between the small size class of Mediterranean ling and poor cod as well as greater forkbeard.

The lowest and highest trophic levels were inferred for silvery pout (trophic level=3.51) and the large size class of Mediterranean ling (trophic level=4.49), respectively. Within this range, only Mediterranean ling and the large size classes of European hake and blue whiting were determined to be at a trophic level ≥4, representative of top predators (Table 2). For all species, with the exception of the greater forkbeard, which had no changes in trophic level with size, the large size classes were at a higher trophic level. The greatest increases in trophic level linked to an ontogenetic shift occurred in European hake (from 3.95 to 4.24) and blue whiting (from 3.98 to 4.21).

Feeding strategies

Four groups of predators were identified on the basis of different feeding strategies (Fig. 3). The first group consisted of species with strong preferences for decapods, such as the Mediterranean bigeye rockling, poor cod, and greater forkbeard. The red snapping shrimp was the dominant prey species for the large size class of greater forkbeard (%V=35.3%) and for poor cod (%V=44.1%), and *Calocaris macandreae* (%V=32.0%) and angular crab (%V=15.6%) were the main prey species for Mediterranean bigeye rockling and the small size class of greater forkbeard. The second group was composed of both size classes of Mediterranean ling, with silvery pout as the dominant prey (with %V values of 52.4% and 24.3% for the small and large size classes, respectively).

The third group identified was composed of both size classes of silvery pout, which had a high preference for large plankton, although in the case of small silvery pout, species of Peracarida were also consumed. In both size classes, euphausiids were the most common prey item (with %V values of 46.8% and 36.8% for the small and large size classes, respectively).

Table 4

Simplified Morisita index values, which indicate trophic niche overlap between pairs of 12 categories of gadiform species for which stomach contents from specimens caught in the western Mediterranean Sea from 2011 through 2017 were examined. Categories combine species and size class (small [S] and large [L]; length ranges for size classes are provided in Table 2). Asterisks indicate extreme index values, defined as those ≥0.9 and <0.1. The species studied were the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), Mediterrenean ling (*Molva macrophtalma*) (MOL), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI).

Category	$\mathrm{GAD_S}$	$\mathrm{GAD_L}$	GAI	$\mathrm{MOL_S}$	$\mathrm{MOL_L}$	$\mathrm{MER_S}$	$\mathrm{MER_L}$	$\mathrm{MIC_S}$	$\mathrm{MIC_L}$	$\mathrm{PHY_S}$	$\mathrm{PHY_L}$	TRI
$\mathrm{GAD_S}$	1.00											
$\mathrm{GAD_L}$	0.92*	1.00										
GAI	0.18	0.17	1.00									
$\mathrm{MOL_S}$	0.16	0.31	0.04*	1.00								
$\mathrm{MOL_L}$	0.17	0.31	0.13	0.90*	1.00							
$\mathrm{MER_S}$	0.64	0.80	0.24	0.30	0.46	1.00						
$\mathrm{MER_L}$	0.22	0.36	0.12	0.35	0.38	0.67	1.00					
$\mathrm{MIC_S}$	0.83	0.91*	0.04*	0.42	0.39	0.71	0.39	1.00				
$\mathrm{MIC_L}$	0.57	0.79	0.11	0.73	0.71	0.72	0.53	0.78	1.00			
$\mathrm{PHY_S}$	0.46	0.43	0.88	0.00*	0.03*	0.37	0.17	0.21	0.24	1.00		
$\mathrm{PHY_L}$	0.10	0.33	0.53	0.03*	0.12	0.47	0.32	0.10	0.36	0.56	1.00	
TRI	0.09*	0.32	0.49	0.03*	0.11	0.47	0.33	0.08*	0.35	0.54	1.00*	1.00

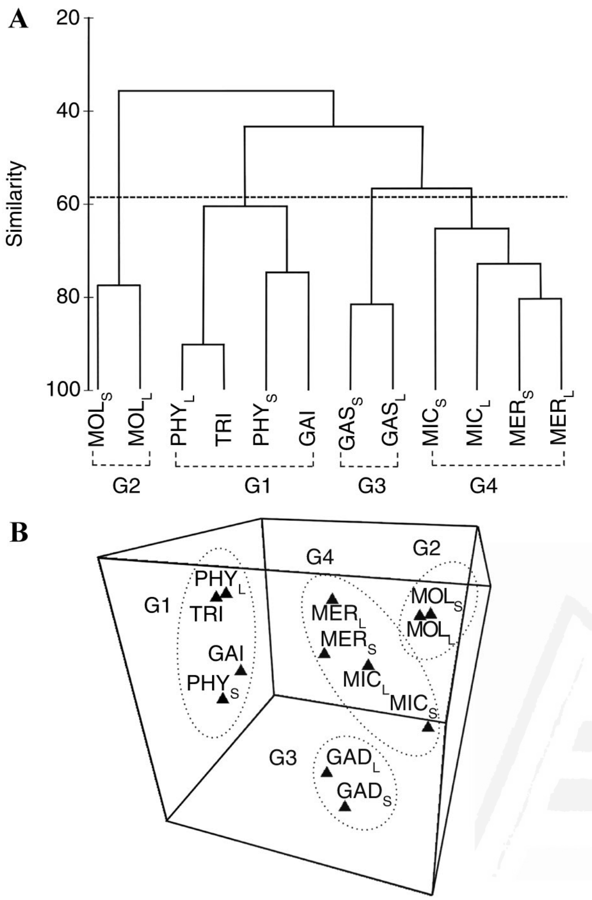

Figure 3

Multidimensional scaling ordination of stomach contents of specimens of 7 species of Gadiformes caught in the western Mediterranean Sea from 2011 through 2017. In the (**A**) 2-dimensional and (**B**) 3-dimensional plots, dashed lines indicate or dotted lines surround predator groups (G1, G2, G3, and G4) identified by using cluster analysis based on feeding strategies. Results are given for 12 categories that combine species and size class (small [S] and large [L]; length ranges for size classes are provided in Table 2). The horizontal dashed line in panel A indicates the threshold similarity for group selection. The species studied include the Mediterrenean ling (*Molva macrophtalma*) (MOL), greater forkbeard (*Phycis blennoides*) (PHY), poor cod (*Trisopterus minutus*) (TRI), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), silvery pout (*Gadiculus argenteus*) (GAD), blue whiting (*Micromesistius poutassou*) (MIC), and European hake (*Merluccius merluccius*) (MER).

The last group was represented by both size classes of blue whiting and European hake. The small size classes of both of these species preyed mostly on large plankton, with euphausiids as the most prevalent prey (with %V values of 51.3% and 24.3%, respectively). Benthopelagic fish species, namely the horned lanternfish (%V=19.3%) and the jewel lanternfish (*Lampanyctus crocodilus*) (%V=17.9%), were the main prey for the large size class of blue whiting. Pelagic fish species, such as the European anchovy (*Engraulis encrasicolus*) (%V=30.3%) and European pilchard (*Sardina pilchardus*) (%V=9.9%), were the species most widely consumed by the large size class of European hake.

Co-occurrence and trophic overlap

The highest percentages of co-occurrence were found for the associations of European hake with poor cod (75.8%) and blue whiting with greater forkbeard (64.1%) (Fig. 4). Conversely, the lowest values of co-occurrence were observed for Mediterranean ling with poor cod (11.3%) and European hake with Mediterranean ling (14.1%). These results, together with analysis of trophic levels, indicate a high niche overlap between silvery pout and blue whiting and a low degree of overlap between Mediterranean ling and poor cod.

All species had an intraspecific trophic overlap greater than 0.50. Greater forkbeard had the lowest value (0.56), and silvery pout had the highest value (0.92). On the other hand, low co-occurrence was found for both blue whiting and Mediterranean ling (0.16 and 0.20, respectively), and high values of co-occurrence were found for European hake, greater forkbeard, and silvery pout (0.77, 0.69, and 0.68, respectively).

Discussion

Our comprehensive study of feeding habits and trophic relationships among 7 fish species of the order Gadiformes that are important to fisheries in the western Mediterranean Sea explored ecological patterns such as those of ontogenetic variation in diet or trophic and spatial segregation of species. The results of this work can inform efforts to improve management of resource partitioning within and among these species in a broad geographic area (i.e., the entire GSA-06).

Our data indicate that the species studied are structured into 4 major guilds based on their feeding habits. The first group comprises the Mediterranean bigeye rockling, poor cod, and greater forkbeard. These species occupy medium-high positions within the food web. Their diets have previously been reported to consist of decapods and other small crustaceans, for example, for poor cod or greater forkbeard in the Catalan Sea (Macpherson, 1978b), in the Gulf of Valencia (Morte et al., 2001, 2002), and in the Adriatic Sea (Dulčić and Dulčić, 2004). However, for Mediterranean bigeye rockling, our results differ from those of Macpherson (1978b), who identified *Eusergestes arcticus* and northern krill (*Meganyctiphanes norvegica*) as the predominant prey. Our results indicate that *Calocaris macandrae* was the primary prey species of Mediterranean bigeye rockling, and it is worth noting that this species was also found to be cannibalistic. These differences may be related to the 38-year gap between the 2 studies or are possibly a result of the fact that our sampling did not explore seasonal dietary

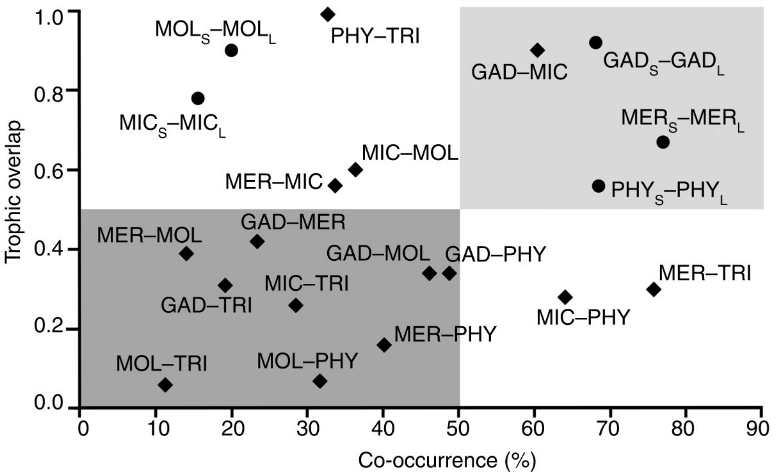

Figure 4

Level of trophic overlap and percentage of co-occurrence for pairs of 12 categories of 7 gadiform species for which stomach contents from specimens caught in the western Mediterranean Sea during 2011–2017 were examined. The 12 categories combine species and size class (small [S] and large [L]; length ranges for size classes are provided in Table 2). Diamonds and circles indicate interspecific and intraspecific interactions, respectively. Pairs in the dark gray area had low niche overlap, and pairs in the light gray area had high niche overlap. The species studied include the silvery pout (*Gadiculus argenteus*) (GAD), Mediterranean bigeye rockling (*Gaidropsarus biscayensis*) (GAI), European hake (*Merluccius merluccius*) (MER), blue whiting (*Micromesistius poutassou*) (MIC), Mediterrenean ling (*Molva macrophtalma*) (MOL), greater forkbeard (*Phycis blennoides*) (PHY), and poor cod (*Trisopterus minutus*) (TRI).

changes; we restricted our study to the spring, when the MEDITS is carried out. This high degree of predation on decapod crustaceans by greater forkbeard and poor cod is indicative of a narrow trophic niche breadth compared with that of the Mediterranean bigeye rockling, which was found to have more generalist feeding habits. Moreover, and in agreement with results reported by Morte et al. (2002), an ontogenetic shift occurred in the diet of greater forkbeard in our study, but our findings differ from those of Morte et al. (2001) for poor cod in that no ontogenetic dietary shift was found.

The second group consists of both size classes of Mediterranean ling, and this species had the highest trophic levels among the 7 species studied. The diet of this species is primarily composed of benthopelagic and demersal fishes, such as the silvery pout and poor cod. This evidence indicates that the Mediterranean ling occupies a narrow trophic niche, a finding that is in agreement with the results previously reported by Macpherson (1981) for the same study area.

A third trophically distinct group is composed of both size classes of silvery pout, which is the only species primarily exploiting resources at the base of the food web, playing an important role in the energy flow from the lowest levels to the top of the food web. The majority of the diet of the silvery pout consists of a variety of small crustaceans, such as euphausiids and shrimp species, confirming the feeding habit observations previously reported by Macpherson (1978a) for silvery pout in the western Mediterranean. Therefore, these results indicate that the silvery pout consumes a broad range of prey items, a diet characteristic of a generalist feeder. We also found ontogenetic variation for this species, with it becoming a more specialized predator as its trophic level increased. This result contrasts with the findings reported by Macpherson (1978a), who observed no clear link between diet and size for the silvery pout.

The last of the 4 feeding guilds we identified is represented by both size classes of European hake and blue whiting, which occupy a position high in the food web. As has been observed for Mediterranean ling, both the European hake and blue whiting seem to be primarily piscivorous, although their diets in addition include shrimp species (*Pasiphaea* spp.) and large plankton, particularly euphausiids (e.g., northern krill). For European hake, our findings are consistent with those of other studies from the western Mediterranean Sea (Bozzano et al., 1997; Cartes et al., 2009). However, slight differences were found when comparing the diets of fish sampled in waters of the North Atlantic Ocean and the eastern Mediterranean Sea, where crustaceans were relatively less important and mackerels play the role reserved for sardines in our study area (Guichet, 1995; Velasco and Olaso, 1998; Philips, 2012). Regarding blue whiting, our results agree with those reported by Olaso and Rodríguez-Marín[6], Velasco et al.[7], and Gutiérrez-Zabala et al.[8] for this species in the Cantabrian Sea off the northern coast of Spain, but they contrast with the findings of Preciado et al. (2002) for blue whiting in the south of Galicia in the northwest of Spain and of Torres et al. (2013) for this species in the Gulf of Cadiz off the southern coasts of Portugal and

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[6] Olaso, I., and E. Rodríguez-Marín. 1995. Alimentación de veinte especies de peces demersales pertenecientes a la división VIIIc del ICES. Otoño 1991. Inst. Esp. Oceanogr., Inf. Téc. 157, 56 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

[7] Velasco, F., I. Olaso, and F. de la Gándara. 1996. Alimentación de veintidós especies de peces demersales de la división VIIIc del ICES. Otoños de 1992 y 1993. Inst. Esp. Oceanogr., Inf. Téc. 164, 62 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

[8] Gutiérrez-Zabala, J. L., F. Velasco, and I. Olaso. 2001. Alimentación de veintiuna especies de peces demersales de la división VIIIc del CIEM. Otoños de 1994 y 1995. Inst. Esp. Oceanogr., Datos Resúm. 16, 61 p. [In Spanish.] [Available from Inst. Esp. Oceanogr., Calle Corazón María 8, 28002 Madrid, Spain.]

Spain. In these latter 2 papers, a higher dependency on crustaceans, particularly euphausiids, was reported.

As far as differences in diet compositions between the European hake and blue whiting in our study are concerned, the European hake was found to prey mainly on pelagic fish species (i.e., sardines and European anchovy), as well as on benthopelagic (e.g., blue whiting) and demersal (e.g., poor cod) fish species, and the blue whiting was found to feed mainly on benthopelagic fish species (e.g., the horned lanternfish and jewel lanternfish). This ability of European hake to prey on different groups resulted in the European hake occupying the broadest trophic niche of all the species studied. Hence, in relation to ontogenetic shifts in diet, both species are characterized by a decreasing consumption of euphausiids and an increasing proportion of fish species with size. All of these results agree with those reported by Bozzano et al. (1997) for work in the Gulf of Lion and by Cartes et al. (2009) for a study in the Balearic Islands, a small archipelago off the northeastern coast of Spain.

Results for examination of niche breadth indicate a pattern that relates size class to niche breadth. The small size classes had a broader trophic niche than that of the large size classes, for all species studied except the Mediterranean ling, with ontogenetic growth leading to greater specialization in these species. In contrast, the Mediterranean ling is a specialist piscivorous species, the larger size of the specimens of which, in comparison to the size of individuals of other species studied, allowed it to have access to a greater number of potential prey in its diet. Therefore, its trophic niche increased with the ontogenetic development of specimens. Our findings for the Mediterranean ling indicate a relationship between size class and trophic level, with the trophic level being lower in the small size classes and increasing after the ontogenetic shift. This difference in the trophic level between size classes was greater for those species located higher in the trophic web (e.g., the European hake, blue whiting, and Mediterranean ling).

We found that the studied species of Gadiformes exploit food resources at different trophic levels of the food web, indicating ontogenetic shifts in diet and resource partitioning. The silvery pout, for example, plays a role closer to that of a primary consumer, with the specimens that composed the small size class being those with the lowest trophic level. Fish species that play a similar role within the food web include species of *Gobius*, *Mullus*, *Symphodus*, and *Diplodus*, according to Karachle and Stergiou (2017). An intermediate trophic position is occupied by the poor cod, greater forkbeard, Mediterranean bigeye rockling, and the small size classes of blue whiting and European hake, as well as of the blackmouth catshark (*Galeus melastomus*) and species of *Serranus*, *Pagellus*, and *Chelidonichthys* (Karachle and Stergiou, 2017). Large specimens of European hake and blue whiting have a position in the upper part of the food web, along with species of *Raja* and *Scorpaena* (Karachle and Stergiou, 2017). Finally, the Mediterranean ling, primarily a piscivorous species, is in the highest trophic level, similar to other piscivorous species such as the common dentex (*Dentex dentex*), greater amberjack (*Seriola dumerili*), bluefin tuna (*Thunnus thynnus*), and John dory (*Zeus faber*) (Karachle and Stergiou, 2017).

If an ecosystem is structured in accordance with the hypothesis of niche complementarity (Ebeling and Hixon, 1991), on the basis of the distribution and diet of the species involved, the structure should have consistently low niche overlap such that the coexistence of similar species occurs because of differences in resource use (Pianka, 1973; Schoener, 1974). We investigated the dietary overlap of coexisting species for which a partitioning of trophic resources was found among species and size classes. This finding indicates that the 7 species studied occupy different trophic positions, ranging from a generalized feeding behavior to specialized piscivorous habits. These results might complement those reported by Macpherson (1978a) and Morte et al. (2001, 2002), who investigated changes with season and depth, respectively, in the diets of blue whiting, silvery pout, poor cod, and greater forkbeard. They related availability of prey to diet depending on the season. Moreover, differences in the patterns of species distribution reduce niche overlap even further.

Only 3 pairs of species had a co-occurrence greater than 50%, with the pairs of blue whiting and greater forkbeard and of European hake and poor cod having by far the highest values of spatial overlap but correspondingly low values of trophic overlap. This distributional and trophic strategy minimizes interspecific competition. Cases in point are the Mediterranean ling and blue whiting, which may avoid intraspecific competition through this mechanism. Only the species pair of silvery pout and blue whiting had high values for both indices, indicating strong competition for resources between these 2 species.

For 5 of the 7 species, excluding the Mediterranean bigeye rockling and poor cod, ontogenetic shifts in diet were found, shifts that allowed them to occupy several niches or subniches simultaneously (Deselle et al., 1978; Keast, 1978). These ontogenetic shifts were associated with an increase in inferred trophic levels for all the species, contributing to increasing segregation between size classes (Pauly et al., 2001). Although the size classes described in this study are related to shifts in trophic strategies, intraspecific trophic overlap was observed for those 5 species that had ontogenetic shifts in their diets, and the intraspecific overlap was generally higher than the interspecific overlap. This result is in line with that of Bergstad (1991), who found that the effects of competitive interactions are more likely to occur between size classes of the same species than between different species.

Of those 5 species, the greater forkbeard, European hake, and silvery pout had high co-occurrence that involved strong competition for food resources, resulting in high intraspecific trophic overlap. An important aspect of this kind of competition is cannibalism, which was found in European hake, and this result is in agreement with findings reported by Macpherson (1979), Bozzano (1997), and Cartes et al. (2009) for studies in the western Mediterranean Sea, as well as in nearby regions of the Atlantic Ocean (Torres et al., 2013; López-López et al., 2015).

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Supplementary Table 1. Diet composition for the 7 gadiform species studied, based on the volume index (%*V*) for each prey item identified to the lowest taxonomic level possible and prey category found in the stomach contents of specimens caught in the western Mediterranean Sea during 2011–2017.

Prey items and categories	***G. argenteus***	***G. biscayensis***	***M. merluccius***	***M. poutassou***	***M. macrophthalma***	***P. blennoides***	***T. minutus***
Teleosts	**17.34**	**17.61**	**84.49**	**52.62**	**99.08**	**9.04**	**7.36**
Scyliorhinidae						0.11	
Scyliorhinus canicula						0.11	
Clupeiformes			**38.76**	**0.92**			**0.54**
Engraulis encrasicolus			28.40				
Sardina pilchardus			10.19	0.92			0.54
Sprattus sprattus			0.18				
Argentiniformes			**0.09**		**0.62**		
Argentina sphyraena			0.09				
Glossanodon leioglossus					0.62		
Myctophiformes	**1.50**		**1.21**	**42.14**	**1.02**	**0.36**	**0.17**
Benthosema glaciale				4.13			
Ceratoscopelus maderensis			0.11	18.20		0.36	
Lampanyctus crocodilus	1.36		1.07	16.55			
Notoscopelus elongatus			0.03	1.23	1.02		0.17
Myctophum punctatum				0.52			
Unidentified myctophids	0.14		0.00	1.51			
Stomiiformes	**9.29**		**0.20**	**4.79**		**0.27**	
Maurolicus muelleri	2.48		0.06	0.62		0.27	
Stomias boa boa			0.13	3.04			
Vinciguerria sp.	0.42						
Cyclothone sp.	6.39			1.11			
Gonostoma denudatum				0.03			
Gadiformes	**1.14**	**16.39**	**16.73**	**1.90**	**89.29**	**6.15**	**3.83**
Gadiculus argenteus	1.14		0.05		31.98		
Merluccius merluccius			3.77			1.11	0.51
Micromesistius poutassou			10.82	0.77	44.62		
Gaidropsarus biscayensis		16.39	0.38		1.47	4.54	3.32
Phycis blennoides			0.55	1.09	1.23	0.03	
Trisopterus minutus			1.16	0.04	9.99	0.47	

Perciformes			**21.10**	**0.77**		**1.43**	**1.95**
Cepola macrophthalma			0.59				
Boops boops			14.45				
Serranus cabrilla			0.01				
Mullus sp.			0.09				
Trachinus draco			0.06				
Deltentosteus quadrimaculatus			0.01				
Gobiidae			0.21				0.44
Lesueurigobius sp.			0.10				0.49
Callionymus sp.			0.11				1.02
Aulopiformes			**5.46**	**0.77**		**1.43**	
Lestidiops sp.				0.77		1.43	
Paralepididae			1.03				
Spicara smaris			0.43				
Spicara maena			1.37				
Trachurus sp.			2.63				
Scorpaeniformes			**0.04**				
Trigla lyra			0.04				
Pleuronectiformes							**0.03**
Arnoglossus sp.							0.03
Teleost larvae	0.01	0.39		0.07			
Unidentified teleosts	5.40	0.83	6.35	2.03	8.15	0.72	0.84
Mollusca			**5.65**	**0.75**		**0.69**	**2.84**
Cephalopoda			**5.65**	**0.75**		**0.69**	**2.83**
Abralia veranyi				0.42			
Illex coindetii			3.43			0.32	
Rondeletiola minor			0.08				
Sepia elegans			1.32				
Sepietta oweniana			0.53				0.71
Unidentified sepiolids			0.29			0.03	1.92
Unidentified teuthids				0.28			
Unidentified cephalopods			0.01	0.05		0.34	0.20
Pteropoda							0.01

Crustacea	**82.46**	**82.04**	**9.86**	**46.62**	**0.92**	**90.14**	**89.71**
Decapoda	**10.26**	**62.82**	**5.24**	**17.41**	**0.47**	**81.13**	**83.56**
Alpheus glaber		9.86	0.41			34.08	44.10
Athanas sp.							0.03
Chlorotocus crassicornis			1.29			7.15	6.32
Crangonidae			0.00				
Gennadas elegans	0.55				0.24		
Pasiphaea sp	0.07		0.29	11.15		0.69	
Philocheras sp.			0.04			0.05	0.20
Plesionika acanthonotus						0.07	
Plesionika edwardsii		2.62					
Plesionika gigliolii		1.38	0.14	0.15			
Plesionika heterocarpus			0.02				
Aegaeon sp.			0.21			0.20	
Pontophilus sp.			0.04				0.03
Processa sp.	2.66	1.81	0.36	0.14		4.17	4.29
Eusergestes arcticus		4.15		0.95	0.23		
Deosergestes henseni				0.06			
Robustosergia robusta				2.37			
Solenocera membranacea			1.04			9.93	1.02
Calocaris macandreae	0.16	28.28		0.01		6.09	0.04
Galathea sp.						0.04	0.03
Goneplax rhomboides		10.92				7.75	4.36
Jaxea sp.							0.08
Liocarcinus sp.			0.10			1.80	10.87
Macropipus tuberculatus						0.13	0.12
Portunidae			0.01				0.03
Monodaeus couchii		1.18				0.80	0.16
Munida sp.		0.87				1.17	0.59
Nephrops norvegicus				0.11			
Paguridae						0.02	
Scyllarus sp.			0.01			0.14	
Upogebia sp.			0.01			0.14	0.10
Unidentified carideans	6.41	0.96	0.95	2.31		5.46	5.84

Unidentified brachyurans		0.46	0.02			0.39	0.76
Unidentified decapods	0.41	0.33	0.31	0.16		0.87	4.59
Stomatopoda			**0.04**			**2.67**	**0.22**
Rissoides pallidus			0.04			2.67	0.22
Peracarida	**3.21**	**13.55**	**0.23**	**0.22**	**0.14**	**2.78**	**2.28**
Amphipoda	**1.11**	**3.25**	**0.11**	**0.10**	**0.04**	**0.76**	**0.80**
Caprellidae		0.03				0.02	
Ampelisca sp.			0.00			0.02	
Epimeria sp.						0.02	0.03
Eusirus sp.						0.02	
Idunella sp.						0.02	
Lysianassa sp.			0.00			0.02	0.12
Lysianassidae	0.25					0.02	
Moerella sp.							0.05
Monoculodes sp.		0.44					
Rhachotropis sp.						0.04	0.03
Scopelocheirus sp.							0.11
Tryphosites sp.							0.02
Westwoodilla sp.	0.27	0.44			0.04		
Brachyscelus sp.			0.05	0.04		0.04	
Hyperiidea	0.14		0.01	0.01			
Phronima sedentaria			0.02	0.01		0.40	0.38
Vibilia sp.	0.08		0.02	0.03			0.02
Unidentified amphipods	0.37	2.34	0.01	0.01		0.12	0.03
Isopoda	1.07	0.44	0.00	0.10	0.03	1.04	0.32
Lophogastrida		**6.83**	**0.06**	**0.01**		**0.45**	**0.93**
Lophogaster typicus		6.83	0.06	0.01		0.45	0.93
Mysida	1.03	3.04	0.05	0.00	0.06	0.52	0.23
Tanaidacea						0.02	
Copepoda	9.48	1.56	0.00			0.02	
Ostracoda						0.02	
Euphausiacea	**53.18**	**2.84**	**4.19**	**28.89**	**0.31**	**3.31**	**2.74**
Euphausia krohnii	17.69			0.05			
Meganyctiphanes norvegica	4.28		0.06	4.85		2.54	2.11
Nematoscelis sp.	1.14		0.01	0.35			

	Nyctiphanes couchii			0.71	1.30			
	Unidentified euphausiaceans	30.07	2.84	3.41	22.34	0.31	0.76	0.62
	Unidentified crustaceans	6.34	1.27	0.16	0.09		0.21	0.92
Annelida		0.20	0.35		0.01		0.12	0.09
Hydrozoa					**0.01**		**0.02**	
	Diphyidae				0.01		0.02	

Supplementary Table 2. Summary of the composition of taxa and species identified in the stomach contents of specimens of 7 gadiform species caught in the western Mediterranean Sea during 2011–2017. Trophic levels of prey items and groups and the references used as sources of this information on trophic levels are provided.

Prey items	**Trophic level**	**Reference**
CEPHALOPODA		
Abralia veranyi	3.20	Cortés (1999)
Eggs	1.00	
Illex coindetii	3.85	Rosas-Luis et al. (2014)
Rondeletiola minor	3.20	Cortés (1999)
Sepia elegans	3.20	Cortés (1999)
Sepietta oweniana	3.20	Cortés (1999)
Sepiolidae	3.20	Cortés (1999)
Teuthida	3.85*	Rosas-Luis et al. (2014)
Undefined cephalopoda	3.20	Cortés (1999)
CRAB, LOBSTER, AND MANTIS SHRIMP SPECIES		
Brachyura	2.88	Corrales et al. (2015)
Calocaris macandreae	2.88	Corrales et al. (2015)
Galathea sp.	2.88	Corrales et al. (2015)
Goneplax rhomboides	2.88	Corrales et al. (2015)
Jaxea nocturna	2.88	Corrales et al. (2015)
Liocarcinus sp.	2.88	Corrales et al. (2015)
Macropipus tuberculatus	2.88	Corrales et al. (2015)
Monodaeus couchii	2.88	Corrales et al. (2015)
Munida sp.	2.88	Corrales et al. (2015)
Paguridae	2.88	Corrales et al. (2015)
Portunidae	2.88	Corrales et al. (2015)
Unidentified crabs	2.88	Corrales et al. (2015)
Upogebia sp.	2.88	Corrales et al. (2015)
Nephrops norvegicus	2.88	Corrales et al. (2015)
Rissoides sp.	2.88	Corrales et al. (2015)
Scyllarus sp.	2.88	Corrales et al. (2015)
BENTHOPELAGIC FISH SPECIES		
Argentina sphyraena	3.44	Pinnegar et al. (2002)
Benthosema glaciale	3.24	Cortés (1999)
Cepola macrophthalma	3.18	This study
Ceratoscopelus maderensis	3.24	Cortés (1999)
Cyclothone sp.	3.20	Fanelli et al. (2011)
Gadiculus argenteus	3.32	This study

Glossanodon leioglossus	3.44	Froese and Pauly (2019)
Gonostoma sp.	3.24	Cortés (1999)
Lampanyctus crocodilus	3.65	This study
Lestidiops sp.	3.24	Cortés (1999)
Maurolicus muelleri	3.24	Cortés (1999)
Merluccius merluccius	3.89	This study
Micromesistius poutassou	3.58	This study
Myctophidae	3.24	Cortés (1999)
Myctophum punctatum	3.60	Fanelli et al. (2011)
Notoscopelus elongatus	3.24	Cortés (1999)
Paralepididae	3.24	Cortés (1999)
Stomias boa boa	4.60	Fanelli et al. (2011)
Vinciguerria sp.	3.24	Cortés (1999)
DEMERSAL FISH SPECIES		
Arnoglossus sp.	3.57	This study
Callionymus sp.	3.09	Karachle and Stergiou (2017)
Deltentosteus quadrimaculatus	3.24	Karachle and Stergiou (2017)
Gaidropsarus biscayensis	3.69	This study
Gobiidae	3.32	Karachle and Stergiou (2017)
Lesueurigobius friesii	3.23	Froese and Pauly (2021)
Mullus sp.	3.52	This study
Phycis blennoides	3.46	This study
Scyliorhinus canicula	3.80	This study
Serranus cabrilla	3.77	This study
Spicara maena	3.46	This study
Trachinus draco	3.94	This study
Triglidae	3.48	This study
Trisopterus minutus	3.59	This study
PELAGIC FISH SPECIES		
Boops boops	3.29	This study
Engraulis encrasicolus	3.02	Corrales et al. (2015)
Sardina pilchardus	2.91	Corrales et al. (2015)
Spicara smaris	3.02	This study
Sprattus sprattus	3.02	Corrales et al. (2015)
Trachurus sp.	4.10	This study
PERACARIDA		
Ampelisca sp.	3.18	Ebert and Bizzarro (2007)
Undefined amphipods	3.18	Ebert and Bizzarro (2007)
Caprellidae	3.18	Ebert and Bizzarro (2007)
Epimeria cornigera	3.18	Ebert and Bizzarro (2007)
Eusirus longipes	3.18	Ebert and Bizzarro (2007)
Idunella sp.	3.18	Ebert and Bizzarro (2007)
Isopoda	3.18	Ebert and Bizzarro (2007)

Lophogaster typicus	2.25	Ebert and Bizzarro (2007)
Lysianassa sp.	3.18	Ebert and Bizzarro (2007)
Lysianassidae	3.18	Ebert and Bizzarro (2007)
Moerella sp.	3.18	Ebert and Bizzarro (2007)
Monoculodes sp.	3.18	Ebert and Bizzarro (2007)
Mysida	2.25	Ebert and Bizzarro (2007)
Rhachotropis sp.	3.18	Ebert and Bizzarro (2007)
Scopelocheirus sp.	3.18	Ebert and Bizzarro (2007)
Tanaidacea	2.40	Ebert and Bizzarro (2007)
Tryphosites sp.	3.18	Ebert and Bizzarro (2007)
Westwoodilla sp.	3.18	Ebert and Bizzarro (2007)
SMALL PLANKTON		
Copepoda	3.00	Fanelli et al. (2011)
Ostracoda	2.20	Fanelli et al. (2011)
Pelagic eggs	1.00	
LARGE PLANKTON		
Brachyscelus crusculum	3.18	Ebert and Bizzarro (2007)
Diphyidae	2.10	Cortés (1999)
Euphausia krohnii	2.25	Cortés (1999)
Euphausiacea	2.25	Cortés (1999)
Euthecosomata	2.10	Cortés (1999)
Fish larvae	3.00	
Hyperiidea	3.18	Ebert and Bizzarro (2007)
Meganyctiphanes norvegica	3.50	Fanelli et al. (2011)
Nematoscelis megalops	3.50	Fanelli et al. (2011)
Nyctiphanes couchii	3.50	Fanelli et al. (2011)
Phronima sedentaria	3.40	Fanelli et al. (2011)
Tunicata	2.10	Jacobsen and Bennett (2013)
Vibilia sp.	2.00	Fanelli et al. (2011)
POLYCHAETA		
Polychaeta	2.05	Corrales et al. (2015)
SHRIMP SPECIES		
Alpheus glaber	2.94	Corrales et al. (2015)
Athanas sp.	2.94	Corrales et al. (2015)
Chlorotocus crassicornis	2.94	Corrales et al. (2015)
Crangonidae	2.94	Corrales et al. (2015)
Deosergestes henseni	3.60	Fanelli et al. (2011)
Eusergestes arcticus	3.60	Fanelli et al. (2011)
Gennadas elegans	3.60	Fanelli et al. (2011)
Pasiphaea multidentata	3.70	Fanelli et al. (2011)
Pasiphaea sivado	3.70	Fanelli et al. (2011)
Philocheras sp.	2.94	Corrales et al. (2015)

Plesionika acanthonotus	2.94	Corrales et al. (2015)
Plesionika edwardsii	2.94	Corrales et al. (2015)
Plesionika gigliolii	2.94	Corrales et al. (2015)
Plesionika heterocarpus	2.77	Fanelli and Cartes (2008)
Pontocaris sp.	2.94	Corrales et al. (2015)
Pontophilus sp.	2.94	Corrales et al. (2015)
Processa sp.	2.94	Corrales et al. (2015)
Sergia robusta	3.60	Fanelli et al. (2011)
Solenocera membranacea	2.94	Corrales et al. (2015)
Unidentified shrimps	2.94	Corrales et al. (2015)

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The full references for all the other information sources are provided in the “Literature cited” section of the main article.

Supplementary Table 3. Results of analysis of similarity by size class (small [S] and large [L]) for the 7 gadiform species studied to detect intraspecific food habit differences. The number of stomachs examined (*n*), length range (total lengths in millimeters), and Global *R*, a comparative measure of the degree of separation between size classes, are provided. An asterisk (*) indicates a probability below the significance level of 0.05. Specimens of the species were caught in the western Mediterranean Sea during 2011–2017.

Species	Size class	*n*	Length range	Global *R*	*P*
G. argenteus	S	44	60–92	0.146	0.012*
	L	219	93–133		
G. biscayensis	S	86	40-110	0.138	0.097
	L	30	111–180		
M. macrophthalma	S	107	83–165	0.124	0.016*
	L	57	166–740		
M. merluccius	S	405	87–149	0.161	0.001*
	L	849	150–549		
M. poutassou	S	172	89–169	0.112	0.006*
	L	614	170–377		
P. blennoides	S	75	85–149	0.478	0.001*
	L	211	150–393		
T. minutus	S	169	78–169	0.002	0.351
	L	154	170–272		

Supplementary Table 4. Results of the similarity percentage analysis of the stomach contents from specimens of species of Gadiformes caught in the western Mediterranean Sea during 2011–2017, based on the average dissimilarity between size classes (small [S] and large [L]) to determine which prey groups contributed the most to the dissimilarity in diet composition. Of the 7 studied species, 2 of the species did not have shifts in diet according to size and are not included in this table.

Species	**Av. Diss**	**Prey group**	**Av. Abund S**	**Av. Abund L**	**Av. Diss**	**Diss/SD**	**Contrib%**	**Cum%**
Gadiculus argenteus	63.43	LARGE PLANKTON	0.53	0.60	17.72	1.23	27.94	27.94
		PERACARIDA	0.27	0.21	13.57	0.95	21.40	49.34
Molva macrophthalma	41.66	DEMERSAL FISH SPECIES	0.27	0.44	19.44	1.12	46.67	46.67
		BENTHOPELAGIC FISH SPECIES	0.88	0.60	17.70	0.95	42.49	89.15
Merluccius merluccius	75.12	PELAGIC FISHES	0.19	0.50	18.26	1.11	24.31	24.31
		LARGE PLANKTON	0.35	0.12	14.02	0.92	18.66	42.97
		SHRIMP SPECIES	0.28	0.25	13.20	0.98	17.57	60.54
Micromesistius poutassou	60.2	LARGE PLANKTON	0.67	0.36	20.34	1.31	33.78	33.78
		BENTHOPELAGIC FISH SPECIES	0.36	0.58	19.24	1.30	31.97	65.75
Phycis blennoides	62.02	SHRIMP SPECIES	0.31	0.75	18.45	1.54	29.74	29.74
		PERACARIDA	0.45	0.06	14.38	1.18	23.19	52.93

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A food-web comparative modeling approach highlights ecosystem singularities of the Gulf of Alicante (Western Mediterranean Sea)

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ABSTRACT

A food-web comparative modeling approach using Ecopath with Ecosim (EwE) was built to characterize the ecosystem of the Gulf of Alicante (GoA) and investigate its singularities. The GoA differs from neighboring ecosystems of the Western Mediterranean Sea because of its different oceanographic characteristics. We developed a model of the study area representing early 2010s, covering a total area of 7085 km^2, and including the continental shelf and upper slope with depths from 50 to 800 m. In total, 45 functional groups considering all components of the food web (fish, marine mammals, seabirds, invertebrates, primary producers, and detritus) were selected to build the ecological model. The fishery was represented by the four main fleets operating in the area (i.e., bottom trawl, purse seine, longlines, and small-scale fisheries) and we included official landing data and estimated percentage of discarded species. Results were then compared with available outputs of available models representing adjacent ecosystems such as the Gulf of Cadiz (in the Atlantic side) and the North Western Mediterranean Sea (north of the study area). The study revealed that the major differences found between models were due to the lower primary production in the GoA. This led to lower catches and higher importance of the demersal compartment, where the most biomass was associated to the detritus. The main trophic flows in the GoA were originated at the basis of the food web, likely related to bottom-up flow control. Interactions between pelagic and demersal groups were weaker than in neighboring areas. Despite the high values of ecotrophic efficiencies and mortality rates, results showed a lower fishing pressure than in neighboring areas, suggesting a moderate exploitation level of marine resources in the GoA. This study fills a knowledge gap in the area and sets the baseline to develop future studies to test scenarios of change and management options.

1. Introduction

The declining trend of several marine resources is being observed worldwide and the main drivers behind are climate change and anthropogenic pressures such as overfishing and industrial and agricultural activity (Díaz et al., 2019; Halpern et al., 2019).

Overall, it is recognized that the impacts and interactions between species and fisheries have induced the seeking of alternative ways to better manage marine resources. The conventional management of marine resources has been based on the assessment of single-species, which has resulted incomplete (Pitcher and Cochrane, 2002). Therefore, an Ecosystem Approach to Fisheries (EAF) has been suggested worldwide as a common starting point for the appropriate management of marine resources (Garcia et al., 2003).

In this context, ecosystem models can be useful tools to contribute to fisheries management by providing relevant information to describe the trophic structure and functioning of marine ecosystems and the ecosystem impacts caused by human activities (Link, 2011; Christensen and Walters, 2011). Within the variety of ecosystem models available, Ecopath with Ecosim (EwE) (Polovina, 1984; Christensen and Pauly, 1992, 1993) is one of the most frequently used modeling frameworks for ecosystem approaches, leading to its applications worldwide by a growing body of scientists (e.g. Coll et al., 2015a; Colléter et al., 2015).

This approach has been also frequently used in the Mediterranean Sea (e.g., Tsagarakis et al., 2010; Coll and Libralato, 2012; Corrales et al., 2015, 2017), a hotspot of biodiversity largely threatened by

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multiple stressors (Coll et al., 2010, 2012). The biodiversity of the Mediterranean Sea depends strongly on the heterogeneity of habitats. In particular, habitat disruption has become a problem, leading to biodiversity loss and a decreasing trend in commercial stocks and catches of main target species in recent years (Ballesteros, 2006; Coll et al., 2010; Bellido et al., 2014; Fernandes et al., 2017; FAO, 2018).

Focusing on the Western Mediterranean and adjacent Atlantic waters, different food-web models have been developed, such as the South Catalan Sea model (CSM) (Coll et al., 2006); the deep-sea ecosystem model in the NW Mediterranean (DSM) (Tecchio et al., 2013); the Gulf of Lion model (GoL) (Banaru et al., 2013); the Northwestern Mediterranean model (NWM) (Corrales et al., 2015) covering the geographical sub-areas (GSAs) 6 and 7 of the General Fisheries Commission for the Mediterranean (GFCM, FAO); or the Gulf of Cadiz model (GoC) in the adjacent Atlantic (Torres et al., 2013). In addition to these models, there are also two EwE models in the region developed to study trophic structure and energy fluxes in an aquaculture system (Forestal et al., 2012; Bayle-Sempere et al., 2013), one to study the Fisheries Restricted Area (FRA) area in the GoL (Vilas et al., 2021) and several to study smaller coastal protected and adjacent areas (Corrales et al., 2020; Vilas et al., 2020).

Even though the Mediterranean Sea is generally considered an oligotrophic sea (Estrada, 1996), the Northern part of the Western Mediterranean basin presents a cyclonic circulation with some relative productive regions (Estrada and Margalef, 1988). These are the cases of the Gulf of Lion (GoL), where the strong prevailing NW winds during winter result in local upwelling processes (Minas, 1968), and to a lesser extent the Catalano-Balearic basin with a permanent southwestward current which flows from the Ligurian Sea to the Catalan Sea and follows the continental slope at the north of Cape La Nao (Millot, 1987). In this region, this current splits, and one branch flows eastward along the south of the Balearic Islands (Castellón et al., 1990) forming the thermohaline front that separates the central waters of the Catalan Sea from modified Atlantic waters (Font et al., 1988), configuring the Gulf of Alicante (GoA) as a transition area to Gulf of Vera and Alboran Sea (Almeria-Oran front), with a marked Atlantic influence.

The case of the Gulf of Alicante (GoA) seems to be specific because it is still under the influence of the Atlantic flow when leaving the Alboran Sea and is linked to the existence of an anticyclone circulation between Cape Palos and Cape La Nao. These features highlight the presence of two anticyclonic eddies, one very marked outside and another inside the continental shelf (Gil, 1992). Similarly, the thermohaline front located to the north of Cape La Nao that separates the GoA and the Catalan Sea could give certain singularity to the composition and dynamics of the marine ecosystems associated with the GoA. However, to date, there are no food-web modeling studies conducted in this area and thus our understanding of the functioning of the marine ecosystem of the GoA is still limited.

Despite the lack of information regarding the structure and functioning of the GoA, the hypothesis derived from the oceanographic conditions is that this ecosystem presents elements of singularity concerning those found north of Cape La Nao. Hence, the aim of the present study is to describe the trophic structure and functional integrity of the GoA marine ecosystem for the first time using a food-web modeling approach. Particularly, and following previous initiatives, we develop a food-web model for the first time that allows us to analyze various aspects of the structure and functioning of the ecosystem, including trophic interactions and the effects of fishing. Afterwards, we compare our results with other existing models located north to the Cape La Nao (Northwestern Mediterranean) and southeastwards Cape Palos (in the Atlantic Gulf of Cadiz). To develop the comparison, we first use robust ecosystem indicators to model comparisons (Heymans et al., 2014; Moloney et al., 2005). Secondly, we also use the ECOIND plug-in (Coll and Steenbeek, 2017) to complement the ecological indicators and obtain further insights into the GoA marine ecosystem properties. One of the interesting aspects of the approach presented here is that it opens the possibility to compare these indicators with those proposed for the EU Marine Strategy Framework Directive (MSFD: EU-COM, 2008) in future studies. The MSFD aims to monitor food-web status and trends in order to collect information needed to assess the current situation and implement the necessary preventive measures to ensure a Good Environmental Status (GES). Our study is a first step forward in this direction in the Gulf of Alicante, complementing available modeling experiences of the Western Mediterranean Sea. It also sets the baseline to develop scenarios of climate change and management options in the area.

2. Material and methods

2.1. Study area

The study was conducted in the Gulf of Alicante (GoA), which is located in the Western Mediterranean Sea, one of the fourth sub-regional divisions defined by the Marine Strategy Framework Directive (MSFD; 2008/56/EC) (38°44′2.44″N – 0°44′33″W; 37°38′10″N – 0°36′27″E) (Fig. 1). The study area includes several important harbors where diverse commercial and recreational activities are carried out. It covers a total area of 7085 km^2 including the continental shelf and upper slope. It covers a depth range between 50 and 800 m. The Alicante continental shelf average width from Cape La Nao to Cape Palos is 32 km, with a minimum and a maximum of 23 km and 40 km, with a dominance of sandy and muddy bottoms (Díaz del Río et al., 1986). The slope has a uniform relief with a width between 30 and 52 km. There are two major canyons: the one from Alicante is gently sloping and the other in Benidorm is narrower and rough with a head that originates at the foot of the continental slope at a depth of 650 m (Díaz del Río, 1991).

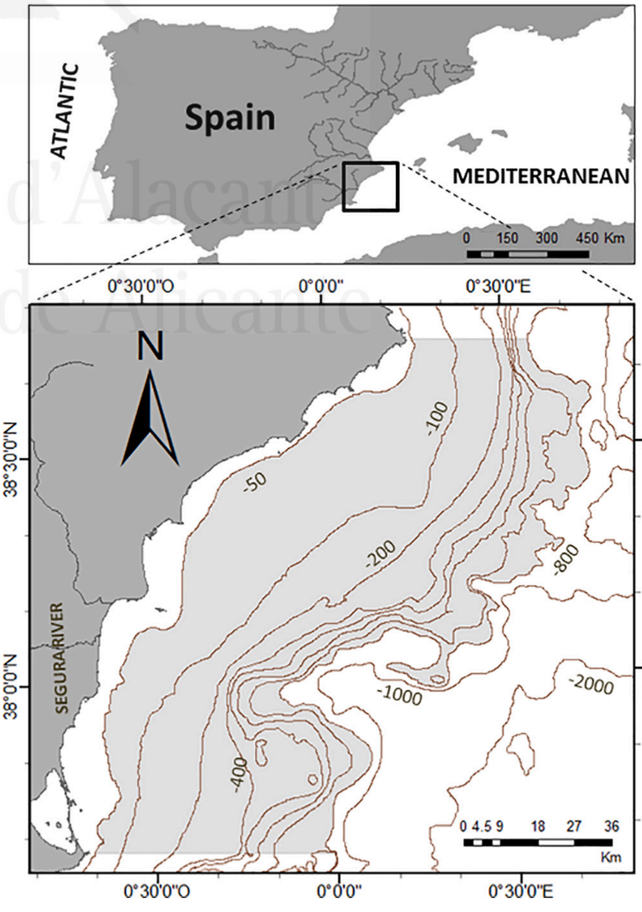

Fig. 1. Map of the Northwestern Mediterranean Sea including the Gulf of Alicante.

2.2. Ecopath mass-balanced model

A trophic model was developed to provide a static description of the GoA ecosystem in early 2010s, when the best data regarding biomass of the demersal community were available in terms of stability along the time series. The model was constructed using the Ecopath with Ecosim (EwE) software version 6.6 (Christensen et al., 2008) and we followed the best practices and applied the PREBAL approach (Heymans et al., 2016; Link, 2010).

Several functional groups were defined and required information for biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and diet. In addition, estimates of catches and discards for fished groups were compiled.

The Ecopath modeling framework, based on the pioneering work of Polovina (1984), estimates the flows among different food-web components (Christensen and Walters, 2004). These components, also called functional groups, can be single-species, ontogenetic phases of a species (or multi-stanza groups), or species groups representing similar ecological guilds in the ecosystem (i.e., have similar growth rates, consumption rates, diets, habitats, and predators) (Christensen et al., 2008; Heymans et al., 2016).

The Ecopath model is based on two master equations, the first of which splits the production term for each functional group i into its components:

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + M0_i \tag{1}$$

where P_i is the total production rate of group *i*, Y_i is the total fisheries catch rate, B_i is the biomass, $M2_i$ is the total predation rate, E_i is the net migration rate (emigration -immigration), BA_i is the biomass accumulation rate, and $M0_i$ is the so-called "other mortality," which includes mortality caused by diseases, starvation, etc.…, or being consumed by

Table 1

Modified input parameters and outputs obtained from the Gulf of Alicante (GoA) model in 2011. Bf = final biomass; P/B = production/biomass ratio; Q/B = consumption/biomass ratio; EE = ecotrophic efficiency; P/Q = production/consumption ratio; R/B = respiration/biomass ratio; R/A = respiration/assimilation ratio; P/R = production/respiration ratio; NE = net efficiency; F = fishing mortality (years^{-1}); M2 = predation mortality (years^{-1}); M0 = other natural mortality (years^{-1}); F/Z = exploitation rate; OI = omnivory index; FD = flow to detritus (t·km^{-2}·years^{-1}); TL = trophic level.

Functional group	Bf	P/B	Q/B	EE	TL	P/Q	R/B	R/A	P/R	NE	F	M2	MO	F/Z	OI	FD
1. Dolphins	0.010	0.03	12.32	0.00	4.07	0.002	9.83	0.997	0.003	0.003	0.00	0.00	0.03	0.000	0.58	0.02
2. Seabirds	0.003	4.47	70.89	0.00	3.01	0.063	52.24	0.921	0.086	0.079	0.00	0.00	4.47	0.000	0.76	0.05
3. Large pelagic fishes	0.095	0.20	1.45	0.28	3.63	0.139	0.96	0.826	0.211	0.174	0.06	0.00	0.15	0.281	1.02	0.04
4. Benthic sharks	0.068	0.65	5.30	0.58	3.43	0.123	3.58	0.846	0.182	0.154	0.30	0.08	0.27	0.459	0.70	0.09
5. Rays and skates	0.006	1.20	4.36	0.72	4.00	0.276	2.29	0.655	0.526	0.345	0.85	0.01	0.34	0.709	0.20	0.01
6. Demersal ichthyophagous fishes	0.038	1.56	5.48	0.99	3.96	0.285	2.82	0.643	0.554	0.357	0.88	0.67	0.02	0.560	0.35	0.04
7. Pelagic ichthyophagous fishes	0.096	1.42	4.65	0.47	3.97	0.305	2.30	0.619	0.615	0.381	0.61	0.05	0.75	0.432	1.40	0.16
8. Anglerfishes	0.034	1.16	3.90	0.72	4.15	0.297	1.96	0.629	0.590	0.371	0.83	0.00	0.32	0.719	0.74	0.04
9. Juvenile hake	0.032	1.53	10.83	0.85	3.64	0.141	7.14	0.824	0.214	0.176	0.00	1.30	0.23	0.000	0.18	0.08
10. Adult hake	0.112	1.48	4.58	0.13	3.85	0.323	2.18	0.596	0.678	0.404	0.00	0.19	1.29	0.000	0.44	0.25
11. Mullets	0.031	1.85	6.36	0.99	3.46	0.292	3.23	0.636	0.574	0.364	1.25	0.58	0.02	0.674	0.21	0.04
12. Blue whiting	0.196	0.83	6.07	0.99	3.71	0.136	4.03	0.830	0.205	0.170	0.48	0.33	0.01	0.586	0.11	0.24
13. Sardine	2.848	0.81	9.56	0.88	2.17	0.084	6.84	0.894	0.118	0.106	0.11	0.60	0.10	0.136	0.19	5.72
14. Anchovy	0.293	1.05	9.87	0.96	3.26	0.107	6.84	0.867	0.154	0.133	0.30	0.71	0.04	0.285	0.10	0.59
15. Small pelagics	0.230	2.59	8.98	0.92	3.08	0.288	4.60	0.640	0.563	0.360	1.81	0.56	0.22	0.699	0.04	0.46
16. Flatfishes	0.036	0.87	8.40	0.96	3.50	0.104	5.84	0.870	0.149	0.130	0.30	0.53	0.04	0.347	0.41	0.06
17. Benthopelagic fishes	0.186	1.17	10.11	0.95	3.28	0.115	6.92	0.856	0.169	0.144	0.41	0.70	0.06	0.351	0.10	0.39
18. Mesopelagic fishes	0.368	1.33	10.26	0.99	3.12	0.130	6.88	0.838	0.193	0.162	0.00	1.31	0.02	0.002	0.28	0.76
19. Mackerels	0.125	0.70	5.95	0.88	3.52	0.118	4.06	0.853	0.172	0.147	0.34	0.27	0.08	0.490	0.12	0.16
20. Horse mackerels	0.276	0.79	7.02	0.90	3.41	0.112	4.83	0.860	0.163	0.140	0.34	0.36	0.08	0.437	0.10	0.41
21. Gobiids	0.127	1.05	10.57	0.97	3.11	0.099	7.41	0.876	0.141	0.124	0.05	0.96	0.03	0.051	0.23	0.27
22. Gelatinous plankton feeders	0.153	1.67	6.55	0.98	3.66	0.255	3.57	0.682	0.467	0.318	0.29	1.34	0.03	0.176	0.10	0.21
23. Sparids	0.006	2.64	6.64	0.99	3.43	0.398	2.67	0.502	0.990	0.498	1.95	0.66	0.03	0.737	0.21	0.01
24. Suprabenthos feeders	0.030	1.06	7.00	0.98	3.40	0.151	4.54	0.811	0.233	0.189	0.38	0.66	0.02	0.356	0.17	0.04
25. Natantia feeders	0.086	1.33	6.78	0.95	3.57	0.196	4.09	0.755	0.325	0.245	0.79	0.47	0.06	0.596	0.39	0.12
26. Benthopelagic cephalopods	0.042	3.20	9.10	0.96	3.66	0.352	4.08	0.560	0.784	0.440	1.52	1.56	0.12	0.475	0.57	0.08
27. Benthic cephalopods	0.014	3.10	8.80	1.00	3.74	0.352	3.94	0.560	0.787	0.440	1.19	1.91	0.00	0.385	0.43	0.03
28. Octopuses	0.070	3.00	8.50	0.85	3.42	0.353	3.80	0.559	0.789	0.441	2.31	0.23	0.46	0.769	0.66	0.15
29. Blue and red shrimp	0.011	2.11	20.57	0.94	3.34	0.103	14.35	0.872	0.147	0.128	1.17	0.82	0.12	0.553	0.16	0.04
30. Deep water rose shrimp	0.013	2.40	24.12	0.29	2.96	0.099	16.89	0.876	0.142	0.124	0.67	0.02	1.71	0.277	0.15	0.09
31. Norway lobster	0.029	5.16	19.84	0.20	2.94	0.260	10.71	0.675	0.481	0.325	0.57	0.48	4.10	0.111	0.50	0.23
32. Crabs	0.396	1.93	7.07	0.99	2.92	0.273	3.73	0.659	0.518	0.341	0.14	1.78	0.01	0.070	0.32	0.56
33. Other shrimps	0.731	1.89	8.49	0.94	2.98	0.222	4.90	0.722	0.385	0.278	0.02	1.76	0.11	0.012	0.42	1.32
34. Suprabenthos	0.616	7.87	52.10	0.90	2.13	0.151	28.60	0.784	0.275	0.216	0.00	7.04	0.83	0.000	0.12	10.14
35. Worms	6.180	5.61	30.00	0.30	2.03	0.187	12.39	0.688	0.453	0.312	0.00	1.70	3.91	0.000	0.03	98.33
36. Echinoderms	0.849	0.24	2.75	0.98	2.02	0.086	1.83	0.886	0.129	0.114	0.01	0.22	0.00	0.041	0.02	0.59
37. Bivalves and gastropods	2.118	1.63	6.78	0.13	2.10	0.240	2.44	0.600	0.667	0.400	0.00	0.22	1.41	0.000	0.10	8.74
38. Other benthic invertebrates	1.244	1.04	4.00	0.21	2.29	0.260	1.76	0.629	0.591	0.371	0.01	0.21	0.82	0.008	0.26	2.51
39. Microzooplankton	3.705	32.32	120.0	0.41	2.02	0.269	63.68	0.663	0.507	0.337	0.00	13.32	18.99	0.000	0.02	159.29
40. Meso- and macrozooplankton	0.682	14.97	49.82	0.99	2.63	0.300	19.90	0.571	0.752	0.429	0.00	14.83	0.14	0.000	0.28	10.29
41. Gelatinous plankton	0.247	12.89	49.38	0.38	2.75	0.261	26.61	0.674	0.484	0.326	0.00	4.91	7.99	0.000	0.26	4.41
42. Phytoplankton	6.220	146.2	–	0.38	1.00	–	–	–	–	–	0.00	56.20	89.95	0.000	–	559.46
43. Benthic macrophytes	0.405	1.08	–	0.95	1.00	–	–	–	–	–	0.00	1.03	0.05	0.000	–	0.02
44. Discards	0.106	–	–	0.86	1.00	–	–	–	–	–	–	–	–	–	–	0.03
45. Detritus	75.6	–	–	0.41	1.00	–	–	–	–	–	–	–	–	–	0.29	–

predators not included in the model ($M0_i = P_i \cdot (1 - EE_i)$, where EE_i is the ecotrophic efficiency of group *i*).

The second master equation describes the energy balance within each functional group:

$$Q_i = P_i + R_i + U_i \tag{2}$$

where Q_i stands for consumption, P_i for the total production rate, R_i for respiration, and U_i for unassimilated food. The Ecopath model uses a linear system of equations to estimate one parameter per equation and functional group, either B, P/B, Q/B, or EE (a detailed description of the model's foundations is given in Christensen et al., 2008; Christensen and Walters, 2004).

2.3. Input data

The selection of the functional groups represents a compromise between the biological and ecological characteristics of the modeled species. As a result, we identified 45 functional groups consisting of 23 fish groups, one group of marine mammals, one group of seabirds, 16 invertebrate groups, two primary producers, and two groups of detritus (Tables 1 and A.1).

One of the consumers, *Merluccius merluccius*, was split into a multi-stanza group to ensure consistency between ontogenetic groups, capturing diet shifts and/or different exploitation patterns (Christensen and Walters, 2004; Heymans et al., 2016), i.e. *adult hake* (i.e. $\geq$ 15 cm) and *juvenile hake* (i.e. $<$ 15 cm). The fishery in the model is represented by the four main fleets targeting the modeled species: bottom trawl, purse seine, longlines, and small-scale fisheries. Both the official landing data and the estimated percentage of discarded species were taken from the IEO Database (Table A.2).

Most biomass data (Table 1) were estimated from a series of scientific bottom trawl surveys (MEDITS) by the swept area method taking into account the weight of each stratum in the total surface area (Bertrand et al., 1998).

Phytoplankton biomass was estimated using satellite imagery data (https://neo.sci.gsfc.nasa.gov). Also, the biomass of detritus was estimated using the empirical equation by Pauly et al. (1993):

$$\text{Log D} = -2.41 + 0.954 \cdot \text{Log Pp} + 0.863 \cdot \text{Log E} \tag{3}$$

where D is detritus biomass (gr $C \cdot m^{-2}$), Pp is primary production (gr $C \cdot m^{-2} \cdot yr^{-1}$), and E the depth of the light penetration (m).

The P/B and Q/B ratios were estimated through empirical equations (Palomares and Pauly, 1998; Christensen et al., 2005) obtained from literature or using assumptions from other models and corrected following Opitz (1996) (Tables A.3 and A.4).

The diet data matrix was constructed based on either field studies in GSA6 (i.e., stomach contents) (García-Rodríguez et al., 2020, 2021 in press) or diet data obtained from the literature for the same species in similar ecosystems in cases where information was not available for the studied area (Table A.5).

To build the diet composition matrix, a statistical analysis was previously performed to determine which of these species showed differences in their dietary preferences between the Gulf of Alicante and the rest of the GSA6. Further differences between diets were explored with non-parametric analysis of similarities (ANOSIM) that are based on multi-dimensional scaling (MDS) of the Bray–Curtis dissimilarity index. In the case of those species showing differences in their dietary patterns, the specific diets of the Gulf of Alicante were used. For the rest of the species that did not show differences, the diet characterized in GSA6 was used.

Migratory patterns of mammals, seabirds, and large pelagic fishes were included in the ecosystem by modeling a proportion of their diet composition as an import (following Coll et al., 2006; Christensen et al., 2008). 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).

For the mass-balancing model, it is required to maintain the laws of thermodynamics following the rules described by Darwall et al. (2010). Therefore, once the model has been balanced and all the Ecotrophic Efficiencies (EE) were $<$ 1; Gross food conversion efficiency (GE) presented, in general, values between 0.1 and 0.3; Net efficiency (NE) presented a default value of 0.2; Respiration/Assimilation Biomass ratio $<$ 1; Production/Respiration ratio $<$ 1. In addition, it was useful to check the PREBAL diagnostics, including estimates of biomasses, biomass ratios, vital rates, and vital rates ratios (Link, 2010). More information about the balancing procedure is provided in the Supplementary Material (A.1).

2.4. Pedigree index

To check the uncertainty and quality of input data sources, the pedigree index was applied (Christensen et al., 2008). We used the default value of uncertainty or confidence intervals assigned to each parameter for each functional group to estimate an overall index of model quality. This index varies between 0 (low quality) and 1 (high quality), enabling a comparison between models.

2.5. Ecosystem structure and functioning

The Ecopath model implemented provides a snapshot of the interactions of the Gulf of Alicante ecosystem in early 2010 and can be used to calculate several ecological indicators. In this study, we selected ecological indicators related to functional groups and trophic interactions, to the theory of ecosystem maturity (sensu Odum, 1969; Christensen, 1995) that were robust to model comparisons (Heymans et al., 2014; Moloney et al., 2005) and using the ECOIND plug-in (Coll and Steenbeek, 2017).

2.5.1. Functional groups and trophic interactions

The indicators that allow analysis of each functional group to investigate their roles within the GoA ecosystem (Table 1) werenatural mortality rate (M) that can be split into non-predation natural mortality rate (M0) and the predation natural mortality rate (M2). The trophic level (TL) per functional group was also calculated, which identifies the trophic position of organisms within food webs by identifying the source of energy for each organism. Following an established convention, fractional TLs are calculated by assigning producers (and often also detritus) to TL = 1 and consumers to a TL = 1 plus the average TL of their prey, weighted by their proportion in weight in the predator's diet (Christensen, 1996). The TL is computed as $TL = 1 + (\Sigma\ DC_{ij})\ (NT_j)$, where DC_{ij} is the proportion of prey *j* in the diet of the predator *i* and NT_j is the trophic level of prey *j* (Christensen and Pauly, 1992). Besides, the Omnivory Index (OI) was included, highlighting the trophic specialization of each group and is computed as the variance of the TL of their prey *i* (Christensen et al., 2008) (Table 1).

The Mixed Trophic Impact analysis (MTI) quantifies the trophic impact that a hypothetical change in the biomass of a functional group would have on each group including fisheries (Ulanowicz and Puccia, 1990). Thus, it is possible to investigate the total effect of one functional group on all the others in a given model, allowing the estimation of keystoneness (KS) for the functional groups. A keystone species is defined as one whose impact on the community or ecosystem is high and disproportionately large relative to its abundance (Power et al., 1996).

The KS index attempts to reconcile the importance of a species concerning its biomass and the relative importance in the ecosystem. There are currently three formulations of the KS in EwE that formulate the biomass ratio differently (Power et al., 1996; Libralato et al., 2006; Valls et al., 2015). We selected the Valls Keystone Index, which tries to reach a compromise between the biomass and impact components of the indicator (Valls et al., 2015). The index is calculated as $KS = IC \cdot BC$, where IC is the impact component and BC is the biomass component.

The IC represents the overall effect of group *i* on all other groups in the food web excluding the impact on *i* itself and the impacts on dead groups and fleets (Libralato et al., 2006). The BC is defined as the rank of the group according to their biomass values in descending order (Valls et al., 2015).

2.5.2. *Ecosystem indicators*

Several indicators allowed us to analyze the ecosystem again criteria describing the stage of maturity, efficiency, health, and development. Several indicators were used to describe the structure and functioning of GoA ecosystem: Total System Throughput (TST, $t \cdot km^{-2} \cdot year^{-1}$), considered as an overall measure of the "ecological size" of the system and the sum of all trophic flows within the system; Total Consumption (TQ, $t \cdot km^{-2} \cdot year^{-1}$); Exports (E, $t \cdot km^{-2} \cdot year^{-1}$); Total Respiration (TR, $t \cdot km^{-2} \cdot year^{-1}$) and Total Flow to Detritus (TFD, $t \cdot km^{-2} \cdot year^{-1}$) (Ulanowicz, 1986); Total Production (TP, $t \cdot km^{-2} \cdot year^{-1}$); Net Production (NP, $t \cdot km^{-2} \cdot year^{-1}$); Total Biomass excluding detritus (TB, $t \cdot km^{-2}$); the ratios Primary production/TST (Pp/TST); TFD/TST; TQ/TST; TR/TST; E/TST; Pp/P; Total Primary Production/Total Respiration (Pp/R) and total Primary Production/Total Biomass (Pp/B, $t \cdot km^{-2} \cdot year^{-1}$).

Other indicators of food-web complexity were estimated: the System Omnivory Index (SOI), defined as the average of the OIs of each consumer group, weighted by the logarithm of their consumption (Christensen and Walters, 2004); and the Finn's Cycling Index (FCI, %), defined as the percentage of all flows that are recycled in the trophic network (Finn, 1976). FCI is an index used to measure the recycling and development of an ecosystem, although it is also linked to stress and its stability (Odum, 1969). Thus, ecosystems, where recycling is considerable, are stable and have a greater capacity to resist disturbances (Christensen, 1995). Finally, Finn's mean Path Length (MPL) represents the number of functional groups that a flow connects within the ecosystem (Finn, 1976).

We calculated the Transfer Efficiency (TE) from primary producers and from detritus, which is the fraction of total flows of each discrete trophic level that are either exported out of the ecosystem or transferred to higher trophic levels through consumption (Lindeman, 1942).

2.5.3. *Ecological indicators: ECOIND*

In addition, the ECOIND plug-in (Coll and Steenbeek, 2017) was used to calculate standardized ecological indicators. This plug-in uses additional species traits and adds new capabilities to EwE facilitating its applications into biodiversity and conservation-based frameworks. ECOIND allows calculation of the following type of indicators:

2.5.3.1. Biomass-based indicators. Based on the abundance of organisms in the food web. These indicators include total biomass (Total B) of species in the ecosystem; biomass of commercial species (Commercial B); biomass of fish (Fish B); invertebrates (Invertebrates B) and the ratio of the two latter (Invertebrates/Fish B); biomass of demersal (Demersal B) and Pelagic (Pelagic B) organisms and their ratio (Demersal/Pelagic B) and the Kempton's biodiversity index (Q). The Q index is proportional to the inverse slope of the species-abundance curve and is a proxy of ecosystem biodiversity (Ainsworth and Pitcher, 2006).

2.5.3.2. Catch-based indicators. Based on the catch and discard species in the ecosystem. These indicators include total catch (Total C) and the catch of fish (Fish C); invertebrates (Invertebrates C) and their ratio (Invertebrates/Fish C); demersal (Demersal C); Pelagic (Pelagic C); catch of organisms and their ratio (Demersal/Pelagic C); catch of predatory organisms (Predatory C), defined as organisms with trophic level (TL) ≥ 4, and total discarded catch (Discards).

2.5.3.3. Trophic-level based indicators. Since fishing selectively removes organisms from the food web, the trophic and size structure of the ecosystem may be altered. Therefore, these six indicators based on the trophic level concept and can be used to understand this effect (Shannon et al., 2014). These indicators include Tropic level (TL) of the catch (TL catch) (Christensen, 1996; Pauly et al., 1998); the Marine Trophic Index (MTI, or TLc including organisms with TL ≤ 3.25) (Pauly et al., 2005); TL of the community including all organisms (TL co); TLco including organisms with TL ≤ 2 (TLco 2); TLco including organisms with TL ≤ 3.25 (TLco 3.25), and TLco including organisms with TL ≤ 4 (Tlco 4).

2.5.3.4. Species-based indicators. Includes eight indicators specifically based on species traits and conservation status: The Intrinsic Vulnerability Index of the catch (IVIc) is a weighted mean of the vulnerability of exploited fish species (Cheung et al., 2007); the biomass (B) of endemic species in the community (Endemics B) and in the catch (C) (Endemics C) provide a measure of how abundant endemic species are in the ecosystem (Coll et al., 2012, 2016, 2015b); the biomass of endangered species in the community (UICN species B) and in the catch (IUCN species C) using the IUCN (International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015).

2.5.4. *Role of fishing activities*

We selected those indicators that can give information regarding fishing intensity and impacts in the ecosystem: the mean trophic level of the catch (mTLc), calculated as the weighted average of the TL of caught species and the mean trophic level of the community (mTLco), which was estimated as the weighted average of the TL for functional groups with a TL > 2 (Christensen, 1996); the Primary Production Required to sustain the fishery (%PPR, considering Pp); and the Primary Production Required to sustain the fishery (%PPR, considering Pp + detritus) (Pauly and Christensen, 1995), the loss in production index (L_{index}), which represents the loss in secondary production due to fishing, and the probability of an ecosystem being sustainably fished (Psust), which can be used to determine the ecosystem effects of fishing (Libralato et al., 2008).

Finally, the fishing mortality 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 ecological group.

2.5.5. *Comparative analysis with other adjacent ecosystems*

To test our original hypothesis, we contrasted results obtained from our GoA model with other models previously implemented in the Mediterranean Sea as the Northwestern Mediterranean model (NWM) (Corrales et al., 2015) and in the Atlantic area as the Gulf of Cadiz model (GoC) (Torres et al., 2013). A similar methodology was used to build the three models, which are similar in terms of ecological structure (Heymans et al., 2016) and cover similar bathymetric range along the Spanish Mediterranean Coast including the Gulf of Cadiz in the Atlantic side.

3. Results

3.1. *Quality and uncertainty of the model*

The Pedigree index calculated by the model was 0.55. The majority of sources of uncertainty were associated with the biomass estimations for several groups, in particular for the invertebrate groups (Table 2). However, most of the diet composition data for predators representing the food web in the study area as well as data regarding landings and discards were all collected at local level and therefore showed a low degree of uncertainty.

3.2. *Description by functional group*

Overall, ecotrophic efficiencies were high (EE > 0.95), mainly for those groups specially predated and exploited in the system, such as fish and invertebrate groups (e.g., *Demersal ichthyophagous fishes*, *Mullets* and

Table 2

Summary statistics and ecosystem indicators for the Gulf of Alicante in comparison with models of nearby areas. GoA = Gulf of Alicante; NWM = Northwestern Mediterranean Model; GoC = Gulf of Cadiz. All units are provided in the table.

	GoA	NWM	GoC	Units
Ecosystem Information				
Years modeled	2011	1999–2003	2009	
Depth range	50–800	0–1000	15–800	m
Area modeled	7085	45,547	7224	km^2
Number of functional groups	45	54	43	
Number of primary producers	2	4	1	
Ecopath Pedigree index	0.55	0.62	0.63	
Ecosystem Indicators				
Sum of all Consumptions (TQ)	789.04	897.27	1946.9	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all Exports (E)	511.93	1088.08	2233.7	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all Respiratory Flows (TR)	398.19	279.55	955.1	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all Flows to Detritus (TFD)	866.77	1493.14	2599.2	$t \cdot km^{-2} \cdot year^{-1}$
Total System Throughput (TST)	2565.93	3758.03	7734.9	$t \cdot km^{-2} \cdot year^{-1}$
Sum of all Production (TP)	1095.33	1599.93	3704.4	$t \cdot km^{-2} \cdot year^{-1}$
Calculated Total Net Primary Production (NPp)	909.47	1366.1	3187.7	$t \cdot km^{-2} \cdot year^{-1}$
Total Primary Production/Total Respiration (Pp/R)	2.28	4.89	3.3	
Net System Production (NT)	511.27	1086.55	2231.6	$t \cdot km^{-2} \cdot year^{-1}$
Total Primary Production/Total Biomass (Pp/B)	31.30	32	39.8	
System Omnivory Index (SOI)	0.26	0.19	0.18	
Total Biomass (excluding detritus) (TB)	29.06	42.69	80.02	$t \cdot km^{-2}$
Mean Trophic Level of the community (mTLco)	1.18	1.38	1.61	
mTLco (excluding TL = 1)	2.32	2.48	2.55	
Fishery Indicators				
Total Catches (TC)	1.94	4.18	4.55	$t \cdot km^{-2} \cdot year^{-1}$
Mean Trophic Level of the Catch (mTLc)	3.16	3.13	3.32	
Gross Efficiency of the fishery (GE)	0.002	0.003	0.001	
Primary Production Required to sustain the fishery (PpR, considering Pp)	16.28	12.08	12.97	%
Primary Production Required to sustain the fishery (PpR, considering Pp + detritus)	22.67	17.36	16.45	%
Psust	66.2	28.4	22.8	%
Recycling Indicators				
Finn's cycling index (of total throughput) (FCI)	9.33	9.12	3	% of TST
Finn's mean Path Length (MPL)	2.82	2.75	2.43	
Predatory cycling index (PCI)	2.04	0.56	8	% of TST without detritus
Mean Transfer Efficiency (mTE)	13.9	14.3	14.3	%
TE From primary producers	14.8	15.4	15.5	%
TE From detritus	12.9	13.3	18.6	%

Crabs), pointing out that total mortality in the system was mainly driven by predation and fishing. On the other hand, those groups without predation mortality or exploitation such as top predators showed lower EE (e.g., *Dolphins*, *Seabirds* and *Large pelagic fishes*) (Table 1).

Trophic levels ranged from TL = 1 for primary producers and detritus group, to TL = 4.15 for *Anglerfishes* and 4.07 for *Dolphins*. Within the fish community, *Sardine* and *Small pelagics* showed the lowest values (2.17 and 3.08, respectively) due to the dominant presence of phytoplankton and zooplankton groups in their diet. In the case of Cephalopods, TLs ranged between 3.74 for *Benthic cephalopods* to 3.42 for *Octopuses*. For crustaceans, natantia presented higher trophic levels (e.g., *Blue and red shrimp*, 3.34) than reptantia (*Crabs*, 2.92) (Table 1).

The partition of natural mortality (M) beyond planktonic groups showed higher values of mortality caused by predation (M2) for *Benthic cephalopods*, *Crabs*, *Other shrimps*, *Worms*, *Benthopelagic cephalopods*, Gelatinous plankton feeders and *Mesopelagic fishes*. Concerning non-predation natural mortality (M0) and also beyond planktonic groups, *Seabirds*, *Norway lobster*, *Worms* and *Deep water rose shrimp* showed the highest values (Table 1).

3.3. Mixed trophic impact and Keystoneness

The results of the mixed trophic impact routine (MTI) showed that all groups had a negative impact on themselves due to within-group competition, especially for *Worms*, *Microzooplankton*, *Gelatinous plankton*, *Large pelagic fishes*, *Gelatinous plankton feeders*, and *Phytoplankton* (Fig. 2). An increase of *Adult hake* would have a negative impact on *Juvenile hake* due to cannibalism. In addition, an increase of *Microzooplankton* could have an indirect negative impact on *Bivalves and gastropods* and *Sardine* due to competition for preys. Numerous functional groups in the model were positively impacted by the groups at the base of the food web such as *Phytoplankton*, *Micro-*, *Meso- Macrozooplankton*, *Suprabenthos* and *Other benthic invertebrates*.

Regarding the fishing activity, the bottom trawling fleet had the highest impact on most ecosystem compartments and the largest impacts on some demersal groups, primarily *Anglerfishes*, *Deep water rose shrimp*, *Rays and skates*, *Benthic sharks*, *Octopuses*, *Blue and red shrimp*, *Adult hake* and, to a lesser extent *Norway lobster*, *Blue whiting* and *Mullets*. The purse seine fishery showed important negative impacts on their target species (small pelagics) and *Demersal ichthyophagous fishes* possibly due to the removal of prey. There was a slight negative impact on *Dolphins* because they compete for their prey. The small scale fishery had a negative impact on *Sparids* and, to a lesser extent, on *Octopuses*, *Pelagic ichthyophagous fishes* and *Mullets*. The longline fishery presented large negative impacts on its main target species (*Large pelagic fishes*).

With respect to the interactions between fleets, bottom trawls produced the highest negative impact on small-scale fisheries. Bottom trawl, longlines, and purse seine revealed strong competition between themselves while small-scale fisheries did not.

The keystoneness index analysis using Valls Keystone Index identified top predators such as *Adult hake*, *Dolphins*, *Anglerfishes* and *Octopuses* as potential keystone species in the GoA ecosystem (Fig. 3).

3.4. Trophic flows and ecosystem indicators

The flow diagram representing the main links between functional groups and the flow of energy illustrated that main trophic flows originated from the trophic groups located at the base of the trophic web (*Detritus* and *Phytoplankton*), which transfer their energy to groups with higher TLs (Fig. 4). Among fish groups, small pelagics such as *Sardine* were the most important component in terms of flows to detritus.

Of the Total System Throughput (TST%), 30.8% of the flows were consumed in the ecosystem, 33.8% became part of the detritus, 15.5% were attributed to respiration, and of the remaining 20% considered as export outside the ecosystem, 99% was due to detritus. Thus, the ecosystem was dominated mainly by detritus flow and consumption.

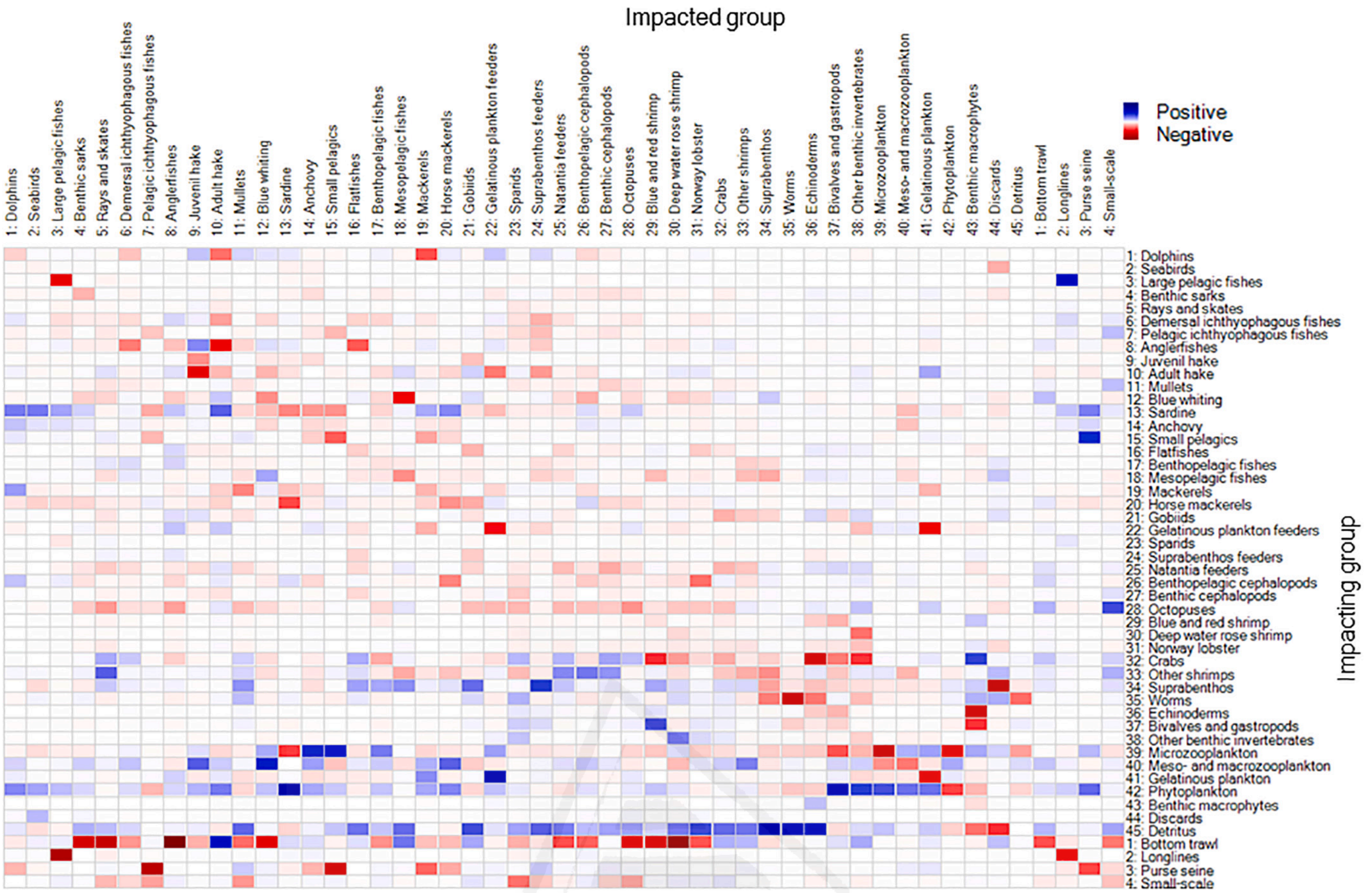

Fig. 2. Mixed trophic Impact (MTI) analysis of the GoA model. Negative (red) and positive (blue) impacts are represented. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The mean transfer efficiency (mTE) obtained from primary producers up the food web (14.9%) was higher than the mTE of the detritus food web (13.0%), which highlighted that the GoA ecosystem was more limited by primary producers than by detritus (Table 2).

The total biomass supported by the ecosystem was estimated at 104.8 t*km^{-2}, which corresponded to 48.3%, 13.8%, and 37.9% of the demersal, pelagic, and planktonic domains, respectively. The dominance of *Phytoplankton* (21.3%), *Worms* (21.2%), *Microzooplankton* (12.7%) and *Sardine* (9.8%) was remarkable. In addition, 93.9% of the total production came from *Phytoplankton* (83.0%) and *Microzooplankton* (10.9%), while *Microzooplankton* (56.4%) and *Worms* (23.5%) concentrated the 79.8% of the total consumption. In the case of flow to detritus, it was dominated by *Phytoplankton* (64.6%), *Microzooplankton* (18.4%) and *Worms* (11.4%).

The Pp/R ratio, close to unity in mature ecosystems, was high in the GoA, which indicates that there was a higher production (2.28 times more) of energy in the ecosystem. In the case of the Pp/B, the GoA presented a high value (31.3), reflecting a low level of biomass accumulation within the system compared to its productivity. The system omnivory index, also correlated with system maturity, showed an intermediate value (0.26) when compared with other Mediterranean regions, highlighting a certain level of food chain complexity of the system. In this context, it is noteworthy to mention the low values of the functional groups *Microzooplankton* (0.02), *Echinoderms* (0.02), *Worms* (0.03) and *Sardine* (0.19), whilst those found with a more diverse diet were *Pelagic ichthyophagous fishes* (1.4), *Large pelagic fishes* (1.02) and *Seabirds* (0.76). The importance of cycling through Finn's cycling index and the mean Path Length revealed differences between the GoA and GoC ecosystems (Table 2).

3.5. *ECOIND analysis*

Concerning the Demersal/Pelagics Biomass-based indicator (1.35), the dominance of the demersal compartment in the GoA model was highlighted (Table 3), which is in line with results from the GoC (1.57), and in contrast with those obtained from the NWM (0.42). In the same line were the results of the ratio Invertebrates/Fish Biomass-based indicator. Similarly, this ratio showed a high proportion of the invertebrate compartment in the GoA (3.09) and GoC areas (1.67), in contrast with the NWM results (0.29), with low relevance of invertebrates. In turn, the biomass of fish species was much lower in GoA (5.47 t*km^{-2}) if compared with the values obtained for NWM (10.59 t*km^{-2}) and GoC (16.27 t*km^{-2}) (Table 3).

Regarding Catch-based indicators, total catch in GoA (1.84 t*km^{-2}) was lower than that obtained in NWM (4.14 t*km^{-2}) and GoC (4.55 t*km^{-2}). In the case of the pelagic fraction, the lowest catches were observed in GoA (1.16 t*km^{-2}). In this case, the Demersal/Pelagics Catch-based indicator showed intermediate values (0.55 t*km^{-2}) between NWM and GoC (0.30 and 0.80 t*km^{-2} respectively). Likewise, Trophic-based indicators analyzed showed intermediate values for the GoA model (3.16) between NWM and GoC (0.11 and 3.32, respectively) (Table 3).

With respect to Species-based indicators, the 'Intrinsic vulnerability index of the catch' (IVIc) in the GoA showed the lower values in comparison with the other two models. Similar results were obtained for the 'biomass of endangered species in the community using the IUCN' (International Union for Conservation of Nature (IUCN) Red List of species at risk (IUCN, 2015) (IUCN species B) and in the 'catch of endangered species in the community using the IUCN' (IUCN species C) (Table 3).

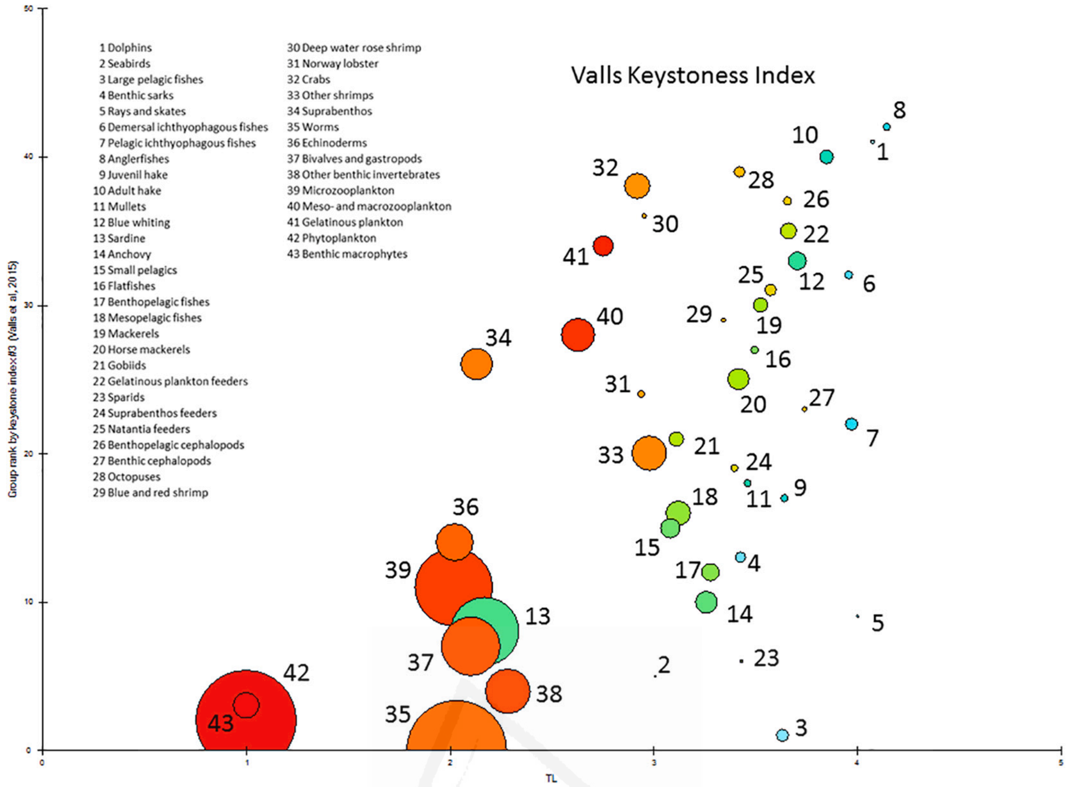

Fig. 3. Functional groups plotted against keystone index of Valls and trophic level. The numbers identify the functional groups of the model (see Table 1). Circle size is proportional to the biomass of the functional group.

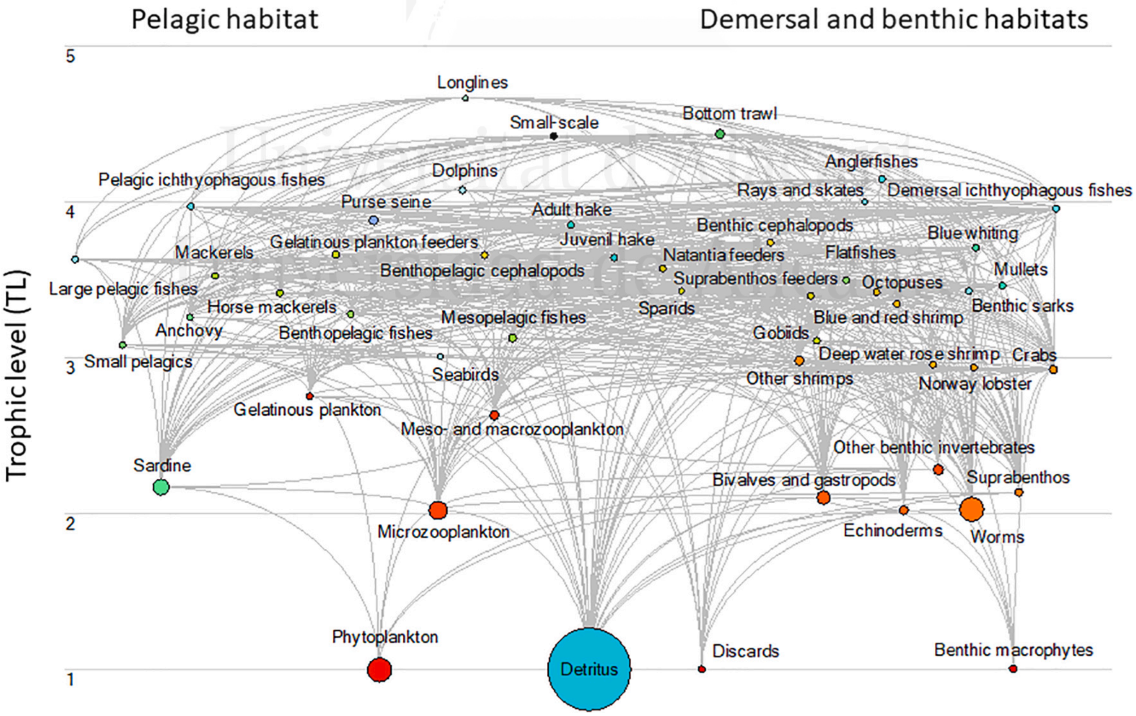

Fig. 4. Flow diagram defining the structure of the Gulf of Alicante Ecopath model. The scale on the left corresponds to the trophic level and circles are scaled to the group's biomass.

3.6. Fishing impacts

Octopuses, *Sparids*, *Small pelagics*, *Benthopelagic cephalopods* and *Mullets* presented the highest values of fishing mortality (F). Despite the high exploitation rates (F/Z), just a few groups (*Sparids* or *Octopuses*) exceeded the recommended rates (0.5) for overexploited demersal stocks (Mertz and Myers, 1998; Rochet and Trenkel, 2003) while *Small pelagics*, *Mackerel*, *Horse mackerel* and *Pelagic ichthyophagous fishes*

Table 3

Ecological indicators comparing across the Gulf of Alicante (GoA) (results from this study), the North Western Mediterranean (NWM) (Corrales et al., 2015) and the Gulf of Cadiz (GoC) (Torres et al., 2013).

Indicator	Description	NWM (1999–2003)	GoC (2009)	GoA (2011)	Units
A. Biomass-based					
Total B	Total biomass (B)	130.48	152.10	104.76	t*km^{-2}
Commercial B	Biomass (B) of commercial species	16.64	29.26	9.23	t*km^{-2}
Fish B	Biomass (B) of fish species	10.59	16.27	5.47	t*km^{-2}
Invertebrates B	Biomass (B) of invertebrate species	3.05	27.24	16.89	t*km^{-2}
Invertebrates/ Fish B	Biomass (B) of invertebrates over fish	0.29	1.67	3.09	
Demersal B	Biomass (B) of demersal species	4.10	19.63	12.38	t*km^{-2}
Pelagic B	Biomass (B) of pelagic species	9.65	12.50	9.15	t*km^{-2}
Demersal/ Pelagic B	Biomass (B) of demersal over pelagic species	0.42	1.57	1.35	
Predatory B	Biomass (B) of predatory organisms with trophic level $\leq$ 4	0.86	0.49	0.05	t*km^{-2}
Kempton's Q	Kempton's biodiversity index (Q)	8.05	5.49	6.39	
B. Catch-based					
Total C	Total Catch (C)	4.14	4.55	1.84	t*km^{-2}
Fish C	Catch (C) of all fish species	3.60	3.23	1.47	t*km^{-2}
Invertebrate C	Catch (C) of all invertebrate species	0.53	1.32	0.32	t*km^{-2}
Invertebrates/ Fish C	Catch (C) of invertebrates over fish	0.15	0.41	0.22	
Demersal C	Catch (C) of demersal species	0.95	2.02	0.63	t*km^{-2}
Pelagic C	Catch (C) of pelagic species	3.18	2.53	1.16	t*km^{-2}
Demersal/ pelagic C	Catch (C) of demersal over pelagic species	0.30	0.80	0.55	
Predatory C	Catch (C) of predatory organisms with trophic level 4	0.20	0.28	0.03	t*km^{-2}
Discards	Total discarded catch	0.86	1.13	0.19	t*km^{-2}
C. Trophic-based					
TL catch	Tropic level (TL) of the catch	3.11	3.32	3.16	
MTI	Marine trophic index, trophic level (TL) of the catch (including organisms with TL $\leq$ 3.25)	3.64	3.68	3.55	
TL co.	Trophic level (TL) of the community (including all organisms)	1.39	1.61	1.28	
TL co. 2	Trophic level (TL) of the community (including organisms with TL $\leq$ 2)	2.49	2.55	2.32	
TL co. 3.25	Trophic level (TL) of the community (including organisms with TL $\leq$ 3.25)	3.63	3.71	3.54	
TL co. 4	Trophic level (TL) of the community (including organisms with TL $\leq$ 4)	4.13	4.18	4.11	
D. Species-based					
Intrinsic Vul. Index	Intrinsic Vulnerability Index of the catch	35.94	38.31	38.62	
Endemics B	Biomass (B) of endemic species in the community	0.08	0.00	0.00	t*km-2
Endemics C	Endemic species in the catch (C)	0.05	0.00	0.00	t*km-2
IUCN species B	Biomass (B) of IUCN-endangered species in the community	0.42	0.60	0.13	t*km-2
IUCN species C	IUCN-endangered species in the catch (C)	0.10	0.12	0.07	t*km-2

exceeded the 0.4 recommended rate for overexploited pelagics stocks (Patterson, 1992) (Table 1).

The primary production required to sustain the fishery (%PPR) in the GoA during 2011 was 16.28%, taking into account only the primary producers. When considering both the primary producers and detritus, the value was 22.67%, suggesting the importance of detritivorous organisms within the catch. These values were the highest of all three compared models (Table 2). In turn, the probability of the GoA being sustainably exploited (P_{sust}) using the estimated Loss in production index (L_{index}) score was low (66%), but higher than values obtained for NWM and GoC ecosystems (28% and 23%, respectively) (Table 2).

4. Discussion

From a trophodynamic point of view, marine ecosystems off the Eastern Iberian coast have been poorly studied and there is still a need to fulfill that knowledge gap, particularly in the meso-scale. The underlying hypothesis of our study was that the singular characteristics of the Gulf of Alicante would cause an organization of the ecosystem that would differentiate it from neighboring ecosystems. These features should be reflected in a different food-web structure and functioning; thereby the Ecopath model presented here is the first attempt to test this hypothesis. The addition of the GoA model to the list of published studies available from the Western Mediterranean Sea (e.g., Coll et al., 2006; Torres et al., 2013; Corrales et al., 2015) allows the possibility of further comparing these meso-scale marine ecosystems, testing the variability and similarities in the ecosystem structure along the north-south axes on the east coast of the Iberian Peninsula (Western

Mediterranean), including the Gulf of Cádiz in the Atlantic coast. With this study we cover an existing knowledge gap in terms of ecosystem modeling, with relevance to trophic ecology and the fisheries management. This study will also be relevant in the context of the MSFD and the new steps to follow towards the achievement of a Good Environmental Status (GES) within European Seas.

Our model was primarily based on data collected from local studies giving a pedigree index value of 0.55, in line with those obtained for nearby Ecopath models. This value places the model at the mid-upper end of the range reviewed for a large number of models worldwide (Morissette, 2007) and suggests that the inputs used in this model were of relatively high quality. This is especially true for the trophic data used in this model (García-Rodríguez et al., 2020, García-Rodríguez et al., 2021). However, the continuous incorporation of new empirical data from the region into the model can improve these results in the future. For example, estimations of IUUs and recreational fleet data may be used in the future for a better understanding of the real impacts of fishing activity in the area.

Results from the trophic model (GoA) showed that the main differences found in comparison with neighboring areas are related to the lower primary production of the system (mainly influenced by local oceanographic conditions), which determines the higher importance of the demersal compartment, where most biomass was associated to the detritus food web, and lower catches.

4.1. *Ecosystem structure and functioning of the Gulf of Alicante*

High values of ecotrophic efficiencies and mortality rates suggested that the ecosystem is highly constrained by predation and fishing mortalities. The case of exploited fishes and invertebrate groups for which the EE were almost 1 is remarkable. The phytoplankton group also showed relatively high values in agreement with the oligotrophic nature of this ecosystem. These results contrast with those reported by Coll et al. (2006) and Corrales et al. (2015), who found in their models located northwards of GoA lower values of EE for some functional groups, suited to more productive ecosystems (Estrada, 1996; Agostini and Bakun, 2002).

Concerning the trophic levels, they were overall consistent with values published for those species in the Mediterranean Sea (Karachle and Stergiou, 2017) and other ecological models of nearby areas (Coll et al., 2006; Corrales et al., 2015; Torres et al., 2013). The low values of TL of *Seabirds* ($TL = 3.01$), which are considered top predators, were in agreement with previously reported values as a consequence of the high percentage of discards in their diet, which is assumed to be parameterized as a detritus group and therefore, resulting in underestimated trophic levels (Coll et al., 2006).

The mixed trophic impact analysis highlighted the importance of groups located at the base of the food web such as *Phytoplankton*, *Micro-*, *Meso- Macrozooplankton*, *Suprabenthos*, *Other benthic invertebrates*, highlighting the importance of bottom-up flow control interactions occurring in the ecosystem. All of these findings, together with the important role of the detritus as a source of food, are consistent with those observed in the NWM and GoC models. However, we did not find a notable interaction between the pelagic and the demersal groups, which is in contrast with important bentho-pelagic coupling observed in other Mediterranean ecosystems (Agnetta et al., 2019; Ricci et al., 2019). This could be related to the higher productivity and high fishing pressure reported in these areas (Coll et al., 2006; Torres et al., 2013; Corrales et al., 2015).

The keystoness index highlighted the importance of top predators in the ecosystem. Indeed, *Dolphins* and *Octopuses* were selected as keystone groups in other Mediterranean models (e.g. Southern Catalan Sea, Coll et al., 2006, 2013; Northeastern Ionian Sea, Piroddi et al., 2010; Carlucci et al., 2021).

4.2. *Trophic flows and ecosystem statistics of the Gulf of Alicante*

The main trophic flows in the GoA were originated from the functional groups located at the lower levels of the trophic network. Likewise, a large percentage of primary production flowed to the detritus, highlighting its role within the ecosystem, which evidenced the importance of this compartment. Similarly, the levels of primary production were shown to be lower than those obtained in the NWM and GoC models, which consequently resulted in a smaller size of the entire system in terms of flows (Ulanowicz, 1986). These results agreed with the TST values obtained for the three models compared, where the GoA has, by far, a different size in terms of total energy flow.

Regarding the transfer efficiencies (TEs), the highest values were observed for TLs II-IV, which can be related to the low productivity of the ecosystem (Shannon et al., 2003; Coll et al., 2006). This suggests a good coupling between preys and their predators, showing more efficient use of energy if compared to the average value of 10% estimated by Pauly and Christensen (1995) for marine ecosystems. The ecosystem then may be food limited (Shannon et al., 2003), in line with findings reported in the other three models. According to the attributes of maturity sensu Odum (1969), the Pp/R ratio in the GoA was the lowest value of the three compared models, especially in the case of NWM. Also, the Pp/B ratio, which is supposed to decrease in developing ecosystems, presented a high value in the GoA, in line with the results of NWM, but lower than GoC, where higher values of Pp/B ratio reflected a low level of biomass accumulation within the system.

In addition, the proportion of throughput cycled within the ecosystem (%FCI) was higher than in the other two models, which may be related to lower levels of stress, just as could be the case of NWM and GoC (e.g., higher fishing pressure). Likewise, food-web complexity indices such as the System Omnivory Index and Finn's mean Path Length showed higher values than those obtained for compared models.

These results suggest that the GoA presents a higher level of complexity of internal flows, which is correlated with stability and maturity. This indicates that the system looks more like a web-like than a chain-like structure (Christensen, 1995), in contrast with the linearity detected in the food web of NWM and GoC ecosystems. Hence, the GoA may be in a higher development stage sensu Odum (1969), which remains efficient and stable, but is also delicate and vulnerable because it depends on the efficient and circular use of its biomass and it is primary production limited. These features may be partially related to the relatively lower fishing activity carried out in the area (see next section).

4.3. *The impact of fishing activities in the Gulf of Alicante*

The GoA showed lower values of catch per unit of surface compared to neighboring areas (Table 2) but high values of fishing mortality for most of the commercial groups in 2011 (*Octopuses*, *Sparids*, *Small pelagics* and *Benthopelagic cephalopods*) (Table 1). These results were in line with results obtained in available independent stock assessments (GFCM, 2012a, 2012b) and with results reported by nearby models. Regarding exploitation rates (F/Z), taking into account the recommended rates for overexploited demersal (0.5) and pelagics (0.4) stocks (Mertz and Myers, 1998; Rochet and Trenkel, 2003; Patterson, 1992), the three ecosystems compared presented high values for demersal and pelagic target species. In the case of the GoA, both, demersal and pelagic functional groups presented high exploitation rate values, namely for *Rays and skates*, *Anglerfishes*, *Mullets*, *Octopuses*, *Small pelagics*, *Mackerels*, *Horse mackerels* and *Pelagic ichthyophagous fishes*. In the NWM, exploitation rates were remarkable for *Atlantic bluefin tuna* and *Adult sardine* too, while in the GoC, *Common octopus, Anglerfishes* and *Mackerels* had values above the recommended rates.

The primary production required to sustain the fishery (%PPR) in the GoA during 2011 was the highest of all three compared models but was within the range of values from temperate shelves recorded by Pauly and Christensen (1995). However, the probability of the ecosystem being sustainably exploited (P_{sust}), based on the estimated loss in production index (Libralato et al., 2008), pointed out a moderate exploitation, lower than those achieved in NWM or GoC ecosystems. This is mainly due to a lower total amount of catches and an intermediate Trophic Level of the catch (see next section).

Similarly, the 'Intrinsic vulnerability index of the catch' (IVIc) (Cheung et al., 2007), the 'Biomass of IUCN-endangered species in the community' (IUCN species B), and the 'Biomass of IUCN-endangered species in the community' (IUCN species C) showed lower values for the GoA, pointing out again to the lower fishing pressure in the area with the consequent decrease of the proportion of endangered species captured.

4.4. The Gulf of Alicante and its neighboring systems

Total catches in the GoA were lower than in ecosystems compared, consistent with the lowest biomasses, especially in the case of fish biomass, and hence in accordance with the low levels of primary production in the area (Estrada, 1996). In this regard, our results revealed the importance of the demersal versus pelagic compartment in the GoA ecosystem, exhibiting a high recycling efficiency. As a result of this, the mean trophic level of the catch in the GoA was slightly higher than in the NWM but lower than the GoC, probably due to the larger proportion of demersal species, with an overall high trophic level reported in the landings of these ecosystems. Despite a low value of mTLc, it is considered as a sign of a distinguished characteristic of Mediterranean exploited ecosystems (Pauly et al., 1998; Bas et al., 1985). In the case of the three ecosystems studied, it seemed to be related with 'Demersal/Pelagic biomasses ratio'. Indeed, the ratios 'D/P biomasses' used as standardized ecological indicators (Pennino and Bellido, 2012; Coll and Steenbeek, 2017), evidenced to be opposite to those described in the NWM, where the pelagic compartment plays a stronger role (Coll et al., 2006; Corrales et al., 2015). Consequently, small pelagics catches northwards in the GoA ecosystem were almost three times higher. This may be associated with the influence of river inputs, which were significantly low in the GoA (e.g., Segura River), impacting the low productivity of the area, in contrast with the highest values of river discharges (e.g., Ebro) in the Catalan sea (Estrada, 1996).

4.5. Conclusions

The comparisons undertaken in this study revealed common features between the three ecosystems considered. However, the GoA ecosystem did show differences in structural features with the two other models located north and south of the study area. This information allows us to link these features to some observed patterns and ecosystem properties, such as low productivity and low catches. According to our results, the GoA should be defined as a detritus-based system, bottom-up controlled, and dominated by the demersal compartment. Despite being an exploited ecosystem, the GoA presents a higher development stage than compared neighboring models likely due to lower fisheries pressure. The approach presented here contributes to our understanding of Mediterranean marine ecosystems functioning, from both ecological and fisheries perspectives, providing a comprehensive image of an ecosystem by following a comparative approach of nearby areas. This study represents a baseline from where to develop simulations of different exploitation scenarios taking into account climate change and alternative management options.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table A.1 Species composition by functional group

Functional group	Species composition. Description
1.Dolphins	*Stenella coeruleoalba, Tursiops truncates*.
2.Seabirds	*Alca torda, Chroicocephalus ridibundus, Larus audouinii, L. fuscus, L. melanocephalus, L. michahellis, Morus bassanus, Phalacrocorax aristotelis, Puffinus mauretanicus, P. yelkouan, Stercorarius skua*.
3.Large pelagic fishes	*Thunnus thynnus, Xiphias gladius*.
4.Benthic sharks	*Etmopterus spinax, Galeus melastomus, Scyliorhinus canicula*
5.Rays and Skates	*Raja asterias, Raja brachyura, Raja clavata, Raja montagui, Torpedo marmorata*
6.Demersal ichthyophagous fishes	*Conger conger, Helicolenus dactylopterus, Lepidopus caudatus, Molva dypterygia, Pagrus pagrus, Scorpaena elongata, Scorpaena scrofa, Trachinus draco, Uranoscopus scaber, Zeus faber*
7.Pelagic ichthyophagous fishes	*Auxis rochei rochei, Euthynnus alletteratus, Lichia amia, Sarda sarda, Seriola dumerili, Sphyraena sphyraena*.
8.Anglerfishes	*Lophius budegassa, L. piscatorius*
9.Juvenile hake	*Merluccius merluccius* < 15 cm
10.Adult hake	*Merluccius merluccius* ≥ 15 cm
11.Mullets	*Mullus barbatus, M. surmuletus*
12.Blue whiting	*Micromesistius poutassou*
13.Sardine	*Sardina pilchardus*
14.Anchovy	*Engraulis encrasicolus*
15.Small pelagics	*Sardinella aurita, Spicara smaris*
16.Flatfishes	*Arnoglossus imperialis, A. laterna, A. rueppelii, A. thori, Citharus linguatula, Lepidorhombus boscii, L. whiffiagonis, Microchirus variegatus, Solea solea*
17.Benthopelagic fishes	*Argentina sphyraena, Capros aper, Cepola macrophthalma, Gadiculus argenteus argenteus, Glossanodon leioglossus, Macroramphosus scolopax*
18.Mesopelagic fishes	*Ceratoscopelus maderensis, Hymenocephalus italicus, Lampanyctus crocodilus, Maurolicus muelleri, Myctophum punctatum, Notoscopelus elongatus, Stomias boa boa*
19.Mackerels	*Scomber colias, S. scombrus*
20.Horse mackerels	*Trachurus mediterraneus, T. picturatus, T. trachurus*
21.Gobiids	*Aphia minuta, Blennius ocellaris, Callionymus maculatus, Crystallogobius linearis, Deltentosteus quadrimaculatus, Gobius niger, Lesueurigobius friesii, Synchiropus phaeton*
22.Gelatinous plankton feeders	*Boops boops, Pagellus bogaraveo*
23.Sparids	*Diplodus annularis, D. vulgaris, Spondyliosoma cantharus*
24.Suprabenthos feeders	*Lepidotrigla cavillone, Lepidotrigla dieuzeidei, Nezumia aequalis, Pagellus acarne, Spicara maena*
25.Natantia feeders	*Chelidonichthys cuculus, Chelidonichthys lastoviza, Chelidonichthys obscurus, Coelorinchus caelorhincus, Eutrigla gurnardus, Gaidropsarus biscayensis, Pagellus Erythrinus, Phycis blennoides, Scorpaena notata, Scorpaena porcus, Serranus cabrilla, Serranus hepatus, Trachyrincus scabrus, Trigla lyra, Trisopterus minutus*
26.Benthopelagic cephalopods	*Abralia veranyi, Alloteuthis media, Alloteuthis subulata, Illex coindetii, Loligo vulgaris, Todarodes sagittatus*
27.Benthic cephalopods	*Callistoctopus macropus, Octopus salutii, Pteroctopus tetracirrhus, Rossia macrosoma, Scaeurgus unicirrhus, Sepia elegans, Sepia officinalis, Sepia orbignyana, Sepietta oweniana*
28.Octopuses	*Eledone cirrhosa, Eledone moschata, Octopus vulgaris*
29.Blue and red shrimp	*Aristeus antennatus*
30.Deep water rose shrimp	*Parapenaeus longirostris*
31.Norway lobster	*Nephrops norvegicus*
32.Crabs	*Atelecyclus rotundatus, Calocaris macandreae, Dardanus arrosor, Ebalia* spp., *Ethusa mascarone, Eurynome aspera, Galathea* spp., *Geryon longipes, Goneplax rhomboides, Inachus* spp., *Liocarcinus* spp., *Macropipus tuberculatus, Macropodia* spp., *Medorippe lanata, Monodaeus couchii, Munida* spp., *Pagurus* spp., *Palinurus* spp., *Parthenope* spp., *Pisa armata, Polycheles typhlops, Rissoides desmaresti, Scyllarus* spp., *Squilla mantis, Upogebia* spp.
33.Other shrimps	*Aegaeon* spp., *Alpheus glaber, Athanas* spp., *Chlorotocus crassicornis, Eusergestes arcticus, Gennadas elegans, Pasiphaea multidentata, P. sivado, Philocheras* spp., *Plesionika acanthonotus, P. antigai, Plesionika edwardsii, P. gigliolii, P. heterocarpus, P. martia, P. narval, Pontophilus* spp., *Processa* spp., *Sergia robusta, Solenocera membranacea*
34.Suprabenthos	Amphipods, cumaceans, isopods, mysids
35.Worms	Nematods, annelids
36.Echinoderms	*Antedon mediterranea, Astropecten aranciacus, A. irregularis, Cidaris cidaris, Echinaster sepositus, Gracilechinus acutus, Echinus melo, Holothuroidea, Luidia* spp., *Marthasterias glacialis, Ophidiaster ophidianus, Ophiura ophiura, Parastichopus regalis, Spatangus purpureus, Sphaerechinus granularis, Tethyaster subinermis*

37.Bivalves and gastropods	*Acanthocardia* spp., *Aporrhais serresianus, Bolma rugosa, Atrina fragilis, Bolinus brandaris, Calliostoma granulatum, Bivetiella cancellata, Galeodea echinophora, Cuspidaria cuspidata, Neopycnodonte cochlear, Nucula* spp., Opistobranchia, *Pteria hirundo, Scaphander lignarius, Tellina* spp,, *Turritella* spp., *Venus* spp., *Xenophora crispa*
38. Other benthic invertebrates	Porifera, Cnidaria, *Scalpellum scalpellum, Veretillum cynomorium, Funiculina quadrangularis, Pennatula rubra, Aplidium conicum, Diazona violacea,* Ascidiidae, *Ascidiella aspersa, Ascidiella scabra, Ascidia mentula, Phallusia mammillata, Polycarpa pomaria, Botryllus schlosseri, Microcosmus* spp., *Molgula* spp., Hydrozoa, *Geodia* spp., *Epizoanthus* spp., *Alcyonium palmatum, Pteroeides spinosum, Suberites domuncula, Halocynthia papillosa, Microcosmus sabatieri, Ircinia oros, Microcosmus vulgaris, Molgula appendiculata, Polycarpa mamillaris, Ascidiella* spp.
39.Microzooplankton	Copepoda, Ostracoda, *Branquiostoma, Acrania*, Planktonic eggs
40.Meso- and macrozooplankton	Hyperiidea, Euphausiacea, Crustacean larvae, Fish larvae, Pteropoda
41.Gelatinous plankton	Cnidaria, Diphyidae, Salpida, Hydrozoa, Scyphozoa, *Pyrosoma atlanticum, Cymbulia peronii*

Table A.2. Landings (t·km^{-2}·year^{-1}) by functional group and fleet

Functional group	Bottom trawl	Longlines	Purse seine	Small-scale	Total
1. Dolphins	-	-	-	-	-
2. Seabirds	-	-	-	-	-
3. Large pelagic fishes	0.000	0.005	-	0.000	0.005
4. Benthic sharks	0.007	0.000	-	0.001	0.008
5. Rays and skates	0.004	0.000	-	0.001	0.005
6. Demersal ichthyophagous fishes	0.025	0.001	0.000	0.005	0.031
7. Pelagic ichthyophagous fishes	0.002	0.000	0.045	0.011	0.059
8. Anglerfishes	0.027	-	-	-	0.027
9. Juvenile hake	-	-	-	-	-
10. Adult hake	0.097	0.001	-	0.006	0.104
11. Mullets	0.027	0.000	-	0.011	0.038
12. Blue whiting	0.094	-	-	0.000	0.094
13. Sardine	0.006	-	0.298	0.003	0.308
14. Anchovy	0.012	-	0.075	0.000	0.087
15. Small pelagics	0.003	0.000	0.410	0.000	0.413
16. Flatfishes	0.009	-	-	0.001	0.010
17. Benthopelagic fishes	0.001	-	-	-	0.001
18. Mesopelagic fishes	-	-	-	-	-
19. Mackerels	0.005	0.000	0.031	0.000	0.037
20. Horse mackerels	0.038	0.000	0.041	0.001	0.081
21. Gobiids	0.001	-	-	0.000	0.001
22. Gelatinous plankton feeders	0.014	0.000	0.009	0.001	0.023
23. Sparids	0.006	0.000	0.001	-	0.007
24. Suprabenthos feeders	0.003	-	-	0.001	0.004
25. Natantia feeders	0.056	0.000	0.000	0.007	0.064
26. Benthopelagic cephalopods	0.063	-	0.000	0.000	0.063
27. Benthic cephalopods	0.011	0.000	-	0.005	0.017
28. Octopuses	0.126	0.000	-	0.033	0.159
29. Blue and red shrimp	0.012	-	-	-	0.012
30. Deep water rose shrimp	0.009	-	-	-	0.009
31. Norway lobster	0.016	-	-	-	0.016
32. Crabs	0.051	0.000	-	0.001	0.052
33. Other shrimps	0.008	-	-	0.009	0.017
34. Suprabenthos	-	-	-	-	-
35. Worms	-	-	-	-	-
36. Echinoderms	0.000	-	-	-	0.000
37. Bivalves and gastropods	0.000	-	-	0.000	0.000
38. Other benthic invertebrates	-	-	-	-	-
39. Microzooplankton	-	-	-	-	-
40. Meso- and macrozooplankton	-	-	-	-	-
41. Gelatinous plankton	-	-	-	-	-
42. Phytoplankton	-	-	-	-	-
43. Benthic macrophytes	-	-	-	-	-
44. Discards	-	-	-	-	-
45. Detritus	-	-	-	-	-
Sum landings	0.734	0.009	0.910	0.098	1.750
Sum discards	0.178	0.000	0.006	0.011	0.195

Table A.3 Main equations and references used to estimate basic input parameters of the Gulf of Alicante model for 2011. Biomass ($t\cdot km^{-2}$); P/B = production/biomass ($year^{-1}$); Q/B = consumption/biomass ($year^{-1}$); P/Q = production/consumption ratio.

Functional group		***Value***	***Sources and References***
1.Dolphins	Biomass	0.001	Based on abundance estimates for Gulf of Alicante waters (Arcos, pers. comm). Toothed whales that stay in the study area a 95% of the total time
	P/B	0.03	Coll et al., 2006
	Q/B	12.32	Innes et al., 1987 & Trites et al., 1997
	Diet		Astruc, 2005
2.Seabirds	Biomass	0.003	Based on population estimates in the study area from SEO/Birdlife, 2014. Seabirds that stay in the study area a 60% of the total time
	P/B	4.47	Pinnegar, 2000. Data corrected following Optiz, 1996
	Q/B	70.89	Nilsson and Nilsson, 1976
	Diet		Data compiled out of Oro, 1996; Oro et al., 1997; Granadeiro et al., 1998; Arcos, 2001
3.Large pelagic fishes	Biomass	0.095	ICCAT, 2012. Large pelagic fishes that stay in the study area a 50% of the total time
	P/B	0.20	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	1.45	From the empirical equation of Pauly et al., 1990
	Diet		Compiled out of Stergiou and Karpouzi, 2002; Carmona-Antoñanzas et al., 2006
4.Benthic sharks	Biomass	0.068	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.65	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.30	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
5.Rays and Skates	Biomass	0.006	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.19	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.36	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *T. marmorata* (Romanelli et al., 2006)
6.Demersal ichthyophagous fishes	Biomass	0.038	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.56	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.48	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
7.Pelagic ichthyophagous fishes	Biomass	0.096	Estimated by the model
	P/B	1.42	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.65	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Allam et al., 1999; Andaloro and Pipitone, 1997; Falautano et al., 2007; Fletcher et al., 2013; Hajjej et al., 2018
8.Anglerfishes	Biomass	0.034	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.16	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	3.90	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
9.Juvenile hake	Biomass	0.032	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.53	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.83	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
10.Adult hake	Biomass	0.112	Estimated from EwE as multistanza group (lead by Juvenil hake)
	P/B	1.48	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	4.58	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
11.Mullets	Biomass	0.031	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.85	Z=F+M; M= empirical equation from Pauly, 1980

	Q/B	6.36	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
12.Blue whiting	Biomass	0.196	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.83	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.07	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
13.Sardine	Biomass	2.848	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	0.81	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	9.56	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Stergiou and Karpouzi, 2002
14.Anchovy	Biomass	0.293	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	1.05	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	9.87	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Tudela and Palomera, 1997; Costalago et al., 2012
15.Small pelagics	Biomass	0.23	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	2.59	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	8.98	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *S. aurita*, compiled out of Tsikliras et al., 2005
16.Flatfishes	Biomass	0.036	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.87	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	8.40	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *S. solea* and *M. variegatus*, compiled out of Stergiou and Karpouzi, 2002
17.Benthopelagic fishes	Biomass	0.186	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.17	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.11	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *A. sphyraena, G. leioglossus, M. scolopax,* compiled out of Sever et al., 2013; Carpentieri et al., 2016
18.Mesopelagic fishes	Biomass	0.368	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.33	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.26	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020, except for *C. maderensis*, *H. italicus*, *M. muelleri*, *M. punctatum*, *N. elongatus*, *S. boa boa* , compiled out of Sutton and Hopkins, 1996; Stergiou and Karpouzi, 2002; www.fishbase.org
19.Mackerels	Biomass	0.125	Based on abundance estimates from the acoustic surveys MEDIAS (IEO database)
	P/B	0.70	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	5.95	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
20.Horse mackerels	Biomass	0.276	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 and acoustic surveys MEDIAS using Landing factor 2011/2016 (IEO database)
	P/B	0.79	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	7.02	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
21.Gobiids	Biomass	0.127	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.05	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	10.57	From the empirical equation of Pauly et al., 1990
	Diet		www.fishbase.org
22.Gelatinous plankton feeders	Biomass	0.153	Based on abundance estimates from bottom trawl surveys MEDITS and acoustic surveys MEDIAS in 2011 (IEO database)
	P/B	1.67	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.55	From the empirical equation of Pauly et al., 1990

	Diet		García-Rodríguez et al., 2020
23.Sparids	Biomass	0.006	Based on abundance estimates from bottom trawl surveys MEDITS in 2011-2017 (IEO database)
	P/B	2.64	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.64	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020 and data compiled tergiou and out of Stergiou and Karpouzi, 2002; www.fishbase.org
24.Suprabenthos feeders	Biomass	0.030	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.06	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	7.00	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
25.Natantia feeders	Biomass	0.086	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.33	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	6.78	From the empirical equation of Pauly et al., 1990
	Diet		García-Rodríguez et al., 2020
26.Benthopelagic cephalopods	Biomass	0.042	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.20	Sánchez y Olaso, 2004
	Q/B	9.10	Sánchez y Olaso, 2004; Coll et al., 2006
	Diet		Data compiled out of Quetglas et al., 1999; Pierce et al., 2010; Valls et al., 2015; Martinez-Baena et al., 2016; Valls et al., 2017
27.Benthic cephalopods	Biomass	0.014	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.1	Sánchez y Olaso, 2004
	Q/B	8.8	Sánchez y Olaso, 2004; Coll et al., 2006
	Diet		Data compiled out of Bernardino and Guerra, 1990; Quetglas et al., 2005; 2009; Mendes Alves et al., 2006; Giordano et al., 2010; Torres, 2013; Jereb et al., 2015
28.Octopuses	Biomass	0.070	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	3.00	Sánchez y Olaso, 2004
	Q/B	8.50	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Data compiled out of Quetglas et al., 1998; Krstulovic, 2009; Regueira, 2017
29.Blue and red shrimp	Biomass	0.011	Based on stock assessment of Esteban et al., 2011
	P/B	2.11	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	20.57	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Cartes and Sarda, 1989
30.Deep water rose shrimp	Biomass	0.013	Based on stock assessment of Perez Gil et al., 2018
	P/B	2.40	Z=F+M; M= empirical equation from Pauly, 1980
	Q/B	24.12	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Nouar et al., 2011
31.Norway lobster	Biomass	0.029	Based on stock assessment of Esteban et al., 2018
	P/B	5.16	Estimated by the model
	Q/B	19.84	From the empirical equation of Pauly et al., 1990
	Diet		Data compiled out of Cristo and Cartes, 1998
32.Crabs	Biomass	0.396	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.93	Corrales, 2013
	Q/B	7.07	Corrales, 2013
	Diet		Data compiled out of Abello and Cartes, 1987; Abello, 1989; Cartes, 1993a;1993b;1993c; Mili et al., 2013

33.Other shrimps	Biomass	0.731	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.89	Z=F+M; M = Multi-Parameter P/B-Model (Brey, 2001)
	Q/B	8.49	Corrales, 2013
	Diet		Data compiled out of Cartes, 1993b;1993c; Fanelli and Cartes, 2004

34.Suprabenthos	Biomass	0.616	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	7.87	Cartes & Maynou, 1998
	Q/B	52.1	Cartes & Maynou, 2001
	Diet		Data compiled out of Cartes et al., 2001
35.Worms	Biomass	6.180	Based on estimated data of Banarú, 2013
	P/B	5.61	Ropert, 1999; Sanchez and Olaso, 2004
	Q/B	30.00	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Data compiled out of Fauchald and Jumars, 1979
36.Echinoderms	Biomass	0.849	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	0.24	Z=F+M; M = Multi-Parameter P/B-Model (Brey, 2001)
	Q/B	2.75	Albouy et al., 2010; Hattab et al., 2013. Data corrected following Opitz, 1996
	Diet		Data compiled out of Millar, 1971; Rodríguez, 1972; Coulon and Jangoux, 1993; De Juan et al., 2007
37.Bivalves and gastropods	Biomass	2.118	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.63	Estimated by the model
	Q/B	6.78	Pinnegar, 2000; Coll et al., 2006; 2007
	Diet		Based on data compiled out of Perron and Turner, 1978; Lalli and Gilmer, 1989
38.Other benthic invertebrates	Biomass	1.244	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.04	Estimated by the model
	Q/B	4.00	Sanchez and Olaso, 2004; Coll et al., 2006
	Diet		Based on data compiled out of Millar, 1971; Rodríguez, 1972; Coulon and Jangoux, 1993; De Juan et al., 2007
39.Microzooplankton	Biomass	3.705	Based on estimated data of Corrales, 2013
	P/B	32.32	Based on data of Plounevez and Champalbert, 2000; Gaudy et al., 2003
	Q/B	120.00	Pinnegar, 2000. Data corrected following Optiz, 1996
	Diet		Calbet et al., 2002
40.Meso- and macrozooplankton	Biomass	0.682	Based on data estimated by Coll et al., 2006
	P/B	14.97	Based on estimated data by Labat and Cuzin-Roudy, 1996
	Q/B	49.82	Baamstedt and Karlson, 1998
	Diet		Baamstedt and Karlson, 1998
41.Gelatinous plankton	Biomass	0.247	Based on data estimated by Coll et al., 2006
	P/B	12.89	Based on data compiled by Malej, 1989. Data corrected following Opitz, 1996
	Q/B	49.38	Malej (1989). Data corrected following Opitz, 1996
	Diet		Data compiled out of Graham and Kroutil, 2001; Örek, 2000
42.Phytoplankton	Biomass	6.22	From Chl-a via satellite (https://neo.sci.gsfc.nasa.gov); conversion factors from Jorgensen et al., 1991; Dalsgaard and Pauly, 1997
	P/B	146.146	Primary production from via satellite data (https://neo.sci.gsfc.nasa.gov)
43.Benthic macrophytes	Biomass	0.405	Based on abundance estimates from bottom trawl surveys MEDITS in 2011 (IEO database)
	P/B	1.08	Data compiled out of McClanahan et Sala, 1997; Sala and Boudouresque, 1997
44.Discards	Biomass	0.195	From IEO on board observer programme database
45.Detritus	Biomass	75.6	From the empirical equation of Pauly et al., 1993

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TABLE A.4 References of data used for parameterizing the Gulf of Alicante model. Linf: asymptotic length (cm); K: von Bertalanffy growth constant (year); a: intercept; b: allometric constant

Functional groups	L_{inf}		***k***	***Reference***	***a***	***b***	***Reference***
3.Large pelagic fishes							
Thunnus thynnus	315	Fishbase	0.09	Fishbase	0.0196	3.01	Fishbase
Xiphias gladius	237	Mejuto and Serna, 1995	0.12	Fishbase	0.000001	3.55	Fishbase
4.Benthic sharks							
Etmopterus spinax	87.4	MEDITS survey	0.20	Fishbase	0.0030	3.13	Fishbase
Galeus melastomus	48.4	IEO Database	0.42	Darna et al., 2018	0.0025	3.02	Fishbase
Scyliorhinus canicula	76.8	IEO Database	0.20	Fishbase	0.0016	3.16	Fishbase
5.Rays and Skates							
Raja asterias	93.2	MEDITS survey	0.45	MEDITS survey	0.0018	3.27	MEDITS survey
Raja brachyura	91.1	MEDITS survey	0.10	MEDITS survey	0.0028	3.23	MEDITS survey
Raja clavata	93.7	MEDITS survey	0.10	MEDITS survey	0.0024	3.20	MEDITS survey
Raja montagui	76.8	MEDITS survey	0.20	MEDITS survey	0.0002	3.89	MEDITS survey
Torpedo marmorata	61.1	IEO Database	0.19	Duman and Basusta, 2013	0.0273	2.91	MEDITS survey
6.Demersal ichthyophagous fishes							
Conger conger	160.0	IEO Database	0.07	Fishbase	0.0006	3.21	MEDITS survey

Helicolenus dactylopterus	36.8	IEO Database	0.10	Fishbase	0.0127	3.04	MEDITS survey
Pagrus pagrus	47.4	IEO Database	1.90	Fishbase	0.0282	2.80	MEDITS survey
Trachinus draco	41.1	IEO Database	0.08	Fishbase	0.0074	2.93	MEDITS survey
Scorpaena elongata	54.7	MEDITS survey	0.11	Fishbase	0.0249	2.89	MEDITS survey
Uranoscopus scaber	36.3	MEDITS survey	0.20	Fishbase	0.0106	3.15	MEDITS survey
Molva dypterygia	94.7	IEO Database	0.11	Fishbase	0.0009	3.26	MEDITS survey
Zeus faber	64.2	IEO Database	0.30	Fishbase	0.0186	2.88	MEDITS survey
Scorpaena scrofa	50.0	MEDITS survey	0.08	Fishbase	0.0220	2.94	MEDITS survey
Lepidopus caudatus	126.3	IEO Database	0.14	Fishbase	0.0003	3.19	MEDITS survey
7.Pelagic ichthyophagous fishes							
Sarda sarda	85.3	IEO Database	0.72	Fishbase	0.0095	3.10	IEO Database
Euthynnus alletteratus	128.4	Fishbase	0.13	Fishbase	0.0213	2.92	IEO Database
Auxis rochei rochei	52.6	Fishbase	0.70	Fishbase	0.0101	3.13	IEO Database
Lichia amia	121.1	IEO Database	0.22	Smith, 2008	0.0086	2.97	IEO Database
Seriola dumerili	184.2	Fishbase	0.19	Fishbase	0.0273	2.74	IEO Database
Sphyraena sphyraena	118.9	IEO Database	0.12	Fishbase	0.0648	2.32	IEO Database
8.Anglerfishes							
Lophius piscatorius	153.7	IEO Database	0.34	IEO Database	0.0206	2.89	IEO Database

Lophius budegassa	103.2	IEO Database	0.19	Data call 2019	0.0563	2.60	IEO Database
9.Juvenile hake							
Merluccius merluccius	15.0	Data call 2019	0.18	Data call 2019	0.0055	3.07	Data call 2019
10.Adult hake							
Merluccius merluccius	115.8	MEDITS survey	0.18	MEDITS survey	0.0068	3.04	MEDITS survey
11.Mullets							
Mullus barbatus	36.3	Data call 2019	0.34	Data call 2019	0.0076	3.13	Data call 2019
Mullus surmuletus	37.9	Data call 2019	0.16	Data call 2019	0.0091	3.09	Data call 2019
12.Blue whiting							
Micromesistius poutassou	44.2	IEO Database	0.16	Data call 2018	0.0043	3.15	Data call 2018
13.Sardine							
Sardina pilchardus	23.7	Data call 2018	0.31	Data call 2018	0.0038	3.25	Data call 2018
14.Anchovy							
Engraulis encrasicolus	20.0	Data call 2018	0.32	Data call 2018	0.0050	3.34	Data call 2018
15.Small pelagics							
Sardinella aurita	34.7	IEO Database	0.44	Fishbase	0.0068	2.99	MEDITS survey
Spicara smaris	23.7	IEO Database	0.40	IEO Database	0.0245	2.62	MEDITS survey

16.Flatfishes							
Solea solea	45.8	MEDITS survey	0.36	Fishbase	0.0014	3.52	MEDITS survey
Microchirus variegatus	18.9	MEDITS survey	0.39	Fishbase	0.1759	1.92	MEDITS survey
Citharus lingutaula	32.6	IEO Database	0.25	Fishbase	0.0030	3.30	MEDITS survey
Lepidorhombus whiffiagonis	51.6	IEO Database	0.16	Fishbase	0.0064	2.99	MEDITS survey
lepidorhombus boscii	41.1	IEO Database	0.11	Fishbase	0.0643	2.27	MEDITS survey
Arnoglossus imperialis	17.4	MEDITS survey	0.25	Fishbase	0.0045	3.17	MEDITS survey
Arnoglossus laterna	16.3	MEDITS survey	0.55	Fishbase	0.0025	3.45	MEDITS survey
Arnoglossus thori	14.2	MEDITS survey	0.33	Fishbase	0.0064	3.17	MEDITS survey
Arnoglossus rueppelii	15.8	MEDITS survey	0.33	Fishbase	0.0051	3.01	MEDITS survey
17.Benthopelagic fishes							
Argentina sphyraena	22.6	MEDITS survey	0.28	Fishbase	0.0047	3.05	MEDITS survey
Glossanodon leioglossus	16.3	MEDITS survey	0.44	Fishbase	0.0022	3.32	MEDITS survey
Capros aper	16.8	MEDITS survey	0.42	Fishbase	0.0282	2.81	MEDITS survey
Cepola macrophthalma	69.5	IEO Database	0.21	Fishbase	0.0119	2.22	MEDITS survey
Gadiculus argenteus argenteus	18.4	MEDITS survey	0.19	Fishbase	0.0562	2.11	MEDITS survey
Macroramphosus scolopax	20.0	MEDITS survey	0.36	Fishbase	0.0040	3.15	MEDITS survey

18.Mesopelagic fishes							
Stomias boa boa	28.6	MEDITS survey	0.28	Fishbase	0.0051	2.98	MEDITS survey
Maurolicus muelleri	7.6	MEDITS survey	0.88	Fishbase	0.0016	3.96	MEDITS survey
Myctophum punctatum	10.2	MEDITS survey	0.17	Fishbase	0.0080	3.00	MEDITS survey
Notoscopelus elongatus	14.4	MEDITS survey	0.89	Fishbase	0.0135	3.00	MEDITS survey
Ceratoscopelus maderensis	11.3	MEDITS survey	0.40	Fishbase	0.0135	3.00	MEDITS survey
Lampanyctus crocodilus	23.4	MEDITS survey	0.89	Fishbase	0.0051	2.98	MEDITS survey
Hymenocephalus italicus	5.5	MEDITS survey	0.23	Fishbase	0.1277	2.80	MEDITS survey
19.Mackerels							
Scomber colias	47.4	IEO Database	0.15	Data call 2019	0.0024	3.40	Data call 2019
Scomber scombrus	41.6	IEO Database	0.50	Data call 2019	0.0042	3.21	Data call 2019
20.Horse mackerels							
Trachurus picturatus	39.5	MEDITS survey	0.25	Fishbase	0.0089	2.96	MEDITS survey
Trachurus mediterraneus	41.1	MEDITS survey	0.22	Data call 2019	0.0138	2.76	Data call 2019
Trachurus trachurus	44.2	IEO Database	0.17	Data call 2019	0.0099	2.96	Data call 2019
21.Gobiids							
Crystallogobius linearis	4.9	MEDITS survey	0.97	Fishbase	0.0096	3.45	MEDITS survey
Deltentosteus quadrimaculatus	14.2	MEDITS survey	0.37	Fishbase	0.0074	3.05	MEDITS survey

Callionymus maculatus	14.2	MEDITS survey	0.58	Fishbase	0.0156	2.49	MEDITS survey
Aphia minuta	5.3	MEDITS survey	2.23	Fishbase	0.0096	3.45	MEDITS survey
Lesueurigobius friesi	8.4	MEDITS survey	0.70	Fishbase	0.0392	2.13	MEDITS survey
Blennius ocellaris	20.0	MEDITS survey	0.38	Fishbase	0.0168	2.91	MEDITS survey
Synchiropus phaeton	23.2	MEDITS survey	0.58	Fishbase	0.0615	2.11	MEDITS survey
Gobius niger	20.0	IEO Database	0.30	Fishbase	0.0089	3.09	MEDITS survey
22.Gelatinous plankton feeders							
Boops boops	36.8	IEO Database	0.17	Fishbase	0.0082	3.00	MEDITS survey
Pagellus bogaraveo	49.5	IEO Database	0.09	Fishbase	0.0130	2.99	MEDITS survey
23.Sparids							
Diplodus annularis	25.3	MEDITS survey	0.46	Fishbase	0.0115	3.17	MEDITS survey
Diplodus vulgaris	35.8	IEO Database	0.39	Fishbase	0.0149	3.01	MEDITS survey
Spondyliosoma cantharus	48.4	IEO Database	0.18	Fishbase	0.0015	3.71	MEDITS survey
24.Suprabenthos feeders							
Spicara maena	24.2	MEDITS survey	0.17	Fishbase	0.0062	3.20	MEDITS survey
Lepidotrigla dieuzeidei	16.8	IEO Database	0.42	Fishbase	0.0078	3.12	MEDITS survey
Lepidotrigla cavillone	18.9	IEO Database	0.56	Fishbase	0.0058	3.26	MEDITS survey
Nezumia aequalis	6.8	MEDITS survey	0.16	Fishbase	0.1279	2.82	MEDITS survey

Pagellus acarne	31.6	MEDITS survey	0.37	Fishbase	0.0066	3.21	MEDITS survey
25.Natantia feeders							
Chelidonichthys lastoviza	31.6	MEDITS survey	0.28	Fishbase	0.0178	2.82	MEDITS survey
Eutrigla gurnardus	32.6	MEDITS survey	0.22	Fishbase	0.0029	3.49	MEDITS survey
Chelidonichthys cuculus	32.1	MEDITS survey	0.35	Fishbase	0.0051	3.20	MEDITS survey
Chelidonichthys obscurus	24.7	MEDITS survey	0.18	Fishbase	0.0067	3.08	MEDITS survey
Coelorinchus caelorhincus	12.6	MEDITS survey	0.12	Fishbase	0.0925	3.14	MEDITS survey
Gaidropsarus biscayensis	15.8	MEDITS survey	0.31	Fishbase	0.0040	3.20	MEDITS survey
Pagellus Erythrinus	54.2	MEDITS survey	0.14	Fishbase	0.0219	2.82	MEDITS survey
Phycis blennoides	67.4	IEO Database	0.22	Fishbase	0.0069	2.97	MEDITS survey
Scorpaena notata	18.9	MEDITS survey	0.22	Fishbase	0.0169	3.04	MEDITS survey
Scorpaena porcus	31.6	MEDITS survey	0.18	Fishbase	0.0183	3.02	MEDITS survey
Serranus cabrilla	28.4	IEO Database	0.30	Fishbase	0.0092	3.07	MEDITS survey
Serranus hepatus	20.0	MEDITS survey	0.25	Fishbase	0.0091	3.24	MEDITS survey
Trachyrincus scabrus	20.0	MEDITS survey	0.17	Fishbase	0.0410	3.06	MEDITS survey
Trigla lyra	35.8	MEDITS survey	0.17	Fishbase	0.0082	2.96	MEDITS survey
Trisopterus minutus	30.5	IEO Database	0.39	Fishbase	0.0075	3.06	MEDITS survey

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TABLE A.5 Diet composition matrix for the Gulf of Alicante model.

	Prey / Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Dolphins																				
2	Seabirds																				
3	Large pelagic fishes																				
4	Benthic sarks				0.009	0.009	0.003		0.004												
5	Rays and skates							0.000													
6	Demersal ichthyophagous	0.050		0.003	0.002	0.003	0.007	0.001	0.098		0.001	0.003					0.000				
7	Pelagic ichthyophagous fishes							0.010													
8	Anglerfishes					0.000	0.000														
9	Juvenil hake	0.010		0.002			0.012	0.000	0.009	0.024	0.042						0.006				
10	Adult hake	0.050			0.000	0.028	0.013		0.078												
11	Mullets					0.007	0.000	0.000	0.026		0.001									0.017	0.000
12	Blue whiting			0.015	0.005	0.001	0.064		0.016	0.020	0.057		0.003				0.009			0.000	0.001
13	Sardine	0.210	0.250	0.281	0.141	0.019	0.111	0.043	0.116	0.251	0.442		0.020				0.042			0.352	0.380
14	Anchovy	0.100	0.040	0.072	0.056	0.013	0.049	0.032	0.004	0.057	0.026						0.001			0.031	0.012
15	Small pelagics	0.090	0.010	0.032		0.036	0.017	0.153	0.003	0.008	0.036									0.001	0.007
16	Flatfishes				0.001	0.003	0.008		0.069								0.006				0.000
17	Benthopelagic fishes			0.002	0.028	0.070	0.080	0.002	0.066	0.005	0.030	0.008	0.008				0.019	0.002		0.000	0.003
18	Mesopelagic fishes			0.006	0.031	0.000	0.053	0.021		0.023	0.015		0.208					0.009	0.013	0.000	0.008
19	Mackerels	0.200					0.013	0.005			0.010									0.000	
20	Horse mackerels	0.040		0.002			0.018	0.003	0.072		0.031									0.010	0.007
21	Gobiids			0.000	0.000	0.013	0.020	0.000	0.040	0.043	0.002	0.003					0.057				0.011
22	Gelatinous plankton feeders				0.046		0.029	0.026	0.160		0.168									0.000	
23	Sparids					0.020	0.002	0.001	0.004												
24	Suprabenthos feeders					0.024	0.020	0.007	0.044		0.011										
25	Natantia feeders			0.000	0.010	0.026	0.028	0.002	0.027	0.000	0.009	0.002	0.002				0.022				
26	Benthopelagic cephalopods	0.100		0.032	0.014	0.046	0.013	0.008	0.013		0.017	0.004	0.008				0.004			0.006	
27	Benthic cephalopods	0.010		0.000	0.006	0.009	0.005	0.004	0.009	0.001	0.002	0.012					0.005			0.000	0.001
28	Octopuses	0.020			0.018		0.020		0.004		0.000										
29	Blue and red shrimp				0.002														0.001		
30	Deep water rose shrimp				0.001	0.001		0.000													
31	Norway lobster				0.001		0.005						0.001				0.009				
32	Crabs			0.022	0.092	0.249	0.144	0.009	0.011	0.007	0.002	0.175	0.000				0.203	0.004	0.001	0.001	0.005
33	Other shrimps			0.011	0.090	0.340	0.094	0.049	0.032	0.111	0.046	0.178	0.073			0.008	0.157	0.050	0.035	0.001	0.016
34	Suprabenthos				0.004	0.062	0.018	0.013	0.000	0.011	0.001	0.217	0.001			0.042	0.188	0.220	0.255	0.056	0.084
35	Worms				0.118	0.004	0.030		0.000			0.286	0.000			0.002	0.159	0.083	0.140	0.001	0.002
36	Echinoderms				0.000		0.003		0.000			0.016						0.000			
37	Bivalves and gastropods				0.001	0.001	0.000	0.006				0.043					0.004	0.001		0.000	0.000
38	Other benthic invertebrates				0.002							0.000						0.000		0.000	
39	Microzooplankton				0.004	0.000	0.000	0.000		0.050		0.000	0.100	0.095	0.595	0.866	0.013	0.354	0.164	0.004	0.059
40	Meso- and macrozooplankton			0.022	0.128	0.001	0.078	0.005	0.000	0.389	0.053	0.052	0.577	0.045	0.400	0.080	0.022	0.271	0.256	0.201	0.401
41	Gelatinous plankton				0.003	0.001	0.014						0.000			0.001		0.005	0.002	0.319	0.002
42	Phytoplankton													0.860							
43	Benthic macrophytes																				
44	Discards	0.010	0.100		0.019	0.001	0.000	0.000	0.005												
45	Detritus	0.035			0.167	0.014	0.028	0.000	0.091						0.005	0.001	0.076		0.133		
	Import	0.075	0.600	0.500				0.600													
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

TABLE A.5 (continued)

	Prey / Predator	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
1	Dolphins																					
2	Seabirds																					
3	Large pelagic fishes																					
4	Benthic sarks					0.000	0.001															
5	Rays and skates																					
6	Demersal ichthyophagous					0.004	0.001	0.003														
7	Pelagic ichthyophagous fishes						0.001															
8	Anglerfishes																					
9	Juvenil hake					0.004	0.000	0.019														
10	Adult hake						0.000	0.009	0.001													
11	Mullets					0.001																
12	Blue whiting					0.001	0.003															
13	Sardine		0.000		0.037	0.007	0.121	0.025	0.139													
14	Anchovy					0.005	0.061	0.033	0.024				0.004									
15	Small pelagics						0.001	0.016														
16	Flatfishes		0.001	0.010	0.007	0.003		0.015														
17	Benthopelagic fishes		0.000			0.010	0.004	0.032	0.021	0.026			0.007									
18	Mesopelagic fishes		0.001			0.004	0.072	0.022		0.026				0.011								
19	Mackerels																					
20	Horse mackerels			0.003			0.115															
21	Gobiids			0.044	0.053	0.022	0.018	0.039	0.033													
22	Gelatinous plankton feeders						0.006		0.083				0.004									
23	Sparids						0.002	0.008														
24	Suprabenthos feeders						0.000															
25	Natantia feeders					0.009		0.018	0.007													
26	Benthopelagic cephalopods		0.000	0.009		0.001	0.006		0.013													
27	Benthic cephalopods		0.001	0.002	0.004	0.008	0.006	0.006	0.003			0.000		0.000								
28	Octopuses			0.005	0.004			0.003	0.002													
29	Blue and red shrimp							0.000					0.002									
30	Deep water rose shrimp																					
31	Norway lobster						0.016		0.003													
32	Crabs	0.071	0.000	0.275	0.069	0.228	0.015	0.234	0.224	0.115		0.053	0.010	0.000								
33	Other shrimps	0.080	0.039	0.016	0.106	0.302	0.291	0.293	0.066	0.095		0.106	0.009	0.008								
34	Suprabenthos	0.350	0.041	0.048	0.375	0.112	0.015	0.045	0.040	0.223	0.136	0.087	0.193	0.190								
35	Worms	0.299	0.015	0.259	0.126	0.143	0.006	0.056	0.119	0.098	0.282	0.225	0.304	0.153		0.030		0.100				
36	Echinoderms	0.004	0.000	0.043	0.034	0.011		0.011	0.015	0.086		0.022	0.042	0.001								
37	Bivalves and gastropods	0.038	0.000	0.098	0.056	0.002	0.005	0.014	0.040	0.296		0.049	0.057	0.008			0.020					
38	Other benthic invertebrates		0.042	0.091	0.007	0.000	0.000				0.213	0.058	0.040	0.000								
39	Microzooplankton	0.063	0.002	0.061	0.003	0.000	0.006			0.007	0.232			0.050	0.130				0.200	0.020	0.570	0.640
40	Meso- and		0.034	0.027	0.062	0.045	0.087	0.015	0.000	0.029		0.087	0.090	0.311					0.050		0.030	0.050
41	Gelatinous plankton		0.801	0.007	0.058	0.000	0.007						0.004									0.010
42	Phytoplankton																	0.640	0.400	0.680	0.300	0.200
43	Benthic macrophytes		0.020		0.001		0.001						0.006				0.100	0.010				
44	Discards						0.013		0.017			0.016	0.002		0.003		0.001					
45	Detritus	0.095	0.002	0.003	0.000	0.080	0.118	0.084	0.150		0.136	0.296	0.226	0.268	0.867	0.970	0.879	0.250	0.350	0.300	0.100	0.100
	Import																					
	Total	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

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Balancing procedure

Model balancing was carried out manually following a top-down strategy (Fig.1). For all modeled groups, Ecotrophic efficiencies were the missing parameter and were estimated by EwE while Biomass, (P/B), and (Q/B) were inputs to the model. One exception concerned the “Pelagic ichthyophagous fishes” group due to the absence of reliable biomass estimations. In this case, we used an input value of 0.47 for EE, following recommendations from Christensen et al. (2005), and we let the model estimate the biomass. In the same way, P/B values for Norway lobster, Bivalves and gastropods and other benthic invertebrates (F.G. 31, 37 and 38, respectively) were estimated by the model. When attempting to balance the model, many of the Ecotrophic Efficiencies were greater than 1 meaning that more of the group was being consumed than produced, and thus had to be reduced. For that reason, inconsistent values were slightly modified following the criteria given by Christensen et al. (2008).

Biomasses were the first parameters modified during model balancing due to they were obtained from scientific surveys, where the sampling method, specifically, the swept-area method (i.e., estimation of biomass per area sampled by trawling), has been reported to underestimate biomass of the sampled species (Sánchez and Olaso, 2004, Tsagarakis et al., 2010, Torres et al., 2013). Thus, their biomass input values were based on a guesstimate to reach the mass balanced ecosystem model requirements. The biomasses of these groups were indeed too low and had to be increased (e.g., F.G. 37. F.G. 18, F.G. 21, F.G. 33, F.G.38, F.G.16 and F.G. 15). This is a common problem in prebalanced EwE models, where invertebrate biomass estimates are frequently too low to support predation mortality (Christensen et al. 2008). In the same way, P/B values were modified according to these criteria. Also and to complete the final mass balance model, we adjusted the diet matrix as a data source with some uncertainty, especially for those groups for which diet information was not from the modeled area.

The resulting input data were tested through ecological and fishery principles used in conjunction with PREBAL diagnostics to identify issues of model structure and data quality before network model balancing. Hence, following Link (2010), a set of diagnostics, i.e., biomasses, biomass ratios, vital rates, vital rate ratios, total production, and total removals (and slopes thereof) across the taxa and trophic levels could be tested through graphical representation. Regarding biomasses, results showed that Worms (F.G 35), Phytoplankton (F.G. 42), Microzooplankton (F.G. 39), Sardine (F.G. 13), Bivalves and gastropods (F.G. 37) could potentially be overestimated (Fig.1) while Flatfishes (F.G 16), Mullets (F.G 11), Sparids (F.G 23), Benthic sharks (F.G 4), Octopuses (F.G 28), Blue and red shrimp (F.G 29) and Norway lobster (F.G 31) could be underestimated. As we mentioned at the beginning of the balancing procedure, the biomass estimations determined with the survey could generate this kind of uncertainty, therefore, some adjustments were necessary to balance the model.

In addition, in the GoA model, the P/B ratios were low for all groups in general, except for Phytoplankton (F.G. 42) and Microzooplankton (F.G. 39). In the case of P/Q ratios, the highest values were detected for Microzooplankton (F.G. 39), Suprabenthos (F.G. 34), Meso- and macrozooplankton (F.G. 40), Gelatinous plankton (F.G. 41) and Seabirds (F.G. 2).

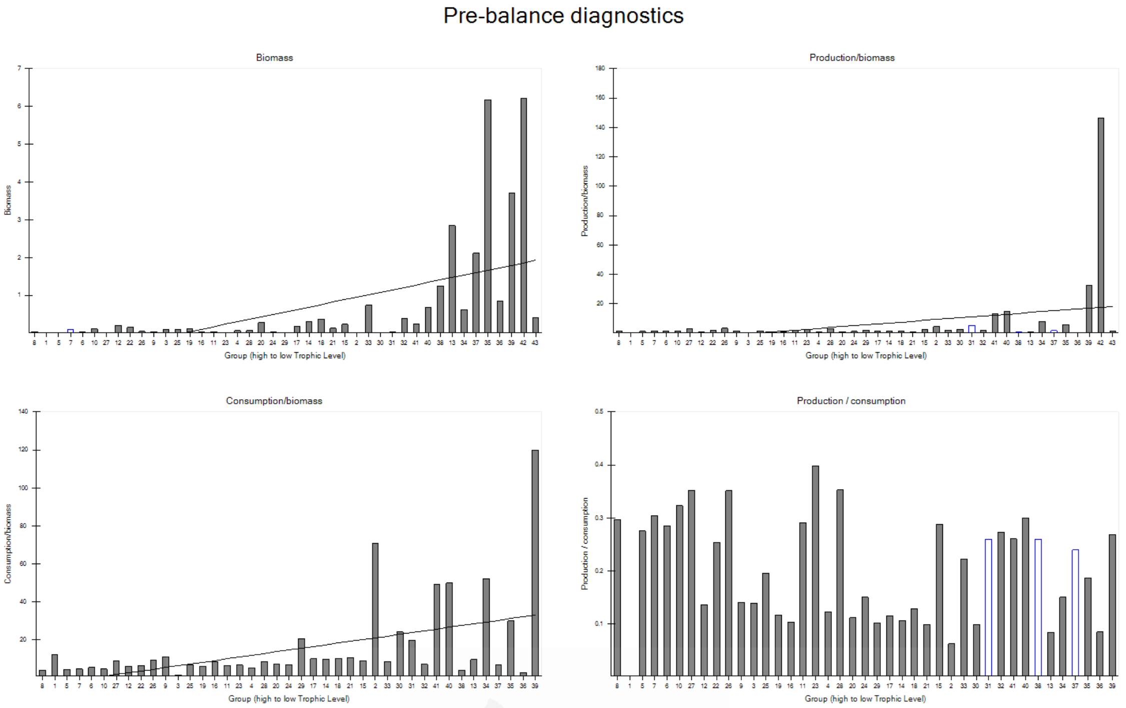

Fig. 1. Results of the PREBAL analysis regarding the trends of Biomass, Production/Biomass, Consumption/Biomass and Production/Consumption along the functional groups arranged by trophic level.

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