

Large-scale distribution of a deep-sea megafauna community along Mediterranean trawlable grounds

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Summary: The large-scale distribution pattern of megafauna communities along the Mediterranean middle slope was explored. The study was conducted between 500 and 800 m depth where deep-water fishery occurs. Although community studies carried out deeper than 500 m are partly available for some geographic areas, few large-scale comparative studies have been carried out. Within the framework of the MEDITS survey programme, we compared the megafauna community structure in ten geographical sub-areas (GSAs) along the Mediterranean coasts. Additionally, the spatial distribution of fishing was analysed using vessel monitoring by satellite information. Overall, the community showed a significant difference between sub-areas, with a decreasing eastward pattern in abundance and biomass. Longitude was the main factor explaining variation among sub-areas (by generalized additive models). However, we found a region which did not follow the general pattern. GSA 6 (northern Spain) showed significantly lower abundance and a different composition structure to the adjacent areas. The decrease in community descriptors (i.e. abundance and biomass) in this area is probably a symptom of population changes induced by intense fishery exploitation. Overall, a combination of environmental variables and human-induced impacts appears to influence the benthic-pelagic communities along the slope areas of the Mediterranean.

Keywords: distribution pattern; fishing impact; continental slope; deep sea; megafauna; red shrimp; community.

Distribución espacial a gran escala de la megafauna de aguas profundas en fondos arrastrables del Mediterráneo

Resumen: En este estudio se describe la estructura y patrones de distribución de la comunidad de megafauna que habita en el margen continental medio a lo largo del Mediterráneo. El estudio se realizó entre los 500 y 800 m, coincidiendo espacialmente con las pesquerías de profundidad. A pesar de que se conoce parcialmente la estructura de las comunidades que habitan por debajo de 500 m, existe la necesidad de estudiar estas comunidades a una escala espacial más amplia. Dentro del marco del proyecto internacional MEDITS, se comparó la estructura de las comunidades en diez sub-áreas geográficas (GSAs) a lo largo de las costas mediterráneas. Además se analizó la distribución espacial del esfuerzo pesquero utilizando la información de los datos de seguimiento de buques. En general los resultados mostraron diferencias significativas entre subáreas mostrando un patrón decreciente en los valores de biomasa hacia el este, siendo la longitud el principal factor explicativo del modelo de distribución (GAMs). Sin embargo, encontramos una subárea que no seguía el patrón general, la GSA6 (norte de España). La GSA6 mostró una biomasa y estructura de la comunidad diferente a las áreas adyacentes. La disminución de la biomasa en esta área parece ser un síntoma de los cambios poblacionales causados por la elevada intensidad de pesca en la zona. Los resultados sugieren que la distribución y estructura de las comunidades bento-pelágicas parecen estar moduladas por la combinación de las variables ambientales y los impactos producidos por la actividad humana.

Palabras clave: distribución; impacto pesca; margen continental; mar profundo; megafauna; gamba roja; comunidad.

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INTRODUCTION

The continental slopes are the connecting habitat between the shelf (200 m) and the deep basins (4000 m). They play an important role in the global carbon cycle, cycling nutrient and providing valuable food and energy resources (Levin and Dayton 2009). These biological systems cannot support high levels of exploitation due to their low productivity and the presence of productive but not yet well-identified habitats (de Juan and Leonart 2010, Norse et al. 2012, Watson and Morato 2013). Several deep-water species have biological characteristics that make them more vulnerable to fishing exploitation: K-type life-history traits, low fecundity and aggregation behaviour in restricted topographic areas (Merrett and Haedrich 1997, Clark et al., 2016, Fernandez-Arcaya et al. 2016). However, several major sources of impacts are threatening continental slopes around the world (i.e. fishing, marine litter, chemical contamination, species invasion, ocean acidification and climate change-related stressors) (Galil 2009, Pham et al. 2014, Fernandez-Arcaya et al. 2017), including those of the Mediterranean Sea, whose physical characteristics make it particularly sensitive to these impacts (Coll et al. 2012, Ramirez-Llodra et al. 2010, 2013). The Mediterranean is a semi-enclosed area characterized by oligotrophic conditions (Margalef 1985). The biological production decreases from north to south and west to east and is inversely related to the increase in temperature and salinity, being the eastern basin one of the poorest marine areas in the world (Azov 1991, Danovaro et al. 2010).

Among the human activities that are impacting the Mediterranean continental slope and its associated biological communities, bottom trawling is the most important and the cause of most concern (Guijarro et al. 2017, Piroddi et al. 2017). Mediterranean deep-water fisheries began in the first decades of the last century,

coinciding with the development of new technologies that made fisheries in deeper waters possible (Relini and Orsi Relini 1987, Spedicato et al. 1995, Sardà and Demestre 1987). Larger vessels with more powerful winches and stronger cables were increasingly used from Mediterranean harbours (Farrugio et al. 1993, Guijarro et al. 2011, Quetglas et al. 2017). Two main deep-sea bottom fisheries have extended along the Mediterranean continental slope: (i) an upper slope (~200-600 m) fishery targeting *Nephrops norvegicus* and *Parapenaeus longirostris*, and ii) a middle slope (~400-800 m) fishery targeting *Aristaeomorpha foliacea* and *Aristeus antennatus* (Sardà et al. 2004a).

The scientific assessment conducted on deep-sea Mediterranean shrimp fisheries is giving rise to alarm about overexploitation and major damage to the associated fauna (Gorelli et al. 2016, Colloca et al. 2017, Vielmini et al. 2017). However, the community associated with red shrimp is not well known and large spatial scale analysis is still lacking. Mediterranean Sea community studies carried out in continental margin areas deeper than 500 m are partly available for some geographic areas. Most of these studies have been conducted in the NW Mediterranean Sea, which is currently one of the most studied deep-sea regions of the world (Sardà et al. 2004b, Massutí and Reñones 2005, Fernandez-Arcaya et al. 2016, among others). Additionally, the published data focus on specific taxonomic groups such as crustaceans (Company et al. 2004, Follesa et al. 2009), cephalopods (Keller et al. 2016) and fishes (D'Onghia et al. 2004, Moranta et al. 2008, Granger et al. 2015), while studies of non-crustacean invertebrate communities are still very limited (Cartes et al. 2009, Gori et al. 2013, Mecho et al. 2014). Thus, there is an increasing need for better understanding of the community distribution patterns as a whole, in particular in the context of an ecosystem management approach that assesses the whole community rather than evaluating single resources (Quetglas

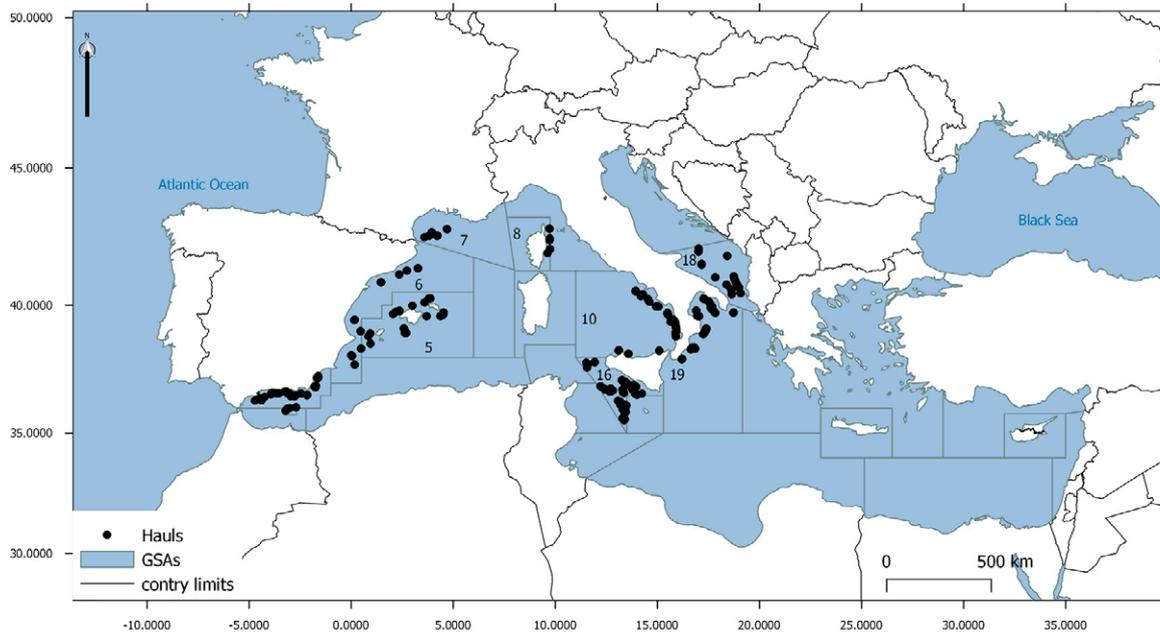


Fig. 1. – Map of the Mediterranean Sea showing the sampling stations in each GSA. The number of hauls in each GSA is shown in parenthesis. GSA 1 (48), GSA 2 (16), GSA 5 (40), GSA 6 (35), GSA 7 (17), GSA 8 (11), GSA 10 (92), GSA 16 (122), GSA 18 (60), GSA 19 (119).

et al. 2017). Additionally, it is essential to identify the main drivers affecting the spatial distribution of deep-sea communities in order to evaluate their distribution patterns (Navarro et al. 2016, Rowden et al. 2017, Allen et al. 2018). This information is also needed in order to identify the major impacts and implement effective management plans within deep-sea habitats. Previous studies suggest that, in addition to the environmental variables, human-induced impacts also affect species composition, abundance and distribution (Worm et al. 2006, Colloca et al. 2017, Navarro et al. 2016). However, these patterns are far from being well understood.

The objective of the present work is to describe and compare abundance, biomass and assemblage structure of the whole megafauna community along the Mediterranean continental slope, using independent MEDITS fishing cruise data. A second objective is to analyse the relationship between environmental variables, fishing intensity and the megabenthic community distribution in deep-water shrimp fishing grounds in order to better understand the dominant forces driving the distribution patterns of deep-sea assemblages.

MATERIALS AND METHODS

The study area comprised a wide area of the Mediterranean Sea, from the Alboran Sea to the western Ionian Sea (Fig. 1). The study covers ten geographical sub-areas (GSAs) with specific environmental and biological characteristics defined by the General Fisheries Commission for the Mediterranean (GFCM): the northern Alboran Sea (GSA 1), Alboran Island (GSA 2), the Balearic Islands (GSA 5), northern Spain (GSA 6), the Gulf of Lions (GSA 7), eastern Corsica (GSA 8), the central-southern Tyrrhenian Sea (GSA 10), the Strait of Sicily (GSA 16), the southern Adriatic Sea (GSA 18) and the western Ionian Sea (GSA 19).

The sampling of benthic megafauna was carried out with an experimental bottom trawl net (IFREMER reference GOC73), the standard sampler for study of deep-sea megafauna (Cartes et al. 2017, Foveau et al. 2017), following a standardized survey design and sampling methodology. The average haul rate for all the GSAs was proportional to the total surface area (one station per 60 km²). The details of sampling methodology can be found on Bertrand et al. 2002a, b and in the MEDITS Handbook (<http://www.sibm.it/MEDITS%202011/principaledownload.htm>).

Only hauls between 500 and 800 m (559) were selected, in order to analyse the preferred habitat of deep shrimp fishing grounds (Sardà et al. 2004a) from 2012 to 2015. The total catch from each haul was sorted, identified to the lowest taxonomical level possible, counted and weighed following the MEDITS survey protocol. Only taxonomical groups that were appropriately sampled and identified in all GSAs were included. The species were grouped by phylum, except for Actinopterygii and Mollusca, which were grouped by subgroups because of their different life history and moving capacity. As a result, nine groups were used for the analysis: Osteichthyes, Chondrichthyes, Crustacea, Cephalopoda, other Mollusca, Echinodermata, Cnidaria, Porifera and Tunicata.

Total abundance (n km⁻²) and biomass (g km⁻²) indexes of each species were standardized by swept area (in km²). Net horizontal opening and recorded distances were used to calculate the swept area. After standardization, specific data were placed in the above groups and their percentage and biomass index descriptors were box-plotted by GSAs.

One-way ANOVA tests on log₁₀-transformed data of abundance and biomass indexes of the entire community, followed by pairwise Tukey honestly significant difference tests, were applied to test for significant

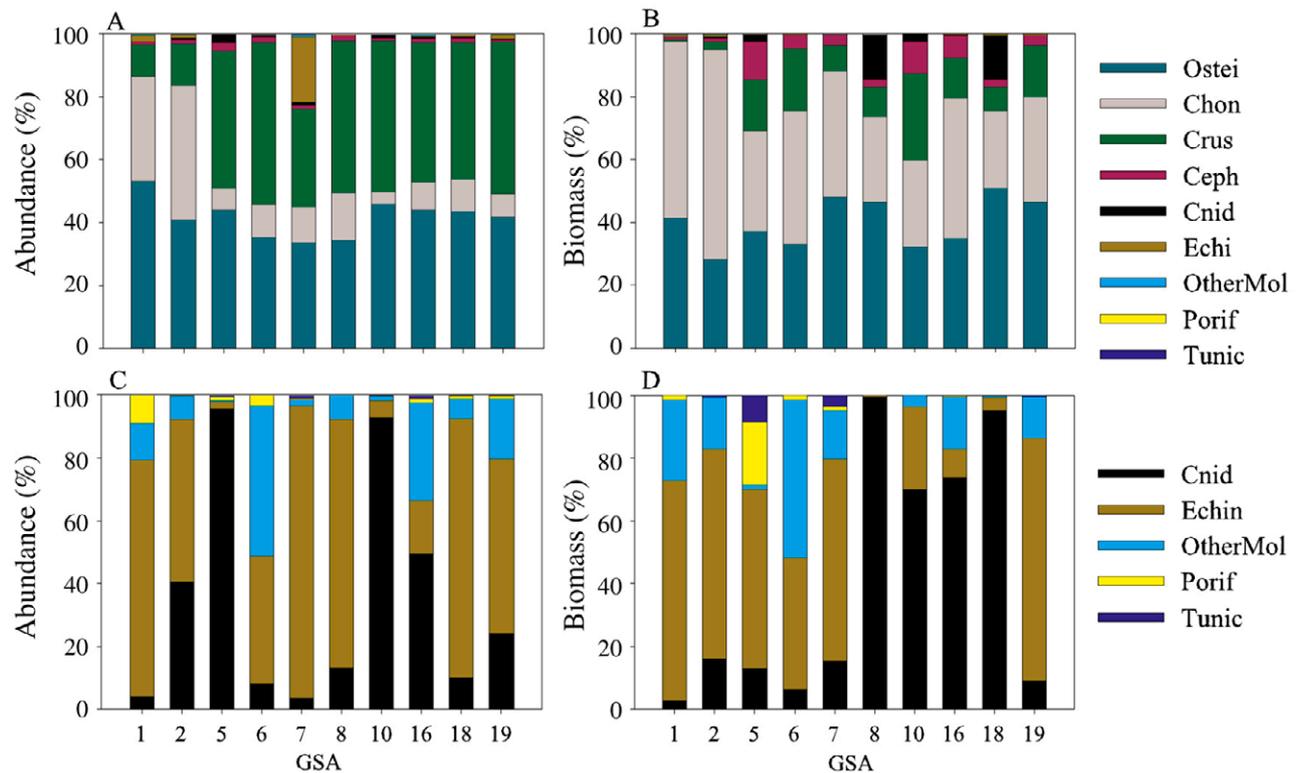


Fig. 2. – Percentage of abundance ($N\ km^{-2}$) (A) and biomass ($g\ km^{-2}$) indexes (B) for each taxonomic group by GSAs. Below, detailed figure of abundance (C) and biomass indexes (D) of the most sessile taxonomic groups. Ostei, Osteichthyes; Chon, Chondrichthyes; Crus, Crustacea; Cepha, Cephalopoda; Cnid, Cnidaria; Echi, Echinodermata; OtherMol, other Mollusca (non-cephalopod); Porif, Porifera; Tunic, Tunicata.

(N) differences among GSAs. Previously, all data were tested for normality using the Shapiro-Wilk test. In this and forward analyses, the selected index was biomass because for several groups it can be complicated to enumerate the individuals caught, as is the case of colonial organisms (like corals or tunicates) or sponges (see Results section for more details).

In addition, data matrices (species biomass vs haul) were square-root transformed and similarity between all samples was calculated using the Bray-Curtis measure. A group average cluster analysis on transformed biomass indices was carried out, and a similarity profile test (SIMPROF) permutation routine (1000 restarts) was applied to test for the significance of genuine clustering. Similarities between sampled hauls were also visualized using a multidimensional scaling plot (MDS) and similarity percentage (SIMPER) analyses were run to determine species contributions to the observed communities. Analysis of similarity (ANOSIM) was used to test for differences in community composition by zones and years. Ecological analyses were performed with the PRIMER-E 6 and PERMANOVA software (Clarke and Gorley 2006).

Generalized additive models (GAMs) were used to determine significant relationships between biomass index (response variables) and latitude and longitude of the hauls (explanatory variables) for each group and for the entire community. The models were defined as follows: $(y) \sim \beta_0 + s_1(x_1) + s_2(x_2)$, where β_0 is the intercept, s represents a polynomial smooth function, substituting the slope parameter in a linear regression, and x represents explanatory variables (Wood 2006).

The response variable (biomass index) was log-transformed to approximate normal distribution. The most parsimonious models were identified for the forward selection using the GCV scores (Burnham and Anderson 2003). The *mgcv* statistical package in R statistical software (R3.3.2) (<http://www.r-project.org/>) was used to fit the models.

Fishing effort

The fishing effort in the area was assessed by means of the Vessel Monitoring System (VMS). To reduce the spatial derived effect on community distribution (e.g. the longitude effect), we used the available VMS data from the Spanish Mediterranean Area (GSAs 1, 2, 5 and 6) for the two-years study period (2013 and 2014). VMS data were provided by the Spanish Ministry of Agriculture, Food and Environment and consisted of records containing data on the geographic position, date, time and instantaneous velocity for each boat, approximately every two hours. Bottom trawlers usually fish at velocities of between 2 and 3.5 knots, so only signals showing these velocities were included in the analysis so as to remove VMS signals from boats transiting to fishing grounds or ports. To estimate the fishing effort, a grid of 0.03×0.03 degrees was created around each haul to calculate the number of VMS signals associated with it.

GAM models were applied to analyse the effect of fishing effort and spatial distribution (latitude and longitude) on the community biomass (see above for more details).

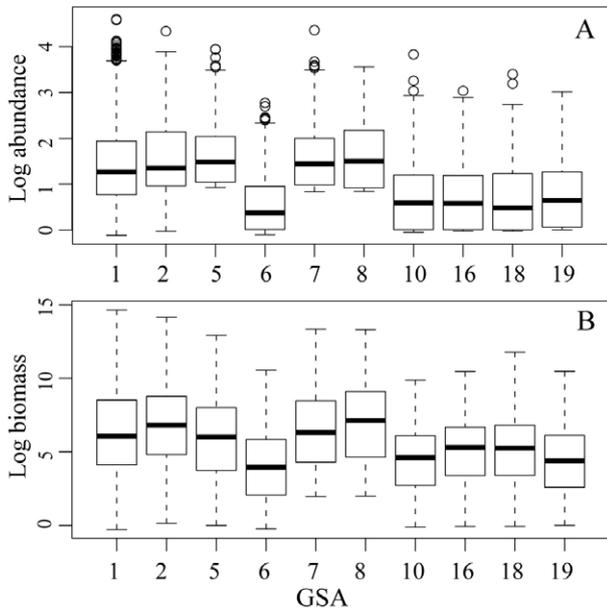


Fig. 3. – Total catch in the ten sampled GSAs, considering standardized abundance ($N\ km^{-2}$) and biomass ($g\ km^{-2}$) indexes. Boxes are the lower to the upper quartile and the centre line is the median with whiskers from minimum to maximum values.

RESULTS

A total of 432 species belonging to 9 different taxonomical groups were selected. The overall taxonomic composition showed that the most diverse groups were Osteichthyes (127 sp.) and Crustacea (91 sp.), followed by the other 6 groups (54 Echinodermata, 38 Cephalopoda, 36 Cnidaria, 26 Chondrichthyes, 36 Mollusca (non-cephalopod), 10 Tunicata and 8 Porifera). The percentages of abundance and biomass for each taxonomic group for all GSAs are shown in Figure 2. In abundance, Osteichthyes and Crustacea dominated the fauna overall, except in Alboran Sea (GSAs 1 and 2) where Chondrichthyes were the dominant taxa (33.7% and 43%, respectively, considering the biomass indexes). In terms of biomass Osteichthyes and Chondrichthyes (mostly *Galeus melastomus* species) dominated the community in these GSAs. The more sessile taxonomical groups (benthic species) showed a lower contribution to the overall community. They were therefore plotted separately in order to visualize their patterns of dominance (Fig. 2C, D). Echinodermata and Cnidaria dominated the benthic fauna in terms of abundance and biomass. However, abundance and biomass showed different patterns, possibly because of the high weight of some hauls conducted over mud facies of corals, such as *Isidella*. In fact, biomass was composed of Cnidaria in the central basin (GSA 8, 99.5%, GSA 10, 79%, GSA 16, 73.7%, GSA 18, 95%), mostly the coral *Isidella elongata*, and of the actinia *Actinauge richardi* in GSA 16 (Fig. 2D). In contrast, the biomass in the western GSAs was dominated by several species of holothurians (*Molpadia musculus* and *Parastichopus regalis*), ophiouras (*Leptometra* sp. and *Hymenodiscus coronata*) and sea-urchins (*Cidariscidaris*) (all the mentioned species together: GSA 1, 69.7%; GSA 2, 66.6%; GSA 5, 56.8%; and GSA 7,

Table 1. – P values of Tukey post hoc tests after one-way ANOVA for biomass with GSAs as fixed factors, $F=227.9$. * significant differences $p<0.01$.

GSA	1	2	5	6	7	8	10	16	18
1									
2	0.29								
5	0.88	0.02							
6	*	*	*						
7	*	*	0.20	*					
8	0.99	0.39	0.99	*	*				
10	*	*	*	1.0	*	0.25			
16	*	*	*	0.59	*	*	0.24		
18	*	*	*	0.70	*	*	0.34	0.96	
19	*	*	*	0.16	*	*	0.16	0.98	*

64.5%) (Fig. 2D). In terms of abundance, in GSA 6 (northern Spain) other Mollusca represent more than 50% of the community. This percentage was mostly caused by the high densities of the species *Aporrhais serresianus* (Fig. 2C).

The overall community box-plot (Fig. 3) showed a significant difference between areas (one-way ANOVA, $F=227.9$, $p<0.001$), with a decreasing eastward pattern in abundance and biomass indices, except in GSA 6 (northern Spain). GSA 6 showed lower levels than the rest of the sub-areas of the western Mediterranean (GSAs 1, 2, 5, 7 and 8, with no significant differences), and equivalent ones to those in the more eastern areas. The sampled sub-areas in the eastern area (GSAs 10, 16, 18 and 19) showed no significant difference among them (Table 1, Fig. 3). The spatial pattern was consistent within all taxa, showing significantly lower values for demersal (e.g. Osteichthyes, Chondrichthyes Crustacea and Cephalopoda) and benthic taxa (Cnidaria, Echinodermata, other Mollusca, Porifera and Tunicata) in GSAs 6, 10, 16, 18 and 19 (Fig. 4). A haul conducted over the crinoid beds (*Leptometra* sp.) in 2013 was responsible for the abundance peak (and high standard error) observed in GSA 7 (Fig 4B). A close-up of Figure 4D showed a peak of biomass values in GSAs 8 and 18 caused by several hauls conducted over an octocoralline community of *I. elongata* and a peak of Echinodermata *Holothuria tubulosa* (GSA 2).

Table 2. – Pairwise test conducted by ANOSIM using the factor Cluster. $p<0.01$ for all pairwise comparisons. Global $R=0.85$.

Clusters	CENTM	ALBO	BAL-GL	COR-GL
CENTM				
ALBO	1.00			
BAL-GL	0.92	0.76		
COR-GL	0.94	0.95	0.67	
ESPN	0.57	1.00	0.62	0.99

Table 3. – Pairwise test conducted by ANOSIM using the factor GSA. $p<0.01$ for all pairwise comparisons. ' no significant difference ($p=36.1$). Global $R=0.67$.

GSA	10	1	16	18	19	2	5	6	7
10									
1	1.00								
16	0.40	0.99							
18	0.73	0.98	0.31						
19	0.43	0.99	0.33	0.24					
2	1.00	0.02	1.00	1.00	1.00				
5	0.97	0.82	0.96	0.96	0.94	0.80			
6	0.83	0.97	0.76	0.84	0.69	1.00	0.74		
7	1.00	0.66	0.96	0.96	0.96	0.69	0.69	0.92	
8	1.00	0.77	0.92	0.93	0.97	0.99	0.83	1.00	0.57

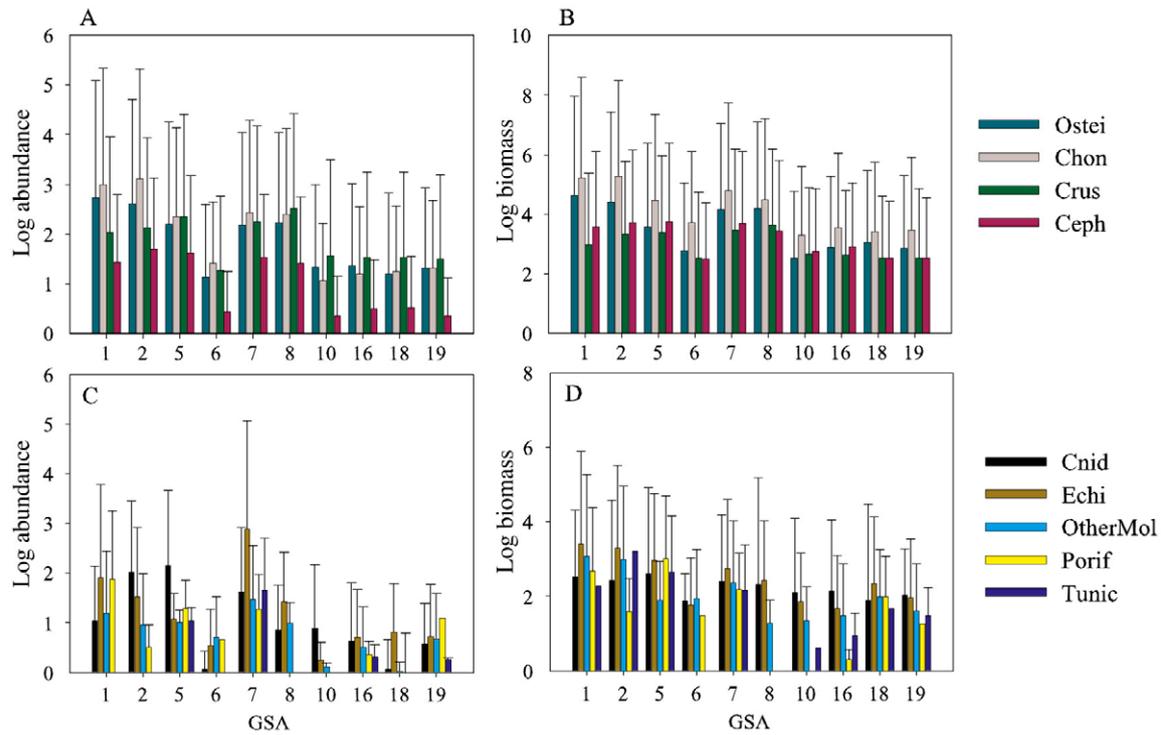


Fig. 4. – Abundances ($N\ km^{-2}$) and biomass ($g\ km^{-2}$) indexes by GSAs of demersal taxonomic groups (A and B) and more sessile taxonomic groups (C and D) (values are mean \pm SE). Ostei, Osteichthyes; Chon, Chondrichthyes; Crus, Crustacea; Ceph, Cephalopoda; Cnid, Cnidaria; Echi, Echinodermata; OtherMol, other Mollusca (non-cephalopod); Porif, Porifera; Tunic, Tunicata.

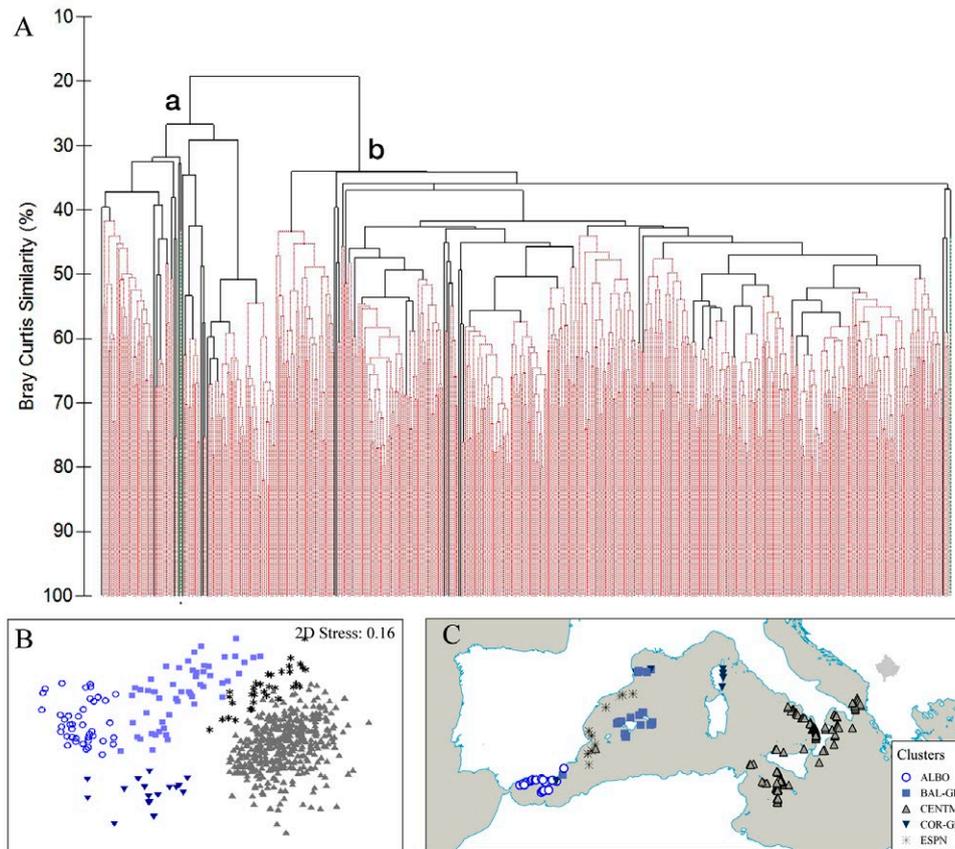


Fig. 5. – Cluster sorting dendrogram showing the percentage similarity of the hauls in relation to the fauna collected (A) and the corresponding two-dimensional MDS ordination (B) by the sorting cluster based upon an arbitrary level of similarity of 0.35; a and b are the two main groups. C, a map of the Mediterranean Sea showing the haul distribution by sorting cluster. ALBO, Alboran Sea and Alboran Island; ESPN, northern Spain; GL-COR, Gulf of Lions and Corsica; CENTM, central Mediterranean Basin; BAL-GL, Balearic basin and Gulf of Lions.

A group average sorting dendrogram showing the percentage similarity of the megabenthic community and the corresponding MDS ordination at each station sampled is shown in Figure 5. Grouping appeared to be strongly influenced by zone and suggests a longitudinal pattern of species distribution. The analysis delineated five clusters in two main community-level groups at the 25% level of similarity (Fig. 5A). These two main groups delineated species from the western and central basin as follows: Group a) a more heterogeneous group formed by samples from the western Mediterranean Basin (GSAs 1, 2, 5, 7 and 8); and Group b) a more homogeneous group formed by samples from the central Mediterranean Basin (GSA 10, 16, 18 and 19) and northern Spain (GSA 6). Three subgroups were formed by western basin samples, based again on longitude. These subgroups overlapped with GSAs, except GSA 7, which is widely distributed in space and showed a transitional zone between the Balearic basin and Corsica (Fig. 5B, C). From Group b, all hauls from the central basin were clustered together and separated by samples from northern Spain (Fig. 5A).

Ordination of data showed good correspondence with clusters, with the samples being adequately represented (stress=0.16) in two-dimensional space (Fig. 5B). The ANOSIM test performed on the groupings showed that the clusters were significantly different from one another (global $R=0.86$, $p<0.01$; Table 2). Analysis of similarities of the complete data set showed an overall significant difference between GSAs ($R=0.67$, $p<0.01$; Table 3). In contrast, there were no significant temporal differences among samples ($R=0.03$, $p=0.1$).

SIMPER analysis was used to identify the species that contributed to the highest similarity within clusters (Supplementary material, Table S1). The clusters formed exclusively by areas, such as ALBO (Alboran Sea and Alboran Island) and ESPN (northern Spain) showed the highest values of average similarity, 55.6% and 48.3% respectively, and three other clusters showed a similar percentage of similarity (close to 40%). According to SIMPER, although 43 species were listed, there were four dominant species: *Phycis blennoides*, *Galeus melastomus*, *Plesionika martia* and *Todarodes sagittatus*. These four species showed a wide range of distribution, appearing within all clusters. However, they showed a decreasing eastward pattern in their average biomass, except *Plesionika martia*, which showed an opposite trend (Supplementary material Table S1). The analysis also showed the presence of species exclusive to certain zones: for example, *Nezumia sclerorhynchus* appeared only in Corsica and the central basin (clusters GL-COR and CENTM), while *Nezumia aequalis* was limited to the western Mediterranean (ALBO, ESPN and BAL-GL). *Aristaeomorpha foliacea* contributed greatly to the community of the central Mediterranean (CENTM), while *Aristeus antennatus* did so to the community of northern Spain and the Balearic Islands (BAL-GL and ESPN) and *Nephrops norvegicus* to the cluster of the Gulf of Lions and Corsica (GL-COR). Six species of Chondrichthyes (*G. melastomus*, *Galeus atlanticus*,

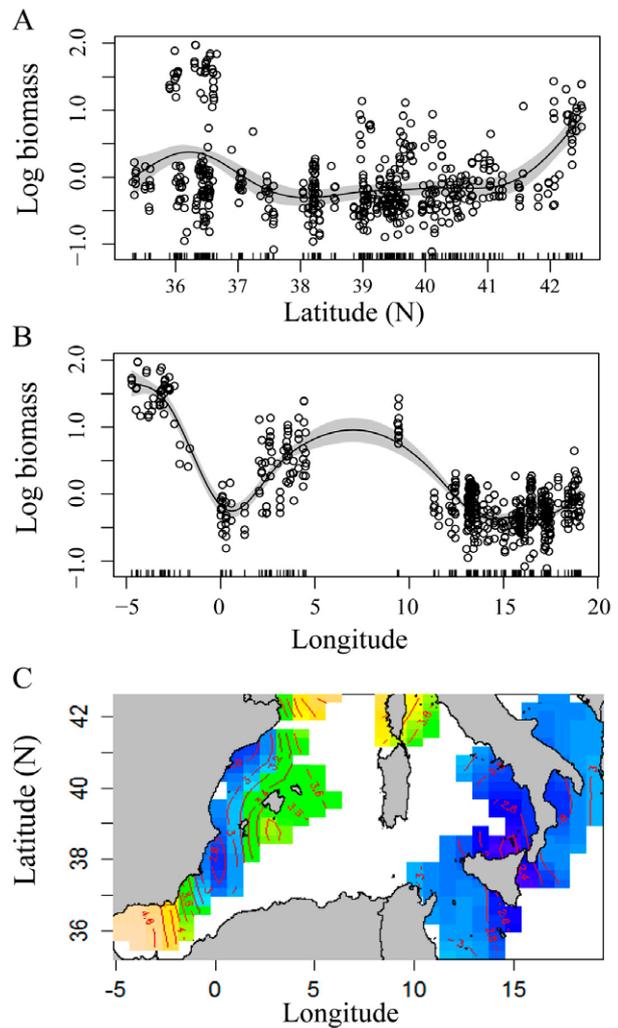


Fig. 6. – Results of significant regression models fitted for overall community to assess the connection of log-transformed biomass (g km^{-2}) index with latitude (A), longitude (B; negative values: West, positive values: East), and with the interaction of latitude and longitude (C). Shaded areas represent 95% confidence intervals. The colour gradient of the geographical effect codes from low values (darker colours) to high values (lighter colours). The statistical summary of all models for the entire community and for different groups is summarized in Table 4.

Etmopterus spinax, *Chimaera monstrosa*, *Dipturus oxyrinchus* and *Scyliorhinus canicula*) contributed to the overall similarity within groups. *G. melastomus* and *S. canicula* showed the highest percentage of contribution in the northern Spain cluster (ESPN). In contrast, *E. spinax* contributed to all clusters except ESPN. *G. atlanticus* contributed exclusively to ALBO, and *D. oxyrinchus* exclusively to GL-COR. Additionally, one species of Cnidaria, *Isidella elongata*, and the Gastropoda *Galeodea rugosa* contributed to the overall similarity within GL-COR and ALBO, respectively.

Based on generalized cross-validation and Aikake information criterion values, the best models explained 85.2% of the deviance variability of total biomass, including the additive effect of latitude and longitude (Table 4). The GAM models identified a significant statistical decrease in biomass eastward, but with minimum values in the longitude corresponding to GSA6

Table 4. – Generalized additive models (GAM) fitted to assess the effect of latitude and longitude on biomass index for the overall sampled community (Total) and by species group. GCV, Generalized cross-validation; AIC, Akaike Information Criterion; Num, Number of samples; %Dev, percentage of explained deviance. Ostei, Osteichthyes; Chon, Chondrichthyes; Crus, Crustacea; Cepha, Cephalopoda; Cnid, Cnidaria; Echi, Echinodermata; OtherMoll, other Mollusca (non-cephalopod).

Species group	Response variable	Factor	GCV	AIC	Num	%Dev	p
Total	LogBiom (g km ⁻²)	~ lat	0.29	854	534	24.4	<0.001
	LogBiom (g km ⁻²)	~ long	0.08	214	534	77.2	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.06	17	534	85.2	<0.001
Cnid	LogBiom (g km ⁻²)	~ lat	0.92	816	296	23.9	<0.001
	LogBiom (g km ⁻²)	~ long	0.51	643	296	57.8	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.45	603	296	66.5	<0.001
Cepha	LogBiom (g km ⁻²)	~ lat	0.46	984	476	14.2	<0.001
	LogBiom (g km ⁻²)	~ long	0.34	848	476	36.2	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.31	801	476	45.5	<0.001
Crus	LogBiom (g km ⁻²)	~ lat	0.17	568	534	13.8	<0.001
	LogBiom (g km ⁻²)	~ long	0.11	346	534	43.6	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.08	213	534	58.7	<0.001
Echi	LogBiom (g km ⁻²)	~ lat	0.71	592	237	16.3	<0.001
	LogBiom (g km ⁻²)	~ long	0.36	429	237	58.7	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.34	417	237	64.5	<0.001
Chon	LogBiom (g km ⁻²)	~ lat	0.44	1072	532	21.2	<0.001
	LogBiom (g km ⁻²)	~ long	0.18	623	532	66.3	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.15	512	532	74.4	<0.001
OtherMoll	LogBiom (g km ⁻²)	~ lat	0.64	510	212	5.08	<0.05
	LogBiom (g km ⁻²)	~ long	0.21	277	212	69.9	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.2	268	212	74.2	<0.001
Oste	LogBiom (g km ⁻²)	~ lat	0.64	993	534	21.3	<0.001
	LogBiom (g km ⁻²)	~ long	0.21	455	534	71.5	<0.001
	LogBiom (g km ⁻²)	~ (lat, long)	0.2	310	534	79.8	<0.001

Table 5. – Summary of regression models results assessing the effects of fishing effort (FE), latitude and longitude on mean biomass values for the Spanish area.

Response variable	Factor	GCV	AIC	Num	%Dev	p
LogBiom (g km ⁻²)	~ lat	0.11	46.3	68	84.5	<0.001
LogBiom (g km ⁻²)	~ long	0.09	34.5	68	86.7	<0.001
LogBiom (g km ⁻²)	~ FE	0.53	150.6	68	16.4	<0.001
LogBiom (g km ⁻²)	~ s(FE) + s(lat, long)	0.06	10.4	68	90.7	<0.001

(i.e. -1° to 3.16° , Fig. 6B). Longitude was the single variable which explained the highest variability for biomass. These results were observed for the overall community as well as for all species groups analysed (Table 4). For latitude, the highest values seem to be related to higher latitude, although there was also a maximum around $36-37^\circ$, around which both low and high values were found (Fig. 6B), as they correspond to different trends found in the Alboran area (GSAs 1 and 2) and the Strait of Sicily (GSA 16).

Regarding the assessment of the possible effect of fishing effort on biomass values, the best models explained 90.7% of the deviance variability of total biomass, including latitude, longitude and fishing effort (Table 5). Spatial distribution explained higher variability than fishing effort. However, a significant decreasing pattern between biomass index and fishing effort was found, explaining 16.4% of the variability (Table 5, Fig 7A). The spatial effect in biomass and fishing effort showed opposite patterns, with the highest biomass in the areas with the lowest fishing effort (GSA 1), and the lowest biomass overlapped with the highest fishing effort (north of GSA 6) (Fig. 7B, C). An exception was found in GSA2, which was relatively high impacted but showed high biomass values.

DISCUSSION

The present study explores long-term distribution patterns of megafauna in the Mediterranean Basin and

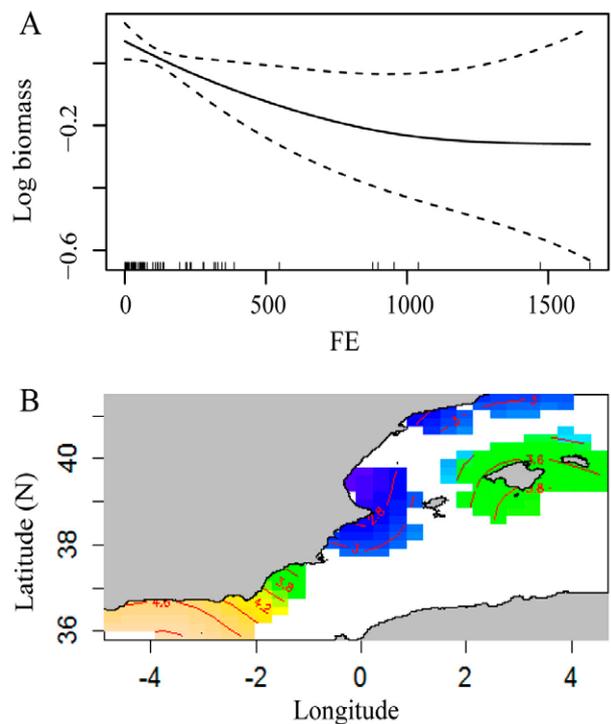


Fig. 7. – Partial effects of fishing effort (FE), and spatial distribution on the biomass index (g km⁻²) in the western Mediterranean (GSAs 1, 2, 5 and 6) using logarithmic transformation of the biomass index (A). The colour gradient of the geographical effect codes from low values (darker colours) to high values (lighter colours) (B). The statistical summary of plots is summarized in Table 5.

how it may be affected by fishing. The results, overall, showed an eastward decreasing pattern in the abundance of megafauna assemblages collected with a trawl net of 500 to 800 m on the Mediterranean continental slope. This finding was observed for all the analysed taxonomic groups (Osteichthyes, Chondrichthyes, Crustacea, Echinodermata, Cephalopoda, other Mollusca, Tunicata and Porifera).

The decreasing eastward pattern observed is consistent with the available information limited to a single studied taxon (Cartes et al. 2002, Company et al. 2004, D'Onghia et al. 2004) and with results reported for deeper areas (below 800 m depth) (Danovaro et al. 2010, Tecchio et al. 2011a), and is primarily related to a decreasing west-east gradient of biological production (Coll et al. 2010). The Mediterranean Sea is characterized by a well-known west to east decrease in nutrient concentration, phytoplankton biomass and surface primary production (Moutin and Raimbault 2002) that seems to be mirrored by a similar decrease in benthic megafaunal biomass. The contrasting results in community descriptors obtained between the western and central Mediterranean basins in this study suggest that differences in biological production (or more generally, in food availability) between the two basins might be the strongest driver for community abundance and biomass. However, other drivers such as fishing effort may also modulate the pattern.

We observed that communities from northern Spain (GSA 6) do not follow the general eastward decreasing trend, showing different compositions and lower abundance values in all the studied taxonomic groups in comparison with adjacent areas. It is well known that the deep NW Mediterranean Basin is an area of high productivity in comparison with the other parts of the Mediterranean Sea, because of higher surface productivity, coastal inputs and exposure to massive inputs of organic matter caused by cyclic cascading events (Margalef 1985, Canals et al. 2006, 2009). However, deep-water bottoms in this area have been intensively trawled during the last century (Gorelli et al. 2016, Pitcher et al. 2017), and thus the presence of the lowest biomass values in these communities inhabiting more productive waters suggest that fishing exploitation might have an important impact on communities in this area. In fact, our results showed that deep trawl-fishing exploitation in GSA 6 is two to four times higher than that in adjacent areas of the Spanish continental slope margin, with the exception of Alboran Island. (Fig. 7B). These results suggest that in this area human activity is an important factor in describing species community and partially modulates community descriptors. This is particularly true on the continental margins, where the life-history characteristics of several deep-sea species make them potentially more vulnerable to human impacts. These results are in accordance with those of previous studies showing that trawl-fishing exploitation in GSA 6 is very intense and much higher, for instance, than in the Balearic Islands (GSA 5) and the Alboran Sea (GSA 1), two sites that were also found to have healthier communities (Ramírez-Amaro et al. 2016, Quetglas et al. 2017).

Following the present study trends but in a whole Mediterranean context, Colloca et al. (2017) identified GSA 6 (with GSA 9 and 17) as the fisheries with the lowest ecosystem sustainability. Moreover, Company et al. (2004) in a comparative study of Mediterranean decapods, found the same general eastward decreasing pattern in species dwelling below 1000 m depth, but not in species from the middle slope (between 600 and 800 m depth), also potentially due to the intense fishing activity targeting *A. antennatus* (western Mediterranean) and *A. foliacea* (in Greek waters). Note that in the present study the results of the fishing pressure in deep-water communities were skewed by the high effort values found at Alboran Island: in fact, if we deleted the eight trawls conducted in this area, the fishing effort explained 34% of the biomass variability. Alboran Island is a seamount of volcanic origin characterized by high productivity (Maldonado and Comas 1992) that has a special fishing regulation (BOE 1998). While it is becoming increasingly clear that human activities are impacting deep-sea Mediterranean communities (Cartes et al. 2004, Navarro et al. 2015, Piroddi et al. 2017), in order to set up effective mitigation strategies, the effects of fishing impacts need to be better quantified. Thus, these results are still preliminary and an analysis of a wider spatial scale will be conducted.

The longitudinal gradient found in this study for biomass and abundance was also observed in the assemblage composition. The MDS results showed samples clearly grouped among geographic sub-areas, except again for samples from northern Spain (GSA 6). The cluster analysis showed different species in the community composition between the western and central Mediterranean (the most significant examples were the two species of *Nezumia* spp. and Aristeids: *N. aequalis* was exclusively found in the western basin and *N. sclerorhynchus* in the central basin of Mediterranean; *A. antennatus* dominated the Balearic Sea, while *A. foliacea* was more abundant in Adriatic and Ionian Sea communities). These species could be preferentially distributed due to their biology and fishing could also potentially alter the community compositions in highly exploited areas (e.g. GSA 6). Additionally, we found higher homogeneity between samples from the central basin than those from the western basin. The more complex oceanographic dynamism of the western Mediterranean Basin (Béranger et al. 2005) and the human-induced changes may have driven the observed results and may indicate that each sub-area is characterized by the presence of a specific assemblage with high biogeographic complexity.

An increase in small and fast-growing species has been observed to be a general community response to trawling (Hiddink et al. 2006). The dominance of crustaceans (which are show the highest percentage of the community) throughout the Mediterranean middle slope suggests that they may be more competitive in a overfishing context than other megabenthos groups (e.g. elasmobranchs and non-crustacean invertebrates). High values of crustacean density have been related to medium and high levels of fishing effort (Guijarro et al. 2011) and, in fact, high catches of *A. antennatus*

have been related to the ability of fishermen to remove competitors at a higher rate (Sardà and Maynou 1998). Interestingly, the only exception was the Alboran Basin (GSA 1 and 2) where the community was dominated by Chondrichthyes. The dominance of species characterized by slow population growth, such as sharks and rays, might be due to the fact that the open slope has remained almost unexploited at depths lower than 500 m (Torres et al. 2001, Rey et al. 2005, Ramírez-Amaro et al. 2016), in addition to the particular oceanographic conditions, river discharges and the presence of submarine canyon which result in very productive areas (Millot 1999, Moranta et al. 2007). Moreover, sessile fauna has been suggested to be the first to undergo the negative effects of fishing (Jennings and Kaiser 1998, Roberts 2002). In accordance, the abundance and biomass of invertebrate non-crustaceans was much lower than that of more mobile fauna, such as fish and crustacean decapods, in the whole Mediterranean continental slope, except for punctual peaks in the values of Echinodermata (GSA 7) and Cnidaria (GSAs 8 and 18). The high densities and biomasses of these two taxonomic groups were caused by isolated hauls conducted over *Leptometra* sp. grounds and deep coral facies of *Isidella elongata*. The compact mud facies with *Isidella elongata* have been listed by the GFCM as sensitive habitats because of their importance as an essential habitat for certain crustacean species (*Aristeus antennatus* and *Aristaeomorpha foliacea*) (GFCM 2009, Fabri et al. 2014). Recent studies have shown that *I. elongata* is only present in areas where the fishing effort is low or absent (Maynou and Cartes 2012, Lauria et al. 2017), a finding that may explain the isolated presence of this species in the present study. This apparent impact of fishing on the Mediterranean continental slope is consistent with earlier descriptions of deep-sea communities in some areas of the Mediterranean (e.g. the Balearic Islands, Farriols et al. 2017) and recent analyses of sediment cores from the NW Mediterranean continental slope (Cartes et al. 2017), which found significant quantities of deep-water coral aggregates that have almost disappeared, indicating their previous/historic presence in these areas. However, further analysis, including the combined use of different gears (e.g. OTMS and the Agassiz dredge or benthic sledge) would be required in order to provide an integrated image of the megafaunal compartment, particularly regarding non-crustacean invertebrates (i.e. echinoderms), for which little information is currently available on their distribution (Tecchio et al. 2011b, Mecho et al. 2015).

In conclusion, the present study is the first attempt to describe the middle slope community along a wide spatial scale. It is in agreement with previous works which report a general eastward decreasing pattern in community descriptors (e.g. Coll et al. 2010, Keller et al. 2016) potentially related to environmental drivers (primary production and temperature). In addition, fishing activity also potentially modulates the deep Mediterranean community. This statement is particularly reflected in highly impacted areas, such as the northwestern Spanish middle slope, where the commu-

nity does not and may be no longer follow the general eastward decreasing pattern, suggesting that the human activity has largely modified the community structure in this area.

Further investigations would require high-spatial resolution data (i.e. data from VMS or the Automatic Information System coupled to information on gear impact on the seabed) to determine the potential impact of fishing on a large spatial scales (Eigaard et al. 2015, 2017). Other alternative approaches need to be developed in order to assess the impact on ecosystem functioning and the response to fishing pressure and other human stressors. These could be based on life-history and biological traits of impacted species (de Juan and Demestre 2012, Rijnsdorp et al. 2016) or on community functional diversity indicators (Mouillot et al. 2013, Beauchard et al. 2017). They could be based on modelling approaches that estimate the reduction in community biomass or the shift in community composition corresponding to the estimated fishing intensity relative to system carrying capacity and natural disturbances (Pitcher et al. 2017). Additionally, the use of habitat suitability modelling, which predicts the suitability of a location for a species or group of species, based on their observed relationship with environmental conditions (Davies et al. 2015, Rowden et al. 2017), could help in spatially managing the impact of fishing on Mediterranean continental margins.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available through the on-line version of this article and at the following link:

<http://scimar.icm.csic.es/scimar/supplm/sm04852esm.pdf>

Table S1. – Results of similarity percentage analysis (SIMPER) of the overall community on each GSA. Av.Abund (average abundance), Av.Sim (average similarity), Sim/SD (ratio of the average similarity and the standard deviation), Contrib% (percentage contribution), Cum% (cumulative percentages).

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Large-scale distribution of a deep-sea megafauna community along Mediterranean trawlable grounds

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Supplementary material

Table S1. – Results of similarity percentage analysis (SIMPER) of the overall community on each GSA. Av.Abund (average abundance), AvSim (average similarity), Sim/SD (ratio of the average similarity and the standard deviation), Contrib% (percentage contribution), Cum% (cumulative percentages).

Cluster ALBO

Average similarity: 55.65

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Galeus melastomus</i>	924.6	17.71	3.09	31.82	31.82
<i>Nezumia aequalis</i>	332.57	6.73	5.81	12.09	43.91
<i>Trachyrincus scabrus</i>	434.23	4.72	1.04	8.48	52.39
<i>Phycis blennoides</i>	200.33	4.14	4.61	7.43	59.82
<i>Chimaera monstrosa</i>	202.13	2.75	1.23	4.95	64.77
<i>Etmopterus spinax</i>	161.12	2.54	1.72	4.56	69.33
<i>Todarodes sagittatus</i>	109.2	1.7	1.17	3.05	72.39
<i>Helicolenus dactylopterus</i>	131.92	1.56	0.99	2.8	75.19
<i>Hoplostethus mediterraneus</i>	104.06	1.55	1.96	2.78	77.97
<i>Lampanyctus crocodilus</i>	80.52	1.24	1.8	2.22	80.19
<i>Galeus atlanticus</i>	130.38	1.02	0.53	1.83	82.02
<i>Plesionika martia</i>	59.24	1	1.81	1.8	83.83
<i>Coelorinchus caelorhincus</i>	108.42	0.91	0.51	1.64	85.47
<i>Conger conger</i>	81.52	0.9	1.03	1.62	87.09
<i>Galeodea rugosa</i>	48.67	0.74	1.26	1.33	88.42
<i>Alepocephalus rostratus</i>	119.15	0.72	0.36	1.3	89.72
<i>Lophius budegassa</i>	81.09	0.61	0.45	1.09	90.81

Cluster BAL-GR

Average similarity: 39.92

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Galeus melastomus</i>	207.01	7.66	1.84	19.2	19.2
<i>Phycis blennoides</i>	110.59	5.03	1.69	12.6	31.79
<i>Aristeus antennatus</i>	90.87	4.47	1.47	11.2	42.99
<i>Lampanyctus crocodilus</i>	79.93	3.32	1.48	8.32	51.31
<i>Geryon longipes</i>	63.77	2.01	0.84	5.03	56.35
<i>Plesionika martia</i>	48.02	1.95	1.65	4.87	61.22
<i>Todarodes sagittatus</i>	65.72	1.51	0.6	3.78	65
<i>Etmopterus spinax</i>	44.06	1.45	0.87	3.63	68.63
<i>Nezumia aequalis</i>	39.49	1.23	0.92	3.07	71.7
<i>Pasiphaea multidentata</i>	23.17	0.9	0.88	2.26	73.97
<i>Trachyrincus scabrus</i>	61.12	0.81	0.39	2.02	75.99
<i>Conger conger</i>	39.46	0.8	0.5	2	77.99
<i>Plesionika acanthonotus</i>	17.11	0.62	1.13	1.56	79.54
<i>Polycheles typhlops</i>	15.16	0.54	1.26	1.35	80.9
<i>Histioteuthis reversa</i>	23.39	0.53	0.52	1.33	82.23
<i>Lepidion lepidion</i>	22.19	0.5	0.54	1.25	83.47
<i>Notocanthus bonaparte</i>	16.23	0.45	0.62	1.13	84.61
<i>Hymenocephalus italicus</i>	16.9	0.44	0.71	1.09	85.7
<i>Merluccius merluccius</i>	26.12	0.35	0.26	0.88	86.58
<i>Nephrops norvegicus</i>	28.5	0.34	0.43	0.85	87.42
<i>Sergia robusta</i>	9.69	0.3	0.82	0.75	88.18
<i>Stomias boa boa</i>	11.56	0.29	0.56	0.72	88.9
<i>Chauliodus sloani</i>	11.44	0.27	0.47	0.68	89.58
<i>Micromesistius poutassou</i>	19.75	0.26	0.32	0.65	90.23

Cluster COR-GL

Average similarity: 44.87

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Galeus melastomus</i>	300.12	7.82	3.04	17.43	17.43
<i>Nephrops norvegicus</i>	174.34	4.29	2.46	9.57	27
<i>Helicolenus dactylopterus</i>	158.7	3.95	2.65	8.81	35.81
<i>Coelorinchus caelorhincus</i>	113.65	3.33	2.22	7.43	43.24
<i>Pagellus bogaraveo</i>	186.79	2.61	0.7	5.81	49.05
<i>Plesionika martia</i>	85.17	2.39	1.94	5.33	54.39
<i>Chimaera monstrosa</i>	112.45	2.3	1.14	5.13	59.51
<i>Phycis blennoides</i>	80.49	2.05	1.95	4.56	64.07
<i>Hoplostethus mediterraneus</i>	86.16	1.55	0.97	3.46	67.53
<i>Lepidorhombus boscii</i>	57.02	1.32	1.42	2.95	70.48
<i>Etmopterus spinax</i>	52.8	1.26	1.52	2.8	73.29
<i>Nezumia sclerorhynchus</i>	58.92	1.26	0.99	2.8	76.08
<i>Hymenocephalus italicus</i>	38.18	1.02	1.71	2.28	78.37
<i>Dipturus oxyrinchus</i>	78.41	1.02	0.51	2.27	80.63
<i>Chlorophthalmus agassizi</i>	58.42	0.85	0.94	1.9	82.53
<i>Parapenaeus longirostris</i>	28.52	0.59	0.9	1.32	83.85
<i>Polycheles typhlops</i>	22.28	0.58	2.22	1.29	85.14
<i>Isidella elongata</i>	99.66	0.57	0.26	1.28	86.42
<i>Lophius piscatorius</i>	94.83	0.55	0.34	1.23	87.65
<i>Micromesistius poutassou</i>	79.65	0.39	0.41	0.88	88.53
<i>Merluccius merluccius</i>	45.86	0.37	0.39	0.84	89.36
<i>Todarodes sagittatus</i>	39.59	0.37	0.32	0.82	90.18

Cluster ESPN
Average similarity: 48.30

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Galeus melastomus</i>	89.36	12.56	2.14	26.01	26.01
<i>Phycis blennoides</i>	42.71	6.29	2.42	13.02	39.03
<i>Aristeus antennatus</i>	34.51	5.05	1.54	10.46	49.49
<i>Lampanyctus crocodilus</i>	31.37	3.91	2.06	8.1	57.59
<i>Geryon longipes</i>	33.32	3.07	0.84	6.36	63.96
<i>Nephros norvegicus</i>	15.44	1.62	1.31	3.35	67.31
<i>Plesionika martia</i>	12.76	1.56	1.41	3.24	70.54
<i>Todarodes sagittatus</i>	16.07	1.38	0.71	2.86	73.4
<i>Polycheles typhlops</i>	9.21	1.37	2.58	2.84	76.23
<i>Trachyrincus scabrus</i>	19.15	1.36	0.9	2.82	79.06
<i>Nezumia aequalis</i>	11.85	1.25	1.1	2.58	81.64
<i>Merluccius merluccius</i>	15.25	0.87	0.39	1.81	83.45
<i>Pasiphaea multidentata</i>	6.62	0.81	1.37	1.68	85.12
<i>Conger conger</i>	10.98	0.71	0.51	1.48	86.6
<i>Micromesistius poutassou</i>	9.23	0.66	0.53	1.37	87.97
<i>Scyliorhinus canicula</i>	9.38	0.55	0.43	1.14	89.11
<i>Plesionika acanthonotus</i>	3.83	0.4	1.08	0.82	89.93
<i>Histioteuthis reversa</i>	6.73	0.37	0.47	0.77	90.7

Cluster CENTM
Average similarity: 43.56

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
<i>Galeus melastomus</i>	67.95	9.1	2.21	20.9	20.9
<i>Phycis blennoides</i>	32.36	4.22	1.98	9.68	30.59
<i>Nezumia aequalis</i>	26.11	3.41	1.97	7.84	38.42
<i>Hoplostethus mediterraneus</i>	35.73	3.33	1.18	7.63	46.06
<i>Aristaeomorpha foliacea</i>	28.1	3.29	1.29	7.55	53.61
<i>Etmopterus spinax</i>	21.09	2.66	1.47	6.11	59.72
<i>Plesionika martia</i>	16.68	2.03	1.76	4.66	64.38
<i>Hymenocephalus italicus</i>	12.43	1.56	1.58	3.57	67.95
<i>Lampanyctus crocodilus</i>	13.43	1.54	1.05	3.52	71.47
<i>Aristeus antennatus</i>	16.4	1.35	0.58	3.1	74.57
<i>Polycheles typhlops</i>	9.07	1.17	1.8	2.69	77.26
<i>Todarodes sagittatus</i>	17.35	1.12	0.52	2.56	79.83
<i>Coelorinchus caelorhincus</i>	15.55	0.96	0.6	2.21	82.04
<i>Merluccius merluccius</i>	17.3	0.9	0.44	2.06	84.1
<i>Helicolenus dactylopterus</i>	15.47	0.78	0.48	1.79	85.89
<i>Nettastoma melanorum</i>	6.56	0.54	0.68	1.23	87.12
<i>Parapenaeus longirostris</i>	8.38	0.51	0.49	1.16	88.28
<i>Nephrops norvegicus</i>	8.74	0.5	0.51	1.15	89.43
<i>Chimaera monstrosa</i>	10.02	0.4	0.33	0.91	90.34