

## Decapod crustacean assemblages on trawlable grounds in the northern Alboran Sea and Gulf of Vera

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**Summary:** This study analyses the samples collected annually (2012 to 2018) on circalittoral and bathyal soft bottoms (30 to 800 m) by the MEDITS surveys in the northern Alboran Sea (including Alboran Island) and the Gulf of Vera to determine the composition, structure and distribution of decapod crustacean assemblages. A total of 94 decapod crustacean species were identified. Non-metric multidimensional scaling showed depth to be the main factor for distinguishing four main decapod assemblages: the inner shelf (30-100 m depth), outer shelf (101-200 m), upper slope (201-500 m) and middle slope (501-800 m). PERMANOVA analyses revealed further significant depth-related differences between three established geographical sectors of the study area (northern Alboran Sea, Gulf of Vera and Alboran Island). Generalized additive model analyses were used to assess the bathymetrical, geographical and environmental effects on the ecological indices of each assemblage. Results showed that depth and the geographical effect were the main drivers in all cases. Decreases in abundance and increases in species richness, Shannon-Wiener diversity and Pielou's evenness indices with depth were detected. This study shows the primacy of depth and geographical effect on the distribution of decapod species in the study area, in alignment with findings from other parts of the Mediterranean Sea.

**Keywords:** Alboran Sea; crustaceans; decapods; assemblages; GAM; circalittoral; bathyal; biodiversity.

### Asociaciones de crustáceos decápodos en fondos arrastrables del norte del mar de Alborán y golfo de Vera

**Resumen:** En este estudio se analizan muestras obtenidas anualmente (2012 al 2018) en fondos blandos circalitorales y batiales (30 a 800 m) del norte del mar de Alborán (incluida la Isla de Alborán) y golfo de Vera durante siete campañas de arrastre de fondo, MEDITS, con el fin de determinar la composición, estructura y distribución de las asociaciones de crustáceos decápodos. En total se identificaron 94 especies de decápodos. El escalamiento multidimensional no métrico indicó la profundidad como factor principal en la diferenciación de cuatro asociaciones de decápodos: plataforma interna (30-100 m de profundidad), plataforma externa (101-200 m), talud superior (201-500 m) y talud medio (501-800 m). Los análisis PERMANOVA revelaron diferencias significativas relacionadas con la profundidad entre los tres sectores geográficos establecidos en el área de estudio (norte del mar de Alborán, golfo de Vera e Isla de Alborán). Los modelos aditivos generalizados se utilizaron para evaluar los efectos batimétricos, geográficos y ambientales sobre los índices ecológicos de cada una de las asociaciones encontradas. Los resultados mostraron la profundidad y el efecto geográfico como los principales factores en todos los casos. Se detectó una disminución de la abundancia con la profundidad mientras que la riqueza de especies, el índice de diversidad de Shannon-Wiener y el índice de equidad de Pielou aumentaron. Este estudio muestra la importancia de la profundidad y el efecto geográfico en la distribución de las especies en el área de estudio en consonancia con lo descrito en otras áreas del mar Mediterráneo.

**Palabras clave:** mar de Alborán; crustáceos; decápodos; asociaciones; GAM; circalitoral, batial, biodiversidad.

**Citation/Como citar este artículo:** Ciércoles C., García-Ruíz C., Abelló P., Hidalgo M., Torres P., González M., Mateo-Ramírez A., Rueda J.L. 2022. Decapod crustacean assemblages on trawlable grounds in the northern Alboran Sea and Gulf of Vera. *Sci. Mar.* 86(3): e039. <https://doi.org/10.3989/scimar.05265.039>

**Editor:** J. Templado.

**Received:** January 12, 2022. **Accepted:** June 9, 2022. **Published:** August 23, 2022.

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## INTRODUCTION

The Alboran Sea, located in the westernmost part of the Mediterranean Sea, is a transitional area between the Atlantic Ocean and the Mediterranean Sea that has been reported as a self-standing ecoregion harbouring a large marine biodiversity and a wide variety of habitats (Spalding et al. 2007, Rueda et al. 2021, Templado et al. 2021). Because of its distinctive geomorphological and oceanographical features, the Alboran Sea has been identified as a specific biogeographical sector for several marine groups (Real et al. 2021), including demersal fish (Gaertner et al. 2005, González et al. 2021), molluscs (Gofas et al. 2011, Ciércoles et al. 2018) and crustaceans (Abelló et al. 2002).

Crustaceans are one of the most morphologically diverse taxonomic groups of the aquatic ecosystems, where they are one of the top dominant groups (Martin and Davis 2001). Within the crustaceans, the order Decapoda constitutes a dominant component of Mediterranean benthic and demersal communities of both the continental shelf and slope (Maynou and Cartes 2000, Guijarro 2012). Their relative importance in the Mediterranean Sea has been hypothesized because of their very high competitive trophic strategy (Cartes and Sardà 1992, Maynou and Cartes 2000). Moreover, decapods are a key taxon linking lower and higher trophic levels (Cartes 1998, Fanelli 2007). Several decapod species are of commercial interest and form an important component of the catches of the bottom trawl fishery in the Alboran Sea and the Gulf of Vera. In fact, some decapod species, such as the deep-water rose shrimp, *Parapenaeus longirostris*, the Norway lobster, *Nephrops norvegicus*, and the red shrimp *Aristeus antennatus* are economically valuable target species in demersal fisheries, so their populations are regularly assessed in the Alboran Sea (González et al. 2021), as well as in other parts of the Mediterranean Sea (Guijarro 2012; Regulation (EU) 2019/1022). Knowledge of the distribution and abundance of species along environmental gradients has traditionally been important to characterize and understand the role of biological communities in aquatic systems (Wenner and Boesch 1979). Studies of biological communities are also essential tools for understanding the dynamics of exploited species from an ecosystem point of view, which is a key element in considering separate management units (Abelló et al. 2002). Additionally, species-specific studies on decapod species have revealed geographical variability patterns throughout the Mediterranean Sea, reflecting the importance of studies at a small-scale geographical level. This approach has been shown to be more efficient for the management of certain species in contrast to large regional approaches (Gaertner et al. 2005, Guijarro et al. 2019) and it is particularly important for scientifically sustaining spatial management. The Alboran Sea, together with the Gulf of Vera, can be considered a transition zone between the Mediterranean and Atlantic biota of crustaceans, since it also constitutes a semipermeable barrier for genetic population exchanges between the Mediterranean Sea and the At-

lantic Ocean (Abelló et al. 2002, Mateo-Ramírez et al. 2015, Pascual et al. 2016).

Several studies on decapod assemblages have been carried out in different habitats of the Alboran Sea, particularly those of the infralittoral zone (soft bottoms, García Muñoz et al. 2008; seagrass meadows, García-Raso 1990, García Raso et al. 2006, Mateo-Ramírez et al. 2016; macroalgal communities, Mateo-Ramírez et al. 2018). However, despite their ecological and economical interest, few studies of decapod assemblages in circalittoral and bathyal soft bottoms have been carried out in the Alboran Sea using beam-trawl samples (Mateo-Ramírez et al. 2015) or including the Alboran Sea as part of studies with a wider scope covering the Spanish Mediterranean waters (Abelló et al. 2002).

The aims of this study were to (1) update faunistic inventories of decapod crustacean species in the Alboran Sea and the adjacent Gulf of Vera; (2) identify and characterize the main decapod assemblages; (3) analyse significant differences between assemblages in the ecological indices considered as community descriptors (decapod abundance, species richness, Pielou's evenness and the Shannon-Wiener diversity index) in order to study the spatial and temporal changes of the composition and structure of the decapod assemblages; and (4) model spatio-temporal trends of ecological indices in terms of potential environmental driving.

## MATERIALS AND METHODS

### Study area

The study area covers approximate 12753 km<sup>2</sup> and encompasses the northern Alboran Sea and Gulf of Vera, from Punta Europa (Strait of Gibraltar) to Cabo de Palos (Cartagena), including also the Alboran Island (Fig. 1). The main hydrological characteristics of this area are the mixture of Atlantic and Mediterranean water masses with (1) Atlantic surficial water masses entering the Mediterranean Sea and extending from the surface to 200 m depth; (2) Intermediate Levantine water masses from the Mediterranean Sea, flowing towards the Atlantic Ocean and usually extending from 200 to 600 m depth; and (3) deep water masses extending below the Levantine water masses to the sea bottom (Parrilla et al. 1986, Vargas-Yáñez et al. 2017). The different physico-chemical characteristics of these water masses, together with the density contrast and the geomorphology of the Alboran basin, are responsible for the complex hydrodynamic processes that take place in the area, along with the presence of the Alboran Gyre and nutrient-rich coastal upwellings (Tintoré et al. 1991, Vargas-Yáñez et al. 2010, 2021). The seafloor of the study area has a high geomorphological complexity with a wide variety of reliefs, such as depressions, banks, ridges and canyons (Parrilla and Kinder 1987, Ercilla et al. 1992, 2021). The northern Alboran Sea and the Gulf of Vera are both characterized by a very narrow continental shelf with alternating predominance of sands and muds, while the continental slope is mainly composed of very fine sediments (Rey and

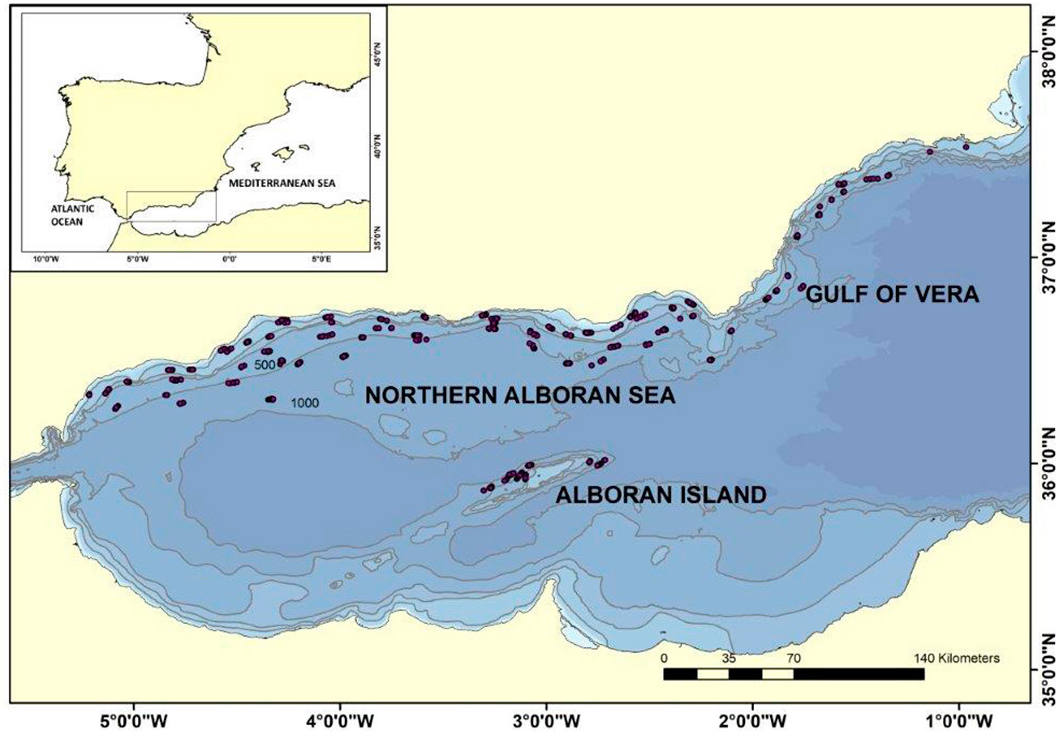


Fig. 1. – Map of the study area showing the sampling stations (black points) used during MEDITS surveys (2012 to 2018) and the sectors considered.

Medialdea 1989, Ercilla et al. 2021). In addition, the Alboran Sea, together with the Gulf of Lion and the mouth of different rivers (e.g. the Ebro River on the northeastern Spanish Mediterranean coast), is one of the areas with the highest primary production in the western Mediterranean (Vargas-Yáñez et al. 2010). This is due to several processes (e.g. nutrient flows from rivers and nutrient-rich coastal upwelling) that favour the injection of nutrients into the photophilous zone of the water column (Báez et al. 2021). The Gulf of Vera is also a strategic location in the western Mediterranean since it is adjacent to the Almería-Oran front, which forms a semi-permanent hydrographic barrier and a transition zone between the Alboran Sea (an area with greater Atlantic water influence) and the rest of the western Mediterranean basin (Tintoré et al. 1988, Millot 1999). The meridional sector of the Alboran Sea is characterized by the presence of an old volcanic ridge oriented SW-NE, on which Alboran Island is located (Vázquez 2005). This island is affected by the circulation of the water masses present in the Alboran basin and has been described as an anticyclonic area located between two geostrophic gyres of the incoming Atlantic surface water. These peculiar hydrological characteristics result in the singularity and extraordinary biodiversity of the benthic communities of the Alboran Island (Gofas et al. 2014), as well as of the Alboran Sea (Rueda et al. 2021). This high diversity promoted the protection of the Alboran Island and its surrounding bottoms through protection measures such as a Marine and Fishing Reserve, a Site of Community Importance and a Specially Protected

Area of Mediterranean Importance (Mateo-Ramírez et al. 2021).

### Sampling

The data for this study were obtained from 413 hauls performed on circalittoral and bathyal soft bottoms (30-800 m depth) of the northern Alboran Sea and the Gulf of Vera during seven MEDITS surveys (International Trawl Surveys in the Mediterranean Sea) between 2012 and 2018 (Bertrand et al. 2002, Spedicato et al. 2019), which are carried out annually in spring (Fig. 1). A stratified random sampling design was applied in the surveys, with the following bathymetric strata: 30-50, 51-100, 101-200, 201-500 and 501-800 m depth. No samples could be obtained at depths shallower than 100 m at Alboran Island as the depths shallower than 100 m around the island are a Marine and Fishing Reserve where trawling is not allowed (see study area section). Haul duration was a function of depth, with 30-minute duration for stations located at less than 200 m (continental shelf) and a 60-minute duration for those located at more than 200 m depth (continental slope) (Bertrand et al. 2002, Spedicato et al. 2019). According to the MEDITS protocol, the number of sampling stations (hauls) in each stratum is proportional to the area of these strata (MEDITS-Handbook 2017). Except for unusual problems (damage noted in previous years, etc.), the hauls are made at the same sampling stations from year to year. In the present study the number of hauls in each of the three established geo-

graphical sectors were 309 for the northern Alboran Sea sector, 51 for the Alboran Island sector and 53 for the Gulf of Vera sector.

The geographical position of each haul was recorded using the global positioning system of the research vessel. Haul performance and gear geometry were monitored using SCANMAR and, more recently, MARPORT sensors. The sampling device was a bottom trawl gear (GOC-73) with a cod-end mesh size of 20 mm, an average horizontal opening of 21.5 m and an average vertical opening of 2.5 m (Fiorentini et al. 1999). Temperature and salinity were recorded close to the bottom using a CTD SBE-37 coupled to the net. Every specimen caught was identified to the lowest possible taxonomic level. Finally, specimens of each species were counted and weighed on board. Scientific names for species followed the nomenclature of the World Register of Marine Species (WoRMS 17/02/2021).

### Data analysis

The swept area from each haul was estimated by monitoring the horizontal opening of the gear and the distance covered during the haul. These values were used to standardize catches in the trawled area, in order to obtain an estimation of abundance as the number of individuals per square km (ind. km<sup>-2</sup>). The frequency index (%F, percentage of hauls in which the species was present in relation to the total hauls carried out) and the dominance index based on abundance (%DN, percentage of individuals caught of a species over the total number of caught species in the total hauls of the study) were estimated for each species.

In order to analyse the potential differences in assemblages over the study area, three geographical sectors were assessed according to their different oceanographic characteristics (Sarhan et al. 2000, Vargas-Yáñez et al. 2010): (1) northern Alboran Sea (from Gibraltar to Cabo de Gata), characterized by a high Atlantic influence and the presence of permanent nutrient-rich coastal upwellings; (2) Gulf of Vera (from Cabo de Gata to Cabo de Palos), with a higher influence of the typical western Mediterranean conditions; and (3) Alboran Island, an insular area located at the top of the Alboran Ridge, which is far away from the continental margin and influenced to a certain extent by the eastern anticyclonic gyre of the Alboran Sea.

The decapod crustacean assemblages were identified using non-parametric multivariate classification (cluster) and ordination (non-metric multidimensional scaling, nMDS) techniques (Clarke 1993, Clarke and Warwick 2001). The resemblance matrix was calculated using the Bray-Curtis similarity index, with a previous square root data transformation in order to reduce the differences in the abundance of highly dominant species (Clarke and Warwick 2001). One-way SIMPER analysis was applied to determine the contribution of each species to the dissimilarity between the groupings of samples obtained in the cluster and nMDS analyses, which are defined as different assemblages (Clarke and Warwick 2001). A distance-based

permutational multivariate analysis of variance (PERMANOVA) (McArdle and Anderson 2001) based on the Bray-Curtis similarity matrix was used to test significant differences between the obtained assemblages (except for shallowest depths), with sector (fixed factor, three levels) and depth (fixed factor, three levels) as a source of variation. The PERMANOVA routine performs a partitioning of the total sum of squares according to the full experimental design, calculating an appropriated distance-based pseudo-F statistic for each term in the model, based on the expectations of mean squares. P-values are obtained using a permutation procedure (a permutation of residuals under a reduced model in our analysis) (Anderson et al. 2008). All these multivariate analyses were performed using PRIMER v6.0 & PERMANOVA+ software.

The abundance (N, ind. km<sup>-2</sup>), species richness (S), Shannon-Wiener diversity index (H') and Pielou's evenness index (J') were calculated for the crustacean decapods of each haul using PRIMER 6.0 software, and mean values were calculated for the main assemblages obtained after the multivariate analyses. The differences between assemblages were tested using the non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952) because the data did not fit the conditions for parametric analyses (e.g. ANOVA). These analyses were carried out using SPSS v15.0 software.

Generalized additive modelling (GAM, Hastie and Tibshirani 1990) was used to test the relationships of abundance, species richness, Shannon-Wiener diversity index and Pielou's evenness index with depth, geographic location and environmental variables: chlorophyll *a* (Chl *a*) concentration (Chl-*a*; mg m<sup>-3</sup>), nitrate (NO<sub>3</sub>), phosphate (PO<sub>4</sub>), sea bottom temperature (SBT; °C), sea bottom salinity (SBS; psu) and the annual NAO index. Year was considered as a factor in these analyses. Data of Chl *a*, NO<sub>3</sub> and PO<sub>4</sub> were obtained from satellite-data with a monthly time resolution developed within the Copernicus Programme (<http://marine.copernicus.eu>). Temperature and salinity were obtained from the CTD SBE 37 placed on the net. The North Atlantic Oscillation climate annual index (NAO) was obtained from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>. A Pearson correlation test was previously performed and environmental variables that had a high correlation (more than 0.9) were eliminated. A two-dimensional smoother was used by combining latitude and longitude to account for the geographical effect, representing the remaining spatially structured variance once the effect of the rest of covariates was removed. A one-dimensional smoother was used to investigate the geographical and environmental effects. The logarithmically transformed values (log[x+1]) of abundance were used to ensure a Gaussian distribution of the residuals. We adopted a backwards stepwise produced from an initial GAM model including all the variables, removing one non-significant covariate at time. The selection of the best model for each variable was based on the minimization of the Akaike information criterion in models with all covariates statistically significant (i.e. p<0.05). For all GAM analyses, residual



plots were checked and the assumptions of variance homogeneity and normal distribution were confirmed. The *mgcv* package in R (<http://www.r-project.org>) was used in the GAM analyses (Wood 2017).

## RESULTS

### Composition and structure of decapod crustaceans

A total of 94 decapod species were collected. The families showing the largest number of species were the Pandalida (epibenthic caridean shrimps), with nine spp., followed by the Inachidae (Brachyuran crabs) and the Paguridae (Anomuran hermit crabs) (with eight spp. each of them), and the Crangonidae (benthic caridean shrimps) (5 spp.) (Table 1).

The most abundant species were *Plesionika heterocarpus* ( $13094.81 \pm 10812$  ind.  $\text{km}^{-2}$ , mean per haul  $\pm$  standard error) (%DN: 70) followed by *Pasiphea sivado* ( $635.92 \pm 403.65$  ind.  $\text{km}^{-2}$ ) (%DN: 6) and *Dardanus arrosor* ( $547.59 \pm 153.90$  ind.  $\text{km}^{-2}$ ) (%DN: 2.49). Other dominant decapods were *P. martia* (%DN: 4.02), *Pagurus prideaux* (%DN: 1.91), *Liocarcinus depurator* (%DN: 1.58) and *P. longirostris* (%DN: 1.97). The most frequently captured species were *D. arrosor* (%F: 79), which also displayed the widest depth range (40-839 m), followed by *Macropodia longipes* (%F: 57), *L. depurator* (%F: 43), *P. martia* (%F: 42), and *Solenocera membranacea* (%F: 42). A total of 27 species (29% of the total decapods) were only recorded in one or two hauls, such as *Polybius henslowii*, *Alpheus platydactylus*, *Ebalia nux* and *Calocarides coronatus* (Table 1).

Table 1. – Decapod crustacean species caught with bottom trawl during MEDITS surveys (2012-2018) in circalittoral and bathyal soft bottoms of the northern Alboran Sea, Alboran Island and the Gulf of Vera. Depth range for collected specimens (metres);  $N_t$ , total abundance (individuals); %DN, dominance index of abundance expressed as a percentage; %F, frequency of occurrence expressed as a %. Systematic and taxonomical classification according to WoRMS.

	Depth range	$N_t$	%DN	%F
Family Acantheephyridae				
<i>Acantheephyra pelagica</i> (Risso, 1816)	449-794	27	<0.01	3.39
Family Alpheidae				
<i>Alpheus dentipes</i> Guérin, 1832	93	30	<0.01	0.24
<i>Alpheus glaber</i> (Olivi, 1792)	40-668	795	0.18	30.51
<i>Alpheus platydactylus</i> Coutière, 1897	641	1	<0.01	0.24
<i>Synalpheus gambarelloides</i> (Nardo, 1847)	154	4	<0.01	0.24
Family Aristeidae				
<i>Aristaeomorpha foliacea</i> (Risso, 1827)	554	1	<0.01	0.24
<i>Aristeus antennatus</i> (Risso, 1816)	393-879	2993	0.67	13.32
Family Atelecyclidae				
<i>Atelecyclus rotundatus</i> (Olivi, 1792)	43-362	20	<0.01	3.63
Family Axiidae				
<i>Calocarides coronatus</i> (Trybom, 1904)	667	1	<0.01	0.24
<i>Calocaris macandreae</i> Bell, 1846	363-869	198	0.04	12.11
Family Benthesicymidae				
<i>Gennadas elegans</i> (Smith, 1882)	431-794	11	<0.01	1.94
Family Calappidae				
<i>Calappa granulata</i> (Linnaeus, 1758)	43-529	25	<0.01	1.94
Family Crangonidae				
<i>Aegaeon cataphractus</i> (Olivi, 1792)	43-86	44	0.01	5.33
<i>Aegaeon lacazei</i> (Gouret, 1887)	119-762	98	0.02	13.32
<i>Philocheas echinulatus</i> (M. Sars, 1862)	135-554	123	0.02	9.69
<i>Philocheas sculptus</i> (Bell, 1847)	135	2	<0.01	0.24
<i>Pontophilus spinosus</i> (Leach, 1816)	78-538	494	0.11	17.43
Family Diogenidae				
<i>Dardanus arrosor</i> (Herbst, 1796)	40-839	10975	2.49	79.42
<i>Paguristes eremita</i> (Linnaeus, 1767)	74	1	<0.01	0.24
Family Dorippidae				
<i>Medorippe lanata</i> (Linnaeus, 1767)	49-573	31	<0.01	5.08
Family Dromiidae				
<i>Dromia personata</i> (Linnaeus, 1758)	54	1	<0.01	0.24
Family Epialtidae				

	Depth range	N <sub>t</sub>	%DN	%F
<i>Lissa chiragra</i> (Fabricius, 1775)	56	1	<0.01	0.24
<i>Pisa armata</i> (Latreille, 1803)	46-86	104	0.02	2.42
<i>Scyramathia carpenteri</i> (C. W. Thomson, 1873)	329-879	232	0.05	16.71
Family Ethusidae				
<i>Ethusa mascarone</i> (Herbst, 1785)	46	1	<0.01	0.24
Family Galatheidae				
<i>Galathea dispersa</i> Bate, 1859	59-249	34	<0.01	3.63
<i>Galathea intermedia</i> Lilljeborg, 1851	40-327	17	<0.01	3.39
<i>Galathea strigosa</i> (Linnaeus, 1761)	61	3	<0.01	0.24
Family Geryonidae				
<i>Geryon longipes</i> A. Milne-Edwards, 1882	440-869	259	0.05	14.77
Family Goneplacidae				
<i>Goneplax rhomboides</i> (Linnaeus, 1758)	40-766	600	0.13	30.51
Family Homolidae				
<i>Homola barbata</i> (Fabricius, 1793)	74-288	7	<0.01	1.21
<i>Paromola cuvieri</i> (Risso, 1816)	654	1	<0.01	0.24
Family Inachidae				
<i>Dorhynchus thomsoni</i> C. W. Thomson, 1873	329-808	32	<0.01	4.60
<i>Inachus aguiarii</i> Brito Capello, 1876	116	1	<0.01	0.24
<i>Inachus communissimus</i> Rizza, 1839	43-132	25	<0.01	3.87
<i>Inachus dorsettensis</i> (Pennant, 1777)	42-540	238	0.05	12.59
<i>Inachus thoracicus</i> P. Roux, 1830 [in P. Roux, 1828-1830]	46-118	27	<0.01	1.21
<i>Macropodia linaresi</i> Forest & Zariquiey Álvarez, 1964	42-95	73	0.01	2.91
<i>Macropodia tenuirostris</i> (A. Milne-Edwards & Bouvier, 1899)	40-774	2335	0.53	57.38
<i>Macropodia rostrata</i> (Linnaeus, 1761)	43-123	102	0.02	3.63
Family Leucosiidae				
<i>Ebalia nux</i> A. Milne-Edwards, 1883	554	1	<0.01	0.24
Family Lysmatidae				
<i>Ligur ensiferus</i> (Risso, 1816)	357-668	3	<0.01	0.73
Family Majidae				
<i>Eurynome aspera</i> (Pennant, 1777)	45-117	5	<0.01	1.21
Family Munididae				
<i>Munida intermedia</i> A. Milne-Edwards & Bouvier, 1899	121-664	52	0.01	5.08
<i>Munida rugosa</i> (Fabricius, 1775)	122	1	<0.01	0.24
<i>Munida speciosa</i> von Martens, 1878	85-554	457	0.10	11.14
<i>Munida perarmata</i> Sars, 1872	374-779	5	<0.01	0.97
Family Nephropidae				
<i>Nephrops norvegicus</i> (Linnaeus, 1758)	143-852	1301	0.29	30.51
Family Oregoniidae				
<i>Ergasticus clouei</i> A. Milne-Edwards, 1882	362-774	42	0.01	4.36
Family Paguridae				
<i>Anapagurus bicorniger</i> A. Milne-Edwards & Bouvier, 1892	249	1	<0.01	0.24
<i>Anapagurus laevis</i> (Bell, 1845)	49-424	9	<0.01	1.69
<i>Pagurus alatus</i> Fabricius, 1775	329-879	2252	0.51	32.20
<i>Pagurus anachoretus</i> Risso, 1827	54	1	<0.01	0.24
<i>Pagurus cuanensis</i> Bell, 1845	44-118	8	<0.01	1.45
<i>Pagurus excavatus</i> (Herbst, 1791)	40-529	119	0.02	16.71
<i>Pagurus mbizi</i> (Forest, 1955)	50-361	42	0.01	5.81
<i>Pagurus prideaux</i> Leach, 1815	40-831	8459	1.91	32.69
Family Palaemonidae				
<i>Ascidonia flavomaculata</i> (Heller, 1864)	62	1	<0.01	0.24
<i>Periclimenes granulatus</i> Holthuis, 1950	301	1	<0.01	0.24

	Depth range	N <sub>t</sub>	%DN	%F
Family Palinuridae				
<i>Palinurus elephas</i> (Fabricius, 1787)	114-118	3	<0.01	0.73
<i>Palinurus mauritanicus</i> Gruvel, 1911	251-664	21	<0.01	3.63
Family Pandalidae				
<i>Chlorotocus crassicornis</i> (A. Costa, 1871)	74-441	356	0.08	8.96
<i>Pandalina profunda</i> Holthuis, 1946	256-296	3	<0.01	0.48
<i>Plesionika acanthonotus</i> (Smith, 1882)	424-879	3903	0.88	29.30
<i>Plesionika antigai</i> Zariquiey Álvarez, 1955	79-534	1590	0.36	8.72
<i>Plesionika edwardsii</i> (J.F. Brandt in von Middendorff, 1851)	256-585	9756	2.21	12.83
<i>Plesionika gigliolii</i> (Senna, 1902)	117-650	3269	0.74	23.00
<i>Plesionika heterocarpus</i> (A. Costa, 1871)	56-764	309314	70.1	40.44
<i>Plesionika martia</i> (A. Milne-Edwards, 1883)	161-879	17740	4.02	42.37
<i>Plesionika narval</i> (Fabricius, 1787)	247-362	3955	0.89	0.73
Family Parthenopidae				
<i>Spinolambrus macrochelos</i> (Herbst, 1790)	251-424	3	<0.01	0.73
<i>Parthenopoides massena</i> (P. Roux, 1830)	65-331	2	<0.01	0.48
Family Pasiphaeidae				
<i>Pasiphaea multidentata</i> Esmark, 1866	336-879	1044	0.23	28.33
<i>Pasiphaea sivado</i> (Risso, 1816)	58-779	26473	6.00	24.46
Family Penaeidae				
<i>Parapenaeus longirostris</i> (Lucas, 1846)	61-688	8716	1.97	34.38
<i>Penaeopsis serrata</i> Spence Bate, 1881	586	1	<0.01	0.24
Family Pilmunidae				
<i>Pilmunus hirtellus</i> (Linnaeus, 1761)	43	1	<0.01	0.24
<i>Pilmunus spinifer</i> H. Milne-Edwards, 1834	43-394	104	0.02	8.72
Family Pinnotheridae				
<i>Pinnotheres pisum</i> (Linnaeus, 1767)	46-47	9	<0.01	0.48
<i>Pinnotheres bicristatus</i> Garcia Raso & Cuesta, 2019	63	1	<0.01	0.24
Family Polybiidae				
<i>Bathynectes maravigna</i> (Prestandrea, 1839)	329-840	200	0.04	14.29
<i>Liocarcinus depurator</i> (Linnaeus, 1758)	40-773	6974	1.58	42.86
<i>Macropipus tuberculatus</i> (P. Roux, 1830)	65-766	782	0.17	20.34
<i>Polybius henslowii</i> Leach, 1820	116	1	<0.01	0.24
Family Polychelidae				
<i>Polycheles typhlops</i> Heller, 1862	288-879	1198	0.27	30.27
Family Porcellanidae				
<i>Pisidia longicornis</i> (Linnaeus, 1767)	44-120	31	<0.01	3.39
Family Processidae				
<i>Processa canaliculata</i> Leach, 1815	74-688	400	0.09	19.61
<i>Processa noveli</i> Al-Adhub & Williamson, 1975	43-527	171	0.03	8.72
Family Sergestidae				
<i>Deosergestes arachnipodus</i> (Cocco, 1832)	541-831	1044	0.23	8.72
<i>Eusergestes arcticus</i> (Krøyer, 1855)	291-644	3791	0.86	5.08
<i>Robustosergia robusta</i> (Smith, 1882)	95-879	2276	0.51	32.20
Family Solenoceridae				
<i>Solenocera membranacea</i> (Risso, 1816)	61-679	4605	1.04	42.37
Family Stenopodidae				
<i>Richardina fredericii</i> Lo Bianco, 1903	311-431	2	<0.01	0.48
Family Xanthidae				
<i>Monodaeus couchii</i> (Couch, 1851)	66-879	346	0.07	29.30

Table 2. – Abundance (ind. km<sup>-2</sup>) of each decapod species caught during MEDITS surveys (2012-2018) in each geographical sector (See Fig 1. for location of the geographical sectors).

Species	Northern Alboran	Alboran Island	Gulf of Vera
<i>AcanthePHYra pelagica</i>	68.77	85.45	99.93
<i>Aegaeon cataphractus</i>	898.01	0.00	66.92
<i>Aegaeon lacazei</i>	689.11	38.36	206.73
<i>Alpheus dentipes</i>	0.00	0.00	583.23
<i>Alpheus glaber</i>	12434.05	19.75	299.92
<i>Alpheus platydactylus</i>	10.44	0.00	0.00
<i>Anapagurus bicorniger</i>	8.53	0.00	0.00
<i>Anapagurus laevis</i>	172.21	0.00	0.00
<i>Aristaeomorpha foliacea</i>	8.51	0.00	0.00
<i>Aristeus antennatus</i>	5352.82	10198.05	13400.08
<i>Ascidonia flavomaculata</i>	25.51	0.00	0.00
<i>Atelecyclus rotundatus</i>	353.73	74.90	0.00
<i>Bathynectes maravigna</i>	557.31	1297.15	27.20
<i>Calappa granulata</i>	96.15	192.73	29.67
<i>Calocarides coronatus</i>	8.89	0.00	0.00
<i>Calocaris macandreae</i>	1910.65	79.56	0.00
<i>Chlorotocus crassicornis</i>	2786.01	98.91	834.97
<i>Dardanus arrosor</i>	194955.77	21378.80	9820.69
<i>Deosergestes arachnipodus</i>	9729.64	269.66	165.71
<i>Dorhynchus thomsoni</i>	233.26	82.45	0.00
<i>Dromia personata</i>	22.09	0.00	0.00
<i>Ebalia nux</i>	0.00	8.83	0.00
<i>Ergasticus clouei</i>	107.79	314.10	0.00
<i>Ethusa mascarone</i>	20.32	0.00	0.00
<i>Eurynome aspera</i>	96.83	22.67	0.00
<i>Eusergestes arcticus</i>	35430.99	0.00	1135.72
<i>Galathea dispersa</i>	696.09	0.00	0.00
<i>Galathea intermedia</i>	350.71	0.00	0.00
<i>Galathea strigosa</i>	75.04	0.00	0.00
<i>Gennadas elegans</i>	76.34	23.04	8.13
<i>Geryon longipes</i>	1257.82	983.33	263.06
<i>Goneplax rhomboides</i>	10731.09	0.00	859.18
<i>Homola barbata</i>	23.57	0.00	114.61
<i>Inachus aguiarii</i>	0.00	24.19	0.00
<i>Inachus communissimus</i>	575.34	0.00	0.00
<i>Inachus dorsettensis</i>	4983.92	74.91	182.96
<i>Inachus thoracicus</i>	573.32	38.46	0.00
<i>Ligur ensiferus</i>	29.57	0.00	0.00
<i>Liocarcinus depurator</i>	158769.15	566.18	594.13
<i>Lissa chiragra</i>	23.85	0.00	0.00
<i>Macropipus tuberculatus</i>	5736.43	3446.73	1948.39
<i>Macropodia linaresi</i>	1709.79	0.00	23.93
<i>Macropodia tenuirostris</i>	42188.56	298.78	766.04
<i>Macropodia rostrata</i>	2246.16	0.00	0.00
<i>Medorippe lanata</i>	223.37	52.87	108.70
<i>Monodaeus couchii</i>	3015.45	256.68	251.24
<i>Munida intermedia</i>	260.07	274.12	20.68
<i>Munida rugosa</i>	19.39	0.00	0.00



Species	Northern Alboran	Alboran Island	Gulf of Vera
<i>Munida speciosa</i>	5289.25	8.87	1066.52
<i>Munida perarmata</i>	10.14	0.00	39.21
<i>Nephrops norvegicus</i>	7186.43	920.90	4001.20
<i>Paguristes eremita</i>	23.57	0.00	0.00
<i>Pagurus alatus</i>	14597.01	6349.94	607.52
<i>Pagurus anachoretus</i>	28.71	0.00	0.00
<i>Pagurus cuanensis</i>	142.57	0.00	47.42
<i>Pagurus excavatus</i>	1806.95	10.71	108.70
<i>Pagurus mbizi</i>	856.28	0.00	0.00
<i>Pagurus prideaux</i>	117912.81	35838.64	11569.99
<i>Palinurus elephas</i>	0.00	62.89	0.00
<i>Palinurus mauritanicus</i>	30.98	147.74	30.45
<i>Pandalina profunda</i>	9.34	0.00	18.97
<i>Parapenaeus longirostris</i>	72582.60	6830.78	13401.46
<i>Paromola cuvieri</i>	10.62	0.00	0.00
<i>Spinolambrus macrochelos</i>	10.41	11.34	9.86
<i>Parthenopoides massena</i>	20.95	10.28	0.00
<i>Pasiphaea multidentata</i>	3676.74	2128.73	4074.06
<i>Pasiphaea sivado</i>	235411.79	11.34	27214.36
<i>Penaeopsis serrata</i>	0.00	10.82	0.00
<i>Periclimenes granulatus</i>	10.38	0.00	0.00
<i>Philocheras echinulatus</i>	1247.97	32.14	25.77
<i>Philocheras sculptus</i>	47.49	0.00	0.00
<i>Pilumnus hirtellus</i>	21.80	0.00	0.00
<i>Pilumnus spinifer</i>	2012.36	0.00	350.42
<i>Pinnotheres pisum</i>	196.44	0.00	0.00
<i>Pinnotheres bicristatus</i>	22.36	0.00	0.00
<i>Pisa armata</i>	2196.13	0.00	0.00
<i>Pisidia longicornis</i>	712.28	0.00	0.00
<i>Plesionika acanthonotus</i>	23724.90	9813.55	3268.71
<i>Plesionika antigai</i>	2420.22	9241.23	3740.36
<i>Plesionika edwardsii</i>	23044.95	5302.86	61761.50
<i>Plesionika giglioli</i>	4569.02	46.49	26194.99
<i>Plesionika heterocarpus</i>	5221700.78	43885.18	142573.02
<i>Plesionika martia</i>	122055.52	27724.52	17985.68
<i>Plesionika narval</i>	0.00	10.71	45811.89
<i>Polybius henslowii</i>	0.00	24.19	0.00
<i>Polycheles typhlops</i>	10118.58	867.70	367.17
<i>Pontophilus spinosus</i>	5357.67	10.71	95.65
<i>Processa canaliculata</i>	5310.32	112.49	203.37
<i>Processa nouveli</i>	712.73	21.42	957.59
<i>Richardina fredericii</i>	19.12	0.00	0.00
<i>Scyramathia carpenteri</i>	1841.02	236.72	52.22
<i>Robustosergia robusta</i>	6561.02	13732.13	1930.25
<i>Solenocera membranacea</i>	44110.91	365.55	2139.31
<i>Synalpheus gambarelloides</i>	0.00	0.00	100.42
Number of species present	86	55	54

Of the 94 decapod species collected, 28 were only recorded in the northern Alboran Sea; 5 in the Alboran Island and 2 in the Gulf of Vera. Overall, 43 species were collected in each of the three geographical sectors (Table 2).

**Affinity between samples**

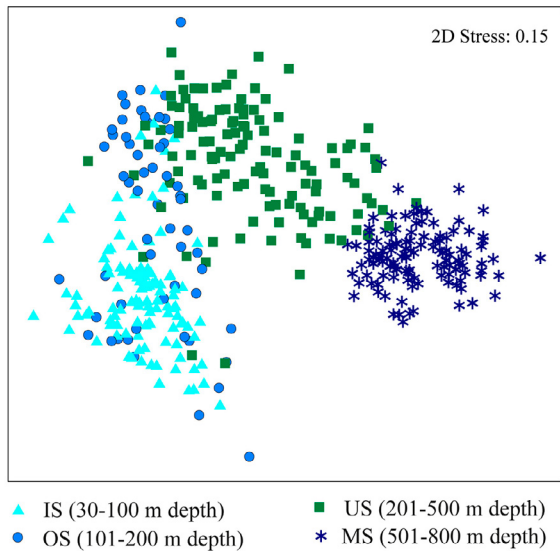


Fig. 2. – Results of the nMDS analysis performed on samples using the Bray-Curtis similarity index based on decapod abundance data (square-root transformed) during MEDITS surveys (2012-2018). IS, inner shelf assemblage; OS, outer shelf assemblage; US, upper slope assemblage; MS, middle slope assemblage.

Cluster and nMDS analyses performed on abundance data revealed four groups of samples (interpreted as different decapod assemblages) that were mainly related to depth: the first group corresponded to an inner/shallow shelf (IS) assemblage at 30 to 100 m depth; the second group corresponded to an outer shelf (OS) assemblage at 101 to 200 m depth; the third corresponded to an upper slope (US) assemblage at 201 to 500 m depth and the fourth corresponded to a middle slope (MS) assemblage to 501 to 800 m depth (Fig. 2). SIMPER analyses showed that the decapods *D. arrosor*, *L. depurator*, *M. longipes* and *P. prideaux* characterized the IS assemblage, whereas *P. heterocarpus*, *D. arrosor*, *P. prideaux* and *M. longipes* characterized the OS assemblage. The US assemblage was characterized by *P. heterocarpus*, *P. longirostris*, *S. membranacea* and *D. arrosor*, and the MS assemblage was characterized by *P. martia*, *P. acanthonotus*, *Pagurus alatus* and *Sergia robusta* (Table 3). The largest differences were observed between the shelf assemblages (IS and OS) and the MS assemblage (av. diss. >96%). These differences were mainly due to the higher abundance of *D. arrosor* and *L. depurator* in the IS assemblage, *P. heterocarpus* and *P. prideaux* in the OS assemblage, *P. longirostris* and *S. membranacea* in the US assemblage, and *P. martia*, *P. acanthonotus*, *P. alatus* and *S. robusta* in the MS assemblage.

The PERMANOVA test revealed significant differences between geographical sectors of the study area (Table 4). Pairwise comparisons after PERMANOVA analyses showed that: significant differences for the

Table 3. – Results of the SIMPER analyses displaying the species contribution to the similarity of each detected decapod assemblage using multivariate methods. Av. Abund, average abundance; Contrib%, percentage contribution to the similarity; Cum%, cumulative percentage of species contribution, up to ca. 90%.

Inner shelf: 30-100 m				Outer shelf: 101-200 m			
Average similarity: 33.11				Average similarity: 29.64			
species	Av.Abund	Contrib%	Cum%	species	Av.Abund	Contrib%	Cum%
<i>Dardanus arrosor</i>	25.1	49.53	49.53	<i>Plesionika heterocarpus</i>	132.44	41.88	41.88
<i>Liocarcinus depurator</i>	20.16	20.35	69.88	<i>Dardanus arrosor</i>	24.55	28.31	70.19
<i>Macropodia longipes</i>	10.93	14.97	84.85	<i>Pagurus prideaux</i>	19.84	12.37	82.56
<i>Pagurus prideaux</i>	10.24	6.6	91.45	<i>Macropodia longipes</i>	8.29	8.26	90.82
Upper Slope: 201-500 m				Middle Slope: 501-800 m			
average similarity: 32.49				average similarity: 51.81			
species	Av.Abund	Contrib%	Cum%	species	Av.Abund	Contrib%	Cum%
<i>Plesionika heterocarpus</i>	48.92	27.53	27.53	<i>Plesionika martia</i>	26.28	1.79	28.11
<i>Parapenaeus longirostris</i>	18.81	15.15	42.68	<i>Plesionika acanthonotus</i>	15.65	1.81	46.04
<i>Solenocera membranacea</i>	12.85	9.25	51.92	<i>Pagurus alatus</i>	11.27	1.68	57.8
<i>Dardanus arrosor</i>	8.2	8.43	60.35	<i>Sergia robusta</i>	10.58	1.57	68.22
<i>Plesionika martia</i>	12.66	6.49	66.84	<i>Polycheles typhlops</i>	7.96	1.31	76.72
<i>Pasiphaea sivado</i>	21.03	6.43	73.27	<i>Pasiphaea multidentata</i>	7.02	7.02	83.74
<i>Nephrops norvegicus</i>	5.83	3.99	77.26	<i>Aristeus antennatus</i>	8.45	3.57	87.32
<i>Macropodia longipes</i>	4.87	3.64	80.89	<i>Rochinia carpenteri</i>	2.76	1.97	89.29
<i>Plesionika gigliolii</i>	7.92	3.38	84.27	<i>Solenocera membranacea</i>	3.39	1.91	91.19
<i>Macropipus tuberculatus</i>	3.56	1.72	85.99				
<i>Liocarcinus depurator</i>	3.97	1.71	87.7				
<i>Alpheus glaber</i>	3.28	1.5	89.2				
<i>Processa canaliculata</i>	2.78	1.48	90.69				

Table 4. – Results of the PERMANOVA analyses testing differences between three of the four detected assemblages (OS, US, MS) and the three considered sectors (northern Alboran Sea, Gulf of Vera and Alboran Island).

Source	df	MS	Pseudo-F	<i>p</i>
Assemblages (AS)	2	98888	56.56	0.001
Sector (SE)	2	22716	12.99	0.001
ASxSE**	4	10419	5.95	0.001
Res	292	1748.4		
Total	300			

OS assemblage were detected between the Alboran Island-northern Alboran Sea and Alboran Island-Gulf of Vera sectors ( $p < 0.05$ ), while significant differences for the US and the MS assemblages were detected between the three sectors ( $p < 0.05$  in all cases). As mentioned previously, this analysis was not carried out for the IS assemblage since this bathymetric stratum could not be sampled in Alboran Island.

### Ecological indices

Significant differences were found between assemblages for all ecological indices tested. With regard to the mean abundance data, the significant maximum values were for the OS and US assemblages, while the minimum ones were detected for the MS assemblage, followed by the IS assemblage (Kruskal-Wallis test:  $\chi^2 = 92.6$ ;  $p < 0.01$ ) (Fig. 3A). Mean species richness showed significant maximum values in the US and MS assemblages and minimum ones in the IS assemblage (Kruskal-Wallis test:  $\chi^2 = 187.6$ ;  $p < 0.01$ ) (Fig. 3B). The mean Shannon-Wiener diversity index displayed significant maximum values in the deepest assemblages (US and MS) and minimum ones in the OS assemblage (Kruskal-Wallis test:  $\chi^2 = 190.5$ ;  $p < 0.01$ ) (Fig. 3C). The mean Pielou's evenness index displayed significant maximum values in the MS and IS assemblages and minimum ones in the OS assemblage (Kruskal-Wallis test:  $\chi^2 = 58.80$ ;  $p < 0.01$ ) (Fig. 3D).

### GAM models for testing spatio-temporal variability of ecological indices

For all ecological indices, GAM analyses showed a statistically significant effect of depth and the latitude-longitude bivariate smoother (hereafter referred to as the geographical effect). The best models included depth and the geographical effect, together with year as a factor, and explained 46.2% of the deviance (DE) for abundance, 64.6% for species richness, 49.6% for Shannon-Wiener diversity index and 34.4% for Pielou's evenness index (Table 5) (Appendix 1 and 2). No significant effect was found for the selected environmental variables of this study, including the NAO index. The depth influence was related to (1) a peak of abundance at 200 m with a progressive decrease with depth (Fig. 4A); (2) a continuous increase in species richness with a peak at 400 m followed by a slight decrease (Fig. 4B); and (3) a minimum value at 200 m with two peaks at 400 and 600 m depth for the Shannon-Wiener diversity

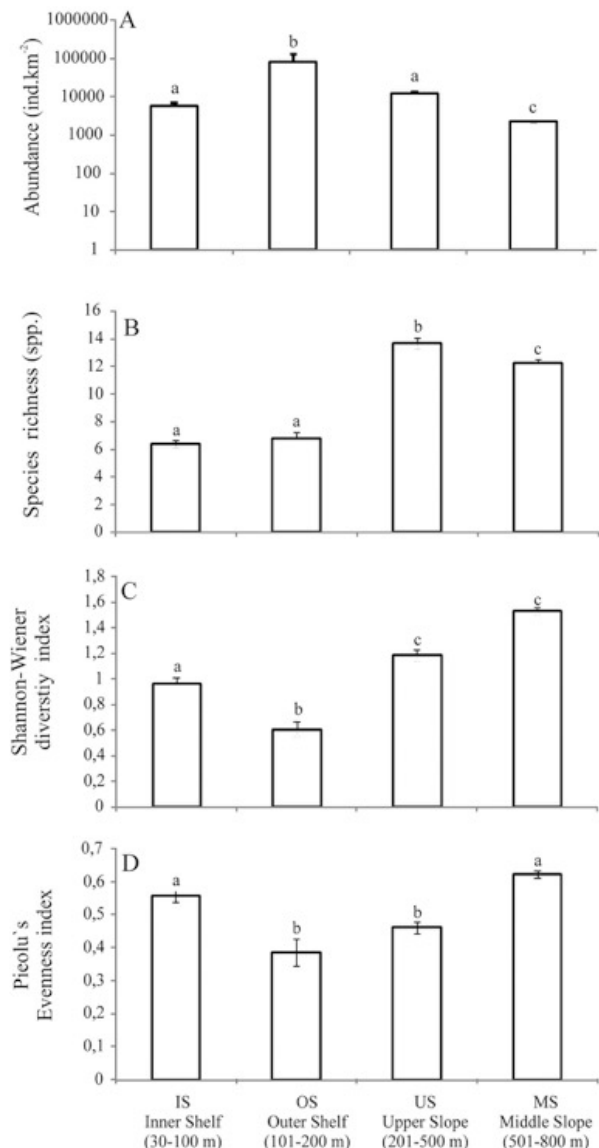


Fig. 3. – Mean values of the ecological indices: (A) abundance (ind. km<sup>-2</sup>); (B) species richness; (C) Shannon-Wiener diversity index; (D) Pielou's evenness index for each decapod assemblages detected in multivariate analyses. Mean $\pm$ SE. Letters above error bars display the results of Kruskal-Wallis pairwise test: different letters distinguish significantly different means at  $p < 0.01$ .

and Pielou's evenness index (Fig. 4C, D). The geographical effect was related to (1) maximum abundance values in the westernmost part of the study area and at Cabo de Gata (Fig. 4A); (2) maximum species richness in the westernmost and easternmost parts of the study area (Fig. 4B); (3) maximum Shannon-Wiener diversity index values in the Gulf of Vera (Fig. 4C); and (4) a similar and high Pielou's evenness index throughout the study area (Fig. 4D). Regarding the factor "year", abundance and species richness showed similar temporal patterns with a slight trend to decrease over successive years and with maximum values in 2012 and 2018 (Fig. 4A, B). For the Shannon-Wiener diversity index, the highest value was recorded in 2012, but no clear temporal trend was detected, as observed for Pielou's

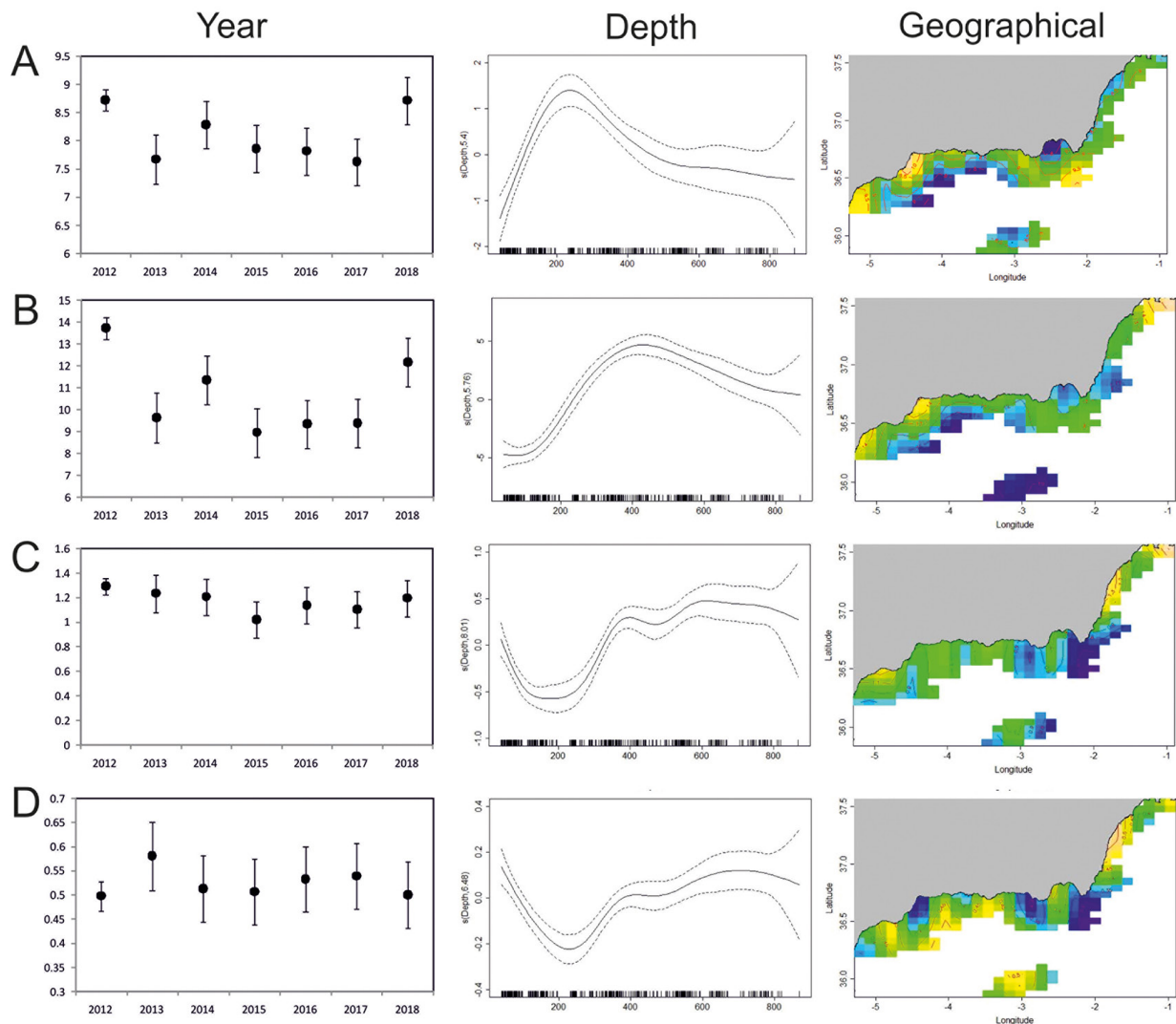


Fig. 4. – Partial effects of year (left column), depth (middle column), and geographic distribution (combination of longitude and latitude) (right column) for (A) abundance (ind. km<sup>-2</sup>) (log-transformed), (B) species richness, (C) Shannon-Wiener diversity index and (D) Pielou's evenness index. The colour gradient of the geographical effect ranges from low values (darker-blue colours) to high values (lighter-green colours).

Table 5. – Results of generalized additive models (GAM) for the ecological indices analysed. N, abundance (log transformed); S, species richness; H', Shannon-Wiener diversity index; J', Pielou's evenness index. Lat and long, latitude and longitude for geographical effect; Chl a, chlorophyll a concentration (mg·m<sup>-3</sup>); SBT, sea bottom temperature; SBS, sea bottom salinity. Values refer to the edf (degrees of freedom). DE(%), percentage of variance explained. ns, Non-significant effect. Asterisks denote significance levels: \*\*\*, p<0.001; \*\*, p<0.01; \*, p<0.05.

Model	Depth	Lat and long	NAO	Chl a	NO <sub>3</sub>	SBT	SBS	DE(%)
N	5.40**	23.38***	ns	ns	ns	ns	ns	46.2
S	5.76***	18.50***	ns	ns	ns	ns	ns	64.6
H'	8.01***	19.93**	ns	ns	ns	ns	ns	49.6
J'	6.48***	20.81**	ns	ns	ns	ns	ns	34.4

evenness index, which showed similar values throughout the time series (Fig. 4C, D) (Appendices 1 and 2).

DISCUSSION

The present study reports a high number of decapod species on circalittoral and bathyal soft bottoms

of the northern Alboran Sea, including Alboran Island and the Gulf of Vera, and increases the number of previously recorded species for these sedimentary habitats (15 additional species to those reported by Abelló et al. 2002). Nevertheless, all the species detected in the present study were previously listed in the Alboran Sea by Marco-Herrero et al. (2017) and García-Raso et al.

(2018) in a bibliographic compilation of marine decapod crustaceans from the Iberian Peninsula. A high decapod richness for the Alboran Sea was already reported by García Muñoz et al. (2008) in infralittoral sedimentary habitats, and this was related to a high diversity of bottom and habitat types and the confluence of Atlantic and Mediterranean waters and organisms. Abelló et al. (2002) highlighted that the exceptional and highly diverse decapod assemblages of the shelf and slope of the northern Alboran Sea, with a biogeographical boundary around Cabo de Palos, made this area very different from other western Mediterranean areas.

Comparing the geographical sectors of the study area, the highest number of species was detected in the northern Alboran Sea (86 spp.), whereas the lowest number was found at Alboran Island and in the Gulf of Vera (55 and 54 spp., respectively). It is important here to reiterate that no sampling could be carried out at depths shallower than 100 m around Alboran Island because it is a Marine and Fishing Reserve and bottom trawling is not allowed because of the occurrence of vulnerable marine ecosystems (Mateo-Ramírez et al. 2021). Species with Atlantic affinities, most of them with a low frequency of occurrence ( $F < 0.73\%$ ) (such as *P. henslowii*, *Ergasticus clouei*, and *Pagurus mbizi*), were recorded in the northern Alboran Sea and/or Alboran Island sectors but not in the Gulf of Vera sector, in agreement with Abelló et al. (2002). This could be due to the effect of the semi-permanent Almeria-Oran oceanographic front that acts as an effective barrier for gene flow and/or species dispersion for these species, as has also been detected for some other decapod species (García Raso et al. 2014, García Lafuente et al. 2021). It is worth mentioning the occurrence of the subtropical Atlantic hermit crab *P. mbizi* (Forest 1955). It was initially reported in 2014 in the westernmost sector of the northern Alboran Sea (an exclusive occurrence in European waters and the Mediterranean Sea) by García Raso et al. (2014) in a depth range of 50 to 150 m. In the present study, specimens of *P. mbizi* were collected in the central and eastern parts of the northern Alboran Sea over a wider bathymetric range (50–361 m), showing a similar depth range to that recorded in Atlantic waters (30–650 m) (Forest 1961). However, *P. mbizi* was absent in the Gulf of Vera, so its expansion is so far restricted to the Alboran Sea. On the other hand, the crab *Scyramathia carpenteri* (previously known as *Rochinia carpenteri*) was first recorded in the northern Alboran Sea sector (Abelló et al. 2002), but the present study provides records for the Gulf of Vera sector, thus suggesting a possible expansion to other western Mediterranean areas. The presence and, in some cases, potential eastward expansion of typical Atlantic species (e.g. *S. carpenteri*) and African species (e.g. *P. mbizi*) through the Alboran Sea could be a result of climate change effects, favouring a northwards expansion of thermophilic Atlantic species along the Atlantic coasts and into the Mediterranean Sea (i.e. meridionalization) (García Raso et al. 2014, 2018), once they manage to surpass the colder waters of the Alboran Sea.

Marine species distribution is generally related to dynamic environmental variables such as temperature

and other variables such as food availability (Snelgrove and Butman 1994, Cartes et al. 2004, Martins et al. 2014), but it is also related to structural properties such as depth and the substrate type of the seabed. As in previous studies (Cartes and Sardà 1993, Follesa et al. 2009, Deval et al. 2017, among others), depth was the main structuring factor for decapod crustacean distribution in the present study, probably because of a combination of other depth-related factors such as light, temperature and food availability (Cartes et al. 2004). In the present study, four decapod assemblages were detected in relation to depth, in agreement with previous studies on the northern Alboran Sea (Mateo-Ramírez et al. 2015), adjacent Mediterranean areas (Abelló et al. 2002, García-Rodríguez et al. 2011, Deval et al. 2017, among others) and adjacent Atlantic waters (López de la Rosa 1997, Muñoz et al. 2012, Castillo et al. 2014). A similar segregation has also been detected for cephalopods (Quetglas et al. 2000, González and Sánchez 2002, Ciércoles et al. 2018), fish (Gouraguine et al. 2011, García-Ruiz et al. 2015, Ramírez-Amaro et al. 2015) and megabenthic fauna (Abad et al. 2007), highlighting the importance of depth as a structuring factor in marine communities of the Mediterranean Sea.

The continental shelf assemblages (IS and OS) showed a high level of overlap between each other because they shared the most dominant species, but the two slope assemblages (US and MS) displayed marked differences and different dominant species. These greater differences in the slope assemblages could be attributed to some hydrological differences between the two depth strata (Abelló et al. 1988). Although a thermally stable environment can be assumed below 200 m in the Mediterranean Sea (Hopkins 1985), small changes in some environmental parameters (such as salinity) must be present at the species level, affecting their distribution and abundance, as shown in other studies (García-Rodríguez et al. 2011, Keller et al. 2017, Quattrocchi et al. 2020). Additionally, the dominant decapod species in each detected assemblage were similar to those found in the same area with the same sampling gear (Abelló et al. 2002). This similarity could be related to the stability of the demersal structures over time, as shown by other authors in the Mediterranean Sea (Gaertner et al. 2005).

The decapod assemblages displayed geographical differences in composition and structure between the sectors of the study area. Although sampling effort was different between sectors, the annual repeat of the same sampling stations and the long temporal database reinforce the idea that the differences between these sectors are mainly driven by differences in the composition and structure of decapod assemblages between sectors. The main differences were due to the pandalid shrimp *P. heterocarpus*, which was dominant in the OS assemblage of the northern Alboran Sea and Gulf of Vera sectors, but not at Alboran Island. Also, *P. heterocarpus* was far less abundant in the Alboran Island sector, and seemed to have a deeper and more restricted bathymetric range (328 to 566 m depth). This may be related to the influence of the nutrient-rich coastal upwellings present along the northern Alboran Sea sec-

tor, which allow the species to reach shallower waters (Carbonell et al. 2003). In contrast, *P. edwardsii* was more abundant in the US assemblage of the Gulf of Vera than in the same assemblage of other sectors, in agreement with García-Rodríguez et al. (2000). Finally, a higher abundance of *A. antennatus* was detected in the MS assemblages of the Alboran Island and Gulf of Vera, probably because of the greater presence of submarine canyons in both sectors, which are a preferred habitat for this species (Martínez-Baños 1997). In fact, the presence of populations of *A. antennatus* attracts a large deep-water trawling fishery to Alboran Island, the northeastern part of the Alboran Sea and the Gulf of Vera (Sardà et al. 2004; García-Rodríguez 2003, Fernandez-Arcaya et al. 2019).

Although no sampling could be carried out in the present study at depths shallower than 100 m around Alboran Island (owing to the presence of a marine reserve), when we compared the fauna from shallow depths around the island (<100 m depth) with those in other geographical sectors found in other studies based on beam-trawl samples (Gofas et al. 2014), we observed that the hermit crab *D. arrosor* is the only dominant species shared by all three sectors. The rest of the dominant decapods in the shallow sedimentary habitats around the island, such as *Scyllarus pygmaeus*, the hermit crab *Paguristes eremita* and several species of crabs of the genus *Pisa*, were absent or displayed low abundances on the continental shelf of the northern Alboran Sea. These differences in the dominant species are probably due to the fact that the sedimentary habitats in the island are mainly composed of bioclastic and coarse sands and rhodoliths, which are less common on the continental shelf, where muddier bottoms generally occur (Gofas et al. 2014).

In the present study, the composition of the decapod assemblages of the shallowest strata (shelf) of the Alboran Sea is similar to those of other parts of the Mediterranean Sea and adjacent Atlantic waters. Similar dominant species (but with a different percentage of contribution) were found for the shelf (IS, OS) and US assemblages of the Alboran Sea in comparison with other Mediterranean areas (Abelló et al. 1988, 2002, García-Rodríguez et al. 2011, Deval et al. 2017). One exception was detected in those of the Italian margin of the Tyrrhenian sea, where *D. arrosor* was scarce or not recorded at all (Fanelli et al. 2007). Moreover, it is worth mentioning that *P. longirostris* showed a different bathymetric range between the Alboran Sea and the Tyrrhenian Sea, being more abundant in shallower waters characterizing the OS assemblages (<200 m) in the latter (Fanelli et al. 2007). Some authors have suggested that the main drivers of high abundances of *P. longirostris* are the increase in water temperature (Quattrocchi et al. 2020), the interaction between wind and current circulations (Ligas et al. 2011), high salinity (Benchoucha et al. 2008) and high primary productivity (Colloca et al. 2004). Regarding the deepest assemblages, differences were detected between those of the northern Alboran Sea and others parts of the Mediterranean and adjacent Atlantic water. The dominant species in the deepest assemblage (MS) of

the present study were mostly different from those of the central and eastern Mediterranean Sea, where *A. antennatus*, *N. norvegicus*, *Aristaeomorpha foliacea* and *P. martia* are dominant (Fanelli et al. 2007, Deval et al. 2017, Fernandez-Arcaya et al. 2019). This fact contributes to the faunistic differentiation of the Alboran Sea, which is important for fisheries management. The rare presence of *A. foliacea* in the Alboran Sea, with only one individual captured in the present study, is noteworthy and similar to the observations made in the southern Alboran Sea, where just one record was observed some decades ago (Maurin 1962). The small populations of *A. foliacea* in the study area could be related to environmental drivers because its abundance declines with temperature and salinity rises, as detected in the western Mediterranean basin (Balearic Basin) (Cartes et al. 2011, 2014). The continental slope decapod assemblages of the northern Alboran Sea are also well differentiated from those in adjacent areas of the Atlantic Ocean. Only one decapod, *S. membranaea*, was shared with the slope assemblages of southern Spain (Gulf of Cádiz), which are dominated by *N. norvegicus*, *Philocheles echinulatus*, *S. membranaea*, *Processa canaliculata* and *P. sivado* (López de la Rosa 1997). In the Atlantic waters of northwest Africa, the slope assemblages (200-500 m depth) displayed a lower contribution of *P. longirostris* and *P. heterocarpus* than those found in the present study (Muñoz et al. 2012). Moreover, two dominant species, *P. narval* and *D. arrosor*, were shown to share the US assemblages and another two (*P. martia* and *Polycheles typhlops*) share the MS assemblage in the Canary Islands (González-Pajuelo et al. 2006).

Regarding ecological indices, GAM analyses showed clear depth trends for the four ecological indices: abundance, species richness, Shannon-Wiener diversity and Pielou's evenness. Decapod abundance increased with depth, peaking around 200 m, which is related to the high abundance of some gregarious dominant species, such as *P. heterocarpus*. Species richness also increased with depth, peaking at 400 to 500 m, thus making the US assemblage a transition zone with the coexistence of characteristic species from adjacent shallow and deep assemblages, in agreement with the findings for other faunal groups in the northern Alboran Sea, such as molluscs (Ciercoles et al. 2018). However, Shannon-Wiener diversity and Pielou's evenness decreased with depth, with a minimum at 200 m, but increased afterwards. These results could be related to the fact that the OS assemblage was characterized by few, very abundant species, while the slope assemblages showed a higher number of species which were less dominant. Similar results were found by Mateo-Ramírez et al. (2015) in the northern Alboran Sea, by Cartes and Sardà (1992) and Fanelli et al. (2007) in the western and Central Mediterranean Sea, and by López de la Rosa (1997) and Muñoz et al. (2012) in Atlantic waters. The increased environmental stability of the deep areas is likely to be a potential explanation for a high diversity (Sanders and Hessler 1969, Rex 1973), which may allow the development of a more mature and complex assemblage, as indicated by Abelló et al. (1988).



The four GAM models also revealed geographical effects (a combination of longitude and latitude), with a greater abundance, species richness and Shannon diversity index in the westernmost part of the Alboran Sea, probably related to the high productivity associated with the major nutrient-rich coastal upwellings in this area (Rubín et al. 1997, Sarhan et al. 2000), the nutrient-rich water transport through the strait of Gibraltar, and the cyclonic vorticity that accumulates nutrients and produces permanent fertilization in the westernmost part of the Alboran Sea (Skloris and Beckers 2009, Vargas-Yáñez et al. 2019). Similarly, a high diversity was detected in the easternmost part, which is a transition area with the coexistence of Mediterranean and Atlantic species. Slight temporal patterns were found for abundance and species richness. However, the present study showed the absence of consistent temporal trends and the presence of annual oscillations of the decapod assemblages in the study area. Temporary changes in the abundance of benthic and demersal species could be the result of biological processes, such as recruitment, mortality and predation, in addition to variations in the fishing impact (increased or decreased fishing effort) in some commercial decapod species or even in commercial species feeding on decapods (Snelgrove and Butman 1994, Ólafsson et al. 1994).

The results of the present study improve knowledge of the decapod assemblages inhabiting the trawlable bottoms of a specific part of the European margin and the western Mediterranean Sea. The study area corresponds to the geographical subareas GSA01 and GSA02 established by the General Fisheries Commission for the Mediterranean (GFCM) for fishing management. Faunistic studies are an essential tool in managing fisheries, especially because both fisheries management and conservation policies apply to an ecosystem-based approach (Pikitch et al. 2004, Bellido et al. 2011). Moreover, this study provides a baseline for characterizing specific components (decapod crustaceans in this case) of benthic and demersal communities on sedimentary habitats under the framework of the Marine Strategy Framework Directive (MSFD, 2008/56/EC). This is especially important in areas with a high marine diversity that are regarded as self-standing ecoregions, such as the Alboran Sea (Abelló et al. 2002, Spalding et al. 2007, Coll et al. 2010).

#### ACKNOWLEDGEMENTS

The authors thank all the participants in the MEDITS surveys. MEDITS surveys, in the study area, are carried out in the framework of the DEMALBORAN project. This project has been funded by the Spanish Institute of Oceanography and the EU through the European Maritime and Fisheries Fund (EMFF) within the National Programme of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. We also thank Timothy Dobinson for his revision of the English grammar of the present study. PA acknowledges partial support from the Severo Ochoa Centre of Excellence accreditation (CEX2019-000928-S)

to the Institut de Ciències del Mar (ICM-CSIC) and the project CLIFISH CTM2015-66-400-C3-3-R, MINECO/FEDER. JLRR acknowledges partial support from the 18-ESMARES2-CIRCA project of the Instituto Español de Oceanografía (IEO-CSIC), under the framework of the tasks commissioned to the IEO by the Ministerio de Transición Ecológica y Reto Demográfico (MITERD) of the Spanish government for the application of the Marine Strategy Framework Directive (MSFD) in Spanish waters.

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## APPENDICES

Appendix 1. – Best-fit general additive models (GAMs) obtained for each ecological index analysed: abundance (N) (log-transformed); species richness (S); Shannon-Wiener diversity index (H') and Pielou's evenness index (J') and results of each GAM model test. s, smoothing functions; Std. Error, Standard error; edf, degrees of freedom; Ref.df, reference degrees of freedom used in computing test statistic and the p-values; F, F-test values. Signif. codes: \*\*\*, p<0; \*\*, p<0.001; \*, p<0.01.

Abundance (LOGPONN)				
(LOGPONN) ~ factor(Year) + s(Depth) + s(Longitude, Latitude)				
Parametric coefficients	Estimate	Std. Error		
(Intercept)	8.723	0.186		
factor(Year)2013	-1.048	0.25		
factor(Year)2014	-0.434	0.238		
factor(Year)2015	-0.86	0.234		
factor(Year)2016	-0.905	0.232		
factor(Year)2017	-1.097	0.231		
factor(Year)2018	-0.007	0.235		
Smooth terms	edf	Ref.df	F	p-value
s(Depth)	5.402	6.448	17.92	<2e-16***
s(Longitude, Latitude)	23.382	26.919	3.84	1.32e-09***
R-sq.(adj)=0.412		Deviance explained= 46.2%		
Species richness (S)				
(S) ~ factor(Year) + s(Depth) + s(Longitude, Latitude)				
Parametric coefficients	Estimate	Std. Error		
(Intercept)	13.716	0.489		
factor(Year)2013	-4.076	0.657		
factor(Year)2014	-2.369	0.626		
factor(Year)2015	-4.759	0.614		
factor(Year)2016	-4.369	0.609		
factor(Year)2017	-4.333	0.608		
factor(Year)2018	-1.549	0.617		
Smooth terms	edf	Ref.df	F	p-value

s(Depth)	5.76	6.821	44.246	<2e-16***
s(Longitude, Latitude)	18.5	22.935	2.345	0.000637***
R-sq.(adj)=0.618		Deviance explained= 64.6%		
Shannon-Wiener diversity index (H)				
(H) ~ factor(Year) + s(Depth) + s(Longitude, Latitude)				
Parametric coefficients	Estimate	Std. Error		
(Intercept)	1.293	0.065		
factor(Year)2013	-0.058	0.087		
factor(Year)2014	-0.087	0.083		
factor(Year)2015	-0.272	0.082		
factor(Year)2016	-0.154	0.081		
factor(Year)2017	-0.187	0.081		
factor(Year)2018	0.097	0.082		
Smooth terms	edf	Ref.df	F	p-value
s(Depth)	8.012	8.697	18.261	<2e-16***
s(Longitude, Latitude)	19.929	24.272	1.875	0.00752**
R-sq.(adj)=0.45		Deviance explained= 49.6%		
Pielou's evenness index (J)				
(J) ~ factor(Year) + s(Depth) + s(Longitude, Latitude)				
Parametric coefficients	Estimate	Std. Error		
(Intercept)	0.498	0.03		
factor(Year)2013	0.083	0.04		
factor(Year)2014	0.015	0.038		
factor(Year)2015	0.008	0.038		
factor(Year)2016	0.035	0.037		
factor(Year)2017	0.041	0.037		
factor(Year)2018	0.002	0.038		
Smooth terms	edf	Ref.df	F	p-value
s (Depth)	6.478	7.536	11.284	1.08e-13***
s (longitude, latitude)	20.811	25.008	2.121	0.00155**
R-sq.(adj)=0.285		Deviance explained= 34.4%		

Appendix 2 – Basic residual plots for checking each generalized additive model fitting process. The upper left normal (Q-Q) plots close to a straight line, suggesting reasonable distributional assumption. The upper right, Residuals vs linear predictor plots suggest that variance is approximately constant as the mean increases. The histogram of residuals at the lower left appears consistent with normality. The lower right plot of response against fitted values shows a positive linear relation with a good deal of scatter: nothing problematic. Resids., residuals; pred., predictor; Q-Q, QuantilesQuantiles. N, abundance (LOGPONN); S, species richness, H', Shannon-Wiener diversity index; J', Pielou's evenness index.

