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; circalitoral; 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 batales (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 bathymétricos, 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, bathyal; 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, Círcules 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 (Martín 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 Aristaeus 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 Atlantic 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 km² 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
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-
The abundance (N, ind. km$^{-2}$), 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$^{-3}$), nitrate (NO$_3$), phosphate (PO$_4$), 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$_3$, and PO$_4$ 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 for parametric analyses (e.g. ANOVA). These analyses were carried out using SPSS v15.0 software.

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$^{-2}$). 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.

Data analysis

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 and 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).

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**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±10812 ind. km⁻², mean per haul±standard error) (%DN: 70) followed by *Pasiphea sivado* (635.92±403.65 ind. km⁻²) (%DN: 6) and *Dardanus arrosor* (547.59±153.90 ind. 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 *Calocaris 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 Alborán Sea, Alboran Island and the Gulf of Vera. Depth range for collected specimens (metres); N, 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.

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

The mgcv package in R (http://www.r-project.org) was used in the GAM analyses (Wood 2017).
| Depth range       | N  | %DN | %F   |
|-------------------|----|-----|------|
| **Lissa chiragra** (Fabricius, 1775) | 56 | 1   | <0.01 | 0.24 |
| **Pisa armata** (Latreille, 1803)   | 46-86 | 104 | 0.02  | 2.42 |
| **Scyramathia carpenteri** (C. W. Thomson, 1873) | 329-879 | 232 | 0.05  | 16.71 |
| **Family Ethusidae** | | | | |
| **Ethusa mascarone** (Herbst, 1785) | 46 | 1 | <0.01 | 0.24 |
| **Family Galatheidae** | | | | |
| **Galathea dispersa** Bate, 1859 | 59-249 | 34 | <0.01 | 3.63 |
| **Galathea intermedia** Lilljeborg, 1851 | 40-327 | 17 | <0.01 | 3.39 |
| **Galathea strigosa** (Linnaeus, 1761) | 61 | 3 | <0.01 | 0.24 |
| **Family Geryonidae** | | | | |
| **Geryon longipes** A. Milne-Edwards, 1882 | 440-869 | 259 | 0.05 | 14.77 |
| **Family Goneplacidae** | | | | |
| **Goneplax rhomboides** (Linnaeus, 1758) | 40-766 | 600 | 0.13 | 30.51 |
| **Family Homolidae** | | | | |
| **Homola barbata** (Fabricius, 1793) | 74-288 | 7 | <0.01 | 1.21 |
| **Paromola cuvieri** (Risso, 1816) | 654 | 1 | <0.01 | 0.24 |
| **Family Inachidae** | | | | |
| **Dorhynchus thomsoni** C. W. Thomson, 1873 | 329-808 | 32 | <0.01 | 4.60 |
| **Inachus aquilarii** Brito Capello, 1876 | 116 | 1 | <0.01 | 0.24 |
| **Inachus communissimus** Rizza, 1839 | 43-132 | 25 | <0.01 | 3.87 |
| **Inachus dorsettensis** (Pennant, 1777) | 42-540 | 238 | 0.05 | 12.59 |
| **Inachus thoracicus** P. Roux, 1830 [in P. Roux, 1828-1830] | 46-118 | 27 | <0.01 | 1.21 |
| **Macropodia linaresi** Forest & Zariquey Álvarez, 1964 | 42-95 | 73 | 0.01 | 2.91 |
| **Macropodia tenuirostris** (A. Milne-Edwards & Bouvier, 1899) | 40-774 | 2335 | 0.53 | 57.38 |
| **Macropodia rostrata** (Linnaeus, 1761) | 43-123 | 1020 | 0.02 | 3.63 |
| **Family Leucosiidae** | | | | |
| **Ebalia nux** A. Milne-Edwards, 1883 | 554 | 1 | <0.01 | 0.24 |
| **Family Lysmatidae** | | | | |
| **Ligur ensiferus** (Risso, 1816) | 357-668 | 3 | <0.01 | 0.73 |
| **Family Majidae** | | | | |
| **Eurynome aspera** (Pennant, 1777) | 45-117 | 5 | <0.01 | 1.21 |
| **Family Munididae** | | | | |
| **Munida intermedia** A. Milne-Edwards & Bouvier, 1899 | 121-664 | 52 | 0.01 | 5.08 |
| **Munida rugosa** (Fabricius, 1775) | 122 | 1 | <0.01 | 0.24 |
| **Munida speciosa** von Martens, 1878 | 85-554 | 457 | 0.10 | 11.14 |
| **Munida perarmata** Sars, 1872 | 374-779 | 5 | <0.01 | 0.97 |
| **Family Nephropidae** | | | | |
| **Nephrops norvegicus** (Linnaeus, 1758) | 143-852 | 1301 | 0.29 | 30.51 |
| **Family Oregoniidae** | | | | |
| **Ergasticus cloueli** A. Milne-Edwards, 1882 | 362-774 | 42 | 0.01 | 4.36 |
| **Family Paguridae** | | | | |
| **Anapagurus bicorner A. Milne-Edwards & Bouvier, 1892** | 249 | 1 | <0.01 | 0.24 |
| **Anapagurus laevis** (Bell, 1845) | 49-424 | 9 | <0.01 | 1.69 |
| **Pagurus alatus** Fabricius, 1775 | 329-879 | 2252 | 0.51 | 32.20 |
| **Pagurus anachoretus** Risso, 1827 | 54 | 1 | <0.01 | 0.24 |
| **Pagurus cuanensis** Bell, 1845 | 44-118 | 8 | <0.01 | 1.45 |
| **Pagurus excavatus** (Herbst, 1791) | 40-529 | 119 | 0.02 | 16.71 |
| **Pagurus mbizi** (Forest, 1955) | 50-361 | 42 | 0.01 | 5.81 |
| **Pagurus prideaux** Leach, 1815 | 48-831 | 8459 | 1.91 | 32.69 |
| **Family Palaemonidae** | | | | |
| **Ascidonia flavomaculata** (Heller, 1864) | 62 | 1 | <0.01 | 0.24 |
| **Periclimenes granulatus** Holthuis, 1950 | 301 | 1 | <0.01 | 0.24 |
## Decapods in northern Alborán Sea and Gulf of Vera

### Family Palinuridae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Palinurus elephas (Fabricius, 1787) | 114-118     | 3 | <0.01 | 0.73 |
| Palinurus mauritanicus Gruvel, 1911 | 251-664   | 21 | <0.01 | 3.63 |

### Family Pandalidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Chlorotocus crassicornis (A. Costa, 1871) | 74-441 | 356 | 0.08 | 8.96 |
| Pandalina profunda Holthuis, 1946 | 256-296 | 3 | <0.01 | 0.48 |
| Plesionika acanthonotus (Smith, 1882) | 424-879 | 3903 | 0.88 | 29.30 |
| Plesionika agilis Zariguey Álvarez, 1955 | 79-534 | 1590 | 0.36 | 8.72 |
| Plesionika edwardsi (J.F. Brandt in von Middendorf, 1851) | 256-585 | 9756 | 2.21 | 12.83 |
| Plesionika gigliolii (Sena, 1902) | 117-650 | 3269 | 0.74 | 23.00 |
| Plesionika heterocarpus (A. Costa, 1871) | 56-764 | 309314 | 70.1 | 40.44 |
| Plesionika martia (A. Milne-Edwards, 1883) | 161-879 | 17740 | 4.02 | 42.37 |
| Plesionika narval (Fabricius, 1787) | 247-362 | 3955 | 0.89 | 0.73 |

### Family Parthenopidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Spinolambrus macrochelos (Herbst, 1790) | 251-424 | 3 | <0.01 | 0.73 |
| Parthenopoides massena (P. Roux, 1830) | 65-331 | 2 | <0.01 | 0.48 |

### Family Pasiphaeidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Pasiphaea multidentata Esmark, 1866 | 336-879 | 1044 | 0.23 | 28.33 |
| Pasiphaea sivado (Risso, 1816) | 58-779 | 26473 | 6.00 | 24.46 |

### Family Penaeidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Parapenaeus longirostris (Lucas, 1846) | 61-688 | 8716 | 1.97 | 34.38 |
| Penaeopsis serrata Spence Bate, 1881 | 586 | 1 | <0.01 | 0.24 |

### Family Pinnotheridae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Pinnotheres pisum (Linnaeus, 1767) | 46-47 | 9 | <0.01 | 0.48 |
| Pinnotheres bicristatus Garcia Raso & Cuesta, 2019 | 63 | 1 | <0.01 | 0.24 |

### Family Polybiidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Bathynectes maravigna (Prestandrea, 1839) | 329-840 | 200 | 0.04 | 14.29 |
| Liocarcinus depurator (Linnaeus, 1758) | 40-773 | 6974 | 1.58 | 42.86 |
| Macrociptus tuberculatus (P. Roux, 1830) | 65-766 | 782 | 0.17 | 20.34 |
| Polybius henslowii Leach, 1820 | 116 | 1 | <0.01 | 0.24 |

### Family Polycheilidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Polychele typlogphs Heller, 1862 | 288-879 | 1198 | 0.27 | 30.27 |

### Family Porcellanidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Pisidia longicornis (Linnaeus, 1767) | 44-120 | 31 | <0.01 | 3.39 |

### Family Processidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Processa canaliculata Leach, 1815 | 74-688 | 400 | 0.09 | 19.61 |
| Processa nouveli Al-Adhub & Williamson, 1975 | 43-527 | 171 | 0.03 | 8.72 |

### Family Sergestidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Deosergestes arachnipodus (Cocco, 1832) | 541-831 | 1044 | 0.23 | 8.72 |
| Eusergestes arcticus (Kroyer, 1855) | 291-644 | 3791 | 0.86 | 5.08 |
| Robustosergia robusta (Smith, 1882) | 95-879 | 2276 | 0.51 | 32.20 |

### Family Solenoceridae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Solenocera membranacea (Risso, 1816) | 61-679 | 4605 | 1.04 | 42.37 |

### Family Stenopodidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Richardina fredericii Lo Bianco, 1903 | 311-431 | 2 | <0.01 | 0.48 |

### Family Xanthidae

| Genus/Species                  | Depth range | N | %DN | %F |
|--------------------------------|-------------|---|-----|----|
| Monodaeus couchii (Couch, 1851) | 66-879 | 346 | 0.07 | 29.30 |
Table 2. – Abundance (ind. km$^{-2}$) 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 |
|------------------------------|------------------|----------------|--------------|
| Acanthephyra pelagica        | 68.77            | 85.45          | 99.93        |
| Aegaeon cataphractus         | 898.01           | 0.00           | 66.92        |
| Aegaeon lacazei              | 689.11           | 38.36          | 206.73       |
| Alpheus dentipes             | 0.00             | 0.00           | 583.23       |
| Alpheus glaber               | 12434.05         | 19.75          | 299.92       |
| Alpheus platyactylus         | 10.44            | 0.00           | 0.00         |
| Anapagurus bicorniger        | 8.53             | 0.00           | 0.00         |
| Anapagurus laevis            | 172.21           | 0.00           | 0.00         |
| Aristaeomorpha foliacea      | 8.51             | 0.00           | 0.00         |
| Aristeus antennatus          | 5352.82          | 10198.05       | 13400.08     |
| Ascidonia flavomaculata      | 25.51            | 0.00           | 0.00         |
| Atelecyclus rotundatus       | 353.73           | 74.90          | 0.00         |
| Bathynectes maravigna        | 557.31           | 1297.15        | 27.20        |
| Calappa granulata            | 96.15            | 192.73         | 29.67        |
| Calocarides coronatus        | 8.89             | 0.00           | 0.00         |
| Calocaris macandreae         | 1910.65          | 79.56          | 0.00         |
| Chlorotocus crassicornis     | 2786.01          | 98.91          | 834.97       |
| Dardanus arrosores           | 194955.77        | 21378.80       | 9820.69      |
| Deosergestes arachnipodus    | 9729.64          | 269.66         | 165.71       |
| Dorhynchus thomsoni          | 233.26           | 82.45          | 0.00         |
| Dromia personata             | 22.09            | 0.00           | 0.00         |
| Ebalia nux                   | 0.00             | 8.83           | 0.00         |
| Ergasticus clouei            | 107.79           | 314.10         | 0.00         |
| Ethusa mascarone             | 20.32            | 0.00           | 0.00         |
| Eurynome aspera              | 96.83            | 22.67          | 0.00         |
| Eusergestes arcticus         | 35430.99         | 0.00           | 1135.72      |
| Galathea dispersa            | 696.09           | 0.00           | 0.00         |
| Galathea intermedia          | 350.71           | 0.00           | 0.00         |
| Galathea strigosa            | 75.04            | 0.00           | 0.00         |
| Gennadas elegans             | 76.34            | 23.04          | 8.13         |
| Geryon longipes              | 1257.82          | 983.33         | 263.06       |
| Goneplax rhomboides          | 10731.09         | 0.00           | 859.18       |
| Homola barbata               | 23.57            | 0.00           | 114.61       |
| Inachus aguiarrii            | 0.00             | 24.19          | 0.00         |
| Inachus communissimus        | 575.34           | 0.00           | 0.00         |
| Inachus dorsettensis         | 4983.92          | 74.91          | 182.96       |
| Inachus thoracicus           | 573.32           | 38.46          | 0.00         |
| Ligur ensiferus              | 29.57            | 0.00           | 0.00         |
| Liocarcinus depurator        | 158769.15        | 566.18         | 594.13       |
| Lissa chiragra               | 23.85            | 0.00           | 0.00         |
| Macropipus tuberculatus      | 5736.43          | 3446.73        | 1948.39      |
| Macropodia finarei           | 1709.79          | 0.00           | 23.93        |
| Macropodia tenairostri       | 42188.56         | 298.78         | 766.04       |
| Macropodia rostrata          | 2246.16          | 0.00           | 0.00         |
| Medorippe lanata             | 223.37           | 52.87          | 108.70       |
| Monodaeus couchii            | 3015.45          | 256.68         | 251.24       |
| Munida intermedia            | 260.07           | 274.12         | 20.68        |
| Munida rugosa                | 19.39            | 0.00           | 0.00         |
### Decapods in northern Alborán Sea and Gulf of Vera

| Species                   | Northern Alboran | Alboran Island | Gulf of Vera |
|---------------------------|------------------|----------------|--------------|
| Munida speciosa           | 5289.25          | 8.87           | 1066.52      |
| Munida perarmata          | 10.14            | 0.00           | 39.21        |
| Nephrops norvegicus       | 7186.43          | 920.90         | 4001.20      |
| Paguristes eremita        | 23.57            | 0.00           | 0.00         |
| Pagurus alatus            | 14597.01         | 6349.94        | 607.52       |
| Pagurus anachoretus       | 28.71            | 0.00           | 0.00         |
| Pagurus cuanensis         | 142.57           | 0.00           | 47.42        |
| Pagurus excavatus         | 1806.95          | 10.71          | 108.70       |
| Pagurus mbizi             | 856.28           | 0.00           | 0.00         |
| Pagurus prideaux          | 117912.81        | 35838.64       | 11569.99     |
| Palinurus elephas         | 0.00             | 62.89          | 0.00         |
| Palinurus mauritanicus    | 30.98            | 147.74         | 30.45        |
| Pandalina profunda        | 9.34             | 0.00           | 18.97        |
| Parapeneaus longirostris  | 72582.60         | 6830.78        | 13401.46     |
| Paromola cuvieri          | 10.62            | 0.00           | 0.00         |
| Spinolambrus macrochelos  | 10.41            | 11.34          | 9.86         |
| Parthenopoides massena    | 20.95            | 10.28          | 0.00         |
| Pasiphaea multidentata     | 3676.74          | 2128.73        | 4074.06      |
| Pasiphaea sivado          | 235411.79        | 11.34          | 27214.36     |
| Penaeopsis serrata        | 0.00             | 10.82          | 0.00         |
| Periclimenes granulatus   | 10.38            | 0.00           | 0.00         |
| Philocheras echnulatus    | 1247.97          | 32.14          | 25.77        |
| Philocheras sculptus      | 47.49            | 0.00           | 0.00         |
| Pilumnus hirtellus        | 21.80            | 0.00           | 0.00         |
| Pilumnus spinifer         | 2012.36          | 0.00           | 350.42       |
| Pinnotheres pisum         | 196.44           | 0.00           | 0.00         |
| Pinnotheres bicristeratus | 22.36            | 0.00           | 0.00         |
| Pisa armata               | 2196.13          | 0.00           | 0.00         |
| Pisidia longicornis       | 712.28           | 0.00           | 0.00         |
| Plesionika acanthotonotus | 23724.90         | 9813.55        | 3268.71      |
| Plesionika antigai        | 2420.22          | 9241.23        | 3740.36      |
| Plesionika edwardsii      | 23044.95         | 5302.86        | 61761.50     |
| Plesionika gigliolii      | 4569.02          | 46.49          | 26194.99     |
| Plesionika heterocarpus   | 5221700.78       | 43885.18       | 142573.02    |
| Plesionika martia         | 122055.52        | 27724.52       | 17985.68     |
| Plesionika narval         | 0.00             | 10.71          | 45811.89     |
| Polybius henslowii        | 0.00             | 24.19          | 0.00         |
| Polycheles typhlops       | 10118.58         | 867.70         | 367.17       |
| Pontophilus spinosus      | 5357.67          | 10.71          | 95.65        |
| Processa canaliculata     | 5310.32          | 112.49         | 203.37       |
| Processa novelii          | 712.73           | 21.42          | 957.59       |
| Richardina fredericii    | 1841.02          | 236.72         | 52.22        |
| Scyramathia carpenteri    | 6561.02          | 13732.13       | 1930.25      |
| Robustosergia robusta     | 44110.91         | 3655.55        | 2139.31      |
| Solenocera membranacea    | 0.00             | 0.00           | 100.42       |
| Synalpheus gambarelloides | 86               | 55             | 54           |

Number of species present: 86
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

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

![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.](image)

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%.

| Species                          | Av. Abund | Contrib% | Cum%  | Species                          | Av. Abund | Contrib% | Cum%  |
|----------------------------------|-----------|-----------|-------|----------------------------------|-----------|-----------|-------|
| Inner shelf: 30-100 m            |           |           |       | Outer shelf: 101-200 m           |           |           |       |
| Dardanus arrosor                 | 25.1      | 49.53     | 49.53 | Plesionika heterocarpos          | 132.4     | 41.88     | 41.88 |
| Liocarcinus depurator            | 20.16     | 20.35     | 69.88 | Dardanus arrosor                 | 24.55     | 28.31     | 70.19 |
| Macropodia longipes              | 10.93     | 14.97     | 84.85 | Pagurus prideaux                 | 19.84     | 12.37     | 82.56 |
| Pagurus prideaux                 | 10.24     | 6.6       | 91.45 | Macropodia longipes              | 8.29      | 8.26      | 90.82 |
| Upper Slope: 201-500 m           |           |           |       | Middle Slope: 501-800 m          |           |           |       |
| Plesionika heterocarpos          | 48.92     | 27.53     | 27.53 | Plesionika martia                | 26.28     | 1.79      | 28.11 |
| Parapeneaus longirostris         | 18.81     | 15.15     | 42.68 | Plesionika acanthonotus          | 15.65     | 1.81      | 46.04 |
| Solenocera membranacea           | 12.85     | 9.25      | 51.92 | Pagurus alatus                   | 11.27     | 1.68      | 57.8  |
| Dardanus arrosor                 | 8.2       | 8.43      | 60.35 | Sergia robusta                   | 10.58     | 1.57      | 68.22 |
| Plesionika martia                | 12.66     | 6.49      | 66.84 | Polychetes typhlops              | 7.96      | 1.31      | 76.72 |
| Pasiphaea sivado                 | 21.03     | 6.43      | 73.27 | Pasiphaea multidentata           | 7.02      | 7.02      | 83.74 |
| Nephrops norvegicus              | 5.83      | 3.99      | 77.26 | Aristeus antennatus              | 8.45      | 3.57      | 87.32 |
| Macropodia longipes              | 4.87      | 3.64      | 80.89 | Rochinia carpenteri              | 2.76      | 1.97      | 89.29 |
| Plesionika gigliolii             | 7.92      | 3.38      | 84.27 | Solenocera membranacea           | 3.39      | 1.91      | 91.19 |
| Macropipus tuberculatus          | 3.56      | 1.72      | 85.99 | Alpheus glaber                   | 3.28      | 1.5       | 89.2  |
| Liocarcinus depurator            | 3.97      | 1.71      | 87.7  | Processa canaliculata            | 2.78      | 1.48      | 90.69 |

Sci. Mar. 86(3), September 2022, e039. ISSN-L 0214-8358 https://doi.org/10.3989/scimar.05265.039
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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 (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 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

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**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 | p   |
|----------------------|----|---------|----------|-----|
| 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|         |          |      |

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**Fig. 3.** – Mean values of the ecological indices: (A) abundance (ind. km$^{-2}$); (B) species richness; (C) Shannon-Wiener diversity index; (D) Pielou’s evenness index for each decapod assemblages detected in multivariate analyses. Mean±SE. Letters above error bars display the results of Kruskal-Wallis pairwise test: different letters distinguish significantly different means at p<0.01.
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 closei, 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 Sicyonahia 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 sub-marine 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, Fernández-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 dominants 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 (García-Rodríguez et al. 2011, Deval et al. 2017). 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 (Ciércoles 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). 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).

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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 (Skliiris 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. Temporal 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 (Snellgrove and Butman 1994, Olafsson 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 ecocoregions, 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, MI-NECO/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)

\[
\text{LOGPONN} \sim \text{factor(Year) } + s(\text{Depth}) + s(\text{Longitude}, \text{Latitude})
\]

| Parameter | 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)

\[
S \sim \text{factor(Year) } + s(\text{Depth}) + s(\text{Longitude}, \text{Latitude})
\]

| Parameter | 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 |
|--------------|-----|--------|---|---------|

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SCI. MAR. 86(3), September 2022, e039. ISSN-L 0214-8358 https://doi.org/10.3989/scimar.05265.039
Decapods in northern Alborán Sea and Gulf of Vera

R-sq.(adj)=0.618  Deviance explained= 64.6%

\( s(\text{Depth}) \)

| Depth | 5.76  | 6.821 | 44.246 | <2e-16*** |
|-------|-------|-------|--------|-----------|

\( s(\text{Longitude, Latitude}) \)

| Longitude, Latitude | 18.5  | 22.935 | 2.345  | 0.000637*** |

Shannon-Wiener diversity index (H)

\( (H) \sim \text{factor(Year)} + s(\text{Depth}) + s(\text{Longitude, Latitude}) \)

| 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(\text{Depth}) | 8.012 | 8.697  | 18.261 | <2e-16***   |
| s(\text{Longitude, Latitude}) | 19.929 | 24.272 | 1.875  | 0.00752***  |

R-sq.(adj)=0.45  Deviance explained= 49.6%

Pielou’s evenness index (J)

\( (J) \sim \text{factor(Year)} + s(\text{Depth}) + s(\text{Longitude, Latitude}) \)

| 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(\text{Depth}) | 6.478 | 7.536  | 11.284 | 1.08e-13*** |
| s(\text{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.