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Joan E. Cartes

Diego F. Figueroa

The University of Texas Rio Grande Valley

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Deep Sea Isopods from the western Mediterranean: distribution and habitat.

Joan E. Cartes¹, Diego F. Figueroa²

¹Institut de Ciències del Mar, ICM-CSIC, P/Marítim de La Barceloneta, 37-49, 08003 Barcelona, Spain

²School of Earth, Environmental, and Marine Sciences, University of Texas Rio Grande Valley,
Brownsville, Texas, 78520, USA

Abstract. Isopods are a highly diversified group of deep-sea fauna, with a wide variety of shapes which must reflect a similar great variety of adaptations to the deep environments. The deep Mediterranean, however, has a low diversity of isopods related to its oligotrophy, the thermal stability of deep-water masses (~12.8 °C below 150 - 200 m) and rather homogeneous geomorphology. The main factor defining isopod habitats in the Balearic Basin is insularity vs mainland influence. Desmosomatidae and Ischnomesidae, examples of epibenthic species (with lack of paddle-shaped legs and non/low-natatory capacity) are mainly linked to mainland areas with higher % organic matter (OM) and labile C, indicating food availability. By contrast, suprabenthic species like Munnopsidae (with some paddle-shaped, natatory, legs) are more dominant in insular areas. Compared with the Atlantic, the degree of impoverishment in diversity (number of species, S) of deep-Mediterranean asellotes is higher among epibenthos (with a lot of families/genera absent in the deep Mediterranean) than for suprabenthic species, with potential natatory capacity (natatory legs). This suggests that the high diversity of deep sea asellotes may depend on the trophic niches (sediment richness and diversity of habitats) available. In the 20 yrs period (1991-2011) of our (non-continuous) sampling series we identified some climatic influence (higher ENSO index) on the high densities reported in 1991-1992 samples, related to species taken at submarine canyons in mainland areas. Higher food availability (by advection) in canyons during 1991 and 1992 related with an increase of rainfall regime may enhance recruitment (e.g. in March 1992 inside canyons) and abundance/diversity of asellotes, especially for epibenthic species (Desmosomatidae).

Introduction.

Isopods are one of the most diversified group of deep-sea fauna, especially regarding their wide variety of shapes (Wolff, 1962; Hessler, 1970; Hessler et al., 1979), which must reflect a great variety of adaptations to the environment. Compared with Eucarids (euphausiids, decapods) among peracarids, including isopods, the lack of larvae dispersal limits their capacity to colonize new areas, increasing isolation and speciation. Therefore, isopods have been one of the main examples used to explain the high biodiversity of deep-sea fauna (Hessler, 1970; Hessler and Thristle, 1975). Numerous exploratory studies on isopods (by extension to macrofauna) have been carried out in the last decades in the North Atlantic (Harrison, 1988; Svavarsson et al., 1990; Brandt et al., 2005; Brix and Svavarsson, 2010; Schnurr et al., 2014; Brökeland, and Svavarsson, 2017), South Atlantic (Brix et al, 2018a) and other oceanic regions (e.g. N Pacific: Brandt et al., 2013; Elsner et al., 2015) with a large list of species reported (Brandt et al., 2009; Elsner et al., 2015). Deep-sea isopods are dominated by species of the suborder Asellota, whose taxonomic classification is extremely difficult (Wilson, 2008). Most published research in the last decades related to the Asellota are primarily taxonomic and include new and revised species descriptions and lists of species reported from new localities that are pending species determination (e.g. in Kurile-Kamchatka: Elsner et al., 2015). Such gaps in taxonomic determination are not only from remote, newly explored areas. In the deep NE Atlantic, for example, there are entire genera with species pending description, as discussed by Wilson and Hessler (1981) for *Disconectes* spp. Distribution and community structure of peracarids are poorly documented in the deep-sea Atlantic-Mediterranean zone (Rowe and Menzies 1969; Bellan-Santini 1985, 1990; Elizalde et al. 1991; Dauvin and Sorbe 1995; Cartes and Sorbe 1997), and none of these studies focus on isopods. In the deep Mediterranean, taxocoenoses of main Orders (Mysida, Amphipoda, Cumacea) have been analyzed, establishing patterns of species richness distribution and zonation along the slope (i.e. with community change around 1000 m depth, Ledoyer 1987; Bellan-Santini 1990, Cartes and Sorbe 1993, 1997).

The water-sediment interface, defined as the Benthic Boundary Layer (BBL), is still one of the least known marine compartments regarding its faunal composition and functioning (Frutos et al., 2018). It extends a few tens of meters into the water column immediately overlying the sea bed, and it is, especially at great depths, a difficult zone to sample properly. The BBL is an environment of great complexity both from a physical (Gage and Tyler, 1991) and biological (Smith and Hinga, 1983) perspective. Over the slope the BBL occupies a layer of *ca.* 0-50 m above the bottom. These limits, however, cannot be precisely defined because they may depend on the resuspension of particulate organic matter (POM), which is not a constant factor. Some organisms living in the BBL have unique characteristics, and different concepts have been used to define them. For example, the terms suprabenthos (Brunel et al., 1979) or its synonym hyperbenthos (Mees and Jones, 1997) have connotations with the idea of a “special benthos with special features” while hypoplankton (Mauchline and Gordon, 1991) define rather a zooplankton living in a concrete habitat. All of them refers to macrofauna (epibenthos), with some degree of natatory capability, that inhabit the interface closest to the sea bed (Sainte-Marie and Brunel, 1985; Elizalde et al., 1999). Terms like suprabenthos are linked to the use of specific sampling methodology, in this case the suprabenthic sledges, especially designed to catch

and quantify this mobile fauna. The idea is to move a zooplankton net as close to the bottom-sediment interface as possible to capture animals that can easily escape other samplers (e.g. to dredges or corers) due to their swimming capacity. At the same time, we must avoid collecting sediment, and fauna living in, and nekton and zooplankton living in the water column above the BBL. The task is technically complex and the final result of samples obtained is the capture of a mixture of organisms that live nearby, in and on the water column near the bottom, planktonic species that e.g. with seasonal periodicity arrive to the sea bottom and endo- or epibenthic species that emerge into the water column e.g. along diel cycles (Mees and Jones, 1997).

It is difficult to determine to what extent all fauna collected in such interface habitat is autochthonous of the BBL. It is a common practice to differentiate between permanent suprabenthos - its entire life cycle develops in the BBL - and not permanent - only some life phases live there (Mees and Jones, 1997). Among the permanent suprabenthos, peracarid crustaceans are probably the most characteristic taxon. The taxonomic richness of the suprabenthos is highlighted by the most diverse group of peracarids, the amphipods, with about 7,000 benthic species (compare to only 233 planktonic species, Vinogradov et al., 1996). Many of these benthic amphipods are epibenthic-suprabenthic. Mysids (Mysida) form another diverse group with over 1,000 species, mostly suprabenthic (hyperbenthic). Isopods are arguably the least known group of peracarids which are comprised of approximately 4,500 species with the majority forming part of the epibenthic-suprabenthic such as the suborder Asellota. Within this high diversity of deep-sea isopods (asellotes) there is still uncertainty on whether certain species are infauna or epifauna (Harrison, 1989, Bober et al., 2018, Brix et al., 2018b), and to this uncertainty we could add the question whether certain species are really suprabenthic due to their natatory capacity.

Deep-sea isopods are not just an important group due to their high taxonomic diversity but also because of their ecological role in deep-sea habitats, playing a crucial role in deep-trophic webs, e.g. in the Balearic Basin (Cartes and Abelló, 1992; Cartes, 1994). Seasonal environmental signals like phytodetritus deposition stands operate rapidly and favor aspects of its biological cycle (recruitment, gametogenesis) (Cartes et al., 2000), as happens among other deep peracarids (Bishop and Shalla, 1994; Tyler et al., 1994; Cartes and Sorbe, 1996), and among macrofauna, in general (Howell et al., 2002; Hudson et al., 2004). Because of their size and high densities, isopods (peracarids) act as a link between the surface production and the megafauna, being a fundamental part of the diet of large lobsters, shrimps and deep-water fish (Cartes and Abelló, 1992; Cartes, 1994; Cartes and Carrassón, 2004; Papiol et al., 2013; Modica et al., 2014).

In the Mediterranean Sea, the typical high diversity of deep-sea peracarids is somewhat limited due to the geological history of the region. The Mediterranean Sea is a peripheral sea (Thistle, 2003), a semi-isolated basin with a recent history of colonization (since the Messinian Crisis, 7-5 million years ago) compared with the neighboring Atlantic Ocean, that has resulted in a low diversity of deep-sea fauna. The deep Mediterranean is characterized by the annual thermal stability of the water mass (~12.8 °C) below around 150 - 200 m and to their deepest basins (Margalef, 1985), and in general it is considered oligotrophic (Moutin et al., 2012). Due to this oligotrophy and the recent extinction of fauna during the Messinian Crisis, it is generally accepted that the deep Mediterranean has not developed a true abyssal

fauna (except perhaps for some few pre-Messinian relict species, [Pèrès, 1985](#)). However, there are areas, with local enrichment spots due to dynamic structures like submarine canyons ([Buscail et al., 1990](#)), seamounts ([Rovere and Würtz, 2015](#); [Vázquez et al., 2015](#)) or upwelling areas acting like hotspots of production. Speciation in the deep sea seems associated with the gradient depth and with the environmental variables linked to depth ([Glazier and Etter, 2014](#)), among which trophic availability and food-related niche diversification might be important. The high environmental stability and oligotrophy of the deep Mediterranean – compared to neighboring Atlantic Ocean, for example – seems an unlikely scenario for higher diversification of fauna. In general, the possibility that species adopt diverse feeding strategies, linked to the temporal stability of diverse food resources, is a factor for enhancing their diversity ([Karr, 1976](#), among birds). In this way, the high environmental stability of the deep Mediterranean can give us some clue to analyze other factors, e.g. trophic factors, responsible for the diversification of deep-sea asellotes. In this way congeneric species are often separated bathymetrically in the deep Mediterranean (e.g. with deep shrimps *Plesionika* spp., [Cartes, 1993](#)), and when these species co-occur there is a size segregation.

Within this general context, the present work pursues two key objectives: (1) To establish the composition and distribution of deep-sea isopods living in the BBL in the north-western Mediterranean; (2) to analyze possible variables responsible for the changes identified in isopod distribution and diversity as a function of habitat. Changes considered were both spatial (influence of “insularity”, i.e. distribution of isopods over mainland/insular slopes) and temporal, including a long-term analysis. Such aspects have been analyzed for other faunistic groups in the Balearic Basin ([Fanelli et al., 2013](#); [Cartes et al., 2015](#)). Such analyses will help resolve the ecology of this important group in the Deep Sea and give clues to the mechanisms and adaptations that have resulted in the high diversification in this environment. The deep Mediterranean is in this sense a natural laboratory ([Margalef, 1985](#)) due to its high stability, somehow a simplified scenario compared to more productive deep oceanic systems.

Material and methods

Study area.

The study area in the western Mediterranean included the Balearic basin and the Algerian Basin ([Figure 1](#)). The Balearic Basin (Balearic Sea or Catalan Sea) has the structure of a large canyon open to the N-NE, flanked by the Iberian Peninsula (mainland) at NW-W and by the Balearic Islands at SE-E. The mainland side has important tributary canyons debouching to the Valencia Trough, where maximum depths in the Basin are recorded (to ca. 2300 m). Canyons are practically absent in the insular side. The Algerian Basin is open to the south, to the Alboran Sea and the north coast of Africa ([Figure 1](#)).

Different water masses, mostly permanent, are distributed in the Basin over the slope (at > 150 – 200 m depth). The Winter Intermediate Water (WIW) is distributed to ca. 200 m, especially marked in colder years ([Pinot et al. 2002](#)). WIW is generated in the Gulf of Lions by vertical convection ([Pinot et al. 2002](#)). During warmer winters WIW cannot form and the deeper water mass, the Levantine Intermediate Water (LIW) can occupy subsurface depths in the Balearic/Algerian basins. The LIW layer is distributed between ca. 300 to 900 m and it is characterized by high salinity; the Western Mediterranean Deep Water

(WMDW), distributed below the LIW, covers all the Basin at > 900 m. Both water masses flow throughout the south (Alboran Sea, Strait of Gibraltar) in winter, in parallel to the mainland coast.

Water masses are more or less defined depending of seasonality. Seasonally, main faunal changes in offshore (deep-water) fish and large invertebrates are associated with the stratification/homogeneity of the entire water column (Papiol et al., 2013). A thermocline is yearly developed around from May to November, with long term tendencies suggesting a prolongation of the stratification period in the last decades in coastal waters (Coma et al., 2009). This may also occur offshore, where a thermocline is formed at *ca.* 150 m depth during late spring- early summer to early-mid autumn (Papiol et al., 2012; Rumolo et al., 2015). Surface production is enhanced after cold winters (Estrada et al. 1993), transferring more organic matter to deep-sea ecosystems by vertical flux (Balbín et al. 2013; Pasqual et al. 2014, 2015). During the stratification period, there is a decrease of nutrient flow from the photic zone. Particulate organic matter (org C) derived from the surface arrives near the bottom well into the mid-summer (Guidi-Guilvard et al., 2007), as deep as 2300 m in the E Ligurian Sea. At the mainland side (Catalan slope), through advective flux, submarine canyons channeling river flows can also contribute important fluxes to the slope, as evidenced by stable isotope and C/N signals (Rumolo et al., 2015). Some local increases of biomass of meio/macrofauna (Cartes et al., 2010; Mamouridis et al., 2011) also suggest that POM can also arrive at high depths, via advection, within the period of stratification (e.g. in July).

Finally, the circulation pattern off the Catalan coast is characterized by surface current flows in a south-westerly direction (Wang et al., 1988; Font et al., 1988; Masó and Tintore, 1991). Oceanic eddies, temporary structures that can reach slope bottoms to 300-400 m depth, can also arise. The vertical extension of fronts/eddies (Ruiz et al., 2002) may generate local enrichment in the Balearic Basin.

Sampling

Isopods (suprabenthos) were collected with a Macer-GIROQ suprabenthic sledge in the sediment-water interface (0 - 1.5 m above the bottom, see Cartes et al., 2003; Frutos et al., 2018) in hauls taken over 134-2159 m. The sampling, trying to cover different bottom features (within canyons, adjacent slopes, insular slopes) followed rather the structure of perpendicular transects (e.g. between the coasts off Barcelona and the N of Mallorca). We compiled samples performed in the last 20 yrs, between 1991 and 2012 in the framework of different projects (see detailed information on sampling station in Table S1).

A total of 110 Macer-GIROQ samples were compiled for analyses of isopod fauna. Hauls were:

- i) ReTro: 1991-1992, 24 hauls covering the four seasons between 393-1858 m;
- ii) BatMan: March 1994 (7 hauls between 1167-1830 m) and July 1995 (2 haul at 1194-1300 m);
- iii) Prova96: October 1996, 3 hauls between 405-1287 m;
- iv) LEA: March 1998 (2 hauls between 194-642 m) and September 1998 (5 haul between 208-1647 m);
- v) QUIMERA: 8 hauls in 1998 between 249-1549 m, with a transect in SW Eivissa (Algerian Basin);
- vi) IDEA: 43 hauls in a by-monthly sampling in 2003-2004 between 139-735 m in the N and S Mallorca;
- vii) BIOMARE: 10 hauls covering the four seasons in 2007 at between 661-811 m off Barcelona; and
- viii) ANTROMARE (PreTrend): 5 hauls in June-July 2010-2011 at 609-649 and 1 haul in May 2012 at 2151-2159 m (Figure 1).

The Macer-GIROQ sledge was equipped with an opening-closing mechanism in the mouths (see [Cartes et al., 1997](#)). The mouths (2-3 superimposed) are closed by the force exerted by a spring once the sledge takes off from the sea floor, reducing contamination along the water column during sledge recovery. Once the suprabenthic sledge contacted the seafloor it was trawled for 10-20 minutes (longer times were used for deeper sites). Contact and detachment with the seafloor were verified by SCANMAR sensors attached to the sledge (in hauls taken after 1998). In the Macer-GIROQ model there is a distance of 10 cm between the lower mouth and the ground, which in theory impedes sediment from going into the net. In practice, however, and on certain sediments (with fluid mud, on steep slopes) it was inevitable to collect a variable, and sometimes considerable, amount of sediment.

Suprabenthic sledges were equipped with 500 μm mesh and trawled at a speed of 1.5 knots. Standard 2030 flowmeters (General Oceanics Inc.) were attached to the mouths of nets to measure the amount of water filtered and to estimate the distance/area covered in each haul. Volume of filtered water ranged between 134 to 805 m^3 in hauls at < 1000 m and between 395 to 2542 m^3 in hauls at > 1000 m, with an effective trawling time ranging between *ca.* 5-25 minutes, with time increasing with depth. Most of the samplings were performed during daytime. Samples were fixed in buffered formaldehyde, ethanol or frozen at -20°C on board. Isopods were sorted in the wet laboratory with forceps under a stereomicroscope (at $\times 10$ – $\times 40$), identified to the lowest possible taxonomic level, using various keys and species descriptions (e.g. [Hessler, 1970](#); [Brix et al., 2015](#) for Desmosomatidae; [Thistle, 1980](#) for *Ilyarachna* spp.; [Wilson and Hessler, 1981](#) for *Eurycope* genus; [Wagele, 1981](#) for Paranthuridae; and references cited therein) and the currently valid names of species were checked on the World Register of Marine Species (WoRMS, www.marinespecies.org). **Specimens are being deposited in collections of the Institut de Ciències del Mar of Barcelona (CSIC), meanwhile they are on personal collections of J.E. Cartes.** Specimens were counted and abundance data were obtained after standardizing number of specimens (to per 1000 m^3) for each haul.

Analysis of isopod communities.

Mann-Withney U test were used to compare the depth breadth (the range of depths) occupied by asellotes with and without paddle-shape (natatory) legs, i.e. between suprabenthic and epibenthic asellotes.

Tendencies of species diversity related to depth were analyzed for isopod taxocoenosis. For each station we calculated traditional indexes used to define species diversity, including Species richness (S), Equitability (J') and Shannon index (H') ([Pielou, 1975](#)). Regarding S , we further analyzed trends in the appearance/ disappearance of species with depth, according to [Gage and Tyler \(1991\)](#).

Species composition (abundance) was analysed by non-metric Multidimensional Scaling (nMDS: [Clarke and Warwick, 1995](#)), using Bray-Curtis distances after log-transformation of the data. Species with low frequencies of occurrence ($< 5\%$ of samples) were removed from the matrices prior to analyses. PERMANOVA tests (distance-based Permutational Analysis of Variance; [Anderson et al., 2008](#)) were performed on the same abundance matrices (999 permutations) to evaluate whether assemblages differed

among the factors defined in the area. The PERMANOVA designs were based on two factors (crossed design): Factor I was defined as “insularity” classifying hauls as belonging to 1 mainland and 2 insular zones (see Figure 2). The mainland zone is off the Catalonia coasts, the 2 “insular” zones around the Balearic Islands were at the Balearic Basin (N Mallorca) and within the Algerian Basin (S Mallorca and Pitiuses Islands: Eivissa- Formentera). Factor II was “depth interval” with 5 intervals: 100-200 m (shelf-slope break); 300-400 m (upper slope); 500-900 m and 1100-1400 m (middle slope); and 1500-2200 m (lower slope), intervals defined from previous analyses performed in the same area for a number of taxocenoses (e.g. Cartes et al., 1993; Cartes and Sorbe 1997; Papiol et al., 2012).

Environmental variables (%OM, %orgC) collected/compiled.

Environmental variables were measured at 5 m above the bottom (mab) with corresponding sensors attached to a CTD Searbird 25, with the exception of %OM which was measured from surface sediments. Both physical (Temperature, T_{5mab} ; salinity, S_{5mab}) and biological (dissolved oxygen, $O_{2\ 5mab}$; fluorescence, f_{5mab} , % of total organic matter, %OM) variables were included. In long-term analyses were considered the variables: i) sledge location (LAT, LONG) and ii) climatic variables, both NAO/winter NAO and MEI-ENSO, see <https://climatedataguide.ucar.edu/climate-data> ; <https://www.esrl.noaa.gov/psd/enso/mei/#data> and Sun spots number, see <http://www.sidc.be/silso/datafiles>).

We compiled available data of these variables in a ca. 20 years (between 1991 and 2012) period in the study area. In short, since 2000s, data was obtained, in general (see Figure 3, Table S1), in the same cruises (simultaneously) where suprabenthos was sampled. In previous (1990s) cruises environmental data was generally compiled from other cruises taken in the Catalan Sea (as explained in detail in Cartes et al., 2015). Sediment samples, i.e. the percentage of organic matter, %OM and (in some cases) percentage of organic Carbon (% orgC) were available in recent cruises (2007-2011, BIOMARE-ANTROMARE projects) in our area (28 data at depths between 63 and 2174 m) not only at stations where suprabenthos were sampled. We included also compiled data from previous projects (e.g. 33 data off the Ebro Delta between 102 and 670 m depth, between Cape Salou and Ebro Delta, see map in Figure 3; Geodelta, May1994; LEA cruises, 9 data taken off Barcelona at depths between 189 - 1634 m; IDEA cruises, see Table S1). With this field data set we generated %OM vs depth equations to complete gaps in our data matrices. The %OM and %orgC were obtained following standard protocols on surficial (0-2 cm) sediment (Cartes et al., 2002; Rumolo et al., 2015).

Analysis of isopod community composition vs environmental variables

Relationships between isopods abundance (ind./1000 m³), as the dependent variable and environmental conditions of sampled sites were analysed using Canonical Correspondence Analyses (CCA), a multivariate technique for extracting synthetic environmental gradients from ecological data (Ter Braak and Verdonschat, 1995). Ordination axes in CCA are linear combinations of environmental variables (arrows on plots) and arrow length is proportional to the importance of each variable for explaining, in this case, the ecological requirements of the species analysed (Ter Braak, 1986). In our ecological

analyses we distinguished (grouped) between: i) asellotes without paddle-shaped legs, probably without/low natatory capacity (e.g. Desmosomatidae and Ischnomesidae) as example of epibenthic species; ii) Those taxa with some paddle-shaped legs, probably with higher natatory capacity, like Munnopsidae, defined as suprabenthic species. Such criterion of behavior classification may have some exceptions. Among the former group some males of Desmosomatidae can swim actively, though the vast majority of Desmosomatidae collected in our study were females.

Our analysis had some limitations because of the lack of availability for all samples of more specific variables, e.g. orgC, C/N, or any other variables reflecting better than TOM (%OM) the nutritional value of organic matter deposited in sediments and/or suspended into the near-bottom water column. All data (variables) were log-transformed. The software XLStat (AddinSoft Inc.) was used for CCA.

Three CCAs were performed under different considerations: i) a general CCA on the composition of isopods on the whole dataset (110 hauls) available; ii) a CCA to analyse the effect of submarine canyons on isopod communities. For this only 45 hauls (taken at comparable depths: 350-650 m) were included in the matrix (hauls taken inside canyon were from depths of 387-537 m); and iii) a CCA built on climatic indices (NAO, MEI-ENSO) and related variables (Sun spots number) together with haul location (LAT, LONG). Only 37 hauls taken between 387-809 m (excluding hauls at > 1000 m), exclusively from the mainland (Catalan slope) area were included in this data matrix.

Results

Depth breadth and diversity tendencies.

Mean depth ranges (depth breadths) along the slope (over 134-2159 m) for epibenthic asellotes = 890.3 m, while for suprabenthic asellotes = 1158.2 m. Mann-Whitney U test = 31.0, being significant ($p=0.049$) when comparing the depth range inhabited by asellotes with and without paddle-shape (natatory) legs, i.e. our epibenthic asellotes occupy narrower depth ranges.

Species diversity related to depth shows different tendencies depending of the index used. Although over the same depth intervals we can find very different diversity values in the three studied areas, some tendencies can be identified:

i) Species richness (S) increased from 100 - 200 m to 300 - 400 and 500 - 900 m, reaching highest values ($S \geq 15$) between 376 - 637 m (Figure 2); S decreased at > 1000 m ($S < 12$) with the exception of 3 hauls at 1210 - 1263 ($S = 15-16$). The highest S values at the Balearic slope are a little displaced over shallower depths (>500 m) compared to the mainland slope;

ii) equitability (J') is maintained at similar high levels ($J' > 0.8$) along all the slope, though we found the lowest values of J' , being mostly between 0.45 - 0.78, at the middle slope (500-900 m) (Figure 2). This is due to the dominance of the suprabenthic species *Munnopsurus atlanticus*;

iii) Shannon index (H') showed a similar trend to J' . Over 100-200 m H' values are low (0.15 - 0.76), reaching highest values ($H' > 0.8$) at 300 - 400 m (to 1.05), but decreasing also at the middle slope (500 -

900 m) due to the dominance of *M. atlanticus*. High values of H' are also maintained at depths exceeding 1000 m (to 1355 m). The highest H' are at shallower depths (>500 m) over the Balearic slope, compared to the mainland slope.

Trends in the appearance/ disappearance of species with depth, showed an increase of species appearance from 134 m to 399 - 405 m, reaching 31 and 19 species for all isopods and for asellotes, respectively (Figure 3). There are no new species appearance at the interval 450 - 600 m. The tendency of increasing species with depth restarts deeper at 748 - 780 m where the 39 isopods (25 asellotes) identified in this study appeared.

Disappearance of species starts at 340 - 475 m (depending on taxon), and progressively increases to 804 m (12 isopods, among them 4 asellotes, reaching their maximal depths of occurrence), this rate of disappearance is maintained to 1194 - 1204 m (not influenced by the sampling gap at 805 - 1194 m), but deeper there is a progressive decrease to 2259 m (Figure 3).

In summary, the main renewal of isopod species occurs at: i) ca. 134 - 400 m with species appearance; ii) between 600 - 800 m, both with species appearance and disappearance; iii) below 1200 m, with any species appearance and progressive disappearance of practically all isopods to maximum depths sampled.

Community composition.

15143 isopods were classified to the lowest possible taxonomic level belonging to no less than 39 species. In MDS results are based on all the sampling performed (Figure 4). Testing the factor “insularity” there are significant differences in isopod community composition comparing mainland (Catalan slope) and the 2 sites around Balearic Islands, the “insular” samples (with N Mallorca PERMANOVA test $t=2.57$, $p=0.001$; with the Algerian Basin $t=2.49$, $p=0.001$). There are no significant differences between the two insular sites ($t=1.29$, $p=0.10$). Therefore, fauna around islands is significantly different than that on the mainland slope, independently of the Basin where hauls were taken.

Because of the significant community differences between the mainland sites and the insular sites, the factor “depth” was considered separately for each (Figure 4, ii). This shows a consistent ordination of samples as a function of depth, with some significant differences between contiguous depth intervals (PERMANOVA test, intervals with low n, e.g. 100-200 m at mainland, > 1000 m at insular not included): i) at mainland the depth intervals 300 - 400 m vs 500 - 900 m (test $t=1.81$, $p=0.009$); 500 - 900 m vs 1100 - 1400 m ($t=3.03$, $p=10^{-4}$); and ii) at insular slope the levels 100 - 200 m vs 300 - 400 m (test $t=2.17$, $p=4 \cdot 10^{-4}$); 300 - 400 m vs 500 - 900 m ($t=1.98$, $p=3 \cdot 10^{-4}$). So significant faunal changes occur at shallower depths over insular (at 200 - 300 and 400 - 500 m) than over mainland (at 400 - 500 and 900 - 1100 m) slopes. Interaction between the two factors ($t=1.9$) was significant ($p=0.004$).

The factor “canyon” with MDS performed only with samples taken at comparable depths (between 350 - 650 m, not represented) show significant differences in isopod composition between hauls taken inside canyons and those not in canyons ($t=1.38$, $p=0.03$). Differences were based on abundance data, i.e. there

are no species exclusively distributed inside canyons (except the rare species *Pleurogonium* sp. with only 2 specimens collected, Table 1), but species abundance is greater.

Environmental variables

The percentage of organic matter (%OM) is always higher over mainland than over insular areas (Figure 5), especially at the upper-middle slope to 1000 m. Briefly, OM increases from 200 to 550 in the mainland area and then it is maintained above *ca.* 12%. The highest values of OM > 12% are found over mainland depths between *ca.* 550 - 1680 m. Over insular depths, the highest values range between *ca.* 6 - 8 %OM with maximum OM at *ca.* 600 - 700 m. Although OM declines deeper (at 1050-1570 m), values are still high (7.5-8.2%). At 2174 m in the middle of Valencia Trough %OM reaches a high (9.4%) value, although this in fact is a boundary between the insular and mainland sides of the Balearic basin. The %orgC (data available only over the mainland area) shows a similar pattern to %OM, with an increase to 0.8% at *ca.* 450 - 600 m. There is high variability between the rather scarce data available at > 1000 m (0.93% at 1170 m, 0.44% at 1285 m and 1.5% of orgC at 1634 m).

Results for the remaining variables (near-bottom data) has been published in previous articles (Cartes et al., 2013; Rumolo et al., 2015). Depth-related trends for (near-bottom) temperature (T), salinity (S) and O₂ shows how T reaches the lowest values (*ca.* 13.07°C) at 1010 - 1282 m, S decreases linearly from 400 m (38.52 pss) to 1010 - 1217 (38.48 pss) and the O₂ concentration has a minimum at 400 m (3.98 ml/l) reaching maximum values (4.38–4.40 ml/l) from 1010 to 1282 m (see Figure 4 in Cartes et al., 2013).

CCA Results.

The CCA of isopod species shows a tendency with a horse-shoe effect in the distribution of hauls (represented in the plot by their respective mean depths) (Figure 6, upper). CCA explained variance – 2 axes represented - is 72.45%. The shallowest hauls, over the shelf-slope break (134 - 211 m), are at the lower right of the CCA plot. Above them and to the left, we progressively find hauls from 300 - 400 and 500 - 900 m depth intervals, and the horse-shoe distribution is completed at the lower left of the plot where we find practically all hauls taken at depths exceeding 1000 m. Species mainly distributed over the shelf-slope break (e.g. *Aega* sp. 1, *Syscenus infelix*, *Rocinela* sp., *Eurydice* cf. *truncata*) are associated with high levels of near-bottom $f_{5\text{mab}}$ (fluorometer data) and low levels of deposited organic matter (%OM). *Natatolana borealis* is preferentially linked to high S (LIW) and %OM, while most species, including a high number of Asellota are preferentially distributed over the middle and lower slope (*ca.* 600 - 1400 m) linked (in this general CCA) to lower T and/or rather high amount of %OM in sediments. Among them we find practically all epibenthic (defined previously as not having paddle-shape legs) Desmosomatidae (see also next CCA). The two *Ilyarachna* spp. preferentially distributed over the lower slope (*ca.* at 1200-1300 m) with *Eurycope* sp. are linked to low T and rather high levels of O₂ near the bottom at these depths (see depth-related results for T and O₂ in Cartes et al., 2013).

CCA performed for hauls taken at the interval 350 - 650 m (Figure 6, lower) included all samples taken inside submarine canyons (C) and the adjacent slope at comparable depths. CCA explained variance was

74.13%. The main axis of the CCA separates mainland vs insular slope samples. Together with this, all C samples are at the left of the CCA plot, linked to practically all Desmosomatidae, with conditions of low T and rather higher %OM. Together with C samples we find (at the same part in the 2-D plot) all hauls taken at mainland region over the adjacent slopes (As), close to canyons. By contrast, asellid isopods with paddle-shape legs, assumed as natatory legs (including all *Disconectes* spp.) are distributed opposite to Desmosomatidae, associated mainly to hauls taken over insular waters, with higher T (and S). Exceptions include the *Eurycope* sp., linked to high levels of O₂ and *Munnopsurus atlanticus* linked to high S.

Based on the CCA results, the mapping of the distribution of asellote families with different morphological characteristics in legs (Desmosomatidae and Ischnomesidae without any paddle-shape, natatory leg, Ilyarachnidae with two pairs (P5 - P6) of paddle-shape legs, Munnopsidae and Eurycopinae with three pairs (P5 to P7) of paddle-shape legs, we find: i) Desmosomatidae and Ischnomesidae are mainly distributed over the Catalan slope, on the mainland part of the Balearic Basin; ii) species with some paddle-shape, natatory, legs are more equally distributed in both mainland and insular areas, around the Balearic Islands (Figure 7).

The CCA based on climatic information (performed for hauls exclusively taken at mainland and at 350-650 m, Figure 8), shows that all samples at the left of the CCA plot are linked to practically all Desmosomatidae (excluding *Eugerdia tenuimana*) and the Anthuridae *Pilosanthura fresii*, with conditions of El Niño (MEI-ENSO index) event in 1991 and especially in 1992 (index values of 52.6, 55.4 respectively) and with high Sun spot numbers (mean Jan-May months). By contrast, asellid isopods with paddle-shape legs (including all dominant species: *Munnopsurus atlanticus*, *Disconectes* spp.) and other highly mobile species (the scavenger *Natatolana borealis*) are mainly found opposite to Desmosomatidae, and more dispersed (in the right part of the CCA plot), linked to rather low/neutral MEI-ENSO indexes, (14 in 2011, close to the accepted limit for La Niña event: 13) and with low Sun spot numbers. CCA explained variance was 80.46%.

Discussion

Faunistic remarks.

Detailed biogeographic comparisons among isopod fauna from different basins/seas is limited by a number of factors, from sampling strategy (Harrison, 1988) to the high amount of species pending to be described/classified to species level. To date we do not find among Mediterranean isopods any confirmed endemic species to add to the 6 deep-sea species listed by George and Menzies (1968), among which we collected the two Munnopsidae, *Aspidarachna sekhari* and *Ilyarachna calidus*. It is possible, pending future detailed taxonomic analyses, that some of the species identified here, such as some Ilyarachninae and *Balbidocolon* sp. may be discovered to be new, undescribed species. The genus *Balbidocolon* was collected in the Eastern Mediterranean (Aegean Sea, Koukouras et al., 2002). It is unlikely that our specimens belong to the 2 only congeneric species described to date, both from abyssal depths (N Atlantic, *B. atlanticum* Hessler 1970; Polar Sea, *B. polaris* Malyutina and Kussakin 1996). The Cirolanid sp. A found over the Catalan slope is blind, a common characteristic among cirolanids inhabiting caves. However, after a complete sampling of the bathyal environment of the deep Mediterranean, we conclude

that the vast majority of isopods identified are not endemics (as suggested by [George and Menzies, 1968](#)), since their distribution also includes the Atlantic Ocean. More detailed conclusions would require further specialized taxonomic and molecular work to clearly define and identify species. We attempted genetic analyses, but extraction of DNA yielded very low concentrations (0.05 to 0.2 ng/uL) and PCR amplification for mitochondrial and nuclear markers using universal and isopod specific primers failed. The issues seem to be specific for isopods as copepods collected from these same hauls yielded 25-fold DNA concentrations and good PCR amplifications ([Figuerola et al. 2019](#)). This failure in molecular work is likely due to the collection and preservation methods not being optimal for isopods. [Riehl et al. \(2014\)](#) summarize similar issues and demonstrate that collection methods highly impact the successful recovery of DNA from deep-sea isopods. [Riehl et al. \(2014\)](#) improved their collection and preservation methods, increasing the success rate of PCR amplification from no amplification to 40%-80% success. Their final recommendation is to use collectors that can be sealed at the collection depth retrieving samples in cool temperature waters of the same sampling depth, immediately preserving samples in chilled ethanol and placing them at -20°C.

Species richness and diversity

Fish ectoparasite isopods (*Rocinela* sp., *Aega* sp.) preferentially occupied the shelf-slope break, linked to the maximum of fish biomass found at the shelf-slope break ([Cartes et al., 1994](#)). Within free-living species, asellotes are, as expected, the most diversified group of deep-sea isopods. High inter-sample variability appears to be inherent in epibenthic sled sampling ([Harrison, 1988](#)). In addition, isopod composition may depend on the type of sampler used.

With a lower sampling effort than that performed in the deep Mediterranean, twelve families and 79 species of asellote isopods were identified at a single site in the southern Rockall Trough (NE Atlantic) by [Harrison \(1988\)](#), while further North at the Iceland-Faroe Ridge (IFR) and the Norwegian Channel (NC), [Brix et al. \(2018\)](#) identified to 100 species in a similar depth range (118 - 2750 m) than ours. By contrast, only 25 asellote species were collected in the western Mediterranean. This, together with the low endemism of fauna, confirms that the deep Mediterranean isopod fauna is an impoverished version of the deep Atlantic fauna. The degree of species impoverishment depends on the Family and species' habits (see below). In the deep Mediterranean we find quite higher species impoverishment among epifaunal asellotes, in this study those species are considered as not having natatory (paddle-shape) legs. For example, the genus *Ischnomesus* was represented in our area by a single species, *Ischnomesus bispinosus*, while [Harrison \(1988\)](#) identified 6 species in the Rockall Trough and [Brix et al. \(2018\)](#) 3 species in IFR-NC. From IFR-NC isopods, only 7 - 8% of species (e.g. *Ilyarachna longicornis*, *Ischnomesus bispinosus*, *Disconectes furcatus* or *D. phalangium*) have been found in the deep Mediterranean. Regarding the nearest area (Rockall) to ours, the ratio of impoverishment of species comparing Mediterranean and Atlantic ranged from 1:2 (*Eugerdia* spp., *Chelator* spp.) to 1:6 in *Ischnomesus* sp., with several genera without representatives in the deep Mediterranean like *Heteromesus* sp. (9 species in Rockall) and *Mirabilicoxa* sp. (12 species in Gay-Bermuda Head transect in [Hessler, 1970](#)). By contrast, among "natatory" asellotes, this impoverishment is more moderate, with genera such as *Ilyarachna* sp. or

Belonectes sp. having the same number of species in both seas, and other (*Munnopsurus* sp., *Munnopsis* sp.) only having 2-3 species in the deep Atlantic vs only one in the Mediterranean. Exceptions include *Eurycope* sp., which are clearly more diversified in the Atlantic (Schnurr et al., 2018), and the small species in *Disconectes* sp., which are more diversified in the deep Mediterranean, though this genus does have a large number of undescribed species from the deep Atlantic (Wilson and Hessler, 1980). In summary, among the 79 species identified by Harrison (1988) 56.5% were epibenthic (without paddle-shape, natatory, legs), while in the deep western Mediterranean these epibenthic species only represent 40% of asellotes. In our study area the most abundant epibenthic asellotes were also regularly collected in samplings performed with box/multi-corers, (e.g. *Chelator chelatus*, *Eugerdia filipes* and *Desmosoma lineare*, Mamouridis et al., 2011, author's unp. data), while among species with paddle-shape (natatory) legs, only some of the smallest (*Ilyarachna longicornis* and *Disconectes latirostris*) can be accidentally collected in such sediment sampling.

Preferent habitats occupied by isopods.

Epibenthic asellotes (as defined above) occupy mainly the continental (mainland) areas in the Balearic Basin, linked to high %OM in sediments (less oligotrophy), likely due to the enrichment effect of mainland, via submarine canyons. Lower dispersal capability is expected among epibenthic (non-swimming) Desmosomatidae or Ischnomesidae. This has been reported comparing asellote fauna from West and East of the Middle Atlantic Ridge (MAR). The MAR acts as a dispersal barrier for non or weakly-swimming Macrostylidae, Desmosomatidae and Nannoniscidae, while gene flow across the MAR was observed for swimming asellotes (Bober et al., 2018). Some Desmosomatidae males have setae at the posterior legs, which may give males some natatory capacity (S. Brix, pers. comm.). In spite of this, compared with asellotes with paddle-shape (natatory) legs (suprabenthic), our epibenthic asellotes occupy along the slope (over 134-2159 m) narrower depth ranges, suggesting they have a narrower, more localized, habitat linked to food availability in /near mainland, influenced by submarine canyons.

Only one species, *Munnopsurus atlanticus*, was regularly collected (72 specimens, 1.4% of total individuals collected) in the upper nets of the suprabenthic Macer-GIROQ, operating above ca. 0.5 m over the sea floor (Cartes et al., 1994). This is the species with the clearest suprabenthic habits (never collected with corers), in our area. *Munnopsurus atlanticus* was the largest asellote in the deep Mediterranean (to ca. 7.5 mm TL), with 3 pairs of natatory legs. *Munnopsurus atlanticus* also suffered important seasonal fluctuations, with low densities in winter (3.4 ind/100 m²) increasing to 60.9 ind/100 m² in summer (Cartes et al., 2000). The mobility of this species could allow it to colonize local patches of food, e.g. by (phyto)detritus deposition, in an oligotrophic area like the deep Mediterranean. In fact, its population dynamics run parallel to the dynamics of %orgC (TOC) of sedimented POM, which increased from winter to summer in the adjacent slope off canyons (Rumolo et al., 2015). The origin of this C in sediments is mainly marine (orgC_{marine} > 70%; mean $\delta^{13}\text{C}$ = -22.4‰; C/N < 10) derived from phytoplankton, and the depleted isotopic signal of *M. atlanticus* ($\delta^{13}\text{C}$ = -20.38/-21.38, Madurell et al., 2008; Fanelli et al., 2009) suggests exploitation of resources of pelagic origin. The link between orgC and *M. atlanticus* response in the Catalan sea populations would be via foraminiferans (Cartes et al., 2000).

Asellotes is not a group with high swimming capacity compared with other isopods, like Cirolanidae, Aegidae or Gnathidae and the spatial partitioning of species over the sea bottom must occur at small spatial scales. In fact, only *Munneurycope murrayi* appeared off the sea bottom at distances of 50 m above it, being collected in sediment traps into Nazaré Canyon (Martin et al., 1996).

Svavarsson et al., (1990) linked the distribution of the asellotes to different sediment types, with differences in grain size and associated foraminiferans, one of the main prey for some asellotes (Svavarsson et al., 1993; Cartes et al., 2000, 2001). Other authors, however, put emphasis on the importance of different water masses and thermoclines (Brix and Svavarsson, 2010 for Desmosomatidae; Brix et al, 2018) in northern waters (IFR-NC region). Different causes can be argued for the poor diversification of deep asellotes in the Mediterranean. First, the particular paleoecological history of this sea with the Messinian extinction of deep fauna, and lack of speciation of Atlantic colonizers. This lack of speciation could likely happen because speciation rate might be slow in more homogeneous habitats like those in the deep Mediterranean. Among lizards, comparative studies between desert species in Australia and North America evidenced how large environmental heterogeneity favor higher diversity of coexisting species (Pianka, 1969). After the Messinian crisis, 5-7 million years, it seems it would be enough time for a higher diversification of Atlantic isopod colonizers in the deep Mediterranean than what is currently observed. Speciation does not necessarily happen slowly as it is commonly assumed. Some changes in the migratory behavior of birds (e.g. *Sylvia atricapilla*), induced by humans, can accelerate the evolution of adaptive phenotypic divergence within periods even observable in a human-life scale (Rohlshausen et al., 2009). The deep Mediterranean is very stable with absence of strong physical or thermal barriers at > 150 m, so we cannot expect the high influence of thermoclines on diversity found at high latitudes (Brix et al., 2018). In the deep Mediterranean we did not find natural barriers either like the MAR (Bober et al., 2018), the number of seamounts for example is rather low, most are close to the coasts (Vázquez et al., 2015) and, due to the hydrographic stability of the deep Mediterranean below 150 m (Furnestin, 1960; Hopkins, 1985), with water masses of similar conditions of temperature or salinity both at summits and seamount flanks. Since DNA of deep-sea isopods seems to be especially sensible to temperature changes during sampling collection (Riehl et al., 2014), we can hypothesize, at an evolutionary scale, that the lack of thermal barriers (temperature changes) in the Mediterranean along wide depth gradients (from 150 m to the deepest abyssal plains) did not favor changes— mutations - in the DNA of deep Mediterranean isopods, hence their poor diversification.

Another important aspect that can make speciation difficult is the poor trophic quality, and rather low – always in comparative terms - habitat patchiness of deep Mediterranean sediments. Diversification depends of how species can occupy different niches with low competition among species. The different characteristics of sediments, type of sediments (Svavarsson et al., 1990), organic richness of sediments, is important, because they can generate a patchy distribution of species. Large phytodetritus aggregations reported in the deep Atlantic (Rice et al, 1986, 1994), for example, have not been documented in the deep Mediterranean, where the phytoplankton biomass on sediment surface is low (< 0.2 µg Chl a l⁻¹), with the lowest values on the insular part of the Balearic Basin compared to the mainland Catalan slope (Riaux-

Gobin et al., 2004). Some labile matter, e.g. derived from Chl *a*, arrives to the bottom of the slope where it is consumed by meiofauna (Riaux-Gobin et al., 2004) and deep macroinvertebrates (Papiol et al., 2014). In general, the values of TOC (a good indicator of food for the benthos) found at the upper part (200-1200 m) of the Catalan slope (0.65 ± 0.12 , present results, Rumolo et al., 2015) are lower than those reported in Atlantic areas, even at abyssal depths (mean %TOC=1%, Escobar-Briones et al., 2009). This low %TOC is typical for all the deep Mediterranean with %TOC <0.5% in the Cretan slope (Tselepides et al., 2000), even lower at the deep Cretan Sea basin (1570 m, %TOC <0.4%). Ecological speciation is the result of ecologically based divergent selection between environments (Jennings et al., 2014), so less (trophic) niche variety may imply less diversification.

Compared to the Atlantic Ocean, deep asellote fauna in the Mediterranean are dominated by suprabenthic species, with 60% of species identified having natatory (based on the paddle shape structure) legs, while in the closest (Rockall) deep Atlantic the relationship epibenthos/suprabenthos is rather inverse, i.e. Harrison (1988) shows that 56.5% of species are epibenthic and 43.5% species have natatory legs. Accordingly, in the list by Brix et al., (2018), Munnopsidae were clearly less diversified than the rest of Families without paddle-shape legs. This tendency also happens in abyssal asellote fauna from the NW Pacific (Elsner et al., 2015), with 62.8% epibenthic species and only 37.2% species (Munnopsidae) with natatory legs (from 215 asellotes counted, see Table 2 in Elsner et al., 2015). In addition, epibenthic asellotes in the Mediterranean are linked primarily to mainland areas, where %OM and, in general, food sources for benthos in sediments is higher. So, the higher diversification of epibenthic species in an area with more favorable trophic conditions suggests that asellote diversification is basically linked to the quantity and quality of OM in sediments. Depth, and the environmental gradients that are associated with depth, play a fundamental role in the diversification of deep marine organisms (Glazier and Etter, 2014). Among these “environmental gradients” the quantity and quality of OM in sediments could be a key factor. To this, we can add the physical characteristics of sediments (grain size, particle distribution) themselves that may allow isopods to burrow with a markedly different degree of success (Hult, 1941, Svavarsson et al., 1990). In addition, among the rather few common species living both in the N Atlantic and the deep Mediterranean we found examples of species living at quite different depths (and habitats), which suggests an adaptative plasticity without speciation along wide latitudinal/depth ranges. There are examples of deep Mediterranean species (peracarids like the mysid *Boreomysis arctica* Tattersall and Tattersall, 1951; isopods: *Syscenus infelix*, *Ilyarachna longicornis*, some *Disconectes* spp.) being described in shallow waters (50 to 550 m) in N Atlantic (e.g. *Ilyarachna longicornis* 55-91 m in Sars, 1899), while they live at depths exceeding 1000 - 2000 m in the Mediterranean. Again, a plausible explanation is the absence of thermal barriers in the deep Mediterranean below 150-200 m, barriers that these species find in the deep Atlantic. Although more direct relationships with sediment characteristics and OM quality (OrgC, lipids, etc...) should be evaluated to justify diversification of asellote species, the general relationship found between epibenthos and %OM, and the higher impoverishment of epibenthic vs suprabenthic species in an oligotrophic environment like the deep Mediterranean indicates what important is to do more effort to characterize trophic niches occupied by asellotes.

Long term tendencies.

No indication of significant temporal change in species composition is found at Rockall Trough (Harrison, 1988), from analyses spanning a period of eleven years. Here, in a series, though non continuous, of *ca.* 20 years we find how species are related with climatic indices depending on their basic life habits – suprabenthos or epibenthos. While practically all epibenthic species (Desmosomatidae) are grouped together, and are related to high MEI-ENSO values (and high number of Sun spots), swimming species seem to have a more variable strategy. Some abundant species like *Munnopsurus atlanticus* and the cirolanid *Natatolana (Cirolana) borealis* have an opposite pattern of association that that of the Desmosomatidae. Other abundant swimmers (*Belonectes parvus*) are not so clearly linked to any climatic tendency, while *Ilyarachna longicornis* or *Eurycope* sp. are also linked to the same conditions followed by epibenthic asellotes. The phenomenon of El Niño (ENSO index) seems to be linked to Mediterranean climate, in spite of the remoteness of the focus of this phenomenon. Some local studies report an increase of rain in the Mediterranean during El Niño years (Laita Ruíz de Asúa, 1998), with rainfall increasing in the preceding autumn to ENSO peak (Mariotti et al., 2002; Shaman, 2014). This would explain higher food availability (by advection) in canyons during 1991 and 1992 with a logical increase in recruitment (e.g. in March 1992 inside canyons, Cartes et al., 2010) and abundance/diversity of asellotes, especially epibenthic species (desmosomatids).

In summary, the analysis of deep-sea isopod fauna in the western Mediterranean, from a 20 year period (1991-2011), collected over mainland and insular areas, demonstrates changes in faunal composition between mainland and insular areas and depending on isopod habits, with epibenthic (non-natatory) species (e.g. Desmosomatidae) mainly linked to mainland areas with higher food availability (%OM, labile C). The impoverishment of deep Mediterranean asellote fauna when compared to the neighboring Atlantic ocean is more accentuated among epibenthos (where entire families are absent from the deep Mediterranean) than for species with higher natatory capacity (natatory legs), suggesting that the high diversity of deep-sea asellotes may, in general, depend significantly on the trophic niches (sediment richness and diversity of habitats) available. In spite of our series not being continuous, some climatic influences on the high densities reported in 1991-1992 cannot be ignored. These higher densities are likely due to increase food availability through increased sediment transport via submarine canyons in mainland areas due to the higher precipitation experienced during these years.

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References

- Anderson M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER-E. Plymouth, UK.
- Balbin, R., Lopez-Jurado, J. L., Flexas, M. M., Reglero, P., Vélez-Velchi, P., González-Pola, C., Rodríguez, J. M., García, A., Alemany, F., 2014. Interannual variability of the early summer circulation around the Balearic Islands. *Journal of Marine Systems*, 178, 70-81. DOI:10.1016/j.jmarsys.2013.07.004.
- Bellan-Santini, D., 1985. Etude de la faune profonde de Méditerranée: les Amphipodes des trois campagnes Polymede I, Polymede II et Biomedes I. Rapport Commission internationale Mer Méditerranée 29, 333–334.
- Bellan-Santini, D., 1990. Mediterranean deep-sea Amphipoda: composition, structure and affinities of the fauna. *Progress Oceanography* 24, 275–387.
- Bishop, J.D.D., Shalla, S.H., 1992. Discrete seasonal reproduction in an abyssal peracarid crustacean. *Deep-Sea Research I* 41, 1798–1800.
- Bober, S., Brix, S., Riehl, T., Schwentner, M., Brandt, A., 2018. Does the Mid-Atlantic Ridge affect the distribution of abyssal benthic crustaceans across the Atlantic Ocean? *Deep-Sea Research II*, 148: 91–104.
- Brandt, A., Brenke, N., Andres, H. G., Brix, S., Guerrero-Kommritz, J., Mühlenhardt-Siegel, U., Wägele, J.W., 2005. Diversity of peracarid crustaceans (Malacostraca) from the abyssal plain of the Angola Basin. *Organisms, Diversity and Evolution* 5, 105–112.
- Brandt, A., Linse, K., Schüller, M., 2009. Bathymetric distribution patterns of Southern Ocean macrofaunal taxa: Bivalvia, Gastropoda, Isopoda and Polychaeta. *Deep Sea Research I* 56, 2013–2025.
- Brandt, A., Elsner, N., Brenke, N., Golovan, O., Malyutina, M.V., Riehl, T., Schwabe, E., Würzburg, L., 2013. Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems, *Deep Sea Research II*, 86-87, 43-55.
- Brix, S., Svavarsson, J., 2010. Distribution and diversity of desmosomatid and nannoniscid isopods (Crustacea) on the Greenland-Iceland-Faeroe Ridge. *Polar Biology*, 33, 525–530.

- Brix, S., Bober, S., Tschesche, C., Kiharac, T.C., Driskell, A., Jennings, R.M., 2018a. Molecular species delimitation and its implications for species descriptions using desmosomatid and nannoniscid isopods from the VEMA fracture zone as example taxa. *Deep-Sea Research Part II*, 148, 180–207.
- Brix, S., Stransky, B., Malyutina, M. Pabis. K., Svavarsson, J., Riehl, T., 2018b. Distributional patterns of isopods (Crustacea) in Icelandic and adjacent waters. *Marine Biodiversity*, <https://doi.org/10.1007/s12526-018-0871-z>
- Brökeland, W., Svavarsson J. 2017. Distribution of haploniscids (Isopoda, Asellota, Haploniscidae) in Icelandic waters, with description of *Haploniscus astraphes* n. sp. from the Iceland basin and the Southeast Atlantic Ocean. *Zootaxa* 4231 (3), 301–326.
- Brunel, P., Besner, M., Messier, D., Poirier, L., Granger, D., Weinstein, M., 1978. Le traineau Macer-GIROQ: appareil amélioré pour l'échantillonnage quantitatif étagé de la petite faune nageuse au voisinage du fond. *Internat. Revue gesamten Hydrobiologie*. 63, 815-829.
- Buscail R., Pockington R., Daumas R., Guidi L., 1990. Fluxes and budget of organic matter in the benthic boundary layer over the northwestern Mediterranean margin. *Continental Shelf Research* 10, 1089-1122.
- Cartes, J.E., 1993. Diets of deep-water pandalid shrimps on the Western Mediterranean slope. *Marine Ecology Progress Series* 96, 49-61.
- Cartes, J.E., 1994. Influence of depth and season on the diet of the deep-water aristeid *Aristeus antennatus* along the continental slope (400 to 2300 m) in the Catalan Sea. *Marine Biology* 120, 639-648.
- Cartes, J.E., Abelló, P., 1992. Comparative feeding habits of Polychelid lobsters in the Western Mediterranean Deep-Sea Communities. *Marine Ecology Progress Series* 84, 139-150.
- Cartes, J.E., Sorbe, J.C., 1993. Les communautés suprabenthiques de la Mer Catalane (Méditerranée occidentale): données préliminaires sur la repartition bathymétrique et l'abondance des crustacés péracarides. *Crustaceana* 64, 155–171.
- Cartes, J.E., J.B. Company, F. Maynou, 1994. Deep-water decapod crustacean communities in the Northwestern Mediterranean: Influence of submarine canyons and season. *Marine Biology* 120, 221-230.
- Cartes, J.E., Sorbe, J.C., 1996. Temporal population structure in deep-water cumaceans along the western Mediterranean slope (between 400 to 1300 m). *Deep-Sea Research I* 43, 1423–1438.
- Cartes, J.E., Sorbe, J.C., 1997. Bathyal Cumaceans of the Catalan Sea (north-western Mediterranean): faunistic composition, diversity and near bottom distribution along the slope (between 389–1859 m). *Journal of Natural History* 31, 1041–1054.

- Cartes, J. E., Carrassón, M., 2004. The influence of trophic variables in the depth-range distribution and zonation rates of deep-sea megafauna: the case of the Western Mediterranean assemblages. *Deep Sea Research* 51, 263-279.
- Cartes, J.E., Elizalde, M., Sorbe, J.C., 2000. Contrasting life histories and secondary production of populations of *Munnopsurus atlanticus* (Isopoda: Asellota) from two bathyal areas of the NE Atlantic and the NW Mediterranean. *Marine Biology* 136, 881-890.
- Cartes, J. E., A. Grémare, F. Maynou, S. Villora-Moreno, Dinét, A., 2002. Bathymetric changes in the distributions of particulate organic matter and associated fauna along a deep-sea transect down the catalan sea slope (Northwestern Mediterranean). *Progress in Oceanography* 53, 29-56.
- Cartes, J.E., D. Jaume, Madurell, T., 2003. Local changes in the composition and community structure of suprabenthic peracarid crustaceans on the bathyal Mediterranean: influence of environmental factors. *Marine Biology* 143, 745-758.
- Cartes, J.E. Fanelli, E., Papiol, V., Maynou, F., 2010. Trophic relationships at intrannual spatial and temporal scales of macro and megafauna around a submarine canyon off the Catalan coast (western Mediterranean). *Journal of Sea Research* 63, 180-190.
- Cartes, J.E., F. Maynou, E. Fanelli, C. López-Pérez, V. Papiol. 2015. Changes in deep-sea fish and crustacean communities at 1000–2200m in the Western Mediterranean after 25 years: Relation to hydro-climatic conditions. *Journal of Marine Systems*. 143: 138–153.
- Clarke, K.R., Warwick, R.M., 1995. *Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Natural Environment Research Council, United Kingdom.
- Coma, R., Ribes, M., Serrano, E., Jiménez, E., Salat, J., Pascual, J., 2009. Global warming-enhanced stratification and mass mortality events in the Mediterranean. *Proceedings National Academy Sciences* 106(15), 6176-6181. <https://doi.org/10.1073/pnas.0805801106>
- Dauvin, J. C., Sorbe, J.C., 1995. Suprabenthic amphipods from the southern margin of the Cap Ferret Canyon (Bay of Biscay, north-eastern Atlantic Ocean): abundance and bathymetric distribution. *Polski Archiwum Hydrobiologii* 42, 441–460.
- Elizalde, M., Dauvin, J. C., Sorbe, J.C., 1991. Les Mysidacés suprabenthiques de la marge sud du canyon du Cap Ferret (golfe de Gascogne): répartition bathymétrique et activité natatoire. *Annales Institut Oceanographique Paris* 67, 129–144.

- Elizalde, M., Weber, O., Pascual, A., Sorbe, J.C., Etcheber, H., 1999. Benthic response of *Munnopsurus atlanticus* (Crustacea Isopoda) to the carbon content of the near-bottom sedimentary environment on the southern margin of the Cap Ferret Canyon (Bay of Biscay, Northeastern Atlantic Ocean). Deep-Sea Research II 46, 2331–2344.
- Elsner, O., M.V. Malyutina, O. A. Golovan, N. Brenke, T. Riehl, Brandt, A., 2015. Deep down: Isopod biodiversity of the Kuril–Kamchatka abyssal area including a comparison with data of previous expeditions of the RV Vityaz Nikolaus. Deep-Sea Research II 111, 210–219.
- Estrada, M., Marrase, C., Latasa, M., Margalef, R., Delgado, M., Riera, T., 1993. Variability of deep chlorophyll maximum characteristics in the Northwestern Mediterranean. Marine Ecology Progress Series 92, 289–300.
- Fanelli, E., J.E. Cartes, P. Rumolo, Sprovieri, M., 2009. Food-web structure and trophodynamics of mesopelagic–suprabenthic bathyal macrofauna of the Algerian Basin based on stable isotopes of carbon and nitrogen. Deep Sea Research I 56(9), 1504–1520.
- Fanelli E., Papiol V., Cartes J.E., Rumolo P., López-Pérez C., 2013. Trophic webs of deep-sea megafauna on mainland and insular slopes of the NW Mediterranean: a comparison by stable isotope analysis. Marine Ecology Progress Series. 490: 199–221.
- Figuerola, D., Figuerola, N., Cartes, J.E., 2018. Genetic structure of *Calanus helgolandicus* (Calanoidea: Copepoda) from the deep Balearic Sea. 9th International Crustacean Congress, Washington, D.C., May 22–25, 2018.
- Font, J., Salat, J., Tintoré, J., 1988. Permanent features of the circulation in the Catalan Sea. In: H. J. Minas, P. Nival (Eds.), Océanographie pélagique Méditerranéenne. Oceanologica Acta 9, 51–57.
- Frutos, I., Brandt, A., Sorbe, J.C. 2018. Deep-Sea Suprabenthic Communities: The Forgotten Biodiversity. In: Rossi S., Bramanti L., Gori A., Orejas C. (eds) Marine Animal Forests. Springer, Cham: Marine Animal Forests pp. 475–503. DOI https://doi.org/10.1007/978-3-319-21012-4_21
- Furnestin, J., 1960. Hydrologie de la Méditerranée occidentale: Golfe du Lion, Mer Catalane, Mer d’Alboran et Corse Orientale. Revue Travaux Institut Pêches maritimes 24, 5–119.
- Gage, J.D., Tyler, P.A., 1991. Deep-sea biology: a natural history of organisms at the deep-sea floor, Cambridge University Press, 504 pp.
- George, R. Y., Menzies, R. J., 1968. Additions to the Mediterranean deep-sea isopod fauna (Vema-14). Revue Roumaine Biologie (Zool.) 13(6), 367–383.

- Glazier, A. E., Etter, R.J. 2014. Cryptic speciation along a bathymetric gradient. *Biological Journal of the Linnean Society* 113, 897–913.
- Guidi-Guilvard, L.D., Thistle, D., Khripounoff, A., Gasparini, S., 2007. Dynamics of benthic copepods and other meiofauna in the benthic boundary layer of the deep NW Mediterranean Sea. *Marine Ecology Progress Series* 396, 181–195.
- Harrison, K., 1988. Deep-sea Asellota (Crustacea: Isopoda) of the Rockall Trough: preliminary faunal analysis. *Ophelia* 28, 169-182.
- Harrison, K. 1989. Are Deep-Sea Asellote Isopods Infaunal or Epifaunal ? *Crustaceana* 56(3), 317-319.
- Hessler, R. R., 1970. The Desmosomatidae (Isopoda, Asellota) Of The Gay Head-Bermuda Transect. *Bulletin of the Scripps Institution of Oceanography* 15, 1-185.
- Hessler, R.R., Thistle, D., 1975. On the place of origin of deep-sea isopods. *Marine Biology* 32, 155–165.
- Hessler, R. R., Wilson, G. D., Thistle, D., 1979. The deep-sea isopods: A biogeographic and phylogenetic overview. *Sarsia*, 64(1-2), 67-75.
- Hopkins, T.S., 1985. *Physics of the Sea*. In: R. Margalef (ed.): Western Mediterranean, Pergamon Press. Oxford.
- Howell, K.L., Billett, D.S.M., Tyler, P.A., 2002. Depth-related distribution and abundance of seastars (Echinodermata: Asteroidea) in the Porcupine Seabight and Porcupine Abyssal Plain, N.E. Atlantic. *Deep-Sea Research I* 49, 1901–1920.
- Hudson, I.R., Pond, D.W., Billett, D.S.M., Tyler, P.A., Limpitt, R.S., Wolff, G.A., 2004. Temporal variations in fatty acid composition of deep-sea holothurians: evidence of benthic-pelagic coupling. *Marine Ecology Progress Series* 281, 109-120.
- Karr, J.R., 1976. Seasonality, resource availability, and community diversity in tropical bird communities. *American Naturalist* 110, 973-994.
- Koukouras, A., Chartosia, N., Apostolaki, E., 2002. New records of isopod crustaceans from the Continental Rise of the Aegean Sea. *Crustaceana* 75(7), 915-923.
- Laita Ruiz de Asúa, M., 1998. El Niño y su influencia en el régimen de lluvias en Baleares Territoris: *Revista del Departament de Ciències de la Terra*, 1, 187-202.

- Ledoyer, M., 1987. Les cumacés méditerranéens profonds (Crustacea) des campagnes Biomedes I et II et Balgim. Synthèse de la distribution bathyale du groupe en Méditerranée occidentale. *Mesogée* 47, 59-70.
- Madurell, T., Fanelli, E., Cartes, J.E., 2008. Isotopic composition of carbon and nitrogen of suprabenthos fauna in the NW Balearic Islands (western Mediterranean). *Journal of Marine Systems*. 71(3-4), 336-345.
- Mamouridis, V., Cartes, J.E., Parra, S., Fanelli, E., Saiz Salinas, J.I., 2011. A temporal analysis on the dynamics of deep-sea macrofauna: Influence of environmental variability off Catalonia coasts (western Mediterranean). *Deep-Sea Research I* 58, 323–337.
- Mariotti, A., Zeng, N., Lau, K.M., 2002: Euro-Mediterranean rainfall and ENSO—A seasonally varying relationship. *Geophysical Research Letters*, 29(12), doi:10.1029/2001GL014248.
- Mauchline, J., Gordon, J.D.M., 1991. Oceanic pelagic prey of benthopelagic fish in the benthic layer of a marginal oceanic region. *Marine Ecology Progress Series* 74, 109–115.
- Margalef, R., 1985. *Western Mediterranean (Key Environments)*, Pergamon Press, New York, 363 pp.
- Martín J., Cartes J.E., Palanques A., Sorbe J.C., Vitorino J., 2006. Preliminary Results on suprabenthic peracarids collected in near-bottom sediment traps deployed in the Nazaré submarine canyon. 11th Deep-Sea Biology Symposium, National Oceanography Centre, Southampton, 9-14 July 2006.
- Masó, M., Tintoré, J., 1991. Variability of the shelf water off the northeast Spanish coast. *Journal of Marine Systems* 1(4), 441-450. DOI: 10.1016/0924-7963(91)90008-I.
- Mees, J., Jones, M.B., 1997. The hyperbenthos. *Oceanography Marine Biology Annual Review* 35, 221-255.
- Modica, L., Cartes, J.E., Carrassón, M., 2014. Food consumption of five deep-sea fishes in the Balearic Basin (western Mediterranean): are there daily feeding rhythms in fishes living below 1000 m? *Journal Fish Biology* 85(3), 800-820.
- Moutin, T., Van Wambeke, F., Prieur, L., 2012. Introduction to the Biogeochemistry from the Oligotrophic to the Ultraoligotrophic Mediterranean (BOUM) experiment. *Biogeosciences*. 9, 3817-3825.
- Papiol, V., Cartes, J.E., Fanelli, E., Maynou F., 2012. Intrannual changes in benthic-pelagic assemblages over the middle slope in the Balearic Basin (NW Mediterranean Sea): influence of environmental variables. *Deep Sea Research I* 61, 84-99.

- Papiol, V., Cartes, J.E., Fanelli, E., Rumolo, P., 2013. Trophic web structure and seasonality of slope megafauna of the NW Mediterranean elucidated by stable isotope analyses: relationship with available food sources. *Journal of Sea Research* 77, 53–69.
- Pasqual, C., Goñi, M. A., Tesi, T., Sanchez-Vidal, A., Calafat, A., Canals, M., 2013. Composition and provenance of terrigenous organic matter transported along submarine canyons in the Gulf of Lion (NW Mediterranean Sea). *Progress in Oceanography*, 118, 81-94. doi:10.1016/j.pocean.2013.07.013
- Pasqual, C., Calafat, A., Lopez-Fernandez, P., Pusceddu, A., 2015. Organic carbon inputs to the sea bottom of the Mallorca continental slope. *Journal of Marine Systems* 148, 142–151. <http://dx.doi.org/10.1016/j.jmarsys.2015.02.006>
- Pérès, J.M., 1985. History of the Mediterranean biota and the colonization of depths. In: Margalef, R. (Ed.), *Key Environments: Western Mediterranean*. Pergamon Press Ltd., Oxford, pp. 198–232.
- Pianka, E.R., 1969. Habitat Specificity, Speciation, and Species Density in Australian Desert Lizards. *Ecology* 50, 498-502. DOI: 10.2307/1933908
- Pielou, E.C., 1975. *Ecological Diversity*, John Wiley & Son, New York, 165 p.
- Pinot, J. M., López-Jurado, J. L., Riera, M., 2002. The canales experiment (1996-1998): interannual, seasonal, and mesoscale variability of the circulation in the Balearic Channels. *Progress Oceanography* 55(3-4), 335-370, doi: 10.1016/S0079-6611(02)00139-8.
- Rice, A.L., Billett, D.S.M., Fry, J., Johns, A.W.G., Lampitt, R.S., Mantoura, R.F.C., Morris, J., 1986. Seasonal deposition of phytodetritus to the deep-sea floor. *Proceedings Royal Society Edinburg B* 88, 265–279.
- Rice, A.L., Thurston, M.H., Bett, B.J., 1994. The IOSDL DEEPSEAS programme: photographic evidence for the presence and absence of seasonal input of phytodetritus at contrasting abyssal sites in the north-eastern Atlantic Ocean. *Deep-Sea Research I* 41, 1305–1320.
- Riehl, T., Brenke, N., Brix, S., Driskell, A., Kaiser, S., Brandt, A., 2014. Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. *Polish Polar Research* 35(2), 203–224.
- Rolshausen, G., Segelbacher, G., Hobson, K. A., Schaefer, H. M. 2009. Contemporary Evolution of Reproductive Isolation and Phenotypic Divergence in Sympatry along a Migratory Divide *Current Biology*, 19 (24), 2097-2101.

- Rovere, M., Würtz, M., 2015. Atlas of the Mediterranean seamounts and seamount-like structures. IUCN Publication, Malaga : IUCN, 2015, 275p. DOI: <https://doi.org/10.2305/IUCN.CH.2015.07.en>.
- Rowe, G. T., Menzies, R.J., 1969. Zonation of large benthic invertebrates in the deep-sea off the Carolinas. *Deep Sea Research. Oceanography Abstracts*, 16(5): 531-532.
- Ruiz, S., Font, J., Emelianov, M., Isern-Fontanet, J., Millot, C., Salas, J., Taupier-Letage, I., 2002. Deep structure of an open sea eddy in the Algerian basin, *Journal Marine Systems* 33, 179–195.
- Rumolo, P., Cartes, J.E., Fanelli, E., Papiol, V., Sprovieri, M., Mirto, S., Gherardi, S., Bonanno, A., 2015. Seasonal variations in the source of sea bottom organic matter off Catalonia coasts (western Mediterranean): links with hydrography and biological response. *Journal of Oceanography* 71, 325–343.
- Sainte-Marie, B., Brunel, P., 1985. Suprabenthic gradients of swimming activity by cold-water gammaridean amphipod Crustacea over a muddy shelf in the Gulf of Saint Lawrence. *Marine Ecology Progress Series* 23, 57-69.
- Sars, G.O. 1899. Account of the Crustacea of Norway; Vol. 2: Isopoda, Kessinger Publishing, Norway, 590 pp.
- Smith, K. L., Hinga, K. R., 1983. Sediment community respiration in the deep-sea. In *The Sea*, Vol. 8, ed. G. T. Rowe, pp. 331-70. New York: Wiley-Interscience.
- Schnurr, S., Brandt, A., Brix, S., Fiorentino, D., Malyutina, M., Svavarsson, J., 2014. Composition and distribution of selected munnopsid genera (Crustacea, Isopoda, Asellota) in Icelandic waters. *Deep Sea Research I*, 84, 142-155 . doi: 10.1016/j.dsr.2013.11.004.
- Schnurr, S., Osborn, K.J., Malyutina, M., Jennings, R., Brix, S., Driskell, A., Svavarsson, J., Martinez Arbizu, P., 2018. Hidden diversity in two species complexes of munnopsid isopods (Crustacea) at the transition between the northernmost North Atlantic and the Nordic Seas. *Marine Biodiversity* 48, 813–843.
- Svavarsson, J., Brattegard, T., Stromberg, J.O., 1990. Distribution and diversity patterns of asellote isopods (Crustacea) in the deep Norwegian and Greenland Seas. *Progress Oceanography* 24, 297-310.
- Svavarsson, J., Gudmundsson, G., Brattegard, T., 1993. Feeding by asellote isopods (Crustacea) on foraminifers (Protozoa) in the deep sea. *Deep Sea Research I* 40(6), 1225-1239.
- Tattersall, O.S., Tattersall, W.M. 1951. *British Mysidacea*. Ray Society, London, 460 pp.

- Ter Braak, C.J.F., 1986. Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. *Ecology* 67(5), 1167-1179.
- Ter Braak, C.J.F., Verdonschot, P.F.M., 1995. Canonical correspondance analisys and related multivariate methods in aquatic ecology. *Aquatic Sciences* 57, 255-289.
- Thistle, D., 1980. A revision of Ilyarachna (Crustacea, Isopoda) in the Atlantic with four new species *Journal of Natural History* 14, 111-143.
- Thistle, D., 2003. The deep-sea floor: an overview. In P. A. Tyler (Ed.), *Ecosystems of the World* 28 (pp. 5-37). New York, Elsevier Science.
- Tyler, P.A., Campos-Creasy, L.A., Giles, L.A., 1994. Environmental control of quasi-continuous andseasonal reproduction in deep-sea benthic invertebrates. In: Young, C.M., Eckelbarger, K.J. (Eds.), *Reproduction, Larval Biology and Recruitment of the Deep-sea Benthos*. Columbia University Press, New York, pp. 158–178.
- Vázquez, J.T., Alonso, B., Fernández-Puga, M.C., Gómez-Ballesteros, M., Iglesias, J., Palomino, D., Roque, C., Ercilla, G. and Díaz-del-Río, V., 2015. Seamounts along the Iberian Continental Margins. *Boletín Geológico y Minero*, 126 (2-3): 483-514.
- Wägele, J. W., 1981. Study of the paranthuridae (Crustacea: Isopoda: Anthuridea) from the mediterranean. *Israel Journal of Zoology* 30, 211-229.
- Wang, D. P., Vieira, M., Salat, J., Tintoré, J., La Violette, P. E., 1988. A shelf/slope frontal filament off the northeast Spanish Coast. *Journal of Marine Research* 46, 321–332.
- Wilson, G. D., 2008., Local and regional species diversity of benthic Isopoda (Crustacea) in the deep Gulf of Mexico. *Deep-Sea Research II* 55, 2634–2649.
- Wilson, G. D., Hessler, R.R., 1981. A revision of the genus Eurycope (Isopoda, Asellota) with descriptions of three new genera. *Journal Crustacean Biology* 1(3), 401-423.
- Wolff, T., 1962. The systematics and biology of bathyal and abyssal Isopoda Asellota. *Galathea Report* 6, 1–320.

Figure 1. Maps of the study area in the Balearic and Algerian basins (north-western Mediterranean), with the locations of the Macer-GIROQ sledges performed in the period 1991-2012 (●).

Figure 2. Depth-related patterns in the distribution of diversity of isopods in the north-western Mediterranean, over the Catalan slope (mainland, ●), and around the Balearic Islands, both in the Balearic (●) and Algerian basins (○).

Figure 3. Appearance (●) and disappearance (○) of accumulative number of species, S , both for all isopods and asellotes as a function of depth over the whole study area (mainland and insular samples combined).

Figure 4. nMDS ordination plot of abundance data of isopods collected in Macer-GIROQ samples in the north-western Mediterranean: i) over all the areas sampled: the Catalan slope (mainland, ●), and around the Balearic Islands, both in the Balearic (●) and Algerian basins (○); ii) over the mainland and insular slopes by separate indicating main depth ranges.

Figure 5. Distribution in sediments of the percentage of organic matter (%OM) in the Balearic Basin (map) and the percentage of organic Carbon (%orgC) off the Catalan coasts (mainland slope) as a function of depth. Results based on field data, from different cruises (see Table S1).

Figure 6. Canonical Correspondence Analysis (CCA) for the composition of north-western Mediterranean deep-sea isopods. upper) CCA on the composition of isopods on the whole dataset (110 hauls) available; lower) CCA analysing the effect of submarine canyons on isopod communities (only 45 hauls taken at comparable depths: 350-650 m, included in the matrix. **C: canyon hauls; As: Adjacent slope (out of canyon) hauls**. Encircled hauls are from insular slopes.

Epibenthic Asellota species (without paddle-shape, natatory, legs) marked in grey. Environmental (near-bottom) variables: T (temperature); O₂ (dissolved oxygen); S (salinity); f (fluorescence); %OM, % of (total) organic matter.

Figure 7. Distribution maps of asellote families with different theoretical swimming capacity associated with morphology. Desmosomatidae and Ischnomesidae are epibenthos without any paddle-shape (natatory) leg, *Ilyarachna* spp. have two pairs (P5-P6) of natatory legs, *Munnopsurus atlanticus* and Eurycopinae have three pairs (P5 to P7) of natatory legs.

Circles size is proportional to species density, but size is different for each taxa represented. Maximum circle size represented 1497 ind/1000 m³ for Desmosomatidae, 414 ind/1000 m³ for Ischnomesidae, 3543 ind/1000 m³ for *Ilyarachna* spp., and 4210 ind/1000 m³ for the sum of Eurycopinae and *Munnopsurus atlanticus* densities.

Figure 8. Canonical Correspondence Analysis (CCA) for the long-term composition of north-western Mediterranean deep-sea isopods.

1022 Supplementary material.

1023

1024 **Table S1.** List of sampling stations with their characteristics and associated environmental variables.

1025 Data in blue were not collected on board at the same time of isopod sampling but comes from parallel cruises (same
1026 depth, same year, same month whenever possible; detailed explanations in Cartes et al., 2015).

1027 C/As: Canyon vs Adjacent slope samples, Cont. Samples taken at mainland slope.

1028

1029 **Table S2.** List of species with their frequency of occurrence (% FO), and the hauls where they were
1030 collected in the current sampling (see references in Table S1).

1031 Table 1. List of isopod species identified in the deep-western Mediterranean, with total number of
 1032 individuals collected, depth range and geographic distribution.
 1033 ¹ species for which molecular analyses were attempted.
 1034

Species		Family(subFamily)	n ^o	depth range (m)	distribution	Observations
Idoteidae	Samouelle, 1819	Idoteidae	1	336-342	S Mallorca	small specimens
<i>Leptanthura apalpata</i>	Wägele, 1981	Anthuridae	8	376-2159	Balearic Basin	
<i>Pilosanthura fresii</i>	(Wägele, 1980)	Anthuridae	73	208-1355	Balearic Basin	
Anthuridae (<i>Apanthura</i> sp.)	Stebbing, 1900	Anthuridae	2	656-661	Catalan slope	
Anthuridae (D)	Leach, 1814	Anthuridae	2	738-1263	Balearic Basin	
<i>Eurydice</i> cf. <i>truncata</i>	(Norman, 1868)	Cirolanidae	47	155-1279	Balearic Basin - S Mallorca	
<i>Natatolana borealis</i>	(Lilljeborg, 1851)	Cirolanidae	621	134-1224	Balearic/Algerian Basin	
<i>Natatolana</i> cf. <i>borealis</i>		Cirolanidae	9	405-752	Balearic/Algerian Basin	
Cirolanidae sp. A	Dana, 1852	Cirolanidae	3	780-1265	Catalan slope	without eyes
<i>Aega</i> sp. 1	Leach, 1815	Aegidae	10	148-752	Algerian Basin (S Mallorca)	
<i>Rocinela</i> sp.	Leach, 1818	Aegidae	7	161-696	Catalan slope- Mallorca (N, S)	
<i>Syscenus infelix</i>	Harger, 1880	Aegidae	5	362-750	Mallorca (N, S)	
<i>Gnathia maxillaris</i>	(Montagu, 1804)	Gnathiidae	1	159-162	S Mallorca	male
<i>Caecognathia</i> cf. <i>elongata</i>	(Kroyer, 1849)	Gnathiidae	4	398-504	Catalan slope	male
<i>Gnathia</i> spp. (<i>pranizza</i>)	Leach, 1814	Gnathiidae	1356	134-2159	Balearic/Algerian Basin	at least from two species
Suborder Asellota						<i>n</i> paddle legs
<i>Balbidocolon</i> sp.	Hessler, 1970	Desmosomatidae	21	385-1228	Balearic Basin	0 probably new species
<i>Chelator chelatus</i>	(Stephensen, 1915)	Desmosomatidae	711	340-1594	Balearic/Algerian Basin	0
<i>Desmosoma lineare</i>	G.O. Sars, 1864	Desmosomatidae	381	365-1408	Balearic/Algerian Basin	0
<i>Echinopleura</i> cf. <i>aculeata</i>	(Sars G.O., 1864)	Desmosomatidae	19	356-775	Balearic Basin - S Mallorca	0
<i>Eugerdia</i> cf. <i>tenuimana</i>	(Sars G.O., 1866)	Desmosomatidae	40	249-1355	Catalan slope- SW Pitiuses	0
<i>Eugerdia filipes</i>	(Hult, 1936)	Desmosomatidae	229	208-1408	Balearic/Algerian Basin	0
Desmosomatidae	G. O. Sars, 1897	Desmosomatidae	1	747	S Mallorca	0 uropod uniramous, engraved teguments
Desmosomatidae (D)		Desmosomatidae	4	628-1254	Catalan slope	0
<i>Janirella</i> sp. (D)	Stephensen, 1915	Janirellidae	1	1790-1830	Catalan slope	0
<i>Janirella nanseni</i>	Bonnier, 1896	Janirellidae	106	615-1830	Balearic/Algerian Basin	0
<i>Pleurogonium</i> sp.	(Sars G.O., 1866)	Munnidae	2	430-470	Catalan slope	0 submarine canyon
<i>Ischnomesus bispinosus</i>	(G.O. Sars, 1866)	Ischnomesidae	255	376-2159	Balearic/Algerian Basin	0
Munnopsidae						
<i>Belonectes parvus</i>	(Bonnier, 1896)	Eurycopinae	1238	173-1647	Balearic/Algerian Basin	3 rostrum deeply cleft
<i>Disconectes</i> cf. <i>furcatus</i>	(Sars G.O., 1870)	Eurycopinae	402	143-1408	Balearic/Algerian Basin	3
<i>Disconectes</i> cf. <i>latirostris</i>	(G.O. Sars, 1883)	Eurycopinae	59	194-1287	Balearic/Algerian Basin	3
<i>Disconectes phalangium</i>	(G.O. Sars, 1864)	Eurycopinae	333	153-1594	Balearic/Algerian Basin	3
<i>Disconectes</i> sp. (D)		Eurycopinae	58	194-1287	Balearic/Algerian Basin	3 rostrum roof tile shaped
<i>Disconectes</i> sp. 2	Wilson & Hessler, 1981	Eurycopinae	37	345-1301	Balearic/Algerian Basin	3
<i>Eurycope</i> sp. 1	G. O. Sars, 1864	Eurycopinae	1281	161-1830	Balearic/Algerian Basin	3
<i>Tytthocope</i> (<i>megalura</i>)	(G. O. Sars, 1872)	Eurycopinae	25	345-1195	Balearic Basin - S Mallorca	3
Eurycopinae (D)	Hansen, 1916	Eurycopinae	16	151-1224	Balearic/Algerian Basin	3
<i>Aspidarachna</i> sp.	(G.O. Sars, 1870)	Ilyarachninae	2	1216-1224	Catalan slope	2
<i>Aspidarachna sekhari</i>	(George & Menzies, 1968)	Ilyarachninae	2	1586-1594	Algerian Basin (SW Pitiuses)	2
<i>Ilyarachna</i> cf. <i>affinis</i>	Barnard, 1920	Ilyarachninae	243	802-2159	Catalan slope- SW Pitiuses	2
<i>Ilyarachna</i> cf. <i>antarctica</i>	Vanhöffen, 1914	Ilyarachninae	22	732-1858	Balearic Basin	2
<i>Ilyarachna longicornis</i>	(G.O. Sars, 1864)	Ilyarachninae	2319	155-1647	Balearic/Algerian Basin	2
<i>Ilyarachna</i> cf. <i>calidus</i>	George & Menzies, 1968	Ilyarachninae	9	670-1694	Algerian Basin	2
<i>Ilyarachna</i> sp. (D)	G. O. Sars, 1869	Ilyarachninae	21	601-1830	Catalan slope	2
<i>Munnopsurus atlanticus</i>	(Bonnier, 1896)	Munnopsidae	5154	356-2159	Balearic/Algerian Basin	3
<i>Pseudomunnopsis beddardi</i>	(Tattersall, 1905)	Munnopsidae	2	150-682	N Mallorca	3
Bopyridae, <i>Athelges</i> sp. (female)	Gerstaecker, 1862	Bopyridae	1	405-408	Catalan slope	parasite

Figure 1.

Figure 2.

1045 Figure 3

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1049 Figure 4.

1050 i)

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1052 ii)

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1054 Figure 5.

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1057 Figure 6.

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1060 Figure 7

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Figure 8.

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10.

Ref.	Sample name	Date	Depth (m)	LAT	LONG	Year	Season	C/As	Insularity	T	S	O ₂	Chla	%OM	MEI-EN:NAO	Winter NAO	SunSpots (Jan-May)
1	R1 MG1	25/04/1991	549	41.0660	2.1090	1991	Spr	As	Cont	13.07	38.47	4.87	0.051	10.82	5.3	1.1	203.6
2	R1 MG2	25/04/1991	504	41.0810	2.0430	1991	Spr	C	Cont	13.11	38.47	4.87	0.051	10.54	5.3	1.1	203.6
3	R1 MG3	26/04/1991	1355	41.0230	2.2790	1991	Spr	As	Cont	12.80	38.43	4.54	0.128	8.04	5.3	1.1	203.6
4	R2 MG1	09/12/1991	549	41.0620	2.1040	1991	Aut	As	Cont	13.07	38.47	4.45	0.087	7.12	5.3	1.1	203.6
5	R2 MG2	09/12/1991	552	41.0580	2.0850	1991	Aut	As	Cont	13.07	38.47	4.45	0.087	7.14	5.3	1.1	203.6
6	R2 MG3	09/12/1991	400	41.0890	2.0870	1991	Aut	As	Cont	13.20	38.47	4.40	0.087	6.38	5.3	1.1	203.6
7	R2 MG4	09/12/1991	450	41.0800	2.0400	1991	Aut	C	Cont	13.16	38.47	4.40	0.087	6.66	5.3	1.1	203.6
8	R2 MG5	09/12/1991	1244	40.5461	2.0650	1991	Aut	As	Cont	12.81	38.43	4.54	0.218	7.18	5.3	1.1	203.6
9	R2 MG6	09/12/1991	1258	40.5420	2.0630	1991	Aut	As	Cont	12.81	38.43	4.54	0.218	7.12	5.3	1.1	203.6
10	R3 MG1	14/03/1992	1253	40.5430	2.0450	1992	Win	As	Cont	12.80	38.44	4.50	0.144	5.31	5.5	2.5	154.7
11	R3 MG2	14/03/1992	1263	40.5440	2.0710	1992	Win	As	Cont	12.80	38.44	4.50	0.144	5.18	5.5	2.5	154.7
12	R3 MG3	14/03/1992	524	41.0580	2.1020	1992	Win	As	Cont	13.11	38.49	4.34	0.016	8.19	5.5	2.5	154.7
13	R3 MG4	14/03/1992	601	41.0680	2.1050	1992	Win	As	Cont	13.05	38.48	4.39	0.016	8.48	5.5	2.5	154.7
14	R3 MG5	14/03/1992	600	41.0640	2.1220	1992	Win	As	Cont	13.05	38.48	4.39	0.016	8.47	5.5	2.5	154.7
15	R3 MG6	14/03/1992	398	41.0930	2.1010	1992	Win	As	Cont	13.14	38.49	4.35	0.055	7.42	5.5	2.5	154.7
16	R3 MG7	14/03/1992	395	41.0780	2.0450	1992	Win	C	Cont	13.14	38.49	4.35	0.055	7.39	5.5	2.5	154.7
17	R4 MG1	27/07/1992	1279	40.5530	2.1070	1992	Summ	As	Cont	12.80	38.44	4.51	0.138	11.71	5.5	2.5	154.7
18	R4 MG2	27/07/1992	1275	40.5430	2.0740	1992	Summ	As	Cont	12.80	38.44	4.51	0.138	11.70	5.5	2.5	154.7
19	R4 MG3	28/07/1992	1858	40.4890	2.3540	1992	Summ	As	Cont	12.80	38.45	4.48	0.096	10.78	5.5	2.5	154.7
20	R4 MG4	28/07/1992	585	41.0560	2.0990	1992	Summ	As	Cont	13.05	38.48	4.39	0.020	9.63	5.5	2.5	154.7
21	R4 MG5	28/07/1992	603.5	41.0575	2.1063	1992	Summ	As	Cont	13.05	38.48	4.39	0.020	9.73	5.5	2.5	154.7
22	R4 MG6	28/07/1992	393	41.0790	2.0480	1992	Summ	As	Cont	13.14	38.49	4.35	0.035	8.45	5.5	2.5	154.7
23	R4 MG7b	28/07/1992	387	41.0893	2.0976	1992	Summ	C	Cont	13.14	38.49	4.35	0.035	8.40	5.5	2.5	154.7
24	R4 MG7	28/07/1992	405	41.0890	2.0880	1992	Summ	C	Cont	13.14	38.49	4.35	0.035	8.53	5.5	2.5	154.7
25	BatMan1/MG3	21/03/1994	1220	41.0212	2.1703	1994	Win	As	Cont	12.83	38.44	4.51	0.020	5.71	5.0	2.9	50.1
26	BatMan1/MG6	21/03/1994	1210	41.0138	2.1723	1994	Win	As	Cont	12.83	38.44	4.51	0.020	5.82	5.0	2.9	50.1
27	BatMan1/MG14	23/03/1994	1404.5	40.5820	2.1710	1994	Win	As	Cont	12.81	38.44	4.52	0.020	12.92	5.0	2.9	50.1
28	BatMan1/MG12	23/03/1994	1220	41.0138	2.1723	1994	Win	As	Cont	12.83	38.44	4.51	0.020	5.71	5.0	2.9	50.1
29	BatMan1/MG13	23/03/1994	1210.5	41.0050	2.1700	1994	Win	As	Cont	12.83	38.44	4.51	0.020	5.82	5.0	2.9	50.1
30	BatMan1/MG15	23/03/1994	1212.5	41.0050	2.1710	1994	Win	As	Cont	12.83	38.44	4.51	0.020	5.79	5.0	2.9	50.1
31	BatMan1/MG18	23/03/1994	1810	40.4830	2.3268	1994	Win	As	Cont	12.79	38.43	4.53	0.020	13.03	5.0	2.9	50.1
32	BatMan2/MG2	06/07/1995	1194	40.5518	2.0494	1995	Summ	As	Cont	12.86	38.45	4.47	0.010	11.64	3.8	-1.1	4.0
33	BatMan2/MG1	06/07/1995	1299.5	40.5390	2.0719	1995	Summ	As	Cont	12.84	38.45	4.47	0.010	11.71	3.8	-1.1	4.0
34	Pr96-MG1	12/10/1996	1284	40.5468	2.0041	1996	Aut	As	Cont	12.84	38.44	4.51	0.010	7.01	2.5	-2.0	-3.8
35	Pr96-MG2	13/10/1996	601	41.0556	2.0909	1996	Aut	As	Cont	13.13	38.50	4.29	0.036	7.32	2.5	-2.0	-3.8
36	Pr96-MG3	13/10/1996	406.5	41.0875	2.0767	1996	Aut	As	Cont	13.18	38.48	4.37	0.045	6.42	2.5	-2.0	-3.8
37	Q1/MG8	28/10/1996	403.5	41.0796	2.0758	1996	Aut	C	Cont	13.18	38.48	4.37	0.045	6.40	2.5	-2.0	-3.8
38	Q1/MG1	26/10/1996	249	38.5000	1.3644	1996	Aut	As	Algerian	13.00	38.26	4.19	0.052	3.36	2.5	-2.0	-3.8
39	Q1/MG2	26/10/1996	399	38.4159	1.4053	1996	Aut	As	Algerian	13.23	38.48	4.16	0.039	4.09	2.5	-2.0	-3.8
40	Q1/MG3	26/10/1996	602	38.3373	1.4816	1996	Aut	As	Algerian	13.14	38.48	4.02	0.031	4.85	2.5	-2.0	-3.8
41	Q1/MG4	26/10/1996	599	38.3247	1.4825	1996	Aut	As	Algerian	13.14	38.48	4.02	0.031	4.84	2.5	-2.0	-3.8
42	Q1/MG5	27/10/1996	805.5	38.2992	1.4882	1996	Aut	As	Algerian	13.07	38.46	4.15	0.039	5.47	2.5	-2.0	-3.8
43	Q1/MG6	27/10/1996	1204	38.2492	1.4788	1996	Aut	As	Algerian	13.03	38.44	4.19	0.048	8.14	2.5	-2.0	-3.8
44	Q1/MG7	27/10/1996	1590	38.1264	1.4775	1996	Aut	As	Algerian	13.06	38.43	4.19	0.049	8.96	2.5	-2.0	-3.8
45	LEA1/MG1	04/03/1998	197.5	41.1432	2.1101	1998	Win	As	Cont	13.36	38.13	4.22	0.032	3.80	4.2	1.0	0.7
46	LEA1/MG3	04/03/1998	641.5	41.0568	2.0755	1998	Win	As	Cont	13.36	38.54	4.08	0.002	6.04	4.2	1.0	0.7
47	LEA2/MG1	22/09/1998	1640.5	40.5221	2.2333	1998	Aut	As	Cont	13.36	38.52	4.21	0.002	9.03	4.2	1.0	0.7
48	LEA2/MG2	22/09/1998	1262.5	40.5590	2.0750	1998	Aut	As	Cont	13.37	38.55	4.04	0.003	8.30	4.2	1.0	0.7
49	LEA2/MG3	23/09/1998	211	41.1538	2.1248	1998	Aut	As	Cont	13.36	38.13	4.22	0.037	3.97	4.2	1.0	0.7
50	LEA2/MG4	23/09/1998	406.5	41.0842	2.0850	1998	Aut	As	Cont	13.41	38.53	4.18	0.001	4.46	4.2	1.0	0.7
51	LEA2/MG5	23/09/1998	616	41.0534	2.0913	1998	Aut	As	Cont	13.36	38.54	4.08	0.001	5.92	4.2	1.0	0.7
52	ID0803-MG1	03/08/2003	155	39.1255	2.7682	2003	Summ	As	Algerian	13.09	38.23	4.57	0.041	2.73	4.3	-0.1	0.2
53	ID0803-MG2	03/08/2003	670	39.0531	2.6236	2003	Summ	As	Algerian	13.20	38.51	4.24	0.021	6.65	4.3	-0.1	0.2
54	ID0803-MG3	04/08/2003	340	38.9726	2.7066	2003	Summ	As	Algerian	13.28	38.47	4.40	0.027	4.67	4.3	-0.1	0.2
55	ID0803-MG4	05/08/2003	747	39.0346	2.6376	2003	Summ	As	Algerian	13.17	38.50	4.27	0.032	5.86	4.3	-0.1	0.2
56	ID0803-MG5	06/08/2003	134	39.6379	2.1854	2003	Summ	As	N Mallorca	13.14	38.18	4.45	0.076	1.70	4.3	-0.1	0.2
57	ID0803-MG6	06/08/2003	732	39.7424	2.1586	2003	Summ	As	N Mallorca	13.15	38.50	4.28	0.059	6.96	4.3	-0.1	0.2
58	ID0803-MG7	07/08/2003	376	39.7379	2.2905	2003	Summ	As	N Mallorca	13.26	38.45	4.49	0.050	5.69	4.3	-0.1	0.2
59	ID0803-MG8	07/08/2003	682	39.7906	2.3003	2003	Summ	As	N Mallorca	13.20	38.51	4.23	0.039	7.00	4.3	-0.1	0.2
60	ID0903-MG1	25/09/2003	751.5	38.9736	2.6420	2003	Aut	As	Algerian	13.19	38.49	4.34	0.033	7.19	4.3	-0.1	0.2
61	ID0903-MG2	26/09/2003	356	38.9841	2.6929	2003	Aut	As	Algerian	13.27	38.47	4.43	0.030	9.09	4.3	-0.1	0.2
62	ID0903-MG3	26/09/2003	696	39.0226	2.6406	2003	Aut	As	Algerian	13.21	38.49	4.32	0.023	5.20	4.3	-0.1	0.2
63	ID0903-MG4	27/09/2003	161	39.1226	2.7569	2003	Aut	As	Algerian	13.20	38.22	4.55	0.045	2.17	4.3	-0.1	0.2
64	ID0903-MG5	29/09/2003	727	39.7531	2.1729	2003	Aut	As	N Mallorca	13.20	38.52	4.21	0.063	5.28	4.3	-0.1	0.2
65	ID0903-MG6	30/09/2003	663	39.7539	2.3178	2003	Aut	As	N Mallorca	13.27	38.49	4.34	0.073	4.92	4.3	-0.1	0.2
66	ID1103-MG1	13/11/2003	666	39.0227	2.3849	2003	Aut	As	Algerian	13.20	38.52	4.21	0.043	4.47	4.3	-0.1	0.2
67	ID1103-MG2	13/11/2003	335	39.0121	2.4098	2003	Aut	As	Algerian	13.28	38.50	4.30	0.054	3.98	4.3	-0.1	0.2
68	ID1103-MG3	14/11/2003	753	38.5649	2.3777	2003	Aut	As	Algerian	13.17	38.51	4.24	0.067	5.63	4.3	-0.1	0.2
69	ID1103-MG4	15/11/2003	148	39.0840	2.4703	2003	Aut	As	Algerian	13.13	38.29	4.66	0.082	2.69	4.3	-0.1	0.2
70	ID1103-MG5	20/11/2003	362	39.4580	2.2093	2003	Aut	As	N Mallorca	13.27	38.50	4.31	0.094	3.46	4.3	-0.1	0.2
71	ID1103-MG6	20/11/2003	695	39.4753	2.1806	2003	Aut	As	N Mallorca	13.58	38.51	4.24	0.072	3.02	4.3	-0.1	0.2
72	ID1103-MG8	21/11/2003	150	39.6390	2.1895	2003	Aut	As	N Mallorca	13.23	38.28	4.66	0.146	2.22	4.3	-0.1	

Species	FO(%)	Samples with occurrence (references)
Idoteidae	0,9	89
<i>Leptanthura apalpata</i>	3,6	58,59,93,110
<i>Pilosanthura fresii</i>	14,5	2,3,5,11-13,15,18,20,22,24,48-50,58,107
Anthuridae (<i>Apanthura</i> sp.)	0,9	97
Anthuridae (D)	1,8	11,91
<i>Eurydice</i> cf. <i>truncata</i>	22,7	11-13, 17,30,52,55,58,59,62-65,74,75,77,80 82,83-85,98,105,109
<i>Natatolana borealis</i>	47,3	1,2,5,6,13-16,20,24,28,39,41,42,49,51,53-57 61,62,65,66,67,74-77,80,90,92,95-105
<i>Natatolana</i> cf. <i>borealis</i>	5,5	36,46,62,87,92,95
Cirolanidae sp. A	1,8	48,98
<i>Aega</i> sp. 1	2,7	60, 62, 69
<i>Rocinela</i> sp.	3,6	36,61,62,63
<i>Sysenus infelix</i>	2,7	70,77,88
<i>Gnathia maxillaris</i>	0,9	63
<i>Caecognathia</i> cf. <i>elongata</i>	1,8	2,15
<i>Gnathia</i> spp. (<i>pranizza</i>)	95,5	All except 8,23,24,37,83
Suborder Asellota		
<i>Balbidocolon</i> sp.	9,1	5,16,20-23,26,85,93,107,109
<i>Chelator chelatus</i>	47,3	1-7,8-16,18,20-22,24,26,30-32,34,39,43,44,46,48 50,54,55,58,59,74,77,81,82,85,86,91,93,99,102,105-109
<i>Desmosoma lineare</i>	40,9	1-17,20-22,24,26,30,33,34-37,41,42,46,48 55,58,86,89,93,99,105,107-109
<i>Echinopleura</i> cf. <i>aculeata</i>	10,0	2, 20,21,36,60,89,92,100, 107-109
<i>Eugerdia</i> cf. <i>tenuimana</i>	19,1	2-6,16,20,21,28,29,32,36,38,39,42,46,97,105-107,109
<i>Eugerdia filipes</i>	33,6	2,4-7,12-16,18,20,21,24,26-29,32,35,36,41,49 58-60,80,86,89,91,92,99,107-109
Desmosomatidae	0,9	55
Desmosomatidae (D)	1,8	29,108
<i>Janirella</i> sp. (D)	0,9	31
<i>Janirella nanseni</i>	14,5	3,9,11,17,26-31,34,42,43,47,48,76,107
<i>Pleurogonium</i> sp.	0,9	7
<i>Ischnomesus bispinosus</i>	28,2	1-9,11-13,15,16,20,21,24,29,30,35,40,42,44,48 55,58,62,92,97,102,107
Munnopsidae		
<i>Belonectes parvus</i>	42,7	6,7,20,26-35,40-44,47,48,53,56,57-59,61,62 71,75,76,79,80,86,90-94,96,99,100,102,106-109
<i>Disconectes</i> cf. <i>furcatus</i>	37,3	16,26-30,40,49,52-55,58,61-65 70,72,73,77,78,80-84,86-94,105-107,109
<i>Disconectes</i> cf. <i>latirostris</i>	13,6	7,26,30,34,42,45,48,53,54,58,62,77,84,89,109
<i>Disconectes phalangium</i>	33,6	2,7,8,15,16,18,22,24,36,39,41-44,45,49,53,55,58,59 62,70,75,80,81,83,86,89-94,99,107,109
<i>Disconectes</i> sp. (D)	20,9	6,9,11,15,16,20,29,30,34,35,39,45,49,55,58 61,62,74,89-91,107,109
<i>Disconectes</i> sp. 2	9,1	26,33,36,39,41,42,81,89,91,92
<i>Eurycope</i> sp. 1	48,2	1,3-7,9-18,26-36,20-22,24,40-44,45,48,51,55,58,59 61,63,65,75-77,91-93,99
<i>Tytthocope (megalura)</i>	3,6	32,81,86,89
Eurycopinae (D)	8,2	28,30,
<i>Aspidarachna</i> sp.	0,9	28
<i>Aspidarachna sekhari</i>	1,8	44,89
<i>Ilyarachna</i> cf. <i>affinis</i>	20,0	3,5,8-11,17-19,26-34,42,47,48,99,110
<i>Ilyarachna</i> cf. <i>antarctica</i>	5,5	8,11,26,17-19,57
<i>Ilyarachna longicornis</i>	70,0	All except 19,25,28,31,33,38-40,46,48,50,56 64,66-70,73,74,79,84,85,88,95-98,101,103,104,110
<i>Ilyarachna</i> cf. <i>calidus</i>	1,8	43,44
<i>Ilyarachna</i> sp. (D)	7,3	6,11,13,17,28-31
<i>Munnopsurus atlanticus</i>	80,0	All except 14,21-24,38,45,52,54,56,62,63,67-69,72-74,81,83,84,88,93,94
<i>Pseudomunnopsis beddardi</i>	1,8	59,63
1071 Bopyridae, <i>Athelges</i> sp. (female)	0,9	36