

Trophic webs of deep-sea megafauna on mainland and insular slopes of the NW Mediterranean: a comparison by stable isotope analysis

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ABSTRACT: Food web structure of deep-sea megafauna in the Balearic Basin (NW Mediterranean) was investigated using carbon and nitrogen stable isotopes. A total of 71 species (including 26 fish species and 19 decapod species) were analysed from samples collected with a semi-balloon otter-trawl in 2 contrasting oceanographic settings: the Catalanian Slope (CS), a continental slope area indented by several submarine canyons and an insular slope area north of Mallorca (the Balearic Slope, BS). Three faunally distinct depth zones were sampled in each area in July 2010: 450 to 600 m (upper slope), 1000 to 1300 m (middle slope) and 1400 to 2200 m (lower slope). Different physical-chemical variables and potential food sources were analysed as possible explanatory variables of trophic web variability. A $\delta^{15}\text{N}$ – $\delta^{13}\text{C}$ scatterplot indicated a complex food web with fish (i.e. Macrouridae and deep-sea sharks) occupying the highest trophic position. Significant differences occurred in the isotopic composition of species among upper, middle and lower slope assemblages and between the areas (CS vs. BS). Generally, higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were observed with increasing depth (especially among benthic feeders), and on the CS compared with the BS. Similarly, based on generalized linear models, different environmental-trophic variables explained the observed trends. On the BS, $\delta^{13}\text{C}$ of species was mainly linked to physical variables and to chlorophyll *a* concentration at 5 m above the bottom as a proxy of marine snow, suggesting assemblages were mainly linked to vertical inputs. Conversely, on the CS, $\delta^{13}\text{C}$ was related to trophic variables, indicating that species are linked to prey availability and less directly to primary production. The comparison suggests longer food webs over the mainland slope.

KEY WORDS: Bathyal megafauna · Stable isotopes · Trophic diversity · Environmental variables · Western Mediterranean

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INTRODUCTION

Deep-sea communities usually obtain their energy through downward flux of marine 'snow' from the epipelagic zone (Sumich 1999). This flocculent material is a combination of aggregated detritus (e.g. exopolymers, mucus, phytoplankton, plankton exoskeletons, faecal pellets and bacteria). They may also eat deep-living zooplankton and micronekton (Vino-

gradov 1970, Vinogradov & Tseitlin 1983). The downward transit of this organic matter may be rapid (Riemann 1989), but the mass flux tends to decrease with increasing depth (Miquel et al. 1994, Sumich 1999), and the particles change in both their chemical nature (Williams & Gordon 1970) and nutritious quality. Flux tends to vary spatially and temporally in response to changes in surface production (Riemann 1989, Miquel et al. 1994). Additionally, in proximity

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to canyon systems, deep-sea species may obtain food from strong down-channel advection of terrestrial material and marine macrophyte remains to the deep-sea floor (Vetter & Dayton 1998, 1999, Fanelli et al. 2011a).

Thus, food sources for deep-sea communities vary depending on the distance from the coast (continental–oceanic gradient) and on the occurrence of advective fluxes. Food supplies near the continental margin may derive from both advective and sinking fluxes (Fanelli et al. 2011a), and deep-sea species there have more abundant benthic prey whose stocks are enhanced by copious organic matter flux. Thus, continental slopes are relatively rich compared to insular slopes (Cartes et al. 2004). Zooplankton are also more abundant near the continent (Cartes et al. 2013) and may augment the available prey there (Papiol et al. 2012). Conversely, on insular slopes deep-sea communities seem to rely almost exclusively on zooplankton, and thus in turn on marine snow (Polunin et al. 2001). At the impoverished extreme of these mainland-to-insular and continental-to-oceanic gradients are seamounts—steep-sided submerged mountains of volcanic origin, widely spread throughout the world’s oceans. On those distinct topographic features, food webs seem to be driven exclusively by zooplankton (Genin et al. 1988, Haury et al. 1995), which in turn are sustained by surface production through sinking of ungrazed phytoplankton, faecal pellets, crustacean moults and other detritus from the surface to deeper waters. Vertical migration of zooplankton is also likely to be important, as migrators may be intercepted and concentrated by seamounts. Generally, zooplankton vertical migrations influence slope communities to ca. 1200 m (Cartes 1998); however, abundant near-bottom zooplankton concentrations have been reported even deeper (Hargreaves 1984, Angel 1989, Cartes et al. 2013).

An important question is whether, despite such migrations, different trophodynamics occur among communities in different depth zones, considering that community structure changes markedly as a function of depth (Gage & Tyler 1991, Stefanescu et al. 1993). In the Balearic Basin, including both the Catalan margin and the slope north of Mallorca, there are 3 distinct deep-sea assemblages: an upper slope assemblage (US) from 450 to 700 m depth, a middle slope assemblage (MS) from 1000 to 1300 m and a lower slope assemblage (LS) below 1400 m (Fanelli et al. 2013). Specifically, the MS is characterised by a biomass peak of Alepocephalidae at 1200 to 1400 m (northwestern Mediterranean:

Stefanescu et al. 1993, Fanelli et al. 2013; North Atlantic: Gordon 1986, Merrett et al. 1991), which has been linked to increases of near-bottom jellyfish (Hargreaves 1984)—important prey for alepocephalid fishes (Carrassón & Cartes 2002, Lebrato et al. 2012).

In recent years, analysis of stable isotopes has become popular for gaining insight into the function of marine and estuarine food webs (Cabana & Rasmussen 1996, Pinnegar & Polunin 2000). Carbon isotope composition in living animals usually provides clues to the origin of the ingested organic matter, and generally $\delta^{13}\text{C}$ increases of ca. 1‰ per trophic level (De Niro & Epstein 1978, Wada et al. 1991). It is useful for distinguishing between primary food sources (e.g. macroalgae, seagrasses or phytoplankton), discriminating between the pelagic vs. benthic origin of food (France 1995) and between terrestrial vs. marine sources (Hobson 1987). Nitrogen isotope signatures can be used to define the trophic level of organisms, since $\delta^{15}\text{N}$ usually increases ca. 2.5 to 3.4‰ from food to consumer (Minagawa & Wada 1984, Post 2002).

Only a few studies have used stable isotope analyses to elucidate trophic relationships among megafauna in deep-sea benthopelagic environments (Polunin et al. 2001, Cartes et al. 2007, Jeffreys et al. 2009, Papiol et al. 2013). Some studies focused on single or congeneric species (Fanelli & Cartes 2008, 2010) or on low trophic-level species/taxa (suprabenthos: Madurell et al. 2008, Fanelli et al. 2009; benthos: Iken et al. 2001, Fanelli et al. 2011a; zooplankton: Koppelman et al. 2009, Fanelli et al. 2011b). The structure of deep-sea food webs encompassing low (e.g. sponges, jellyfish) to top trophic-level species and primary food sources remains far from fully investigated. Trophic structure of deep-sea benthopelagic fauna over a wide bathymetric range (450 to 2200 m) and at mesoscale sampling separations (ca. 150 km) has never been explored.

Here, we report analyses of the isotopic composition of dominant megafaunal species from the Balearic Basin in 2 contrasting settings characterized by different oceanographic conditions (Fanelli et al. 2013), sampled over a wide bathymetric range (from 450 to 2200 m), in order to assess geographical and bathymetric variations in their biochemical response to differences in food supply (i.e. input of phytodetritus vs. possible advective fluxes from the continental shelf).

The Catalan coastal zone and the waters north of Mallorca (Balearic Islands) are on opposite sides of the Balearic Basin (northwestern Mediterranean),

separated by ca. 150 km. They have some contrasting features regarding primary production and sediment granulometry (fine, mostly silty sediment particles off the mainland; coarser sand on the insular slope). In addition, the area north of the Balearic Islands is open and far from a large land mass, in comparison to the Catalan Sea, which is situated close to the influence of continental processes. The Catalan margin is indented by several canyons, which channel significant amounts of sediment and associated organic matter (OM) across the slope (Buscail et al. 1990, Palanques et al. 2006).

The main aim of our study was to explore the trophic pathways potentially supporting Mediterranean bathyal slope communities. The specific hypotheses were that (1) deep-sea food webs vary at the spatial mesoscale (ca. 150 km), (2) food-web structure differs between depth zones, and (3) both the continental-versus-island and depth-zone contrasts relate to food availability. We sought to test these hypotheses by analyses of the stable isotopes of carbon and nitrogen.

MATERIALS AND METHODS

Study area

The study was performed in the Balearic Basin, NW Mediterranean (Fig. 1), encompassing an area ca. 150 km wide, extending from the Catalan coast to the Balearic Archipelago (Mallorca Island). The Balearic Basin has a structure resembling a large submarine canyon, with the Valencia Trough separating the Catalanian (CS) and Balearic Island (BS) Slopes. The CS extending along the Catalanian coast is crossed by a complex system of tributary canyons (e.g. Palamós, Besós and Berenguera canyons). This feature produces 2 different oceanographic settings: the CS, influenced by advective fluxes through submarine canyons channeling terrigenous material to the deep-sea; and the BS, characterized by more oceanic conditions, with advective fluxes of terrigenous inputs practically absent (Cartes et al. 2004). On the BS, pelagic detrital material dominates in near-shore areas, and hemipelagic material of biogenic origin dominates offshore (Emelyanov 1972).

Primary production dynamics in the Balearic Basin are characterised by a late winter bloom at the surface, and in summer by a deep chlorophyll maximum (DCM) in open waters. Surface primary production is generally higher over the CS than over the BS (Fanelli et al. 2013).

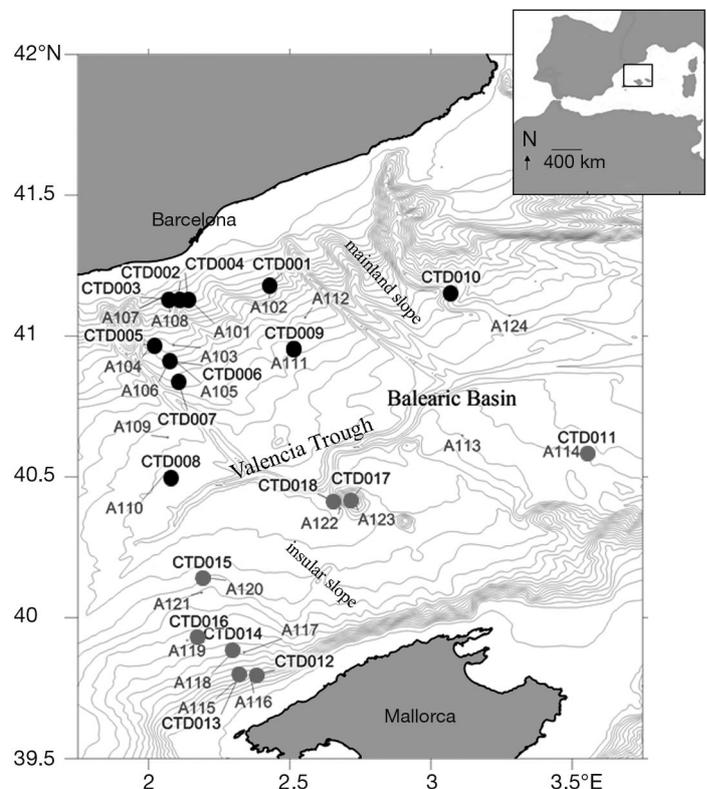


Fig. 1. Study area with indications of CTD station locations (named CTD001 to CTD018 consecutively) and trawl hauls (from A101 to A124 consecutively)

Environmental data

Eighteen CTD casts were performed during the ANTRMARE survey, approximately coinciding with the biological sampling stations, using an SBE 32 coupled with a fluorometer, a transmissometer and an oxygen sensor. Values of temperature (T), salinity (S), oxygen, fluorescence and turbidity were recorded for each CTD profile. The values of these variables at 5 m below the surface (5m) and at 5 m above the sea bottom (5mab) were obtained, although only 5mab values were then used for analyses.

Values of surface primary production (SPP, $\text{mg C m}^{-2} \text{ d}^{-1}$), obtained from www.science.oregonstate.edu/ocean.productivity/index.php, were used to compare productivity in the 2 areas. Monthly average readings of SPP at the positions of the bottom trawls were used (Cartes et al. 2004), considering different lag intervals before the sampling periods (from 1 to 4 mo before, designated SPP1, SPP2 and so on).

Sediments were collected at 10 stations with a multicorer, and the upper 2 cm were analysed. The per-

centage of organic matter (%TOM) in sediment was estimated according to $\%TOM = [(A - B)/A] \times 100$, where A is the dry weight (>72 h at 50°C) and B is the ash weight (incineration at 550°C for 2 h then cooled in a desiccator).

Water samples for the analysis of $\delta^{13}C$ of particulate organic matter (POM_{wat}) were collected with Niskin bottles during all the cruises at the surface, intermediate depths and just above the bottom and then filtered on board onto precombusted (450°C for 4 h) GF/F filters (Whatman, 0.7 μm pore size) using an HCl-cleaned 5 l glass filtration unit. From 8 to 15 l of seawater were filtered (e.g. Struck et al. 2004, Coban-Yildiz et al. 2006). After collection, the filters were immediately frozen at -20°C.

Biological data

Samples were collected on cruises performed on the slope of the Balearic Basin from 445 to 2198 m depths during the Spanish-funded project ANTROMARE (ref. CTM2009-12214-C02-01/MAR). During July 2010, 23 trawl hauls were carried out using a semi-balloon otter trawl (OTSB-14: Merrett & Marshall 1980) from the RV 'García del Cid' (see Fanelli et al. 2013 for further details on the methodology). Once captured, individual specimens were identified to species level, kept frozen and analysed subsequently in the laboratory where they were measured to the nearest mm and weighed to the nearest 0.1 g. Other invertebrates (e.g. jellyfish or echinoderms) were identified to species level, counted and weighed.

Stable isotope analysis (SIA)

Species selected for isotopic analysis were those dominant in the megafaunal assemblage in terms of both abundance and biomass (Cartes et al. 2004, Papiol et al. 2012, Fanelli et al. 2013). Tissues used for isotopic analysis of fish were white muscle close to the dorsal fin. In this study we did not rinse shark tissues with deionized water to extract the urea, as has been suggested by various authors (Logan & Lutcavage 2010, Kim & Koch 2012, Hussey et al. 2012a), since results of the urea extraction are quite contradictory: the response seemed to be species-specific, and generally with negligible changes in both carbon and nitrogen in most of the species studied (Logan & Lutcavage 2010). In addition, trophic position (TP) estimates based on $\delta^{15}N$ values

for several elasmobranchs closely matched estimates from stomach contents, suggesting that urea concentration was not causing underestimation of TP (Logan & Lutcavage 2010 and references therein). Thus, the use here of non-urea extracted samples did not compromise our considerations about the shark's TP. For decapods, we used caudal muscle; for cephalopods, pieces of the mantle (octopuses) or of wings (squids). We used the whole body (without shell) for bivalves, sponges, gelatinous zooplankton (i.e. jellyfish, pteropods, thaliaceans) ophiuroids and echinoids. We used the body wall for holothurians. Samples were dried to constant weight at 60°C, then ground to a fine powder. For species in which carbonate structures were present (e.g. spicules in echinoderms and the exoskeleton in small crustaceans), 2 sub-samples (out of 4 replicates) for carbon isotope analysis were acidified by adding 1 M HCl drop-by-drop to remove inorganic carbonates (the cessation of bubbling was the criterion for the amount of acid to add; for further details, see Fanelli et al. 2011a,b), and then samples were dried again at 60°C for 24 h. Acidification is required because carbonates present a higher $\delta^{13}C$ than organic carbon (De Niro & Epstein 1978).

Although some authors suggest extracting lipids in samples prior to stable isotope analysis (see references in Hoffmann & Sutton 2010), we did not use a defatting approach in order to allow comparisons with isotope data from other studies on deep-sea megafauna (Iken et al. 2001, Polunin et al. 2001, Jeffreys et al. 2009, Papiol et al. 2013). A study carried out on 21 elasmobranch species showed that the mean increase in $\delta^{13}C$ between bulk and lipid-extracted samples was minimal (ca. 0.6‰) for most species (Hussey et al. 2012b). Notwithstanding, to evaluate whether lipids may affect the isotopic signatures, a relationship was used between C:N ratios and $\delta^{13}C$ signatures (sensu France 1996). Values of %C and %N for C:N ratios were measured simultaneously during stable isotope analysis from the elemental percentages. The bulk $\delta^{13}C$ values for decapods and other invertebrates were normalized for lipid concentration according to the equation of Post et al. (2007): $\delta^{13}C_{lipidfree} = \delta^{13}C_{bulk} - 3.32 + 0.99 \times C:N_{bulk}$. For fish, we used the correction proposed by Hoffman & Sutton (2010) for deep-sea fishes: $\delta^{13}C_{lipidfree} = \delta^{13}C_{bulk} + [-6.39\text{‰} \times (3.76 - C:N_{bulk})]/C:N_{bulk}$. The $\delta^{13}C_{lipidfree}$ values were then compared with $\delta^{13}C_{bulk}$ with Student's t -test.

Comparisons between $\delta^{13}C_{bulk}$ and $\delta^{13}C_{lipidfree}$ values showed no significant differences for fish or decapods, both of which had low C:N values (3 to 4).

A few significant differences were found for other invertebrates with higher C:N ratios, such as echinoderms, sponges and the thaliacean *Pyrosoma atlanticum* (C:N >5 up to 8). Given that these organisms (i.e. sponges, echinoderms) have low lipid content (Drazen et al. 2008), the high C:N is probably attributable to structural compounds with high C content. Thus, the following analyses were carried out on untreated samples.

Stable isotope measurements of biological, POM_{wat} and sediment (POM_{sed}) samples were carried out by a ThermoFisher Flash EA 1112 elemental analyser coupled to a Thermo Electron Delta Plus XP isotope ratio mass spectrometer (IRMS) through a ConFloII interface at the Geochemistry Laboratory of the IAMC-CNR Institute in Naples, Italy.

Biological samples were weighed (ca. 1 mg of dry weight) in tin cups. Filters for POM_{wat} analysis were also packed in tin cups. POM_{sed} for analyses of % total organic carbon (%TOC, by mass) and $\delta^{13}\text{C}_{\text{OC}}$ were initially weighed (~5 mg) in silver capsules; then the carbonate fraction was removed by treatment with 1 M HCl followed by drying (60°C until constant weight). Nitrogen analyses of sediments (%TN and $\delta^{15}\text{N}$) were carried out on bulk-powdered samples of 15 to 20 mg placed into tin capsules.

Samples were run against blank cups and analytical grade urea of certificated isotopic composition. Experimental precision (based on the standard deviation of replicates of the internal standard) was <0.2‰ for $\delta^{15}\text{N}$ and <0.1‰ for $\delta^{13}\text{C}$. Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are expressed in parts per thousand (‰) relative to Vienna Pee Dee Belemnite and atmospheric N₂ standards, respectively, according to the following formula: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

When possible, a minimum of 3 replicates was analysed for each species (72% of cases), and each replicate included just 1 individual to reduce pseudo-replication (Hurlbert 1984). In addition, POM_{wat} and POM_{sed} samples were analysed in triplicate.

Relative proportions of terrestrial (%OC_{ter}) and marine (%OC_{mar}) organic carbon in the sedimentary organic matter (%OC_{ter} + %OC_{mar} = 1) at each depth range and for each area were calculated using the equation proposed by Harmelin-Vivien et al. (2008): $\delta^{13}\text{C}_{\text{sample}} = \% \text{OC}_{\text{ter}} \times \delta^{13}\text{C}_{\text{ter}} + \% \text{OC}_{\text{mar}} \times \delta^{13}\text{C}_{\text{mar}}$, where $\delta^{13}\text{C}_{\text{sample}}$ is the isotopic composition of each sample, quantities $\delta^{13}\text{C}_{\text{ter}}$ and $\delta^{13}\text{C}_{\text{mar}}$ are the isotopic compositions for terrestrial ($\delta^{13}\text{C}_{\text{ter}} = -27.9\text{‰}$, our own data) and marine ($\delta^{13}\text{C}_{\text{mar}} = -20.1\text{‰}$, Harmelin-Vivien et al. 2008) end-members, respectively.

In addition, a Bayesian mixing model (SIAR: Inger et al. 2006) was run in order to determine the contribution of phytoplankton, terrestrial leaves and POM_{wat} to POM_{sed} in each of the 2 areas (Inger et al. 2006).

Data analyses

We tested for normality of isotope data case by case (i.e. across depth ranges and between the 2 areas). Since data were normally distributed, they were not transformed for univariate and multivariate analyses.

Values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, %TOC and %TN of POM_{sed} and $\delta^{13}\text{C}$ of POM_{wat} were tested for differences among areas and depths by means of 2-way (crossed) ANOVA. The $\delta^{13}\text{C}$ estimates of the 2 carriers POM_{sed} and POM_{wat} were also compared by 1-way ANOVA.

First, to obtain a general overview of the trophic structure of bathyal communities, $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ plots were made for mean values of each megafauna species and macrofaunal group (benthic suspension feeders, sub-surface suspension feeders, surface suspension feeders, planktonic POM consumers, planktonic carnivores and omnivores, suprabenthic carnivores and omnivores) and POM_{sed} for the 3 depth ranges (US, MS and LS) and the 2 areas (CS and BS) separately. Values for macrofaunal species were obtained from ANTROMARE (this study), from Fanelli et al. (2009, 2011a) and from our unpublished data (suprabenthos, benthos). Comparisons of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data were made at species level among the 3 depth ranges using 1-way ANOVA ($\alpha = 0.05$), or Student's *t*-tests ($\alpha = 0.05$) where there was material from only 2 ranges; the latter tests were also performed for comparisons between sampling areas (CS vs. BS). All species compared were approximately the same size to avoid size-dependent shifts (see Tables 2 to 4). The values of correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for each group are also given, in order to assess the strength of the association (Polunin et al. 2001).

Community-wide metrics developed by Layman et al. (2007a) were calculated for each data set (US, MS, LS, each separately for CS and BS) to reveal key aspects of trophic structure. Briefly, the community metric 'total area' (TA) can be converted directly to a measure of population niche area (Layman et al. 2007b). However, 'convex hull area' (i.e. the outer envelope of the $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ scatterplot) is influenced by sample size and generally

increases with it, even if the underlying population has remained the same (Jackson et al. 2011). Thus, we also used 'standard ellipse area' (SEA) as a measure of the mean core population isotopic niche, which is robust to variation in sample size (Jackson et al. 2011). Additionally, SEA_c , a sample-size corrected version of the standard ellipse area, was calculated to circumvent the bias that arises when sample sizes are small (Jackson et al. 2011, 2012). All metrics were calculated using the package 'siar' for R (<http://cran.r-project.org/web/packages/siar/index.html>). See Jackson et al. (2011) for detailed methodology and Layman et al. (2007a) for original descriptions of the community-level metrics.

In order to give an indication of the size of fish and decapods collected and analysed for SIA, mean weight per individual (biomass/abundance) by each depth interval (every 100 m) were calculated for the most abundant species (Cartes et al. 2004, Papiol et al. 2012, Fanelli et al. 2013) in each area.

To evaluate megafauna species groups, a non-metric multi-dimensional scaling (nMDS) (untransformed data, Euclidean distance) was performed (including replicates rather than means), but considering only fish and decapods since they are the most abundant taxa (Stefanescu et al. 1992, Fanelli et al. 2013). The groups obtained were compared with trophic groups based on data acquired from literature or from gut content analyses according to Papiol et al. (2013): benthic feeders (BF), non-migratory macroplankton feeders (nmMF) and migratory macroplankton feeders (mMF). PERMANOVA (Anderson 2001) was employed on the same matrix to test the significance of differences among trophic groups, and then a pair-wise comparison was done. Significance was set at $p = 0.05$ and p -values were obtained using 9999 permutations under unrestricted permutation of the raw data, which is recommended when there is only 1 factor. In addition, a permutational univariate ANOVA (Anderson et al. 2008) was carried out based only on $\delta^{13}\text{C}$ values of the same matrix. Bathymetric trends of each group were also explored by regression analysis for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ separately.

After that, $\delta^{13}\text{C}$ values for each feeding group identified for fish and decapods, separately for each area (considering the 3 depth strata together), were compared with environmental variables using generalized linear models (GLM)—a flexible generalisation of ordinary least squares regression. The distribution family used was Gaussian. Model selection was based on minimising Akaike's Information Criterion (AIC) values.

GLMs were generated using 3 different variable sets (Fanelli et al. 2013): (1) physical variables, recorded *in situ* (T , S , $[\text{O}_2]$) and turbidity at 5mab from CTD casts; (2) trophic variables, measured in sediments (%TOC, C:N and $\delta^{13}\text{C}$) and in the water close to the bottom (chl a at 5mab as recorded by CTD) and those indicating prey availability, such as the biomasses of large polychaetes, the burrowing shrimp *Calocaris macandreae*, gelatinous zooplankton, euphausiids and *Boreomysis arctica* obtained by the OTSB-14; and (3) mid-term primary production variables (SPP recorded from 1 to 4 mo before sampling dates as obtained by satellite imagery), and %TOM, which in a sense represents the recent history of the environment that the analysed communities inhabit. Before the analyses, a draftsman plot (i.e. scatter plots of all pairwise combinations of variables; Clarke & Ainsworth 1993) was applied to chemical-physical/trophic variables to identify those strongly correlated and thus providing redundant information. Redundant variables ($\rho > 0.70$) were discarded, simplifying the matrix.

All analyses were performed using PRIMER6 and PERMANOVA+ (Clarke & Warwick 1995, Anderson et al. 2008) and R 2.14.2 (www.r-project.org).

RESULTS

Results for spatial and temporal trends of %TOC and surface primary production are detailed in Papiol et al. (2012). They are not repeated here, as they are taken into account only for GLM development.

Food web structure of megafaunal communities

The analyses of POM_{sed} showed significant differences in both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between the areas ($\delta^{15}\text{N}$: $F_{1,29} = 15.97$, $p < 0.001$; $\delta^{13}\text{C}$: $F_{1,29} = 11.09$, $p < 0.01$), with higher values on the BS than on the CS (Table 1). No significant depth-related differences were detected. On the CS, the proportion of organic matter of terrestrial origin contributing to POM_{sed} was greater than on the BS (Table 1), where the organic carbon was mainly (ca. 79%) of marine origin. Based on SIAR, both terrestrial leaves and phytoplankton contributed to the isotopic composition of POM_{sed} on the CS, by 20 and 38%, respectively. On the BS, the contribution of terrestrial leaves was negligible while phytoplankton contributed an average of 45%.

Results for $\delta^{15}\text{N}$ of POM_{wat} were obtained in only a few cases, so a statistical analysis cannot be per-

Table 1. Isotopic composition and C:N ratios of potential food sources collected on the Catalan (CS) and Balearic (BS) Slopes at upper, middle and lower slope zones (US, MS, and LS, respectively). POM_{wat}: particulate organic matter in the water column close to the bottom; POM_{sed}: POM in sediments. Calculated percentage of marine (%OC_{mar}) and terrestrial (%OC_{ter}) organic carbon contributions of settling particles are also given

Source	Zone	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	C:N	%OC _{mar}	%OC _{ter}
<i>Phyllophora</i> sp.	MS	0.4	-31.24			
<i>Sargassum acinarium</i>	MS	0.22	-15.1			
<i>Posidonia oceanica</i>	MS	8.02	-13.13 ± 0.57			
Terrestrial vascular plants	LS	-	-25.6			
Wood remains	LS	-	-26.49			
Cane remains	LS	2.79	-23.15			
POM _{wat} CS	US	5.83 ± 0.97	-24.10 ± 0.14			
	MS	-	-25.38 ± 0.48			
	LS	1.86	-24.02 ± 0.67			
POM _{wat} BS	US	-	-24.98 ± 0.07			
	MS	-	-25.26 ± 0.27			
	LS	4.65	-25.28 ± 0.12			
POM _{sed} CS	US	2.59 ± 0.01	-22.66 ± 0.65	6.7	67	33
	MS	3.09 ± 0.02	-23.01 ± 1.22	7.9	63	37
	LS	3.02 ± 0.05	-22.04 ± 0.24	8.3	75	25
POM _{sed} BS	US	3.60 ± 0.09	-21.30 ± 0.27	5.9	85	15
	MS	3.62 ± 0.31	-21.55 ± 0.31	8.3	83	17
	LS	3.02 ± 0.07	-21.37 ± 0.07	7.0	75	25

formed; they ranged from 1.86 to 6.94‰. The $\delta^{13}\text{C}$ of near-bottom POM_{wat} was significantly lower than $\delta^{13}\text{C}$ of POM_{sed} ($F_{1,35} = 92.91$, $p < 0.001$) and fell among values typical for this area (between -24.02‰ and -25.38‰; Table 1). Significant differences in $\delta^{13}\text{C}$ of bottom POM_{wat} were detected between the 2 areas, among depth ranges (area: $F_{1,17} = 28.66$, $p < 0.001$; depth: $F_{2,17} = 12.82$, $p < 0.01$) and for the area × depth interaction ($F_{1,17} = 11.66$, $p < 0.01$). On average, higher $\delta^{13}\text{C}$ values were observed on (1) the CS compared with the BS and (2) over the US vs. the two deepest depth ranges (Table 1). Values of other potential carbon sources for deep-sea communities are also shown in Table 1.

Overall, a total of 71 species were analysed, among them 26 fish species, 19 decapods and 4 cephalopods (see Tables 2 to 4). The $\delta^{15}\text{N}$ values of decapod crustaceans ranged between 4.19‰ for the burrowing shrimp *Calocaris macandreae* and 9.60‰ for the polychelid *Stereomastis sculpta* over the mainland slope, and from 5.01‰ for the mesopelagic shrimp *Sergestes hanseni* to 10.53‰ for *Pontophilus norvegicus* over

the insular slope (Table 2, Fig. 2). The $\delta^{15}\text{N}$ values of fishes collected during July 2010 ranged from 6.1‰ for *Cyathone braueri* to 12.05–12.63‰ for *Nezumia aequalis* over both the CS and the BS (Table 3, Fig. 2).

Generally, the $\delta^{15}\text{N}$ range exhibited by fishes was wider than that for decapods, and the highest $\delta^{15}\text{N}$ values were always those of fishes. Cephalopods occupied the same trophic level as decapods, with $\delta^{15}\text{N}$ values ranging from 6.55‰ (the small octopus *Opisthoteuthis calypso*) to 9.00‰ (the small squid *Heteroteuthis dispar*; Table 2). Among other invertebrates caught by the otter trawl, the thaliacean *Pyrosoma atlanticum* and the pteropod *Cymbulia peroni* showed the lowest $\delta^{15}\text{N}$ values (on average 3.36‰ ± 0.4 SD) in both the areas, while the sponges *Polymastia tissieri* (11.25‰) and *Hyalinema thomsoni* (11.81‰) had the highest values over the mainland and insular slopes, respectively (Table 4).

The mesopelagic shrimp *Sergia robusta* and the crangonid *Pontophilus norvegicus* had the two extreme $\delta^{13}\text{C}$ values among decapod crustaceans in both areas. The $\delta^{13}\text{C}$ values of *S. robusta* were -19.79‰ and -18.38‰ over the mainland and insular slopes, respectively, whereas $\delta^{13}\text{C}$ values of *P. norvegicus* were from -13.54‰ (CS) to -12.01‰ (BS). The $\delta^{13}\text{C}$ values of fishes ranged from -18.94‰ for *Alepocephalus rostratus* to -14.40‰ for *Helicolenus dactylopterus* over the mainland slope, and from -19.13‰ for the small myctophid *Myctophum punctatum* to -14.24‰ for the shark *Centroscymnus coelolepis* over the insular slope (Table 3, Fig. 2). Among cephalopods, the jewel squid *Histioteuthis reversa* was the most depleted in ^{13}C ($\delta^{13}\text{C} = -18.28‰$) and *Bathypolipus sponsalis* the least depleted (-16.20‰; Table 2). The $\delta^{13}\text{C}$ values of other invertebrates ranged from -21.32‰ (the tunicate *Pyrosoma atlanticum*) to -12.58‰ (the holothuroid *Pseudostichopus ocellatus*) over the mainland slope and from -21.77‰ (the pteropod *Cymbulia peroni*) to -14.94‰ (the asteroid *Ceramaster grenadiensis*) over the insular slope (Table 4). The $\delta^{13}\text{C}$ values of benthic feeders were generally higher than those for plankton feeders among both fishes and decapod crustaceans.

Relationships between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data in food webs

Ascending the food web—from POM in sediments to the low trophic level species, including suprabenthos, macrozooplankton/micronekton (gelatinous plankton, euphausiids, small decapods and small mesopelagic fish) and benthos (Tables 1 to 4), to decapod crusta-

ceans and cephalopods and finally to macrourids and sharks—there was a general increase in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 2). Correlations were generally greater for deep-sea communities inhabiting the CS than for those on the BS; and on both slopes, correlations were greater in the MS than in the other depth zones. The correlations in both areas were significant from all depth zones (Fig. 2) except from the US on the BS ($p > 0.05$).

Table 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for decapods and cephalopods from the upper (US), middle (MS) and lower (LS) slope zones during July 2010. Key abbreviations are used in Fig. 5. N: number of replicates analysed. BF: benthic feeders; nmMF: non-migratory macroplankton feeders; mMF: migratory macroplankton feeders. Size of specimens in mm (\pm SD) is carapace length for decapods and mantle length for cephalopods

Species	Key	Feeding guild	Zone	Catalan Slope				Balearic Slope			
				$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size
Decapoda											
<i>Aristeus antennatus</i>	Aant	BF	US	–	–	–	–	8.72 ± 0.32	-15.94 ± 0.46	2	33 ± 0.88
			MS	9.67 ± 0.79	-15.25 ± 0.25	4	32.98 ± 0.87	8.33	-14.28	1	33.23
			LS	8.77 ± 0.53	-15.53 ± 0.32	5	32.78 ± 2.50	8.48 ± 0.55	-13.83 ± 0.32	4	34.07 ± 6.37
<i>A. antennatus</i> juveniles	Aantjuv	BF	LS	7.76 ± 0.03	-15.14 ± 0.73	3	12.95 ± 0.72	6.69 ± 0.22	-15.40 ± 0.41	3	12.83 ± 0.83
<i>Acanthephyra eximia</i>	Aexi	nmMF	MS	8.43 ± 0.04	-15.99 ± 0.32	4	27.95 ± 0.74	8.13 ± 0.75	-15.95 ± 0.21	4	32.88 ± 5.79
			LS	7.49 ± 0.29	-16.17 ± 0.24	7	28.15 ± 0.71	6.93 ± 0.21	-16.31 ± 0.520	3	28.63 ± 0.17
<i>A. eximia</i> juveniles	Aexijuv	nmMF	LS	6.77 ± 0.14	-17.37 ± 0.73	3	7.97 ± 0.55	–	–	–	–
<i>Acanthephyra pelagica</i>	Apel	mMF	LS	6.86 ± 0.54	-17.43 ± 1.46	6	21.13 ± 1.03	6.69 ± 0.57	-16.65 ± 0.13	3	20.05 ± 2.00
<i>Geryon longipes</i>	Glon	BF	US	–	–	–	–	9.47 ± 0.28	-16.61 ± 0.37	3	45.32 ± 1.33
<i>Munida tenuimana</i>	Mten	nmMF	MS	7.44 ± 0.51	-15.55 ± 0.13	2	17.09 ± 0.86	7.29 ± 0.07	-14.27 ± 0.13	2	17.21 ± 0.37
			LS	6.91 ± 0.27	-15.07 ± 0.07	3	15.67 ± 0.57	7.47 ± 0.34	-14.60 ± 0.49	3	15.89 ± 0.35
<i>Nematocarcinus exilis</i>	Nexi	nmMF	LS	7.20 ± 0.77	-15.31 ± 0.58	8	13.57 ± 0.67	7.69 ± 0.81	-14.93 ± 0.45	4	14.01 ± 0.36
<i>Nephrops norvegicus</i>	Nnor	nmMF	US	7.00 ± 0.84	-16.07 ± 0.26	3	32.60 ± 1.71	6.08 ± 0.34	-16.60 ± 0.99	3	34.22 ± 0.97
<i>Plesionika acanthonotus</i>	Paca	nmMF	MS	8.13 ± 0.47	-14.96 ± 0.62	3	15.06 ± 0.96	7.10 ± 0.50	-15.78 ± 0.52	3	15.37 ± 0.40
<i>Plesionika martia</i>	Pmar	nmMF	US	6.73 ± 0.51	-16.24 ± 0.90	3	18.68 ± 2.45	6.95 ± 0.29	-15.85 ± 0.53	3	18.13 ± 0.71
<i>Pasiphaea multidentata</i>	Pmul	mMF	US	7.37 ± 0.18	-16.44 ± 0.98	2	22.43 ± 0.88	7.50 ± 0.41	-16.61 ± 0.29	3	32.93 ± 0.46
			MS	8.32	-16.38	1	26.4	–	–	–	–
			LS	8.10 ± 0.90	-16.93 ± 0.84	3	29.45 ± 3.92	–	–	–	–
<i>Pontophilus norvegicus</i>	Pnor	BF	MS	9.41 ± 0.15	-13.54 ± 0.43	3	8.73 ± 0.31	10.27 ± 0.18	-13.76 ± 0.85	5	9.03 ± 0.29
			LS	9.03 ± 0.18	-13.80 ± 0.29	3	8.44 ± 0.08	10.53 ± 0.06	-12.82 ± 0.38	3	9.13 ± 0.06
<i>Polychaetes typhlops</i>	Ptyp	BF	MS	8.97 ± 0.87	-15.89 ± 0.03	3	19.62 ± 1.11	9.60 ± 0.68	-15.74 ± 0.16	3	20.31 ± 0.69
<i>P. typhlops</i> juveniles	Ptypjuv	BF	MS	9.49 ± 0.14	-16.04 ± 0.07	2	13.87 ± 0.19	9.49 ± 0.35	-17.02 ± 0.27	3	12.36 ± 0.96
<i>Sergia robusta</i>	Srob	mMF	US	7.30	-19.79	1	11.32	–	–	–	–
			MS	6.69 ± 0.81	-19.63 ± 1.59	2	13.45 ± 3.32	6.57 ± 0.15	-18.21 ± 0.25	2	11.33 ± 0.90
			LS	6.19 ± 0.86	-18.16 ± 0.95	5	17.97 ± 0.11	6.95 ± 0.42	-17.04 ± 0.79	3	19.21 ± 0.90
<i>Stereomastis sculpta</i>	Sscu	BF	LS	9.60 ± 0.47	-14.64 ± 0.18	3	25.88 ± 1.42	9.23 ± 0.72	-14.81 ± 0.45	6	26.09 ± 2.25
Cephalopoda (Mollusca)											
<i>Bathypolipus sponsalis</i>			MS	7.22 ± 0.22	-16.20 ± 0.39	4	51.50 ± 17.8	–	–	–	–
<i>Heteroteuthis dispar</i>			LS	9	-17.36	1	33.1	8.01	-16.73	1	36.0
<i>Histioteuthis reversa</i>			MS	8.22	-17.97	1	23.0	8.48	-18.28	1	31.0
<i>Opisthoteuthis calypso</i>			LS	6.55	-17.07	1	30.0	8.84 ± 0.11	-16.39 ± 0.18	2	52 ± 21

SEA_c for the 2 areas generally overlapped for all depth ranges (Table 5, Fig. 3). However, overlap was low for communities inhabiting the upper slope, increasing deeper. Population metrics showed that, except in the US, the trophic diversity was greater on the BS than on the CS, as indicated by the higher values of TA and SEA_c (Table 5).

Comparisons between Catalan and Balearic Islands Slopes

The isotopic compositions of 35 species (out of the 71), abundant both on CS and BS, were compared between mainland vs. insular slopes. The general tendency was greater values of δ¹³C and δ¹⁵N in species inhabiting on the CS compared to those from

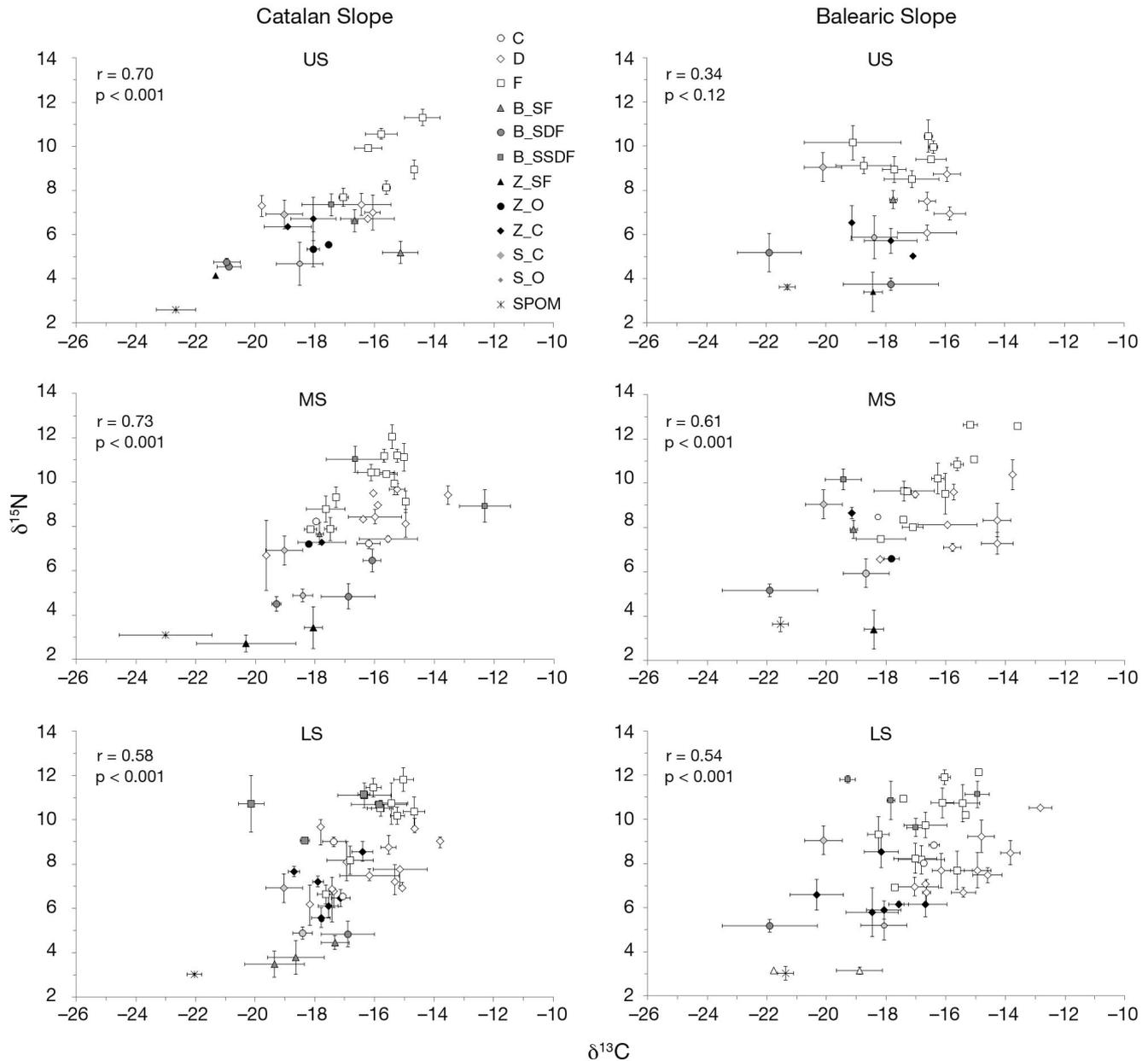


Fig. 2. Mean (±SD) isotopic values of fish (F), decapods (D), cephalopods (C), macrofauna (B_SF: benthic suspension feeders; B_SDF: benthic surface deposit feeders; B_SSDF: benthic sub-surface deposit feeders; Z_SF: zooplanktonic POM feeders; Z_O: zooplanktonic omnivores; Z_C: zooplanktonic carnivores; S_O: suprabenthic omnivores; S_C: suprabenthic carnivores) and POM_{sed} (SPOM) in the Catalan and Balearic upper (US), middle (MS) and lower (LS) slopes. Correlation r- and p-values are also given

Table 3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for fish and sharks from the upper (US), middle (MS) and lower (LS) slope zones during July 2010. Key abbreviations are used in Fig. 5. N: number of replicates analysed. Feeding guilds as in Table 2. Size of specimens in cm (\pm SD) is total length for all except macrourids (*), for which pre-anal length was measured

Species	Key	Feeding	Zone	Catalan Slope				Balearic Slope			
				$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size
Osteichthyes											
<i>Argyrolepecus</i>	Ahem	mMF	MS	7.87 \pm 0.19	-18.16 \pm 0.13	3	3.20 \pm 0.36	7.49 \pm 0.10	-18.18 \pm 0.83	2	3.30 \pm 0.14
<i>hemygimnus</i>			LS	7.94 \pm 0.72	-17.45 \pm 0.21	3	3.07 \pm 0.06	8.00 \pm 0.44	-17.02 \pm 0.78	9	3.57 \pm 0.27
<i>Alepocephalus</i>	Aros	nmMF	MS	8.79 \pm 0.48	-17.64 \pm 0.59	4	32.83 \pm 1.56	9.64 \pm 0.45	-17.40 \pm 1.01	4	33.61 \pm 2.26
<i>rostratus</i>			LS	9.68 \pm 0.33	-17.81 \pm 0.83	3	32.53 \pm 2.25	9.32 \pm 0.79	-18.25 \pm 0.36	5	33.80 \pm 3.54
<i>Bathypterois</i>	Bmed	BF	LS	11.45 \pm 0.42	-16.03 \pm 0.26	4	19.75 \pm 0.21	11.90 \pm 0.33	-16.03 \pm 0.19	5	14.03 \pm 0.29
<i>mediterraneus</i>											
<i>Cataethyx</i>	Call	BF	MS	10.44 \pm 0.73	-15.96 \pm 0.16	3	9.70 \pm 0.57	9.63 \pm 0.08	-17.29 \pm 0.13	2	9.07 \pm 0.05
<i>alleni</i>			LS	10.52 \pm 0.36	-15.79 \pm 0.30	3	9.50 \pm 0.00	10.2	-15.33	1	10.9
<i>Cataethyx</i>	Clat	BF	LS	11.82 \pm 0.53	-15.02 \pm 0.33	3	39.33 \pm 4.63	-	-	-	-
<i>laticeps</i>											
<i>Chalinura</i>	Cmed	BF	LS	10.74 \pm 0.93	-15.42 \pm 0.55	4	4.95 \pm 0.31	10.73 \pm 0.84	-15.43 \pm 0.58	7	5.03 \pm 0.38
<i>mediterranea*</i>											
<i>Chauliodus</i>	Cslo	mMF	US	-	-	-	-	10.16 \pm 0.78	-19.10 \pm 1.63	4	-
<i>sloani</i>			MS	-	-	-	-	8.36	-17.42	1	-
			LS	-	-	-	-	6.91	-17.7	1	-
<i>Coryphaenoides</i>	Cgue	BF	LS	10.19 \pm 0.38	-15.23 \pm 0.24	7	5.43 \pm 0.16	9.74 \pm 0.57	-16.68 \pm 0.72	3	5.37 \pm 0.21
<i>guentheri*</i>											
<i>Coelorhynchus</i>	Clab	BF	MS	9.32 \pm 0.38	-17.29 \pm 0.45	3	20.83 \pm 1.04	11.07	-15.06	1	18.60
<i>labiatus*</i>			LS	-	-	-	-	10.94	-17.43	1	18.80
<i>Helycolenus</i>	Hdac	BF	US	11.31 \pm 0.36	-14.40 \pm 0.65	3	26.05 \pm 1.91	10.46 \pm 0.72	-16.56 \pm 0.15	3	24.95 \pm 1.02
<i>dactylopterus</i>											
<i>Hymenocephalus</i>	Hita	nmMF	US	7.69 \pm 0.42	-17.04 \pm 0.61	3	3.13 \pm 0.15	-	-	-	-
<i>italicus*</i>											
<i>Lampanyctus</i>	Lcro	mMF	US	-	-	-	-	8.50 \pm 0.39	-17.12 \pm 0.92	5	15.15 \pm 1.20
<i>crocodilus</i>			MS	7.88 \pm 0.72	-17.48 \pm 0.53	4	16.07 \pm 0.83	8.02 \pm 0.04	-17.11 \pm 0.35	4	16.35 \pm 0.35
			LS	-	-	-	-	8.23 \pm 0.67	-17.03 \pm 0.72	2	15.15 \pm 0.21
<i>Lepidion</i>	Llep	BF	MS	10.43 \pm 0.80	-16.12 \pm 0.37	4	21.80 \pm 1.29	10.21 \pm 0.70	-16.26 \pm 0.21	2	20.77 \pm 0.85
<i>lepidion</i>			LS	10.52 \pm 0.14	-15.81 \pm 0.43	3	20.5 \pm 0.75	10.75 \pm 0.68	-16.12 \pm 0.38	2	19.97 \pm 1.95
<i>L. lepidion</i>	Llepjuv	BF	LS	6.63 \pm 0.42	-17.64 \pm 0.28	3	8.13 \pm 0.15	-	-	-	-
juveniles											
<i>Merluccius</i>	Mmer	nmMF	US	-	-	-	-	9.41 \pm 0.09	-16.47 \pm 0.51	3	37.00 \pm 1.91
<i>merluccius</i>											
<i>Micromesistius</i>	Mpou	nmMF	US	9.91	-16.21	1	28.00	9.12 \pm 0.37	-18.74 \pm 0.92	3	25.10 \pm 0.15
<i>poutassou</i>											
<i>Myctophum</i>	Mpun	mMF	US	-	-	-	-	6.52 \pm 0.78	-19.13	2	-
<i>punctatum</i>											
<i>Mora moro</i>	Mmor	BF	MS	9.92 \pm 0.21	-15.35 \pm 0.50	4	33.20 \pm 1.93	10.86 \pm 0.30	-15.63 \pm 0.21	6	32.83 \pm 1.04
<i>Nezumia</i>	Naeq	BF	MS	12.05 \pm 0.39	-15.42 \pm 0.54	3	25.73 \pm 1.19	12.63 \pm 0.12	-15.18 \pm 0.24	2	23.20 \pm 0.66
<i>aequalis*</i>											
<i>Notacanthus</i>	Nbon	BF	US	8.95 \pm 0.43	-14.68 \pm 0.36	3	22.60 \pm 0.00	8.94 \pm 0.58	-17.70 \pm 0.40	3	17.47 \pm 0.55
<i>bonapartei</i>			MS	9.12 \pm 0.86	-14.96 \pm 0.49	4	19.70 \pm 1.99	-	-	-	-
			LS	10.36 \pm 0.67	-14.66 \pm 0.36	4	22.07 \pm 0.21	7.78 \pm 0.86	-15.62 \pm 0.52	3	22.75 \pm 2.62
<i>Phycis</i>	Pble	BF	US	10.56 \pm 0.24	-15.78 \pm 0.20	3	29.30 \pm 0.96	9.97 \pm 0.28	-16.40 \pm 0.15	3	27.95 \pm 0.35
<i>blennoides</i>											
<i>Polyacanthonotus</i>	Pris	BF	MS	11.19 \pm 0.04	-15.69 \pm 0.29	2	18.20 \pm 0.85	-	-	-	-
<i>rissoanus</i>											
<i>Trachyrhynchus</i>	Tsca	BF	MS	11.12 \pm 0.55	-15.02 \pm 0.63	3	38.30 \pm 2.86	-	-	-	-
<i>scabrus*</i>											
<i>T. scabrus</i>	Tscajuv	BF	MS	11.20 \pm 0.55	-15.25 \pm 0.29	3	17.37 \pm 0.15	-	-	-	-
juveniles*											
Chondrichthyes											
<i>Centroscymnus</i>	Ccoe	BF	MS	-	-	-	-	12.59	-13.59	1	-
<i>coelolepis</i>			LS	-	-	-	-	12.14	-14.90	1	-
<i>Dalatias licha</i>	Dlic	BF	MS	9.83 \pm 0.06	-17.32 \pm 0.20	2	-	-	-	-	-
<i>Etmopterus</i>	Espi	nmMF	US	-	-	-	-	9.47 \pm 0.30	-19.33 \pm 0.38	3	-
<i>spinax</i>			MS	10.37	-15.61	1	44.3	-	-	-	-
<i>Galeus</i>	Gmel	nmMF	US	8.12 \pm 0.31	-15.6 \pm 0.21	3	41.10 \pm 1.31	-	-	-	-
<i>melastomus</i>			MS	-	-	-	-	9.53 \pm 0.92	-16.02 \pm 0.01	3	44.50 \pm 8.59

Table 4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for suprabenthic, zooplanktonic and benthic species from the upper (US), middle (MS) and lower (LS) slope zones during July 2010. N: the number of replicates analysed. B_SF: benthic suspension feeders; B_SDF: benthic surface deposit feeders; B_SSDF: benthic sub-surface deposit feeders; Z_SF: zooplanktonic POM feeders; Z_O: zooplanktonic omnivores; Z_C: zooplanktonic carnivores; S_O: suprabenthic omnivores; S_C: suprabenthic carnivores. Size or weight of specimens is also given (CL for euphausiids, mysids and decapods in mm, TL for *Cylothone braueri* and *Phronima sedentaria*; weight in g for sponges, cnidarians and echinoderms)

	Zone	Feeding guild	Catalan Slope				Balearic Slope			
			$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size
SUPRABENTHOS										
Mysidacea										
<i>Boreomysis arctica</i>	US	S_O	–	–	–	–	5.86	–18.38	1	6.40
	MS		4.68 \pm 0.97	–18.51 \pm 0.77	4	6.60 \pm 0.36	5.93 \pm 0.65	–18.67 \pm 0.59	4	6.53 \pm 0.10
	LS		4.88 \pm 0.27	–18.41 \pm 0.33	3	6.67 \pm 0.45	5.19 \pm 0.69	–18.07 \pm 0.24	7	6.55 \pm 0.21
MACROZOOPLANKTON										
Cnidaria										
Hydrozoa										
<i>Abylopsis tetragona</i>	US	Z_SF	4.73 \pm 0.44	–15.86 \pm 0.21	3	–	–	–	–	–
Scyphozoa										
<i>Pelagia noctiluca</i>	US	Z_SF	–	–	–	–	5.01 \pm 0.82	–17.41 \pm 0.33	3	–
	MS		5.59 \pm 0.40	–16.08 \pm 0.75	3	–	–	–	–	–
	LS		4.46 \pm 0.33	–17.32 \pm 0.46	4	–	–	–	–	–
<i>Peryphilla peryphilla</i>	MS	Z_C	–	–	–	–	8.66 \pm 0.25	–19.15 \pm 0.55	3	–
	LS		–	–	–	–	8.52 \pm 0.70	–18.17 \pm 0.57	5	–
Mollusca										
Gastropoda										
<i>Cymbulia peroni</i>	MS	Z_SF	3.43 \pm 0.94	–18.06 \pm 0.31	5	2.15 \pm 1.06	–	–	–	–
	LS		3.79 \pm 0.76	–18.64 \pm 0.95	4	–	3.15	–21.77	1	1.52
Crustacea										
Mysidacea										
<i>Eucopeia hanseni</i>	LS	Z_C	7.21 \pm 0.24	–17.89 \pm 0.18	3	5.97 \pm 0.50	6.58 \pm 0.70	–20.33 \pm 0.89	4	6.00 \pm 0.60
Euphausiacea										
<i>Euphausia khronii</i>	US	Z_O	5.34 \pm 0.80	–18.05 \pm 0.21	3	–	–	–	–	–
<i>Meganyctiphanes norvegica</i>	US	Z_O	5.53	–17.55	1	5.9	–	–	–	–
	MS		7.19	–18.20	1	5.5	6.59 \pm 0.11	–17.82 \pm 0.26	3	6.07 \pm 0.46
	LS		5.49 \pm 0.57	–17.77 \pm 0.27	5	6.00 \pm 0.00	–	–	–	–
<i>Nematoscelis megalops</i>	LS	Z_C	7.66 \pm 0.24	–18.73 \pm 0.19	4	4.80 \pm 0.24	–	–	–	–
Amphipoda Hyperiidea										
<i>Phronima sedentaria</i>	MS	Z_C	7.28	–17.77	1	–	–	–	–	–
	LS		8.56 \pm 0.44	–16.40 \pm 0.35	4	29.30 \pm 0.60	5.79 \pm 1.10	–18.47 \pm 0.88	2	28.00 \pm 0.00
Decapoda										
<i>Gennadas elegans</i>	US	Z_C	6.36 \pm 0.05	–18.91 \pm 0.80	3	7.12 \pm 0.56	5.71 \pm 0.57	–17.83 \pm 0.89	3	6.57 \pm 0.15
	LS		6.46 \pm 0.39	–17.13 \pm 0.32	5	7.13 \pm 0.14	6.15 \pm 0.12	–17.58 \pm 0.33	5	7.22 \pm 0.20
<i>Sergestes arcticus</i>	US	Z_C	6.71 \pm 0.98	–18.06 \pm 0.76	3	9.43 \pm 0.40	–	–	–	–
	LS		5.58 \pm 0.44	–17.79 \pm 0.32	3	9.40 \pm 1.57	5.90 \pm 0.41	–18.07 \pm 0.58	3	10.2 \pm 2.50
<i>Sergestes henseni</i>	US	Z_C	6.53	–	1	12	5.01	–17.08	3	12
Tunicata										
<i>Pyrosoma atlanticum</i>	US	Z_SF	4.14	–21.32	1	–	3.39 \pm 0.89	–18.42 \pm 0.32	3	–
	MS		2.71 \pm 0.39	–20.31 \pm 1.66	4	–	–	–	–	–
	LS		3.48 \pm 0.58	–19.35 \pm 1.00	5	–	3.14 \pm 0.16	–18.89 \pm 0.77	2	–
Osteichthyes										
<i>Cylothone braueri</i>	LS	Z_C	6.11 \pm 0.51	–17.54 \pm 0.33	3	29.70 \pm 0.23	6.15 \pm 0.57	–16.68 \pm 0.72	3	28.70 \pm 0.21
MACROZOOBENTHOS										
Porifera										
<i>Hyalinema thomsoni</i>	LS	B_SDF	10.72	–20.13 \pm 0.20	4	0.83 \pm 0.08	11.81 \pm 0.17	–19.29 \pm 0.26	3	0.84 \pm 0.05
<i>Polymastia tissieri</i>	MS	B_SDF	11.02 \pm 0.59	–16.66 \pm 0.96	5	0.44 \pm 0.04	10.17 \pm 0.47	–19.44 \pm 0.60	3	0.33 \pm 0.09
	LS		11.16 \pm 0.78	–16.35 \pm 0.57	11	0.55 \pm 0.04	10.85 \pm 0.87	–17.84 \pm 0.14	5	0.40 \pm 0.07
Cnidaria										
Anthozoa										
<i>Hormathia alba</i>	US	B_SF	–	–	–	–	7.57 \pm 0.41	–17.74 \pm 0.17	3	0.85 \pm 0.09
<i>Isidella elongata</i>	MS	B_SF	7.67 \pm 0.25	–17.84 \pm 0.11	4	–	7.92 \pm 0.23	–19.09 \pm 0.17	3	–

(continued on next page)

Table 4 (continued)

	Zone	Feeding guild	Catalan Slope				Balearic Slope			
			$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	N	Size
Mollusca										
Bivalvia										
<i>Abra longicallus</i>	US	B_SF	6.63 ± 0.49	-16.67 ± 0.12	3	0.67 ± 0.24	-	-	-	-
Gastropoda										
<i>Philine</i> sp.	US	B_SF	5.19 ± 0.50	-15.14 ± 0.60	3	-	-	-	-	-
Crustacea Decapoda										
<i>Calocarides coronatus</i>	MS	B_SDF	6.46 ± 0.50	-16.09 ± 0.19	3	8.03 ± 0.06	-	-	-	-
<i>Calocaris macandreae</i>	MS	B_SDF	4.84 ± 0.57	-16.89 ± 0.90	4	8.25 ± 0.13	-	-	-	-
Echinodermata										
<i>Brisingella coronata</i>	LS	B_SDF	11.1	-16.34 ± 0.93	3	-	9.62 ± 0.41	-17.01 ± 0.30	5	-
<i>Bryssopsis lyrifera</i>	US	B_SSDF	7.35 ± 0.50	-17.44 ± 0.99	3	44.76 ± 6.87	-	-	-	-
<i>Ceramaster grenadiensis</i>	LS	B_SSDF	10.70 ± 0.14	-15.85 ± 0.15	5	0.50 ± 0.09	11.13 ± 0.61	-14.94 ± 0.41	5	0.50 ± 0.14
<i>Mesothuria intestinalis</i>	LS	B_SSDF	9.06 ± 1.28	-18.33 ± 0.42	3	-	-	-	-	-
<i>Pseudostichopus oculatus</i>	MS	B_SSDF	8.92 ± 0.73	-12.31 ± 0.85	6	3.75 ± 1.21	-	-	-	-
<i>Ypsilothuria bitentaculata</i>	MS	B_SDF	4.50 ± 0.33	-19.29 ± 0.15	3	0.32 ± 0.01	-	-	-	-

Table 5. Population metrics (TA: total area; SEA_c : standard ellipse area, corrected for sample size) calculated from isotopic signatures of consumers (decapods, fish and cephalopods) from 3 depth ranges of the Catalan (CS) and Balearic (BS) Slopes

Metric	Upper slope		Middle slope		Lower slope	
	CS	BS	CS	BS	CS	BS
TA	20.99	19.00	26.45	29.28	26.40	34.30
SEA_c	7.02	5.63	5.97	7.65	6.21	7.94

Table 6. Significant results of Student's *t*-tests carried out on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of species from the Catalan Slope (CS) and the Balearic Slope (BS). **p* < 0.05, ***p* < 0.01, ****p* < 0.001

Species	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
CS > BS		
<i>Cataethyx alleni</i>	-2.71*	
<i>Eucopeia henseni</i>		-4.14**
<i>Gennadas elegans</i>	-2.40*	
<i>Helicolenus dactylopterus</i>	-2.36*	-5.63**
<i>Isidella elongata</i>		-3.38*
<i>Notacanthus bonapartei</i>		-2.98**
<i>Phycis blennoides</i>	-2.76*	-4.30*
<i>Plesionika acanthonotus</i>	-2.58*	
<i>Plesionika martia</i>		-2.52*
<i>Phronima sedentaria</i>	-3.57*	-2.83*
<i>Polymastia tissieri</i>		-5.58***
CS < BS		
<i>Munida tenuimana</i>		4.14**
<i>Pontophilus norvegicus</i>	10.91***	

over the BS (Tables 2 to 4). Indeed, among species showing significant differences between the 2 areas, the bulk was more enriched in ^{13}C near the mainland (the fishes *Helicolenus dactylopterus* and *Phycis blennoides*, the decapods *Plesionika martia* and *P. acanthonotus*, the bamboo coral *Isidella elongata*, the hyperiid *Phronima sedentaria*, the mysid *Eucopeia henseni* and the sponge *Polymastia tissieri*; Table 6) than over the insular slope; the only exception being *Munida tenuimana*. Similarly, significantly higher $\delta^{15}\text{N}$ values were observed off the mainland in the majority of the species compared from the 2 areas (see Table 6) with the exception of *Pontophilus norvegicus*.

The analysis of mean weight of individual by area showed a general tendency in fish and decapods towards greater size in species on the CS than those on the BS, although differences were not always significant (Fig. 4, Kruskal-Wallis test, *p* < 0.05 in 60% of species analysed). No species showed the inverse trend, i.e. higher mean weight (size) on the BS.

Comparisons between depth ranges

Data were merged for those species having non-significant differences between the 2 areas, whereas for species showing significant or almost significant ($0.06 > p > 0.05$) differences, the analyses to untangle bathymetric variations in isotopic composition were carried out separately for each zone. Comparisons

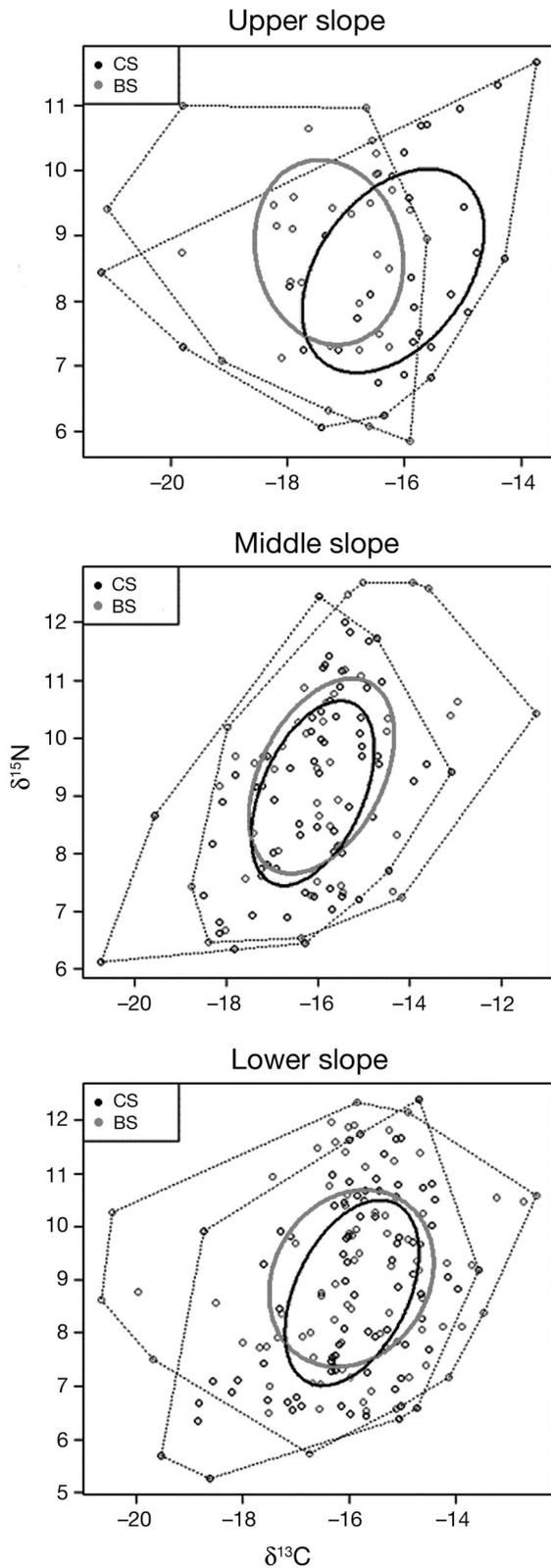


Fig. 3. Stable isotope bi-plots for depth zone. The open circles represent species used in the analysis. The lines enclose the standard ellipse area (SEA_c) for species from the Catalan Slope (CS, black) and Balearic Slope (BS, grey)

Table 7. Significant results of Student's *t*-tests carried out on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of species from the 3 depth ranges (US: upper slope; MS: middle slope; LS: lower slope). CS: species analysed from the mainland slope; BS: those from the insular slope; A: all, when isotopic values were merged from the 2 areas, since no significant differences existed between them (see 'Results: Comparisons between depth ranges')

Species	<i>t</i> -values	Pair-wise	Site
$\delta^{15}\text{N}$			
<i>Alepocephalus rostratus</i>	-2.73*	MS<LS	CS
<i>Notacanthus bonapartei</i>	8.80*	US=MS<LS	CS
<i>Pontophilus norvegicus</i>	2.84*	MS<LS	BS
<i>Polycheles typhlops</i>	2.53*	US<MS	BS
<i>Meganyctiphanes norvegica</i>	3.93**	MS>LS	A
$\delta^{13}\text{C}$			
<i>Aristeus antennatus</i>	-8.50***	US<LS	A
<i>Munida tenuimana</i>	-5.83**	MS<LS	A
<i>Periphylla periphylla</i>	-2.70*	MS<LS	A

Table 8. Results of PERMANOVA pair-wise tests carried out on $\delta^{15}\text{N}$ - $\delta^{13}\text{C}$ mean values of feeding guilds of decapods and fish from the Catalan (CS) and the Balearic (BS) Slopes. Feeding guilds as in Table 2. **p* < 0.05, ****p* < 0.001

Guilds	CS	<i>t</i>	Guilds	BS	<i>t</i>
mMF vs. nmMF	5.05***		mMF vs. nmMF	2.20*	
mMF vs. BF	11.31***		mMF vs. BF	8.26***	
nmMF vs. BF	7.58***		nmMF vs. BF	6.25***	

among depth zones were possible for 23 species (7 fishes, 9 decapods and 7 other invertebrates).

Among fishes, there were significant depth differences in $\delta^{15}\text{N}$ for *Alepocephalus rostratus* and *Notacanthus bonapartei* (Table 7) over the mainland slope (always comparing the same size fish). Only 2 significant differences (*Pontophilus norvegicus* and *Polycheles typhlops*) were detected for the decapod crustaceans, both on the insular slope (Table 7). There were only a few significant differences in $\delta^{13}\text{C}$ among depth ranges: it was greater at greater depth in the decapods *Aristeus antennatus* and *Munida tenuimana* and in the jellyfish *Periphylla periphylla* (Table 7). No fish species differed significantly in $\delta^{13}\text{C}$ among the 3 depth zones.

Feeding groups and relation with depth

The nMDS analyses carried out separately for CS and BS for fish and decapods showed a separation of species as a function of their feeding guild, with benthic feeders clearly separated from planktonic feed-

ers in both areas (Fig. 5, PERMANOVA test $p < 0.001$ in both areas). Pair-wise testing showed that differences were significant among all *a priori* established groups (BF, nmMF, and mMF), both for CS and BS (Table 8); feeding groups were also segregated when

the analysis was carried out on $\delta^{13}\text{C}$ (for nmMF vs. mMF in CS $p < 0.05$; in the rest of cases $p < 0.001$).

Overall, at group level $\delta^{15}\text{N}$ values of BF decapods were higher at MS and lower at US and LS (Fig. 6a). Their $\delta^{13}\text{C}$ values increased significantly with depth

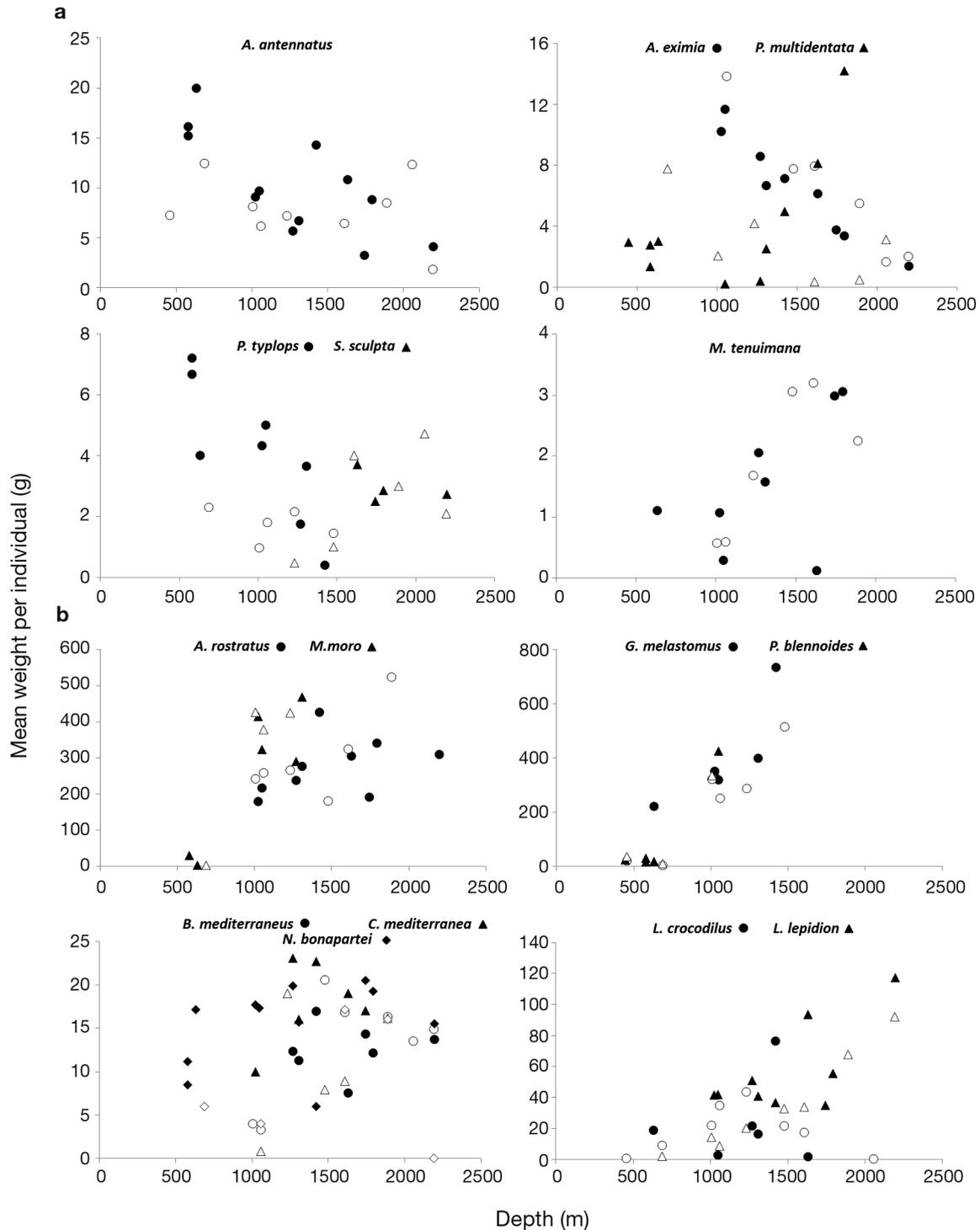


Fig. 4. Mean weight (g) per individual of the most abundant (a) decapod and (b) fish species collected over the Catalan (filled symbols) and Balearic (white symbols) Slopes during ANTRMARE and analysed for stable isotopes

($r = 0.47$, $p = 0.03$; Fig. 6c). $\delta^{15}\text{N}$ values of mMF decapods decreased with depth ($r = -0.46$, $p = 0.04$), while $\delta^{13}\text{C}$ values showed an opposite (though non-significant) trend, increasing with depth (Fig. 6c). Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of BF fishes were greater at increasing depth, although results were significant only for $\delta^{15}\text{N}$ ($r = 0.62$, $p = 0.001$; Fig. 6b).

Correlation with environmental variables

Draftsman plots showed strong positive correlation of *Calocaris macandreae* with polychaetes, of SPP2 with SPP1, and negative correlation between O_2 and %TOC. Thus, after excluding auto-correlated variables, GLM models were run with (1) the physical

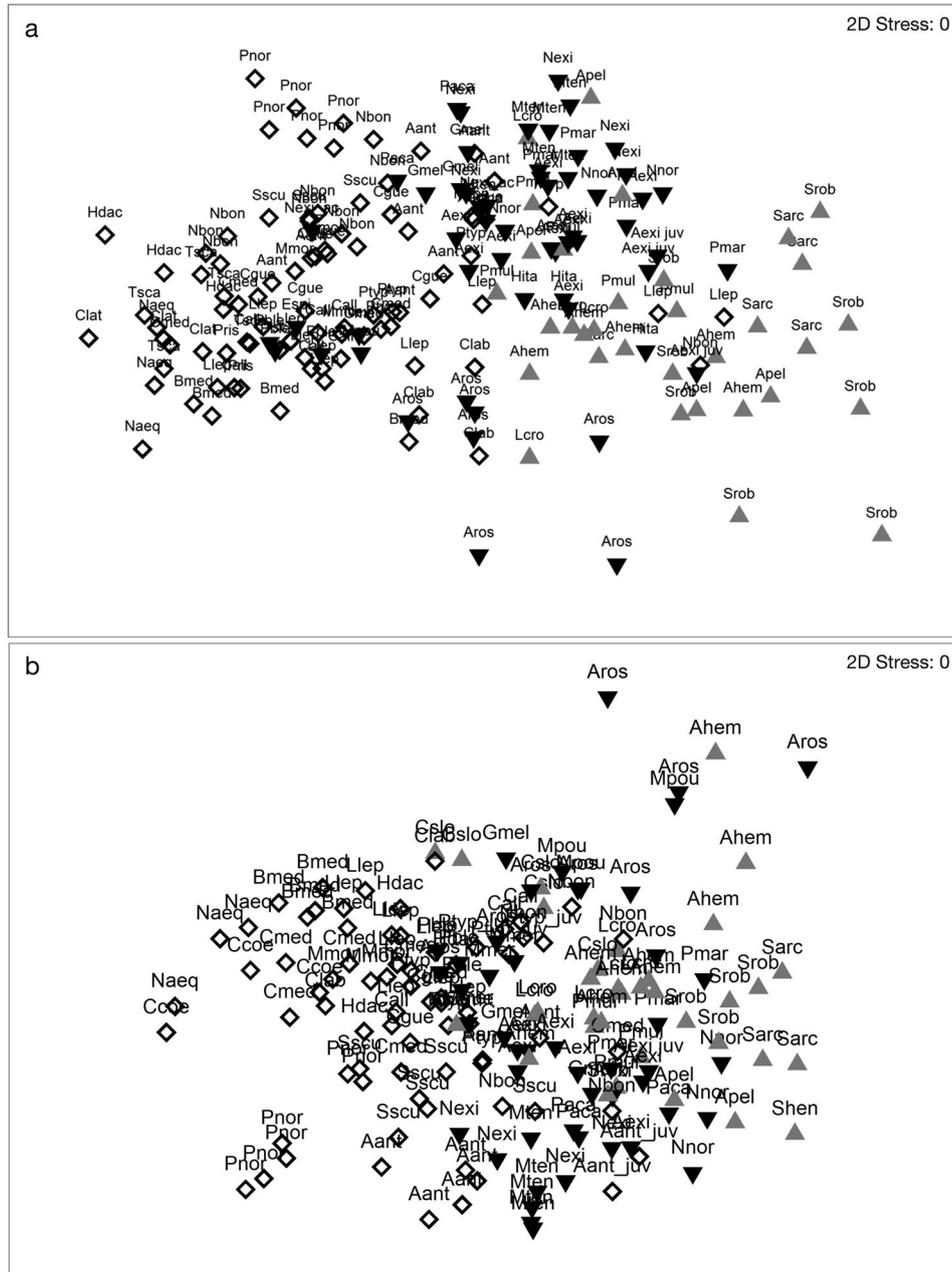


Fig. 5. nMDS based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of decapods and fishes collected on the (a) Catalan and (b) Balearic Slopes. Grey triangles: migratory plankton feeders; black triangles: non-migratory plankton feeders; white diamonds: benthic feeders. Label abbreviations as in Tables 2 & 3

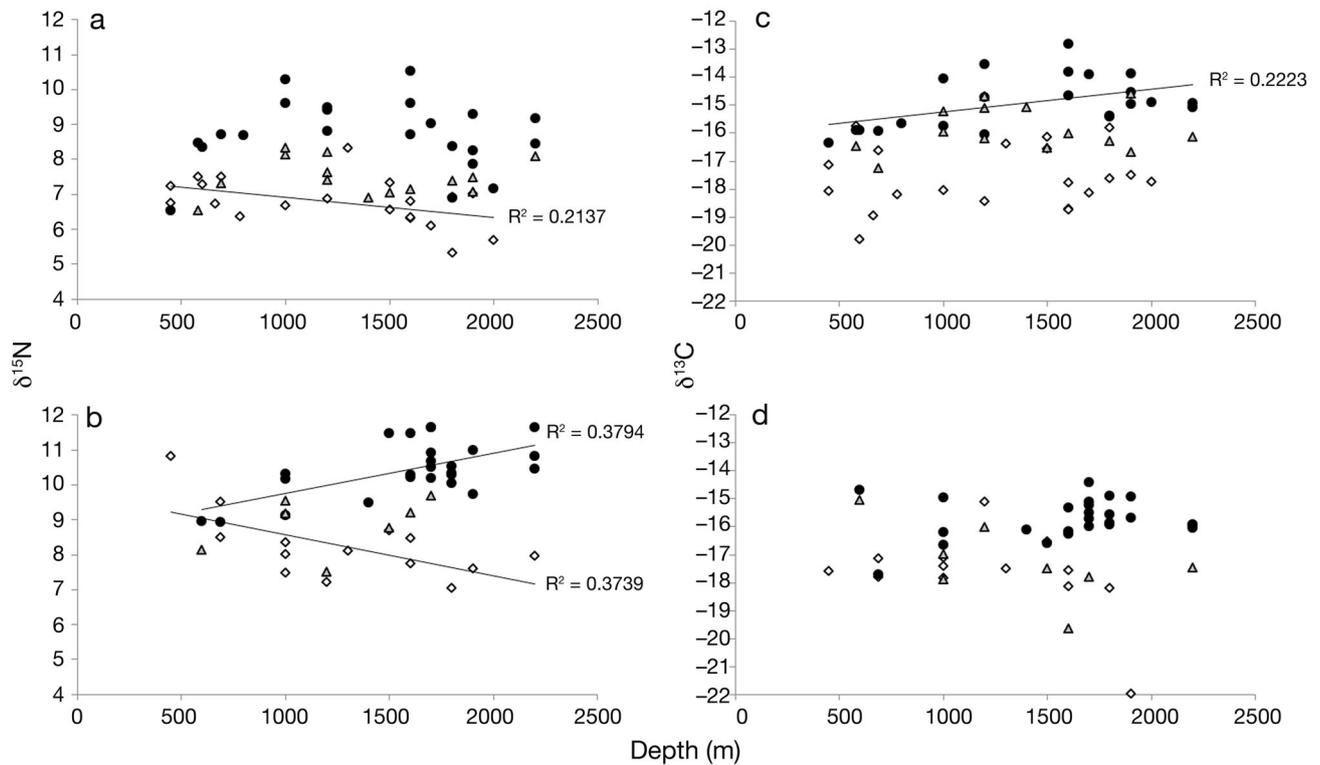


Fig. 6. Depth-related trends of (a,b) $\delta^{15}\text{N}$ (on the left) and (c,d) $\delta^{13}\text{C}$ values for (a,c) decapods and (b,d) fishes along the bathymetric range explored in the study. Black circles: benthic feeders; white diamonds: migratory macroplankton feeders; grey triangles: non-migratory macroplankton feeders. Regression lines and R^2 values are given also for significant correlations

Table 9. Results of generalized linear models (GLMs) performed on $\delta^{13}\text{C}$ of the different trophic guilds of fish and decapods (see Table 2) from the Catalan and the Balearic Slopes. F values of models are indicated, and the sign of the estimate is given in parentheses. T : temperature; S : salinity; Turb: turbidity; $\text{Chl } a_{5\text{mab}}$: chl a recorded 5 m above the bottom (as for all physical variables); CMAC: *Calocaris macandreae* biomass; MYS: mysids (*Boreomysis arctica* biomass); EUP: euphausiids; SPP2, SPP3: surface primary production recorded 2 and 3 mo before sampling. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Factor	Catalan Slope						Balearic Slope					
	Decapods			Fish			Decapods			Fish		
	BF	nmMF	mMF	BF	nmMF	mMF	BF	nmMF	mMF	BF	nmMF	mMF
Physical												
T	-	-	-	-	-	-	-	31.48 (+)	-	-	11.02 (+)	-
S	6.82 (+)	-	-	21.35 (-)	-	-	-	8.95 (+)	-	-	-	-
O_2	-	-	-	10.22 (+)	46.82 (-)	-	-	35.37 (+)	-	-	-	-
Turb	-	-	-	-	-	-	-	-	-	29.50 (-)	10.98 (-)	-
Trophic												
$\text{Chl } a_{5\text{mab}}$	-	-	3.11 (-)	-	-	-	-	-	5.81 (-)	4.11 (-)	-	-
CMAC	-	-	-	8.41 (-)	-	-	-	-	-	-	-	-
MYS	-	-	-	-	9.17 (+)	-	-	-	-	-	-	-
EUP	9.07 (-)	4.27 (+)	-	-	-	-	-	-	-	-	-	-
SPP2	-	-	-	-	19.46 (+)	-	42.49 (+)	-	-	-	-	-
SPP3	8.67 (+)	-	-	-	-	-	-	-	-	-	-	-
% deviance explained	60.55	11.47	14.06	33.03	87.27	-	65.69	67.85	82.34	45.65	42.26	42.34
df	34	37	20	64	14	10	23	23	10	42	17	16
AIC	36.77	68.16	66.27	153.32	25.63	-	51.70	47.22	9.45	81.25	48.99	27.53

variables T , S , O_2 and turbidity and (2) the trophic variables chl a_{5mab} , SPP2, SPP3, SPP4, mysids, euphausiids, gelatinous plankton and *C. macandreae*. GLM models, carried out on groups defined above (BF, nmMF and mMF; Papiol et al. 2013), showed clearly that $\delta^{13}C$ signatures in the 2 areas were explained by different environmental and trophic variables (Table 9).

In general, trophic variables were the foremost explanatory variables of CS fish and decapod $\delta^{13}C$ (according to GLMs). Food sources (prey) of high trophic levels (euphausiids for decapods; mysids and *Calocaris macandreae* for fish) were the most strongly explanatory variables of $\delta^{13}C$. All were inversely correlated with $\delta^{13}C$ (i.e. the lower the $\delta^{13}C$, the greater the available prey biomass). Among physical (taken *in situ*) variables, $[O_2]$ was the main explanatory factor for BF and nmMF fish, being positively correlated with $\delta^{13}C$. Salinity was an important variable for BF decapods and fish (Table 9). Trophic variables, indicating primary food sources (SPP3 and SPP2), contributed to give the best models for BF decapods (SPP3) and nmMF fish (SPP2). No significant models were found for mMF fish.

On the BS, physical and SPP records best explained $\delta^{13}C$ trends in fish and decapods (Table 9). Specifically, salinity and $[O_2]$ were important variables for nmMF decapods, while turbidity and salinity were significant for nmMF and mMF fish. Chl a_{5mab} was the second explanatory variable for BF fish and mMF decapods, while BF decapods were best explained by SPP2.

DISCUSSION

Food web structure

The present study included 17 taxonomic groups with emphasis on fish and decapod crustaceans, but also most of the dominant megabenthic invertebrates in the deep Mediterranean (e.g. 6 species of echinoderms). Previous information regarding the role of these groups in deep-sea food webs is not readily available. Despite the low sample size for some species, the overall dataset completes the information given by Polunin et al. (2001) for the Algerian Basin, and by Papiol et al. (2013) for the Catalan margin. Ours is one of the few attempts to compare the isotopic composition of species over a spatial mesoscale in the deep-sea (compare with Madurell et al. 2008, Fanelli et al. 2009).

Overall, the carbon and nitrogen dual-isotope plot of all organisms sampled confirms that fishes represent the highest trophic level, while decapods and cephalopods occupy similar trophic positions. However, the low trophic position of cephalopods compared to oceanic species preyed on by tunnids or sharks (Logan & Lutcavage 2013) and to benthopelagic species found in stomachs of sperm whales (Cherel et al. 2009) is likely attributable to the low size of slope-dwelling species collected with the OTSB14.

Generally, decapods showed higher $\delta^{13}C$ values than fish, likely due to the greater dominance of benthic prey in their diets than in those of fishes in the same trophic guilds (Papiol et al. 2013). According to the literature, fish and decapods are divided into 3 main trophic guilds (see Papiol et al. 2013 and references therein), with BF species of fish and decapods located closer to the top of the trophic web (Papiol et al. 2013), and mMF presenting the lowest $\delta^{15}N$ and $\delta^{13}C$ values. At bathyal depths, higher $\delta^{13}C$ has been described for benthic macrofauna in comparison to zooplankton (Polunin et al. 2001, Fanelli et al. 2011a,b, present study), likely because they eat sediment microorganisms, meiofauna and refractory organic matter (Gooday & Turley 1990, Roberts et al. 2001, Iken et al. 2001, Amaro et al. 2009).

Among invertebrates, surface deposit feeders (SDF; i.e. the sponges *Polymastia tissieri* and *Hyalinema thomsoni* and the asteroid *Brisingella coronata*) and sub-surface deposit feeders (SSDF; the asteroid *Ceramaster grenadensis*) showed the highest $\delta^{15}N$ values, which were comparable to fish. They probably feed on more refractory and frequently recycled POM_{sed} and POM_{wat} (Iken et al. 2001, Fanelli et al. 2011a) in which bacteria play an important role (Amaro et al. 2009). Thus, the high $\delta^{15}N$ values of sponges may relate to either the restriction of sponge diet to the smallest, most degraded POM (i.e. ^{15}N -enriched; Mintenbeck et al. 2007), or to the heavy colonization of sponge surfaces and interstices by bacteria (e.g. Webster et al. 2004) that are included in the analysed tissue samples. Further, several SSDF (such as deep-sea holothurians) exploit bacteria directly as food, or their symbiotic bacteria provide them with essential nutrients (Deming et al. 1981, Deming & Colwell 1982, Eardly et al. 2001).

Spatial changes and potential food sources

We began this analysis by excluding POM_{wat} from the data set due to the high variability of its $\delta^{15}N$

(ranging from 1.86‰ to 6.94‰). This high variability has also been found in other Mediterranean deep-sea communities (Carlier et al. 2009).

The $\delta^{13}\text{C}$ in sinking (POM_{wat}) and deposited (POM_{sed}) POM showed characteristic differences between mainland and insular sites. In deep waters, $\delta^{13}\text{C}$ values of POM_{wat} (5mab) were significantly lower than those of POM_{sed} at both sites. However, over the CS the difference between POM_{wat} and POM_{sed} was less (~2‰) than over the BS (~4‰). The CS has a narrow continental shelf cut by submarine canyons that transfer organic matter from the continent to the deep sea (Puig & Palanques 1998, Sanchez-Vidal et al. 2009, Cartes et al. 2010a,b). Closely similar isotopic carbon values for POM_{wat} and POM_{sed} on the CS reveal that the organic matter in both samples was a mixture of terrigenous ($\delta^{13}\text{C} \approx -25.2\text{‰}$) and marine organics ($\delta^{13}\text{C} \approx -21.9\text{‰}$) (Font 1987, Monaco et al. 1990, Millot 1999). Consistently, terrestrial leaves contributed to POM_{sed} on the CS (SIAR results), where the proportion of organic carbon of terrestrial origin was relatively high (on average 33%) compared to the BS (on average 21%).

In contrast, sediments on the insular slope had more marine characteristics, and mean $\delta^{15}\text{N}$ values ($3.7 \pm 0.3\text{‰}$) of POM_{sed} were close to the mean $\delta^{15}\text{N}$ (~4‰) of phytoplankton over deep bottoms in the western Mediterranean Sea (Pantoja et al. 2002, Harmelin-Vivien et al. 2008), while the range of $\delta^{13}\text{C}$ has the isotopic variability of marine organic matter.

The large difference between POM_{wat} and POM_{sed} found on the insular slope is likely attributable to the greater oligotrophy on the BS (Fanelli et al. 2013), which may lead to almost complete consumption of the sinking matter and a much remineralised sedimented matter.

Stronger $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ correlations were observed on the CS than on the BS in all depth ranges. High $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ correlations indicate a single and isotopically homogenous food source, and suggest the dietary importance of pulsed inputs from new production, while low correlations point to a wide array of food sources sustaining the food web (Pinnegar & Polunin 1999, Fanelli et al. 2011a) or to high isotopic variability of a single food source. Stronger correlations over the CS than those observed on the BS are likely generated by the greater SPP in the CS, which provides fresh material from the surface, sustaining the community as observed by Papiol et al. (2013) on the US.

Despite the availability of fresh OM of terrestrial origin on the CS, $\delta^{13}\text{C}$ values of terrigenous material (i.e. algae, seagrasses and terrestrial remains) were

not consistent (either too high or too low) with the isotopic ranges found for macrofaunal and megafaunal species (Fanelli et al. 2011a, present study) suggesting that it was not incorporated into the biota. Thus, terrestrial-derived OM was probably less bioavailable to the benthic community.

On the other hand, deep-sea communities on the BS were supplied by less abundant fresh food (lower SPP, more oligotrophic) and rely on scarce phyto-detritus (Fanelli & Cartes 2008). Here, greater oligotrophy likely results in a multivorous food web (Pomeroy 2001).

These considerations are supported by population metrics (Layman et al. 2007a, Jackson et al. 2011) that indicate slightly higher trophic diversity (by exploitation of low abundance food) in the BS than in the CS, at the highest depths (MS, LS). In ultra-oligotrophic conditions, animals are generally omnivores (Pomeroy 2001), exploiting all available resources. For this reason, greater trophic diversity is found at greater depths, where food is even scarcer.

Alternatively, the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ correlations could reflect temporal variations in the baseline (plankton/suprabenthos) isotope values coupled with varying rates of isotopic incorporation (Fanelli et al. 2009, 2011b).

Significant differences were observed in POM_{sed} and in several species between the 2 areas, but whereas the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of POM_{sed} were greater at BS than at CS (see above), the opposite trend was found when comparing species. The consumers of POM suspended in the water (e.g. the thaliacean *Pyrosoma atlanticum*; $\delta^{15}\text{N} = 3.45\text{‰}$ on CS and $\delta^{15}\text{N} = 3.27\text{‰}$ on BS; this study) or of POM in sediments (e.g. cumaceans that are SDF; $\delta^{15}\text{N} = 4.10\text{‰}$ on CS: Papiol et al. 2013; $\delta^{15}\text{N} = 3.72\text{‰}$ on BS: Fanelli et al. 2009) were more enriched in ^{15}N at CS than at BS. One hypothesis as to why this might be so is that POM consumers have on average more trophic steps between them and the basal materials at CS than at BS. The greater availability of OM at CS (Fanelli et al. 2013) could enhance higher bacterial biomass and in turn more meiofauna (Danovaro et al. 2000, Mintenbeck et al. 2007), potentially exploited by POM consumers, which become themselves enriched. Such enrichment was finally reflected by secondary consumers, especially benthic feeders (Papiol et al. 2013).

In addition to SIA results, the generalized greater size (in terms of mean weight) of species inhabiting the mainland slope compared to those on the insular reinforced the idea of a longer (and probably more

complex) food chain on the mainland (CS) than around insular (BS) areas.

Another hypothesis might be the greater anthropization of the Catalan coast compared to the Balearic archipelago. Cabana & Rasmussen (1996) demonstrated large differences in $\delta^{15}\text{N}$ of baseline materials and at higher levels in the food web that correlated with the human population density in the local watershed. In the Catalan sea, nitrate concentration (^{15}N -enriched) has increased in recent decades (Moutin et al. 1998), together with a decrease in phosphates (Raimbault et al. 2009) due to phosphate treatment in purification plants (Souchu et al. 1997), likely causing the enrichment in ^{15}N .

Variations with depth

Generally higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were observed at greater depths. Changes in $\delta^{15}\text{N}$ with depth were observed for SSDF and SDF, and appear to be linked to the increase of $\delta^{15}\text{N}$ in POM with depth (Mintenbeck et al. 2007). The generally higher $\delta^{15}\text{N}$ values found at greater depths for 14 out of 23 species—even though not significant for all—points toward the propagation of the depth-related increase in $\delta^{15}\text{N}$ of POM along the food web (Rau et al. 1989, Polunin et al. 2001). Accordingly, high $\delta^{15}\text{N}$ in *Notacanthus bonapartei* on the LS, where it feeds mainly on sessile invertebrates such as bryozoans and sponges and ophiuroids (Mauchline & Gordon 1986, Macpherson 1989) is parallel to the increase in POM for SSDF and SDF described by Mintenbeck et al. (2007). Values of $\delta^{13}\text{C}$ also tended to increase at greater depths which, as for nitrogen, is consistent with the biodegradation of marine snow leaving residues of more refractory materials (Williams & Gordon 1970, Müller-Niklas et al. 1994). Those include inorganic carbonates and chitin, which are known to be enriched in ^{13}C compared to other biochemical fractions (Bunn et al. 1995).

Dietary changes resulting from variation in prey availability may also account for the enrichment in ^{15}N with depth. A clear example is the plankton feeder *Alepocephalus rostratus*, which preyed mainly on *Pyrosoma atlanticum* on the MS (stomach contents data from Carrassón & Matallanas 1998), but had a more diversified diet as well as passive consumption of sedimented (^{15}N -enriched) material below 1200 to 1400 m. That was likely fostered by the decrease of near-bottom zooplankton resources below 1400 m (Cartes et al. 2013). An inverse trend (i.e. ^{15}N depletion at greater depths) was detected for

the crangonid *Pontophilus norvegicus*, which is a selective feeder of ^{15}N -enriched carnivorous polychaetes (Fanelli et al. 2011a) in shallower water (Cartes et al. 2007, Papiol et al. 2013), but probably feeds at lower trophic levels at greater depth where polychaetes are scarce (Cosson-Sarradin et al. 1998).

The higher $\delta^{13}\text{C}$ values of the decapod *Aristeus antennatus* and *Munida tenuimana* at greater depth (Table 2) seem to corroborate the available gut-content data. For example, *Munida tenuimana* feeds on a large array of benthopelagic resources, especially on euphausiids, siphonophores and hyperiids. The contribution of these groups to the diet of *M. tenuimana* decreased progressively with depth, while sedimented detritus may increase (Lagardère 1971, Cartes 1993a).

These considerations are also supported by the depth-related trends for whole trophic guilds, with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values increasing with depth for BF fish, whereas BF decapods showed highest $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values at intermediate (1000 to 1500 m) depths. Opposite to this general ^{15}N -enrichment with depth, we observed general ^{15}N -depletion in both mMF fish and decapods with increasing depth. This followed the downward depletion of their pelagic prey (^{15}N ca. 1‰ lower at LS than at US and MS in *Pelagia noctiluca*, *Meganycthiphanes norvegica* and *Sergestes arcticus*). These species even rely directly on sinking particles from the surface that are ^{15}N -depleted when flux is low (Altabet et al. 1991), as during our sampling cruises in June-July. Indeed, zooplankton are known to become relatively ^{15}N -depleted when ammonia is the main nitrogen source for phytoplankton (Mullin et al. 1984). This occurs when surface waters become oligotrophic and primary production is based on recycled ^{15}N -depleted ammonium (Polunin et al. 2001).

Correlation with environmental variables

The variables that exert strong influence on trophic dynamics over the Catalan Slope are mainly of a 'trophic' nature, related to prey availability (i.e. euphausiids, *Calocaris macandreae* and the mysid *Boreomysis arctica*) or to detritus arriving at the seafloor from surface production (chl $a_{5\text{mab}}$). Chl $a_{5\text{mab}}$ may be related to phytodetritus deposition, as documented over the CS (Riaux-Gobin et al. 2004), and its abundance explained mMF fish dynamics. The seasonal peak of chl $a_{5\text{mab}}$ enhances proliferation of the main prey taxa (i.e. copepods and euphausiid larvae) for carnivorous zooplankton (Buscail et al. 1990),

even as deep as 2300 m on the northwestern Mediterranean slope (copepod nauplii; Guidi-Guilvard et al. 2007), which in turn are prey for mMF fish (Carrassón & Cartes 2002, Papiol et al. 2013). Dissolved O₂ is also an explanatory variable for trophic dynamics of BF and nmMF fishes. Oxygen availability was directly related with near-bottom zooplankton biomass (Cartes et al. 2013) and indirectly with %TOC—which is considered a good indicator of food availability for benthos (Danovaro et al. 1995). Moreover, in our region sedimentary %TOC is linked to higher densities of deposit feeders along the CS (Cartes et al. 2010a, Mamouridis et al. 2011).

In contrast to the situation on the Catalan margin, trophic variables related to high trophic levels (i.e. secondary production by prey) in the food web did not appear in the models of the BS. On the insular slope, different physical (temperature, turbidity) and 'low trophic level' variables (i.e. SPP, chl *a*_{5mab}) explain the dynamics of isotopic composition of fish and decapods (i.e. δ¹³C as indicator of food sources). We found a positive correlation between δ¹³C of mMF feeders (both fish and decapods) and temperature, and increasingly higher ¹³C values have been observed in phytoplankton with increasing growth temperature (Johnston 1996). The mMF feeders, e.g. pasiphaeid shrimps (Cartes 1993b), perform diel vertical migrations for feeding on zooplankton at shallower depths where temperature is greater, and thus they may be linked to phytoplankton through their prey.

Finally, a different delay between input of SPP and the biochemical response as ¹³C-enrichment was observed comparing BF decapods between the 2 areas. Isotopic dynamics of BF decapods on the CS were largely explained by SPP3, whereas those on the BS were related to SPP2. This longer delay between the input of primary production from the surface over the CS and the response observed there is consistent with the pattern described above: a longer food chain over the mainland slope versus a more direct connection to vertical flux of benthopelagic trophic webs on the BS (Fanelli et al. 2013). Thus, food chain length on the BS should be shorter, due to lower SPP, than in the more productive margins over the CS (more production = longer food chain length: Elton 1927, Vander Zanden & Fetzer 2007). Shorter trophic chains may compensate for less SPP; this being also suggested by the lower benthopelagic megafauna biomass over the insular slope (Fanelli et al. 2013) as well as by the lower size of species from the BS compared with those from the CS (this study).

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