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Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: Insight from stable isotopes

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ABSTRACT

Food web structure of the macroplankton/micronekton fauna on the continental slope of the Catalan Sea (Balearic basin, NW Mediterranean) was investigated using carbon and nitrogen stable isotope tracers on a total of 34 taxa. Samples were collected close to Barcelona, Spain, on the middle slope, at a seasonal scale. Mean $\delta^{13}C$ values ranged from −22.1‰ (*Salpa maxima*) to −16.9‰ (the mysid *Eucopia hanseni*). Values of $\delta^{15}N$ ranged from 2.5‰ (the hyperiid *Vibilia armata*) to 9.8‰ (the pelagic polychaete *Tomopteris* sp.). The stable isotope ratios of this fauna displayed a continuum of values over the $\delta^{15}N$ range of 7‰, confirming a wide spectrum of feeding strategies (from filter feeders to predators). High annual mean $\delta^{15}N$ values were found among carnivorous large zooplankton and micronekton, including species that prey on gelatinous plankton (i.e. salps, siphonophores), euphausiids, natantian decapod crustaceans and fish (i.e. myctophids and stomiiformes). In agreement with the available information on diets of planktonic taxa, the lowest isotope ratios were found for filter feeders (*V. armata*, *S. maxima*, the pteropods *Cymbulia peroni* and *Cavolinia inflexa*, ostracods and the thaliacean *Pyrosoma atlanticum*), all of which feed on particulate organic matter. We found three trophic levels in macroplankton/micronekton food webs based on a ^{15}N-enrichment factor of ~2.5‰ per level. The range of $\delta^{13}C$ was particularly wide among carnivores (−20.7‰ to −16.6‰), suggesting predation on a variety of prey from gelatinous zooplankton (which displayed more depleted $\delta^{13}C$ signatures) to small fishes and decapods. Correlation between $\delta^{13}C$–$\delta^{15}N$ was generally weak, likely due to the consumption of different kinds of sinking particles (e.g. marine snow, phytodetritus), some constituted of multiply recycled particulate organic matter (POM). However, higher $\delta^{13}C$–$\delta^{15}N$ correlations were observed during winter and spring, periods of water column homogenization, suggesting that the planktonic community assimilates pulses of new production from the photic zone (peaking in January–February). Low correlations were observed during periods of water column stratification, particularly in summer, when production is especially low, suggesting that in this period macroplankton–micronekton community rely on sources other than surface primary production such as POM derived from river discharge.

1. Introduction

The deep-sea ecosystem depends mostly on organic material from the epipelagic zone. Organic particles, produced by photosynthesis in the euphotic surface layer, partly sink to greater depths. Food is also transferred downward by the vertical migration of zooplankton and micronekton (see Vinogradov, 1970; Vinogradov and Tseitlin, 1983), both in their gut contents and their tissue, some of it remaining at depth as a result of predation (Angel, 1989; Longhurst and Harrison, 1989). However, the particle-sinking flux is probably the greater source (Angel, 1984; Fowler and Knauer, 1986). Zooplankton in the deep sea are active in the recycling of organic matter moved down by both of these processes (Angel, 1989; Lampitt, 1992; Wishner, 1980; Koppelmann et al., 2000). Despite this general understanding, quantitative knowledge of the relationships among primary production, particle flux and active swimming flux rates and consumption by zooplankton are extremely limited for the deep-sea environment (see Banse, 1994).

Approximately 90% of particulate organic matter (POM) is remineralized as it sinks through the water column. Portions of sinking POM are transferred from lower to higher trophic levels via the food chain (Koppelmann and Frost, 2008).

In the last decades stable isotope analyses have been widely used in food-web studies, although investigations on deep-sea organisms remain scarce, particularly on deep-sea zooplankton (Burd et al., 2002; Koppelmann et al., 2003; Blachowiak-Samolyk et al., 2007; Tamelander et al., 2008). In the Mediterranean, knowledge of the ecology of single deep-sea species (Fanelli and Cartes, 2008, 2010) or compartments such as suprabenthos (Madurell et al., 2008; Fanelli et al., 2009a) or fish and decapods (Polunin et al., 2001) is steadily increasing. However, the structure of deep-sea food webs remains far to be well known and particularly the trophic structure of deep-sea zooplankton

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has never been investigated, despite its importance in linking POM and the lowest trophic levels to top predators such as fish and decapod crustaceans.

Analysis of stable isotope composition provides indications of the origin and transformations of organic matter. Stable isotopes of carbon and nitrogen integrate short-term variations in diet and thus are less subject to temporal bias. In deep-sea fish, tissue turnover rates may be as slow as 0.1–0.2% day^{-1} (Hesslein et al., 1993). The $\delta^{15}N$ in tissues of consumers are typically greater by 2–3‰ relative to their prey, so that stable N-isotope data have been used to estimate the trophic levels of organisms (Owens, 1987). In contrast, tissues tend to be rather weakly enriched in ^{13}C at progressively higher trophic levels (<1‰), and thus ^{13}C may act as a useful indicator of primary organic carbon sources of an animal's diet. Investigations of $\delta^{15}N$ and $\delta^{13}C$ values have been very helpful to understand particle dynamics in the ocean (Altabet et al., 1991; Voss et al., 1996).

A notable gap in understanding the linkage between different trophic levels (from top predators to primary consumers) in pelagic food webs is the lack of information about gelatinous organisms. They are widely distributed and occasionally occur in large numbers with biomass exceeding that of fish. This can greatly impact food web dynamics. A likely explanation for the paucity of knowledge of gelatinous organisms is the inherent difficulty of sampling them. Most gelatinous organisms are fragile and break into pieces when sampled with commonly used nets. Thus, information on their ecological role is very limited.

We present here an overview of deep-sea zooplankton food web structure and trophodynamics (macrozooplankton and micronekton), including gelatinous organisms such as siphonophora and salps, on a temporal scale, and its role in organic matter cycling, while addressing gaps in knowledge.

Within the Spanish funded BIOMARE project, the present study aims, by means of stable isotope analysis, to (1) identify the trophic guilds within the macrozooplankton–micronekton community on the Catalan slope; (2) elucidate temporal patterns in isotopic signatures; and (3) explore and identify which environmental variables best explain the observed patterns.

2. Materials and methods

2.1. Study area and samples collection

The study area encompasses a portion of the Catalan Sea slope (Balearic Basin, NW Mediterranean: Fig. 1) between 650 and 800 m.

In the Catalan Sea primary production is characterised by a late winter bloom at the surface and by a deep chlorophyll maximum (DCM) in open waters in summer (Estrada et al., 1993). Advective inputs depend on river discharges through submarine canyons, which are numerous in the area (Cartes et al., 2010a). Besòs River, close to our sampling station (*ca.* 31 km northeast), had maximum flow in April–May (6–4.5 m^3/s) with a secondary peak in October 2007 (4.4 m^3/s). Llobregat River close to Berenguera canyon (*ca.* 25 km northwest) had a similar seasonal pattern, always with greater flow (peak in April = 14.9 m^3/s) than Besòs (data available at http://mediambient.gencat.net/aca/es). Both rivers in the study period (February 2007–February 2008) showed the typical torrential regime of Mediterranean rivers. Stratification of the water column takes place from April to November (Papiol et al., 2008).

Meso/macrozooplankton/micronekton in the water column was sampled using a WP2 net with a mouth area of 1 m^2, equipped with 0.5 mm mesh size net and a system of closure, in horizontal–oblique hauls performed as close to the sea bottom as possible (closest distance to the bottom estimated to be between 13 and 90 m by means of SCANMAR sensors). This gear allows to collect mesoplankton (species ranging from 0.2 mm to 2 mm, such as copepods, ostracods and some small pteropods), macroplankton (2–20 mm, i.e. hyperiids, euphausiids, jellyfish) and micronekton (small but actively swimming organisms ranging in size between 2 and 10 cm, i.e. mesopelagic fish, natantian decapods). However, considering the mesh size of the net (0.5 mm) it is more suitable for macrozooplankton/micronekton, being the mesoplanktonic fraction not well sampled.

A total of 10 hauls were performed off Barcelona, between February 2007 and February 2008, 2 in February 2007 and 2008 (BIOMARE 1 and BIOMARE08, both indicated as B1), 2 in April 2007 (BIOMARE 2 or B2), 4 in June–July 2007 (BIOMARE 3 or B3), and 2 in October 2007 (BIOMARE 4 or B4). All samples were collected on board of the R/V García del Cid (38 m long, 1500 HP).

Samples of particulate organic matter (POM) were collected by Niskin bottles during all the cruises at ca. 800 m depth and filtered on board onto precombusted (450 °C for 4 h) GF/F filters (Whatman, 0.7 μm pore size) using a HCl-cleaned 5 l glass filtration unit. From 2 to 8 l of seawater were filtered (e.g. Struck et al., 2004; Coban–Yıldız et al., 2006). After collection the filters were immediately frozen (−20 °C).

2.2. Gut contents data

Data on the feeding habits of micronekton/macroplankton species were compiled by gut contents analysis which have been carried out in this and in previous studies (see Table 1). Briefly, the guts of some specimens were examined under a compound microscope (×100–×600). The relative proportions (in terms of volume) of phytodetritus, sediment, and animal remains were determined semi-quantitatively. Information on

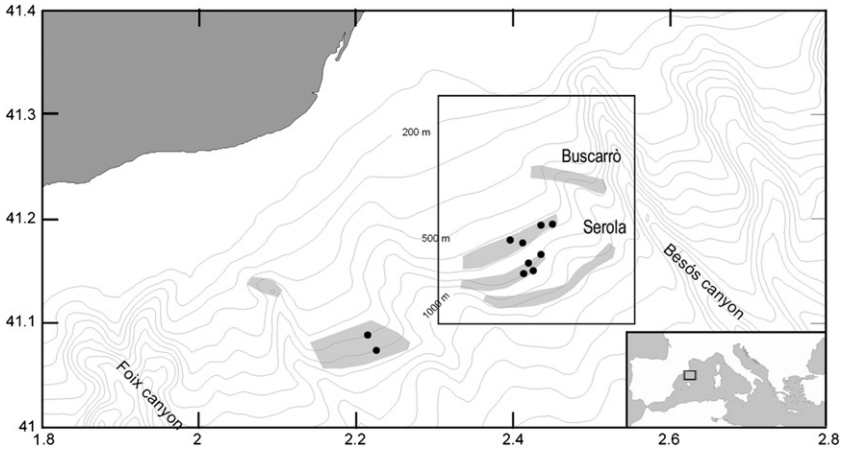

Fig. 1. Map of the whole BIOMARE study area. The quadrate indicates the area where samples used in this study were collected and in grey the sites where trawl hauls and CTDs were carried out, black dots indicate stations sampled by WP2.

Table 1
Species analysed for stable isotopes of N and C during each sampling period. Feeding modes listed in literature are also given: FF = Filter Feeders; O = Omnivores; CSZ = Carnivores on mesozooplankton; CZ = Carnivores on macrozooplankton–micronekton. Feb = February 2007 and 2008; Apr = April 2007; Jun/Jul = June/July 2007; Oct = October 2007. § indicate species for which seasonal analysis were untangled.

Phylum/Class/Order	Taxon	Abbreviation	Feb	Apr	Jun/Jul	Oct	Feeding mode	Source
Cnidaria	*Periphylla periphylla*	Pper	*	*	*		CSZ	Sørnes et al. (2008)
Cnidaria	*Solmissius* sp.	Solm				*	?	
Siphonophora	*Chelophyes appendi culata* §	Capp	*	*	*	*	CSZ	Purcell (1981)
Siphonophora	*Lensia* sp.	Lens				*	?	
Chaethognatha	Chaetognatha §	Chaet	*	*	*	*	CSZ	Pearre (1980)
Copepoda	*Candacia tenuimana*	Cten	*	*			?	
Copepoda	*Candacia* sp.	Cand				*	CZ	Ohtsuka and Onbé (1989)
Copepoda	Calanoidea Unid	Cop	*	*	*		O	
Copepoda	*Calanus helgolandicus*	Chel	*		*	*	O	Paffenhöfer and Strickland (1970)
Copepoda	*Neoscolecithrix* sp.	Neos	*		*	*	?	
Ostracoda	Ostracoda	Ostr		*			FF	Kluijver & Ingalsuo[1]
Hyperiidea	*Vibilia armata*	Varm		*			FF	Madin and Harbison (1977)
Hyperiidea	*Phronima sedentaria*	Psed		*			CZ	Madin and Harbison (1977)
Hyperiidea	*Euprimno macropus*	Emac		*			FF	Madin and Harbison (1977)
Euphausiacea	*Meganycthiphanes norvegica*	Mnor	*	*	*		O	Onsrud and Kaartvedt (1998)
Euphausiacea	*Nematoscelis megalops* §	Nmeg	*	*	*	*	CSZ	Barange et al. (1991)
Mysidacea	*Eucopia henseni*	Ehan		*	*	*	CSZ	Hopkins et al. (1994)
Decapoda	*Gennadas elegans* §	Gele	*	*	*	*	CSZ	Heffernan and Hopkins (1981)
Decapoda	*Sergestes arcticus*	Sarc	*		*	*	CSZ	Vestheim and Kaartvedt (2009)
Decapoda	*Pasiphaea multidentata*	Pmul	*	*	*		CZ	Cartes (1993a)
Decapoda	*Sergia robusta* §	Srob	*	*	*	*	CZ	Cartes (1993b)
Polychaetha	*Tomopteris* sp.	Tomop				*	CZ	Rakusa-Suszczewski (1968)
Pteropoda	*Cavolinia inflexa*	Cinf		*			FF	Gilmer and Harbison (1986)
Pteropoda	*Cymbulia peroni*	Cper	*	*			FF	Gilmer (1972)
Tunicata	*Pyrosoma atlanticum*	Patl	*		*		FF	Drits et al. (1992)
Tunicata	*Salpa maxima*	Smax	*	*			FF	Madin (1974)
Osteichthyes	*Argyropelecus hemigymnus*	Ahem			*	*	CSZ	Kinzer and Schulz (1988)
Osteichthyes	*Chauliodus sloanei*	Cslo		*	*		CZ	Roe and Badcock (1984)
Osteichthyes	*Cyclothone braueri* §	Cbra	*	*	*	*	CSZ	Roe and Badcock (1984)
Osteichthyes	*Cyclothone pygmaea*	Cpyg		*		*	CSZ	Roe and Badcock (1984)
Osteichthyes	*Lampanyctus crocodilus* §	Lcro	*	*	*	*	CZ	Stefanescu and Cartes (1992)
Osteichthyes	*Myctophum punctatum*	Mpun	*		*		CZ	Scotto Di Carlo et al. (1982)
Osteichthyes	*Symbolophorus veranyi*	Sver		*		*	CZ	Watanabe et al. (2002)
Osteichthyes	*Stomias boa*	Sboa	*		*		CZ	Roe and Badcock (1984)

1 http://nlbif.eti.uva.nl/bis/crustacea.php?menuentry=soorten&id=2.

gut contents and trophic guilds of species analyzed within the framework of BIOMARE project is summarized in Cartes et al. (2009); other data on the feeding habits of micronekton/macroplankton species from the Catalan Sea were obtained from literature (*Candacia* sp.: Paffenhöfer and Strickland, 1970; *Lampanyctus crocodilus*: Stefanescu and Cartes, 1992; *Pasiphaea multidentata*: Cartes, 1993a,b; *Calanus helgolandicus*: Ohtsuka and Onbé, 1989; *Periphylla periphylla*: Sørnes et al., 2008).

2.3. Stable isotope analysis

Once collected, biological samples were immediately frozen at −20 °C and later sorted in the laboratory as quickly as possible, identified to species level and prepared for analysis. Species selected were those dominant in both abundance and biomass throughout the sampling period in the macrozooplankton–micronekton assemblage (Cartes et al., 2008, 2010b; see Table 1). Tissues used for isotope analysis of invertebrates were the whole body of hyperiids and copepods, the body wall of siphonophorans, salps, cnidarians, chaetognaths and pteropods, caudal muscle for decapods and euphausiids and dorsal white muscle for fish, except for *Cyclothone* species for which the whole body was used. Samples were dried to constant weight at 60 °C, then ground to a fine powder. For species analyzed whole in which carbonate structures were present (e.g. the exoskeleton in crustaceans, bones in *Cyclothone* spp.), one sub-sample for carbon isotope analysis was acidified by adding 1 M HCl drop-by-drop to remove inorganic carbonates (the cessation of bubbling was used as criterion to determine the amount of acid to add; Jacob et al., 2005), and then samples were dried again at 60 °C for 24 h. Acidification is required because carbonates present a less negative $\delta^{13}C$ than organic carbon (DeNiro and Epstein, 1978). The other sub-sample for nitrogen isotope analysis was not acidified, as acidification results in enrichment (Pinnegar and Polunin, 1999) or depletion (Authors' unpubl. data) in $\delta^{15}N$.

Although some authors suggest extracting lipids from samples prior to stable isotope analysis, a defatting technique is unusual for invertebrates (Iken et al., 2001; Nyssen et al., 2002, 2005; Carlier et al., 2007), and all the (few) published and most recent works on deep-sea invertebrates present isotope data from non-defatted analyses (e.g., Iken et al., 2001; Madurell et al., 2008; Jeffreys et al., 2009; Fanelli et al., 2009a, 2011). Thus, we preferred to use untreated samples for direct comparison with the available literature and for investigation of natural signals of fresh food inputs, after assessing the effects of lipid contents on our results through the relationship between C/N ratios and $\delta^{13}C$ signatures (i.e. higher lipid samples have higher C/N ratios; Tieszen et al., 1983; France, 1996). $\delta^{13}C$ values of untreated samples (not defatted) were converted to $\delta^{13}C_{normalized}$ ($\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 * C/N_{sample}$) according to Post et al. (2007).

As expected, the difference between normalized and untreated samples was small (our samples had low lipid concentrations, i.e. low C/N ratios) and similar for all the species, thus our choice to use untreated samples, was fully justified.

Biological samples were weighed (ca. 1 mg of dry weight) in tin analysis cups. Analyses of filters were run on dried (at 60 °C for 24 h) samples of disks of about 13 mm packed into tin capsules and loaded onto a ThermoFisher Flash EA 1112 elemental analyzer coupled to a Thermo Electron Delta Plus XP isotope ratio mass spectrometer (IRMS) at the geochemistry laboratory of the IAMC–CNR Institute at Naples (Italy).

Samples were run with blank cups and known urea standards. Standards were prepared by weighing (from 0.5 to 2 mg) of analytical grade urea (CH_4N_2O mw=60, C=20% N=46%) of certificated isotopic

composition ($\delta^{13}C = 47.37‰$ vs. Vienna Pee Dee Belemnite {VPDB} and $\delta^{15}N = 0.02‰$ vs. atmospheric N_2).

Three capsules of urea were analysed at the beginning of each sequence and one every six samples to compensate for potential machine drift and as a quality control measure. Experimental precision (based on the standard deviation of replicates of the internal standard) was <0.2‰ for $\delta^{15}N$ and <0.1‰ for $\delta^{13}C$. $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to VPDB and N_2 standards, respectively, according to the following formula:

$$\delta^{13}C \text{ or } \delta^{15}N = \left[\left(R_{sample} / R_{standard}\right) - 1\right] \times 10^3,$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$

A minimum of three replicates (when sufficient samples were available; in a few cases only one sample was processed) were analyzed for all of the species (Tables 1 and 2) and each replicate included just one individual. Only in the case of copepods several specimens were pooled to obtain sufficient mass for the isotope measurement.

Analyses to untangle temporal variations in isotope signatures were performed for 10 species (species marked with § in Table 1).

For POM, the analyses were carried out in triplicate; reproducibility was better than ±10%.

2.4. Environmental variables

CTD casts were performed at each station using an SBE 32 coupled with a fluorometer, a transmissometer and an oxygen sensor. Values of temperature, salinity, oxygen, fluorescence and turbidity were recorded for each CTD profile. The values of these variables at 5 m below the surface and at 5 m above the sea bottom were also obtained.

Phytoplankton pigment concentration (ppc, mg Chl-*a*/m^3), obtained from NASA website (http://reason.gsfc.nasa.gov/Giovanni), was used as indicator of the productivity of the area. Monthly average readings of ppc at the positions of the bottom trawls were used (Cartes et al., 2004), considering different lag intervals before the sampling periods (simultaneously and 1, 2 and 3 months before). In addition we used the primary productivity data downloaded from the Ocean Productivity webpage of the Oregon State (USA) (http://www.science.oregonstate.edu/ocean.productivity/; Behrenfeld and Falkowski, 1997) for the same period.

Mean monthly flow volumes at the mouths of the two main rivers discharging in the area, the Besòs and Llobregat, were obtained from the ACA website (Catalan Agency for Water at http://aca-web.gencat.cat/aca/appmanager/aca/aca/).

2.5. Data analyses

Our isotope data are normally distributed (Kolgomorov–Smirnov test for both $\delta^{15}N$ and $\delta^{13}C$: $p > 0.05$); thus they were not transformed for univariate and multivariate analyses. First, in order to give an overall picture of the food web structure of macrozooplankton and micronekton, a hierarchical cluster analysis (average grouping methods) was carried out on the resemblance matrix (Euclidean distance) of $\delta^{13}C$ and $\delta^{15}N$ mean values per species and per sampling date (month). The groups obtained were compared with postulated trophic groups based on the literature and on our own data, as previously explained. Groups are filter feeders—FF; carnivores on mesozooplankton (copepods, ostracods etc.)—CSZ; carnivores on macrozooplankton and micronekton (gelatinous plankton, euphausiids and decapods)—CZ; and omnivores—O, as listed in Table 1 and also provided in Cartes et al. (2009). A Permutational Multivariate ANOVA (PERMANOVA: Anderson et al., 2008) was performed on this same matrix to compare trophic groups and then a pair-wise comparison was done. Since for some species the feeding guild is unknown (species identified in Table 1 with a "?") the PERMANOVA test also allows to assign them to a trophic category, by comparing their isotopic signatures with those of species with known diet. Significance was set at $p = 0.05$ and p-values were obtained using 9999 permutations, under unrestricted permutation of raw data, which is recommended when there is only one factor.

Secondarily, in order to detect whether there was a general pattern of seasonal variation in stable isotope composition, a non-parametric Multidimensional Scaling (nMDS) were carried out on the triplicate $\delta^{13}C$ and $\delta^{15}N$ values of seven dominant taxa (*Chelophyes appendiculata*, Chaetognatha, *Gennadas elegans*, *Nematoscelis megalops*, *Sergia robusta*, *Cyclothone braueri* and *L. crocodilus*), which belong to different taxonomic groups and trophic guilds (see Table 1), for each sampling date (season). This analysis was carried out separately for $\delta^{15}N$ and $\delta^{13}C$ values. On the two matrices generated, cluster analyses were also performed and the results were overlaid onto the same nMDS plots as circles which represent the highest resemblance level. Two PERMANOVA tests were then performed on the two matrices to compare groups identified, and then pair-wise comparisons were done on the average $\delta^{13}C$ and $\delta^{15}N$ of these groups.

Correlations were used to assess the strength of association between $\delta^{15}N$ and $\delta^{13}C$ data across all sampled materials (see Polunin et al., 2001) and then within each season. Only those species for which data from at least three surveys were available, were included in these analyses.

Finally $\delta^{15}N$ and $\delta^{13}C$ data recorded at each station/sampling period were compared with environmental variables using Spearman's correlation coefficients, separately, and using the BIOENV routine available in PRIMER6 (Clarke and Warwick, 1995) in order to find the best match between the two isotopic values and the environmental variables. For those analyses, only those species analyzed in both

Table 2
Mean $\delta^{15}N$ and $\delta^{13}C$ values (±SD) of taxa analysed from February to October 2007. Trophic levels (TL) are based on the equation reported in the text. Abbreviations as in Table 1. "J" indicates juvenile specimens of *Lampanyctus crocodilus*, "L" means adults. The number (N) of replicates analysed for each species is also given.

	$\delta^{15}N$	$\delta^{13}C$	TL	N
Varm	2.53 (0.12)	−21.67 (0.34)	2.0	3
Smax	2.56 (1.75)	−22.08 (1.15)	2.0 (0.32)	6
Cper	2.80 (0.34)	−20.08 (0.81)	2.1 (0.22)	6
Ostr	3.19	−21.26	2.2	1
Patl	3.45 (0.65)	−21.94 (0.23)	2.3	6
Cinf	3.70 (0.15)	−21.73 (0.99)	2.4	3
Emac	3.65(0.20)	−20.18(0.31)	2.4	3
Capp	4.03 (0.59)	−19.38 (0.82)	2.6 (0.23)	12
Lcro_J	5.02 (0.62)	−19.79 (0.39)	3.0	6
Cten	5.17 (1.49)	−21.43 (1.85)	3.0 (0.59)	6
Chel	5.36 (0.38)	−21.76 (1.12)	3.1 (0.15)	9
Lens	5.37	−18.71	3.1	1
Cbra	5.59 (1.08)	−18.74 (1.06)	3.2 (0.43)	12
Chaet	5.65 (0.84)	−20.38 (0.69)	3.2 (0.33)	12
Cop	5.77 (0.60)	−21.10 (0.37)	3.2 (0.28)	9
Ahem	6.23 (0.10)	−18.51 (0.09)	3.4 (0.04)	6
Psed	6.26	−21.18	3.4	1
Solm	6.29 (1.27)	−17.60 (0.17)	3.5	3
Nmeg	6.29 (0.39)	−20.00 (0.23)	3.5 (0.16)	12
Mnor	6.45 (0.45)	−19.49 (0.20)	3.5 (0.18)	9
Pper	6.49 (0.95)	−20.62 (0.50)	3.5 (0.37)	9
Gele	6.57 (0.94)	−17.88 (1.21)	3.6 (0.237)	12
Srob	6.57 (0.50)	−18.54 (1.30)	3.6	12
Cand	6.58 (0.28)	−20.39 (0.22)	3.6	3
Mpun	6.60 (0.98)	−19.63 (0.44)	3.6	6
Sarc	6.72 (0.24)	−18.94 (0.26)	3.6 (0.09)	9
Pmul	7.02 (0.82)	−18.36 (0.62)	3.7 (0.15)	9
Cpyg	7.12 (0.49)	−20.70 (0.50)	3.8 (0.19)	6
Neos	7.36 (0.58)	−20.48 (0.90)	3.9 (0.23)	9
Sver	7.52 (0.32)	−20.23 (0.69)	3.9	6
Lcro_L	7.62 (0.64)	−17.17 (1.21)	4.0 (0.25)	12
Ehan	7.70 (0.56)	−16.90 (1.00)	4.0 (0.22)	9
Cslo	9.00 (0.84)	−18.82 (0.34)	4.5	6
Sboa	9.18 (0.71)	−18.64 (0.31)	4.6	6
Tomop	9.78 (0.12)	−19.50 (0.21)	4.8	3

periods (February/April vs. June–July/October) were considered. Before the analysis, a draftsman plot (Clarke and Warwick, 1995) was performed on environmental variables in order to look at collinear variables and to reduce the number of environmental variables to be used in the following analyses.

All the analyses were performed using PRIMER6 & PERMANOVA+ (Clarke and Warwick, 1995; Anderson et al., 2008) and STATISTICA 6 software.

3. Results

3.1. Gut contents analysis

Our data and literature sources on the feeding habits of macroplankton/micronekton species allowed to identify the main trophic guilds, summarized in Table 1: 1) filter feeders (FF) encompassed species which feed on POM, marine snow, phytodetritus, such as ostracods, small hyperiids (i.e. *Vibilia armata*, *Euprimno macropus*), pteropods (*Cymbulia peroni*, *Cavolinia inflexa*), salps and pyrosomids; 2) carnivores on small zooplankton, i.e. mesozooplankton (CSZ), include species which prey on small copepods and ostracods, such as Scyphozoan medusae (*P. periphylla*), siphonophora (*C. appendiculata*) and chaethognats; 3) carnivores on zooplankton (CZ) include species which prey on euphausiids, myctophids, hyperiids and small natantian decapods, such as *P. multidentata*, *S. robusta* and mesopelagic fish; 4) omnivores (O) comprises species which alternatively feed on zooplankton and phytodetritus such as *Meganycthiphanes norvegica*.

3.2. Isotope analysis

POM $\delta^{13}C$ values varied temporally (ANOVA test $F_{3,8}=22.96$, $p<0.001$; SNK post-hoc test: February<April–June/July<October), being more depleted during winter (February 2007; $\delta^{13}C=26.40\pm0.41$), increasing in spring and summer ($\delta^{13}C=22.88‰\pm0.04$ SD and $-23.01‰\pm0.56$ SD, in April and June–July respectively) and finally being more positive during autumn (October 2007, $\delta^{13}C=21.23\pm1.41$).

Thirty-four taxa were analyzed on an annual basis (Table 1). Information on feeding habits and diets used in the following is also presented in Table 1.

All the species analysed in our study belong to macrozooplankton and micronekton and even in the case of typically mesozooplanktonic groups (i.e. copepods), we collected large individuals. Thus no considerations on size differences (Bode et al., 2007) have been made in this study.

Isotopic analyses revealed a considerable range of $\delta^{13}C$ and $\delta^{15}N$ values for macrozooplankton–micronekton species (Table 2). $\delta^{13}C$ values ranged from −22.1‰ (*Salpa maxima*) to −16.9‰ (the mysid *Eucopia hanseni*). $\delta^{15}N$ ranged from 2.5‰ (the hyperiid *V. armata*) to 9.8‰ (*Tomopteris* sp.).

Distinct differences were detected in $\delta^{15}N$ values of filter feeders: *V. armata*, *S. maxima* and the pteropod *C. peroni* occupied the lowest trophic levels, positioned at level 2.0, while the other filter feeders (ostracods, *Pyrosoma atlanticum* and *C. inflexa*) ranged from 2.2 to 2.4. Carnivores on mesozooplankton (i.e. on copepods, ostracods etc.) and on larger zooplankton such as the siphonophoran *C. appendiculata*, euphausiids, decapods or small fish had implied TL values higher than 2.6 (Table 2); among carnivores eating macrozooplankton–micronekton, the carnivorous polychaete *Tomopteris* sp. (with a mean wet weight of 0.2 g) was positioned at the highest level (TL = 4.8).

The trophic groups identified by cluster analysis (Fig. 2) are in general agreement with the postulated feeding habits of the group members (Table 1). The cluster analysis based on $\delta^{15}N$ and $\delta^{13}C$ identified two main groups, designated I and II, and three subgroups within II. Group I included filter feeders, for examples the hyperiid *V. armata* and pseudothecosome *C. peroni*, and also the siphonophoran *C. appendiculata* that feeds on small copepods and exhibited the lowest TL among carnivores on mesozooplanton (TL = 2.6). Group II

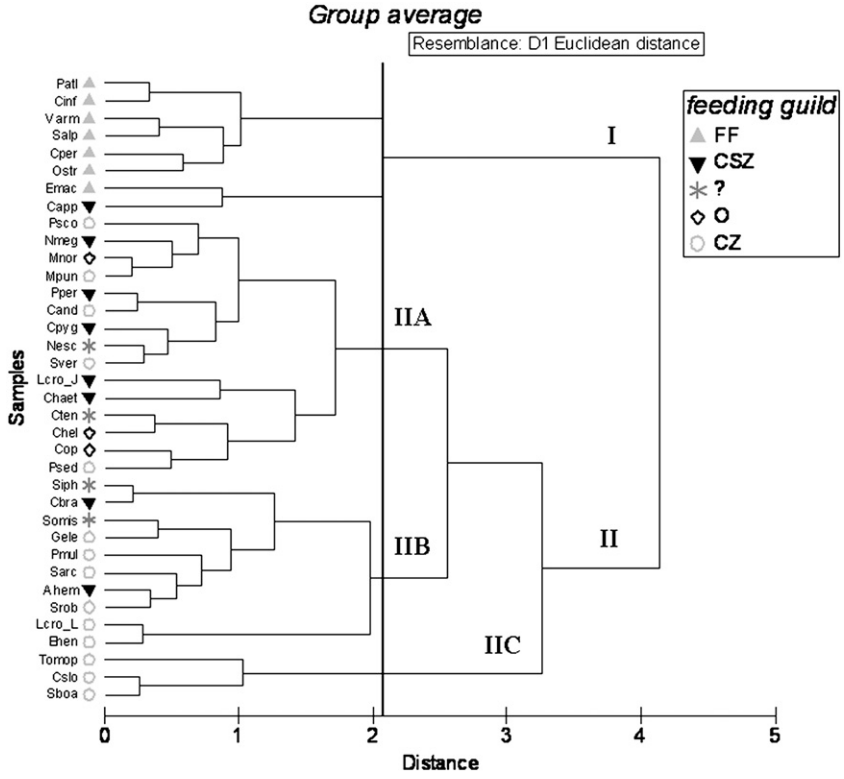

Fig. 2. Hierarchical clustering (Euclidean distance of untransformed data subjected to pair-averaged grouping) of $\delta^{13}C$ and $\delta^{15}N$ for 34 macrozooplankton and micronekton taxa. Roman numerals at the tree branches identify groups of taxa belonging to different trophic guilds. Abbreviations of species as in Table 1.

comprised the remaining species. Within subgroup IIA the cluster algorithm placed carnivores on mesozooplankton from the lowest trophic levels, such as juveniles of the lantern fish *L. crocodilus* and chaetognaths, to carnivores on macrozooplankton–micronekton such as the myctophids *Symbolophorus verany* and *Myctophum punctatum* and also omnivores (i.e. calanoid copepods, *Calanus helgolandicus*, *M. norvegica*). Within subgroup IIB there are only carnivores, both on mesozooplankton (the teleosts *Argyropelecus hemygimnus* and *C. braueri*) and on macrozooplankton–micronekton (*P. multidentata*, Sergestidae, large *L. crocodilus*), together with species of unknown feeding habits (the jellyfish *Solmissius* sp. and the siphonophoran *Lensia* sp.). Finally in subgroup IIC there were only carnivores on macrozooplankton–micronekton, those species positioned at the highest trophic level, such as the polychaete *Tomopteris* sp. and the stomiids *Chauliodus sloani* and *Stomias boa*.

Average stable isotopic ratios differed significantly among trophic groups identified by cluster analysis (PERMANOVA $F_{4,33}=11.51$, $p<0.001$). The pair-wise comparisons showed significant differences between the isotopic signatures of filter feeders and all the other groups (Table 3). Species with unknown feeding habits differed significantly only from filter feeders; thus these species may be included in the trophic guilds of either omnivores or carnivores on zooplankton. More specifically, *Candacia tenuimana* fell in the group of omnivores, *Lensia* sp. in the group of carnivores on mesozooplankton, while the jellyfish *Solmissius* sp. and the copepod *Neoscolecithryx* sp. were carnivores on macrozooplankton–micronekton (Fig. 3).

3.3. Temporal isotopic variations in dominant species

nMDS analysis carried out on the stable isotopic ratios of seven dominant species at a temporal scale showed a good separation of both $\delta^{15}N$ and $\delta^{13}C$ signatures of the specimens obtained in February–April from those obtained in June/July and October (Fig. 4a–b). $\delta^{15}N$ signatures from April were less dispersed than signatures from February, while $\delta^{13}C$ values from February were more closely grouped. PERMANOVA tests performed on both the $\delta^{15}N$ and $\delta^{13}C$ signatures of the species showed significant differences among the seasons (main test on $\delta^{15}N$ values: $F_{3,11}=6.44$, $p<0.001$; main test on $\delta^{13}C$: $F_{3,11}=6.70$, $p<0.001$).

At a species level, $\delta^{15}N$ values of taxa feeding on copepods (*C. appendiculata*, Chaetognatha, *N. megalops* and *P. periphylla*) showed the same trend (Fig. 5), increasing from February to October.

3.4. Relationship between $\delta^{13}C$ and $\delta^{15}N$ data in food webs

The correlation including all seasons between $\delta^{15}N$ and $\delta^{13}C$ was weak ($N=176$, $r=0.35$).

The strength of the correlations of species in common among the four seasons, was higher when the water column was homogenized

Table 3
Results of PERMANOVA pair-wise tests comparing isotopic ratios of postulated feeding groups based on 9999 permutations. FF = Filter Feeders; O = Omnivores; CSZ = Carnivores on small zooplankton (mesozooplankton); CZ = Carnivores on macrozooplankton/micronekton; ? = taxon with unknown feeding habits. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

Groups	t
FF, CSZ	5.76***
FF, ?	4.30***
FF, O	4.76***
FF, CZ	6.99***
CSZ, CZ	2.08*
O, CZ	2.15*

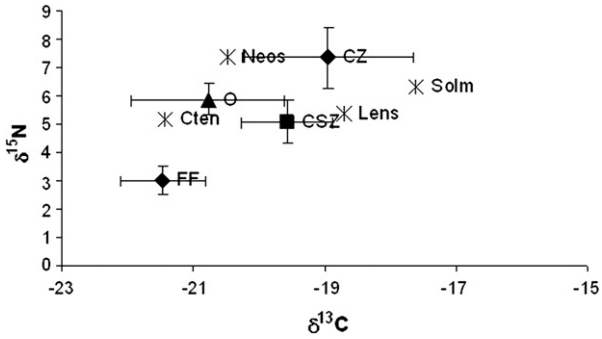

Fig. 3. Scatterplot of mean $\delta^{15}N$ (‰) vs. $\delta^{13}C$ (‰) values of each major trophic group, as obtained by cluster analysis for zooplankton. The average $\delta^{13}C$ and $\delta^{15}N$ values of all the species that could not be attributed to a particular trophic group from data in the literature are also shown (open symbols). Vertical and horizontal bars are standard deviations. Neos = *Neoscolecithrix* sp.; Solm = *Solmissius* sp.; Cten = *Candacia tenuimana*; Lens = *Lensia* sp.

($r=0.41$, $p=0.02$ in February and $r=0.41$, $p=0.004$ in April) compared to when it was stratified ($r=0.29$, $p=0.04$ in June/July and $r=0.36$, $p=0.02$ in October). A general trend of $\delta^{13}C$ enrichment, as observed for $\delta^{13}C$ POM values, was recorded from February–April to June/July–October.

3.5. Correlation between isotopes data and environmental variables

The results of Spearman correlation showed that $\delta^{15}N$ values were not influenced by any of the environmental variables we explored. $\delta^{13}C$ values were positively correlated (indicating more enriched $\delta^{13}C$) with the concentration of Chlorophyll *a* (recorded simultaneously and one month before sampling), with Primary Productivity (PP) data (recorded simultaneously and one month before sampling), with river discharge recorded one month before sampling, with salinity recorded at 5 m from

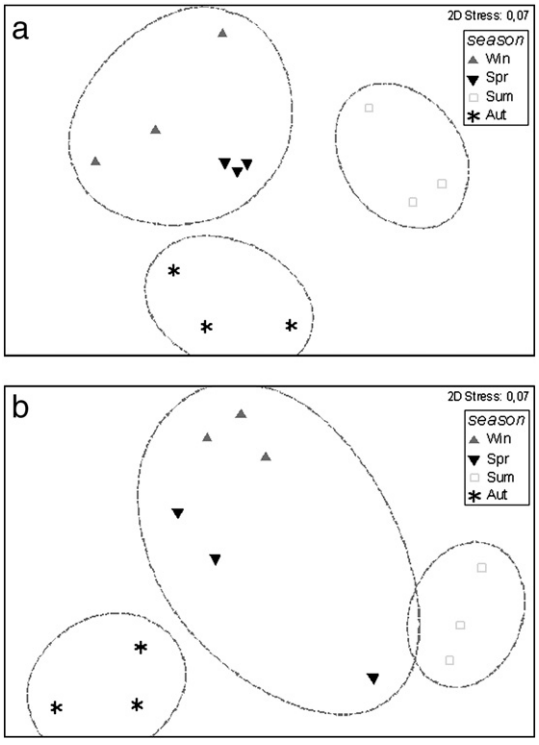

Fig. 4. nMDS plots of a) $\delta^{15}N$ and b) $\delta^{13}C$ values of 9 dominant species. The results of the cluster analysis are superimposed on the figure showing 3 groupings at 2.7 (Euclidean) distance (dashed line). Win = Winter (February 2007–08); Spr = Spring (April 2007); Sum = Summer (June–July 2007); Aut = Autumn (October 2007).

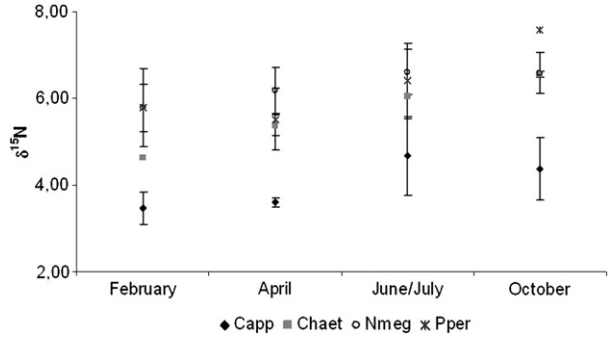

Fig. 5. Mean $\delta^{15}N$ (‰) values of taxa feeding on mesozooplankton (i.e. copepods) throughout the sampling period (February–October). Vertical bars are standard deviations. Capp = *Chelaphyes appendiculata*; Chaet = Chaetognatha; Nmeg = *Nematoscelis megalops*; Pper = *Periphylla periphylla*.

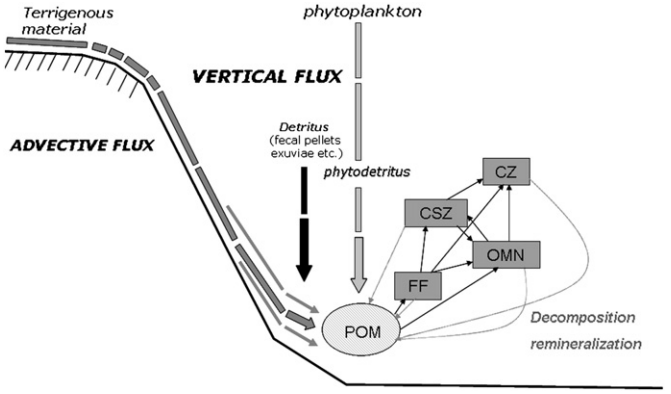

Fig. 6. Scheme of the food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope and of the carbon fluxes arriving to the bottom.

the surface and with the depth at which the maximum turbidity was recorded (Table 4). $\delta^{13}C$ values were negatively correlated (indicating more depleted $\delta^{13}C$) with maximum turbidity (Table 4). The BEST analysis (BIOENV method) showed that the best match between isotopic values and environmental variables was obtained with five variables ($R = 0.715$; $p < 0.01$): temperature and turbidity recorded at 5 m above the bottom and readings of Chlorophyll *a* recorded two and three months before the sampling and simultaneously to sampling.

4. Discussion

This is the first attempt to elucidate the trophic web structure of deep(open)-sea zooplankton species based on a multi-taxon data set (from gelatinous plankton to fish), with the only exception of some results reported by Polunin et al. (2001). They analyzed macrozooplankton only at a broad taxonomic level (i.e. order or higher group such as "gelatinous plankton" or "macrozooplankton"), reporting data also on some micronektonic decapods (*Sergestes arcticus*, *S. robusta* and *P. multidentata*) and fish (*C. sloani*, *S. boa*, *L. crocodilus* and *C. braueri*). In addition, most of the species/genera considered in our study are cosmopolitan (*M. norvegica*, *S. boa*, *C. sloani*, *Cyclothone* spp., *S. arcticus* etc.), so our results may be extrapolated to other geographic areas and located in a broad context beyond the Mediterranean.

4.1. Trophic structure of deep macrozooplankton–micronekton community on the Catalan slope

Our results allowed to depict a complex food web, far from the trophic chain normally described for pelagic environments, in which multiple trophic linkages among the species occurred (Fig. 6).

Table 4
Spearman correlation of $\delta^{13}C$ values with environmental variables recorded for each collection of macrozooplankton/micronekton fauna. Only significant correlations are given. S = salinity; Turb = Turbidity; PP = Primary productivity. * $p<0.05$, ** $p<0.01$, *** $p<0.001$.

$\delta^{13}C$	Valid N	Spearman R	p-level
S 5 m	137	0.18	*
Chl *a* max (+5 m)	137	-0.21	*
Turb 5 m	137	-0.35	***
ΣTurb (0–50/200 m)	137	-0.33	***
Turb max	137	-0.26	**
Depth Turb max	137	0.31	***
Chl *a* 1 month before	137	0.24	**
Chl *a* simultaneous	137	0.22	**
PP 1 month before	137	0.32	***
PP simultaneous	137	0.24	**
River discharge 1 month	137	0.18	*

We identified a general tendency in the distribution of species in the multi–species analysis, where secondary carnivores (e.g. Stomiiformes and the polychaete *Tomopteris* sp.) and filter feeders (primary consumers) were located at the two extremes of the trophic web, with omnivores and carnivores on small zooplankton (mesozooplankton) at intermediate trophic levels. Secondary carnivores prey on organisms from several trophic levels (from gelatinous zooplankton to other decapods and fish, i.e. filter feeders, carnivores on mesozooplankton and omnivores; see Fig. 6) as well as omnivores, which alternatively act as either particle feeders or carnivores (see below), thus creating a complex web in which an organism (except those located at the top) may be prey and/or predator.

Our results for stable carbon and nitrogen isotopes of macrozooplankton–micronekton are consistent with previously reported values evaluated at species level (Fanelli et al., 2009a) based on data obtained at the South of Mallorca (Algerian Basin). The isotopic signatures of our target species fit well with gut content findings in the literature (when it is available) and based on our own data (see Table 1). However data from the Catalan sea slope differed from those reported for some common species from Eivissa island (Algerian basin: Polunin et al., 2001). $\delta^{15}N$ signatures in our study were in general 1–2‰ more depleted than those observed by Polunin et al. (2001) for the same species (see above). Accordingly our baseline was also more depleted than that reported by Polunin et al. (2001; $\delta^{15}N$ of gelatinous plankton in the study of Polunin et al. ranged from 5 to 7‰ vs. our values which ranged from 3 to 4‰).

This study revealed wide ranges of both $\delta^{15}N$ and $\delta^{13}C$ values (Table 2) for all the species which suggest that zooplankton above the Catalan slope probably exploit different sources of primary production ($\delta^{13}C$ varied from −22.1‰ to −16.9‰). Conversely in the Algerian basin a narrower range of $\delta^{13}C$ values ($\delta^{13}C$ varied from −21.1‰ to −19.9‰; Fanelli et al., 2009a) were found, implying that zooplankton there mainly exploit a single source of primary production, i.e. locally produced phytoplankton and marine snow derived from it. Additionally our $\delta^{13}C$ values were generally more enriched from those reported for some common species from Eivissa island (Algerian basin: Polunin et al., 2001). The Algerian basin, due to the near absence of river discharges, is a more oceanic and oligotrophic area than the Balearic basin (Cartes et al., 2009). Our study area within the Balearic basin is indented by several submarine canyons (the nearest *Besós* and *Berenguera*) that channel downward flow of water and suspended POM (Puig and Palanques, 1998). Canyons, which heads coincide with areas of high surface primary production (Vetter, 1995) may enhance the available POM for filter-feeders such as salps. The wide range of POM ^{13}C signatures (from −21‰ to −26‰) is consistent with the idea of the occurrence of both a vertical flux toward the deep ocean from the uppermost layers of the water column (i.e. the euphotic zone) and

a lateral flux driven by physical processes related to sediment transfer (Tesi et al., 2007), such as canyon transport.

Variability in the relationship between $\delta^{13}C$ and $\delta^{15}N$ was particularly great among carnivores on macrozooplankton–micronekton, animals that prey on organisms from several trophic levels (from gelatinous zooplankton to other decapods and fish) and among omnivores (Fig. 3). Indeed, the omnivore designation was somewhat arbitrary, as they are feeding at several different trophic levels and could therefore be considered either particle feeders or carnivores (Burd et al., 2002). For example, pelagic omnivores include species such as the krill *M. norvegica*, a key organism in food webs of temperate and cold waters, utilizing diverse food sources and also a prominent prey for fish, birds and marine mammals (Pearcy et al., 1979; Mauchline, 1980; Falk-Petersen and Hopkins, 1981). Microscopic investigations of stomach contents from *M. norvegica* have revealed items such as detritus, ctenophores, chaetognaths and copepod remains (e.g. Mauchline, 1980; Sameoto, 1980; Beyer, 1992; Buchholz et al., 1995; Båmstedt and Karlson, 1998), and measurements of gut fluorescence have assessed its herbivorous food intake (Simard et al., 1986; Onsrud and Kaartvedt, 1998).

The group of carnivores on mesozooplankton showed the narrowest range of $\delta^{13}C$, although their $\delta^{15}N$ range was particularly wide. This suggests that a wide range of species belonging to different trophic levels exploited a single food source (probably copepods). Copepods are the most abundant taxon in deep Mediterranean suprabenthos and zooplankton (Cartes, 1998), constituting a superabundant food resource. So, this exploitation of a single food does not necessarily imply competition among carnivores consuming copepods.

Among those species with unknown feeding habits (i.e. there are no data on gut contents), stable isotope analyses assigned the copepod *C. tenuimana* to an omnivorous trophic guild. This conclusion is consistent with gut content data for closely-related species (i.e. *Candacia bipinnata*, Ohtsuka and Onbé, 1989). Several copepod species exhibit an expansion of trophic niches; they tend to be omnivorous to avoid competition for food (Gage and Tyler, 1991; Jarre-Teichman et al., 1997). For example, *C. helgolandicus* feeds not only on living organisms, but also on dead particles (dead diatoms and faecal material: Paffenhöfer and Strickland, 1970). Again, the omnivory attributed to deep-sea zooplankton species may be better described as a mixed behavior in which species may feed both on organic particles and prey on small invertebrates (e.g. larvaceans in the case of *C. bipinnata*: Ohtsuka and Onbé, 1989; present study). Conversely the copepod *Neoscolecithrix* sp. fits well with the trophic guild of carnivores on zooplankton, according to its mouthpart morphology (Bradford-Grieve, 2002). The jellyfish *Solmissius* sp. is also a carnivorous species, likely similar in diet to the other deep-sea jellyfish analysed in this study, *P. periphylla* that feeds on copepods and remains of euphausiids. The main prey items found in the stomachs of *P. periphylla*, which displayed a similar isotopic composition, are calanoid copepods, especially *Calanus* spp., together with exoskeletons of the northern krill *M. norvegica*, ostracods of the genus *Conchoecia* and chaetognaths (Youngbluth and Båmstedt, 2001; Sørnes et al., 2007).

As in our study, previous findings (deep-sea benthic ecosystem off the NE Atlantic Ocean: Iken et al., 2001; Algerian basin, northwest and southeast off Mallorca: Madurell et al., 2008; Fanelli et al., 2009a; benthic food web off the Catalan Sea slope, Fanelli et al., 2011) have shown that there is significant overlap in nitrogen isotopic values between trophic levels, suggesting a smaller stepwise enrichment than the most widely assumed 3.4‰ (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Post, 2002) and in general in deep-sea ecosystems, it seems unrealistic to use a single fractionation factor to characterise the food web structure (Caut et al., 2009). As an example, small *P. multidentata* (with $\delta^{15}N$ signature of 7.0‰) consume prey (e.g. *V. armata*, euphausiids; Cartes, 1993a,b) for which the $\delta^{15}N$ signature ranged between 2.5% and 6.4%, providing fractionation factors of 4.5 and 0.6, respectively. Thus the macrozooplankto/micronekton food web seemed to imply a complex set of trophic linkages which cannot be easily separated in a step-wise way. In an attempt of simplification, we can assume an average trophic enrichment between consumers and their diet of 2.75‰, as proposed by Caut et al. (2009; based on 268 estimates of $\Delta^{15}N$ from reviewed papers, e.g. the difference between the isotopic composition of a consumer with respect to its diet), or of 3.1‰ (as calculated according to the equation proposed by the same authors for invertebrates) which seem to be consistent with the dietary information available for the bulk of carnivores. Under this assumption, at least three trophic levels were identified within the macrozooplankton assemblage off the Catalan slope. As a consequence, the zooplankton food web there seems to be more complex than that southeast off Mallorca (Fanelli et al., 2009a). At the latter site, zooplankton was found to be organized in only two trophic levels.

In summary, over the Catalan slope, assemblages ran from a lower trophic level occupied by filter feeders such as *C. peroni* and *S. maxima*, both strictly phytophagous species (with low contribution of detrital particles and nanoplankton: Gilmer, 1972; Madin, 1974) up to the swimming polychaete *Tomopteris* sp. (a large specimen of total length >5 cm) that feeds on chaetognaths, tunicates and fish larvae (Fauchald and Jumars, 1979). A similarly wide range of $\delta^{15}N$ values was observed for zooplankton living in the upper ocean (<800 m depth) close to the Endeavour Ridge hydrothermal vent plume (Northeast Pacific off the Canadian coast), where $\delta^{15}N$ ranged from 7‰ to 16.8‰ (Burd et al., 2002). Low $\delta^{15}N$ values occur in zooplankton feeding directly on living autotrophs in the epipelagic zone and values increase with each trophic step. Filtering organisms (such as pteropods in our study) and predators (siphonophores and chaethognaths) showed $\delta^{15}N$ values of 2–4‰ and 4–5‰, respectively, values comparable to those found for filtering copepods and chaethognaths from the epipelagic North Pacific Central Gyre (about 20–30°N) (Mullin et al., 1984).

As mentioned above, the lower trophic level in this study was occupied by filter feeders (e.g. hyperiids and salps) which are analogous to the suspension feeders found at the base of the benthic food web off the Catalan slope (Fanelli et al., 2011). Although $\delta^{15}N$ values found for *Amphiura chiajei* and *Amphipholis squamata*, the suspension feeders found at the lowest trophic level in the benthic food web, with a mean $\delta^{15}N = 4.25‰ \pm 0.29$ (Fanelli et al., 2011), were higher than those of hyperiids and salps (mean $\delta^{15}N = 2.60‰ \pm 0.02$). In spite of this, the same number of TLs was found in both systems. Three levels were also suggested by $\delta^{15}N$ for the deep-sea benthic food web of Porcupine Abyssal Plain (Iken et al., 2001). This comparability is quite unexpected, since in general the length of pelagic food webs is shorter than that of benthic ones (Bode et al., 2007; Fanelli et al., 2009a, b). A possible explanation for this discrepancy might be that we worked on fauna collected in the proximity of submarine canyons, animals likely exploiting two different basic food sources, both marine phytodetritus and terrestrial POM (Tesi et al., 2007). This could allow a diversification of trophic strategies among zooplankton species. In fact, gut content studies performed in our study area on *Pasiphaea* spp. (Cartes, 1993a,b) and on the lanternfish *L. crocodilus* (Stefanescu and Cartes, 1992) showed some feeding on both suprabenthic and benthic resources (*Boreomysis arctica*, gammaridean amphipods, sigalionid worms) in addition to zooplankton prey.

4.2. Temporal patterns in isotopic signatures and influence of environmental variables

In general the low $\delta^{13}C$–$\delta^{15}N$ correlation observed for zooplankton close to the Catalan slope was likely due to the exploitation of both newly synthesized and older recycled material (Burd et al., 2002). Indeed, high $\delta^{13}C$–$\delta^{15}N$ correlations would likely indicate a single food source (as, for example, in deep-sea communities; Polunin et al., 2001) and suggest pulses of 'fresh' organic matter from primary production arriving after phytoplankton blooms in the euphotic zone. In contrast, weak correlations point to an array of possible sources of production.

The highest $\delta^{13}C$–$\delta^{15}N$ correlations were found in February–April, coinciding with the trend of surface chlorophyll-*a* concentration in the area. This is also consistent with the significant correlation found between $\delta^{13}C$ values and surface chlorophyll-*a* concentration recorded simultaneously to sampling. Thus zooplankton communities may be sustained in winter–spring mainly by primary production. Zooplankton migrates vertically in the western Mediterranean (Sardou et al., 1996) generating substantial and rapid transport (the *swimmer flux*; Miquel et al., 1994) of new production from the euphotic zone downward. In the open ocean, swimming by zooplankton produces a major portion of downward organic matter transfer, and zooplankton also aggregate small particles as fecal 'shuttles' that sink rapidly (Wefer, 1989). On the other hand, the weaker correlations found in summer and autumn suggest a multiple sources of carbon sustaining deep-sea zooplankton in these periods (both vertical and advective fluxes). Suspended sediment supplied by river discharges is transferred down the slope in near-bottom nepheloid layers along the entire shelf, but especially within canyons (Puig and Palanques, 1998). Over the Catalonian mid-slope there is a permanent nepheloid layer located at 350–400 m (Puig and Palanques, 1998), the position and intensity of which change seasonally (i.e. depending of changes in water masses and shelf-slope fronts).

Temporal changes in food sources for zooplankton were also evident in $\delta^{13}C$–$\delta^{15}N$ relationships observed SW of Mallorca (off Cabrera) in the northwestern Mediterranean (Fanelli et al., 2009a), however there correlations were much stronger than off the Catalan slope indicating a single source of nutrition for those zooplankton communities.

A second increase in the $\delta^{13}C$–$\delta^{15}N$ correlation was found among zooplankton in October, when both the $\delta^{13}C$ and $\delta^{15}N$ signatures of some dominant species differed consistently from those of July. This could be related with a second peak of food input in October, in turn related with i) the formation of the DCM at *ca.* 60–110 m (Turley et al., 2000) in late spring–summer (Estrada et al., 1993) in the western Mediterranean Basin, and/or ii) a second peak of river discharge found in the area between August and October (http://aca-web.gencat.cat/aca/appmanager/aca/aca/). A DCM is characteristic of oligotrophic waters, including the Mediterranean (Estrada et al., 1993; Turley et al., 2000), in which production is based on diatoms that are more $\delta^{13}C$-enriched than dinoflagellates (Gearing et al., 1984). This is consistent also with the progressive $\delta^{13}C$ enrichment found for dominant species from summer (July) to early autumn (October) in the area. Conversely, in July zooplankton probably exploited only older recycled material (Burd et al., 2002), since primary production was low in this period and river discharge was also at a minimum (http://aca-web.gencat.cat/aca/appmanager/aca/aca/).

In any case, $\delta^{13}C$–$\delta^{15}N$ correlations were higher for planktonic than for benthic species ($r = 0.11$; Fanelli et al., 2011), although in both cases couplings with inputs from both surface primary production and river discharge were detected, as demonstrated by the significant correlation of $\delta^{13}C$ values with surface chrorophyll-*a* and river discharge.

In conclusion, deep near-bottom zooplankton is a key-compartment in food webs close to submarine canyons, where infauna are also an important resource for fish and decapods (Cartes and Maynou, 1998). In this continental area (the Catalan slope), deep zooplankton are also influenced by advective fluxes, and the zooplankton food chain is more complex than in insular areas.

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