

Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data

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ABSTRACT: Fishes and invertebrates were collected from the continental slope southwest of the Balearic Islands, Mediterranean, in October 1996 and May 1998 from 3 faunally-distinct depth zones: 200 to 800 m (upper slope), 800 to 1425 m (middle slope) and 1425 to 1800 m (lower slope). Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between October 1996 and May 1998 were observed only in the crustaceans *Aristeus antennatus* and *Nematocarcinus exilis*. There were few differences among depths in $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ of benthic fishes or crustaceans: the shrimps *A. antennatus* and *Acanthephyra eximia* showed higher $\delta^{15}\text{N}$ values at greater depth, and $\delta^{13}\text{C}$ values of the fishes *Alepocephalus rostratus* (Alepocephalidae) and *Coelorhynchus coelorhynchus* (Macrouridae) also tended to increase with increasing depth. Differences in plankton and suprabenthos were also observed among zones (at depth, greater $\delta^{15}\text{N}$ values of gelatinous plankton, calanoid copepods and peracarids were recorded, along with smaller $\delta^{13}\text{C}$ values of gelatinous plankton and peracarids). These are attributed to a microbially-mediated increase in $\delta^{15}\text{N}$ and a reduction in $\delta^{13}\text{C}$ of the particulate material remaining after preferential utilization of labile organic matter in the stable and relatively high (13°C) temperature of the Mediterranean water column. Strong positive correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data for plankton, fishes and crustaceans indicated a single primary source material for these communities, which is attributed to marine snow.

KEY WORDS: Deep-sea · Mesozooplankton · Fishes · Crustaceans · Suprabenthos · Mediterranean · Bathyal

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INTRODUCTION

Studies of the feeding relationships of deep-sea organisms are very limited and have concentrated primarily on gut-content data, and these data have substantial limitations. For example, gut contents reflect diets at particular points in time and space, and severely neglect certain types of dietary materials such as gelatinous plankton and detritus that may nevertheless be very important in the sustenance of marine

food-webs. Other limitations include problems associated with the voiding of gut contents upon capture, and the very sporadic feeding of many carnivorous species. Furthermore, many animals crush or grind their food, such that identification of prey becomes very difficult, and it is not often clear which components of diets are actually assimilated, particularly when refractory or amorphous foods are ingested (Pinnegar & Polunin 2000). Such difficulties are especially great in the study of food webs in the deep ocean.

The use of stable nitrogen and carbon isotopes for the study of trophic interactions is now common in aquatic ecosystems (e.g. Pinnegar & Polunin 2000).

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Stable isotopes can provide an indication of the prey assimilated over a considerable period of time (Hesslein et al. 1993) and elucidate aspects of both the origin and transformation of organic matter ingested. Stable nitrogen isotopes have been used to help define the trophic level of organisms (Vander Zanden et al. 1997). Carbon isotopes may be useful indicators of sources of production (e.g. Harrigan et al. 1989). Given the constraints and paucity of gut-content data, stable isotopes can clearly help to elucidate some aspects of the structure of deep-sea food webs.

Inputs of material to the deep ocean include falls from large animals such as sharks (e.g. Witte 1999) and export of material from littoral plants such as macroalgae (Vetter & Dayton 1999). However, the main input of primary production into this environment is considered to be the downward flux from the epipelagic zone of aggregated detrital material (e.g. faecal pellets and plankton exoskeletons) and zooplankton (e.g. Miquel et al. 1994) which constitute what is loosely referred to as 'marine snow' (e.g. Sumich 1999). The flux of this material may be rapid (Riemann 1989), and phytodetritus can at times be up to 1 cm thick on the sea floor (Smith et al. 1996). With increasing depth, the flux tends to decrease (Miquel et al. 1994, Sumich 1999) and change in character (Williams & Gordon 1970); it also tends to vary temporally in response to changes in production (Riemann 1989, Miquel et al. 1994). The supply of food is generally considered as the main limiting factor for most deep-sea communities (Gage & Tyler 1991), and consequently marine snow constitutes a valuable food resource for deep-sea microbes, metazoans and bathyal detritivores (Smith et al. 1996). Bacteria may have important ecological roles in the highly oligotrophic deep-Mediterranean environments, for example through decomposition of particulate matter derived from the upper layers (Danovaro et al. 1993). In spite of the evident role of marine snow in food supply, there has been little attempt to assess the diversity of source materials consumed by organisms in the Mediterranean bathyal.

Relative to the Atlantic coast of western Europe, the Mediterranean bathyal assemblage (1500 to 2500 m) is impoverished in numbers of species (although exhibiting some endemism; e.g. Moranta et al. 1998). Overall abundance is also well below that of Atlantic coasts (Pérès 1985), and generally declines with depth (e.g. Cartes 1998). The Mediterranean deep sea constitutes a distinct environment, with a high and almost constant temperature (around 13°C) and salinity (Fredj & Laubier 1985) below 200 m. It has a characteristically low concentration of oxygen (Randall & Farrell 1997) and there is often a scarcity of food available to the benthos (Pérès 1985). In the western Mediterranean, picoplankton (>2 µm) is responsible for up to 50% of

the primary production; this is exploited by the microbial food web (Azam et al. 1983) and may only inefficiently support the requirements of fishes (Randall & Farrell 1997). Waters around the SW Balearic Islands are as a rule particularly oligotrophic (e.g. Emeilyanov 1972); however phytoplankton blooms do sometimes occur, and winter and summer peaks in primary production have been recorded (Estrada et al. 1985). Temporal changes in the food available to bathyal communities are therefore to be expected and may be detectable in isotopic data.

Community structure changes markedly as a function of depth (Stefanescu et al. 1993), and within the region adjacent to the SW Balearic Islands there are 3 different fish assemblages; an upper slope assemblage (US) from 200 to 800 m depth, a middle slope assemblage (MS) from 800 to 1425 m and a lower slope assemblage (LS) below 1425 m (Moranta et al. 1998). The MS is characterized by higher biomass, abundance and mean fish weight than the LS (Moranta et al. 1998), and similar depth zones exist for assemblages of decapod crustaceans (Maynou & Cartes 2001). In the neighbouring Catalan Sea, the LS is characterized by smaller, more sedentary species with lower energy requirements (Stefanescu et al. 1993, Cartes 1998). Vertical migrations occur, but movements and distributions tend to be complex and their implications for vertical material fluxes from the epipelagic are unknown (Andersen et al. 1992, Macquart-Moulin 1993); an important question is whether, in spite of such migrations, trophodynamic differences occur among communities at different depths.

Among deep-sea fishes are benthic species which ambush prey, forage slowly on the sediment surface, or scavenge large carcasses falling from above, and bathypelagic species, which possess buoyancy mechanisms and enter the water column to feed (Mahaut et al. 1990, Koslow 1996). The scavengers have been observed by the use of baited cameras, but very little is known about them.

The main aim of the present study was to explore the pathways potentially supporting Mediterranean bathyal slope communities. The specific hypotheses were that (1) food-web structure differs between depth zones, (2) deep-sea food webs respond to seasonal changes in the photic zone, and (3) there is only 1 main food source in the Mediterranean deep-sea, i.e. marine snow. We sought to test these hypotheses by analyses of the stable isotopes of carbon and nitrogen.

METHODS

Sample collection was carried out from the EV 'Garcia del Cid' in October 1996 and May 1998 off the

Balearic Islands (Algerian Basin, western Mediterranean) south of the Ibiza and Formentera islands (Fig. 1). Samples of large fishes and decapod crustaceans were obtained by a semi-balloon otter trawl towed at a speed of 5 km h^{-1} with a single warp and codend, mesh-size 6 mm. A total of 46 trawls (32 in the October 1996 cruise and 14 in May 1998) were conducted. The trawls were carried out between 200 and 1800 m depth. Samples of small suprabenthos/zooplankton were obtained simultaneously during the May 1998 cruise with a small plankton net ($40 \times 60 \text{ cm}$ mouth; $500 \mu\text{m}$ mesh size) attached to the bottom trawl. Also 6 suprabenthonic hauls were completed at 200 m intervals between 200 and 1800 m. Materials were sorted to the lowest possible taxonomic level and freeze-dried. Fishes and decapod crustaceans were classified to species level, the principal authority for the fishes being Whitehead et al. (1986). Due to the minimum weight required for isotope analysis, suprabenthos/zooplankton was not identified to species level and organisms were grouped into broad taxa. Suprabenthos animals were exclusively caught in the benthic boundary layer (~ 1 to 2 m above bottom), whilst zooplankton (mainly copepods and euphausiids, but also gelatinous plankton) were caught in this zone and in the water column due to the lack of a closing mechanism on the plankton net. Gelatinous plankton included siphonophores, medusae and chaetognaths, whilst the macrozooplankton was composed of pelagic crustaceans (mainly euphausiids and pelagic decapods). Suprabenthic mysids consisted almost exclusively of the species *Boreomysis arctica*, and suprabenthic peracarids consisted largely of amphipods, but also of isopods and cumaceans.

White muscle tissue was sampled from each fish, freeze-dried, and ground to a fine homogeneous powder, while most invertebrate samples consisted of whole organisms. The crustacean samples had to be decalcified to remove the inorganic carbon from the exoskeleton, since inorganic carbonates tend to be less negative in $\delta^{13}\text{C}$ than other bodily fractions (DeNiro & Epstein 1978). A small quantity of 1 M hydrochloric acid was added to the samples and left for 3 h. The samples were then rinsed with distilled water, dried at 60°C for 12 h and reground. Since this process results in enrichment of ^{15}N (Pinnegar & Polunin 1999), crustacean samples required analysis before (for $\delta^{15}\text{N}$) and after (for $\delta^{13}\text{C}$) decalcification. Some suprabenthos samples could not be analyzed after decalcification due to the small size of the initial sample.

^{15}N , ^{14}N , ^{13}C and ^{12}C concentrations in the samples were determined using continuous-flow isotope-ratio mass spectrometry (CF-IRMS) (Preston & Owens 1983). One milligram ($\pm 0.1 \text{ mg}$) of ground material was oxidized and the N_2 and CO_2 passed into a single inlet

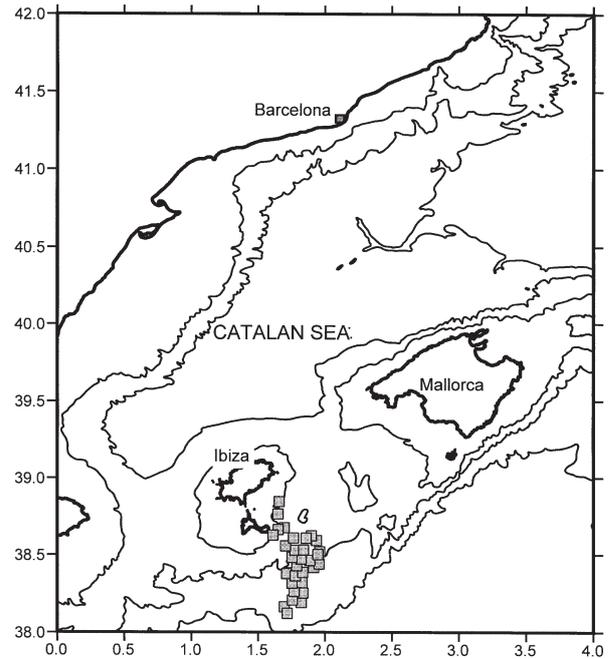


Fig. 1. Location of the study area and specifically of the trawl hauls in October 1996. Depth contours are 200, 1000 and 2000 m. \blacksquare : haul sites

dual mass spectrometer (Automated Nitrogen Carbon Analysis [ANCA] SL 20-20 system; PDZ Europa, Crewe, UK). Two samples of an internal reference material (homogenized cod white-muscle tissue) were analyzed after every 6 tissue samples to calibrate the system and compensate for drift with time. Isotope ratios are expressed as parts per thousand (‰) differences from a standard reference material:

$$\delta X = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \times 10^3$$

where X is ^{15}N or ^{13}C , R is the ratio of $^{14}\text{N}:^{15}\text{N}$ or $^{13}\text{C}:^{12}\text{C}$ for N or C isotopes respectively, and δ is the index of heavy to light isotope in the sample. The standard reference materials were Vienna Pee Dee Belemnite (vPDB) for carbon and atmospheric N_2 for nitrogen (Pinnegar & Polunin 1999). Experimental precision based on the standard deviation of replicates of the internal standard was 0.12‰ for $\delta^{15}\text{N}$ and 0.09‰ for $\delta^{13}\text{C}$.

Sample sizes were small ($n < 10$ for all samples), but transformation of data was not found to be necessary. Comparisons of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data were made at species (crustaceans and fishes) and group (suprabenthos and plankton material) levels among the 3 depth zones using 1-way ANOVA ($\alpha = 0.05$), or Student's t -test ($\alpha = 0.05$) where there was material from only 2 zones; the latter tests were also performed for comparisons between sampling periods. Correlations were used to

assess the strength of association between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data across all sampled materials within each depth zone in May 1998; plankton and suprabenthos material were not available for October 1996, and the data from that interval were therefore not correlated. Error terms are expressed as standard deviations (SD) throughout.

RESULTS

The $\delta^{15}\text{N}$ of fishes collected during October 1996 ranged from 7.63‰ for *Alepocephalus rostratus* to 13.78‰ for the shark *Centroscymnus coelolepis* (Table 1, Fig. 2), and from 10.08‰ for *Lampyctus crocodilus* to 13.78‰ for *Nezumia aequalis* during May 1998 (Table 3, Fig. 2). The $\delta^{15}\text{N}$ of decapod crus-

taceans ranged from 7.76‰ for the mesopelagic shrimp *Sergestes arcticus* to 12.43‰ for *Pontophilus norvegicus* in October 1996 (Table 2, Fig. 2), and between 8.78‰ for *S. arcticus* and 12.41‰ for the polychelid *Stereomastis sculpta* during May 1998 (Table 4, Fig. 2). 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 among the fishes. $\delta^{15}\text{N}$ values for the suprabenthos/zooplankton collected in May 1998 ranged between 5.25‰ (gelatinous plankton) and 8.46‰ (macrozooplankton) (Table 5, Fig. 2). These groups of organisms represent a major food source for large fishes and decapods, and consequently the $\delta^{15}\text{N}$ values were generally below those of decapods (Tables 2 & 4) and fishes (Tables 1 & 3).

$\delta^{13}\text{C}$ in fishes ranged from -19.31‰ for the small mesopelagic *Cyclothone braueri* to -16.83‰ for *Con-*

Table 1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for fishes from the upper, middle and lower slope zones during October 1996. Key abbreviations are used in Fig. 2

Family	Species	Key	Zone	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	(n)
Scyliorhinidae	<i>Galeus melastomus</i>	GM	Lower	12.28–12.35	-17.34–17.14	(2)
	<i>Galeus melastomus</i>	GM	Middle	10.34–10.50	-18.00–17.46	(2)
	<i>Scyliorhinus canicula</i>	SC	Upper	12.33–12.37	-17.40–17.23	(2)
Squalidae	<i>Centroscymnus coelolepis</i>	CC	Lower	13.78 \pm 0.48	-16.83 \pm 0.09	(3)
	<i>Dalatias licha</i>	DL	Middle	13.08	-16.92	(1)
	<i>Etmopterus spinax</i>	ES	Middle	12.56–12.96	-17.19–16.80	(2)
Alepocephalidae	<i>Alepocephalus rostratus</i>	AR	Lower	12.04–12.84	-17.96–16.80	(2)
Gonostomidae	<i>Cyclothone braueri</i>	CB	Lower	7.63	-19.31	(1)
Chauliodontidae	<i>Chauliodus sloani</i>	CS	Lower	10.69	-18.38	(1)
	<i>Chauliodus sloani</i>	CS	Middle	9.94	-18.58	(1)
Stomiidae	<i>Stomias boa</i>	SB	Lower	11.29	-18.88	(1)
Argentinidae	<i>Argentina sphyraena</i>	AS	Upper	9.69	-19.28	(1)
Chlorophthalmidae	<i>Bathypterois mediterraneus</i>	BM	Lower	12.90 \pm 0.32	-17.45 \pm 0.09	(4)
Myctophidae	<i>Lampyctus crocodilus</i>	LC	Middle	9.74–10.05	-18.83–18.52	(2)
Nettastomidae	<i>Nettastoma melanurum</i>	NM	Middle	12.35	-17.16	(1)
Congridae	<i>Conger conger</i>	CO	Middle	13.63–13.71	-16.83–16.81	(2)
	<i>Conger conger</i>	CO	Upper	12.51	-17.33	(1)
Notacanthidae	<i>Notacanthus bonapartei</i>	NB	Upper	11.49	-17.05	(1)
Macroramphosidae	<i>Macroramphosus scolopax</i>	MS	Upper	12.39–12.89	-19.35–18.07	(2)
Macrouridae	<i>Chalinura mediterranea</i>	CM	Lower	11.31 \pm 1.11	-17.96 \pm 0.41	(4)
	<i>Coelorhynchus coelorhynchus</i>	CC	Upper	11.17–11.50	-17.48–17.32	(2)
	<i>Coelorhynchus labiatus</i>	CL	Lower	12.40 \pm 0.36	-17.66 \pm 1.44	(4)
	<i>Nezumia aequalis</i>	NA	Middle	14.18	-16.57	(1)
	<i>Trachyrhynchus trachyrhynchus</i>	TT	Middle	12.84–13.07	-17.60–17.38	(2)
Merlucciidae	<i>Merluccius merluccius</i>	MM	Middle	13.92	-16.73	(1)
	<i>Merluccius merluccius</i>	MM	Upper	9.96 \pm 0.21	-18.87 \pm 0.13	(3)
Gadidae	<i>Gadiculus argenteus</i>	GA	Upper	9.14–9.83	-18.92–18.72	(2)
	<i>Micromesistius poutassou</i>	MP	Upper	10.66–10.67	-18.38–18.16	(2)
	<i>Phycis blennoides</i>	PB	Upper	12.30 \pm 0.26	-18.03 \pm 0.28	(4)
Moridae	<i>Lepidion lepidion</i>	LL	Lower	13.42 \pm 0.28	-16.97 \pm 0.20	(3)
	<i>Lepidion lepidion</i>	LL	Middle	11.27–11.29	-18.40–17.94	(2)
	<i>Mora moro</i>	MO	Middle	12.78–12.88	-17.07–16.91	(2)
Apogonidae	<i>Epigonus denticulatus</i>	ED	Upper	10.33	-18.55	(1)
Trichiuridae	<i>Lepidopus caudatus</i>	LE	Upper	9.74	-19.13	(1)
Trachichthyidae	<i>Hoplostethus mediterraneus</i>	HM	Middle	12.96–14.03	-17.88–17.27	(2)
Scorpaenidae	<i>Helicolenus dactylopterus</i>	HD	Upper	11.76 \pm 0.38	-17.82 \pm 0.28	(3)
Peristidae	<i>Peristedion cataphractum</i>	PC	Upper	10.46–12.21	-18.43–18.05	(2)
Scophthalmidae	<i>Lepidorhombus boschii</i>	LB	Upper	9.30 \pm 0.63	-18.46 \pm 0.49	(4)

ger conger and *Centroscymnus coelolepis* during October 1996 (Table 1, Fig. 2), and from -19.57‰ for the epipelagic *Trachurus trachurus* to -16.52‰ for the macrourid *Coelorrhynchus coelorrhynchus* in May 1998 (Table 3, Fig. 2). The $\delta^{13}\text{C}$ in decapod crustaceans spanned from -20.20‰ for the mesopelagic shrimp *Sergestes arcticus* to -16.11‰ for *Pontophilus norvegicus* during October 1996 (Table 2), and from -19.64‰ for the crab *Geryon longipes* to -17.06‰ for the polychelid *Stereomastix sculpta* during May 1998 (Table 4). The $\delta^{13}\text{C}$ values of supra-benthos and zooplankton ranged from -22.55‰ (calanoid copepods) to -18.97‰ (gelatinous plankton: Table 5). The $\delta^{13}\text{C}$ values of plankton feeders were generally higher (less negative) than those for benthic feeders among both fishes and decapod crustaceans (the latter with the exception of *Geryon longipes*).

Comparisons between depth zones and sampling periods

Comparisons among depth zones were possible for 11 species of fishes and 9 species of crustaceans. Among these species, there were no significant depth differences in $\delta^{15}\text{N}$ for any of the fishes, and only 2 significant differences for the decapod crustaceans; these were for *Aristeus antennatus* between the US and LS ($\delta^{15}\text{N}$ of US > LS; $t = 4.6$, $p = 0.044$) and *Acanthephyra eximia* between the MS and LS ($\delta^{15}\text{N}$ of MS > LS; $t = 8.92$, $p = 0.012$) (Table 4). For the calanoid copepods ($t = 80.83$, $p = 0.008$), $\delta^{15}\text{N}$ was significantly lower in the MS than in the LS. Gelatinous plankton and peracarids differed among all 3 zones (ANOVA, $F = 15.16$, $p = 0.027$ and $F = 108.59$, $p = 0.002$, respectively), both being significantly higher in $\delta^{15}\text{N}$ at greater depths (US < MS/LS [$t = 33.71$, $p = 0.019$] in gelatinous plankton; US/MS < LS [$t = 21.76$, $p = 0.029$] in peracarids) (Table 5). There were few significant differences in $\delta^{13}\text{C}$ among depth zones, $\delta^{13}\text{C}$ being greater at depth in the fishes *Alepocephalus rostratus* (US < MS, $t = 7.11$, $p = 0.019$) and *Coelorrhynchus coelorrhynchus* (US < LS, $t = 15.05$, $p = 0.004$) (Table 3). No decapod crustacean species differed significantly in $\delta^{13}\text{C}$ between depth zones

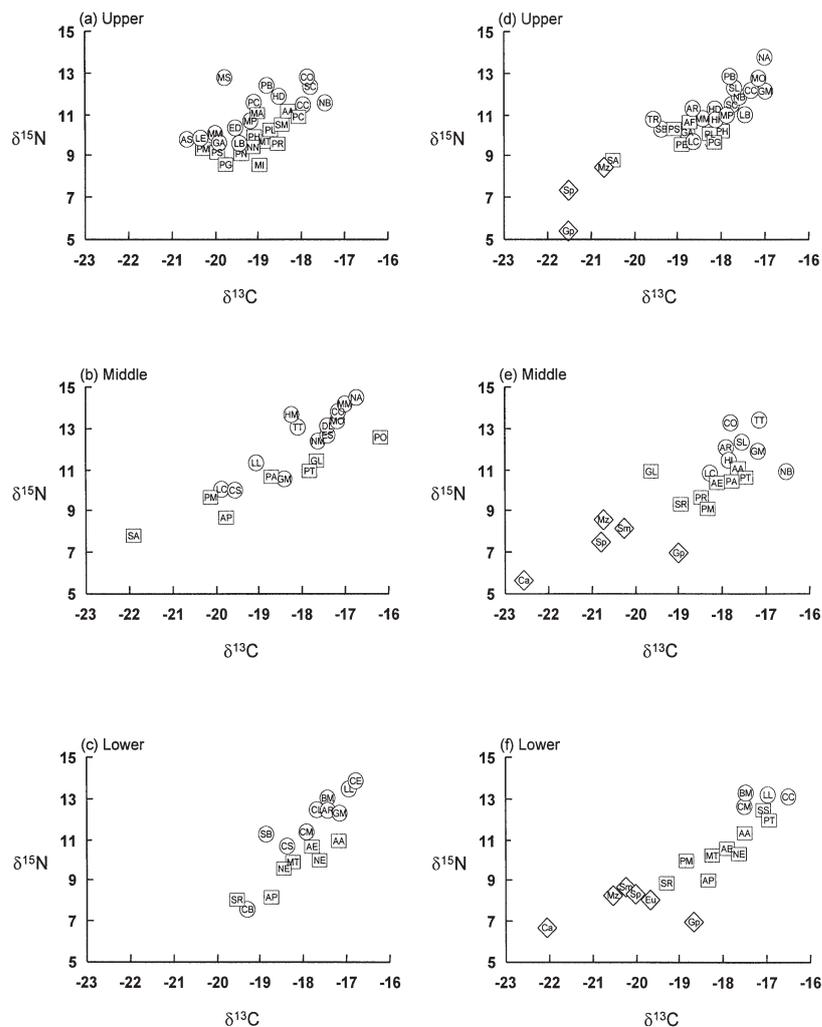


Fig. 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of fishes (O), crustaceans (□) and supra-benthos (◇) in upper (a) middle (b) and lower slope (c) assemblages in October 1996, and in upper (d), middle (e), and lower slope (f) assemblages in May 1998. (a)–(c) Species' key codes as in Tables 1 (fishes) and 2 (crustaceans); (d)–(f) species' key codes as in Tables 3 (fishes), 4 (crustaceans) and 5 (supra-benthos)

(Tables 2 & 4), while $\delta^{13}\text{C}$ tended to increase (become less negative) at depth in gelatinous plankton (ANOVA, $F = 53.24$, $p = 0.005$, US < MS/LS) and in peracarids (ANOVA, $F = 14.60$, $p = 0.028$; US > MS/LS) (Table 5). There were no significant depth-related differences in macrozooplankton or supra-benthic mysids in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$.

Five comparisons were feasible ($n \geq 3$) in fish species within zones between time periods, and 10 in crustacean species, but there were differences between sampling intervals for only 2 crustaceans: in the LS, mean $\delta^{15}\text{N}$ was greater in May 1998 than in October 1996 in the shrimps *Aristeus antennatus* and *Nematosquilla exilis*, neither of the $\delta^{13}\text{C}$ differences being significant (Tables 2 & 4).

Table 2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for crustaceans from the upper, middle and lower slope zones during October 1996. Key abbreviations are used in Fig. 2

Family	Species	Key	Zone	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	(n)
Aristeidae	<i>Aristeus antennatus</i>	AA	Upper	10.96 \pm 0.13	-17.59 \pm 0.18	(3)
	<i>Aristeus antennatus</i>	AA	Lower	10.91 \pm 0.28	-17.20 \pm 0.27	(6)
Crangonidae	<i>Pontophilus norvegicus</i>	PO	Middle	12.43 \pm 0.16	-16.11 \pm 0.31	(3)
Pandalidae	<i>Plesionika acanthonotus</i>	PA	Middle	10.52 \pm 0.64	-17.93 \pm 0.45	(3)
	<i>Plesionika antigai</i>	PN	Upper	9.06 \pm 0.14	-18.37 \pm 0.10	(3)
	<i>Plesionika giglioli</i>	PG	Upper	8.56 \pm 0.04	-18.69 \pm 0.21	(3)
	<i>Plesionika heterocarpus</i>	PH	Upper	9.76 \pm 0.13	-18.17 \pm 0.15	(3)
	<i>Plesionika martia</i>	PR	Upper	9.51–9.70	-17.95–17.75	(2)
Pasiphaeidae	<i>Pasiphaea multidentata</i>	PM	Upper	9.18	-18.99	(1)
	<i>Pasiphaea multidentata</i>	PM	Middle	9.52–9.64	-19.21–18.63	(2)
	<i>Pasiphaea sivado</i>	PS	Upper	9.13 \pm 0.14	-18.87 \pm 0.09	(3)
Nematocarcinidae	<i>Nematocarcinus exilis</i>	NE	Lower	9.40–9.71	-18.45–18.40	(2)
	<i>Nematocarcinus</i> sp.	NE	Lower	9.92 \pm 0.10	-17.64 \pm 0.28	(3)
Oplophoridae	<i>Acanthephyra pelagica</i>	AP	Middle	8.33–8.82	-19.01–18.29	(2)
	<i>Acanthephyra pelagica</i>	AP	Lower	8.16 \pm 0.26	-18.74 \pm 0.28	(3)
	<i>Acanthephyra eximia</i>	AE	Lower	10.57 \pm 0.39	-17.82 \pm 0.50	(6)
Penaeeidae	<i>Parapenaeus longirostris</i>	PL	Upper	9.92 \pm 0.19	-17.99 \pm 0.17	(3)
Sergestidae	<i>Sergestes arcticus</i>	SA	Middle	7.76 \pm 0.53	-20.20 \pm 0.41	(3)
	<i>Sergia robusta</i>	SR	Lower	8.02 \pm 0.11	-19.51 \pm 0.92	(3)
Processidae	<i>Processa caniculata</i>	PC	Upper	10.69–11.11	-17.64–17.43	(2)
Solenoceridae	<i>Solenocera membranacea</i>	SM	Upper	10.41 \pm 0.10	-17.78 \pm 0.17	(3)
Galatheidae	<i>Munida tenuimana</i>	MT	Upper	9.62–9.99	-18.26–17.86	(2)
	<i>Munida tenuimana</i>	MT	Lower	9.78 \pm 0.84	-18.34 \pm 0.24	(3)
	<i>Munida iris</i>	MI	Upper	8.50 \pm 0.17	-18.12 \pm 0.30	(3)
Nephropidae	<i>Nephrops norvegicus</i>	NN	Upper	9.25 \pm 1.31	-18.27 \pm 0.47	(3)
Polychelidae	<i>Polycheles typhlops</i>	PT	Middle	10.78 \pm 0.19	-17.27 \pm 0.25	(3)
Geryonidae	<i>Geryon longipes</i>	GL	Middle	11.28 \pm 0.07	-17.17 \pm 0.21	(3)
Portunidae	<i>Macropipus tuberculatus</i>	MA	Upper	10.97 \pm 0.48	-18.20 \pm 0.36	(3)

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

Ascending the food web, from the suprabenthos/zooplankton via decapod crustaceans to the macrourids and sharks, there was a general increase in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of consumers (Fig. 2). The correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of all groups in May 1998 were highly significant in all depth zones (US $r = 0.89$, MS $r = 0.82$, LS $r = 0.87$; all $p < 0.0001$).

DISCUSSION

Like gut-content data, stable isotopes have several limitations in the extent to which they can elucidate the complex dynamisms of food webs. Among these is the resolution of only broad categories of dietary organisms, distinguishable in terms of $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ values (Polunin & Pinnegar in press). The high lipid content of many deep-sea animals may represent another problem, because lipid synthesis favours the lighter isotope ^{12}C over ^{13}C (DeNiro & Epstein 1977), such that any material which is rich in lipids will be relatively depleted in ^{13}C , potentially reducing the

chances of correctly identifying types of source material (Pinnegar & Polunin 1999). Some workers have specifically chosen to sample tissue lipids, since these generally have a fast turnover and integrate short-term dietary histories, but with the high lipid content found among deep-sea animals, we chose to focus on tissues with low levels of lipid wherever possible (e.g. the white muscle of fish). Despite such constraints, stable isotopes have helped here to elucidate ecological features which would otherwise have been very difficult to assess, given the paucity of available dietary data for many deep-sea species.

Temporal changes

Only 2 significant differences in stable isotope data between the October 1996 and May 1998 intervals were noted, and both of these were increases in $\delta^{15}\text{N}$ in the latter. Seasonal variations in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of planktonic material occur widely (e.g. Wainwright & Fry 1994), including the Mediterranean (Dauby et al. 1990). $\delta^{15}\text{N}$ values of surface plankton collected off Corsica were found to be much higher in the spring than in the autumn, since turbulent mixing and

Table 3. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for fishes from the upper, middle and lower slope zones during May 1998. Key abbreviations are used in Fig. 2

Family	Species	Key	Zone	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	(n)
Scyliorhinidae	<i>Galeus melastomus</i>	GM	Middle	11.84 \pm 0.42	-17.20 \pm 0.15	(3)
	<i>Galeus melastomus</i>	GM	Upper	12.13 \pm 0.38	-17.10 \pm 0.36	(3)
	<i>Scyliorhinus canicula</i>	SC	Upper	11.52 \pm 0.15	-17.74 \pm 0.03	(3)
Alepocephalidae	<i>Alepocephalus rostratus</i>	AR	Middle	12.07 \pm 0.51	-17.91 \pm 0.19	(3)
	<i>Alepocephalus rostratus</i>	AR	Upper	11.35 \pm 0.46	-18.65 \pm 0.04	(3)
Stomidae	<i>Stomias boa</i>	SB	Upper	10.36	-19.21	(1)
Chlorophthalmidae	<i>Bathypterois mediterraneus</i>	BM	Lower	13.28 \pm 0.16	-17.48 \pm 0.04	(3)
Myctophidae	<i>Lampanyctus crocodilus</i>	LC	Middle	10.76 \pm 0.66	-18.27 \pm 0.80	(3)
	<i>Lampanyctus crocodilus</i>	LC	Upper	10.08 \pm 0.44	-18.73 \pm 0.31	(3)
Congridae	<i>Conger conger</i>	CO	Middle	13.26	-17.78	(1)
Notacanthidae	<i>Notacanthus bonapartei</i>	NB	Middle	10.89 \pm 0.11	-16.53 \pm 0.40	(3)
	<i>Notacanthus bonapartei</i>	NB	Upper	11.65 \pm 0.05	-17.70 \pm 0.41	(5)
Macrouridae	<i>Chalinura mediterranea</i>	CM	Lower	12.57 \pm 0.03	-17.52 \pm 0.06	(3)
	<i>Coelorhynchus coelorhynchus</i>	CC	Lower	13.05 \pm 0.49	-16.52 \pm 0.11	(3)
	<i>Coelorhynchus coelorhynchus</i>	CC	Upper	12.14 \pm 0.33	-17.32 \pm 0.03	(3)
	<i>Nezumia aequalis</i>	NA	Upper	13.78 \pm 0.61	-17.02 \pm 0.34	(6)
	<i>Trachyrincus trachyrincus</i>	TT	Middle	13.36	-17.14	(1)
Merlucciidae	<i>Hymenocephalus italicus</i>	HI	Middle	11.31 \pm 0.06	-17.80 \pm 0.02	(3)
	<i>Hymenocephalus italicus</i>	HI	Upper	10.82 \pm 0.46	-18.21 \pm 0.15	(3)
	<i>Merluccius merluccius</i>	MM	Upper	9.86–11.85	-19.11–17.62	(2)
Gadidae	<i>Gadiculus argenteus</i>	GA	Upper	10.32 \pm 0.46	-18.86 \pm 0.11	(3)
	<i>Micromesistius poutassou</i>	MP	Upper	10.99 \pm 0.18	-17.94 \pm 0.25	(3)
	<i>Phycis blennoides</i>	PB	Upper	12.74 \pm 0.15	-17.79 \pm 0.44	(6)
Moridae	<i>Lepidion lepidion</i>	LL	Lower	13.17 \pm 0.29	-16.97 \pm 0.21	(3)
	<i>Mora moro</i>	MO	Upper	12.69 \pm 0.42	-17.15 \pm 0.19	(3)
Scorpaenidae	<i>Helicolenus dactylopterus</i>	HD	Upper	11.00 \pm 0.33	-18.21 \pm 0.25	(3)
Scophthalmidae	<i>Lepidorhombus boschii</i>	LB	Upper	11.07	-17.48	(1)
Cynoglossidae	<i>Symphurus ligulatus</i>	SL	Middle	12.33 \pm 0.41	-17.54 \pm 0.27	(3)
	<i>Symphurus ligulatus</i>	SL	Upper	12.28 \pm 0.08	-17.67 \pm 0.05	(3)
Carangidae	<i>Trachurus trachurus</i>	TR	Upper	10.58–11.02	-20.62–18.52	(2)

Table 4. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for crustaceans from the upper, middle and lower slope zones during May 1998. Key abbreviations are used in Fig. 2

Family	Species	Key	Zone	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	(n)
Aristeidae	<i>Aristeus antennatus</i>	AA	Middle	11.27 \pm 0.33	-17.68 \pm 0.42	(14)
	<i>Aristeus antennatus</i>	AA	Lower	11.34 \pm 0.17	-17.52 \pm 0.32	(9)
	<i>Aristaeomorpha foliacea</i>	AF	Upper	10.47–10.69	-18.97–18.57	(2)
Pandalidae	<i>Plesionika acanthonotus</i>	PA	Middle	10.53 \pm 0.38	-17.76 \pm 0.82	(5)
	<i>Plesionika edwardsi</i>	PE	Upper	9.67 \pm 0.11	-18.90 \pm 0.25	(6)
	<i>Plesionika giglioli</i>	PG	Upper	9.97 \pm 0.17	-18.21 \pm 0.27	(4)
	<i>Plesionika heterocarpus</i>	PH	Upper	10.04 \pm 0.30	-18.08 \pm 0.70	(3)
	<i>Plesionika martia</i>	PR	Middle	9.67 \pm 0.18	-18.48 \pm 0.44	(3)
Pasiphaeidae	<i>Pasiphaea multidentata</i>	PM	Middle	9.16	-18.33	(1)
	<i>Pasiphaea multidentata</i>	PM	Lower	9.93–10.02	-18.95–18.73	(2)
	<i>Pasiphaea sivado</i>	PS	Upper	10.29 \pm 0.09	-19.10 \pm 0.19	(4)
Nematocarcinidae	<i>Nematocarcinus exilis</i>	NE	Lower	10.03–10.61	-17.75–17.53	(2)
Oplophoridae	<i>AcanthePHYra pelagica</i>	AP	Lower	9.07 \pm 0.49	-18.34 \pm 0.21	(6)
	<i>AcanthePHYra eximia</i>	AE	Middle	10.56 \pm 0.46	-18.00 \pm 0.34	(8)
	<i>AcanthePHYra eximia</i>	AE	Lower	10.62 \pm 0.47	-17.91 \pm 0.49	(9)
Penaeidae	<i>Parapenaeus longirostris</i>	PL	Upper	10.02 \pm 0.20	-18.21 \pm 0.34	(6)
Sergestidae	<i>Sergestes arcticus</i>	SA	Upper	8.67–8.89	-20.08–20.52	(2)
	<i>Sergia robusta</i>	SR	Middle	9.27 \pm 0.50	-18.95 \pm 0.61	(4)
	<i>Sergia robusta</i>	SR	Lower	8.89 \pm 0.38	-19.32 \pm 0.47	(3)
Galatheididae	<i>Munida tenuimana</i>	MT	Lower	10.25 \pm 0.12	-18.25 \pm 0.06	(3)
Polychelidae	<i>Polycheles typhlops</i>	PT	Middle	10.77	-17.58	(1)
	<i>Polycheles typhlops</i>	PT	Lower	12.03	-16.97	(1)
	<i>Stereomastis sculpta</i>	SS	Lower	12.41	-17.06	(1)
Geryonidae	<i>Geryon longipes</i>	GL	Middle	10.86	-19.64	(1)

Table 5. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (mean \pm SD where appropriate) for suprabenthos from the upper, middle and lower slope zones during May 1998. Key abbreviations are used in Fig. 2

Family	Key	Zone	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	(n)
Gelatinous plankton	Gp	Upper	5.03–5.46	–21.63–21.32	(2)
Gelatinous plankton	Gp	Middle	6.90 \pm 0.53	–18.97 \pm 0.92	(4)
Gelatinous plankton	Gp	Lower	6.92 \pm 0.38	–18.67 \pm 0.94	(4)
Calanoid copepods	Ca	Middle	5.47–5.59	–22.77–22.33	(2)
Calanoid copepods	Ca	Lower	6.57 \pm 0.32	–22.04 \pm 0.21	(4)
Euphausiids	Eu	Lower	7.91 \pm 0.31	–19.70 \pm 0.17	(3)
Macrozooplankton	Mz	Upper	8.36 \pm 0.25	–20.67 \pm 0.40	(7)
Macrozooplankton	Mz	Middle	8.46 \pm 0.35	–20.70 \pm 0.71	(4)
Macrozooplankton	Mz	Lower	8.21 \pm 0.60	–20.51 \pm 0.33	(8)
Suprabenthic mysids	Sm	Middle	8.16 \pm 1.05	–20.23 \pm 0.56	(3)
Suprabenthic mysids	Sm	Lower	8.49	–20.21	(1)
Suprabenthic peracarids	Sp	Upper	7.26–7.39	–21.59–21.38	(2)
Suprabenthic peracarids	Sp	Middle	7.39–7.59	–21.18–20.33	(2)
Suprabenthic peracarids	Sp	Lower	8.41 \pm 0.34	–20.01 \pm 0.78	(3)

upwelling caused by offshore winds bring nitrate which is high in $\delta^{15}\text{N}$ to the surface where it is taken up by phytoplankton (Michener & Schell 1994). As this mixing and upwelling ceases, the surface waters rapidly become oligotrophic and primary production becomes largely dependent on recycled nitrogen, especially in the form of ammonia which is generally depleted in ^{15}N . Many small invertebrates feed non-selectively on the fallen detritus or plankton, and because they generally possess rapid tissue turnover times, they might be expected to exhibit isotopic compositions which follow these seasonal patterns in the plankton. The shrimps *Aristeus antennatus* and *Nematocarcinus exilis* did show higher $\delta^{15}\text{N}$ values in the spring of 1998 than autumn of 1996. However we would not generally expect organisms feeding at higher trophic levels (e.g. fishes and large crustaceans) to express seasonal patterns in isotope composition, because of their much slower rates of tissue turnover (e.g. Hesslein et al. 1993).

Depth changes

Of the only 2 macroconsumer species showing significant differences in stable isotope data among depth zones, one, *Aristeus antennatus*, has a diet which varies from primarily benthic invertebrates (mainly polychaetes and other infaunal taxa) and suprabenthic crustaceans in shallow water to a high proportion of less-mobile prey from low trophic levels such as foraminiferans and pteropod-shell remains in deeper regions (Cartes 1994). The other macroconsumer species, *Acanthephyra eximia*, is generally carnivorous in shallower water, but shifts to a more detritivorous mode of feeding in the deeper zone (Cartes 1993). In

both cases, feeding at lower trophic levels at greater depth is indicated, and this was corroborated by the $\delta^{15}\text{N}$ data. In contrast, calanoid copepods (1 to 3.5 mm), peracarids (2 to 20 mm) and the gelatinous plankton (4 to 20 mm), all exhibited significantly higher $\delta^{15}\text{N}$ values at greater depth; there are 2 hypotheses as to why this might be so. One hypothesis is that the consumers of the suprabenthos and zooplankton have on average more trophic steps between them and the basal materials at depth, while the other is that the food-web basal materials become ^{15}N -enriched at depth.

Longer food chains leading to the planktonic animals are another possible explanation for the greater $\delta^{15}\text{N}$ of

these consumers in deeper water. Changes in the dominant feeding type of copepods and other mesozooplankton have been observed with increasing depth, with an increase in carnivorous forms occurring in deeper water (Vinogradov & Tseitlin 1983). Although the feeding habits of suprabenthos are poorly known, the mysid *Boreomysis arctica* and the amphipod *Rhachotropis caeca*, which are dominant suprabenthic species off Ibiza, feed on crustacean remains (particularly copepods), and become more common with increasing water depth (Cartes & Sorbe 1998).

Saprotrophic fungi and other microbes are known to enrich organic matter in ^{15}N by preferentially utilizing the labile matter that is relatively abundant in ^{14}N (Gleixner et al. 1993, Hobbie & Macko 1999). Refractory substances like the chitin from copepod exoskeletons thus become relatively more abundant in marine snow as it sinks (Miquel et al. 1994). Chitin is often overlooked as an important source of nitrogen in the marine environment (Shimmelmann et al. 1998), and the ability to utilise chitin has been demonstrated for bacteria (Kichner 1995) and many types of crustaceans (Bucholz & Vetter 1993, Watanabe et al. 1998) which are common consumers in the deep sea. The high and depth-stable temperature in the Mediterranean Sea (Fredj & Laubier 1985) must facilitate microbial degradation of particulate organic matter in the water column. Bacteria are recognised as having an important role in sustaining the benthos of many deep oligotrophic areas of this sea (Danovaro et al. 1993).

$\delta^{13}\text{C}$ values may be useful indicators of source materials, since fractionation of the carbon isotopes with each trophic level is small relative to that exhibited by nitrogen isotopes, and there are often distinct differences among types of basal materials in ecosystems. In the present study, species depleted in ^{13}C generally fed

near the base of the food web and were more closely associated with the plankton. The higher $\delta^{13}\text{C}$ values of the fishes *Alepocephalus rostratus* and *Coelorhynchus coelorhynchus* at greater depth (Table 3) did not seem to corroborate available gut-content data. The related *Coelorhynchus labiatus* appears to feed more on suprabenthos and zooplankton in deeper waters (Carrassón 1994). *A. rostratus* feeds primarily on macroplankton on the lower slope (Carrassón & Matallanas 1990). These are both diets which might have been expected to produce lower values of $\delta^{13}\text{C}$ at greater depth. In fact, $\delta^{13}\text{C}$ values of the suprabenthos and zooplankton tended also to increase at greater depth and, as for nitrogen, this is consistent with the biodegradation of marine snow leaving residues of more refractory materials (Williams & Gordon 1970, Mullerniklas et al. 1994) such as inorganic carbonates and chitin, which are known to be enriched in ^{13}C compared to other biochemical fractions (Bunn et al. 1995).

Food-web structure

The strong correlations observed between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (Fig. 2) are indicative of a single type of primary source material supporting deep-sea communities. Vertical fluxes of organic particulate matter have been measured in the study region, the rates of organic carbon at 800 to 1000 m depth being 1 to 5 g m⁻² yr⁻¹ (Miquel et al. 1994). The correlations between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ contrast with those in communities of the Mediterranean littoral (e.g. cf. Lepoint et al. 2000 and Pinnegar & Polunin 2000), where an array of possible sources of production including plankton, macroalgae and seagrasses, are available, and the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is much weaker (e.g. consumers in Pinnegar & Polunin 2000, $r = 0.46$; non-epiphytic consumers in Lepoint et al. 2000, $r = 0.24$). Being a short distance away from the Balearic Islands, our study area experienced lower vertical flux rates than oceanic areas closer to land (Danovaro et al. 1999), and the sediments have very little input of terrigenous material (Emelyanov 1972). If falls of large epipelagic predators such as sharks or tunas had been significant food sources, the materials apparently supporting the bathyal food webs studied here would have been higher and more variable in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. If macrophytes such as large algae had been significant contributors, then higher and more variable values of $\delta^{13}\text{C}$ would have been indicated for the source materials of the deep-sea food webs than were found. Marine snow almost certainly constitutes the main supply of food materials to the sea floor in the study area. However, values for the slope of regression between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of consumers differed from the value would

be expected (a slope of ~ 3) if $\delta^{15}\text{N}$ increased by 3 to 3.4‰ and $\delta^{13}\text{C}$ by 1‰ (DeNiro & Epstein 1978) at each trophic level.

The spread of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values presented here for fishes and decapods is generally consistent with the highly diversified diets of large consumers in the western Mediterranean bathyal zone, as indicated by gut-content data (e.g. Macpherson 1977, Cartes 1998). There appear to be 3 groups of fishes, namely those with a low trophic level, which consume a variety of planktonic foods (copepods, gelatinous plankton, mesopelagic decapods and euphausiids), those which preferentially consume benthic/suprabenthic invertebrates, and the top predators (e.g. sharks, some macrourids and *Conger conger*) which prey on large decapods, other fishes and cephalopods (e.g. Carrassón et al. 1992).

Trophic level

We estimated the trophic level (TL) of the top predators based on their $\delta^{15}\text{N}$ data and using calanoid copepods as a reference material (with an assumed trophic level of 2) and an increase in $\delta^{15}\text{N}$ of 3.4‰ per trophic level (Vander Zanden et al. 1997). In this way, the maximum trophic level exhibited by any fish species was 4.4 for both the shark *Centroscymnus coelolepis* (October 1996) and the macrourid *Nezumia aequalis* (May 1998). This is equivalent to the trophic level occupied elsewhere by large sharks (Cortés 1999), and generally agrees with the suggestion that aquatic food chains typically have no more than 4 or 5 trophic steps (Hall & Raffaelli 1993). Bathyal fishes off the Balearic Islands appeared to be foraging over 2 to 3 full trophic levels, while decapods fed over 2 trophic levels, as did the suprabenthos/zooplankton. Calanoid copepods appeared to feed at a lower trophic level than did the macrozooplankton, euphausiids and suprabenthic peracarid groups. The gelatinous plankton generally exhibited very low $\delta^{15}\text{N}$ values, and this may indicate a greater reliance on POM or microzooplankton (Malej et al. 1993).

Comparing the results presented here for deep-sea consumers with those from littoral environments (e.g. Lepoint et al. 2000, Pinnegar & Polunin 2000), zooplankton at shallower depths generally exhibited lower $\delta^{15}\text{N}$ values (~ 3.5 ‰) than those of zooplankton from the deep waters (~ 5.5 to 6.5 ‰), and this was also the case for gelatinous plankton, decapod crustaceans, fishes, mysids and peracarids. This suggests that it is variation in the underlying $\delta^{15}\text{N}$ of the basal organisms that is responsible for apparent TL differences between littoral and deep-sea organisms, and not any fundamental difference in TL of the large consumers in the food webs concerned.

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