Food web structure and trophodynamics of mesopelagic-suprabenthic bathyal macrofauna of the Algerian basin based on stable isotopes of carbon and nitrogen.

Fanelli E.^{1*}, Cartes J.E.¹, Rumolo P.², Sprovieri M.²

¹ ICM-CSIC P.g Maritim de la Barceloneta 37-49 – 08003 – Barcelona, Spain

² IAMC-CNR Calata Porta di Massa – 80100 – Naples, Italy

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* corresponding author:

Emanuela Fanelli ICM-CSIC P.g Maritim de la Barceloneta 37-49, 08003 Barcelona Spain
Tel. +34932309500; Fax +34932309555; e-mail: efanelli@icm.csic.es

18 **Abstract.** The trophodynamics of mesopelagic (macrozooplankton/micronekton) and Benthic
19 Boundary Layer (suprabenthos = hyperbenthos) faunas from the Algerian basin were characterized
20 on a seasonal scale through stable carbon and nitrogen isotopic analyses of a total of 34 species and
21 two broad taxa (Copepoda and Cumacea). This is the first study simultaneously focused on
22 trophodynamics of deep-sea zooplankton and suprabenthos. Samples were collected southeast of
23 Mallorca (Algerian Basin, Western Mediterranean), on the continental slope close to Cabrera
24 Archipelago, at 650-780 m depths, *ca.* bi-monthly between August 2003 and June 2004. Mean $\delta^{13}\text{C}$
25 values of suprabenthos ranged from -21.1‰ (*Munnopsurus atlanticus*) to -16.7‰ (*Cyclaspis*
26 *longicaudata*). Values of $\delta^{15}\text{N}$ ranged from 2.8‰ (*Lepechinella manco*) to 9.9‰ (larvae of *Gnathia*
27 sp.). The stable isotope ratios of suprabenthic fauna displayed a continuum of values, confirming a
28 wide spectrum of feeding guilds (from filter feeders/surface deposit feeders to predators). According
29 to the available information on diets for suprabenthic species, the highest annual mean $\delta^{15}\text{N}$ values
30 were found for the hematophagous isopod *Gnathia* sp. parasite on fish (represented by *Praniza*
31 larvae) and carnivorous amphipods (e.g. *Rhachotropis* spp., *Nicippe tumida*) consuming copepods,
32 and the lowest $\delta^{15}\text{N}$ values were found for two cumaceans (*Cyclaspis longicaudata* and *Platysympus*
33 *typicus*) feeding on detritus. Assuming a ^{15}N -enrichment factor of 2.5‰ and deposit feeders as
34 baseline we found three trophic levels in suprabenthic food webs. $\delta^{13}\text{C}$ ranges were particularly wide
35 among deposit feeders (ranging from -21.8 to -17.3‰) and omnivores (from -20.5 to -18.8‰),
36 suggesting exploitation of particulate organic matter (POM) of different characteristics. Our isotopic
37 analyses revealed lower ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for macrozooplankton/micronekton, compared with
38 suprabenthos. $\delta^{13}\text{C}$ values of zooplankton taxa ranged from -21.1‰ (the hyperiid *Phrosina*
39 *semilunata*) to -19.9‰ (the decapod *Pasiphaea multidentata*), while $\delta^{15}\text{N}$ values ranged from 3.9‰
40 (*P. semilunata*) to 7.5‰ (*P. multidentata*). Among zooplankton, more enriched $\delta^{15}\text{N}$ values were
41 found among carnivores (e.g. the fish *Cyclothone* spp. and *Pasiphaea multidentata*) preying on
42 copepods, hyperiids, euphausiids and small fish. The lowest $\delta^{15}\text{N}$ values were found for hyperiids

43 that feed on the mucus nets of salps (e.g. *Vibilia armata*). After contrasting isotope analysis with
44 dietary data, we conclude there were two trophic levels among zooplankton/micronekton. Strong
45 correlation between the mean annual $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values was found for zooplankton ($R^2=0.7$), but
46 not for suprabenthos, which suggests a single source of carbon for plankton. We found a general
47 seasonal trend for $\delta^{13}\text{C}$ enrichment from late autumn (November) to late winter-spring (February-
48 April) for both suprabenthos and zooplankton. The $\delta^{13}\text{C}$ enrichment in February-April was
49 correlated in zooplankton with higher surface chlorophyll *a* concentration one month before
50 sampling. As evidenced by $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations, the response of zooplankton to the peak of
51 surface primary production was almost immediate (an increase of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations in
52 February), and stronger than for suprabenthos. The response among suprabenthos was weak, with
53 slight increase in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ relationships in April-June.

54

55 **1. Introduction**

56 Studies of trophodynamics of benthopelagic resources, including compartments such as
57 suprabenthos and near-bottom zooplankton, are fundamental to understand the functional
58 mechanisms of deep-sea communities. Swimming macrofauna in the deep sea, including permanent
59 suprabenthos (=hyperbenthos) and near-bottom zooplankton (for terminology see reviews by
60 Vereshchaka, 1995, and Mees & Jones, 1997), have been the subject of increasing studies of their
61 ecology in recent decades (Sorbe, 1999; Cartes et al., 2001, 2003; among others). These studies have
62 shown that crustaceans (mainly peracarids) constitute the dominant fauna of these assemblages, and
63 they are key taxa linking POM and the lowest trophic levels to top predators such as fish and
64 decapod crustaceans (Cartes, 1994; 1998; Carrasson & Cartes, 2002; Cartes et al., 2004). In the
65 same way substantial trophic transfer to the suprabenthos by mesopelagic organisms forming the
66 deep scattering layer (DSL) is indicated by the copious prey from the DSL found in stomachs of
67 benthopelagic fish and decapods at bathyal depths. In subtropical Atlantic waters the DSL undergoes
68 daily displacements from ca. 600-900 m during daylight to the surface at night (Mozgovoy &
69 Bekker, 1991). These migratory movements by oceanic zooplankton have usually been characterized
70 as vertical (Hopkins & Baird, 1981; Mauchline & Gordon, 1991). In the northwestern
71 Mediterranean, zooplankton constitutes a “swimmer flux” (Miquel et al., 1994), composed mainly of
72 amphipods (*Phronima sedentaria*), Thecosomata, copepods and small euphausiids. They are one of
73 the major components in the export of organic matter, both living migrant organisms and faecal
74 pellets, from the euphotic zone to depth.

75 Despite the important role played by suprabenthic and zooplanktonic species, the trophic structure of
76 these organisms is still far from well understood (Cartes et al., 2001). In fact, suprabenthos was not
77 properly sampled in previous studies of deep-sea trophic webs using isotopic composition (e.g. Iken
78 et al., 2001). Different functional guilds or feeding habits have been determined for some taxa,
79 though based on limited information about diets (Svavarsson et al., 1993; Elizalde et al., 1999;

80 Cartes et al., 2002), behaviour and morphological features. For example, Lysianassidae are generally
81 considered to be scavengers (Sainte-Marie, 1992), while Eusiridae appear to be carnivores because
82 they have large gnathopods (Enequist, 1949) and contain animal lipid biomarkers (Nyssen et al.,
83 2005). No data are available on the temporal trophodynamic variation (i.e. trophic level and food
84 sources exploited) of swimming macrofauna as important prey for deep-sea fish. Seasonal
85 environmental signals, among which phytodetritus deposition stands out, appear to operate rapidly
86 and favour aspects of the biological cycle (recruitment, gametogenesis) in some groups of deep-sea
87 macrofaunal species (Bishop and Shalla, 1994; Tyler et al., 1994; Cartes and Sorbe, 1996), and some
88 megafaunal species (Tyler and Gage, 1984; Féral et al., 1990).

89 Traditional food-web analysis, such as examining gut contents or conducting field and laboratory
90 experiments is restricted for macrofauna by technical difficulties. However, indirect techniques, such
91 as stable isotopes (Fry & Sherr 1984, Peterson & Fry 1987) and lipid biomarkers (Nyssen et al.,
92 2005), have appeared as new proxies for examining trophic interactions. The combined analysis of
93 carbon and nitrogen stable isotopes is useful for identifying the ultimate organic matter sources and
94 trophic position of consumers. The use of stable isotopes relies on the fact that the carbon isotope
95 ratio ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$) of consumers reflects that of their food sources, with minimal enrichment or
96 fractionation (0-1‰, Fry and Sherr, 1984; Michener and Schell, 1994; McCutchan et al., 2003),
97 while the heavy nitrogen isotope ^{15}N ($^{15}\text{N}/^{14}\text{N}$ or $\delta^{15}\text{N}$) displays a stepwise enrichment of about 3.0-
98 3.4‰ with each trophic level (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001;
99 Post, 2002). A meta-analysis based on 134 estimates of $\delta^{15}\text{N}$ enrichment from the literature,
100 (Vanderklift and Ponsard 2003) found a value of 2.54‰ for trophic fractionation. These stepwise
101 enrichments were deduced from a large variety of both freshwater and marine studies, but nothing is
102 known about stable isotope accumulation in tissues of deep-sea species.

103 This point is quite controversial, because isotopic fractionation by a consumer of its diet depends on
104 different factors, among them trophic strategies, food biochemical compositions and metabolism
105 (Vander Zanden and Rasmussen, 2001; Vanderklift and Ponsard, 2003; McCutchan et al., 2003). As

106 a consequence, we expect faster response to changes in food source among small, fast-growing
107 macrofauna, and among suprabenthos in comparison to infauna, because suprafafauna has a higher
108 P/B ratio (Cartes et al., 2002) according to recent studies on marine plankton that showed $\delta^{15}\text{N}$
109 fractionation values generally lower than the average 3.4‰ (Bode et al., 2006; Bode et al., 2007).

110 Stable isotope analysis has been successfully carried out to analyze the trophic links in deep-sea
111 corals (e.g. Kiriakoulakis et al 2005), in foraminiferans (e.g. Corliss et al., 2002), and in polychaetes
112 from hydrothermal vents (e.g. Levesque et al., 2003). However, in the study of macrofauna this
113 approach has rarely been adopted (Iken et al., 2001, 2005; Polunin et al., 2001), and the application
114 of isotopic analysis to suprabenthic fauna at species level has been limited to the Antarctic Ocean
115 (for amphipods: Nyssen et al., 2002, 2005) and to the deep Mediterranean (Madurell et al., 2008),
116 with little consideration of temporal variation. Studies of isotopic signature seasonality in deep-sea
117 fauna are almost nonexistent (Corliss et al., 2002; Fanelli & Cartes, 2008). Food sources in the deep
118 sea tend to vary temporally in response to changes in primary production (Billett et al., 2001), and
119 probably to changes in the general flux of POM in the water column (Miquel et al., 1994). This
120 seasonal input has an effect on suprabenthos and zooplankton biomass (Cartes et al., 2008).
121 Suprabenthos and zooplankton, because they possess rapid tissue turnover times (Cartes et al.,
122 2002), might exhibit isotopic compositions that follow these seasonal patterns in food sources. The
123 use of $\delta^{13}\text{C}$ vs $\delta^{15}\text{N}$ relationships can be a useful indicator if there is one or more source material
124 supporting biological communities (Polunin et al., 2001). In fact weak correlations between $\delta^{13}\text{C}$ and
125 $\delta^{15}\text{N}$, such as those found in littoral communities of the Mediterranean (e.g. cf. Lepoint et al. 2000;
126 Pinnegar & Polunin 2000; Fanelli et al., 2009), are indicative of an array of possible sources of
127 production including plankton, macroalgae and seagrasses. Conversely strong correlations are
128 indicative of a single type of primary source as the case of deep-sea communities (Polunin et al.,
129 2001). Studies on isotopic composition and its temporal variation in marine zooplankton are scarce,
130 most of them concerning specific species of coastal copepods observed in experimental conditions

131 (Tamelander et al., 2006) or the whole zooplankton compartment (Checkley & Miller, 1989; Rolff,
132 2000; Bode et al., 2003, 2006, 2007; Bode & Alvarez-Ossorio, 2004).

133 We focus here on the trophodynamics of bathyal suprabenthos and macrozooplankton/micronekton
134 from the Algerian basin (western Mediterranean) on a seasonal scale. The Algerian Basin, like all of
135 the deep Mediterranean, has relatively stable temperature and salinity below ~150 m (Hopkins,
136 1985) and marked oligotrophy in surface waters (Turley et al., 2000). The high temperature (~13°C)
137 below 150 m provokes rapid degradation down the water column of fresh POM produced in the
138 photic zone, resulting in limited availability of fresh POM for communities in the benthic boundary
139 layer (BBL).

140 By means of stable isotope analysis we want to achieve the following objectives: i) to establish the
141 different trophic levels found among suprabenthic and mesopelagic fauna, thus supporting the idea
142 of a high complexity among the benthic-pelagic compartment, normally associated with a single
143 trophic level; ii) to identify possible food sources for suprabenthos and
144 macrozooplankton/micronekton fauna; iii) to identify temporal variations in $\delta^{15}\text{N}/\delta^{13}\text{C}$ relationships
145 in both these compartments.

146 **2. Materials and methods**

147 *2.1. Study area and sampling strategy.*

148 The study was performed on the middle slope of Cabrera Archipelago situated to the southeast of
149 Mallorca (Balearic Islands, western Mediterranean) within the framework of the multidisciplinary
150 project IDEA (CICYT, Spain) (Figure 1). Sampling was carried out every two months between
151 August 2003 and June 2004 (see details in Cartes et al., 2008) in both the two compartments. The
152 site (39° 68'N- 2° 18'E; 39° 81'N- 2° 37'E) is included in the Algerian basin.

153 Suprabenthos and macrozooplankton/micronekton (from now on referred to as zooplankton) were
154 sampled at two bathyal stations (650 and 780 m). A total of 24 Macer-GIROQ sledges and 24 WP2
155 plankton nets were performed during six cruises from August 2003 to June 2004 at ca. bi-monthly

156 intervals (Cartes et al., 2008). The Macer-GIROQ sledge collects suprabenthos between 0 and 1.5 m
157 above bottom; it is equipped with 0.5 mm mesh size nets (Cartes et al., 2008).
158 Macrozooplankton/micronekton in the water column was sampled using a WP2 net with a mouth
159 area of 1 m², equipped with 0.5 mm mesh size net, in horizontal-oblique hauls performed as close to
160 the sea bottom as possible (closest estimated distance to the bottom estimated to be between 13 and
161 90 m by means of an inclinometer).

162 2.2. *Stable isotopes analyses*

163 Once collected, samples were immediately frozen at -20 °C and later sorted in the laboratory as
164 quickly as possible, identified to species level and prepared for analyses. Species selected for
165 isotopic analysis were those dominant in both abundance and biomass throughout the sampling
166 period (Cartes et al., 2008; unpubl. data). Tissues used for isotope analysis in invertebrates and fish
167 were always whole body, except for decapods and euphausiids, for which caudal muscle was
168 utilized. Afterwards samples were dried to constant weight at 60 °C, then ground to a fine powder.
169 One sub-sample, for carbon isotope analysis, was acidified by adding 1M HCl drop-by-drop to
170 remove inorganic carbonates from the exoskeleton (the cessation of bubbling was used as criterion to
171 determine the amount of acid to add: Nieuwenhuize et al., 1994; Jacob et al., 2005), and then
172 samples were dried again at 60 °C for 24 h. The acidification was required because carbonates
173 present a less negative $\delta^{13}\text{C}$ than organic carbon (De Niro and Epstein 1978). The other subsample,
174 for nitrogen isotope analysis, was not acidified, as acidification results in enrichment (Pinnegar and
175 Polunin 1999) or depletion (authors' unpubl. data) in $\delta^{15}\text{N}$.

176 Although some authors have suggested extracting lipids in the samples prior to stable isotopes
177 analysis, in this study we did not. Lipid extraction is made because tissues rich in lipids are depleted
178 in $\delta^{13}\text{C}$ relative to those rich in proteins because of fractionation occurring during lipid synthesis
179 (DeNiro and Epstein, 1978); thus trophic interpretations based on $\delta^{13}\text{C}$ signatures may be
180 confounded by lipid effects (e.g. Wada et al., 1987). However, this procedure is more common with
181 large fish and invertebrates (i.e. decapods) and not for small invertebrates as in our case.

182 Alternatively, we used as indicator of lipid content the relationship between C/N ratios and $\delta^{13}\text{C}$
183 signatures (*sensu* France, 1996). C/N ratios are a relatively good surrogate for tissue lipid content
184 (i.e. higher lipid samples have higher C/N ratios; Tieszen et al., 1983), and percent lipid explained
185 nearly 90% of the variation in $\Delta\delta^{13}\text{C}$ for aquatic animals (Post et al., 2007).

186 Organic carbon and total nitrogen elemental composition were determined from the residues of CO_2
187 and N_2 gases. C/N ratios were measured simultaneously during stable isotope analysis from the
188 percent element data.

189 In addition $\delta^{13}\text{C}$ values were also normalized for lipid concentration according to Post et al. (2007),
190 thus $\delta^{13}\text{C}$ values of untreated samples (not defatted) were converted to $\delta^{13}\text{C}$ normalized
191 ($\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \cdot \text{C:N}_{\text{sample}}$)

192 Samples were weighed (ca. 1 mg of dry weight) into tin cups. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of benthopelagic
193 samples were determined by a ThermoFisher Flash EA 1112 elemental analyzer coupled to a
194 Thermo Electron Delta Plus XP isotope ratio mass spectrometer (CNR-IAMC, Naples, Italy).

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

201 $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$ where
202 $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$.

203 Four replicates were analyzed for all of the species (Table 1), and when it was possible each
204 replicate included just one individual in order to reduce pseudo-replication (Hulbert, 1984). When
205 the biomass of a specimen was not sufficient, several were pooled to obtain sufficient mass for the
206 isotope measurement (as in the cases of calanoid copepods and some cumaceans).

207 2.3. Data analysis

208 Isotope data are normally distributed, thus they were not transformed for univariate and multivariate
209 analyses. A hierarchical cluster analysis (Euclidean distance, average grouping methods) was carried
210 out on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ mean values per species and per sampling date (month). The groups thus
211 obtained were compared with postulated trophic groups based on literature and on our own data (i.e.
212 filter-feeders, deposit-feeders, omnivores, zooplankton carnivores, meiobenthos carnivores,
213 parasites, as given in Table 1). A distance-based permutational analysis of variance (PERMANOVA,
214 Anderson, 2001) based on Euclidean distance, was performed on the same matrix to compare groups
215 obtained from the cluster analysis; then a pair-wise comparison was done on the average $\delta^{13}\text{C}$ and
216 $\delta^{15}\text{N}$ of these groups. Significance was set at $p=0.05$; p-values were obtained using 9999
217 permutations of residuals under unrestricted permutation of raw data, which is recommended when
218 there is only a single factor (Anderson, 2001).

219 Linear regressions between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated separately for suprabenthos and
220 zooplankton by averaging monthly values to obtain a single mean “annual” value for each species.
221 Afterwards, temporal variations were explored for each sampling period (month) by using mean
222 values per species from August 2003 to June 2004.

223 Finally $\delta^{13}\text{C}$ data were coupled with environmental variables using Spearman’s correlation
224 coefficients (Fanelli & Cartes, 2008). Variables tested were means of surface temperature and
225 salinity, temperature and salinity near the bottom (at five meters above the bottom), maximum
226 fluorescence and depth of maximum fluorescence (see López-Jurado et al., 2008 for details) taken
227 during IDEA02 (February) and IDEA04 (April), percentage of organic matter in surficial sediment,
228 sediment grain size (mean, mode) and chlorophyll *a* recorded in surface waters at different time
229 intervals (simultaneous with sampling; one, two, and three months before sampling). This last
230 information was obtained from the Ocean Colour Time-Series Online Visualization and Analysis
231 System (available at: reason.gsfc.nasa.gov/Giovanni).

232 The possible confounding effect of lipids was examined by Spearman rank correlations between
233 $\delta^{13}\text{C}$ and C/N for each sampling period and separately for suprabenthos and zooplankton.

234 All the analyses were performed using PRIMER6 & PERMANOVA+ (Clarke & Warwick, 1995;
235 Anderson, 2001) and STATISTICA 6 software.

236 2.4. Trophic level estimates

237 Because of sampling constraints, POM was not sampled in this study, thus in the lack of the baseline
238 we estimated the trophic levels of zooplanktonic/suprabenthic fauna from the $\delta^{15}\text{N}$ data using two
239 different references: 1) deposit feeders for suprabenthos and 2) filter feeders for zooplankton. $\delta^{15}\text{N}$
240 values were converted to trophic level based on the assumption of a $\sim 2.54\text{‰}$ fractionation per
241 trophic level (Vanderklift and Ponsard, 2003) and that the base material (filter feeders or deposit
242 feeders) had a trophic level of 2: $\text{TL}_i = (\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{PC}} / 2.54) + 2$; where TL_i is the trophic level of
243 species i , $\delta^{15}\text{N}_i$ is the mean $\delta^{15}\text{N}$ of species i , and $\delta^{15}\text{N}_{\text{PC}}$ is the mean $\delta^{15}\text{N}$ of the primary consumers
244 for the six months combined. Deposit feeders are a large, very heterogeneous group as there are
245 many specializations in terms of particle size, particle location (surface, sub-surface) and particle
246 freshness. The group that could be most convincingly argued to be primary consumers is selective
247 surface deposit feeders (Fanelli et al., 2009), consuming the more freshly deposited particles on the
248 seabed surface, which have not been reworked by biological processes numerous times and are thus
249 isotopically lighter (Nyssen et al., 2005). The low values of $\delta^{15}\text{N}$ found for *Cyclaspis longicaudata*
250 and *Platysypus typicus* (mean $\delta^{15}\text{N} = 3.72\text{‰} \pm 0.26$), together with their mouth appendages
251 morphology and their swimming behaviour (Cartes & Sorbe, 1997; Macquart-Moulin, 1991; Cartes
252 et al., 2002), allowed them to be classified as selective surface deposit feeders.

253 As a reference for zooplankton we used the two hyperiids *Phosina semilunata* and *Vibilia armata*
254 (mean $\delta^{15}\text{N} = 4.06\text{‰} \pm 0.14$; Madin & Harbison, 1977; Coleman, 1994); they were the most feasible
255 candidates to use as reference, because they feed on mucus nets (including phytoplankton) of salps.

256 3. Results

257 3.1. Isotopic composition of suprabenthic and mesopelagic fauna and trophic levels estimates

258 3.1.1. *Suprabenthos*

259 Twenty-two species (15 amphipods, 1 decapod, 3 isopods, 1 mysid and 4 cumaceans) and other
260 cumaceans as a broad taxon were analyzed on an annual basis (Table 1). Information used here on
261 feeding habits and diets is also given in Table 1.

262 Our isotopic analyses revealed a considerable range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for suprabenthic species
263 (Table 2). $\delta^{13}\text{C}$ values of suprabenthos taxa ranged from -21.9‰ (*Calocaris macandreae*) to -16.7‰
264 (*Cyclaspis longicaudata*). $\delta^{15}\text{N}$ ranged from 2.8‰ (*Lepechinella manco*) to 9.9‰ (*Gnathia* sp.).

265 The trophic groups identified by cluster analysis (Fig. 2) were in good agreement with postulated
266 feeding habits as provided by information on feeding habits and diets (Table 1). The cluster analysis
267 based on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ identified two main groups, I and II, and two main subgroups within II.
268 Group I included mostly deposit feeders such as two cumaceans (*Platysympus typicus* and *Cyclaspis*
269 *longicaudata*), the amphipod *Lepechinella manco* and the thalassiniid shrimp *Calocaris*
270 *macandreae*. Group II comprised the remaining species, predominantly carnivore predators and
271 omnivores. Within subgroup IIA we found, in addition to *Rhachotropis* spp. and *Nicippe tumida*, all
272 preying on copepods, the hematophagous isopod *Gnathia* sp. (Praniza larvae, the second stage of
273 larval development of *Gnathia* spp.) and scavengers (*Natatolana borealis*). The group IIB was more
274 heterogeneous and comprised species in part preying on meiofauna, such as the isopod *Munnopsurus*
275 *atlanticus* (consuming foraminiferans), cumaceans of the Family Nannastacidae (*Campylaspis* and
276 *Procampylaspis* spp.) and omnivores (the case of the mysid *Boreomysis arctica* that may
277 facultatively act as a filter feeder and as a carnivore feeding on plankton). This group also included
278 *Rhachotropis integricauda*, a carnivore with a lower $\delta^{15}\text{N}$ value than other *Rhachotropis* spp.

279 Assuming a trophic fractionation of 2.54‰ the overall range of $\delta^{15}\text{N}$ values implied three trophic
280 levels, with surface/sub-surface deposit feeders and carnivores positioned at the two extremes.
281 Deposit/suspension feeders ranged from 2.0 to 2.6 (C. *macandreae*) while carnivores on
282 mesozooplankton had a TL of 3.9 and the parasite *Gnathia* sp. was positioned at the highest level

283 (TL=4.4). An intermediate trophic level between these two points was represented by omnivores
284 (TL=3.1) and meiobenthic feeders (TL=3.7; see also Figure 3).

285 Average stable isotopic ratios differed significantly between trophic groups identified by cluster
286 analysis (PERMANOVA $F_{4,21}=6.50$; $p<0.05$). Excluding parasite species, the pair-wise comparisons
287 showed significant differences between deposit feeders and the remaining groups, except omnivores,
288 whilst no significant differences were found between zooplankton and meiobenthos carnivores
289 (Table 3). Differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the species that could not be attributed *a priori* to
290 a trophic group based on the literature (Figure 3) were not significant; therefore their isotopic
291 signatures were similar to those of omnivores and meiobenthos carnivores (Table 3). By contrast,
292 “unknown” species (see Table 1) isotope values were significantly different from those exhibited by
293 deposit feeders and copepod carnivores. The isotopic compositions of *Stegocephaloides*
294 *christianensis*, *Epimeria parasitica*, *Tryphosites longipes* and *T. alleni* were within the range for
295 omnivores, while the stable isotope ratios of the amphipod *Bruzelia typica* were within the range for
296 meiobenthos carnivores (Figure 3).

297 3.1.2. Zooplankton

298 Twelve species (3 euphausiids, 3 hyperiids, 4 decapods and 2 fish) and copepods were analyzed on
299 an annual basis (Table 1).

300 There was a narrower range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for zooplankton species (Table 2) than for
301 suprabenthic species, especially for $\delta^{13}\text{C}$ that ranged from -21.1‰ (*Phrosina semilunata*) to -19.9‰
302 (*Pasiphaea multidentata*). $\delta^{15}\text{N}$ ranged from 3.9‰ (*P. semilunata*) to 7.4‰ (*P. multidentata*).

303 The narrow ranges of isotopic values accord with a narrow range of trophic strategies and fit quite
304 well with the trophic classifications based on gut contents and isotopic analyses in the literature
305 (Table 1). Thus, species with more enriched $\delta^{15}\text{N}$ values are carnivores (e.g. the mesopelagic fish
306 *Cyclothone braueri* and *C. pygmaea*, the decapod *Pasiphaea multidentata* and the euphausiid
307 *Nematoscelis megalops*) that prey on copepods, hyperiids, other euphausiids and small fish (Fig. 4;

group II). Low $\delta^{15}\text{N}$ values identify mainly filter-feeders (more closely dependent on mesoplankton, feeding on phytoplankton and other particles in the water column; Fig. 4 group I) or small carnivores (e.g. small decapods and the hyperiid *Phronima sedentaria*; Fig. 4 group IIa) that prey on copepods and gelatinous plankton. In general more depleted $\delta^{13}\text{C}$ values were found in omnivores (copepods and *M. norvegica*) consuming prey at several trophic levels and likely also detritus. A more enriched signature (as found in *Cyclothone* spp.) corresponds to strict carnivores and was also found in bathypelagic species with low migratory habits (i.e. *Gennadas elegans* and *Pasiphaea multidentata*). Accordingly *P. sedentaria*, which is known to feed on salps, was separated from the other two hyperiids *P. semilunata* and *V. armata* (see also Figure 5). A one-way PERMANOVA test showed significant differences between groups I and II ($F_{1,12}=33.13$, $p<0.05$). The overall range of $\delta^{15}\text{N}$ is indicative of two trophic levels, provided we accept a $\delta^{15}\text{N}$ enrichment of 2.54‰ per trophic step, with *P. multidentata*, *N. megalops* and *C. braueri* positioned at the uppermost level (TL ranged from 3.0 to 3.4), *V. armata*, *P. semilunata* and copepods on the lowest level (2.0) and the rest of the species occupying an intermediate level.

3.2. Seasonal changes and relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of suprabenthos and zooplankton

The only variation in the mean $\delta^{15}\text{N}$ of suprabenthos was a decrease of the mean trophic level in February and April (Fig. 6a). However, differences in the mean $\delta^{15}\text{N}$ were not significant (one-way ANOVA, $p>0.05$) due to high variance. $\delta^{13}\text{C}$ was more depleted in August-September and more enriched in February and June (Fig. 6b); the same trend was observed when $\delta^{13}\text{C}$ values were corrected for lipid content (via C/N ratio). The peak in February was significant (one-way ANOVA, $F_{5,59}=4.54$, $p<0.05$) compared to August and September (*post-hoc* Tukey test, $p<0.05$). $\delta^{15}\text{N}$ for zooplankton showed no significant trend (Fig. 6c); in September we found the lowest $\delta^{15}\text{N}$ values and in February the highest ones. Regarding $\delta^{13}\text{C}$, the most enriched values were found in February and April/June (Fig. 6d), with significant differences from September (one-way ANOVA $F_{4,32}=4.83$, $p<0.05$; *post-hoc* Tukey test with $p<0.05$), when we found the most depleted $\delta^{13}\text{C}$ values.

333 Over the sampling interval as a whole, the relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values was
334 considerably stronger for zooplankton ($R^2=0.67$; $\delta^{15}\text{N} = 2.30*\delta^{13}\text{C} + 53.04$) than for suprabenthos
335 ($R^2=0.02$; $\delta^{15}\text{N} = -0.22*\delta^{13}\text{C} + 2.63$).

336 The relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of suprabenthos was generally weak in all periods (Fig. 7).
337 The $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ relationships for suprabenthos were slightly higher in summer (August and
338 September) and spring (April-June). In August and September $\delta^{13}\text{C}$ values were more depleted
339 (ranging from -19.4 to -22.2‰), then started to be slightly enriched from November to February
340 (values ranged from -17.6 to -20.9‰). Thus, in April-June they were on average more depleted
341 (ranging from -18.5 to -22.5‰).

342 A different trend in the $\delta^{15}\text{N}$ to $\delta^{13}\text{C}$ relationship was detected for zooplankton (Fig. 8); the strongest
343 correlations were observed in August and February, while correlations were weaker in September
344 and exhibited the lowest R^2 value in November. A pattern of $\delta^{13}\text{C}$ enrichment similar to that
345 observed for suprabenthos was displayed by zooplankton; the most depleted $\delta^{13}\text{C}$ signatures
346 occurred from August to September with a shift to more enriched values from November to April.

347 3.3. Correlation of $\delta^{13}\text{C}$ signatures with environmental variables

348 Spearman correlation between mean $\delta^{13}\text{C}$ values of all the suprabenthic species in each month and
349 the available environmental variables showed significantly negative correlation with the
350 concentration of organic matter in the sediment surface ($R=-0.943$, $p= 0.004$). $\delta^{13}\text{C}$ values of
351 zooplanktonic species were correlated with the surface Chl *a* concentration recorded one month
352 before the sampling ($R=0.828$, $p= 0.041$).

353 3.4. Correlations between $\delta^{13}\text{C}$ signatures and C/N

354 The correlations between $\delta^{13}\text{C}$ and C/N ratio for suprabenthos were always negative, although not
355 significant. Correlation was closed to the significance level (Spearman $R=-0.345$; $p=0.057$) in
356 February, explaining ~12% of the variation. For zooplankton species $\delta^{13}\text{C}$ vs. C/N ratio correlations

357 were negative in August ($R=-0.314$; $p>0.05$) and June ($R=-0.800$; $p>0.05$), then positive significant
358 correlations were found in September ($R=0.942$; $p<0.01$), February ($R=0.705$; $p<0.01$) and almost
359 significant ($R=0.468$; $p=0.078$) in April. In September and February correlation explained up to 50%
360 of the variation. In general C/N ratios seemed to be less variable in zooplankton (ranging from 3.7 to
361 4.8) than in suprabenthos (from 3.1 to 5.9). There was a clear increase in lipid content from August
362 to April, both in suprabenthos and zooplankton. C/N ratios increased from August to April, being
363 maxima in February (C/N suprabenthos 5.9 ± 1.2 ; C/N for zooplankton 4.8 ± 0.9).

364

365 **4. Discussion**

366 *4.1. Methodological approach*

367 Based on our results, our approach to trophic level estimates and the value of fractionation chosen
368 (2.54‰, Vanderklift and Ponsard, 2003), has proven to be consistent with the dietary information
369 available for some of the species analysed in this study.

370 Small ($CL < 28$ mm) *P. multidentata* (with $\delta^{15}\text{N}$ signature of 7.5‰) consume prey (e.g. *Vibilia*
371 *armata*, Phrosinidae, euphausiids; Cartes, 1993) for which the $\delta^{15}\text{N}$ signature ranged between 3.9
372 and 6.3 ‰, providing an average fractionation of ~ 2.4 ‰. This agrees with recent findings on marine
373 plankton which showed $\delta^{15}\text{N}$ fractionation values considerably lower than the assumed 3.4‰ (Bode
374 et al., 2006) and enrichment between size classes even much smaller (Rau et al., 1990; Fry &
375 Quinones, 1994; Rolff, 2000; Bode et al., 2007).

376 As far as concerns lipid extraction in this study we did not extract lipids from samples, because
377 defatting is unusual for small invertebrates (Iken et al 2001, Nyssen et al 2002, 2005; Carlier et al,
378 2007a, b) and most of the (few) published works on deep-sea small invertebrates present data on
379 isotopes with non-defatted analysis (e.g., Iken et al 2001; Polunin et al., 2001; Nyssen et al 2002;
380 2005). Thus the use here of defatted samples would have made impossible comparison with other
381 studies. Besides removing lipids prior to isotope analysis (or even ‘normalising’ the $\delta^{13}\text{C}$ based on

382 C/N ratio, *sensu* McConnaughey & McRoy, 1979; Leggett, 1998) might be contrary to the goals of
383 our analysis using $\delta^{13}\text{C}$, because in freshwater zooplankton lipids are typically dietary in origin
384 (Goulden & Place, 1990). In deep waters most of the seasonal shifts in isotopic carbon signatures are
385 attributable to inputs of fresh OM (e.g. Chl *a*) in sediments and later in animal tissues. Because of
386 the lipid nature of this pigment, lipids were significantly correlated with Chl *a* concentration
387 (Fabiano et al., 1993), so lipid extraction may lead to a removal of the signal of food input for these
388 communities. We are reassured by the fact that as C/N ratios increase in the time series the ^{13}C
389 values are enriched, not depleted as one would expect from the effect of lipid enrichment. Thus it is
390 very likely that changes in OM flux will affect both lipid levels of consumers (through greater
391 feeding and increased lipids) and the ^{13}C signature of the OM. This means that changes in ^{13}C ratios
392 could be the result of changes in the type of OM or the amount of OM.

393 In our analysis of the bathyal benthopelagic food webs of the Algerian Basin based on $\delta^{13}\text{C}$ and
394 $\delta^{15}\text{N}$ shifts, we focused on the dynamics of suprabenthos and macrozooplankton/micronekton. Both
395 compartments are the basis of diets for megafauna (fish, decapods) in open-sea trophic chains in the
396 western Mediterranean (Cartes and Carrassón, 2004). Although it is a useful and increasingly
397 employed technique, isotope composition gives only an average indication of the trophic level of
398 food that has been assimilated into tissues (see Johnston and Kennedy, 1998; Owens and Watts,
399 1998 for a review). For that reason we have compiled here both our own data and published results
400 on the gut contents of suprabenthic peracarids and macrozooplankton/micronekton (see Table 1).
401 Original and novel information was provided by carrying out the simultaneous and comparative
402 analysis of zooplankton and suprabenthos.

403 *4.2. Trophic structure of deep suprabenthos and zooplankton.*

404 *4.2.1 Relationships with gut content data.*

405 Our results for stable carbon and nitrogen isotopes of suprabenthos are consistent with previously
406 reported values for deep Mediterranean suprabenthos as a whole group (Polunin et al., 2001) and
407 complete the information given at species level (Madurell et al., 2008) based on data obtained north

408 of Mallorca (Balearic Basin: *ca.* 100 km to the northwest of Cabrera). Although there is not
409 information on isotopic data for deep zooplankton at species level, the isotopic signatures of our
410 target species fit well with gut content findings in the literature (see Table 1).

411 The isotope data on suprabenthos also agreed with scarce information on gut contents (Table 1). We
412 identified a general tendency in the distribution of species in the multi-species analysis, with
413 carnivores (e.g. *Rhachotropis* spp., and *Nicippe tumida*) and deposit feeders occupying the two
414 extremes of the “trophic gradient”. An important group of predators seems to be species feeding on
415 meiobenthos: nannastacids (e.g. *Campylaspis* and related genera, based on the piercing structure of
416 mouthparts: Jones, 1976) and the isopod *Munnopsurus atlanticus*, which often consumes
417 foraminiferans (Elizalde et al., 1999; Cartes et al., 2002). Among those species with unknown
418 feeding habits (i.e. there are no data on gut contents), stable isotope analyses assigned the
419 stegocephalid amphipod *Stegocephaloides christianensis*, *Tryphosites* spp., and *Epimeria parasitica*
420 to an omnivorous trophic guild. This conclusion was based both on the morphology of mouth parts
421 (e.g. stegocephalids, Ruffo & Vader, 1998; *Tryphosites* spp. Saint-Marie, 1985) and on gut content
422 data for closely-related species (i.e. the stegocephalid *Andaniexis mimonectes*, close to *S.*
423 *christianensis*, feeds on detritus: Cartes et al., 2002). Deep-sea macrobenthos (mostly detritus
424 feeders) exhibit an expansion of trophic niches; species tend to be omnivorous to avoid competition
425 for food (Gage and Tyler, 1991; Jarre-Teichman et al., 1997). The isopod *Eurycope inermis* preys on
426 medium-sized foraminifera and consumes detritus (Svavarsson et al., 1993). Hence the omnivory
427 attributed to deep-sea species may be better described as a mixed behaviour in which species may
428 both feed on organic particles and prey on microinvertebrates (e.g. some *Epimeria* spp., Nyssen et
429 al., 2005; present study). Most Lyssianassidae are generally considered as scavengers, based on
430 images of bait-attending animals (Blankenship and Levin 2007). However, detritus often occurs in
431 guts of deep-water lysianassids such as *Scopelocheirus hopei* (Cartes et al., 2002). These facultative
432 adaptations to exploit different food sources likely explain the isotope results obtained for
433 omnivorous species.

434 At assemblage level, we found a wider range of $\delta^{15}\text{N}$ values than of $\delta^{13}\text{C}$ values (Table 2), which
435 suggests partition of a similar source of primary production (narrow range of $\delta^{13}\text{C}$ values) among a
436 variety of trophic levels (wide range of $\delta^{15}\text{N}$ values) among suprabenthic species. The variability in
437 the relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was particularly high among deposit feeders and omnivores
438 (Fig 3), suggesting exploitation of POM at different stages of degradation: from patches of fresh
439 phytodetritus to highly refractory or recycled material. For example, at Porcupine Abyssal Plain
440 (PAP) suspension feeders can expand the spectrum of the food they utilize to include resuspended,
441 more refractory, material (Iken et al., 2001) because of low availability of fresh POM (Lampitt,
442 1985). They show higher $\delta^{15}\text{N}$ values than deposit feeders (Iken et al., 2001; Mintenbeck et al.,
443 2007), because they likely consume the smallest particles of POM, which are the most degraded. In
444 our study, *Calocaris macandreae* exhibited the highest $\delta^{15}\text{N}$ values among POM consumers (e.g. the
445 amphipod *Lepechinella manco*, the cumaceans *Platysymphus typicus* and *Cyclaspis longicaudata*) in
446 the Algerian Basin. This must be attributed to its burrowing behaviour and also larger size. *C.*
447 *macandreae* finds an optimal habitat (with its highest abundance) in muddy bottoms off the Catalan
448 coasts, a slope area influenced by advective fluxes through submarine canyons (Monaco et al.,
449 1990). POM must be increasingly metabolized while being mixed into the sediment (Conte et al.,
450 1994; Santos et al., 1994), thus showing an enriched $\delta^{15}\text{N}$ in a burrowing species such as *C.*
451 *macandreae*.

452 Among meiobenthos feeders, it was evident that $\delta^{13}\text{C}$ signatures exhibited a wider range of values
453 than $\delta^{15}\text{N}$ (high ratio between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges), which suggests exploitation of different
454 meiofaunal compartments, such as medium-sized foraminifera or hard-tested, agglutinant
455 foraminifera. As foraminifera quickly consume inputs of fresh OM to the seabed (Gooday and
456 Lambshead, 1989), even competing with macrofauna for labile OM (Gooday et al., 1996), it seems
457 logical that foraminiferan-feeders off Cabrera (e.g. *Munnopsurus atlanticus*) should have lower $\delta^{15}\text{N}$
458 and more depleted $\delta^{13}\text{C}$ than species consuming meiobenthos with slower responses to particle

459 fluxes (e.g. nannastacid cumaceans). The group of copepod carnivores had the lowest ratio between
460 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges, suggesting exploitation of a single food source (copepods) and maybe high
461 competition for food. Copepods, however, are the most abundant taxon in deep Mediterranean
462 suprabenthos (Cartes, 1998), and they may constitute a superabundant food resource, which may
463 reduce possible competition among carnivorous amphipods. The ratio between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ranges
464 among zooplankton was comparable to that among carnivorous suprabenthos. Zooplankton probably
465 exploited a single source of primary production ($\delta^{13}\text{C}$ varied from -21.1‰ to -19.9‰) in comparison
466 with suprabenthos. This indicates lower diversification of primary food sources and, consequently,
467 of feeding strategies among macrofauna in pelagic than in benthic ecosystems. Our data suggest that
468 benthic food webs tend to be more complex, as also confirmed by the low variation of C/N ratios in
469 zooplankton compared to suprabenthos.

470 4.2.2 Trophic levels

471 As in our study, Iken et al. (2001) showed that in the deep-sea benthic ecosystem of the northeastern
472 Atlantic Ocean (Porcupine Abyssal Plain), there is significant overlap in nitrogen isotopic values
473 between trophic levels, suggesting a smaller stepwise enrichment than the most widely assumed
474 3.4‰ (DeNiro and Epstein, 1981; Minawaga and Wada, 1984; Post, 2002). Thus assuming a trophic
475 enrichment of 2.54‰ (Vanderklift and Ponsard, 2003) between consumers and their diet, at least
476 three trophic levels were identified within suprabenthos of the Algerian Basin. Assemblages ran
477 from the lowest level occupied by deposit feeders to the uppermost where we found the fish parasite,
478 *Gnathia* sp. A similarly wide range of $\delta^{15}\text{N}$ values was observed for amphipods sampled in the
479 eastern Weddell Sea, where three levels of the food web were covered among eight species
480 examined (Nyssen et al., 2005). However, the lowest level in the Weddell Sea was occupied by
481 species feeding on algae and phytoplankton (e.g. *Ampelisca richardsoni*), absent from deep-sea
482 environments. We observed two trophic levels among suprabenthos at bathyal depths in the Catalan
483 Sea based only on gut content data (Cartes et al., 2002).

484 Compared to suprabenthos, trophic levels for zooplankton were at the most two: the lowest
485 represented by the hyperiids *Vibilia armata* and *Phrosina semilunata*, feeding on mucus net
486 (including phytoplankton) of salps (Madin & Harbison, 1977; Coleman, 1994), the highest by the
487 mesopelagic decapod *Pasiphaea multidentata* ($\delta^{15}\text{N}$: 7.5‰).

488 4.3. Trophic dynamics

489 4.3.1 Seasonal variability in stable isotopes signatures

490 As shown by $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations, there were some clear differences between zooplankton and
491 suprabenthos in their coupling with peaks of new production (nitrate-based production or export
492 production). High $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations likely indicate a single food source (e.g. in deep-sea
493 communities; Polunin et al., 2001) and suggest pulses of new production. In contrast, weak
494 correlations (low R^2 values) point to an array of possible sources of production.

495 Among zooplankton, increase of $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations in February was almost immediate after the
496 peak of surface chlorophyll *a* concentration and stronger than for suprabenthos. Zooplankton migrate
497 vertically in the western Mediterranean (Sardou et al, 1996), and there is substantial, active and rapid
498 transport (the *swimmer flux*; Miquel et al., 1994) of new production from the euphotic zone
499 downward. In the open ocean, swimming by zooplankton produces a major portion of downward
500 organic matter transfer, and zooplankton also aggregate small particles as fecal shuttles that sink
501 rapidly (Wefer, 1989). The higher correlation between carbon and nitrogen isotopes in zooplankton
502 during the most productive period of the year may reflect the coupled effects of a nitrogen isotope
503 positive excursion triggered by Rayleigh fractionation (according to the conceptual scheme proposed
504 by Mariotti et al., 1981) and classical biological pump effects on the carbon isotopes due to the
505 preferential removal of the lighter isotopes by phytoplankton.

506 As indicated, the response among suprabenthos was weak, with slight increase in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$
507 relationships in April-June (delayed relative to the peak of Chl *a*). In general the low correlation
508 observed for suprabenthos was likely due to the exploitation of different kinds of sinking particles

(e.g. marine snow, fresh POM, phytodetritus) or sedimented and frequently recycled POM. Seasonal changes in food sources for suprabenthos were also evident in $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ relationships northeast of Mallorca (off Soller) in the northwestern Mediterranean (Madurell et al., 2008), where the correlations were stronger than off Cabrera. Despite being only *ca.* 100 km north of Cabrera, Soller is a more productive area (Cartes et al., 2008) because of different local factors: wind regime with formation of deep water and an influence of Winter and Levantine Intermediate Waters (López Jurado et al., 2008). Although generally weak, the highest $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ correlations were found among suprabenthos in August and September off Cabrera. This suggests a second peak of food input, which could be related with i) the formation of the deep chlorophyll maximum (DCM) at *ca.* 60-110 m (Turley et al., 2000) in late spring-summer (Estrada et al., 1993) in the western Mediterranean Basin, or ii) the maximum mass flux of POM in mid-June (Miquel et al., 1994). A DCM is a characteristic feature of oligotrophic waters, including the Mediterranean (Estrada et al., 1993; Turley et al., 2000), in which production is based on diatoms. The signature of fluxes combining dinoflagellates and flagellates in upper layers and diatoms at the DCM can give a different $\delta^{13}\text{C}$ than that of spring phytoplankton blooms. Dinoflagellates, being more depleted (Gearing et al., 1984), even dominate over diatoms under highly stratified conditions in late spring-summer (e.g. in the middle of the Adriatic Sea; Totti et al., 2000).

4.3.2. *Hypotheses for winter-spring enrichment of $\delta^{13}\text{C}$*

In the Algerian Basin we found a general trend for $\delta^{13}\text{C}$ enrichment from late autumn (November) to late winter-spring (February-April), both for suprabenthos and zooplankton, which is also correlated with increase in C/N ratios. This pattern was consistent with that observed off Galicia (NE Iberian Peninsula) for mesozooplankton (Bode & Alvarez-Ossorio, 2004). In that upwelling ecosystem there is $\delta^{13}\text{C}$ enrichment in mesozooplankton simultaneous with the peak of Chl *a* in surface waters. The $\delta^{13}\text{C}$ enrichment off Cabrera in February-April was correlated with higher surface Chl *a*, though recorded one month before the plankton samplings, and with lower concentration of organic matter

534 on the sea bottom (Figure 9), the last (negative) indicating a delay after the Chl *a* peak. $\delta^{13}\text{C}$ of
535 suprabenthos was higher in April-June, lower in November-February: this enrichment from April to
536 June probably coincided with higher, increasingly refractory, total organic matter in sediments.
537 Bathyal suprabenthic fauna undergoes noticeable seasonal variations in biomass around the Balearic
538 Islands (Cartes et al., 2008), with a peak of abundance in summer parallel to an increase in organic
539 matter in the sediment, which in turn is coupled to the peak of Chl *a* recorded in January-March,
540 with a delay of two/three months. In any case, shifts of $\delta^{13}\text{C}$ values off Cabrera seemed to be a
541 consequence of variations in surface production, successional changes in phytoplankton composition
542 and the general vertical flux of particles (Miquel et al., 1994). In fact flagellates (small
543 phytoplankton with slow growth rates) have been shown to exhibit more negative $\delta^{13}\text{C}$ than co-
544 existing diatoms (Gearing et al., 1984), and these differences are also seen during the seasonal
545 succession of diatoms to flagellates. Low enrichment could be due to an increase of more depleted
546 dinoflagellates (Gearing et al., 1984) in late spring-summer (Gilabert, 2001). In parallel, production
547 in late spring must be based on a mass flux of faecal pellets, which change depending on
548 zooplankton succession (Miquel et al., 1994). Pellet flux in August is dominated by those of
549 euphausiids and large copepods. Tamelander et al. (2006) showed depletion of $\delta^{13}\text{C}$ from faecal
550 pellets of copepods, in agreement with the low enrichment in $\delta^{13}\text{C}$ found in August-September.
551 Oceanographic processes, in this case the water column regime, may also influence shifts in isotope
552 composition. The rapid sedimentation rates in late winter-spring may be enhanced in the western
553 Mediterranean under conditions of water-mass homogeneity in that period (López-Jurado et al.,
554 2008), so shifts in $\delta^{13}\text{C}$ were almost simultaneous with the peak of surface Chl *a* (February-March).
555 By contrast, the reduced sedimentation of more $\delta^{13}\text{C}$ depleted particles in late spring, when water
556 masses are stratified, may contribute to the (weak) response in $\delta^{13}\text{C}$ of bathyal suprabenthic species
557 in August-September, after the decrease of mass flux in the water column (Miquel et al., 1994).

558 *4.4. The benthopelagic food web in the Algerian Basin*

Bathyal suprabenthos is distributed mainly on the sediment water interface between 0 and 1 m above the bottom (Angel, 1990). This fauna is trophically dependent on the arrival of POM at the seabed. The bulk of photosynthetically produced organic matter exported from the photic zone usually reaches the sea floor in the form of detrital particles that are the main food source for the deep-sea benthos (Pfannkuche, 1993; Thiel, 1983). The particular oceanographic conditions of the Mediterranean influence the quantity and quality of POM reaching deep waters. Basically, the general oligotrophy of Mediterranean waters, which increases eastward (Turley et al., 2000), couples with the thermal stability below 150 m at an approximately constant temperature around 13°C (Hopkins, 1985) to enhance rapid degradation of OM down the water column (Wishner, 1980). The Algerian Basin south of the Balearic Islands is an insular area, with little influence from advective inputs (Cartes et al., 2008) because of low river discharge and uncertain influence from mainland-associated events such as the cascade fluxes through submarine canyons farther north in the Gulf of Lyons (Palanques et al., 2006). Under these conditions, only low quantities of POM can arrive on the seabed off Cabrera. This explains why detritus feeders (e.g. *Calocaris macandreae*) were not dominant among macrofauna in the area (Cartes et al., 2008, authors' unpubl. data), a difference from the mainland part of the Catalanian coasts (Cartes et al., 2002) influenced by advective fluxes channelled through submarine canyons. Canyons have higher and probably more enriched POM than surrounding areas (Rowe et al., 1982; Vetter & Dayton, 1998). Conversely, in the western Algerian Basin the guild of meiobenthos carnivores (e.g. *Munnopsurus atlanticus*), mainly exploiting foraminifera, was well represented (Cartes et al., 2008; authors' unpublished data). This suggests that inputs of fresh organic matter to the seabed must be rapidly consumed by meiofauna competing for fresh food with macrobenthos. This role has been previously attributed in the eastern Mediterranean to meiofauna (Danovaro et al., 1999) because of its relatively high biomass and the low biomass of macrofauna. High levels of meiofauna in the Algerian Basin would explain the dominance of meiobenthos feeders.

584 Patterns of food sources in the western Mediterranean are quite different from those in areas where
585 studies on food webs have previously been performed; however, this is the first study focused on the
586 mesopelagic- suprabenthic food web, so there is not direct available data for comparison. In the
587 northeastern Atlantic (Porcupine Abyssal Plain, PAP) at abyssal depths, phytodetritus arrives at the
588 sea floor in late May-early June, only 4-6 weeks after the peak of primary production at the surface
589 (Bett et al., 2001). As a consequence deposit feeders are often the main trophic guild found at PAP
590 based on both isotopic composition and gut content results (Iken et al., 2001). This massive arrival
591 of phytodetritus, sometimes densely covering the bottom, has never been observed in the bathyal
592 Mediterranean (e.g. at the surface of multi-corer samples). In spite of the greater depth (4800 m) of
593 PAP compared to the Algerian Basin, PAP is situated in a eutrophic area (e.g. based on the trophic
594 structure of macrobenthos: Sokolova, 1972). The arrival of new production at bathyal depths of the
595 Algerian Basin is probably weaker than at PAP. Hence, in the deep Mediterranean off Cabrera we
596 found a high density of carnivores, represented mainly by amphipods of the genus *Rhachotropis*
597 (Cartes et al., 2008; authors' unpubl. data) feeding on copepods, with a wide variety of trophic
598 guilds, without the clear dominance of any (i.e. high diversity) and distributed in three trophic levels.
599 In an oligotrophic system such as the deep Algerian basin (Turley et al., 2000) the scarcity of any
600 dominant food source may enhance exploitation of different trophic pathways.

601 5. Conclusions

602 The most innovative aspect of our study is the simultaneous and comparative study of zooplankton
603 and suprabenthos, which allowed us to put both compartments at different trophic levels and to
604 distinguish a different source of carbon based on the different $\delta^{13}\text{C}$ signature for zooplankton and
605 suprabenthos. The majority of benthic macrofaunal organisms are considered to be deposit feeders or
606 generalists (Gage and Tyler, 1991). However, our study based on swimming macrofauna living in
607 the entire or just near-bottom water column described a more complex food web, in which species
608 with mixed diets (feeding alternately on detritus and small invertebrates) and carnivores were

609 dominant. Hence the trophic web of the suprabenthic community is organized in three trophic levels
610 (Madurell et al., 2008; this study) with organisms that exploit fresh food, deposited/resuspended
611 POM, small invertebrates (e.g. foraminiferans) and other crustaceans and generally depending more
612 on the deposited or resuspended detritus in the BBL (Cartes et al., 2008). Conversely zooplankton
613 are organized in two trophic levels, comprising organisms which feed directly on
614 phytoplankton/phytodetritus by daily movements to the photic zone and carnivores feeding on them.
615 In any case, both compartments are linked to the primary production cycle and are exposed to a
616 seasonal shift in food availability and quality, as deduced by seasonal changes in $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$
617 relationships. The high diversification found in suprabenthos food strategies evidenced by stable
618 isotope analysis indicated the complexity of food webs in deep environments. Both bottom-up and
619 top-down processes played an important role in deep trophic webs. Particularly, by the role of
620 croppers (*sensu* Dayton and Hessler, 1972) top-down processes must help to maintain high levels of
621 diversity among suprabenthic macrofauna in comparison, for instance, to deep zooplankton. This
622 trend should be evidenced in the future, once highlighted the contribution of suprabenthos in the
623 diets of fish and decapod in the area.

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