



Deep-sea macroplankton distribution (at 400 to 2300 m) in the northwestern Mediterranean in relation to environmental factors

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ABSTRACT

Changes in the composition and biomass distribution of deep-living zooplankton over wide gradients of depth (400–2300 m) and longitude (~180 km) have been analyzed in the Balearic Basin (western Mediterranean), seeking the environmental variables responsible for these changes. Zooplankton tends to aggregate at different levels of the water column (forming Deep Scattering Layers, DSL) and in the Benthic Boundary Layer (BBL). Macrozooplankton biomass and composition were analyzed along a transect performed in July 2010 in midwater (between ~350 and 450 m) and near the bottom (at ~5–200 mab), over soundings of 450–2263 m, including the top of Valencia Seamount (at ~40° 25' N–02° 42' E, 1076 m). Zooplankton changed significantly in composition at the mesoscale (~180 km) in both the DSL and the BBL. Siphonophores and calanoid copepods were the most dominant deep zooplankton taxa, calanoids reaching higher abundance in the BBL (1761–5177 individuals/1000 m³) than in the DSL (1568–1743 individuals/1000 m³). There was a significant increase in near-bottom zooplankton biomass over the middle slope, at 1000–1300 m, linked to an increase in scyphozoans and siphonophores (*Lensia* spp. and *Abylopsis tetragona*) with peaks of 1.5–2.0 gWW/1000 m³. The peak of near-bottom zooplankton at 1000–1300 m coincided with the lowest temperatures (13.08 °C) and maximum O₂ concentration (4.40 ml/l) near the bottom and below 1000 m with higher records in near-bottom turbidity. Gelatinous zooplankton are the main prey in the diet of the demersal fish *Alepocephalus rostratus* in the western Mediterranean, fish responsible for the peak of megafauna biomass reported at around 1200–1400 m in the deep Mediterranean and at similar depths in other oceanic areas (e.g. the NW Atlantic). We suggest that deep-sea environmental conditions can govern peaks of near-bottom zooplankton, as well as influence the structure of the demersal fish community.

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1. Introduction

Zooplankton and micronekton communities tend to aggregate at different levels in midwater and at the seabed interface (Genin, 2004; Simard et al., 1986; Vereshchaka, 1995). Near the bottom, zooplankton aggregate around physical features such as shelf breaks (Genin, 2004; Vereshchaka, 1995) and canyon heads (Macquart Moulin and Patriiti, 1996). In midwater they may aggregate close to thermohaline fronts (boundaries between water masses with different T and S) that may constitute physical barriers for zooplankton migrations. Zooplankton both form Deep Scattering Layers (DSL) (Opdal et al., 2008) and interact with features of the seafloor on the continental shelf and slope. This has been described by observations and sampling (e.g. Hargreaves, 1984; Omori and Otha, 1981; Reid et al., 1991) and by the occurrence of typical DSL fauna in the diet of benthopelagic fish and crustaceans living on the continental slope to

~1000 m (Cartes, 1994; Cartes et al., 2008a,b; Fock et al., 2002; Gordon and Mauchline, 1990; Mauchline and Gordon, 1991). Interaction of mesopelagic zooplankton layers with the bottom occurs typically around 200–700 m (Hargreaves, 1984; Omori and Otha, 1981; Reid et al., 1991). For example, aggregations of the scyphomedusa *Parumbrosa polylobata* in the benthopelagic layer occur off Suruga Bay at 270–510 m (Miyake et al., 2005). Zooplankton also tends to aggregate near the bottom beyond the mesopelagic domain (Smith et al., 1987; Wishner, 1980). That is the case of: i) the pelagic holothurid *Scotoanassa* sp. and gelatinous organisms at 20–100 m above the sea bottom over 1800–1900 m depths (Childress et al., 1989) and ii) zooplankton and nekton at 2000 m on Juan de Fuca Ridge over hydrothermal vents (Skebo et al., 2006).

The benthopelagic or near-bottom (Mauchline and Gordon, 1991; Mees and Jones, 1997) fauna is composed of a wide variety of taxa (e.g. cnidarians, decapod crustaceans, mysids and fish) inhabiting the water layer immediately adjacent to the sea bottom, the so-called Benthic Boundary Layer (BBL). Some taxa that are permanent residents are called *suprabenthos* or *hyperbenthos*. This assemblage is composed

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mainly by peracarid crustaceans, whereas the *near-bottom zooplankton* are composed of taxa, including euphausiids and natantian decapods, that occupy this zone on a more temporary basis as phases of vertical or ontogenetic migrations (Cartes et al., 2010). The BBL community has a diverse composition and complex ecological dynamics, both of which are still poorly known. This community is an important source of food for demersal fishes and crustaceans situated at the top of deep-sea trophic webs. Yet, it is not clear what environmental variables control the distributions and abundance of zooplankton in intermediate and deep waters. Mesopelagic zooplankton and micronekton (small fishes, shrimps and squids) are distributed worldwide (Reid et al., 1991), and they support key biological processes in all bathyal and benthopelagic trophic webs (Cartes et al., 2008a). Small fishes, shrimps and squids are energy-rich items in comparison with gelatinous zooplankton that are mostly water (Lucas et al., 2011). Zooplankton is the most important component in the diets of slope fish (Cartes and Carrassón, 2004; Percy and Ambler, 1974) and of some decapod crustaceans (Cartes, 1993a, 1994). Aggregations of zooplankton may enhance fish biomass near the bottom. For example, the abundance peak of Alepocephalidae at 1200–1400 m over the continental slope in the western Mediterranean (Stefanescu et al., 1993) and North Atlantic (Gordon, 1986; Merrett et al., 1991) has been linked to increases of near-bottom gelatinous plankton (Cartes and Carrassón, 2004; Lebrato et al., 2012). This also has an influence on the success in reproduction of some deep-water shrimps (e.g. *Aristeus antennatus* and *Plesionika martia*; Cartes et al., 2008b; Fanelli and Cartes, 2008), which is linked to seasonal consumption of zooplankton prey.

It is especially important to understand which environmental factors control the distribution of deep zooplankton in the deep Mediterranean basin, because changes in deep and intermediate water masses (the Mediterranean deep-water, WMDW, and the Levantine intermediate water, LIW) have occurred since the 1950s (Rixen et al., 2005). These modifications are partially related to human activities such as river damming (Rohling and Bryden, 1992; Skliris and Lascaratos, 2004), changing the abundance of benthopelagic organisms, such as the shrimp *Aristaeomorpha foliacea*. That particular change is likely related with long-term changes in the deep water column T, S and O₂ (Cartes et al., 2011a, b). Moreover, dramatic effects on the distribution of deep-sea zooplankton following changes in O₂ concentration are suggested, based on zooplankton responses to extreme conditions found in Oxygen Minimum Zones (OMZs, Childress, 1995; Wishner et al., 2000). Dissolved oxygen concentrations in OMZs are <22 µM at intermediate depths (50–1000 m), thus, it is important to study responses to oxygen availability in other areas where depletion has developed progressively in recent times.

In this context, questions addressed in the study we report here are: 1) What mesoscale changes occur in the composition and biomass distribution of deep zooplankton over wide depth ranges (400–2300 m) and longitudinal (~180 km) gradients? And, 2) what environmental variables are related with these zooplankton changes in mid-water (DSL) and especially in the BBL? We also discuss possible relationships between the distributions of the BBL zooplankton and those of the deep-sea benthopelagic fish (e.g. alepocephalids), based on the important role of gelatinous zooplankton in their diets below 1000 m, as previously observed in the area. Our results are the first multidisciplinary, mesoscale approach for study of near-bottom zooplankton, their relationship with environmental factors and their trophic role.

2. Material and methods

2.1. Study area

Macrozooplankton and environmental parameters were sampled in July 2010 along a transect between the Catalanian coast (off Barcelona, 41° 11' N–2° 27' E) and the NW side of the Island of Mallorca (39° 47'

N–2° 22' E, Balearic Islands) in the Balearic Basin (northwestern Mediterranean; Fig. 1). Sampling was conducted in the framework of Project ANTRIMARE (ref. CTM2009-12214-C02-01-MAR) that focused on the analysis of natural variability and anthropogenic impact on the biotic diversity and trophic webs of the bathyal zone.

2.2. Sampling

2.2.1. Macroplankton sampling

Macroplankton was sampled at 14 stations along the Catalonia–Mallorca transect (Fig. 1) over soundings of 450–2263 m (Table 1). Hauls were performed in intermediate waters (in the DSL through a fixed depth interval between ~350 and 450 m) and near the bottom (in the BBL). Hauls at 12 stations were performed in the DSL and 12 in the BBL. In 10 cases DSL and BBL hauls were performed at the same station, while at 4 stations only DSL or BBL hauls were performed. We analyzed the composition and distribution of biomass of macroplankton along the slope of the Balearic Basin separately for the DSL and BBL samples. The two stations situated over 450 m soundings were at the intersection on the slope of the DSL with the bottom, and they were used for the analyses of both the DSL and BBL zooplankton. Thus, the numbers of samples were 14 for the DSL and 12 for the BBL. Two hauls in the BBL were performed over distinctive environments: W8 in La Berenguera Canyon (over ~615 m) and W23 on the top of Valencia Seamount (at ~40° 25' N–02° 42' E, 1076 m). At midwater depths, the DSL was located with the help of echosounders (Simrad Single-beam biological echo sounder EK500:

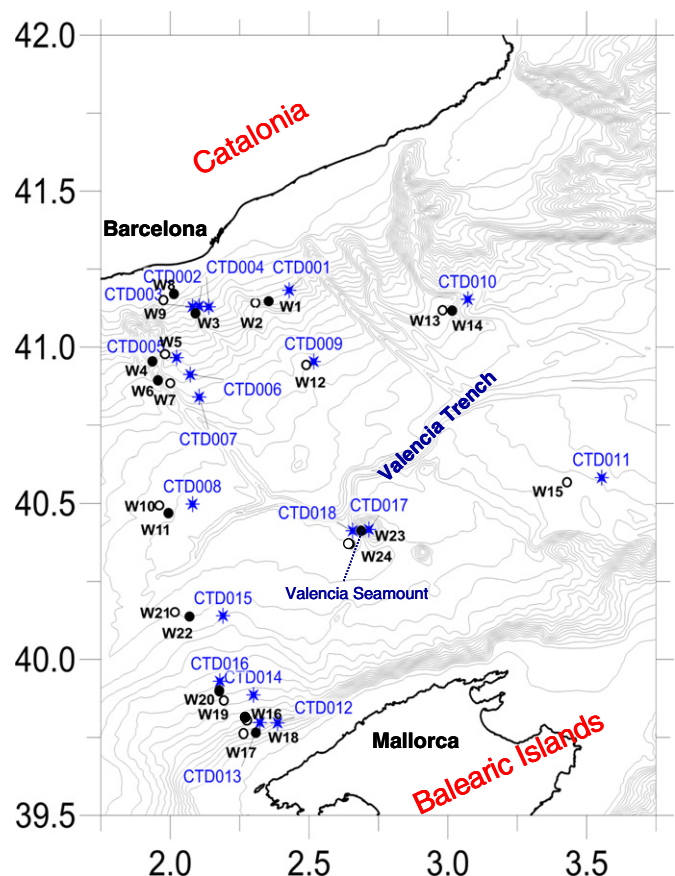


Fig. 1. Map of the Balearic Basin with locations of zooplankton sampling stations: i) in intermediate waters (o), at fixed depths between ~350 and 500 m within the Deep Scattering Layer (DSL); ii) close to the bottom (*) in the Benthic Boundary Layer (BBL) between ~10 and 150 mab over soundings between 450 and 2250 m. Locations (s) of CTD profiles performed from surface to 5 mab.

Table 1

Abundance (ind/1000 m³) of main taxa and species of zooplankton collected in the Deep Scattering Layer and in the Benthic Boundary Layer over the two slopes of the Balearic Basin (C: Catalan slope; B: Balearic slope). Codes for taxa/species analyzed in CCAs were included. n = number of hauls.

Code	Taxa/species	Benthic Boundary Layer				Deep Scattering Layer		
		400–663 m		1010–1282 m		1500–2123 m	Catalan slope	Balearic slope
		C n = 3	B n = 2	C n = 2	B n = 2	n = 3	n = 9	n = 5
Dlarv	Decapod larvae	7.9	5.8	3.0	2.2	0.1	4.7	6.0
Alpl	<i>Alpheus glaber</i> (L)	2.8	3.8	0	0.2	0	1.5	1.7
	Pandalidae (L)	2.6	0.7	1.7	0	0	0.1	0
SergL	Sergestidae (L)	1.5	0.8	1.7	0.7	0.1	0.5	0.7
Dec	Decapoda	1.9	0	1.7	1.2	0.4	0.1	0
Gele	<i>Gennadas elegans</i>	1.2	0	1.7	1.2	0.3	0.1	0
Elarv	Euphausiid larvae	97.8	263.7	66.4	50.9	14.9	59.1	150.7
Euph	Euphausiacea	10.5	10.2	5.1	7.9	2.7	36.1	13.7
Ekro	<i>Euphausia krohni</i>	0.2	6.5	0.3	0.6	0.1	2.9	5.5
Nmeg	<i>Nematoscelis megalops</i>	7.3	3.3	4.8	6.6	1.7	32.1	7.8
Slon	<i>Stylocheiron longicorne</i>	0.4	0	0	0.3	0.7	0.1	0.4
Mys/Ehan	Mysidacea (<i>Eucopia hanseni</i>)	0	0	1.3	1.1	0.6	0	0.1
Hyp	Hyperiid	4.5	13.5	5.4	5.6	3.6	15.0	7.8
	<i>Anchilomera blossenvilei</i>	0	0	0	0	0.2	0.2	0
	<i>Brachyscelus cruscum</i>	0	0	0.4	0	0	0.2	0
Hsch	<i>Lestrigonus schizogeneios</i>	1.0	3.6	0.7	0.8	0.5	5.1	3.2
Hlon	<i>Hyperoides longipes</i>	0.7	1.7	0.7	0	0.2	2.1	0.8
Psed	<i>Phronima sedentaria</i>	0.2	0.5	0.7	0.6	0.4	0.3	0.6
Psem	<i>Phrosina semilunata</i>	1.0	0.8	0	0.6	0.2	0.5	0
Pmac	<i>Primno macropa</i>	0.3	3.8	0.4	0.6	0	1.2	1.7
	<i>Scina borealis</i>	0	0	0	0	0.4	0	0
Scra	<i>Scina crassicornis</i>	0	0.5	1.0	0.8	0	0.2	0.4
Varm	<i>Vibilia armata</i>	1.0	2.7	1.7	2.0	1.6	5.2	1.0
Cal	Copepoda Calanoidea	1761.2	2222.8	5177.2	2173.9	1882.5	1568.2	1743.7
	Copepoda Cyclopoidea	2.8	0	0	0	0	0.9	0
Ostr	Ostracoda	34.2	31.7	90.0	83.0	23.7	14.6	18.7
	Cladocera	2.8	0	0	0	0	0.9	0
Siph	Siphonophora	132.3	43.1	90.7	24.8	22.5	52.4	25.5
Atet	<i>Abylopsis tetragona</i>	1.6	2.0	1.0	0.2	5.8	1.4	1.7
Chap	<i>Chelophyes appendiculata</i>	2.2	2.3	1.9	1.0	3.2	4.4	4.1
Lens	<i>Lensia</i> spp.	128.4	37.4	87.8	23.6	13.5	41.4	18.8
	Ctenophora	6.0	0.4	0	0.3	0	1.6	0
Scy	Scyphozoa	1.5	17.2	3.2	32.5	3.9	0.8	12.0
Per	<i>Periphylla periphylla</i>	0	4.8	0.4	0.2	0.3	0	3.9
Solm	<i>Solmissius</i> spp.	0.5	11.9	0.3	31.3	3.2	0	6.9
	<i>Pelagia noctiluca</i>	0	0	0	0.9	0.4	0	0.4
Poly	Polychaeta (Tomopteridae)	1.7	0.9	0	0.9	1.1	1.3	0.2
	Nemertina	0.6	0	0	1.7	0.4	0	1.2
	Opisthobranchia Thecosomata	9.6	13.0	47.2	0.9	0.9	15.9	10.8
Cym	<i>Cymbulia peroni</i>	0	0	0	0.3	0	0.1	0.6
Pter	Pteropoda	9.6	13.0	47.2	0.6	0.9	15.8	10.2
Cinf	<i>Cavolinia inflexa</i>	0	0	3.8	0	0.4	0.3	1.9
Cpyr	<i>Clio pyramidata</i>	2.2	0	3.2	0.3	0	0.1	2.1
	<i>Creseis acicula</i>	0.4	0	0	0	0	0.1	1.9
Linf	<i>Limacina inflata</i>	7.0	12.2	40.1	0.3	0	14.3	6.2
	Clionidae	0	0.9	0	0	0.4	0	0
Chaet	Chaetognatha	33.8	98.4	33.6	51.8	34.1	35.8	68.6
	Thaliacea	0	0	0.4	0	0.3	0	0
	Appendicularia	3.1	0	0	0	0	0.1	0
Oste	Osteichthyes	7.0	3.3	2.4	2.8	2.2	4.5	4.5
Cbra	<i>Cyclothone braueri</i>	7.0	3.2	2.1	0.8	1.3	4.5	3.6
Cpyg	<i>Cyclothone pygmaea</i>	0	0	0.3	1.7	0.8	0	0.6
	<i>Argyropelecus hemigymnus</i>	0.4	0	0	0	0.1	0.3	0.4
	<i>Ceratoscopelus maderensis</i>	0	0	0	1.4	0.3	0	0.1
Flarv	Fish larvae	0.4	0.8	0.4	1.9	2.5	4.3	1.4

34, 120, and 200 kHz), although specific acoustical sampling was not performed. The sonar-identified DSL roughly coincided with the layer of maximum temperature and salinity in intermediate waters.

Sampling was by means of a cylindro-conical WP2 (or WP3) type plankton net with a 1 m² mouth equipped with an opening-closing mechanism: 1000DT General Oceanics Ltd. The WP2 has both greater maneuverability close to the seafloor and a lower cost than multinet systems such as MOCNESS or BIONESS. In difficult and risky maneuvers performed as close to the bottom as 5 m at great depths (up to 2200 m) this net has been our best option for sampling the BBL

zooplankton. Mouth diameter (1.1 m) of our net fit better with the WP3 definition, but we used 0.5 mm mesh instead the more standard 1 mm for the WP3. The depth of DSL samples and distance to the bottom of BBL samples were recorded by a SCANMAR sensor attached to the net depressor to a depth of ~1200 m, indicating distance to the sea floor. Below this, the SCANMAR sensors do not operate, and distance to the bottom was estimated with a cable-angle inclinometer. The deployment of the net (with an iron depressor of ~75 kg) was visualized on the EK500 screen, helping us to situate the net as close as possible to the sea bed. The SCANMAR-recorded depths were in

agreement with the relationships found among cable angles and cable paid out for the deepest hauls performed with those sensors. Distance of the net from the bottom for BBL hauls was between ~5 and 60 m at soundings between 450 and 650 m and to 5–207 m below 1000 m, with increasing mab distance at greater depths.

The WP2 net was equipped with 500 μm mesh and trawled at ~1.5–2 knots. The duration of horizontal tows was 10 min both for DSL and BBL hauls. Standard 2030 flowmeters (General Oceanics) were attached to the mouths of nets to measure the amount of water filtered and/or the distance covered in each haul. Volume of water filtered ranged between 775 and 2223 m^3 , typically between 866 and 1617 m^3 . All hauls were performed during daytime, except for one W3 sample over 450 m off Barcelona performed at sunset.

Zooplankton samples were immediately fixed in buffered formaldehyde (4%) on board (except some fish, crustaceans as large as mysids or euphausiids and some gelatinous taxa frozen at -20°C for stable isotope analyses, once identified). Specimens were sorted in the ship's wet laboratory with forceps under a stereomicroscope (at $\times 10$ – $\times 40$). A few large medusae (*Pelagia noctiluca*) were accidentally collected in two 1 m^2 WP2 hauls. As they represented between 3 and 10 times the biomass of the rest of sample we excluded them from assemblage/biomass analyses. All taxa were counted and weighed (wet weight after eliminating blotting water) based on aliquots from 1/2 to 1/8 of samples from the fraction of smaller organisms (ca. <20 mm, i.e. copepods, ostracods, and euphausiid larvae). Zooplankton were identified to general taxonomic levels (e.g. siphonophores, polychaetes, euphausiids, and calanoid copepods) and to genus or species for the most dominant taxa of crustaceans (excluding copepods and ostracods) and jellyfish under a stereomicroscope (at $\times 10$ – $\times 40$). One haul was performed per station as has been done in other zooplankton studies in open water (e.g. Scotto di Carlo et al., 1984). A single haul can represent in detail the faunistic composition of zooplankton in a specific depth and period. Both taxa and species were standardized to individuals/1000 m^3 or gWW/1000 m^3 per haul prior to data presentation (for instance by depth strata) and statistical analyses.

2.2.2. Environmental variables

Environmental parameters were recorded by casts with a SBE25 CTD profiler equipped with Niskin bottles and sensors for the P (pressure), T (temperature in $^\circ\text{C}$), S (salinity in pss), O_2 (oxygen concentration in ml/l), turbidity (*turb*) and fluorescence (the last two in voltage units). One CTD profile was performed at each zooplankton sampling station to 5 m above the seafloor. For each variable averages were calculated for the depths trawled in the DSL and in the BBL close to the bottom. Profiles of turbidity were recorded for all CTD stations, from surface to 5 m above the bottom. As a measure of the degree of scattering light, turbidity is mainly a function of the amount of suspended particulate matter in the water column, including resuspended matter near the bottom. Particulate matter includes both inorganic (sand and mud) and organic particles (phytodetritus, fecal pellets, and organisms), so it roughly indicates possible food sources for zooplankton. Thus, we present here the entire profiles for *turb*.

2.3. Data treatment

We analyzed tendencies in the composition of zooplankton by means of Multidimensional Scaling (MDS) analyses at two taxonomic levels: i) based on 19 higher-level taxa and; ii) based on 27 genera-species. Analyses were performed on Bray–Curtis resemblance matrices of log-transformed biomass data, after removing those species which appeared less than twice in all hauls. A distance-based Permutational Analysis of Variance (PERMANOVA, Anderson et al., 2008) was then applied to the two matrices (higher level taxa and species) in order to establish whether the observed patterns/groups indicated by

nMDS were significantly different. Factors compared (both for higher level taxa and species) were water-column layers (DSL vs. BBL) and geographic areas (Catalonia vs. Balearic slopes, i.e. mainland vs. insular). One-way SIMPER analyses (Clarke and Ainsworth, 1993) were performed with Bray–Curtis distances among standardized biomasses to identify the main species contributing to each assemblage (cluster). Because a degree of consistency in ordination of BBL hauls as a function of depth was identified by the MDS, SIMPER was also used for BBL hauls to analyze the factor “depth interval”. Three depth ranges – upper slope (400–663 m), middle slope (1010–1282 m), and lower slope (1500–2163 m) – over the Catalonia slope were compared with SIMPER. Ordinations of hauls vs. depth were not observed among DSL hauls or over the Balearic slope in the BBL, so no further analyses were performed for those samples. Analyses were carried out with PRIMER 6.0+ PERMANOVA software (Anderson et al., 2008; Clarke and Warwick, 1995).

Possible relationships between zooplankton biomass (at both higher taxon and species levels) and environmental gradients/variables were explored using two types of statistical analyses: i) Canonical Correspondence Analysis (CCA: Ter Braak, 1986); and ii) Generalized Linear Models (GLMs) (Gill, 2000). CCA is a multivariate technique for extracting synthetic environmental gradients from ecological data (Ter Braak and Verdonschot, 1995). CCA ordination axes are chosen based on the recorded environmental variables. Axes are linear combinations of these variables, and arrows in plots are proportional in length to the importance of each variable (Ter Braak, 1986) for explaining community variability. Data were log-transformed. The software XLStat (AddinSoft Inc.) was used for CCA.

Generalized linear models (GLM) are flexible generalizations of ordinary least squares regressions. A GLM allows the linear model to be related to a response variable (zooplankton biomass in this case) based on a link function and relates the variance of each measurement with a function of its predicted value. To test for relationships between zooplankton biomass and environmental factors, a GLM based on a Gaussian distribution and a log link were employed. The GLM identified the environmental variables significantly related to the distribution of zooplankton in our sampling. We built GLMs for those taxa regularly represented in all (or most) hauls, excluding taxa with a large number of zeros in the data matrix and thus not likely to be fit by a Gaussian distribution. GLMs were built using the software R for statistical computing (see <http://www.r-project.org>).

3. Results

3.1. Zooplankton composition

Zooplankton in both the DSL and the BBL showed similar levels of total biomass (2 to 3.2–3.4 gWW/1000 m^3) across the entire slope, but the highest biomass values were found in both the DSL and the BBL over depths between 1000 and 1300 m, the middle slope (Fig. 2). Thus, as suggested by tendency lines fitted to the data, there was an increase of biomass (on average) from the upper slope (400–650 m) to the middle slope (1010–1282 m), and then a decrease of biomass (especially in the BBL) over the lower slope (1500–2163 m). Biomass over La Berengueria Canyon (Station W8, over ~615 m) was 2.43 gWW/1000 m^3 , lower than over the adjacent slope (4.20 gWW/1000 m^3) at a similar depth (Station W1, over ~624 m). Station W23 on the top of Valencia Seamount also had low biomass (2.17 gWW/1000 m^3).

In the BBL calanoid copepods and siphonophores were dominant in biomass in all three depth intervals defined (Fig. 3), reaching 2.1 gWW/1000 m^3 and 1.1 gWW/1000 m^3 respectively over the middle slope (~1000–1300 m). Also over the middle slope, jellyfish biomass increased as a peak of scyphozoans of 1.4 gWW/1000 m^3 over the Balearic slope. This tendency would be clearer if we included the large medusa *P. noctiluca* (Fig. 3) that reached 14.6 gWW/1000 m^3 at

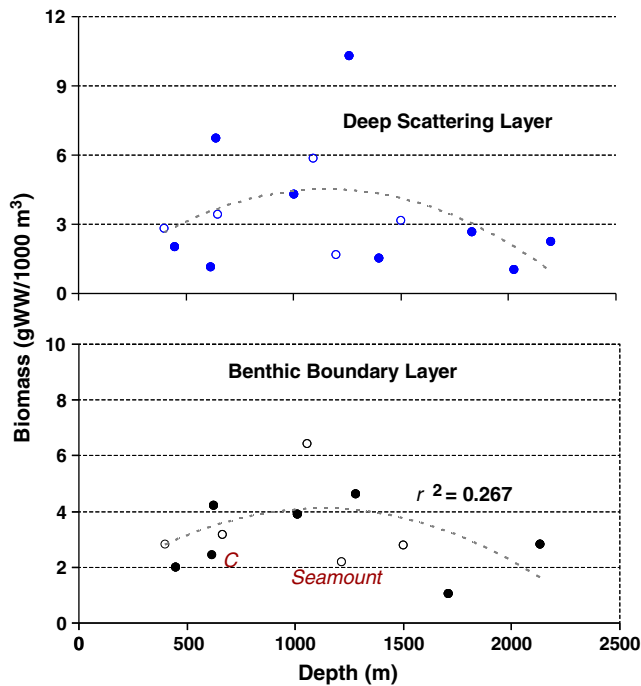


Fig. 2. Depth trends for zooplankton biomass in the Deep Scattering Layer and in the Benthic Boundary Layer in the Balearic Basin. Results given for the Catalan (•) and Balearic (o) slopes. Hauls collected in Berenguer Canyon (C) and adjacent to Valencia Seamount are indicated; r^2 for BBL hauls was calculated after excluding C and Seamount hauls (fitted line is a second-degree polynomial curve).

1058 m and 38.5 gWW/1000 m³ at 1500 m. Other taxa were secondary regarding biomass. Euphausiids and fish were important (0.3–0.4 gWW/1000 m³) over the upper slope (400–650 m) while decapod biomass (mainly *Gennadas elegans*) increased in the deepest interval (0.1 gWW/1000 m³).

Calanoid copepods were numerically dominant in both the DSL and BBL, reaching the highest abundance in the BBL over bottoms at 1010–1282 m (5177 ind/1000 m³, Table 1). Calanoids reached higher densities in the BBL (1761–5177 ind/1000 m³) than in the DSL (1568–1743 ind/1000 m³). Siphonophores and euphausiid larvae (including also juveniles) were also numerically important in the BBL, although the latter only on the upper slope (97.8–263.7 ind/1000 m³). On the middle and lower slopes, other taxa (ostracods, chaetognaths and locally pteropods) dominated in the BBL (23.7–90.0 ind/1000 m³). In the DSL, euphausiid larvae and chaetognaths (35.8–150.7 ind/1000 m³) ranked after calanoid copepods and were followed by siphonophores (Table 1). Total zooplankton biomass did not differ between DSL and BBL at any depth (upper, middle or lower slope) (t tests, $p > 0.3$). Comparing densities (Table 1), decapods, ostracods, copepods, and scyphozoans reached significantly higher average abundances in the BBL than in the DSL (t tests, $p < 0.05$), with mysids and siphonophores less markedly showing the same tendency ($p < 0.1$). Fish larvae were more abundant in the DSL ($p < 0.05$).

3.2. Environmental variables

Environmental variables showed different tendencies as a function of bottom depth in the DSL and in the BBL (Fig. 4). In the DSL, T_{DSL} along the Catalan slope decreased from 13.23 °C over 400 m to 13.05 °C over 1400 and 2025 m, without any similar trend along the Balearic slope. There was a tendency toward lower S_{DSL} offshore over Catalan and Balearic slopes with values between 38.49 and 38.52 psu. O_2 was almost constant over the Catalan slope with values ranging from 4.09 to 4.24 ml/l, while O_2 increased offshore over the

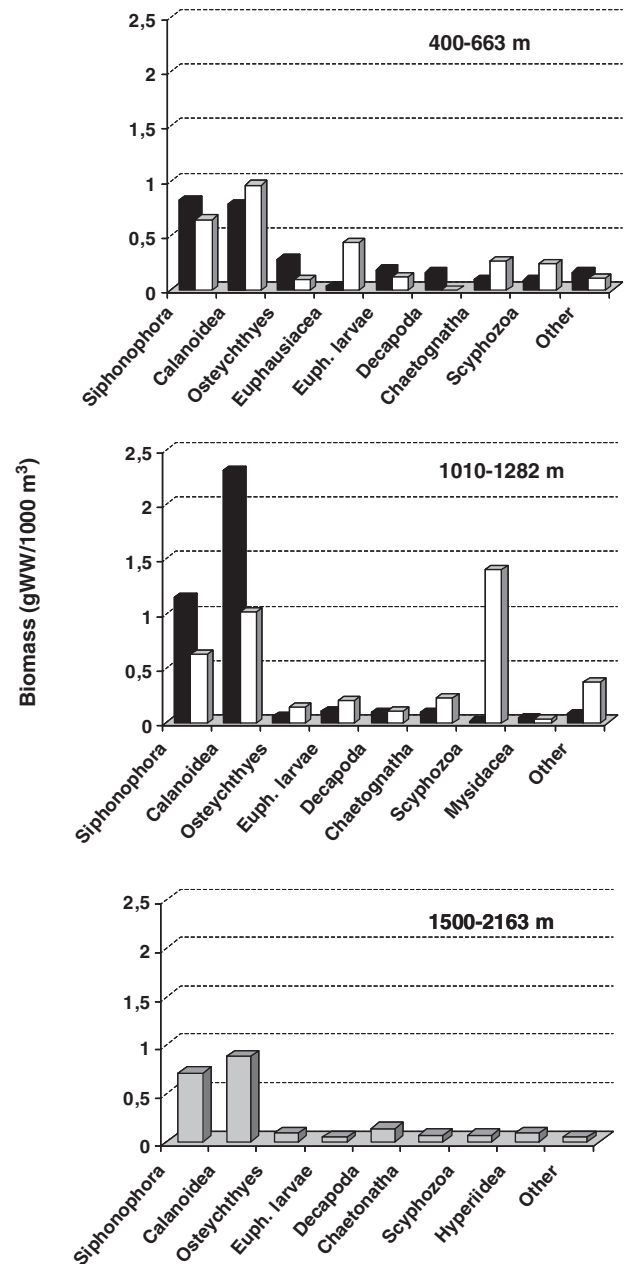


Fig. 3. Composition of higher level taxa of zooplankton (in biomass) in the Benthic Boundary at three different depth levels (400–663, 1010–1282, and 1500–2163 m) on the slope. Results presented for the Balearic slope (white bars) and Catalanian slope (black bars) except at 1500–2163 m.

Balearic slope (between 3.99 and 4.19 ml/l). The O_2 concentration in the DSL was always lower than in the BBL over bottom depths greater than 1000 m (4.32–4.40 ml/l). Turbidity in the DSL ($turb_{DSL}$) showed a progressive decrease to seaward, similar to the turbidity readings near the bottom ($turb_{BBL}$). Turbidity values were lower on average in midwater than close to the bottom.

In the BBL, temperature near the bottom was maximum at 400–625 m (13.22–13.19 °C) and at 2132–2236 m (13.21–13.23 °C) and lower (13.06–13.08 °C) at 1010–1282 m (Fig. 4). Similar trends were found on the Catalan and the Balearic slopes. Salinity (S) decreased linearly from 400 m (38.52 psu) to 1010–1217 (38.48 psu) with constant values deeper. The O_2 concentration was minimum at 400 m (3.98 ml/l) increasing to 4.2 ml/l at 450–663 m, reaching maximum values (4.38–4.40 ml/l) from 1010 to 1282 m, then slightly

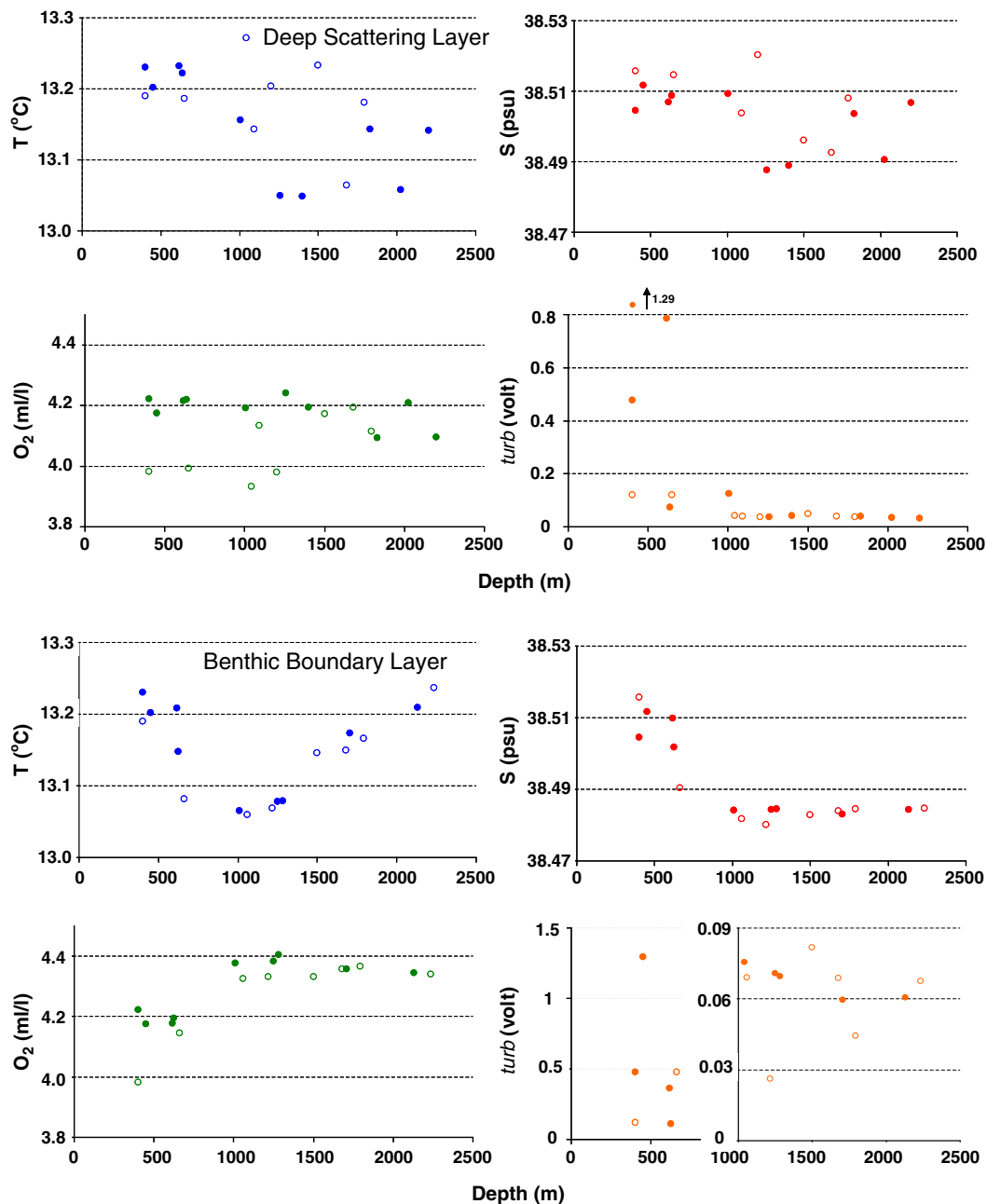


Fig. 4. Depth-related trends for four variables taken simultaneously with zooplankton hauls by means of CTD profiling, both at intermediate (top of figure) and near-bottom (bottom) depths. T: temperature (°C); salinity (psu); oxygen (ml/l); turbidity (voltage). (o) Data taken over the Balearic slope; (•) data from the Catalan slope.

decreasing with depth (4.34 ml/l at 2263 m). The O_2 values were slightly higher over the Catalan slope than over the Balearic slope to depths of ~1500 m (Fig. 4). Turbidity (*turb*) ranged between 0.109 and 1.290 V over the upper slope, decreasing below 1000 m to <0.09 V. Below 1000 m (Fig. 4, right), *turb* was moderately higher in the interval 1000–1500 m (0.069 to 0.081 V) than at >1500 m (0.044–0.068 units), except over the Seamount station (0.026 V).

Profiles of *turb* along the Balearic Basin exhibited (Fig. 5) peaks (to 1.4 V) on the upper Catalanian slope at 400 m but especially at 650 m. These correspond to a thick, widespread across the slope, nepheloid layer (NL). This intermediate NL seemed to arrive with lower *turb* (ca. 0.1 V) over 1000 and 1200 m bottoms (at ca. 200–300 mab), and it disappeared offshore. An intermediate NL can also be observed over the Balearic slope (at 600 and 1000 m

soundings), weaker (0.2–0.8 V) than that over the mainland slope (Fig. 5). *Turb* also increased near the bottom (from ca. 150–200 mab) between 1000 and 1400 m (to 1600 m on the Balearic slope) on both mainland and insular slopes, increasing from <0.04 V to ca. 0.1 V at 5 mab. This increase of *turb* in the BBL was less marked inshore, over the upper slope to 1000 m, and in the depth range of 1600–2200 m (Fig. 5). Scarcely any increases of near-bottom *turb* were found over the seamount station or in La Berenguera canyon at 650 m.

3.3. Multivariate analyses

MDS analysis performed on higher level taxa of zooplankton (excluding calanoid copepods) taken in the Deep Scattering Layer (DSL) and in the Benthic Boundary Layer (BBL) showed significant

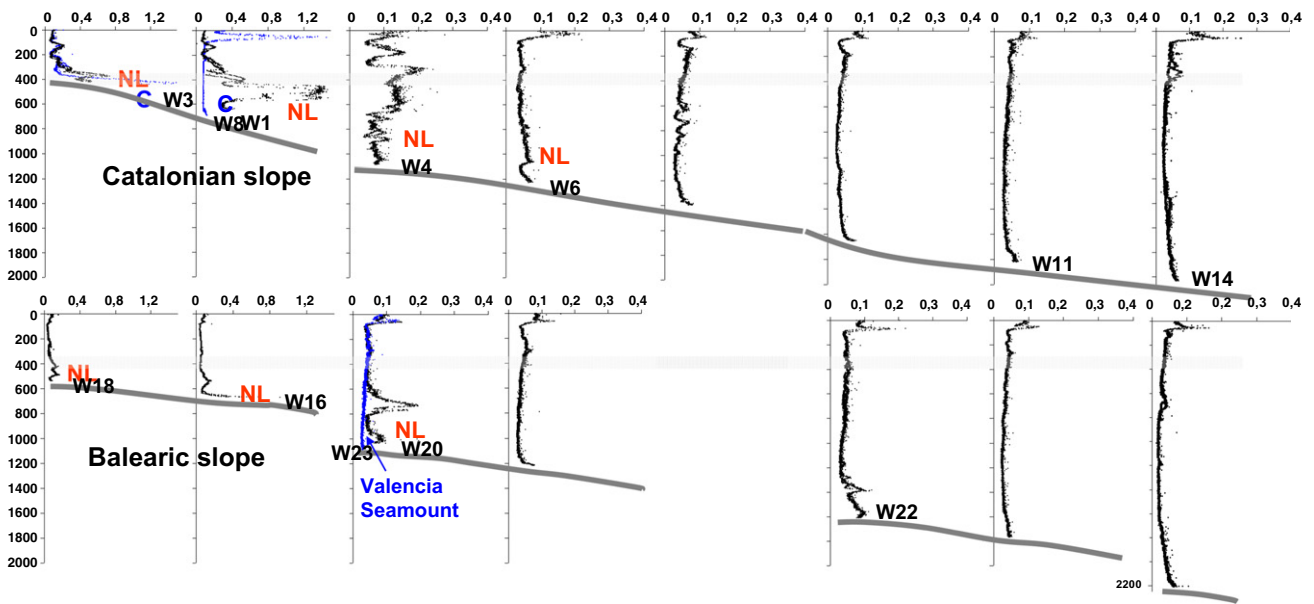


Fig. 5. Profiles of turbidity along the transect performed across the Balearic Basin, over slopes seaward of Catalonia and the Balearic Islands. WP2 hauls performed in the BBL are adjacent to the base of their corresponding profiles. NL: Intermediate Nepheloid Layer. Shadowed area around 400 m depth is the DSL.

segregation of hauls ($n=24$) taken in the DSL from those in the BBL (Fig. 6a; stress=0.13; PERMANOVA: $t=1.62$, $p=0.02$). The BBL hauls also showed significant segregation between the Catalanian and Balearic hauls in the MDS (PERMANOVA: $t=1.82$, $p=0.005$). The MDS analyses done at species level (excluding copepods) also showed significant segregation of hauls between the DSL and the BBL (PERMANOVA: $t=1.43$, $p=0.02$; Fig. 6b). Hauls taken in the DSL did not follow any ordination sequence as a function of the depth over which they were collected or over the station's distance from the coast (Fig. 6b). In contrast, BBL hauls had a partial ordination sequence vs. depth, with hauls taken over the upper and middle slopes (450–1282 m) distributed in the upper half of plot (encircled hauls, upper) and hauls over the lower slope (1707–2163 m) in the lower part. SIMPER found some significant differences in the composition of zooplankton between the DSL and the BBL (Table 2), with a dissimilarity of 68.2%. Siphonophores (*Abylopsis tetragona*, *Chelophyes appendiculata*, and *Lensia* spp.) dominated in the BBL, while the euphausiid *Nematoscelis megalops* and the gonostomatid fish *Cyclothone braueri* were dominant in the DSL.

Further analyses for species data, only considering BBL hauls, showed: i) significant differences between hauls over Catalanian and Balearic slopes (Fig. 7; stress=0.13; PERMANOVA: $t=1.54$, $p=0.01$); ii) no ordination as a function of depth in hauls taken over the Balearic slope; iii) a degree of ordination for the Catalan slope, where upper and middle slope hauls (450–1282 m) were distributed toward the right end of the first MDS axis and lower slope (1707 and 2132 m) hauls on the left (PERMANOVA comparing upper-middle vs. lower slope hauls: $t=2.66$, $p=0.04$). SIMPER showed that the composition of the BBL zooplankton over the Balearic slope was dominated by gelatinous plankton (including siphonophores and the scyphozoan *Solmissus* spp.) and chaetognaths (Table 3a). In addition to siphonophores (*Lensia* spp., *A. tetragona*, *C. appendiculata*), *N. megalops* and *C. braueri* were important contributors to similarity over the Catalan slope (Table 3a). Dissimilarity between Catalan and Balearic slope zooplankton was high (74.1%).

The BBL zooplankton species over the Catalan slope were distinct between the 3 depth zones adopted in this study. Two siphonophores (*Lensia* spp. and *A. tetragona*) dominated assemblages, especially below 1000 m where they accumulated 66.5–68.4% of biomass similarity. On the upper slope (400–650 m), *N. megalops* and *C. braueri*

contributed more to the assemblage biomass than at >1000 m (Table 3b). Dissimilarity was less between upper and middle slope (36.9%) than between middle and lower slope (58.1%).

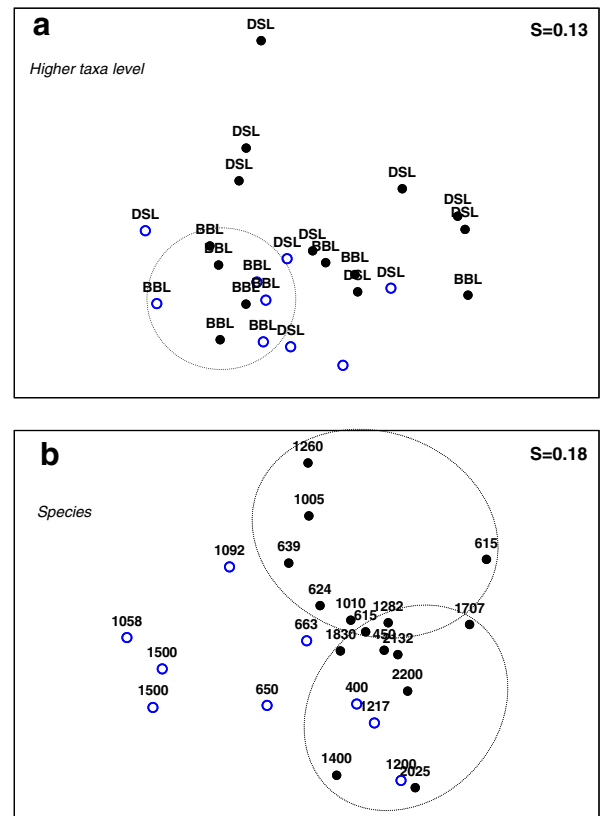


Fig. 6. MDS analysis performed on 24 zooplankton samples (higher level taxa (a) and dominant species (b) by biomass) in the Deep Scattering Layer (DSL) and in the Benthic Boundary Layer (BBL). Depths (soundings) where sampling was performed are included behind each sample in the species plot. Balearic slope (o); Catalonia slope (•). Circle (in higher level taxa plot) includes the major part of the BBL hauls.

Table 2

SIMPER analysis comparing zooplankton composition (species level, biomass) in intermediate depths (Deep Scattering Layer, DSL) and in the Benthic Boundary Layer (BBL) in the Balearic Basin. Copepods were excluded of analysis.

Group BBL Average similarity: 43.54			
Species	Av.Biom	Contrib.%	Cum.%
<i>Lensia</i> spp.	0.13	29.3	29.3
<i>Abylopsis tetragona</i>	0.09	23.0	52.3
<i>Chaetognatha</i>	0.06	13.5	65.8
<i>Chelophyes appendiculata</i>	0.05	11.5	77.3
<i>Nematoscelis megalops</i>	0.04	7.9	85.2
<i>Cyclothone braueri</i>	0.04	7.2	92.4
Group DSL Average similarity: 29.74			
Species	Av.Biom	Contrib.%	Cum.%
<i>C. appendiculata</i>	0.06	25.4	25.4
<i>N. megalops</i>	0.21	18.9	44.3
<i>Chaetognatha</i>	0.05	16.3	60.6
<i>C. braueri</i>	0.08	13.6	74.2
<i>A. tetragona</i>	0.09	11.5	85.7
<i>Lensia</i> spp.	0.03	7.1	92.8

Av.Biom (average biomass, gWW/1000 m³); percentage of contribution (Contrib.%) and cumulative percentage (Cum.%) of similarity.

CCA analyses related taxa/species (and hauls) with environmental variables that can influence their distributions both at the DSL and the BBL. At the DSL no higher level taxon was directly related with T or S, so it seems that most taxa in the DSL avoid the highest values of T and S. Some taxa were related with high (the case of osteichthyans and euphausiid larvae) or low (e.g. adult euphausiids and scyphozoans) values of O₂ concentration (Fig. 8a) or with high fluorescence (the case of hyperiids). Some taxa (euphausiids, decapod larvae and scyphozoans) were abundant in hauls taken in the Balearic part of the Catalan Sea, while others (euphausiid larvae and fishes) were more common in hauls performed on the Catalan side. CCA accumulated 85.9% of variance among higher level taxa. Result at the species level was similar (Fig. 8b), as shown in the CCA plots. Only the euphausiid *Euphausia krohni* and the siphonophores *Lensia* spp. were related to high T and S values; another euphausiid, *N. megalops*, clearly appeared to be related with high values of O₂ concentration (Fig. 8b). The hyperiid *Primno macropa* and fish larvae (mainly *Argyropelecus hemigymnus*) were more strongly related with high fluorescence. The greatest number of species appearing to be related to low levels of O₂ was found on the Balearic side of the Catalan Sea (see also Fig. 2), comprising siphonophores (*A. tetragona* and *C. appendiculata*), hyperiids (*Scina crassicornis*, *Hyperia schizogeneios*, *Hyperoides longipes* and

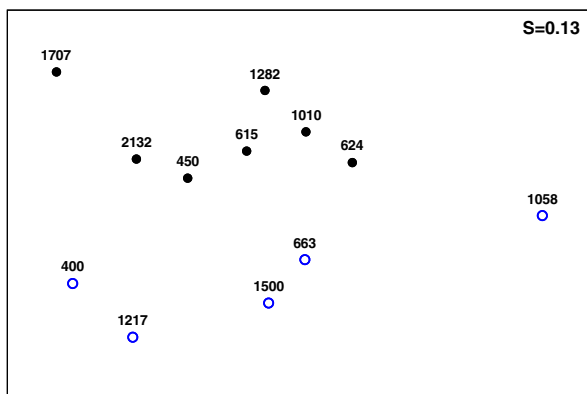


Fig. 7. MDS analysis (dominant species by biomass) performed on the 12 Benthic Boundary Layer (BBL) hauls performed over the Catalan slope (•) and the Balearic slope (○). Depths (soundings) where sampling was performed are included behind each haul.

Table 3

SIMPER analysis comparing zooplankton composition (dominant species, biomass) in the Benthic Boundary Layer (BBL) in the Balearic Basin: a) between Catalonia (C) and NW of Balearic Islands (B) and b) in three depth strata: upper slope – 400–650 m; middle slope – 1000–1300 m; and lower slope – 1500–2300 m, over Catalanian and Balearic slopes. Copepods were excluded from the analysis.

a) Balearic slope Average similarity: 29.56			
Species	Av.Biom	Contrib.%	Cum.%
<i>Chaetognatha</i>	0.09	27.9	27.9
<i>Chelophyes appendiculata</i>	0.07	16.9	44.8
<i>Pelagia noctiluca</i>	0.50	15.5	60.3
<i>Abylopsis tetragona</i>	0.10	10.6	70.9
<i>Lensia</i> spp.	0.06	7.1	78.0
<i>Solmissius</i> spp.	0.15	6.8	84.8
<i>Cyclothone braueri</i>	0.05	3.7	88.5
<i>Nematoscelis megalops</i>	0.05	3.6	92.1
b) Catalan slope Average similarity: 36.01			
Species	Av.Biom	Contrib.%	Cum.%
<i>Lensia</i> spp.	0.09	21.2	21.2
<i>A. tetragona</i>	0.08	18.9	40.1
<i>N. megalops</i>	0.17	16.1	56.2
<i>C. appendiculata</i>	0.05	15.0	71.2
<i>C. braueri</i>	0.07	14.0	85.3
<i>Chaetognatha</i>	0.03	10.2	95.5
400–663 m Average similarity: 59.38			
Species	Av.Biom	Contrib.%	Cum.%
<i>A. tetragona</i>	0.12	29.2	29.2
<i>Lensia</i> spp.	0.14	27.5	56.6
<i>C. braueri</i>	0.10	12.2	68.9
<i>N. megalops</i>	0.07	10.5	79.3
<i>Chaetognatha</i>	0.04	10.4	89.7
<i>C. appendiculata</i>	0.04	9.6	99.3
1010–1282 m Average similarity: 65.41			
Species	Av.Biom	Contrib.%	Cum.%
<i>Lensia</i> spp.	0.25	54.2	54.2
<i>A. tetragona</i>	0.10	12.3	66.5
<i>N. megalops</i>	0.04	10.4	76.9
<i>Chaetognatha</i>	0.04	10.3	87.2
<i>C. appendiculata</i>	0.03	7.2	94.4
1500–2163 m Average similarity: 45.79			
Species	Av.Biom	Contrib.%	Cum.%
<i>A. tetragona</i>	0.07	39.6	39.6
<i>Lensia</i> spp.	0.05	28.8	68.4
<i>C. braueri</i>	0.04	10.6	79.0
<i>C. pygmaea</i>	0.02	7.0	86.0
<i>Vibilia armata</i>	0.01	3.6	89.6
<i>C. appendiculata</i>	0.04	3.4	92.9

Phronima sedentaria) and decapod larvae (*Alpheus* sp. and *Sergestidae*). The CCA accumulated 88.3% of the variance among species.

The CCA for higher level taxa at the BBL (Fig. 9a) showed a relationship of decapod and euphausiid larvae, large euphausiids and pteropods and osteichthyans with the highest values of T and S. This coincided with hauls performed over the upper part of the slope between 400 and 663 m (right half of the MDS plot). Mysids, decapods and to a lesser extent calanoids and siphonophores captured over intermediate and deep bottoms (1010–2163 m) were related with O₂ maxima; left-bottom part of the plot: Fig. 9a. Scyphozoans were negatively related with T, appearing basically in two hauls

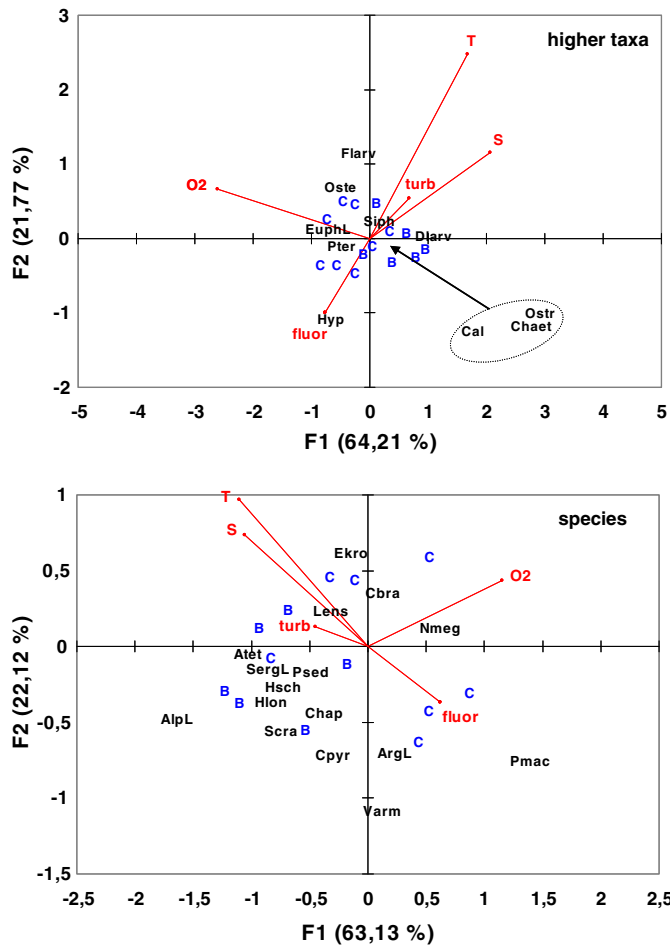


Fig. 8. CCA for zooplankton biomass (higher level taxa and dominant species) in the Deep Scattering Layer along the transect between Catalonia (C) and NW of Balearic Islands (B). Depths (soundings) of sampling sites are also included. Taxa and species codes are in Table 1.

from 1058 to 1217 m. CCA explained 90.7% of total variance in the first two dimensions. At species level (Fig. 9b) maxima of T and S (indicating entry of Levantine Intermediate waters, LIW) coincided (right part of the plot) with upper slope hauls (400–663 m) and with the euphausiids *E. krohni* and *Stylocheiron longirostris*, the gonostomatid *C. braueri* and the hyperiid amphipods *H. longipes* and *P. sedentaria*. In the upper-left part of the biplot the decapod *G. elegans* and the mysid *Eucopeia hanseni*, captured over mid-slope bottoms (1010–1282 m), were associated with the highest concentration of dissolved O_2 (Fig. 9b). Sergestid larvae and to a lesser extent the siphonophore *Lensia* spp. followed a similar trend. The fish *Cyclothone pygmaea* was most abundant in the deepest hauls (1500–2132 m) and two siphonophores (*A. tetragona* and *C. appendiculata*) were more abundant in these waters, characterized by low turbidity but similar O_2 levels than at the middle slope, as was the case of the amphipod *L. schizogeneios* and less clearly for the medusa *Periphylla periphylla*. Total variance explained by the first two dimensions of CCA (58.4%) was moderate.

The GLM models suggested different factors that can be used as explanatory variables for the distribution of biomass in the DSL and the BBL (Table 4). In the DSL, the number of significant explanatory variables for zooplankton biomass was greater than in the BBL, probably because there is greater environmental variability in midwater layers than close to the bottom. Total biomass was correlated with turbidity, although the model only accounted for 22.5% of the variance. Temperature was the main explanatory variable for siphonophore biomass, but for most taxa (euphausiids, chaetognaths, and

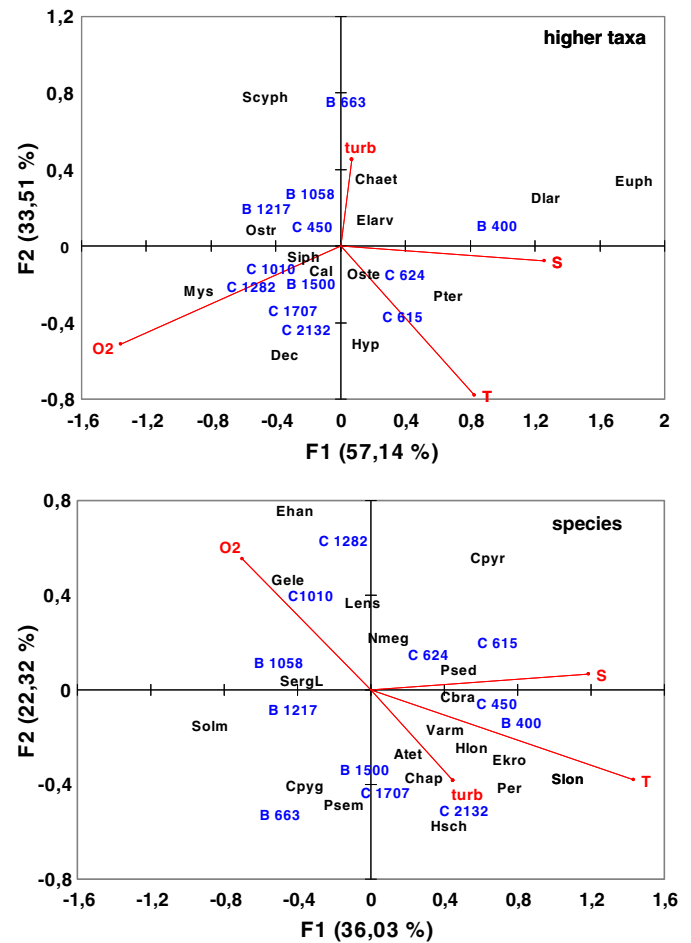


Fig. 9. CCA for zooplankton biomass (higher level taxa and dominant species) in the Benthic Boundary Layer along the transect between Catalonia (C) and NW of Balearic Islands (B). Depths (soundings) of sampling sites are also included. Taxa and species codes are in Table 1.

osteichthyes) S and O_2 concentration were more strongly related to biomass variation (Table 4). Models for higher taxa explained between 48.3% (siphonophores) and 96.8% (euphausiids) of the total deviance.

In the BBL, the GLM for total zooplankton biomass explained 35.8% of the deviance, with T_{BBL} being the only explanatory variable. It was inversely related: greater biomass occurred at the lowest T_{BBL} . A similar result was obtained for the biomass values of the dominant taxa; with the GLMs explaining higher levels of deviance than that for combined zooplankton biomass (from 46.0% for euphausiids to 98.1% for scyphozoans). Furthermore, T_{BBL} was inversely related with scyphozoan, chaetognath and copepod biomass. Concentration of O_2 was also an important explanatory variable for distributions of zooplankton biomass for different taxa, entering more models than did T_{BBL} (Table 4). Concentration of O_2 was inversely related with euphausiid and chaetognath biomass and positively related with calanoid and scyphozoan biomasses.

4. Discussion

Midwater and near-bottom zooplankton of the Balearic Basin show significant changes in composition at the scale of ~180 km separating the coasts of Catalonia and the NW of Balearic islands. Such changes have been identified in previous studies in the north-western Mediterranean, where with spatial changes in composition are influenced by W–E gradients (for non-gelatinous zooplankton:

Table 4
GLMs performed on total biomass (wet weight) of zooplankton and on the biomass of the most dominant taxa of the Deep Scattering Layer (DSL) and Benthic Boundary layer (BBL) zooplankton. Explanatory variables included in the models are T, S, O₂, turbidity (*turb*) for both DSL and BBL, adding longitude and fluorometry in the analysis of some DSL models.

BBL						DSL					
Variable	Estimate	Explained deviance	Residual deviance	% expl. deviance	p	Variable	Estimate	Explained deviance	Residual deviance	% expl. deviance	p
1 Total biomass		Df= 11				1 Total biomass		Df= 13			
Null		22.134				Null		86.511			
T	−6.808	7.924	14.210	35.8	0.027	Turb	−1.062	19.425	67.086	22.5	0.046
						T	−3.3177	19.425	50.636	19.0	0.066
			Total	35.8					Total	41.5	
2 Euphausiacea		Df= 11				2 Euphausiacea		Df= 13			
Null		0.604				Null		0.588			
S	3.364	0.165	0.439	27.3	0.018	T	179.452	0.012	0.576	2.0	0.046
O ₂	−1.369	0.113	0.326	18.7	0.050	S	−1190.01	0.096	0.480	16.4	9.1 e−14
			Total	46.0		O ₂	−187.217	0.461	0.019	78.4	2.2 e−16
									Total	96.8	
3 Calanoidea		Df= 11				3 Siphonophora		Df= 13			
Null		5.178				Null		2.133			
O ₂	6.835	1.595	3.583	30.8	0.029	T	6.879	0.740	1.393	34.7	6.3 e−4
T	−5.463	1.077	2.506	20.8	0.074	Turb	2.6708	0.291	1.102	13.6	0.032
4 Scyphozoa		Df= 11				4 Chaetognatha		Df= 13			
Null		6.629				Null		0.089			
T	−499.2	6.286	0.343	94.8	2.2 e−16	O ₂	−0.940	0.044	0.046	48.7	2 e−4
O ₂	143.0	0.212	0.132	3.2	1.1 e−5						
Turb	180.1	0.003	0.129	0.04	0.026				Total	48.7	
			Total	98.1							
5 Chaetognatha		Df= 11				5 Osteichthyes		Df= 13			
Null		0.096				Null		0.599			
T	−7.768	0.020	0.077	20.3	0.01	T	1.399	0.053	0.546	8.8	0.048
S	−22.656	0.025	0.052	25.8	0.004	S	7.042	0.093	0.454	15.5	0.009
O ₂	−6.039	0.025	0.026	26.4	0.004	O ₂	2.291	0.070	0.384	11.6	0.023
			Total	72.5		Turb	−0.286	0.234	0.150	39.0	3.1 e−5
									Total	74.9	

Cartes et al., 2010; for euphausiids: Casanova, 1974). Similar shifts have been observed over wider areas (e.g. along the Mid-Atlantic Ridge). There are also latitudinal and vertical changes in the water column associated with the origins of distinct water masses (Gaard et al., 2008; Hosia et al., 2008). In the benthic boundary layer (BBL) we have found an increase in near-bottom zooplankton biomass over the middle slope (at 1000–1300/1400 m) that is mainly linked to greater abundance of cnidarians (scyphozoans and siphonophores, 1.5–2.0 gWW/1000 m³). In the few studies available on BBL zooplankton, similar increases of gelatinous zooplankton have been reported; for example, more medusae of *Aglantha digitale* above the slopes of Porcupine Seabight in the NE Atlantic between 900 and 1600 m (Hargreaves, 1984). In addition, indirect evidence of peaks in gelatinous zooplankton biomass in the vicinity of 1100–1300 m in the study area has come from analysis of the gut contents of Alepocephalid fishes, which feed primarily on gelatinous prey (Cartes and Carrassón, 2004).

In the Balearic basin, the depths at which near-bottom zooplankton reached the greatest biomass, 1000–1300 m, were characterized by the lowest temperatures (T_{BBL} : 13.06–13.08 °C) and to a lesser extent the lowest salinities (S_{BBL} : 38.48 pss). Also, and of greater biological significance, maximum O₂ concentration (4.38–4.40 ml/l) was also reached at 1000–1300 m. In this same way, at depths greater than 1000 m higher near-bottom turbidity (particulate matter including organic particles) was found between 1000 and 1500 m, suggesting more food availability for zooplankton. Below ca. 1300 m down to 2200 m, O₂ had greater concentrations than were found over the upper slope and was also similar than that found in the BBL at 1000–1300 m. Consistently O₂ and turbidity entered as significant variables in models explaining the biomass distributions of two of the main taxa in the BBL: copepods and scyphozoans. Low dissolved oxygen (DO) in Oxygen

Minimum Zones (OMZs with DO<0.5–0.1 ml/l: Sewell and Fage, 1948; Vinogradov and Voronina, 1961) drives physiological and biochemical adaptations in zooplankton and micronekton (Childress, 1995). Outside OMZs, neritic zooplankton (e.g. copepods in Chesapeake Bay, Roman et al., 1993) display seasonal declines in abundance and distribution in periods when DO<2 ml/l (Roman et al., 1993) with inhibition of egg hatching in some copepod species (Roman et al., 1993). Decline in the abundance of coastal copepods occurs when DO falls below 3 mg/l (Keister et al., 2000). In general, both the density of neritic zooplankton as a whole (Moon et al., 2006; Olson, 1987), and more particularly cnidarians (Pavez et al., 2010), seems to be positively correlated with DO. Waters exceeding 300 or 400 m have narrower changes in DO than do coastal systems (e.g. in the Balearic basin O₂ is usually between 3.98 and 4.40 ml/l, and it has been 4.0–4.8 ml/l in LIW since the 1970s, Segura, 2007). Although deep-living species may be adapted to different O₂ ranges than coastal ones, a similar relation may occur between zooplankton biomass and dissolved O₂ in the deep sea. The greatest values of zooplankton biomass were linked to the highest near-bottom O₂ values in the BBL, as suggested by our GLM results for copepod and scyphozoan biomass. This has not been previously reported in deep-sea ecosystems.

4.1. The trophic role of zooplankton in deep benthopelagic communities

Peaks of near-bottom zooplankton in the deep sea have been found previously for total zooplankton and for jellyfish (Angel, 1990; Cartes, 1998; Wishner, 1980). Density of copepods also increases close to the bottom (Cartes, 1998; Gaard et al., 2008). Copepods are at the base of BBL trophic webs, as deduced both from stomach contents of fish (Cartes and Carrassón, 2004) and decapods (Cartes, 1993b; Cartes

and Carrassón, 2004) and from analysis of stable isotopes (Fanelli et al., 2011). *Calanus helgolandicus*, the dominant near-bottom copepod over the middle slope in the Balearic Basin, shows depleted $\delta^{15}\text{N}$ values (4.36‰; Fanelli et al., 2011). The biomass increase of calanoids and gelatinous zooplankton at ~1200 m over the Balearic Basin slope represents an increase of food availability for highest trophic levels.

The underlying reasons behind zooplankton biomass peaks between 1000 and 1300 m are uncertain. A possible explanation is that the minimum T in this layer reduces O_2 consumption of organisms living there. A metabolic advantage of copepods at 1000–1300 m could also be related to the increase in their mean size (0.46 mg/WW/individual), compared to species living at 400–610 m (0.39 mg/WW/individual). Although we considered copepods as a higher level taxon, their species assemblages change with depth in the western Mediterranean, e.g., at 100–600 m and below 1000 m (Scotto di Carlo et al., 1984). As deduced from analysis of citrate synthase activity, a biomarker of aerobic metabolism, wet-weight oxygen consumption rates decline significantly with increasing copepod size (Thuesen et al., 1998). Minimum T coincided with an increase of DO only in the interval 1000–1300 m, where, in addition, the greater turbidity below 1000 m suggests greater food availability. Below 1300 m, T increased again, which may increase zooplankton oxygen consumption, while turbidity decreased below 1500 m. Considering the decrease of oxygen consumption by copepods in deeper, colder waters (Ikeda, 2008), we suggest that the small increase of O_2 at 1000–1300 m (0.4 ml/l) in a highly stable environment such as the deep Mediterranean combined with a possible increase of food particles (turbidity) could be enough to explain the increase of copepod biomass in this layer. Also important is the low range of T variations in the mesopelagic zone in the Mediterranean where ΔT is scarcely 0.4 °C below 200 m (Font, 1987; Rixen et al., 2005). That is negligible compared to oceanic areas where most respiration data have been obtained (Ikeda et al., 2007; Thuesen et al., 1998). Thus, deep organisms may be more sensitive to small variations in DO in a very stable thermal environment such as the deep Mediterranean.

On the middle slope, peaks of biomass in the BBL were not significantly lower than the biomass found in the DSL. In other words, there was an accumulation of zooplankton near the bottom, as already reported in other areas (Hargreaves, 1984; Smith et al., 1987; Wishner, 1980; also suggested by Gaard et al., 2008 for copepods at the Middle Atlantic Ridge). The DSL coincided with the layer of maximum T and S in intermediate waters, a layer established in the western Mediterranean by the influx of Levantine Intermediate Water (LIW; Font, 1987). In intermediate strata, the LIW is characterized by maxima of T and S and also by minimum values of O_2 concentration (see Cartes et al., 2011a; Roether and Well, 2001). Within the DSL, we found (as deduced from CCA) that no taxa/species (excepting some siphonophores such as *Lensia* sp.) were related with high levels of T and S, suggesting that zooplankton somehow tend to avoid increasingly warm and saline waters with minimal O_2 , as are found at the LIW core. This possible avoidance of LIW core conditions by zooplankton can also be deduced from the negative relationship between zooplankton biomass and T in our GLM models. This suggests the hypothesis that the long-term increase of S (and of T to a lesser extent) in LIW since the 1950s (Rixen et al., 2005) could have induced a decrease of zooplankton biomass in intermediate waters in the Mediterranean.

The relationships found between species and O_2 concentration are partially in agreement with trends in oxygen consumption found off California (an area with an OMZ and, thus, different from the Catalano–Balearic slope) by Childress and collaborators. They analyzed oxygen consumption of dominant taxa of zooplankton/micronekton (Childress, 1995; Thuesen et al., 1998), and postulated that some visually orienting taxa (visual predators of zooplankton) like fish, shrimps and cephalopods can adapt their rates of oxygen consumption as a function of depth (see Thuesen et al., 1998), in

contrast to non-visually orienting animals (e.g. jellyfish and copepods). Among copepods the contrary trend has also been reported (Ikeda, 2008). In any case, in our among-species analysis (by CCA) found that species with well developed eyes were those associated with high levels of O_2 , specifically the shrimp *G. elegans* and the mysid *E. hansenii* in the BBL, and the euphausiid *N. megalops* in the DSL. Species related with lower levels of O_2 were siphonophores (*A. tetragona* and *C. appendiculata*) in midwater and the medusa *P. periphylla* in the BBL. However, a large number of hyperiidean amphipods (*S. crassicornis*, *L. schizogeneios*, *H. longipes* and *P. sedentaria*) having large eyes also appeared to be associated with low levels of O_2 , which could be explained by the close association, even symbiotic relationships, between hyperiideans and gelatinous organisms like siphonophores, medusae and salps (Gasca and Haddock, 2004). Such relationships were less clear in the analysis performed on higher level taxa (e.g. O_2 was negatively related with euphausiids in GLMs), but this could be explained by the substantial heterogeneity of strategies of species within the same broad taxon, as pointed out by Thuesen et al. (1998) from oxygen consumption and enzymatic activity in deep-water copepods. So, the visual interaction hypothesis, based on the idea of a decrease of activity with a decrease of visual ranges with depth among visual predators, probably requires further evaluation considering: i) the high vertical mobility (daily migrations) of macroplankton (e.g. crustaceans such as *N. megalops* and *G. elegans*; Franqueville, 1971), with species having their main predatory activity in upper levels of the water column at night (e.g. Pasiphaeidae, Cartes, 1993b), and ii) that many predator–prey relationships in mesopelagic and bathypelagic depths are based on bioluminescence (Herring, 2002), which is not linearly dependent on depth. By contrast, species having positive relationships with O_2 levels generally occupied a higher trophic level (deduced from $\delta^{15}\text{N}$ values: *N. megalops* – 6.29‰, *E. hansenii* – 7.70‰ and *G. elegans* – 6.57‰) than those having negative relationships with O_2 levels (cnidarians: *C. appendiculata*, 4.03‰; *Lensia* spp., 5.37‰; *P. periphylla* 6.49‰, and especially hyperiids: *Vibilia armata*, 2.53‰; *P. macropa* 3.65‰; for a complete data set see Fanelli et al., 2011). Trophic position indicated by $\delta^{15}\text{N}$ can in turn be correlated with swimming capacity of species and with their energy content (basically lipid content). Both swimming capability and lipid content generally indicate the greater metabolic activity and oxygen demand of organisms that accumulate in strata with higher O_2 availability.

The high levels of benthopelagic zooplankton (siphonophores and scyphozoans and copepods) found at mid-slope depths below 1000 m were related with a T minimum near the bottom and with increases of dissolved O_2 (from 4 to 4.4 ml/l) compared to the upper slope. Near-bottom turbidity was also significant. Increase of zooplankton in the BBL may enhance aggregation of benthopelagic fish, probably explaining peaks of fish biomass located at ~1000–1400 m in the western Mediterranean (authors' unpubl. data; Stefanescu et al., 1993). At these depths, dominant species mainly feed on gelatinous zooplankton (i.e. the fish *Alepocephalus rostratus*, Carrassón and Cartes, 2002; shrimps including *Plesionika acanthonotus*, Cartes, 1993b). This conclusion is based on a single transect performed in a single, relatively brief time period (July 2011). However, the depth-trends described here for T, S and O_2 over the slope have been found in previous surveys in the area (Fig. 10) performed at different seasons. Copepods have consistently been the most abundant near-bottom zooplankton taxon (Cartes, 1998), and they are at the base of most trophic webs over the slope (Mauchline and Gordon, 1991), as deduced from both stomach contents (Cartes, 1993a,b; Stefanescu et al., 1993) and depleted $\delta^{15}\text{N}$ ratios of the dominant calanoids in the BBL (4.36‰ in *C. helgolandicus*; Fanelli et al., 2011). In conclusion, the increase of near-bottom zooplankton biomass may support a complex food webs and peaking of fish biomass at mid-slope depths. This is the case in the Mediterranean and also in Atlantic areas where Alepocephalidae dominate near-bottom fish

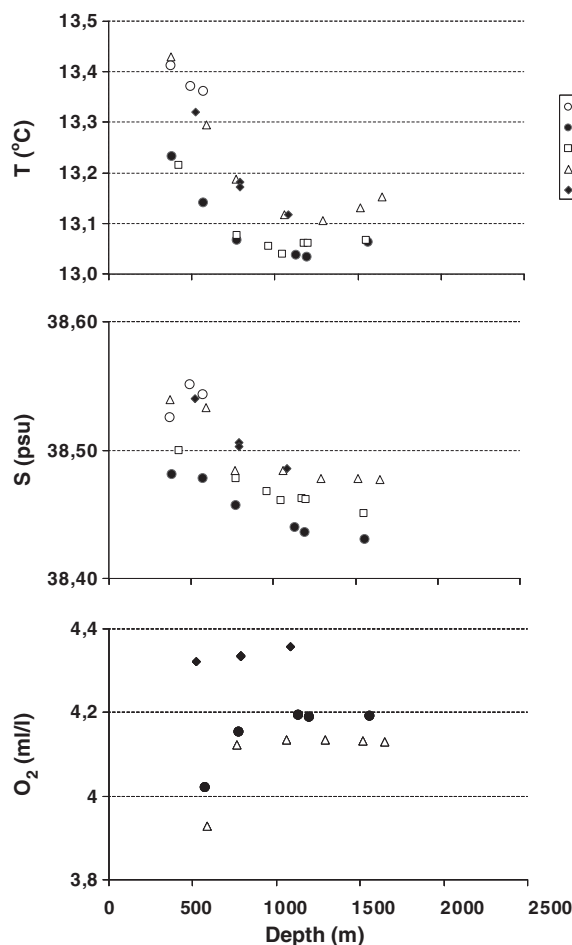


Fig. 10. Depth-trends recorded for near-bottom T, S and O₂ over the middle slope in different seasons and locations in the western Mediterranean, comparing surveys performed in the 1990s and 2007. Off the coasts of Catalonia in March 1998 (○), February 2007 (△) and July 2007 (◊); to the SE of Eivissa, Balearic Islands, in October 1996 (●) and May 1998 (□).

communities at ca. 1000–1500 m. By means of similar multidisciplinary approaches to those presented here, future research should determine whether relationships like those we found in the northwest Mediterranean are common in other slope areas with peaks of benthopelagic fish biomass.

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