

Composition and distribution of the larval decapod community in the deep sea of the Western Mediterranean Sea Balearic Sub-basin

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Abstract

Mechanisms facilitating larvae transport from continental to more oceanic areas were investigated in the Balearic sub-basin (BSB), Western Mediterranean Sea. The abundance, distribution, and development stages of decapod larvae were recorded for a transect of 28 stations crossing the central eddy of the BSB. Zooplankton samples were taken to 1,800 m depth by horizontal and oblique 500- μ m mesh size nets hauls towed near the benthic boundary (BBL) and in deep scattering layers (DSL). In total, 67 taxa belonging to Decapoda and one Stomatopoda were identified. Advanced development represented 75% of the individuals recorded. 75% of the species corresponded to adults of deep-sea species, 9% were sergestids (mesopelagic species), and the remaining 16% corresponded to shelf and coastal species. Cluster assemblages formed were related to the hydrological conditions, water masses dynamics, and geomorphologic structures mainly associated with nepheloid layers. Advanced and juvenile specimens of commercial species such as *Parapenaeus longirostris*, *Geryon longipes*, and *Aristeus antennatus* were found close to seafloor BBL. The influence of trophic ecology should be considered as the priority factor of larvae concentrations in deep.

KEYWORDS

Balearic sub-basin, benthic boundary layer, decapod larvae, deep sea, fishery species, nepheloid layers, Northwestern Mediterranean Sea

1 | INTRODUCTION

Factors linked to the development cycle of larvae can significantly contribute to determining the demography of adult populations, influencing biodiversity and fishery maintenance of exploited species (Cowen & Sponaugle, 2009). The oceanographic context, including hydrodynamics, bathymetry, and biological factors, defines the specific environment where larvae are developing. Identifying the effects of such factors is therefore crucial to understand dispersal and connectivity processes for particular populations (Sponaugle et al., 2002). Besides, connectivity between larvae and adults' habitats, as well as between more and less productive zones, can mitigate threats and recover depleted populations, being able to hold adult populations well above disappearance

in a context of climatic change or habitat patchiness (Hillman et al., 2018). A growing body of studies evidenced self-supplied recruitment processes for shelf demersal marine species (Swearer et al., 2002), contrasting with the open ocean model supported by significant evidences of gene flow for species over wide geographic regions (Hellberg, 2009) or far dispersion of larvae from adults habitats (Cowen et al., 2000).

Hydrodynamics, at regional and local scales, mixing vertical and horizontal water masses, enhance ocean productivity (Dufois et al., 2016; Gaube et al., 2014) and transport (Marshall et al., 2009). Steep topography, as that found in slopes like submarine canyons and channels or straits restricting the exchange of water between basins, interacts with eddies margins producing detachment of particulate matter by lateral and vertical advection,

known as nepheloid layers (NL). Those constitute important pathways to channeling advective inputs of productivity from the shelf and slope to the bottoms (Canals et al., 2009) and offshore by horizontal advection, dispersing plankton from their surroundings (Marshall et al., 2009).

In the Northwestern Mediterranean Sea, the Balearic sub-basin (BSB) presents hydrological conditions and topography that incorporates many geomorphologic and oceanographic structures that cause trophic and environmental interactions, with intermittent hydrographic cyclonic and anticyclonic eddies for lengthy periods, in which micro- and macro-plankton communities are concentrated (Cartes, Fanelli et al., 2013).

Decapods dominate slope communities in the BSB (Cartes & Sardà, 1993), and several studies exploring the distribution and the composition of larvae community have been carried at sub-surface water layers (Olivar et al., 1998; Peña et al., 2015; Torres et al., 2014). Yet, larvae assemblages in deep waters remain virtually unknown. The available studies showed a limited larval dispersal capacity and larvae distribution in patches, suggesting that hydrography drivers model larval distribution (Rodríguez et al., 2013; Carbonell et al., 2014). Given the opportunity to explore these environmental and hydrographic conditions in deep, the present study analyses the decapod larvae spatial distribution and composition in the deep BSB and discusses the potential oceanographic modeling connectivity and dispersion.

2 | MATERIAL AND METHODS

2.1 | Study area

The BSB represents an old depression, the Valencia Trough, flowing to the N-NE between the Catalan coasts in the Iberian Peninsula (mainland) at NW-W and the Balearic Islands at SE-E (Figure 1). The area is approximately 22,708 km² with maximum depths at 2,200–2,300 m. The mainland has important tributary canyons and the Delta River plain, while the insular area presents narrow connections through channels of about 75 km wide between the islands and the mainland and with the southern open waters of the Alboran Sea. Both channels are the route for the northward progression of surface fresh less haline waters from the Algerian Basin, the named Atlantic Water (AW), and at the same time the southward progression of surface warm waters, the Modified Atlantic Water (MAW) from the north of BSB.

2.2 | Oceanographic features

The inflow of comparatively less haline and oxygen-rich surface North Current (NC), situated in the upper water body, flowing southwards anticlockwise along the mainland shelf (Masó et al., 1990) together with two more deeper water layers: the Levantine Intermediate Water (LIW), distributed between 200–900 m, with

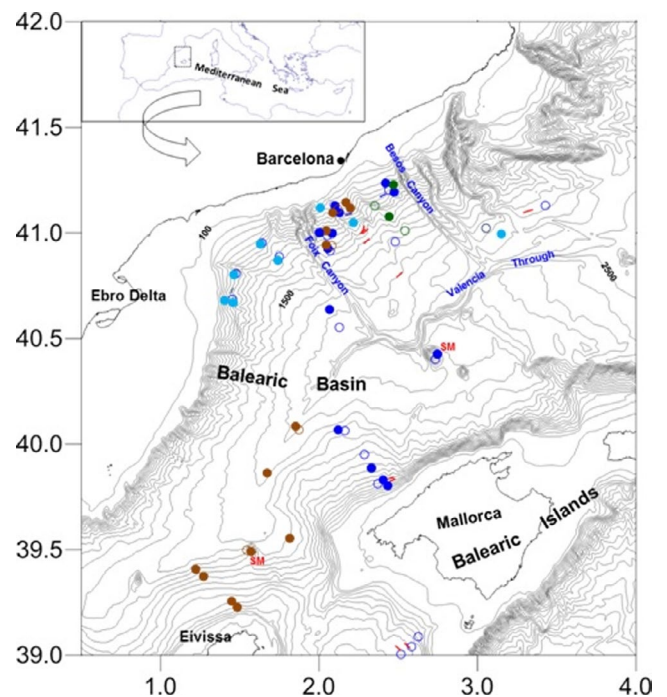


FIGURE 1 Study area in the Northwest Mediterranean Sea, Balearic sub-basin (BSB). Blue Circles represented WP2 zooplankton hauls, dark blue filled circles are hauls taken at the BBL (close to the seafloor), and empty circles correspond to hauls taken at the DSL. Brown circles corresponded to Macer-GIROQ suprabenthic hauls performed over a submarine mount

a core around 400 m, more haline than surrounding waters, transported southwards with the NC along the mainland shelf and slope (Bosse et al., 2015; Masó et al., 1990); whereas the Balearic Current (BC) flows northwards along the Balearic Archipelago shelf and slope to depths of 250 m (García-Ladona et al., 1996). Below these layers, the Western Mediterranean Deep Water (WMDW) covers all the BSB at depths greater than 900 m (Balbín et al., 2012). In some winters, the Winter Intermediate Water (WIW) is generated, in the north of the BSB, in the Gulf of Lions by the cooling and mixing the surface MAW, which lies right above the LIW in the BSB (Gasparini et al., 1999; Juza et al., 2019). The WIW enhances the formation of anticyclonic eddies from spring to summer and brings oxygen to the lower water body layers. This circulation pattern shows high spatial variability, especially in spring (Pinot et al., 2002). The vertical extension of the eddy structures is variable, reaching up to 900 m (Amores et al., 2013) and ultimately boosting the transfer of organic matter to the deep-sea benthic boundary layer (BBL) by vertical both passive and active fluxes (Pasqual et al., 2014). The mainland coast presents important pathways inputs of productivity, favoured by geomorphologic structures, like canyons and rivers runoff, that increase suspended particulate organic matter (POM) with potential food availability for larvae and zooplankton. Particles fluxes are usually greatest in late-winter and spring, associated with a bloom in surface production and water column homogeneity associated with vertical

TABLE 1 Hauls characteristics sampled in the Balearic sub-basin (BSB) from 2008 to 2011

Station	Month	Year	Zone	Area	Period	Canyon
A2W3	6	2011	BBL	M	EST	Out
A2W1	6	2011	BBL	M	EST	Out
B08W1	2	2008	Obl	M	HOM	Out
A1W3	7	2010	BBL	M	EST	Out
A2W2	6	2011	DSL	M	EST	Out
B08OT6	2	2008	Obl	M	HOM	In
A2W4	6	2011	BBL	M	EST	Out
A1W18	7	2010	BBL	I	EST	Out
A1W9	7	2010	DSL	M	EST	In
A1W2	7	2010	DSL	M	EST	Out
A1W1	7	2010	BBL	M	EST	Out
A1W8	7	2010	BBL	M	EST	In
A1W19	7	2010	DSL	I	EST	Out
A1W10	7	2010	DSL	M	EST	Out
A1W17	7	2010	DSL	I	EST	Out
A1W15	7	2010	DSL	M	EST	Out
A1W16	7	2010	DSL/BBL	I	EST	Out
A1MG2	7	2010	BBL	M	EST	Out
A2MG2s	6	2011	BBL	M	EST	Out
A1W21	7	2010	DSL	I	EST	Out
A1W7	7	2010	DSL	M	EST	Out
A1W6	7	2010	BBL	M	EST	Out
A1W24	7	2010	DSL	M	EST	Out
A2W9	6	2011	BBL	M	EST	Out
A3W6	10	2011	BBL	I	TR	Out
A2W5	6	2011	BBL	M	EST	Out
A2W6–8	6	2011	DSL	M	EST	Out
A3W4–5	10	2011	BBL	M	TR	Out
A1W2	7	2010	DSL	M	EST	Out
A1MG1	7	2010	BBL	M	EST	Out
A3W11	10	2011	Obl	I	TR	Out
A2W7	6	2011	BBL	M	EST	Out
A3W10	10	2011	BBL	I	TR	Out
A3W12	10	2011	BBL	I	TR	Out
A3W15	10	2011	BBL	M	TR	Out
A1W5	7	2010	DSL	M	EST	In

Note: Code of station; month and year; zone (sampling depth zone at benthic boundary layer (BBL) and deep scattering layer (DSL)); area (the situation of each station at mainland (M) or insular (I) area); period (sampling period of the water column conditions for stratified water column (EST), for homogenized water column (HOM), for mixing transition period (TR)).

mixing (Estrada, 1991). During summer, the water column is stratified and surface production is low, resulting in reduced vertical passive transport of organic material (Miquel et al., 1994). Instead, the Balearic Archipelago lacking such type of structures presents oligotrophic waters and a food web more supported by only zooplankton production (Cartes, Fanelli, et al., 2013; Cartes, Lolacono et al., 2013).

2.3 | Sampling

A total of 28 stations located at the open ocean between the Catalan mainland and Insular coasts (Figure 1) were sampled at different depth strata and during different seasons/years. Sixteen zooplankton samples with WP2 type nets were taken near the bottom (the benthic boundary layer, BBL), 4 at midwater (oblique) hauls and 16 more were taken at intermediate waters, at a depth interval between

350–450 m, in the deep scattering layer, DSL (Table 1). Moreover, sixteen zooplankton samples taken near the sediment–water interface (0–1.5 m above the bottom, see Cartes et al., 2003) obtained from with a Macer-GIROQ suprabenthic sledge over 610–1840 m (performed in the framework of the projects BIOMARE, CTM2006-13508-CO2-02/MAR, MEC, and ANTRMARE, CTM2009-12214-CO2-01/MAR) were investigated for decapod larvae community near bottom and included in the study (details of the stations are in Annex Table S1).

The WP2 plankton net was equipped with an opening–closing mechanism 1000DT General Oceanics Ltd, and tows were performed horizontally (i.e. somehow oblique but in a rather narrow, depth range within a selected water layer) at the DSL and BBL with the net open only in these depth strata. A net depressor (iron depressor weighing 75 kg) was attached to the WP2 in order to maintain the net at the desired depth range. The DSL was previously located using echosounders (biological Simrad Single-beam echosounder EK500: 34, 120, 200 kHz). The depth of the net in DSL samples and the distance to the bottom in BBL samples were recorded by a SCANMAR sensor attached to the WP2 net depressor, until a depth of 1,200 m. Below this depth, the SCANMAR sensors do not operate, and the depth of the sampling was estimated with a cable-angle inclinometer. The deployment of the WP2 net was visualized at the EK500 screen, which helped to situate the net as close as possible to the sea bottom in BBL hauls. Distance of the net to the bottom was between ca. 5–60 m at soundings between 450–650 m and between 5–207 m at depth up to 1,000 m, with increasing distance at greater depths. The duration of WP2 tows was around 10 min (8–13 min) both in DSL and BBL hauls, with time in general increasing with depth. In the four midwater (oblique) hauls, the WP2 net was used without the opening–closing mechanism. More details on WP2 maneuver are in Cartes et al., 2010; Cartes, Fanelli et al., 2013. The Macer-GIROQ suprabenthic sledge was towed horizontally over the seafloor during ca. 5–20' (time also increasing with depth); contact of the sledge with the seafloor was verified by SCANMAR sensors attached to the sledge (details in Cartes et al., 2010. Cartes, Fanelli et al., 2013).

Both the WP2 and suprabenthic Macer-GIROQ sledge were equipped with 500 μm mesh and towed at a speed of ca. 1.5 knots. In both cases, standard 2030 flowmeters (General Oceanics) were attached to the mouths of the nets to measure the amount of water filtered and to estimate the distance covered in each haul. Volume of filtered water ranged between 424–2,464 m^3 in WP2 hauls (both DSL-BBL and oblique hauls, the latter filtering the highest water volumes) and between 207–2,292 m^3 in Macer-GIROQ hauls (increasing volume at increasing depth). All samples were collected during daytime.

Sampling to collect near-bottom zooplankton was adapted to the topography (slope, canyons); thus, it could not follow a pre-established regular grid/transect (e.g. fixed stations each n miles) as usually performed for surface zooplankton sampling. Samples were immediately fixed in buffered formaldehyde or ethanol on board. Larvae were sorted in the wet laboratory under a stereo

microscope identified to the lowest possible taxonomic level and counted.

Specimens were identified to species level and development stages, using illustrated keys (Ingle, 1992; Paula., 1996), different taxa descriptions (dos Santos & Gonzalez-Gordillo, 2004; Santos & Lindley, 2001), and specific species descriptions for *Callinectes sapidus* (Costlow & Bookhout, 1959); *Geryon* (Ingle, 1992); *Aristeus* (Sarda and Cartes, 1997), *Palinurus* (Guerao et al., 2006), and *Squilla* spp. (Ahyong et al., 2014). The identification was at species level when possible; alternatively, the generic “spp” was used. For some cases, when it lacks of accurate specific descriptions, it was indicated in parenthesis the most probable species, after review the reproduction biology and adults' distribution habitats available information. This was the case of phyllosomas and puerulus of *Palinurus* (Guerao et al., 2006; Hunter, 1999; Maigret, 1978; Palero & Abelló, 2007) and for *Geryon* genre (Attrill et al., 1991; Marco-Herrero et al., 2015).

Additionally, information of some advanced larvae (megalopes) and juveniles of 4 species was included (not in the analyses), due to the interest in detecting “close to settlement” of deep-sea species. They were collected with a Macer-GIROQ suprabenthic sledge in SW of Balearic Islands (QUIMERA 1 cruise, 27/10/96, 1,586–1,594 m), an otter trawl semi-balloon OTSB-14 a trawl with a 2 door, 1-warp trawl system with mesh size at the cod end of 6 mm.

2.4 | Environmental variables

Environmental parameters were recorded simultaneously with zooplankton sampling using a CTD SBE25 profiler with sensors for temperature (T in $^{\circ}\text{C}$), salinity (S in PSU), dissolved oxygen concentration (O_2 in mg/L), variables of turbidity (NTU), and fluorescence (RFU). Whenever possible, one CTD profile was performed over each zooplankton sampling station along the entire water column to 5 m above the seafloor. For each variable, the mean value in the water column (at DSL) and close to the bottom (at the BBL) was calculated at each station.

To evaluate the influence of water speed in deep, vorticities (ω), data obtained from satellite imagery dynamic height (absolute values, gradients or edges, and correlations) available from 2010 year, and following algorithm developed by Amores et al. (2014), that estimated relative speed from the daily sea surface height (SSH) satellite images at different water column depths were used. Vorticities are defined by a vector field that provides a local measure of the rotation of a water mass, and waters in cyclonic gyres display positive vorticity, while those in anticyclonic gyres have negative vorticity. Product used to obtain ω of each sample at their depth was SEALEVEL_MED_PHY_L4_REP_OBSERVATIONS_008_051 provided by COPERNICUS (<https://www.copernicus.eu/en/services/marine>) with a spatial resolution of $1/8^{\circ} \times 1/8^{\circ}$. These vorticities were calculated as the curl of the velocity field, but only the third component was retained as it represents the vorticity of a horizontal field. Then, vorticity average was computed in a two degrees side square around the sampling stations field. The area selected was big

TABLE 2 GAM models tested for zoea and megalopa functional groups and Caridea and Dendrobranchiata taxonomic densities

Model	Hypothesis	Statistical model
M1	There is one single smoother effect	$K_{ni} = \alpha + \beta_1 * s(S_i, T_i, O_{2i}, \text{turb}, \text{fluor}, \text{fluoBBL}, \text{vort}) + \epsilon_i$
M2	There is one single smoother effect and one underlying influence	$K_{ni} = \alpha + \beta_1 * s(S_i, T_i, O_{2i}, \text{turb}, \text{fluor}, \text{fluoBBL}, \text{vort}) + f(\text{CAN}, \text{AREA}, \text{ZONE}) + \epsilon_i$
M3	There is two smoother effect with one underlying influence factor	$K_{ni} = \alpha + \beta_1 * s(S_i, T_i, O_{2i}, \text{turb}, \text{fluor}, \text{fluoBBL}, \text{vort}) + \beta_2 * s(S_i, T_i, O_{2i}, \text{turb}, \text{fluor}, \text{fluoBBL}, \text{vort}) + f(\text{CAN}, \text{AREA}, \text{ZONE}) + \epsilon_i$

Note: The notation smoother applied for hydrographic salinity, temperature and dissolved oxygen (S, T and O₂) and food web trophic-related variables turbidity (turb), fluorescence and fluorescence at BBL (fluor or fluoBBL), and vorticity (vort) covariates with Gaussian residual distributions (function $\epsilon_i \sim N(0, \sigma^2)$), and three different linear underlying effect factors: Canyon in/out samples localization (CAN) in the Mainland, samples geographic localization Mainland/Insular (AREA) or sampling depth localization, at seep scattering layer (DSL), or at benthic boundary layer (BBL), or oblique haul from a specific depth to surface (ZONE).

enough to include the Northern (mainland) and Balearic (insular) currents because they are potential to eddy generation. The land and a buffer around it were excluded from the square.

2.5 | Data analysis

Species densities were calculated considering the water volume filtered in each haul, and individuals were standardized to individuals per 1,000 m³. Developmental stages were grouped in three classes: for early stage "protozoas and zoeas I-IV" (Pz, Z); advanced stages "zoeas above stage IV," "decapodites," "mysis," "phyllosoma" (D, My, Ph); and stages close to the settlement for "puerulus," "pseudozoeas," "megalopes," and "juveniles" (P, Ps, M, J). Notwithstanding, for few species with low densities and several different stages, they were grouped together. For the analysis purposes, a $\log(x + 1)$ transformation was applied to the larvae matrix.

To characterize decapod larval assemblages, multivariate analyses were performed using Bray-Curtis similarity index. A cluster analysis was done to classify hauls as a function of species composition similarity. To visualize the cluster results, a "map" of the configuration of the samples in a 2 dimensions was constructed by a non-metric multidimensional scaling (nMDS: Clarke & Warwick, 2001). Differences in species composition by sampling season (i.e. periods of water column stratification (May-September) or homogeneity (December-April), and a transition period of thermocline breaking (October-November) (Houpert et al., 2015), as well as area of sampling (mainland vs. insular), were tested by means of one-way PERMANOVA tests (Anderson et al., 2008). SIMilarity of PERcentages was used to identify species most responsible for intra-group similarities and between-group dissimilarities. Analyses were performed using the software PRIMER 7.1 (Anderson, 2001; Clarke & Warwick, 2001).

The relationship between trophic and environmental variables and species was assessed with canonical correspondence analysis (CCA) (ter Braak & Smilauer, 2002) using XLStat. CCA is a multivariate

method to elucidate the relationships between assemblages of species and their environment (ter Braak & Verdonschot, 1995). The two ordination axes represented in CCA are linear combinations of the environmental variables considered. Variables are graphically represented by arrows with lengths proportional to their importance for explaining density variability (ter Braak, 1986). Rare species (Occurrence < 5%) were not included in the analysis. The explanatory variables were temperature (T), salinity (S), fluorescence (fluor) at surface and near the bottom (fluoBBL), turbidity (turb), dissolved oxygen (O₂), and relative vorticity (ω). Two CCA were performed for hauls carried out between 2010 and 2011, one excluding winter samples, for which the effects of vorticity could be evaluated.

A series of statistical generalized additive models (GAMs: Wood, 2006) for larvae densities from the WP2 hauls were used to explore the influence of variables on the main functional development stages and taxonomic groups (model hypothesis, Table 2). Prior to the analyses, a detailed data exploration was carried out, with special emphasis on collinearity. Factors considered to seek over fixed influences were as follows: geographic localization at mainland or at insular area (AREA); sampling depth localization: at DSL, BBL, or Oblique hauls to surface (ZONE); and samples localization in-out of canyons (CAN). The best model was selected using the Akaike information criterion (AIC) and Akaike weights (w_i) gave the probabilities of the best model (Anderson & Burnham, 2002). The optimal model was validated using a variogram (i.e. a plot of the residuals against the space coordinates) (Zuur et al., 2009) Analyses were carried out using the "mgcv" library in R package (R Development Core Team, 2017).

3 | RESULTS

3.1 | Environment and larvae composition

Environment conditions were quite homogeneous; salinity remained around 38.44 PSU throughout the area and periods sampled, while temperature showed seasonal cycle with the lowest

temperature in March (12.89°C) and the highest at the end of summer in September (13.39°C). The area of study corresponded to a semi-enclosed sub-basin (BSB) of the northwestern Mediterranean Sea. The range of temperatures and salinities was examined to a station small scale. Salinity and temperature influence larvae survival and growth rate. Thus, we provide information on these factors that conditioning juvenile recruits' strength of species inhabiting the slope habitats. Hydrographic periods studied were stratification (summer), transition and mixing (autumn–winter). They correspond to different fluxes caused by seasonal winds, influencing currents and hydrography. Summing up the estimates at BBL and DSL layers, for salinities were in summer over the isohaline of 38.50 PSU, at isobathic of 400–1,000 m depth, in both mainland and insular zones. Whereas in autumn–winter period, it decreased in the mainland stations to 38.40 PSU and remained similar to summer values in the insular zone. Temperatures averaged values at the same depth intervals were in summer between 13.00–13.15°C, decreasing to 12.80°C in winter in the mainland stations and remained at the same summer values in the insular zone. Dissolved oxygen (O₂) levels were slightly superior in the mainland for whatever period, and in average between 4.10 and 4.30 mg/L, while in the insular area ranged between 4.03 and 4.25 mg/L, in all cases decreased in summer and increased in autumn–winter. Fluorescence was between 0.1 and 0.2 RFU and presented maximum values between 310–582 m depth, coinciding with the minimum O₂ values. Turbidity as a measure of the amount of the seawater particles composition, including sediments, particulate organic matter (POM), and phytoplankton, was higher in the stratification period at DSL, but overall at BBL. Higher values in the mainland were around 0.32 NTU, decreasing to minimum values between 0.13 and 0.05 NTU in the mixing period. In the insular area raised the maximum of 0.48 NTU at the BBL in the stratification period and remained similar to the mainland during the mixing period.

The hydrography assessed by geostrophic currents in surface and deep presented negative (anticyclonic) vorticities, with values fluctuating from high to low speed, during the stratification period in summer (both 2010 and 2011 surveys), and positive an less fluctuating values in the autumn–winter mixing period in the insular area and always cyclonic geostrophic currents in the mainland. The 2010 summer anticyclonic eddy was situated centrally in the BSB, between the Catalan coast and the Balearic Archipelago, with negative geostrophic vorticities reaching deep stations. In contrast, in summer of 2011 the eddy was situated slightly northwards, nearest Delta Ebro plain mainland slope with weakly vorticities values in deep. In winter 2011, positive and higher vorticities values matched with the cyclonic winter gyre also reaching deep stations.

A total of 541 specimens identified belonged to 67 Decapoda taxa and to one Stomatopoda. The number of taxa identified at species level was 37, and the rest were identified at genre of family level (Table 3). Over the total number of specimens identified 75% of them corresponded to advanced larval stages (decapodites, megalopes, *Puerulus* and *Phyllosoma* stages, pseudozoas

TABLE 3 List of species collected at the 28 sampling sites in the Catalan mainland area (M) and in the oceanic Balearic Archipelago (I)

Code	Species	M	I
Shrimps (Dendrobranchiata)			
Arist J	<i>Aristeus antennatus</i>		1
Shen Pz	<i>DeoSergestes henseni</i>	1	
Shen My	<i>DeoSergestes henseni</i>		1
Sarc Pz	<i>EuSergestes arctitus</i>	3	1
Sarc My	<i>EuSergestes arcticus</i>		1
Gele Z	<i>Gennadas elegans</i>	3	
Gele D	<i>Gennadas elegans</i>	2	1
Gele My	<i>Gennadas elegans</i>	2	
Plon My	<i>Parapenaeus longirostris</i>	1	
Pen Z	<i>Pennaes sp1</i>		1
Pen Z	<i>Pennaes sp2</i>		1
Svig Pz	<i>ParaSergestes vigilax</i>	2	1
Svig My	<i>ParaSergestes vigilax</i>	2	1
Srob Pz	<i>Sergia robusta</i>	1	1
Srob My	<i>Sergia robusta</i>	1	1
Srob J	<i>Sergia robusta</i>	3	
Serg D	<i>Sergestes spp.</i>	3	2
Smem J	<i>Solenocera membranacea</i>	1	
Smem My	<i>Solenocera membranacea</i>	3	1
Smem Z	<i>Solenocera membranacea</i>	2	
Shrimps (Caridea)			
Acan Z	<i>Acantheephyra spp.</i>	1	1
Plac Z	<i>Aegaeon lacazei</i>		2
Plac M	<i>Aegaeon lacazei</i>		3
Aglab Z	<i>Alpheus glaber</i>	3	1
Aglab M	<i>Alpheus glaber</i>	1	
Alph Z	<i>Alpheus spp.</i>	1	
Anit M	<i>Athanas nitescens</i>	2	
Car D	<i>Caridea</i>	1	2
Car Z	<i>Caridea</i>	2	1
Car1 Z	<i>Caridea1</i>	1	
Car2 Z	<i>Caridea2</i>	1	
Ccra J	<i>Chlorotoccus crassicornis</i>		1
Lys Z	<i>Lysmata spp.</i>	1	
Pal Z	<i>Palaemon spp.</i>	1	
Pand Z	<i>Pandalidae sp1</i>		1
Pcan Z	<i>Processa canaliculata</i>	1	
Pedu Z	<i>Processa edulis</i>	1	
Pmod Z	<i>Processa modica</i>	1	
Pnou Z	<i>Processa novelli</i>	3	
Pnou J	<i>Processa novelli</i>	1	
Proc Z	<i>Processa spp.</i>	2	1
Pmul J	<i>Pasiphaea multidentata</i>	1	

(Continues)

Table 3 (Continued)

Code	Species	M	I
Phil Z	<i>Philocheras</i> spp.	-	
Pech M	<i>Philocheras echinulatus</i>		1
Ples Z	<i>Plesionika</i> spp.	3	1
Heremit crabs (Paguridae)			
Anap Z	<i>Anapagururs</i> spp.	-	
Ctub Z	<i>Calcinus tubularis</i>	1	1
Dpug Z	<i>Diogenes pugilator</i>	-	
Nlon Z	<i>Nematopagurus longicornis</i>	1	1
Ppri M	<i>Pagurus prideaux</i>	2	3
Pag Z	<i>Pagurus</i> spp.	1	1
Pag M	<i>Pagurus</i> spp.	3	2
Ghost shrimps (Axiidea and Gebiidea)			
Axiid D	<i>Axiidae</i>	2	
Ctrun Z	<i>Callinassa subterranea</i>	2	
Call Z	<i>Callinassa</i> spp.	1	
Jnoc Z	<i>Jaxea nocturna</i>	1	
Laom Z	<i>Laomediidae</i>	1	
Upo Z	<i>Upogebia</i> spp.	-	
Slipper lobster (Palinuridae and Scyllaridae)			
Pmau J	<i>Palinurus (mauritanicus)</i>	1	
Palin Ph	<i>Palinurus</i> spp.	1	
Scyar Ph	<i>Scyllarus arctus</i>	1	1
Squar lobsters (Galatheidae and Polychelidae)			
Galat M	<i>Galathea</i> spp.		1
PolycM	<i>Polycheloes typhlops</i>	-	
Mun Z	<i>Munida</i> spp.	1	
Mun M	<i>Munida</i> spp.		2
Crabs (Brachyura)			
Bmar Z	<i>Bathynectes maravigna</i>	1	
Brach1	<i>Brachyura sp1</i>	1	1
Csap M	<i>Callinectes sapidus</i>		1
Ccas M	<i>Corystes cassivelannus</i> (exhuvia)	-	
Geryon	<i>Geryon (longipes)</i>	1	
Grho Z	<i>Goneplax rhomboides</i>	4	1
Grho M	<i>Goneplax rhomboides</i>	3	
Inuc Z	<i>Illia nucleus</i>	1	1
Inachus	<i>Inachus</i> spp.	1	
Ldep Z	<i>Liocarcinus depurator</i>	4	
Ldep M	<i>Liocarcinus depurator</i>	3	1
Mcou Z	<i>Monadeus couchii</i>	2	
Mtub Z	<i>Macropipus tuberculatus</i>	1	1
Pmac Z	<i>Parthenope macrocheles</i>	2	
Pmac M	<i>Parthenope macrocheles</i>		1
Pspi Z	<i>Pilumnus spinifer</i>		1
Pisa M	<i>Pisa sp1</i>		2

(Continues)

Table 3 (Continued)

Code	Species	M	I
Polyb Z	<i>Polybiinae</i> spp.	1	
Xan Z	<i>Xantho</i> spp.	1	
Mantis shrimps Stomatopoda (Squilla)			
Squilla	<i>Squilla</i> spp.	1	1

Note: Areas were split for the Valencia Trough in the middle of the sub-basin. CODE (code of species included and development stage; was used in the CCAs graphics).

The identification was at species level when possible; afterward, the generic "spp" were used. For some cases the most probable species was indicated in parenthesis.

Species stages were grouped in three classes for early stage "Protozoas and zoeas I-IV" (Pz, Z); advanced stages of "Zoeas above stage IV and decapodites," "mysis" and "phyllosoma" (D, My, Ph); and stages close to the settlement for "puerulus," "pseudozoeas," "megalopes," and "juveniles" (P, Ps, M, J).

When few different stages occur for a species, they were grouped together.

For some species (without accurate identification), the most likely species is included in parentheses.

Densities were transformed to abundance classes, as follows: for: "-" for abundance <1; "1": 1-5; "2": 5.1-20; "3": 20.1-100; "4": 100.1-500 individuals. per 1,000 m³.

and zoeas over stage IV). Larvae of species inhabiting slope and deep bottoms represented 75% of recorded specimens. Of the remaining larvae, 16% were of species with adult populations typical of the continental shelf, and 9% corresponded to mesopelagic *Sergestidae* species, living between 200 and 900 m depth in the water column. Insular stations comprising 15% and the lowest percentage was recorded in stations over submarine canyons with 2% of specimens. The highest densities were recorded at the mainland area on the BBL, in samples taken between 485 and 611 m, and between 1,042 and 1,404 m, and they decreased with depth (except for a sample taken at 1,577 m) (Figure 2a-b), and maximum densities at the DSL occurred at the mainland slopes, at depths between 346-486 m in the mainland and between 325-555 m in the insular area.

The suborder Dendrobranchiata was the most numerous group accounting 168 individuals of which the Superfamily *Sergestoidea* represented 43%. The rest corresponded to *Penaeoidea* Superfamily, formed for *Gennadas elegans*, *Solenocera membranacea*, and among other *Penaeoidea* one *Aristeus antennatus* juvenile and one *Parapenaeus longirostris* mysis records. The suborder Pleocyemata was represented by seven infraorders: Caridea with 163 specimens, of which Pandalidae with 41% of individuals was the most abundant; Brachyuran species with 156 specimens followed by Anomura (32), and Gebiidae, Polychelida, and Achelata (22).

The highest densities by species in the mainland corresponded to Brachyuran crabs *Liocarcinus depurator* in spring-summer (May-July), *Goneplax rhomboides*, and *Monodeus couchii* in summer (June-July) and *Macropipus tuberculatus* in winter (February-March). In the Insular area, the most abundant orders were Caridea, especially

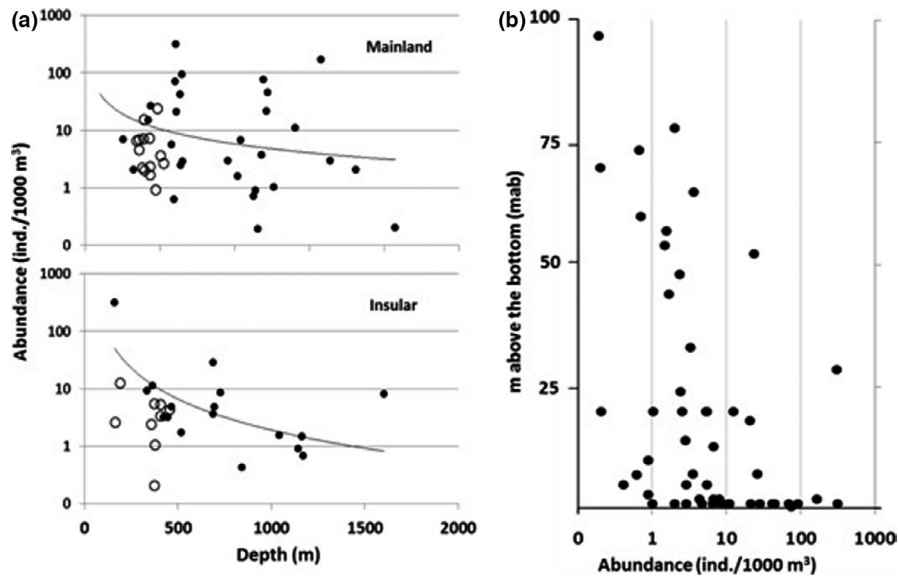


FIGURE 2 Abundance of decapod larvae (a) as a function of depth in the Balearic sub-basin (BSB) filled circles and at the deep scattering layer (DSL) empty circles for samples in Balearic sub-basin (BSB). (b) Abundances as a function of hauls distance to seafloor bottom in the BSB

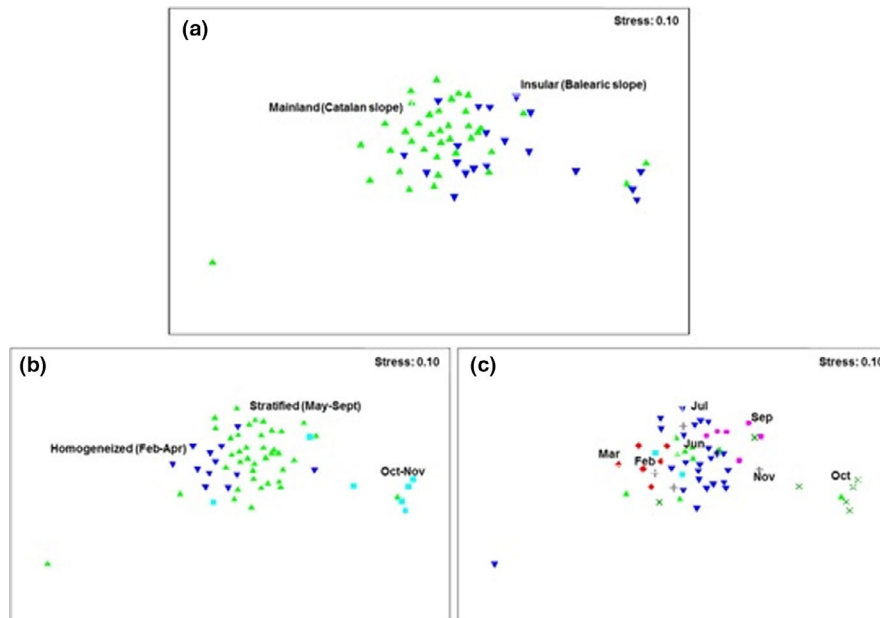


FIGURE 3 Multidimensional scaling analysis of decapod larvae collected in the Balearic sub-basin (BSB). (a) Plot represented main (significant) factors explaining the distribution of larval communities over the mainland (green triangles) and over the insular (inverted blue triangles) areas. (b) Plot represented main (significant) factors explaining the distribution of larval communities as function of different periods from water masses stratification (green triangles), homogenizations (inverted blue triangles), and transition periods (light blue squares). (c) Plot represented main significant factors explaining the distribution of larval communities as function of monthly temporality

Pandalidae family, and Anomura species of *Paguridae* and *Galatheidae* families (*Pagurus* spp., *Munida* spp.).

Regarding larvae distribution in the water column close to the seabed, at the BBL (Figure 2b), the highest densities were found at ca. 1–20 m above the bottom (mab), with modal abundance of ca. 6–11 larvae/1,000 m³. Further away of the seabed (25–100 mab) densities diminished to less than 2 larvae/1,000 m³. Spring–summer (May–July) was the period with high larval densities over the mab, and the lowest were recorded in autumn (October–November) in both areas.

Due to the scarce information on larvae of deep-sea species, we complemented our results with some sparse information on

advanced stages collected at depths ranging 1,590–1,758 m with other sampling gear in the framework of other different projects. It was registered one juvenile of *A. antennatus* (CL 4.6 mm) in the SW of Balearic Islands (in 27/10/1996 at 1,586–1,594 m), collected with a suprabenthic sledge, one megalope *Eryoneicus* of *Polycheles typhlops* (in 05/05/2012, at 1,661–1,622 m) one megalope–juvenile of *Geryon longipes* (CL 5.6 mm) in a stomach content of the fish *Cataetyx alleni* (in 16/10/2011, at 1,753–1,748m) quite intact, likely ingested in the codend by the fish, and several megalopes of *Monadeus couchii* attached to wood pieces (in 16/10/2011 at 1,753–1,748 m) caught in the middle of the Trough, collected from the seafloor by OTBS-14 trawling.

3.2 | Community structure

Results of nMDS Bray–Curtis distance similarity matrix produced an ordination of the stations according to their location in the mainland or insular (open waters) areas (Figure 3a). Besides, a small number of samples split—to the right of MDS plot—forming a small group of hauls corresponding to the deep hauls (1,000–1,500 m) performed in both areas mainland and insular of the Valencia Trough. Cluster analysis consistently revealed two main groups including the samples obtained in each area with a stress nMDS value of 0.10. Plotting the nMDS as a function of seasonality, an ordination

according to the water column, from stratified through transition and homogenized water column condition appeared (Figure 3b). Ordination of samples according to the month was additionally plotted, emerging the ordination with independence of the area, except for the same small group of hauls distributed at right, corresponding to hauls taken at deepest depths which appeared grouped regardless the month they were taken (Figure 3c). PERMANOVA analysis evidenced significant results between samples taken at insular and mainland slopes and when comparing water column condition (Table 4).

TABLE 4 PERMANOVA *t* tests and average similarities between groups of larval assemblages taken at mainland (M) and insular (I) slopes and comparing periods with different water column conditions: stratified (ST), homogenized (HOM) and transition period (TR) 999 permutations

Groups	<i>t</i>	<i>p</i>	Perms
Averaged Similarity between/within groups			
M, I	16.635	0.001	999
M	78.524		
I	56.362	10.575	
Averaged Similarity between water column condition			
ST, HOM	17.452	0.001	999
ST, TR	19.838	0.002	999
HOM, TR	18.874	0.004	995
ST	98.321		
HOM	47.187	10.906	
TR	32.105	25.646	24.161

3.3 | Environmental drivers

The canonical correspondence analysis (CCA) for years 2010 and 2011 (Figure 4a), for which relative vorticity (vorticity with sign positive or negative) data were available, showed a great segregation of brachyuran species closely related to high fluorescence and positive vorticities (associated with cyclonic circulation), which would indicate a strong link with the NC along the mainland coastline. There were some seasonal effects, with higher vorticities linked to winter hauls and relatively low O₂ and temperature. The second axis split samples of high and low larvae density on stations where Caridea and Dendrobranchiata were dominant taxa respectively, with relatively high positive vorticities for hauls of low densities. The CCA showed that the species and samples are split depending on the environmental on the trophic conditions at the different depths (Oblique, DSL, or BBL) aggregating species depending on their feeding preferences and development stages. Two mainland assemblages were found: (a) the upper slope at the mainland coasts, composed by crab larvae, in a more productive zone (characterized by high fluorescence, a proxy of phytoplankton residual activity) occurring especially in spring–summer and autumn; and (b) a zone perpendicular

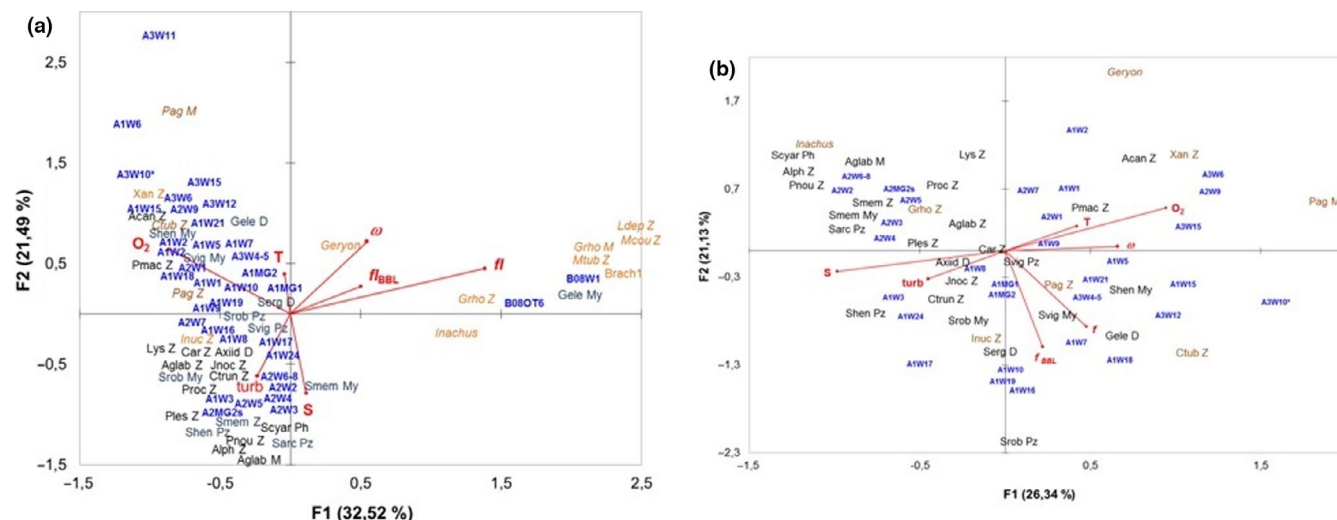


FIGURE 4 CCA of decapod larvae collected in the Balearic sub-basin (BSB) in the Northwest Mediterranean Sea. (a) Distributed as a function of environmental variables, including vorticity (ω) data based only on years 2010–2011 (BIOMARE08, ANTROMARE surveys). (b) Analysis was repeated after removing all winter samples. See codes of hauls and species in Tables 1 and 3, respectively

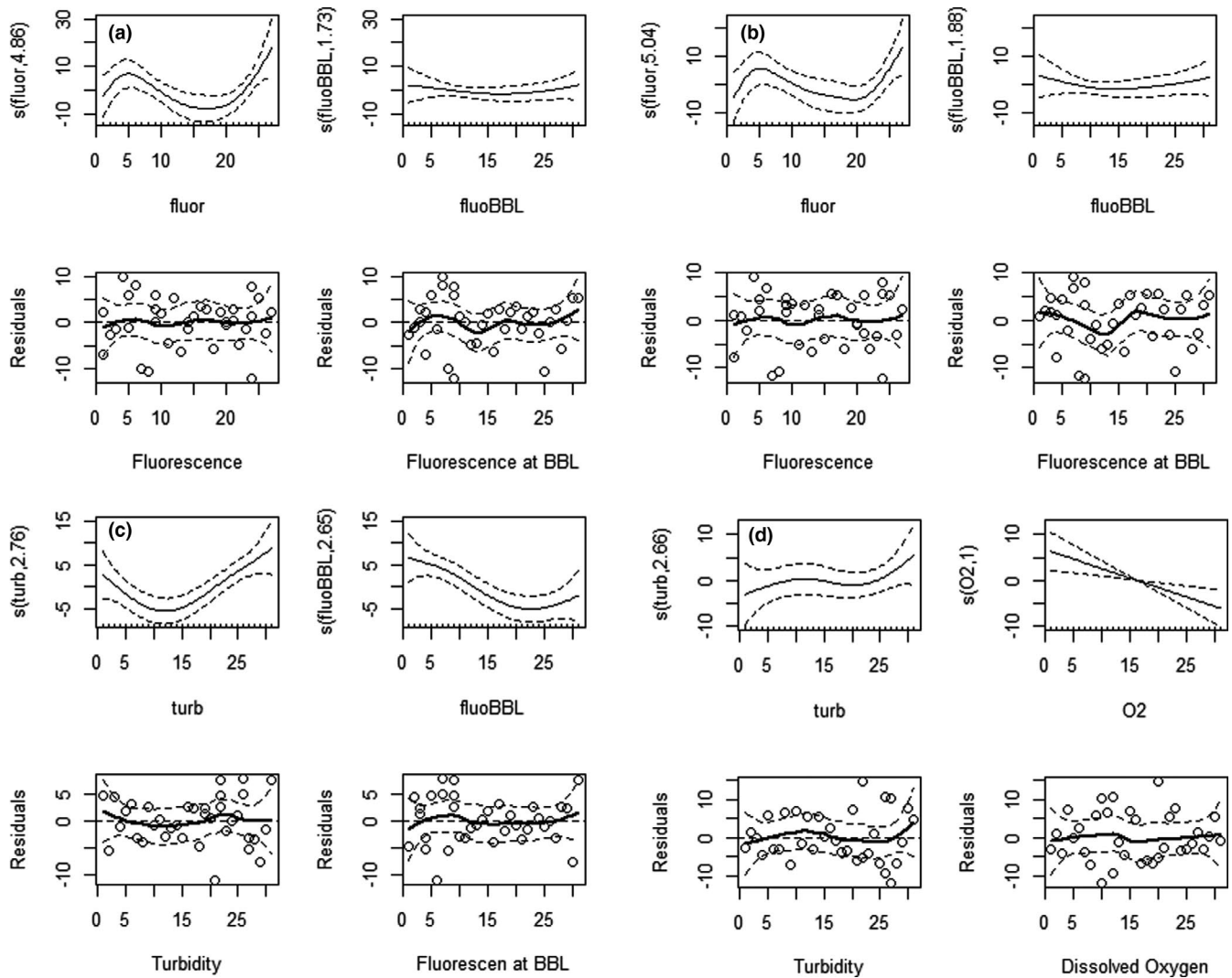


FIGURE 5 Fitted values of field observations based on smoothers of fluorescence and turbidity for (a) zoae and megalopes functional groups; and for (b) taxonomic (c) Caridea and (d) Dendrobranchiata groups. The vertical axes show the fitted values. Semi-variance variogram of residuals values against distance in the x-axis (x-axis is converted in distance scaled between 0 and 100), for each best models. No distance dependence is indicated, since there is no pattern of increasing band width among point residuals

to Ebro Delta plain (mainland zone) with concentrations of Pandalids and Sergestids in late-spring (early summer, June), a period with higher turbidity conditions likely related to resuspended organic matter (OM) at the BBL coinciding with the stratification period at mainland and insular areas; and (c) a third assemblage dominated by different pelagic species (also as adults) of sergestids and anomuran crabs at the DSL, linked to stations in the oceanic insular area in summer. This draft persisted in CCA even when winter samples were removed from the analysis (Figure 4b).

Generalized the taxonomic group of additive models (GAMs) for the groups of zoae (Figure 5a), and megalopes (Figure 5b) best model fit with added complexity (two smoother and one underlying factor effect) applied for trophic sources of fluorescence for zoae, which explained 62.9% and for fluorescence at BBL for megalopes explaining 57.9% of the total deviance. Both models included zone as underlying effect for zoae and megalopes stages (Tables 5 and 6). For Caridea the best model (Figure 5c), explained 69.4% of

total deviance, and the significant variables include turbidity and fluorescence at BBL, while the significant factor zone was the DSL layer. Finally, Dendrobranchiata best model (Figure 5d) fit for turbidity and dissolved oxygen low concentrations, but significance was only proved for dissolved oxygen (deviance explained 33.9%) (Tables 5 and 6). GAM best models showed significant underlying effect for zone or insularity, confirming that the zoae (early development stages) and megalopes and advanced zoae occurred mainly in the stratification and transition periods out of canyons.

4 | DISCUSSION

The interest of exploring the deep-sea biology is centered here on the decapod larval community occurring in the benthopelagic domain of the Northwestern Mediterranean Sea. The larvae found coincide at the upper slope, with the community of (adult) decapods

TABLE 5 Best fitted model for functional groups of zoeas and megalopes and Caridea and Dendrobranchiata response variables (Resp. Var.); degree of freedom (Df); significance (Δ i) of the Akaike information criterion (AIC), and the Akaike weights (wi)

Resp. Var.	Model	smoothers	factor	df	AIC	Δ i	wi
Zoeas	M3	Fluor	ZONE	9.075	252.326	0.000	0.629
		FluorBBL					
Megalopes	M3	Fluor	AREA	14.712	215.918	0.000	0.579
		FluorBBL					
Caridea	M3	Turb	ZONE	3.682	210.669	0.000	0.694
		FluorBBL					
Dendrobranchiata.	M3	Turb	AREA	3.000	277.004	0.000	0.339
		O ₂					

Note: Explanatory variables: Fluor (Fluorescence); Turb (Turbidity); FluorBBL (Fluorescence at benthic boundary layer), O₂ (Dissolved Oxygen); sampling at DSL or BBL depth (ZONE); localization mainland or insular area (AREA).

Resp. Var.	Smoother	Sig. edf	Sig. Ref.df	F	p-value	Sig.
Zoea	Fluor	4.865	5.913	4.470	0.00268	***
	FluorBBL	1.726	2.117	0.529	0.54827	
	ZONE (DSL)	5.299	2.611	2.030	0.053	.
Megalope	Fluor	5.042	6.138	2.970	0.0218	**
	FluorBBL	1.881	2.367	0.987	0.4423	
	AREA	-3.292	3.152	-1.044	0.306	
Caridea	Turb	2.757	3.396	6.132	0.00194	***
	FluorBBL	2.651	3.244	5.695	0.00311	***
	ZONE(DSL)	4.307	2.255	1.910	0.067	.
Dendroranchiata.	Turb	2.659	3.305	1.009	0.365	
	O ₂	1.000	1.000	9.303	0.00464	***
	AREA	-2.365	2.651	-0.892	0.379	

Significance;

*<0.01.

**<0.05.

***<0.005.

inhabiting the Balearic sub-basin (Abelló et al., 2002), while larvae of species inhabiting depth below 1,000 m (Cartes & Sardà, 1993) were hardly collected, despite we sampled the maximum depth in the area (ca. to 2,300 m). Similar assemblage analyses were restricted in the BSB to the epipelagic (0–200 m) of the water column (Carbonell et al., 2014), so the present study is somehow completing what happens in the meso (at the deep scattering layer, DSL) and bathypelagic near the seafloor (the benthic boundary layer, BBL). We identified different assemblages (regarding their composition and abundance) in the mainland and insular areas and at different layers of the water column (DSL and BBL). Furthermore, at a local geographic scale, impoverished decapod larvae assemblages were observed inside canyons and in open ocean insular waters. Also, new factors explaining the spatial distribution patterns of decapod larvae communities in the deep sea, such as the influence of vorticities in the dynamics of concentration of brachyuran species, were found (CCA results). The species dominant in mainland and insular areas were quite different,

suggesting that the exchange for the larval community is low (Pires et al., 2018), and the environment favors the presence of different species and communities in a geographic gradient at midscale. The structure of the assemblages and the presence of specific taxonomic groups were closely related to changes in the productivity and food supply (accounted by fluorescence and/or turbidity).

Ecotones (transition zones between neighboring ecological systems) shaped by environmental gradients over a range of space and time scales play an important role in ecosystem dynamics. The BBL, basically an ecotone between the pelagic and benthic system, seems to be a good habitat for advanced stages of decapod larvae. The BBL may play an important role in fauna dynamics due to the re-suspension of particles (near-bottom turbidity) associated with this level (Cartes, Lolocono, et al., 2013; Papiol et al., 2019), important for suprabenthic fauna (Mees & Jones, 1997).

The great deltaic plain (Ebro river) in the mainland concentrated shrimp larvae advanced zoea stages near the bottom (at ca. 10–150 m

TABLE 6 ANOVA results for best GAM models. Explanatory variables: Fluor (Fluorescence); Turb (Turbidity); FluorBBL (Fluorescence at benthic boundary layer), O₂ (Dissolved Oxygen); sampling at DSL or BBL depth (ZONE); localization mainland or insular area (AREA)

above the seafloor) coinciding with the occurrence of bottom nepheloid layers (BNL), at 400–600 m and at 1,000 m off the continental coastline, and at 700 m off the Northern of the Insular Balearic area (see figure 7 in Cartes, Lolocono, et al., 2013). Suspended particulate organic matter (POM) may constitute an attractive food source for shrimp (Caridea and Dendrobranchiata), which were more abundant not immediately on the bottom or in the water column off the seabed, but at 1–25 m above it. Dissolved oxygen is another factor influencing zooplankton density (Cartes, Fanelli, et al., 2013; Cartes, Lolocono et al., 2013; Papiol et al., 2019), but in this case the density of *Sergestidae*, which increased during stratification period (CCA-GAM results).

The BSB is characterized by an offshore general cyclonic circulation, which results in a dome-like structure that enhances the down-top food web. The cyclonic eddies entrain nutrient-rich deep waters toward the coast, enhancing Portunid and Anomuran crabs recruits aggregations in the vicinity of the shelves. However, this pattern was seasonal more frequent in spring–summer and interrupted by anticyclonic episodes that modify the oceanographic dynamics, probably facilitating the top-down settlement of offshore swimming species of Caridea and Dendrobranchiata larvae. The temporal variability in the nepheloid layers (NL) can also cause changes in the species distribution and composition, since NL are, in most cases, not permanent structures, reflecting monthly/seasonal, and probably inter-annual, peaks in mass export offshore (Rumolo et al., 2015; Thomsen & van Weering, 1998). Successful colonization of NL by larvae could be subjected to their dynamics, that may contribute to the larval dispersion. In other words, the dispersal capability of (advanced stages) decapod larvae may depend on their ability to find NL in order to feed on these habitats. When larvae reach near-bottom BBL or DSL, they find a mechanism that may facilitate their transport from mainland to more oceanic areas, advecting larvae offshore. In agreement with this model, in the whole Western Mediterranean Sea there is a recruitment of smallest (recently settled) juveniles of *A. antennatus* at over 1,000 m depths (Sardá & Cartes, 1993; Follesa et al., 2009; Cartes et al., 2018) and there are evidences of a common genetic pool for these important commercial shrimps, for example *A. antennatus*, *Aristaeomorpha foliacea* (Heras et al., 2019).

Brachyuran species with similar life cycle strategies, but with different recruitment periods, appeared together in the same CCA quadrant plot, suggesting that they occur under similar environmental conditions and take advantage of seasonal peaks of production. They have, in general, abbreviated larval life cycle, and larvae occurred according to the recognized reproduction periods of the adults' populations, of species such as *M. turbeculatus*, *M. couchi*, and *L. depurator*. Their growth and feeding are coupled with periods of high productivity and phytoplankton peaks—in spring–summer or early winter (Estrada, 1996; Pochelon et al., 2014) to avoid starvation. By contrast, the groups with extended development life cycle (e.g. Dendrobranchiata), and are rather *r*-strategist, having greater dispersal capacities, probably they are able to exploit other sources of food, like POM or detritus resuspended in Benthic Nepheloid Layers (BNL) detached offshore from the continental slope. Such hypothesis is reinforced by the collection of first settled—or “close

to settlement”—specimens of deep species at great depths (1,590–1,758 m) near the bottom (at the BBL).

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CONFLICT OF INTERESTS

I hereby declare that none of the authors of this manuscript has any potential sources of conflict of interest that influences their objectivity regarding the content of the present manuscript.

AUTHOR CONTRIBUTIONS

A. Carbonell and J.E. Cartes conceived the research idea and wrote the manuscript. A. Carbonell identified the larvae and with J.E. Cartes did the data analysis. A. Aparicio provide vorticity oceanographic data product. V. Papiol participated in discussion of the results and critically reviewed the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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