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PRIMARY RESEARCH PAPER

Effects of contrasting oceanographic conditions on the spatiotemporal distribution of Mediterranean cephalopod paralarvae

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Abstract Cephalopods are sensitive to environmental conditions due to their fast growth rates and short life cycles, being thus considered good ecological indicators. Here, we analyzed western Mediterranean cephalopod paralarvae communities during two consecutive summers (2004 and 2005) characterized by contrasting oceanographic conditions. Our main aim was to determine to what extent such contrasting scenarios affected the spatial distribution of the cephalopod early life stages and decipher the main environmental factors affecting each particular taxon. The contrasting oceanographic conditions during 2004 and 2005 included differences in the shape and location of a regional frontal system, which brought about differences in the sea circulation and the temperature regime. Such contrasting scenarios were reflected in the spatial distribution and the frequencies of appearance of both the whole community and the individual taxa. There was not any major factor affecting most taxa equally, which points to differences in species sensitivity to external conditions. Moreover, our results evidenced that paralarvae populations were more influenced by regional sea salinity and temperature than by mesoscale hydrographic features. Our study reveals that moderate changes in sea temperature have a major effect on the presence of paralarvae populations, which has profound implications in the context of the current global warming.

Keywords Environmental effects · Temperature · Salinity · Cephalopod · Paralarvae · Mediterranean

Introduction

Cephalopods are key components of marine trophic webs, where they constitute major food resources for a large variety of predators (Piatkowski et al., 2001). Octopuses, squids, and cuttlefishes also represent important fractions in many fisheries around the world (FAO, 2012). As living resources, cephalopods are particularly relevant in the Mediterranean, where the common octopus (*Octopus vulgaris*) represents between 20 and 40% of the bottom trawl landings (Quetglas et al., 1998); the cuttlefish *Sepia officinalis* is also pivotal for the maintenance of the small-scale fleet (Keller et al., 2014), whereas the squid *Loligo vulgaris* is a main target for recreational fishers (Morales-Nin et al., 2005). Most cephalopods are

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typical r-strategists having fast growth rates and short life span, dying soon after the reproduction takes place (Boyle & Rhohouse, 2005). This makes cephalopod populations strongly dependent on the success of reproduction and recruitment. As a consequence of these life-history traits, cephalopod populations are very sensitive to external factors and display a high plasticity to changing environmental conditions. Thus, cephalopods are expected to anticipate much faster responses to environmental disturbances than longer-lived marine species, making them both drivers of ecosystem changes and potential ecological indicators of natural and human-induced alterations in marine ecosystems (André et al., 2010).

Despite the practical interest in analyzing the expected close-knit relationships between reproductive success and fishery yields in commercially exploited cephalopods, the ecology of their early life stages has traditionally been scarcely studied compared to other main taxonomical groups such as fishes and crustaceans. The inadequacy of most commonly used zooplankton sampling methods, the subsequent under-representation of paralarvae in such standard plankton samples and the uncertainties of species identification are major limitations to those studies (Boyle & Rhohouse, 2005). Pending on future improvements on taxonomic aspects, many current studies have focused on the effects of oceanographic parameters on paralarvae distribution in different areas of the world's ocean (e.g., Röpke et al., 1993; Diekmann & Piatkowski, 2002; Roberts & Berg, 2005). Though several studies investigated the influence of the regional oceanographic variability in the northeast Atlantic (González et al., 2005; Moreno et al., 2009; Otero et al., 2009), there is not a single study in the Mediterranean Sea. In fact, the ecology of cephalopod early life stages from Mediterranean waters has scarcely been studied since most existing works focus on the paralarvae species composition without reference to its relationships with external factors (e.g., Roper, 1974; Sánchez & Molí, 1985; Salman et al., 2003; Lefkaditou et al., 2005). The waters surrounding the Balearic Islands constitute a highly hydrodynamic area in the western Mediterranean (Fig. 1) that straddles the transition between the Algerian and Balearic sub-basins and play a key role in the sea circulation of the area by conditioning the water mass exchanges between these two basins (López-Jurado et al., 1995; Pinot et al., 2002). During summer, when the winter atmospheric forcing ceases, the density gradient forces become dominant, allowing the northward progress of recent Atlantic water (AW) across the Balearic channels. The confluence of recent AW (fresher and warmer) with resident AW (saltier and colder) generates salinity driven oceanic density fronts. The location and intensity of these fronts also depend on the seasonal and interannual variability (López-Jurado et al., 2008) and the interaction between surface and intermediate waters (Balbín et al., 2013).

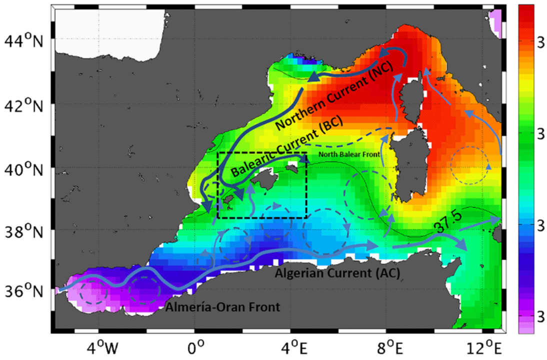


Fig. 1 Average July salinity for the western Mediterranean (map adapted from Reglero et al., 2012) with the Balearic Archipelago identified by a *black dashed square*. The isohaline 37.5 approximately separates the fresh Atlantic waters to the south from the resident Atlantic waters to the north. Major currents are shown by *arrows*: the Algerian current (*light blue solid line*), the Northern Current (*wide dark blue solid line*), the Balearic current (*narrow dark blue solid line*), the North Balear front (*dark blue dashed line*) and gyres (*light blue dashed lines*)

In the framework of the general oligotrophy of the Mediterranean, the Balearic Sea sustains a relatively diverse and abundant summer larval fish community, as reported by Alemany et al. (2006) and Rodríguez et al. (2013) who identified up to 61 and 128 taxa, respectively. Larval fish communities showed a patchy distribution, depth and water masses being the main factors shaping these strong horizontal structures. It was also found that anticyclonic eddy boundaries constitute favorable habitats for fish larvae. The Balearic Archipelago also represents an important spawning area of many large pelagic fishes, both highly migratory and resident species (Alemany et al., 2006, 2010; Rodríguez et al., 2013). Taking advantage of this, summer ichthyoplankton surveys were conducted in the area during 2004 and 2005 to study the larval ecology of Atlantic bluefin tuna and related large pelagic fishes (Alemany et al., 2010).

Besides the early life stages of these target species, the surveys also provided extensive samples of other fish species and other taxonomical groups such as crustaceans and cephalopods. Recent studies suggest that the hydrographic conditions of these two consecutive summers were notably contrasting, with higher stability and a lack of water mass interchange between the Algerian and Balearic sub-basins and weak surface currents in 2005 (Balbín et al., 2013; Rodríguez et al., 2013). Such contrasting environmental scenarios triggered a different horizontal distribution and structure of fish larvae assemblages (Rodríguez et al., 2013), underlying potential influence on other taxonomic groups of the meroplankton community.

In this study, we analyzed the cephalopod paralarvae communities from the Balearic Sea during two consecutive summers (2004 and 2005) characterized by contrasting oceanographic conditions. Our main aim was to determine to what extent such contrasting scenarios affected the presence of the cephalopod early life stages and decipher the main environmental factors affecting the paralarvae distribution of each specific taxon.

Materials and methods

Field sampling and laboratory processing

The sampling was conducted during the summers of two consecutive years (18 June to 10 July 2004 and 27 June to 23 July 2005) in the Balearic Sea (western Mediterranean). The nodes of a regular grid of 10 × 10 nautical miles (see Fig. 4) were systematically sampled using two different Bongo nets of 60 and 90 cm mouth diameter (henceforth referred to as B60 and B90, respectively); the B60 was equipped with 200- and 335-µm mesh and the B90 with 500-µm mesh. A total of 367 (181 in 2004, 186 in 2005) and 396 (197 in 2004, 199 in 2005) sampling stations were performed using the B60 and B90, respectively, during daytime and night-time hours. The B60 was towed on depth-integrated oblique hauls from 70 m depth, whereas the B90 was towed at subsurface down to 5 m depth, in both cases using towing speeds of two knots. The oblique tow operations were monitored with a Minilog time/temperature/depth recorder and the water volume filtered was estimated using general oceanic flowmeters mounted in the centre of the gear mouths. Vertical profiles of temperature, salinity, fluorescence, and pressure were also taken using a CTD probe SBE911. Mesozooplankton dry weight was obtained from samples collected with a 200-µm mesh mounted on the B60 net, which were frozen on board and analyzed afterward following Lovegrove (1966); weights were standardized to mg m^{-3}. Plankton samples were preserved on board with 4% formaldehyde in seawater and subsequently sorted under a stereoscopic microscope in the laboratory. Once sorted, all paralarvae were classified to the lowest taxonomic level possible using published taxonomic descriptions (e.g., Sweeney et al., 1992; Diekmann et al., 2002; Moreno, 2008).

Data analysis

Dynamic topography (height of the sea surface relative to the particular gravitational equipotential surface known as the geoid) can be used to diagnose the ocean circulation, and, in particular, the currents that redistribute heat and thus regulate the Earth's climate (Bingham & Haines, 2006). We calculated the dynamic height in order to estimate the geostrophic velocity, which in our study area is positively correlated with the intensity of the fronts due to the confluence of fresh and older Atlantic water in the channels. Dynamic height was calculated by vertical integration of the specific volume, using 600 m as the level of no motion (Pinot et al., 1995), and was used to estimate the geostrophic velocities. These velocities were obtained by the first-derivative of the dynamic height profiles objectively analyzed onto a regular grid (see Balbín et al. (2013), for more details on the interpolation method) and were used as a proxy of current intensity close to fronts due to the confluence of water masses of different origins. Maps of hydrographic variables were obtained from an objective analysis on to a 3 × 3 nm regular grid by using minimum error variance methods. Finally, surface chlorophyll-*a* concentration (Chla, mg m^{-3}) from the study area was obtained from satellite data as the spatial mean in a 15 km^2 window from the MODIS-Aqua 8 day composite 4 km resolution Level-3 files (htpp://oceancolor.gsfc.nasa.goc/); the depth range of these Chla data for the summer season in the study area is about 20–50 m.

In the study area, salinity maps are useful to detect salinity fronts separating recent and resident Atlantic water (AW). The saltier and colder surface water that has stayed longer in the Mediterranean will be henceforth denoted in this study as resident AW ($S \geq 37.8$), the fresher and warmer water recently arrived through the Strait of Gibraltar as new or recent AW ($S < 37.5$) and the waters with intermediate salinity values ($S \sim 37.5$) corresponding to the mixing of these two masses as mixed AW (López-Jurado et al., 2008).

The use of two gear types with different characteristics and sampling different water layers prevented the joint analysis of samples. This was further reinforced by cluster analysis, which clearly separated the samples from both nets (results not shown). Consequently, all analyses were performed separately by the B60 and B90 nets. Owing to the low number of paralarvae taken by taxon (see below), we modeled presence/absence data instead of densities. Firstly, we determined the spatial distribution of paralarvae presences by year. Secondly, we used generalized additive models (GAMs) to analyze the relationship between paralarvae presences and several biological and hydrographical parameters. These analyses were performed for the individual taxa containing ≥16 individuals.

The following environmental variables, which best summarize the hydrographic conditions in the upper water column (Balbín et al., 2013), were selected: temperature at mixed layer, 5 m (T_5), 10 m, and 25 m (T_{25}) depth and salinity at mixed layer, 5 m (S_5), 10 m, and 25 m (S_{25}) depth, in addition to depth of the mixed layer (MLD), geostrophic velocity, surface Chla, depth-integrated (10–100 m) fluorescence and mesozooplankton dry weight. In order to remove collinear effects among environmental covariates, we applied a variance inflation factor (VIF) with a cut-off VIF value of 5 (Zuur et al., 2009), and dropped all collinear variables before starting the GAM analyses. Given that the two Bongo nets used sample different water layers (whereas the B90 focuses on subsurface waters, the B60 integrates 70 m depth), we selected the most appropriate hydrographical covariates depending on the net type: (1) B90: S_5, T_5, mixed layer depth (MLD), geostrophic velocity, and surface Chla; and (2) B60: S_{25}, T_{25}, MLD, geostrophic velocity, and depth-integrated (10–100 m) fluorescence. We also included log-transformed actual depth (log-depth) and two temporal covariates, the year (treated as a factor) and hour of sampling. Presence/absence data were modeled using a binomial family (logit link), which is commonly applied when the data set is characterized by an excess of zeros. The GAMs were fitted using smoothing splines with a maximum of four degrees of freedom (i.e., five knots). The model selection was based on the following three criteria: (1) minimization of the unbiased risk estimator (UBRE), an error index penalized for excessive nonlinear smoothers; (2) deviance explained (DE); and (3) statistical significance of the covariates included in the model. All covariates were included in the model and eliminated one at a time when they were not statistically significant. The order in which covariates were excluded was based on the significance of their smooth-term effect, expressed by the P value. All GAMs were fitted with the mgcv library using the R software (www.r-project.org/).

Results

Description of the two oceanographic scenarios

As our samples were collected in subsurface waters (B90) and in oblique hauls from 70 m depth (B60), the oceanographic conditions at the average depth (35 m) was used to describe the main general processes in the study area (Fig. 2). In June 2004 (Fig. 2a), seawater temperature was rather homogeneous along the study area, ranging from 14.0 to 17.5°C (mean 16.1°C). The year 2005 was warmer (Fig. 2b), with temperature ranging from 14.9 to 22.5°C (mean 17.5°C); during this year, temperature values were close to 16–17 and 18–19°C west and east off Mallorca, respectively, with a broad area of 20–22°C at the southeast of the island. In 2004 (Fig. 2c), the most important hydrographical feature was the presence of mixed recent and resident AW ($37.4 < S < 37.5$) south of Mallorca and Menorca islands, and this structure was associated with currents reinforcing an anticyclonic gyre south of Menorca (Fig. 2e). In 2005 (Fig. 2d), recent AW occupied the southwestern part of the study area, including the Ibiza and Mallorca channels and there were northward inputs of recent AW through the Ibiza channel. The salinity driven front separating recent and resident AW meandered between Ibiza and Mallorca, returning into the Algerian basin through the Mallorca channel (Fig. 2f). Resident AW was observed to occupy most of the eastern part of the

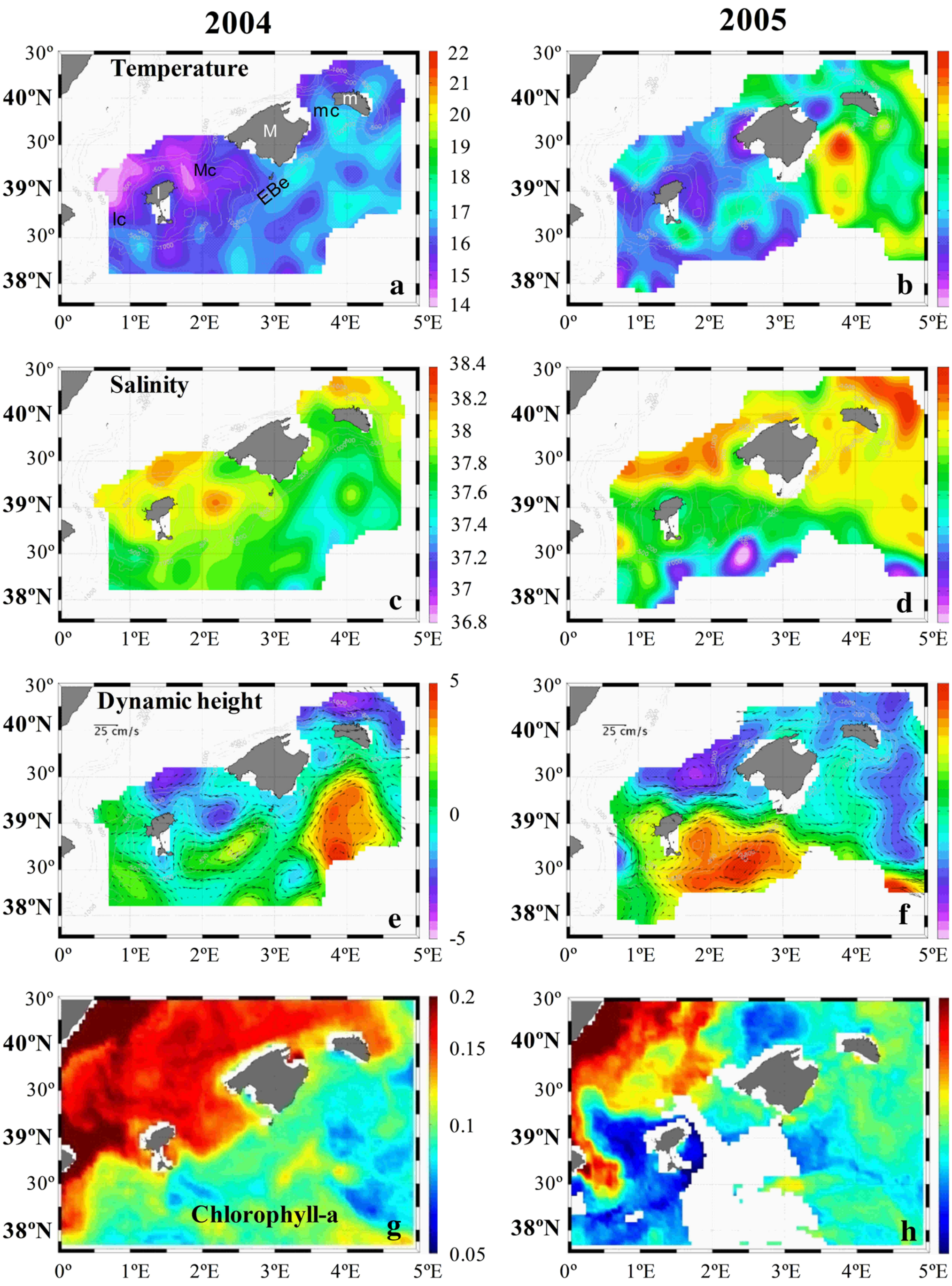


Fig. 2 Hidrographic conditions (temperature, salinity, dynamic height and chlorophyll-*a* concentration) around the Balearic Islands (western Mediterranean) at 35 m depth during the summer (June) of two consecutive years (2004, 2005). The labels in the upper left hand side map a for the islands of Mallorca (M), Menorca (m) and Ibiza (I), together with the corresponding channels between them (Ibiza channel, Ic; Mallorca channel, Mc; Menorca channel, mc) and the Emile Boudot escarpment (EBe). Temperature, salinity, and dynamic height maps were elaborated with our own data collected during two scientific surveys, whereas chlorophyll-*a* data was obtained from http://oceancolor.gsfc.nasa.gov/

domain. The scenario was different in 2004, since there was a distinct front of Chla running from the southwest to the northeast, separating the waters situated between the Archipelago and the mainland (0.15–0.20 mg·m^{-3}) from those southeast of the Archipelago (0.1 mg m^{-3}) (Fig. 2g); by contrast, in 2005 the front did not reach the Archipelago (Fig. 2h). Finally, the frequency distributions of salinity, temperature at 35 m, and depth-integrated (10–100 m) fluorescence during 2004 and 2005 (Fig. 3a–c) revealed that while the thermal regime was clearly different between years, the other two parameters did not show important variations.

Taxonomic composition

A total of 1,162 paralarvae were collected (302 with B60, 860 with B90), from which ten taxa were identified to the species level, one to genera and four to family (Table 1). The most abundant taxon was the family Ommastrephidae, accounting for 72.72% of the paralarvae, followed by far by the families Onychoteuthidae (6.88%) and Octopodidae (6.45%), and the species *Thysanoteuthis rhombus* (4.82%); the contribution in number of the remaining taxa ranged between 0.09 and 1.55%. Three species were recorded only once: *Cranchia scabra, Stoloteuthis leucoptera,* and *Rossia macrosoma.* With the only exception of the family Ommastrephidae, the mean densities of all other paralarvae were always higher in B60 than in B90. The most frequent taxon in both nets was Ommastrephidae (39.20% in B60, 27.87% in B90), followed by Onychoteuthidae (17.33% in B60) and Octopodidae (7.73% in B60). The spatial distribution of the whole paralarvae community showed striking differences between years, since they were much more widely distributed along the sampling grid in 2005 compared to 2004 (Fig. 4). Whereas paralarvae were only present in 35% (B60) and 46% (B90) of the sampling stations in 2004, they occurred in about 80% of those performed with both nets in 2005.

Modeling paralarvae distribution

From the whole set of covariates tested using GAMs, the geostrophic velocity, MLD, surface Chla, depth-integrated (10–100 m) fluorescence, and T_{25} did not significantly affect any of the taxa modeled. All other covariates and factors showed significant effects for some individual taxa (Table 2). In both Bongo nets, paralarvae presences were significantly higher in 2005 than in 2004.

The taxa containing ≥16 individuals (Table 1), and hence used for GAM modeling included six taxa for B60 (*Abralia veranyi*, Loliginidae, Octopodidae, Ommastrephidae, Onychoteuthidae, and *Thysanoteuthis rhombus*) and four taxa for B90 (Octopodidae, Ommastrephidae, Onychoteuthidae, and *T. rhombus*). Most taxa collected with the B60 (*C. sicula,* Loliginidae, Octopodidae, Onychoteuthidae, and Ommastrephidae) displayed a scattered spatial distribution around the Balearic Islands (Fig. 5b–f). By contrast, *A. veranyi* (Fig. 5a) was not present in any of the stations located between the Archipelago and the mainland, while *T. rhombus* (Fig. 5g) was exclusively taken in the Ibiza Channel. Considering the B90 sampling, the taxa Octopodidae and Ommastrephidae also displayed a scattered distribution (Fig. 5h, j, respectively). However, Onychoteuthidae (Fig. 5i) was restricted to the south and east off Menorca and

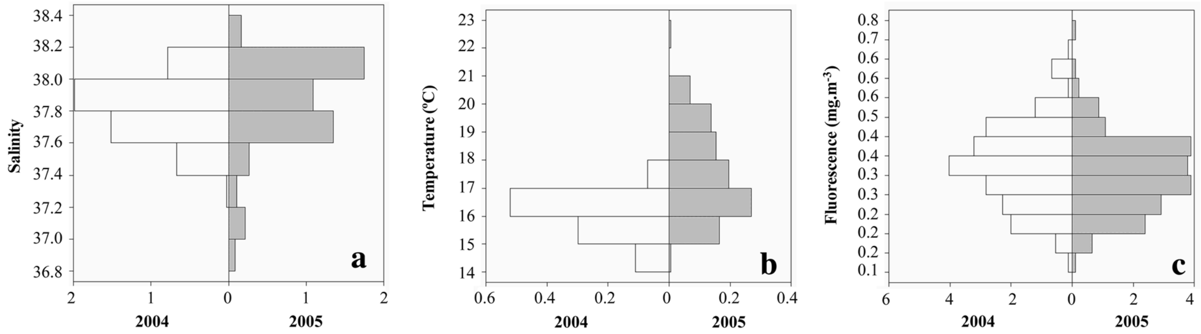


Fig. 3 Frequency distributions of temperature, salinity at 35 m depth, and depth-integrated (10–100 m) fluorescence off the Balearic Islands (western Mediterranean) during the summer (June) of two consecutive years (2004, 2005)

Table 1 Taxonomic composition of the cephalopod paralarvae collected using two Bongo nets (60 and 90) during early summer of two consecutive years in the western Mediterranean

Family	Species	Bongo 60			Bongo 90			Bottom depth (m)	Nt	%Nt
		N	%F	(AA +) ± SD	N	%F	(AA +) ± SD			
Ancistrocheiridae	*Ancistrocheirus lesueurii*	6	2.78	0.687 ± 0.086	6	1.33	0.177 ± 0.021	104–2,515	12	1.03
Brachioteuthidae	*Brachioteuthis riisei*				2	0.45	0.203 ± 0.009	1,339–2,566	2	0.17
Chtenopterygidae	*Chtenopteryx sicula*	10	4.58	0.643 ± 0.123				545–2,735	10	0.86
Cranchiidae	*Cranchia scabra*				1	0.22	0.190	130	1	0.09
Enoploteuthidae	*Abralia veranyi*	16	7.37	0.616 ± 0.103	2	0.44	0.181 ± 0.0138	71–2,735	18	1.55
	Abraliopsis morisii	1	0.45	0.647	1	0.22	0.195	426–2,312	2	0.17
Histioteuthidae	*Histioteuthis sp.*	2	0.91	0.685 ± 0.115				1,610–2,021	2	0.17
Loliginidae	Unidentified	17	6.36	0.722 ± 0.310	1	0.22	0.212	55–2,673	18	1.55
Octopodidae	Unidentified	18	7.77	0.654 ± 0.229	57	7.73	0.289 ± 0.177	73–3,452	75	6.45
Ommastrephidae	Unidentified	139	39.20	0.970 ± 0.518	706	27.87	1.051 ± 1.416	55–3,452	845	72.72
Onychoteuthidae	Unidentified	51	17.33	0.826 ± 0.494	29	3.10	0.388 ± 0.271	107–2,887	80	6.88
Sepiolidae	*Heteroteuthis dispar*	2	0.92	0.596 ± 0.107				855–1,002	2	0.17
	Stoloteuthis leucoptera	1	0.45	0.537				55	1	0.09
	Rossia macrosoma	1	0.47	0.723				1,653	1	0.09
Thysanoteuthidae	*Thysanoteuthis rhombus*	19	4.09	1.48 ± 2.784	37	5.32	0.267 ± 0.139	71–3,019	56	4.82
Unidentified		19	7.32	0.749 ± 0.290	18	3.10	0.230 ± 0.122	113–2,725	37	3.18
Total		302			860				1,162	

For each gear type, the following parameters are shown: number of individuals (N), frequency of occurrence (%F) and average abundance (±SD) considering exclusively the stations where paralarvae were present (AA+; expressed as individuals per 100 m^3). The bottom depth range, total number of individuals (Nt) and its corresponding contribution in percentage (%Nt) are also displayed for each taxon

south of Ibiza and *T. rhombus* (Fig. 5k) was mainly observed south of the Archipelago.

The summary of the GAMs fitted to these paralarvae taxa is in Table 2. Models for *T. rhombus* and Octopodidae were only significant considering the B90, which suggests contrasting vertical distribution of these taxa. For the other taxa (Ommastrephidae and Onychoteuthidae), models were significant in both Bongo nets. The family Loliginidae did not show significant effects of any environmental variable. In the entire set of models, deviance explained (DE) ranged between 10.1% in *A. veranyi* and 35.7% in Octopodidae. In the three taxa with significant models for both nets, the B90 model always had higher DE values than the B60 model.

In the following paragraphs, the significant results of the GAMs are described by species and Bongo net (Figs. 6, 7). The squid *A. veranyi* collected with the B60 showed positive linear effects of both the log-depth (Fig. 6a) and W_{meso} (Fig. 6b).

In both Bongo nets, the presence of Ommastrephidae paralarvae was higher in 2005 than in 2004 (Figs. 6c, 7f). Together with differences between years, the presence of Ommastrephidae at B60 displayed positive linear effects of log-depth (Fig. 6d) and S_{25} (Fig. 6e). By contrast, the B90 sampling displayed non-linear effects of S_5, log-depth, W_{meso}, and T_5 (Fig. 7g–j). The partial effect of log-depth (Fig. 7h) decreased gradually from values close to 5 (i.e., 150 m depth) down to 7 (i.e., 1,100 m depth), but

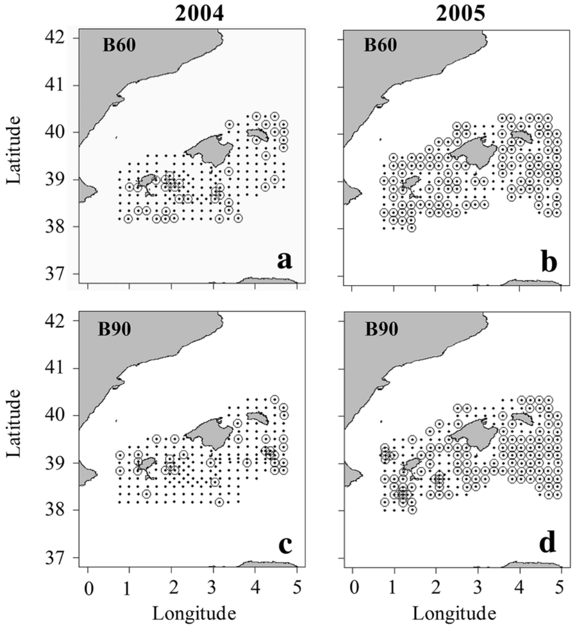


Fig. 4 Spatial distribution of stations with presences of cephalopod paralarvae (*open circles*) from the total set of sampling stations (*black dots*) performed during early summer of two consecutive years (2004, 2005) using two different Bongo nets (Bongo 60 and 90) in waters around the Balearic Islands (western Mediterranean)

increased markedly afterward. The partial effect of W_{meso} (Fig. 7i) displayed a non-linear effect with a peak at about 5 µg. The effect of T_5 (Fig. 7j) suggests no presence of Ommastrephidae in waters of temperature values between 22.5 and 24°C, while that of S_5 (Fig. 7g) evidences that the presence of Ommastrephidae was mainly related to resident AW (salinity ∼ 37.8).

The family Onychoteuthidae collected with the B60 showed significant effects of year, hour, log-depth, and S_{25} (Fig. 6f–i). Paralarvae presences were higher in 2005 than in 2004 (Fig. 6f). The covariate hour showed a periodicity of about 12 h, with the highest values at about 4:00 a.m. and 9:00 p.m. and the lowest values at 1:00 p.m (Fig. 6g). The log-depth (Fig. 6h) showed a positive linear effect with higher presences associated to values higher than 7 (i.e., 1,100 m depth). The effect of S_{25} was non-linear, with minimum values in mixed waters of salinity around 37.5 (Fig. 6i). For B90, this family showed a significant effect of the hour (Fig. 7c) similar to that observed for B60, in addition to an increasing linear effect of S_5 (Fig. 7d).

The squid *Thysanoteuthis rhombus* caught with the B60 did not show significant effects of any environmental variable. The species only displayed a cyclic effect of the hour of capture in the B90 sampling, with the lowest values at about 11:00 a.m. and highest values at 00:00 a.m. and 8:00 p.m. (Fig. 7e).

Finally, whereas the family Octopodidae collected with the B60 neither showed significant effects of any environmental variable, it was affected by the factor year and the covariate hour in the B90 sampling (Fig. 7a,b). Octopus presences were higher in 2005 than in 2004. The daily cycle was similar to that found for the family Onychoteuthidae, with higher presences during night hours and a clear minimum between 8:00 a.m. and 3:00 p.m.

Table 2 Main outputs of the generalized additive models (GAMs) modelling the presence/absence of paralarvae against the following explanatory variables: year (as a factor), temperature and salinity at 5 and 25 m depth (T_5, T_{25}, S_5, S_{25}, respectively), hour, chlorophyll-*a* concentration (Chla), mixed layer depth (MD; in m) and dry weight of mesozooplankton (W_{meso})

Taxa	Net	Year 2004	Year 2005	T_5	S_5	S_{25}	Hour	Depth	W_{meso}	Dev (%)	N
Abralia veranyi	B60							1*	1*	10.1	309
Octopodidae	B90	−5.12 (0.65)	−2.32 (0.30)				2.84***			35.7	396
Ommastrephidae	B60	−2.24 (0.26)	−0.62 (0.16)			1*		1*		12.8	367
	B90	−1.92 (0.32)	−0.61 (0.37)	3.20*	2.15**			3.72***	3.42*	27.4	312
Onychoteuthidae	B60	−3.34 (0.41)	−2.33 (0.29)			2.37**	3.78**	1*		21.6	367
	B90				1*		2.59**			28.8	370
Thysanoteuthis rhombus	B90						3.86**			20.0	396

Outputs are shown by the two different Bongo nets used (B60, B90). Values for year include the estimate and standard error within parentheses. In all other variables, values denote the effective degrees of freedom indicating departure from linearity. For each model, the percentage of deviance explained (Dev %) and number of data (N) are also shown. Significance at $P < 0.001$***, 0.01**, 0.05*

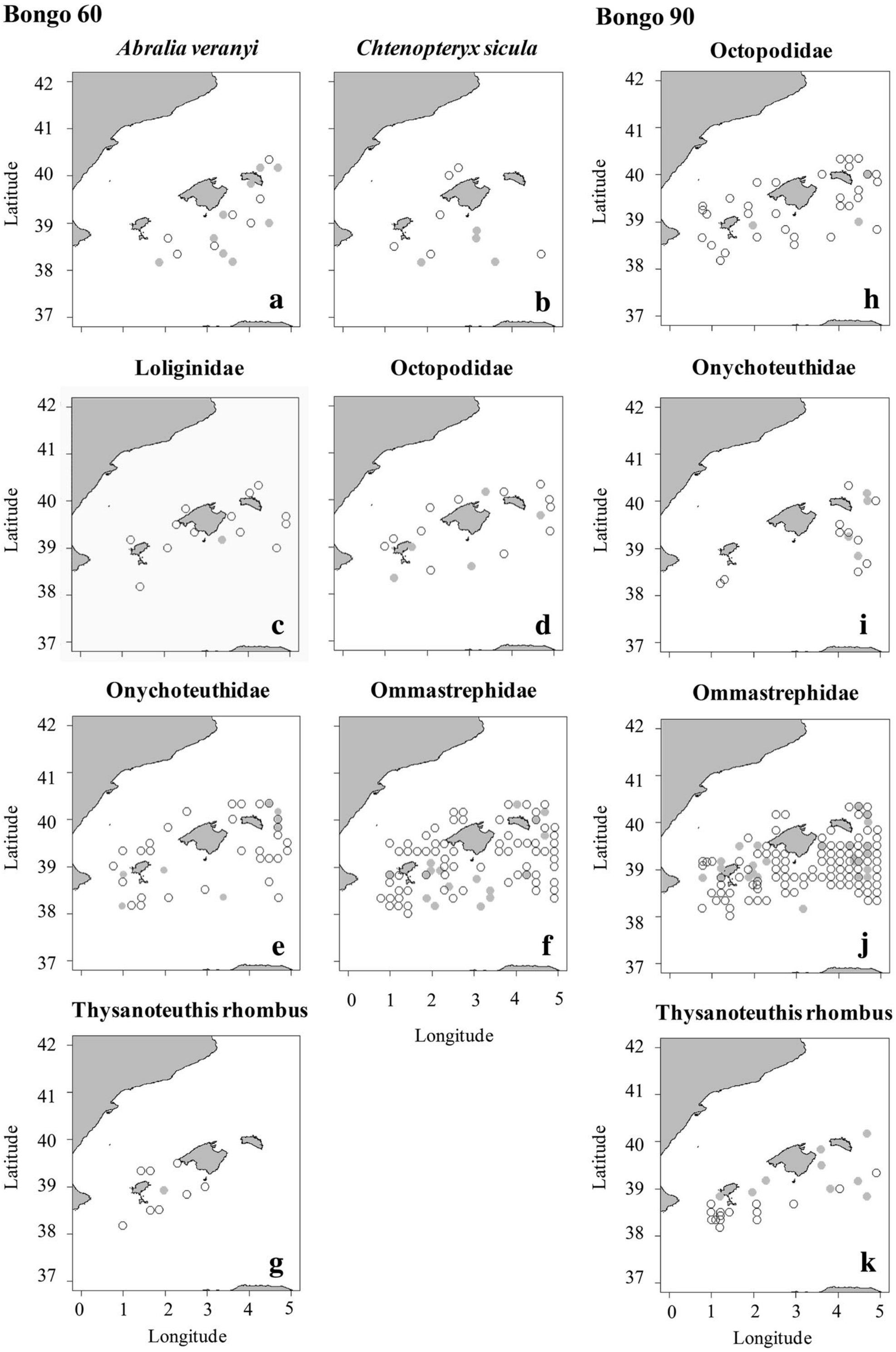
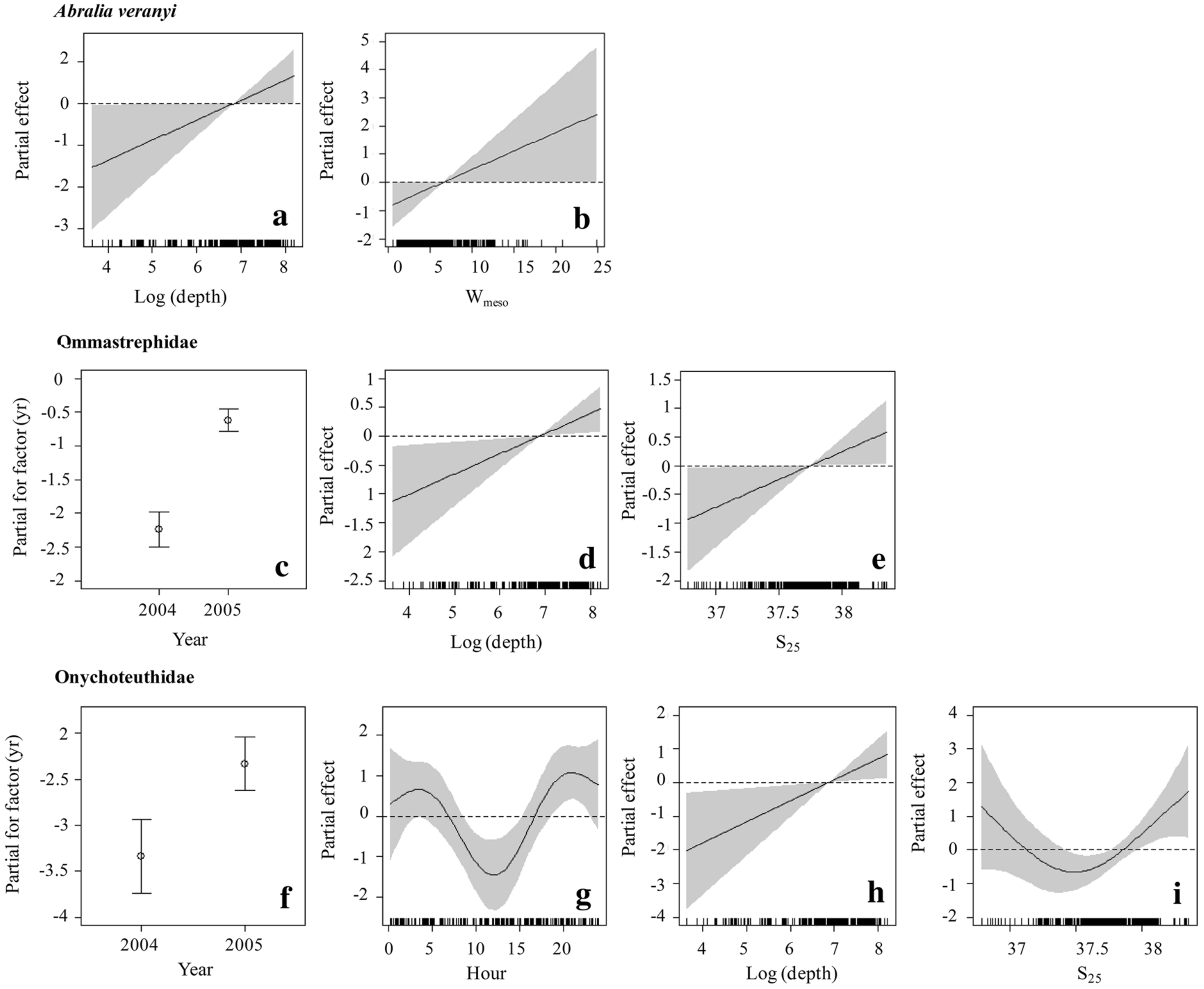


Fig. 5 Spatial distribution of the most abundant taxa of cephalopod paralarvae collected during 2004 (*gray*) and 2005 (*white*) using two different Bongo nets (Bongo 60 and 90) in waters around the Balearic Islands (western Mediterranean)


Abralia veranyi

Ommastrephidae

Onychoteuthidae

Fig. 6 General additive model (GAM) outputs modeling the presences/absences of the most abundant cephalopod taxa (*Abralia veranyi*, Ommastrephidae and Onychoteuthidae) collected in waters around the Balearic Islands (western Mediterranean) using the Bongo 60 net. The partial effect of factor year and the following explanatory variables are shown: hour, depth (log-transformed), dry weight of mesozooplankton (W_{meso}), salinity at 25 m (S_{25}). Fitted lines (*solid line*) and 95% confidence intervals (*gray shaded areas*) are shown

Discussion

A total of 15 different taxa of cephalopod paralarvae were identified in the sampling conducted in waters around the Balearic Islands (western Mediterranean) during two consecutive years characterized by contrasting oceanographic conditions. Owing to the difficulties of identifying the species of some families, which are important in the study area according to the adult phases such as Octopodidae, Ommastrephidae, or Loliginidae (Quetglas et al., 2000), exclusively 10 species could be classified to the species level. This number only accounts for about 19% of the 52 species currently reported in the Balearic Sea (Quetglas, 2003). Furthermore, the species composition of the paralarvae from our sampling contrasts with that of adults, since most paralarvae belonged to species rarely caught as adult in the study area such as *Ancistrocheirus lesueurii, Brachioteuthis riisei, Cranchia scabra, Abraliopsis morisii,* or *Stoloteuthis leucoptera* (Quetglas et al., 2013a). However, it is also true that the occurrence of these species was sporadic and only collected once or twice. The Ommastrephidae was the most abundant family,

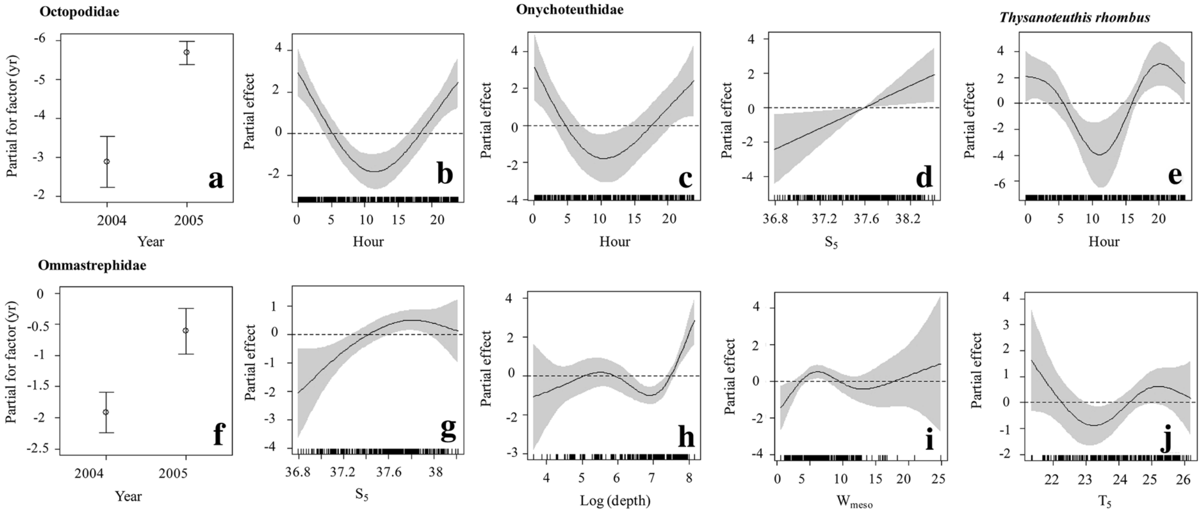


Fig. 7 General additive model (GAM) outputs modeling the presences/absences of the most abundant cephalopod taxa (Octopodidae, Ommastrephidae Onychoteuthidae and *Thysanoteuthis rhombus*) collected in waters around the Balearic Islands (western Mediterranean) using the Bongo 90 net. The partial effect of factor year and the following explanatory variables are shown: hour, depth (log-transformed), dry weight of mesozooplankton (W_{meso}), salinity, and temperature at 5 m (S_5, T_5). Fitted lines (*solid line*) and 95% confidence intervals (*gray shaded areas*) are shown

which includes three species in the Mediterranean Sea, *Illex coindetii*, *Todarodes sagittatus,* and *Todaropsis eblanae*. Since all three species have a protracted spawning period in the area (Mangold-Wirz, 1963; Sánchez, 1984; Quetglas et al., 1998), it is not possible to infer to what species our paralarvae most likely belonged to.

The contrasting oceanographic conditions during the summers of 2004 and 2005 included differences in the shape and location of a regional frontal system which brought about differences in the sea circulation and the temperature regime, with 2005 significantly warmer than 2004. Such contrasting oceanographic scenarios conditioned the spatial distribution and frequencies of appearance of the individual taxa. This might be due to lower hydrographic activity in 2005 allowing an evenly distribution of some taxa with high contribution to the whole community (i.e., Ommastrephidae, Onychoteuthidae, and Octopodidae). This effect was already reported for the ichthyoplankton community collected concurrently with our samples (Rodríguez et al., 2013). Fittingly, the models also showed significantly higher presences in 2005 than in 2004.

Our results revealed, in agreement with previous works (e.g., Diekmann & Piatkowski, 2002; González et al., 2005; Moreno et al., 2009), that there was not any major factor affecting most taxa equally, since each taxon was influenced by different covariates. This would point to differences in the species-specific sensitivity to abiotic factors that might be related to contrasting life-history characteristics among taxa. However, it is worth noting that the results for the species *Abralia veranyi* must be taken with caution owing to the low sample size. The most influential parameters were the factor year, hour of the day, salinity, and depth. The presences of the most abundant taxa (Octopodidae, Ommastrephidae and Onychoteuthidae) were significantly higher in 2005 than in 2004, which might be due to two non-independent processes. Firstly, the warmer conditions during 2005 compared to 2004, since it is well known that warmer temperature enhances both paralarvae growth and the reproductive success of adults (Boyle & Rhohouse, 2005). Secondly, it might be related to the inherent interannual differences in spawners abundance, which has been demonstrated to be highly variable and cyclic in the study area (Quetglas et al., 2013b).

The daily cycle was found to affect the families Onychoteuthidae and Octopodidae and the squid *Thysanoteuthis rhombus*. In both net types, there appeared a common daily cycle with the lowest paralarvae presences occurring during the day (between 8:00 a.m. and 4:00 p.m.) and two distinct maximums during night hours (4:00 a.m. and 9:00 p.m.). Such a cycle would reflect the nychthemeral migrations already reported in many paralarvae studies (e.g., Röpke et al., 1993; Piatkowski, 1998; Moreno et al., 2009). Coinciding with our results, representatives of the family Octopodidae (e.g., common octopus, *Octopus vulgaris*) were also found to undertake dial vertical movements both in the Atlantic (Otero et al., 2009) and Pacific (Sakaguchi et al., 1999) oceans. Nychthemeral migrations have also been reported for the squid *Onychoteuthis banksii* (family Onychoteuthidae) in Mediterranean (Roper, 1974) and, to a lesser extent, Great Meteor Seamount populations (subtropical North-east Atlantic; Diekmann & Piatkowski, 2004). The family Ommastrephidae also showed vertical movements in the Arabian Sea (Piatkowski, 1998), but not in the case of the Great Meteor Seamount (Diekmann & Piatkowski, 2004). Such different responses within the same family might be due to differences in species composition with contrasting day-night migration patterns.

The bathymetry gradient of the study area affected three out of the five taxa analyzed, though with different effects. In the B60 sampling, the effect of depth on the squid *Abralia veranyi* and the families Ommastrephidae and Onychoteuthidae showed the same increasing linear trend, suggesting that these paralarvae occur preferentially in oceanic environments coinciding with the distribution of adults. Both the squid *A. veranyi* and the two representatives of the family Onychoteuthidae (*Onychoteuthis banksii, Ancistroteuthis lichtensteinii*) inhabit exclusively continental slope grounds deeper than 200 m in the Balearic Sea (Quetglas et al., 2000). The three squid species of the family Ommastrephidae occur both on the shelf-break and slope, though *Todarodes sagittatus* and *Todaropsis eblanae* predominates on the slope and *Illex coindetii* on the shelf-break (Quetglas et al., 2000). However, the spawning of all these ommastrephids seems to take place on slope grounds (Quetglas et al., 1998; Lefkaditou et al., 2008).

The oceanographic conditions (temperature and salinity) also affected the paralarvae populations, salinity being the most influential factor. Despite the importance of the thermal regime for cephalopod growth and survival (Boyle & Rhohouse, 2005), sea temperature only affected the family Ommastrephidae. However, there is an important difference between salinity and temperature responses, given that the global effect of temperature is also included in the factor year as a well-differentiated thermal regime, while this is not the case with salinity that did not vary between years (Fig. 3). The important effect of temperature on paralarvae distribution has already been reported in previous works. The thermal front represented a distinct boundary for the distribution of paralarvae in the Sargasso Sea (Diekmann & Piatkowski, 2002), whereas temperature and upwelling were shown to be the most important variables in modulating seasonality and distribution of paralarvae in the western Iberia (Moreno et al., 2009).

Considering salinity, we found contrasting responses depending on the taxa: a linear increasing trend (Ommastrephidae and Octopodidae) and a nonlinear trend with a minimum close to 37.5 (Onychoteuthidae). According to the salinity values, the families Ommastrephidae and Octopodidae would be associated with resident Atlantic Waters (AW) characterized by salinities higher than 37.8. By contrast, the salinity effect identified on the Onychoteuthidae suggests lower presences of this family in areas of mixture of water masses associated to the haline front (i.e., salinity values close to 37.5). It indicates that Onychoteuthidae would actively avoid areas of mixed waters formed by mesoscale events (e.g., eddies and filaments) associated to the front (Alemany et al., 2010). This is further supported by the lack of significant effects of the geostrophic velocity on any paralarvae taxon, which contrast with the importance of this parameter for fish larvae taken concurrently with our samples (Reglero et al., 2012).

We finally consider the effects of primary (chlorophyll-*a* concentration and depth-integrated fluorescence) and secondary (mesozooplankton biomass) trophic resources on the paralarvae taxa. The phytoplankton concentration did not affect any individual taxon. Although high concentrations of phytoplankton generally improve hatching survival (e.g., Gónzalez et al., 2005; Otero et al., 2009), the effect of primary production depends on the temperature, which plays a major role than food availability (Moltschaniwskyj & Martínez, 1998). However, it is worth noting that the dry weight of mesozooplankton affected the squid *Abralia veranyi* and the family Ommastrephidae. Since paralarvae and juvenile cephalopods feed directly on secondary production (Roura et al., 2012), the lack of relationships between mesozooplankton and paralarvae presences might be due to the existence of lag times accounting for the incorporation of prey resources into paralarvae populations as has been reported in adult cephalopods (Quetglas et al., 2011).

To conclude, our results evidenced that the populations of early life stages of cephalopods were more influenced by regional sea salinity and temperature than by mesoscale hydrographical features or the regional seascape of primary or secondary producers. Paralarvae displayed clear responses to changing environmental conditions, both at the whole community and at lower taxonomical levels. We also found that there is not any major factor affecting most taxa equally, which points to specific differences in sensitivity to external influences. Our study reveals that moderate changes in sea temperature have major effects on paralarvae populations, which has profound implications in the context of the current global warming. This is especially relevant in the Mediterranean Sea, which is expected to be one of the most affected regions by the climate change (e.g., Danovaro et al., 2001, 2004; Coma et al., 2009).

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