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Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia

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The present study analyses the distribution of cephalopod paralarvae off the Portuguese coast. The effects of temporal and physical variables on Loligo vulgaris, Octopus vulgaris, sepiolid and ommastrephid abundances are analysed with generalized linear models. Their distribution patterns are discussed in relation to mesoscale features, including currents, thermal fronts and coastal upwelling cross-shelf transport, prevailing in the western Iberia upwelling system. Paralarvae of the neritic species occur during a considerably extended period of the year with two or three abundance peaks within the highly productive upwelling system of the western Portuguese coast and contrasting with the Gulf of Cadiz area. Temperature and upwelling were shown to be the most important variables in modulating seasonality and distribution of these paralarvae. The influence of the physical environment is particularly pronounced for the paralarvae of O. vulgaris, following distinct patterns according to the oceanography of the western Iberia and the Gulf of Cadiz systems. The paralarvae of oceanic species, which in many cases have their northern limit of distribution at these latitudes, were mainly found in the southern part of the sampling area. The distribution of these species indicates that the prevailing oceanographic features of the Gulf of Cadiz system, especially fronts, together with temperature act as boundaries to geographic dispersal, contributing to an area of high cephalopod biodiversity in the southern Portuguese waters.

INTRODUCTION

Cephalopods represent a major fishery resource in Europe, specifically in Portugal and Spain. The most important cephalopod species as a fisheries resource, which have planktonic early life stages, hereafter called paralarvae (Young and Harman, 1988), are *Octopus vulgaris*, *Loligo vulgaris*, *L. forbesi*, *Illex coindetii* and *Todaropsis eblanae*. These are neritic species, whose adults and juveniles occur mainly in the middle-shelf (*O. vulgaris* and *Loligo* spp.) or in the outer-shelf region (*I. coindetii* and *T. eblanae*). *Octopus vulgaris* is presently the fourth most important fishery resource in Portuguese waters with landings of about 7000 tons and a commercial value of 28.7 million € in 2006 (DGPA, 2007), and supports many local fishing communities.

The neritic loliginid, octopus and sepiolid females lay their eggs in capsules/clusters attached to hard substratum or branched sessile organisms on the sea bottom, while in ommastrephids and most other oceanic squids the eggs are laid as large masses that drift submerged in the open sea (Jereb and Roper, 2005). Embryonic development lasts from a few weeks to a few months, depending on water temperature (Villanueva *et al.*, 2003). Soon after hatching, cephalopod paralarvae are active predators on other zooplankton and are active swimmers using jet propulsion; however, during this life

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stage, their distribution is essentially dependent on the oceanic circulation (Hanlon *et al.*, 1985). Information on the distribution of paralarvae and knowledge of the spawning grounds of the most important European cephalopod resources are scarce. However, such information is of major relevance for the understanding of the dispersal behaviour of paralarvae stages with important implications for recruitment success and variability. Some studies have analysed the oceanographic influences on cephalopod paralarvae distribution in the Atlantic (e.g. Diekmann and Piatkowski, 2002, 2004; Roberts and Berg, 2005), but besides studies in Galicia (NW Spain), that relate the distribution of cephalopod paralarvae and the circulation associated to coastal upwelling events (Rocha *et al.*, 1999; González *et al.*, 2005; Otero, 2006), little research has been undertaken in the eastern Atlantic. Thus, cephalopod early life-history dynamics in coastal upwelling systems are poorly understood in this region. Furthermore, information about the vertical distribution of cephalopod paralarvae is even scarcer, being almost exclusively related to pelagic oceanic squid species in non-European waters (e.g. Roepke *et al.*, 1993; Filippova and Pakhomov, 1994; Bower and Takagi, 2004).

Relevant aspects of the oceanography of the study area

The western Iberian region is the northernmost part of the Canary Current upwelling system, one of the four major eastern boundary current systems of the world that stretches from Cape Finisterra (NW Spain; ~43°N; Fig. 1) to the south of Cape Vert (Senegal; ~10°N) and is characterized by optimum conditions for phytoplankton blooms and consequent high zooplankton abundance (Arístegui *et al.*, 2006; Valdés *et al.*, 2007). At Cape S. Vicente (37°N), the meridional alignment of the coastline of western Iberia changes radically to a zonal orientation, which is a characteristic of almost all the northern Gulf of Cadiz (Fig. 1). Since equator-ward

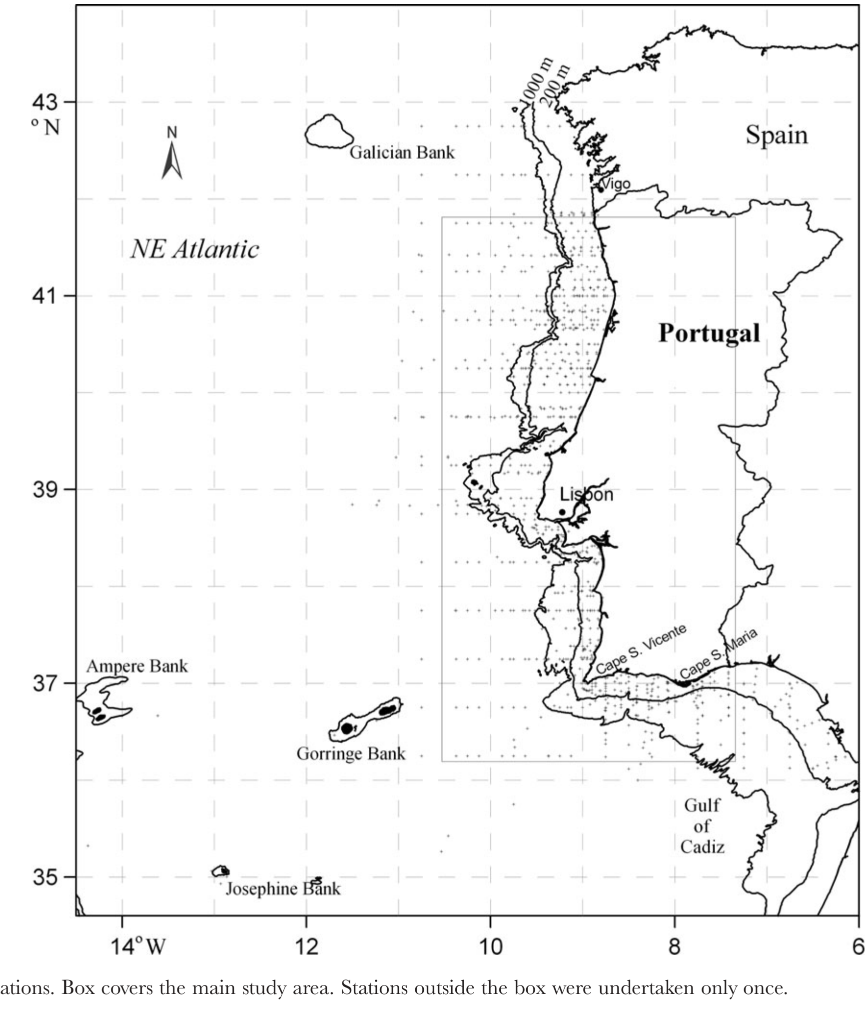

Fig. 1. Sampling stations. Box covers the main study area. Stations outside the box were undertaken only once.

winds in the region are dominant during a substantial part of the year, this change in the orientation of the coastline has important implications for the coastal oceanography, mainly in relation to coastal upwelling. Thus, on the western coast, upwelling occurs from spring to early autumn (April to September) in response to the intensification and steadiness of favourable equator-ward winds, but with maximum offshore Ekman transport in summer (e.g. Wooster *et al.*, 1976; Fiúza *et al.*, 1982). At the same time, the east–west orientation of the south coast (northern Gulf of Cadiz) does not favour upwelling under northerly winds. Here, local upwelling events under westerly winds tend to be weak, intermittent and less frequent (Relvas and Barton, 2002). However, the northern Gulf of Cadiz is partially influenced by the equator-ward-jet of cold water upwelled further north on the western coast, which extends around Cape S. Vicente (Relvas and Barton, 2002, 2005) flowing eastward with the Gulf of Cadiz slope Current (GCC) along the southern Portuguese coast (Peliz *et al.*, 2007a). During upwelling relaxation and under easterly winds, an inshore warm and salty counter-current flows westward along the northern Gulf of Cadiz, turns around Cape S. Vicente and progresses poleward along the southwest coast (Relvas and Barton, 2005; Garcia-Lafuente *et al.*, 2006; Teles-Machado *et al.*, 2007).

In autumn and winter, the prevailing direction of the winds is poleward (south-southwesterlies) leading to the predominance of general coastal convergence conditions. Nevertheless, winter upwelling events have been observed on the western Iberian coast (Santos *et al.*, 2001; Vitorino *et al.*, 2002; Santos *et al.*, 2004) in association with positive values of the North Atlantic Oscillation (NAO) index (Borges *et al.*, 2003). The Iberian Poleward Current (IPC) is a persistent feature of the winter circulation off western Iberia (Wooster *et al.*, 1976; Frouin *et al.*, 1990; Haynes and Barton, 1990). Although still a subject of debate, there is some evidences that during the rest of the year, the IPC is still present but weaker and flowing more offshore (e.g. Peliz *et al.*, 2002, 2005). The IPC is a warm and salty current driven primarily by the interaction of a meridional density gradient with a meridionally oriented slope and shelf. The generation of the IPC is closely related to the location of the Western Iberia Winter Front (WIWiF), which is a recurrent thermal front located at about 39–40°N, separating colder northern waters from southern warmer ones (e.g. Peliz *et al.*, 2005). A second frontal system, the subtropical front, is associated to the Azores Current (AC) at about 34–36°N (Fernández and Pingree, 1996). The AC transports warm and salty water eastwards into the Gulf of Cadiz (Fernández and Pingree, 1996; Martins *et al.*, 2002). There is also some evidence that this current could re-circulate northward in the vicinity of Cape S. Vicente and form a southern branch of the IPC (Peliz *et al.*, 2005).

Besides the AC, the Portugal Current, that roughly marks the northern extent of the Canary Current, is the main feature of the large scale circulation off western Iberia. This is a broad equator-ward slow current that extends from about 10° to about 24°W longitude (e.g. Pérez *et al.*, 2001; Martins *et al.*, 2002) and connects the North Atlantic Current (Dietrich *et al.*, 1980) or at least the inter-gyre (subarctic and subtropical) transition zone (Krauss, 1986) with the AC.

The present study aims to explain the cephalopod paralarvae distribution in Portuguese waters based upon knowledge of the regional oceanography and coastal transition zone processes. Since cephalopod paralarvae are rare in plankton samples (Vechione, 1987), the analysis is based on information from 19 years of plankton sampling (1986 to 2004) off the Portuguese and adjacent Spanish waters. To understand the distribution of paralarvae according to changes in their physical environment, we test the following key questions: are the differences in the main oceanographic features and processes between the Western Iberian upwelling system and the Gulf of Cadiz reflected in paralarvae abundance and distribution within each species in western and southern Portuguese waters? Do the shelf processes related to upwelling dynamics affect the distribution of loliginid and octopus paralarvae in the same manner? Does water temperature influence paralarvae abundance and distribution patterns along the Portuguese coast?

METHOD

Sampling

Cephalopod paralarvae distribution and seasonality were analysed based on plankton samples carried out during 57 survey cruises between October 1986 and December 2004 in Portuguese waters, and occasionally in adjacent Spanish waters (Fig. 1). Table I summarizes the fieldwork and sampling methodologies used in this study. The sampling area covers latitude 33.23 to 42.75°N and longitude 6.15° to 14.37°W in the NE Atlantic. The majority of cruises were performed on a monthly or seasonal basis on board the Portuguese research vessels “Noruega”, “Capricórnio” and “Mestre Costeiro”, as part of sampling programmes targeting fish eggs and larvae. The main gear was a bongo net with a 60 cm mouth aperture diameter fitted with 335 and 500 μm mesh size nets. The net was towed on

Table I: *Plankton sampling summary*

Date	Target	Area	No. of samples	CTD	Haul type	Net type	Mesh size	Method
October 1986 to January 1989 (monthly)	Fish eggs and larvae	West coast: three transects at 41°05′N, 40°05′N, 38°00′N from shoreline to 9°35′W South coast: 1 transect at 8°35′W, from shoreline to 36°50′N	506	Yes	Oblique	Bongo 60 cm ϕ	335 and 500 μm	Hauls from near bottom to surface, or from 200 to surface, where the ocean floor >200 m
June/July 1990/92; March/April 1995	Fish eggs and larvae	Along the coast: 36°07′ to 42°45′N and 7°30′ to 10°45′W	1756	No				
February/March 1992/93; October/November 1991/93 June/July 1993; May 1994; January/February/March 1998/2001/04				Yes				
August 1993	Crustacean larvae	South coast: 33°14′ to 37°17′N and 7°25′ to 14°22′W	62	No				
June 1994	Cephalopods			Yes				
February 2000	Fish larvae	North coast: 40°24′ to 41°36′N and 8°45′ to 10°00′W	111	No				
June 1995	Cephalopods	North coast: 39°45′ to 41°50′N and 8°44′ to 9°45′W	160	Yes	Horizontal and Oblique	Bongo 60 cm ϕ	335 and 500 μm	Hauls towing 10′ near bottom and oblique to surface
November 1996; August 1996				No				
August/September 1995; November 1995	Cephalopods	SW and south coast: 36°48′ to 38°38′N and 7°48′ to 9°56′W	97	No; Yes				
December 2004	Fish eggs			Yes				
February/March 1996 (WP2)	Fish eggs/larvae	NW coast: 38°17′ to 41°31′N and 8°34′ to 11°30′W	1010	Yes	Oblique	WP2, LHPR or Mocness	200 μm, 280 μm, or 335 μm	Stratified hauls in 3 to 8 depth layers from near bottom to surface or from 200 m to surface, where the ocean floor >200 m
May 1996 (WP2)	Cephalopods			No				
May 2002 (LHPR)	Crustacean larvae			Yes				
June 1994 (Mocness)	Cephalopods	SW and south coast: 33°14′ to 38°45′°N and 6°20′ to 14°22′W	314	Yes				
March/April 1995 (WP2)	Fish larvae			Yes				
November 2002/03 (WP2)	Fish larvae			No				
November/December 1999/00/01[a]	Fish eggs	Along the coast: 36°07′ to 41°52′N and 6°09″ to 10°00′W	140	No	Vertical	Calvet	150 μm	Hauls from near bottom to surface, or from 200 m to surface, where the ocean floor >200 m
January 2002[a]				No				

[a]denote sampling excluded in the horizontal distribution analyses of neritic species.

depth-integrated oblique hauls at ~2 knots from surface to 10 m above the bottom or until 200 m when the bottom was deeper. Filtered water volumes were estimated using calibrated flowmeters mounted on both net mouth apertures.

On the cruises targeting cephalopod paralarvae on board "R/V Mestre Costeiro" and the German "R/V Poseidon", the bongo net was towed horizontally for 10 min near bottom between double oblique tows to surface (Moreno, 1998). Most vertical distribution data were obtained from a survey targeting crustacean larvae, in which a Pro-LHPR system and neuston net were used. The Pro-LHPR system collected samples at ~5 m depth intervals in the first 25 m and at 10 m depth intervals down to near bottom (for more complete description of this cruise, see dos Santos *et al.*, 2007). Scattered data on vertical distribution were obtained from depth stratified sampling during several cruises, with a WP-2 and a MOCNESS multiple net sampler. Environmental data, when collected, were obtained from CTD casts (see Table I for details).

All samples were preserved in 4% borax-buffered formaldehyde, prepared using seawater. A total of 4156 samples were examined and 914 cephalopod paralarvae identified to the lowest taxonomic level possible, and the dorsal mantle length (DML) was measured as defined by Sweeney *et al.* (Sweeney *et al.*, 1992).

Data analysis

Catches of the neritic species were standardized to numbers per 100 m^{-3}, using flowmeter information, to study their distribution and seasonality. Latitude, longitude and bottom depth of each sampling station were included in the time series of paralarvae abundances to account for spatial variability.

The following oceanographic and climatic factors were included in the dataset, assigned to each sampling station: sea surface temperature (SST), upwelling indices (UI) and the NAO index. These were used as proxies for the oceanographic processes of the continental shelf as they have been pointed out to be key variables to explain distribution and abundance during the life cycle of several marine species (e.g. Bakun, 1996; Santos *et al.*, 2007). SST data for most sampling stations were extracted from CTD temperature profiles. SST data (weekly, 1° grid) were also extracted to fill in SST gaps in 14% of the sampling stations, from the integrated Global Ocean Services System—Meteorological Center "IGOSS nmc" database (Reynolds and Smith, 1994). The SST source effect on paralarvae distribution was accessed on a subset of samples and considered unimportant in the context of our analysis. UI provided by the NOAA-NMFS-Pacific Fisheries Environmental Laboratory (http://www.pfel.noaa.gov/) were computed from monthly mean pressure fields on a 1° mesh grid. The coastal angle needed to compute UI was estimated for each 1° latitude along the Portuguese coast. Monthly mean UI and SST for the west and south shelves are shown in Fig. 2. The Climate Research Unit of the University of East Anglia provided the NAO index, based on the monthly difference of normalized sea level pressures between Gibraltar and Reykjavik (http://www.cru.uea.ac.uk/).

The relationships between paralarvae abundances and environmental factors were analysed with generalized linear models (GLM), using R software (R Development Core Team, 2005). GLM are an extension of linear models allowing the incorporation of non-normal distributions of the response variable and transformations of the dependent variables to linearity (McCullagh and Nelder, 1989). The GLM analysis was conducted in a two steps procedure, because of the very

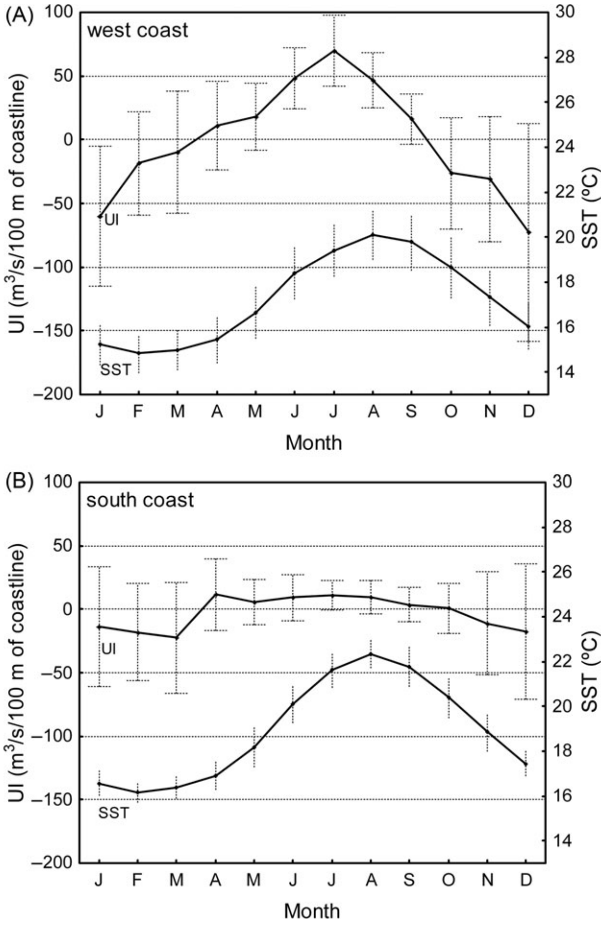

Fig. 2. Mean monthly sea surface temperature (SST) and upwelling index (UI) over the continental shelf on the west (**A**) and south Portuguese coasts (**B**). Vertical bars denote standard deviation.

high proportion of null samples (e.g. 83% for loliginids) and to account for both the probability of occurrence and the abundance by sampling station (Sousa *et al.*, 2007): (i) a logistic regression model with the logit link (Hosmer and Lemeshow, 1989) was used to evaluate which factor/factors are important for the presence/absence of paralarvae (data follow a binomial distribution); and (ii) the gamma regression model with a log link to assess the factor/factors that influence abundance (paralarvae abundance) (McCullagh and Nelder, 1989). The occurrence/abundance was analysed as a response to the following explanatory variables (predictors): year, month, latitude, longitude, depth, NAO, UI and SST. First-order interactions (multiplicative interactions of combinations of predictors, included additively in the models together with the predictors considered) were included in the model whenever considered adequate (based on their contribution to the deviance explained). The goodness-of-fit of the models was assessed by comparing their relative contribution to total deviance explained. A significance level of 0.05 was considered in all test procedures.

The cross-shelf distribution on the west coast was evaluated in more detail by testing the differences in abundances by season and depth range with a factorial ANOVA. For each species, the categorical predictor season grouped samples were carried out during distinct hatching seasons. Knowing that oceanographic conditions associated with upwelling may be determinant in the cross-shelf distribution of zooplankton off the west Portuguese coast (e.g. Santos *et al.*, 2004; Queiroga *et al.*, 2005; dos Santos *et al.*, 2007), the cross-shelf differences were also tested for loliginids and octopus with a factorial ANOVA, grouping samples carried out each year during months under prevailing downwelling conditions versus months under prevailing upwelling conditions (UI <0 versus UI >0).

All depth-stratified samples were pooled together to provide data on loliginid and octopus vertical distribution and diel vertical migrations.

RESULTS

Neritic species

The most abundant cephalopod paralarvae off the Portuguese coast belong to the neritic species of the families Loliginidae (40%), Octopodidae (*O. vulgaris*) (27.5%), Sepiolidae (11%) and Ommastrephidae (10%). Table II gives a summary of the spatial and temporal distribution of the different taxa found, as well as additional information about paralarvae size, total number caught, bottom depth and SST range where they were found.

Loliginids

Loliginid paralarvae were found year round over the shelf, with two distinct hatching seasons: a main season between December and April and a secondary season between July and September, with highest mean abundances in March and August, respectively (Fig. 3). The relatively high mean abundance observed in April depends mainly on catches in a single year (1988) of the three that have been sampled in April.

In general, higher abundances were found between the 50 and 125 m isobaths, particularly along the north-west coast of Portugal (between 39.5°N and 41.5°N) (Fig. 4). The spatial distribution displayed differences between hatching seasons: during the winter hatching season, paralarvae occurred all over the sampling area with higher abundances over the 100 m isobath (Fig. 4A); during the summer hatching season, paralarvae occurred mainly on the north-west shelf in more coastal waters (Fig. 4B). Despite the fact that the high mean abundances in April were allocated to the first hatching season, during this month loliginids occurred inshore of the 100 m isobath and concentrated on the north-west coast, more similar to the summer distribution (Fig. 4C).

GLM results (Table III) support the significant role of month, latitude and depth, but also the importance of low temperatures (<19°C) and high upwelling in loliginid distribution. Moreover, the analysis indicates that there was a significant influence of the interactions month versus latitude (e.g. absence of the summer hatching peak on the south) and SST versus latitude (e.g. occurrences associated to the northern lower SST) (Fig. 5A and B). On the other hand, the gamma model (Table IV) indicated that oceanographic conditions alone had the main influence on loliginid abundance. This model essentially reflects seasonality rather than the spatial distribution, i.e. higher abundances associated with the SST and UI conditions of the winter hatching season. Nevertheless, the logistic model fitted to presence/absence of loliginids explained only about 8.4% and the gamma model 12.4% of total variability for the whole area.

A detailed analysis of the bathymetric distribution on the west coast highlighted the differences between hatching seasons, with significantly higher abundances (ANOVA season versus depth range effect, $F(4, 641) = 2.711$, $P < 0.05$) offshore (75 to 125 m isobaths) during the winter hatching season (December to April) and close inshore (50 to 75 m isobaths) during the summer hatching season (June to September). However, the

Table II: List of paralarvae species (taxa) collected on 57 research cruises (1986–2004) in Portuguese and adjacent waters

Family	Species	Latitude range (°N)	Bottom depth range (m)	SST range (°C)	Seasonality (month)	DML range (mm)	N
Loliginidae	Loliginidae indet.	36.13–42.75	15–500	13.0–22.7	all	1.5–7.5	371
Octopodidae	*Octopus vulgaris*	35.06–41.83	14–1378	13.9–22.7	all	1.2–4.2	254
Sepiolidae	Sepiolidae indet.	36.24–41.86	21–740	13.2–20.8	all	1.2–9.5	102
	Heteroteuthis dispar[a]	36.24–36.70	587–750	17.8–20.9	1, 7	10.6	2
Ommastrephidae	Ommastrephidae indet.	33.23–42.75	20–4142	13.2–20.8	all	0.7–8.7	91
Pyroteuthidae[a]	*Pterygioteuthis* sp.	35.75–38.00	65–2000	16.0–17.3	1, 2, 4, 6, 7	1.9–13.3	9
	Pyroteuthis margaritifera	36.24–36.49	614–4788	17.3–19.4	1, 2, 3	2.1–9.4	5
	Pyroteuthidae indet.	36.25–36.87	132–4788	17.0–19.4	1, 3	1.5–4.4	6
Enoploteuthidae[a]	*Abraliopsis atlantica*	36.12–36.69	745–3681	17.2–17.3	1, 2, 3, 6	2.5–7.8	5
	Abralia cf. veranyi	36.12	310	17.7	1	2.1	1
Ancistrocheiridae[a]	*Ancistrocheirus lesueurii*	36.24–37.06	20–2400	15.6–17.2	1, 3	3.0–5.3	2
Enoploteuthid group[a]	Enoploteuthid group indet.	36.12–36.99	63–900	17.1–17.7	1, 5	1.5–2.5	5
Cranchiidae[a]	*Leachia* sp.	36.24–36.75	2043–3400	17.0–17.3	1	26.8–52	4
	Taonius pavo	36.25–36.57	800–4000	17.2–19.5	1, 2	2.5–15.6	11
	Helicocranchia pfefferi	36.34–36.72	742–3681	—	5, 6	2.4–8.3	5
	Bathothauma lyromma	36.25–37.75	3000–4765	16.2–18.1	1, 2	7.0–24.3	2
	Megalocranchia sp.	36.17–36.75	800–3000	16.9–19.1	2, 3	5.5–11.8	5
	Teuthowenia megalops	40.25–41.08	45–3850	13.8–15.0	2, 3	4.4–28	5
	Taoninae indet.	34.93–37.71	228–1290	18.3	3, 6	2.2–4.1	5
Mastigoteuthidae[a]	*Mastigoteuthis* sp.	36.12–40.75	310–3460	15.6–18.8	1, 2, 3, 4	4.9–9.9	9
Onychoteuthidae[a]	*Onychoteuthis banksii*	36.24–40.75	230–3000	15.0–18.8	2, 3, 5, 6, 8	6.8–11.2	6
	Onychoteuthidae indet.	39.75–40.30	162–1030	15.4–16.9	2, 5	2.7–3.7	2
Chiroteuthidae[a]	*Chiroteuthis veranyi*	36.25–37.25	210–3000	16.0–19.4	1, 2, 3	4.8–16.8	4
Brachioteuthidae[a]	*Brachioteuthis reesei*	36.24	968	17.8	2	3.2	1
Chtenopterygidae[a]	*Chtenopterix siculus*	36.00	2000	—	4	2.1	1
Ocythoidae[a]	*Ocythoe tuberculata*	35.32	4318	—	6	6	1

Summary of the spatial and temporal distribution, size range and total number caught.

[a] Oceanic taxa.

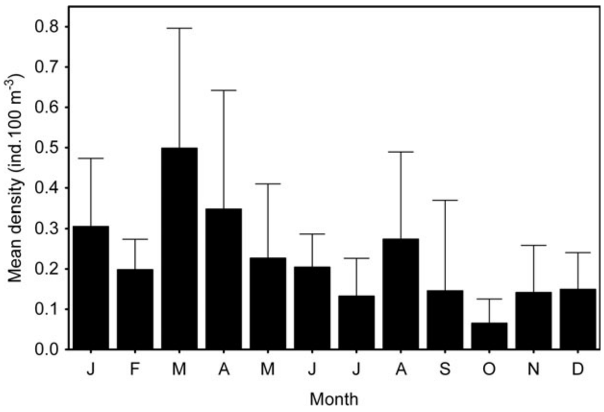

Fig. 3. Monthly mean abundances of loliginid paralarvae within their distribution area (bottom depth < 200 m). Vertical bars denote 0.95 confidence intervals.

cross-shelf distribution was not significantly different when grouping months with contrasting upwelling levels (ANOVA UI level versus depth range effect: $F(4, 641) = 1.495$, $P > 0.05$).

Loliginid paralarvae showed a consistent diel vertical migration (Fig. 6), being in surface layers at night and deeper during daylight. However, these results were based only on few numbers of paralarvae. No paralarvae were found in the neuston layer at any time.

Octopus vulgaris

Octopus paralarvae occurred mainly in the second half of the year, with peaks in July and November (Fig. 7). These two distinct peaks, a minor peak in summer and a major peak in autumn, were present throughout the sampled area. Paralarvae hatching in spring-summer were distributed over the shelf and slope between the 14 and 1400 m isobaths and at the Gorringe and Ampere Banks (Fig. 8A). During autumn-winter, they were found more inshore (Fig. 8B).

The GLM analysis revealed an important contribution of several variables, and interactions between them, to explain the occurrence of octopus paralarvae (total explained = 59.2%, Table III). The variable, month and its interaction with depth, and SST and its interaction with UI, depth or latitude were the most significant contributors to explain the distribution. Overall, the probability of finding paralarvae increased during the year (higher in autumn), with increasing SST and upwelling, and decreasing latitude (higher in the south) and depth (higher inshore). Nevertheless, the probability of finding

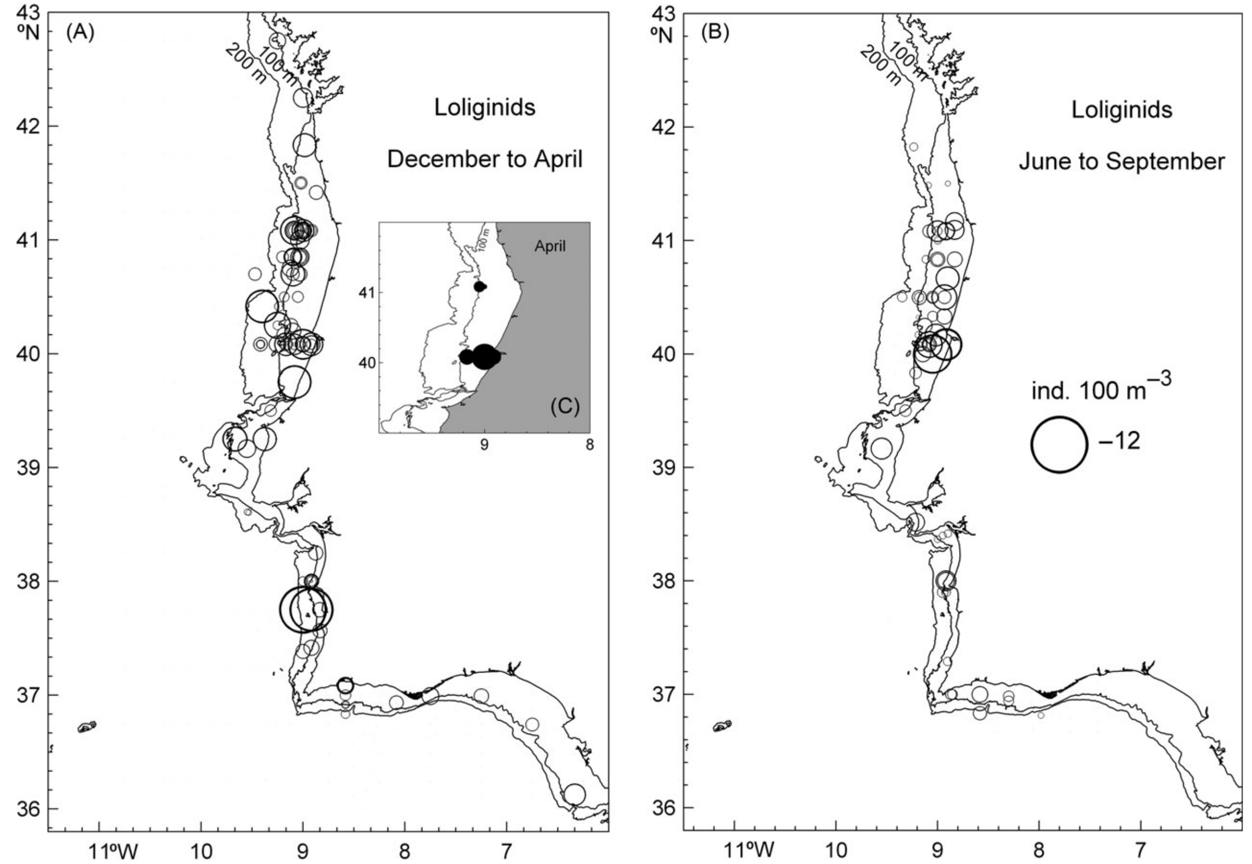

Fig. 4. Horizontal distribution of loliginid paralarvae in Portuguese waters and adjacent Spanish regions from plankton surveys during the two main hatching seasons: December to April (**A**) and June to September (**B**) plankton surveys. Detail of the distribution in April (**C**).

paralarvae was positively correlated with stronger upwelling (Table III), but abundance inversely correlated (Table IV). Differences between the west and the south coasts, which may be inferred by the significant influence of the association of latitude with UI and SST, could introduce some contradictory influence of environmental variables in the analysis for the whole coast. For example, the influence of upwelling was rather different on the west coast (>37.2°N) than on the south coast (<37.2°N). On the west, abundance was highly correlated with favourable upwelling conditions independently of hatching season (ANOVA, $F(1,\ 1156) = 7.20$, $P < 0.05$). On the other hand, on the south coast no relationship was detected between octopus abundance and UI (ANOVA, $F(1,\ 420) = 2.26$, $P > 0.05$), despite the higher abundances found under downwelling conditions (Fig. 9A). On the other hand, higher abundances were found at 18–19°C independently of area or even season and the probability of finding paralarvae increased with SST on both the west and south coasts (Fig. 9B).

In spite of the fact that the gamma model did not show any significant influence for the whole area in relation to the interaction between month and depth (Table IV), the west coast showed a cross-shore distribution significantly different between hatching seasons (ANOVA season versus depth range effect, $F(4,\ 646) = 2.642$, $P < 0.05$): during the summer hatching season (June–September), the abundance was significantly higher offshore (150–200 m) and during the autumn/winter hatching season, higher abundances were observed close inshore (15–50 m). The cross-shelf distribution was also significantly different when grouping months of contrasting upwelling intensity, with evidence of higher abundances on the outer-shelf (100–200 m) under prevailing upwelling conditions and inshore (<100 m) under favourable convergence conditions (ANOVA UI level versus depth range effect: $F(4,\ 646) = 2.753$, $P < 0.05$).

The diel vertical distribution pattern of octopus is not clear from the data available, which were compiled from different stations, seasons and areas. No paralarvae were found in the neuston layer at any time.

Sepiolids

Sepiolids were found mainly over the continental shelf (only three specimens deeper than 200 m) in two

Table III: Deviance tables for loliginid, octopus, ommastrephid and sepiolid paralarvae logistic models (probability of positive capture)

Source of variation	Deviance %	Estimates		
		βi	SE	*P*-value
Loliginids				
Month	0.8	−0.062	0.023	0.006
Latitude	0.8	0.144	0.050	0.004
Depth	1.7	−0.006	0.001	0.000
UI	1.3	0.007	0.002	0.001
SST	0.6	−0.097	0.038	0.012
Month × latitude	1.4	0.029	0.014	0.041
Latitude × SST	1.8	0.074	0.027	0.007
Total explained	8.4%			
Octopus vulgaris				
Month	10.3	0.248	0.026	<2E−16
Latitude	1.0	−0.152	0.049	0.002
Depth	0.6	−0.001	0.000	0.021
UI	0.7	0.005	0.002	0.009
SST	6.4	0.299	0.038	0.000
Month × depth	11.0	0.000	0.000	0.024
Latitude × depth	3.2	0.001	0.000	0.001
Latitude × UI	2.1	0.003	0.001	0.048
Latitude × SST	7.3	0.074	0.025	0.004
Depth × SST	8.2	−0.001	0.000	0.009
UI × SST	8.4	−0.005	0.001	0.000
Total explained	59.2%			
Ommastrephids				
Year	4.2	−0.131	0.030	0.000
Latitude	2.8	0.291	0.079	0.000
Year × month	5.7	−0.026	0.010	0.008
Year × depth	5.3	0.000	0.000	0.024
Month × latitude	5.4	0.068	0.024	0.004
Total explained	23.4%			
Sepiolids				
Year	1.0	0.051	0.022	0.021
Depth	1.8	0.008	0.003	0.002
Total explained	2.8%			

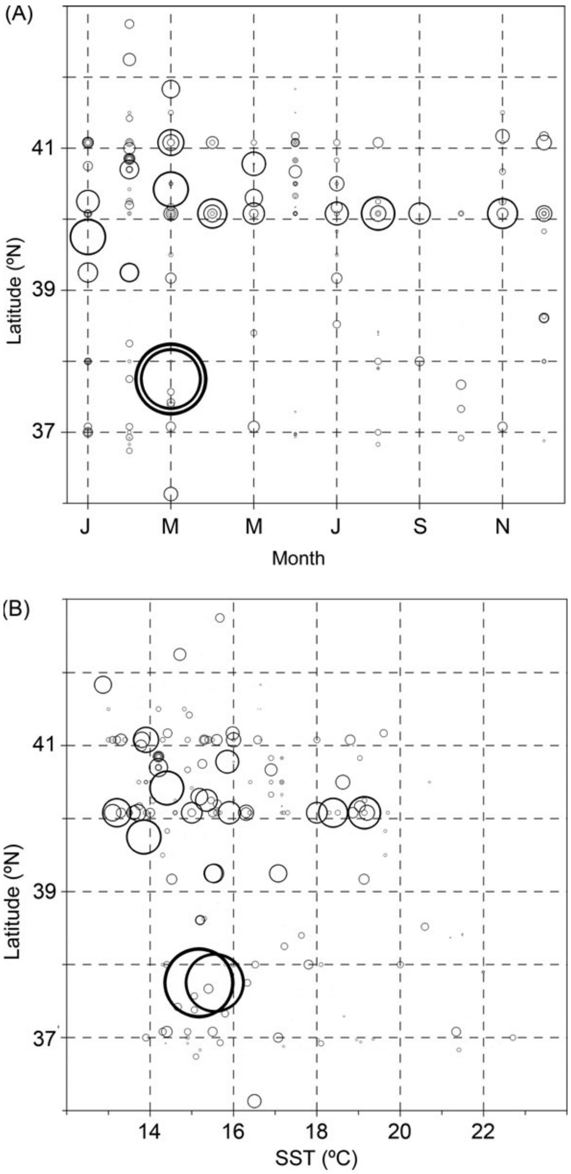

Fig. 5. Interaction of latitude and month (**A**) and interaction of latitude and SST (**B**) in loliginid paralarvae abundance. The size of dots represents abundances of 1 up to 12 ind. 100 m^{-3}.

separate areas (Fig. 10): one in the northwestern shelf between 40° and 42°N, mainly inshore of the 100 m isobath and the other one in the southwestern and southern shelves, south to 38°N, mainly offshore of the 100 m isobath. The variables included in the GLM modelling poorly explain the distribution of these paralarvae for the whole area (2.8%), with year and depth being the only significant contributors (Table III), reflecting mainly the higher occurrences in 2002 and 2004 and generally offshore of the 80 m isobath. At the same time, the gamma model explained 23.7% of the total variance, with month and SST as the major contributors (Table IV). Abundance was significantly higher during the first part of the year (Fig. 10) when the average SST is lower throughout the whole sampling area and this could explain the inverse relationship with this variable. A separate detailed analysis for the northwestern shelf and the southwestern/southern shelf showed no seasonal depth range differences within each area (ANOVA, $F(3, 689) = 0.118$, $P > 0.05$, $F(3, 425) = 0.351$, $P > 0.05$, respectively, in the north and south).

Ommastrephids

Ommastrephids were mostly in the rhyncoteuthion stage (only seven specimens showed some proboscis division, DML > 5.3 mm). Paralarvae were found throughout the whole year (Table II), with three distinct peaks in January, April/May and October and distributed mainly in the northwestern shelf and shelf break north of 40°N (Fig. 11), between the 50 and 300 m isobaths. GLM results (Table III) significantly highlight the

Table IV: Deviance tables for loliginid, octopus, ommastrephid and sepiolid paralarvae gamma models (abundance in positive captures)

		Estimates		
Source of variation	Deviance %	βi	SE	*P*-value
Loliginids				
UI	5.0	−0.004	0.002	0.038
SST	7.4	−0.097	0.036	0.008
Total explained	12.4%			
Octopus vulgaris				
Year	11.9	−0.060	0.015	0.000
Longitude	5.2	0.416	0.153	0.007
Depth	7.6	−0.001	0.000	0.009
UI	3.4	−0.005	0.002	0.032
Year × depth	33.6	0.001	0.000	0.000
Total explained	61.6%			
Sepiolids				
Month	15.4	−0.103	0.030	0.001
SST	8.3	−0.114	0.052	0.031
Total explained	23.7%			

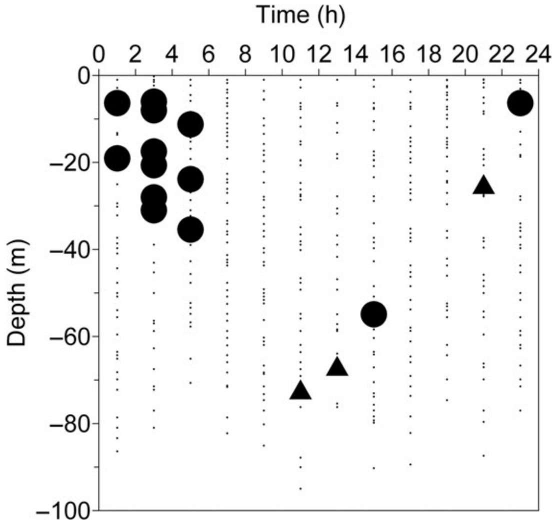

Fig. 6. Diel vertical distribution of loliginid paralarvae. Big dots (LHPR sampling) and triangles (WP2 and MOCNESS sampling) represent paralarvae presence, small dots represent absences. Real depth sampling standardized to 100 m water column. Sampling at −1 m indicates the neuston net sampling.

higher probability of capture ommastrephid paralarvae at northern latitudes. The interaction latitude versus month was also significant, reflecting the seasonal variation in the spatial distribution: during spring/summer most paralarvae occurred on the northern shelf and a meridional spread from the centre of distribution was detected in autumn/winter (Fig. 11). During winter,

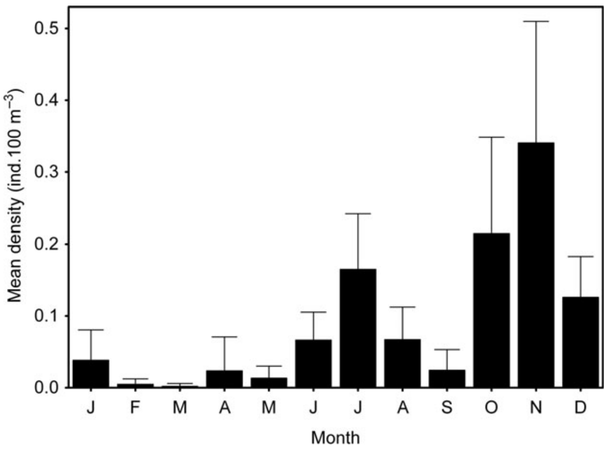

Fig. 7. Monthly mean abundances of octopus paralarvae within their distribution area (bottom depth <1500 m). Vertical bars denote 0.95 confidence intervals.

some specimens occurred in oceanic waters, namely between the continental shelf-break and oceanic seamounts (Galicia and Gorringe Banks). There is also a significant role of year and of the interactions year versus month and year versus depth, suggesting high interannual variability. A more detailed analysis revealed higher abundances offshore (100−300 m) between April and September under the summer upwelling conditions and close inshore (50−100 m) between October and January, during the autumn/winter convergence (ANOVA, season versus depth range effect, $F(5,\ 868) = 3.9273$, $P < 0.05$). The paralarvae distribution was limited to SST between 13 and 20°C.

Oceanic species

Ninety-six paralarvae and early juveniles of 19 different taxa of oceanic cephalopod species occurred in the sampling area. The majority of them belonged to the Enoploteuthid group and the family Cranchiidae. Details of distribution, seasonality and size for each of the taxa are summarized in Table II. The occurrence of oceanic paralarvae peaked during January and decreased until August. Most taxa were found only during winter months (*Chiroteuthis veranyi*, *Pyroteuthis margaritifera*, *Abralia cf. veranyi*, *Ancistrocheirus lesueurii*, *Leachia* sp., *Taonius pavo*, *Bathothauma lyromma*, *Megalocranchia* sp., *Teuthowenia megalops* and *Brachioteuthis reesei*), while others were found during winter and spring (*Abraliopsis atlantica*, *Mastigoteuthis* sp.), only in spring (*Helicocranchia pfefferi*, *Chtenopterix siculus*, *Ocythoe tuberculata*) or throughout winter to summer (*Pterygioteuthis* sp., *Onychoteuthis banksii*, *Heteroteuthis dispar*). No oceanic paralarvae were found between September and December,

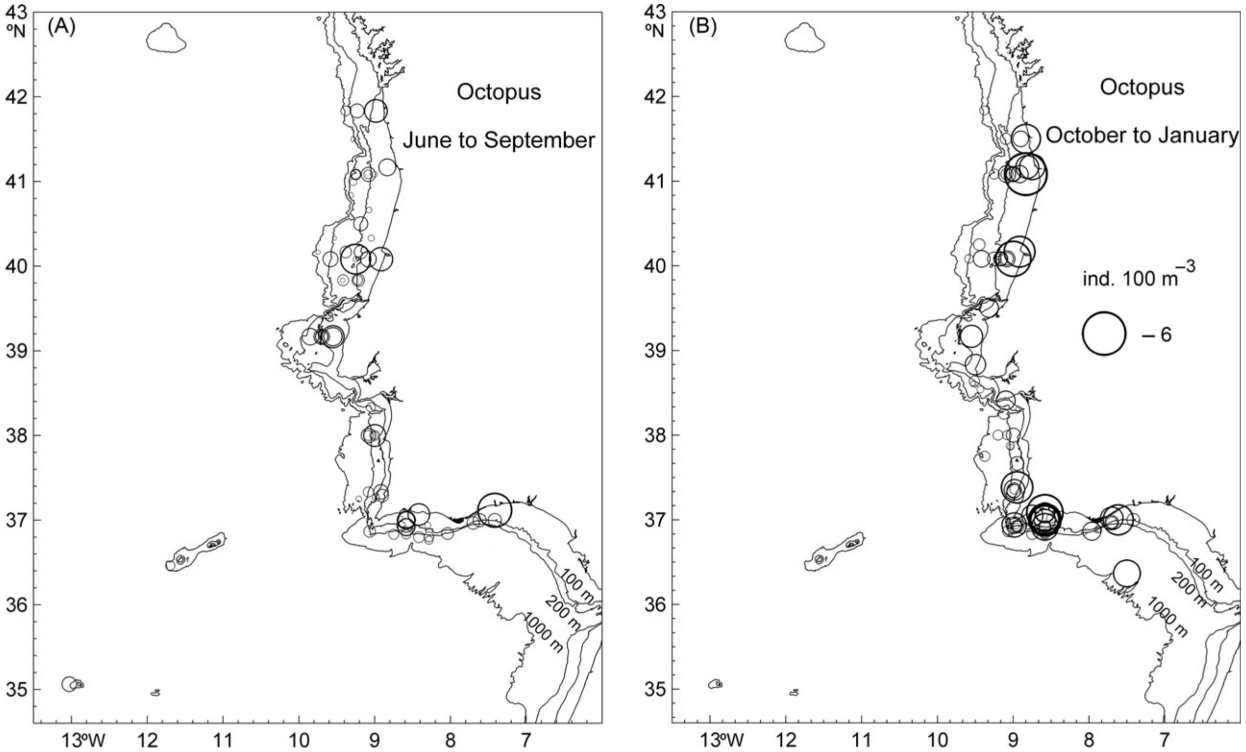

Fig. 8. Horizontal distribution of octopus paralarvae in Portuguese waters and adjacent Spanish regions from plankton surveys during the two main hatching seasons: June to September (**A**) and October to January (**B**).

despite the offshore sampling (over bottom depths >200 m) undertaken during those months.

Teuthowenia megalops, the only species whose main distribution is in north temperate to sub-arctic waters in the Atlantic, was captured off western Iberia only in winter, north of 40°N and SST below 15°C. During this season, only *Mastigoteuthis* sp. and *Onychoteuthis banksii* paralarvae occurred also north of 38°N. Most oceanic paralarvae (91%) were distributed in the southern part of the sampling area, at the warmer oceanic stations and few on the colder continental shelf. Subtropical and tropical species were restricted to the southern area, south of the Gulf of Cadiz northern recirculation front and mostly within SST ~17°C (Fig. 12).

DISCUSSION

Portuguese waters are an important area for the spawning of numerous neritic and oceanic species, which is reflected in the high biodiversity found. This study was based on plankton sampling from several cruises and different programmes, throughout a 19 year period. Sampling methodology bias was minimized by the standardization of catches, and the adjustment of the analysis to the data available (e.g. high number of zero catches). Despite the net efficiency being different between sampling gears (e.g. Stehle *et al.*, 2007), we considered this effect to be of limited relevance to the establishment of distribution and abundance patterns of paralarvae, as most sampling was done with bongo nets with extended spatial and time coverage.

Loligo vulgaris

Loliginid paralarvae are very similar in shape and thus difficult to identify to species level, especially when chromatophore pattern is absent, as it is the case of old preserved plankton samples. However, the relatively low abundance of *Loligo forbesi* off the Portuguese coast (Chen *et al.*, 2006); the occasional recoveries of loliginid egg masses, all identified as being *L. vulgaris* (e.g. Cunha *et al.*, 1995; Villa *et al.*, 1997), and the size at hatching measured in reference collections of preserved specimens, lead us to assume that the loliginid paralarvae caught were mainly *L. vulgaris*, with a small percentage of *Alloteuthis subulata*. Furthermore, the hatching period inferred from loliginid paralarvae abundances matches the spawning season of *L. vulgaris*. The spawning peaks

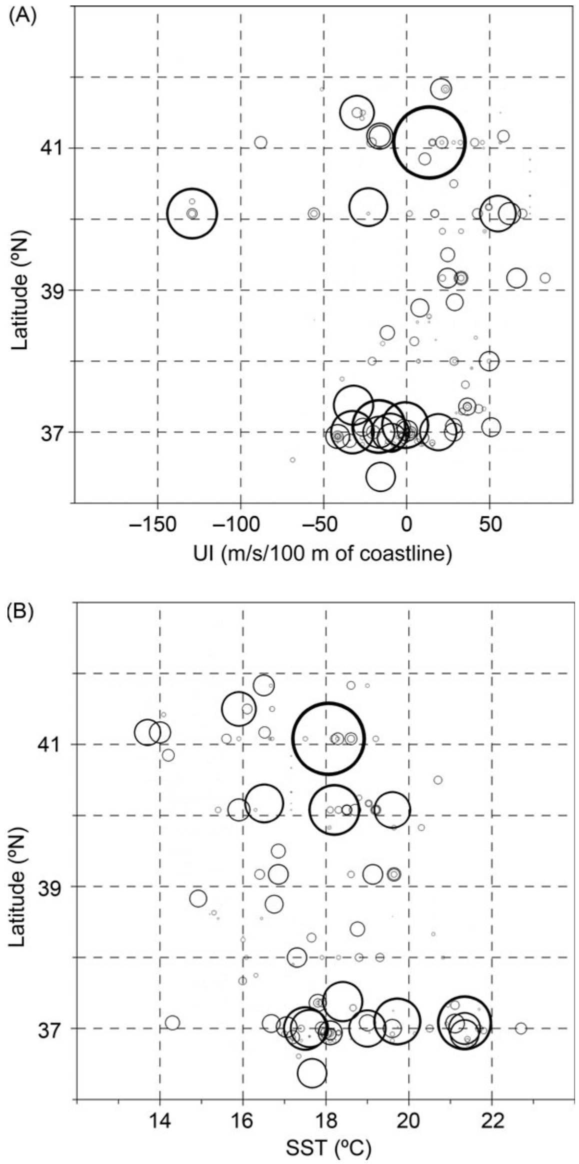

Fig. 9. Interaction of latitude and UI (**A**) and interaction of latitude and SST (**B**) in octopus paralarvae abundance. The size of dots represents abundances of 1 up to 6 ind. 100 m^{-3}.

in December/January and June/July (Moreno *et al.*, 2002), followed by an embryonic development of 40–47 days on average (Villanueva *et al.*, 2003), would produce two seasons of higher abundances of hatchlings with peaks around March and August, as detected in our analysis. The winter hatching season may extend into spring in years of stronger upwelling, such as observed in April 1988.

SST was found to be the most important environmental factor, enough to determine species seasonality and distribution, in agreement to other studies that demonstrate the role of temperature in *L. vulgaris* life history traits (e.g. Moreno *et al.*, 2005). Therefore, higher abundances and a broader distribution were found in winter, when average SST is relatively low throughout the area, whereas in the summer, the higher abundances were located in areas with lower temperature (SST < 20°C), i.e. mainly on the west coast.

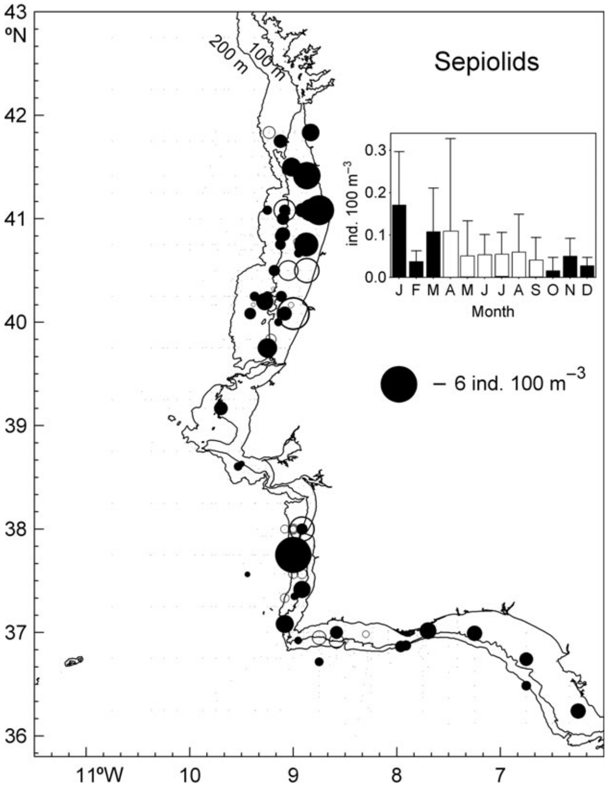

Fig. 10. Horizontal distribution of sepiolid paralarvae in Portuguese waters and adjacent Spanish regions during October to March (black dots) and April to September (open circles) plankton surveys. Monthly mean abundances within their distribution area (bottom depth <200 m), where vertical bars denote 0.95 confidence intervals.

Despite the location of an important spawning ground on the south coast (9 to 8°W) in summer (Cunha *et al.*, 1995), covering relatively warm coastal waters (17–19°C; Villa *et al.*, 1997), we found low abundance of *L. vulgaris* paralarvae in this area and total absence to the east of 8°W, where temperatures are higher. We can speculate that hatchlings can be advected from the south coast by the warm inshore counter-current. This current extends westwards and turns northwards along the western coast after reaching Cape St Vincente (Relvas and Barton, 2005; Garcia-Lafuente *et al.*, 2006; Teles-Machado *et al.*, 2007). This drift may be a potential mechanism that allows squid paralarvae to be exposed to colder but more productive upwelled waters of the west coast and thus enhances their survival, since the temperature difference between areas is not enough to affect the survival rate (see Villanueva, 2000). The positive influence of

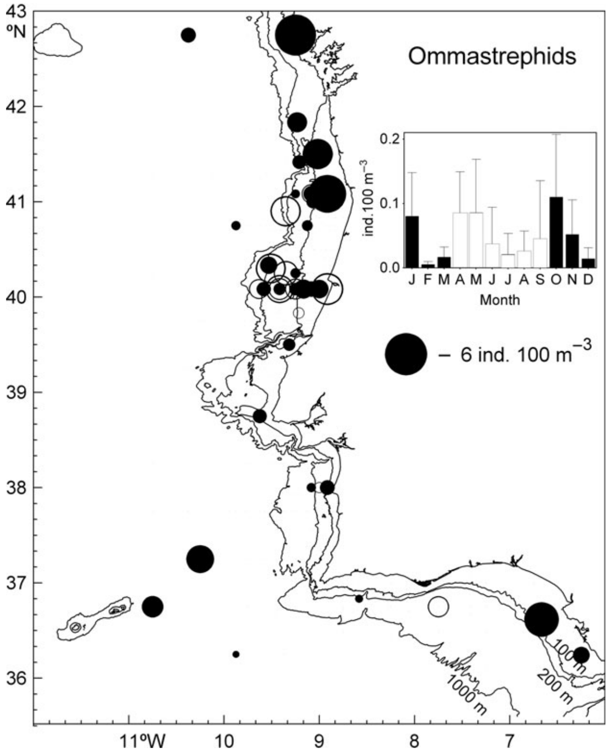

Fig. 11. Horizontal distribution of ommastrephid paralarvae in Portuguese waters and adjacent Spanish regions during October to March (black dots) and April to September (open circles) plankton surveys. Monthly mean abundances within their distribution area (bottom depth <1500 m), where vertical bars denote 0.95 confidence intervals.

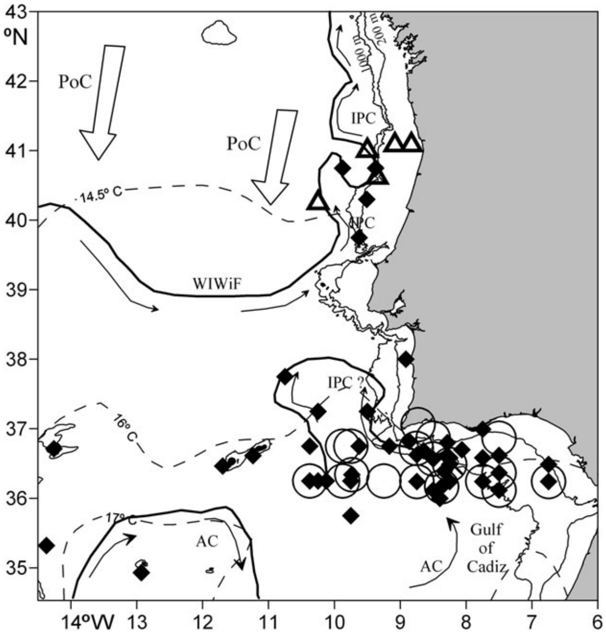

Fig. 12. Distribution of paralarvae of oceanic species. Open triangles are the *Teuthowenia megalops* records, open circles are the tropical/sub-tropical species (*Abralia cf. veranyi*, *Ancistrocheirus lesueurii*, *Pyroteuthis margaritifera*, *Helicocranchia pfefferi*, *Megalocranchia* sp. and *Leachia* sp.) and dots represent the remaining species distribution. Overlay of winter sea surface temperature (SST) and major winter surface circulation features, after Peliz *et al.* (Peliz *et al.*, 2005): PoC, Portugal Current; IPC, Iberian Poleward Current; AC, Azores current eastern branch (arrows); WIWiF, Western Iberia Winter front, Gulf of Cadiz northern re-circulation and STF/AC frontal systems (thick lines).

upwelling on the abundance of *L. vul*garis paralarvae was previously observed during summer in the vicinity of Ria of Vigo (Rocha *et al.*, 1999; González *et al.*, 2005).

The distribution and seasonality of *L. vulgaris* paralarvae on the northwest shelf were quite distinct from the south and reflect the different mesoscale dynamics of western Iberia. Therefore, in summer, although paralarvae are under the influence of upwelling conditions and consequently cross shelf transport in the Ekman layer is expected to advect them towards the open ocean, the higher abundances were found mainly on the middle shelf, broadly located in the vicinity of the main northern spawning ground (Cunha *et al.*, 1995). Furthermore, our data suggest that *L. vulgaris* paralarvae can perform diel vertical migrations, similar to other cephalopod paralarvae (Piatkowski *et al.*, 1993). Thus, the cross-shelf net transport associated with upwelling dynamics coupled to larval diel migration patterns could result in favourable conditions for their retention over the spawning grounds during summer as hypothesized for crustacean larvae in the same geographic area using observations and models (Marta-Almeida *et al.*, 2006; dos Santos *et al.*, 2008). In winter, when paralarvae abundance is higher, a part of the new generation is able to spread offshore but retained over the shelf break by the blocking effect of the IPC which in the long run could promote also a net poleward advection (Santos *et al.*, 2004; Peliz *et al.*, 2005). At the same time, the absence of paralarvae close to the shore on the northwestern coast during winter is likely to avoid the low saline coastal waters derived from intense river runoff (Ribeiro *et al.*, 2005).

Since we observed that the loliginid paralarvae bathymetric distribution on the west coast is better explained by hatching season than the prevailing cross-shelf transport, this may reflect seasonal differences in the spawning grounds location. Although at present there is no direct evidence of seasonal changes of the squid spawning areas on the west Portuguese shelf, embryonic statolith measurements suggest that *L. vulgaris* changes depth range to spawn as a function of ambient temperature (Villanueva *et al.*, 2003).

Octopus vulgaris

Octopus vulgaris is widespread over mainland shelf waters, as well as off distant oceanic islands and seamounts. The length of embryonic development has an inverse relationship with temperature and it may take from 1.5 to 4 months until hatching (Mangold and Boletsky, 1973) under the temperature range the eggs may experience within Portuguese waters at depths <100 m.

Year round spawning is observed in fisheries and survey data off northwestern Portugal with two distinct peaks in March and July (unpublished data). Giving that mean bottom temperature at depths <100 m is ~14°C (IPIMAR cruise data), two main abundance peaks of paralarvae would be expected ~100 days later (Mangold and Boletsky, 1973). These would correspond to higher abundances of octopus paralarvae in June/July and in October/November, which matches well with our observations. The autumn hatching peak could be magnified as a result of faster development of the eggs laid by the end of the summer spawning season, since with the end of the upwelling season bottom temperatures rise abruptly at shallow depths. Further north, in Galician waters, a unique peak of early hatched octopus occurs at the end of summer and autumn months, just after the upwelling season (Otero, 2006).

On the north-west coast, the seasonal distribution of octopus seems to agree well with the Ekman dynamics of cross-shelf transport, showing higher abundances offshore during the upwelling season and near the shore during the convergence period. Unlike loliginids, the variability in octopus paralarvae bathymetric distribution was better explained by the prevailing cross-shelf transport than by the hatching season. Thus, it is improbable that the location of the main hatching peak on the inner-shelf (<50 m) is a result of spawning migration towards the coast. The spatial dynamics of the *O. vulgaris* benthic phase off western Iberia is poorly studied, but we expect a similarity to the Moroccan coastal upwelling system (Faraj and Bez, 2007), where a displacement of spawners to coastal waters is not observed, contrary to what occurs on Mediterranean waters (e.g. Sánchez and Obarti, 1993).

Despite the fact that a more offshore distribution of octopus paralarvae is observed in spring/summer off the north-west Portuguese coast, they are still retained over the shelf. A probable explanation for this is the double frontal system on the wide north-west continental shelf described by Peliz *et al.* (Peliz *et al.*, 2002) that makes it a major retention area, preventing massive larvae advection and consequent loss into the open ocean, as demonstrated for several species (e.g. Santos *et al.*, 2004). The retention capabilities of this area minimize the potentially unfavourable conditions induced by the strong upwelling events, allowing a regional spring/summer octopus hatching season. A similar coupling between the spawning strategy and the enrichment/retention shelf processes was described for the Arguin Bank (Mauritania), where *O. vulgaris* also shows two spawning/hatching peaks (Demarcq and Faure, 2000).

On the other hand, in the northern Gulf of Cadiz, the spawning season occurs from February until November with higher intensity from June to August both in the western (IPIMAR unpublished data) and the eastern areas (Silva *et al.*, 2002), and very similar to the reproductive strategy in the western Mediterranean (Rodriguez-Rúa *et al.*, 2005). A single paralarvae peak would be expected in southern Portuguese waters ~80 days later (Mangold and Boletsky, 1973), taking into account the mean local bottom temperature (~15°C) that follows the main spawning season (IPIMAR cruise data). This is in agreement with the dominant autumn peak observed in paralarvae abundance. However, it does not adequately explain the distribution of paralarvae during summer in this area.

A plausible explanation is a drift of the new hatchlings, equatorward within the western upwelling-derived flow, and eastwards around Cape St Vincente (Relvas and Barton, 2002, 2005) within the GCC along the southern Portuguese coast, which in summer is connected upstream with the upwelling current (Peliz *et al.*, 2007a). This water mass with SST below 19°C (Relvas *et al.*, 2007) coincides with the distribution of paralarvae along the southern shelf break until ~8°W and over the shelf east of Cape Santa Maria (see Fig. 7A). As the swimming capacity of newly hatchlings (<3 cm s^{-1}) is very weak (Villanueva *et al.*, 1995), some may be carried as far as ~190 km within the upwelling jet (~16–22 cm s^{-1}) (Sánchez and Relvas, 2003) and the GCC (~20 cm s^{-1}) (Peliz *et al.*, 2007a), from the west to the south coast in 10 days. This should be enough to reveal a paralarvae abundance peak in July on the south coast.

Following this oceanic circulation, a few specimens could also be advected offshore by the long upwelling filament that protrudes close to Cape St Vincente (Relvas *et al.*, 2007), and be caught in June at the Gorringe and Ampere seamounts. Nevertheless, we do not exclude the possibility that the paralarvae on the banks result from resident populations.

The drift hypothesis from the west to the south coast is supported by the significant influence of SST and upwelling on *O. vulgaris* paralarvae distribution that is demonstrated by our study, which denotes a strong association of these paralarvae and water masses properties, namely the 17–18°C upwelled waters. Additionally, the distribution of paralarvae during summer on the southern coast may also be an indication that a significant part of the summer spawning would occur in shallow waters, at areas with high bottom temperatures, producing significant offspring within a month time.

The different distribution of *L. vulgaris* and *O. vulgaris* paralarvae on the west coast during summer may be related to distinct diel vertical migration patterns coupled with Ekman transport. However, knowledge about the vertical distribution and behaviour of those paralarvae is still very scarce.

Sepiolids

The poor correlation observed between paralarval sepiolid distribution and environmental variables is caused by the occurrence of several species with different distributions and spawning seasonality. Indeed, the paralarvae found, which were not identified to the species level, may include a mixture of *Rossia macrosoma*, *Sepietta oweniana* and *Rondeletiola minor* that are the most abundant species within the surveyed area (Guerra, 1992). Some paralarvae caught could also belong to the less abundant species: *Sepietta neglecta*, *Sepiola atlantica* and *Sepiola rondeleti*. Nevertheless, our observations are consistent with the knowledge that all those species undergo spawning all year round (Jereb and Roper, 2005). The most interesting finding was that paralarvae were retained on the continental shelf, in spite of the fact that adult distribution range spreads far offshore (until 500 m or even 1000 m depth). This could be an indication that these species migrate inshore for spawning in Atlantic waters, as observed for many species in the Mediterranean Sea (Jereb and Roper, 2005). Unlike the other cephalopod paralarvae, no seasonal oceanographic effects on paralarvae dispersal were observed. Thus, the distinct depth distribution detected between the northern and southern areas may be more related to the actual geographic differences between those areas. Namely, in the northern area, the shelf is much wider (∼60 km) than in the southern area (∼25 km) (Peliz *et al.*, 2005), and distinct depth range distributions suggest similar distances from the coast.

Ommastrephids

Some morphological differences were detected among ommastrephids, however, as there were no paralarvae descriptions available yet, all specimens were analysed as a single group. The most abundant species, *Illex coindetii* and *Todaropsis eblanae* spawn all year round throughout Atlantic European waters. *I. coindetii* has a main spawning season between spring and summer (González and Guerra, 1996; Arvanitidis *et al.*, 2002; Hernández-García, 2002) and *T. eblanae* spawns mainly during summer in northern waters (Hastie *et al.*, 1994; Robin *et al.*, 2002; Zumholz and Piatkowski, 2005) and in early spring and early autumn south of 44 °N (González *et al.*, 1994; Arkhipkin and Laptikovsky, 2000). The high paralarvae abundance in spring matches the spawning peak of both species, giving ∼15 days for egg development (Sakai *et al.*, 1998). On the other hand, the paralarvae of the October peak may represent mainly the *T. eblanae* second spawning season.

Paralarvae of *Todarodes sagittatus* could be considered to be negligible as a component of this group, since the spawning females that approach the Portuguese continental waters are few, occurring from May until December (IPIMAR cruise data). Nevertheless, *T. sagittatus*, in spite of having an extended spawning season, shows a well-pronounced winter peak in the northwestern African waters (Arkhipkin *et al.*, 1999) and thus the January peak of ommastrephids in our samples could correspond to *T. sagittatus* paralarvae, including those specimens found between the continental shelf-break and oceanic seamounts.

Ommastrephid spawning grounds in the northeast Atlantic are unknown, but it is possible to suggest their location based on the occurrence of females in spawning condition, namely regarding *T. eblanae*, which is less migratory than the sympatrics *I. coindetii* and *T. sagitattus* (Lordan, 2001). *Illex coindetii* and *T. eblanae* spawning females may be found mainly in the southwest and southern areas during spring and summer months (IPIMAR cruise data). During this season, there is a clear mismatch between the spatial distribution of spawning females and paralarvae, which were found mainly confined to the continental shelf between 42 and 40°N. Although paralarvae may be rapidly transported within water masses (Trites, 1983), it is more likely that the mature fast swimming ommastrephids migrate northwards, namely by taking advantage of the subsurface IPC in the vicinity of the shelf-break. This northward migration in spring and summer months allows females to meet favourable environments for spawning in more productive areas with moderate temperatures, because eggs and paralarvae fail to develop at temperatures >20°C (Boletzky *et al.*, 1973).

The area of higher abundance of ommastrephid paralarvae was, during all seasons, within that already described as retentive for biogenic material of northwestern Iberia. These results emphasize the importance of the productive upwelling areas for the reproduction and early growth of migratory pelagic species. Thus, the lack of significant influence of temperature or upwelling in the statistical analysis of distribution and abundance was hidden by the mixture of species.

Oceanic species

The oceanic species composition in Portuguese waters was similar to other sub-tropical eastern Atlantic areas.

In spite of histioteuthids being rather more common in this region (Nixon and Young, 2003; Clarke, 2006), their early young stages were not found, and the mesopelagic enoploteuthids and cranchiids, whose hatchlings occur in near-surface waters (e.g. Gibbs and Roper, 1970), dominated the catches. The adults of most of the paralarvae identified may be found off northwest Africa (Adam, 1983) and in Madeiran waters (Rees and Maul, 1956; Clarke and Lu, 1995) towards the mid-Atlantic ridge, in the vicinity of seamounts and in waters off the Azores (Diekmann and Piatkowski, 2004; Clarke, 2006). Those species have their northernmost range of distribution in Portuguese waters, approaching for spawning, between January and June. They take advantage of the major circulation regimes, illustrated in Fig. 12, such as the eastern branch of the AC and the Gulf of Cadiz northern recirculation, which transports warm subtropical water, as well as the flow associated with the WIWiF formed around 39–40°N in winter.

On the contrary, the cranchiid *Teuthowenia megalops*, which is a common species west of the British Islands (Collins *et al*., 2002), extends its spawning ground further south in winter and its paralarvae will reach the northwest Portuguese coastal waters. For the northern species, warmer temperatures are likely to be a major boundary to equatorward dispersal. *Teuthowenia megalops* specimens were all found in the same geographic area, and are a good example of adult or larval drift equatorwards by the broad southward-flowing Portugal Current (Pérez *et al*., 2001), and inshoreward advection by the prevailing winter convergence in northwest Portuguese waters (Peliz *et al*., 2007b).

Despite the wide geographic sampling coverage, the oceanic paralarvae were mainly concentrated in the Gulf of Cadiz system, including many cosmopolitan species, such as *Brachioteuthis reesei* or *Heterotheuthis dispar.* The persistent fronts between the shelf and deep waters close to Cape S. Vicente (Sánchez and Relvas, 2003; Peliz *et al*., 2005), together with water temperature, may represent a boundary to poleward dispersal, which would result in the concentration of oceanic cephalopod paralarvae off the southwestern Iberian Peninsula, within the transition from subtropical to temperate ecosystems.

Concluding remarks

With this study, we can conclude that temperature along with mesoscale features, including horizontal currents, thermal fronts, coastal upwelling and related features are important in modulating seasonality and distribution of cephalopod planktonic paralarvae, as they do for other plankton communities (e.g. Bakun, 1996; dos Santos *et al*., 2007, 2008; Santos *et al*., 2007).

Loligo vulgaris paralarvae are more abundant and occur over a larger part of the year on the western than on the southern shelf. The western Iberia upwelling area provides more favourable environmental conditions for these paralarvae, with relatively low temperatures throughout the year, even in summer, due to the presence of cold upwelled waters over the shelf. The eventual advection from the shelf during upwelling events is probably prevented by their diel migration behaviour. The summer inshore counter-current is suggested to advect *L. vulgaris* paralarvae from the warm summer spawning grounds on the northern Gulf of Cadiz to the western upwelled waters around Cape S. Vicente.

On the other hand, *O. vulgaris* paralarvae occur in the plankton during a more restricted period of the year, mainly associated with 17–19°C upwelled waters. On the west coast, higher abundances are located on the outer-shelf during spring and summer and near the shore during autumn, possibly following the Ekman dynamics of cross-shelf transport. The abundance is higher after the upwelling season, but a summer peak also exists on the north-west shelf and the eventual advection from the outer-shelf during upwelling events is avoided by the retention characteristics of this area. Two hatching peaks occur also on the southern coast, though preceded by a single regional spawning peak. A drift of the new hatchlings from the west to the south within the upwelling and other mesoscale currents is proposed.

The poor correlation observed between paralarval sepiolidae and ommastrephidae distribution and environmental variables is considered to be related to the occurrence of several unidentified species within each family, with different distributions and spawning seasonality. Nevertheless, our data show that their spawning areas occur over the continental shelf despite the fact that the adult distribution range spreads far offshore. In the case of ommastrephids, the distribution of paralarvae reveals that the spawning area in spring and summer is restricted to the north-west continental shelf, where water temperature is not a limiting factor for embryonic development.

Off the Portuguese coast, paralarvae of the neritic species occur during a considerably extended period of the year with two or three abundance peaks, namely within the highly productive upwelling system of the western Portuguese coast and contrasting with the Gulf of Cadiz area. Important differences were noted in the reproductive strategies between species (or groups of species), translated in the seasonality and/or the distribution of paralarvae. The relationship between environmental factors and paralarvae distribution was particularly significant in *O. vulgaris*, giving further evidence that the reproductive strategy of this species follows the seasonal dynamics of the regional environmental processes. Nevertheless, these are complex relationships and we are still far from having a comprehensive knowledge of how they work.

A better knowledge of the spawning areas and the vertical distribution of the planktonic stage for each species are still required to fully understand and predict dispersion/retention patterns on the Portuguese coast. New technologies for tagging and tracking paralarval cephalopods may be one of the most promising approaches to address this question as pointed out in Semmens *et al*. (Semmens *et al*., 2007).

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