

# Decapod larval retention within distributional bands in a coastal upwelling ecosystem

Cátia Bartilotti<sup>1,\*</sup>, Antonina dos Santos<sup>1</sup>, Margarida Castro<sup>2</sup>, Álvaro Peliz<sup>3</sup>,  
A. Miguel P. Santos<sup>1,2</sup>

<sup>1</sup>Instituto Português do Mar e da Atmosfera (IPMA), Av. Brasília s/n, 1449-006 Lisboa, Portugal

<sup>2</sup>Centro de Ciências do Mar do Algarve, Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

<sup>3</sup>Instituto Dom Luiz, Faculdade de Ciências, Universidade de Lisboa. Campo Grande, 1749-016 Lisboa, Portugal

**ABSTRACT:** The spatial distribution and ontogenetic vertical migrations of decapod larvae in the northwestern Portuguese upwelling ecosystem were analyzed to explore the hypothesis of retention over the shelf and the related mechanisms involved. The sampled decapod crustacean larvae were retained on the continental shelf along 3 meridional bands parallel to the coast, independent of larval phase duration or taxonomic group. All larval stages belonging to inner shelf or estuarine species were found close to the shore, mainly restricted to a 10 km wide band. The larvae of shelf species were mainly distributed in the middle of the shelf. However, some of these species were widely distributed over the shelf, whereas others were more abundant in the northern or southern transects (as a consequence of the advection of a warmer water mass from the south). The outer shelf band included larvae from slope species. This distribution pattern (i.e. in bands) corroborates observations from other coastal upwelling systems and results from the relationship between larval behavior and local oceanographic processes. Ontogenetic vertical migration behavior was evident for almost all the taxa analyzed, in which the older stages (last zoeal stages, decapodids and megalopae) were usually found in deeper strata of the water column.

**KEY WORDS:** Decapod larvae · Retention · Ontogenetic vertical migrations · Distributional bands · Upwelling · Portugal

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## INTRODUCTION

Population connectivity is a biophysical process that results from the interaction between physical transport and biological traits, such as larval behavior, growth and mortality (e.g. Pineda et al. 2007, Cowen & Sponaugle 2009). Several recent studies have demonstrated that many species of decapod larvae remain close to parental populations throughout development (e.g. dos Santos et al. 2008, Morgan et al. 2011, Landeira et al. 2012, Yannicelli et al. 2012).

The study area (see Fig. 1) is located in the northern part of the Canary Current upwelling system (CCUS) and is characterized by a complex mesoscale

variability with a strong seasonality, namely the occurrence of coastal upwelling during the spring-summer season (Peliz et al. 2002, Relvas et al. 2007) similar to that observed off the coasts of northern California and Oregon, USA (e.g. Mackas et al. 2006). Frouin et al. (1990) and Haynes & Barton (1990) reported the presence of a poleward current—the Iberian Poleward Current (IPC)—along the coast of northwestern Iberia, generally described as a slender poleward flow along the upper slope/shelf break zone, carrying warm and salty waters in the upper 200 to 300 m during autumn and winter. Peliz et al. (2003a,b, 2005) showed that the IPC is driven by density forcing associated with larger-scale meridional

\*Corresponding author: catia\_bartilotti@hotmail.com

thermal gradients, and although it intensifies during winter it is present year-round. River runoff is significant on this northwestern coast, contributing a fresh water input to the shelf that generates a low salinity lens: the Western Iberia Buoyant Plume (WIBP, Peliz et al. 2002). The WIBP is low-salinity ( $<35.75$ ) and chlorophyll-rich ( $>0.75 \text{ mg m}^{-3}$ ), with a thickness of 20 to 40 m. It can be advected from the inner shelf (~20 km from coast) and responds rapidly to changes in wind direction, being displaced offshore with northerly winds or converging to the coast with southerlies (Peliz et al. 2002, Santos et al. 2004, Ribeiro et al. 2005, Otero et al. 2008). Intermittent upwelling conditions together with the presence of the WIBP, and the slope circulation associated with the IPC, could induce convergence zones for planktonic organisms in this region. Examples include the retention of phytoplankton in shallow stratified nutrient-rich waters (Ribeiro et al. 2005), the evident association of fish larvae with the waters of the WIBP (Santos et al. 2004, Garrido et al. 2009), the retention of cirripede cyprids along a band in the inner shelf (dos Santos et al. 2007), and the influence on the dispersal of decapod larvae over the shelf (dos Santos et al. 2008).

The 3-dimensional larval decapod distributions studied by dos Santos et al. (2008) confirmed along-shore dispersal and retention over the middle shelf due to the combination of an intermittent wind-driven circulation regime and an active diel vertical migration (DVM) behavior, as proposed by 2 previous modeling studies of the study area (Marta-Almeida et al. 2006, Peliz et al. 2007). Dos Santos et al. (2008) suggested that the larval decapod retention over the shelf was related to their probable settlement areas. According to these authors (dos Santos et al. 2008), under upwelling conditions, the larvae located at the middle shelf would not reach the coast within a realistic time to settle, so only those larvae retained in the inner shelf would settle and recruit inshore or in the lagoon or estuarine systems. Additionally, inshore cirripede cyprid species that have to return to the coast for settlement seemed to be rare offshore of the inner shelf zones and were usually restricted to a narrow band near and along the coast (dos Santos et al. 2007). These observations are in agreement with those made by other authors for other upwelling systems. Morgan et al. (2009a) found most coastal crustacean larvae 6 km from the shore after upwelling conditions in northern California, and considered that many of the sampled species were able to complete their development in that area. Shanks & Shearman (2009) described a similar

pattern of distribution for intertidal invertebrates on the Oregon coast, concluding that the average distance from the shore did not vary with upwelling or downwelling, and that all taxa and larval stages were found between 0.9 and 4 km from the coastline.

The ontogenetic vertical migrations, defined as a change in the average depth of distribution during the larval phase, is an obligatory process for benthic crustaceans that hatch close to the bottom, feed at the surface, and at the end of their larval life must return to the adult habitat (Queiroga & Blanton 2004). Several studies describe these ontogenetic migrations but most of them only consider brachyuran species (see Queiroga & Blanton 2004 for details and references therein). The larval transport in decapods depends greatly on their capacity to perform DVM (Queiroga & Blanton 2004). The larval vertical positioning is under strong behavioral control and has been assumed to be a determinant in the timing of recruitment (Morgan et al. 2009b).

There have been several studies on larval cross-shelf distribution, retention and dispersion in coastal upwelling systems but they considered mainly taxa of intertidal invertebrate species (e.g. Shanks & Shearman 2009). The aims of this study were to (1) test the hypothesis that in a coastal upwelling ecosystem, decapod larvae are distributed along meridional patches (bands) reflecting their parental origins, and (2) investigate the ontogenetic vertical migrations of the larvae along the shelf. Thus, it was expected that all larval developmental stages of each species should be retained in alongshore bands according to the distribution of their parental populations over the shelf.

## MATERIALS AND METHODS

### Field study

To test the above hypothesis, we selected the 17 most abundant taxa (2 inner shelf species, 12 shelf species and 3 slope species, according to the adult distributions; Table 1) collected during an oceanographic cruise carried out off the northwest coast of Portugal (northern CCUS), from 9 to 22 May 2002 aboard the IPMA RV 'Noruega' (Fig. 1). The following 9 (3 Caridea, 3 Anomura and 3 Brachyura) of the 17 taxa (Table 1) were selected to verify the existence of ontogenetic vertical migrations based on their abundance and the presence of the complete larval series at fixed point stations (see this section, last paragraph): *Processa nouveli* (first to ninth zoeae and decapodid), *Pandalina brevivrostris* (first to seventh

Table 1. List of the selected taxa, respective decapod crustacean group and Family (De Grave et al. 2009), distribution range when adults (according to Zariquiey-Álvarez 1968 and d'Udekem d'Acóz 1999) and grouping of the sampled larval stages. Protozoa (PZ), zoea (Z) (new [ZN] or old [ZO]), decapodid (D), megalopa (M)

Taxa	Decapod group	Family	Distributional range	ZN	ZO	D or M
<i>Diogenes pugilator</i>	Anomura	Diogenidae	Inner shelf (up to 35–40 m)	Z I–II	Z III–IV	M
<i>Necora puber</i> <sup>a</sup>	Brachyura	Macropipidae	Inner shelf (up to 15 m)	Z I–II	Z III–V	M
<i>Philocheas bispinosus</i> <sup>a</sup>	Caridea	Crangonidae	Shelf (up to 130 m)	Z I–II	Z III–V	D
<i>Eualus occultus</i>	Caridea	Hippolytidae	Shelf (up to 150 m)	Z I–IV	Z V–IX	D
<i>Pandalina brevisrostris</i> <sup>a</sup>	Caridea	Pandalidae	Shelf (up to 180 m)	Z I–III	Z IV–VII	D
<i>Processa nouveli</i> <sup>a</sup>	Caridea	Processidae	Shelf (10–330 m)	Z I–IV	Z V–IX	D
<i>Callianassa subterranea</i>	Axiidea	Callianassidae	Shelf (35–500 m)	Z I–II	Z III–IV	-
<i>Upogebia</i> spp.	Gebiidea	Upogebiidae	Shelf (up to 65 m)	Z I–II	Z III–IV	-
<i>Anapagurus</i> spp. <sup>a</sup>	Anomura	Paguridae	Shelf (up to 200 m)	Z I–II	Z III–IV	M
<i>Pagurus bernhardus</i> <sup>a</sup>	Anomura	Paguridae	Shelf (up to 140 m)	Z I–II	Z III–IV	M
<i>Pisidia longicornis</i> <sup>a</sup>	Anomura	Porcellanidae	Shelf (up to 100 m)	Z I	Z II	M
<i>Atelecyclus rotundatus</i> <sup>a</sup>	Brachyura	Atelecyclidae	Shelf (9–100 m)	Z I–II	Z III–V	M
<i>Liocarcinus</i> spp. <sup>a</sup>	Brachyura	Carcinidae	Shelf (50–100 m)	Z I–II	Z III–V	M
<i>Polybius henslowii</i>	Brachyura	Carcinidae	Shelf (2–518 m)	Z I–II	Z III–V	M
<i>Solenocera membranacea</i>	Dendrobranchiata	Solenoceridae	Slope (beyond 400 m)	PZ II–III	Z I–II	-
<i>Parthenope</i> spp.	Brachyura	Parthenopidae	Slope (beyond 400 m)	Z I–II	Z III–IV	-
<i>Goneplax rhomboides</i>	Brachyura	Goneplacidae	Slope (beyond 400 m)	Z I–II	Z III–IV	M

<sup>a</sup>Taxa used in the ontogenetic vertical migrations analyses

zoeae and decapodid), *Philocheas bispinosus* (first to fifth zoeae and decapodid), *Anapagurus* spp. (first to fourth zoeae and megalopa), *Pagurus bernhardus* (first to fourth zoeae and megalopa), *Pisidia longicornis* (first to second zoeae and megalopa), *Atelecyclus rotundatus* (first to fifth zoeae and megalopa), *Li-*

*ocarcinus* spp. (first to fifth zoeae and megalopa), and *Necora puber* (first to fifth zoeae and megalopa).

The cruise was previously described by dos Santos et al. (2008), so only a brief description of the survey is given here. A quasi-synoptic view of the mesoscale circulation patterns prior to biological sampling was obtained with 5 transects perpendicular to the coast (Leg 1; Fig. 1a), from 11 to 14 May 2002 using

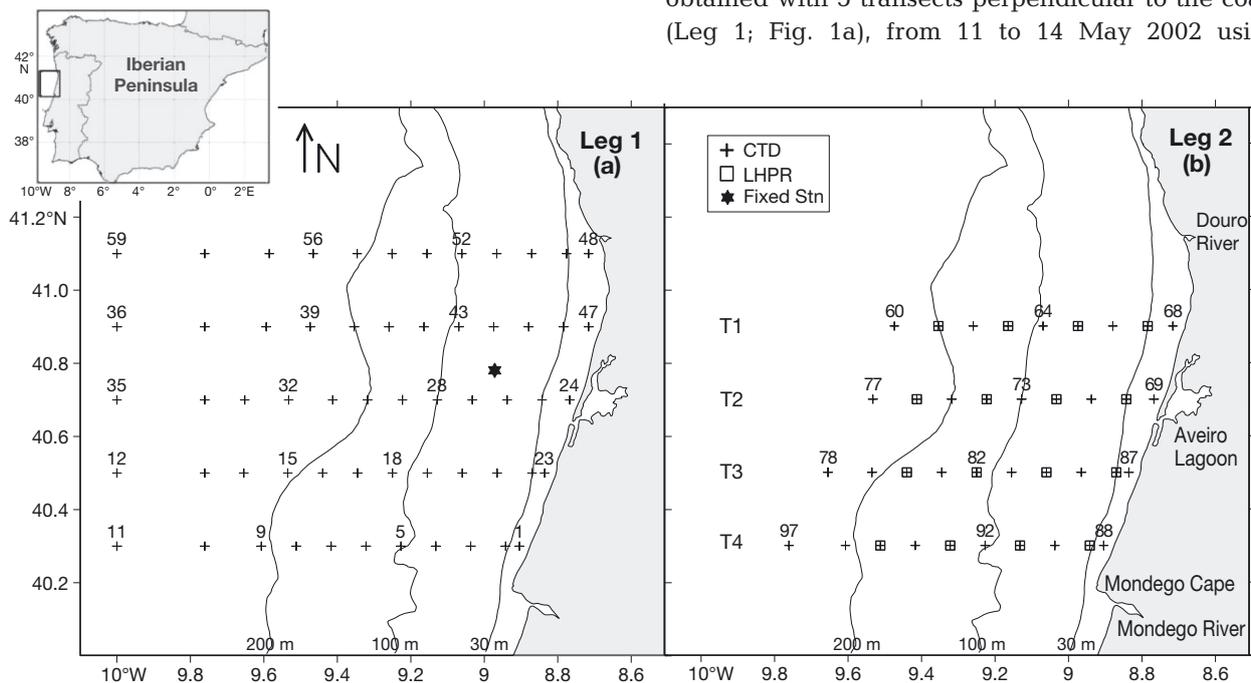


Fig. 1. ProRecruit cruise stations off Portugal's northwest coast carried out (a) from 11 to 14 May 2002 (Leg 1: only CTD casts) and (b) from 15 to 17 May 2002 (Leg 2: CTD casts and Longhurst-Hardy Plankton Recorder [LHPR] hauls). Transects of Leg 2 are identified as T1, T2, T3 and T4. The fixed point station is indicated by a star in (a). Stations are identified by a sequential number above their location. The 30, 100 and 200 m bathymetric lines are also presented

a SBE911p CTD (conductivity/temperature/depth). From 15 to 17 May, the plankton sampling (Leg 2) was carried out in a 16 station grid along the 4 southernmost transects (Fig. 1b) using a Pro-LHPR system (mouth aperture of 0.42 m and 280  $\mu\text{m}$  mesh size), a commercially updated version of the Longhurst-Hardy Plankton Recorder (Williams et al. 1983). The Pro-LHPR was towed at 3 to 4 knots on oblique hauls. The stratified samples were collected in 5 m depth intervals for the first 25 m of the water column, in 10 m depth intervals from 25 to 65 m, in 20 m depth intervals from 65 m to 105 m and until 5 to 10 m above the bottom or 150 m at deeper stations. Each transect (T1 to T4; Fig. 1b) had 4 stations separated by approx. 16 km, the first station in each transect being approx. 8 km offshore.

From 18 to 21 May 2002, a fixed station was sampled at 2 h intervals over a period of 69 h (Fig. 1). The first 20 cm of the water column was sampled using a Neuston net with a rectangular mouth aperture of  $0.2 \times 1.0$  m, 335  $\mu\text{m}$  mesh size, with a flowmeter mounted in the mouth aperture, and towed horizontally for 3 min periods at a velocity of 1.5 knots. The stratified samples were collected with the Pro-LHPR at 5 m depth intervals in the first 25 m and 10 m depth intervals from 25 m until near the bottom. Temperature and salinity were measured every hour with a SBE 911p CTD.

### Sample processing

Plankton samples were preserved in 4% borax-buffered formaldehyde prepared with seawater. Samples were sorted for decapod larvae, and identified to species level and developmental stage whenever possible, based on dos Santos & Lindley (2001) and dos Santos & González-Gordillo (2004), and confirmed by larval descriptions listed in González-Gordillo et al. (2001). Data were standardized to individuals per cubic meter of water filtered ( $\text{ind. m}^{-3}$ ). The Weighted Mean Depth (WMD, in m, Pearre 2003) was calculated for each species as explained in dos Santos et al. (2008).

### Statistical analysis

In order to reduce the zero values and improve the statistical analysis, the larvae were grouped based on morphological characters that identify the larval stages throughout development. Three larval groups were considered (Table 1): (1) the early zoeal stages

(ZN) (in the particular case of *Solenocera membranacea*, these correspond to the protozoae [PZ] stages), (2) the later zoeal stages (ZO) (for *S. membranacea* these correspond to the mysis stages [My]), and (3) the decapodid (D) (for shrimps in general) or megalopa (M) (for all other decapod species).

Larval decapod horizontal distribution in relation to particular environmental parameters was analyzed for each species and larval group separately. The 2-step approach was used to deal with the problem of zero-inflated data (Wenger & Freeman 2008). Two response variables were considered: (1) log transformed abundance ( $\text{ind. m}^{-3}$ ) and (2) presence/absence (1 or 0) of a given taxa and larval group. All environmental variables that were available and potentially useful to explain presence and/or abundance of larvae were investigated in the first phase of the exploratory data analysis. These variables were BOTTOM (depth at the station, in meters, a continuous variable), DEPTH\_CAT (upper limit of the depth stratum, in m, a discrete variable), MAX\_TOW\_DEPTH (tow maximum depth, in m, a continuous variable), DEPTH\_STR (midpoint depth of the stratum, in m, a discrete variable), DIST\_COAST (distance to the coast, in km, 0 was considered the coastline, a continuous variable), REAL\_TIME (time of day, 00:00 to 23:59 h, a continuous variable), HOUR1 (night and day, in accordance with the sunrise [6:00] and sunset hours [20:00], categorical variable with 2 levels), HOUR2 (night, dawn, day and dusk, in accordance with the sunrise and sunset hours with 'dawn' and 'dusk' corresponding to the 2 h that follow sunrise [06:00 to 07:59] and sunset [20:00 to 21:59], respectively, a categorical variable with 4 levels), HOUR\_WAVE (hour defined as a circular function of the time of day, sunrise = 0, noon = 1, sunset = 0 and midnight = -1, a continuous variable generated by the function  $\sin[(\text{hour} \times 2\pi/24) + 3\pi/2]$ , where 'hour' is the time of day from 00:00 to 23:59), WIBP (Western Iberia Buoyant Plume, presence/absence, with presence corresponding to a water mass with salinity  $<35.75$ ), ISWM (Intermediate Salinity Water Mass, presence/absence, with presence corresponding to a water mass with salinities  $\geq 35.75$  and  $<35.90$ ), IPC (Iberian Poleward Current, categorical variable representing the presence of a high salinity water mass with salinity  $\geq 35.90$ ), SAL (salinity, no units, a continuous variable), and TEMP (temperature, in  $^{\circ}\text{C}$ , a continuous variable). Since most of these variables were not significant in any of the studied cases (species and larval group), they were excluded and the variables used in the construction of the final models were DIST\_COAST, HOUR\_WAVE, TEMP and WIBP.

In the first step, the larval presence or absence was predicted using a Logistic Model (LM) with the chosen explanatory variables (above). The results from this model were then used in a second step for situations where at least 1 of the variables was significant and for data points where 'presence' was predicted. For these data points, the measured values of abundance were modeled with a Generalized Additive Model (GAM) using linear predictors for DIST\_COAST, HOUR\_WAVE, TEMP and WIBP, and a spline for TEMP, with 2 degrees of freedom. The statistical analysis was performed using SAS v. 9.2 (SAS Institute 2008) using PROC LOGIT for fitting the logistic model (stepwise option) and PROC GAM for the generalized additive models.

To investigate if there were significant ontogenetic vertical migration differences between the 9 taxa selected, a nonparametric statistical analysis (Kruskal-Wallis by ranks and median tests,  $H$ ) was applied (Fowler & Cohen 1990), as data were not normally distributed even after logarithmic transformation. The  $z$ -values and their associated probabilities ( $p$ -values) were computed for post-hoc comparisons of mean ranks of all pair groups (Siegel & Castellan 1988).

## RESULTS

### Oceanographic conditions

Favorable winds for upwelling (northerlies) prevailed in the weeks prior to the oceanographic cruise. As a result, there was a displacement of the WIBP over the shelf and slope for more than 100 km off the coast. A reversal of the wind conditions, from northerlies to southerlies, occurred during the first leg of the cruise (Leg 1), which may have caused a partial retraction and deepening of the plume, as well as an erosion of it by mixing and overturning its offshore edge. Southerly winds continued during the first part of the plankton sampling (Leg 2), causing further mixing of the WIBP with the saltier and warmer offshore waters (Fig. 2). This change led to coastal convergence conditions during Leg 2, and to a progressive poleward advection and invasion of the shelf by saltier and warmer waters (Figs. 3 & 4), namely by the Iberian Poleward Current (IPC) slope waters with salinities  $>35.90$  (Fig. 3). The relaxation of the upwelling happened simultaneous to an intensification of the northward currents in the middle to inner shelf (Fig. 4; see also current meter data in Fig. 3 of Santos et al. 2006), leading to the intrusion of warmer waters near the coast (Fig. 5). As a conse-

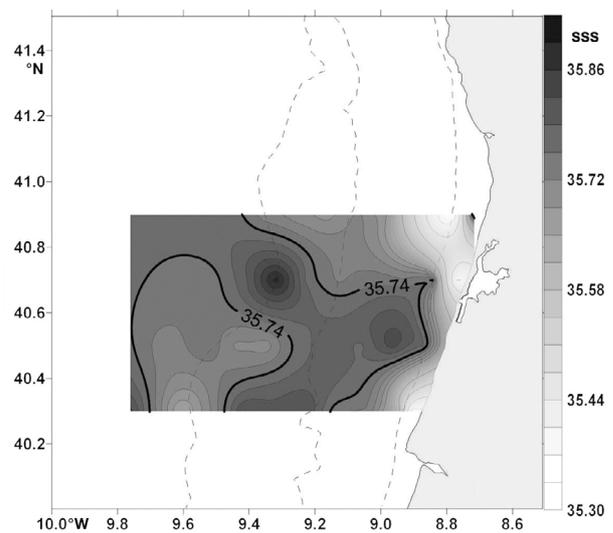


Fig. 2. Distribution of sea surface salinity (SSS) during Leg 2 (15 to 17 May 2002) of the ProRecruit cruise. The bold black line delimits the Western Iberia Buoyant Plume (WIBP). Note the onshore regression of the WIBP and the intrusion of oceanic waters (higher salinities) over the shelf disrupting the plume's integrity. The dashed lines represent the 30, 100 and 200 m isobaths

quence of the advection from the south of these warmer and saltier waters, a thermal front developed at the latitude of the Aveiro lagoon (Fig. 5) and a regression of the WIBP was observed (Fig. 2). Nevertheless, the main features of the thermohaline structure and circulation related to the upwelling conditions observed before the oceanographic cruise were still seen in the outer shelf (white arrow in Fig. 4), meaning that the current reversal was not very significant over that area.

### Larval distribution of the inner shelf species

The species sampled at the stations nearer to the shore were *Diogenes pugilator* (Fig. 6a) and *Necora puber*. Both species had all the larval developmental stages (ZN, ZO and M) captured, with higher abundances in the northern transects (T1 and T2) over the 30 m isobath approx. 8 km from the shore (Fig. 6a). Early zoeal stages (ZN) were more abundant than old (ZO) and megalopa (M) stages. Maximum abundance was 2.79 ind.  $10\text{ m}^{-3}$  for *D. pugilator* (ZN) in T2, and 1.62 ind.  $10\text{ m}^{-3}$  for *N. puber* in T1. The 2-step statistical modeling showed that DIST\_COAST was negatively correlated, and TEMP was positively correlated, with the zoeal distributions of these inner shelf species (Table 2). Neither of these species distributions was statistically correlated with HOUR\_WAVE.

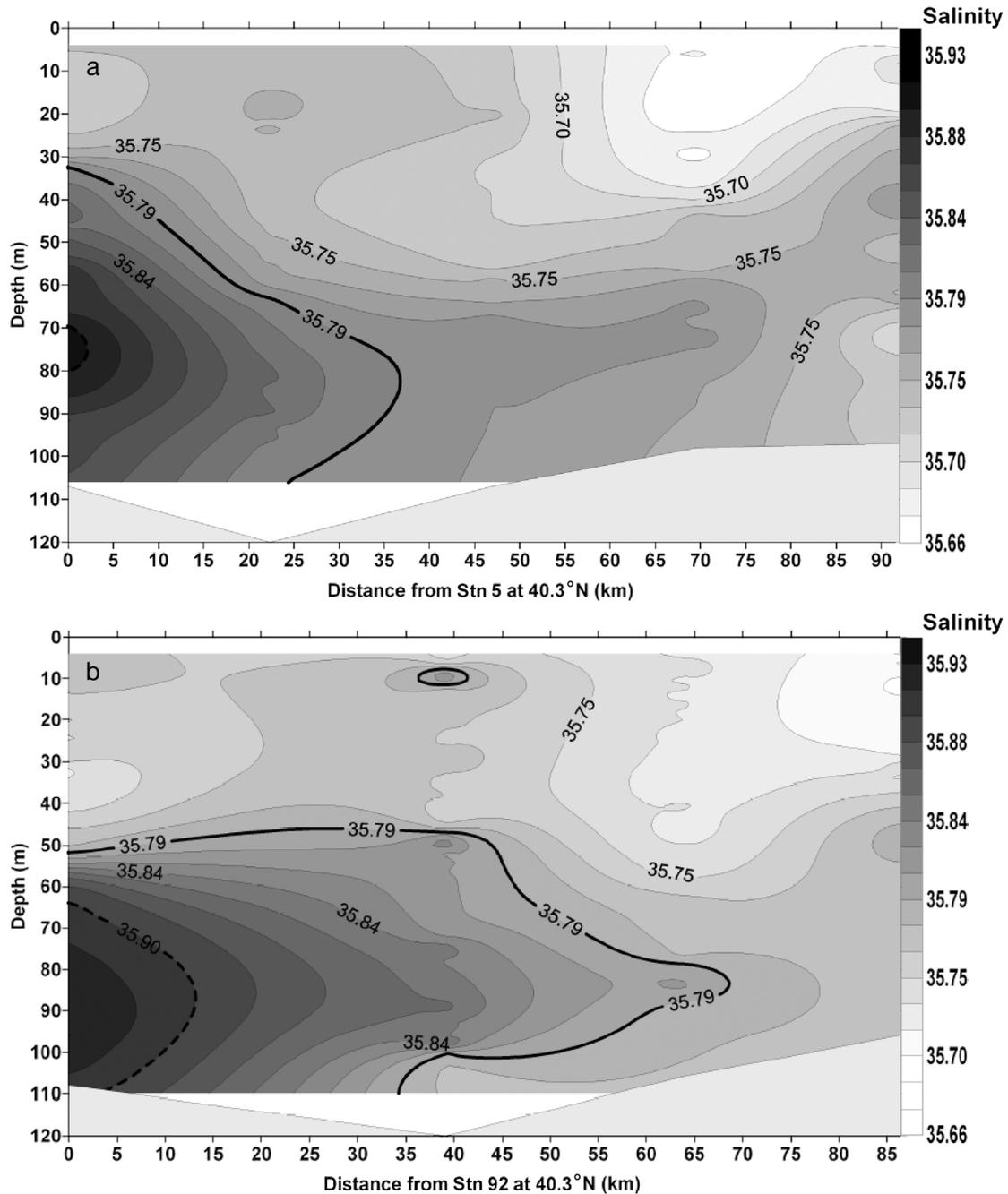


Fig. 3. Meridional transects of salinity along the 100 m isobath during (a) 11 to 14 May 2002 (Leg 1) and (b) 15 to 17 May 2002 (Leg 2). The solid black line defines the northward advection of the Iberian Poleward Current (IPC) waters over the shelf; the dashed black line represents the core of the IPC. Distances are relative to cruise Stn 5 (Leg 1) and Stn 92 (Leg 2), both located at latitude 40.3°N, in a northward direction

#### Larval distribution of the shelf species

Most of the larvae considered as being from shelf taxa were concentrated along the middle shelf; namely *Eualus occultus*, *Processa noveli*, *Pandalina brevirostris*, *Philocheras bispinosus*, *Callianassa subterranea*, *Upogebia* spp., *Anapagurus* spp., *Atelecyclus rotundatus*, *Liocarcinus* spp. and *Polybius hens-*

*lowii* (a subset of which is shown in Fig. 6b–d). Although the shelf species had a wider distribution over the shelf, it was possible to identify 3 different patterns. *Upogebia* spp. and *Anapagurus* spp. had higher abundances in the northern transects (T1 and T2) inshore of the 100 m isobath at a distance of approx. 20 km from the shore (*Anapagurus* spp. shown in Fig. 6b). Old zoeal stages (ZO) were the

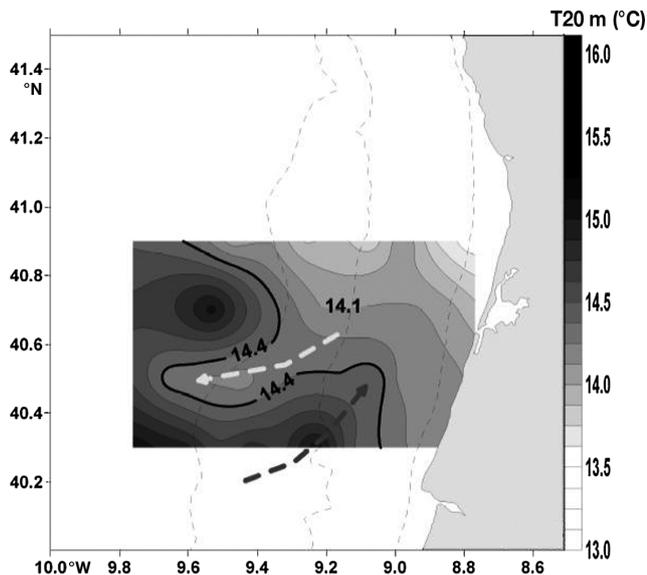


Fig. 4. Distribution of sea temperature ( $^{\circ}\text{C}$ ) at 20 m depth during Leg 2 (15 to 17 May 2002). The bold black line defines the remains of an upwelling filament. The dashed bold arrows are a schematic representation of the circulation (direction of the currents). The dashed lines represent the 30, 100 and 200 m isobaths

most abundant (2.15 and 6.82 ind.  $10\text{ m}^{-3}$  for *Upogebia* spp. and *Anapagurus* spp. respectively in T2). On the contrary, *P. nouveli* and *C. subterranea* were more concentrated in the southern transects (T3 and T4), but also inshore of the 100 m isobath at a distance of approx. 20 km from the shore (*C. subterranea* shown in Fig. 6c). *C. subterranea* was not collected in the northernmost transect (T1) and *P. nouveli* had very low abundances in the same transect. Early zoeal stages (ZN) were the most abundant for both of these species, reaching their maximum value in T4 (2.02 ind.  $10\text{ m}^{-3}$  for *P. nouveli*, and 4.50 ind.  $10\text{ m}^{-3}$  for *C. subterranea*). *P. nouveli* decapodid (D) and *C. subterranea* old zoeae (ZO) were exclusively sampled in T4 (the most southern transect) (*C. subterranea* ZO shown in Fig. 6c). The remaining 6 shelf taxa (*E. occultus*, *P. brevirostris*, *P. bispinosus*, *A. rotundatus*, *Liocarcinus* spp. and *P. henslowii*) had an extended distribution throughout the shelf (*P. henslowii* shown in Fig. 6d), and higher larval abundances were found along a wide band inshore of the 200 m isobath, 8 to 60 km from the coastline. For all of these taxa, the old zoeal stages (ZO) were the most abundant and *P. henslowii* was the most abundant species in the area (25.06 ind.  $10\text{ m}^{-3}$ ; Fig. 6d).

The statistical results (Table 2) showed that the presence of the early zoeal stages (ZN) of *E. occultus*

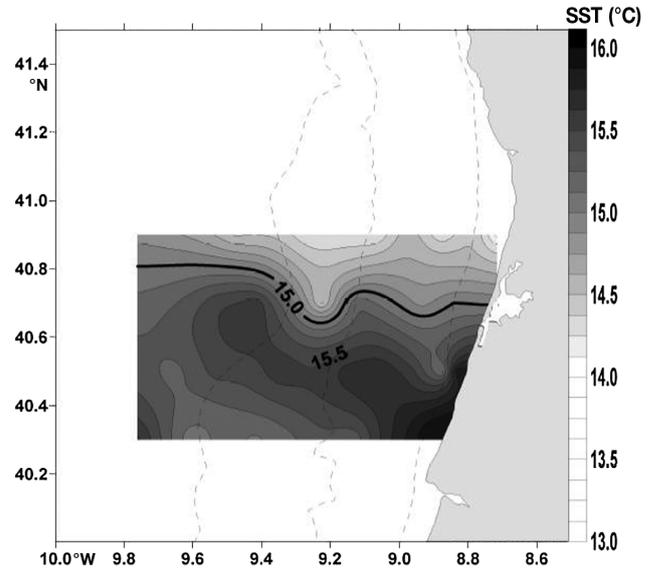


Fig. 5. Distribution of sea surface temperature ( $^{\circ}\text{C}$ ) during Leg 2 (15 to 17 May 2002). The bold black line defines a zonal thermal front. The dashed lines represent the 30, 100 and 200 m isobaths

*tus*, *P. nouveli*, *P. brevirostris*, and *C. subterranea* was positively related to the WIBP. *Upogebia* spp. old zoeae (ZO) and the megalopae (M) of shelf crabs (*A. rotundatus*, *Liocarcinus* spp., and *P. henslowii*) were negatively related with this plume. The distributions of the 3 larval groups (ZN, ZO and D or M) of most shelf species were negatively related to TEMP, the exceptions being *E. occultus* and *P. brevirostris* decapodids (D) and *C. subterranea* early zoeal stages (ZN) which were positively related to it. *Liocarcinus* spp. and *P. henslowii* were ubiquitous in the area, so temperature did not explain the presence or abundance of their larval stages. HOUR\_WAVE reflected the diel vertical migration behavior previously described by dos Santos et al. (2008); thus, *P. nouveli* (ZN and ZO), *P. brevirostris* (D), *P. bispinosus* (D), *Anapagurus* spp. (ZN and M), *A. rotundatus* (ZN and ZO), *Liocarcinus* spp. (M), and *P. henslowii* (ZN and M) larval distributions were significantly related to this parameter. DIST\_COAST explained the distribution of the decapodids of *E. occultus* and *P. bispinosus* closer to the shore, as well as the distribution of shelf crab older stages (ZO and M) further from the shore. *P. henslowii* had all larval stages (ZN, ZO and M) significantly related to the distance to the coast; *Anapagurus* spp. early zoeal stages (ZN) and megalopa (M) presences were also significantly and negatively related to the distance to the coast.

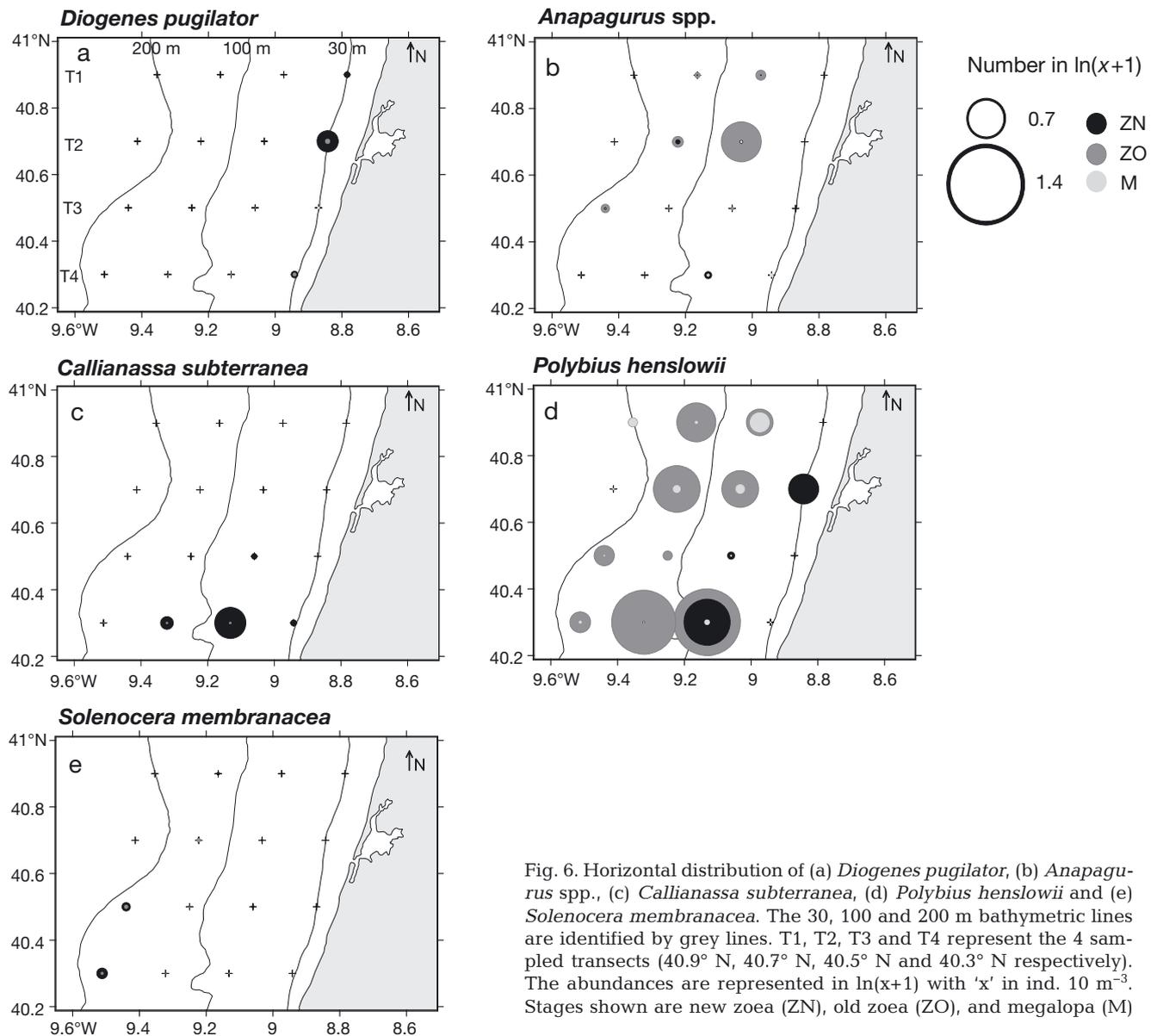


Fig. 6. Horizontal distribution of (a) *Diogenes pugilator*, (b) *Anapagurus* spp., (c) *Callianassa subterranea*, (d) *Polybius henslowii* and (e) *Solenocera membranacea*. The 30, 100 and 200 m bathymetric lines are identified by grey lines. T1, T2, T3 and T4 represent the 4 sampled transects (40.9° N, 40.7° N, 40.5° N and 40.3° N respectively). The abundances are represented in  $\ln(x+1)$  with 'x' in  $\text{ind. } 10^{-3}$ . Stages shown are new zoea (ZN), old zoea (ZO), and megalopa (M)

### Larval distribution of the slope species

*S. membranacea*, *Parthenope* spp. and *G. rhomboides* larvae were mainly present in the southern transects (T3 and T4), in a band offshore of the 100 m isobath 40 to 56 km from the coastline (*S. membranacea* shown in Fig. 6e). The maximum abundances registered were 1.66  $\text{ind. } 10^{-3}$  for ZN of *S. membranacea* in T4 (Fig. 6e), 1.02  $\text{ind. } 10^{-3}$  for ZN of *Parthenope* spp. in T3, and 1.65  $\text{ind. } 10^{-3}$  for ZO of *G. rhomboides* in T3. The majority of the zoeal presences, the protozoae and mysis of *S. membranacea*, *Parthenope* spp. ZN, and *G. rhomboides* ZO, were positively related to DIST\_COAST

and were never associated with the WIBP (Table 2). The ZN of these species were more abundant in the southern transects where an intrusion of slope waters was occurring (Figs. 3 & 4). TEMP was always negatively correlated with the distribution of the slope species. All the larval stages of the 3 taxa were distributed throughout the whole water column, from the surface to close to the bottom. However, the bulk of these larvae were found between 25 and 80 m (not shown). Vertical migration behavior was clear and HOUR\_WAVE explained the distribution of *S. membranacea* (protozoae) and *G. rhomboides* (ZO and M) larvae (Table 2).

Table 2. Coefficients of significant explanatory variables of the 2-step model (presence or absence predicted using a Logistic Model in the first step, values of abundance modelled with a Generalized Additive Model in the second step) describing the distribution of decapod larvae of selected taxa. Larval groups: zoea new (ZN), zoea old (ZO), decapodid (D) or megalopa (M); Model phases: number of measured points (n) for presences (P) and, from estimated points, abundances (A); Western Iberia Buoyant Plume (WIBP); time of day (HOUR\_WAVE); distance to the coast (DIST\_COAST), temperature (TEMP; see 'Materials and methods: Statistical analysis for definition of 'linear' and 'spline'). '-': variable not included in the model, or abundances not estimated due to the low number of predicted presences. \*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05, ns: not significant

Species	Larval group	Model phases	n	Coefficients of significant explanatory variables				
				WIBP	HOUR_WAVE	DIST_COAST	TEMP (linear)	TEMP (spline)
<i>Diogenes pugilator</i>	ZN	P	148	ns	ns	-0.289***	ns	-
		A	18	ns	ns	ns	0.044*	ns
	ZO	P	148	ns	ns	-0.069**	1.517**	-
		A	-	-	-	-	-	-
<i>Necora puber</i>	ZN	P	148	ns	ns	-0.079***	1.287*	-
		A	-	-	-	-	-	-
	ZO	P	148	ns	ns	ns	1.470**	-
		A	-	-	-	-	-	-
<i>Anapagurus</i> spp.	ZN	P	148	ns	-1.466*	-0.057**	ns	-
		A	-	-	-	-	-	-
	ZO	P	148	ns	ns	ns	-0.627*	-
		A	19	ns	ns	ns	ns	ns
	M	P	148	ns	-1.466*	-0.057**	ns	-
		A	12	ns	4.001**	ns	-0.017**	0.007
<i>Upogebia</i> spp.	ZO	P	148	-0.740*	ns	ns	ns	-
		A	-	-	-	-	-	-
<i>Callianassa subterranea</i>	ZN	P	148	0.850***	ns	-0.033*	1.602***	-
		A	45	ns	ns	ns	ns	ns
<i>Processa nouveli</i>	ZN	P	148	0.646**	0.823**	ns	ns	-
		A	-	-	-	-	-	-
	ZO	P	148	0.564**	1.535***	ns	ns	-
		A	17	ns	0.621**	-0.008*	-0.025*	ns
<i>Eualus occultus</i>	ZN	P	148	0.394*	ns	ns	-1.290***	-
		A	20	ns	ns	ns	ns	ns
	ZO	P	148	ns	ns	ns	-0.837**	-
		A	34	ns	ns	ns	ns	ns
	D	P	148	ns	ns	-0.102**	1.717**	-
		A	-	-	-	-	-	-
<i>Pandalina brevis</i>	ZN	P	148	0.573*	ns	ns	ns	-
		A	-	-	-	-	-	-
	ZO	P	148	ns	ns	ns	-1.110***	-
		A	41	0.348**	ns	ns	ns	ns
	D	P	148	ns	-2.253**	ns	1.379**	-
		A	-	-	-	-	-	-
<i>Philocheas bispinosus</i>	ZO	P	148	ns	ns	ns	-1.493***	-
		A	-	-	-	-	-	-
	D	P	148	ns	-1.931*	-0.110***	ns	-
		A	12	ns	4.497*	ns	-0.024*	ns
<i>Atelecyclus rotundatus</i>	ZN	P	148	ns	-1.064*	ns	ns	-
		A	-	-	-	-	-	-
	ZO	P	148	ns	ns	0.829***	ns	-0.857**
		A	85	ns	ns	0.0039*	ns	ns
	M	P	148	-0.781***	ns	0.049***	-1.557***	-
		A	36	ns	ns	ns	ns	0.044
<i>Liocarcinus</i> spp.	M	P	148	-0.517**	-0.560*	ns	ns	-
		A	25	ns	0.604*	ns	ns	ns
<i>Polybius henslowi</i>	ZN	P	148	ns	-1.017***	-0.025*	ns	-
		A	12	ns	ns	ns	ns	ns
	ZO	P	148	ns	ns	0.050***	ns	-
		A	126	ns	ns	-0.008*	ns	ns
	M	P	148	-0.591**	-1.149***	0.072***	ns	-
		A	68	-0.086**	-0.070***	ns	ns	ns
<i>Solenocera membranacea</i>	ZN	P	148	ns	0.641*	0.041**	-1.601***	-
		A	34	ns	0.130*	ns	ns	ns
	ZO	P	148	ns	ns	0.051**	ns	-
		A	-	-	-	-	-	-
<i>Parthenope</i> sp.	ZN	P	148	ns	ns	0.137*	ns	-
		A	-	-	-	-	-	-
<i>Goneplax rhomboides</i>	ZO	P	148	ns	ns	0.065***	-1.536***	-
		A	22	ns	0.191*	ns	ns	ns
	M	P	148	ns	-1.154*	ns	-3.505***	-
		A	-	-	-	-	-	-

### Ontogenetic migrations

All the taxa analyzed showed significant vertical migration behavior differences among stages, with the exception of the caridean shrimps *P. nouveli* and *P. bispinosus*, and the brachyuran crab *N. puber* (Table 3).

The decapodids (D) of the 3 species of caridean shrimps were always absent from the neuston (minimum WMD was 10.6 m for *P. bispinosus*, 13.0 m for *P. brevirostris* and 40.7 m for *P. nouveli*) and were always found deeper than the zoeal stages. We did not find any decapodids of these species during the day; the only zoeal stages found in the neuston layer during the day belonged to *P. nouveli*. The ZO stages of *P. brevirostris* were distributed shallower than the other stages (ZN and D) especially during the night (Table 3, Fig. 7a).

Anomuran megalopa and zoeal stages never reached the neuston layer, with the exception of *Anapagurus* spp. during the night. In general, older larval stages (ZO and M) of the anomuran taxa were found deeper than the first and second zoeal stages (e.g. Fig. 7b). However, *Anapagurus* spp. only showed statistically significant differences for ZN vs. ZO (ND), *P. bernhardus* for ZN vs. ZO (ND and N) and ZN vs. M (ND), and *P. longicornis* for ZN vs. ZO (ND) and ZO vs. M (ND and N) (Table 3).

The megalopae of the brachyuran *A. rotundatus* were only found in the neuston layer during the night and never caught during the day. *N. puber* megalopae could reach the neuston layer during the day but never during the night (minimum WMD was 0.8 m). *Liocarcinus* spp. megalopae were always absent from the neuston layer (minimum WMD was 2.0 m at night and 1.6 m during the day). The ZO of *A. rotundatus* and *N. puber* never reached the neuston layer during the day (minimum WMD was 1.6 m and 3.9 m, respectively). The ZO of *A. rotundatus* were found deeper than the early zoeal (ND and N) and megalopa stages (ND and N) (Table 3). *Liocarcinus* spp. megalopa were always distributed deeper than the zoeal stages (Fig. 7c) and these differences were always statistically significant ( $p < 0.05$  and  $p < 0.001$ ) with the ex-

Table 3. Summary of Kruskal-Wallis by ranks and median statistics ( $H$ ) testing the significance of ontogenetic vertical migrations between larval stages of 9 decapod taxa, as well as the significant z-values for the pairwise comparisons between larval groups. Time of day: night and day (ND), night (N), and day (D); n = number of measured points. Larval groups: zoea new (ZN), zoea old (ZO), decapodid (D) or megalopa (M) \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns: not significant

Taxon	Time	n	df	$H$	z-value		
					ZN vs. ZO	ZN vs. D or M	ZO vs. D or M
<i>Pandalina brevirostris</i>	ND	161	2	6.177 <sup>ns</sup>			
	N	89	2	13.275 <sup>**</sup>	3.210 <sup>**</sup>		2.365 <sup>*</sup>
	D	72	2	0.000 <sup>ns</sup>			
<i>Philocheras bispinosus</i>	ND	94	2	0.522 <sup>ns</sup>			
	N	64	2	2.095 <sup>ns</sup>			
	D	30	2	0.000 <sup>ns</sup>			
<i>Processa nouveli</i>	ND	142	2	1.723 <sup>ns</sup>			
	N	73	2	2.876 <sup>ns</sup>			
	D	69	2	0.000 <sup>ns</sup>			
<i>Anapagurus</i> spp.	ND	85	2	8.239 <sup>*</sup>	2.867 <sup>**</sup>		
	N	55	2	3.845 <sup>ns</sup>			
	D	30	2	5.056 <sup>ns</sup>			
<i>Pagurus bernhardus</i>	ND	87	2	12.269 <sup>**</sup>	3.463 <sup>**</sup>	2.871 <sup>**</sup>	
	N	52	2	9.413 <sup>**</sup>	3.060 <sup>**</sup>		
	D	35	2	2.999 <sup>ns</sup>			
<i>Pisidia longicornis</i>	ND	63	2	17.402 <sup>***</sup>	3.401 <sup>**</sup>		3.465 <sup>**</sup>
	N	40	2	8.260 <sup>*</sup>			2.671 <sup>*</sup>
	D	23	2	7.179 <sup>*</sup>			
<i>Atelecyclus rotundatus</i>	ND	123	2	20.736 <sup>***</sup>	3.963 <sup>***</sup>		2.584 <sup>*</sup>
	N	68	2	19.494 <sup>***</sup>	3.837 <sup>***</sup>		2.683 <sup>*</sup>
	D	55	2	0.000 <sup>ns</sup>			
<i>Liocarcinus</i> spp.	ND	171	2	31.654 <sup>***</sup>	2.597 <sup>*</sup>	5.622 <sup>***</sup>	3.761 <sup>***</sup>
	N	86	2	23.993 <sup>***</sup>		4.777 <sup>***</sup>	4.086 <sup>***</sup>
	D	85	2	18.509 <sup>***</sup>	3.173 <sup>**</sup>	4.067 <sup>***</sup>	
<i>Necora puber</i>	ND	56	2	5.010 <sup>ns</sup>			
	N	29	2	5.384 <sup>ns</sup>			
	D	27	2	1.383 <sup>ns</sup>			

ception that during the day ZO were distributed as deep as megalopae (Fig. 7c) and the differences were no longer statistically significant ( $p = 0.362$ ). The first and second zoeal stages of this taxa always presented statistically significantly lower WMD ( $p < 0.05$  and  $p < 0.001$ ) than the older stages (ZO and M; Fig. 7c).

### DISCUSSION

Our study demonstrates that decapod crustacean larvae are retained in meridional patches (bands) off the northwest Portugal continental shelf, a coastal upwelling region similar to other eastern boundary upwelling systems. This was hypothesized by dos Santos et al. (2008) and Peliz et al. (2007) as a consequence of the local circulation, the coastline orientation, and the ability of the larvae to perform diel vertical migrations (DVM). The decapod larval distri-

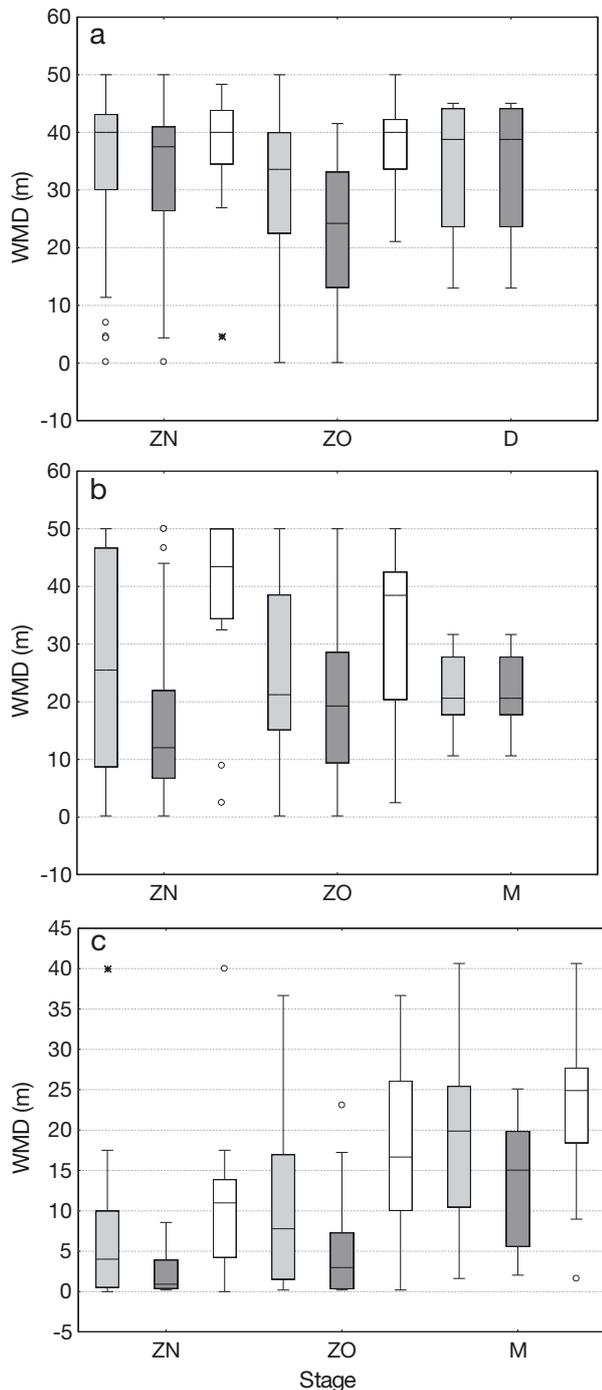


Fig. 7. Box plots of larval weight mean depth (WMD) at the fixed station (45°45.9' N 08°59.0' W) by stage group and time of day. (a) *Pandalina brevivirostris* (caridean shrimp); (b) *Pisdia longicornis* (anomuran crab); and (c) *Liocarcinus* spp. (brachyuran crab). The mid-line in the boxes represents the median, the box the upper and lower quartile, the whiskers the non-outlier range (coefficient = 1), the circles the outliers (coefficient = 1.5) and the \* denotes extreme values (coefficient = 3). Larval states: new zoea (ZN), old zoea (ZO), decapodid (D) and megalopa (M) (see Table 1 for more details). Light grey bars represent the night + day periods combined; dark grey the night; and white the day

bution in bands is in accordance with the known depth cline and distributional range of their adult populations. The larval stages of the inner shelf species were found very close to the shore in an 'inner shelf band', the larvae of shelf species were distributed over the middle shelf constituting a 'shelf band', and the larvae of the slope species were observed in the area adjacent to the shelf break forming the 'outer shelf band'. This distributional pattern is in accordance with the biophysical model study of Peliz et al. (2007), where it was proposed that with alternating episodes of north/south winds, larvae would tend to aggregate in alongshore band-like meridional patches in the same area.

Our results confirm that all larval developmental stages of the inner shelf species were retained near-shore and mainly restricted to a 10 km wide band parallel to the coast (Fig. 6a) even under coastal upwelling conditions, i.e. as observed just prior to our plankton sampling. The aggregation of intertidal invertebrate larvae close to the coast has been observed previously under weak upwelling conditions (Shanks & Brink 2005), moderate upwelling conditions (Shanks & Shearman 2009, Morgan et al. 2009b), and strong upwelling conditions (Morgan et al. 2009a). This clearly demonstrates that larvae of intertidal invertebrates remain close to the coast (5 to 6 km from the coastline) during both upwelling and downwelling conditions. In this present study, the observed upwelling relaxation allowed the intrusion of warmer waters near the coast (cf. Figs. 4 & 5) as well as an intensification of the northward currents at the inner shelf (Santos et al. 2006). As a consequence, the inner shelf species larvae experienced an alongshore transport across the potential settlement sites adjacent to the Aveiro coastal lagoon. This distribution and retention pattern has already been described for barnacles, cyprids, and *Carcinus maenas* larvae in the same area (dos Santos et al. 2007, 2008). Although the mechanisms that allow decapod larval retention in the inner shelf area remain unknown, it has been proposed that it is a consequence of their depth-keeping behavior (Shanks & Brink 2005, Yannicelli et al. 2006, dos Santos et al. 2008, Morgan et al. 2009b, Shanks & Shearman 2009, Morgan & Fisher 2010).

Based on a biophysical modeling study of crab larvae dispersal, Peliz et al. (2007) demonstrated that the distribution of decapod shelf species larvae in meridionally elongated bands parallel to the shore was a combination of local wind-driven circulation, buoyancy input from adjacent rivers, local topography and synchronized vertical migration behavior. Their results showed that about 50% of the larvae

stayed close to their release sites and the remainder were advected alongshore under intermittent upwelling conditions. Peliz et al. (2007) also demonstrated that the WIBP was a critical feature for crab larval retention over the shelf and their alongshore dispersion. Our results suggest the same conclusions, since the larvae of the shelf species band were only associated with the WIBP in the statistical analysis (cf. Table 2). Furthermore, dos Santos et al. (2008) observed that decapod larvae were retained over the northwestern Portuguese shelf, and hypothesized that this was due to their active DVM behavior. We found 3 different distributional patterns for the larvae in the 'shelf band'. One pattern was clearly shown by the higher abundances of *Upogebia* spp. and *Anapagurus* spp. larvae in the northern transects (*Anapagurus* spp. shown in Fig. 6b), whereas the other pattern was characterized by the concentration of *P. nouveli* and *C. subterranea* larvae in the southern transects (*C. subterranea* shown in Fig. 6c). Both pairs of species appear to be separated by the frontal structure perpendicular to the coastline (Fig. 5) that split the northern transects (T1 and T2) from the southern ones (T3 and T4). In reality, the distributional patterns probably reflected the recent advection of a water mass from the south (Figs. 3 & 4) and were not the result of the front. This hypothesis is reinforced by the fact that *Upogebia* spp. and *Anapagurus* spp. larvae that were concentrated in the northern transects belonged mainly to older stages (ZO; *Anapagurus* spp. shown in Fig. 6b), whereas larvae of *P. nouveli* and *C. subterranea*, more abundant in the southern transects, were mainly from early stages (ZN; *C. subterranea* shown in Fig. 6c). The third pattern shows that the remaining shelf species (*E. occultus*, *P. brevisrostris*, *P. bispinosus*, *A. rotundatus*, *Liocarcinus* spp. and *P. henslowii*) were widely distributed over the shelf and had higher abundances adjacent to the 100 m isobath (*P. henslowii* shown in Fig. 6d). This widespread pattern in an across shore distribution is most probably a consequence of the coupled dynamics of the upwelling front with the jet observed over the middle shelf. An upwelling front, meridionally oriented along the 100 m isobath, is a typical feature that occurs in this area during the coastal upwelling season with an equatorward jet associated with it (Peliz et al. 2002). The double-core upwelling jet flows parallel to, and on both sides of, the front; this recirculates onshore and offshore waters as the jet flows southward (Peliz et al. 2002). Thus, in our opinion, the natal origins and the larval vertical behavior of shelf species coupled to the coastal upwelling dynamics described above consti-

tutes an adequate mechanism to explain the third pattern of widely distributed larvae over the middle shelf (e.g. dos Santos et al. 2008). Most studies suggest that larval behavior mediates the cross-shelf transport (e.g. dos Santos et al. 2008), so ontogeny is a possible explanation for the transport of larvae of the same species in different directions. Our results show an ontogenetic-related response by the larvae of the widely distributed shelf species (the third group referred to above). For instance, the temperature preferences by *E. occultus* and *P. brevisrostris* zoeal stages were opposite to those observed for the decapodid stage of these species, which preferred warmer waters (temperature negatively related to the zoeal stages distribution, but positively related to their decapodids, see Table 2). Also, the early zoeal stages of *P. henslowii* were found closer to the shore than the older stages (ZN negatively related with the distance to the coast, while both ZO and M were positively related with this predictor, see Table 2).

As expected, the larvae of slope taxa (*S. membranacea*, *Parthenope* spp. and *G. rhomboides*) were positively related to the distance to the coast. Their negative relationship with temperature was explained by the higher concentrations in the 25 to 80 m depth layer inside the water mass of the outer shelf. This water mass had maintained the characteristics of the waters upwelled in the weeks prior to the plankton sampling (Fig. 4). It was expected that the zoeal stages of the outer shelf species were advected to the shelf by the intrusion of the slope waters during the upwelling relaxation (convergence conditions). Nevertheless, their decapodid or megalopal stages were virtually absent from this zone, suggesting an apparent migration to their adult habitats (where they will metamorphose and settle). This migration probably occurs throughout the offshore advection during the upwelling conditions observed prior to the survey.

Knowing that depth preferences can also be a result of ontogeny, contributing to interspecific differences in cross-shelf transport (e.g. Morgan et al. 2009a), the ontogenetic migrations were studied for some of the species in the present study. As stated before, in a 2 layer circulation pattern typical of upwelling systems, the ontogenetic shifts in the mean distribution depth of the larvae may result in different cross-shelf transport strategies (e.g. Yannielli et al. 2006, Morgan et al. 2009a). The DVM is a behavior that keeps the larvae close to their parental populations, but the deeper WMD through development is probably a strategy to enhance larval retention, survival and settlement success. In general, all the stages of the 9 species studied have a WMD

deeper (>15 m) than the surface Ekman layer, especially during the daytime period (Fig. 7). This means that the net vertical depth distributions of the larvae are outside the main offshore transport layer during coastal upwelling, which could be a strategy to be retained in, and not to be washed out from the shelf (Marta-Almeida et al. 2006, Morgan et al. 2009a). At the same time, the later stages of the 9 species analyzed (decapodids of the 3 caridean shrimps, and the older zoeal stages and megalopae of the anomuran and brachyuran species with the exception of *A. rotundatus*) were distributed closer to the bottom than the early zoeal stages. This deeper distribution closer to the adult populations will be an advantage when the time of metamorphosis and settlement approaches.

The paradigm of larval cross-shelf transport in coastal upwelling systems, in which circulation limits the supply of larvae to coastal populations through their offshore transport and favors it in relaxation or downwelling conditions (e.g. Connolly & Roughgarden 1999, Connolly et al. 2001, Menge et al. 2004) has been recently questioned by several studies carried out offshore of California and Oregon (north-eastern Pacific) (e.g. Wing et al. 2003, Morgan et al. 2009a, Shanks & Shearman 2009, Morgan & Fisher 2010, Morgan et al. 2011, 2012). All these studies concluded that intertidal invertebrate larvae remained close to the shore, avoiding high offshore dispersal and wastage independently of upwelling or downwelling conditions. The shifting currents over upwelling–relaxation cycles alter larval behavior (e.g. Morgan et al. 2012), and the dynamic interaction between physics and larval behavior is fundamental to determine the fate of larvae in a highly advective upwelling regime. We demonstrate that the detailed description of different water masses and ocean processes concurrently with the sampling of many species is fundamental to reveal the different responses in the vertical and horizontal distribution patterns of decapod larvae. The genetic homogeneity of the shore crab *Carcinus maenas* along the Atlantic coast of Iberia (Domingues et al. 2010) and the predicted demographic connectivity over this region are consistent with the local larval production (Domingues et al. 2012), suggesting a genetic exchange (effective migration) at a scale of 100s of km. Our results further support this view and extend it to a broader number of shelf/slope species whose larvae tend to be retained in bands according to their natal origins. Thus, larval distribution and retention in alongshore bands related to their parental populations, at least for estuarine, intertidal and shelf inver-

tebrate species seems to be a rule across different coastal upwelling systems. However, local oceanographic and topographic features (e.g. the WIBP and the IPC in the northern CCUS and headlands in the northern California Current upwelling system) could introduce site-specific particularities, mediating the dispersal/retention in a particular coastal upwelling system. At least along the northern CCUS coast, the current regimes and oceanographic features do not seem to act as barriers to larval dispersal and the close proximity of estuaries may in fact facilitate the exchange of migrants between rivers (Domingues et al. 2012). Peliz et al. (2007) estimated that the connectivity of crab populations on the northern CCUS shelf should be between 40 and 80 km, and suggested that some estuaries might be larval sources for other locations. As our results suggest, the alongshore retention of larvae and the oceanographic processes in the northern CCUS explain this potential connectivity over a relatively large geographic scale. Larval retention seems to be the rule when taking into account our study and comparing it to results from other regions with weak (e.g. North Carolina, northwestern Atlantic: Shanks & Brink 2005), moderate (e.g. Oregon, northeastern Pacific: Shanks & Shearman 2009; Chile, southwestern Pacific: Yannicelli et al. 2012) and strong coastal upwelling conditions (e.g. California, northeastern Pacific: Morgan et al. 2009a; Canary Islands, northeastern Atlantic: Landeira et al. 2012).

*Acknowledgements.* This study was supported by Fundação para a Ciência e Tecnologia (FCT) through the research project 'Pro-Recruit—shelf processes controlling recruitment to littoral populations in an eastern oceanic boundary: using barnacles and crabs as models' (POCTI/1999/BSE/36663), excellently coordinated by Henrique Queiroga. Many thanks to the crewmembers and technicians on the 2002 Pro-Recruit survey, and to Fátima Quintela for the laboratory support. C.B. is supported by FCT through the postdoctoral fellowship SFRH/BPD/63888/2009. This is a contribution to IMPROVE (PTDC/MAR/110796/2009) and MODELA (PTDC/MAR/098643/2008) FCT-funded projects were coordinated by A.d.S. and A.M.P.S., respectively.

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*Editorial responsibility: Steven Morgan,  
Bodega Bay, California, USA*

*Submitted: August 3, 2012; Accepted: April 5, 2014  
Proofs received from author(s): June 26, 2014*