

Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport

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ABSTRACT: The vertical distribution of decapod larvae off the northwest Portuguese coast was analysed in relation to associated environmental conditions from sampling during a 69 h period around a current meter mooring located on the shelf, approximately 21 km off the coast. Plankton samples were collected every 2 h at the surface with a neuston net and through the water column with a Longhurst Hardy Plankton Recorder (Pro-LHPR), allowing a very detailed resolution of larval vertical distribution. Environmental data (temperature, salinity, and chlorophyll *a*) were obtained every hour. To investigate the horizontal distribution of decapod larvae in relation to the coast, a plankton-sampling grid was carried out before the 69 h fixed station. Larvae of shelf decapod species were widely distributed over the shelf, while those of inshore species were found much closer to the coast. Decapod larvae (zoeae and megalopae) showed clear diel vertical migrations, only appearing in the upper 20 m at night, a migration that did not appear to be affected by physical conditions in the water column. Larval densities were highly variable, 0.01 to 215 ind. m⁻³ for zoeae and 0 to 93 ind. m⁻³ for megalopae, the zoeae being generally more abundant. The results indicated that during the day larvae accumulate very close to the bottom. The diel vertical migration behaviour is discussed as one of the contributing mechanisms for larval retention over the shelf, even with offshore transport conditions promoted by coastal upwelling, and is hence of major relevance for the recruitment success of decapod species that inhabit inshore and shelf zones of coastal upwelling systems.

KEY WORDS: Decapod larvae · Diel vertical distribution · Portuguese shelf · Transport processes

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INTRODUCTION

Most studies on marine invertebrate larval ecology emphasise the importance of understanding dispersal processes because of their influence on recruitment and population dynamics (Connell 1985, Underwood & Fairweather 1989). Transport processes during the larval phase are a critical component of the supply mechanism of larvae to habitats suitable for settlement and juvenile development (e.g. Botsford 1986). These processes also result in partition of time between

different environments during the different stages of larval development, exposing the larvae to different mortality factors (Queiroga & Blanton 2005).

Offshore studies focusing on spatial and temporal distribution of decapod larvae are rare (e.g. Lindley et al. 1994, Shanks & Eckert 2005), with most studies carried out in estuaries and inner coastal zones (e.g. Garrison 1999, DiBacco et al. 2001). Physical processes such as upwelling, downwelling and other wind-driven components of the circulation, internal waves and tidal bores, and density-driven flow have been

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proposed to explain variations in larval decapod supply rate (Shanks 1995, Queiroga & Blanton 2005). Larval vertical distribution and migration of inshore decapod species when offshore, as well as of species inhabiting different zones of the shelf, are probably important in determining retention over the shelf and eventual recruitment, as has been shown for other invertebrate larvae (Shanks & Brink 2005). Recent modelling studies on the Portuguese shelf (Marta-Almeida et al. 2006, Peliz et al. 2007) certainly indicate that larval decapod diel vertical migration between water masses moving in different directions at different depths may constitute a mechanism that contributes to their retention on the inner shelf near their release sites. Diel vertical migration behaviour has already been demonstrated for cirripede cyprids and sardine *Sardina pilchardus* larvae in the region (Santos et al. 2006, dos Santos et al. 2007).

The Ria Aveiro lagoon system and northern Portuguese offshore shelf region have recently been the focus of much work on the larvae of the shore crab *Carcinus maenas*. The first zoea and the megalopa developmental stages of this species are the only larval stages found inside the lagoon system (Queiroga et al. 1997), while the intermediate zoeae stages are found over the shelf (Queiroga 1996), a situation typical of many estuarine and inshore decapods. Vertical distribution studies on the larvae in the lagoon have shown vertical migration behaviour, particularly in relation to tidal cycles, that enhances the transport of the first zoea stage to the shelf (Queiroga et al. 1997) and the returning megalopae up the estuary (Queiroga 1998). Supply of megalopae to estuaries is thought to be partly controlled by the interaction of upwelling/downwelling circulation, driven by along-shore winds with the vertical position occupied by the larvae in the water column (Queiroga et al. 2006).

Available information indicates that larvae of virtually all decapod species perform some kind of diel vertical migration (Queiroga & Blanton 2005). However, in most cases this evidence is indirect and comes from studies on horizontal patterns of distribution and abundance. Most studies addressing vertical migrations in shelf waters over time have used only neuston sampling or sampling at discrete depths (e.g. Shanks 1986, Abelló & Guerao 1999) rather than high-resolution vertical sampling (Lindley 1986, Lindley et al. 1994).

The objective of the present study is to investigate the fine scale vertical distribution and migration behaviour of decapod larvae on the northern Portuguese shelf in relation

to environmental conditions, to contribute to a better understanding of the processes that control larval supply to littoral and shelf populations in eastern boundary upwelling systems, as found off Western Iberia. We focused on *Carcinus maenas* larvae in particular detail, because their life history is better understood than any of the other species occurring in the area. Information on this species could help in the interpretation of the distribution and behaviour of the other species.

MATERIALS AND METHODS

Fieldwork. A research cruise was carried out aboard RV 'Noruega' from 9 to 22 May 2002 on the Portuguese shelf (Fig. 1). Just after the beginning of the cruise on 11 May 2002, a mooring—with 3 current meters (Aanderaa RCM 9), located at 5, 15 and 35 m depths, and 2 high-accuracy conductivity, temperature and pressure recorders (SBE MicroCats)—was deployed on the inner shelf at 40° 45.9' N 08° 59.0' W, approximately 21 km offshore (Fig. 1). It was positioned at a bottom depth of 60 m, in an area adjacent to the Aveiro coastal lagoon where decapod larvae were expected to be abundant, including *Carcinus maenas* larvae (Queiroga 1996). The mooring was recovered on 16 June 2002.

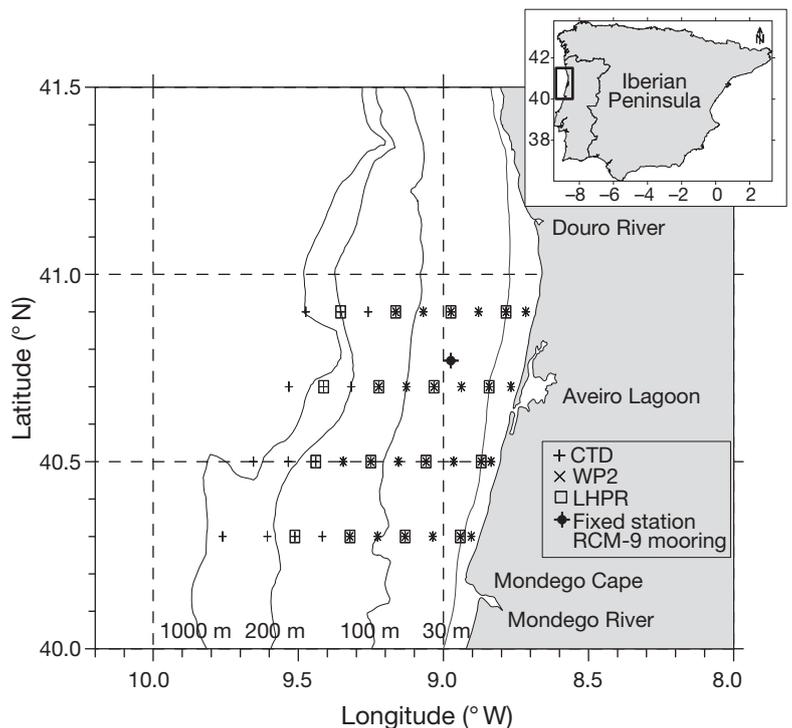


Fig. 1. Cruise stations and sampling details, 9 to 22 May 2002. CTD: conductivity, temperature, depth profiler; WP2: Working Party No. 2 plankton net; LHPR: Longhurst Hardy plankton recorder

From 18 to 21 May 2002, the fixed current meter station position was sampled continuously for 69 h. Temperature, salinity and chlorophyll *a* (chl *a*) concentration were measured every hour with a Seabird SBE 9 plus CTD (conductivity/temperature/depth) fitted with a Seapoint fluorometer. Depth-stratified zooplankton samples were collected every 2 h with a Pro-LHPR system, a commercially updated version of the Longhurst Hardy plankton recorder (Williams et al. 1983) to examine short timescale variability and detailed resolution of the vertical distribution of decapod larvae. The Pro-LHPR had a mouth opening of 0.42 m diameter and was fitted with a 280 μm mesh net and towed at ~ 4 knots, sampling on oblique hauls from the surface to 10 m above the bottom. This system collects zooplankton between 2 rolls of 280 μm filtering gauze. The gauze is advanced at operator specified time intervals inside a cod-end box to give, for each haul, a series of consecutive samples over the water column. The total sampling time for each haul was approximately 30 min and samples were collected at approximately 5 m depth intervals in the first 25 m, then at 10 m depth intervals down to near bottom. Flow rate was monitored by a flowmeter mounted in the mouth aperture, and each sample represented approximately 25 m^3 of water filtered. Neuston net samples were also collected every 2 h. This net had a single rectangular mouth opening of 0.2×1.0 m, a net of 335 μm mesh and a flowmeter mounted in the mouth aperture. It was towed horizontally for 3 min at a ship speed of ~ 1.5 knots, sampling the upper 20 cm of the water column.

To obtain environmental data for the region and decapod larval horizontal distribution and abundance, a grid of CTD casts and plankton sampling was carried out prior to the fixed-point sampling. This took place night and day from 15 to 17 May 2002 (60 h total duration) along 4 transects perpendicular to the coast. We used 2 different nets for plankton sampling, as indicated in Fig. 1: (1) a WP-2 (Working Party No. 2: UNESCO 1968) plankton net of 180 μm mesh and 0.58 m mouth aperture, fitted with a calibrated flowmeter, towed obliquely between the surface and 10 m above the bottom; and (2) the Pro-LHPR system. The Pro-LHPR sampling was conducted over a wider area, but the WP-2 sampling was done at higher resolution. The distance between stations was 8 km. The transect sampling is described in more detail in dos Santos et al. (2007).

Sample processing. All zooplankton samples were preserved in $\sim 4\%$ borax-buffered formaldehyde, prepared using seawater. Samples were subsequently sorted for decapod larvae. The WP-2 net samples were only sorted for *Carcinus maenas* larvae, while all decapod larvae were identified in the grid and fixed-station

Pro-LHPR samples and in the fixed station neuston net samples. Decapod zoeae were identified to species level and developmental stage, whenever possible, using descriptions in dos Santos & Lindley (2001) and dos Santos & González-Gordillo (2004). Megalopae were identified to genus or to species level, whenever possible, using the descriptions in González-Gordillo et al. (2001). Data were standardized to ind. m^{-3} using flow information. Zooplankton biomass was estimated using displacement volume.

Statistical analysis. In order to examine temporal changes in the vertical distribution of decapod larvae at the fixed station, the instantaneous average depth of the larvae from the Pro-LHPR samples and the instantaneous abundance of larvae in the neuston layer were calculated. Average depth is a useful measure in representing the vertical distribution of the larvae through the water column (Pearre 2003).

The average depth of zoeae and megalopae for each sampling time was calculated as the weighted abundance of the larvae collected in each stratum z , at each sampling time t :

$$WMD_t = \frac{\sum_{z=1}^9 (A_{zt} \times D_{zt})}{\sum_{z=1}^9 A_{zt}}$$

where WMD is the weighted mean depth of the larvae (m), A is the abundance (ind. m^{-3}), and D is the average depth of each stratum (m) (Pearre 2003).

Also used in the time series analysis of the data was the depth of maximum chl *a* concentration, the total zooplankton biomass (expressed as biovolume) and physical information obtained from CTD casts, including depth of the thermocline, halocline and the 35.6 salinity value, which is used as a proxy of low salinity buoyant plumes in the region (Peliz et al. 2002). Wind velocity and solar radiation data from the meteorological station of the University of Aveiro were also used.

Data on zoeae and megalopae were always analysed separately. The 69 h fixed station sampling was analysed using time series techniques, which usually require a series with at least 4 relevant cycles (Chatfield 1996), but sampling had to be curtailed when just less than three 24 h cycles were completed because of the onset of bad weather. Because of this, standard time series analysis was used, backed up with ANOVA and correlations between variables based on data integrated through time, which effectively removed the serial correlations that were present in the data series.

In order to detect the periods of oscillation, time series on average abundance of the larvae along the water column, abundance of larvae in the neuston layer and average depth of larvae were autocorrelated,

after removing the trend. Average depth and abundance in the neuston were also cross-correlated with the environmental variables. In most cases, the physical and the biological data were autocorrelated at a lag of 2 h. Since this can increase the significance values of the cross-correlations, the data series were differentiated using a time lag of 2 h before the calculation. Because the factors that limit upward migration during the night and set the distribution at depth during the day are not necessarily the same, we calculated cross-correlations separately for samples collected during the night and during the day, and also for the complete data series. The onset of day and night was delineated using sunrise and sunset times. The cross-correlation analyses were intended to test 2 key questions about the reaction of decapod larvae to changes in their physical environment: Do thermocline, halocline and the 35.6 salinity value constitute a barrier to upward migration at night? Does wind velocity and associated vertical mixing increase overall depth distribution of the larvae? The Bonferroni correction for multiple comparisons was used in all cases (Quinn & Keough 2002).

Average abundance through the water column, aggregated within complete 24 h periods, was found not to be autocorrelated and was tested by ANOVA, using the day and night periods as the independent variable. Cochran tests indicated moderate heterogeneity of variances in the case of the megalopae, but since the significance of the test was lower than the significance of the diel effect, transformation of the variable was deemed unnecessary (Underwood 1997). Changes in the diel vertical distribution of larvae were investigated by averaging abundance by depth stratum across all sampling points and scaling abundance in each stratum by total abundance in the water column, separately for day and night. This procedure removes diel differences in overall abundance of larvae and allows comparison of depth distribution patterns. The diel difference in proportions of larvae in each depth stratum was found not to be autocorrelated over depth, and therefore, we used the Pearson correlation coefficient to relate it with depth. If larvae had essentially the same diel vertical distribution, then the differences should be randomly distributed and uncorrelated with depth.

Archive data. Following the cruise, additional data from the Instituto Nacional de Recursos Biológicos (IPIMAR) zooplankton database (A. dos Santos unpubl. data) on *Carcinus maenas* (green crab) and *Atelecyclus rotundatus* (circular crab) larvae were analysed to compare with the cruise data. These were from plankton samples taken on 24 plankton/oceanographic surveys carried out off Portugal between October 1986 and July 1990, initially taken to study sardine *Sardina*

pilchardus spawning. The samples were taken with a 60 cm Bongo net of 305 μm mesh, in oblique hauls from surface to near bottom, in 2 transects perpendicular to the coast ($41^{\circ}05' \text{N}$ with 6 stations and $40^{\circ}05' \text{N}$ with 7 stations). The transects extended from 3 to 60 km off the coast.

RESULTS

Environmental observations

Coastal upwelling conditions occurred in the weeks preceding the survey. Several days before the fixed station was sampled there was a reversal of the wind direction, but this was not enough to significantly change the hydrographic patterns produced by the upwelling. During the fixed station sampling the wind reversed again to favour upwelling (Santos et al. 2006).

The CTD observations for the 69 h at the fixed station showed that, at this location, the depth of the thermocline oscillated between 10 and 20 m, without any obvious trend. Salinity showed a subsurface minimum, also between 10 and 20 m. During the first day of sampling, surface salinity values were ~ 35.7 . However, after the second day, an intrusion of less saline waters (< 35.6) was observed in the upper 10 to 20 m, probably advected from the north, as suggested by current

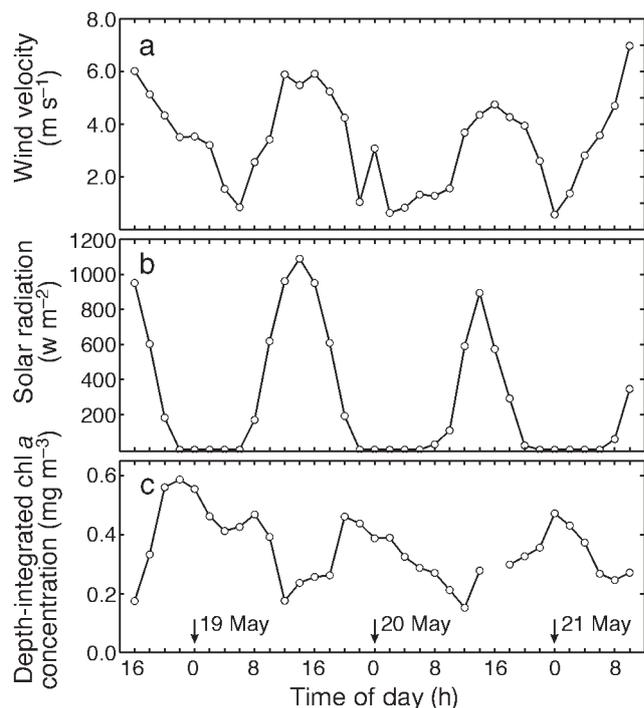


Fig. 2. (a) Wind speed, (b) solar radiation at the surface, and (c) depth-integrated average chl *a* during the 69 h fixed station study. Arrows indicate beginning of each day

meter measurements (Santos et al. 2006). After the second day the thermocline and the halocline were largely coincident and the chl *a* maximum was between 20 and 40 m.

Wind speed, solar radiation and depth-integrated chl *a* all showed cyclic diel variations at the fixed station (Fig. 2). During the first 48 h of the study, wind blew from the northwest, following the pattern typical of the wind regime of the Portuguese west coast, with low values during the night and early morning. Radiation and wind speed both peaked during the afternoon (Fig. 2a,b). The increases in wind speed during the afternoon of May 20 and during the early morning of May 21 were due to the passage of 2 cold fronts and were accompanied by a rotation to the southwest. Average chl *a* concentration over the water column peaked during the early night and decreased slowly through the night and morning (Fig. 2c).

Decapod larvae horizontal distribution

The horizontal distribution of total zoeae (Fig. 3a) showed that they were widely distributed over the shelf and in higher numbers than megalopae (Fig. 3b). Few zoeae were sampled at or beyond the 200 m contour on the 2 most northern transects or at most of the stations along the 30 m contour. Megalopae were most abundant between the 30 and 100 m contours. The most abundant larval species/genera in the area were *Liocarcinus* spp. (portunid crabs) (Fig. 3c), *Atelecyclus rotundatus* (Fig. 3d) and *Anapagurus* spp. (pagurid hermit crabs) (Fig. 3e). They all show a similar horizontal distribution to total zoeae, being more abundant between depths of 50 and 200 m. *A. rotundatus* is a shelf species during its adult phase, while the genera *Liocarcinus* and *Anapagurus* include species that can be both coastal and shelf when adults (Zariquiey-Álvarez 1968). The horizontal distributions of *Necora puber* (velvet swimming crab) and *Carcinus maenas* larvae, the most abundant representatives of coastal/estuarine species sampled, were also plotted for comparison (Fig. 3f,g). They showed a pronounced meridional distribution between the coast and the 30 m contour on the inner shelf, only occasionally being sampled further than 10 km from the coast. There were thus obvious distributional differences between the 2 categories of larvae plotted. *N. puber* and *C. maenas* were concentrated towards the coast and *A. rotundatus* and *Liocarcinus* spp. were widely distributed over the shelf.

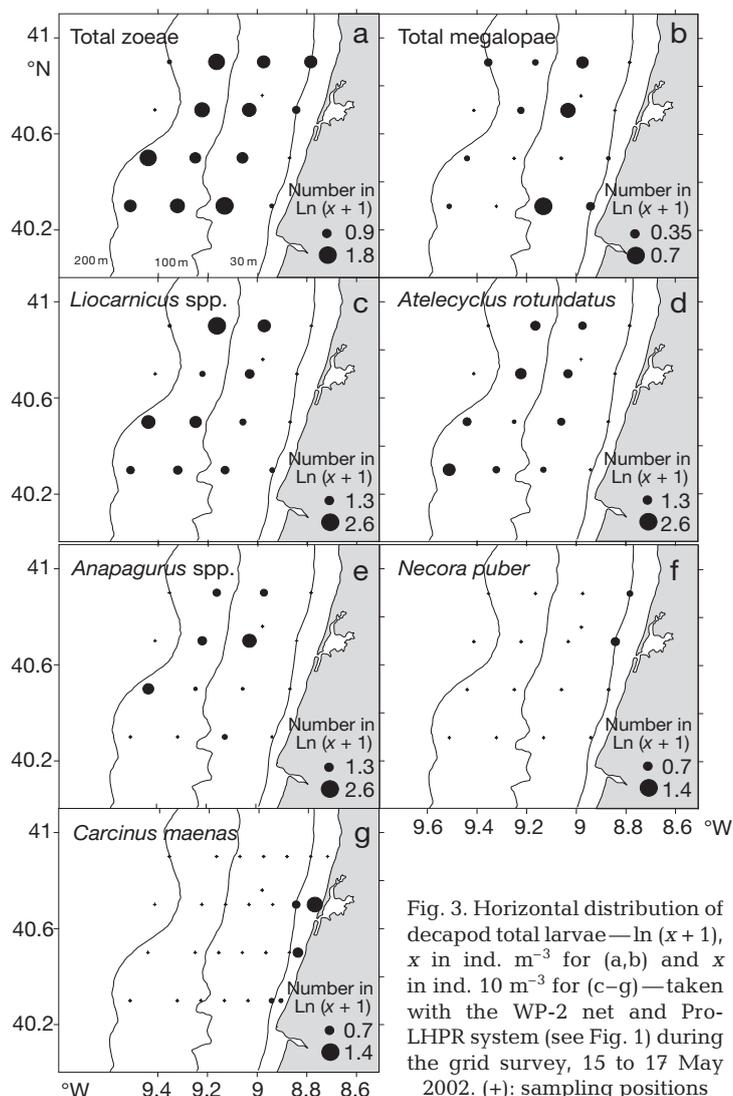


Fig. 3. Horizontal distribution of decapod total larvae— $\ln(x+1)$, x in ind. m^{-3} for (a,b) and x in $\text{ind. } 10 \text{ m}^{-3}$ for (c–g)—taken with the WP-2 net and ProLHPR system (see Fig. 1) during the grid survey, 15 to 17 May 2002. (+): sampling positions

The archive data from the study area, examined subsequent to the cruise, also showed from a series of 24 previous surveys along 2 transects that while *Carcinus maenas* larvae were mainly distributed over the inner shelf, mostly within an area 10 km off the coast throughout the year (Table 1), *Atelecyclus rotundatus* zoeae, but not megalopae, were mainly distributed over the middle shelf in a band between 10 and 20 km off the coast.

Decapod larval species composition at the fixed station

The list of all decapod larval species, or genera, sampled at the fixed station is given in Table 2. Of the 61 categories, most were sampled in very low numbers. Of the total categories, 14 were not sampled in the Pro-

Table 1. Archive data for *Carcinus maenas* (upper rows) and *Atelecyclus rotundatus* (lower rows and ZV, in italics) larvae in the study area, separated into different distance zones from the coast. Percent (average concentration \pm SD in ind. m^{-3}) of zoea (Z) and megalopa (M) stages over the whole area defined by the transects

	0–10 km	10–20 km	20–60 km
ZI	80 (0.65 \pm 0.31) 43 (0.49 \pm 0.34)	2 (0.01 \pm 0.01) 48 (0.54 \pm 0.66)	18 (0.14 \pm 0.17) 9 (0.09 \pm 0.04)
ZII	79 (0.15 \pm 0.21) 15 (0.11 \pm 0.08)	8 (0.01 \pm 0.004) 55 (0.39 \pm 0.34)	13 (0.02 \pm 0.0005) 30 (0.21 \pm 0.22)
ZIII	49 (0.05 \pm 0.03) 11 (0.06 \pm 0.03)	40 (0.04 \pm 0.02) 60 (0.35 \pm 0.39)	11 (0.01 \pm 0.001) 29 (0.16 \pm 0.1)
ZIV	53 (0.05 \pm 0.03) 5 (0.03 \pm 0.002)	29 (0.03 \pm 0.006) 75 (0.41 \pm 0.45)	18 (0.01 \pm 0.009) 20 (0.1 \pm 0.06)
ZV	2 (0.01 \pm 0.005)	81 (0.61 \pm 0.79)	17 (0.12 \pm 0.12)
M	89 (0.07 \pm 0.05) 37 (0.05 \pm 0.03)	11 (0.008 \pm 0.00005) 32 (0.04 \pm 0.06)	– 31 (0.04 \pm 0.03)

LHPR and 13 in the neuston net. Brachyuran larvae accounted for 54 % of the total decapod larvae sampled and were mainly *Liocarcinus* spp., *Atelecyclus rotundatus* and *Polybius henslowi* (swimming crab). Anomuran (hermit crab) and caridean (shrimp) larvae each accounted for 19% of total larvae. The most abundant larval anomuran species were *Anapagurus* spp., *Pisidia longicornis* (long-clawed porcelain crab) and *Pagurus bernhardus* (common hermit crab); the most abundant caridean species were *Philocheas* spp. (crangonid shrimps) *Pandalina brevirostris* (pandalid shrimp) and *Processa* spp. (processid shrimp). Megalopae represented about 21% of all decapod larvae sampled, the most abundant being *Liocarcinus* spp, *Pilumnus* spp. and *Philocheas bispinosus* comprising 47, 14 and 7% of megalopae, respectively.

Table 2. Mean abundance (\pm SD, ind. m^{-3}) of decapod larvae from the most abundant taxa collected with the Pro-LHPR (Longhurst Hardy plankton recorder) system and neuston net at the 69 h fixed station

Taxa	Pro-LHPR	Neuston	Taxa	Pro-LHPR	Neuston
BRACHYURA			<i>Galathea squamifera</i>	0.009 \pm 0.03	0.0003 \pm 0.001
<i>Liocarcinus</i> spp.	15.9 \pm 31.83	10.56 \pm 25.1	CARIDEA		
<i>Atelecyclus rotundatus</i>	5.16 \pm 15.97	3.33 \pm 12.57	<i>Pandalina brevirostris</i>	1.37 \pm 1.4	0.14 \pm 0.44
<i>Polybius henslowi</i>	2.66 \pm 8.87	1.92 \pm 7.07	<i>Philocheas bispinosus</i>	1.25 \pm 1.84	0.07 \pm 0.18
<i>Necora puber</i>	2.17 \pm 10.34	1.48 \pm 8.19	<i>Processa nouveli</i>	0.64 \pm 0.53	0.04 \pm 0.11
<i>Macropipus tuberculatus</i>	1.27 \pm 6.82	0.97 \pm 5.46	<i>Eualus occultus</i>	0.59 \pm 0.69	0.19 \pm 0.42
<i>Thia scutellata</i>	1.01 \pm 2.18	0.69 \pm 1.75	<i>Processa edulis</i>	0.09 \pm 0.13	0.19 \pm 0.87
<i>Pilumnus</i> spp.	0.98 \pm 1.38	0.49 \pm 0.95	<i>Palaemon serratus</i>	0.04 \pm 0.05	0.11 \pm 0.21
<i>Carcinus maenas</i>	0.65 \pm 1.23	0.21 \pm 0.56	<i>Athanas nitescens</i>	0.04 \pm 0.06	0.03 \pm 0.12
<i>Ebalia</i> sp.	0.14 \pm 0.41	0.07 \pm 0.21	<i>Philocheas trispinosus</i>	0.04 \pm 0.08	0.005 \pm 0.02
<i>Eurynome</i> sp.	0.07 \pm 0.11	0.04 \pm 0.1	<i>Processa modica</i>	0.02 \pm 0.06	0.002 \pm 0.008
<i>Pirimela denticulata</i>	0.04 \pm 0.07	0.39 \pm 1.29	<i>Alpheus glaber</i>	0.01 \pm 0.04	0.16 \pm 0.88
<i>Xantho incisus</i>	0.03 \pm 0.12	0.02 \pm 0.09	<i>Dichelopandalus bonnieri</i>	0.01 \pm 0.03	
<i>Brachynotus sexdentatus</i>	0.006 \pm 0.02		<i>Processa canaliculata</i>	0.008 \pm 0.03	0.0005 \pm 0.003
<i>Inachus</i> sp.	0.003 \pm 0.01		<i>Philocheas sculptus</i>	0.007 \pm 0.02	
<i>Parthenope</i> sp.	0.001 \pm 0.006		<i>Caridion steveni</i>	0.005 \pm 0.02	
<i>Pinnotheres pisum</i>	0.0008 \pm 0.004		<i>Crangon crangon</i>	0.003 \pm 0.01	0.05 \pm 0.2
<i>Portumnus latipes</i>		0.02 \pm 0.06	<i>Periclimenes sagittifer</i>	0.003 \pm 0.01	
<i>Monodaeus couchii</i>		0.01 \pm 0.06	<i>Lysmata seticaudata</i>	0.002 \pm 0.01	
<i>Pachygrapsus marmoratus</i>		0.002 \pm 0.01	<i>Thoralus</i> sp.	0.002 \pm 0.008	
<i>Xantho pilipes</i>		0.001 \pm 0.007	<i>Palaemon elegans</i>		0.04 \pm 0.25
<i>Cancer pagurus</i>		0.001 \pm 0.007	<i>Palaemon longirostris</i>		0.01 \pm 0.01
<i>Rochinia carpenteri</i>		0.0006 \pm 0.003	<i>Processa</i> sp.		0.006 \pm 0.03
<i>Geryon</i> sp.		0.0004 \pm 0.002	<i>Palaemon adspersus</i>		0.002 \pm 0.01
<i>Goneplax rhomboides</i>		0.0004 \pm 0.002	<i>Hippolyte</i> sp.		0.0006 \pm 0.003
ANOMURA			<i>Philocheas echinulatus</i>		0.0005 \pm 0.003
<i>Anapagurus</i> spp.	3.9 \pm 5.53	1.44 \pm 2.98	OTHER GROUPS		
<i>Pisidia longicornis</i>	1.65 \pm 2.71	0.24 \pm 0.8	<i>Upogebia</i> spp.	0.76 \pm 0.48	0.03 \pm 0.1
<i>Pagurus bernhardus</i>	0.89 \pm 0.97	0.006 \pm 0.02	<i>Solenocera membranacea</i>	0.04 \pm 0.07	0.002 \pm 0.008
<i>Galathea dispersa</i>	0.43 \pm 0.61	0.16 \pm 0.29	<i>Callianassa subterranea</i>	0.03 \pm 0.05	0.0005 \pm 0.003
<i>Pagurus</i> spp.	0.13 \pm 0.43	0.03 \pm 0.03	<i>Scyllarus arctus</i>	0.009 \pm 0.02	
<i>Galathea nexa</i>	0.07 \pm 0.09		<i>Jaxea nocturna</i>	0.007 \pm 0.02	
<i>Diogenes pugilator</i>	0.01 \pm 0.03	0.0005 \pm 0.003			

Vertical distribution and diurnal migration

To examine the comparative vertical distribution of inshore and shelf decapod larvae, the mean vertical distributions, averaged over the 3 d at the fixed station for each sampling time and depth interval, are given for *Carcinus maenas* and the 3 most abundant larvae, *Liocarcinus* spp., *Atelecyclus rotundatus* and *Anapagurus* spp. (Fig. 4). *C. maenas* was the only inshore species in high enough numbers to plot. Because numbers of larvae were variable over time and between species/genera, they were plotted as percentages to facilitate comparison. All species showed a very similar pattern of diel vertical distribution, generally being deeper in the water column during the day, migrating towards the surface and into the neuston layer at night, and returning to deeper water before or following dawn. There was no clear difference between the behaviour of *C. maenas* and the larvae of shelf species.

As the diel vertical distributions of the most abundant inshore and shelf decapod species/genera larvae at the fixed station appeared to be similar, the diel depth distribution of total decapod zoeae and total megalopae were similarly plotted (Fig. 5) to examine the vertical distribution of the entire decapod larval population.

Densities of zoeae were highly variable, from 0.01 to 215 ind. m⁻³. Below 20 m, there was no marked diel difference in numbers sampled (Fig. 5a). From 16:00 to 20:00 h, in the period prior to night, their distribution was almost bimodal, with some of the lowest numbers in the intermediate depths. Between 22:00 and 02:00 h, during the first period of the night, numbers increased considerably in the upper 20 m, especially in the neuston layer. In the remaining night period up to 06:00 h, numbers in the 0 to 20 m depth layers gradually decreased and zoeae moved out of the neuston layer. Following dawn, between 08:00 and 14:00 h, zoeae numbers reduced further and highest numbers were deeper in the water column.

Megalopae were sampled in lower numbers than zoeae (from 0 to 93 ind. m⁻³), but showed essentially the same vertical distribution. In the period prior to night, numbers were generally low over the whole water column, with some of the highest numbers below 35 m and a bimodal distribution. Numbers gradually increased in the upper 35 m at night until 02:00 h, especially in the neuston layer and then decreased rapidly before dawn. On return to daylight, from 08:00 to 14:00h, numbers gradually increased towards the bottom.

More larvae were generally collected during the night than during the day; 3 and 8 times higher for zoeae and megalopae, respectively. Megalopae showed a more pronounced diel difference in numbers

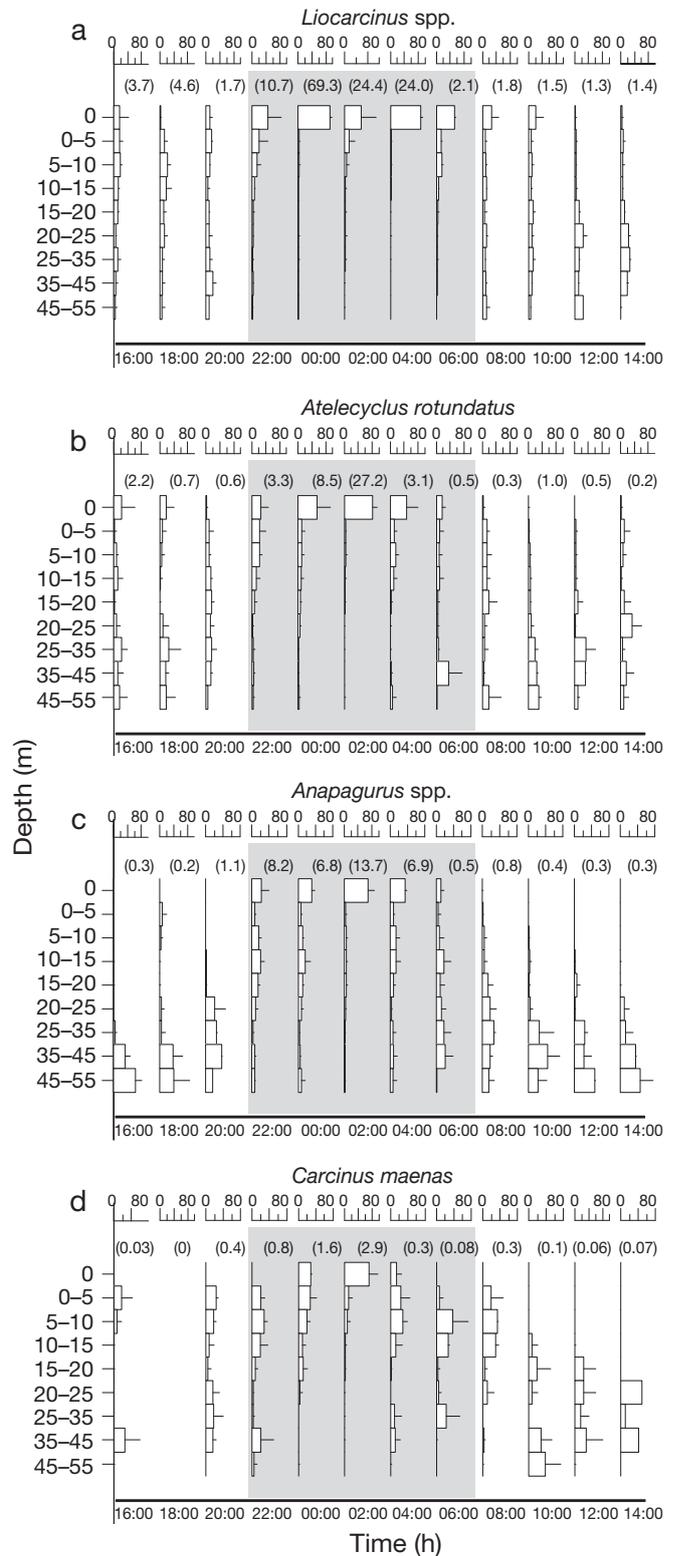


Fig. 4. Vertical distribution of the most abundant decapod larval species (as percentage of total numbers ± SE) from the Pro-Longhurst Hardy plankton recorder and neuston hauls at the 69 h fixed station, averaged over the 3 d. (■): night period. Numbers in brackets are average abundance in ind. m⁻³ for the entire water column at each sampling time

sampled at all depths (Fig. 5b), many more being sampled at night compared to the zoeae. These diel differences were significant, both for zoeae and megalopae (zoeae: $F_s = 10.850$, $df = 1$, $p < 0.05$; megalopae: $F_s = 12.529$, $df = 1$, $p < 0.05$).

The diel difference in proportions of larvae, aggregated across sampling times, was not significantly correlated with depth in the case of the zoeae ($r = 0.55$, $df = 7$, $p > 0.10$), but was with the megalopae ($r = 0.72$, $df = 7$, $p < 0.05$). Proportionally fewer megalopae were collected above 20 m and more below 20 m during the day than at night. The zoeae, despite a non-significant correlation, were proportionally more abundant during the night in the neuston layer and always more abundant during the day in the other depth strata.

Average abundance, abundance in the neuston and average depth of zoeae and megalopae are given in Fig. 6, which consistently shows higher values of abundance and a shallower distribution during the night. Autocorrelation values (Fig. 7) were always positive at a time lag of 24 h, and negative at time lags between 8 and 18 h.

Vertical distribution of larvae in relation to environmental variables

During the day, the average depth distribution and abundance of zoeae were positively correlated with wind velocity ($r = 0.595$, $p < 0.05$), but not with zooplankton biovolume, chl *a* or solar radiation. During the night, average depth of the zoeae and abundance of zoeae and megalopae were not correlated with any of the variables. When the complete data series was tested, only wind speed was positively correlated with average depth of the zoeae ($r = 0.541$, $p < 0.05$).

Transport, retention and diel vertical migration

Larval drift was simulated using the current meter mooring data and the diel vertical migration pattern observed. Results showed that larvae stay in the Ekman surface layer during the night (21:30 h to 06:30 h), migrate to the bottom at 'dawn' (06:30 to 07:30 h), stay in the bottom Ekman layer during the day (07:30 to 20:30 h), and migrate to the surface at 'dusk' (20:30 to 21:30 h). It was considered that average transport was nil during both migrations (dawn and dusk).

The advection in the Ekman surface layer was calculated using the speed and direction data from the current meter located at 15 m depth. Considering that the 35 m current meter measured the interior flow field not affected by the Ekman layers, advection at the bottom was calculated applying a simple parameterisation (correction) to obtain an estimation of the speed and direction in the Ekman bottom layer. The correction was calculated considering that the shelf is weakly stratified at this time of the year and, with a viscosity of $0.02 \text{ m}^2 \text{ s}^{-1}$, the speed of the 35 m current meter is reduced, on average, to about half and the direction about 30° to the left (A. Peliz pers. comm.). Based on this information, a progressive vector diagram, which is a way to simulate a Lagrangian display from Eulerian measurements, was computed for the period 11 May to 15 June 2002 (Fig. 8).

It is clear from Fig. 8 that the main component of the transport is alongshore and very little offshore advection occurs. In the first days there is a northward advection with downwelling conditions until about

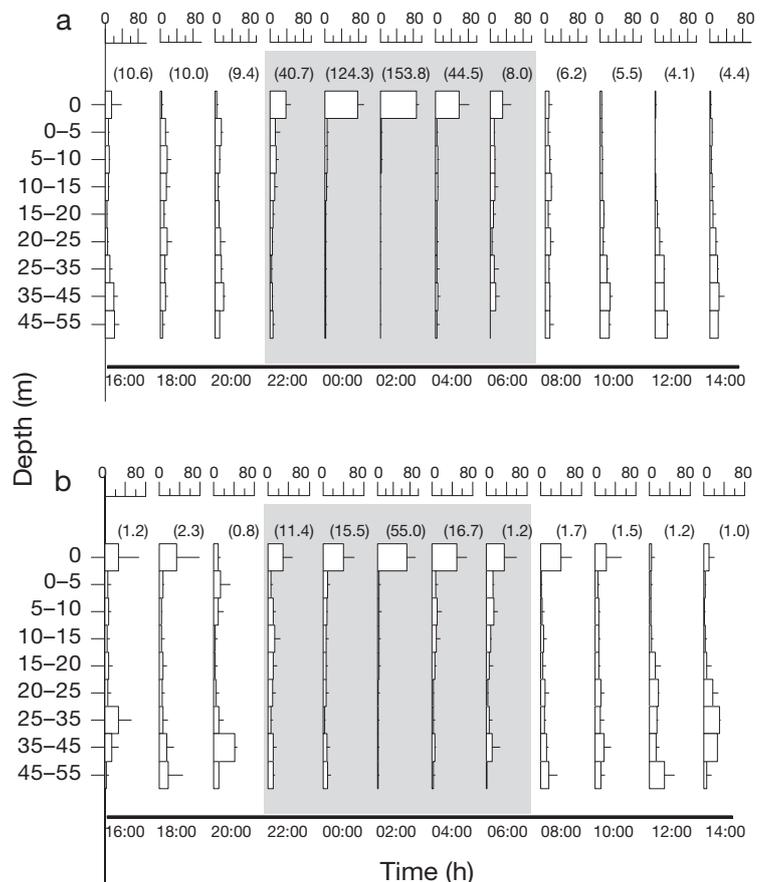


Fig. 5. Vertical distribution of (a) total decapod zoeae and (b) total megalopae (as percentage of total numbers \pm SE) from the Pro-Longhorst Hardy plankton recorder and neuston hauls at the 69 h fixed station, averaged over the 3 d. (■): night period. Numbers in brackets are average abundance in ind. m^{-3} for the entire water column at each sampling time

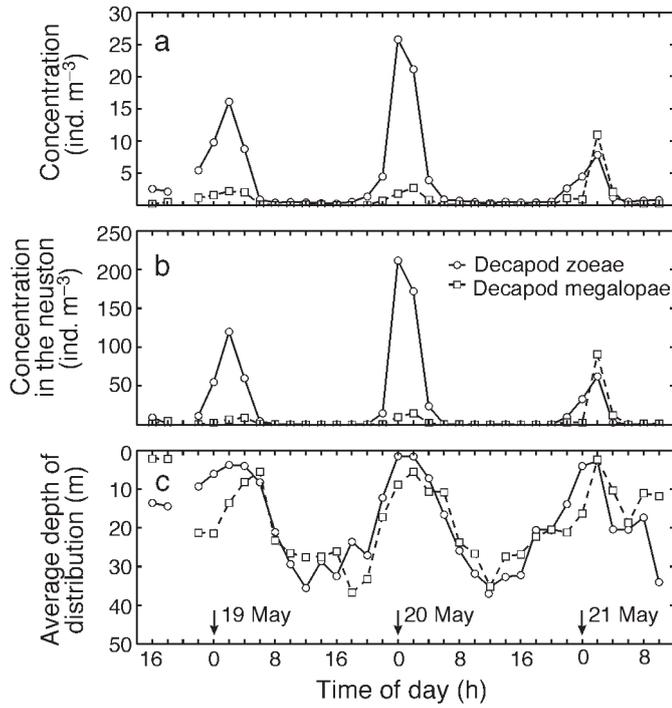


Fig. 6. (a) Integrated abundance in the water column, (b) abundance in the neuston and (c) average depth distribution of decapod zoeae and megalopae from the 69 h fixed station sampling. Arrows indicate beginning of each day

18 May 2002. Following this there is a reversal of the wind direction to favour upwelling, when the advection is almost entirely equatorwards, a situation that generally persisted until the end of the current meter measurements on 15 May 2002. Thus, even with upwelling-favourable conditions for almost 1 mo,

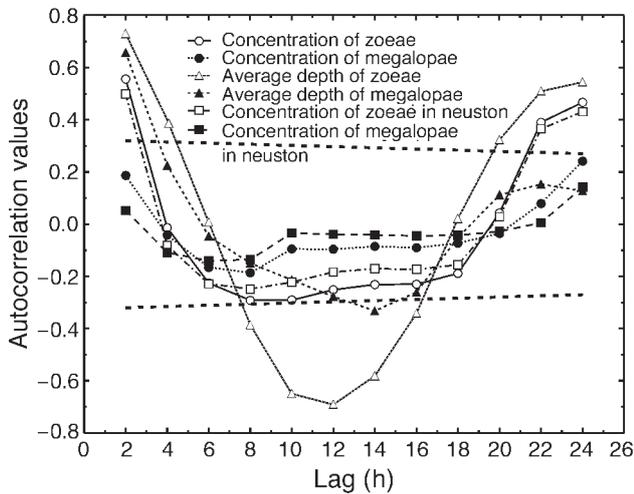


Fig. 7. Autocorrelation values for integrated abundance in the water column, abundance in the neuston and average depth distribution of decapod zoeae and megalopae during the 69 h station study. (----): 5% significance level

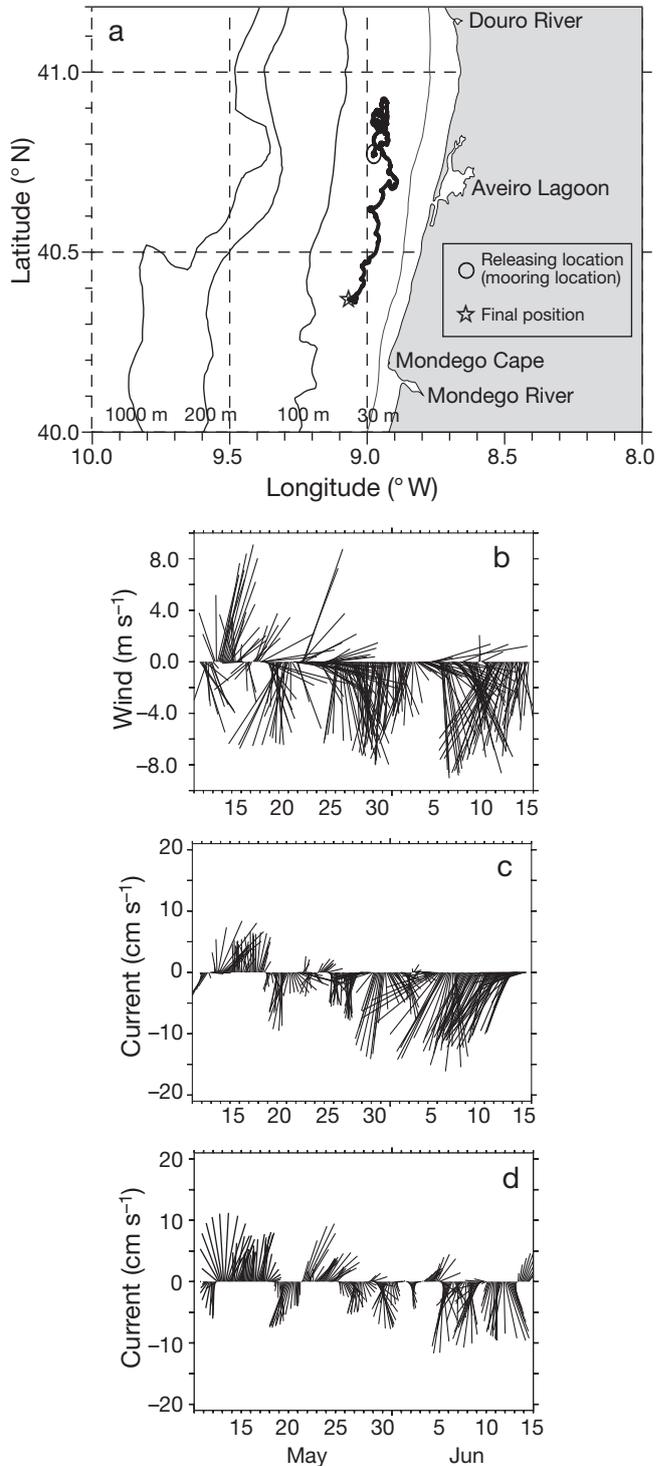


Fig. 8. (a) Progressive vector diagram that simulates larval drift based on their diel vertical migration behaviour. Stick diagrams of (b) wind measured by the Portuguese Meteorological Office (IM) at Cape Carvoeiro (39° 21.6' N, 09° 24.0' W) and (c,d) current meter data at (c) 15 m and (d) 35 m (see 'Materials and methods' for a more detailed explanation). (O): larval release point (corresponding to the location of the current meter mooring array); (☆) final location of larvae after about 1 mo of simulation

cross-shelf dispersal of vertically migrating larvae was highly reduced, and the net result is retention with a meridional distribution over the shelf.

DISCUSSION

Species analysis of the decapod larvae from the LHPR and neuston net samples taken at the fixed station indicated high species diversity, with 61 species/genera recorded, typical of the region (dos Santos 1999). Some only occurred in one or the other of the nets, but this was probably a reflection of the low numbers sampled, rather than a true indication that they were restricted to the neuston layer, or to deeper in the water column. Brachyuran larvae dominated in the samples, comprising 54 % of total decapod larvae, a proportion normal for northern European waters (e.g. Lindley et al. 1994) and for the Portuguese shelf (dos Santos 1999).

Horizontal distributions clearly showed a pattern related to their presumed settlement areas. The inshore species, *Carcinus maenas* and *Necora puber*, were concentrated towards the coast, while the shelf species were widely distributed. The distribution of *C. maenas* larvae was of particular interest, due to its socio-economical importance in the region of the Aveiro Lagoon and previous knowledge on their ecology inside this system (Queiroga et al. 1997). These larvae were expected to be abundant in the region of the fixed station, based on data from a previous cruise (Queiroga 1996), in which zoeal stages, other than the first zoeae, were found over the middle shelf, further offshore than in the present study. However, that cruise may have been in an exceptional period, as the present cruise distributional data and also the archive data showed that the fixed station was located just outside their normal main distribution.

The most abundant taxa were *Liocarcinus* spp., which includes species such as *L. depurator*, *L. arcuatus* and *L. marmoreus* that occur both inshore and over the shelf. All are common in Portuguese waters (Zariquiey-Álvarez 1968), but as they could not be speciated only a general distribution pattern was obtained. Larvae belonging to species that must return to the coast for settlement, such as *Carcinus maenas*, *Necora puber*, *Pisidia longicornis* and *Diogenes pugilator*, were rare at the fixed station, and their horizontal distribution showed that they were mainly restricted to a 10 km-wide band along the coast, over bottom depths less than 30 m. This result is similar to that obtained by Shanks & Eckert (2005), who analysed the distribution of larvae from coastal and shelf species from the California upwelling system and concluded that larvae belonging to inshore species are mainly located within 20 km of the shore.

Diel abundance of decapod larvae was statistically different, there being many more sampled at night, especially in the neuston layer. This could indicate net avoidance, as has been shown for other zooplankton species using different nets (Stehle et al. 2007). However, Lindley et al. (1994), using similar LHPR equipment, concluded that there was no clear evidence for avoidance by decapod larvae. The neuston net was towed at ~1.5 knots (0.77 m s^{-1}), less than half the speed of the Pro-LHPR; therefore, some avoidance during the day is possible, especially by the more motile brachyuran megalopae. However, considering the size and swimming ability of decapod larvae (Mileikovsky 1973, Chia et al. 1984), avoidance would be unlikely to be a problem with either net. Therefore, our results suggest that during the day, both zoeae and megalopae larvae will be in the narrow layer close to the bottom that, for equipment safety reasons, was not sampled by the Pro-LHPR. This deep distribution has been shown to occur with *Pandalus jordani* early juveniles stages off the central Oregon coast (USA) (Rothlisberg & Pearcy 1977).

The Portuguese shelf has a complex hydrography, coastal upwelling events occurring periodically during spring and summer, as they did before the cruise and during the sampling at the fixed station. This upwelling, in conjunction with the Western Iberian Buoyant Plume (WIBP) and the slope circulation associated with the Iberian Poleward Current (IPC) (Peliz et al. 2002, Santos et al. 2004) will influence the dispersal of decapod larvae over the shelf. The WIBP appears to be present all year round off NW Iberia (Peliz et al. 2002, Santos et al. 2004, 2006), changing the buoyancy and stratification of the shelf water column and, consequently, the surface Ekman layer transport and inner shelf circulation. In the case of a well-developed WIBP, the transport, in the surface layers would be mainly offshore during upwelling. However, the presence of the IPC could create a blocking effect to this offshore transport, and the interactions with the WIBP generate a convergence zone at the shelf break and a mechanism of larval retention over the shelf (Santos et al. 2004).

Inshore decapod larvae exported from the Aveiro lagoon system, developing on the inner Portuguese shelf, should experience greater alongshore than cross-shelf transport, as suggested by a modelling study (Peliz et al. 2007). As a result, these larvae should be distributed in the inner and middle shelf in patches parallel to the coast, related to the intermittency of downwelling and upwelling events, the associated alongshore circulation and the presence of buoyant plumes in the area. This is exactly the distribution observed in the current study for *Carcinus maenas* and *Necora puber*, also predicted by the larval drift calcu-

lations based on the current meter data (Fig. 8). Similar distributions were previously reported for cirripede cyprids (dos Santos et al. 2007), although in a more offshore position, and are considered a common event, controlled by the inner shelf circulation (Epifanio & Garvine 2001).

Larval dispersal due to shelf hydrography depends greatly on their vertical distribution and time spent in different water layers, so the capacity to perform diel vertical migrations will be a crucial factor. Decapod larvae, both of inshore and shelf species, showed conventional diel vertical migrations, the majority appearing in the surface layers at night, returning to deeper water during the day. This behaviour is similar to that found for decapod larvae in the North and Celtic Seas (Lindley et al. 1994) and may contribute to their retention on the shelf during upwelling conditions. Results from a modelling study on the retention of larval *Carcinus maenas* off Western Iberia (Marta-Almeida et al. 2006), indicated that there would be high dispersal in the absence of diel vertical migration. By partitioning the time between a surface layer moving seaward and a bottom layer where the compensating counter-current develops, larvae avoid seaward dispersal (Peterson 1998). Physical and biological gradients in the water column have been shown to alter vertical migration in cirripede larvae in the study area (dos Santos et al. 2007) and decapod larvae in other areas (e.g. Hobbs & Botsford 1992, Lindley et al. 1994, Wing et al. 1998). However, the only factor measured which appeared to modify decapod larval vertical distribution in the present study was an increase in wind speed that resulted in zoeae having a deeper average depth distribution. This may have been due to an active migration to avoid turbulence, or a passive re-distribution due to a higher mixing depth.

Another suggested mechanism for transporting inshore decapod megalopa larvae to the coast is by internal waves acting on the surface layer (Shanks 1985). However, the study was based on neuston sampling only and requires that for transport to be accomplished, megalopae should be neustonic and not perform diel vertical migrations. Based on the results of the present study, this mechanism would not operate, as megalopae spent more time close to the bottom, where if they remained they would be transported inshore in the Ekman bottom layer during upwelling events. However, their diel vertical migration away from the bottom would maintain their position around the same location, or take them a little further inshore.

Nevertheless, offshore transport is not a problem for larvae migrating over the middle shelf, as this group was composed of larvae whose adults mainly inhabit the shelf and their megalopae can settle anywhere

over the shelf. Tapia et al. (2004) suggested that larval supply to shore habitats could be associated with daily sea breezes that can produce short-term, strong onshore surface currents. However, megalopae would need to be at the surface during the morning hours and although around 28% were at the surface between the 06:00 and 10:00 h, more were present (48%) at night from 22:00 to 04:00 h, so only a small proportion would benefit from this mechanism.

Off the Portuguese coast, retention of decapod larvae in inshore waters is probably determined by intensification and relaxation of upwelling-favourable winds, which have pulses of ~7 to 10 d (dos Santos et al. 2007). In inshore waters (depths less than 30 m) surface and bottom layers tend to overlap, reducing cross-shelf transport (Peterson 1998), thus diel vertical migration will not be an advantage for larval retention. However, the intermittency of upwelling/downwelling events could be an important mechanism to retain decapod larvae inshore as was showed for bivalve larvae off California (Shanks & Brink 2005).

The modelling of Peliz et al. (2007) predicts that decapod larvae will be distributed alongshore over the middle shelf as a consequence of the upwelling system dynamics. This appears to be true for decapod larvae belonging to shelf species and also for larvae with a distribution on the inner shelf and for some other crustacean larvae inhabiting the area (dos Santos et al. 2007). The other model (Marta-Almeida et al. 2006) predicts that larvae performing diurnal vertical migration and subjected to upwelling conditions will be retained on the shelf during their development, which is also supported by our data. However, the larval drift simulation (Fig. 8) indicates that *Carcinus maenas* zoea found at the fixed station (21 km offshore), and any other shore or estuarine decapod larval species that has been carried to the middle shelf, would not reach the coast within a realistic time to settle. *C. maenas* megalopae has only 12 to 17 d duration at 12.5 to 18°C (Dawirs 1985) so only those larvae retained in the inner shelf zone, as a large proportion appear to be, would be able to settle and recruit. Therefore, the numbers of estuarine and coastal decapod larvae recruiting each year will depend on the interannual differences in hydrographic conditions and the varying distances they are carried from the coast.

Once inshore and estuarine larvae are over the inner shelf they may be able to detect specific cues indicating they are close to the coast and take actions to bring them to their settlement areas, for example changing their migratory behaviour to synchronise with tides (Queiroga et al. 2006). In support of this, it has been observed that some decapod larvae, reared under laboratory conditions, only metamorphose in the presence of settlement cues (Forward et al. 1994, dos Santos et

al. 2004), and that megalopae of estuarine species show different swimming behaviours in the presence of estuarine and oceanic waters (Forward & Rittschof 1994). However, confirmation of this will require further investigations in the coastal zone.

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