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Vertical distribution of the European sardine (*Sardina pilchardus*) larvae and its implications for their survival

A. MIGUEL P. SANTOS[1]*, PEDRO RÉ[2], ANTONINA DOS SANTOS[1] AND ÁLVARO PELIZ[3]

[1]INSTITUTO NACIONAL DE INVESTIGAÇÃO AGRÁRIA E DAS PESCAS-IPIMAR, AVENIDA DE BRASÍLIA S/N, 1449-006 LISBOA, PORTUGAL, [2]LABORATÓRIO MARÍTIMO DA GUIA, DEPARTAMENTO DE BIOLOGIA ANIMAL, FACULDADE DE CIÊNCIAS DA UNIVERSIDADE DE LISBOA, ESTRADA DO GUINCHO, 2750-374 CASCAIS, PORTUGAL AND [3]DEPARTAMENTO FÍSICA-CENTRO DE ESTUDOS DO AMBIENTE E DO MAR, UNIVERSIDADE DE AVEIRO, 3810-194 AVEIRO, PORTUGAL

*CORRESPONDING AUTHOR: amsantos@ipimar.pt

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This study presents results of the vertical behaviour of the European sardine (Sardina pilchardus) larvae as observed at sea off the NW Iberian coast during an oceanographic cruise conducted in May 2002. Samples were taken in a grid of 38 stations (conductivity-temperature-depth [CTD] measurements and Longhurst Hardy Plankton Recorder [LHPR] plankton hauls); a 69-h fixed station study was also performed (hourly CTD measurements and LHPR/neuston hauls every 2 h). The horizontal distribution of larvae is closely related to the circulation patterns measured by a current metre-mooring array deployed during the cruise. Larvae were mainly distributed in the upper 20–25 m of the water column, in evident association with the waters of the Western Iberia Buoyant Plume (WIBP). Large (older) larvae are found mainly in the surface layers, and larval size decreases with depth. A diel rhythm of migration to the neuston layer was observed, correlated with the inflation/deflation activity of the swim bladder. Larvae with lengths greater than 12.5 mm and inflated swim bladders were only found in this layer. Considering the near surface stratification conditions for food availability and Ekman transport in the upper few metres, even small vertical migrations of larvae can be very important for their survival and subsequent recruitment success.

INTRODUCTION

The European sardine *Sardina pilchardus* (Walbaum, 1792) (hereafter called sardine) is one of the most important fisheries in the NE Atlantic, which is essentially confined to the Iberian Peninsula and Moroccan coasts. The decrease in the abundance of this species could cause serious socioeconomic problems for the countries of the region.

Santos *et al.* (2001) and Borges *et al.* (2003) studied changes in recruitment and catches of sardine in relation to upwelling events that occurred during the spawning season (wintertime). They put forward the hypothesis that the offshore transport of larvae during these events could be a major factor for their survival and subsequent recruitment. In fact, the survival of fish's early life-history stages is a major factor that could explain recruitment variability in small pelagic fish species like the sardine, which is closely linked to oceanographic processes related to transport and dispersal. In Western Iberia, the transport/dispersal of sardine larvae is affected by factors such as the wind-driven transport, the structure and circulation of the WIBP and the slope circulation associated with the Iberian Poleward Current (IPC) (Santos *et al.*, 2004). Since some of these oceanographic processes may have a differential impact in relation to depth, it is crucial to know the vertical distribution of the larvae.

Almost all planktonic organisms, including fish eggs and larvae, are found to have heterogeneous vertical distributions, even in well-mixed water columns. Fish eggs are

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often buoyant and tend to float towards the surface (Coombs, 1981), but fish larvae are usually denser than seawater, and their buoyancy can change in relation to physiological condition (e.g. Sclafani *et al.*, 1993). According to Heath (1992), active depth selection (swimming ability and buoyancy) has several advantages, namely (i) preference for avoidance of particular physical conditions such as temperature, light intensity or wave action; (ii) attraction to zones of high prey density; (iii) avoidance of zones with high number of predators; (iv) rhythms of swim bladder inflation/deflation; and (v) optimization of horizontal distribution by vertical shear. Santos *et al.* (2004) and Ribeiro *et al.* (2005) stressed the importance of depth distribution of fish eggs and larvae for their survival off Western Iberia. However, information on the vertical distribution of fish eggs and larvae is scarce, mainly due to sampling difficulties (Conway *et al.*, 1997). Off Western Iberia, only a few studies have addressed the vertical distribution of individual fish larvae (Andres *et al.*, 1992; John and Ré, 1995; John *et al.*, 1996). These studies have provided limited information about the vertical distribution of sardine larvae, and none of it was based on repeated sampling over complete diel periods.

The aim of this study is to contribute to the knowledge of the vertical distribution of sardine larvae in order to allow future numerical modelling studies of fish larval dispersal under different oceanographic scenarios. Several issues were addressed, namely depth preference, association with oceanographic features, rhythms of migration and swim bladder inflation/deflection rhythms based on a vertical stratified sampling for a period of 69 h.

METHODS

A research cruise was carried out aboard RV 'Noruega' (ProRecruit'2002-02050502) from 9 to 22 May 2002 off the northwest Iberian coast (Fig. 1). The main objective of the cruise was the study of the processes that control the supply of invertebrate larvae to coastal systems (Santos, 2002), as well as the vertical and horizontal distribution of fish larvae.

An initial grid of CTD stations (grid1), composed of four transects perpendicular to the coast was carried out from 11 to 14 May 2002, to obtain, in conjunction with the current metre measurements (see below), a quasi-synoptic view of the mesoscale circulation patterns. Temperature and salinity were measured at each station with a CTD SBE 9p (S/N 19860-0530), in its first use after factory calibration, with a sampling rate set to 12 or 24 scans per second and a lowering rate of $\sim$1 m s^{-1}. The same grid was repeated on 15–17 May 2002 (grid2), but in addition to CTD sampling at each station, depth-stratified plankton samples were collected at shelf stations (Fig. 1) using a modified Pro-LHPR system (Williams *et al.*, 1983). A fixed station (fpoint) was carried out for 69 h from 18 to 21 May 2002 at 40°45.9′N and 08°59.0′W over a bottom depth of 60 m and about 30 km from the shore (Fig. 1). This station is located round the current metre-mooring array deployed at the beginning of the cruise (3 Aanderaa RCM-9 at 5, 15 and 35 m depths). Environmental sampling carried out during the fixed station included the measurements of temperature and salinity every hour with the CTD and depth-stratified zooplankton samples collected every 2 h using the Pro-LHPR system and a neuston net. The Pro-LHPR system with a 280 μm mesh net was towed at 3–4 knots on oblique hauls from the surface to near the bottom. This system collects plankton between two rolls of filtering gauze with a 280 μm mesh, which are advanced at intervals inside a cod end box to give a series of consecutive samples. The depth intervals sampled were (i) every 5 m in the first 25 m, (ii) every 10 m from 25 to 55 m depth and (iii) every 20 m hereafter. The neuston net had a rectangular opening of 1×0.20 m^2 (335 μm mesh size) and a flow metre mounted in the mouth. The net was towed horizontally in the first 20 cm of the surface layer at a ship speed of $\sim$1.5 knots for 3 min. All samples were preserved in 4% borax buffered formaldehyde prepared using seawater. Sardine larvae were subsequently sorted, counted and measured. Larvae were measured with the aid of a binocular microscope to the nearest 0.5 mm by placing the larva on a transparent grid marked in millimetres and illuminated from below. All larval lengths correspond to standard lengths. For comparison of vertical distributions between night and day, weighted mean depth (WMD) values were calculated for the fixed station hauls using the formula from Worthington (1931). While acknowledging that such depth data may not be normally distributed, the average of the WMD values was computed for the dark and light period and presented with its 95.0% confidence level (WMD ± CL). ANOVA were also computed using these data.

RESULTS

The horizontal distribution of sardine larvae is presented in Fig. 2. The highest abundance of larvae was sampled along the southern edge of the low salinity and density plume (Fig. 2). The main patterns of this distribution are an increase of abundance in a southwestward direction and a displacement away from the coast. This distribution is probably associated with the upwelling-favourable winds observed during the days preceding the plankton sampling (Fig. 3a), which were responsible for an

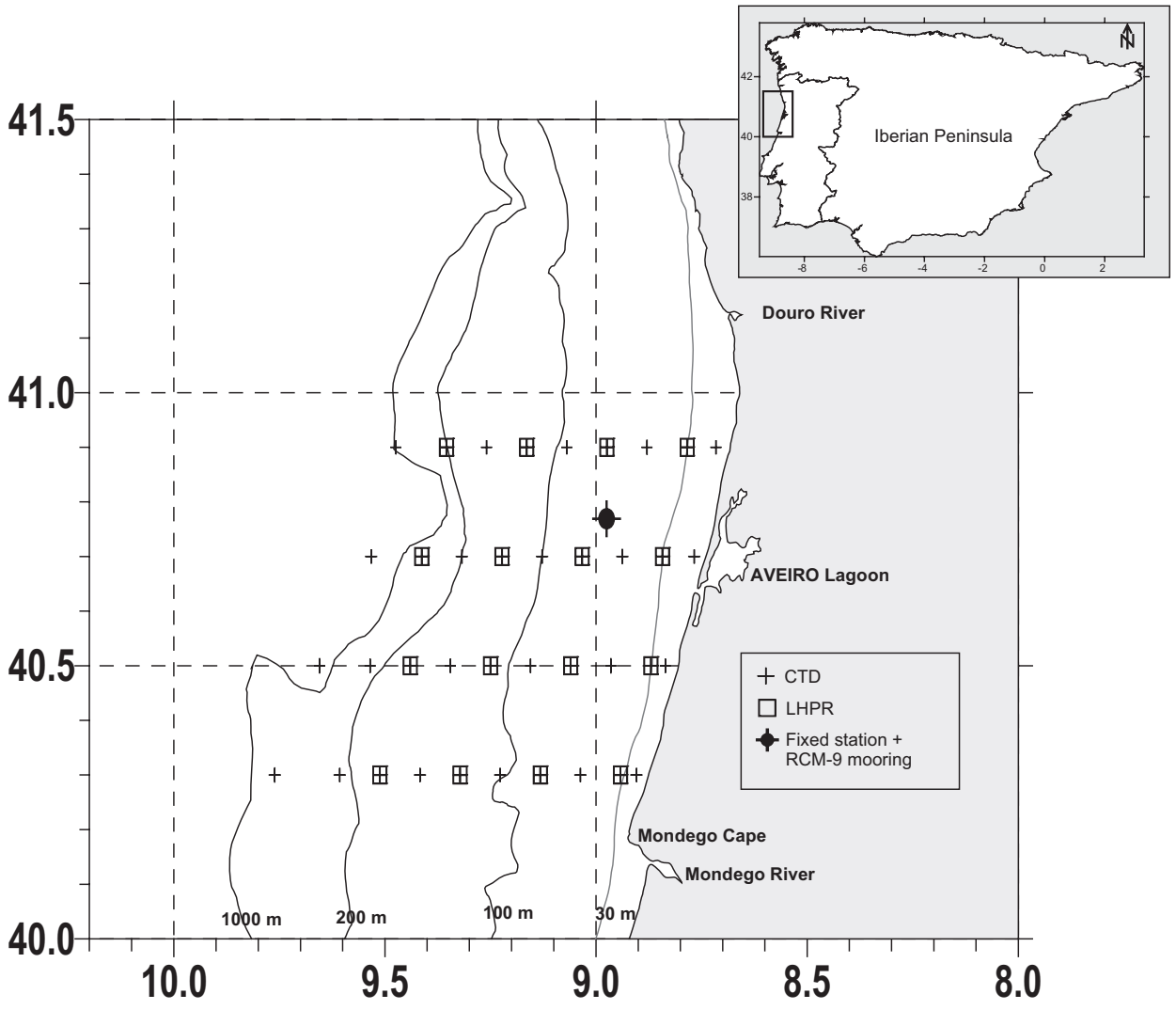

Fig. 1. Location of the sampling stations (ProRecruit'2002 cruise, 15–17 May). The location of the 69-h fixed station and mooring array is also indicated.

upwelling jet with a southwestward direction measured by the current-metre array (Fig. 3b). The upwelling event before the survey leads to the formation and offshore extension of a buoyant plume, which was still observed in the salinity fields of the first leg (not shown), and the reversal of the wind and currents during the end of the first leg was not sufficient to completely break this pattern (Fig. 2). Thus, larval horizontal distribution reflects the southwestward and offshore advection inside this low-salinity plume during the upwelling event before the sampling programme.

The vertical distribution of sardine larvae along the four transepts, superimposed on salinity distributions, is presented in Fig. 4. It is clear that sardine larvae are mainly distributed in the upper 20–25 m water layer within the WIBP, which is a lens of low-density waters characterized by salinity values <35.7–35.8 (c.f. Peliz *et al.*, 2002). This depth distribution of sardine larvae is even more obvious in the fixed station (Fig. 5). The highest concentration of larvae (25.9%) was in the 5–10 m depth interval, and >90% of these were found in the first 20 m of the water column (Fig. 5). The WMD was 8.9 ± 1.7 m.

There was no significant difference (ANOVA, $P = 0.914$) between the average number of individuals per 100 cubic metres during the day (6.9 ± 7.4 larvae per 100 m^{-3}) and night (6.4 ± 2.9 larvae per 100 m^{-3}) periods in the fixed station study as far as the LHPR hauls are concerned (number of hauls: day = 18, night = 15). Although the WMD was similar (ANOVA, $P = 0.196$) between day (10.0 ± 2.5 m) and night (7.8 ± 2.4 m) in the fixed point,

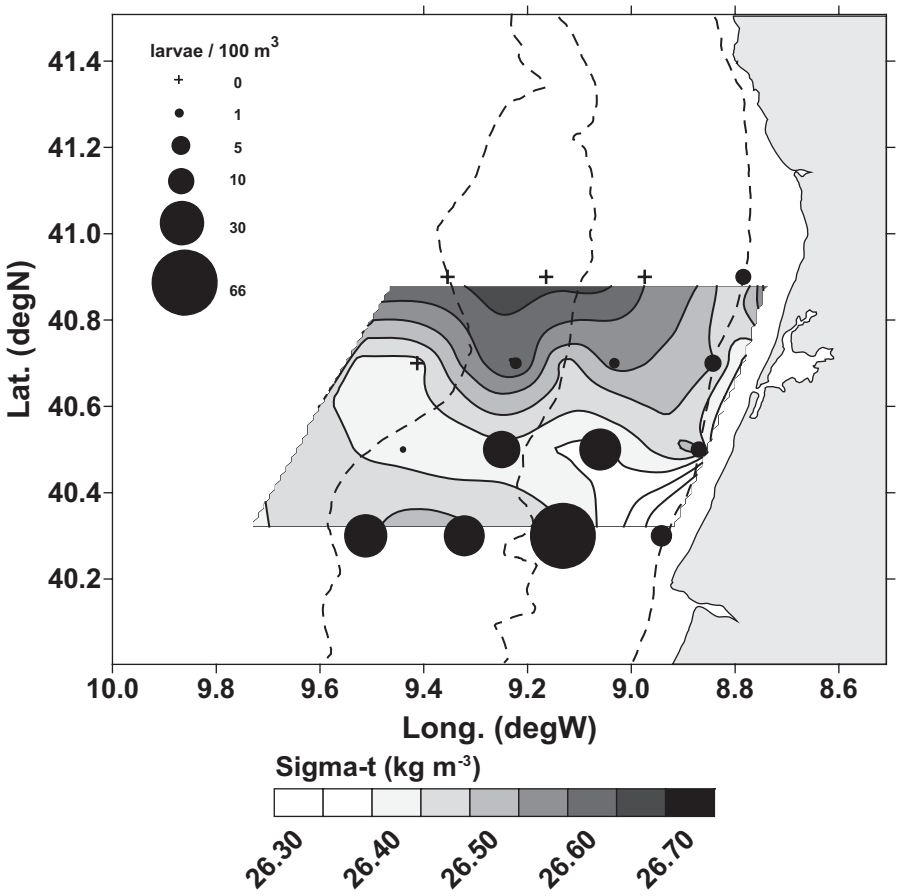

Fig. 2. Horizontal abundance of sardine larvae (number 100 m^{-3}) collected with a Pro-LHPR system superimposed on surface distributions of density σ_t (kg m^{-3}).

there was a highly significant difference (ANOVA, $P = 0.01$) between day (0.9 ± 1.0 larvae per 10 m^{-3}) and night (61.7 ± 52.5 larvae per 10 m^{-3}) in the neuston. Larvae showed a clear preference for the neuston layer during the night period (Fig. 5). This was the only clear diel rhythm observed during the 69-h sampling study. Sardine larvae migrate to the neuston layer at dusk, and the higher abundance was detected between 02:00 and 04:00 hours (Fig. 6). During the day, larvae tend to concentrate (68.5%) at depths between 5 and 20 m (Fig. 5). A very good example of a clear diel vertical migration pattern of sardine larvae is presented in Fig. 4b–d. During the night, they are evenly distributed in the water column; at dawn/dusk they migrate to the surface, and during the day (in the furthest offshore plankton station in Fig. 4d) the bulk of the larvae are located in an intermediate water layer (10–30 m).

The analysis of the length composition reveals that the largest larvae occupy the neuston layer, and there is a displacement for small larval sizes with increasing depth (Fig. 7). Although the size distribution of larvae between depth intervals was highly significant (ANOVA, $P < 0.001$), there is a homogenous group (Tukey HSD, $P = 0.445$–0.997—depth layers >5 m). The only significant difference in length distribution by depth is between the neuston layer and all the other depth strata (Tukey HSD, $P < 0.001$). Larvae with inflated swim bladders were only found in the neuston layer, corresponding to older larvae with sizes raging from 12.4 to 20.4 mm. However, it was observed changes in larval mean length with depth over time (Fig. 8). There were differences in the diel rhythms of migration with size during the 69-h sampling period. Larger larvae start to migrate to the neuston layer first at dusk (18:00–20:00 hours), and smaller ones arrive progressively during the night (22:00–04:00 hours; Figs 8 and 9). At dawn (06:00–08:00 hours), smaller larvae leave the neuston layer first, but larger length classes only leave that layer during the day (10:00–16:00 hours; Figs 8 and 9). During the day (and dawn), all larval length classes are found throughout the vertical range, with the exception of the neuston layer (Fig. 9).

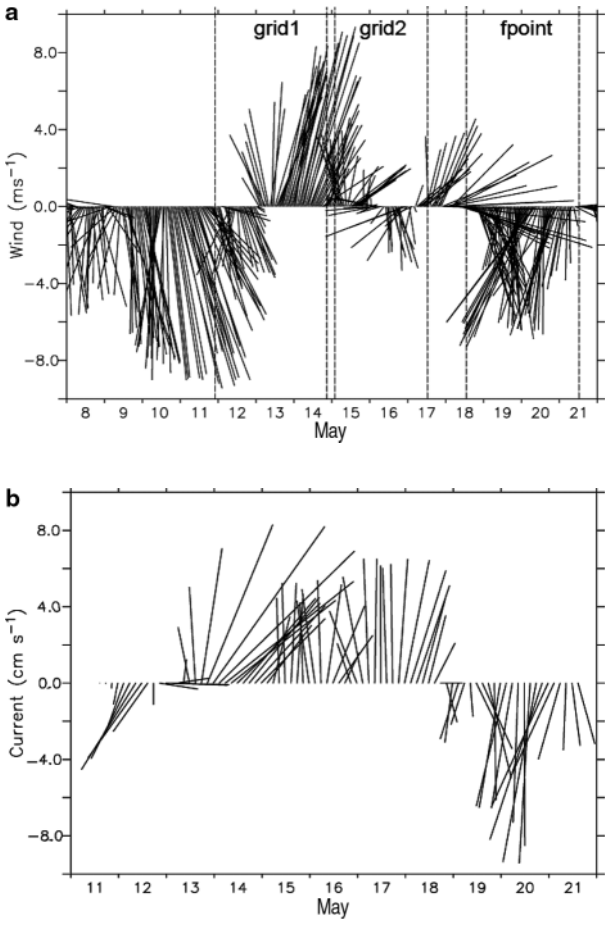

Fig. 3. Stick diagrams of (**a**) wind (m s^{-1}) measured at Cabo Carvoeiro (39.36°N, 9.40°W) by the Portuguese Meteorological Institute during May 2002 and (**b**) 3-h average currents (cm s^{-1}) measured by the RCM-9 current metre located at the 15 m depth level during May 2002.

DISCUSSION

Information on the vertical distribution of sardine larvae is still incomplete, despite study over many decades (Fage, 1920; Fives and O'Brien, 1976; John, 1973, 1978; John *et al.*, 1980; Russell, 1926, 1928). Summing up the available information, sardine larvae stay within the 0–30 m layer during the daylight period. Within this layer, the maximum abundance shows well-marked vertical changes (during the day, it is deepest at about 10–25 m; during the night, the larvae tend to occur close to the surface in the upper 5 or 10 m). John (1973, 1978) and John *et al.* (1980) also showed that sardine larvae are mainly caught in the neuston during the night and only rarely during the day. These results are in agreement with the results presented here, but the fine vertical resolution of our study in conjunction with length composition data allowed a better knowledge of the vertical distribution of sardine larvae. Thus, most sardine larvae were found in depths <20 m, with larger (older) larvae distributed more at the surface than smaller larvae that tend to be deeper. This differential distribution with size is opposite to that reported for the South African pilchard (*Sardinops sagax*) where there is a tendency for bigger larvae to be found deeper (Stenevik *et al.*, 2001). In that study, most of the larvae were found at the 20–40 m depth interval, thus presenting a deeper distribution than the European sardine. Olivar *et al.* (2001) also found somewhat different results in the NW Mediterranean Sea. They observed that larvae are distributed in the 10–30 m depth interval during the day, but were found deeper and with a broader depth distribution at night, with bigger larvae located deeper at night in layers below 35 m. These authors explained that this distribution is regulated by light and food availability, although a slow sinking of sardine larvae may occur during the period of darkness due to conditions of a well-mixed surface layer observed during winter. If local conditions, such as hydrographic structure and/or special ocean features, can influence the vertical distribution of fish larvae (Neilson and Perry, 1990), then the contrasting results observed in Western Iberia could be explained by the presence of the WIBP (see below), which brings stratification and stability to the surface layers and consequently makes food available to the sardine larvae (Chicharo *et al.*, 2003; Ribeiro *et al.*, 2005; Santos *et al.*, 2004).

Ré (1986) showed that the microstructure of sardine larval otoliths was related to certain ecological and physiological events, namely the onset of exogenous feeding, diel rhythms of swim bladder inflation, feeding and vertical migration. In sardine larvae, swim bladder formation occurs at a length of 10 mm (age 12 days), and the diel rhythm of swim bladder inflation/deflation is initiated at a length of ca. 12.5 mm (age 17 days) (Ré, 1986). Thus, the results presented here, in which only larvae with length >12.4 mm present swim bladder inflation and are located only in the neuston layer during the night, support the hypothesis of a diel rhythm of inflation/deflation related to active vertical migration behaviour. Larvae of many clupeoid fishes are know to inflate their swim bladder at night, possibly as an energy sparing mechanism and as a means to decrease the likelihood of capture by predators detecting prey by movement (Hunter and Sanchez, 1976). Larvae with deflated swim bladders sink more rapidly than larvae with inflated swim bladders. This vertical migration behaviour is synchronized by the diurnal light cycle (Hoss *et al.*, 1989). In fact, our observations show that the migration to the neuston layer is initiated at dusk first by older (larger) larvae (Figs 8 and 9), and the peak of abundance is found between 02:00 and 04:00 hours (Fig. 6), due to the progressive arriving of smaller length classes during the night (Fig. 9).

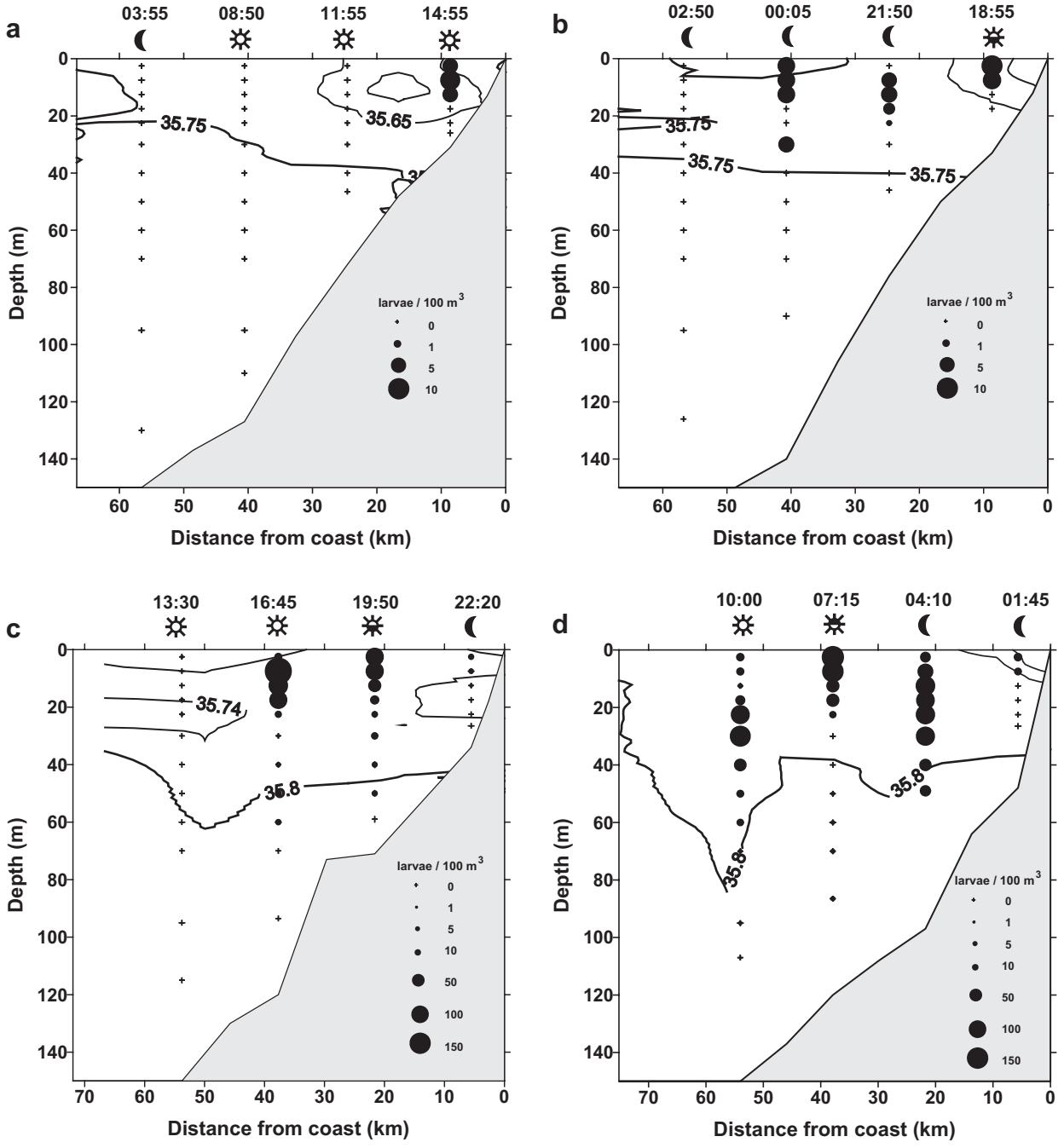

Fig. 4. Vertical distribution of sardine larvae (number 100 m^{-3}) collected with a Pro-LHPR system along four transects during 15–17 May 2002: (**a**) 40.9°N in 15.05.2002; (**b**) 40.7°N in 15–16.05.2002; (**c**) 40.5°N in 16.05.2002 and (**d**) 40.3°N in 17.05.2002. The vertical distribution of salinity (<35.75–35.8) characteristic of the WIBP is represented by the solid lines. Night and day periods are represented by the moon and sun symbols. Over these symbols are presented the hours of the day. Note that the scale of larval abundance is one order of magnitude greater in (**c**) and (**d**) than in (**a**) and (**b**).

The late sinking of larger larvae at the start of the daylight could be explained by the fact that it takes about 1 h for the larvae to shrink the swim bladder (Uotani, 1973). During daylight (including the dawn period), only 3% of larvae are present in the neuston layer, but all larval size spectra are found throughout the other water layers. These changes in size distribution with depth as a function of time of the day have been reported by other

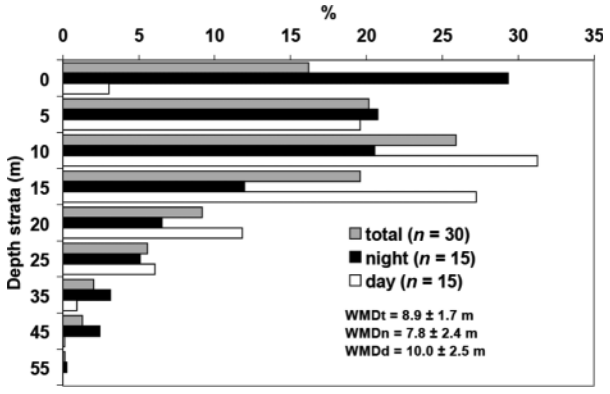

Fig. 5. Vertical distribution of sardine larvae plotted as the mean percentage of abundance on all (night/day) Pro-LHPR hauls during the 69-h fixed station study (18–21 May 2002). Also shown are the weighted mean depth (WMD) and the number of hauls (*n*).

authors for several species (e.g. Neilson and Perry, 1990 and references within; Pearre, 2003 and references within). Moreover, laboratory experiments (Hoss and Phonlor, 1984; Hunter and Sanchez, 1976) showed that in clupeoid fishes filling of the swim bladder is achieved by gulping air at the water surface at dusk. Larvae stay inactive close to the surface during the night period (usually body oriented head-down at an oblique angle to the water surface), and with the onset of the light period, the swim bladder is deflated by passing gas bubbles through the pneumatic duct. There is no histological evidence for gas secretion in sardine larvae. This means that larvae gulp air at the surface to maintain their position close to the surface during the night and descend after the onset of the light period by deflating their swim bladder (Hunter and Sanchez, 1976; Uotani, 1973).

Santos *et al.* (2004) tested the hypothesis, advocated by Santos *et al.* (2001) and Borges *et al.* (2003), of a dependence between larval survival and upwelling events during the sardine spawning season (wintertime). These authors conclude that the association with a surface low-salinity water lens could be a retention mechanism that leads to better survival. Thus, the offshore larval transport is constrained by local features such as the WIBP and the IPC, with the joint effect of both being responsible for retention conditions of the larvae close to the shelf break. However, the vertical distribution of sardine larvae was unknown, so more conclusive results about the real impact of such features and oceanographic conditions on the transport/retention were difficult to support.

In this study, it is shown that sardine larvae are located in the surface layers, mainly in the top 20 m and in clear association with the waters of the WIBP. These results are a further support to the mechanism proposed by Santos *et al.* (2004). This strategy results in larval retention in a layer of high food availability, since the WIBP allows the necessary amounts of nutrients and degree of stratification for phytoplankton growth (Moita, 2001; Peliz and Fiúza, 1999; Ribeiro *et al.*, 2005). The negative impact of the potential offshore transport in this surface layer might be compensated for by interaction with the along slope flux (IPC) that introduces a blocking effect to the seaward extension of the WIBP and leads to the formation of a convergence zone in the shelf break, thereby creating conditions for larval retention over the shelf (Santos *et al.*, 2004). This could explain the contrasting differences observed between our results and the ones by other authors (Olivar *et al.*, 2001; Stenevik *et al.*, 2001). In the former study, the deeper larval distribution is probably related to an active migration out of the Ekman layer in order to reduce offshore loss in a dynamic upwelling system, which in our case study is compensated for by the retention in the convergence zone. In the latter study, the authors relate the vertical behaviour with the tendency of larval aggregation in more productive layers during daylight in order to feed, and to the lack of stratification in winter that may

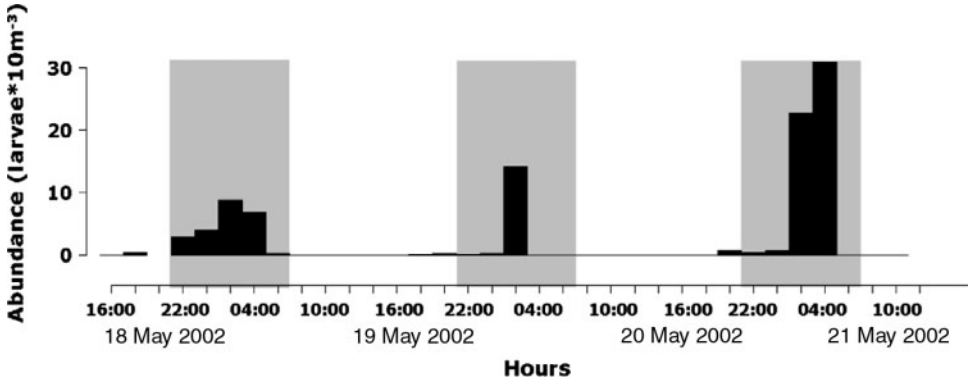

Fig. 6. Abundance distribution of sardine larvae by time in the neuston layer (fixed station study). The grey areas correspond to the night period (22:00–06:00 hours).

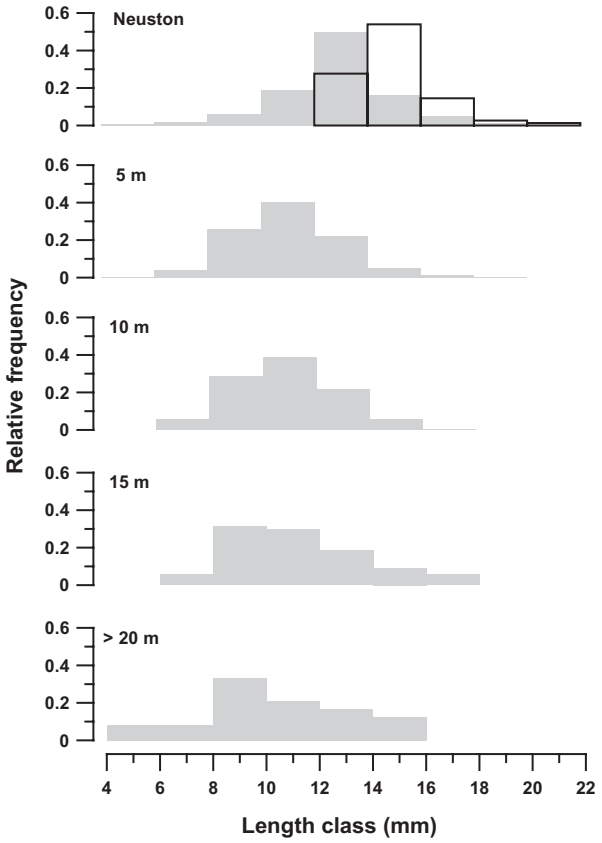

Fig. 7. Length composition of sardine larvae by mean depth strata (fixed station study). Grey bars correspond to the length composition of all sardine larvae. White bars represent only the length composition of larvae with inflated swim bladders.

contribute to the wider larval vertical distribution during the night. In the present study, the productive layer is to be found within the well-stratified WIBP located in the upper 25 m layer.

The results from this study are an important contribution to the knowledge of the vertical behaviour of sardine larvae off Western Iberia, which is required for future studies of larval dispersal and survival, chiefly for simulations of different circulation scenarios using numerical modelling.

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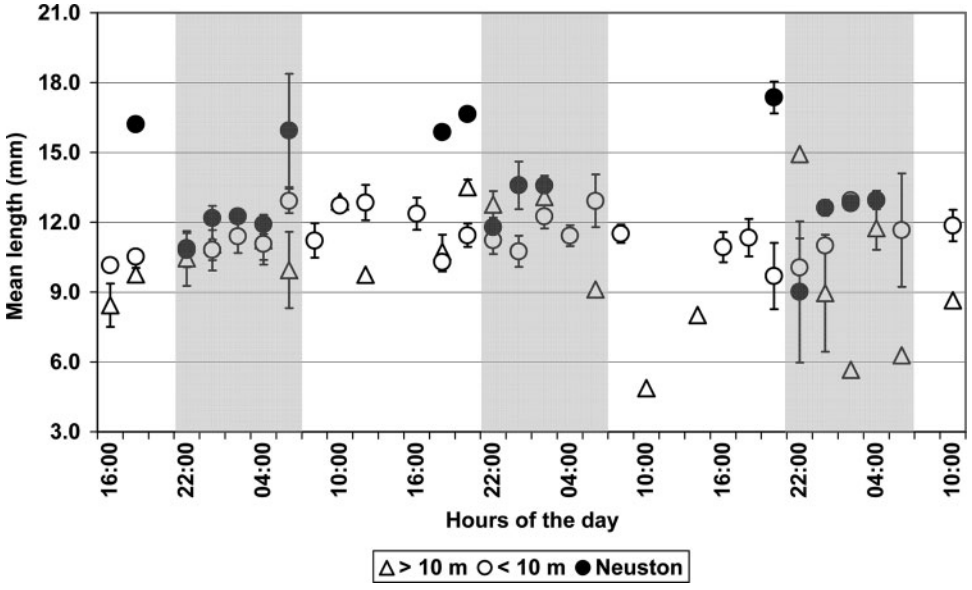

Fig. 8. Larval sardine mean length ± SE by depth strata over time (fixed station study; 18–21 May 2002). The grey areas correspond to the night period (22:00–06:00 hours).

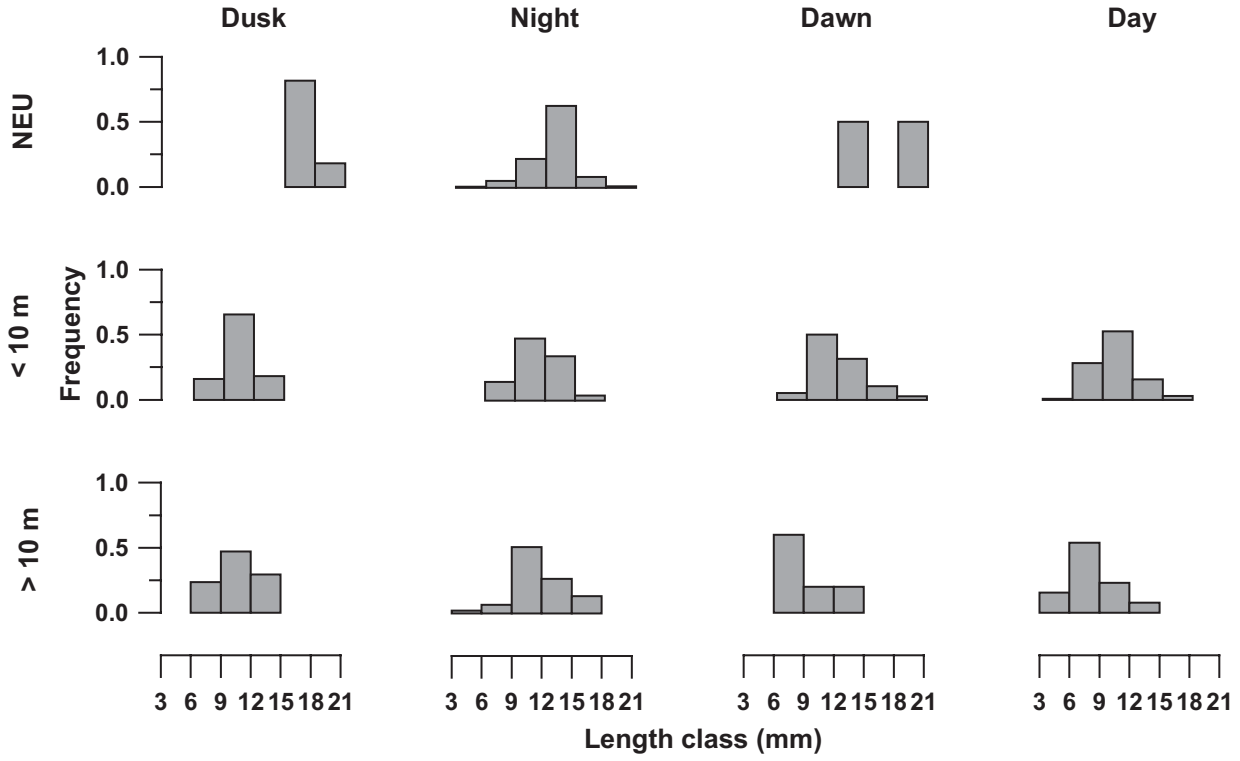

Fig. 9. Larval sardine length composition by depth strata and time of the day (fixed station study; 18–21 May 2002). NEU is the neuston layer; <10 m is the upper 10 m water layer and >10 m is the layer between 10 and 55 m. Dusk corresponds to 18:00–20:00 hours, night from 22:00 to 04:00 hours, dawn from 06:00 to 08:00 hours and day from 10:00 to 16:00 hours.

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