Spatial distribution and vertical migrations of fish larvae communities off Northwestern Iberia sampled with LHPR and Bongo nets

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ABSTRACT
The spatial distribution and diel vertical migration of fish larvae were studied in relation to the environmental conditions off NW Iberia during May 2002. Larvae from 23 families were identified, the most abundant were the Clupeidae, Gobiidae, Callionymidae, Blenniidae, Sparidae and Labridae. Sardina pilchardus was the most abundant species, mean concentrations 1 order of magnitude higher than the other fish larvae species. Larval horizontal distribution was mainly related to upwelling-driven circulation, resulting in an offshore increase of larval abundance while the vertical distribution was closely associated to the Western Iberia Buoyant Plume. Despite this general trend, taxon-specific relationships between the distribution of larvae and environmental variables were observed, and temperature was an important regressor explaining the distribution of most taxa. A comparison between ichthyoplankton samples collected alternatively with the LHPR and Bongo nets resulted in captures of larvae =1 order of magnitude higher for the LHPR, probably related to its higher towing speed. The spatial distribution and relative composition of larvae were also different for both nets, although the most frequent/abundant groups were the same. A fixed station sampled for 69-h showed diel vertical migrations performed by the larvae, with the highest larval concentrations occurring at surface layers during the night and most larvae being found in the neuston layer only during that period.

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1. Introduction
Dispersal and transport of fish larvae are key factors affecting the recruitment of fish populations because the physical and biological processes that promote the aggregation of larvae in appropriate conditions possibly determine their survival (e.g., Hinckley et al., 1996). The heterogeneity of the survival of the early life stages of fish for different taxa, year-classes and areas may therefore be the result of the suitability of the environment for larvae development. However, larvae are not inert particles at the mercy of the physical processes, and can increase the probability of staying in appropriate environments by means of active vertical migrations. Vertical migrations of fish larvae are taxon-specific, can change with ontogeny and can reflect local adaptations, which has complicated the simple determination of the signals that trigger those migrations and their advantages for larval survival. As reviewed in Neilson and Perry (1990), the most commonly accepted candidates as signals for fish larvae vertical migrations are light, prey concentration, thermocline, tides and changes in the buoyancy of larvae. The advantages of the vertical migration are generally proposed to be light-related predator avoidance, choice of optimal prey concentrations, selection of appropriate water temperature to adjust the metabolic rate to the available food in the water, rhythms of swim bladder inflation, and a strategy to guarantee their retention in shallow waters, this latter of crucial importance in upwelling regions. For upwelling areas, the diel vertical position of fish larvae determines if they are retained in shallow and productive waters or advected offshore, and larvae with near-surface distributions are more susceptible to offshore transport associated with coastal upwelling than deeper distributions that render larvae to shoreward transport (Rodríguez, 1990).

The Northwest Iberian coast is characterized by seasonal coastal upwelling during spring and summer (e.g., Wooster et al., 1976) and influenced by significant river runoff. Coastal upwelling is induced by the prevalence and steadiness of northerly winds between April and September, strengthened during summer by a thermal low pressure centre located typically over the Iberian Peninsula at this
time of the year. The presence of filaments reappearing each year at the same locations is a conspicuous characteristic of the Western Iberia upwelling system (e.g., Haynes et al., 1993), promoting an important shelf-ocean exchange of water properties that can have an important impact in the dispersion and survival of fish larvae (e.g., Barton et al., 2001; Rodriguez et al., 2004). The Aveiro filament (e.g., Peliz et al., 2002) is one of these mesoscale features that occur in the region under study.

Besides upwelling events, two important oceanographic features have implications in the transport of fish larvae in the northwestern coast of Portugal: the Western Iberia Buoyant Plume (WIBP) and the Iberian Poleward Current (IPC) having a differential impact on larval fish depending on their vertical distribution (Santos et al., 2004, 2006). The WIBP is a recurrent low-salinity lens extending along the coast with origin in the discharge of many rivers present all year round in the region, despite the seasonal variability of riverine discharges. It is characterized by salinity values <35.7–35.8, a thickness of about 25 m from the surface (Peliz et al., 2002) and a rapid response to changes in wind conditions (Ribeiro et al., 2005; Otero et al., 2008). During upwelling favourable conditions, the WIBP spread offshore over the shelf and slope, being a favourable environment for larval fish survival (Chicharo et al., 2003; Santos et al., 2004, 2006; Ribeiro et al., 2005). On the contrary, during the influence of southerlies the plume is confined to the shelf and near-shore (Ribeiro et al., 2005).

The IPC is a warm and salty surface slope current flowing poleward with mean velocities of about 0.2–0.3 m s\(^{-1}\) and a thickness of about 20 m from the surface (Peliz et al., 2002) and a rapid response to changes in wind conditions (Ribeiro et al., 2005; Otero et al., 2008). During upwelling favourable conditions, the WIBP spread offshore over the shelf and slope, being a favourable environment for larval fish survival (Chicharo et al., 2003; Santos et al., 2004, 2006; Ribeiro et al., 2005). On the contrary, during the influence of southerlies the plume is confined to the shelf and near-shore (Ribeiro et al., 2005). The IPC is a warm and salty surface slope current flowing poleward with mean velocities of about 0.2–0.3 m s\(^{-1}\) and a volume transport of about 1–2 Sv (Frouin et al., 1990; Haynes and Barton, 1990) and it is a clear feature of the autumn–winter season but probably occurs year round (e.g., Peliz et al., 2005). The implication of the IPC for larval fish transport is its blocking effect that prevents the seaward extension of the WIBP and leads to the formation of a convergence zone in the shelf break, thereby creating a mechanism for larval retention over the shelf (Santos et al., 2004). On the contrary, the Aveiro filament can promote the offshore extension of the WIBP in its zone of influence (Ribeiro et al., 2005).

The study of the relationship between oceanographic features and plankton distribution can be influenced by the type of sampling method that is used, given that different methods may have differential efficiency and selectivity while capturing planktonic organisms. The Longhurst–Hardy Plankton Recorder (LHPR) and the Bongo nets are frequently used to capture fish larvae. A detailed comparison of the characteristics of these two nets is given in Stehle et al. (2007), where data collected from the same cruise as the present work has shown that the LHPR net captured 5 times more mesozooplankton biomass than the Bongo net, while the diversity of zooplankton species was similar between both nets. It is crucial to know the differences between the sampling strategies in the estimated abundances and composition of fish larvae communities, to be able to recognize which sampling device is more appropriate for the objective under study, e.g., estimate the diversity of species or directed towards specific larval taxa or specific depth ranges.

The objectives of this study are 1) to examine the spatial distribution and diel vertical migrations of fish larvae communities off NW Iberia during the spring season, when upwelling events occur in this area and 2) to compare the abundance and composition of fish larvae caught by two different nets, the LHPR and Bongo nets. Results of this cruise referring specifically to the vertical distribution of the sardine (*Sardina pilchardus*) captured by the LHPR net were published elsewhere (Santos et al., 2006). As far as we are aware of this is the first time a study is carried out with sufficient temporal and vertical resolution to enable an investigation of the diel vertical migration for a broad number of marine fish larval taxa.

### 2. Materials and methods

The vertical distribution, concentration and community structure of fish larvae were studied off the NW Iberian coast during an oceanographic survey carried out in May 2002 on board of the RV “Noruega”. From 15 to 17 May 2002 plankton samples were collected along four transects perpendicular to the coast, over a grid of 38 stations (Fig. 1). LHPR and Bongo stations were performed alternatively along the 4 transects. The LHPR net (Williams et al., 1983) had a 42 cm diameter aperture and a 280 μm mesh. This net collected vertical-stratified samples at each station, operating at 3–4 knots on oblique tows from the surface to 5–10 m above the ocean floor. The Bongo net had a 60 cm diameter aperture and a 335 μm mesh, was operated at 2 knots and collected double-oblique hauls from the surface until 5–10 m above the bottom. Temperature, salinity and chlorophyll-a concentration profiles were taken in all stations with a SBE 9plus CTD (Conductivity–Temperature–Depth) fitted with a Seapoint fluorometer.

A fixed station positioned at about 20 km away from the coast over a bottom depth of 60 m was sampled continuously for 69 h, from 18 to 21 May 2002 (Fig. 1). At this station, samples were taken every 2 h with LHPR and neuston nets and CTD data were collected hourly. The neuston net had a rectangular opening of 0.20 m\(^2\) and a 335 μm mesh size and was towed at ≈1.5 knots for 3 min in the first 20 cm of the surface layer.

Plankton samples were preserved for posterior analysis in seawater with 4% borax buffered formaldehyde. In the laboratory, samples were sorted for fish larvae and the displacement volume (ml 10 m\(^{-3}\)) was used as a proxy of mesoplankton biomass as described in Stehle et al. (2007). Fish larvae were then identified and quantified using a stereomicroscope.

To estimate the depth at which the fish larvae were found in higher concentrations for the grid of stations, the Weighted mean depth was estimated for each larval group, using the formula of Worthington (1931) to analyse the vertical distribution of larvae:

$$W = \sum \frac{Qi}{Zi}$$

where Qi is the frequency of occurrence of a given larvae group and Zi is the sampling depth. Zi was calculated as the middle point of the depth strata.

In order to compare the diversity of fish larvae taxa caught by the LHPR and Bongo nets, the species richness or the total number of different fish larvae taxa and the Shannon–Wiener diversity index were calculated for each sample.

To study the vertical distribution of the most frequent and abundant fish larval taxa as a function of environmental factors, we build a Hurdle regression model (Gurmu, 1998), given that the concentrations of most taxa in the strata were zero-inflated and overdispersed. Hurdle regression model is a two-component model with a truncated count component for positive counts and a component that models the zero counts (Zeileis et al., 2008). The Hurdle regression model is simpler to interpret than other zero-inflated regression models, because the binomial probability model and the truncated-at-zero count data model are fitted separately (Welsh et al., 1996; Barry and Welsh, 2002). The zero Hurdle models or the probability of finding zero or positive values of larval abundances were adjusted to a binomial distribution with a logit link. The count model was fitted to a truncated at zero negative binomial distribution with a log link. The concentration of fish larvae taxa collected with the LHPR net in each station was grouped for several vertical strata: 0–10 m, 10–15 m, 15–20 m, 20–25 m, 25–35 m, 35–45 m, 45–55 m, 55–65 m, 65–85 m, 85–105 m and >105 m. The following predictors were used: temperature (°C), salinity, depth of
the station (m), chlorophyll-a concentration (mg m$^{-3}$), zooplankton biovolume (ml 10 m$^{-3}$) and the interaction between the categorical variables daytime (day vs. night period) and depth layer (defined as the position in 3 vertical strata: <20 m, >20 to <50 m, and >50 m). To normalise their distributions, the depth of the station, chlorophyll-a concentration and zooplankton biovolume were log-transformed. Backward stepwise algorithm by Akaike’s Information Criterion (Venables and Ripley, 2002) was used to reduce the explanatory variables of the initial model, using the Voung’s non-nested hypothesis to make sure that the final reduced model predictions were not significantly different from the initial model that included all variables.

The comparison between the horizontal distribution of fish larvae caught by LHPR (integrated for each station) and Bongo nets was done using negative binomial generalized linear models, using larval concentrations for each of the most frequent and abundant taxa caught by LHPR as predictors of the larvae caught with the Bongo net for the same station. Since the stations where the Bongo nets were used were not juxtaposed with the ones from LHPR (Fig. 1), we used the average concentration of fish larvae between the two Bongo stations immediately before and after each LHPR of the same transect.

Statistical analysis and graphics were performed using the open source software R 2.8.0 (R Development Core Team, 2008) and the packages MASS (Venables and Ripley, 2002), pscl version 1.02 (Jackman, 2008), car version 1.2.9 (Fox, 2008) and Vegan (Oksanen, 2008).

3. Results

3.1. Oceanographic conditions

The specific oceanographic conditions that characterized the survey where larval fish sampling occurred are described in more detailed in dos Santos et al. (2007). The plankton sampling took place after several weeks of upwelling favourable winds combined with the beginning of upwelling relaxation, as a consequence of the reversal of the wind direction. The change of wind and currents was not sufficient to significantly alter the hydrographical patterns associated with the recent event of coastal upwelling. Consequently, the WIBP presented a noticeable offshore displacement (Fig. 2) and the flow associated to the Aveiro filament with a southwest direction was still present (Fig. 3). However, it was observed the initial development of a weak poleward flow over the shelf (Fig. 3) as a consequence of the relaxation event.

Minimum and maximum temperatures and salinities registered in the vertical-stratified grid of samples were 11.4–15.7 $^\circ$C and 35.5–36.0 respectively. Fresher waters in the first 25–30 m are associated to the presence of a relatively well developed WIBP (Fig. 2). The highest values of chlorophyll-a concentration integrated at each LHPR station were registered for the stations located in the two southern transects and the 4 station of each of the 4 transects nearer to coast (>3 m gm$^{-3}$). Chlorophyll-a concentrations presented a vertical stratification (Fig. 4), being higher in the surface waters (<20 m depth). Chlorophyll-a concentrations were not significantly different from the initial model that included all variables.

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3.2. Horizontal and vertical distribution of fish larvae

3.2.1. Fish larvae communities

A total of 2195 larvae were collected from the grid of samples, 922 with the Longhurst–Hardy Plankton Recorder (LHPR) and 1273 with the Bongo net. Fish larvae from 23 families were identified and the most frequent and abundant families were the Clupeidae, Gobiidae, Callionymidae, Blenniidae, Sparidae and Labridae (Table 1). Sardine (Sardina pilchardus) was the most abundant species, with mean abundance (individuals 1000 m$^{-3}$ ± SD) of
1714 ± 2172 for samples collected with the LHPR net and 41 ± 48 for samples collected with the Bongo net, which in both cases represents concentrations 1 order of magnitude higher than the ones registered for the other fish larvae species. The most abundant taxa following sardine were Callionymus spp., unidentified Gobiidae, Arnoglossus spp., Trachurus trachurus, Parablennius gattorugine, Diplodus spp. and Lebetus spp (Table 1). The higher frequency of occurrence in the sampled grid was of larvae from the taxa Gobiidae, S. pilchardus, Callionymus spp., P. gattorugine, Ammodytes spp., Gadidae and Arnoglossus spp. (Table 1).

3.2.2. Relationship with environmental variables

The horizontal distribution of the fish larvae was different between the taxa, with some species being more frequent and abundant in the inner stations such as Gobiidae and Labridae dominating the near-shore larvae assemblages, others like sardines being especially frequent in the southern transects within the 100–200 m bathmertics, Arnoglossus spp., and several Blenniidae were more frequent in outer stations (Table 1 and Fig. 5). Despite the differences observed for the different taxa, the horizontal distribution of the most abundant and frequent fish larvae showed higher abundances in the southern transects and in the western stations (Fig. 5), associated with southwestward and offshore advection inside the surface plume during the upwelling event (described in Section 3.1).

Regarding the vertical distribution, most fish larvae were concentrated in the buoyant plume located near the surface and characterized by having higher temperature and lower salinity (Fig. 2). All taxa that occurred below this plume were more abundant above it for the same station, like Sardina pilchardus and Callionymus spp. The exceptions to this distribution were two species that had low frequency of occurrence, the deep-sea fish Maurolicus muelleri (Sternoptychidae) and the flatfish Psetta maxima (Scophthalmidae), which were more abundant in deeper waters.

When modelling the distribution of larval taxa in relation to the environmental variables, the total abundance of fish larvae was significantly and positively related to temperature, to the log-transformed biomass of zooplankton and to the depth level of capture (Table 2). Significantly higher concentrations of fish larvae were found in the first depth level (0–20 m) than in the other two levels (20–50 m and >50 m) considered in the regression. Temperature was the most
important factor explaining the distribution of the majority of the abundant/frequent fish larvae species, such as sardine, *Parablennius gattorugine*, *Callionymus* spp., *Diplodus* spp., and *Arnoglossus* spp., the exception being the *Ammodytes* spp. larvae, whose presence was only positively related to zooplankton biomass. Besides temperature, the depth of the station (which is correlated to the longitude and distance to shore) was significant explaining the presence of sardine larvae, found in higher numbers around the 100 m bathymetric, and also the depth strata and its interaction with the period of the day during which the samples were taken (Table 2).

Sardine larvae were preferentially located in the upper 20 m of the water column during the night, and located in higher depths for samples taken during the daylight, which is reflecting diel vertical migrations for the larvae of this species, consistent with the results of the fixed station described in Section 3.3. Although the presence of sardine and *Parablennius gattorugine* larvae was not related to chlorophyll-α concentration, the higher abundances of the larvae were coincident with samples with high chlorophyll-α concentration. On the other hand, unidentified gobiidae larvae, which occurred preferentially near-shore, attained higher concentrations in samples with high levels of zooplankton biomass. *Callionymus* spp. larval abundances were significantly related to the depth strata in the water column, but not with its interaction with the time of the day, meaning that diel vertical migration behaviour was not detected by the model (Table 2), which is similar to the results of the fixed station described in Section 3.3. Finally, *Diplodus* spp. larvae were the only ones whose abundance was explained by salinity.

### 3.2.3. Comparison of LHPR and Bongo nets

The comparison between LHPR and Bongo samples showed that the abundance of fish larvae was ≈ 1 order of magnitude higher for the LHPR than for the Bongo net (Table 1 and Fig. 6) and this was consistent for the majority of larval groups (Table 1). The average concentration of larvae (individuals 1000 m$^{-3}$) collected with the LHPR net was 1752 (ranging from 146.2 to 5646.4) and for the Bongo net was 58.9 (ranging from 10.5 to 207.2). On the other hand, some species that were absent or residual in the LHPR net occurred in high frequencies in the Bongo samples, such as the soleids *Microchirus variegatus* and *Solea vulgaris*, and the horse mackerel *Trachurus trachurus*.

Fish larvae richness or the number of different larvae taxa in each sample ranged in the LHPR from 2 to 16 (mean = 5.6) and from 0 to 11 (mean = 5.5) for the Bongo samples. The Shannon–Wiener
frequent and abundant fish larvae groups (Table 3). Considered, but the relation was not significant for all the other stations. Unidentified Blennidae (50% for Bongo, 6.2% for LHPR samples) and unidentified Gobiidae (50% for Bongo, 0% for LHPR samples). The spatial distribution of the relative frequency of occurrence of the most frequent and abundant larval taxa shown in Fig. 7. The major differences of the relative frequency of fish larvae taxa caught by both nets were for 4 species that occurred in higher frequencies in the Bongo samples compared to LHPR samples: the species Platichthys flesus, distributed in the entire water column of the taxa (Table 4, Fig. 8). Several species were found in the neuston layer in significantly higher abundances during the night than during the day, such as larval sardine, whose frequency of occurrence in the neuston layer compared to deeper strata was significantly higher during the night (29.3%) than during the daytime hours (3.0%). Similarly, the species Parablennius gattorugine was also more frequent in the neuston layer during the night (82.5%) than during the day period (21.2%), which was also the case for Diplodus spp., Symphodus melanops and Spondylus cantharus that occurred in high abundances in the neuston layer and were practically absent of the remaining water column both during the day and night periods (Table 4, Fig. 8).

4. Discussion

The high diversity of larvae observed in this study is typical for the northwestern Portuguese coast during the spring season, when a large number of fish species are known to spawn (John and Ré, 1995). The concentration of fish larvae caught in this study was dominated by the species Sardina pilchardus, a very abundant pelagic fish off Western Iberia that spawns mainly from October to March off Iberian waters. The most frequent and abundant fish larvae species following sardines were Callionymus spp., distributed in the entire water column with similar frequencies of occurrence during the day and night periods and the garfish Belone belone and Gadiforus spp. that occurred in high abundances in the neuston layer and were practically absent of the remaining water column both during the day and night periods (Table 4, Fig. 8).
Fig. 5. Horizontal distribution of the most frequent/abundant fish larvae groups in the LHPR samples.
The highest fish larval abundances were found inshore of the 100 m bathymetric, where a total of 27,688 individuals 1000 m$^{-3}$ were found for the LHPR inner stations, as opposed to 353 individuals 1000 m$^{-3}$ found for the LHPR outer stations. The higher abundances of fish larvae registered for the inner shelf were previously observed in a study carried out during autumn for the same area (Andres et al., 1992). The zonal differences in the composition of larval communities discriminated species associated with coastal environments (e.g., Symphodus melops, Echiichthys vipera) and others preferentially concentrated near the shelf edge (e.g., Arnoglossus spp., Trachurus trachurus). A study conducted off the south Iberian coast has also shown a clear distinction in the distribution of coastal and mesopelagic species, related to distinct coastal–oceanic habitats separated in a wide shelf and prevailing currents (Catalan et al., 2006). Several species of the family Gobiidae presented a wide distribution in coastal and offshore stations, as previously reported by John and Ré (1995). As the authors point out, this reflects the fact that this family includes several species spawning from shallow to shelf edge waters. Sardine larvae were especially abundant in the mid-shelf, which was also noticed by John et al. (1996), describing sardines as totally absent from the freshly upwelled shelf waters of the spring months. The prevalence of sardine larval distribution in the mid-shelf explains why very near-shore studies of fish larvae communities off Western Iberia found comparatively low sardine larval abundances throughout the year (Prista et al., 2003; Borges et al., 2007a,b).

The horizontal distribution of fish larvae was related to the prevailing circulation patterns off the Northwestern Iberia, where upwelling favourable winds led to an increase of fish larval abundance in a southwestward direction, and a displacement of larvae away from the coast. This offshore displacement of fish larvae associated with the upwelling jet was previously described for sardines (Santos et al., 2006) and was also registered in the present study for several other fish larvae species, such as Callophycus spp. and Parablennius gattorugine, the latter being a species widespread along shallow waters (Azeteiro et al., 2006; Borges et al., 2007a) and was found in high numbers in the northern transects close to the shelf, and also in the offshore stations of the southern transects, which may be an indication of offshore transport related to the prevailing circulation during coastal upwelling conditions observed before the survey (Santos et al., 2006; dos Santos et al., 2007). These short-term physical processes such as currents induced by wind can affect the distribution of larvae; particularly those associated to the shelf, and might have a strong impact on larvae survival (Catalan et al., 2006).
The abundance and diversity of fish larvae were higher for surface waters (first 20 m), as observed for other regions of the northeastern Atlantic, like the Irish and North Sea (Conway et al., 1997), and the upwelling region of NW Africa (John, 1982) which has been proposed to be related to the higher food availability near the surface. In fact, most fish larvae in the present study were associated to the more productive surface waters of the WIBP, with a total of 22,638 individuals 1000 m⁻³ caught within the plume and only 2604 larvae found below (Fig. 2), similarly to previous studies conducted in the same area that caught fish larvae mainly within the first 30 m surface layer (Andres et al., 1992; John and Ré, 1995; John et al., 1996; Santos et al., 2006). Furthermore, this result is reinforced by the statistical significant relationship between total larval abundance and the depth strata and mesozooplankton biomass (Table 2). This relationship of fish larval concentrations with mesozooplankton biomass was also observed for the north Iberian waters (Rodriguez et al., 2004). The distribution of the majority fish larvae in the Ekman surface layer implies that most larvae groups described in this study are susceptible of offshore transport associated to upwelling events and the balance between food availability and offshore advection should be compensated by any retention mechanisms over the shelf related to diel vertical migrations behaviour and physical processes (Santos et al., 2004, 2006). The exceptions to this superficial distribution within the buoyant plume were the Sternoptychidae Maurolicus muelleri and the Scophthalmidae Psetta maxima. Maurolicus muelleri was also found in deep waters off the Alboran Sea (Vargas-Yanez and Sabatés, 2007) while no references were found describing the vertical distribution of Psetta maxima larvae.

The relation between the vertical distribution of the most frequent and abundant fish larvae species with the environmental variables was taxon-specific, despite being significantly associated to temperature for the majority of the fish larvae species. Vertical migrations of fish can be modified by the conditions of the environment, and temperature is the most obvious environmental signal affecting those migrations (Neilson and Perry, 1990). However, the gradients of temperature can be associated with the gradients of other important variables such as the dissolved oxygen concentration, which was not measured in the present study, and can be a limiting factor for some fish larvae species (Neilson and Perry, 1990). Besides temperature, the distribution of Ammodytes spp., Diplodus spp. and Gobiidae was also significantly influenced by mesozooplankton biomass, which is probably reflecting their feeding habits. In fact, previous studies have reported the diet of the former two being dominated by copepods (Sanchez-Velasco and Norbis, 1997; Simonsen et al., 2006; Strydom, 2008) but to our knowledge there are no available studies regarding the feeding ecology of Gobiidae larvae. On the other hand, the chlorophyll-a concentration was an important regressor for the distribution of sardine larvae and Parablennius gattorugine. In a study off the Alboran Sea, sardine larvae were located in the upper part of the water column, mainly in the first 60 m and were also significantly correlated with the chlorophyll-a concentrations (Vargas-Yanez and Sabatés, 2007). This was also observed for other clupeid fish larvae such as Sardinella aurita and Engraulis encrasicolus (Rodriguez, 1990; Garcia and Palomera, 1996). For the majority of taxa there was no significant relation between the abundance of fish larvae and chlorophyll-a and mesozooplankton (Table 2). The distribution of fish larvae is probably more significantly associated to the concentration of microplankton than with chlorophyll-a and mesozooplankton biomass, since there are increasing evidences that heterotrophic microplankton is an essential prey for a large number of marine fish larvae species (e.g., Rossi et al., 2006; Pepin and Dower, 2007; de Figueiredo et al., 2007).

The close linkage between fish larvae and physical environmental variables can reflect their ability to position themselves in

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**Table 3**

Coefficients and significance (p-value) of the slope of the negative binomial generalized linear model describing the concentrations of the most frequent/abundant larval taxa collected with the Bongo as a function of the larvae collected for the same stations with the LHPR net. Levels of significance are represented as: **p < 0.0001, *p < 0.001, *p < 0.01, p < 0.05. AIC is the Akaike Information Criterion, LogLik is the log-likelihood of the fitted model, DF are the degrees of freedom.**

<table>
<thead>
<tr>
<th>Larval taxa</th>
<th>LHPR vs. Bongo</th>
<th>Coefficient</th>
<th>p-value</th>
<th>AIC</th>
<th>2 × LogLik</th>
<th>DF</th>
</tr>
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<tr>
<td>Total larvae</td>
<td>1.65 × 10⁻⁴</td>
<td>0.0551</td>
<td>164.49</td>
<td>-158.49</td>
<td>15</td>
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<td>Sardina pilchardus</td>
<td>2.80 × 10⁻⁴</td>
<td>0.0267</td>
<td>151.21</td>
<td>-145.2</td>
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<td>Parablennius gattorugine</td>
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<td>0.448</td>
<td>34.91</td>
<td>-28.91</td>
<td>15</td>
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<tr>
<td>Callionymus spp.</td>
<td>1.09 × 10⁻³</td>
<td>0.351</td>
<td>86.05</td>
<td>-80.05</td>
<td>15</td>
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<tr>
<td>Diplodus spp.</td>
<td>1.45 × 10⁻²</td>
<td>0.2137</td>
<td>16.92</td>
<td>-10.92</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Gobiidae unid.</td>
<td>1.38 × 10⁻³</td>
<td>0.41521</td>
<td>90.84</td>
<td>-84.84</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Ammodytes spp.</td>
<td>-5.99 × 10⁻³</td>
<td>0.9889</td>
<td>13.13</td>
<td>-7.13</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Ammodiscus spp.</td>
<td>3.24 × 10⁻³</td>
<td>0.78</td>
<td>56.11</td>
<td>-50.11</td>
<td>15</td>
<td></td>
</tr>
</tbody>
</table>

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Fig. 7. Relative frequency of the most frequent/abundant fish larval groups for all stations represented in Fig. 1, using LHPR ("L") and Bongo ("B") nets.
particular water masses that are optimal for their growth and survival or be a result of differential survival of larvae in water masses related to different levels of food (Lee et al., 2005). The 69-h sampling in a fixed station showed that the majority of the fish larvae species conducted diel vertical migrations, generally being more concentrated in surface waters during the night and spreading throughout the water column during daylight hours. The most abundant and frequent fish larvae species that were found to follow this pattern of vertical migrations were Sardina pilchardus, Diplodus spp., Symposodus melops, Parablennius gattorugine, and Spondylus canthus, for some of which this behaviour is described here for the first time.

There were some fish larvae species that did not show clear patterns of vertical migration. This was the case of Callionymus sp. that was broadly distributed from deep waters to close to the surface during all day. Olivar and Sabatés (1997), Sabatés (2004) and Röpke (1989) found a similar depth distribution for this species and John and Reé (1995) showed preference for depths of 30–60 m, coincident with an intermediate wedge of higher salinities and as a result of having a deeper distribution allow them to avoid the less saline waters that promote offshore transport. Other species that did not perform diel vertical migrations were the garfish Belone belone and Gaidropsarus spp., whose distribution was restricted to the neuston layer. Garfish larvae were considered euneustonic by Hempel and Weikert (1972) but facultative neustonic by Tully and O’Ceidigh (1989), who also described Gaidropsarus spp. as euneustonic. Our results seem to agree with the results of the former authors for garfish and confirm that both species are obligate members of the ichthyoneuston community for the Western Ibiza. However, the patterns of diel vertical distribution of fish larvae can vary significantly with environmental conditions such as food availability and oceanographic features.

The LHPR net seems to be a more efficient device to catch fish larvae than the Bongo net since larval abundance was about 1 order of magnitude higher for the LHPR than for the Bongo samples. The most likely explanation is the higher towing speed of LHPR, resulting in lower avoidance of high mobile fish larvae. However, Stehle et al. (2007) using data from the same cruise observed that the catching efficiency of the LHPR net for fish eggs was also significantly higher than the Bongo net (mean concentrations of 1760 ± 370 and 520 ± 380 eggs 100 m⁻³, respectively). Furthermore, they also revealed that LHPR was more efficient in capturing mesozooplankton than the Bongo net in terms of biomass, but the diversity and proportion of the different zooplankton taxa were similar between the two nets, allowing the estimation of a conversion factor between them. In relation to fish larvae, our results show that the most frequent and abundant fish larvae taxa were similar between the two nets, but the distribution of larvae inferred from the two nets was only significantly similar when the total number of larvae and of Sardina pilchardus were considered, while for the other larvae groups it was significantly different. The high offshore gradient of fish larvae composition resulting from the patchiness of fish larvae groups is probably the cause of the differences in species composition between contiguous LHPR and Bongo stations, given that they were not juxtaposed, alternating a few miles (3–5 nautical miles) from each other.

Despite the fact that the Bongo net was less efficient in capturing high concentrations of fish larvae, some species that were absent or residual in the LHPR net occurred in high frequencies in the Bongo samples, such as the soleids Microchirus variegatus and Solea vulgaris, and the horse mackerel Trachurus trachurus in the inner stations. One possible explanation might be that the mouth of the Bongo net is wider and sampled larger volumes of water in the same layer when compared to the LHPR.
Fig. 8. Frequency of occurrence (%) of fish larvae at each depth range during the day and night periods for several fish larvae taxa collected at the fixed station during the 69-h period.
maximizing the encounter of less abundant species. However, all of these larvae have a deep distribution in the water column and probably the LHPR was less efficient in capturing larvae communities distributed closer to the bottom because it was decided to keep a wider distance to the sea-floor in order to avoid damaging the net.

5. Conclusions
This study has demonstrated that the distribution of the fish larvae communities off the Western coast of Portugal during the spring season is closely associated with the WIBP, and this surface distribution in the absence of any retention mechanism has the potential to disperse them offshore in the presence of coastal upwelling events that frequently take place in that area during spring and summer months. Retention mechanisms as the one described by Santos et al. (2004), which explain the interaction between the WIBP and the IPC to form convergence zones over the shelf, seem to play a role in limiting larval dispersal. However, these larvae have a deep distribution in the water column and only a fraction of them is likely to remain in the upper layers of the water column.

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