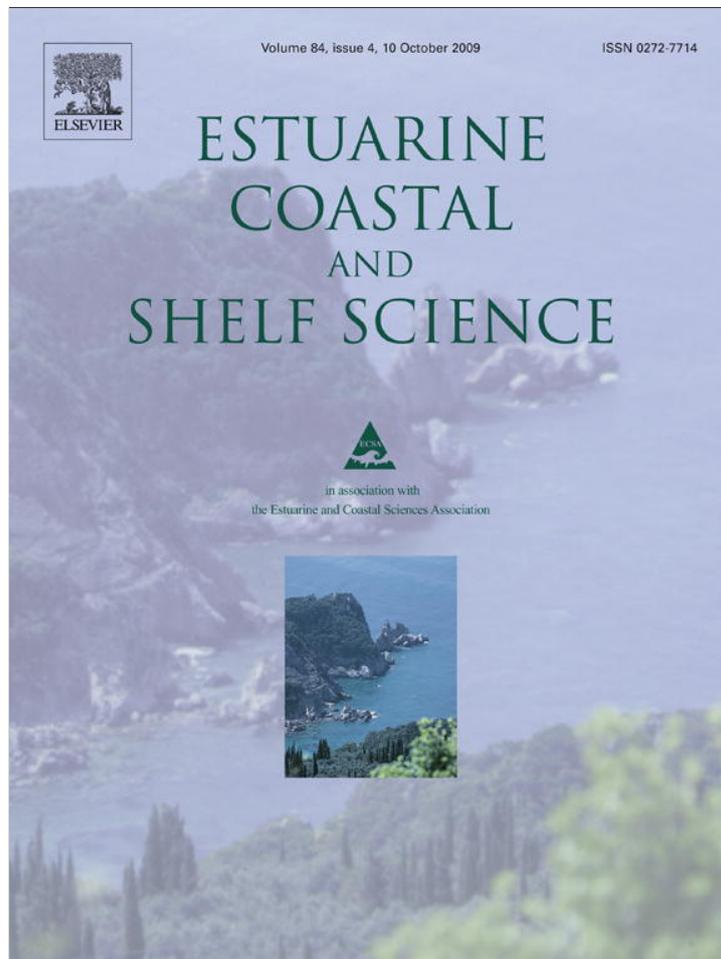


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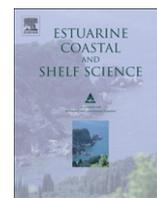
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Spatial distribution and vertical migrations of fish larvae communities off Northwestern Iberia sampled with LHPR and Bongo nets

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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 larvae 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

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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 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 plankton 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 larvae 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 m² 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:

$$W = \sum_i^n O_i Z_i$$

where O_i is the frequency of occurrence of a given larvae group and Z_i is the sampling depth. Z_i 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 larvae 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

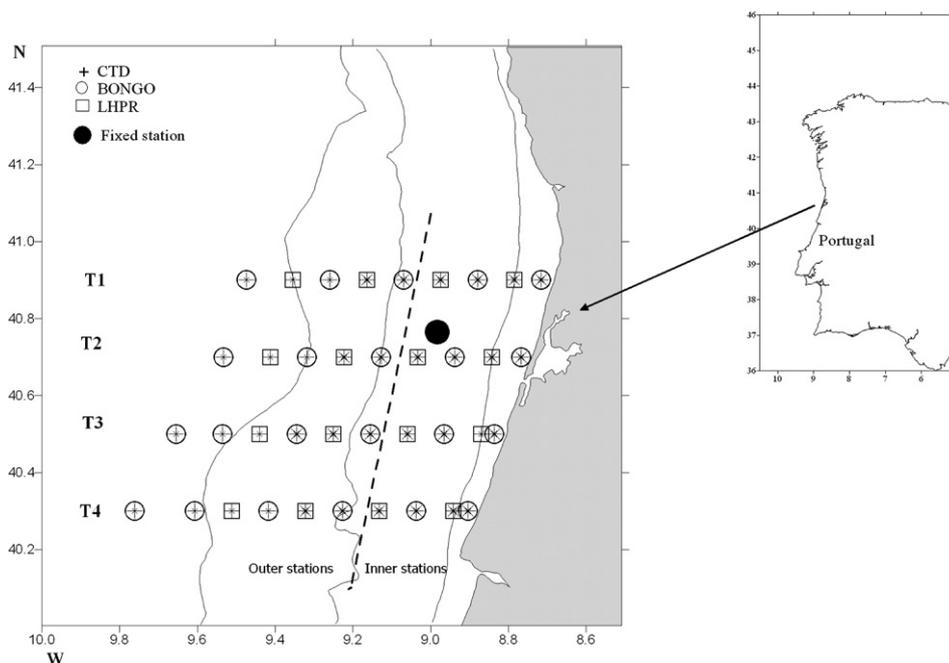


Fig. 1. Map of the Portuguese coast with sampling positions (CTD and plankton samples) collected on board of the RV *Noruega* from 15 to 17 May 2002, Project Pro-Recruit. Transects identified as T1, T2, T3 and T4. The 30, 100 and 200 m bathymetry lines are represented. The fixed station was sampled for 69 h from 18 to 21 May 2002.

the station (m), chlorophyll-*a* concentration (mg m^{-3}), zooplankton biovolume ($\text{ml } 10 \text{ m}^{-3}$) and the interaction between the categorical variables daytime (day vs. night period) and depth layer (defined as the position in 3 vertical strata: $\leq 20 \text{ m}$, $>20 \text{ to } \leq 50 \text{ m}$, and $>50 \text{ m}$). 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 Young'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 $11.4\text{--}15.7^\circ\text{C}$ and $35.5\text{--}36.0$ 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 ($>3 \text{ mg m}^{-3}$). Chlorophyll-*a* concentrations presented a vertical stratification (Fig. 4), being higher in the surface waters ($\leq 20 \text{ m}$ depth) of the WIBP. The mesozooplankton biovolume integrated vertically at each LHPR sample was higher for all outer stations ($>20 \text{ ml } 10 \text{ m}^{-3}$) and was lowest for the stations of the two northern transects closer to coast ($<10 \text{ ml } 10 \text{ m}^{-3}$), reflecting the conditions associated to a previous prevalent coastal upwelling situation. The vertical stratification of mesozooplankton biomass was not as evident as for the chlorophyll, although higher values of mesozooplankton biomass were also registered in surface waters (Fig. 4).

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 $1000 \text{ m}^{-3} \pm \text{SD}$) of

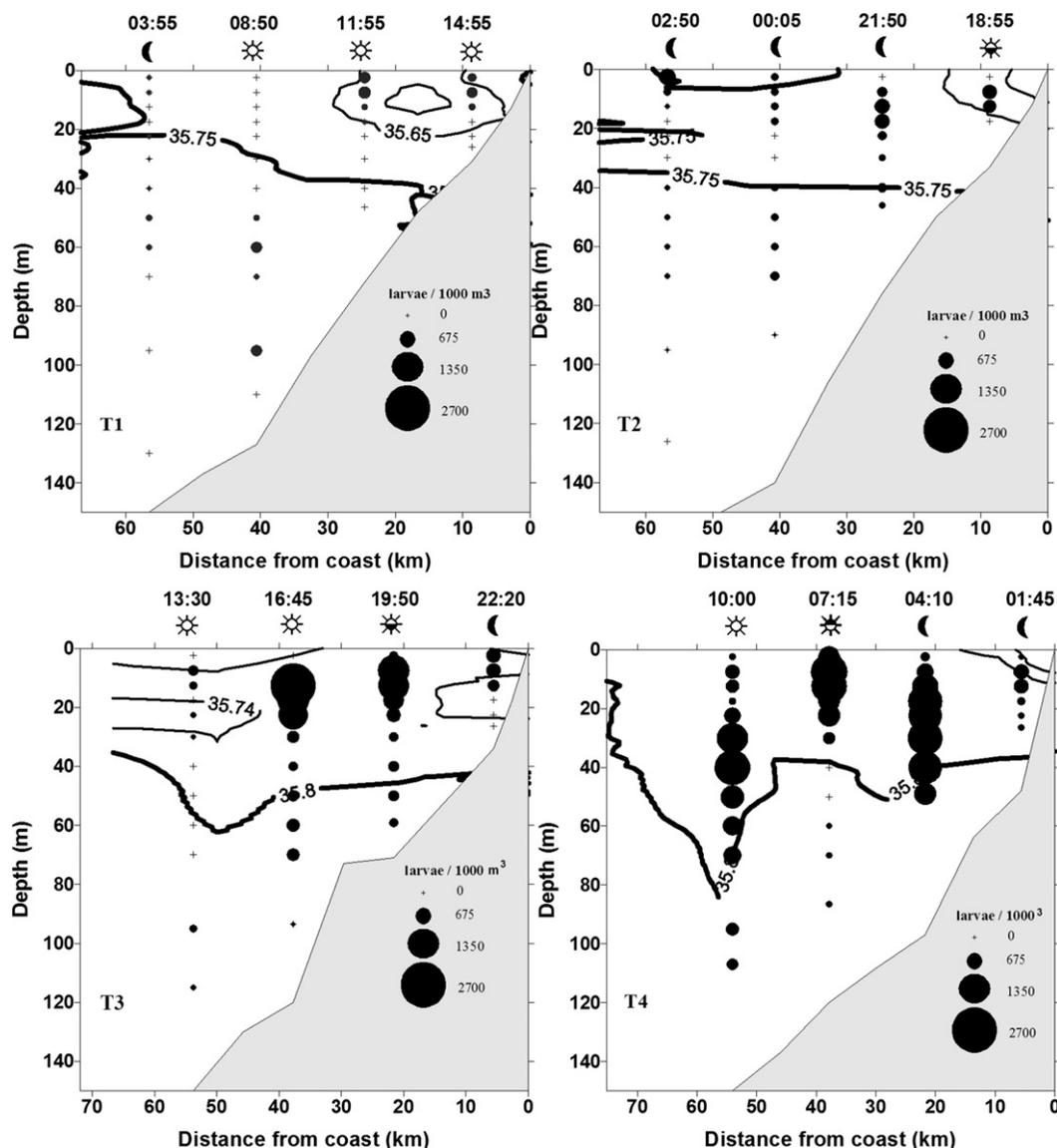


Fig. 2. Vertical distribution of total larval concentrations (individuals 1000 m^{-3}) collected with the LHPR net in the 4 transects (T1–T4) represented in Fig. 1. The vertical profile of salinity, identifying the WIBP is shown.

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 bathymetrics, *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

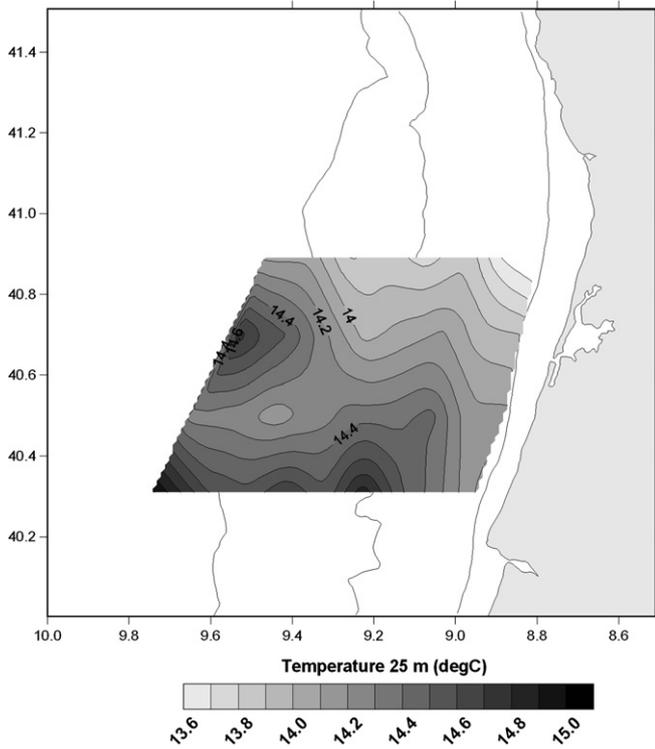


Fig. 3. Horizontal distribution of temperature at 25 m depth in the grid of stations.

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-*a* concentration, the higher abundances of the larvae were coincident with samples with high chlorophyll-*a* 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 variegates* 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

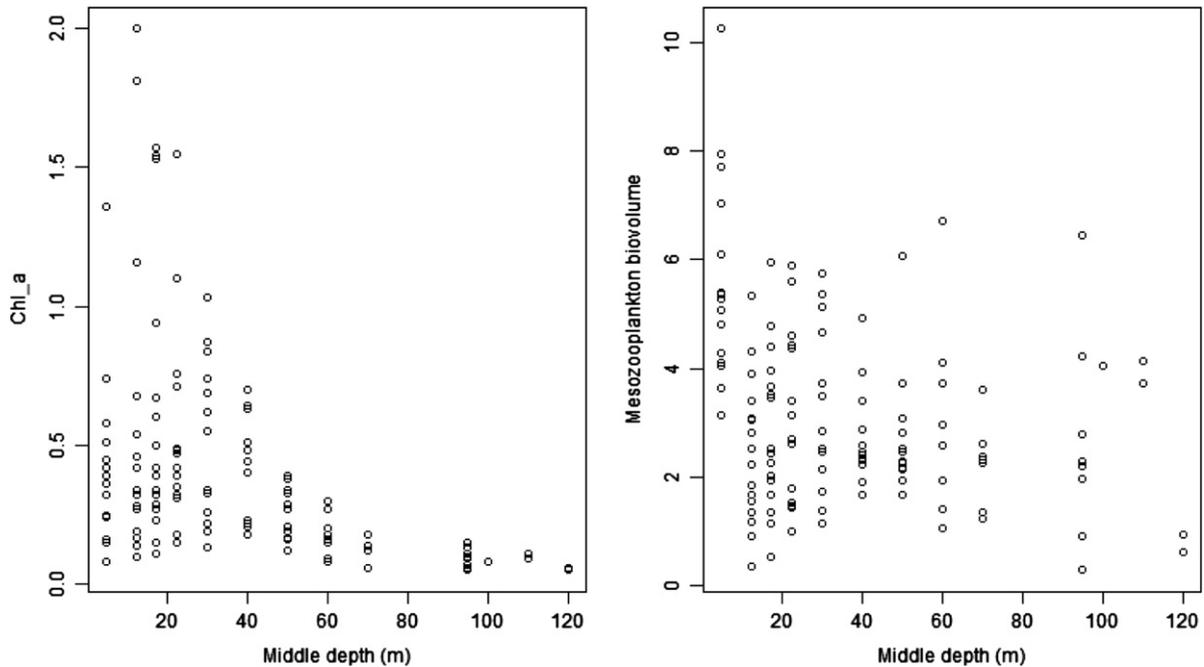


Fig. 4. Vertical distribution of chlorophyll-*a* concentration (left panel, mg m^{-3}) and mesozooplankton biovolume (right panel, $\text{ml } 10\text{ m}^{-3}$) integrated for each depth strata of the grid of LHPR stations. The middle value of each depth strata is represented.

Table 1
Frequency of occurrence (0%) and mean integrated density (individuals 1000 m⁻³) of fish larvae for total, inner and outer LHPR and Bongo stations (represented in Fig. 1). W represents the weighted mean depth of the larvae caught in the LHPR stations.

Fish larvae	LHPR							Bongo						
	0%			Mean if present			W	0%			Mean if present			
	Total	Inner	Outer	Total	Inner	Outer	Total	Total	Inner	Outer	Total	Inner	Outer	
Ammodytidae	<i>Ammodytes</i> spp.	31.25	25	37.5	61.0	5.3	17.6	30.3	43.75	25	62.5	0.8	0.4	0.3
Blennidae	<i>Blennidae</i> unid.	6.25	0	12.5	118.0	0.0	14.7	95.0	50	37.5	62.5	1.1	0.6	0.5
	<i>Parablennius gattorougine</i>	56.25	50	62.5	76.3	39.4	46.5	9.9	43.75	25.0	62.5	1.7	1.2	0.3
	<i>Blennius ocellaris</i>	12.5	0	25	42.7	0.0	10.7	18.2	0	0.0	0.0	0.0	0.0	0.0
	<i>Coryphoblennius galerita</i>	6.25	0	12.5	61.9	0.0	7.7	45.1	12.5	25.0	0.0	1.2	0.1	0.1
Bothidae	<i>Arnoglossus</i> spp.	25	12.5	37.5	153.4	0.0	38.3	38.9	62.5	25	100	4.1	1.1	3.5
Callionymidae	<i>Callionymus</i> spp.	62.5	37.5	87.5	213.5	107.1	106.4	41.4	100	100	100	4.9	5.4	4.5
Carangidae	<i>Trachurus trachurus</i>	12.5	0	25	109.5	0.0	27.4	32.7	68.75	62.5	75.0	1.7	1.0	1.3
Carapidae	<i>Echiodon</i> spp.	0	0	0	0.0	0.0	0.0	0.0	12.5	0	25	0.0	0.0	0.0
Clupeidae	<i>Sardina pilchardus</i>	75	62.5	87.5	1714.4	1105.3	1466.3	15.1	93.75	87.5	100.0	41.4	36.9	40.8
Gadidae	<i>Gadidae</i> spp.	31.25	25	37.5	65.3	0.0	24.5	48.9	50	37.5	62.5	0.6	0.1	0.5
Gobiesocidae	<i>Diplecogaster</i>	0	0	0	0.0	0.0	0.0	0.0	43.75	50	37.5	1.7	1.3	0.2
Gobiidae	<i>Gobiidae</i> unid.	81.25	87.5	75	199.1	153.6	145.0	34.9	87.5	87.5	87.5	6.0	7.6	2.9
	<i>Lebetus</i> sp.	18.75	12.5	25	58.4	22.0	7.2	29.8	0	0.0	0.0	0.0	0.0	0.0
	<i>Pomatochistus</i> spp.	0	0	0	0.0	0.0	0.0	0.0	18.75	12.5	25	1.1	0.3	0.1
Labridae	<i>Symphodus melops</i>	12.5	25	0	54.4	13.6	0.0	5.0	37.5	50.0	25.0	1.5	1.1	0.1
	<i>Ctenolabrus rupestris</i>	6.25	12.5	0	29.4	3.7	0.0	12.5	0	0.0	0.0	0.0	0.0	0.0
Myctophidae	<i>Myctophum</i> sp.	18.75	25	12.5	58.4	0.0	14.6	35.1	0	0	0	0.0	0.0	0.0
Paralepididae	<i>Paralepsis</i> spp.	6.25	12.5	0	29.3	0.0	3.7	50.0	0	0.0	0.0	0.0	0.0	0.0
Pleuronectidae	<i>Platichthys flesus</i>	12.5	0	25	73.7	6.5	11.9	63.4	12.5	0.0	25.0	0.4	0.0	0.1
Scombridae	<i>Scomber</i> spp.	6.25	0	12.5	25.9	3.2	0.0	5.0	25	25	25	0.6	0.2	0.1
Scophthalmidae	<i>Psetta maxima</i>	6.25	0	12.5	30.4	0.0	3.8	95.0	0	0.0	0.0	0.0	0.0	0.0
	<i>Zengopterus punctatus</i>	0	0	0	0.0	0.0	0.0	0.0	12.5	12.5	12.5	1.1	0.3	0.0
Soleidae	<i>Microchirus variegatus</i>	0	0	0	0.0	0.0	0.0	0.0	50	12.5	87.5	1.0	0.2	0.7
	<i>Solea vulgaris</i>	0	0	0	0.0	0.0	0.0	0.0	25	50	0	1.2	0.4	0.1
Sparidae	<i>Diplodus</i> spp.	50	50	50	60.1	49.6	10.4	7.0	25	25	25	1.2	0.4	0.2
Sternoptychidae	<i>Maurolicus muelleri</i>	18.75	25	12.5	29.0	3.9	7.0	58.9	37.5	25.0	50.0	1.2	0.0	0.9
Trachinidae	<i>Echiichthys vipera</i>	12.5	12.5	12.5	68.8	17.2	0.0	12.2	31.25	25.0	37.5	2.6	0.9	0.7
Triglidae	<i>Triglidae</i> spp.	12.5	12.5	12.5	43.6	4.2	6.7	46.2	37.5	25.0	50.0	0.7	0.3	0.3

(S–W) diversity index ranged from 0.39 to 1.91 for the LHPR samples (mean = 1.07) while for the Bongo it ranged from 0 to 1.82 (mean = 0.97). However, the ANOVA comparison of the species richness and S–W diversity index showed no significant differences between both nets ($p > 0.05$).

The most abundant and frequent larvae groups were similar for LHPR and Bongo samples and in general, the relative frequency of fish larvae groups was similar between the two nets (Table 1 and 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 horse mackerel *Trachurus trachurus* (68.8% for Bongo, 12.5% for LHPR stations), *Microchirus variegatus* (50% for Bongo, 0% for LHPR stations), unidentified Blennidae (50% for Bongo, 6.2% for LHPR stations) and *Diplecogaster bimaculata* (43.8% for Bongo, 12% for LHPR stations).

The spatial distribution of the relative frequency of occurrence of the most frequent and abundant fish larvae taxa (Fig. 7) showed a strong offshore gradient of larvae community structure for both types of nets. The generalized linear models relating the abundance of each of the main larval taxa sampled with the Bongo and LHPR nets (Table 3), showed a significant regression coefficient when the total number of larvae and the species *Sardina pilchardus* were considered, but the relation was not significant for all the other frequent and abundant fish larvae groups (Table 3).

3.3. Diel vertical migrations

A total of 2148 fish larvae were collected in the fixed station, 661 with the LHPR net and 1487 using the neuston net. Diel vertical migrations were observed for most larvae groups throughout the 69-h period (Table 4) in the fixed station. The highest concentrations

of fish larvae occurred at surface layers during the night for the majority 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 daylight hours (3.0%). Similarly, the species *Parablennius gattorougine* 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 melops* and *Spondylisoma cantharus* that were almost restricted to the neuston layer at night (>90%) and distributed from surface to the 20–35 m depth during the daylight period (Fig. 8). The exceptions to this vertical migration behaviour of fish larvae being closer to surface at night than during the day were the species *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 *Gaidropsarus* 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).

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., unidentified Gobiidae, *Arnoglossus* spp., *Trachurus trachurus*, *Parablennius*

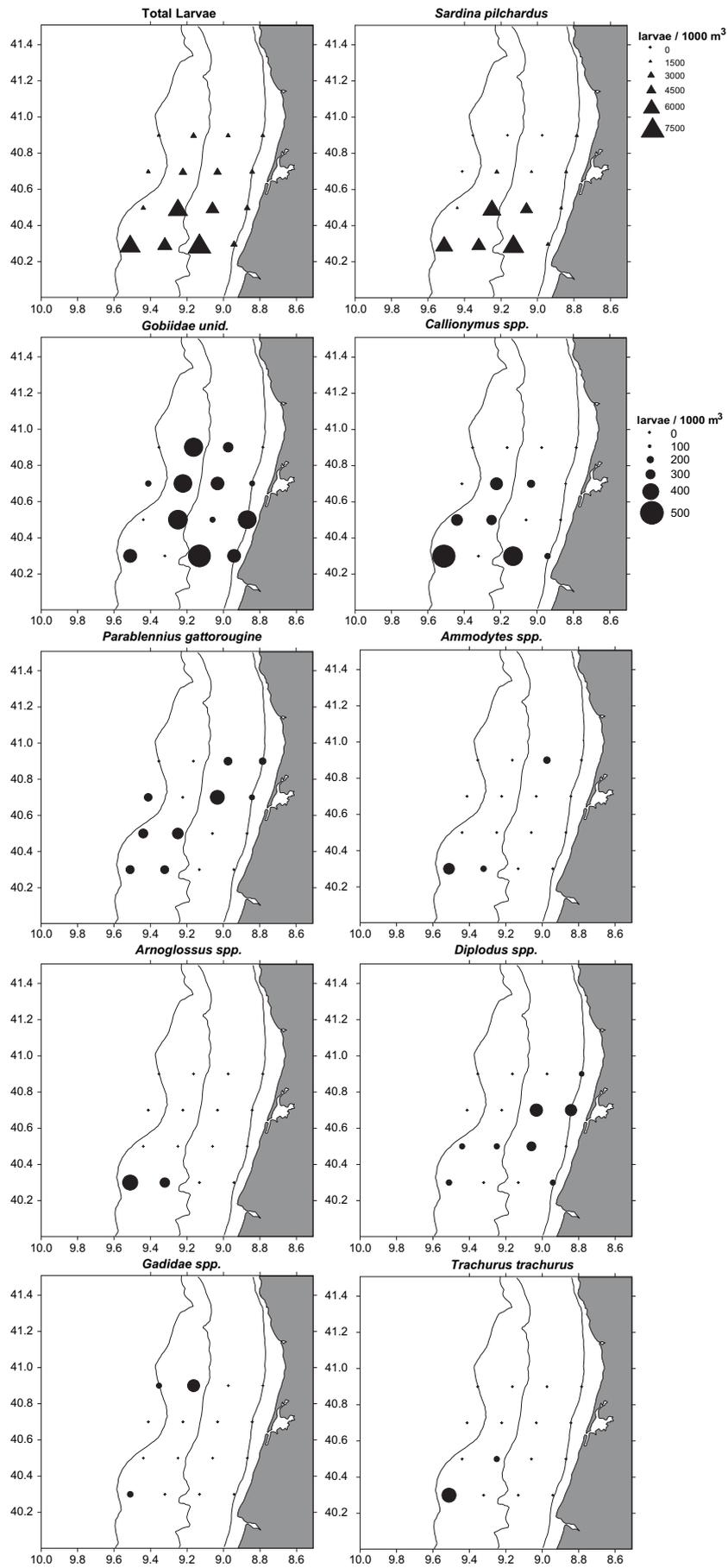


Fig. 5. Horizontal distribution of the most frequent/abundant fish larvae groups in the LHPR samples.

Table 2
Coefficients and significance (p -value) of each of the explanatory variables of the two components of Hurdle regression models (a truncated count component for positive counts and a Hurdle component that models the zero counts) describing the distribution of the most frequent/abundant larvae groups collected with the LHPR net in the vertical-stratified grid of stations. Levels of significance are represented as *** $p < 0.0001$, ** $p < 0.001$, * $p < 0.01$ and n.i. represents variables not included in the final model after backward stepwise regression. LogLik is the log-likelihood of the fitted model, DF are the degrees of freedom.

Coefficients	Independent variables	Total larvae	<i>Sardina pilchardus</i>	<i>Parablennius gattorugine</i>	<i>Callionymus</i> spp.	<i>Diplodus</i> spp.	Gobiidae unid.	<i>Ammodytes</i> spp.	<i>Arnoglossus</i> spp.
Zero Hurdle model	Temperature	2.17***	4.98***	2.37*	1.74**	3.91**	1.78**	2.07	3.03**
	Salinity	n.i.	n.i.	-15.79	n.i.	-13.12	n.i.	n.i.	n.i.
	Depth	n.i.	-1.13*	n.i.	-0.74	-1.52	-0.85*	n.i.	n.i.
	Chl_a	n.i.	-1.31	-3.65	n.i.	-2.70	n.i.	n.i.	n.i.
	Zooplankton	1.15*	n.i.	n.i.	n.i.	0.25	1.14	3.30*	n.i.
	Level	0.87*	1.16*	-0.93	1.41**	0.44	0.89	-0.49	0.65
	Level \times daytime	n.i.	0.59*	n.i.	n.i.	n.i.	n.i.	2.03	1.08
Count model	Temperature	1.58***	1.39***	-0.26	0.10	-0.57*	-0.36***	-0.03	-0.49
	Salinity	n.i.	n.i.	1.35	n.i.	13.82***	n.i.	n.i.	n.i.
	Depth	n.i.	1.03**	n.i.	-0.19	-1.82***	-0.39	n.i.	n.i.
	Chl_a	n.i.	3.63**	-1.80***	n.i.	-2.10*	n.i.	n.i.	n.i.
	Zooplankton	0.03*	n.i.	n.i.	n.i.	-1.83*	0.85***	-1.09	n.i.
	Level	0.16	0.03	0.27	0.35	-1.71**	0.17	-0.56	0.218
	Level \times daytime	n.i.	-0.42*	n.i.	n.i.	n.i.	n.i.	0.03	-0.364
	AIC	1087.71	686.64	162.53	362.40	139.768	454.82	88.86	125.67
	LogLik	-533.9	-330.3	-70.30	-172.1	-170.8	-216.4	-33.43	-53.84
	DF	9	13	11	9	9	11	11	9

gattorugine, *Diplodus* spp., *Lebetus* spp and *Ammodytes* spp. The fish larvae communities described here are similar to the ones found in previous studies off the Iberian coast during the spring/summer seasons (John and Ré, 1995; Azeiteiro et al., 2006), although the relative proportion of sardine larvae (1 order of magnitude higher concentrations than for the other fish larvae groups) was significantly higher for the present study. The dominance of *S. pilchardus* in the spring ichthyoplankton communities was also registered for the Cantabrian Sea, North Iberia (Rodríguez et al., 2004). Total fish larval abundances determined off southern Iberia were within the range of the ones described in the present work, although other pelagic species dominate the spring ichthyoplankton communities; the sardine *Sardinella aurita* and the anchovy *Engraulis encrasicolus* (Baldó et al., 2006; Catalan et al., 2006). The first species is absent from the Western Iberia and anchovy larvae are mainly limited to the estuaries but in summer months can dominate the near-shore ichthyoplankton communities (John and Ré, 1995) although the adult catches of anchovies off the Western Iberian coast are residual compared to sardines.

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 preference of sardine larvae distribution in the mid-shelf explains why very near-shore studies of fish larvae communities off Western Iberia found comparably 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 *Callionymus* spp. and *Parablennius gattorugine*, the latter being a species that is typical of shallow waters (Azeiteiro et al., 2006; Borges et al., 2007a) and was found in high numbers in the northern transects close to coast 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).

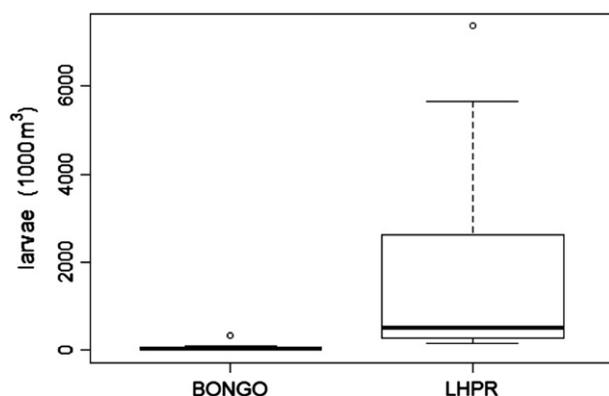


Fig. 6. Boxplots with larval concentrations (individuals 1000 m^{-3}) for all stations using Bongo and LHPR nets.

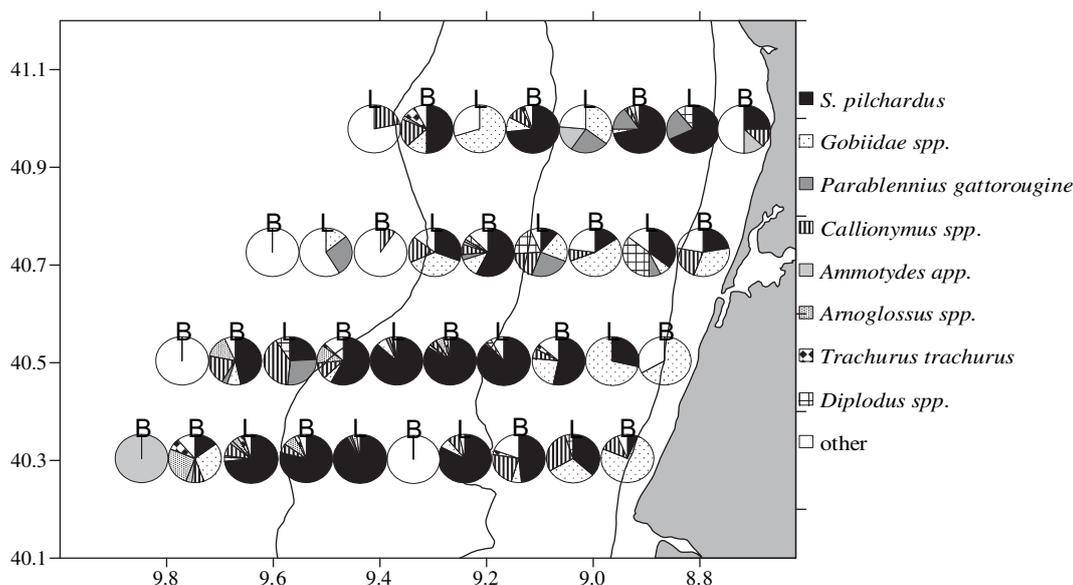


Fig. 7. Relative frequency of the most frequent/abundant fish larvae groups for all stations represented in Fig. 1, using LHPR ("L") and Bongo ("B") nets.

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 (Rodríguez 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 gattorougine*. 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* (Rodríguez, 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

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 larvae 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.

LHPR vs. Bongo	Coefficient	<i>p</i> -value	AIC	2 × LogLik	DF
<i>Larvae taxa</i>					
Total larvae	1.65 × 10 ⁻⁴	0.0551†	164.49	-158.49	15
<i>Sardina pilchardus</i>	2.80 × 10 ⁻⁴	0.0267*	151.21	-145.2	15
<i>Parablennius gattorougine</i>	7.82 × 10 ⁻³	0.448	34.91	-28.91	15
<i>Callionymus</i> spp.	1.09 × 10 ⁻³	0.351	86.05	-80.05	15
<i>Diplodus</i> spp.	1.45 × 10 ⁻²	0.2137	16.92	-10.92	15
Gobiidae unid.	1.38 × 10 ⁻³	0.41521	90.84	-84.84	15
<i>Ammodytes</i> spp.	-5.99 × 10 ⁻¹	0.9989	13.13	-7.13	15
<i>Arnoglossus</i> spp.	3.24 × 10 ⁻³	0.78	56.11	-50.11	15

Table 4
Average densities (\pm SD) of larvae (individuals 1000 m^{-3}) for different depth layers (neuston, <10 m, 10–15 m and >15 m) during day and night periods in the fixed station.

Fish larvae	Neuston		<10 m		10–15 m		>15 m		
	Day	Night	Day	Night	Day	Night	Day	Night	
Ammodytidae	<i>Ammodytes tobianus</i>	0.0	1.9 \pm 7.26	3.6 \pm 8.52	0.0	3.8 \pm 12.18	1.8 \pm 7.02	0.0	1.8 \pm 7.02
	<i>Gymnammodytes semisquamatus</i>	0.0	0.9 \pm 3.51	0.0	0.0	0.0	0.0	0.0	0.0
	<i>Hiperoplus lanceolatus</i>	0.0	14.4 \pm 19.67	0.0	0.0	0.0	0.0	0.0	0.0
Belonidae	<i>Belone belone</i>	114.2 \pm 127.68	163.2 \pm 112.97	0.0	10.4 \pm 32.46	0.0	0.0	0.0	0.0
Blennidae	Blennidae unident.	21.5 \pm 33.18	87.5 \pm 126.90	4.5 \pm 14.10	0.0	0.0	0.0	0.0	0.0
	<i>Parablennius gattorougine</i>	4.0 \pm 10.22	236.6 \pm 310.87	13.0 \pm 23.10	13.69 \pm 24.77	3.0 \pm 8.88	1.7 \pm 6.92	2.8 \pm 12.03	0.35 \pm 1.38
	<i>Coryphoblennius galerita</i>	0.0	0.0	2.4 \pm 10.29	0.0	0.5 \pm 2.32	0.0	3.2 \pm 13.92	0.0
Bothidae	<i>Lipophrys pholis</i>	0.9 \pm 3.87	0.0	0.0	1.6 \pm 6.51	0.0	0.8 \pm 3.25	0.0	0.0
	<i>Arnoglossus lanterna</i>	0.0	0.8 \pm 3.27	0.0	0.0	0.0	0.0	0.0	0.0
Callionymidae	<i>Callionymus unident.</i>	5.8 \pm 14.71	12.6 \pm 29.14	1.6 \pm 4.91	10.3 \pm 16.90	4.1 \pm 12.28	6.8 \pm 13.51	72.2 \pm 74.80	41.2 \pm 50.56
	<i>Callionymus lyra</i>	0.0	0.0	0.0	0.7 \pm 3.03	0.0	1.9 \pm 7.59	0.0	11.8 \pm 28.45
	<i>Callionymus maculatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5 \pm 6.15
Carangidae	<i>Trachurus trachurus</i>	0.3 \pm 1.63	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clupeidae	<i>Sardina pilchardus</i>	8.7 \pm 19.90	617.7 \pm 947.46	339.2 \pm 721.50	381.3 \pm 381.82	211.5 \pm 442.47	137.5 \pm 206.44	69.9 \pm 99.50	140.6 \pm 148.06
Gadidae	<i>Phycis blennoides</i>	38.6 \pm 39.52	53.0 \pm 63.38	0.0	0.0	0.0	0.0	4.0 \pm 16.99	0.0
	<i>Gaidropsarus spp.</i>	38.6 \pm 39.52	53 \pm 63.38	0.0	0.0	0.0	0.0	0.0	0.0
Gobiidae	<i>Gobiidae unident.</i>	1.5 \pm 3.80	21.4 \pm 39.19	3.7 \pm 11.10	28.9 \pm 43.79	1.3 \pm 5.78	32.3 \pm 49.22	1.2 \pm 5.36	42.9 \pm 54.72
Gobiesocidae	<i>Gobiesocidae unident.</i>	0.0	6.1 \pm 17.93	0.0	0.8 \pm 3.13	0.0	2.0 \pm 7.84	0.0	0.0
	<i>Diplecogaster bimaculata</i>	0.0	21.9 \pm 39.35	3.5 \pm 10.36	7.7 \pm 27.21	1.6 \pm 7.10	4.5 \pm 9.92	0.0	14.7 \pm 36.48
Labridae	<i>Labrus bergylta</i>	0.0	0.0	2.1 \pm 6.31	0.0	2.8 \pm 8.71	0.0	0.0	0.0
	<i>Labrus mixtus</i>	0.0	0.0	0.0	0.0	0.0	0.0	2.9 \pm 12.39	0.0
	<i>Symphodus melops</i>	0.0	12.9 \pm 23.92	5.8 \pm 13.68	3.2 \pm 8.71	1.6 \pm 7.10	2.1 \pm 8.34	7.9 \pm 23.39	0.4 \pm 1.66
Scophthalmidae	<i>Ctenolabrus rupestris</i>	1.3 \pm 4.19	88.4 \pm 135.67	0.0	0.0	1.3 \pm 5.66	0.0	4.6 \pm 19.82	0.0
	<i>Zengopterus punctatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3 \pm 23.10
Scombridae	<i>Scomber spp.</i>	7.4 \pm 24.11	32.5 \pm 79.09	0.0	0.0	0.0	0.0	0.0	0.0
Soleidae	<i>Microchirus variegatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.9 \pm 19.10
Sparidae	<i>Diplodus spp.</i>	2.6 \pm 8.44	89.1 \pm 125.63	18.3 \pm 40.22	2.2 \pm 8.79	1.3 \pm 5.85	0.0	4.3 \pm 13.39	0.0
	<i>Spondyliosoma cantharus</i>	0.0	9.5 \pm 27.13	3.0 \pm 10.35	0.0	1.6 \pm 6.94	0.0	0.9 \pm 4.16	0.0
Trachinidae	<i>Echiichthys vipera</i>	3.9 \pm 8.49	2.5 \pm 7.19	0.0	1.9 \pm 7.69	0.0	0.3 \pm 1.53	3.6 \pm 15.31	0.0
Total Larvae		211.3 \pm 182.17	1473.8 \pm 1628.26	401.1 \pm 798.70	463.3 \pm 412.56	235.0 \pm 469.23	192.3 \pm 215.31	178.1 \pm 127.83	268.8 \pm 187.18

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.*, *Symphodus melops*, *Parablennius gattorougine*, and *Spondyliosoma cantharus*, 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 Ré (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 ÓCéidigh (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 Iberia. 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 1000 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,

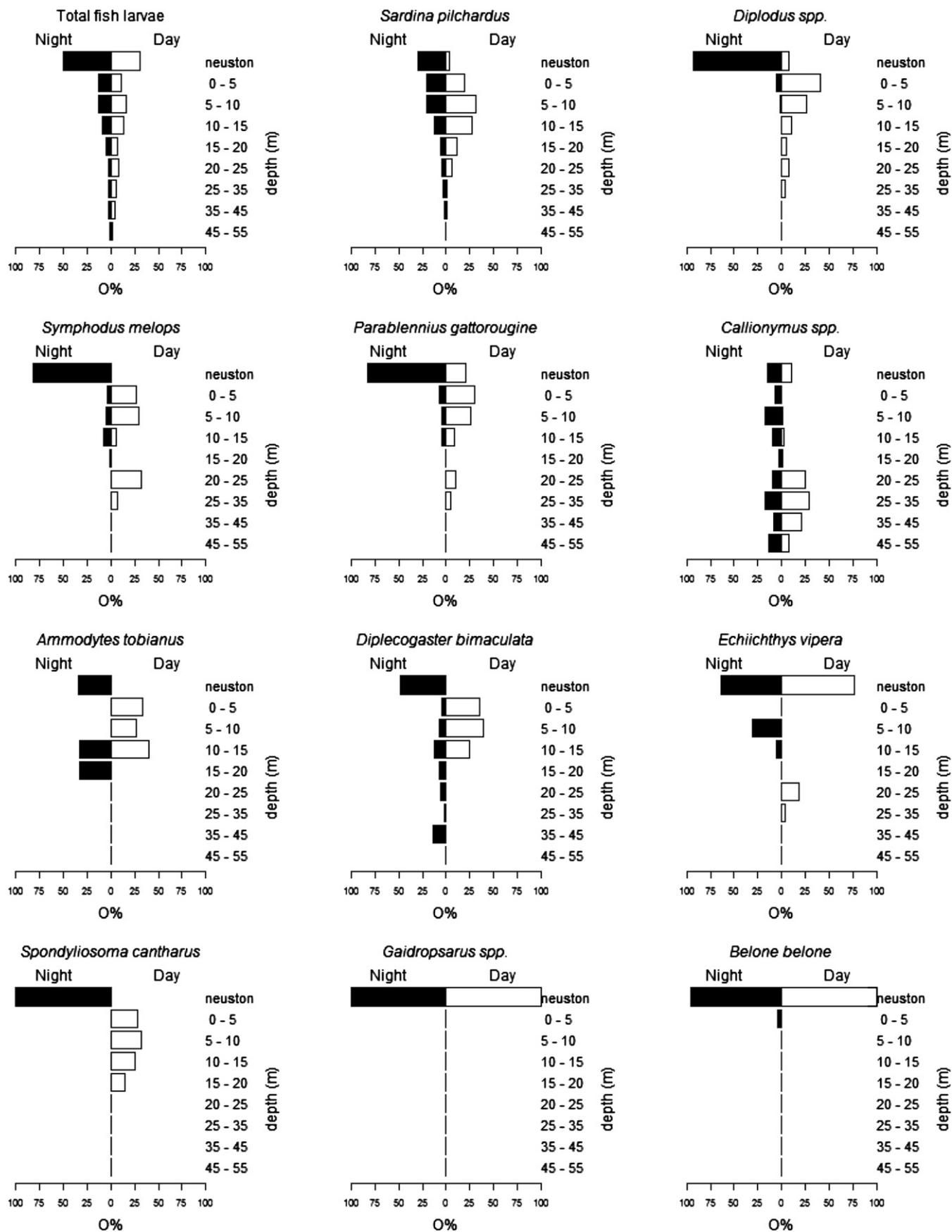


Fig. 8. Frequency of occurrence (%) of fish larvae at each depth range during the day and night periods for several fish larvae taxa collected at the fixed station during the 69-h period.

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 under upwelling conditions, are probably one plausible explanation that allows fish larvae to be in a surface favourable feeding environment (the WIBP) without being washed away from the shelf into unfavourable survival habitats. At the same time, most fish larvae species were able to perform diel vertical migrations, mostly concentrating at surface waters during the night and dispersing through the water column during daylight hours. This behaviour has been demonstrated for other planktonic organisms studied in the same area such as cyprids (dos Santos et al., 2007) and decapods (dos Santos et al., 2008) and may enable them to remain in the more productive waters closer to the coast or return to it by actively changing their vertical position in the water column. The vertical position of the fish larvae taxa was associated with taxon-specific environmental variables, and temperature was an important regressor explaining the presence of the majority of fish larvae species. Our results have also shown that the LHPR is more efficient in capturing fish larvae for most fish species when compared to the Bongo net but further studies are required in order to compare the selectivity of both nets for the different larvae species.

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References

- Andres, H.G., John, H.-Ch., Ré, P., 1992. Fish larvae and gammaridae plankton off Northern Portugal during autumn 1987. *Senckenbergiana maritima* 22, 179–201.
- Azeiteiro, U.M., Bacelar-Nicolau, L., Resende, P., Gonçalves, F., Pereira, M.J., 2006. Larval fish distribution in shallow coastal waters off North Western Iberia (NE Atlantic). *Estuarine, Coastal and Shelf Science* 69, 554–566.
- Baldó, F., García-Isarch, E., Jimenez, M.P., Romero, Z., Sanchez-Lamadrid, A., Catalan, I.A., 2006. Spatial and temporal distribution of the early life stages of three commercial fish species in the northeastern shelf of the Gulf of Cádiz. *Deep-Sea Research II* 53, 1391–1401.
- Barry, S.C., Welsh, A.H., 2002. Generalized additive modelling and zero inflated count data. *Ecological Modelling* 157, 179–188.
- Barton, E.D., Inall, M., Sherwin, T., Torres, R., 2001. Vertical structure, turbulent mixing and fluxes during Lagrangian observations of an upwelling filament system off Northwest Iberia. *Progress in Oceanography* 51, 249–267.
- Borges, R., Ben-Hamadou, R., Chicharo, M.A., Ré, P., Gonçalves, E.J., 2007a. Horizontal spatial and temporal distribution patterns of nearshore larval fish assemblages at a temperate rocky shore. *Estuarine, Coastal and Shelf Science* 71, 412–428.
- Borges, R., Beldade, R., Gonçalves, E.J., 2007b. Vertical structure of very nearshore larval fish assemblages in a temperate rocky coast. *Marine Biology* 151, 1349–1363.
- Catalan, I.A., Jimenez, M.T., Alconchel, J.L., Prieto, L., Munoz, J.L., 2006. Spatial and temporal changes of coastal demersal assemblages in the Gulf of Cadiz (SW Spain) in relation to environmental conditions. *Deep-Sea Research II* 53, 1402–1419.
- Chicharo, M.A., Esteves, E., Santos, A.M.P., Peliz, A., Ré, P., 2003. Are sardine larvae caught off northern Portugal in winter starving? An approach examining nutritional conditions. *Marine Ecology Progress Series* 257, 303–309.
- Conway, D.V.P., Coombs, S.H., Smith, C., 1997. Vertical distribution of fish eggs and larvae in the Irish Sea and southern North Sea. *ICES Journal of Marine Science* 54, 136–147.
- de Figueiredo, G.M., Nash, R.D.M., Montagnes, D.S., 2007. Do protozoa contribute significantly to the diet of larval fish in the Irish Sea? *Journal of the Marine Biological Association of the UK* 87, 843–850.
- dos Santos, A., Santos, A.M.P., Conway, D.V.P., 2007. Horizontal and vertical distribution of cirripede cyprid larvae in an upwelling system off the Portuguese coast. *Marine Ecology Progress Series* 329, 145–155.
- dos Santos, A., Santos, A.M.P., Conway, D.V.P., Bartilotti, C., Lourenço, P., Queiroga, H., 2008. Diel vertical migration of decapod larvae in the Portuguese coastal upwelling ecosystem: implications for offshore transport. *Marine Ecology Progress Series* 359, 171–183.
- Fox, J., 2008. Companion to Applied Regression. Package "car" version 1.2-9. <http://cran.r-project.org/web/packages/car/car.pdf>.
- Frouin, R., Fiúza, A.F., Ambar, I., Boyd, T.J., 1990. Observations of a poleward surface current off the coast of Portugal and Spain during winter. *Journal of Geophysical Research* 95, 679–691.
- García, A., Palomera, I., 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. *Scientia Marina* 60, 155–166.
- Gurmu, S., 1998. Generalized hurdle count data regression models. *Economical Letters* 58, 263–268.
- Haynes, R., Barton, E., 1990. A poleward flow along the Atlantic coast of the Iberian Peninsula. *Journal of Geophysical Research* 95, 11425–11441.
- Haynes, R., Barton, E.D., Pilling, I., 1993. Development, persistence and variability of upwelling filaments off the Atlantic coast of Iberian Peninsula. *Journal of Geophysical Research* 98, 22681–22692.
- Hempel, G., Weikert, W., 1972. The neuston of the subtropical and boreal north-eastern Atlantic ocean: a review. *Marine Biology* 13, 70–88.
- Hinkley, S., Hermann, A.J., Megrey, B.A., 1996. Development of a spatial explicit, individual-based model of marine fish early life history. *Marine Ecology Progress Series* 139, 47–68.
- Jackman, S., 2008. *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory, Stanford University. Department of Political Science, Stanford University, Stanford, California. R package version 1.03.* <http://pscl.stanford.edu/>.
- John, H.-Ch., 1982. Horizontal and vertical distribution of sardine and other fish larvae. *Rapports et Procès-verbaux Réunion des Conseil International pour l'Exploration de la Mer* 180, 359–364.
- John, H.-Ch., Ré, P., 1995. Cross-shelf zonation, vertical distribution and drift of fish larvae off Northern Portugal during weak upwelling. *Arquivos de Museu Bocage* 2, 607–632.
- John, H.-Ch., Ré, P., Zuelicke, Ch., 1996. Sardine larvae in a spring upwelling event off Northern Portugal. *Ciência Biológica. Ecology Sistemática* 16, 193–198.
- Lee, O., Nash, R.D.M., Danilowicz, B.S., 2005. Small-scale spatio-temporal variability in ichthyoplankton and zooplankton distribution in relation to a tidal-mixing front in the Irish Sea. *ICES Journal of Marine Science* 62, 1021–1036.
- Neilson, J.D., Pery, R.I., 1990. Diel vertical migrations of marine fishes – an obligate or facultative process. *Advances in Marine Biology* 26, 115–168.
- Oksanen, J., 2008. *Community Ecology Package. Package Vegan version 1.15-3.* <http://vegan.r-forge.r-project.org/>.
- Olivar, M.P., Sabatés, A., 1997. Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. *Marine Biology* 129, 289–300.
- Otero, P., Ruiz-Villareal, M.R., Peliz, A., 2008. Variability of river plumes off Northwest Iberia in response to wind events. *Journal of Marine Systems* 72, 238–255.
- Peliz, A., Dubert, J., Santos, A.M.P., Oliveira, P.B., Le Cann, B., 2005. Winter upper ocean circulation in the Western Iberian Basin – fronts, eddies and poleward flows: an overview. *Deep-Sea Research I* 52, 621–646.
- Peliz, A., Rosa, T., Santos, A.M.P., Pissarra, J.L., 2002. Jets, eddies and counterflows in the Western Iberian upwelling system. *Journal of Marine Systems* 35, 61–77.
- Pepin, P., Dower, J.E., 2007. Variability in the trophic position of larval fish in a coastal pelagic ecosystem based on stable isotope analysis. *Journal of Plankton Research* 29, 727–737.
- Prista, N., Vasconcelos, R.P., Costa, M.J., Cabral, H., 2003. The demersal fish assemblage of the coastal area adjacent to the Tagus estuary (Portugal): relationships with environmental conditions. *Oceanologica Acta* 26, 525–536.
- R Development Core Team, 2008. *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* Available at: www.R-project.org.
- Ribeiro, A.C., Peliz, A., Santos, A.M.P., 2005. A study of the response of chlorophyll-a biomass to a winter upwelling event off Western Iberia using SeaWiFS and in situ data. *Journal of Marine Systems* 53, 87–107.

- Rodríguez, J.M., 1990. Contribución al conocimiento del ictioplancton del Mar de Alborán. *Boletín del Instituto Español de Oceanografía* 6, 1–20.
- Rodríguez, J.M., Barton, E.D., Hernández-Léon, S., Aristegui, J., 2004. The influence of mesoscale physical processes on the larval fish community in the Canaries CTZ, in summer. *Progress in Oceanography* 62, 171–188.
- Röpke, A., 1989. Small-scale vertical distribution of ichthyoplankton in the Celtic Sea in April 1986. *Meeresforschung* 32, 192–203.
- Rossi, S., Sabatés, A., Latasa, M., 2006. Lipid biomarkers and trophic linkages between phytoplankton, zooplankton and anchovy (*Engraulis encrasicolus*) larvae in the NW Mediterranean. *Journal of Plankton Research* 28, 551–562.
- Sabatés, A., 2004. Diel vertical distribution of fish larvae during the winter-mixing period in the Northwestern Mediterranean. *ICES Journal of Marine Science* 61, 1243–1252.
- Sanchez-Velasco, L., Norbis, W., 1997. Comparative diets and feeding habitats of *Boops boops* and *Diplodus sargus* larvae, two sparid fishes co-occurring in the north-western Mediterranean (May 1992). *Bulletin of Marine Science* 61, 821–835.
- Santos, A.M.P., Peliz, A., Dubert, J., Oliveira, P.B., Angelico, M.M., Ré, P., 2004. Impact of a winter upwelling event on the distribution and transport of sardine (*Sardina pilchardus*) eggs and larvae off western Iberia: a retention mechanism. *Continental Shelf Research* 24, 149–165.
- Santos, A.M.P., Ré, P., Dos Santos, A., Peliz, A., 2006. Vertical distribution of the European sardine (*Sardina pilchardus*) larvae and its implications for their survival. *Journal of Plankton Research* 28, 523–532.
- Simonsen, C.S., Munk, P., Folkvord, A., Pedersen, S.A., 2006. Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. *Marine Biology* 149, 937–952.
- Stehle, M., Dos Santos, A., Queiroga, H., 2007. Comparison of zooplankton sampling performance of Longhurst–Hardy Plankton Recorder and Bongo nets. *Journal of Plankton Research* 29, 169–177.
- Strydom, N.A., 2008. Utilization of shallow subtidal bays associated with warm temperate rocky shores by the late-stage larvae of some inshore fish species, South Africa. *African Zoology* 43, 256–269.
- Tully, O., ÓCéidigh, P., 1989. The ichthyoneuston of Galway Bay (Ireland): I. The seasonal, diel and spatial distribution of larval, post-larval and juvenile fish. *Marine Biology* 101, 27–41.
- Vargas-Yanez, M., Sabatés, A., 2007. Mesoscale high-frequency variability in the Alboran Sea and its influence on fish larvae distributions. *Journal of Marine Systems* 68, 421–438.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S*, fourth ed. Springer, New York.
- Williams, R., Collins, N.R., Conway, D.V.P., 1983. The double LHPR system, a high speed micro- and macroplankton sampler. *Deep-Sea Research I* 30, 331–342.
- Welsh, A.H., Cunningham, R.B., Donnelly, C.F., Lindenmayer, D.B., 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. *Ecological Modelling* 88, 297–308.
- Wooster, W.S., Bakun, A., McLain, D.R., 1976. The seasonal upwelling cycle along the eastern boundary of the North Atlantic. *Journal of Marine Research* 34, 131–141.
- Worthington, E.B., 1931. Vertical movements of freshwater macroplankton. *Internationale Revue des gesamtten Hydrobiologie und Hydrographie* 25, 394–436.
- Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. *Journal of Statistical Software* 27, 1–25.