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Vertical distribution of fish larvae in the Canaries-African coastal transition zone, in summer

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Abstract

This study reports the vertical distribution of fish larvae during the 1999 summer upwelling season in the Canaries-African Coastal Transition Zone (the Canaries-ACTZ). The transition between the African coastal upwelling and the typical subtropical offshore conditions is a region of intense mesoscale activity that supports a larval fish population dominated by African neritic species. During the study, the thermal stratification extended almost to the surface everywhere, and the surface mixed layer was typically shallow or non-existent. Upwelling occurred on the African shelf in a limited coastal sub-area of our sampling. The vertical distributions of the entire larval fish population, as well as of individual species, were independent of the seasonal thermocline. Fish larvae and mesozooplankton were concentrated at intermediate depths regardless of the thermocline position, probably because of its weak signature and spatial and temporal variability. Day/night vertical distributions suggest that some species did not perform diel vertical migration (DVM), whereas others showed either type I DVM or type II DVM. The opposing DVM patterns of different species compensate for each other resulting in no net DVM for the larval fish population as a whole.

KEY WORDS: Fish larvae; Vertical distribution; African coastal transition zone; NW African upwelling

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Introduction

Most neritic and oceanic fish larvae have been reported to occur in the surface mixed layer and upper part of the thermocline (e.g. Ahlstrom 1959; Loeb 1979; Palomera 1991; Boehlert and Mundy 1994; Olivar and Sabates 1997; Smith and Suthers 1999; Coombs et al. 2001), where patterns of vertical distributions and daily migrations are taxon-specific (e.g. Ahlstrom 1959; Roepke 1989; Leis 1991; Gray 1996; Olivar and Sabates 1997; Gray and Kingsford 2003). Temperature and light are important factors in determining these patterns (Roepke 1989; Olla and Davis 1990; Heath et al. 1991; Brodeur and Rugen 1994). Other studies have suggested that vertical distributions and migrations are independent of the thermal stratification and are determined by feeding conditions in the water column (Fortier and Leggett 1983; Southward and Barret 1983; Munk et al. 1989; Palomera 1991; Roepke 1993).

The vertical distributions of fish eggs and larvae and larval migration patterns must be known to understand and predict horizontal distributions in the presence of vertical shear. The interaction between vertical distributions, migrations and hydrodynamic processes is of special importance to the horizontal distribution of fish larvae in coastal upwelling regions and adjacent areas (Parrish et al. 1981; Norcross and Shaw 1984; Olivar 1990; Smith and Suthers 1999). Fish eggs and larvae with near-surface distributions are more susceptible to transport offshore in the Ekman layer associated with coastal upwelling (John 1985; John and Re 1995; Smith and Suthers 1999). Advection of larvae of African neritic species, by Ekman transport and upwelling filaments, is considered the principal cause of domination of the Canaries-ACTZ larval fish population by these larvae during the summer upwelling season (Rodriguez et al. 1999; Rodriguez et al. 2004). In contrast, deeper distributions render eggs and larvae liable to shoreward transport in the deep onshore flow that is also associated with coastal upwelling (Hamann et al. 1981; John 1985; John and Re 1995; Smith and Suthers 1999). In some cases, fish larvae migrate vertically between the two flow regimes daily (Parrish et al. 1981; Myers and Drinkwater 1989) or ontogenetically (Norcross and Shaw 1984; John 1985; Gorbunova et al. 1986) to avoid advection from suitable nursery grounds.

Knowledge of vertical distributions of early life stages of fishes also has practical implications for developing sampling strategies. Sampling to inappropriate depths can

lead to undersampling if the entire depth range of the distribution of target species is not covered, or to wasted sampling time in the case of surface dwelling species.

In this paper, we examine the vertical distributions of the whole larval fish population and of the most common larval fish species that inhabit Canaries-African Coastal Transition Zone (the Canaries-ACTZ) in summer, in relation to the thermal structure of the water column. We also contribute some new information about the daily vertical migrations of these groups.

Oceanography of the Canaries-ACTZ in summer

During the summer upwelling season, the transition (Fig. 1) between the NW African coastal upwelling and typical offshore conditions is characterised by intense mesoscale activity. The Canary Islands' abrupt topography acts as a barrier to the Canary Current and trade winds. This introduces a strong variability in the atmospheric and oceanic flows. Warm lees are formed downwind of the islands, and cyclonic and anticyclonic eddies are shed continuously from the islands to drift southward with the general flow (Aristegui et al. 1994; Aristegui et al. 1997; Barton et al. 1998). Also, upwelling filaments originating on the African shelf may reach the eastern islands of the Canary archipelago to interact with the warm lees and the island-shed eddies (Barton et al. 2000; Basterretxea et al. 2002). Like eddies, these upwelling filaments are structures changing in space and time (Barton et al. 1998; Barton et al. 2004), contributing to the high variability of environmental conditions in the Canaries-ACTZ.

Materials and methods

***Sampling procedures*.** Sampling of the Canaries-ACTZ was conducted aboard the R/V *Hesperides*, from 5 to 27 August, 1999 (Fig. 1). Hydrographic conditions were measured at every station by means of a CTD (Barton et al. 2004). Zooplankton and ichthyoplankton were sampled at 37 stations (19 at night and 18 during the day). These stations (Fig. 1) were arranged in one long section (LS), seven short transects (S, F, Q, W and Y) and two isolated stations (D). Five of the short transects (S, F, Q -F repeated-, W and Y) crossed upwelling filaments perpendicularly at different distances from the African coast. The stations were arranged with one north of an upwelling filament, one or two in the filament itself, and the last south of the filament. Transect V crossed filament F2 and the anticyclonic eddy (A7) located southwest of Fuerteventura and

transect Z crossed the anticyclonic eddy (A6) and the warm island wake south-southeast of Gran Canaria (Fig. 1). All of these structures were apparent in the satellite imagery of the region obtained during the cruise (Barton et al. 2004). The two isolated stations (D2 and D4), corresponded to 24-hour samplings following surface drifters. Only two of the ichthyoplankton stations (D2 and LS24) were located over the African neritic region, while the remainder were in the oceanic region beyond the 200 m isobath.

Zooplankton and ichthyoplankton samples were collected with a Longhurst-Hardy Plankton Recorder (LHPR) (Williams et al. 1983) fitted with a calibrated flow meter. On station, oblique tows, at a speed of 3-4 knots, were made to 200 m depth or to 10 m above the bottom where shallower. The 200 µm mesh screen in the sampler was programmed to increment at 2 minutes intervals during the descent of the net, collecting a series of consecutive samples with a vertical resolution from 10 to 30 m. After recovering the gear, plankton was removed from the meshes and the resulting samples were preserved in a buffered 4% solution of formalin and seawater. At every station, the individual 2-minute strata were aggregated into 9 strata corresponding to the following depth ranges: 0-20, 20-35, 35-50, 50-66, 66-82, 82-100, 100-124, 124-151 and 151-200. At the shallower stations D2 and 24, the bottom depth permitted sampling only to 85 and 80 m, respectively.

Laboratory procedures. All fish eggs and larvae were sorted and counted in the laboratory. Fish larvae were identified to the lowest taxonomic level possible. *Engraulis encrasicolus* larvae were measured to 0.1 mm (standard length) under a microscope, using an ocular micrometer. For all the other fishes, their developmental stage (larvae or juvenile) was determined. Juvenile fishes were only identified to the family level (81 myctophids and 5 gonostomatids) and they were not included in the analysis of average vertical distribution or daily migrations of individual larval fish species. The composition of the entire larval fish assemblage can be found in Rodriguez et al. (2004). The term “larval fish assemblage” used here refers to all larval fish caught at every ichthyoplankton station. Mesozooplankton individuals were counted using a laboratory Optical Plankton Counter (OPC). However, when using an OPC to count zooplanktonic individuals, the fractions of the zooplankton population <250 µm and >2 mm in diameter are lost. The smaller zooplankton, eggs and naupliar through adult stages of copepods constitute the main food items for fish larvae (Hunter 1984). The number of individuals collected in the different sampling strata was standardised to number unit^{-1}

of filtered water (densities): m^3 for mesozooplankton, 10 m^3 for fish eggs, and 1000 m^3 for fish larvae (densities). The number of larval fish taxa recorded at every stratum was standardised to number 100 m^{-3}, and this value was taken as a approximate measure of the taxonomic diversity. Average vertical distributions were calculated using all the stations. Fish larvae caught in the different sampling strata were also integrated to obtain the number of individuals 10 m^{-2} of sea surface (abundances).

The weighted mean depth (WMD) of the vertical distributions of mesozooplankton and fish larvae at each station was calculated as the centre of density:

$$\text{WMD} = \sum_{i=1}^{n}(p_i Z_i) = \sum_{i=1}^{n}(C_i Z_i) / \sum_{i=1}^{n} C_i$$

where p_i and C_i are, respectively, the proportion and the concentration of mesozooplankton individuals (number m^{-3}) and fish larvae (number 1000 m^{-3}) in the *i*th stratum, and Z_i is the mid-depth of the *i*th stratum (e.g. Fortier and Leggett 1983; Heath et al. 1991; Gronkjaer and Wieland 1997).

Data analysis. The relationship between variables was assessed through correlation analysis. We calculated the Pearson's correlation coefficient between the horizontal distributions of mesozooplankton densities and larval fish abundances and also between thermocline depths, fluorescence maximum depths, WMDs of mesozooplankton, WMDs of the larval fish assemblages and WMDs of single larval fish species. The thermocline depth was calculated as the depth of the strongest temperature gradient in the upper 200 m. The gradient was calculated over 5 m-intervals to eliminate small-scale structures that could give anomalous results. The bottom of the thermocline was defined as the depth where a strong change in the slope of the temperature profile was observed. This change coincided in general with the 18.5 ºC isotherm and we choose this isotherm depth as the thermocline bottom.

The amplitude of daily vertical migration (DVM) was calculated as the difference between the average WMD between day and night. A positive value indicated movement towards the surface during the night, or type I DVM, and a negative value indicated reverse vertical migration, or type II DVM (Neilson and Perry 1990). Following Irigoeien et al. (2004), only those organisms whose mean depth varied by more than 10 m between day and night were considered to perform significant DVM.

One-way ANOVA was used to compare the difference in size with depth of *Engraulis encrasicolus* larvae for day and night catches independently. The absence of larvae

during daytime from the two deepest strata prevented us from using a two-way ANOVA.

Results

Hydrographic conditions

The hydrography of the study area during the sampling period was summarised in Barton et al. (2004) on the basis of extensive *in situ* sampling and remote sensing. Features described (Fig. 1) included an anticyclonic eddy (A1) shed from Tenerife, an anticyclone (A6) and a cyclone (C2) shed from Gran Canaria, an eddy spinning anticyclonically south of Fuerteventura (A7) and an upwelling filament (F1). A second filament (F2) subsequently developed further north to merge with F1 some 100 km offshore. The filaments were partially entrained over the slope around a topographically trapped cyclonic eddy (C7). Two more eddies, one cyclonic (C8) and the other anticyclonic (A8), were observed between the filament branches and the African coast. Moreover, the characteristic warm regions in the lee of Gran Canaria and Fuerteventura were also evident.

The water column was thermally stratified. In this subtropical region, off the continental shelf, the seasonal summer thermocline is contiguous with the permanent thermocline. The surface mixed layer, where there was one, was in general shallow. The depth and, to a lesser extent, the intensity of the seasonal thermocline varied greatly between stations. The thermocline was shallow in the core of the cyclonic eddies and in filaments, but deeper in the core of the anticyclonic eddies and warm wakes, and gradually rose to the surface as it approached the coastal upwelling region (Figs. 2-4).

Overall vertical distributions

Chlorophyll-a was highly stratified. All the fluorescence profiles showed a maximum consistently located at the bottom of the thermocline. Differences between maximum fluorescence depths and bottom of the thermocline depths were not significant (T-Student for paired samples, $p=0.82$, $p<0.01$). The dependence of the vertical distribution of phytoplankton on the vertical thermal structure of the water column was corroborated by the high and significant correlation found between thermocline depths and maximum fluorescence depths ($r=0.82$, $p<0.01$).

Mesozooplankton (Fig. 2) and fish larvae (Fig. 3) were distributed throughout the sampled water column, with the highest densities found at intermediate depths. In some

cases (e.g. stations S14 and V8), the vertical distributions were quite uniform. Greatest larval fish diversity was also found at intermediate depths, except at station D2, where it occurred in the surface stratum (Fig. 4).

The mean concentration of mesozooplankton (Fig. 5a) increased from the surface to a maximum at the 35-50 m stratum, then decreased gradually towards deeper layers. However, the average vertical distribution shows that fish larvae were more stratified; most larvae were concentrated between 20 and 66 m depth (Fig. 5b). The maximum larval fish density was recorded in the same stratum (35-50 m) as mesozooplankton. The average vertical distribution shows that maximum larval diversity was found in the 50-66 m stratum, below the maximum larval density (Fig. 5c).

Individual larval fish species followed different patterns of vertical distribution. The vertical distribution of *E. encrasicolus* larvae (Fig. 5d) and *Sardine pilchardus* larvae (Fig. 5f) were similar, although no *S. pilchardus* larvae were found below 151 m. *E. encrasicolus* dominated the larval fish population of the Canaries-ACTZ at the time of our sampling, comprising 29.3% of the total larval fish catch (Rodriguez et al. 2004). Over 97% of the *E. encrasicolus* and all *S. pilchardus* larvae (2.1% of the total larval fish catch) were caught in the oceanic region, outside the 200 m isobath. Also, 1780 *E. encrasicolus* eggs were collected at the two stations located over the African continental shelf, most of which were concentrated in the surface layer (Fig. 5e). Below 35 m, densities were uniformly low. Most of the *E. encrasicolus* eggs (>83%) and all of the smallest larvae (those <3.0 mm in size) were caught in the 0-35 m layers of station D2, located near the root of filament F2.

Anthias anthias (13.0% of the total larval fish catch) was the species that showed the least stratified vertical distribution (Fig. 5g), distinct from the other neritic and oceanic species. All the larvae of this neritic species were caught in the oceanic region.

Most larvae of the mesopelagic species *Cyclothone braueri* (6.3% of the total larval fish catch) were concentrated between 20 and 66 m (Fig. 5h), and they were absent or present in very low densities in the two deepest strata (124-200 m).

Ceratoscopelus maderensis (3.9% of the larval fish catch) had the shallowest distribution of all myctophids studied (Fig. 5i). The maximum density occurred in the 35-50 m stratum, and larvae were almost absent below 82 m. The other myctophid species, *Notolichnus valdiviae* (Fig. 5j), *Diogenicthys atlanticus* (Fig. 5k) and *Myctophum punctatum* (Fig. 5l), with 1.8%, 3.5% and 3.2% of the total larval fish catches respectively, showed vertical distributions with few or no larvae above 35 m.

Their maximum densities were found in the 66-82 m stratum. Almost all of the larvae classified as oceanic species (99.7%) were caught in the oceanic region.

The WMDs of all larvae and individual larval fish species were generally not related to the thermocline or maximum fluorescence depths, but they were positively, and in most cases significantly, related to the WMD of mesozooplankton (Table I). The significant correlation found between the WMD of *D. atlanticus* and thermocline depth must be viewed with caution because the correlation coefficient was small, this significant relation only represented 11.0% of the larval fish groups implicated in the analysis and the number of larvae of this species was relatively low. These considerations are also applicable to the significant correlations found between WMDs of *D. atlanticus* and *N. valdiviae* with maximum fluorescence depths.

The horizontal distribution of larval fish abundances was significantly correlated with the horizontal distribution of the mesozooplankton densities ($r=0.42$, $p=0.01$).

Diel vertical migrations

Mesozooplankton (Fig. 6a) and total larvae (Fig. 6b) followed almost identical patterns of vertical distribution during day and night, although densities in every stratum were higher at night than during the day. Neither group showed daily vertical migration (Table II). Individual larval fish species showed relatively different patterns of vertical distributions for day and night. The neritic species, *E. encrasicolus* (Fig. 6c), *S. pilchardus* (Fig. 6d) and *A. anthias* (Fig. 6e), exhibited a more stratified vertical distribution during day than night. However, only *S. pilchardus* larvae performed significant diel vertical migration (Table II). As for mesopelagic species, *N. valdiviae* and *D. atlanticus* larvae showed normal or type I DVM and *M. punctatum* showed reverse or type II DVM (Table II). It is also apparent from Figure 6 that more mesozooplankton and fish larvae of all groups were caught at night than during the day.

A total of 808 *E. encrasicolus* larvae were measured. They ranged in size from 2.5 to 23.0 mm, with a mean of 9.9 mm. Of these larvae, the 656 specimens caught at night were significantly larger (mean size 10.1 mm), than the 152 caught during the day (mean size 9.1 mm) (T-test, $p < 0.01$). During daytime, the size of the larvae increased steadily with depth, from a mean of 8.1 mm in the surface stratum to 13.0 mm in the 82-100 m stratum. Differences in size between strata were significant (ANOVA, $p < 0.01$). At night, the largest larvae (up to 23.0 mm in length and with a mean size 11.3 mm)

were caught in the surface stratum. In the remaining strata, the mean size ranged from 9.1 to 10.3 mm. The differences in larval *E. encrasicolus* size between strata were also significant (ANOVA, $p < 0.01$).

Discussion

Physical conditions

The continuous permanent and seasonal thermoclines found in the oceanic area, where the great majority of the larvae were caught, is typical of summer conditions in subtropical waters. The distinctive characteristic of the Canaries-ACTZ is the strong mesoscale oceanographic activity in the region, apparent in the satellite imagery of the area at the time of the sampling (Barton et al. 2004), and also reflected in the variability in the distribution of temperature along the different transects (Figs. 2, 3 and 4). Upwelling episodes, with the consequent formation of Ekman transport and upwelling filaments, and eddy shedding from the Canary Islands result in great variability in thermocline depth over short distances (Figs. 2, 3 and 4) and times.

Larval vertical distributions

The distribution of fish larvae was vertically stratified. This was consistent with the vertical distributions reported for fish larvae in coastal (e.g. Ahlstrom 1959; Boehlert et al. 1985; Olivar 1990; Leis 1991; Gray 1993; Conway et al. 1997) and oceanic waters (e.g. Ahlstrom 1959; Loeb 1979; Roepke 1993). The observation that maximum larval diversity occurred below the depth of maximum larval density suggests that the maximum diversity was found where species with shallower distribution met species with deeper distribution.

Vertical distributions of fish larvae have often been related to the thermal stratification of the water column (Loeb 1980; Hamann et al. 1981; Roepke et al. 1993; Boehlert and Mundy 1994; Moser and Pommeranz 1999). The presence of a thermocline was considered important (Loeb 1979; Kendall and Naplin 1981; Boehlert et al. 1985; Roepke et al. 1993; Smith and Suthers 1999) in acting as an upper or a lower barrier for the vertical distribution of the larvae of some species (Ahlstrom 1959; Coombs et al. 1981; Davis et al. 1990; Olla and Davis 1990). However, in the Canaries-ACTZ, the vertical distribution of fish larvae was not conditioned by the thermocline. Independence of vertical distributions from the vertical thermal structure of the water

column has been observed for coastal and oceanic waters in different regions of the world (Southward and Barret 1983; Roepke 1993; Gray 1996; Conway et al. 1997; Gray 1998). According to Olla and Davis (1990), fish larvae possess behavioural mechanisms that enable them to alter position in the water column to deal with environmental gradients and select favourable ones. Gray (1996) argued that larval behaviour, not thermocline location, is the major influence determining vertical distributions of fish larvae in waters characterized by strong physical variability. Gray and Kingsford (2003) provided evidence that thermoclines had no detectable effect on vertical distributions of fish larvae and mesozooplankton in dynamic coastal waters. In the Canaries-ACTZ the seasonal thermocline is relatively weak compared to, say, the sub-tropical Pacific, the Benguela upwelling or temperate seas in summer, and so fish larvae would experience only gradual temperature changes with depth, which may explain the negligible influence of the thermocline on the vertical distribution of fish larvae. However, It should be borne in mind that the combining of data from areas of different stratification and from different species, inevitable because of the sparse sampling, will tend to obscure any particular relationships in different features.

Vertical distributions of individual fish species, apart from the neritic species *E. encrasicolus* and *S. pilchardus* (no information is available concerning the vertical distribution of *A. Anthias*), were similar to patterns previously reported for the same or congener mesopelagic larval fish species in different regions of the world (Gorbunova 1973; Badcock and Merret 1976; Gorbunova 1977; Loeb 1979; Hamann et al. 1981; John 1984; John 1985; Boehlert et al. 1992; Roepke 1993). *E. encrasicolus* and *S. pilchardus* larvae had a deeper and a wider vertical distribution than previously found for these species in the NE Atlantic (Southward and Barret 1983; John 1985; John and Re 1995), in the NW Mediterranean (Palomera 1991; Olivar and Sabates 1997; Olivar et al. 2001) or in the Adriatic Sea (Regner 1972; Coombs et al. 1997). Species within these genres, such as *Engraulis mordax* and *Sardinops coerulea* in the California Current (Ahlstrom 1959; Boehlert et al. 1985; Moser and Pommeranz 1999), *Engraulis capensis* and *Sardinops ocellatus* in the Northern Benguela Region (Olivar 1990), and *Engraulis rigens* and *Sardinops sagax* in the Peru Current (Sameoto 1982) showed also shallower and narrower distribution than that found in this study. However, it must be emphasized that the above studies were carried out in neritic temperate regions or in subtropical upwelling regions, with different vertical distributions of abiotic and biotic properties from those found in this study. In Peruvian waters, Gorbunova et al. (1986)

found for *S. sagax* a shallow distribution in the coastal area but a deep distribution, even more so that in this study, in open ocean waters under conditions of convergent currents. *E. encrasicolus* eggs, all of them collected in the region of coastal upwelling, showed a pattern of vertical distribution similar to that observed for this species in the NE Atlantic ocean (Coombs et al. 2004), and the NW Mediterranean (Palomera 1991; Olivar et al. 2001) and Adriatic (Regner 1972; Coombs et al. 1997; Coombs et al. 2003) seas. The near-surface concentration of anchovy eggs has been related to the spawning location of this species in the water column (Olivar et al. 2001). This near surface location of most *E. encrasicolus* eggs and all of the smallest larvae within the Ekman layer, which in this region has a thickness between 20 and 60 m (Mittelstaedt 1983), results in them being transported away from the spawning site on the African continental shelf (Furnestin and Furnestin 1959). The larvae were then spread throughout the Canaries-ACTZ, in the Ekman layer and in upwelling filaments, where they dominated the larval fish population at the time of our sampling (Rodriguez et al. 2004).

From the above it follows that larval fish species, under similar environmental conditions, seem to occupy similar depth ranges in different regions of the world. This indicates a species-specific depth selection behaviour dependent on some particular environmental conditions of the water column. Ahlstrom (1959) reported that many of the differences observed in depth distributions of larvae of the same species in various sampling series were due to differences in the position of the thermocline. Other authors have reported the importance of vertical distribution of prey to the vertical distribution of fish larvae (Coombs et al. 1981; Sameoto 1982; Fortier and Leggett 1983; Fortier and Harris 1989; Munk et al. 1989; Palomera 1991; Ponton and Fortier 1992; Roepke 1993; Mullin and Cass-Calay 1997). In this study, the significant correlation found between the spatial distributions of fish larvae and mesozooplankton suggests some kind of relationship between them, perhaps trophic. If so, prey distribution would be an important environmental factor influencing the vertical distribution of fish larvae in the Canaries-ACTZ. But we have data neither about the composition of the mesozooplankton population nor about the gut content of the larvae to draw any conclusion. Further studies are required to elucidate this question. In any case, as in other dynamical regions (Gray and Kingsford 2003), the thermocline seems not be an important interface for trophic interactions between zooplankton and fish larvae.

Finally, we must add that to sample adequately the larval fish population in this region, it is necessary to carry out deeper hauls than we did in this study. Only the vertical distribution of *S. pilchardus* larvae seems to have been adequately covered by sampling to 200 m in depth.

Diel vertical migrations

The difficulties involved in the study of daily vertical migration (DVM) of fish larvae are significant (see Pearre 1979), especially considering the four main limitations of our sampling strategy: (1) This sampling was not specifically designated to study DVM. We compared samples collected at different times of day and night and at different locations with quite different environmental conditions. (2) The thickness of the strata could exceed the migration range of some individuals. (3) As we have seen above, our sampling depth did not cover the entire distribution range of most of the organisms studied. And (4) the accuracy of the amplitude estimation is related to the abundance of organisms. Apart from the whole populations of mesozooplankton and fish larvae and, perhaps, *E. encrasicolus* larvae, the other taxa were in relatively low abundance. Despite these limitations, given the particular lack of previous studies on the subject in the Canaries-ACTZ and the general paucity of studies about DVM in oceanic waters, such an investigation is fully warranted.

Although type I DVM is the most common pattern of DVM followed by larval fish species, type II DVM and no DVM have also been reported (Boehlert et al.1985, Neilson and Perry 1990; Olivar 1990; Brodeur and Rugen 1994; Conway et al. 1997). Ontogenetic differences in diel vertical migration have also been observed with more extensive DVM carried out by larger larvae (Fortier and Leggett 1983; Fortier and Harris 1989). In our study, the increase in size with depth during the day and the presence in the surface stratum of the largest *E. encrasicolus* larvae at night suggest normal or type I DVM of larger sized individuals. The size-related DVM has been reported for *E. encrasiclous* larvae (Palomera 1991; Olivar and Sabates 1997; Olivar et al. 2001) and other anchovy species (Hunter and Sanchez 1976; Brewer and Kleppel 1986). According to Hunter and Sanchez (1976), larger anchovy larvae would move to the surface to swallow air and fill their swim bladder in order to save the energy required to maintain a position in the water column during the night, when the larvae do not feed. However, in the absence of a strong physical barrier, even larvae with gas in

their swim bladders might passively sink during the resting period (Sogard et al. 1987; Munk et al. 1989; Brodeur and Rugen 1994; Olivar et al. 2001). This would result in the broader night-time distributions observed for *E. encrasicolus* against the more stratified, light gradient dependent daytime patterns actively maintained by larvae (Heath et al. 1988; Leis 1991; Ponton and Fortier 1992). The net result of active migrations to conform daytime patterns, and passive sinking at night would be no DVM, as found for *E. encrasicolus* larvae in this study (Table II)

The normal or model I of DVM found for *S. pilchardus* contradicts the DVM pattern previously found for this species (Olivar et al. 2001) and *Sardinops sagax* (Fletcher 1999). However, the size of the larvae (between 5.0 and 15.5 mm, mean 9.7 mm) and the size related DVM also reported for the larvae of this species (Olivar et al. 2001) must be considered. Neither, the low number of *S. pilchardus* larvae available for the analysis (67) must be not forgotten. For mesopelagic species there are few studies about larval DVM (see Neilson and Perry, 1990, for a review). In a recent study about diel vertical distribution of fish larvae in the Northwestern Mediterranean, Sabates (2004) reported that most of the mesopelagic species larvae were closer to the surface during the day than at night.

In the Canaries-ACTZ in summer, larval fish species seem to carry out little or no DVM. For those that migrate, the opposed DVM followed by different species compensate each other to produce an overall result of no net DVM for the total larval fish population. Fish larvae generally seem to maintain positions at intermediate depths coinciding with depths of maximum mesozooplankton densities. Perhaps feeding conditions there are optimal, and light levels reduce the predation risk and allow visual avoidance of the sampling gear by the larvae during the daytime. The last point would explain the differences in day/night catches for fish larvae.

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Figure legends

Figure 1. Geographic location of the study area, sampling stations, eddies and filaments as discussed in the text. (•) night stations, (o) day stations.

Figure 2. Vertical profiles of temperature (ºC) and vertical distributions of mesozooplankton (number of individuals m^{-3}) along the sampled transects. Circle size is proportional to densities and circles are centred in the middle of each of the 9 resulting strata for every ichthyoplankton station. The bottom of the thermocline is indicated by the thicker isoline. Station labelled in bold and italic are night stations. The approximate location of the different eddies and filaments discussed in the text is indicated.

Figure 3. Vertical profiles of temperature (ºC) and vertical distributions of larval fish densities (nº of individuals 1000 m^{-3}) along the sampled transects. Circle size is proportional to densities and circles are centred in the middle of each of the 9 resulting strata for every ichthyoplankton station. The bottom of the thermocline is indicated by the thicker isoline. Station labelled in bold and italic are night stations. The approximate location of the different eddies and filaments discussed in the text is indicated.

Figure 4. Vertical profiles of temperature (ºC) and vertical distribution of taxonomic diversity (nº of larval fish taxa 100 m^{-3}) along the sampled transects. Circle size is proportional to densities and circles are centred in the middle of each of the 9 resulting strata for every ichthyoplankton station. The bottom of the thermocline is indicated by the thicker isoline. Station labelled in bold and italic are night stations. The approximate location of the different eddies and filaments discussed in the text is indicated..

Figure 5. Mean vertical concentrations of a) mesozooplankton, b) total fish larvae, c) larval taxonomic diversity, d) *Engraulis encrasicolus* larvae, e) *E. encrasiclous* eggs, f) *Sardina pilchardus* larvae, g) *Anthias anthias* larvae, h) *Cyclothone braueri* larvae, i) *Ceratoscopelus maderensis* larvae, j) *Notolichnus valdiviae* larvae, k) *Diogenichthys atlanticus* larvae and l) *Myctophum punctatum* larvae (horizontal lines indicate positive values of standard error). The mean vertical profile of temperatures recorded at the ichthyoplankton stations is overlapped to the vertical distributions of mesozooplankton and fish larvae.

Figure 6. Mean day (open bars)/night (filled bars) vertical concentrations of a) mesozooplankton, b) total fish larvae, c) *Engraulis encrasicolus* larvae, d) *Sardina pilchardus* larvae, e) *Anthias anthias* larvae, f) *Cyclothone braueri* larvae, g) *Ceratoscopelus maderensis* larvae, h) *Notolichnus valdiviae* larvae, i) *Diogenichthys atlanticus* larvae and j) *Myctophum punctatum* larvae.

Table. I. Correlation coefficients between weighted mean depths (WDMs) of mesozooplankton, larval fish assemblages, and single larval fish species, and depth of the thermocline.

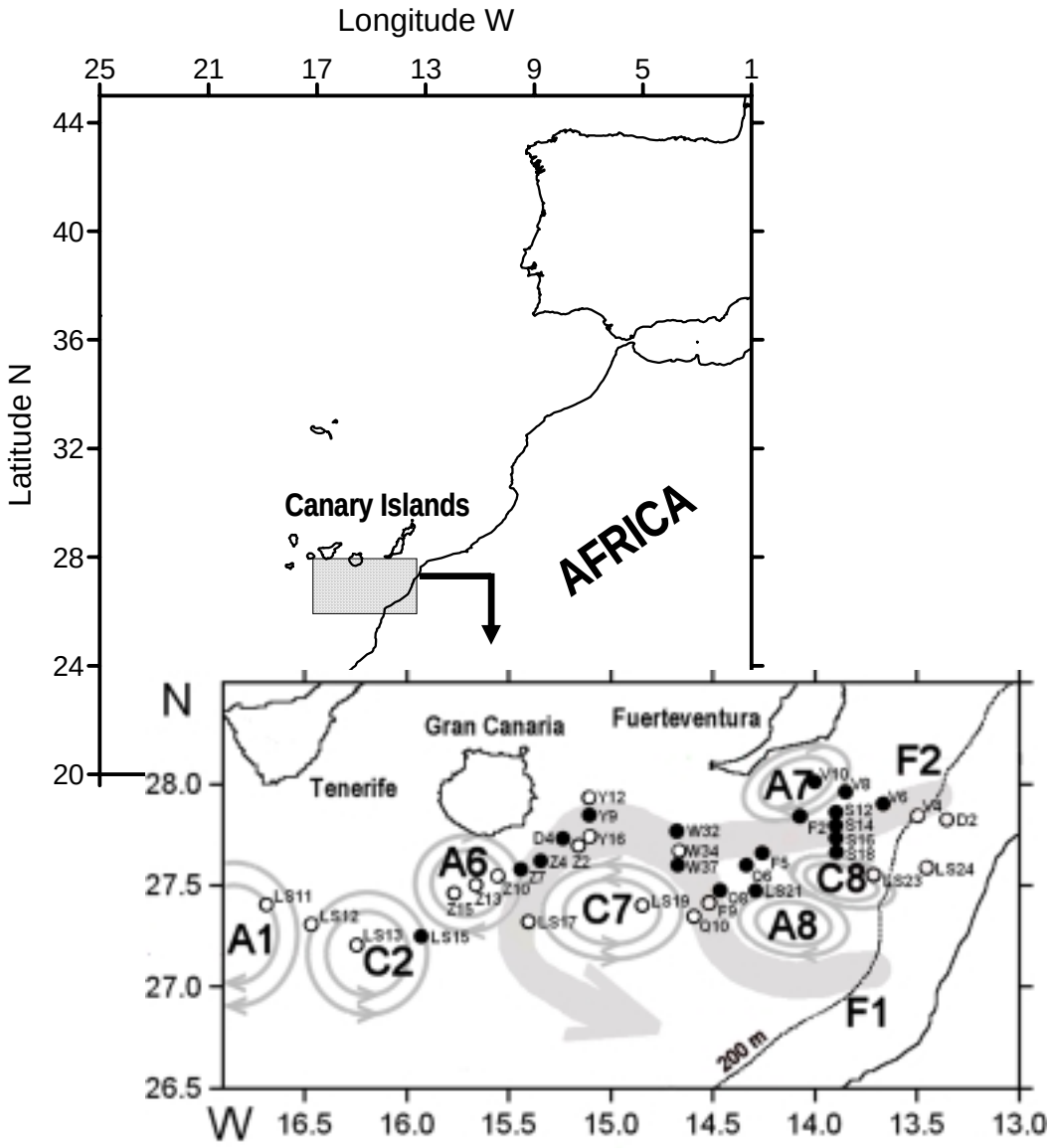
	Thermocline Depths	Maximum fluorescence depths	WMDs of mesozooplankton
Maximum fluorescence depths	0.82**	–	–
WMDs of mesozooplankton	0.09	0.09	–
WMDs of larval fish assemblages	0.15	0.18	0.67**
WMDs of Engraulis encrasicolus	0.10	0.09	0.30
WMDs of Sardina pilchardus	0.28	0.23	-0.05
WMDs of Anthias anthias	0.04	-0.16	0.18
WMDs of Cyclothone braueri	0.23	0.03	0.53**
WMDs of Ceratoscopelus maderensis	-0.12	0.05	0.22
WMDs of *Myctophum punctatum*	0.20	0.32	0.63**
WMDs of *Diogenichthys atlanticus*	0.43*	0.40*	0.49**
WMDs of Notolichnus valdiviae	0.44	0.57**	0.63**

*significant to the 0.05 level, **significant to the 0.01 level

Table II. Daytime weighted mean depth (DWMD) and amplitude of diel vertical migration (DVM, m) of the mesozooplankton, total fish larvae and individual larval fish species. Negative values indicate reverse vertical migration (deeper at night than during the day). Only those organisms whose mean depth varied by more 10 m between day and night were considered to perform DVM.

	DWMD	DVM
Mesozooplankton	65.0	-3.3
Total fish larvae	52.8	-2.1
Engraulis encrasicolus	46.9	4.4
Sardina pilchardus	40.9	15.9*
Anthias anthias	49.8	7.3
Cyclothone braueri	43.6	-6.2
Ceratoscopelus maderensis	45.4	-8.7
Myctophum punctatum	70.8	-12.4*
Diogenichthys atlanticus	96.0	18.6*
Notolichnus valdiviae	84.8	20.0*

* perform significant diel vertical migration



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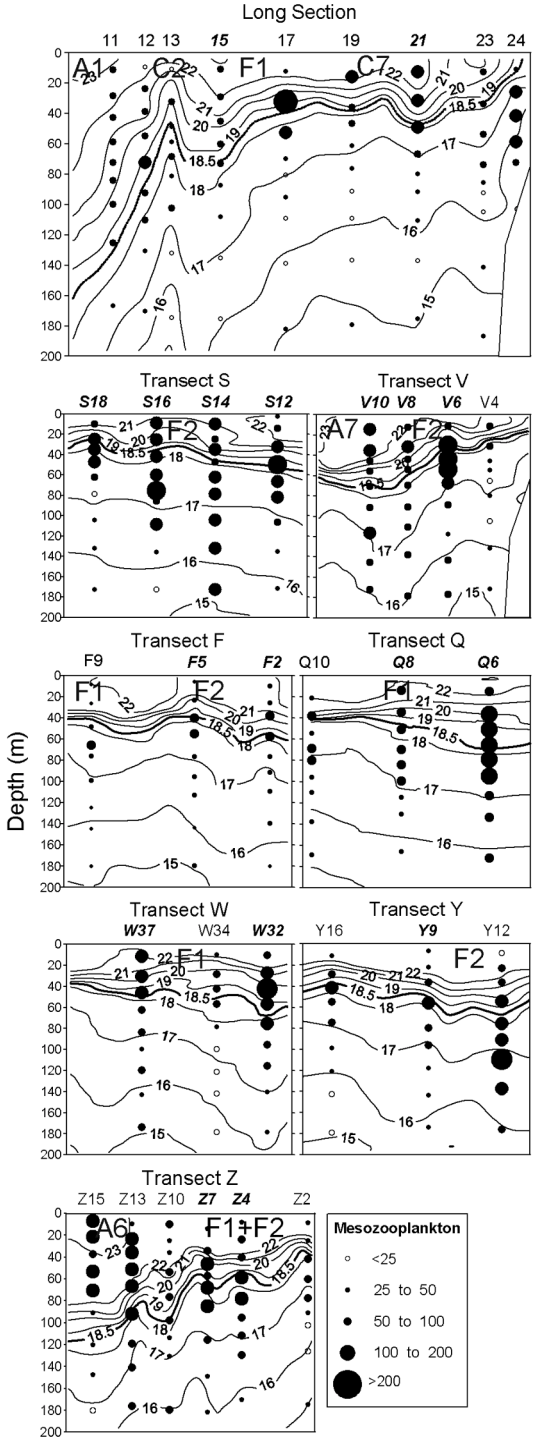
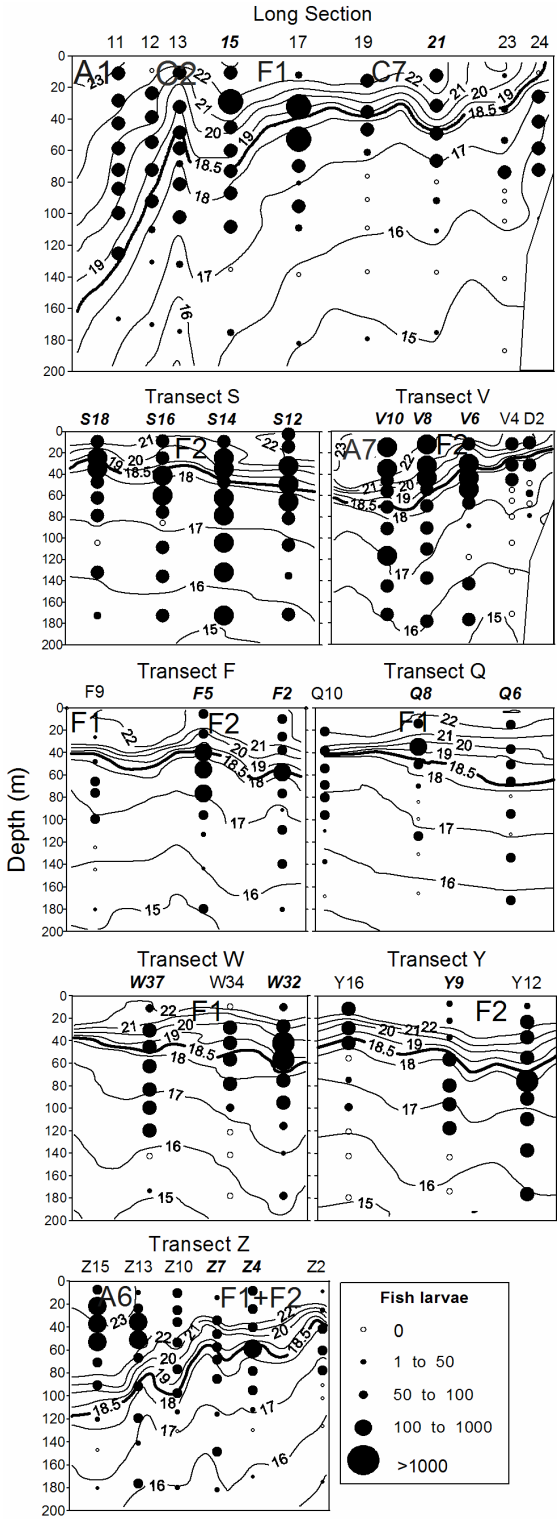


Figure 2. Vertical profiles of temperature (ºC) and vertical distributions of mesozooplankton (number of individuals m^{-3}) along the sampled transects. Circle size is proportional to densities and circles are centred in the middle of each of the 9 resulting strata for every ichthyoplankton station. The bottom of the thermocline is indicated by the thicker isoline. Station labelled in bold and italic are night stations. The approximate location of the different eddies and filaments discussed in the text is indicated.



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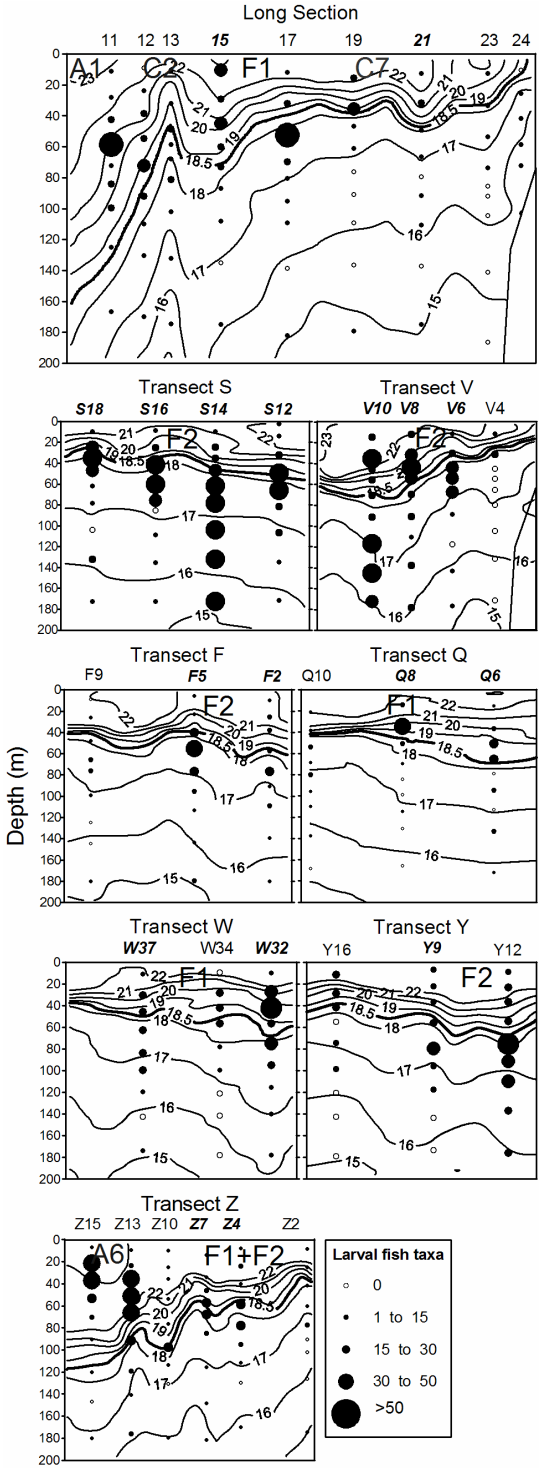

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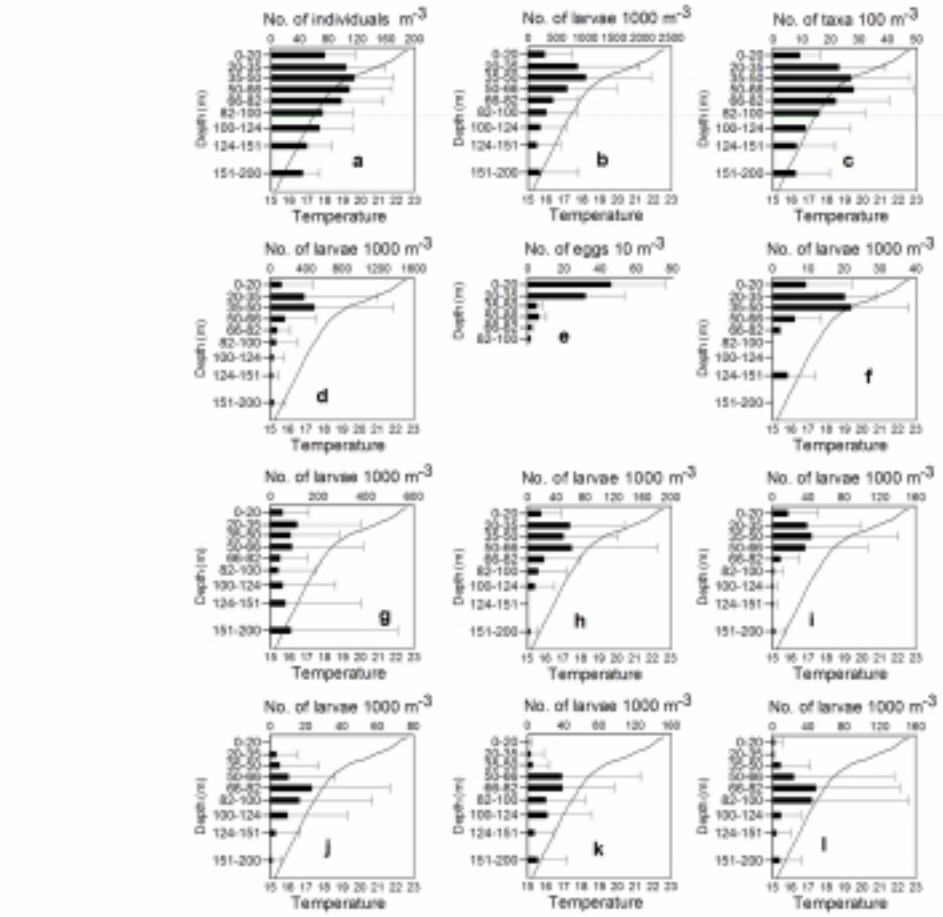

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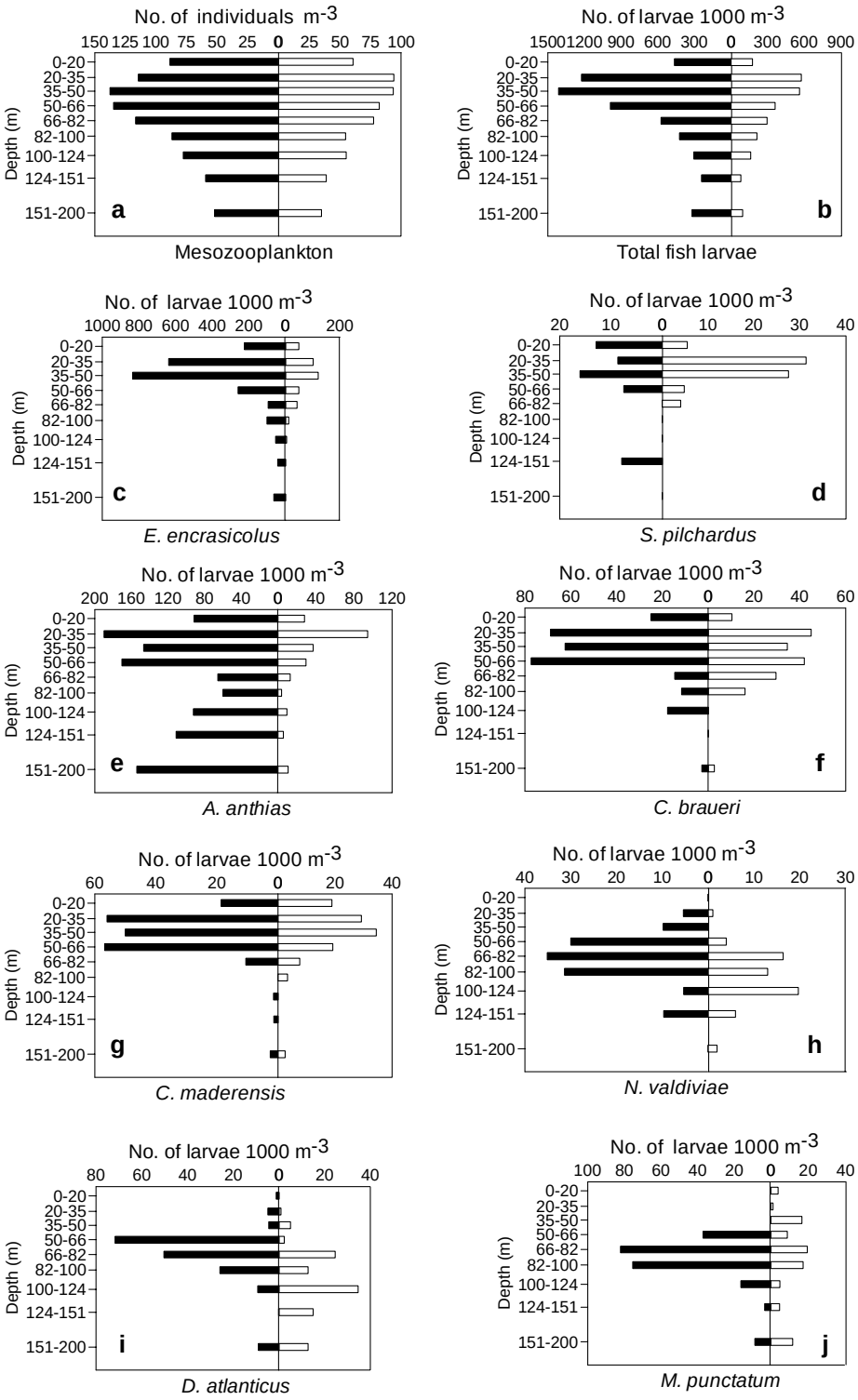

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