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Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea

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ABSTRACT: Anchovy and pilchard are the most abundant pelagic species in the NW Mediterranean Sea. They spawn in different seasons, subject to different environmental conditions: anchovy in summer, when the water column is stratified; pilchard in winter, when the water column is vertically homogeneous. The spatial distribution patterns of eggs and larvae of these 2 species are compared in relation to the main productive features in the region during their respective spawning seasons. The study was performed on the continental shelf off the Ebro River (NW Mediterranean) during June (for anchovy) and February (for pilchard). Sampling comprised a horizontal survey, designed to locate patches of eggs or larvae, followed by a Lagrangian experiment using stratified hauls to study the vertical distributions at different times of day in the water parcel tracked. While pelagic eggs and larvae of both species were present in the upper 70 m of the water column, we recorded differences in the preferential vertical distribution and migration patterns. Maximum concentrations of anchovy eggs and larvae were located in the upper 20 m; pilchard concentrations extended down to 10–40 m. Vertical displacements by the larger larvae at night occurred in both species, but with opposite patterns: anchovy larvae tended to aggregate in the upper 10 m, pilchard larvae exhibited greater dispersal at night, with a preference for levels below 30 m.

KEY WORDS: Pilchard · Anchovy · Ichthyoplankton · Horizontal distribution · Vertical distribution · Diurnal vertical migration · NW Mediterranean

INTRODUCTION

Among the small pelagic species that inhabit the coastal waters of the NW Mediterranean Sea, anchovy *Engraulis encrasicolus* and pilchard *Sardina pilchardus* stand out in their abundance and importance to fisheries. The horizontal and vertical distribution patterns of the early stages of anchovy were addressed by Palomera (1991, 1992) and García & Palomera (1996). Much less attention has been focused on eggs and larvae of pilchard. Direct information on pilchard spawning is limited to adult studies (Gómez-Larrañeta 1960) and a 2-yr survey based on monthly plankton sampling at 2 isolated inshore stations (Palomera & Rubiés 1979, Palomera & Olivar 1996). While the main oceanography and primary production features of the region are well known (e.g. Estrada & Margalef 1988, Estrada & Salat 1989, Font et al. 1990), information on prey distribution and feeding habits of early stages of both species is scarce (Tudela & Palomera 1995, E. Saiz pers. comm.).

In the NW Mediterranean, larvae of anchovy and pilchard are usually found over the continental shelf, and we examined the continental shelf off the Ebro River. It receives considerable input of inland water from the river (around 400 $m^3 s^{-1}$, Guillén & Palanques 1997). On the upper continental slope off the shelf break, water circulation is characterized by a shelf-slope jet, affecting the whole water column, which

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flows to the southwest and transports roughly 1 Sverdrup (10^6 m^3 s^{-1}) (Castellón et al. 1990, Millot 1999). This current (local name: Catalan Current), is in geostrophic balance with a typical shelf-slope density front (Font et al. 1988). Strongly steered by topography, the circulation is also subject to mesoscale variability due to open sea eddies (Tintoré et al. 1990, García et al. 1998), seasonal variability (Font et al. 1995) and frontal oscillations (Alvarez et al. 1996). At the Ebro shelf, the change in the orientation of the shelf break in the northern part of the area has been reported to affect the stability of the slope current in that region (Font et al. 1990). Ageostrophic cross frontal motions, such as filaments, have also been reported in this area (Wang et al. 1988). All these features contribute to enhance local productivity (Salat et al. in press), but they may also exert adverse effects by dispersing the larvae.

Thus, understanding the horizontal distribution patterns of eggs and larvae requires information on coupling between vertical distribution patterns and ocean dynamics. Many studies have dealt with the role of vertical distribution of the early ontogenetic stages of fishes as an important factor affecting advection of those stages (Leis 1986, Neilson & Perry 1990, Govoni & Pietrafesa 1994, John & Ré 1995). The sampling strategy employed, i.e. using fixed stations or following a water parcel and the vertical resolution of the gear used, greatly affects the results obtained on vertical distribution patterns. Previous studies on the vertical distribution of anchovy eggs and larvae in the NW Mediterranean have been based on sampling at fixed stations (Palomera 1991, Olivar & Sabatés 1997, Olivar et al. 1998). These studies disclosed the shallow distribution of these larvae in the upper 30 m. They also showed variability in abundance associated with intrusions of new water masses at the sampling sites. Coombs et al. (1997) analyzed discrete vertical distributions (every 5 m) for the species in the northern Adriatic (a very shallow sea), and reported a more restricted vertical distribution, in the upper 10 m.

No studies exist for the vertical distribution of pilchard eggs and larvae in the NW Mediterranean region. The closest available references are the examinations carried out by Andrés et al. (1992), John & Ré (1995) and Farinha & Lopes (1996) off the Atlantic coast of the Iberian Peninsula. All these studies recorded the main concentrations of eggs and larvae in the upper 60 m.

We examined whether the different environmental conditions during the spawning seasons for anchovy (summer) and pilchard (winter) influenced the horizontal and vertical distribution patterns of the eggs and larvae of these species on the continental shelf off the Ebro River (NW Mediterranean).

MATERIALS AND METHODS

We surveyed the horizontal and vertical distribution of eggs and larvae during the spawning season (summer for anchovy, winter for pilchard). The sampling area was the same in both cases (Fig. 1), off the Ebro River delta (NW Mediterranean).

The anchovy egg and larval study started with a horizontal survey between 31 May and 2 June 1996. A total of 23 stations were sampled using Bongo nets. Hauls were oblique at a vessel towing speed of 2 knots, from 95 m to the surface, depth permitting. The volume of water was measured by a flow meter placed in the center of the net mouth. Egg and larval abundance was standardized to number of individuals under 10 m^2, on the basis of the volume of water filtered through the net and the starting depth of the haul.

The pilchard egg and larval study started with a horizontal survey between 4 and 13 February 1997. Due to the lack of previous data on horizontal distribution of pilchard eggs and larvae in the region, a larger number of stations were sampled during this cruise. A total of 86 samplings were carried out using a Bongo net. Hauls were vertical from 100 m to the surface, depth permitting. Measurement of the volume of water filtered and standardization of egg and larval abundance were the same as in the anchovy survey.

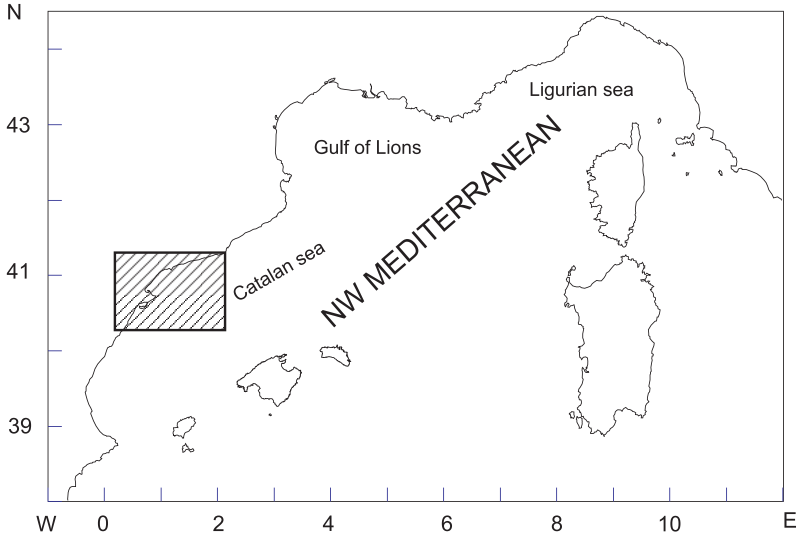

Fig. 1. Map of the study area

In both studies, samples were initially examined on board to locate patches of eggs and/or larvae for release of the drogues, the start of the Lagrangian experiments. Radio-tracked drogues attached to a sea anchor calibrated to a depth of 10 m were launched near the respective patches of eggs and/or larvae. This depth was chosen to track the surface water parcel, where most of the early stages of anchovy were found (Palomera 1991). In the case of pilchard, with an expected larger vertical range, the depth of the anchor is not as critical because in winter the vertical shear is weak. This depth is also useful to avoid the direct effect of wind over the drogue. The distance between drogues at the time of release was 0.7 nautical miles. The water parcels tracked by the drogues were followed and sampled every 4 to 6 h for 44 h during the anchovy survey and 65 h during the pilchard survey. Vertical temperature, salinity and fluorescence profiles were obtained using a Sea Bird 25 CTD (Seabird Electronics Inc, Bellevue, WA), equipped with a Sea-Tech fluorometer (Sea-Tech Inc, Corvallis, OR). Stratified plankton samples were collected using a Longhurst-Hardy Plankton Recorder (LHPR) net system (Spartel, Devon, UK). In the anchovy Lagrangian survey, 7 stations were sampled in the daytime and 3 at night. In the pilchard Lagrangian survey, 7 stations were sampled in the daytime and 6 at night.

LHPR hauls were carried out at a vessel towing speed of 3 to 3.5 knots while the net was descending. Eggs and larvae were counted and pooled into 5 m intervals from the surface to a depth of 70 to 80 m. The volume of water filtered by the net was recorded by a flow meter attached to the mouth of the net. Egg and larval abundance was standardized to number per 100 m^3.

Eggs stages were classified in: (1) eggs without embryo; (2) eggs with early stage embryos (tail still attached); and (3) eggs with late stage embryos in which the tail was free. Larvae were measured to the nearest 0.1 mm and classified by 2 mm size intervals.

Microzooplankton samples were collected during the winter survey with the LHPR net using a mesh size of 53 µm. Nauplii and copepodite concentrations were analyzed for 3 daytime stations. Because no simultaneous microzooplankton data were recorded for the summer cruise, we used data obtained from 3 stations sampled in June 1993 in a comparable situation in the same region (E. Sáiz pers. comm.).

RESULTS

Anchovy

Horizontal egg and larval distributions covered the entire shelf, with the main concentrations near the shelf break (180 to 200 m). Egg densities attained values of 1000 to 7000 per 10 m^2 (Fig. 2). Larval densities were lower, <1000 larvae per 10 m^2. The main center of egg abundance was located over the 150 m isobath, between 15 and 25 nautical miles offshore. This was the position chosen to release 2 drogues for the Lagrangian experiment. The release site was located near the main course of the Catalan Current that flows along the shelf break. The track of the drogues showed a net displacement towards the southeast (Fig. 2).

No significant changes in physical parameters were detected over the Lagrangian study (Fig. 3), indicating that the drogues followed the same water parcel. The distance between the 2 drogues never exceeded 1 nautical mile. Vertical temperature profiles were typical for the season, showing the seasonal thermocline development. The sharpest temperature gradient was

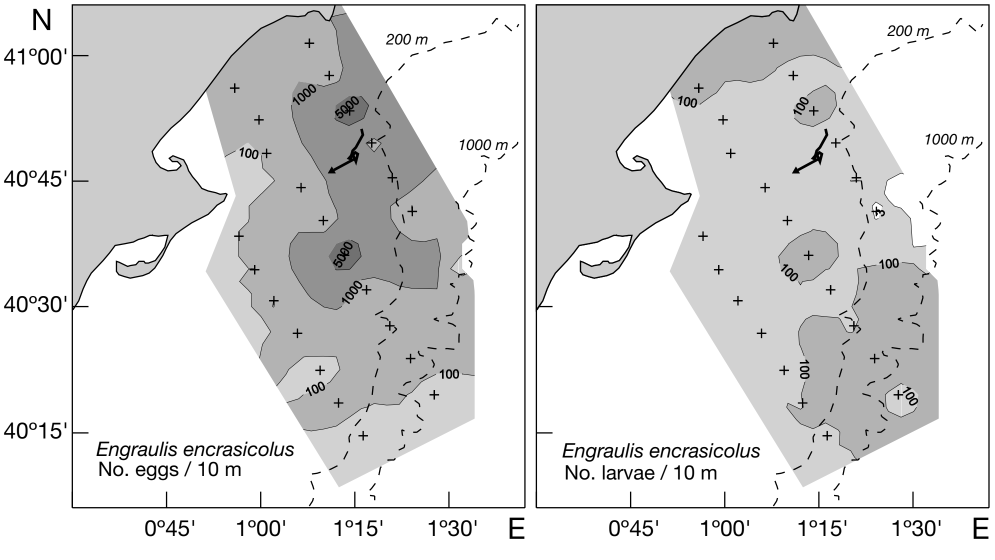

Fig. 2. *Engraulis encrasicolus.* Horizontal distribution of eggs and larvae during the June 1996 survey. Black line inside the contour map shows the mean drogue track, arrow shows direction

recorded between 5 and 30 m in depth. Relatively homogeneous temperature values of between 13.5 and 13°C were found below 60 m. Fluorescence profiles consistently showed a deep fluorescence maximum layer at a depth between 40 and 60 m over the study.

Anchovy eggs and larvae were found throughout the entire water column sampled but were mainly concentrated in the upper 20 m (Fig. 4). Eggs had a shallower distribution, with 90% of the eggs found in the upper 15 m, while the main larval concentrations exhibited a broader depth distribution that spanned the upper 40 m. There were no day/night differences in the vertical distribution of the eggs, whereas larval abundance was concentrated in the upper 10 m at night (Fig. 4).

Early stage eggs (without embryo or before tail separation) were nearly absent below 30 m. Later stage egg abundance increased below that depth (Fig. 5).

The larvae collected ranged in size from ca 2.5 to 15 mm, with a modal size at 3 to 4 mm (Fig. 6). The highest concentrations of larvae smaller than 6 mm were located in the upper 20 m in both daytime and nighttime hauls. Larvae larger than 6 mm followed a different pattern, with a tendency towards concentration in the upper layers at night and a more disperse pattern during daylight hours. No larvae larger than 12 mm were collected in daytime hauls at the surface (Fig. 6).

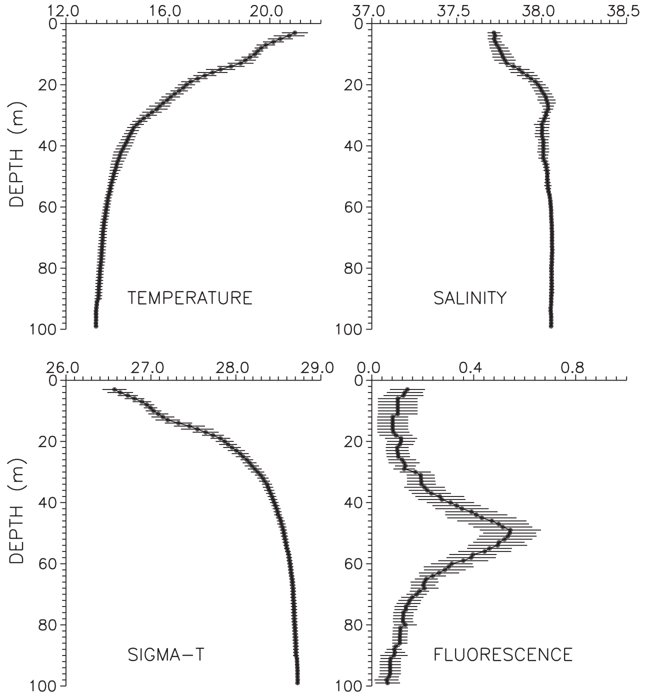

Fig. 3. Mean vertical temperature (°C), salinity (psu), σ_t (kg m^{-3}) and fluorescence profiles during the Lagrangian survey in June 1996 (horizontal lines indicate standard deviations)

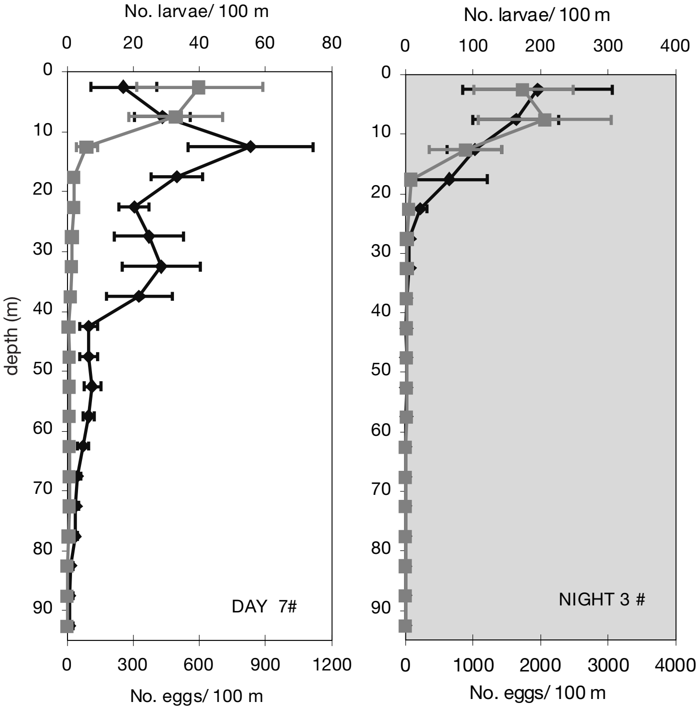

Fig. 4. *Engraulis encrasicolus.* Mean vertical distribution of eggs (grey symbols) and larvae (black symbols) in the daytime and at night in June 1996 (horizontal lines indicate standard errors)

Pilchard

Horizontal distribution of pilchard eggs and larvae in February was more concentrated over the shelf than anchovy distribution in June. Egg densities reached values of from 1000 to ca 10 000 per 10 m^2, while larval densities were from 1000 to ca 4000 per 10 m^2. Pilchard eggs and larvae were mainly present over the broad portion of the shelf south of the Ebro River delta. The main concentrations of both eggs and larvae were between the 70 to 100 m isobaths, 15 nautical miles offshore. That zone was therefore chosen for the release of 3 drogues for the Lagrangian experiment. The zone was located outside the direct influence of the river discharges affecting the coastal strip and far enough from the shelf break to escape the direct influence of the Catalan Current. The track of the drogues revealed a circular clockwise trajectory (Fig. 7).

Temperature and salinity profiles varied slightly during the study (Fig. 8), indicating that the drogues followed the same water parcel. The distance between the drogues was always under 1 nautical mile. Mean vertical temperature profiles revealed a homogeneous water column from the surface to the bottom, with temperatures ranging between 13.1 and 13.4°C,

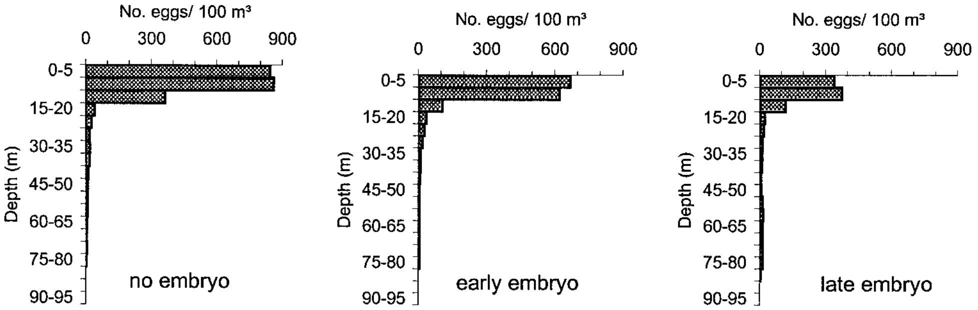

Fig. 5. *Engraulis encrasicolus.* Mean vertical distribution of 3 developmental stages of eggs in June 1996. (See 'Materials and methods' for classification)

the typical situation in this region in winter. Sigma-*t* and salinity profiles showed values slightly higher in the upper 30 m, and quite homogeneous below that depth. The highest fluorescence values during the study were from the surface down to 20 m (Fig. 8).

Nauplii abundance was highest between 10 and 35 m, with a maximum at 15 m. Copepodites were most abundant between 20 and 40 m with peak at 35 m (Fig. 9).

Pilchard eggs and larvae appeared throughout the sampled water column, but were most abundant in the upper 50 m (Fig. 10). Maximum egg abundance (44%) was in the upper 10 m of the water column both during the daytime and at night. Larvae were concentrated mainly between 10 and 30 m in daytime hauls, exhibiting a broader distribution at night and a deeper peak (Fig. 10). The vertical egg distribution pattern showed that early stages were located below 15 m. Later egg stages were more concentrated in the upper 5 m (Fig. 11).

The pilchard larvae collected ranged from 2.5 to 21.5 mm in size, with a modal size at 8 to 9 mm. The vertical larval size distribution revealed the migration pattern of the larger larvae (Fig. 12). The highest concentrations of larvae smaller than 4 mm were located between 40 and 50 m in both daytime and nighttime hauls. Highest abundance of larvae from 4 to 8 mm in size was between 10 and 20 m during the daytime and more dispersed in the water column at night. Larvae larger than 8 mm exhibited distinct differences in distribution, with a pattern similar to that of the smaller sizes in the daytime but increased abundance in the layers below 35 m at night.

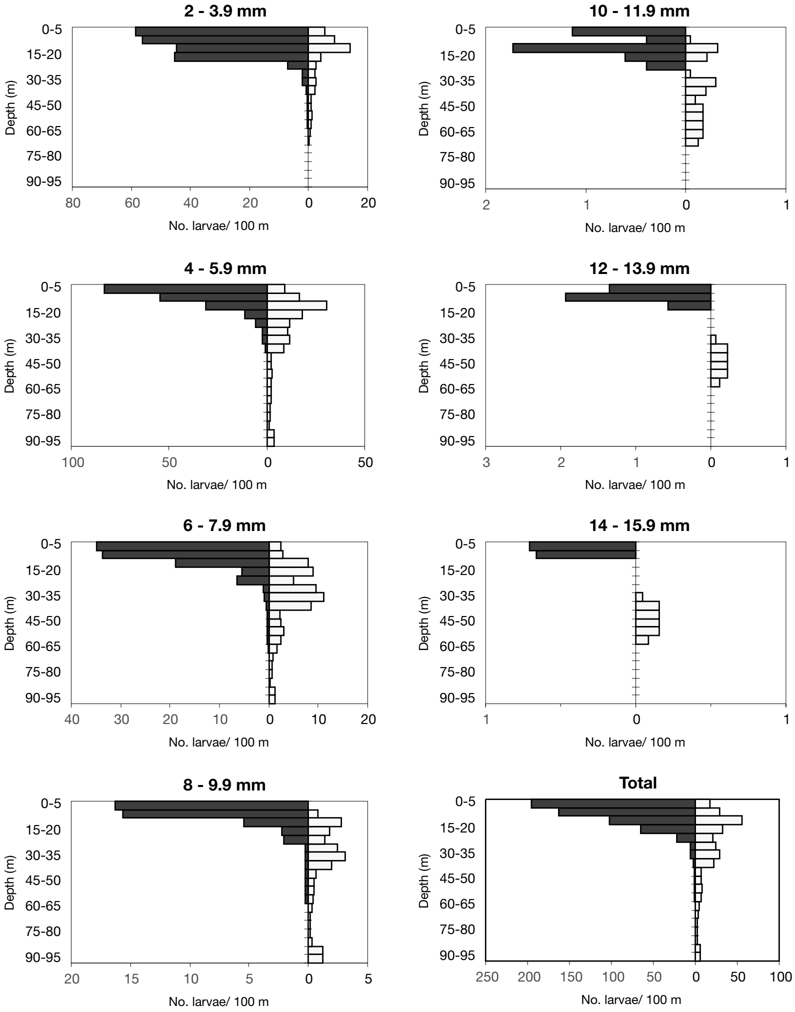

Fig. 6. *Engraulis encrasicolus.* Mean vertical distribution of larvae by size class in daytime (open bars) and nighttime (filled bars) hauls in June 1996

DISCUSSION

As a general rule, during the spawning period of anchovy in the NW Mediterranean (summer), nutrients are depleted at the surface because of the strong thermal stratification. In such conditions productivity in the water column is confined to the Deep

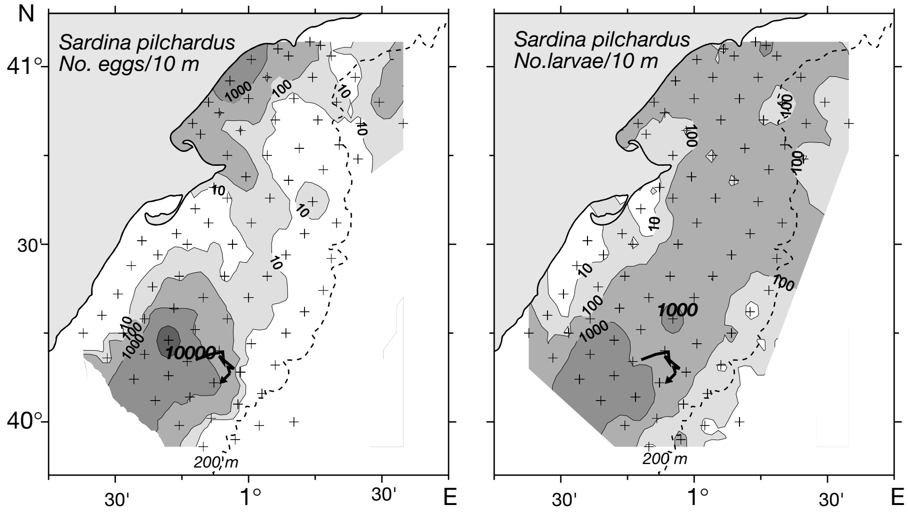

Fig. 7. *Sardina pilchardus.* Horizontal distribution of eggs and larvae in February 1997. Black line inside the contour map shows the mean drogue track, arrow shows direction

Chlorophyll Maximum (DCM) (Estrada & Salat 1989). The presence of a DCM is a generalized feature in most oligotrophic seas in the period of water column stratification (Varela et al. 1994). During the spawning period of pilchard (winter), low temperatures and vertical mixing associated with wind storms affect the entire surface layer (usually >100 m). Mixing over the continental shelf involves the water column as a whole, carrying nutrients to the entire euphotic zone. Consequently, in the winter, maximum productivity over the continental shelf is centered near the surface.

Main environmental features during each survey were those expected for the respective season. The survey carried out in June yielded evidence of seasonal thermocline formation and the presence of a pronounced DCM. In

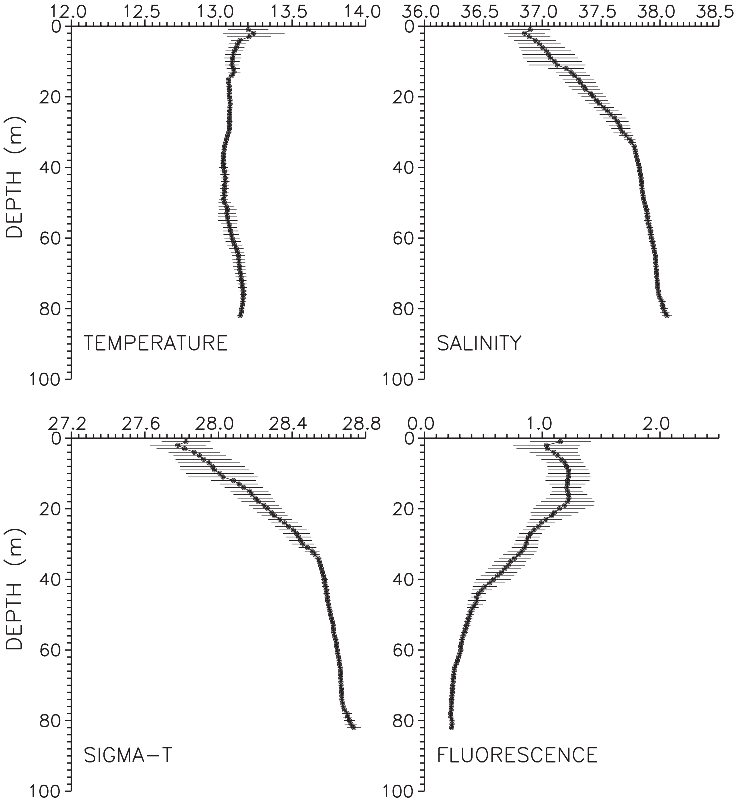

Fig. 8. Mean vertical temperature (°C), salinity (psu), σ_t (kg m^{-3}) and fluorescence profiles during the Lagrangian survey in February 1997 (horizontal lines indicate standard deviations)

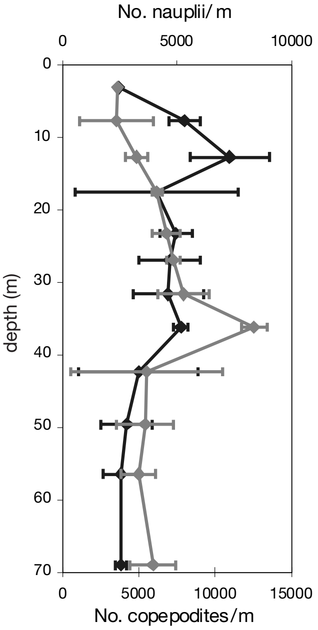

Fig. 9. S*ardinia pilchardus.* Mean vertical distribution of nauplii (black symbols) and copepodites (grey symbols) at 3 daylight stations during February 1997 (horizontal lines indicate standard errors)

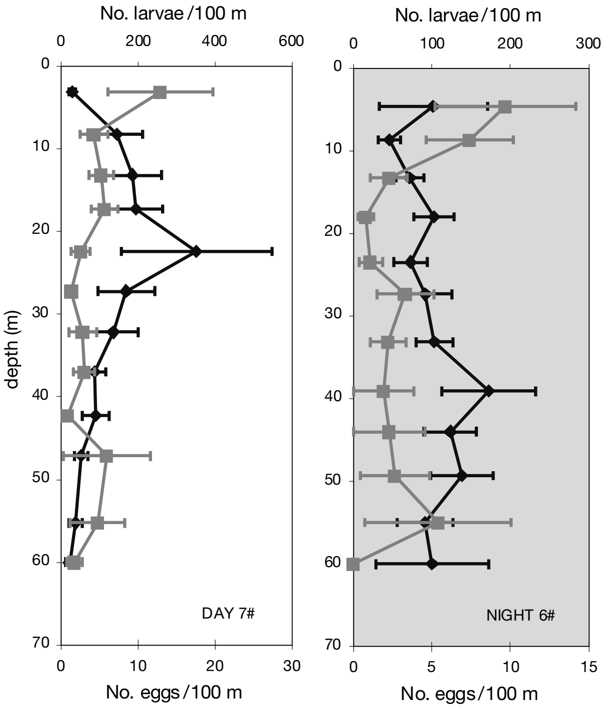

Fig. 10. *Sardina pilchardus.* Mean vertical distribution of eggs (grey symbols) and larvae (black symbols) in the daytime and at night in February 1997 (horizontal lines indicate standard errors)

February there was a well-mixed water column; peak chlorophyll values were found near the surface.

The general vertical egg and larval distributions of both *Engraulis encrasicolus* and *Sardina pilchardus* recorded in the present study were consistent with those reported for other pilchard and anchovy species around the world (John 1982, Boehlert et al. 1985, Fletcher 1999, Matsuura & Olivar 1999, Moser & Pommeranz 1999). From the evidence of the location of the early egg stages, anchovy spawned close to the surface at depths of <10 m; larvae in their first stages of development exhibited the same surface distribution, above the level of the thermocline (15 to 20 m). In contrast, the absence of vertical gradients in winter may contribute to the wider vertical distribution observed for pilchard eggs (>50 m), either due to spawning over a wider vertical range, as compared to anchovy, or by active vertical mixing of the water column.

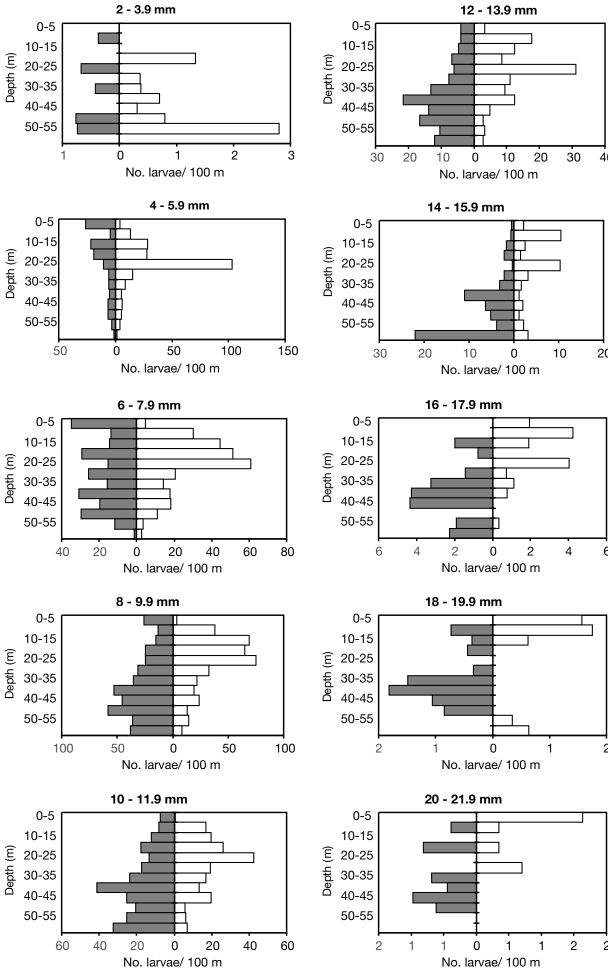

Fig. 12. *Sardina pilchardus.* Mean vertical distribution of larvae by size class in daytime (open bars) and nighttime (filled bars) hauls in February 1997

Anchovy larvae larger than 6 mm displayed a wider vertical range due to vertical migrations towards

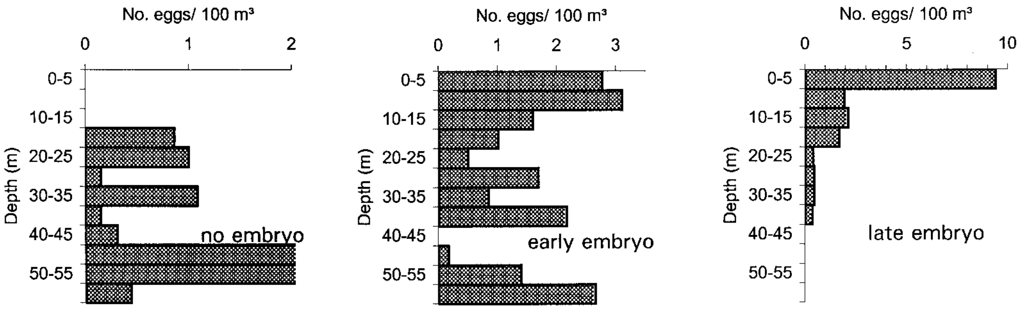

Fig. 11. *Sardina pilchardus.* Mean vertical distribution of 3 developmental stages of eggs in February 1997. (See 'Materials and methods' for classification)

deeper waters during the day. This size-related diel migration is a feature known from larvae of other fish species (Willis & Pearcy 1982, Munk et al. 1989, Lough & Potter 1993, Gronkjaer & Wieland 1997). Blaxter & Hunter (1982) concluded that vertical migrations of larvae should follow the same pattern as those in adults, upwards to the surface at dusk and downwards at dawn. Anchovy, and particularly *Engraulis encrasicolus* larvae larger than 6 mm, kept close to that migration pattern. However, according to our findings, this was not true for the pilchard *Sardina pilchardus*. Fletcher (1999) reported similar results for pilchard off southern Australia. Thus, the night vertical displacement by pilchard larvae, in a direction opposite to that taken by anchovy larvae, merits special attention.

Numerous studies (Pearre 1979, Heath et al. 1988, Munk et al. 1989, Ponton & Fortier 1992) presented evidence that light, food, or a combination of the 2 significantly determined vertical movements of larvae. Perry & Neilson (1988), Davis et al. (1990) and Olivar (1990), however, have noted the importance of well-established thermoclines as barriers to vertical migration, but other research has suggested that a thermocline is not the prime factor influencing vertical larval distributions; food availability and larval behavior are more important (Southward & Barret 1983, Gray 1996). According to Conway et al. (1998), feeding by anchovy occurs mainly during daytime. The vertical distribution of anchovy larvae recorded during the daytime, down to 40–60 m, would appear to be linked to the layer of highest production, the DCM. Main microzooplankton concentrations in this area during summer have been found to be associated with the DCM, above, and at the DCM (E. Sáiz pers. comm.).

Sardina pilchardus spawns when the water column is well mixed. The contrasting hydrography, with respect to anchovy spawning season, has been pointed out to be responsible for the different vertical distributions at early stages of development. This contrast can also influence the migration patterns of larger larvae. Feeding by pilchard, like anchovy, occurs mainly during the daytime (Blaxter 1969, Conway et al. 1994). The daytime distribution of pilchard larvae, between 5 and 40 m, closely conformed to the zone with high concentrations of potential food items. Although the highest fluorescence values were recorded in the upper 20 m, high microzooplankton concentrations ranged somewhat deeper, from 10 to 35 m. The main food items for pilchard larvae are nauplii and the copepodite stages of copepods (Conway et al. 1994). Thus, the vertical location of the larvae during daylight could also be related to feeding.

At night anchovy larvae larger than 6 mm migrated to the surface, as previously reported for Mediterranean anchovy (Palomera 1991, Olivar & Sabatés 1997). This is consistent with the pattern observed in other anchovy species, which has been related to energy-saving mechanisms (Hunter & Sánchez 1976). The broader and relatively deeper nighttime distributions observed for pilchard have also been observed in other fish larvae (Boehlert et al. 1985, Brewer & Kleppel 1986, Heath et al. 1988, Leis 1991, Ponton & Fortier 1992), and have been attributed to passive sinking by larvae (Munk et al. 1989, Richards et al. 1996).

Information on the diel cycle of swim bladder inflation in the larvae of several clupeoid species (see Neilson & Perry 1990, for a review) indicated that larvae migrate to the surface at night to swallow air and fill their swim bladders, but for some species subsequent slow sinking of larvae at night has also been observed. This may provide an explanation for the results recorded in the present study. Anchovy larvae that migrate upward to fill their gas bladders at night are confined to those layers by the thermocline during the nocturnal resting period. In winter, as there are no physical barriers to keep pilchard larvae confined to the upper layers, slow sinking may occur during the period of darkness.

In summary, light and food availability apparently regulate the vertical distributions of the larvae of these 2 species, which spawn in diametrically opposite seasons of the annual cycle. Larvae tend to aggregate in the respectively more productive layers during the hours of daylight. At night, during periods of thermal stratification, anchovy larvae are kept near the surface, while pilchard larvae may be subjected to a passive slow sinking.

The horizontal patterns for the egg and larval distributions of *Engraulis encrasicolus* and *Sardina pilchardus* observed in this study can also be related to the areas of higher productivity. In summer, the chlorophyll values at the DCM are higher in the vicinity of the frontal zone, on account of the associated mesoscale activity (Estrada & Margalef 1988, Masó et al. 1998). In the survey carried out in June 1996, anchovy larvae were mainly concentrated near the shelf break, the main frontal area. Thus, the horizontal distribution of these larvae mirrored the productivity distribution. In winter, productivity is higher over the continental shelf than further offshore, because vertical mixing there spans the entire water column. The horizontal distribution of pilchard larvae found in February 1997 also reflected this pattern, with peak abundance recorded at the center of the continental shelf.

The large concentrations of anchovy larvae found near the main frontal area means that they are exposed to horizontal displacements caused by the shelf-slope current associated with the front. Long-distance entrainment of anchovy larvae along the continental slope in the NW Mediterranean has been reported and explained as a larval export mechanism (Sabatés et al. 2001). In terms of potential dispersal, that pattern contrasts with the central distribution of pilchard on the shelf, where currents are less intense and circulation is usually anticyclonic (Font et al. 1990). Consequently, the early stages of pilchard are less exposed to horizontal displacement and will tend to remain inside the 200 m isobath.

The different distribution patterns found can be attributed to the different seasonal mechanisms that act to enhance productivity. Although our sampling was not specifically addressed to quantify the coupling of prey distributions and ichthyoplankton, both the horizontal and the vertical egg and larval distributions recorded indicate that the spawning strategies of the 2 species are adapted to the seasonality of the productive mechanisms operating in the region.

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