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Vertical distribution of early developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis encrasicolus*

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ABSTRACT: In recent years a northward expansion of *Sardinella aurita* has been reported in the western Mediterranean. Considering the coexistence of its larvae with those of the dominant species *Engraulis encrasicolus*, the present study was conducted to compare their vertical distributions in 2 areas off the Catalan coast with different vertical environmental conditions. During summer, the water column was stratified with a deep chlorophyll maximum (DCM) beneath the pycnocline. However, the southern area, under the influence of the Ebro River, was characterized by a secondary surface chlorophyll maximum. Vertical distribution of larval food, nauplii and copepodites showed good agreement with the high chlorophyll layers. In the earliest stages of development, larvae of both species remained in the upper levels. From 6 mm standard length on they developed a day/night migratory behaviour to search for food during the day (feeding period). Therefore, in the south, where the abundance of potential food in the upper layers was relatively high, larvae of both species remained in the upper levels during the day. However, in the north, where food was restricted to the DCM, only *E. encrasicolus* larvae were able to reach these deep levels. The low temperatures (~15°C) detected at the DCM may restrict the vertical migration of *S. aurita* in accordance with their thermophilic character. This limitation might represent a restriction for the northward expansion of this species in the western Mediterranean.

KEY WORDS: *Sardinella aurita* · *Engraulis encrasicolus* · Larvae · Eggs · Microzooplankton · Vertical distribution · NW Mediterranean

INTRODUCTION

During recent decades, a warming trend in Mediterranean waters has been reported, both at the surface as well as in deep waters (Rohling & Bryden 1992, Bethoux & Gentili 1996, Salat & Pascual 2002). In relation to this tendency, fish species characteristic of the warm waters of the southernmost parts are extending their distribution range, since they are appearing more frequently in the northernmost and colder areas (Francour et al. 1994, Astraldi et al. 1995, Bianchi & Morri 2000). In the NW Mediterranean, the most abundant species of small pelagic fish are the European anchovy *Engraulis encrasicolus* and the sardine *Sardina pilchardus* (Lleonart & Maynou 2003). Another pelagic species, the round sardinella *Sardinella aurita*, is a thermophilic species, found frequently in the warmer waters of the southern Mediterranean (Ben Tuvia 1960). Nevertheless, in the past few years, a gradual northward expansion and an increasing abundance of *S. aurita* in the northern sector has been documented in connection with the warming of the sea in the area (Sabatés et al. 2006).

In the NW Mediterranean, the reproductive period of the 2 dominant species, sardine and anchovy, takes place in completely opposite periods of the year: autumn/winter and spring/summer, respectively. The reproduction of round sardinella occurs in summer, from the end of June to September, when the surface temperature reaches the highest annual values (Oliver

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& Navarro 1952, Palomera & Sabatés 1990, Somarakis et al. 2002). Therefore, the spawning periods of the anchovy and round sardinella coincide during the summer months. Since both species dwell on the continental shelf, their larvae coexist in the plankton during this period of the year.

The summer period in the NW Mediterranean is characterised by a stratified water column, with a marked thermocline (and pycnocline). Consequently, vertical water movement is very limited, and almost all the surface nutrients are depleted. Primary production remains limited to a deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone (Estrada 1985), where there is a compromise between nutrient concentration and light intensity (Estrada et al. 1993). The only nutrient contribution to the surface during the fully stratified season comes from riverine runoff water (Blanc et al. 1969). Although the contribution of this source to the total primary productivity is only between 10 and 20% (Salat et al. 2002), it is relevant because it is able to maintain surface planktonic production in areas under the influence of the river discharges in summer.

In such variable vertical conditions of temperature, density, light and food concentration, it is relevant to determine where the larvae of *Sardinella aurita* and *Engraulis encrasicolus* are located in the water column. In particular, what are the vertical distribution patterns, including the possible day/night variations in relation to the environmental variables? Fish larvae, like many other planktonic organisms, perform diel vertical migrations (Neilson & Perry 1990). Most of them are visual predators that typically cease feeding at night, when light levels fall below the minimum required for successful foraging (Blaxter 1986, Sabatés et al. 2003). Therefore, the position of larvae in the water column will indicate the availability of prey they encounter during the feeding periods, and the foraging environment available to larval fishes will influence their growth and survival.

In the Mediterranean, studies on the vertical distribution of anchovy eggs and larvae reported that the eggs are found largely in the upper 10 m of the water column (Olivar et al. 2001, Coombs et al. 2003). In the case of larvae, some authors indicated that they are found mainly in the surface layers (Olivar & Sabatés 1997, Coombs et al. 2003) during both the day and night, whereas others describe nictemeral migrations in advanced larval developmental stages in relation to the concentration of food, with larvae being found deeper during the day than during the night (Palomera 1991, Olivar et al. 2001). However, there are no studies concerning the vertical distribution patterns of *Sardinella aurita*, either in the Mediterranean or in other geographical areas.

Considering the recent northward expansion of *Sardinella aurita* into the western Mediterranean and the coexistence of its larvae with those of the dominant species *Engraulis encrasicolus*, the present study was conducted to describe the vertical distribution of early developmental stages of both species in 2 areas off the Catalan coast with different environmental conditions. Specific aims were (1) to compare ontogenetic and diel differences in their vertical distributions in relation to the physical structure and distribution of microzooplankton in the water column, and (2) to determine weather the vertical migration behaviour of *S. aurita* could represent a difficulty to the expansion of this species towards the north.

MATERIALS AND METHODS

The Catalan coast (NW Mediterranean) is characterised by a continental shelf, which is, in general, quite narrow. It only widens clearly in the southernmost part, in the vicinity of the delta of the Ebro River, and in the north between the main submarine canyons. The southern shelf of the Catalan coast receives a significant riverine inflow from the Ebro, which, under normal conditions, accounts for around 90% of the total fresh water discharges along the Catalan coast. The northern shelves are more exposed to the winds, which leads to a deeper surface mixed layer with generally lower surface temperatures during the summer. Likewise, the levels of surface chlorophyll are higher on the southern shelf than in the north because of the effect of the waters from the Ebro River.

Sampling was carried out during July 2003 and July 2004, coinciding with the spawning period of *Sardinella aurita* and *Engraulis encrasicolus*. Determination of the basic hydrographic parameters was performed with CTD casts at stations distributed along transects, from near the coast to the shelf edge, along the Catalan coast (NW Mediterranean). Stations on transects were placed 7.5 nautical miles apart, and the distance between transects was 10 nautical miles (Fig. 1). The CTD employed was a Neil Brown Mark III with an attached SeaTech fluorometer. Profiles of temperature, salinity, density and fluorescence were averaged at 1 m intervals. The depth of the pycnocline was established where the maximum of the vertical density gradient (obtained by centred differences at 1 m intervals) was observed.

To determine the vertical distribution of fish eggs and larvae, sampling was focused on 2 areas of the Catalan coast where the continental shelf was relatively wide: one in the southern part, which was called the 'southern area' and the other in the north that was denoted the 'northern area' (Fig. 1). Five stations were

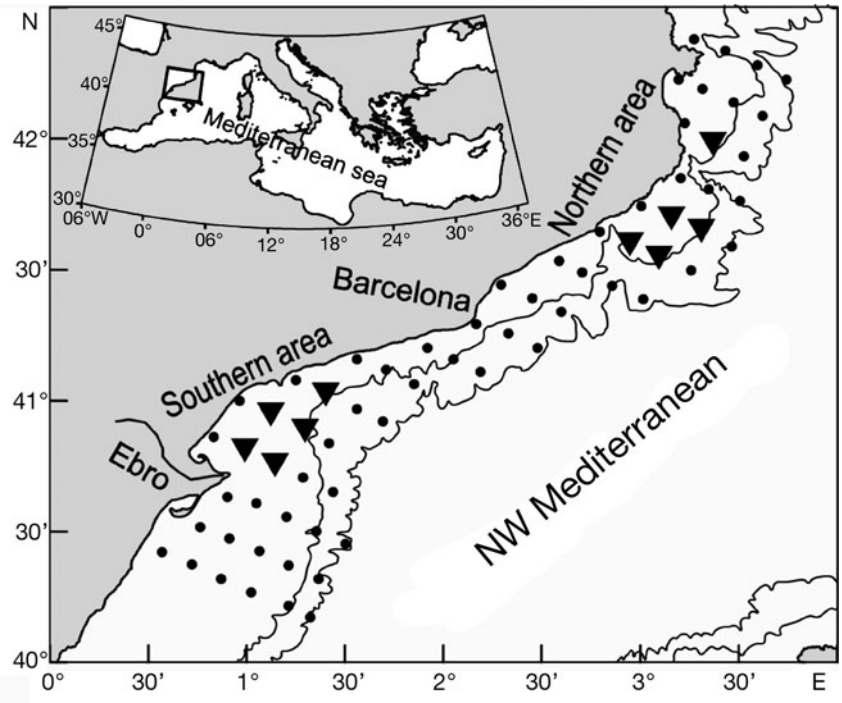

Fig. 1. Study site showing the sampling stations in the southern and northern areas. Circles: CTD casts; triangles: Longhurst-Hardy Plankton Recorder (LHPR) tows.The isobaths shown are 200 and 1000 m

sampled in each area (3 during the day and 2 during the night) during July 2003 and July 2004. Vertically stratified zooplankton samples for fish larvae (45 cm mouth diameter, 333 µm mesh) and microzooplankton (9 cm diameter, 53 µm mesh) were collected simultaneously using a double Longhurst-Hardy Plankton Recorder net (LHPR; Williams et al. 1983). Tows were taken obliquely from the surface down to a maximum depth of 120 m, with a sampling time of 4 min stratum^{-1} and a vertical resolution of 10 m. Towing speed was 3.5 knots. The volume of water filtered by each net was recorded by a flow meter attached to the mouth of the net. The average volume of filtered water was 34 m^3 (6 SD) for the coarse net and 0.35 m^3 (0.08 SD) by the fine mesh. Zooplankton samples were preserved in 5% formaldehyde buffered with sodium tetraborate.

In the laboratory, eggs and larvae of *Sardinella aurita* and *Engraulis encrasicolus* were sorted and identified from the 333 µm samples, and their numbers were standardised to number per 100 m^3. The standard length (SL) of larvae was measured to the nearest 0.1 mm. For the microzooplankton, aliquots were made from the 53 µm samples for counting nauplii and the copepodite stages of copepods. Two aliquots were taken from each sample, and at least 300 individuals in each aliquot were counted. Mean concentration in the aliquots was expressed as the number of individuals per cubic metre.

The mean depth of eggs and larvae, Z_{CM}, in each sample was calculated as the centre of mass of the larval distribution:

$$Z_{CM} = \sum_{i=1}^{n} P_i Z_i$$

where P_i is the proportion of larvae in the ith depth stratum:

$$P_i = \frac{C_i H_i}{\sum_{i=1}^{n} C_i H_i}$$

Z_i is the mean sampling depth of the ith depth stratum, C_i is the concentration of larvae in the ith depth stratum and H_i is the width of the ith depth stratum.

One-way ANOVA was used to assess the significance of differences in thermocline depth between the 2 areas, for each year. In addition, 3-way ANOVA was performed on Z_{CM} values for each species, by size, to determine the interaction between year (2003/2004), area (north/south) and time (day/night). Analyses were performed on log(x + 1)-transformed data. The Dunne test was conducted post hoc when significant differences were observed in interactions.

RESULTS

Hydrography

The horizontal temperature distributions in both years showed a marked surface front of nearly 2°C, perpendicular to the coastline around 41° 30′ N (Fig. 2). However, surface temperatures were higher (between

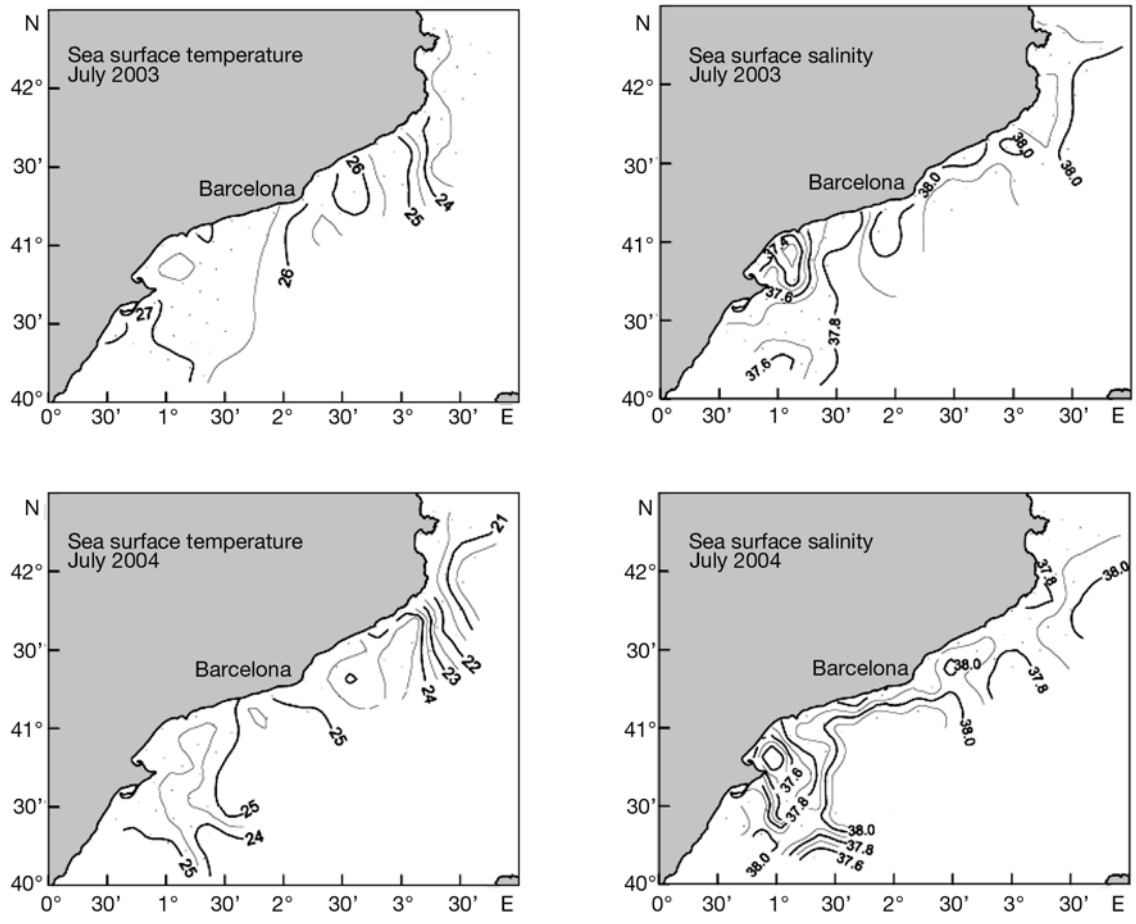

Fig. 2. Surface distribution of temperature (left-hand panels) and salinity (right-hand panels) for July 2003 (upper panels) and July 2004 (lower panels)

1 and 2°C) in July 2003 than in July 2004. In fact, July 2003 was extremely hot. Surface salinity distributions showed uniform values (around 37.9) in the whole area sampled, except near the Ebro River, where values were lower (~37.4 in 2003 and ~37.7 in 2004) (Fig. 2). Relatively high surface chlorophyll patches were found during both cruises on the Ebro shelf, showing good correspondence with areas of low salinity, in association with the effect of riverine nutrient inputs.

The vertical structure of the water column was dominated by thermal stratification, which was typical of full summer (Figs. 3 & 4). In both years, the stations in the north area had a significantly ($p < 0.03$) deeper pycnocline (and thermocline) than those in the southern area (Table 1). Comparing the 2 yr, the thermoclines in 2003 were shallower than in 2004. The maximum density gradient was found in the southern area in 2003 (Table 1). Vertical fluorescence profiles were also typical of the season with a clear DCM located beneath the pycnocline. However, there was also a secondary surface chlorophyll maximum (SCM) in the southern area associated with the presence of low salinity surface waters from the Ebro River. Fluorescence values found at this SCM were close to those at the DCM in this southern area (Figs. 3 & 4).

Microzooplankton

Copepod nauplii and copepodites showed similar distribution patterns throughout the water column in the 2 studied years, although differences were observed

Table 1. Mean (±SD) depth of the pycnocline and vertical density gradient at the pycnocline, by area and year

	Depth of the pycnocline (m)		Vertical density gradient (kg m^{-4})	
	July 2003	July 2004	July 2003	July 2004
South area	12 ± 0.45	16 ± 3.16	0.60 ± 0.07	0.23 ± 0.05
North area	20 ± 4.39	30 ± 13.54	0.23 ± 0.07	0.37 ± 0.20

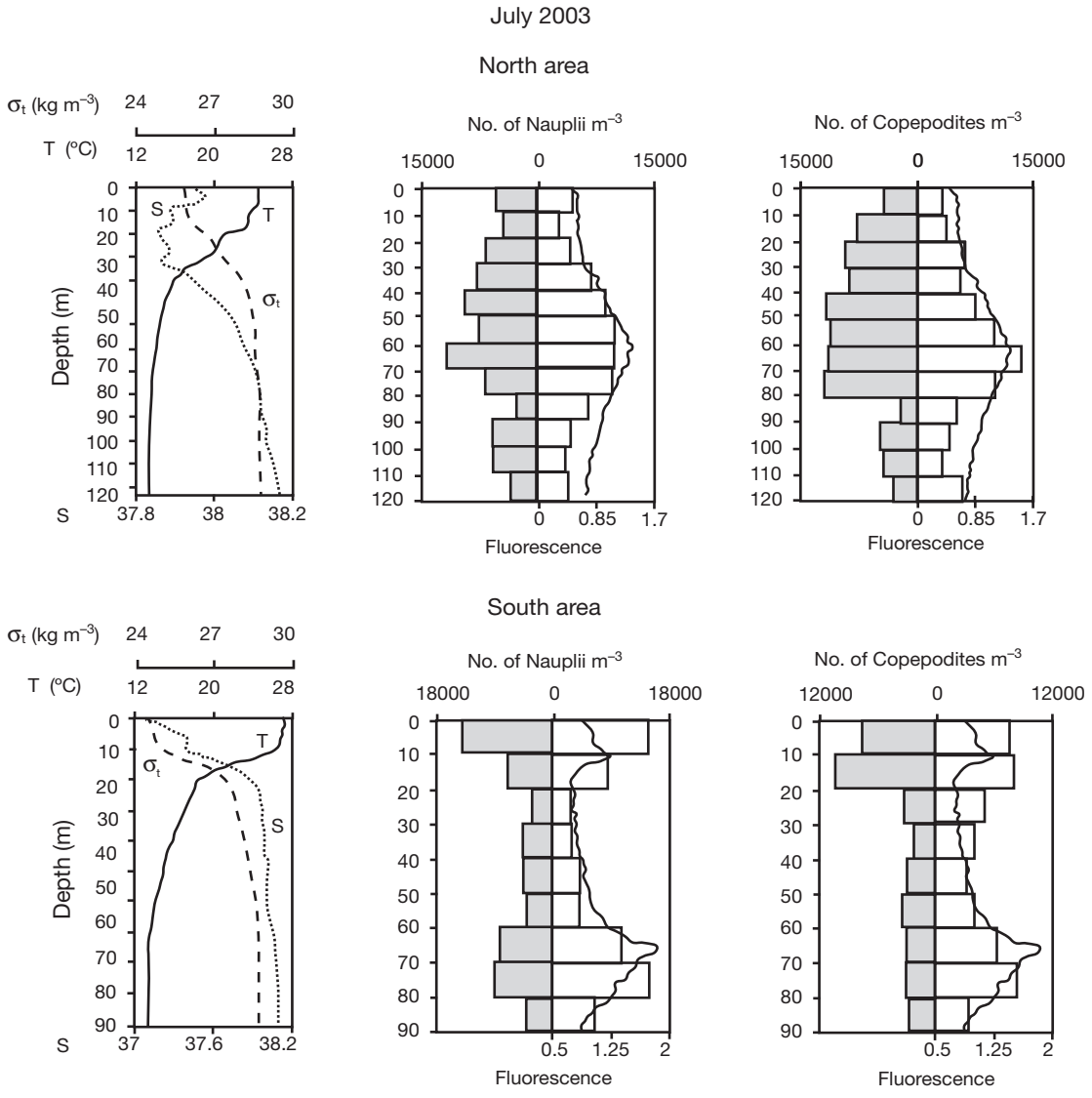

Fig. 3. Mean vertical profiles of temperature (T), salinity (S) and density (σ_t), and mean vertical distributions of fluorescence (—) and nauplii and copepodite stages of copepods in daytime (white bars) and night-time (grey bars) for the south and north sampling areas in July 2003

between the southern and northern areas. The vertical distributions of both microzooplankton groups were well correlated with that of fluorescence at the same depth intervals (correlation significant at $p < 0.05$; $r = 0.47$ for nauplii and $r = 0.40$ for copepodites). Accordingly, in the south, high concentrations were detected in the upper 20 m, which were associated with the SCM (Figs. 3 & 4), although it was not as evident for copepodites in July 2003. Another abundance peak was observed between 60 and 80 m depth, coinciding with the DCM. In the northern area, the highest concentrations were detected between 50 and 80 m, at levels close to the DCM, which was located between 60 and 70 m. In this area, no surface relative maximum was observed, in accordance with the absence of the SCM. Although the copepodites showed a certain tendency to be closer to the surface during the night, no indication of diel vertical migrations was evident for the nauplii (Figs. 3 & 4).

Fish eggs and larvae

The vertical distribution patterns of eggs and larvae of *Sardinella aurita* and *Engraulis encrasicolus* were very similar in the 2 sampling years. Complete data of abundances by size classes and depth stratum are shown in Table 2.

The vertical distribution of eggs (in July 2004), superimposed on density distributions, is presented in Fig. 5. The eggs of *Sardinella aurita* were close to the

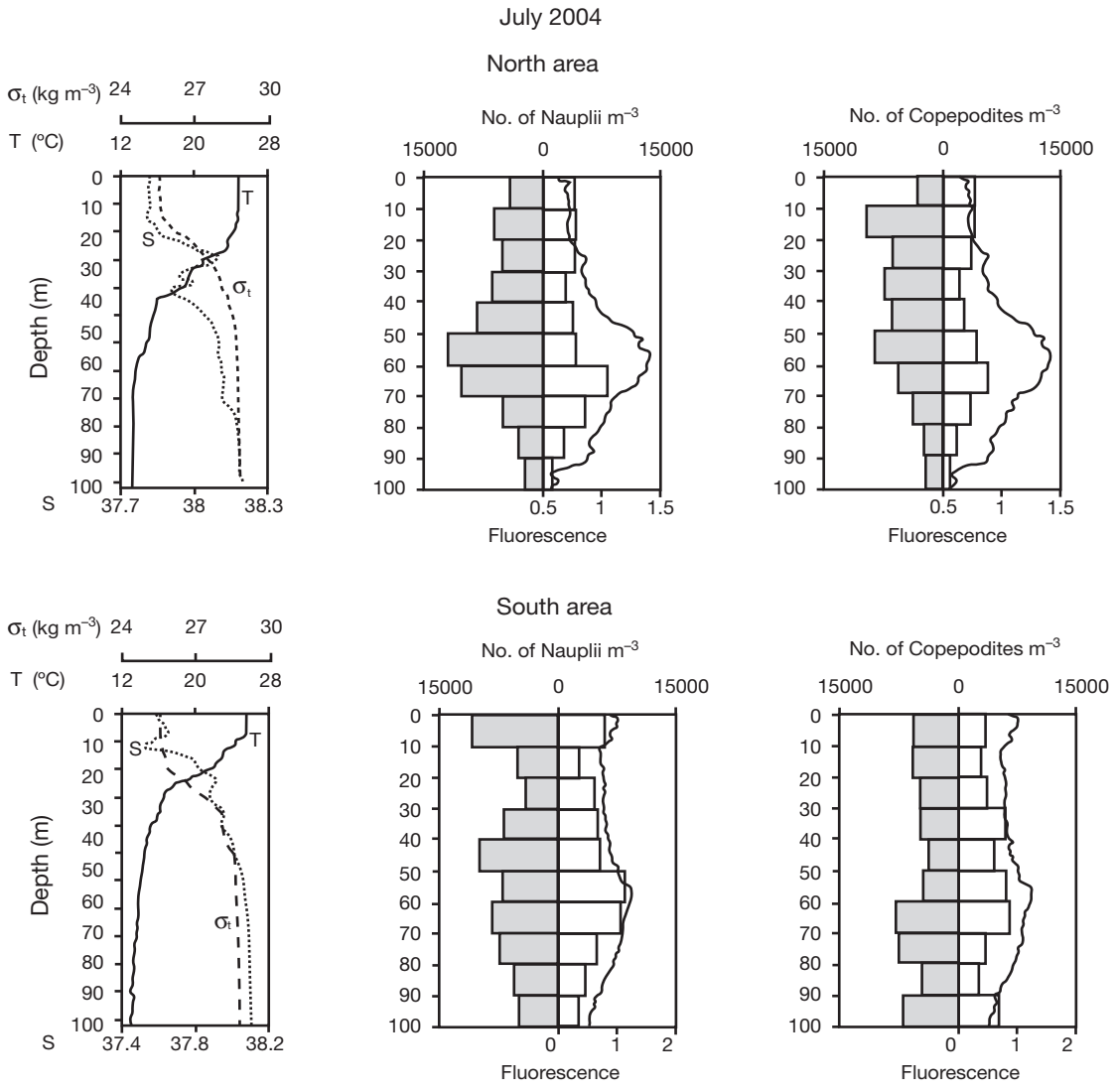

Fig. 4. Mean vertical profiles of temperature (T), salinity (S) and density (σ_t), and mean vertical distributions of fluorescence (—) and nauplii and copepodite stages of copepods in daytime (white bars) and night-time (grey bars) for the south and north sampling areas in July 2004

surface, mainly in the upper 10 m, well above the pycnocline, both in the southern and in the northern areas (Fig. 5). This is also evident in the distribution of the centre of mass (Z_{CM}) versus pycnocline depth (Fig. 6, Table 3). The eggs of *Engraulis encrasicolus* showed a wider distribution, with the maximum abundances associated with the highest density gradient, around the depth of the base of the pycnocline (Fig. 5). The Z_{CM} for anchovy eggs extended down to nearly 30 m (Fig. 6, Table 3) and was well correlated with pycnocline depth ($r = 0.61$; $p < 0.05$).

The larval abundances, by size, at the different depth intervals are presented in Table 2. We used the Z_{CM} at different developmental stages (Fig. 6, Table 3) to quantify vertical patterns of distribution. The results of ANOVAs performed to compare years, areas and day/night are presented in Table 4. These results show that (1) there were no differences between years, (2) the differences between areas were only significant for anchovy >6 mm SL, and (3) day/night differences were significant for both anchovy >6 mm SL and round sardinella >8 mm SL. In addition, these results show that the only significant interaction was time and area for anchovy larvae >8 mm SL, since the Z_{CM} values during the day in the north area were deeper than those in the rest of the cases.

The variability found in the Z_{CM} distributions can be analysed in more detail from the vertical distributions of larvae by size groups and areas (Figs. 7 & 8) in 2003. We used this year, with the highest abundances, because there were no significant differences between years in Z_{CM} distributions. During the night, larvae of

Table 2. *Sardinella aurita* and *Engraulis encrasicolus*. Mean (±SD) densities (no. 100 m^{-3}) of eggs and larvae by size class (mm) at each depth stratum (all stations combined), for July 2003 and July 2004. N: night; D: day

Year	Depth (m)	Time	*S. aurita*				*E. encrasicolus*			
			Eggs	<6	6–8	>8	Eggs	<6	6–8	>8
2003	1–10	N	27 ± 50	57 ± 100	12 ± 20	11 ± 13	97 ± 120	71 ± 66	65 ± 49	20 ± 21
		D	62 ± 117	53 ± 32	23 ± 22	1 ± 0	66 ± 80	40 ± 53	3 ± 3	2 ± 3
	11–20	N	6 ± 11	49 ± 92	5 ± 7	5 ± 7	43 ± 53	74 ± 69	56 ± 48	20 ± 11
		D	40 ± 100	84 ± 71	26 ± 24	5 ± 6	31 ± 43	37 ± 46	3 ± 4	2 ± 2
	21–30	N	–	12 ± 22	1 ± 3	2 ± 4	3 ± 3	70 ± 89	46 ± 40	17 ±15
		D	1 ± 2	17 ± 13	15 ± 20	4 ± 5	17 ± 21	37 ± 41	12 ± 19	3 ± 4
	31–40	N	–	13 ± 26	–	–	2 ± 3	25 ± 24	27 ± 38	19 ± 24
		D	–	7 ± 8	9 ± 8	4 ± 4	4 ± 7	30 ± 43	15 ± 22	7 ± 10
	41–50	N	–	7 ± 14	–	–	1 ± 2	21 ± 32	19 ± 25	6 ± 9
		D		1 ± 1	1 ± 2	1 ± 2	2 ± 3	14 ± 22	16 ± 28	7 ± 13
	51–60	N	–	2 ± 3	–	–	–	6 ± 9	5 ± 10	–
		D	–	–	0 ± 1	–	1 ± 2	2 ± 4	5 ± 10	4 ± 9
	61–70	N	–	–	–	–	2 ± 3	1 ± 1	2 ± 3	–
		D	–	–	–	–	1 ± 2	1 ± 2	2 ± 4	4 ± 6
	71–80	N	–	–	–	–	1 ± 2	2 ± 3	–	–
		D	–	–	–	–	–	1 ± 2	1 ± 2	3 ± 4
	81–90	N	–	–	–	–	–	–	–	–
		D	–	–	–	–	–	2 ± 3	2 ± 4	3 ± 5
	91–100	N	–	–	–	–	–	–	–	–
		D	–	–	–	–	–	2 ± 2	–	1 ± 1
	101–110	N	–	–	–	–	–	–	–	–
		D	–	–	–	–	–	–	1 ± 1	1 ± 1
	111–120	N	–	–	–	–		–	–	–
		D	–	–	–	–		2 ± 2	1 ± 1	3 ± 5
2004	1–10	N	2 ± 82	34 ± 36	33 ± 43	9 ± 8	265 ± 239	17 ± 12	30 ± 32	21 ± 22
		D	145 ± 236	25 ± 22	4 ± 4	–	209 ± 230	2 ± 2	–	1 ± 1
	11–20	N	–	24 ± 35	24 ± 44	9 ± 12	332 ± 265	28 ± 17	29 ± 35	27 ± 24
		D	65 ± 112	100 ± 132	23 ± 26	3 ± 3	554 ± 633	12 ± 10	6 ± 6	3 ± 4
	21–30	N	–	3 ± 5	5 ± 6	3 ± 2	370 ± 532	18 ± 19	13 ±14	10 ± 11
		D	25 ± 44	14 ± 12	8 ± 7	3 ± 6	93 ± 91	7 ± 7	10 ± 10	4 ± 4
	31–40	N	–	–	1 ± 3	–	95 ± 107	9 ± 14	6 ± 8	8 ± 11
		D	5 ± 10	14 ± 28	3 ± 6	1 ± 1	41 ± 40	3 ± 3	5 ± 6	4 ± 5
	41–50	N	–	1 ± 2	–	–	30 ± 35	3 ± 4	1 ± 3	6 ± 6
		D	1 ± 3	11 ± 19	–	–	21 ± 25	3 ± 4	2 ± 4	8 ± 17
	51–60	N	–	–	–	–	7 ± 7	–	1 ± 1	1 ± 1
		D	–	1 ± 2	–	–	10 ± 7	1 ± 1	1 ± 2	28 ± 54
	61–70	N	–	–	1 ± 2	–	6 ± 8	–	–	–
		D	–	2 ± 4	–	1 ± 1	5 ± 3	1 ± 1	–	15 ± 28
	71–80	N	–	–	–	–	–	–	–	–
		D	–	–	1 ± 2	–	4 ± 3	–	1 ± 2	1 ± 2
	81–90	N	–	–	–	–	6 ± 6	–	–	–
		D	–	–	–	–	11 ± 8	–	–	–
	91–100	N	–	–	–	–	10 ± 10	–	–	–
		D	–	–	–	–	7 ± 3	–	–	2 ± 2
	101–110	N	–	–	–	–	–	–	–	–
		D	–	–	–	–	–	–	–	–
	111–120	N	–	–	–	–	–	–	–	–
		D	–	–	–	–	–	–	–	–

all size classes of both species were located in the upper layers (mainly in the first 30 m). The corresponding Z_{CM} were clearly above the pycnocline (Fig. 6). During the day, at the initial developmental stages (<6 mm SL), larvae of both species were largely found in the upper layers of the water column, between the surface and 20 m. Their Z_{CM} was situated above or close to the pycnocline (Fig. 6). As they grew their distribution became wider, although it did not extend beyond 50 m depth in the south (Fig. 8). In the northern area, the patterns of vertical distribution of larger larvae showed differences between species. Larvae of *Sardinella aurita* from 8 mm SL onwards were mainly found between 20 and 40 m, but never deeper than 50 m (Fig. 7). Their Z_{CM} was generally located below the pycnocline, although never below 40 m depth (Fig. 6, Table 3). The maximum abundances of anchovy larvae (6 to 8 mm SL) appeared between

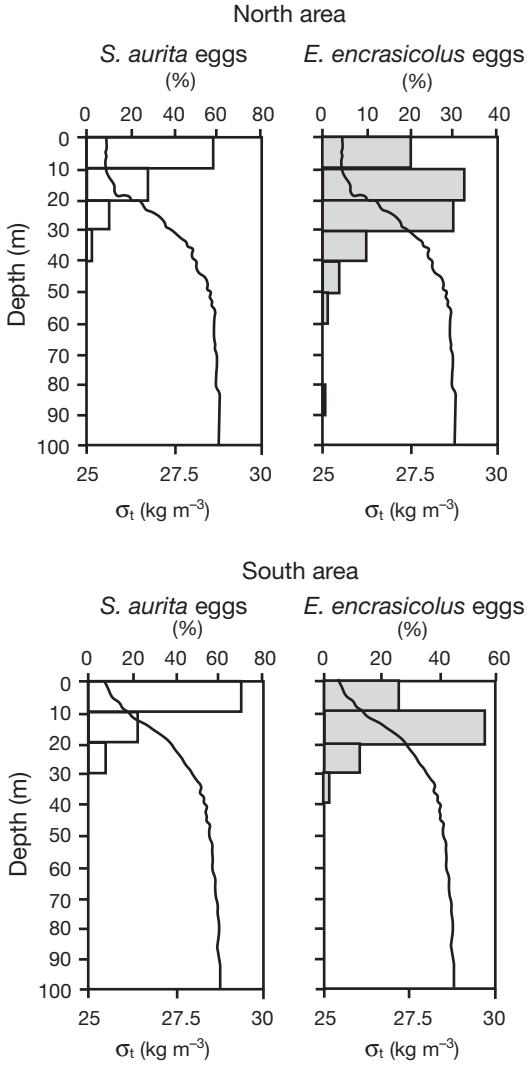

Fig. 5. *Sardinella aurita* and *Engraulis encrasicolus*. Mean vertical distribution of eggs and density (σ_t), for the south and north sampling areas, in July 2004. The percentages calculated are based on the mean abundance at all stations for each depth stratum

Table 3. *Sardinella aurita* and *Engraulis encrasicolus*. Daytime mean (±SD) depth (Z_{CM}) of eggs and larvae by size class, areas and years

	Z_{CM} (m)			
	South		North	
	July 2003	July 2004	July 2003	July 2004
S. aurita eggs	7 ± 5.0	6 ± 1.3	6 ± 2.1	5 ± 3.9
S. aurita <6 mm	16 ± 1.3	12 ± 3.5	14 ± 2.8	18 ± 3.5
S. aurita 6–8 mm	16 ± 6.4	9 ± 6.2	17 ± 2.8	15 ± 1.5
S. aurita >8 mm	27 ± 12.3	18 ± 5.2	24 ± 5.0	27 ± 12.3
E. encrasicolus eggs	11 ± 3.4	17 ± 7.3	16 ± 1.3	20 ± 10.1
E. encrasicolus <6 mm	14 ± 2.1	18 ± 0.2	23 ± 10.4	21 ± 2.0
E. encrasicolus 6–8 mm	24 ± 2.2	21 ± 0.8	31 ± 8.6	34 ± 1.4
E. encrasicolus >8 mm	16 ± 0.5	20 ± 4.0	46 ± 15.0	59 ± 6.6

20 and 50 m, and from 8 mm SL onwards they showed a much more extended distribution, between 30 and 90 m (Fig. 7). Z_{CM} for *Engraulis encrasicolus* was deeper than that of *S. aurita* with a day/night migratory behaviour evident in larvae >6 mm SL (Fig. 6, Table 3). From this size, the Z_{CM} was below the pycnocline, reaching 70 m in larvae >8 mm SL.

DISCUSSION

The environmental conditions found in both years were in general those expected for the season, though the surface temperature in summer 2003 was around 2°C higher than usual in the whole region. This could be explained by the successive heat waves, reported at the time as extremely hot, that affected south-western Europe during the spring and summer of 2003 (Schär & Jendritzky 2004). Consequently, the thermoclines in 2003 were shallower than in 2004. The maximum density gradient was found in the southern area in 2003. The presence of lower surface salinity near the Ebro River and the high temperatures in 2003 might have contributed to the enhancement of this pycnocline (Table 1).

The vertical distribution of nauplii and copepodites showed good agreement with the areas of high phytoplankton concentration, i.e. below the thermocline at the level of the DCM and close to the surface in the southern area affected by the Ebro River runoff. Development of a DCM during the stratified period is a well-known feature in the area (Estrada 1985). DCM phytoplankton cells are preyed on by herbivorous zooplankton (Saiz & Alcaraz 1990), and high zooplankton biomass has been found associated with the DCM during daylight hours (Alcaraz 1985).

The vertical distribution of pelagic eggs, according to Sundby (1991), is determined by a set of interacting biological and physical processes, namely the properties of the eggs (density, diameter) and the ambient sea water (density, viscosity, turbulence). Generally, pelagic fish eggs have a specific density which is lower than that of the upper mixed layer of the sea, and they tend to rise towards the surface (Sundby 1991). In the present study, the eggs of both species were located in relatively superficial waters. Nevertheless, although the eggs of *Sardinella aurita* were clearly located above the pycnocline, the *Engraulis encrasicolus* eggs showed a certain tendency to accumulate at the base of the pycnocline. This suggests that the density of the anchovy eggs is higher than that of *S. aurita* eggs. While eggs of the latter

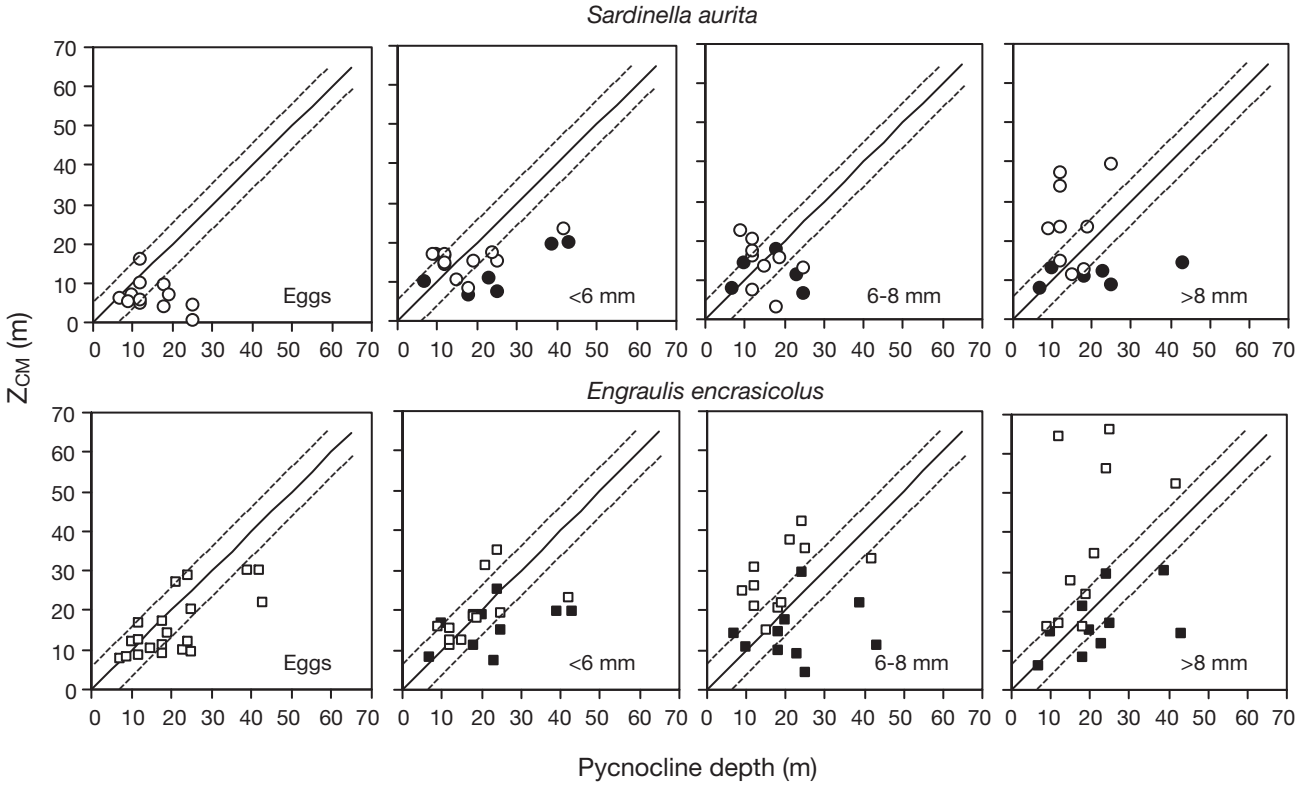

Fig. 6. *Sardinella aurita* and *Engraulis encrasicolus*. Relationships between the depth of the pycnocline and mean depth (Z_{CM}) of eggs and larvae by size class for day (open symbols) and night (filled symbols) (samples 2003 and 2004 combined). The slope line is included to better represent the depth of the pycnocline. Dashed lines are drawn at ±5 m

species are clearly less dense than the surface waters, those of the anchovy have a similar or slightly higher density than the upper mixed layer, on the order of 1026.5 to 1027 kg m^{-3}, which would make them accumulate in the pycnocline. The observed lower density of eggs of *S. aurita* would allow them to develop at slightly higher temperatures than those of the anchovy, in more favourable conditions for a species characteristically from warm waters. Although no references have been found concerning the vertical distribution of *S. aurita* eggs, the concentration of anchovy eggs in the pycnocline has been reported by Motos & Coombs (2000) and Coombs et al. (2004) in the Cantabrian Sea (south of the Gulf of Biscay) at similar densities to those detected in the present work. Olivar et al. (2001), in a study carried out in the NW Mediterranean, indicated that anchovy eggs were largely found in the upper 10 m, clearly above the pycnocline. Nevertheless, the density corresponding to the upper mixed layer observed in this latter work was 1027 kg m^{-3}, higher than that found in the present study. Consequently, the anchovy eggs probably have a density on this order independent of the environmental density. This observation did not match the results of Petitgas et al. (2006), who modelled the vertical distribution of eggs of pelagic species. These authors indicated that the density values of different species (sardine, sprat and anchovy) varied in coherence with each other, meaning that across species there was a similar process of egg density adaptation.

The larvae of both species showed diel vertical movements as larval development progressed. The vertical displacements showed differences between the 2 areas studied, but the patterns observed for each

Table 4. Three-way ANOVA testing for differences in Z_{CM} for each larval size class by year (2003/2004), area (north/south) and time (day/night). The interaction listed is the only one that has some significance. NS: not significant

	Sardinella aurita			*Engraulis encrasicolus*		
	<6 mm	6–8 mm	>8 mm	<6 mm	6–8 mm	>8 mm
Time: day/night	NS	NS	$p < 0.022$	NS	$p < 0.015$	$p < 0.001$
Area: north/south	NS	NS	NS	NS	$p < 0.008$	$p < 0.001$
Year: 2003/2004	NS	NS	NS	NS	NS	NS
Time × Area	NS	NS	NS	NS	NS	$p < 0.015$

species were the same in the 2 studied years. During the night, the larvae of both species were located in the most superficial layers, above the pycnocline, independent of their size. This has already been documented in the larvae of *Engraulis encrasicolus* as well as in other clupeoid species (Neilson & Perry 1990, Olivar et al. 2001), but was not known in the case of *Sardinella aurita*. It is assumed that, in general, clupeoid larvae migrate upwards at night to fill their gas bladders at the sea surface to reduce the energetic cost of swimming during the night, when the larvae do not feed (Hunter & Sánchez 1976). During daylight hours, i.e. the feeding period (Conway et al. 1998), larvae of both species >6 mm SL were located in deeper levels of the water column. Clear evidence of diel vertical migration was especially apparent in anchovy larvae >6 mm SL. This size corresponds with the development of the caudal fin and coincides with behavioural changes, as the onset of vertical migrations (Somarakis & Nikolioudakis 2007). These displacements, however, were much more evident in the northern than in the southern area. If we consider the effort required to cross strong density gradients such as those present in summer, we can argue that the vertical movements might be limited above a certain threshold value of the vertical density gradient. Some studies effectively indicate that strong pycnoclines can act as a physical barrier for the diel vertical migration of fish larvae (Davis et al. 1990). Moreover, the greatest concentrations of fish larvae in stratified water columns have been found in and above the thermocline (Ahlstrom 1959, Kendall & Naplin 1981). In the present study, according to the values recorded in the different situations (Table 1), the 2004 gradient in the north was greater than that in

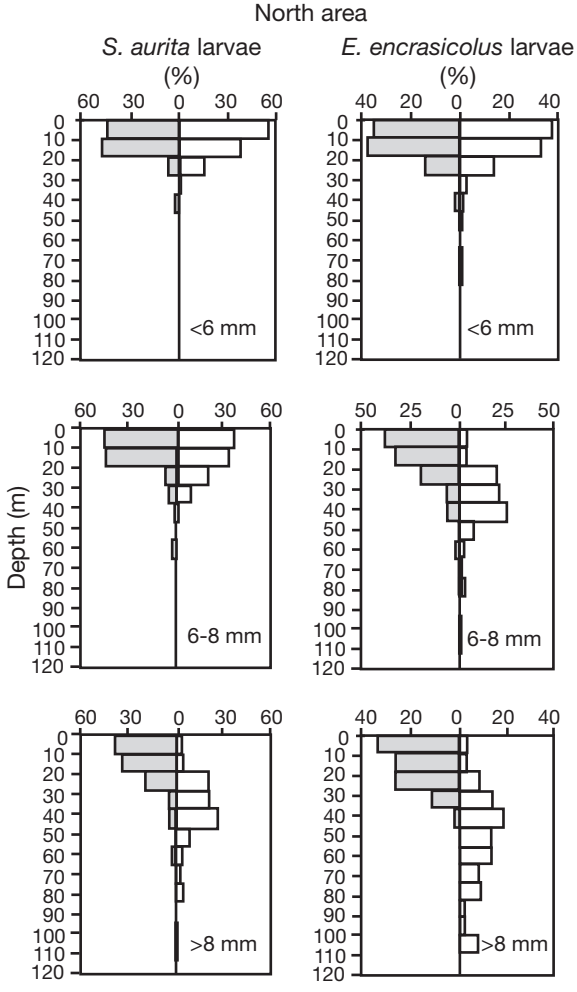

Fig. 7. *Sardinella aurita* and *Engraulis encrasicolus*. Vertical distribution of larvae by size class in daytime (white bars) and night-time (grey bars) for the north area in July 2003. The percentages calculated are based on the mean abundance at all stations for each depth stratum

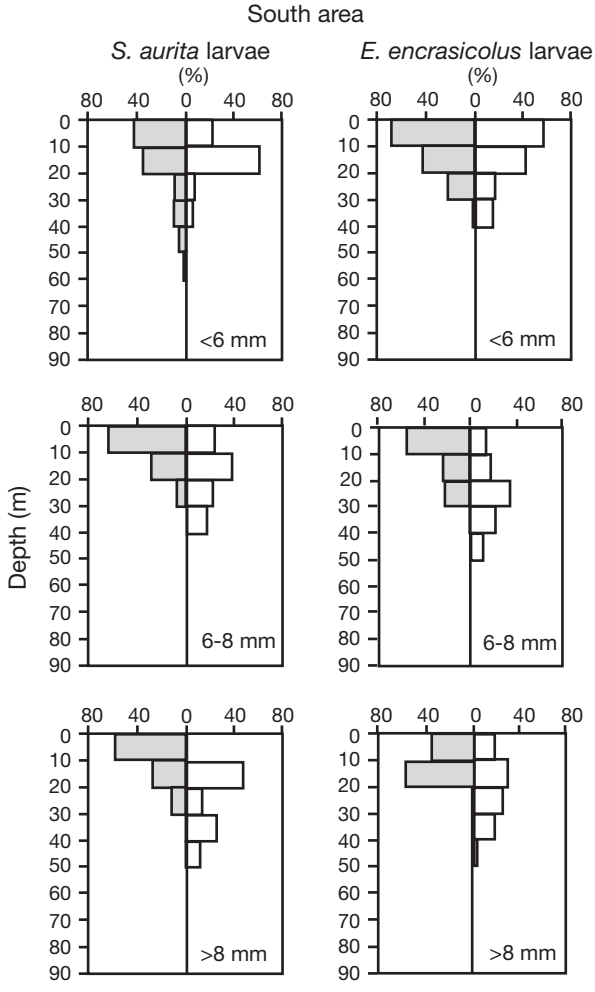

Fig. 8. *Sardinella aurita* and *Engraulis encrasicolus*. Vertical distribution of larvae by size class in daytime (white bars) and night-time (grey bars) for the south area in July 2003. The percentages calculated are based on the mean abundance at all stations for each depth stratum

the south, whereas, in 2003, an opposite trend was observed. Therefore, if fish larvae could cross the pycnocline in the north in 2004 (Table 3), there should be no problem to do so in the south, at least in this same year. Hence, the effort to cross the pycnocline would not be a limiting factor for vertical displacement.

The diel vertical migrations depend on a combination of factors, such as thermal structure, availability of prey and light (Kendall & Naplin 1981, Munk et al. 1989, Olla & Davis 1990). Fish larvae may accumulate where prey are concentrated, either by modifying their behaviour when they find good foraging conditions (Munk & Kiorboe 1985) or in association with physical conditions, such as the thermocline, where prey aggregate (Munk et al. 1989). We could suggest that, in the present study, the differences found in the vertical distribution of larvae between areas could respond to the vertical distribution of their prey. In the southern area, where a SCM was well developed under the influence of Ebro River runoff, the abundance of nauplii and copepodite stages of copepods at the surface was higher than in the northern area at the same levels, and similar to that found at the DCM level, below the pycnocline. Then, the fact that, in the southern area, the larvae of both species were found in relatively superficial layers, independent of their developmental stage, could correspond to the relative abundance of food at these upper levels. We could thus argue that the vertical displacements to feed were not necessary in the southern area. However, in the north, in the absence of surface fertilization mechanisms, the primary production was limited to the DCM, and, accordingly, the highest concentrations of nauplii and copepodites were always found below the pycnocline. In this situation, while the advanced developmental stages of anchovy larvae were found at considerable depths, near the DCM, coinciding with the high abundance of prey, *Sardinella aurita* larvae never reached depths >50 m. This migratory behaviour of anchovy larvae has already been described by Olivar et al. (2001) in a similar stratification situation, and it was justified by the food aggregation at the DCM level.

Why do *Sardinella aurita* larvae not behave similarly? Is there any physical factor that might hinder the vertical migration of *S. aurita* towards deeper levels? Physical factors that can affect the depth distribution of fish larvae are light, turbulence and temperature (Heath et al. 1988, Munk et al. 1989, Olla & Davis 1990). Among these factors, and considering the thermophilic character of *S. aurita* (Ben Tuvia 1960), we suggest temperature could be a limiting factor, since at the levels corresponding to the DCM the temperature (~15°C) could be too low. Fish larvae, as poikilothermic organisms, show a preference for certain temperature ranges that are generally associated with physiological and growth optima (Blaxter 1992). It has been reported that fish larvae are capable of adjusting their depth distribution in order to avoid unfavourable temperatures (Olla & Davis 1990). Therefore, we should explore whether the temperature detected at the DCM is unfavourable for the larvae of *S. aurita*, even though this is where the maximum food abundances are located. It should be pointed out that *S. aurita* is a very abundant species in upwelling regions of the central Atlantic. In these areas, it reproduces when the temperatures reach the local annual maximum (Ettahiri et al. 2003). Compared with conditions in the Mediterranean in summer, in upwelling regions maximum surface temperature is lower (18 to 21°C), vertical stratification is weaker and the surface layers are richer in food for the larvae. In the present study, in the northern area, high food concentrations were only found at the DCM level, below the pycnocline, where temperature is lower than in the upwelling regions.

Whatever the reason, the results of the present study show that the larvae of *Sardinella aurita* have difficulties reaching depths below 50 m. This is a weakness for obtaining food in the zones where surface primary production is limited. This behaviour puts *S. aurita* (in a phase of expansion) at a disadvantage in relation to the anchovy in the areas where larvae of both species coexist. This difficulty, in addition, could control the northward extension of *S. aurita* in the western Mediterranean. Conversely, the presence of productive surface waters on the Ebro shelf could have facilitated the expansion of this species along the southern half of the Catalan coast.

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