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**CROSS-SHELF ZONATION, VERTICAL DISTRIBUTION,  
AND DRIFT OF FISH LARVAE OFF NORTHERN  
PORTUGAL DURING WEAK UPWELLING.**

by

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**Abstract:**

An area off Northern Portugal was surveyed in August 1989, normally a month of strong upwelling, in order to study the horizontal and vertical distribution of fish larvae in relation to the coastal upwelling structures. Stable stratification and anomalously high temperatures caused the unusual offshore spawning of anchovy, *Engraulis encrasicolus*, during the survey. Spawning intensity of anchovy was at maximum during periods of non-upwelling. The observed upwelling event was of short duration only and had low intensity, particularly close to the coast.

The cross-shelf zonation and dispersal of fish larvae depended on the interaction of spawning bathymetry, vertical distribution of larvae and the hydrographical conditions in the respective range, but integrated time scales larger than the survey.

Soleid larvae living in less dense and less wind exposed coastal surface waters appeared to be retained there.

Surface living larvae of midshelf species showed dispersal offshore. For young anchovy larvae dispersal up to about 10 miles from the spawning grounds was directly related to the observed upwelling event, but for elder larvae up to 43 days old occurrences up to 37 miles from the respective zonal spawning depths were related also to two events north of the surveyed area during July.

Larvae from midshelf origin, but with a more extended vertical distribution including the thermocline showed reduced net offshore dispersal, particularly when they avoided the Ekman-layer as e.g. *Callionymus* sp. However, the bottom-near specimens of many taxa showed some advection from midshelf towards the coast.

The inshore boundaries of larvae of several slope or oceanic species were not always as anticipated from their vertical range, the reasons are discussed.

It is presumed that under normal summer conditions (with more consistent and stronger upwelling) all discussed dispersal patterns would become more pronounced.

## Introduction:

An area off the central west coast of the Iberian Peninsula (Fig. 1) was object of a seasonal study of horizontal and vertical distribution patterns of fish larvae in relation to the coastal upwelling structures.

Coastal upwelling in seasonal scales occurs normally off Northern Portugal from late spring to late summer or early autumn (WOOSTER et al. 1976; FIUZA et al. 1982). As in other eastern boundary current areas, coast-parallel, equatorward windstress causes offshore Ekman-transport in the surface layer. A resulting mass-deficit near the coast is partly compensated by an intermediate onshore compensating current. This compensating current feeds cooler, nutrient-rich water into the euphotic layer (MINAS et al. 1982), enhancing primary and subsequent production (e.g. HEMPEL 1982). There exist relations between upwelling intensity and biomass of commercial fish stocks, the effects being positive or negative, depending generally on the species (e.g. ARNTZ 1986; WYATT & PÉREZ-GANDARAS 1988). However, as pointed out by DICKSON et al. (1988), such relations may even reverse sign between adjacent stocks of the same species, and the mechanisms are only partly understood. Among the acting mechanisms are besides trophic enrichment turbulent mixing (affecting prey-density) and cross-shelf dispersal of fish larvae with both Ekman-transport and compensating current, potentially removing larvae from optimum food concentrations or the habitat of adults (e.g. BAKUN & PARRISH 1991, and literature therein). It is assumed that successful recruitment of pelagic stocks in upwelling ecosystems needs an optimum environmental window (CURY & ROY 1989).

This paper describes both the hydrographic structure and the species composition of fish larvae off Northern Portugal during weak upwelling, and analyses specific cross-shelf zonations and vertical distributions as a pilot study to elucidate the space and time scales of cross-shelf dispersal of fish larvae.

## Material and methods:

A grid of 79 fixed standard CTD/plankton stations, organized in 6 cross-shore sections, was carried out off northern Portugal from 08 to 15 August 1989, on board of the German RV "Friedrich Heincke" (cruise no. 279, see Fig. 2). The typical station spacing was  $\leq 10$  km over the shelf and upper slope, increasing to 30 km offshore. The sections were named A to F, from north to south, and the stations numbered, within each section, from coast to the open ocean (1 to 12 - 14), regardless of the direction the observations were carried out (Fig. 2).

CTD-data come from a mini CTD (ME-OTS 1500) installed near the opening of an obliquely towed multiple-opening-closing plankton net (MCN). The system was towed under controlled conditions (ships speed 1.2 m/s, speed of ascent  $< 10$  m/min) from 200 m depth (or about 5 m above the bottom in shallower stations) in an oblique path. The mounting was done in a way to achieve unobstructed flow through both CTD-sensors and net. The dots in Fig. 2 refer to the starting positions of the stations. However, the end positions of CTD (not oxygen) might have been as far as 2 nautical miles away. In order to assess data quality, the T,S properties in the temperature range  $12^{\circ}$  -  $13^{\circ}\text{C}$  were checked against the standards of EMERY & DEWAR (1982), and no significant deviations were found. The salinity values are



therefore believed to be generally correct.

Dissolved oxygen was measured with an independent, but similar, CTD-02 probe that had a slightly deficient conductivity sensor. Due to a slow O<sub>2</sub>-sensor (time constant 60 s), measurements were taken at  $\leq 8$  standard depths between 5 and 300 m, or 3 m above the bottom in shallower stations (see dots in Fig. 7). The oxygen sensor was calibrated twice daily by the WINKLER-method (GRASSHOFF et al. 1983). Due to instrument failure, the oxygen measurements were discontinued before the end of section C.

SEEWETTERAMT HAMBURG provided wind-time series for the period 01 July - 15 August 1989 ("SWA"-data). The data came from stations off Vigo and in Viana do Castelo, Leixoes (Fig. 3) and close to Peniche (the latter was least affected by orographic effects, but showed the highest number of interruptions and worst directional resolution).

Except for the deepest stratum 120 - 200 m, the up to five plankton samples per tow came from steps 30 m wide (or less, see e.g. Fig. 9). The average sample size was 3.91 m<sup>3</sup> ( $s = 2.17$ ;  $n = 311$ ), and the efficiency of the sampler is also comparable to the Bongo net (KLOPPMANN 1990). This paper deals with a representative selection out of a total yield of almost 3700 fish larvae and some 60 taxa.

Abundance values (catch per unit of effort = cpue) are expressed as  $n/1 \text{ m}^3$ , either integrated over the total vertical range sampled for horizontal distributions, or per individual step for vertical distributions.

Preservation of anchovy larvae permitted direct ageing from daily growth increments in sagittal otoliths for 23 specimens only (prevailing 4.5 - 10.0 mm TL). These data showed close agreement with a broader length/age key from the Mira estuary in April 1987 (RÉ 1987; see also for literature and methods), which was therefore applied to assess the age from spawning of the remaining material. We assume that the first growth ring was formed at the end of the fourth day after spawning.

For the spawning bathymetry of the selected species, the reader is generally referred to the original literature reviewed e.g. in HUREAU & MONOD 1973 or WHITEHEAD et al. 1984-86, some additional data of relevance will be quoted below.

#### The hydrographical situation:

Weak and variable wind conditions prevailed the 12 days prior to the survey (SWA-data). The plankton survey coincided with an onset of upwelling favourable, stable wind directions, weak at 08 August and moderate winds up to Beaufort force 5 at 09 - 12 August. The wind ceased and changed direction again during transect D at 13 August, when the survey was about 60 % completed. This development was consistent in time from at least Vigo to Peniche and is below referred to as "the observed event". However, it might be argued that this event could be traced back to 03 August at all 4 stations, though with instabilities in the beginning.

With a response time lag of 1 day (FIUZA et al. 1982; JORGE DA SILVA 1992) transects B to perhaps D should show coastal upwelling, but coastal stations had less wind forcing during the observed event than offshore stations (Fig. 2), in agreement with the meteorological situation (JORGE DA SILVA, pers. comm.).

Horizontally, temperature and salinity (with coastal salinity minima due to river plumes) increased both towards offshore and southwards, from 19.0°C

or 35.4 psu to  $>22.0^{\circ}\text{C}$  and 36.1 psu. Except for an isolated minimum  $18.8^{\circ}\text{C}$  offshore, the minima coincided with the event.

There was a permanent stratification in temperature and density, the discontinuity layer was almost confined to the upper 50 m and the strongest gradients occurred in the upper 30 m (e.g. Figs. 4 & 5). Upwelling did mainly affect the vertical position and width of the thermo- and pycnocline, which ascended near the coast at transects A - D (except in the river plume), and corresponded with a bottom-parallel ascent of 35.7 psu water from some 100 - 150 m to either the river plume or the surface (Fig. 6). The sloping of isopleths and vertical continuity of salinity diminished or disappeared in the upper 100 m at transects E & F, in close response to the wind event. Surface-near waters of  $\leq 35.7$  psu were oxygen-oversaturated (Fig. 7), and the congruency of the distribution patterns of all physical parameters there is striking. The same salinity range at depths was oxygen-depleted.

Some upwelling-like structures were also found consistently below 100 m depth (Figs. 5 - 7), but these structures were uncorrelated to the observed wind event, and the congruency between the parameters was weaker. While generally in the upper 200 m salinity (and temperature) decreased with depth, at intermediate depth a wedge of somewhat higher salinity  $\geq 35.8$  psu was consistently present. Its inshore boundary depended on the vertical movement of 35.7 psu water.

## Results:

### Species composition and vertical distributions:

Among a total catch of 3670 fish larvae some 60 taxa have been identified. As many of these taxa were rare, or, as e.g. for family Gobiidae with at least 3 species, specific identification was not possible for all specimens, some regrouping to higher taxa was done. The 15 resulting taxa listed in Table 1 comprise about 84 % of the total catch (standardised to cpue). Some additional taxa of relevance will be mentioned below. The first ranking species was anchovy, *Engraulis encrasicolus*, with 29.4 % of the unquantified total catch or 24.6 % of total cpue.

Average vertical distributions for more abundant or frequent taxa are listed in Table 1, arranged from surface preference (top) to deep distribution (bottom). The vertical resolution of sampling is with generally 30 m-steps fairly coarse, particularly in respect to the shallow mixed layer and narrow thermocline (Fig. 5). Nevertheless the patterns are not unusual and may also be attributed to a preference for the mixed layer, a mixed layer-thermocline group, a thermocline pattern and a group preferring subthermocline temperatures.

### Zonation and drift:

Among a complex mixture of individual horizontal distribution patterns, the following general patterns emerged:

1. "Stationary" taxa, not revealing any cross-shelf displacement from the spawning grounds of adults. Within the stationary group, the following cross-shelf zonations were observed (Fig. 8A - 8C):

- 1-A. Surface-near living larvae of family Soleidae (almost exclusively *Buglossidium luteum*) remained above the shallow, inshore habitat of adults

and coincided with the less saline, or less wind-exposed, inshore waters (Fig. 8A). No second taxon revealed a similar distribution.

1-B. *Callionymus* sp. larvae remained above the midshelf spawning grounds (Fig. 8B). Preferring depths of some 30 - 60 m, they coincided mostly with the intermediate wedge of somewhat higher salinities. For the deeper living larvae some onshore transport may be assumed from Figure 9, while less saline coastal surface waters were devoid of the species. A corresponding horizontal distribution is found for larvae of the vertically extended family Gobiidae, except that they also occurred at most inshore stations. The taxon is likely to include several species spawning from shallow waters to the shelf edge.

1-C) Generally larvae of oceanic species and extended-shallow distribution remained exclusively beyond the shelf edge (Fig. 8C). An almost identical offshore distribution showed (unexpectedly, see below) larvae of the oceanic-slope dwelling family Paralepididae in spite of a deep vertical range 60 to at least 200 m. Though also of oceanic origin and with shallow distributed larvae (JOHN 1984 and literature therein), larvae of the oceanic meso- to bathypelagic genus *Cyclothone* make an exception. In spite of low overall abundance they occurred until the shelf stations adjacent to the 200 m depth contour, and, with a single specimen, at station B 4.

## 2. Taxa with offshore displacement:

Anchovy, *Engraulis encrasicolus*, larvae hatch from eggs spawned at mid-shelf. Their abundance maxima of larvae and minimum lengths (ages) were encountered (Figs. 10 & 12). Minimum lengths coincided with the zone of deepest occurrences of larvae (Fig. 11), and age distribution showed a U-shape cross-shelf (Fig. 12). Anchovy larvae of mostly larger age (together with few triglid, serranid or sparid larvae mainly at transect D) occurred also offshore of the spawning grounds along the northern transects A - D, but anchovy larvae of any size were absent in offshore waters of transects E & F (a single triglid larva was encountered at E 8). There was a relative paucity of young larvae at all depths of transects B - D in contrast to the surveys at the onset of the event or distinctly after it (transects A and F).

A fairly similar horizontal distribution as found for anchovy, but with less extension seawards due to the absence of larger specimens, was observed for the ecologically well comparable larvae of *Arnoglossus laterna*. Broadly corresponding patterns were found also for *Cepola rubescens* and *Trachurus trachurus*, where with a somewhat more extended vertical distribution a smaller percentage of the larvae should be affected by offshore Ekman-transport.

## 3. Taxa with evident or anticipated onshore displacement:

The occurrence of larvae of the deep-sea genus *Cyclothone* above bottom depths as shallow as 140 m (exceptionally 100 m at station B 4) can only be explained by advection, though probably during the egg stage as larvae live in surface waters. Similar is likely for the single straggler of the slope species *Myctophum punctatum* at station B 3 (see HAMANN et al. 1981).

*Maurollicus muelleri* larvae originate from a pseudoceanic (sensu HULLEY 1981) parental stock and hatch at some 150 - 300 m depth (JOHN & KLOPPMANN 1989). Literature data (JOHN 1985; WEISS et al. 1988) indicated drift with the onshore compensation flow during upwelling. Larvae had their maximum extension towards the shore at transects B & C (Fig. 13), but as the inshore boundary was not beyond the extreme records for adults, such dispersal remains questionable in our survey.

Larvae of other oceanic and slope-dwelling families were almost, deep-living Paralepididae completely, absent above the shelf.

## Discussion:

The increase of surface temperature and salinity both towards offshore and southwards is known for the area (DHI 1967; ANDRES et al. 1992; own, unpublished data). The actual surface temperatures showed upwelling-related coastal minima, but were warmer than long-term means for the month, with anomalies of some +2°C offshore (compared with DHI 1967) and +3.0 to 3.5°C at the coast (compared to data from off Leixoes and Peniche, FIUZA et al. 1982).

It is likely, that the occurrence of the first ranking species anchovy, *Engraulis encrasicolus*, was related to this temperature anomaly. The species was previously not considered to be an important component of Portuguese ichthyoplankton outside of estuaries (RÉ 1991, and literature therein). The relative paucity of young larvae at transects B to D might be interpreted as a consequence of reduced anchovy-spawning during the observed event, which reached or exceeded the critical threshold of 5 - 6 m/s defined by CURY & ROY (1989, assuming prey density to be affected) from 09 - 11 August. A back-calculation of birthdays for all larvae revealed a coincidence of the absolute maximum of larvae born per day, as well as some preceding weak modes, with winds from the south (which occurred during July at northern locations 1 to 2 days earlier than off Leixoes). Assuming a reduction of spawning intensity during northerly winds, the birthday histogram would correspond better to a triggering wind event starting on 03 August (Fig. 3, NW-wind 5 m/s), than to the event scale defined above on base of consistency.

While otherwise the species composition is not unusual for a summer survey, the vertical distributions encountered may partly be a result of the shallow mixed layer and strong temperature gradients (see e.g. RUSSELL 1976, and literature therein).

Considering the coarse vertical resolution of sampling, most vertical distribution patterns agree fairly well with earlier results from the NE-Atlantic boundary current system (e.g. JOHN 1985), but not always with data from shallower and turbulent British waters (RUSSELL 1976). As e.g. corroborated by a much wider vertical distribution of *Sardina pilchardus* larvae in the identical station grid but with a deeper thermocline during autumn 1987 (ANDRES et al. 1992), the vertical distributions described here may also be different from "normal" upwelling seasons.

Besides temperature, some further congruencies between the spatial (horizontal and vertical) distribution of larvae and physical parameters were revealed: anchovy larvae with aged upwelled water (characterized by temperatures >19°C, salinity 35.7 psu and oxygen saturation >100 %), *Buglossidium luteum* larvae with less dense coastal water and *Callionymus* larvae with the intermediate wedge of higher salinities (>35.8 psu).

We regard the coastal temperature and salinity signal plus the time behaviour of the discontinuity layer as evidence for (weak) upwelling. On base of the congruent distribution of all parameters, we assume here that the distribution of 35.7 psu water is broadly representative for the origin and spreading of upwelling water (but as a conservative parameter salinity must have integrated also past events, see below). The upwelling water should thus have originated from some 100 - 175 m depth above the slope, ascended in the bottom-near layer over the shelf and arrived in the surface layer either over midshelf (when the inshore low-density and less wind-exposed river plume appeared to be coupled off from upwelling), or much closer to the coast (in case there was no river plume present). Upwelling water must



have got some 4 - 5°C warmer during the ascent by mixing.

The alternative hypothesis, that upwelling water originated from shallow pycnocline depths only (JORGE DA SILVA, pers. comm.) would conform better with the weak SST-signal, but would fail to explain the salinity signal, the spreading of oxygen depleted waters (the absolute minima were below the values at 300 m above the slope and thus result of local consumption), and the time/depth behaviour of all parameters from mid pycnocline downwards.

Upwelled water displaced again westwards at the surface, where, considering the weak to moderate winds, the oversaturation with oxygen must have been caused by primary production. This water, however, could not have been upwelled during the observed event, as oversaturation was found already from the beginning of the event onwards, instead after the expected time lag of some days. Biological results discussed below suggest, that these waters actually had ages of >10 - <43 days.

Offshore Ekman-drift and the deeper low-salinity layer appeared to be separated by a permanent intermediate (100 - 30 m) layer of elevated salinity and probably reduced cross-shelf motion, separating deeper from surface waters under quiescent conditions, but ending wedge-like off the coast during upwelling.

We presume, that the observed cross-shelf zonations of fish larvae depended on the following interactions between spawning bathymetry, vertical distribution, and hydrography:

The U-shape of anchovy age distribution cross-shelf (Fig. 12) is likely to have been caused by vertically separated, opposite cross-coast dispersal linked with both offshore Ekman-drift (for larvae with preference for surface waters) and the onshore compensation flow (for the deeper stages), as had been shown for *Sardina pilchardus* by JOHN et al. (1980). The bottom-near vertical distribution of cpue for this species (as well as for *Callionymus* larvae) suggests also some onshore transport above the bottom from midshelf to shallow depths.

The shown meridional differences in offshore distribution of surface living anchovy larvae seemed to indicate a coincidence with the time-behaviour of the observed upwelling event, but the time scales actually did fit only partly and to the younger cohorts:

As mentioned, the observed event had a directional consistency of 7 days only, after a variable period of 12 days. A more generous interpretation would yield an event scale of 12 days. Anchovy larvae with an age of 10 - 12 days had modes up to 10 nautical miles offshore of the spawning depths at transects B to D, while for the same age group the spatial difference was almost nil at transect A during the beginning of the event. This dispersal (as well as that of e.g. *Arnoglossus laterna* with a small length range) may thus have been closely related to the observed event.

Contrary to this, anchovy larvae of any size (but not other coastal species) were absent in offshore waters of transects E & F after the event. We had above related the paucity of youngest larvae to an inhibition of spawning during upwelling, but some larvae elder than 10 days should nevertheless have been expected at these southern slope stations.

Anchovy larvae 32 - 43 days old, and dispersed up to 37 nautical miles offshore from the respective zonal spawning bathymetry, must have been dispersed also during the preceding event 06 - 10 July (12 July off Leixoes) and the minor one around 24 July, and were probably born much farther northwards. These larvae were found in water masses showing the characteristics of aged upwelled water. JORGE DA SILVA (pers. comm.) estimated the place of origin to have been some 150 - 300 km to the north, between Viana do Castelo and Cape Finisterre.

As mentioned, for the bottom-near layer from midshelf to the coast some

indication of an onshore transport is indicated for deeper *Callionymus* larvae and respective youngest anchovy, which did not, or less so, extend into the less dense and less wind-exposed coastal waters (the data from soleid larvae also suggest that these waters showed little spreading cross-coast). The overall horizontal distribution of *Callionymus*, however, indicates little cross-shelf net dispersal, as to be anticipated from the prevailing medium-deep vertical distribution of the larvae.

Contrary to our expectations, there is contrasting evidence concerning the onshore advection of deep-living oceanic taxa. Deep-living *Paralepididae* (fairly rare) did not spread at all beyond the shelf edge. Entrainment of eggs, but not of shallow or extended-shallow larvae, by an earlier onshore compensation flow (perhaps about 04 August?) is likely to have caused the occurrence of *Cyclothone* larvae or the individual *Myctophum punctatum* up to the extreme midshelf stations B 3 & B 4.

The inshore limit of the horizontal distribution of *Maurolicus muelleri* is almost identical as found for *Cyclothone*, and for the deep living *M. muelleri* larvae closest inshore at transects B and C a direct relation with the upwelling event seems more likely, though the vertical distribution of cpue of *Maurolicus muelleri* (Fig. 14) along the transects is somewhat ambiguous. It might be reasoned, that there was little volume transport in the Ekman-layer (some 15 m deep), resulting in a much smaller onshore velocity of the vertically wider compensation current. While yolk-sac larvae of *M. muelleri* live at depth, with feeding they show a vertical ascent into the upper layers in time scales of probably few days, but without increasing much in size (JOHN & KLOPPMANN 1989). This ascent could have consequently smeared any indication of onshore transport in Fig. 14, which would have become apparent during stronger upwelling. We consider it likely also, that those drift patterns revealed above would become more pronounced during stronger upwelling, and that larvae of *Buglossidium luteum* would also become subject of Ekman transport.

### Conclusions:

Stable stratification and anomalously high temperatures caused the unusual offshore spawning of anchovy off Northern Portugal in summer 1989. Spawning of anchovy was at maximum during periods with winds from the south. The observed upwelling event was of short duration only and had low intensity, particularly close to the coast. However, additionally signals of preceding upwelling events were evident in the meteorological, hydrographical and biological data.

The cross-shelf zonation and dispersal of fish larvae depended on the interaction of spawning bathymetry, vertical distribution of larvae and the hydrographical conditions in the respective range, not always consistent during the entire planktonic phase before the time of catch.

Surface living larvae of anchovy as well as those of other midshelf species showed dispersal offshore. For young larvae dispersal up to about 10 miles from the spawning grounds was directly related to the observed upwelling event, but for elder larvae up to 43 days old, occurrences up to 37 miles from the respective zonal spawning depths were related also to two events north of the surveyed area during July. Larvae from midshelf origin but with a vertical distribution extending into the thermocline, like e.g. *Trachurus trachurus* or *Cepola rubescens*, showed reduced offshore dispersal. Soleid larvae living in less dense and less wind exposed coastal surface waters appeared to be retained there. Larvae originating from midshelf and with medium-deep (subthermocline) vertical distribution as e.g. *Callionymus*



sp. showed little overall cross-shelf dispersal, though the deepest specimens of the very same group were advected somewhat from midshelf towards the coast.

The inshore boundaries of larvae of several slope or oceanic species were not always as anticipated from their vertical range. Some inshore occurrences of shallow living larvae of e.g. *Cyclothone* were attributed to an earlier entrainment of deeper living eggs. Evidence for an onshore advection of deeper-living larvae of the slope species *Maurolicus muelleri* with the compensation flow is inconclusive, probably because the ontogenetical ascent of feeding larvae occurred in the same or smaller time scale as onshore flow.

It is presumed that under normal summer conditions (with more consistent and stronger upwelling) all discussed dispersal patterns would become more pronounced, and that anchovy would not be a principal component of Portuguese offshore ichthyoplankton.

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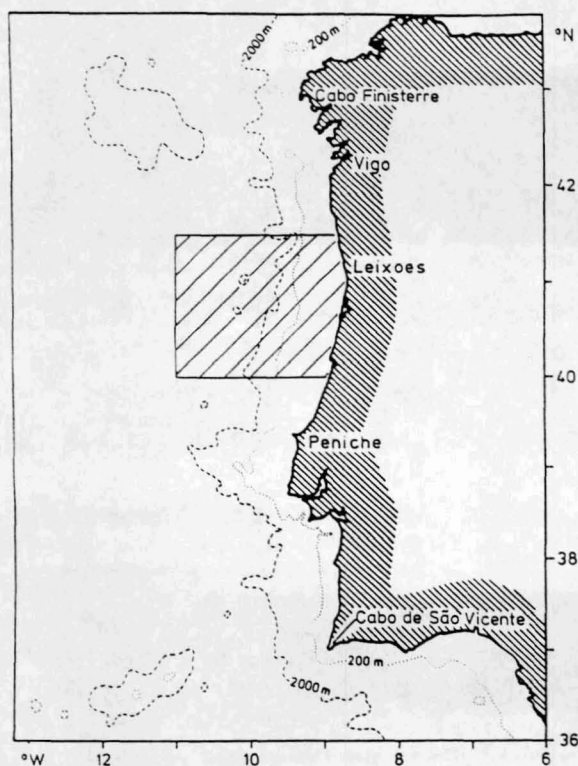


Fig. 1: The survey area off the western Iberian Peninsula and location of reference points mentioned in the text.

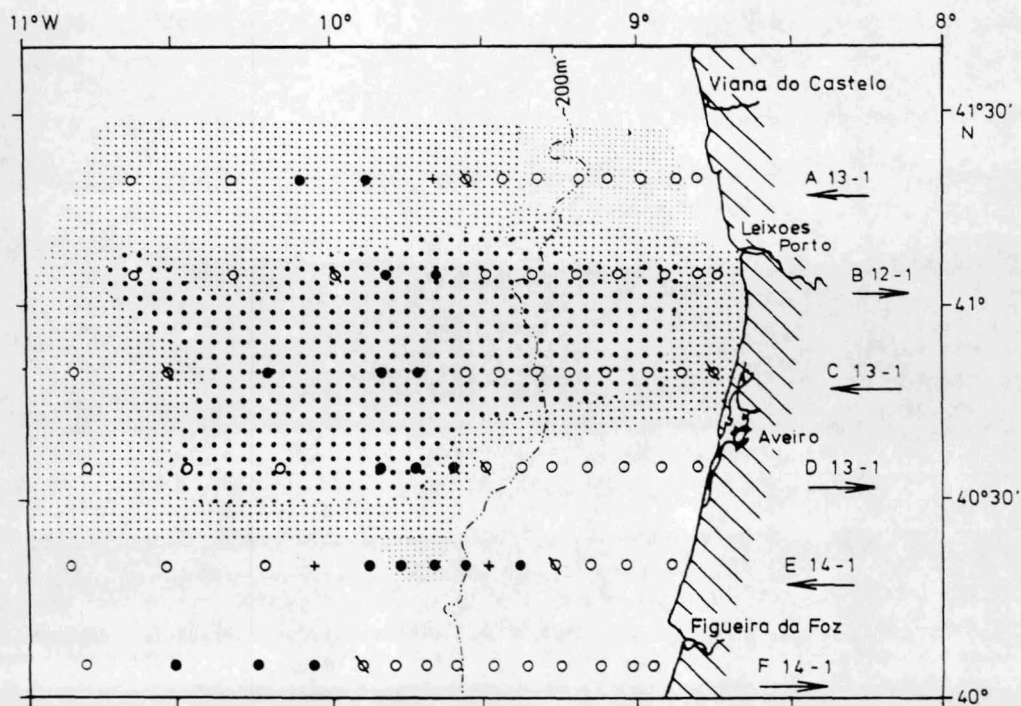


Fig. 2: The grid sampled off Northern Portugal. Letters A to F refer to transects and numerals to standard station numbers ascending from the coast, regardless of the direction (see arrows) of sampling. Crosses represent CTD-casts only. Open circles represent daytime CTD/plankton stations, full circles nighttime stations and crossed circles CTD-casts/twilight plankton tows. Shading depicts upwelling favourable (NW to N) wind directions at stations, different grey shadings represent Beaufort forces 3 (light) to 5 (dark).



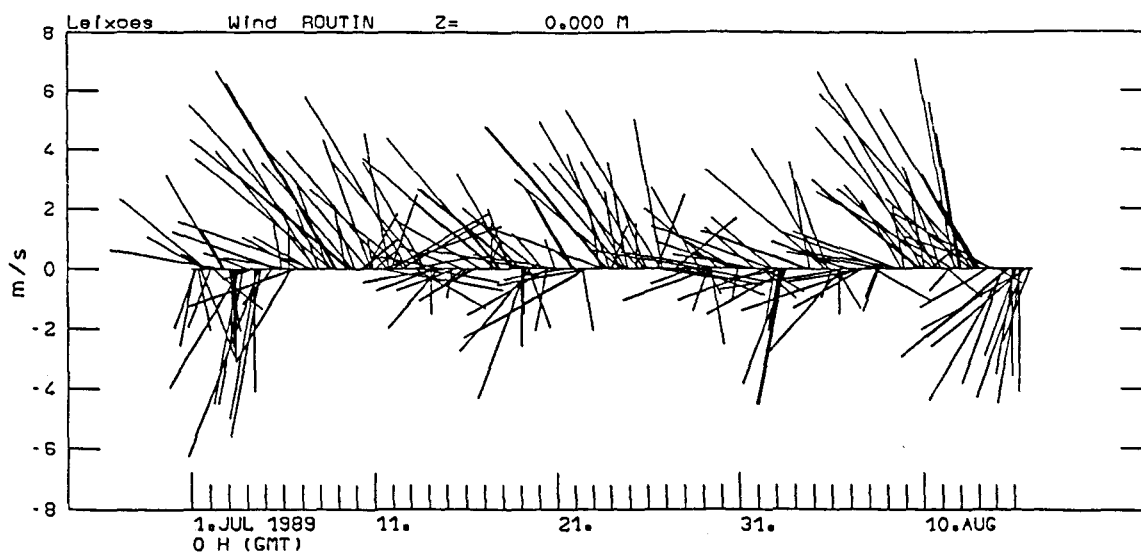


Fig. 3: A wind-vector time-series 01 July - 15 August 1989 from Leixoes. Sticks fly with the wind towards the line of 0 m/s. Positive values thus represent a southward component of windstress.

Table 1: Relative vertical distributions of fish taxa of any abundance or frequency, as based on cumulated catches per unit of effort.

Pattern	Taxon	Stations positive	$\Sigma$ cpue (=100%)	0-30 m %	30-60 m %	60-90 m %	90-120 m %	120-200 m %
	all fish larvae	75	1007.0	58.8	22.2	9.3	4.0	5.7
Shallow	Sparidae	8	8.8	97	0	2	1	0
	<i>E. encrasicolus</i>	40	248.1	86.6	9.9	1.8	1.1	0.6
	<i>A. laterna</i>	34	54.9	80.1	16.4	1.8	0	1.6
	<i>C. rubescens</i>	14	18.5	75.7	22.7	1.6	0	0
	<i>B. luteum</i>	12	25.6	72.7	27.3	0	0	0
	<i>S. pilchardus</i>	15	7.6	70	30	0	0	0
	<i>Cyclothone</i>	17	12.7	68.5	18.1	2.4	0	11.0
Extended-shallow	<i>T. trachurus</i>	17	22.5	52.9	42.7	3.6	0.9	0
	<i>B. glaciale</i>	19	14.2	40.8	45.8	7.7	0	5.6
	<i>M. punctatum</i>	23	14.9	33.6	47.7	12.8	2.7	3.4
	Gobiidae	32	184.8	31.8	48.2	14.8	4.7	0.5
Medium	Triglidae	11	9.7	34	53	10	3	0
	<i>Callionymus</i>	26	136.9	15.1	57.6	20.4	5.7	1.2
Deep	Paralepididae	32	18.6	9.7	10.2	21.0	20.4	38.7
	<i>M. muelleri</i>	41	68.4	6.4	6.4	28.2	15.4	43.6

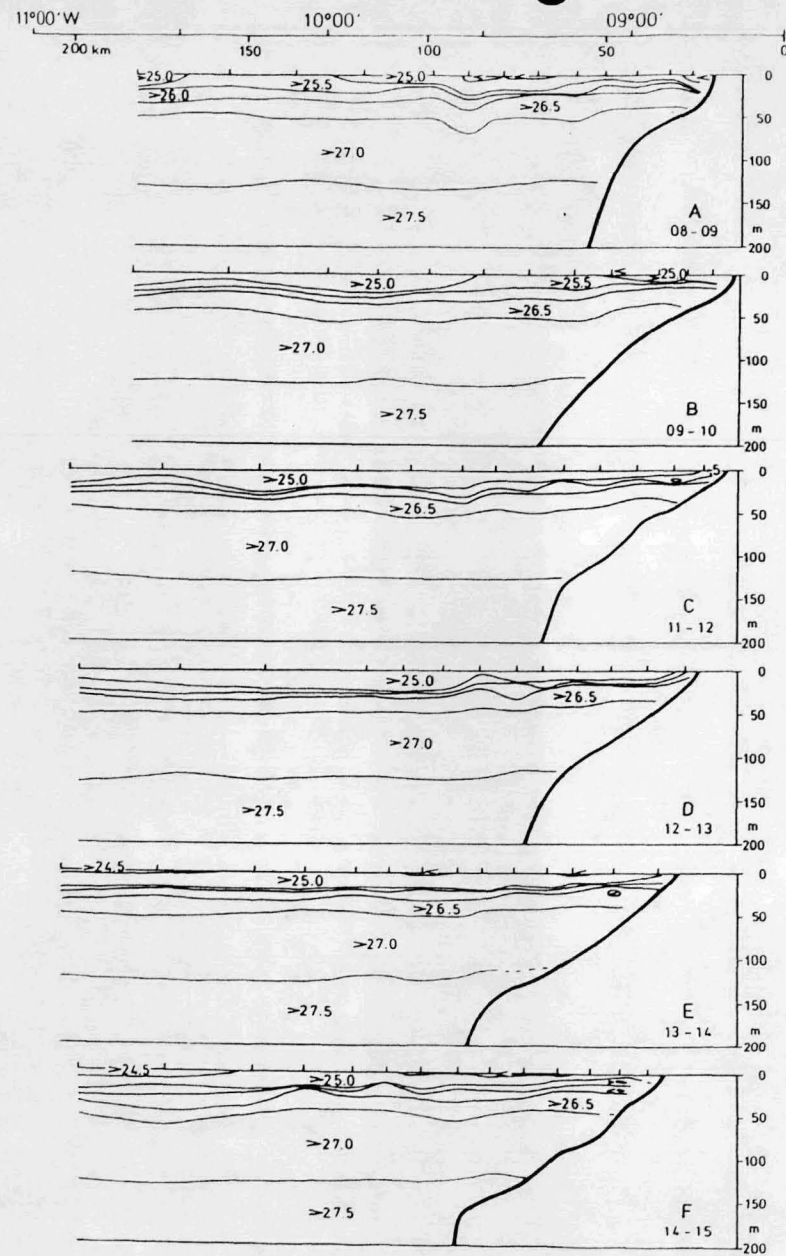


Fig. 4: The vertical structure of in situ density anomaly ( $\text{kg/m}^3$ ) along transects A - F, 08 - 15 August 1989.

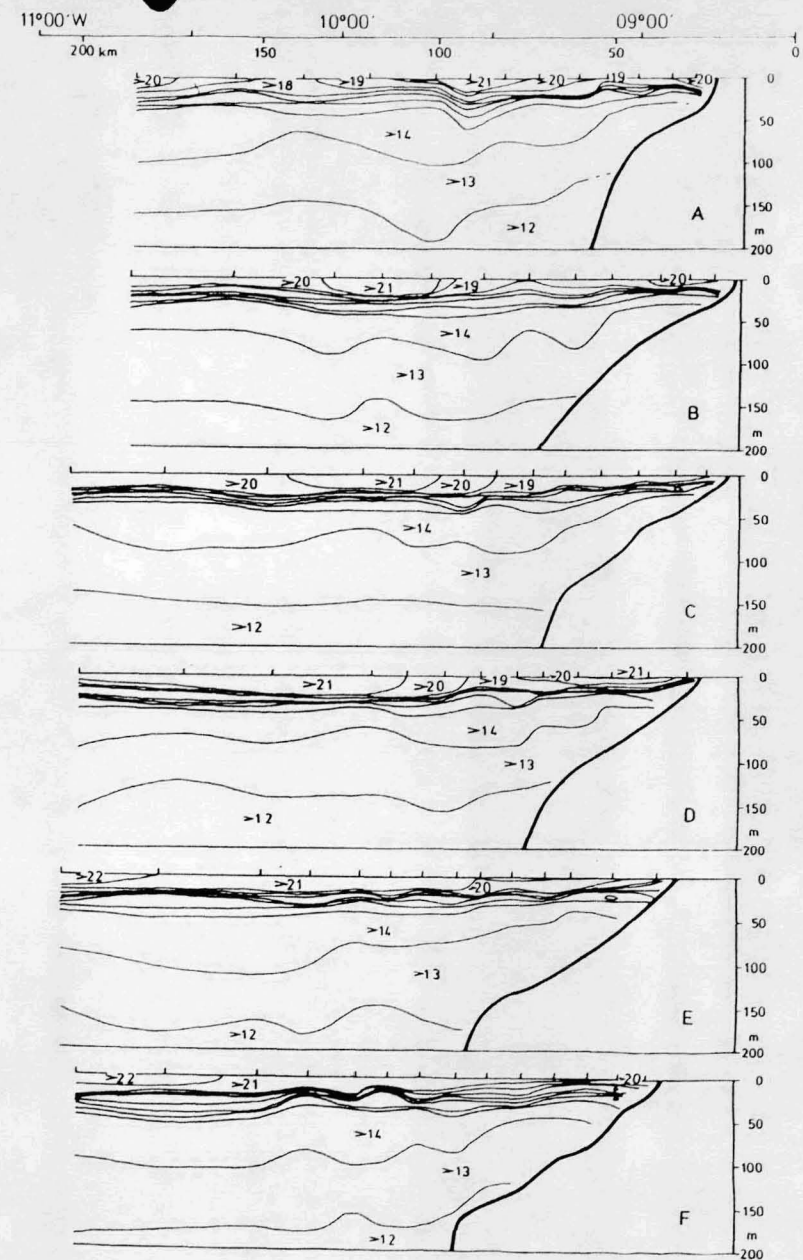


Fig. 5: The vertical distributions of temperature ( $^\circ\text{C}$ , as for Fig. 4).

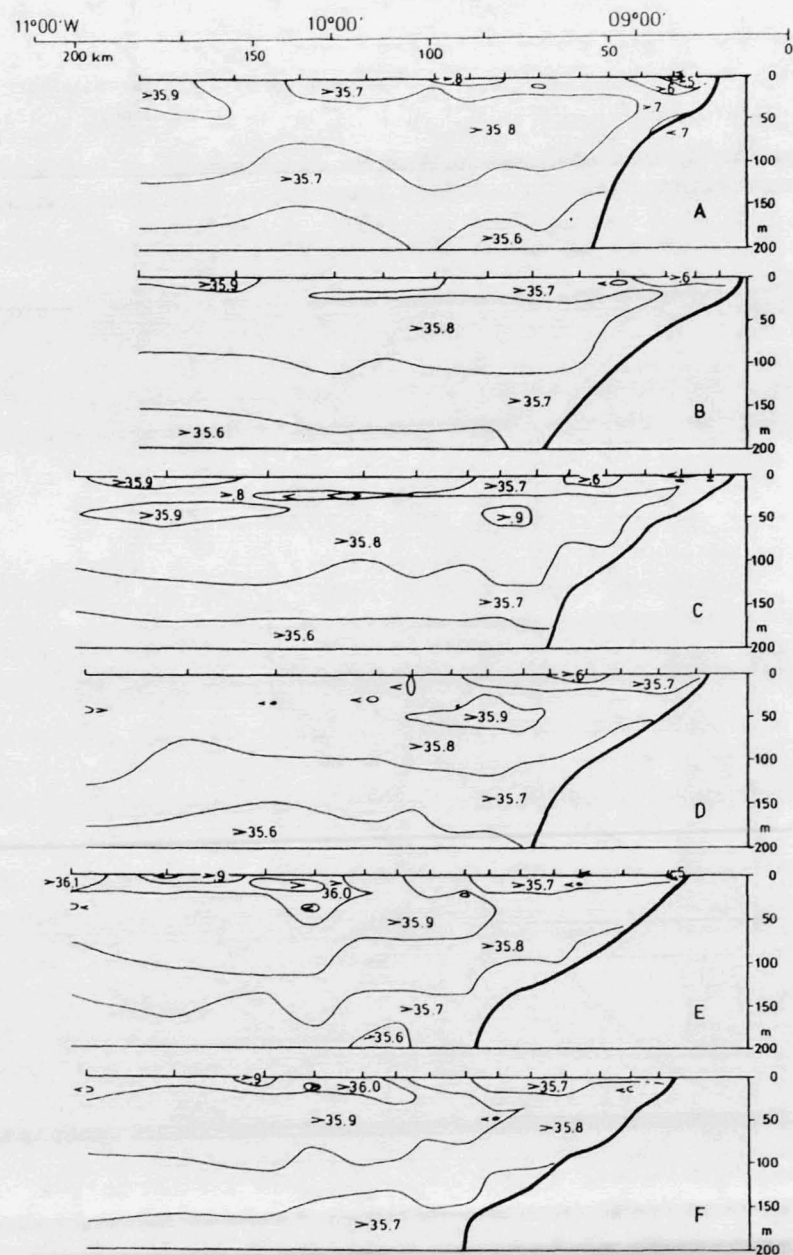


Fig. 6: The vertical distribution of practical salinity (as for Fig. 4).

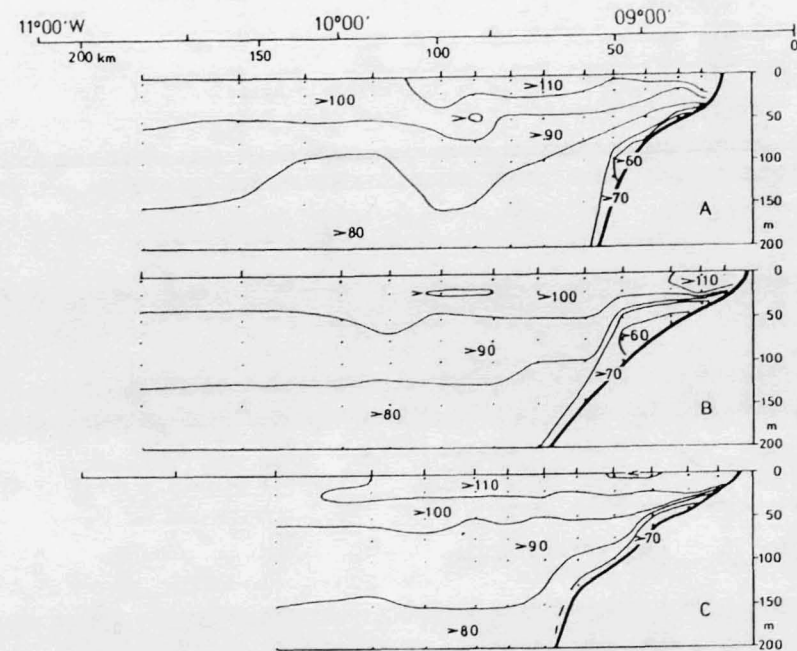


Fig. 7: The vertical distribution of oxygen saturation (%) along transects A to C until failure of the probe.



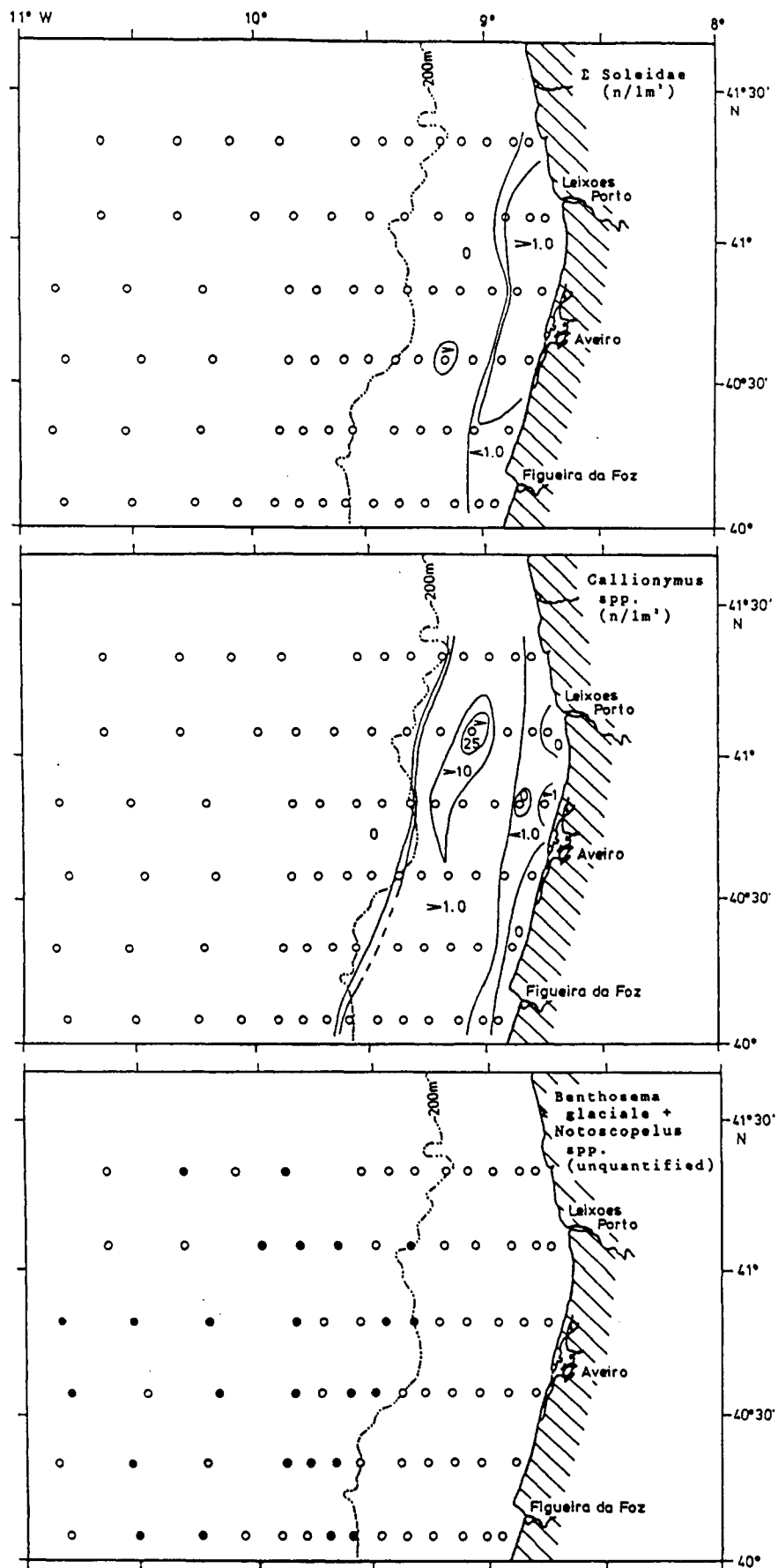


Fig. 8: The cross-shelf zonation of "stationary" taxa.  
 A, top: nearshore, surface-living. B, centre: midshelf, medium-deep. C, bottom: oceanic, extended-shallow vertical distribution.

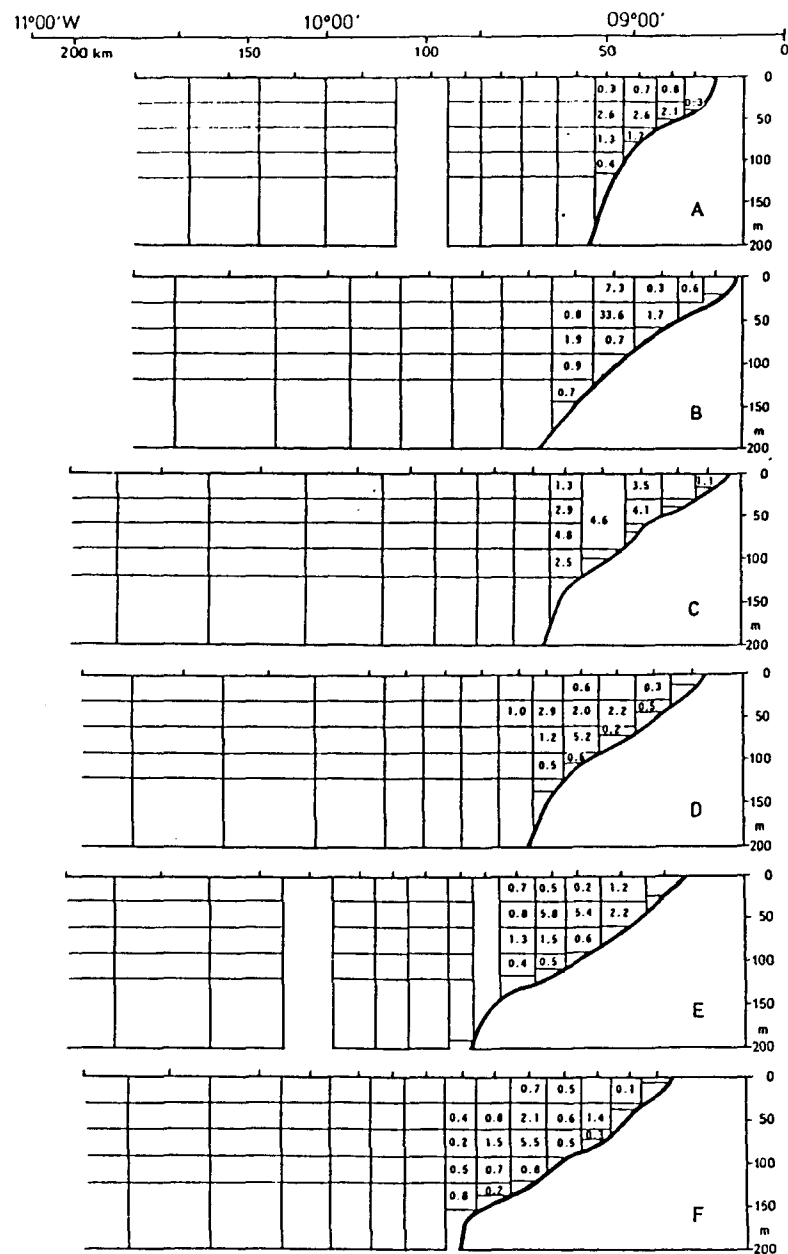


Fig. 9: The vertical distribution of *Callionymus* larvae ( $n/l\ m^2$  for positive steps; zero values are left blank for reasons of clarity).

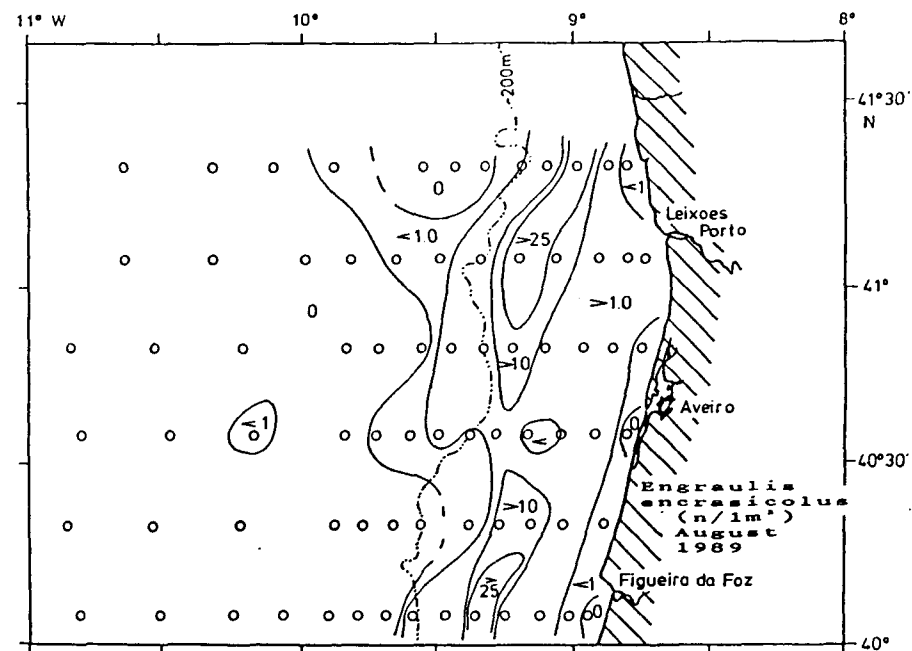


Fig. 10: The horizontal distribution of *Engraulis encrasicolus* larvae.

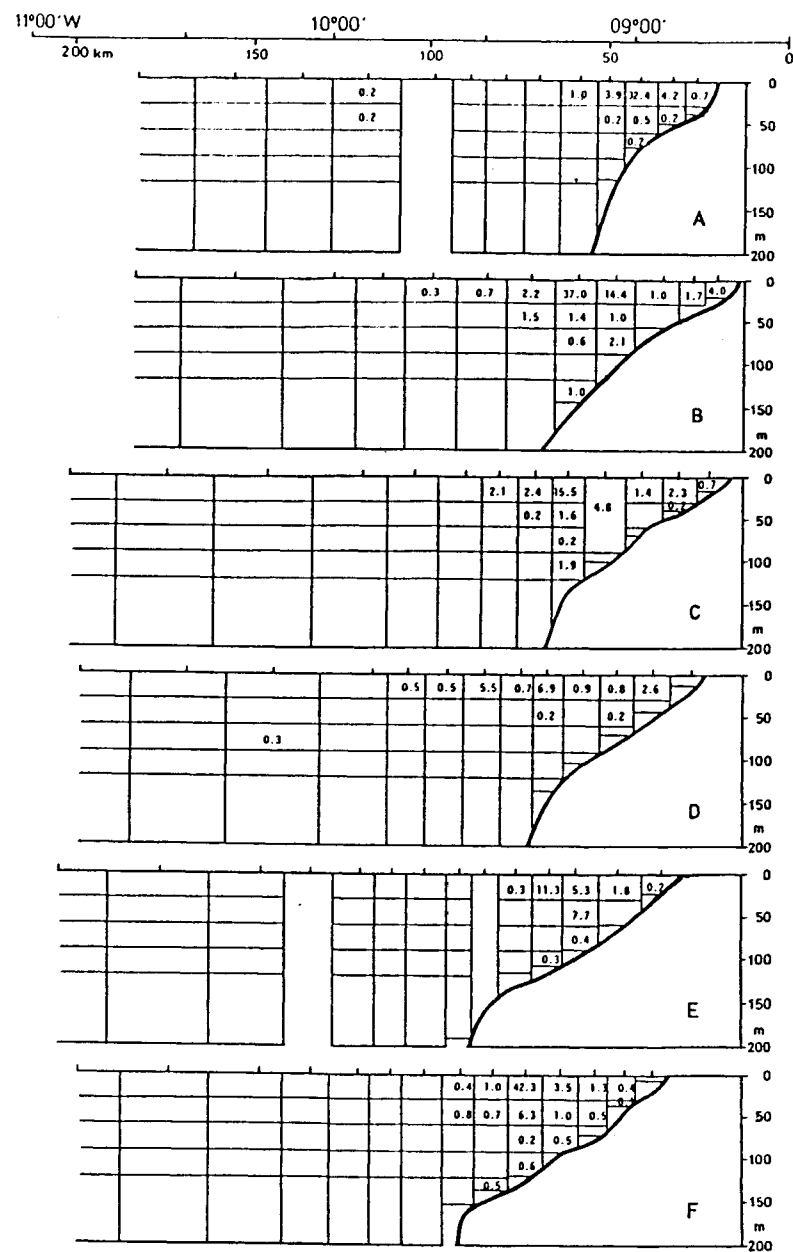


Fig. 11: The vertical distribution of *Engraulis encrasicolus* larvae along the transects (as for Fig. 9).

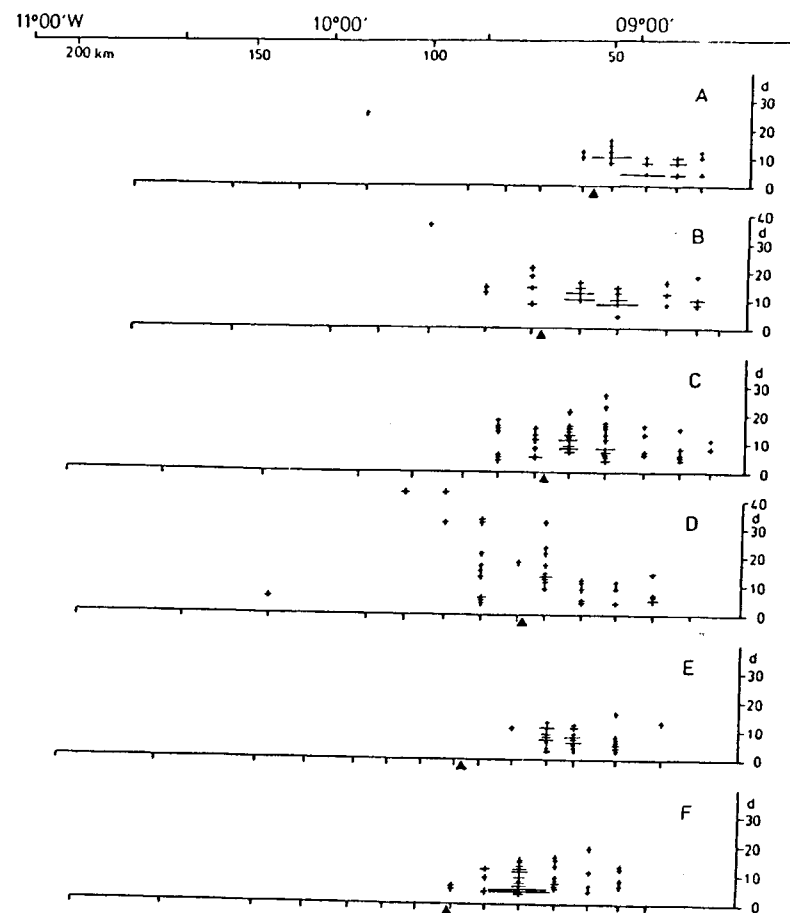


Fig. 12: The cross shelf age-distribution ( $d = \text{days}$ ) of *Engraulis encrasicolus* larvae from the upper 30 m. The length of the horizontal bar in each cross is a relative measure for the number of individuals per age group. The full triangle indicates the position of the 200 m depth contour.



