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A comparative study on the influence of the pycnocline on the vertical distribution of fish larvae and cephalopod paralarvae in three ecologically different areas of the Arabian Sea

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Abstract—Zooplankton sampling took place during cruise 5 Leg 3 of the R.V. *Meteor* (March–June 1987) in three hydrographically and ecologically different areas of the Arabian Sea (Indian Ocean): an upwelling area at the coast of Oman; an oligotroph area in the central Arabian Sea; and a shelf area off the coast of Pakistan. All three areas were expected to have similar ichthyoplankton and cephalopod components and similar light conditions. These are important prerequisites for the present comparative study, which is concerned with the importance of the structure of the water column (physical stability and prey availability), compared with the influence of the light intensity (day/night) on the vertical distribution of species and size classes of fish larvae and cephalopod paralarvae in the subtropical pelagial.

First results show that the vertical structure of the water column, especially the occurrence of a pycnocline and the varying mixed-layer width, either directly or indirectly had important impact on the vertical distribution patterns of both fish larvae and cephalopod paralarvae. In addition, cephalopods were influenced more consistently by the diurnal change of light intensity than fish larvae. Both taxa occurred mainly below the mixed surface layer. However, cephalopod paralarvae preferred shallower depths than fish larvae in all three areas and were closer related to the pycnocline than fish larvae in most cases. In the absence of a significant pycnocline, larvae appeared close to the surface.

INTRODUCTION

THE energy flow through the food chain in the pelagic environment of the oceans is partly a function of the spatial and temporal composition of different size groups of the zooplankton. For a better understanding of structure and function of the pelagic ecosystem, a detailed analysis of the zooplankton biomass distribution is needed.

Fish larvae and cephalopod paralarvae are components of the pelagic food chain. Their chance for survival, a central question in recent fisheries research (see ROTHSCHILD, 1986), depends in part on spatial and temporal match or mismatch with larval food, competitors and predators (CUSHING, 1975; LASKER, 1975; MAY, 1974; HUNTER, 1976; NELLEN, 1986). Climatic and hydrographic factors play a major role in governing these regimes

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(ROTHSCHILD and OSBORN, 1988), and future investigations must strive to define the location of larvae in the water column in relation to abiotic and biotic factors.

A number of factors governing the vertical distribution of fish larvae have been studied in the past, but there is a lack of information on the interaction of these factors and on their relative importance. Answers to these questions are a prerequisite for successful modelling of larval recruitment processes.

Fish larvae are known for their complex behaviour. Their vertical distribution and migration patterns are species specific (see e.g. AHLSTROM, 1959; LOEB, 1979, 1980; KENDALL and NAPLIN, 1981; SOGARD *et al.*, 1987; RÖPKE, 1989). They are also dependent on larval size and stage (see e.g. NELLEN and HEMPEL, 1970; LOEB, 1979; COOMBS *et al.*, 1983; FORTIER and LEGGETT, 1983, 1984; HEATH *et al.*, 1988; FORTIER and HARRIS, 1989; FRANK and CARSCADDEN, 1989). The light intensity (day/night rhythm) is the major factor triggering these behaviours (in the laboratory; WOODHEAD and WOODHEAD, 1955; BLAXTER, 1973) and seems to be responsible for much of the observed variability in those patterns. Thermoclines were shown to influence fish larval distribution and migration patterns (see e.g. AHLSTROM, 1959; LASKER, 1975; SOUTHWARD and BARRY, 1980; KENDALL and NAPLIN, 1981; SAMEOTO, 1982; SOUTHWARD and BARRETT, 1983). However, it is not clear, whether the temperature (or turbulence gradient) influences the larvae directly or whether larval prey associated with the pycnocline (LASKER, 1975) acts as the major attraction for the larvae. Studies contributed during the last decade indicate that larvae of epipelagic fish species can adopt their distribution to peak abundances of prey at a small spatial scale of several m (FORTIER and LEGGETT, 1983, 1984; DE LAFONTAINE and GASCON, 1989; FORTIER and HARRIS, 1989).

To test the importance of water column structure (physical stability and food availability) and light intensity (day/night) on the vertical distribution of different species and size groups of fish larvae and cephalopod paralarvae in the subtropical pelagial, as well as for the variability of the distribution, a comparative study was carried out in the Arabian Sea (Indian Ocean). A similar sampling program was undertaken in three hydrographically and ecologically different areas containing the same species and under similar light conditions. This paper presents first results of the study, dealing with the influence of the pycnocline on the vertical distribution of fish larvae and cephalopod paralarvae.

MATERIALS AND METHODS

Three areas, named "Bioboxes" (Bb), were sampled in the northern Arabian Sea (Indian Ocean) during *Meteor* cruise 5 Leg 3 (18 March–9 June, 1987; Fig. 1) under constant sunny (Fig. 2) and calm weather conditions. Each Biobox consisted of a grid with 5×5 stations and had side lengths of 100×50 nautical miles and was sampled twice in order to assess temporal, as well as spatial variability. Biobox 1 (coast of Oman; centre at 21°20′N, 59°50′E), sampled 31 March–2 April (Grid 1) and 7–10 April (Grid 2) represents a potential upwelling area with a mixed water column, which should provide high food densities for the larvae throughout a wide range of the water column. Biobox 2 (central oceanic area; centre at 18°45′N, 65°05′E), sampled 30 April–3 May (Grid 3) and 8–10 May (Grid 4), was expected to have a stable stratified water column with a sharp pycnocline and low production. Relatively good nutritional conditions for larvae might be expected for the mixed surface layer. Biobox 3 (shelf off Pakistan; centre at 23°20′N, 66°35′E) was sampled 23–26 May (Grid 5) and 2–4 June (Grid 6), and was anticipated as a typical coastal

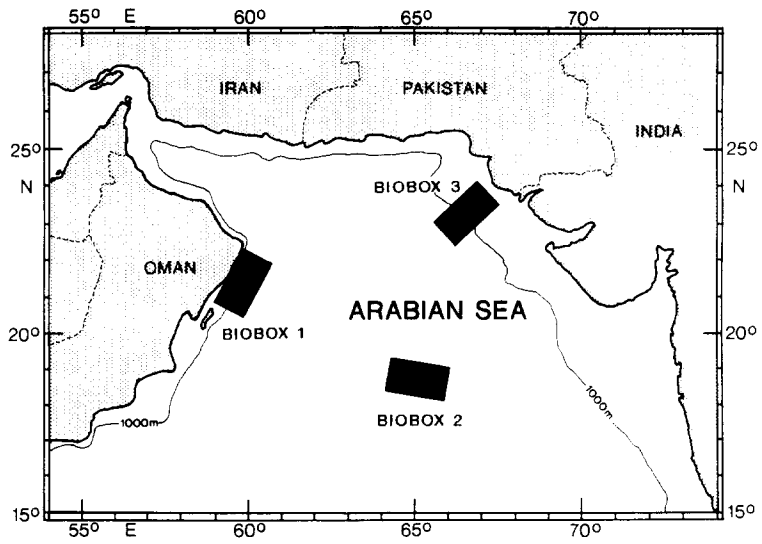

Fig. 1. Area of research during *Meteor* cruise 5 Leg 3 (18 March–4 June 1987) into the Indian Ocean (Arabian Sea). Position of the three Bioboxes.

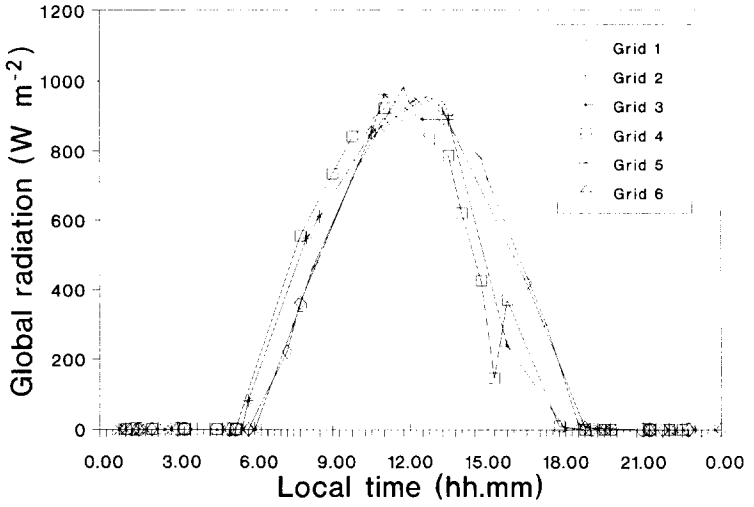

Fig. 2. Global radiation in relation to time of the day during six grid sampling sequences in the three Bioboxes.

shelf area with fresh water influence from the Indus River and a weaker stratification of the water column with enriched nutritional conditions. It was thus expected to be intermediate between Bioboxes 1 and 2.

The plankton samples were taken by a modified MOCNESS-1 (Multiple Opening/ Closing Net and Environmental Sensing System; WIEBE *et al.*, 1985; NELLEN *et al.*, 1988), which has a box-shaped frame designed for improved stability during sampling. The nets had a length of 6 m and a mesh aperture size of 335 μm. The towing speed was 2 knots. The volume of water filtered was determined by an electric flowmeter mounted in the frame

Table 1. *Number of analyzed hauls and samples taken during six grid sampling sequences in the three Bioboxes, verified for day/night and mean depth interval*

Area	**Biobox 1**		**Biobox 2**		**Biobox 3**		
Sampling sequence	Grid 1 N	Grid 2 N	Grid 3 N	Grid 4 N	Grid 5 N	Grid 6 N	Sum N
Hauls (positive)	25	23	21	24	22	17	132
day/night	14/11	8/15	9/12	13/11	14/8	7/10	65/67
Samples (positive)	175	158	156	179	162	117	947
day/night	95/80	61/97	67/89	88/91	101/61	54/63	466/481
Mean depth interval (m)							
0–10	11/10	6/13	7/9	8/9	12/5	6/11	50/57
11–20	12/11	7/13	3/9	11/11	8/6	7/6	48/56
21–30	13/11	7/15	7/11	12/9	14/6	7/8	60/60
31–40	12/11	8/13	8/8	13/11	13/7	8/10	62/60
41–50	13/10	8/12	9/11	12/11	13/7	6/9	61/60
51–60	0/0	1/0	7/5	6/8	12/8	5/4	31/25
61–80	12/9	8/11	9/14	9/9	13/8	7/8	58/59
81–100	11/9	8/10	9/10	4/11	8/9	4/2	44/51
101–150	11/9	8/10	8/12	13/12	8/5	4/5	52/53

opening. Discrete sampling of eight depth strata took place during an oblique haul from 150 m depth up to the surface. At water depths less than 150 m, sampling began 5 m above the sea bed. The sampling intervals were 150–100 m, 100–75 m, 75–60 m, 60–50 m, 50–40 m, 40–30 m, 30–20(15) m and 20(15)–0 m. Since sampling of these intervals could not be performed accurately in each case, the mean sampling depth per interval was used for further analysis. Table 1 shows the location and timing of the hauls.

Samples were stored in a buffered 4% formaldehyde/fresh water solution at 15°C for up to 2 years before being analyzed. The plankton displacement volume was measured before all fish and cephalopod larvae were removed, identified and counted. Afterwards the dry weight of the planktons sample were determined after 66 h of drying at 60°C. Table 2 gives the total sorting data by time of the day for each grid. Catch data for cephalopod paralarvae and fish larvae by mean depth interval are listed in Table 3.

For computation of the standing stock (relative apparent abundance), the different depth strata were integrated. Variation in the vertical distribution of the net biomass and in the larvae was evaluated by the depth of the centre of mass (Z_{cm})

$$Z_{cm} = \sum_{i=1}^{\leq 8} P_i * Z_i \tag{1}$$

and

$$P_i = C_i * H_i \Big/ \sum_{i=1}^{\leq 8} (C_i * H_i) \tag{2}$$

where P_i is the proportion of the stock of biomass or larvae in the ith depth stratum and Z_i is the mean sampling depth of the ith depth stratum. C_i is the concentration of biomass or larvae in the ith depth stratum and H_i is the width of the ith depth stratum.

Table 2. Raw data on the total filtered volume of water, plankton displacement volume, and catches of cephalopod paralarvae and fish larvae by time of the day from six grid sampling sequences in the three Bioboxes

Area	**Biobox 1**		**Biobox 2**		**Biobox 3**		
Sampling sequence	Grid 1	Grid 2	Grid 3	Grid 4	Grid 5	Grid 6	Sum
Filtered Volume (m^3)	58,337	49,920	56,799	69,937	58,690	38,424	332,107
day/night	32,575/25,762	19,601/30,319	22,613/34,183	39,626/30,311	37,520/21,170	17,599/20,825	169,537/162,570
Plankton displacement volume (ml)	8,561	5,122	2,694	3,399	3,085	1,634	24,495
day/night	4,380/4,181	1,280/3,842	1,041/1,653	1,771/1,628	2,046/1,039	658/976	11,176/13,319
Cephalopod paralarvae N	1,599	426	931	890	1,515	567	5,928
day/night	731/868	99/327	282/649	422/468	1,191/324	231/336	2,956/2,972
Fish larvae N	17,255	12,799	4,884	5,701	27,636	17,114	85,389
day/night	7,539/9,716	1,972/10,827	855/4,029	1,652/4,049	17,478/10,158	6,835/10,279	36,331/49,058

Table 3. Raw data on catches of cephalopod paralarve and fish larvae by mean depth interval from six sampled grids in the three Bioboxes

Area	Biobox 1		Biobox 2		Biobox 3		
Sampling sequence	Grid 1 N	Grid 2 N	Grid 3 N	Grid 4 N	Grid 5 N	Grid 6 N	Sum N
(a) Cephalopods	1,599	426	931	890	1,515	567	5,928
(b) Fish larvae	17,255	12,799	4,884	5,701	27,636	17,114	85,389
Mean depth interval (m)							
(a) 0–10	106	69	76	42	60	31	384
(b)	580	1,257	25	43	693	382	2,980
(a) 11–20	253	104	76	97	101	47	678
(b)	2,085	1,861	96	98	1,591	531	6,262
(a) 21–30	374	109	182	129	150	87	1,031
(b)	3,497	2,649	137	123	3,486	1,171	11,063
(a) 31–40	444	70	167	234	267	153	1,335
(b)	4,345	2,978	261	261	5,378	3,120	16,343
(a) 41–50	193	36	160	151	349	104	993
(b)	2,526	1,581	473	391	5,447	4,557	14,975
(a) 51–60	0	0	113	61	355	49	578
(b)	0	3	367	843	5,484	1,881	8,578
(a) 61–80	159	22	95	84	198	87	645
(b)	2,548	1,262	1,290	1,073	4,283	4,584	15,040
(a) 81–100	51	11	39	61	26	6	194
(b)	1,399	881	1,352	1,086	1,055	540	6,313
(a) 101–150	19	5	23	31	9	3	90
(b)	275	327	883	1,783	219	348	3,835

Hydrographical data from all stations were taken by a CTD-system (Multisonde, ME, Kiel) down to a depth of 150 m. The resulting temperature, salinity and density profiles were compiled by RIBBE (1988, unpublished data report). Data on the width of the mixed-layer, the width of the pycnocline (highest grade of density change), and the temperature gradient of the water column down to 150 m depth were taken from these profiles.

RESULTS

Hydrographic stratification of the water column

A schematic overview of the mean temperature profiles during the six sampling sequences is given in Fig. 3. The corresponding mean values (S.D.) of physical stratification parameters are listed in Table 4. The water column of Bb 1 (coast of Oman) was almost unstratified, with an average mixed-layer width of 23–25 m. The pycnocline was very weak and therefore not discerned. Due to lateral advection of a more oceanic water mass (higher salinity and temperature), vertical stratification increased during the second grid of Bb 1. The mixed-layer width in Bb 1 was relatively heterogenous.

The grids in Bb 2 (central oceanic) and 3 (shelf off Pakistan) were very similar and

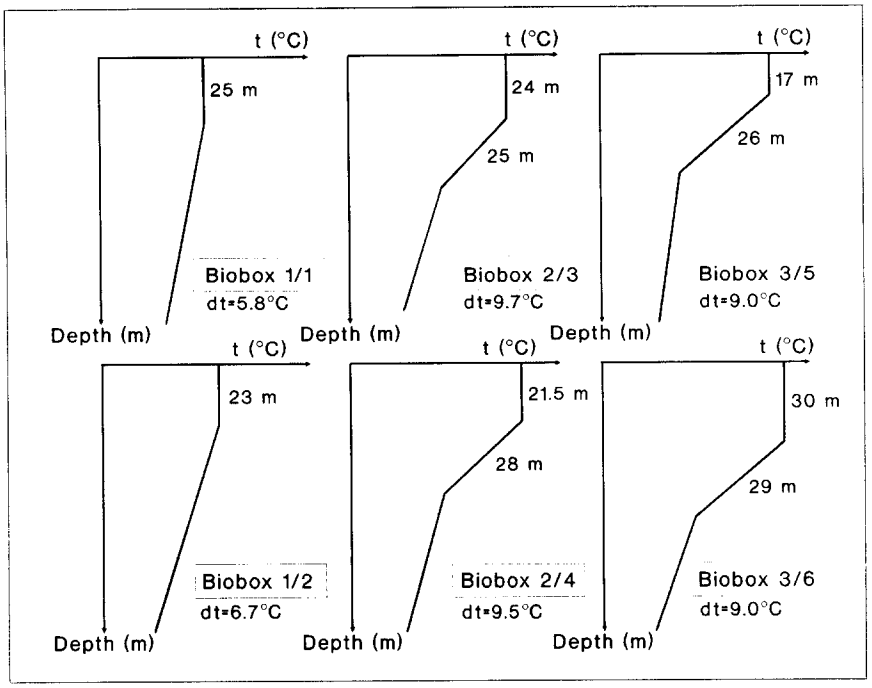

Fig. 3. Schematic overview of the mean temperature profiles during the six sampling sequences in the three Bioboxes. Values for the mixed-layer width, thermocline width and temperature gradient down to 150 m are indicated.

homogeneous in terms of their vertical structure, all being typically oceanic with a pronounced pycnocline, which had an average space width of 25–28 m in Bb 2 and 26–29 m in Bb 3. In Bb 2 the pycnocline began at about 22–24 m depth on average and was very sharp; in Bb 3 it began at 17 m depth during Grid 5 and at 30 m during Grid 6. No coastal low salinity influence was observed at the shelf stations in Bb 3. The surface temperature increased gradually from Bb 1 (25.4–25.8°C) to Bb 3 (29.0–29.4°C), but the highest vertical temperature gradient was found in the oceanic Bb 2, indicating the highest stability of the water body in this area.

Standing stock of net-biomass, cephalopod paralarvae and fish larvae

Bb 1 had the highest values of net-biomass (plankton dry weight) standing stock. The mean value was 47.0 g 100 m^{-2} during the first sampling, and statistically significantly (*U*-Test, $p < 0.05$) lower, 38.7 g 100 m^{-2}, during the second (Table 5). The samples, especially those from the first sampling in Bb 1, contained large numbers of siphonophores and salps, giving relatively high and variable values for the biomass from plankton displacement volumes. The standing stock of net-biomass in Bb 2 and 3 averaged 27.3 and 18.4 g 100 m^{-2}, respectively, and the variability was lower than in Bb 1. Thus, the stock of biomass was higher in the central oceanic area (Bb 2) than in the shelf area off Pakistan (Bb 3).

Pronounced changes occurred in the cephalopod paralarval stock between the two

Table 4. *Mean values (S.D.) on physical stratification parameters during six sampling sequences in the three Bioboxes. "+" signs indicate statistically significant differences* (t-*Test*, $p < 0.05$)

Physical parameter in the water column	Biobox 1 Grid 1 $\bar{x}(SD)$	Biobox 1 Grid 2 $\bar{x}(SD)$	Signif. (5%)	Biobox 2 Grid 3 $\bar{x}(SD)$	Biobox 2 Grid 4 $\bar{x}(SD)$	Signif. (5%)	Biobox 3 Grid 5 $\bar{x}(SD)$	Biobox 3 Grid 6 $\bar{x}(SD)$	Signif. (5%)
Mixed-layer width (m)	24.8 (11.1)	22.9 (10.1)	–	24.1 (6.1)	21.5 (7.4)	–	17.2 (3.4)	29.8 (5.2)	+
Pycnocline width (m)	0	0	–	24.8 (4.7)	27.8 (7.2)	–	26.4 (10.9)	28.9 (7.0)	–
Temperature gradient (°C) (surface–150 m depth)	5.8 (0.6)	6.7 (0.4)	+	9.7 (0.4)	9.5 (0.7)	–	9.0 (0.7)	9.0 (0.5)	–
Surface temperature (°C)	25.4 (0.3)	25.8 (0.2)	+	28.6 (0.1)	28.8 (0.3)	–	29.0 (0.2)	29.4 (0.2)	+

t-Test ($p < 0.05$)

Table 5. Mean values on the standing stocks of net-biomass (dry weight), cephalopod paralarvae, and fish larvae for the six sampled grids. "+" signs indicate statistically significant differences [U-*Test* (*pairs*, $p < 0.05$)] *between night and day sampling, respectively between the two grids of each Biobox*

Area	**Biobox 1**				**Biobox 1**					
Sampling sequence	Grid 1		signif.		Grid 2		signif.		signif.	change
day/night/sum	day	night	(5%)	sum	day	night	(5%)	sum	(5%)	%
Biomass dry weight ($g/100m^{-2}$)	44.3 (15.5)	49.0 (24.7)	–	47.0 (16.4)	37.6 (13.3)	38.7 (12.6)	–	38.7 (12.3)	+	−18
Cephalopods (n/m^{-2})	2.3 (3.3)	2.0 (3.8)	–	2.2 (3.3)	0.6 (0.9)	0.9 (1.2)	–	0.8 (0.9)	+	−64
Fish larvae (n/m^{-2})	24.7 (15.7)	48.5 (28.4)	+	32.1 (29.9)	14.9 (15.1)	32.8 (51.7)	+	23.8 (33.9)	–	−26
Area	**Biobox 2**				**Biobox 2**					
Sampling sequence	Grid 3		signif.		Grid 4		signif.		signif.	change
day/night/sum	day	night	(5%)	sum	day	night	(5%)	sum	(5%)	%
Biomass dry weight ($g\ 100m^{-2}$)	25.3 (2.9)	27.6 (8.1)	–	26.8 (6.8)	24.0 (12.8)	28.0 (6.8)	–	27.8 (12.5)	–	+4
Cephalopods ($n\ m^{-2}$)	1.3 (1.1)	1.8 (1.4)	–	1.8 (1.4)	1.5 (0.8)	1.9 (1.5)	–	1.6 (1.0)	–	−11
Fish larvae ($n\ m^{-2}$)	5.0 (3.0)	14.5 (12.7)	+	9.6 (10.1)	4.3 (4.1)	18.2 (11.0)	+	9.5 (13.9)	–	−1
Area	**Biobox 3**				**Biobox 3**					
Sampling sequence	Grid 5		signif.		Grid 6		signif.		signif.	change
day/night/sum	day	night	(5%)	sum	day	night	(5%)	sum	(5%)	%
Biomass dry weight ($g\ 100\ m^{-2}$)	20.6 (6.1)	19.7 (8.1)	–	20.3 (7.2)	16.5 (7.8)	16.0 (5.0)	–	16.5 (4.9)	+	−19
Cephalopods ($n\ m^{-2}$)	1.2 (4.2)	1.1 (3.2)	–	1.2 (4.2)	1.4 (0.8)	1.2 (1.5)	–	1.4 (1.1)	–	+17
Fish larvae ($n\ m^{-2}$)	38.4 (50.6)	59.7 (15.3)	–	54.8 (42.6)	32.0 (40.0)	34.3 (48.8)	–	33.5 (42.7)	–	−39

Median (Interquartile-range)
***U*-Test (pairs, $p < 0.05$)**

station grids in Bb 1 (coast of Oman), the average standing stock declining from 2.2 to 0.8 n m^{-2} (Table 5). An average value of 1.7 n m^{-2} was derived for Bb 2 with relatively low variability between stations. On the shelf off Pakistan (Bb 3) the cephalopod standing stock was about 1.3 n m^{-2}. Stations with biggest values were those at the edge of the continental shelf in Bb 1 and 3. The enoploteuthid species *Abralia marisarabica* and *Abraliopsis lineata* were dominant in these both Bioboxes, while *Sthenoteuthis oualaniensis* (Ommastrephidae) and *Liocranchia reinhardti* (Cranchiidae) were most abundant in the central Bb 2.

The largest standing stock of fish larvae was found on the shelf off Pakistan (Bb 3), with an average of 44.2 n m^{-2} for both grids (Table 5). In the oceanic area (Bb 2), the mean value was only 9.6 n m^{-2}. In Bb 1 (coast of Oman), the average was 32.1 n m^{-2} during the first sampling, and 23.8 n m^{-2} during the second. The most abundant families were the Myctophidae (*Benthosema pterotum*, *Hygophum proximum*, *Diaphus arabicus*) and the Photichthyidae (*Vinciguerria nimbaria*).

There was no systematic differences between day and night in the standing stocks of net biomass and cephalopod paralarvae (Table 5). Fish larvae were significantly (*U*-Test, $p<0.05$) more abundant at night, probably due to a higher grade of net avoidance during daylight. Extreme fluctuations were observed in the central oceanic area (Bb 2). As a result, differences in sampling effort between day and night do not allow a simple comparison of the different grids in the case of fish larvae. Therefore both grids of each Biobox were combined for analysis of the vertical distribution. Each Biobox contained similar numbers of day and night hauls (Table 1).

Vertical distribution of net-biomass, cephalopod paralarvae and fish larvae

In Bb 1 (coast of Oman) the highest median concentrations of net-biomass (0.4–0.8 g 100 m^{-3}) were found in the upper 50 m of the water column during both sampling sequences. Higher values and higher variability during the first experiment were correlated with high concentrations of gelatinous zooplankton (siphonophores and salps), which were less abundant during the second sampling of the grid. Very low plankton concentrations were observed below 50 m during both sample sequences in Bb 1 (0.1–0.3 g 100 m^{-3}).

The biomass in Bb 2 was relatively low and very homogenous between stations. The plankton consisted mostly of copepods and ostracods. The median concentration peak (0.3–0.4 g 100 m^{-3}) was found between 30 and 50 m water depth. The gradient over the whole water column down to 150 m depth was low. Extremely low concentrations (<0.2 g 100 m^{-3}) were found between 0–30 m and 75–150 m depth. Similar results were gained in Bb 3, where copepods and chaetognaths were dominant. Again there was a peak (0.3–0.4 g 100 m^{-3}) between 30 and 50 m depth. The distribution pattern was similar to Bb 2, but had a stronger gradient between the surface and the bottom, where values were <0.1 g 100 m^{-3}.

Assessment of the vertical distribution patterns of cephalopod paralarvae is difficult because of their low abundance. Highest median concentrations (4–8 n 100 m^{-3}) were found between 20 and 50 m depth. Densities in the surface layers were low (<2 n 100 m^{-3}). Very few cephalopod paralarvae were caught below a depth of 80 m. The low numbers caught during the second sampling sequence of the grid in Bb 1 were more evenly distributed than those of the first.

The vertical distribution patterns of fish larvae showed distinct differences between the Bioboxes. In Bb 1 (coast of Oman), fish larvae had a median concentration peak (50–100 n 100 m^{-3}) between 30 and 40 m depth. Very low concentrations (<20 n 100 m^{-3}) were found in the surface layer and below 80 m. Few larvae were caught below 100 m. In the open ocean (Bb 2) the concentration maximum (20 n 100 m^{-3}) lay between 50 and 100 m depth. Even between 100 and 150 m relatively large numbers (10 n 100 m^{-3}) of fish larvae were caught. Very few larvae (<3 n 100 m^{-3}) were found at the surface (0–30 m). Concentrations computed from night hauls were 2–3 times greater than those from day hauls in both areas, suggesting net avoidance by fish larvae in Bb 1 and 2. However, the influence of this error on the vertical distribution pattern was only quantitative, since there was evidence in the data for a downward directed vertical movement of fish larvae at night, which cannot be produced by a daylight avoidance in the surface layers normally.

Bb 3 (coast off Pakistan) differed from Bb 1 and 2 by a broader depth-distribution pattern of fish larvae. Median concentrations (70–90 n 100 m^{-3}) were consistently high between 30 and 60 m depth. Low values were found at the surface between 0 and 20 m (<30 n 100 m^{-3}) and below 80 m depth (0–10 n 100 m^{-3}). Larvae caught in this area were relatively small. Differential catches between day and night hauls were not found, but there was some evidence for migration towards the surface at night.

Centre of mass of net-biomass, cephalopod paralarvae and fish larvae

The centres of mass (Z_{cm}) of the three groups are shown for each haul in relation to the mixed-layer and the pycnocline in the Figs 4 (net biomass), 5 (cephalopod paralarvae) and 6 (fish larvae). The arithmetic means of the Z_{cm} are listed and shown comparatively in Fig. 7.

The Z_{cm} of the net-biomass generally lay between 40 and 60 m depth in all Bioboxes (Fig. 4). The mixed-layer was, with the exception of one station, totally avoided. The mean Z_{cm} made a 5–10 m upward shift in the water column during the night (Fig. 7). The highest variability of the Z_{cm} was found at Bb 1 (coast of Oman). At stations with narrow, mixed-layers, the Z_{cm} of the net biomass was closer to the surface than at stations with wider mixed-layers. In Bb 3, most Z_{cm} were a few metres below the pycnocline during the day, but they were inside the pycnocline during night sampling. The observed high variability seems to coincide with the variability of the pycnocline width. A very homogenous picture derived from Bb 2 (central oceanic). Most Z_{cm} lay closely related below the pycnocline, ascending a few m during the night. The pycnocline seems to be avoided in this area.

In the case of cephalopod paralarvae (Fig. 5), most Z_{cm} were found between 20 and 50 m depth (30–50 m depth on average), i.e. below the mixed-layer and inside or shortly below the pycnocline. The mean Z_{cm} showed a upward shift during night of about 10 m in all Bioboxes (Fig. 7). This observation coincides with a general upward migration into the pycnocline during night in Bioboxes 2 and 3. Cephalopod paralarvae occupied the uppermost position of the three groups in the water column in all areas where they avoided the mixed-layer.

Fish larvae had mean Z_{cm} in about 45 m depth during day and night sampling in Bioboxes 1 and 3, and were distributed between the net-biomass and the cephalopod paralarvae (Fig. 7). In contrast to these groups, fish larvae occurred extremely deep in Bb 2, at about 70 m during the day and 80 m at night, avoiding the pycnocline (Fig. 6). In

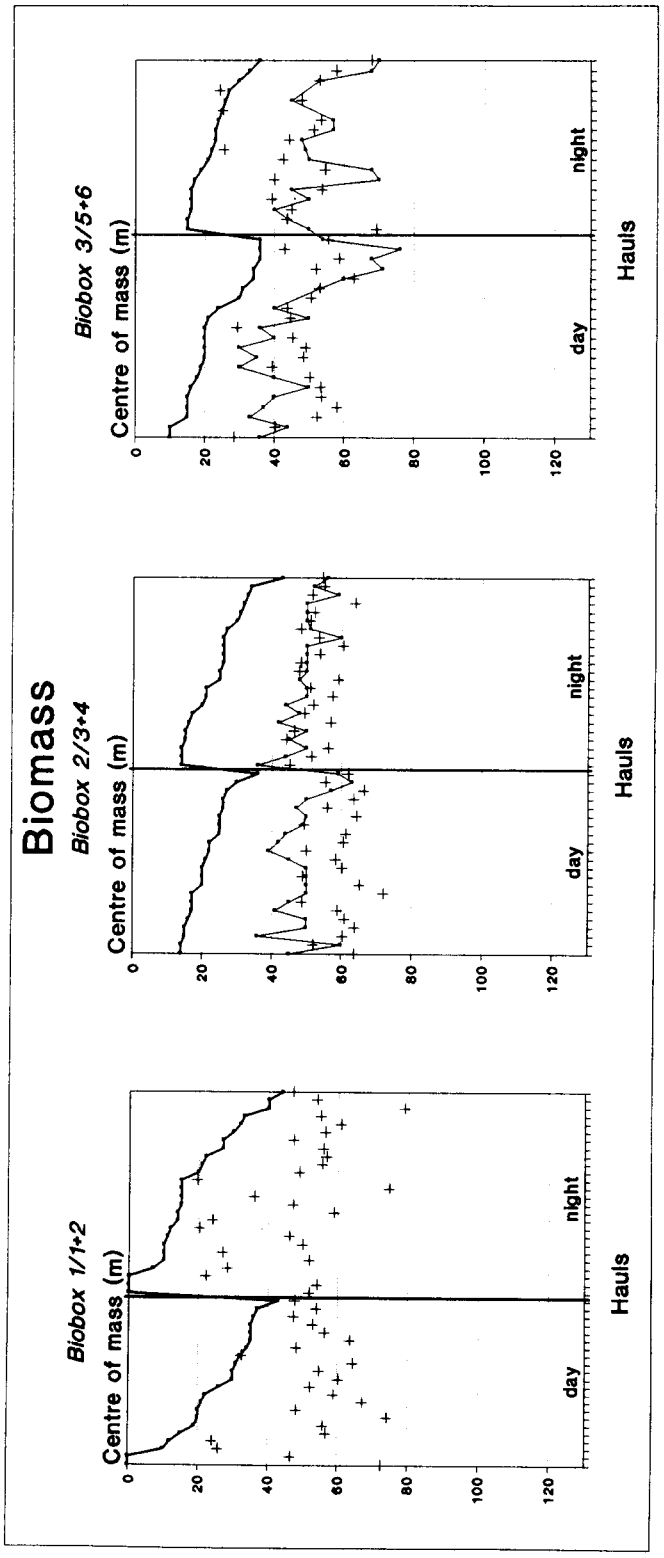

Fig. 4. The centre of mass of the net-biomass for each haul of the three Bioboxes. Day and night hauls are separated. The upper line indicates the lower border of the mixed-layer, whereas the lower line shows that of the pycnocline.

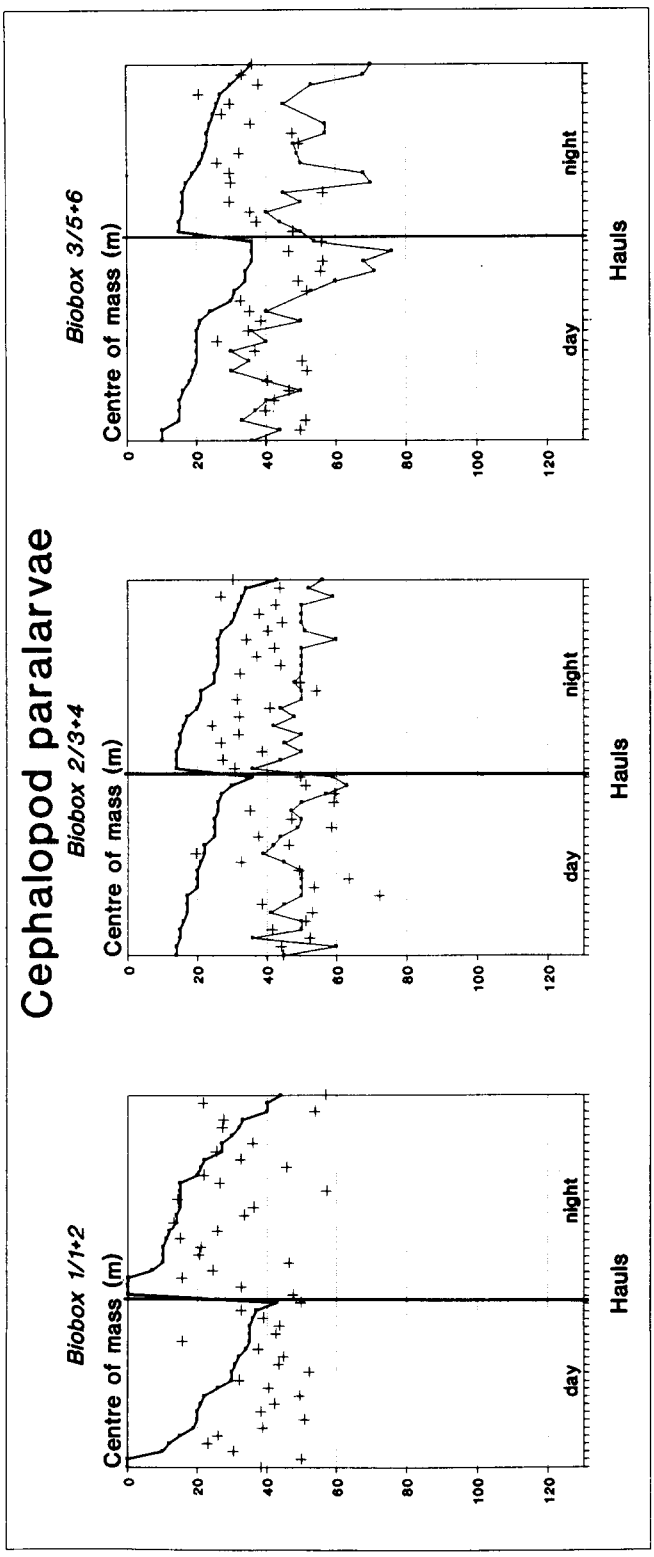

Fig. 5. The centre of mass of the cephalopod paralarvae for each haul of the three Bioboxes. Day and night hauls are separated. The upper line indicates the lower border of the mixed-layer, whereas the lower line shows that of the pycnocline.

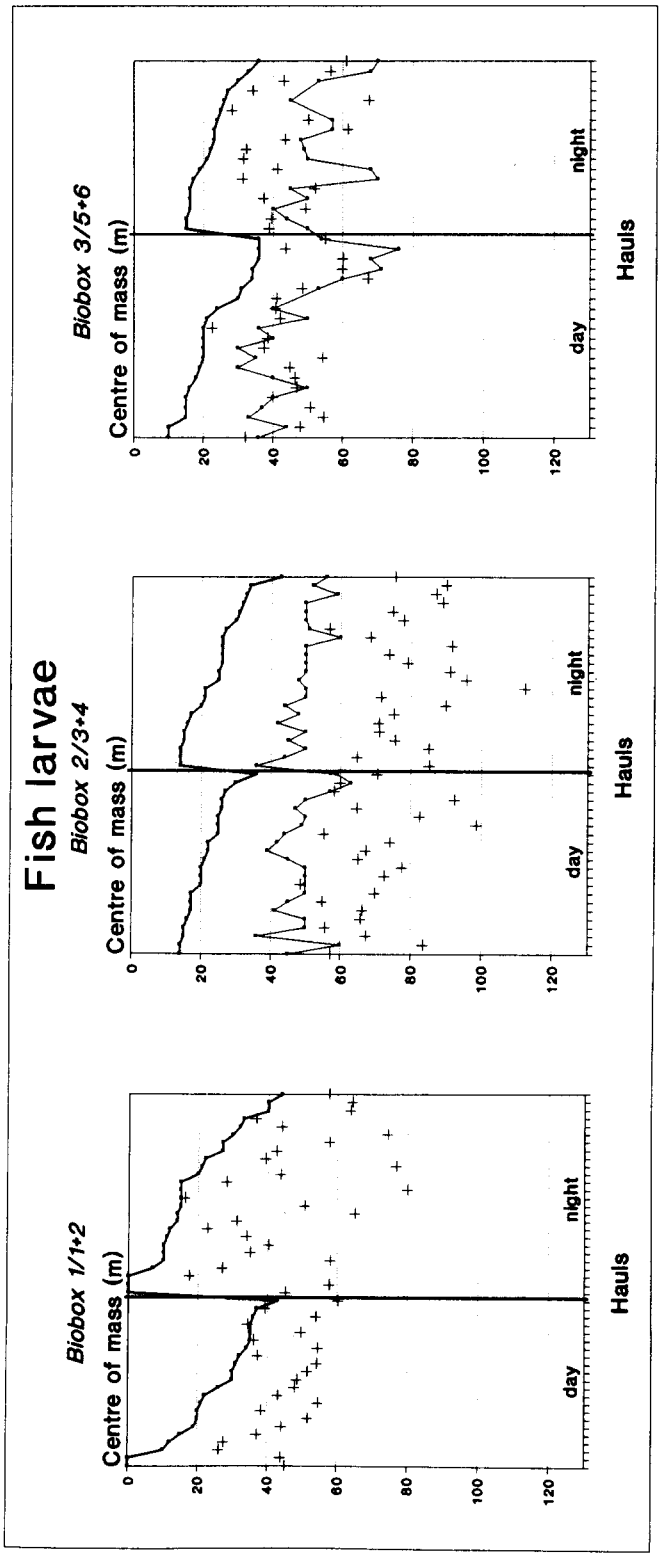

Fig. 6. The centre of mass of the fish larvae for each haul of the three Bioboxes. Day and night hauls are separated. The upper line indicates the lower border of the mixed-layer, whereas the lower line shows that of the pycnocline.

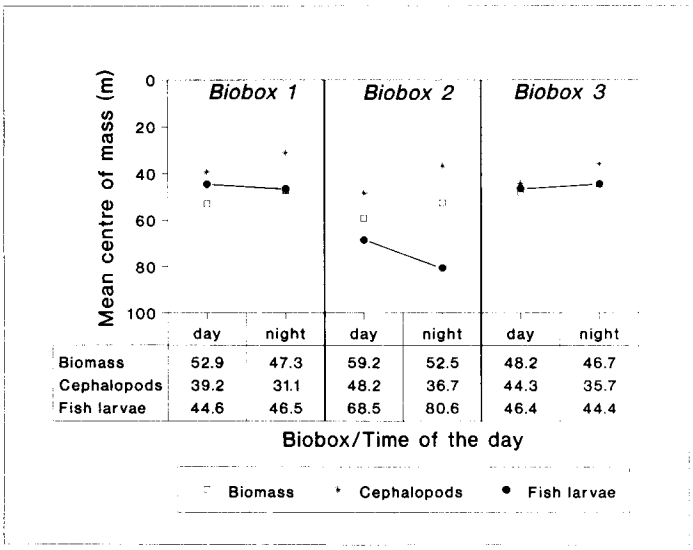

Fig. 7. Mean values of the centre of mass for the net-biomass, cephalopod paralarvae and fish larvae in the three Bioboxes, separated for day and night hauls.

contrast, larvae preferred the pycnocline in Bb 3. The Z_{cm} of fish larvae in Bb 1 were highly variable but seemed to be correlated with the width of the mixed-layer.

Linear regressions between the centres of mass (Z_{cm}) of the different populations and the starting depth of the pycnocline (mixed-layer width) were computed for Bb 1 (Grid 1) and Bb 2 (Grid 3; Figs 8 and 9). The slopes were tested by the t-test ($p < 0.05$). A

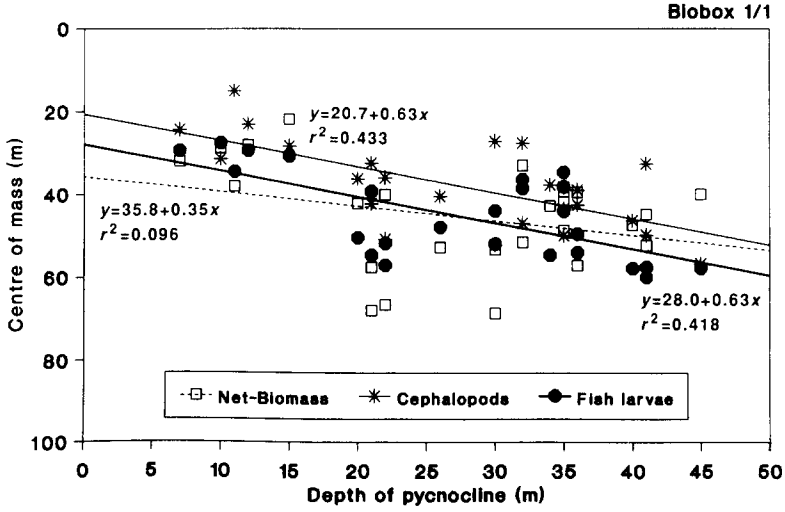

Fig. 8. Linear regression between starting depth of the pycnocline and centre of mass for the net-biomass, cephalopod paralarvae and fish larvae during the first station grid in Biobox 1 (coast of Oman). The slope is statistically significant ($D.F. = 23, p < 0.05$) for cephalopods and fish larvae.

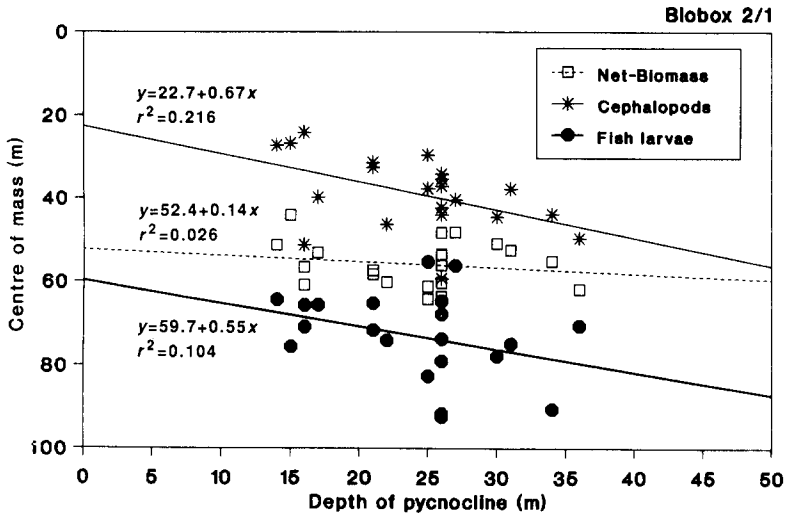

Fig. 9. Linear regression between starting depth of the pycnocline and centre of mass for the net-biomass, cephalopod paralarvae and fish larvae during the first station grid in Biobox 2 (central oceanic). The slope is statistically significant ($D.F. = 19, p < 0.05$) for cephalopods only.

statistically significant slope was found for cephalopod paralarvae and fish larvae in Bb 1 (Fig. 8). According to these results, a downward shift of the pycnocline of 10 m, for example, would result in a 6–7 m deepening of the distribution of cephalopod paralarvae and fish larvae. The net biomass would be 3–4 m deeper. Similar results were obtained for Bb 2 (Fig. 9), but the slope was significantly different from 0 only for the cephalopods. More data on the Z_{cm} of the populations must be evaluated, since the range of data for the depth of the pycnocline is small. As in Bb 1, a 10 m shift of the pycnocline would lead to a shift of 6–7 m in cephalopod paralarvae and fish larvae, but in contrast, the net-biomass would remain unaffected.

DISCUSSION

The occurrence and position of the pycnocline is known to be a major factor in the vertical distribution of plankton organisms. Fish larvae have been found to live mostly above or within the thermocline, using the higher prey concentrations there. AHLSTROM (1959) found that 12 out of 15 species of fish larvae lived in the upper mixed-layer off California and Baja California. Three species lived in or below the thermocline, which extended down to 125 m. Similar results were obtained by KENDALL and NAPLIN (1981) for larvae in the mid-Atlantic Bight. Most species favoured the depth range of 0–30 m, when the thermocline lay between 20 and 30 m. LOEB (1979, 1980) found the highest abundance and diversity of fish larvae at the bottom of the seasonal mixed layer (40 m) in the North Pacific central gyre region. LASKER (1975, 1981) linked similar observations to favourable feeding conditions for anchovy (*Engraulis mordax*) larvae in or above the thermocline in the stable ocean, due to the aggregation of suitable food near the chlorophyll maximum

layer. ELLERTSEN *et al.* (1981) described how cod (*Gadus morhua*) larvae used nauplii at the sea surface. Mackerel larvae (*Scomber scombrus*) have been shown to occur near the surface, in association with copepod eggs, nauplii, and copepodites (COOMBS *et al.*, 1983). The latter studies indicate that food is the primary attraction for fish larvae in the water column. In the absence of thermal stratification, food and fish larvae will be distributed more evenly. HEATH *et al.* (1988) showed this for herring (*Clupea harengus*) larvae. SOGARD *et al.* (1987) and RÖPKE (1989) found different species distributed throughout the poorly or non-stratified water column. Present results on Bb 1 (coast of Oman), which was less stratified than the other areas, support these findings.

Food concentrations in the present study were highest in the layer above the pycnocline in the oceanic area (Bb 2) and in the shelf area off Pakistan (Bb 3) (TRINKAUS, personal communication). The distribution of fish larvae below the pycnocline among lower food concentrations might be a species-specific phenomenon. Most larvae caught in this study belong to the Myctophidae. AHLSTROM (1959) and LOEB (1979, 1980) described that the larvae of this family are deep-dwelling, indicating early adaptations to their later life in the mesopelagial. On the other hand, cephalopod paralarvae were found close to the pycnocline, possibly adopting the role more normally assumed by fish larvae in other regions.

However, the pycnocline (mixed-layer width) is seen to be important in the variance in the vertical distribution of fish larvae and cephalopod paralarvae in this subtropical area. The light intensity (day/night) also plays an important role, especially in case of the cephalopods, in upward migration at night. Whether the influence of the pycnocline is direct (temperature, density, or turbulence) or indirect (food, competitors, or predators) is subject to further investigations. Indirect influences seem more likely. The net-biomass, which can be a vector for the competitor–predator field in this study, seems to be relatively independent from small scale variations of the pycnocline depth.

Factors other than the pycnocline, such as the species and size composition of the fish larvae, may also have had a significant influence on the vertical distribution because the vertical patterns were so different between different areas. Samples from Bb 2 (central oceanic area) contained almost exclusively myctophid species, which are likely to be distributed in deeper water (AHLSTROM, 1959; LOEB, 1979, 1980) than coastal species such as percoids. Ontogenetic vertical migrations minimizing predation and starvation risks (FORTIER and HARRIS, 1989) must also be taken into account. In that study, larger postlarvae were distributed according to their food resources (Ideal Free Distribution model; FRETWELL and LUCAS, 1970), indicating that food was not limiting; density-dependent competition for limited food can theoretically lead to a modification of the distribution patterns of the foragers (Optimal Foraging Theory). Similar mechanisms can be presumed for this study, relating the different results in the three bioboxes to the abundance and distribution of food, competitors and predators.

Unpublished results (TRINKAUS, personal communication) show that the concentration of fish larval food was higher by a factor of 10–20 in the central oceanic area than in the shelf area off Pakistan. The stock of the net-biomass, consisting of potential competitors, was almost the same in both areas. The larval fish stock was higher by a factor of 5 on the shelf. These results suggest that food was not limiting in the oceanic area, and a stratification of the fish larval species therefore is due to specialization, not competition. Histological and biochemical analyses on the nutritional status of larval *Vinciguerria* sp. in Bb 2 and 3 (SIEG *et al.*, 1989) showed that larvae from both areas were in a similarly good

condition. OWEN *et al.* (1989) came to similar conclusions for larval anchovies (*Engraulis mordax*) off southern California. Larvae living offshore had the same chances for survival and recruitment as larvae living near-shore.

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