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Do larvae of mesopelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients?

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ABSTRACT: Size-specific vertical distributions of larvae of the myctophid species *Benthosema pterotum, Bolinichthys longipes, Diaphus arabicus, Diogenichthys panurgus, Hygophum proximum*, and *Myctophum aurolaternatum*, and of the photichthyid species *Vinciguerria nimbaria* were analyzed from 3 hydrographically and ecologically different regions of the northern Arabian Sea (Indian Ocean) during the intermonsoon period (March–June) 1987, using a MOCNESS-1 net system to 150 m depth under comparable circumstances. Regional data on the vertical centres of mass were compared by species and length class. Concurrent measurements of physical stratification and of prey abundance and distribution in the water column were related to larval distribution. Results indicate that larvae of mesopelagic species are found at relatively deep depth. They move downward during early development, adapting to their later life in the mesopelagic zone. Species- and size-specific depth selection was responsible for much of the interregional differences in vertical distribution of fish larvae in general, since the species composition was different between regions. Most of the myctophid and photichthyid species avoided the upper mixed layer, which contained the highest concentrations of potential prey organisms, and their distribution was also not directly related to pycnocline depth (except for *B. pterotum*). Below the mixed surface layer the abundance and vertical distribution of potential prey was more important in determining the vertical distribution of the larvae than the gradient of physical stratification. The low abundance of prey on the shelf off Pakistan was probably responsible for the strong concentration of larvae just below the mixed layer and for their poor nutritional condition in that area. Larvae of identical species and length class occurred on average about 20 m deeper in the central oceanic region compared to the coastal areas off Oman and Pakistan. This was probably due to a deeper and broader distribution of prey organisms.

INTRODUCTION

The understanding of recruitment processes and nutritional relationships in young fish requires knowledge of their small-scale, probably even microscale, distribution in relation to abiotic and biotic parameters (Rothschild & Osborn 1988, Sundby & Fossum 1990, Mackenzie & Leggett 1991). The vertical dimension of the ocean usually has much higher and more consistent gradients of physical, chemical and biological parameters than the horizontal one. The structure of the planktonic system is also more complex on the vertical than on the horizontal plane. This is partly because of active vertical movements of planktonic animals which are related to those gradients.

Fish larvae are known for their complex behaviour. Their vertical distribution and migration patterns are species specific (Ahlstrom 1959, Loeb 1979, 1980, Kendall & Naplin 1981, Sogard et al. 1987, Röpke 1989) and also depend on larval size and stage (Nellen & Hempel 1970, Loeb 1979, Coombs et al. 1983, Fortier & Leggett 1983, 1984, Heath et al. 1988, Fortier & Harris 1989, Frank & Carscadden 1989). Light intensity (day/night rhythm) is the major factor triggering these

behaviours in the laboratory (Woodhead & Woodhead 1955, Blaxter 1973), and seems to be responsible for much of the observed variability in distribution and migration patterns. Thermoclines have been shown to influence these patterns in fish larvae (Ahlstrom 1959, Southward & Bary 1980, Kendall & Naplin 1981, Sameoto 1982, Southward & Barrett 1983, Röpke et al. 1993). However, it is not clear to what extent the temperature change or the larval prey distribution (Lasker 1975) at the thermocline is responsible for this behaviour.

Studies made during the last decade indicate that larvae of epipelagic fish species can adjust their distribution to forage on peak abundances of prey at a small spatial scale of several meters (Fortier & Leggett 1983, 1984, De Lafontaine & Gascon 1989, Fortier & Harris 1989). However, such behavioural responses to prey are considered unlikely in the case of mesopelagic fish larvae. The highest concentrations of potential prey organisms occur in the upper mixed layer of the open ocean, but developing larvae of these species must move progressively to much greater depths (Loeb 1979, 1980) where only low concentrations of potential prey exist. This suggests that mesopelagic fish larvae may not require high concentrations of prey for survival and growth and hence may be less dependent on production processes in the surface layer.

One objective of the interdisciplinary project 'BIOSTAR' (BIOlogical STructures And Recruitment; Nellen et al. 1988) was to determine whether fish larvae of mesopelagic species adapt their vertical distribution to the variable physical and biological structures of the water column as do larvae of epipelagic species, or whether they are relatively inflexible in their vertical distribution behaviour. To answer this question a quasi-synoptical study comparing 3 ecologically different areas containing identical species was conducted during the 1987 'Meteor' expedition in the Arabian Sea.

The Arabian Sea is one of the most productive oceanic areas in the world (Ryther et al. 1966). It has wide and variable ranges of physical and chemical conditions for biological production on relatively small temporal and spatial scales. This is because it is located at the northern border of the western Indian Ocean and is thus subject to the monsoon seasons, causing unique and highly variable circulation systems (Düing 1970, Wyrtki 1973, Qasim 1982, Shetye et al. 1991). The present project was carried out during an intermonsoon period, when high regional differences in physical and chemical stratification can be observed over the northern Arabian Sea. These were responsible for different prey environments for fish larvae as desired for this study.

MATERIALS AND METHODS

Three areas, named 'Bioboxes' (Bb), were sampled in the northern Arabian Sea (Indian Ocean) during cruise 5/leg 3 of the RV 'Meteor' (March 18 to June 9, 1987; Fig. 1). Each Bb consisted of a 5 × 5 station grid with side lengths of 100 × 50 nautical miles. Each grid was sampled twice in order to assess temporal as well as spatial variability. Bb 1 represents a potential upwelling area off the coast of Oman (centred at 21° 20' N, 59° 50' E), featuring a well-mixed water column, and was sampled between March 31 and April 2 (Grid 1) and between April 7 and 10 (Grid 2). Bb 2 (central oceanic area, centred at 18° 45' N, 65° 05' E) was sampled between April 30 and May 3 (Grid 3), as well as between May 8 and 10 (Grid 4), and had a stable and stratified water column with a sharp pycnocline. Bb 3 (shelf off Pakistan, centred at 23° 20' N, 66° 35' E) was sampled between May 23 and 26 (Grid 5) and June 2 and 4 (Grid 6). This area was characterized by an altered oceanic type of water mass which had been advected onto the shelf. All 3 areas were sampled under constant sunny and calm premonsoon weather conditions. Fig. 2 gives the global radiation measured onboard the RV 'Meteor' in relation to local time for the first grid in each area. The variation in light intensity between different areas was low. This is a major prerequisite for a comparative study on the vertical distribution of fish larvae.

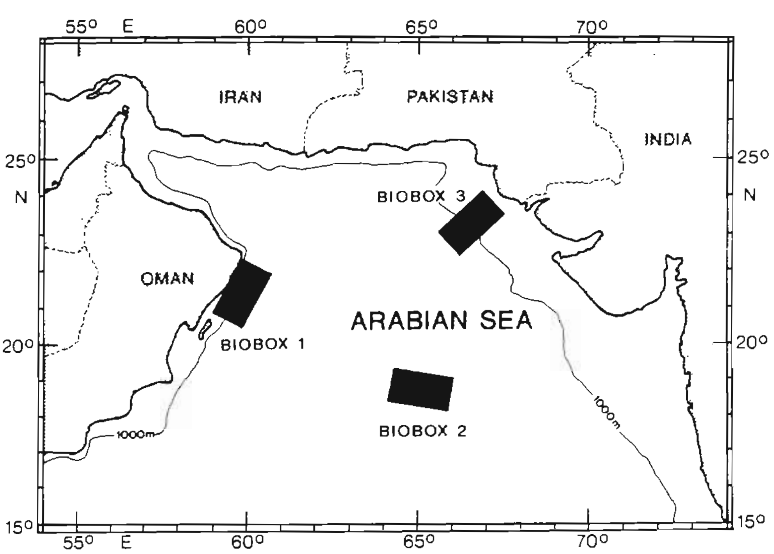


Fig. 1. Positions of the 3 sampling areas (bioboxes) in the northern Arabian Sea during RV 'Meteor' cruise 5/leg 3 (March 18 to June 9, 1987)

Plankton samples were obtained with a modified MOCNESS-1 net system (Wiebe et al. 1985, Nellen et al. 1988) which has a box-shaped frame and is supplied with a stabilizer. These modifications improved the stability of the gear during the sampling process. The nets had a length of 6 m and a mesh aperture size of 335 µm. Towing speed was 1 m s^{-1}. The volume of water filtered was determined from flow counts recorded by an electric flowmeter mounted in the frame opening, corrected for simultaneous net angle data. We sampled 8 discrete depth strata during oblique hauls from 150 m to the surface. At water depths less than 150 m, sampling began 5 m above the sea bed. The strata sampled were 150–100, 100–75, 75–60, 60–50, 50–40, 40–30, 30–20(15), 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 number of analyzed hauls (N = 132) and samples (N = 947) classified by mean depth interval, time of day, and grid. The total volume of water filtered was 332 107 m^3.

Samples were stored in a buffered 4%-formaldehyde/fresh water solution at 15°C for 1 to 2 yr before analysis. The fish larvae (N = 85 389) were removed from the total plankton displacement volume of 24 500 cm^3, identified and counted. The standard length (SL) of undamaged larvae (N = 54 614) of the most abundant mesopelagic species *Benthosema pterotum* (Bb 1, 3), *Bolinichthys longipes* (Bb 2), *Diaphus arabicus* (Bb 1, 2, 3), *Diogenichthys panurgus* (Bb 2), *Hygophum proximum* (Bb 1, 2, 3), and *Vinciguerria nimbaria* (Bb 1, 2, 3) was measured with the help of a planimeter to the nearest 0.1 mm.

Variation in the vertical distribution of larvae was evaluated by the depth of the centre of mass (Z_{CM}),

$$Z_{CM} = \sum_{i=1}^{\leq 8} (P_i Z_i)$$

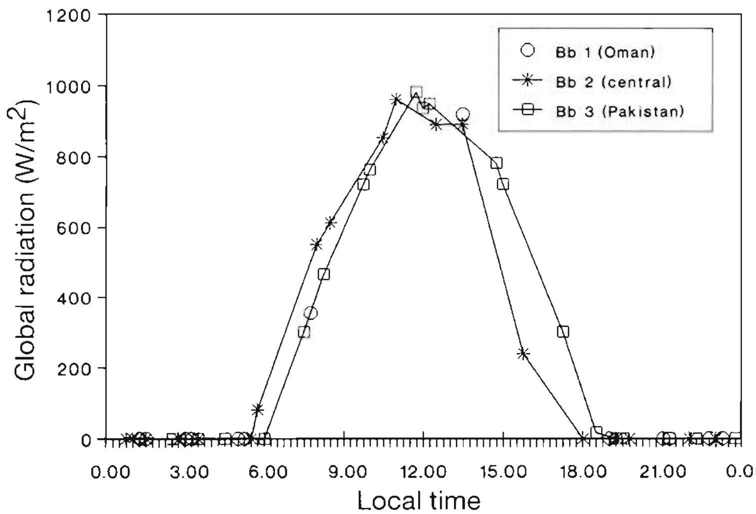


Fig. 2. Global radiation in relation to time of day during sampling of the 3 bioboxes in the northern Arabian Sea

Table 1. Number of analyzed hauls and samples during 6 grid sampling sequences in the 3 bioboxes, classified by day/night sampling and mean depth, made during RV 'Meteor' cruise 5/leg 3 (March–June, 1987)

	Biobox 1		Biobox 2		Biobox 3		Total
	Grid 1	Grid 2	Grid 3	Grid 4	Grid 5	Grid 6	
	N	N	N	N	N	N	N
Hauls analyzed	25	23	21	24	22	17	132
Day/night	14/11	8/15	9/12	13/11	14/8	7/10	65/67
Samples analyzed	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 (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

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

where P_i is the proportion of larvae in the ith depth stratum; 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.

Data of both grids in each Bb were combined for analysis of the vertical distribution of fish larvae in relation to the physical characteristics of the environment – the major point of interest in this paper. This procedure was possible because both grids had a similar physical water column structure. Day and night samples were analyzed separately since the different day/night sampling effort between areas could have caused biased results in the case of pooled samples.

Hydrographical data were obtained with a CTD system (Multisonde, ME, Kiel, Germany) to a depth of 150 m. The resulting profiles were compiled by Ribbe (1988, unpubl. data report). Arithmetric mean and standard deviation values of temperature and density were computed for selected depths in each grid. The resulting mean profiles and the T/S diagrams are illustrated for the first grid of each Bb only, since this was characteristic of both grids. Data on the width of the mixed layer and the pycnocline (depth range with highest density decline), as well as the temperature gradient to 150 m, were taken from the original profiles. Mean values for these physical stratification parameters were computed for both grids of each Bb combined.

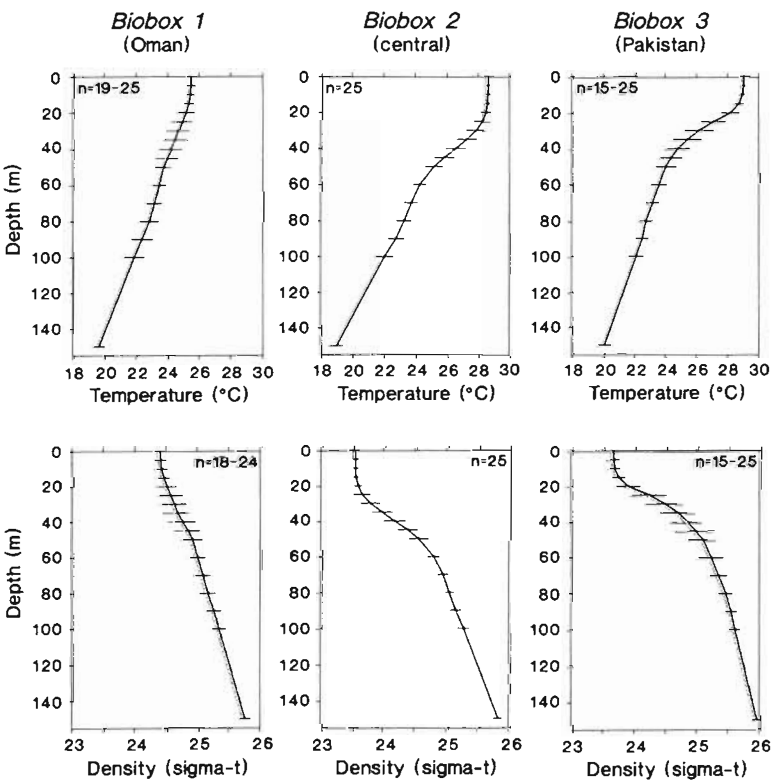


Fig. 3. Mean vertical temperature and density profiles during the first grid sampling in each of the 3 bioboxes in the northern Arabian Sea. Horizontal lines indicate standard deviations around the means

Table 2. Mean ($\bar{x}$) and standard deviation (SD) of physical parameters in the water column of the 3 bioboxes in the northern Arabian Sea

Physical parameter in the water column	Biobox 1 $\bar{x}$ (SD)	Biobox 2 $\bar{x}$ (SD)	Biobox 3 $\bar{x}$ (SD)
Surface temperature (°C)	25.6 (0.25)	28.7 (0.21)	29.2 (0.20)
Surface salinity (ppt)	36.56 (0.05)	36.83 (0.09)	37.05 (0.11)
Mixed-layer width (m)	23.9 (10.7)	22.8 (6.7)	23.5 (4.3)
Pycnocline width (m)	–	26.3 (5.9)	27.6 (9.0)
Temperature gradient 0–150 m (°C)	6.2 (0.5)	9.6 (0.5)	9.0 (0.6)

RESULTS

Hydrography

Mean values of characteristic physical parameters in the water column are given in Table 2. Along the coast of Oman (Bb 1) surface temperature and salinity were relatively low (25.6 °C, 36.56 ppt). There was an almost linear decline of temperature (6.2 °C) down to 150 m depth (19.4 °C). The mixed layer width varied mainly between 13 and 35 m (mean = 23.9 m). There was only a weak signal of a pycnocline between 20 and 50 m depth (Fig. 3).

In contrast to the almost mixed water column in Bb 1, the stratification in Bb 2 (central oceanic area) was much more pronounced (Fig. 3). A significant and very consistent pycnocline, about 20 to 32 m in width (mean = 26.3 m), was measured. The surface temperature averaged around 28.7 °C, which is about 3 °C higher than in Bb 1. The salinity (36.83 ppt) was also higher than in Bb 1. The mixed layer depth varied mainly between 16 and 30 m (mean = 22.8 m).

The data for Bb 3 (shelf off Pakistan) do not confirm any fresh water influence from the Indus River as presumed prior to sampling. The SW monsoon was very late in 1987 and, as a result, oceanic water was

still lying on the shelf off Pakistan at the beginning of June, with a higher temperature and salinity (29.2 °C, 37.05 ppt) than the water in Bb 2. The physical stratification was also stronger in Bb 3 (Fig. 3). The mixed layer depth varied between 20 and 28 m (mean = 23.5 m) and was relatively consistent. In contrast, the width of the pycnocline was highly variable (19 to 37 m, mean = 27.6 m).

The main hydrographical result was that water temperature and salinity, as well as stratification, increased from west (Bb 1) to east (Bb 3) in the northern Arabian Sea during this premonsoon season. This is also visible in the T/S diagrams for the 3 regions (Fig. 4). Yet, regional differences were less spectacular than anticipated: water masses were of a more or less oceanic kind.

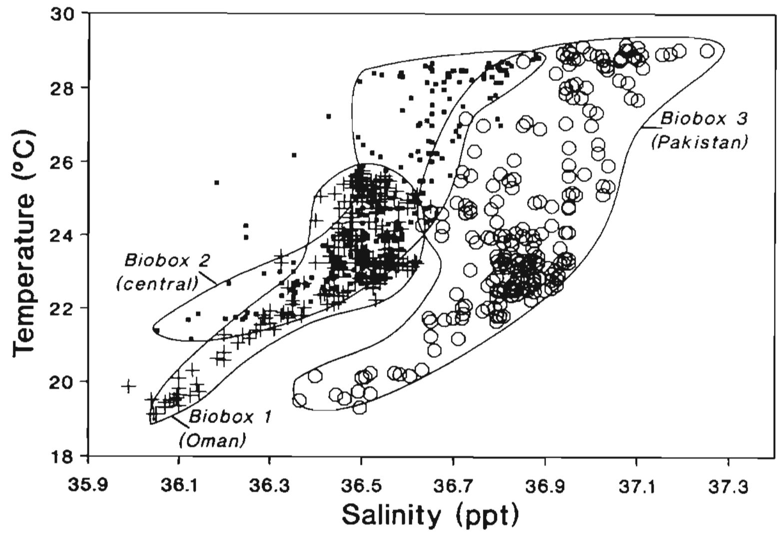


Fig. 4. T/S diagram of temperature vs salinity data for the 3 bioboxes in the northern Arabian Sea. (+) Bb 1; (■) Bb 2; (○) Bb 3. Lines around the 3 clusters are hand-drawn

Taxonomic composition

Of the fish larvae sampled (N = 85 389), 95.5 % were identified at least to family level. A total of 55 families were encountered. The 3 most abundant families, making up 74.36 % of all larvae, were Myctophidae (N = 47 254; 55.34 %), Photichthyidae (N = 13 546; 15.86 %), and Bregmacerotidae (N = 2 701; 3.16 %). The adults of most species within these groups are mesopelagic. Bb 1 (Oman) and Bb 3 (Pakistan) are coastal areas and show a much higher diversity of families (N = 48 to 50) than Bb 2 (central, N = 17), where Myctophidae and Photichthyidae together made up 90.47 % of all fish larvae captured (N = 10 585). These 2 families were also responsible for 70.66 % of all larvae in Bb 3 (N = 44 750) and 65.21 % of all larvae in Bb 1 (N = 30 054).

Table 3 lists the species composition of the Myctophidae and Photichthyidae. Seven out of 8 groups of captured myctophid larvae were identified to species level. There was only 1 photichthyid species, *Vinciguerria nimbaria*, which was the second most abundant species of all, responsible for 15.86 % of all captured larval fishes. The most abundant species was the myctophid *Benthosema pterotum* with 36.21 %. The third most abundant species was *Hygophum proximum* with 12.62 %, followed by *Diaphus arabicus* with 4.46 %.

Table 3. Total number caught and percentage occurrence of species within the mesopelagic families Myctophidae and Photichthyidae, present in the plankton samples from the 3 bioboxes in the northern Arabian Sea

Family Species	Biobox 1 N	 %	Biobox 2 N	 %	Biobox 3 N	 %	Total N	 %
Myctophidae								
Benthosema pterotum	11 056	36.79	36	0.34	19 824	44.30	30 916	36.21
Hygophum proximum	2 861	9.52	6 752	63.79	1 162	2.60	10 775	12.62
Diaphus arabicus	989	3.29	471	4.45	2 347	5.24	3 807	4.46
Diogenichthys panurgus	103	0.34	646	6.10	20	0.04	769	0.90
Myctophum aurolaternatum	13	0.04	421	3.98	24	0.05	458	0.54
Bolinichthys longipes	22	0.07	374	3.53	48	0.11	444	0.52
Symbolophorus evermanni	3	0.01	14	0.13	53	0.12	70	0.08
Lampanyctus sp.	2	0.01	0	0.00	0	0.00	2	0.00
Myctophidae unidentified	6	0.02	3	0.03	4	0.01	13	0.02
Photichthyidae								
Vinciguerria nimbaria	4 544	15.12	860	8.12	8 142	18.19	13 546	15.86

The 3 Bbs varied strongly in their species compositions within the families Myctophidae and Photichthyidae. A very dominant taxon in Bb 2 was *Hygophum proximum* (63.79%). In Bbs 1 & 3 *Benthosema pterotum* was the dominant species (36.79% and 44.30%). However, this species was rarely caught in Bb 2. As in Bb 2 *Vinciguerria nimbaria* was the second most abundant species in Bbs 1 & 3. Its relative importance there was higher than in Bb 2. Much lower values than in Bb 2 were registered for *H. proximum* in Bbs 1 & 3. The species *Diogenichthys panurgus*, *Myctophum aurolaternatum* and *Bolinichthys longipes*, which were relatively important in Bb 2, had very low counts in Bbs 1 & 3.

Species-specific vertical distribution

Vertical distribution patterns for larvae of the 6 most abundant species of midwater fishes in Bb 2 (central) are shown in Fig. 5. Day and night concentrations were drawn separately. Nighttime abundances of all 6 species were much higher than were daytime abundances. This may be due to a generally lower daytime catchability of large fish larvae in Bb 2. For example, large larvae of the near-surface species *Bolinichthys longipes* were totally missed on most stations during daylight sampling in Bb 2. This was probably due to their extremely strong net-avoidance behaviour in the comparatively bright surface water.

However, different species were confined to different vertical niches. Larvae of *Bolinichthys longipes* stayed more or less in the upper 40 to 60 m of the water column, where the mixed layer and the upper part of the pycnocline occurred. The larvae of *Vinciguerria nimbaria* were confined mainly to a depth range between 30 and 80 m, mostly within the pycnocline. *Diaphus arabicus* and *Myctophum aurolaternatum* were distributed relatively evenly between 30 and 100 m depth (below the mixed layer), whereas *Hygophum proximum* larvae had their highest abundances below 50 m depth. High densities of this taxon were found between 100 and 150 m depth. It preferred a depth range strictly below the pycnocline. A very striking behaviour was shown by the larvae of *Diogenichthys panurgus*, whose range of occurrence started at 80 m depth and may have gone deeper than 150 m (the lower limit of sampling during this study).

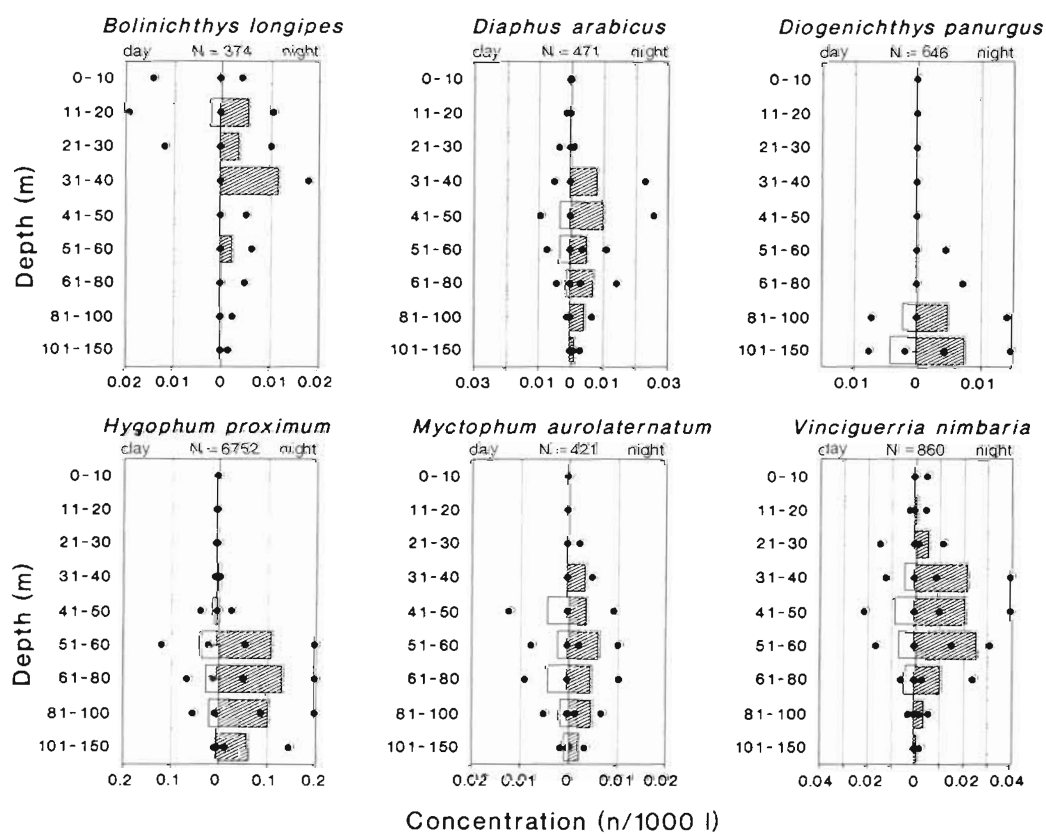


Fig. 5. Day and night vertical distribution profiles for the larval concentrations of 6 mesopelagic fish species in Biobox 2 (central oceanic). Bars represent median concentrations; points indicate interquartile ranges around the medians

Table 4. Measured number and mean standard length (SL; $\bar{x} \pm$ SD) of 6 larval mesopelagic species from the 3 bioboxes in the northern Arabian Sea

Species	Biobox 1 N	Biobox 1 SL (mm) $\bar{x}$ (SD)	Biobox 2 N	Biobox 2 SL (mm) $\bar{x}$ (SD)	Biobox 3 N	Biobox 3 SL (mm) $\bar{x}$ (SD)	Total N
Benthosema pterotum	10381	3.6 (1.2)	0		17333	3.7 (1.0)	27714
Vinciguerria nimbaria	4310	6.2 (2.8)	801	9.5 (3.5)	7788	6.0 (2.0)	12899
Hygophum proximum	2631	3.9 (1.3)	5842	4.6 (1.1)	1116	4.1 (1.0)	9589
Diaphus arabicus	909	5.7 (2.1)	379	5.8 (2.1)	2218	4.1 (0.9)	3506
Diogenichthys panurgus	0		579	4.9 (1.6)	0		579
Bolinichthys longipes	0		327	5.0 (1.4)	0		327
Total	18231		7928		28455		54614

Size-specific vertical distribution

In order to analyze the influence of size on the vertical distribution of mesopelagic fish larvae, the standard length (SL) of all undamaged specimens of the most abundant myctophid species and of *Vinciguerria nimbaria* was measured. The numbers measured for each species and biobox are listed in Table 4 along with the arithmetic means and standard deviations (normal distribution is given).

The majority of larvae caught were relatively small. The myctophid species ranged from 3.6 (± 1.2) mm (*Benthosema pterotum*) to 5.8 (± 2.1) mm (*Diaphus arabicus*). The larvae of *Vinciguerria nimbaria* were much larger (6.2 ± 2.8 to 9.5 ± 3.5 mm). The largest specimens of comparable species were captured in Bb 2 (central), where larval *V. nimbaria* were more than 3 mm longer on average than in Bbs 1 & 3. Larvae of *Hygophum proximum* and *D. arabicus* were also larger in Bb 2.

The illustration (Fig. 6) of the centre of mass at each station for different length classes of larval myctophids in Bb 2 (central) shows that differences in depth selection of species were due to species-specific rather than to size-specific behaviour. Larvae of different species (*Bolinichthys longipes*/*Diogenichthys panurgus*) but identical length classes were confined to different vertical niches. For a given species, larger myctophid larvae occurred deeper in the water column than smaller ones (Table 5). This observation was especially evident during the night, when larger larvae either actively swam or passively sank greater distances downward, away from their daytime depth, than smaller larvae. The higher net avoidance, especially near the surface, during daylight compared to nighttime hours (Fig. 5) cannot be responsible for the observed downward movement of the larvae. Avoidance would have produced the opposite result, i.e. of apparently descending larvae in the day, not at night, especially in the case of larger larvae.

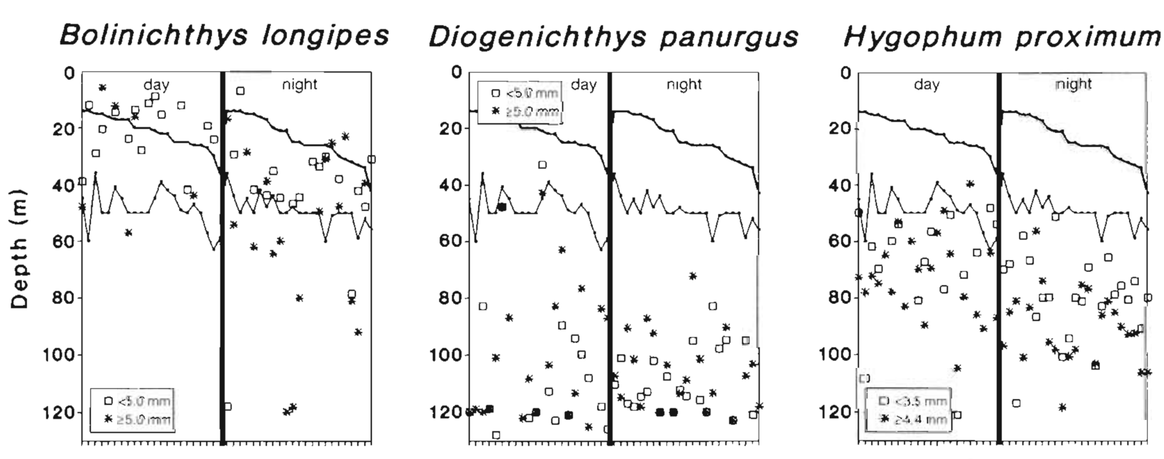


Fig. 6. Centre of mass of 2 size classes of larval *Bolinichthys longipes*, *Diogenichthys panurgus* and *Hygophum proximum* on all analyzed stations of Biobox 2 (central oceanic), separated for day and night sampling. Upper solid line: lower border of the mixed layer (criterion for station order); lower line: bottom of pycnocline

Similar results were obtained for larval *Benthosema pterotum* in Bb 1 (Fig. 7). Larvae <2.5 mm SL occurred just below the mixed layer in the upper pycnocline during both day and night. The subsequent size classes descended gradually, showing increased depth variability which was highest during nighttime. The centre of mass occurred within the mixed layer in only a very few cases. Distribution of larval *B. pterotum* seems to be directly related to the upper limit of the pycnocline (Fig. 8). Linear regressions ($r^2 = 0.3$, $n = 20$ or 21) between the centre of mass of the larval distribution and the depth of the pycnocline (= mixed layer width) were relatively good in the case of this highly abundant species in Bb 1. The slopes were statistically significant (*t*-test, $p < 0.05$) for larvae <2.5 mm and 2.5 to 4.4 mm SL during the day and for larvae <2.5 mm SL during the night. Larvae 2.5 to 3.4 mm SL showed the same downward trend during nighttime as the larger sizes. The higher variance of larger larvae cannot be explained by the depth of the pycnocline alone. The 3 linear regressions, which have statistically significant slopes, are almost parallel, making these results relatively reliable. The slopes are in the range 0.56 to 0.69, meaning that a 10 m descent of the pycnocline results in a 5.6 to 6.9 m deeper distribution of the small larvae of *B. pterotum*. However, this relationship seems to be relevant for small larvae only and mainly during daylight.

Larval *Vinciguerria nimbaria* had a somewhat different behaviour to the myctophids (Fig. 7). The smallest stage (<4.0 mm) was heterogenously distributed below the mixed layer. Larger length classes (4.0 to 6.9 and 7.0 to 9.9 mm) were distributed higher in the water column and were also found in the lower region of the mixed layer. Late larvae (>9.9 mm) descended back into deeper waters. During the night, only a few centres of mass remained in the mixed layer, accounting for the same downward movement as in larval myctophids. As for the myctophids the variability was higher during the night than during the day, but there was no direct relationship (*t*-test, $p > 0.05$) between the vertical distribution of larvae and the depth of the pycnocline.

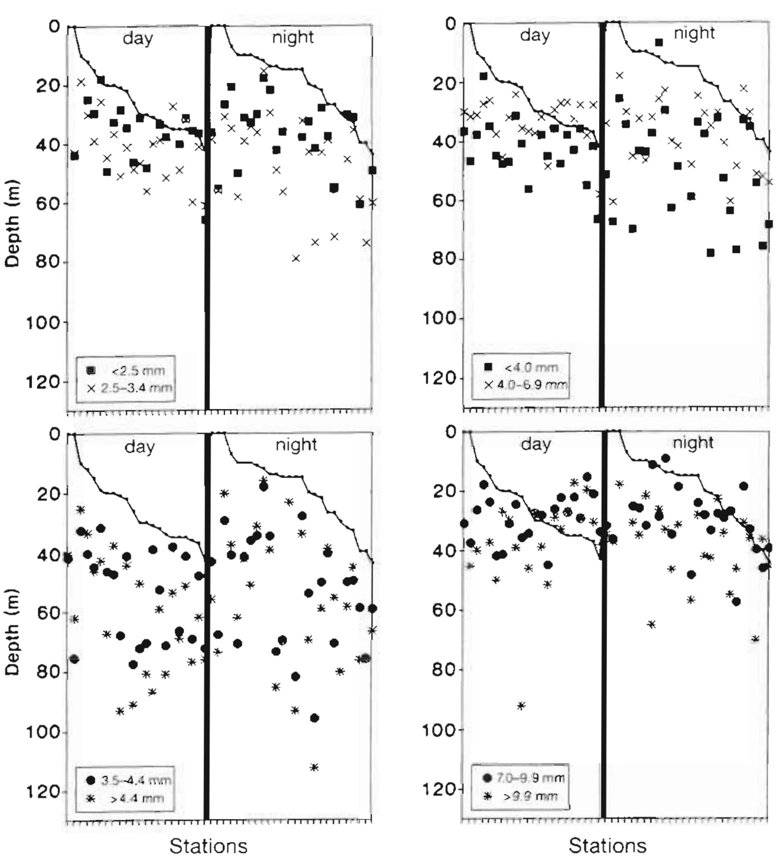


Fig. 7. Centre of mass of 2 small (top) and 2 large (bottom) size classes of larval *Benthosema pterotum* (left) and *Vinciguerria nimbaria* (right) on all analyzed stations of Biobox 1, separated for day and night sampling. Line indicates lower border of mixed layer (criterion for station order)

Regional vertical distribution

Table 5 summarizes the mean centres of mass for 4 comparable mesopelagic fish species in a size- and site-specific way, including a day/night comparison. The data are illustrated in Fig. 9. The observed day/night differences are statistically significant (*t*-test, $p < 0.05$) only for length classes of *Diaphus arabicus* in Bb 2 (oceanic) and for *Hygophum proximum* in all regions. Nevertheless, a slight downward shift during the night was obvious in most species and length classes, with the exception of *Benthosema pterotum* which was shown to be linked more closely to the depth of the pycnocline than other species.

The size-specific differences between the centres of mass were statistically significant (*t*-test, $p < 0.05$) mainly in Bb 1 (4 species, 13 cases) and to a lesser extent in Bb 3 (2 species, 5 cases). In Bb 2 only *Hygophum proximum* showed size-specific differences in vertical distribution for 2 length classes. The vertical spread between length classes was maximum in Bb 1.

Comparing the 3 regions by species, size class and time of day leads to the following general conclusion (Fig. 9): mesopelagic fish larvae had their uppermost

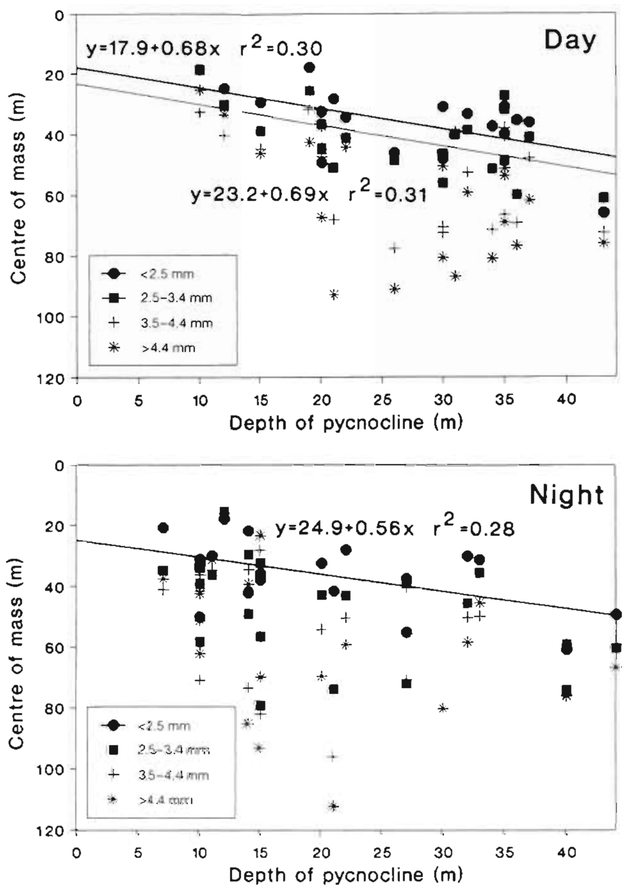


Fig. 8. *Benthosema pterotum*. Centre of mass of 4 size classes of larvae in relation to the depth of the pycnocline (= width of the mixed layer), separated for day (top) and night (bottom) sampling in Biobox 1. Linear regressions are computed and drawn for 3 statistically significant (t-test, $p < 0.05$) slopes

position in the water column of Bb 1 (coast of Oman), followed by Bb 3 (shelf off Pakistan), where the larvae occurred a little deeper on the average. Larvae in Bb 3 were concentrated in the range of the pycnocline, whereas those in Bb 1 were more evenly distributed throughout a wide depth range below the mixed layer. On average, fish larvae of mesopelagic species occurred 10 to 20 m deeper in Bb 2 (central oceanic) than in the other 2 regions.

DISCUSSION

Literature on the analysis of the vertical distribution of larval mesopelagic fishes in the open ocean is rare. Ahlstrom (1959) describes the vertical distribution of midwater fish larvae in relation to the thermocline in the Pacific Ocean along the coast of California and Baja California. In contrast to the present study, he found most species in a wide surface mixed layer and at the top of the thermocline. However, the hydrographical conditions in that study were very variable and the thermocline was relatively deep and weak. Additionally, sampling was limited to non-closing nets at that time, and the genera and species were different from those of this study. Therefore, the results of the present study were not expected to be the same, not even those from the coast of Oman, a region with a similar mixed water column. Nevertheless, Ahlstrom's general observation that species have specific vertical distribution ranges in the epipelagic zone was supported later by Loeb (1979, 1980) in the North Pacific Central Gyre region and by this study in the northern Arabian Sea. The different species composition is the main reason for the previously reported (Röpke et al. 1993) regional variability of the vertical distribution of fish larvae in the Arabian Sea.

Loeb (1979, 1980) and Boehlert et al. (1992) showed that larvae of many mesopelagic fish species live relatively deep as compared to epipelagic species (e.g. Röpke 1989), adjusting themselves ontogenetically to their later life as adults in the mesopelagic zone. More or less consistent interspecific differences in depth selection of the genera *Diaphus* and *Diogenichthys* and the species *Vinciguerria nimbaria*, *Bolinichthys longipes*, and *Hygophum proximum* were found in these studies in different regions of the world which have different production regimes. This indicates an underlying species-specific depth selection behaviour which is independent of actual environmental conditions such as physical stratification and prey distribution. This behaviour is likely to be triggered by light intensity.

However, species in the present study (Bb 2, central) were generally not as concentrated at the bottom of the mixed layer and at the top of the pycnocline as described by Loeb (1979, 1980), in spite of living in a similar physically stratified environment. Rather, they were distributed more evenly over the whole sampling range down to 150 m. In addition, the mixed layer was avoided by all species, with the exception of *Bolinichthys longipes* during daylight hours. *Benthosema pterotum*, the most abundant of all species sampled, was the only one closely associated with the upper part of the pycnocline, especially during daylight hours. *B. pterotum* was responsible for the good linear relationship between the depth of the pycnocline and the centres of mass of all fish larvae in Bb 1 (Oman), shown by Röpke et al. (1993). Data for *Vinciguerria nimbaria* were too variable to show a similar relationship. Other larval fish species seem to be relatively independent of the direct influence of the physical stratification since they live in deeper regions of the water column. However, due to net avoidance, large size groups of some species might have been distributed closer to the

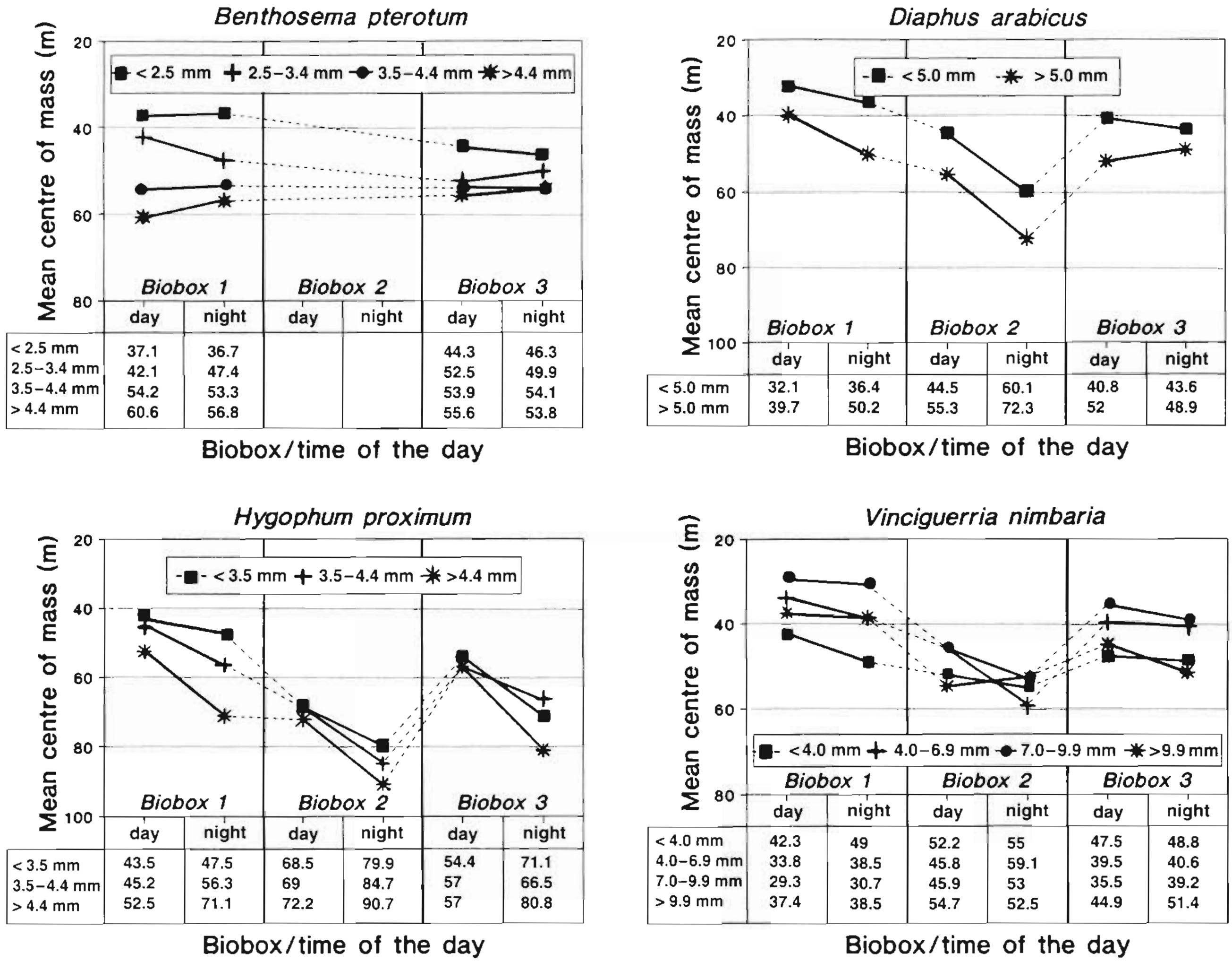
Table 5. Mean centre of mass ($\bar{x} \pm$ SD) in larvae of 4 mesopelagic fish species and their length classes, classified for their regional origin (biobox) and day/night sampling. '+' and '|' signs indicate a statistically significant (t-test, $p < 0.05$) difference between the mean values ('+' day vs night, '|' length classes)

Species Length class (mm)	Biobox 1 Day $\bar{x}$ (SD) N	Biobox 1 Night $\bar{x}$ (SD) N	Signif. (5%) d/n	Signif. (5%) + length	Biobox 2 Day $\bar{x}$ (SD) N	Biobox 2 Night $\bar{x}$ (SD) N	Signif. (5%) d/n	Signif. (5%) + length	Biobox 3 Day $\bar{x}$ (SD) N	Biobox 3 Night $\bar{x}$ (SD) N	Signif. (5%) d/n	Signif. (5%) + length
B. pterotum	44.6 (9.2) 22	46.5 (17.9) 26	–						51.0 (14.4) 21	51.2 (20.1) 18	–	
<2.5	37.1 (10.9) 18	36.7 (11.6) 22	–						44.3 (8.5) 14	46.3 (14.4) 15	–	
2.5–3.4	42.1 (11.2) 21	47.4 (16.6) 24	–						52.5 (12.9) 21	49.9 (20.6) 18	–	
3.5–4.4	54.2 (15.7) 22	53.3 (19.5) 24	–						53.9 (15.1) 21	54.1 (21.3) 17	–	
>4.4	60.6 (19.6) 22	56.8 (23.6) 26	–						55.6 (14.7) 20	53.8 (20.8) 18	–	
D. arabicus	34.0 (13.0) 21	47.4 (21.5) 24	+		49.6 (16.7) 22	70.9 (21.2) 23	+		42.3 (9.6) 14	43.4 (14.2) 17	–	
<5.0	32.1 (10.2) 20	36.4 (13.9) 24	–		44.5 (20.4) 13	60.1 (21.5) 19	+		40.8 (8.8) 14	43.6 (13.4) 16	–	
≥5.0	39.7 (15.2) 19	50.5 (22.4) 22	–		55.3 (12.4) 19	72.3 (25.9) 22	+		52.0 (17.9) 11	48.9 (19.7) 14	–	
H. proximum	44.7 (11.0) 21	56.9 (21.4) 25	+		70.6 (15.5) 22	86.5 (11.9) 23	+		56.3 (8.9) 14	72.2 (21.7) 13	+	
<3.5	43.5 (11.1) 21	47.5 (21.7) 24	–		68.5 (20.6) 15	79.9 (14.8) 23	–		54.4 (8.0) 10	71.1 (22.8) 8	+	
3.5–4.4	45.2 (12.0) 21	56.3 (21.1) 22	+		69.0 (16.6) 20	84.7 (12.3) 23	+		57.0 (9.0) 11	66.5 (19.7) 9	–	
>4.4	52.5 (21.5) 19	71.1 (24.9) 24	+		72.2 (15.3) 22	90.7 (13.5) 23	+		57.0 (10.3) 14	80.8 (18.5) 12	+	
V. nimbaria	35.0 (8.7) 22	38.7 (11.1) 25	–		50.8 (13.9) 22	54.4 (11.3) 23	–		38.3 (13.6) 19	40.5 (12.8) 18	–	
<4.0	42.3 (10.0) 21	49.0 (18.6) 25	–		52.2 (21.5) 4	55.0 (15.3) 8	–		47.5 (10.6) 12	48.8 (12.0) 12	–	
4.0–6.9	33.8 (8.2) 22	38.5 (12.1) 25	–		45.8 (14.4) 17	59.1 (19.0) 20	+		39.5 (11.8) 18	40.6 (12.5) 18	–	
7.0–9.9	29.3 (7.8) 22	30.7 (11.1) 23	–		45.9 (12.3) 18	53.0 (19.9) 23	–		35.5 (14.6) 18	39.2 (16.6) 17	–	
>9.9	37.4 (15.9) 20	38.5 (13.2) 24	–		54.7 (17.2) 18	52.5 (18.7) 23	–		44.9 (18.0) 17	51.4 (19.6) 17	–	

mixed layer in reality than they appeared to be during daylight sampling. But the majority of larvae of most species in this study were small (<5.0 mm), especially in the coastal areas. Net avoidance was not such an important factor there as in the oceanic area (see Röpke et al. 1993).

Only the small length classes of *Benthosema pterotum* stayed immediately below the mixed layer. Larger stages gradually moved into deeper water, as did all the mesopelagic fish species in this study. It is rather speculative to discuss why only small larvae of *B. pterotum* behaved like this. Perhaps they required the high prey concentration in the mixed surface layer and the upper pycnocline for feeding success during daylight hours more than other species and size classes of mesopelagic fish. Nellen (1973) and Röpke (1992) showed that *B. pterotum*, in contrast to other mesopelagic species, appeared to be distributed more in coastal, highly productive areas of the Arabian Sea. However, the highest concentrations of nauplii and copepodites, which were the major food items in the diet of larval myctophids (Nerlich pers. comm.), were consistently found in the mixed surface layer in all 3 bioboxes (Fig. 10).

The vertical prey distribution seems to be more effective than the variation of the mixed layer dimension in explaining some consistent interregional differences in the vertical distribution within species and size classes of fish larvae. The differences in prey distribution were not as large as anticipated prior to the study, since all areas were still under a strong oceanic influence, meaning low primary production and poor prey supply for fish larvae, including those in the coastal areas (Röpke 1992, Sieg 1992). Highest concentrations of copepod nauplii and copepodites <0.4 mm were found in the central oceanic Bb 2 with about 16 l^{-1} between the surface and 40 m depth. Even at 50 m there was a concentration of potential prey organisms for fish larvae higher than the highest concentrations in Bb 1 (5.5 l^{-1}) and Bb 3 (8.5 l^{-1}). These concentrations also occurred in the mixed layer, but were limited to the upper part of it. This pattern might explain the general deeper distribution (about 20 m) of mesopelagic fish larvae in Bb 2 compared to Bb 3



Benthosema pterotum

	Biobox 1 day	Biobox 1 night	Biobox 2 day	Biobox 2 night	Biobox 3 day	Biobox 3 night
< 2.5 mm	37.1	36.7			44.3	46.3
2.5–3.4 mm	42.1	47.4			52.5	49.9
3.5–4.4 mm	54.2	53.3			53.9	54.1
> 4.4 mm	60.6	56.8			55.6	53.8

Diaphus arabicus

	Biobox 1 day	Biobox 1 night	Biobox 2 day	Biobox 2 night	Biobox 3 day	Biobox 3 night
< 5.0 mm	32.1	36.4	44.5	60.1	40.8	43.6
> 5.0 mm	39.7	50.2	55.3	72.3	52	48.9

Hygophum proximum

	Biobox 1 day	Biobox 1 night	Biobox 2 day	Biobox 2 night	Biobox 3 day	Biobox 3 night
< 3.5 mm	43.5	47.5	68.5	79.9	54.4	71.1
3.5–4.4 mm	45.2	56.3	69	84.7	57	66.5
> 4.4 mm	52.5	71.1	72.2	90.7	57	80.8

Vinciguerria nimbaria

	Biobox 1 day	Biobox 1 night	Biobox 2 day	Biobox 2 night	Biobox 3 day	Biobox 3 night
< 4.0 mm	42.3	49	52.2	55	47.5	48.8
4.0–6.9 mm	33.8	38.5	45.8	59.1	39.5	40.6
7.0–9.9 mm	29.3	30.7	45.9	53	35.5	39.2
> 9.9 mm	37.4	38.5	54.7	52.5	44.9	51.4

Fig. 9. Interregional comparison of the mean centres of mass of 4 highly abundant mesopelagic larval fish species in the northern Arabian Sea, classified for different size classes and for day and night sampling

which had a similar gradient of physical stratification. The extraordinarily low concentration of $<1\ l^{-1}$ for water deeper than 30 m in Bb 3 (shelf off Pakistan) might be responsible for the higher concentration of species and size classes just below the mixed layer in this area compared to the more spread-out pattern in Bb 1 (coast of Oman). Thus, prey density and distribution seems to be more critical for the vertical distribution of most species of fish larvae than the gradient of physical stratification.

Summarizing the results of this study, it appears that larvae of most mesopelagic fish species have 2 major boundaries for their vertical occurrence. They prefer to

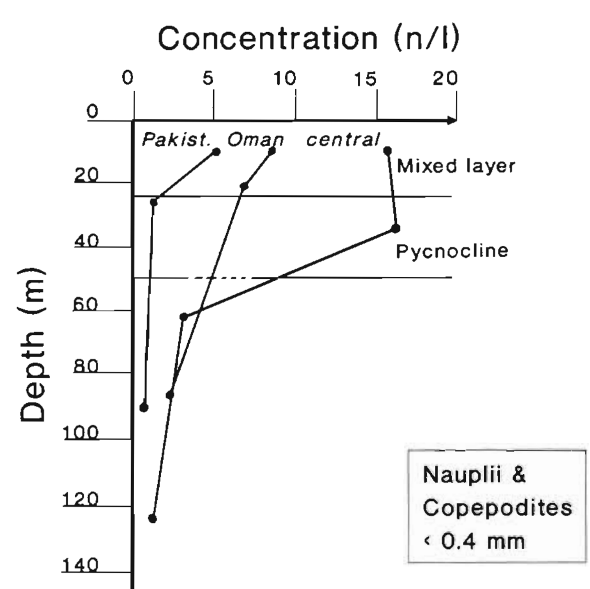


Fig. 10. Interregional comparison of mean vertical distribution profiles for the concentrations of potential fish larval prey organisms (nauplii and copepodites <0.4 mm) in the northern Arabian Sea during March–June 1987 (modified after Trinkaus 1992)

stay below the mixed surface layer, even if there are higher potential prey concentrations than elsewhere in the water column, but they do not occur deeper than depths with a minimum prey supply. If both boundaries are close together, as in Bb 3 (shelf off Pakistan), this could hypothetically lead to higher levels of competition, starvation, predation, and mortality within that narrow depth range. The lower mean length of the larvae observed in Bb 3 compared to Bb 2 might reflect a higher mortality in Bb 3. Slightly lower values for the nutritional condition of larval *Vinciguerria* sp. were reported for Bb 3 compared to Bb 2 elsewhere (Sieg 1992).

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