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A COMPARATIVE STUDY ON THE VERTICAL DISTRIBUTION OF FISH AND CEPHALOPOD LARVAE IN THREE HYDROGRAPHICALLY AND ECOLOGICALLY DIFFERENT AREAS OF THE ARABIAN SEA (PRELIMINARY RESULTS)

by

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ABSTRACT

Studies on the factors influencing the vertical distribution of fish larvae have generally been restricted to monofactorial analyses, neglecting the importance of reciprocal effects of factors. The present study is concerned with the importance of the 'structure of the water column' (physical stability and food availability), compared with the factor 'light intensity' on the vertical distribution of species and size classes of fish and cephalopod larvae in the subtropical pelagial. Zooplankton sampling took place during cruise 5/3 of 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, a central oceanic area, and a shelf area off the coast of Pakistan. All three areas were expected to have similar ichthyoplankton and cephalopod compositions and similar light conditions.

Preliminary results show that the vertical structure of the water column, especially the occurrence and the varying depth of the pycnocline, directly or indirectly (evaluation of data on the distribution of potential prey organisms is still in progress) determined the vertical distribution of fish and cephalopod larvae more strongly than the diurnal change of light intensity. Different larval species largely preferred different water depths, indicating endogenous adaptation mechanisms of the larvae to gradients in the water column. Cephalopods preferred shallower depths than fish larvae in all three areas, but both taxa had their center of distribution below the mixed surface layer closely related to the depth of the pycnocline. In the absence of a pycnocline, larvae appeared relatively close to the surface.

INTRODUCTION

The energy flow through the food chain in the pelagic environment of the oceans is, besides other factors, 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 and cephalopod larvae both are components of the pelagic food chain. Their chance for survival, a central question in recent fisheries research (see ROTHSCHILD, 1986), depends on spatial and temporal match or mismatch with larval food, competitors, and predators (CUSHING, 1975; LASKER, 1975; MAY, 1974; HUNTER, 1976; NELLEN, 1986). Physical factors play a major role in governing these regimes (ROTHSCHILD & OSBORN, 1988), and future investigations must strive to define the probable place of larvae in the water columnn in relation to abiotic and biotic factors.

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

The vertical distribution of fish larvae depends on the species themselves (e.g. AHLSTROM, 1959; LOEB, 1979; BREWER & KLEPPEL, 1986; FORTIER & HARRIS, 1989; RÖPKE, 1989), light intensity for diel vertical migration (see compendium by NEILSON & PERRY, 1990; RÖPKE, 1989), ontogenetic stage (e.g. NELLEN & HEMPEL, 1970; LOEB, 1979; FORTIER & LEGGETT, 1983; FORTIER & HARRIS, 1989), food availability (LASKER, 1975; ELLERTSEN et al., 1977; COOMBS et al., 1983; FORTIER & LEGGETT, 1984; FORTIER & HARRIS, 1989), hydrographic structure of the water column (e.g. AHLSTROM, 1959; LASKER, 1975; HEATH et al., 1988; SOUTHWARD & BARY, 1980; SOUTHWARD & BARRETT, 1983; KENDALL & NAPLIN, 1981). Intra- and interspecific competition for the same resources may also have a significant influence on the vertical distribution of fish larvae (FORTIER & HARRIS, 1989; RÖPKE, 1989).

To test the importance of water column structure (physical stability and food availability) and light intensity (day/night) for the vertical distribution of different species and size groups of fish and cephalopod larvae 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). An identical sampling program was undertaken in three presumedly hydrographically and ecologically different areas with similar light conditions and comparable species compositions.

This paper presents first results of the study, without having the complete overview yet, neither for larval species and length composition, nor for prey distribution. It mainly deals with the influence of the pycnocline on the vertical distribution of fish and cephalopod larvae.

MATERIALS AND METHODS

Three areas, named 'bioboxes', were sampled in the Arabian Sea (Indian Ocean) during the METEOR-cruise 5/3 (March 18 - June 9, 1987; Fig. 1) in the Arabian Sea (Indian Ocean) under sunny and clear weather conditions. Each biobox consisted of a grid with 5 x 5 stations and had side lengths of 80 x 40 nautical miles. Each grid was sampled twice in order to assess temporal, as well as spatial variability. Biobox 1 (at the coast of Oman) was sampled March 31 - April 2 and April 7-10; it represents a potential

upwelling area with a relatively mixed water column, and should provide high food densities for the larvae throughout a wide range of the water column. Biobox 2 (central oceanic area) was sampled April 30 - May 3 and May 8-10 and was expected to have a stable stratified water column with a sharp pycnocline and low production. Relatively good nutritional conditions for larvae have been expected for the mixed surface layer. Biobox 3 (shelf off Pakistan) was sampled May 23-26 and June 2-4 and was thought to be a typically coastal 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 intermediary between bioboxes 1 and 2. At present, evaluation is complete for both series of samples from Biobox 1 and for the first series from Bioboxes 2 and 3.

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 like frame supplied with a stabilizer for improved stability during the sampling process. The nets had a length of 6 m and a mesh size of 335 µm. The towing speed was 2 knots. The volume of water filtered was determined by an electric flowmeter mounted into the frame 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 ground. Table 1 shows the number of hauls and samples by depth strata and time of the day.

The samples were stored in a buffered 4 % formaldehyde/fresh water solution at 15 °C for one to two years before being analyzed. The plankton displacement volume was measured before all fish and cephalopod larvae were sorted out. Table 2 gives the raw data on the larvae caught and the volumes of water filtered. For computation of the standing stock under 1 m^2, the different depth strata were integrated. Vertical distribution patterns are presented as 'Notched-Box-and-Whisker-Plots' (MCGILL et al., 1978). The central box covers the middle 50 % of the data values, between the lower and upper quartiles. The 'whiskers' extend out to the extremes (minimum and maximum values), while the central line is at the median. A notch is added to each box corresponding to the width of the confidence interval (95 %) for the median. Outliers more than 1.5 times beyond the interquartile range are plotted as individual adjacent values. Variation in the vertical distribution of the net-biomass and in the larvae was evaluated by the depth of the center of density of the distribution (Zcd),

$$Zcd = \sum_{i=1}^{8} Pi * Zi$$

where Pi is the proportion of the density (concentration) of biomass or larvae in the ith depth strata and Zi is the average depth of the ith depth stratum.

Hydrographical data from all stations were taken by a CTD-system (Multisonde, ME, Kiel). The resulting profiles were compiled by RIBBE, 1988. Data on the depth of the pycnocline were taken from these profiles by fixing the value at the lower border of the upper mixed layer.

RESULTS

Hydrographic stratification of the water column

Typical vertical profiles for water temperature, salinity and density are shown in Fig. 2. The water column of Bb 1 (coast of Oman) was relatively unstratified, with a weak pynocline starting at about 30 m on average during the first sampling of the grid, and an totally unstratified water column on most stations during the second sampling. This indicates a change in the water body between the two experiments, probably due to lateral advection of water with higher salinity rather than upwelling. The hydrographic conditions in Bb 1 were relatively heterogenous. The Bb 2 (central oceanic) and 3 (shelf off Pakistan) were very similar and homogenous in terms of their vertical structure, both being rather typically oceanic, with a pronouced pycnocline. In Bb 2 it began at about 26 m on average and was very sharp, and in Bb 3 at 17 m. The expected influence of coastal low salinity water was not found at the shelf stations.

Standing stock of net-biomass, cephalopod and fish larvae

Bb 1 had the highest values of net-biomass (plankton displacement volume) standing stock. The mean value was 15.4 ml/m^2 during the first sampling and 11.1 ml/^{2} during the second (Tab. 3). The samples, especially of the first sampling in Bb 1, contained large numbers of siphonophores and salps, indicating relatively high and variable values for the biomass deriving from plankton displacement volumes. The standing stock of net biomass in Bb 2 and 3 averaged 6.8 and 6.1 ml/m^2, respectively (Tab. 3), and the variability was lower than in Bb 1. Thus, the stock of biomass was even higher in the central oceanic area (Bb 2) than in the shelf area off Pakistan (Bb 3).

The largest stock of fish larvae was found on the shelf off Pakistan (Bb 3), with 51.7 n/m^2 (Tab. 3). In the oceanic area (Bb 2) the mean value was 8.9 n/m^2, only. In Bb 1 (coast of Oman) the average was 34.4 fish larvae / m^2 during the first, and 24.9 n/m^2 during the second sampling. The highest variability between stations was again found in Bb 1. The most abundant families were the Myctophidae (Benthosema sp., Hygophum proximum, Diaphus sp., Bolinchthys longipes) and the Photichthyidae (Vinciguerria sp.).

Pronounced changes occurred in the cephalopod larval stock between the two passages of the station grid in Bb 1 (coast of Oman), the average standing stock declining from 2.3 to 0.8 larvae/m^2 (Tab. 3). A similar value was surveyed in Bb 2 with 1.2 n/m^2 and low variability between stations. The biggest cephalopod stock was found on the shelf off Pakistan (Bb 3) with 3.9 n/m^2. Stations with highest values were those at the edge of the shelf in Bb 1 and 3.

Fig. 3 illustrates a possible trend in the data for all stations. There were no systematic differences between day and night in the standing stocks of net-biomass and cephalopod larvae. Fish larvae were most abundant at night, possibly due to net avoidance during daylight. Extreme fluctuations were observed in the central oceanic area (Bb 2). Differences in sampling effort, concerning day/night hauls, don't allow a simple comparison of the different grids.

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

In Bb 1 (coast of Oman) the highest concentrations of net-biomass (10-30 ml/100 cbm) were found in the upper 50 m of the water column during both samplings (Fig. 4, top). The surface layers were avoided during the second trial. Higher values and higher variability during the first experiment were correlated with high concentrations of jelly organisms (siphonophores and salps), which were almost absent during the second sampling of the grid. Very low plankton concentrations were observed below 50 m during both samplings of the grid in Bb 1 (5-10 ml/100 cbm).

The biomass in Bb 2 was relatively low and very homogenous between stations (Fig. 4, bottom). The plankton consisted mostly of copepods and ostracods. A concentration peak (10 ml/100 cbm) was found between 40 and 50 m water depth. The gradient over the whole water column down to 150 m depth was low. Extremely low concentrations (<5 ml/100 cbm) were found between 0 to 30 m and 75 to 150 m depth. Similar results were gained in Bb 3, where copepods and chaetognaths were dominant. Again there was a peak (10-15 ml/100 cbm) at 40 to 50 m depth. The distribution pattern was similar as in Bb 2, but had a stronger gradient up to the surface and down to the bottom.

There were no day/night differences in the distribution patterns of the net-biomass during sampling in the three Bioboxes. This is also true for the following group, the cephalopod larvae.

Assessment of the vertical distribution patterns of cephalopod larvae (Fig. 5) are difficult, because of their low abundance. Highest concentrations (3-5 n/100 cbm) were found between 30 and 50 m depth. Densities in the surface layers were very low (1-2 n/100 cbm). Almost no cephalopod larvae was caught below a depth of 75 m. The low numbers caught during the second sampling of the grid in Bb 1 are more evenly distributed than those of the first.

Concerning the vertical distribution patterns of fish larvae there were prominent differences between the bioboxes (Fig. 6, 7). In Bb 1 (coast of Oman) fish larvae had a concentration peak (70 n/100 cbm) between 40 and 50 m depth (Fig. 6, top). Very low concentrations (<10 n/100 cbm) were found in the surface layer and below 75 m. Few larvae were caught below 100 m. In the open ocean (Bb 2) the concentration maximum (10 n/100 cbm) lay between 60 and 75 m depth (Fig. 7, top left). Even between 100 and 150 m depth relatively large numbers (2-10 n/100 cbm) of fish larvae were caught. Almost no larvae were found at the surface (0-30 m). Concentrations computed from night hauls were two to three times higher than those from day hauls in both areas (Fig. 6 center and bottom and Fig. 7 left center and bottom). This again indicates net avoidance by fish larvae in the Bb 1 and 2. The influence of this error on the vertical distribution patterns should be low, because the larvae seem to make no diel vertical migration.

Bb 3 (coast off Pakistan) differs from Bb 1 and 2 by having a broader distribution pattern in fish larvae (Fig. 7, right top). Concentrations (100-130 n/100 cbm) were constantly high between 30 and 60 m depth. Very low values were found at the surface between 0 and 20 m (30 n/100 cbm) and below 75 m depth (0-10 n/100 cbm). The larvae caught in this area were relatively small. Differential catchability between day and night hauls was not registrated, but the larvae seem to migrate upward at night (Fig. 7, right center and bottom).

Center of density of net-biomass, cephalopod and fish larvae

The 'Centers of Density' (Cd) of the three groups and the depth of the pycnocline are shown for each single haul in Fig. 8. The medians and interquartile ranges of the raw data on the Cd are summarized in Table 4.

During the first sampling of Bb 1 (coast of Oman) the beginning of the pycnocline varied around a depth of about 30 m on average. In the second experiment a pycnocline was mostly absent, with the exception of few stations in the north. The depths of the Cd for the net-biomass, the cephalopod and the fish larvae lay below the pycnocline at almost all stations and varied almost parallel to its depth. The three planktonic groups were distributed very closely to the pycnocline during the first passage of Bb 1. The variability between stations was higher during the second sampling, because the single populations were more strongly spread throughout the water column. In stations without pycnocline fish and cephalopod larvae were distributed nearer to the surface. Cephalopods were distributed highest in the water column (38/32 m depth) and were closely associated with the pycnocline during the first experiment. Fish larvae lived about 10 m deeper (48/43 m depth). The Cd of the fish larvae was closely correlated with the depth of the pycnocline in experiment one. The variability of the Cd of the fish larvae increased with the break-up of the pycnocline during the second sampling. The net-biomass had an intermediate position in the water column (43 m depth) during the first trial and was correlated to the depth of the pycnocline. In the second trial the net-biomass had its cd around 55 m. This was mainly produced by those unstratified stations with single Cds below 60 m depth.

In the central oceanic area (Bb 2) the pycnocline began at an average depth of 26 m (Fig. 8). It tended to be deeper towards the eastern stations. Cephalopods again held the upper position in the water column with an average depth of 38 m, the same depth as in the first passage of Bb 1. Their Cds were correlated with the depth of the pycnocline. This is not true for the net-biomass and the fish larvae. They had average depths of 56 and 72 m, far below the pycnocline. The variability of the Cd was low in all three groups. The light intensity (day/night) did not have any obvious influence on the vertical distribution of the organisms.

The upper mixed layer in Bb 3 (shelf off Pakistan) reached to a depth of 17 m with little variation (Fig. 8). The cephalopod and fish larvae as well as the net-biomass were extremely tight distributed, showing very low variability. The upper position was again prefered by the cephalopods (on average 39 m). Fish larvae followed only 3 m deeper at an average depth of 42 m, and the net-biomass was found at about 49 m.

Linear regressions between the Center of Density (Cd) of the different populations and the depth of the pycnocline were computed for Bb 1 and Bb 2 (Fig. 9, 10), and the correlation coefficient was tested by the T-test ($p < 0.05$). A statistically significant linear correlation was found for cephalopod and fish larvae in Bb 1 (Fig. 9). According to these results, a downward shift of the pycnocline of e.g. 10 m would result in a distribution of cephalopod and fish larvae of 6-7 m deeper. The net-biomass would be 3-4 m deeper. Similar results were obtained for Bb 2 (Fig. 10), but the correlation is statistically significant only for the cephalopods. More data on the Cd 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 and fish larvae, but in contrast, the net-biomass would remain unaffected.

Data on selected species in the central oceanic biobox 2

Table 5 gives the raw data on the three most abundant fish larval taxa in Bb 2. These were Diogenichthys panurgus, Hygophum proximum, and Vinciguerria sp.. They had highly diverse distribution patterns. Larvae of Hygophum proximum preferred relatively great water depths (Fig. 11, left), while those of Vinciguerria sp. were mainly distributed in moderate water depths (Fig. 11, right). Again there was better catchability of the larvae during the night than during daytime. A diel vertical migration was not detected at the species level. Figure 12 illustrates that the species had very distinct vertical preferences in the oceanic area, down to depths of about 100 m in the case of Diogenichthys panurgus. None of these species had its main distribution in the upper mixed layer. The depth of the pycnocline seems to be an important factor for their vertical distribution. The three species showed a trend towards a deeper distribution with increasing depth of the pycnocline (Fig. 13). This trend is not statistically significant.

DISCUSSION

The main aim of this comparative study is to test the importance of the the water column structure (physical stability and food availability) and the light intensity (day/night) for the vertical distribution and its variability in different species and size classes of fish and cephalopod larvae in the subtropical pelagial. The three areas selected had a more or less oceanic character, making it difficult, to extract comparative results. Nevertheless, first results on the influence of the pycnocline and the light intensity on the vertical distribution are promising for future analysis of our material.

The occurrence and position of the pycnocline (thermocline) is known to be a major factor in the vertical distribution of plankton organisms. Mostly, fish larvae have been found to live above or in the thermocline, using the higher prey concentrations there. AHLSTROM (1959) found that 12 out of 15 species of 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 & NAPLIN (1981) for larvae in the Middle Atlantic Bight. Most species favoured the depth range of 0 to 30 m, when the thermocline lay between 20 and 30 m. SOUTHWARD & BARY (1980) and LOEB (1979) 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 good 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 absence of thermal stratification, food and fish larvae will be distributed more evenly. HEATH et al. (1988) show this for herring (Clupea harengus) larvae. SOGARD et al. (1987) and RÖPKE (1989) found different species distributed all over the low or non stratified water column. Present results on Bb 1 (coast of Oman), which was less stratified than the other areas confirm these findings.

Food concentrations in the present study appear to be highest in the layer above the pycnocline in the oceanic area (Bb 2) and in the shelf area off Pakistan (Bb 3) (TRINKAUS, pers. comm.). The distribution of fish larvae below the pycnocline at lower food concentrations might be a species specific phenomenon. Most larvae caught in this study belong to the Myctophidae. AHLSTROM (1959) and LOEB (1979) described larvae belonging to this family as deep-standing, indicating early adaptations to their later life in the mesopelagial. On the other hand cephalopod larvae were found in close relation to the pycnocline. They seem to take over the role normally assigned to fish larvae.

However, the pycnocline is an important cause of variance in the vertical distribution of fish and cephalopod larvae in this subtropical area. The light intensity (day/night) seems to have no influence, because significant diurnal vertical migration did not occur. 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 to be more likely. The net-biomass, which can be a measure for the competitor/predator field in this study, seems to be relatively independent from small scale variation of the pycnocline depth.

Factors other than the pycnocline, such as the species and size composition of the fish larvae, probably had a significant influence on the vertical distribution of fish larvae, too, 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 live in deeper water (AHLSTROM, 1959; LOEB, 1979) than coastal species like percoids. Ontogenetic vertical migrations to minimize predation and starvation risks (FORTIER & HARRIS, 1989) must also be taken into account. With increasing length postlarvae were distributed proportionally to their food resources (Ideal Free Distribution model; FRETWELL & 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.

Preliminary results (TRINKAUS, pers. comm.) show, that the concentration of fish larval food was higher by a factor of 5 to 10 in the central oceanic area than in the shelf area off Pakistan, whereas 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 indicate that food was not limiting in the oceanic area, and the stratification of the fish larval species should thus be due to specialization and not due to 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. These results show that a combination of genetically fixed depth range selection and active search for best feeding conditions within this range seems to be one mechanism for adaptation to variable conditions in the water column.

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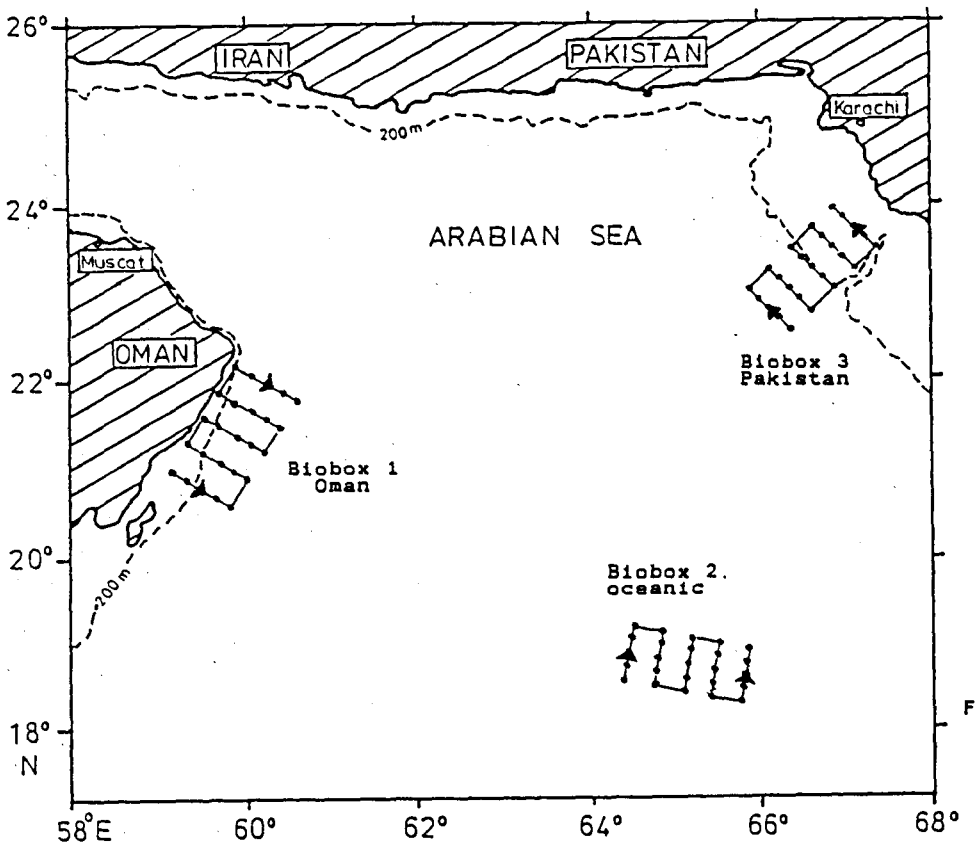


Fig. 1: Area of research during METEOR-cruise 5/3 into the Indian Ocean (Arabian Sea). Position of the three bioboxes.

	Biobox 1/1 Oman	Biobox 1/2 Oman	Biobox 2/1 oceanic	Biobox 3/1 Pakistan
Hauls N day/twilight/night	25 12/4/9	23 7/2/14	21 8/3/10	22 13/3/6
Samples N day/twilight/night	175 83/28/64	158 53/13/92	156 61/22/73	162 98/20/44
Samples per depth interval (m): (day/twilight/night)				
0-20(15) No.1	9/4/8	6/2/12	7/2/8	18/5/7
(15)20-30 No.2	11/4/9	5/2/13	8/3/9	12/3/5
30-40 No.3	10/4/9	7/2/13	7/2/8	13/2/5
40-50 No.4	11/4/9	7/2/12	8/3/8	13/3/5
50-60 No.5	11/3/8	7/2/11	8/3/10	12/2/6
60-75 No.6	11/3/7	7/1/11	8/3/11	11/2/6
75-100 No.7	10/3/7	7/1/10	8/3/9	11/2/6
100-150 No.8	10/3/7	7/1/10	7/3/10	8/1/4

Tab. 1: Number of hauls and samples taken during four passages of the station grids in the three Bioboxes.

Tab. 2: Raw data on the filtered volume of water, plankton volume, and caught larvae of fishes and cephalopods during four passages of the station grids in the three Bioboxes.

	Biobox 1/1 Oman	Biobox 1/2 Oman	Biobox 2/1 oceanic	Biobox 3/1 Pakistan
Filtered volume (cbm) day/twilight/night	58337 29162/9782/19393	49920 17279/3203/29438	56799 19723/7744/29332	58690 34975/6734/16981
Plankton volume (ml) day/twilight/night	8561 3766/1140/3655	5122 1183/1317/2622	2694 885/438/1371	3085 1854/391/840
Fish larvae N day/twilight/night	17083 6643/2404/8036	12545 1578/1355/9612	4826 798/617/3411	27457 16499/2410/8548
Cephalopod larvae N day/twilight/night	1599 598/308/693	426 87/19/320	931 256/123/552	1515 1166/61/288
Depth interval (m): (day/twilight/night)				
0-20(15) No.1				
Filtered vol. (cbm)	1617/819/1559	1580/316/2224	1587/375/1832	4726/967/1584
Plankton vol. (ml)	662/200/500	96/25/234	46/27/93	205/47/72
Fish larvae	129/34/369	49/360/857	12/1/17	615/428/573
Cephalopod larvae	8/12/88	6/3/62	26/5/52	69/9/79
(15)20-30 No.2				
Filtered vol. (cbm)	2939/894/1806	1296/304/3637	1953/1159/3628	2635/2120/1445
Plankton vol. (ml)	601/263/611	132/63/461	80/70/224	200/133/99
Fish larvae	1021/281/808	137/414/1332	18/12/94	1315/634/1476
Cephalopod larvae	77/52/130	15/7/87	26/16/100	60/27/46
30-40 No.3				
Filtered vol. (cbm)	2951/1208/1722	1378/352/3407	1427/417/1758	2971/412/1022
Plankton vol. (ml)	514/128/770	184/124/529	87/45/155	327/41/108
Fish larvae	1177/511/1760	363/148/2031	25/9/143	4075/302/1431
Cephalopod larvae	120/60/176	25/3/75	35/23/104	200/6/72
40-50 No.4				
Filtered vol. (cbm)	2219/2682/1770	1264/392/2174	1605/553/1656	3099/841/1117
Plankton vol. (ml)	461/154/644	196/120/385	142/68/159	429/106/89
Fish larvae	1672/188/2108	512/221/2172	128/19/223	3792/622/1229
Cephalopod larvae	182/7/171	22/1/48	68/31/108	304/14/41
50-60 No.5				
Filtered vol. (cbm)	2361/642/1593	1207/362/2115	1825/678/2202	2706/368/2189
Plankton vol. (ml)	327/62/375	108/946/247	143/75/224	289/30/148
Fish larvae	959/121/1107	290/169/1093	171/97/371	3362/271/1830
Cephalopod larvae	101/7/51	17/3/14	47/27/106	323/1/31
60-75 No.6				
Filtered vol. (cbm)	4217/700/2631	2807/314/3967	2165/864/3164	3390/481/2791
Plankton vol. (ml)	563/132/234	113/12/264	164/58/229	205/16/150
Fish larvae	1016/572/1128	160/34/1040	161/200/916	2548/100/1542
Cephalopod larvae	78/101/49	2/2/18	28/18/49	183/2/13
75-100 No.7				
Filtered vol. (cbm)	4602/807/2963	2954/362/4485	3450/1268/4943	6779/660/3217
Plankton vol. (ml)	299/97/255	167/9/246	114/44/137	130/11/110
Fish larvae	548/544/645	42/8/809	190/189/956	691/39/361
Cephalopod larvae	25/65/19	0/0/11	16/3/20	22/2/2
100-150 No.8				
Filtered vol. (cbm)	8256/2030/5349	4793/801/7429	5711/2430/10149	8669/885/3618
Plankton vol. (ml)	339/104/266	187/18/256	109/51/150	69/7/64
Fish larvae	121/153/111	25/1/278	93/90/691	101/14/106
Cephalopod larvae	7/4/9	0/0/5	10/0/13	5/0/4

Tab. 3: Mean values of the standing stock of the plankton volume, the fish and the cephalopod larvae during sampling of four grid passages in the three Bioboxes. The interquartile range indicates the variability of the raw data.

	Standing stock			
	Biobox 1/1 Oman	Biobox 1/2 Oman	Biobox 2/1 oceanic	Biobox 3/1 Pakistan
Plankton volume (ml/m^2)				
Median	15.4	11.1	6.8	6.1
Interquartile range	6.3	4.2	1.6	1.5
Fish larvae (n/m^2)				
Median	34.4	24.9	8.9	51.7
Interquartile range	32.3	31.9	9.6	43.4
Cephalopod larvae (n/m^2)				
Median	2.3	0.8	1.7	1.1
Interquartile range	3.2	1.0	1.2	3.9

Tab. 4: Mean values of the depth of the pycnocline and the depth of center of density of the plankton volume, the fish and the cephalopod larvae during sampling of four grid passages in the three Bioboxes. The interquartile range indicates the variability of the raw data.

	Biobox 1/1 Oman	Biobox 1/2 Oman	Biobox 2/1 oceanic	Biobox 3/1 Pakistan
Pycnocline (m)				
Median	30	--	26	17
Interquartile range	14	--	5	5
	Depth of center of density (m)			
Plankton volume				
Median	42.9	54.8	56.2	48.5
Interquartile range	13.7	13.0	7.7	12.2
Fish larvae				
Median	48.0	43.4	71.7	41.6
Interquartile range	18.3	26.6	12.2	11.2
Cephalopod larvae				
Median	38.2	32.1	37.8	39.0
Interquartile range	14.8	24.8	11.4	11.8

Tab. 5: Raw data on caught larvae of Diogenichthys panurgus, Hygophum proximum, and Vinciguerria sp. during passage 1 of the station grid in Biobox 2 (oceanic).

		Diogenichthys panurgus n	Hygophum proximum n	Vinciguerria sp. n
All depth intervals day/twilight/night		273 94/59/120	2901 369/473/2059	413 62/14/337
Depth interval (m): (day/twilight/night)				
0-20(15)	No.1	1/0/0	1/1/1	1/0/8
(15)20-30	No.2	0/0/0	3/4/2	6/0/29
30-40	No.3	1/0/1	7/0/3	9/5/44
40-50	No.4	1/1/1	60/1/9	23/2/87
50-60	No.5	0/7/4	111/87/122	11/3/83
60-75	No.6	5/4/2	91/182/656	6/3/55
75-100	No.7	29/26/45	86/158/742	6/0/20
100-150	No.8	57/21/87	10/60/524	0/1/11

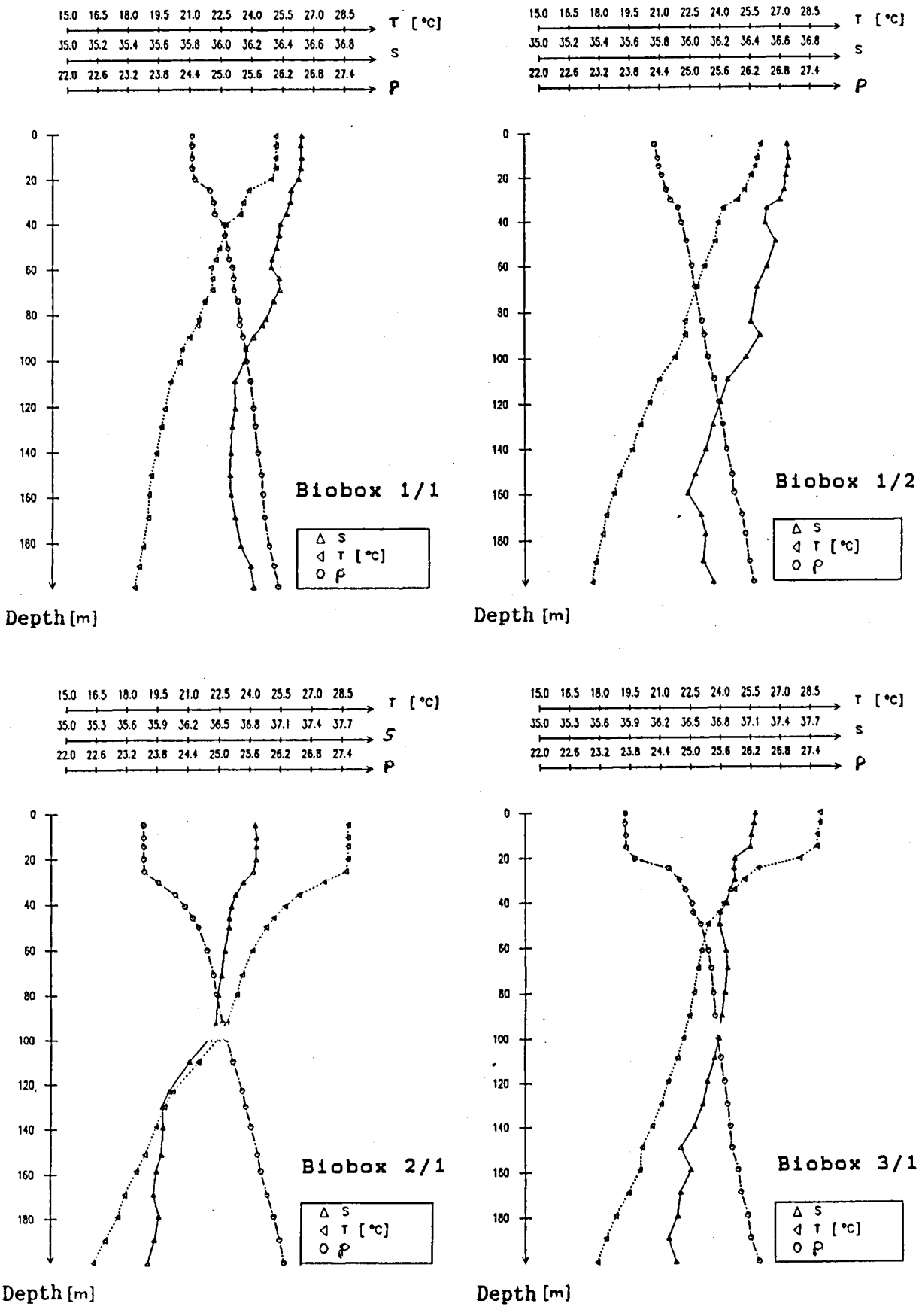
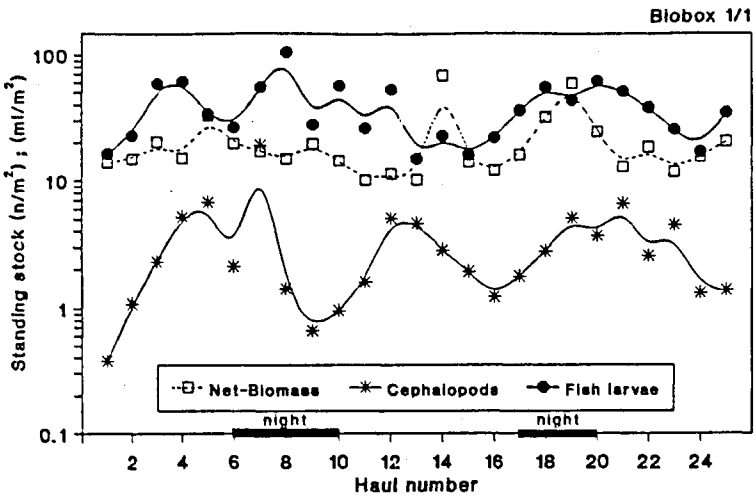
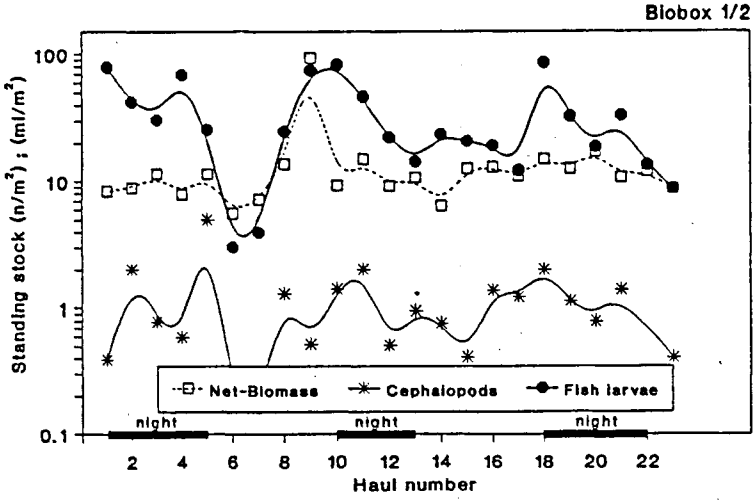
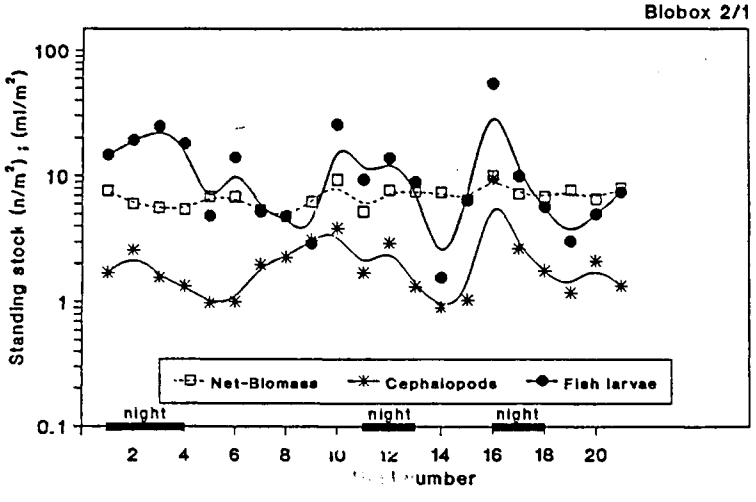


Fig. 2: Hydrographic conditions in the water column. Four typical stations are selected to show the vertical structure of temperature, salinity and density during four passages of the station grids in the three Bioboxes.







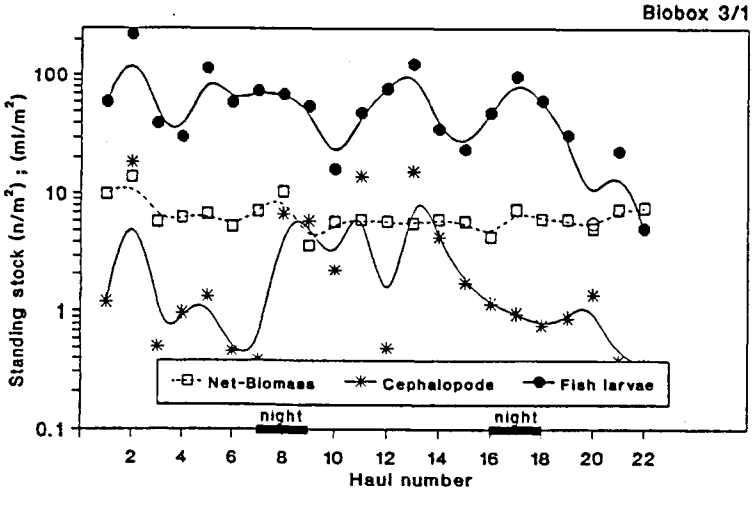


Fig. 3: Standing stock of net-biomass, cephalopod and fish larvae on the different stations of the four samplings in the three bio-boxes. The smoothed lines (moving average) indicate a possible trend in the data. Note the logarithmic scale of the vertical axis.

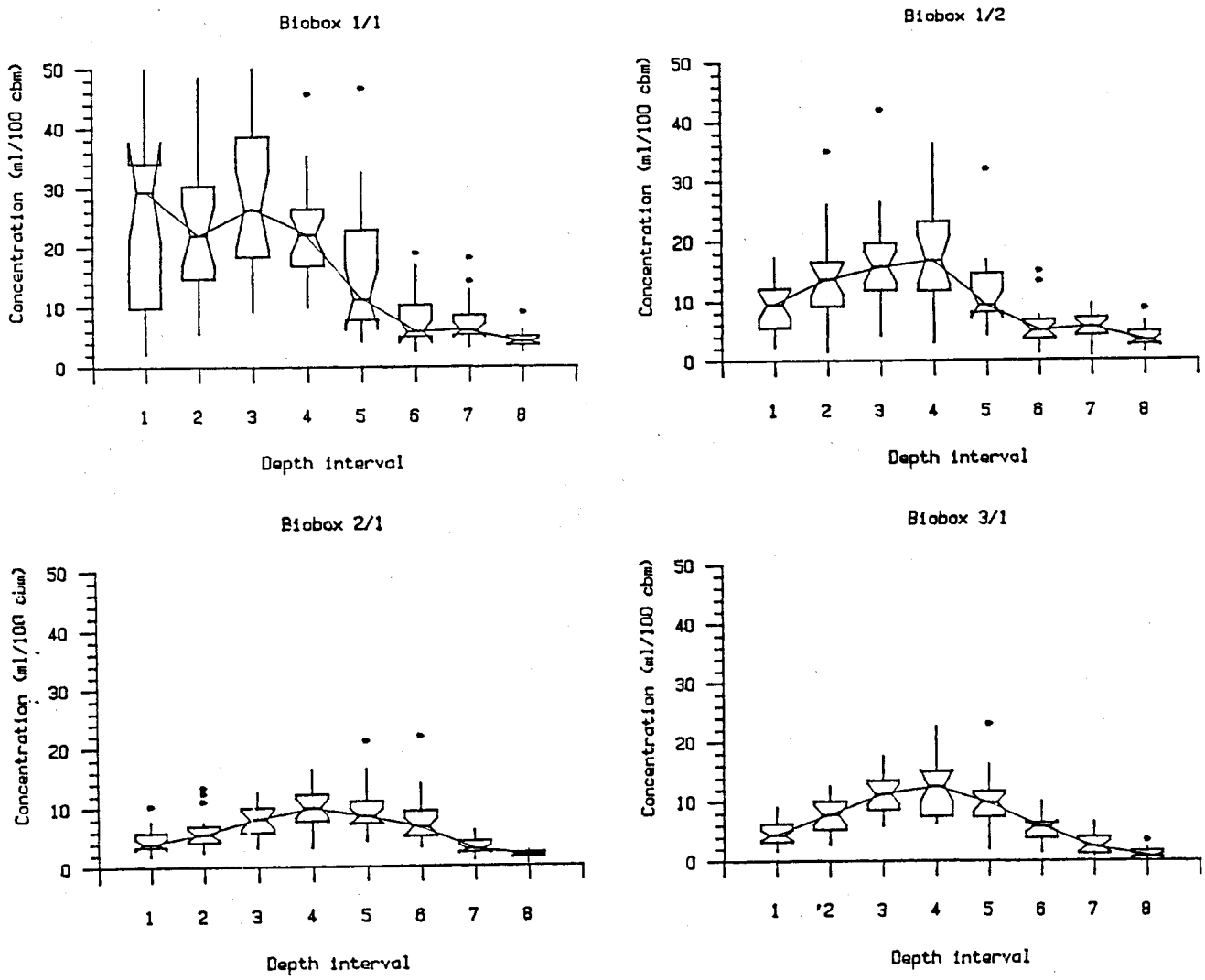


Fig. 4: Mean vertical distribution of the concentration of the net-biomass during four passages of grid sampling in the three bioboxes (Depth intervals ascending: 0-15(20), 15(20)-30, 30-40, 40-50, 50-60, 60-75, 75-100, 100-150 m). The medians are connected by a line (The Notched-Box-and-Whisker-Plot is explained in the text).

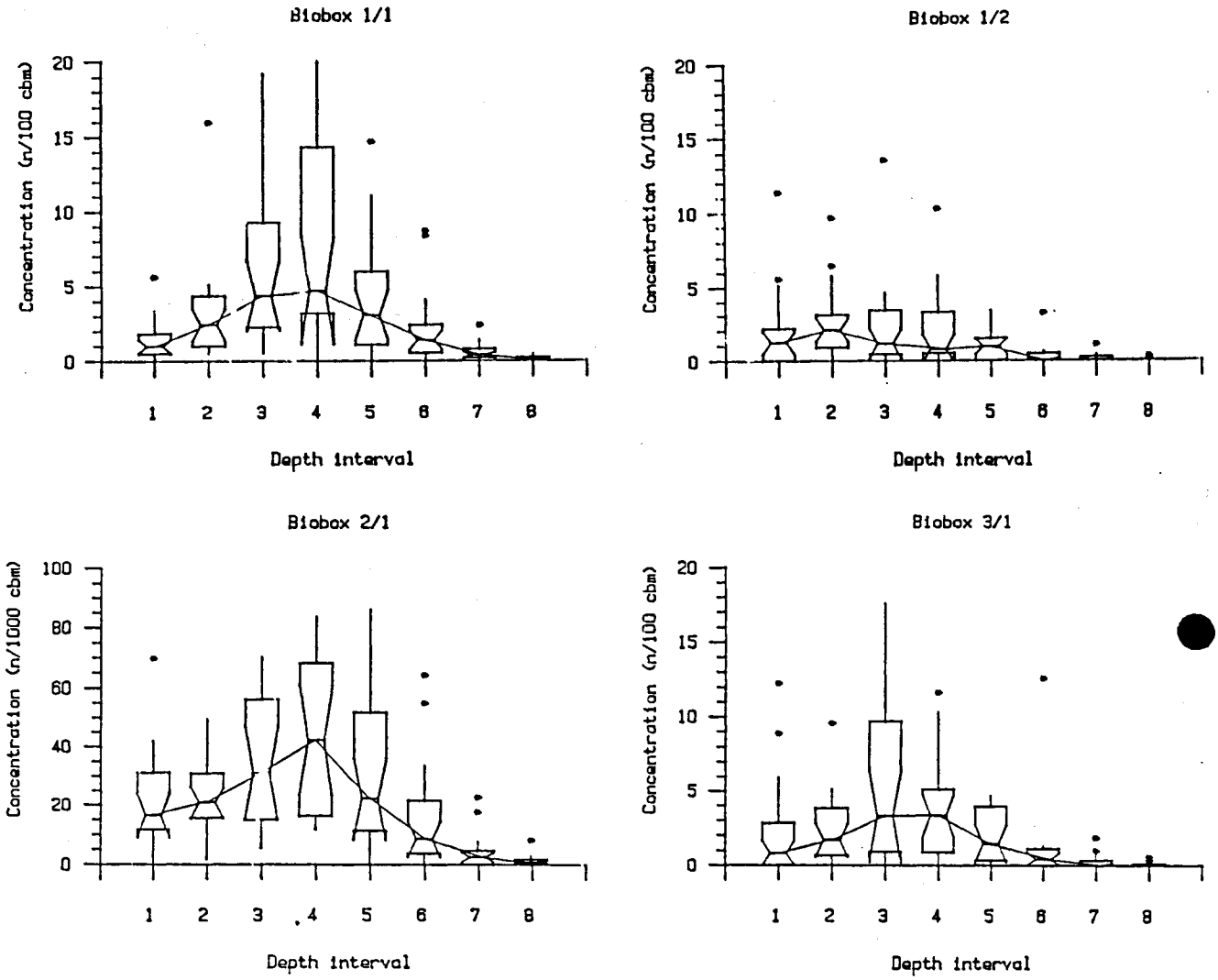


Fig. 5: Mean vertical distribution of the concentration of cephalopod larvae during four passages of grid sampling in the three bioboxes (Depth intervals ascending: 0-15(20), 15(20)-30, 30-40, 40-50, 50-60, 60-75, 75-100, 100-150 m). Note the different scales of the vertical axis. The medians are connected by a line (The Notched-Box-and-Whisker-Plot is explained in the text).

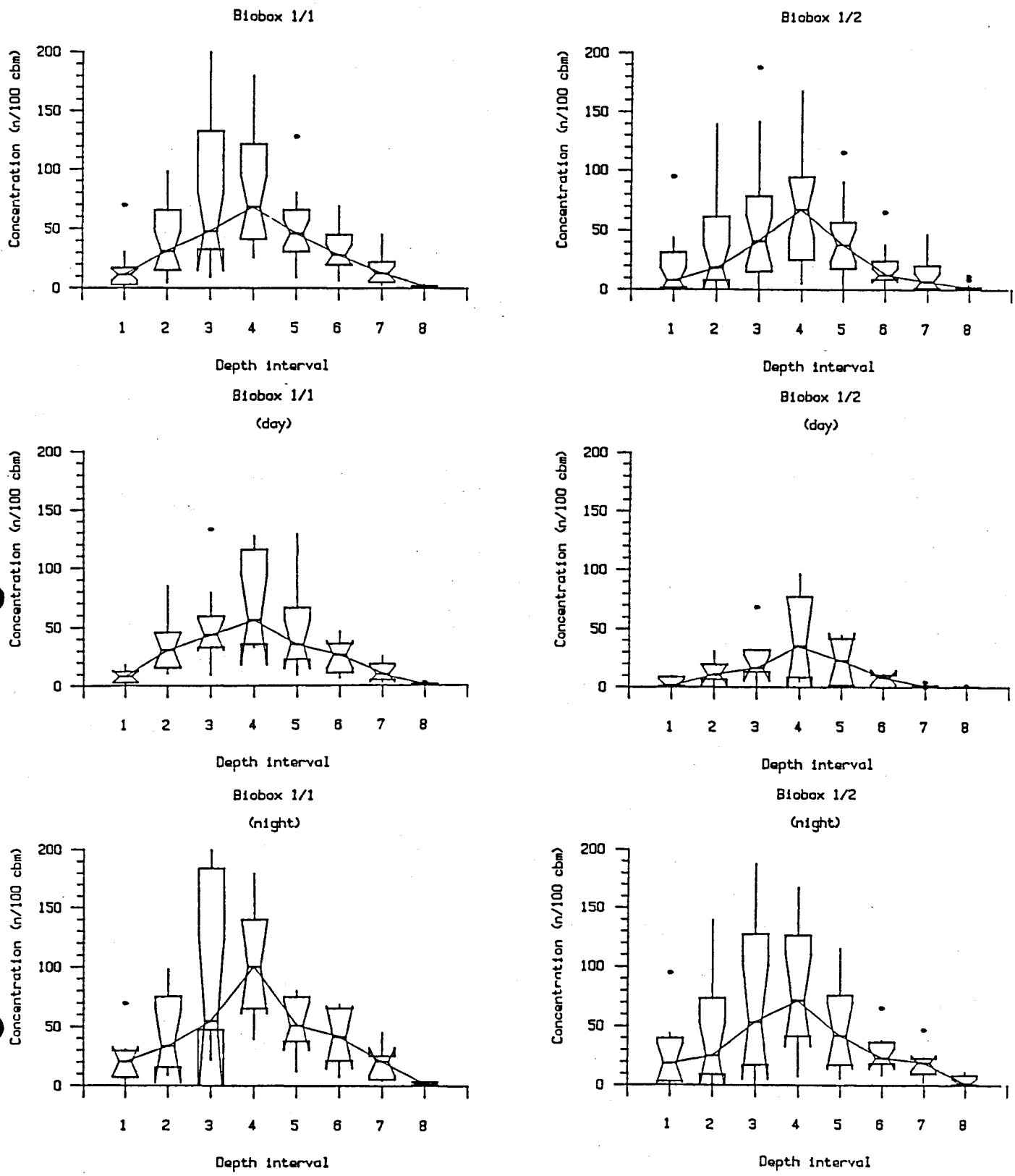


Fig. 6: Mean vertical distribution of the concentration of fish larvae during two passages of grid sampling in Biobox 1 (Oman). Day and night stations are presented separately (Depth intervals ascending: 0-15, 15-30, 30-40, 40-50, 50-60, 60-75, 75-100, 100-150 m). The medians are connected by a line (The Notched-Box-and-Whisker-Plot is explained in the text).

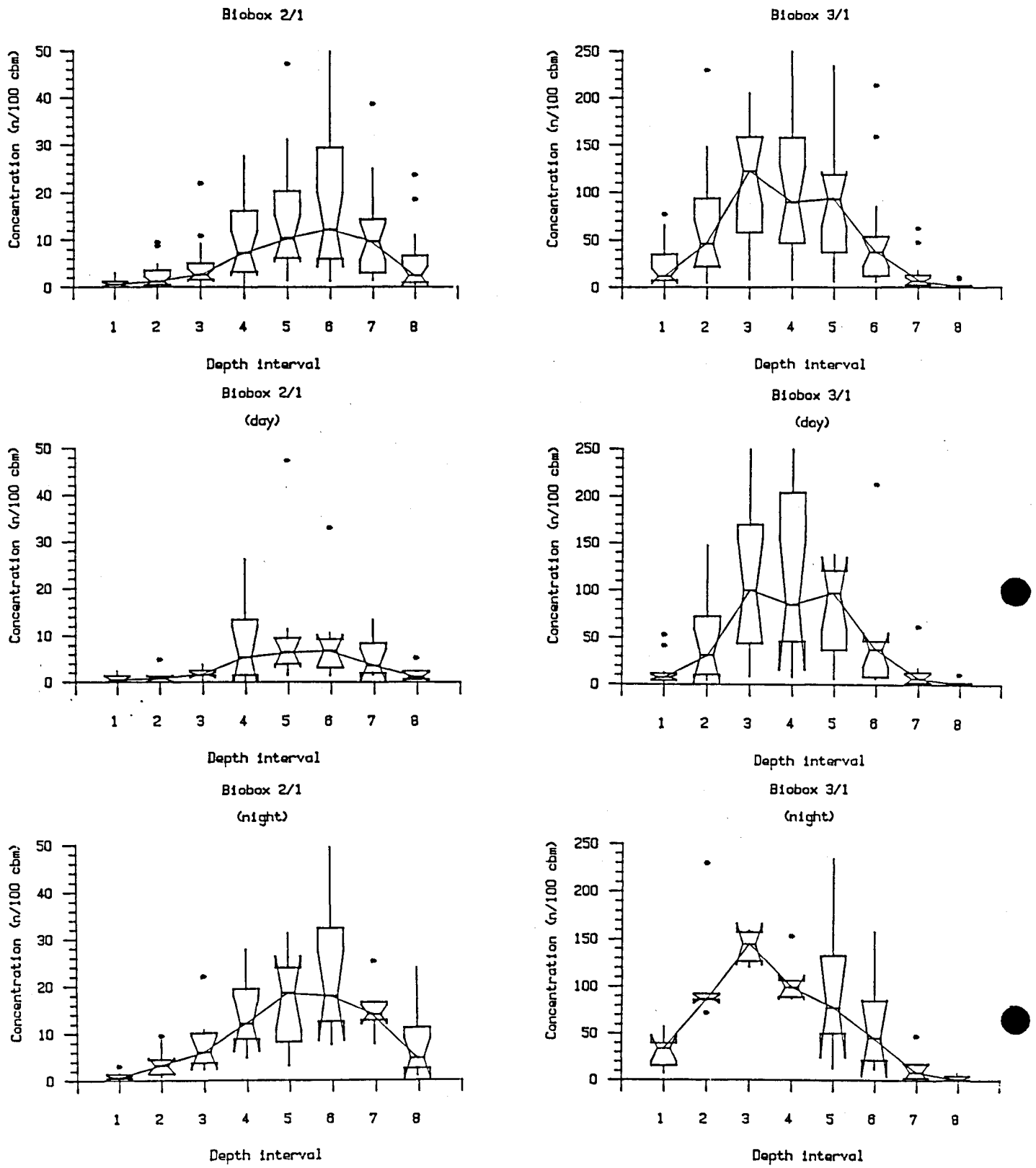
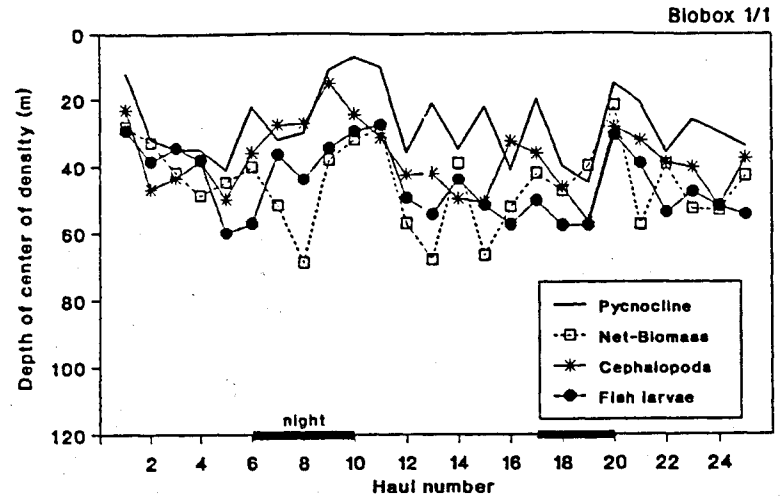
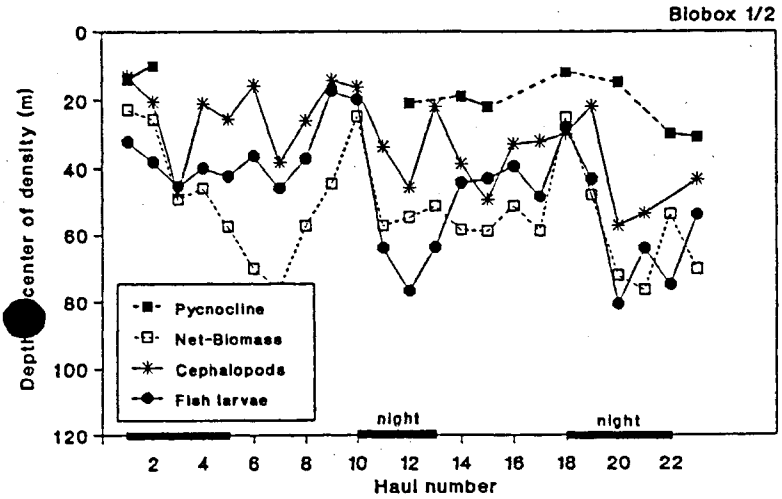
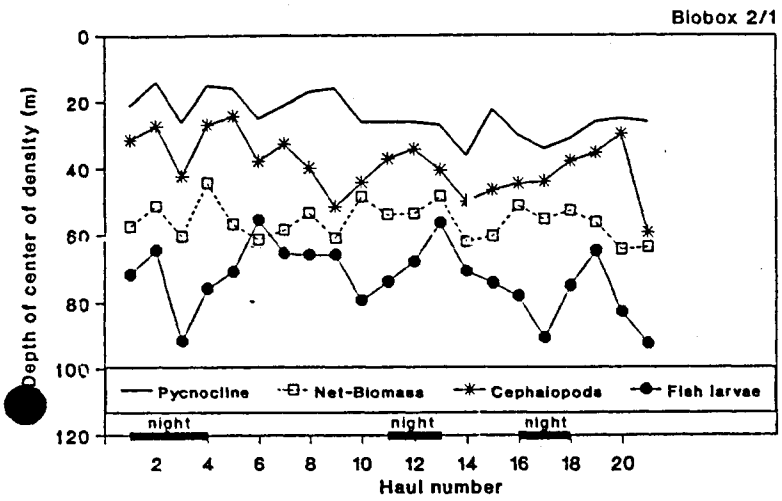


Fig. 7: Mean vertical distribution of the concentration of fish larvae during grid sampling in Biobox 2 (oceanic) and 3 (Pakistan). Day and night stations are presented separately (Depth intervals ascending: 0-20, 20-30, 30-40, 40-50, 50-60, 60-75, 75-100, 100-150 m). The medians are connected by a line (The Notched-Box-and-Whisker-Plot is explained in the text).







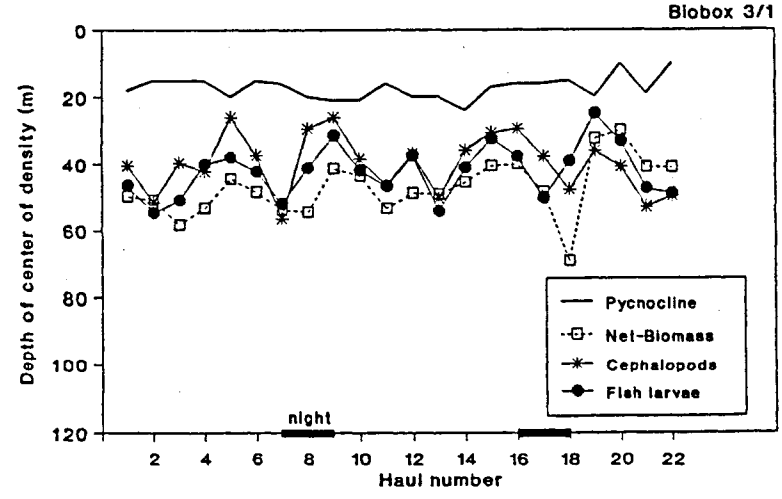


Fig. 8: The depth of the center of density of the net-biomass, the cephalopod and fish larvae on different stations during the four grid passages in the three bioboxes. Note also the position of the pycnocline.

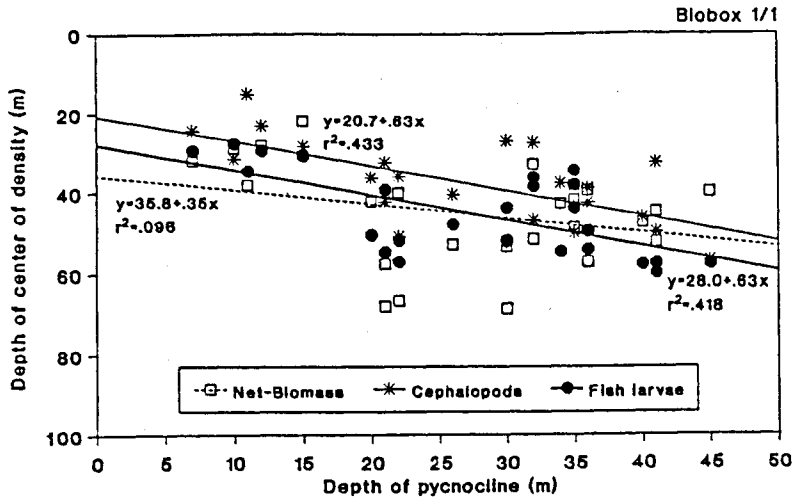


Fig. 9: Linear regression between depth of pycnocline and depth of center of density for the net-biomass, cephalopod and fish larvae during the first passage of the station grid in Biobox 1 (Oman). The correlation is statistically significant (D.F. = 23; $p < 0.05$) for cephalopod and fish larvae.

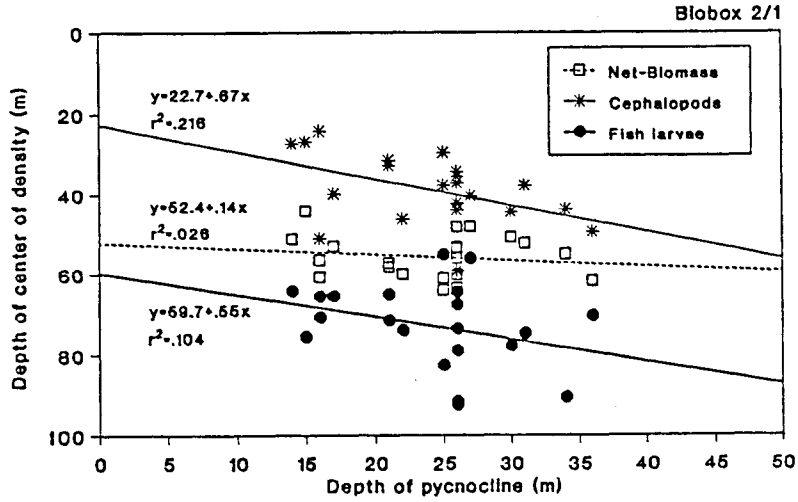


Fig.10: Linear regression between depth of pycnocline and depth of center of density for the net-biomass, cephalopod and fish larvae during the first passage of the station grid in Biobox 2 (oceanic). The correlation is statistically significant (D.F. = 19; $p < 0.05$) for cephalopods only.

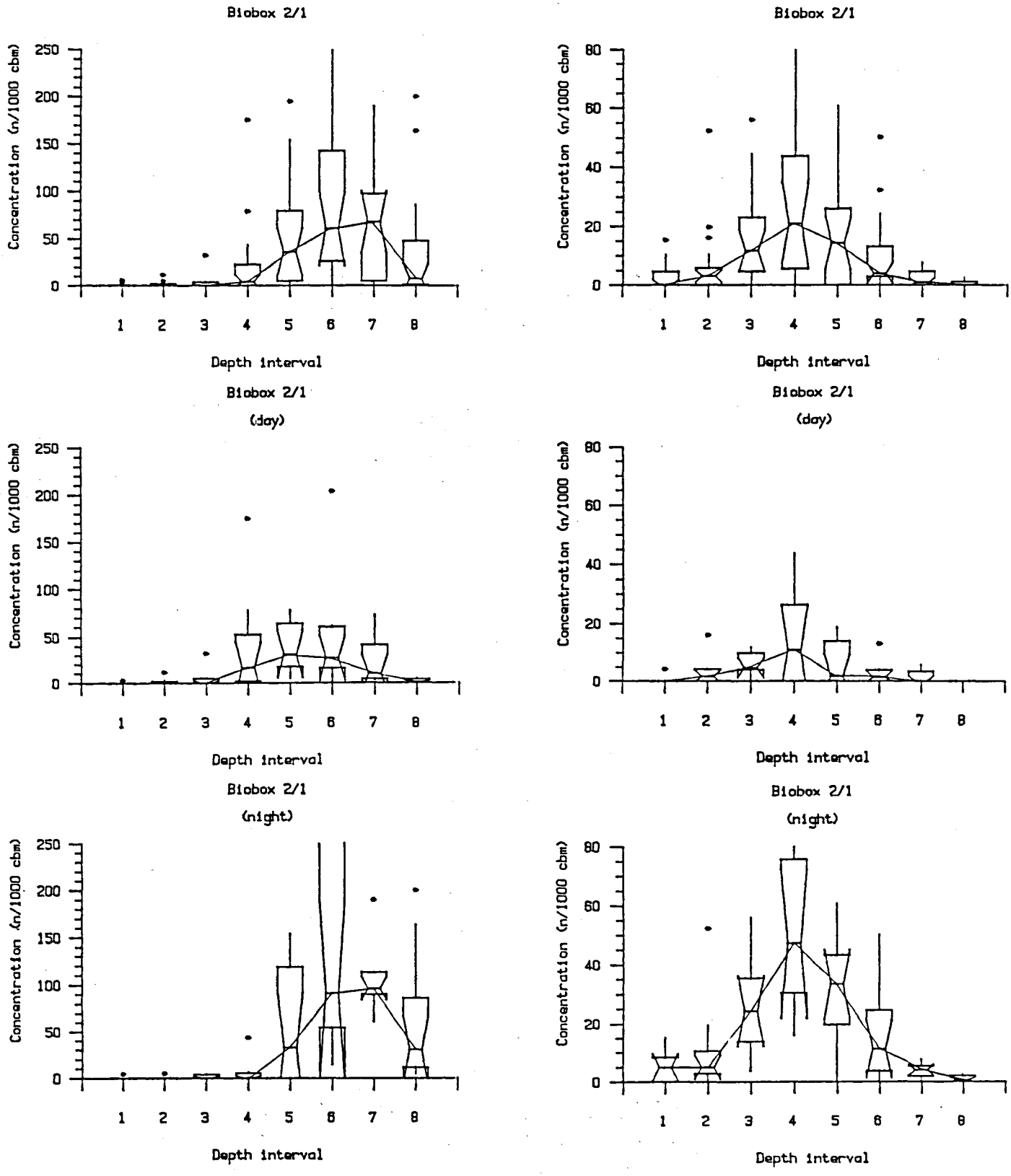


Fig.11: Mean vertical distribution of the concentration of larvae of Hygophum proximum (left) and Vinciguerria sp. (right) during the first passage of the station grid in Biobox 2 (oceanic). Day and night stations are presented separately (Depth intervals ascending: 0-20, 20-30, 30-40, 40-50, 50-60, 60-75, 75-100, 100-150 m). The medians are connected by a line (The Notched-Box-and-Whisker-Plot is explained in the text).

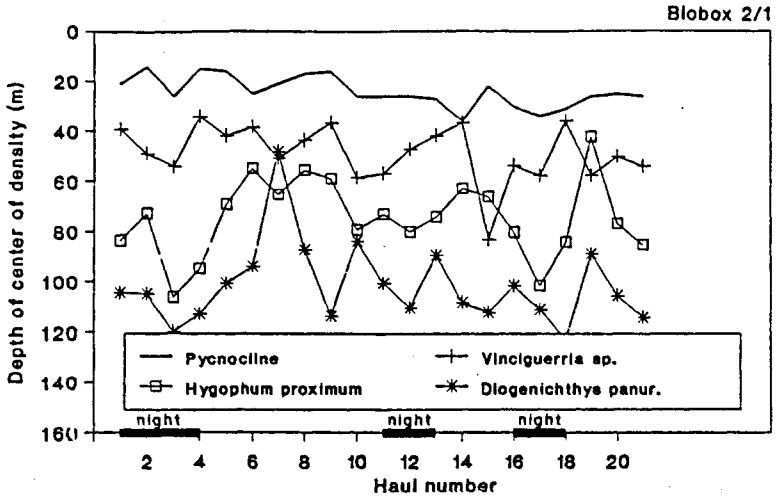


Fig.12: The depth of the center of density of larvae of Vinciguerria sp., Hygophum proximum, and Diogenichthys panurgus on different stations of the first passage in Biobox 2 (oceanic). Note also the position of the pycnocline.

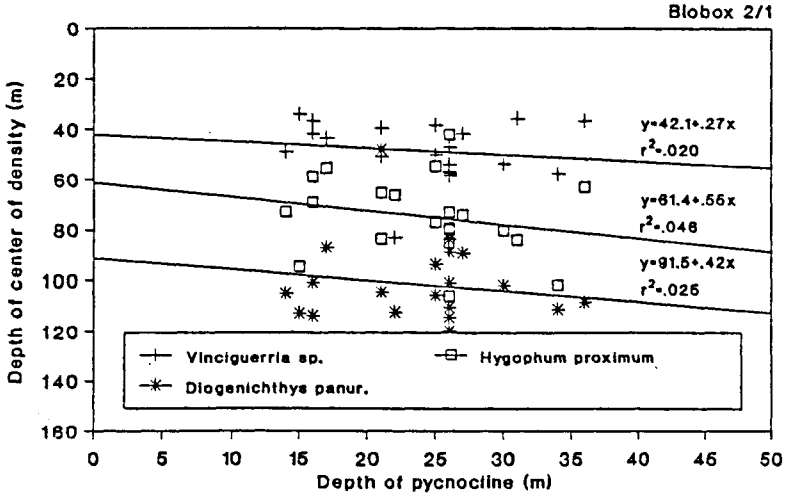


Fig.13: Linear regression between depth of pycnocline and depth of center of density for larvae of Vinciguerria sp., Hygophum proximum, and Diogenichthys panurgus during the first passage of the station grid in Biobox 2 (oceanic). The correlation is statistically not significant (D.F. = 19; $p < 0.05$) in all three cases.