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Distribution Patterns of the Early Life Stages of Pelagic Cephalopods in Three Geographically Different Regions of the Arabian Sea

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Abstract: The present study describes the distribution patterns of the early life stages of pelagic cephalopods in three different areas of the Arabian Sea, Indian Ocean. Specimens were collected during the *Meteor*-expedition to the Indian Ocean in 1987 by means of multiple opening/closing nets in the top 150m of the water column. A total of 3836 specimens were caught at 67 stations. The following taxa were prevailing: *Sthenoteuthis oualaniensis* (Ommastrephidae), *Abralia marisarabica* and *Abraliopsis lineata* (Enoploteuthidae), *Onychoteuthis banksi* (Onychoteuthidae), and *Liocranchia reinhardti* (Cranchiidae). While the enoploteuthid species dominated the two neritic regions (the stations grids off Oman and Pakistan), the ommastrephid and cranchiid species were most abundant in the oceanic waters of the central Arabian Sea. The geographical and vertical distribution patterns of the taxa were analyzed and are discussed along with hydrographic features which characterized the different areas. The data provide new and important information on the spawning areas of pelagic tropical cephalopods.

Introduction

In respect to the strong swimming ability and net-avoidance capability of many adult oceanic cephalopods, reliable quantitative estimates of their abundances may only be possible through sampling their early life stages. Before such estimates can be made, a broad knowledge of the ecology of the early life stages of pelagic cephalopods is necessary to understanding the importance of cephalopods in the marine ecosystem (Vecchione 1987). This is in accordance to the fisheries approved concerning oceanic finfishes where larval surveys form the basis for distribution and abundance studies and, frequently, evaluation of finfish stock-recruitment models (e.g., Hempel, 1973). Only few attempts have been made until present to assess cephalopod stocks by larval surveys (Okutani and Watanabe, 1983).

There are indications of widely unexploited cephalopod resources in the northern Arabian Sea (Silas *et al.,* 1982). However, investigations of species composition and biology of oceanic cephalopods in the Arabian Sea are only fragmentary. The only comprehensive study on the tropical cephalopod fauna of the Indian Ocean dates back to the work of Chun (1910) who described the collection of the *Valdivia* expedition. More recently, Silas (1968) compiled a catalogue of the cephalopod species so far known from the Indian Ocean that was based on the *Varuna* collections. Filippova (1968), Nesis (1970, 1974, 1986), and Okutani (1970, 1971, 1983) have reported on small cephalopod collections from the tropical Indian Ocean. The majority of these studies focused on adult specimens which could not be sampled quantitatively.

The only comprehensive report on the distribution of the early life stages of cephalopods was given by Aravindakshan and Sakthivel (1973) who described the location of cephalopod nurseries in the Indian Ocean. Within the Arabian Sea they found remarkably high densities off Oman and off Pakistan. However, they provided no information on taxonomic composition or more precise distribution patterns.

During the German expedition with R/V *Meteor* to the northern Indian Ocean from March to June 1987, an extensive zooplankton and micronekton sampling programme was conducted in three hydrographically and ecologically different parts of the Arabian Sea (Nellen *et al.,* 1988). A major objective of these studies was a detailed analysis of the distribution patterns of the early life stages of fishes and cephalopods to obtain a better understanding of factors that may effect their recruitment patterns. The present study is a detailed analysis of the spatial distribution patterns of the early life stages of the cephalopods which were sampled during the *Meteor* cruise.

Materials and Methods

Cephalopod specimens were obtained from zooplankton samples that were collected in the northeastern part of the Arabian Sea from March to June 1987 during cruise 5 of R/V *Meteor*. Three grids were sampled, each consisted of 5 × 5 stations and had side lengths of 80 × 40 nautical miles (Fig. 1). The 25 stations in each grid were sampled consecutively in time intervals of four hours. Between the hauls CTD casts and phytoplankton sampling were carried out. The first stations set, Grid A was situated near the coast of Oman and was sampled from 31 March–2 April 1987. It represented a typical upwelling area with a relatively mixed water column at the surface. The second sampling site, Grid B was located in the central Arabian Sea and was sampled from 30 April–3 May 1987. It was chosen to find a stratified water column with a pronounced thermocline in the surface layer. Grid C at the shelf slope region of Pakistan was sampled from 23–26 May 1987. Here, only a weak stratification of the surface layer is typical attributed to the influence of freshwater from the Indus River.

Due to technical problems in grid B and C zooplankton samples could be obtained only from 21 of the 25 grid stations. Numbers of stations and filtered water volumes (m^3) in the three grids are compiled in Table 1.

All sampling was carried out with a modified MOCNESS (Multiple-Opening-Closing-Net and Environemntal Sensing System: Wiebe *et al.*, 1976). In modification to the original MOCNESS design our net system was equipped with a box-shaped frame and a stabilizer underneath the frame to improve stability during the haul. The MOCNESS system allows a sequentially opening and closing of nine nets during one haul. Nets were controlled from a deck unit via a one-conductor cable, and volume of water filtered was determined by an electric flowmeter that was mounted into the frame opening. The nets had a length of 6m and a mesh size of 335 μm. The towing speed was 2 knots; at this speed the mouth opening of the net is approximately 1 m^2.

The standard procedure was a double oblique haul, fishing downward to 150 m with the first net and then upward through eight discrete depth strata ranging from 150 m to the surface which were sampled sequentially by nets 2–9. Standard depths during the phase of hauling were 150–100 m, 100–75 m, 75–50 m, 50–40 m, 40–30 m, 30–20 m, 20–10 m and 10–0 m in Grid A; and 150–100 m, 100–80 m, 80–60 m, 60–50 m, 50–40 m, 40–30 m, 30–15 m and 15–0 m in Grid B and C. Only samples from the upward hauls through the discrete eight depth strata were considered in the present study. In order to document vertical distribution patterns of the cephalopod paralarvae and their diurnal changes day-

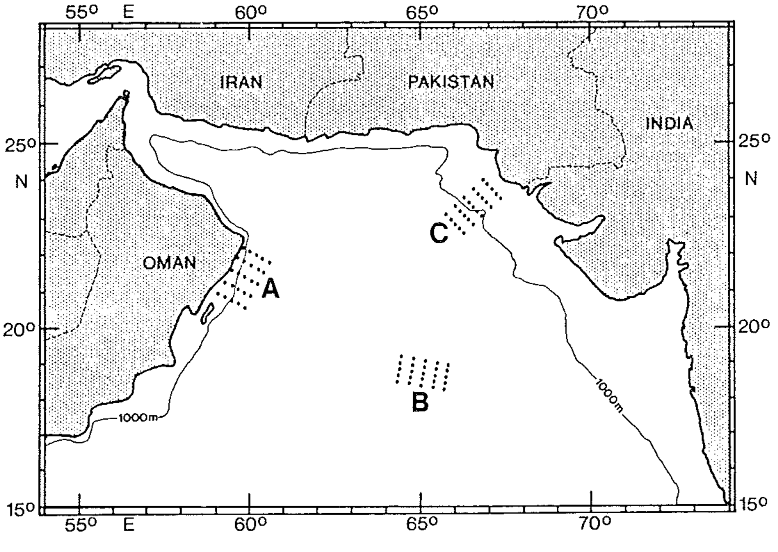

Fig. 1. The northern Arabian Sea and the MOCNESS station grids A–C sampled during cruise 5 of R/V *Meteor* from March to June 1987.

Table 1. Numbers of stations and water volumes filtered (m^3) in the three grids.

	Grid A Off Oman	Grid B Central Arabian Sea	Grid C Off Pakistan
Stations at			
daytime	12	7	12
twilight	4	4	3
night	9	10	6
total	25	21	21
Filtered water volume	58637	56799	57159

time and night stations were treated separately (see Table 1). Twilight catches were excluded from the comparisons as they can strongly bias the night figures. A comprehensive report on station data, sampling procedures and first preliminary results of the cruise is published elsewhere (Nellen *et al.,* 1988).

Immediately after each haul, total zooplankton/micronekton samples were fixed in a buffered 4% formaldehyde-freshwater solution. In the home laboratories fish larvae and cephalopod paralarvae were sorted from the samples. Röpke *et al.* (in press) described first results on abundance and vertical distribution patterns of the early life stages of fish and cephalopods in the region.

The cephalopods were sorted into taxonomic families. Identificaiton to genus or species level was not possible for the majority of the specimens due to their poor condition. Illustrations of chromatophore patterns, an essential feature in identification could be only prepared for a small number of animals. Further, the complete lack of literature on the species identification of early life stage of cephalopods from the Indian Ocean prevented a more precise identification. However, in some cases we succeeded in identificaiton to genus and species level according to figures and descriptions of tropical cephalopods published by Okutani and Tung (1978), Voss (1980), Harman and Young (1985), Young and Harman (1985) and Sweeney *et al.* (1992), and with the comparison of adult specimens sampled during the same expedition (Piatkowski and Welsch 1991; Tsuchiya *et al.,* 1991).

All specimens were counted and densities of the various taxonomic groups in the depth strata were adjusted to individuals per 1,000 cbm (n/1,000 m^3). The abundances at the different sampling sites (geographical distribution) are given as number per m^2 (standing stock) by integrating the eight depth strata. To test whether the observed distribution patterns were patchy, random or even, the dispersion coefficient ($CD = s^2/\bar{Y}$; Sokal and Rohlf 1981) was computed for each of the main cephalopod groups in the various grids and depth strata, separately for daytime and night samples. The coefficient of dispersion (CD) is simply the ratio between variance (s^2) and mean density ($\bar{Y}$). If the value will be near 1, the distribution is random. The distribution is patchy, if the value is much greater than 1, and even, if it is less than 1.

All cephalopod specimens are stored in the Institut für Meereskunde, Kiel, Germany, where additional studies on length frequency distributions and scanning electron microscopy are in progress.

Data on water temperature and salinity from all grid stations were taken by a CTD-system (Multisonde ME, Kiel) and were provided by Joachim Ribbe, Institut für Meereskunde, Hamburg, Germany.

Results

Hydrography

Vertical profiles of water temperature and salinity for the top 150m of the grid stations are shown in Figs. 2a–c. They represent mean values of all the stations within each of the grids. The standard deviations are indicated as horizontal bars.

The water column off Oman (Grid A) was relatively unstratified which is characteristic for this upwelling region. A very weakly pronounced thermocline existed at about 25m depth, where the water temperature of the top surface layer of about 25°C started slightly to decrease (Fig. 2a). No stratification can be recognized in the salinity profile within the top 80m which showed a constant salinity of approximately 36.5‰.

The profiles of Grid B (central Arabian Sea) and of Grid C (off Pakistan) were of similar structure (Figs. 2b, c). A warm surface layer was well established with water temperatures above T = 28.5°C.

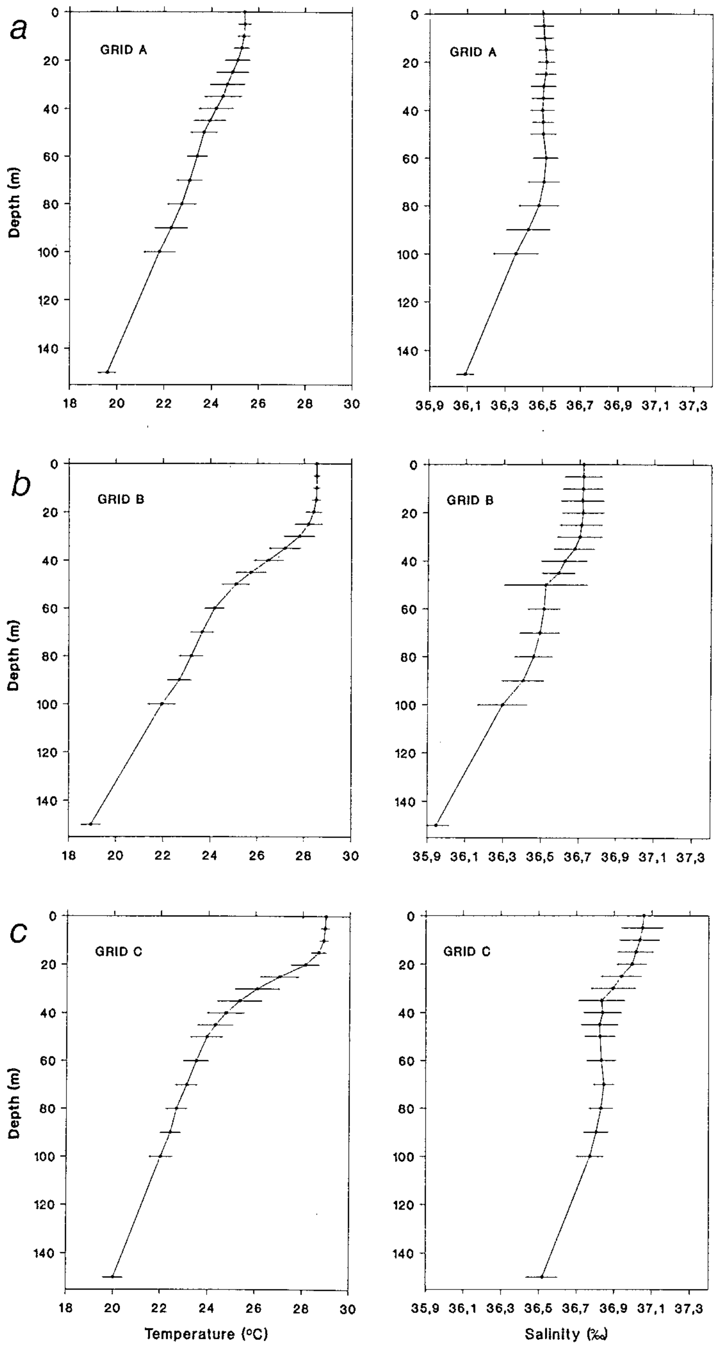

Fig. 2. Depth profiles of temperature (T°C) and salinity (S‰) during cruise 5 of R/V *Meteor*. Mean values for Grid A off Oman (a), Grid B in the central Arabian Sea (b), and Grid C off Pakistan (c).

Table 2. Numbers (n) and concentrations (n/m²) of cephalopod paralarvae sampled in the three grids.

	Grid A Off Oman		Grid B Central Arabian Sea		Grid C Off Pakistan	
	n	n/m²	n	n/m²	n	n/m²
Enoploteuthidae	1011	2.59	0	0	1208	3.17
Ommastrephidae	516	1.32	312	0.82	201	0.52
Cranchiidae	27	0.07	491	1.30	14	0.04
Onychoteuthidae	5	0.01	11	0.03	4	0.01
Octopodidae	6	0.02	0	0	0	0
Others/Unidentified	13	0.03	0	0	20	0.05
Total	1578	4.04	814	2.15	1444	3.79

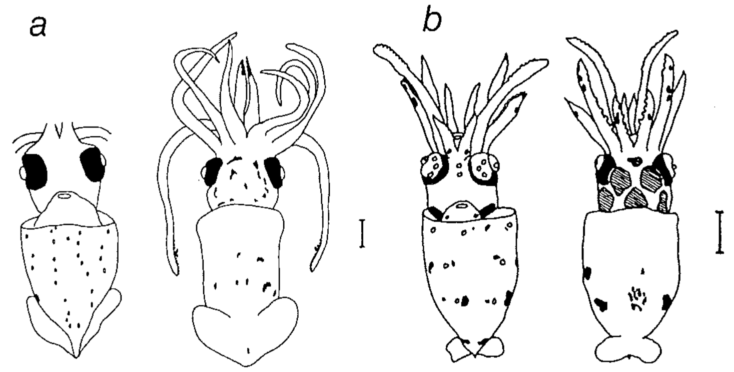

Fig. 3. Paralarval stages of Enoploteuthidae. Ventral and dorsal view of (a) *Abraliopsis lineata* from station Grid C, and (b) *Abralia marisarabica* from station Grid C. Scale bars = 1.0 mm.

Beginning in about 20 to 30 m a sharp thermocline was apparent and temperature decreased steadily to below T = 23°C in ca. 70 to 80 m depth. The salinity profiles corresponded to the temperature gradients. The expected coastal low salinity water at the shelf and shelf break stations off Pakistan induced by the freshwater outflow of the Indus river was not detected. Instead, surprisingly high saline water masses were found with values above S = 37‰ in the top 20 m of the water column which were by far the highest salinities measured in the whole investigated area (Fig. 2c).

Number of cephalopod paralarvae and taxonomic composition

A total of 3836 cephalopod specimens were sorted from the samples and divided into six broad taxonomic units: Enoploteuthidae, Ommastrephidae, Cranchiidae, Onychoteuthidae, Octopodidae and Others/Unidentified (Table 2). Within the last unit were two badly damaged paralarvae of *Ctenopterx* sp. and a number of specimens that could not be identified. The cephalopod fauna was not diverse. In the station grids close to Oman and Pakistan standing stocks of paralarvae were higher than in the central Arabian Sea (Table 2). Enoploteuthidae dominated in the coastal grids but were totally absent in the oceanic grid (Grid B). Ommastrephidae were most abundant in Grid A, off Oman. Cranchiidae appeared in considerable numbers only in the central Arabian Sea. Early life stages of Octopodidae were found only in Grid A.

A more preciese identification was attempted by classifying the specimens into various genus types. This could be easily achieved because the specimens in each of the most abundant families showed the same generic characters. The Enoploteuthidae of both coastal grids could be separated into the *Abraliopsis* and *Abralia* types (Figs. 3a, b) with a ratio of about 1:9. The *Abraliopsis* type possessed the characteristic photophores on the tips of the 4th arms. The *Abralia* type had distinct photophore patterns on the mantle and ventral eye balls (Fig. 3b). Previous studies on the adult and juvenile cephalopod fauna of the region (Okutani 1983; Piatkowski and Welsch 1991; Tsuchiya *et al.*, 1991) showed *Abraliopsis lineata* and *Abralia marisarabica* to be the dominant enoploteuthid species.

The Ommastrephidae were represented by the typical rhynchoteuthion larvae of the *Sthenoteuthis* type (Fig. 4): (1) the suckers on the tip of the proboscis were nearly equal in size, and (2) the bigger specimens (>3.5 mm ML) were characterized by two photophores on the intestine and one on each eye. *Sthenoteuthis oualaniensis* is the only ommastrephid known from the Arabian Sea that has young with these characteristics (Nesis, 1986; Sweeney *et al.*, 1992).

The Cranchiidae were characterized by typical ball-shaped and pear-shaped gelatinous forms (Fig. 5). At a dorsal mantle length of approximately 5 mm they showed two pronounced V-shaped cartilaginous stripes on the anterior part of the ventral side of the mantle and a median stripe along the dorsal side of the mantle (Fig. 5). These stripes, covered by cartilaginous tubercles, are characteristic of the species *Liocranchia reinhardti* (Voss, 1980; Sweeney *et al.*, 1992).

Only a few paralarval stages of the Onychoteuthidae were recorded. They could be easily identified because of the distinct chromatophore pattern on the dorsal side of the head and the sharp point of the gladius at the posterior end of the mantle (Fig. 6). Most probably they belong to the *Onychoteuthis* "*banksi*" complex.

Geographical distribution

The geographical distribution of the major groups over the sampling sites of the station grids and their standing stock densities in the top 150 m expressed as individuals/m² are shown in Figs. 7–9. Off Oman the Enoploteuthidae dominated the southern stations whereas the Ommastrephidae were more abun-

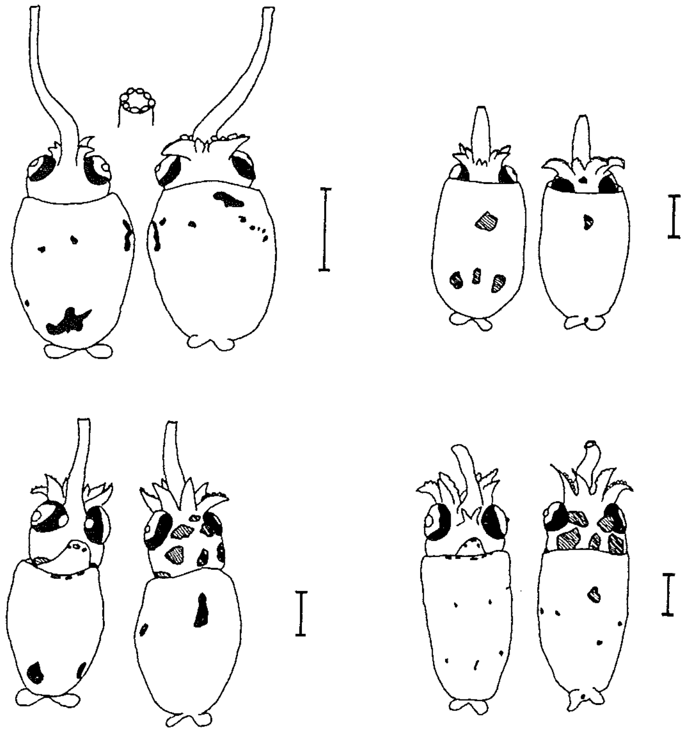

Fig. 4. Paralarval stages of Ommastrephidae (Rhynchoteuthions). Ventral and dorsal view of 4 selected specimens of *Sthenoteuthis oualaniensis* from station Grid B. Scale bars = 1.0 mm.

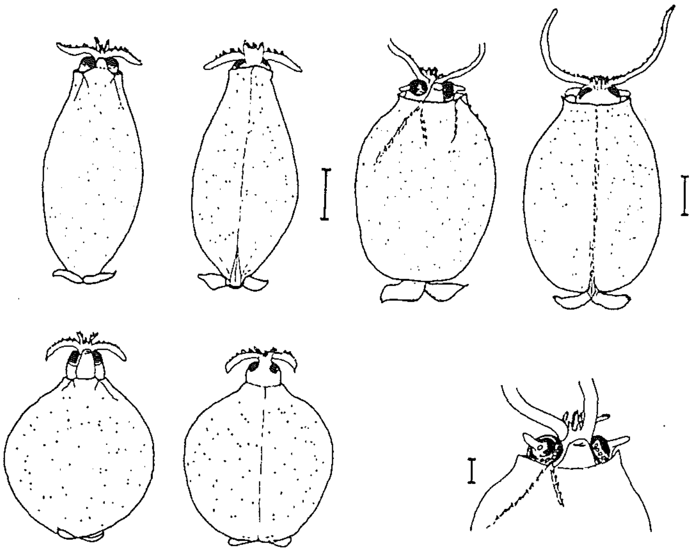

Fig. 5. Paralarval stages of Cranchiidae. Ventral and dorsal view of 3 selected specimens of *Liocranchia reinhardti* from station Grid B. Scale bars = 1.0 mm.

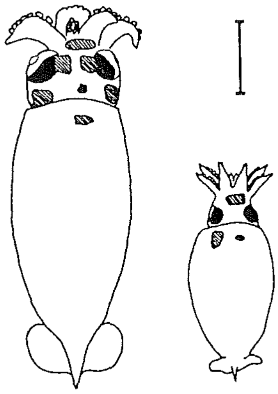

Fig. 6. Paralarval stages of Onychoteuthidae. Ventral and dorsal view of the *Onychoteuthis* "*banksi*" type from station Grid B. Scale bars = 1.0 mm.

dant in the northern region (Fig. 7). The Enoploteuthidae had a maximum density of 16.33 individuals/m^2. They showed a random distribution during the daytime ($\bar{Y}=1.41$ ind./m^2; $s=1.2$; $CD=1.02$) and were extremely patchy at night ($\bar{Y}=2.77$ ind./m^2; $s=5.1$; $CD=9.39$). The Ommastrephidae had a maximum density of 3.34 ind./m^2. They were evenly distributed during daylight ($\bar{Y}=1.12$ ind./m^2; $s=0.98$; $CD=0.86$) and nearly randomly at night ($\bar{Y}=1.19$ ind./m^2; $s=1.16$; $CD=1.13$).

Densities in the central Arabian Sea were considerably lower. The Ommastrephidae were more frequent in the northern part of the grid, the cranchiid paralarvae showed highest densities along the southern end ot the grid (Fig. 8). Maximum values were 1.77 ind./m^2 for the ommastrephids and 8.56 ind./m^2 for the cranchiids. Ommastrephids showed an even distribution both during daytime and night ($\bar{Y}=0.89$ ind./m^2; $s=0.64$; $CD=0.47$, and $\bar{Y}=0.77$ ind./m^2; $s=0.27$; $CD=0.09$, respectively). Cranchiids occurred evenly at daytime ($\bar{Y}=0.45$ ind./m^2; $s=0.31$; $CD=0.22$) and were patchy during the night ($\bar{Y}=1.56$ ind./m^2; $s=2.51$; $CD=4.04$).

The shelf region of Pakistan was dominated by the Enoploteuthidae; ommastrephids only occurred off the shelf break at stations of more than 1,000 m water depth (Fig. 9). The highest density of the enoploteuthid paralarvae was 15.97 ind./m^2. The Ommastrephidae reached a maximum concentraion of 10.52 ind./m^2. Distribution of enoploteuthids was patchy during the day ($\bar{Y} = 3.73$ ind./m^2; $s = 5.32$; $CD = 7.6$) and at night ($\bar{Y} = 2.31$ ind./m^2; $s = 2.91$; $CD = 3.67$). Ommastrephids were sampled only in the night hauls and were extremely patchy ($\bar{Y} = 1$ ind./m^2; $s = 3.01$; $CD = 9.03$).

In all grids no significant differences were detected between densities of daytime and night samples (Mann-Whitney *U*-test, $p < 0.05$).

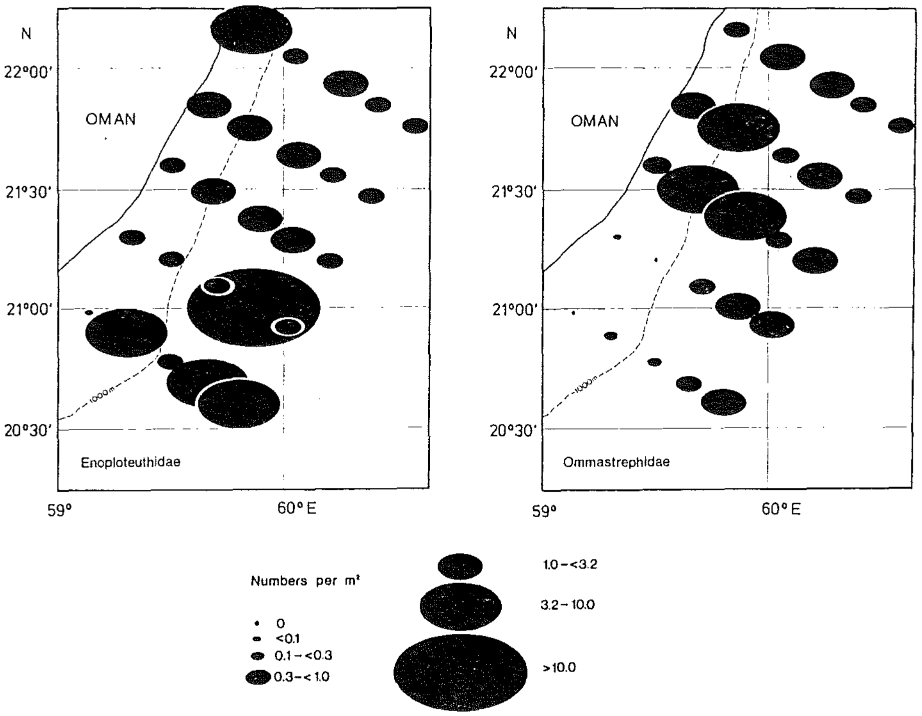

Fig. 7. Geographical distribution and numbers per m^2 of the early life stages of Enoploteuthidae and Ommastrephidae collected in Grid A off Oman from 31 March to 2 April 1987.

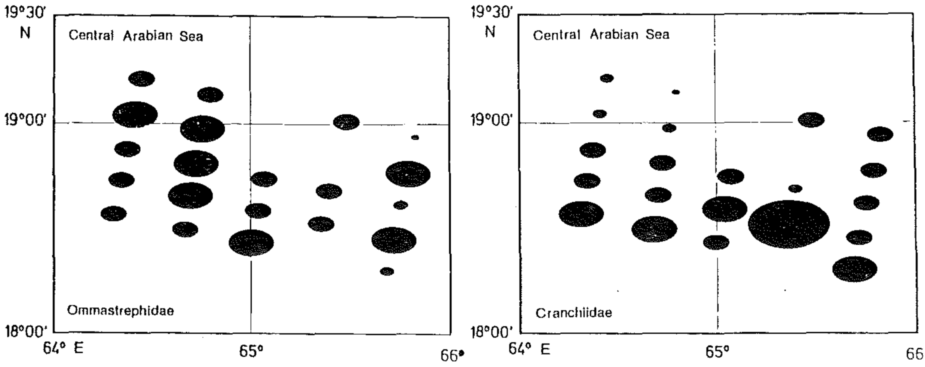

Fig. 8. Geographical distribution and numbers per m^2 of the early life stages of Ommastrephidae and Cranchiidae collected in Grid B in the central Arabian Sea from 30 April to 3 May 1987. See Fig. 7 for scale of abundancee

Vertical stratification

The stratified sampling of the MOCNESS system enabled us to demonstrate the vertical distribution of the cephalopod paralarvae within the surface layers of the various grids. We have further separated day and night hauls in order to search for changes in the diurnal rhythm. Again for the most abundant groups, both, mean and median values of concentrations (ind./1,000 m^3) are given for each depth stratum (Figs. 10–12).

In Grid A, off Oman, Enoploteuthidae and Ommastrephidae showed similar distribution patterns (Fig. 10a, b). Both groups had maximum densities in the layers from 20–50 m. The number of captured enoploteuthid paralarvae increased considerably during the night hauls (N = 483). They reached a maximum value of 522.5 ind./1,000 m^3 and the ommastrephids of 118 ind./1,000 m^3, both in the 30–40 m layer of the same night station. Significant differences between daytime and night samples (Mann-Whitney *U*-test, $p<0.05$) existed for the enoploteuthids only in the 40–50 m layer where they were more frequent during the day ($\bar{Y}=22.3$ ind./1,000 m^3) than at night ($\bar{Y}=11.8$ ind./1,000 m^3), and for the ommastrephids in the top surface layer (> 10 m) with a low mean concentraiton of $\bar{Y}=1.6$ ind./1,000 m^3 at daytime and a significantly higher mean concentration at night ($\bar{Y}=18.1$ ind./1,000 m^3). The distribution of both groups was mostly patchy, particularly in the layers of highest densities (Table 3).

Data on ommastrephids and cranchiids are slightly displaced upwardly the night hauls at the oceanic stations of Grid B (Fig. 11a, b). Highest densities of ommastrephids were in about 40–50 m during the day and in about 15–40 m during the night. Cranchiids were concentrated in the 40–50 m layer during daytime. Their numbers increased substantially during the night samples with highest densities in the 30–60 m strata. Maximum concentrations were recorded during the night with 63.2 ind./1,000 m^3 in the 15–30 m layer for the ommastrephids, and with 224 ind./1,000 m^3 in the 40–50 m layer for the cranchiids. Significant differences between daytime and night samples were only detected once for the cranchiids (Mann-Whitney *U*-test, $p< 0.05$). In the 30–40 m layer they were more abundant during the night ($\bar{Y}=40.8$ ind./1,000 m^3) than at daytime ($\bar{Y}=5.7$ ind./1,000 m^3). Ommastrephid paralarvae were characterized by an even or random distribution, whereas young cranchiids appeared in all layers mostly patchy, especially during the night (Table 3).

Enoploteuthidae and Ommastrephidae were most frequent in the 40–50 m layer during the day in the station grid on the Pakistan shelf region (Figs. 12a, b). This is slightly deeper than in the two other grids. During the night the bulk of enoploteuthid paralarvae was concentrated in the 15–40 m strata (Fig. 12a). Only 8 ommastrephid paralarvae were caught during the night hauls. Their vertical stratification is not illustrated. Maximum densities were 437 ind./1,000 m^3 in the 60–80 m layer for enoploteuthids and 399 ind./1,000 m^3 in the 40–50 m layer for the ommastrephids, both during the day sampling. There was no significant diel variation in the abundance of paralarval enoploteuthids in either depth stratum (Mann-Whitney *U*-test, $p< 0.05$). The Pakistan grid showed the most pronounced patchiness of cephalopod paralarvae (Table 3).

Discussion

The present study provides new information on the spatial distribution patterns of cephalopod paralar-

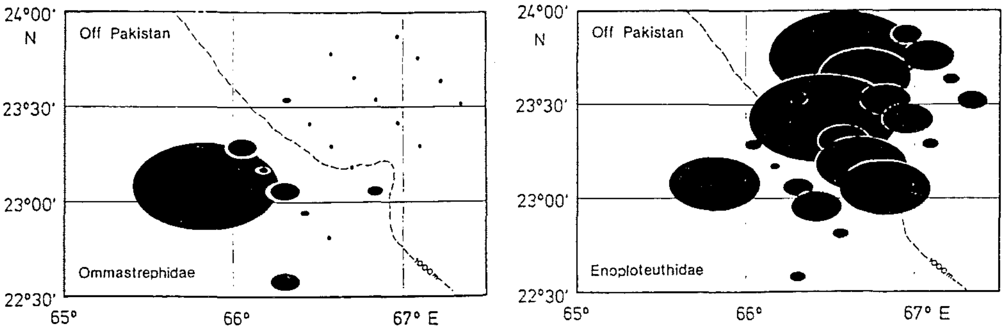

Fig. 9. Geographical distribution and numbers per m^2 of the early life stages of Ommastrephidae and Enoploteuthidae collected in Grid C off Pakistan from 23 to 26 May 1987. See Fig. 7 for scale of abundance

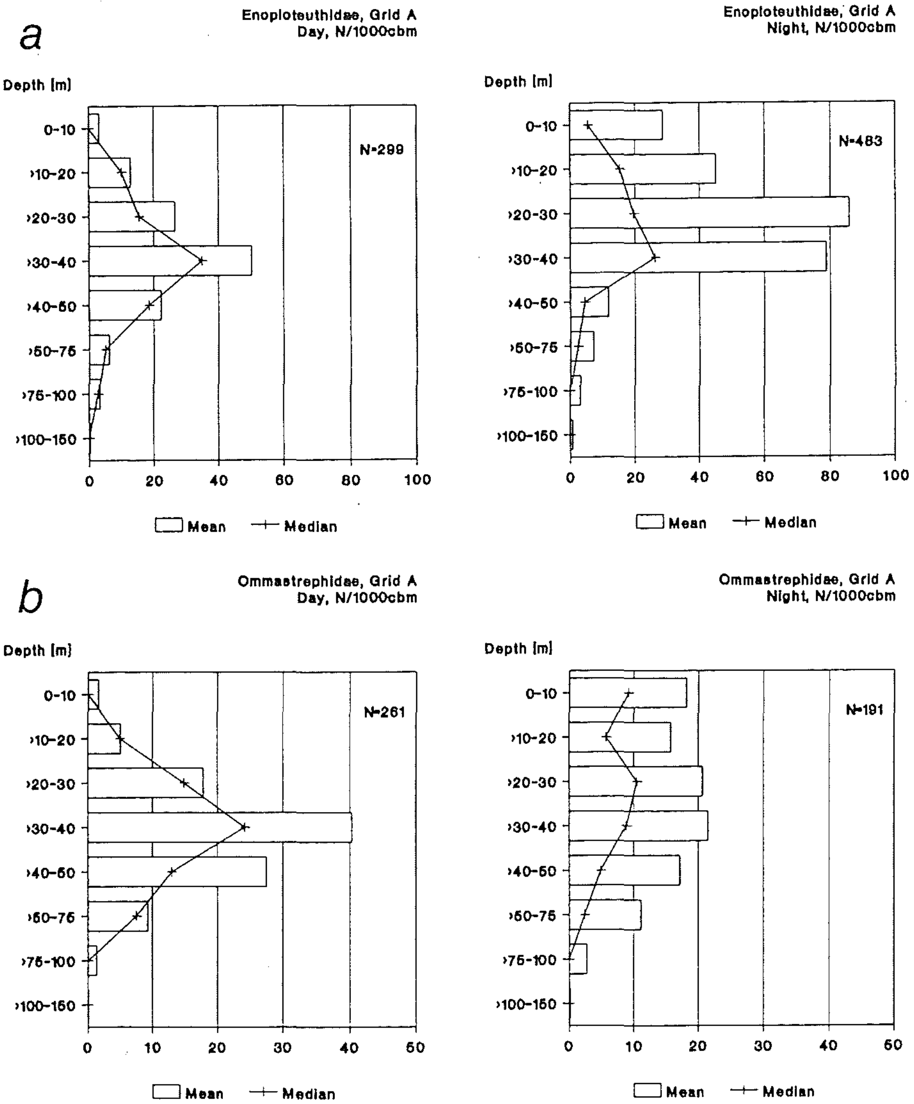

Fig. 10. Mean and median vertical distribution of cephalopod paralarvae at Grid A. (a) Enoploteuthidae from day (left) and night samples (right), and (b) Ommastrephidae from day (left) and night samples (right).

vae in the northern Arabian Sea. By comparing three geographically different regions it is shown that the faunal composition changes considerably from place to place. The station grids off Oman and in the shallower (< 1,000 m water depth) shelf slope region off Pakistan are dominated by relatively high numbers of paralarval enoploteuthids which are absent from the mid-ocean grid. The pattern off Pakistan, if typical, indicates that the coastal shelf break regions play an important role as nursery areas for the members of this family. The adults of *Abraliopsis lineata* and *Abralia marisarabica,* however, seem to be more confined to mesopelagic layers of the oceanic Arabian Sea (Piatkowski and Welsch 1991). This contradictory geographical distribution pattern of enoploteuthid paralarvae and adults demonstrates that nursery areas are well separated from the habitat of the adult populations. Perhaps the enoploteuthid species also belong to a so-called "mesopelagic-boundary community" as it has been report-

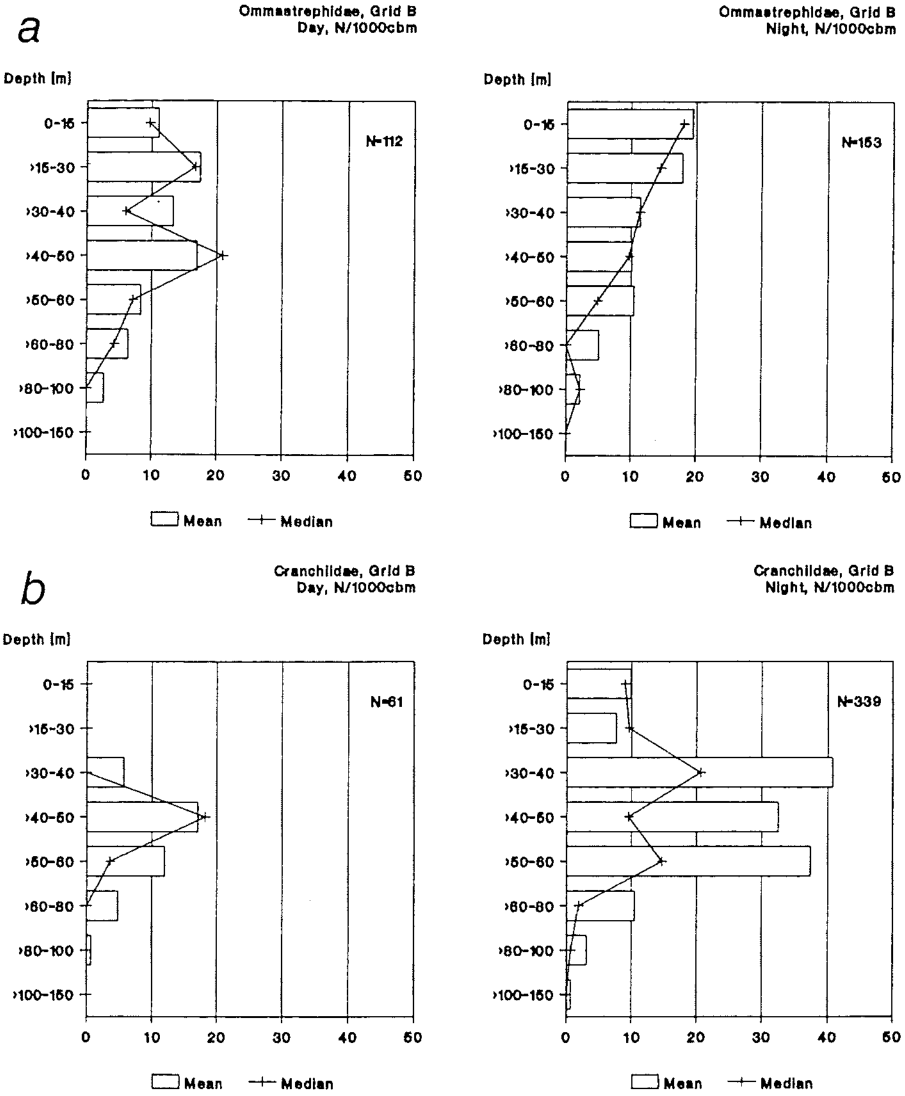

Fig. 11. Mean and median vertical distribution of cephalopod paralarvae at Grid B. (a)Ommastrephidae from day (left) and night samples (right), and (b) Cranchiidae from day (left) and night samples (right).

ed from the Hawaiian islands (Reid *et al.,* 1991). This shelf slope or land-associated community consists of mesopelagic micronekton species and replaces the oceanic mesopelagic community over great bottom depths. Mesopelagic-boundary zones are characterized by mesopelagic water masses bordering the upper slope of land masses, islands or seamounts (Reid *et al.,* 1991). As there are a variety of islands and seamounts in the tropical Indian Ocean, further studies are needed to proof whether these regions are inhabited by a typical mesopelagic-boundary community. The particular importance of these locations for the distribution pattern of pelagic cephalopods in the Indian Ocean (Nesis, 1986) is yet no fully understood.

The distribution pattern of the paralarval stages of the ommastrephid squid *Sthenoteuthis oualaniensis* is similar to that of the enoploteuthids. However, this species was also abundant in the surface layers

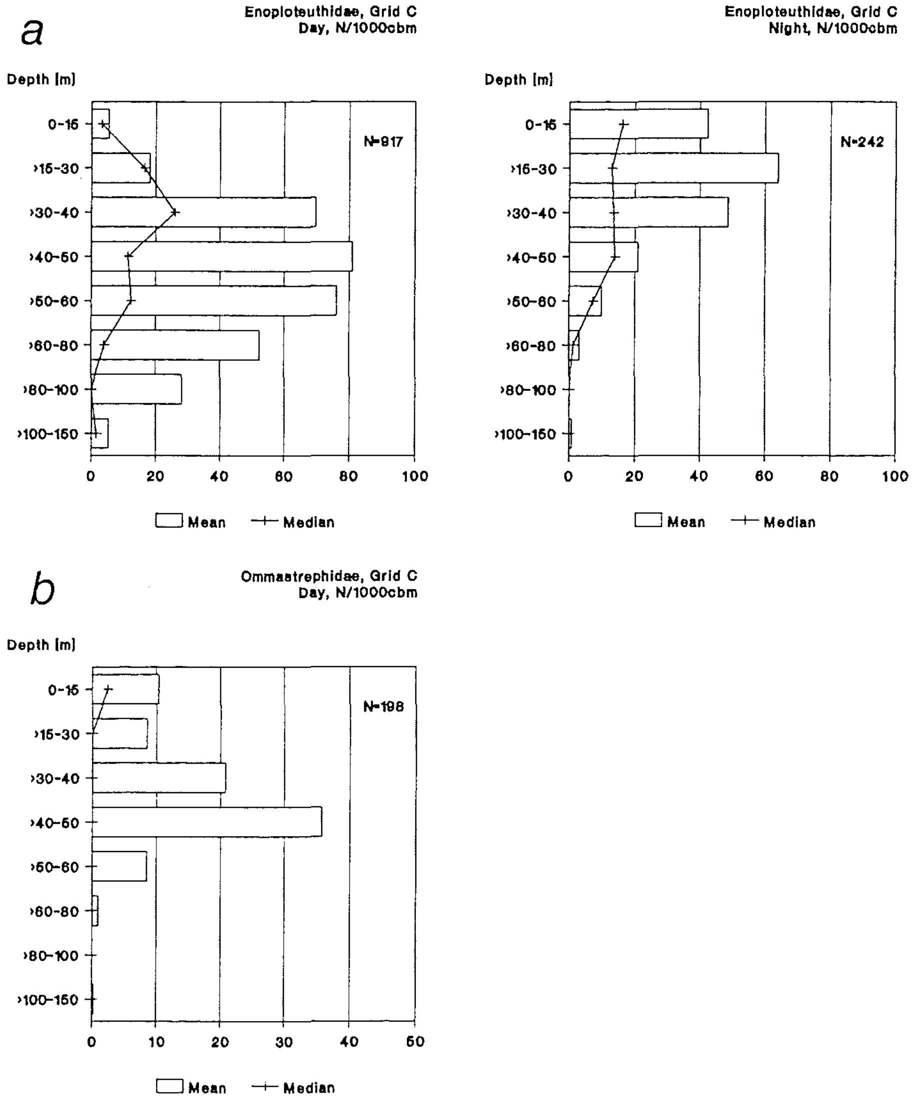

Fig. 12. Mean and median vertical distribution of cephalopod paralarvae at Grid C. (a) Enoploteuthidae from day (left) and night samples (right), and (b) Ommastrephidae from day samples.

of the oceanic grid. In respect to the importance of *Sthenoteuthis oualaniensis* as a commercially exploitable cephalopod species in the Arabian Sea (Aravindakshan and Sakthivel, 1973; Silas *et al.*, 1982; Roper *et al.*, 1986) and the large schools of adult specimens that have been reported from the waters off Karachi (Okutani and Tung, 1978; Silas *et al.*, 1982) the high abundance of the paralarval stages at the continental shelf breaks and in the central Arabian Sea indicate possible spawning areas.

In contrast to Enoploteuthidae and Ommastrephidae, the cranchiids were concentrated in the central Arabian Sea (Fig. 8, Table 2). In terms of abundance they were only of minor importance in the coastal regions. Their whole life cycle seems to be restricted completely to the oceanic regions. *Liocranchia reinhardti* was the only cranchiid species in our collection. Nothing can be said about the distribution patterns of other cephalopod groups, because they were only caught in very low numbers (Table 2).

Table 3 Dispersion coefficients ($CD = s^2/\overline{Y}$) of each of the main cephalopod groups compiled for each depth stratum in each grid and separated into daytime and night catches. The distribution is random if the value of CD is near 1; it is patchy if $CD > 1$; and it is even if $CD < 1$. A "—" means that the group was absent in the depth stratum. Further explanations are given in the Materials and Methods section.

Depth stratum	Grid A				Depth stratum	Grid B				Grid C			
	Enoploteuthidae		Ommastrephidae			Ommastrephidae		Cranchiidae		Enoploteuthidae		Ommastrephidae	
	Day	Night	Day	Night		Day	Night	Day	Night	Day	Night	Day	Night
< 10 m	0.53	11.26	0.38	2.71	< 15 m	1.01	0.58	—	0.81	1.79	6.23	3.49	—
10– 20 m	0.90	18.64	0.35	1.75	15– 30 m	0.59	1.26	—	2.39	1.80	11.31	4.32	—
20– 30 m	3.72	29.74	2.38	2.77	30– 40 m	1.27	0.50	1.93	6.32	14.71	9.46	19.34	—
30– 40 m	9.38	35.42	3.89	6.33	40– 50 m	0.69	0.52	0.74	14.24	17.38	2.78	36.79	—
40– 50 m	1.30	4.91	3.88	6.88	50– 60 m	0.63	3.43	2.04	12.17	20.20	1.20	9.98	—
50– 75 m	0.38	1.16	1.18	4.83	60– 80 m	1.11	2.04	1.92	2.86	30.41	0.88	0.70	—
75–100 m	0.37	0.61	0.23	1.25	80–100 m	1.27	0.32	0.14	1.06	18.00	—	—	—
100–150 m	0.20	0.25	0.80	0.50	100–150 m	0.80	0.80	—	0.11	2.19	0.25	0.27	—

Looking carefully at the illustrations of the geographical distribution of the groups there are indications that the various groups exclude each other; i.e. they do no co-occur with high numbers. This is particularly evident in the reigons off Oman and Pakistan. Off Oman enoploteuthids were more abundant in the southern region of the sampling grid, at stations located over > 1,000 m bottom depth (Fig. 7). Paralarval ommastrephids, however, were mostly distributed in the northern region of the grid close to the 1,000 m isobath (Fig. 7). In the grid off Pakistan dense concentraitons of enoploteuthids were mostly recorded on the shelf region (< 1,000 m bottom depth; Fig. 9) whereas ommastrephids occurred exclusively southeasterly of the shelf break (Fig. 9). Further, they were also frequent in the central Arabian Sea grid (Fig. 8) where no enoploteuthids were caught. This striking figure, although not proofed significantly (Mann-Whitney *U*-test, $p < 0.05$) needs further investigations despite the patchy distribution of enoploteuthid and ommastrephid paralarvae described in the present study.

The vertical distribution patterns revealed a clear stratification of the cephalopod paralarvae (Figs. 10–12). In most cases the animals are concentrated below the mixed layer (> 30 m) during the day and night. At night, however, they seem to be more abundant in the mixed layer than during the day. In the oceanic region and off Oman densities were considerably higher during the night hauls. This can be attributed to the greater net avoidance during the day, to a vertically upward migration from layers below 150m, or it is simply a result of patchiness (see Table 3). In the Pakistan grid, however, highest densities occurred during daytime, particularly if the ommastrephid paralarvae are considered (Fig. 12). They were virtually absent during the night. This conspicuous feature is mot probably an effect of patchiness which was very marked in the Pakistan grid (Table 3). Furthermore, the water masses seem to be more variable in the coastal grids than in the oceanic region where the vertical stratification of the water masses and the cephalopods are more stable (Figs. 2b; 11a, b).

Although the samples only showed a low diversity, they clearly demonstrate the usefulness to study the meso-scale distribution of cephalopod paralarvae, because the results reveal much information on the complex distribution patterns of cephalopod paralarvae in the Arabian Sea. The strengths of paralarval surveys are that hatching paralarvae can be unambiguously associated with spawning sites and times and that they are more numerous and more easily caught than adults. Even the MOCNESS system which is a comparatively small gear to sample motile micronekton organisms adequately (Wormuth and Roper, 1983) caught relatively high densities of cephalopod paralarave. It is most likely that the numbers presented here are still underestimations of the true densities.

The data also document a number of shortcomings in analyzing distribution patterns of cephalopod paralarvae. Besides the difficulties with identification of specimens the most important ones are avoidance and patchiness (Wormuth and Roper, 1983). Avoidance should not be overemphasized here, because most density differences of paralarvae between daytime and night samples were not significant (Mann-Whitney *U*-test, $p < 0.05$). Further studies on the comparison of length frequencies from daytime and night samples of paralarvae will provide additional information on the significance of avoidance (Piatkowski, unpublished).

Patchiness, however, was very much pronounced. It was less distinct in ommmastrephids than in enoploteuthids and cranchiids and more important at night than during daytime (see Table 3). Possibly the cephalopod paralarvae aggregate in the mixed layer strata during the night and are more dispersed during daytime which would explain the more patchy distribution during darkness. Suggestions to overcome patchiness are to take long tows, filter large volumes of water and to take replicates (Wormuth and Roper, 1983). Of course, this would require frequent and expensive cruises, but they would be very advantageous.

The present results detected the spawning sites of pelagic cephalopods in the Arabian Sea. To reduce the effects of patchiness which definitely biased our results to some degree, further fine-scale studies are needed now within the areas of highest cephalopod densities. Time stations within one water body are necessary to follow the same cephalopod population (Lagrangian sampling). This would substantially decrease the effects of patchiness and allow a more reliable modelling of distribution patterns of the cephalopod populations.

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