

## CEPHALOPOD PARALARVAE AROUND TROPICAL SEAMOUNTS AND OCEANIC ISLANDS OFF THE NORTH-EASTERN COAST OF BRAZIL

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### ABSTRACT

Early life cephalopod stages were collected around tropical seamounts and oceanic islands off the north-eastern coast of Brazil. A total of 511 specimens was caught with oblique Bongo net hauls between 150 m depth and the surface during a joint Brazilian/German oceanographic expedition with the RV VICTOR HENSEN in January/February 1995. Mean density of cephalopods was low with 24 ind 1000 m<sup>-3</sup>. Fifteen families representing at least 21 genera, from which 11 species were identified. The findings revealed a typical tropical and oceanic cephalopod assemblage. The most abundant families were Enoploteuthidae (27.6%), Ommastrephidae (20.9%), Onychoteuthidae (11.2%), Cranchiidae (10.4%) and Octopodidae (9.2%). Less abundant families were Octopoteuthidae, Thysanoteuthidae, Ctenopterygidae, Lycoteuthidae, Mastigoteuthidae, Tremoctopodidae, Argonautidae, Chiroteuthidae and Bolitaenidae. Highest cephalopod densities occurred along the Fernando de Noronha Chain (34 ind 1000 m<sup>-3</sup>). Small-sized Enoploteuthidae and Onychoteuthidae dominated in that region. Around the North Brazilian Chain overall cephalopod density was 31 ind 1000 m<sup>-3</sup> where again, Enoploteuthidae were most abundant, closely followed by Ommastrephidae. Cephalopod abundance was the lowest (13 ind 1000 m<sup>-3</sup>) around the St. Peter and St. Paul Archipelago. However, cephalopod diversity was highest in this region (17 genera) with Enoploteuthidae dominating, followed by Cranchiidae. Cephalopod mantle lengths (ML) ranged from 0.8 mm to 25 mm. The majority of specimens were small-sized with 65% below 3 mm ML, and 81% below 4 mm ML. All major genera and species are illustrated and their meso-scale distribution patterns are discussed. The results provide new information on the species composition and distribution patterns of early life cephalopods in tropical seas.

The pelagic regions of tropical oceans are regarded as ‘deserts’, because they are characterised by low primary productivity and low standing stocks of zooplankton and nekton. This is caused by a perennial pycnocline at the bottom or below the euphotic zone that is nearly depleted of nutrients. However, off the north-eastern coast of Brazil there are various seamounts and islands (St. Peter and St. Paul Archipelago, Fernando de Noronha Chain and the North Brazilian Chain; Fig. 1) which provide productive environments with appropriate conditions for all trophic levels and all life stages. They harbor unique ecosystems that are inhabited by characteristic communities (Ekau and Knoppers, 1999), and which support traditional major fishing grounds for tuna and other pelagic fishes (Hazin, 1993).

The maintenance of high standing stocks of pelagic and benthic organisms near islands and seamounts suggests high rates of energy transfer (Boehlert and Genin, 1987; Rogers, 1994; Koslow, 1997). So far it is well documented, (1) that most seamounts show a higher standing stock of organisms in nearly every part of the food chain, (2) that they play an essential role in the reproduction and life history of many species, and (3) that seamounts appear to show significant levels of endemism. Seamount ecosystems are also characterized by the occurrence of higher standing stocks of commercially exploitable pelagic and benthic-pelagic fishes and invertebrates. Three processes might be responsible for this

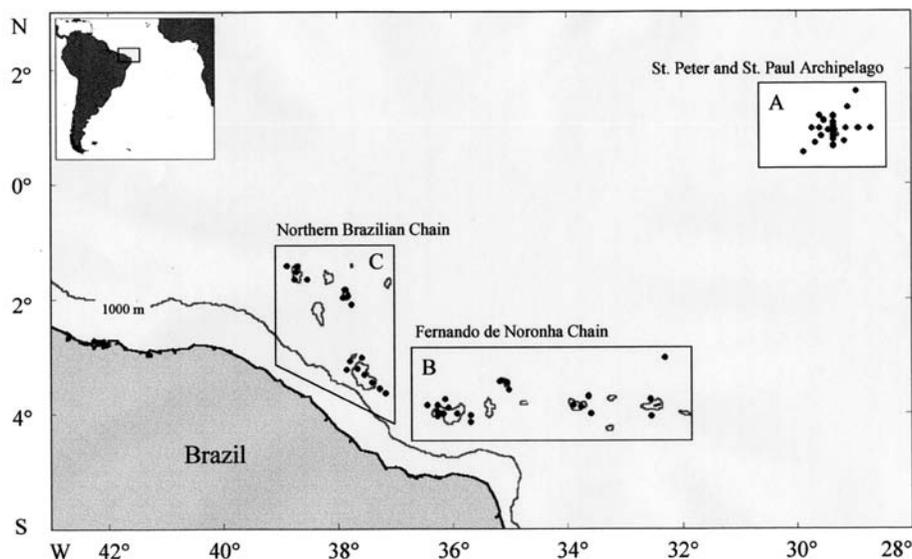


Figure 1. Study areas and locations of Bongo net sampling off the north-eastern coast of Brazil during the expedition of the RV VICTOR HENSEN in January/February 1995.

phenomena: (1) an increased pelagic primary production due to local upwelling processes or within so-called 'Taylor columns', (2) an enhanced benthic primary and secondary production due to a low but steady supply of organic and inorganic nutrients through the prevailing current systems, and (3) migrating zooplankton is transported during its night-time ascent towards the top of a seamount where it serves as food source for benthic and pelagic organisms Rogers (1994).

Unlike other molluscs, cephalopods do not have a true larval stage, but develop without radical metamorphosis which led to the use of the term 'paralarva' for the post-hatching stage of most of them (Vecchione, 1987; Young and Harman, 1988). In general, little is known about the paralarval stages, especially about their abundance and distribution in tropical seas. Sampling paralarvae, however, provides meaningful conclusions on distribution, life cycle and population structure of cephalopods, which is particularly important for commercially interesting species such as the ommastrephid *Illex argentinus* (see review of Haimovici et al., 1998.).

In the present paper we investigated the composition of the early life cephalopod assemblage that was sampled during a joint Brazilian/German oceanographic expedition with the RV VICTOR HENSEN in January/February 1995 off the north-eastern coast of Brazil at various seamounts and islands (St. Peter and St. Paul Archipelago, Fernando de Noronha Chain and the North Brazilian Chain). Besides describing the taxonomic composition, abundance and distribution of cephalopod paralarvae off north-eastern Brazil and relating the findings to the hydrographic conditions in the region, we will further illustrate if an increased pelagic production around the seamounts also results in a higher abundance of early life cephalopods.

## MATERIAL AND METHODS

Sampling was performed in January/February 1995 during a joint Brazilian/German oceanographic expedition with the RV VICTOR HENSEN as part of the JOPS-II project (Ekau and Knoppers, 1999). Cephalopod paralarvae were collected from 66 zooplankton sampling stations in three areas off north-eastern Brazil: around the St. Peter and St. Paul Archipelago (Leg A; 27 stations), along the islands of the Fernando de Noronha Chain (Leg B; 22 stations), and in the vicinity of the seamounts of the North Brazilian Chain (Leg C; 17 stations). The sampling sites are shown in Figure 1.

Samples were collected with Bongo nets that had a mouth opening of 60 cm in diameter and 300  $\mu\text{m}$  and 500  $\mu\text{m}$  meshes. Hauls were performed during daytime obliquely between depths of 50, 100 and 150 m and the surface. Filtered water volumes were 8848  $\text{m}^3$  in leg A, 6882  $\text{m}^3$  in leg B, and 4,717  $\text{m}^3$  in leg C (in total 20447  $\text{m}^3$ ). A detailed compilation of station data, the work at sea, and first results were given in the cruise report. Paralarvae were separated from the zooplankton catches and stored in 4% formaline solution. Identification to the lowest possible taxon and measurements of specimens was done according the manual of Sweeney et al. (1992). Nomenclature followed the guidelines of Sweeney and Roper (1998). The term 'type' was chosen for a distinct taxon, that could not be identified to a lower taxonomic level. Dorsal mantle lengths (ML in mm) of squids (Teuthida) were measured from the anterior edge of the mantle to the tip of the tail and not to the exposed tip of the gladius. Additionally, the proboscis of ommastrephid paralarvae (rhynchoteuthions) was measured and the relative width of the two lateral suckers compared to the other six suckers of the proboscis was recorded. Additional measurements of squids included fin length and width. Mantle length of octopods was measured from the midline between the eyes to the posterior end of the mantle along the dorsal midline.

## RESULTS

**HYDROGRAPHY.**—Physical oceanography in each of the three areas was studied by Travassos et al. (1999) who analyzed temperature, salinity, density profiles and TS diagrams during the cruises. According to the authors, sea surface temperature ranged between 27.2 and 28.6°C and sea surface salinity between 35.4 and 36.6 0 over the entire study region.

Two water masses were dominant in the region: Surface Equatorial Water (>20°C, and 35.5–37.0– 0) and Southern Atlantic Central Water (<20°C, and <35.5 0). In all three areas strong thermoclines were observed at depths between 50 and 200 m. Salinity maxima (>36.0 0) occurred between 50 and 100 m depth. These data suggest a typical equatorial pattern. In contrast to the St. Peter and St. Paul Archipelago, sampling sites around the Fernando de Noronha and the North Brazilian chains showed evidence of topography-flow interaction on thermohaline structures. The major observed features were an uplifting of the isotherms and isohalines and a step-wise gradient in vertical temperature profiles, providing evidence of seamount-induced perturbations. These patterns were more pronounced above seamounts with summits located just below the thermocline base. At one seamount in the North Brazilian Chain, a pronounced cold water upwelling cone was found, suggesting the formation of a Taylor column, that is, a closed streamline anticyclonic vortice above a topographic obstacle in an impinging flow. Consisting of a diameter of 20 km and a height of 90 m, this dome extended into the euphotic zone and presented the greatest potential for enrichment of the surface layers. This area produced the second-highest density of cephalopod paralarvae found in the study site. Distributions of particulate organic carbon (POC) and nitrogen (PON), chlorophyll *a* and pheopigments

in the St. Peter and St. Paul Archipelago were studied by Bröckel and Meyerhöfer (1999). In general, all three study sites showed low productivity at the time of sampling.

**RELATIVE ABUNDANCE OF CEPHALOPOD PARALARVAE.**—Cephalopod paralarvae were found at 57 of 66 zooplankton stations. In total, 511 specimens were caught between 150 m depth and the surface. Mean density was 24 ind 1000 m<sup>-3</sup>. Fifteen families comprising at least 21 genera and eleven species were identified (Table 1). The most abundant families were Enoploteuthidae (27.6%), Ommastrephidae (20.9%), Onychoteuthidae (11.2%), Cranchiidae (10.4%) and Octopodidae (9.2%). Less abundant families were Octopoteuthidae, Thysanoteuthidae, Ctenopterygidae, Lycoteuthidae, Mastigoteuthidae, Tremoctopodidae, Argonautidae, Chiroteuthidae and Bolitaenidae.

Highest cephalopod density occurred along the Fernando de Noronha Chain (34 ind 1000 m<sup>-3</sup>) with small-sized Enoploteuthidae and Onychoteuthidae prevailing. Again Enoploteuthidae were the most abundant around the North Brazilian Chain where cephalopods reached a mean density of 31 ind 1,000 m<sup>-3</sup>. Lowest cephalopod abundance (13 ind 1000 m<sup>-3</sup>) occurred at the St. Peter and St. Paul Archipelago, ML ranged from 0.8 to 25 mm. The majority of specimens were small-sized, with 65% below 3 mm ML, and 81% below 4 mm ML. Due to the small size, identification of paralarvae to genus was possible for 38% of the specimens and to species level for only 17%.

Initially, the number of specimens per filtered water volume (ind 1000 m<sup>-3</sup>) was calculated separately for the most abundant families for each different haul depth (50 m, 100 m, 150 m). Despite some indications that Enoploteuthidae, Ommastrephidae and Onychoteuthidae were more abundant in the upper layers and Cranchiidae in the deeper layers, these differences were not apparent. Thus, for further analysis, samples were not treated separately according to haul depth, but were pooled in each study region.

#### SYSTEMATICS AND DISTRIBUTION

##### LYCOTEUTHIDAE

*Selenoteuthis scintillans* (n = 3; ML < 4.0 mm).— These paralarvae had a stout mantle and were identified by the presence of one large photophore on the tip of the mantle and three photophores (small, large, small) on the eyeball.

##### ENOPLOTEUTHIDAE

Representatives of this family were the most abundant in all three sampling sites, with for a total of 153 specimens (ML = 0.9–6.0 mm). Most specimens (n = 130) with an appearance shown in Figure 2A could not be identified to genus or species level. They were very small (ML = <3 mm) with cone-shaped mantles, which were generally everted. Eyes were prominent and the arm crown was short with no apparent photophores. Tentacles and arms were moderately long, except for the fourth arm that was very short (arm formula 2>1>3>>4). Considering their body shape we believe that most of them belonged to the genera *Abralia* or *Abraliopsis* (Fig. 2B,C).

*Enoploteuthis* sp.—One specimen (ML = 4.8 mm) was identified by its head, which showed the typical presence of five photophores on the ventral surface of each eye, one at the base of each arm IV and two on the ventral surface of the head (Fig. 2D). Heads of *Abralia* and *Abraliopsis* of similar size did not possess photophores on the ventral side of the head and possessed only three on the ventral surface of the eyes.

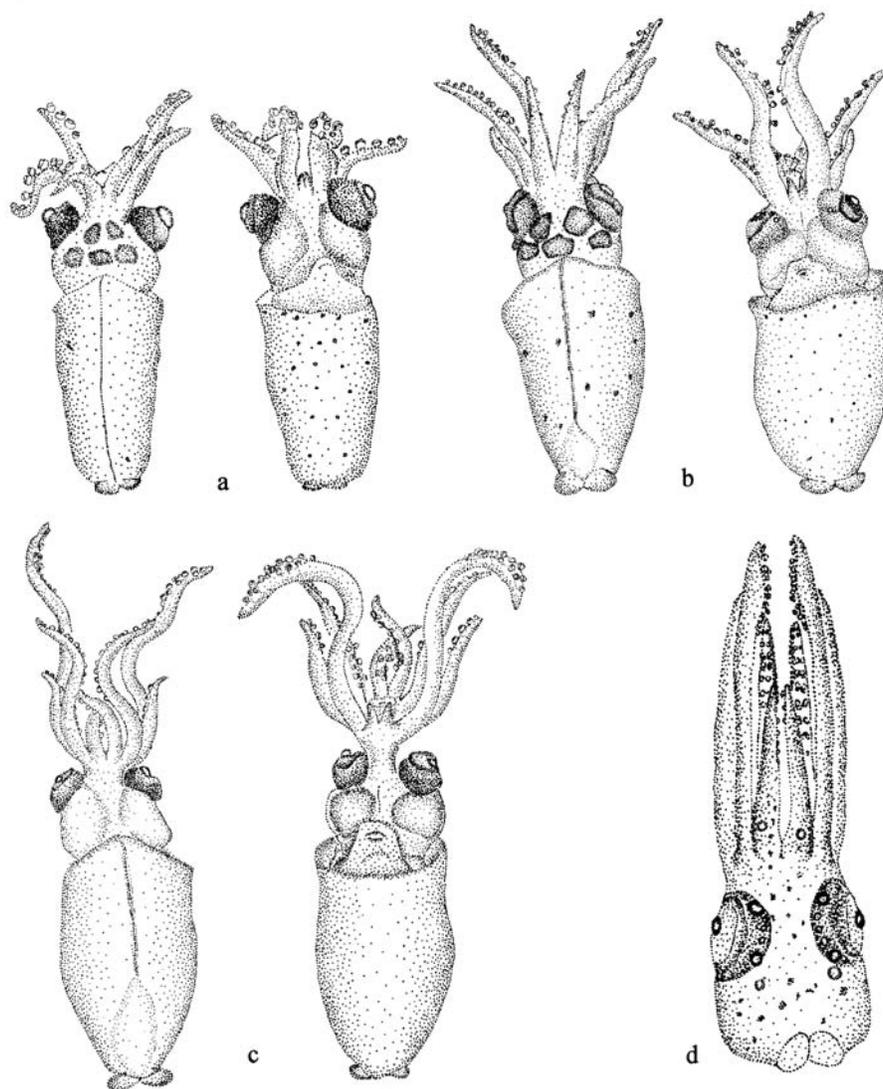


Figure 2. Cephalopod paralarvae from Bongo samples off the north-eastern coast of Brazil during the expedition of RV VICTOR HENSEN in January/February 1995. a), b) and c) Enoploteuthidae unidentified (dorsal and ventral views) ML= 1.1, 2.5 and 2.1 mm, respectively; d) *Enoploteuthis* sp (head); e) (*e-h* on page 319) *Abralia* sp (ventral and dorsal view) ML= 4.0 mm; f) *Abraliopsis* sp (dorsal and ventral view) ML= 5.2 mm; g) *Ancistrocheirus lesueuri* (dorsal and ventral view) ML= 5.0 mm; h) *Octopoteuthis* sp (dorsal and ventral view) ML= 2.0 mm; i) (*i-m* on page 320) *Onychoteuthis* sp type 1 (dorsal and ventral view) ML= 7.2 mm; j) and k) *Onychoteuthis* sp type 2 (dorsal and ventral views) ML= 2.5 and 8.4 mm respectively; l) and m) *Onychoteuthis* sp type 3 (dorsal and ventral views) ML= 2.2 and 5.1 mm respectively; n) (*n-q* on page 322) *Chtenopterix sicula* (dorsal view) ML= 2.5 mm; o) *Chiroteuthis* sp (dorsal and ventral view) ML= 20.0 mm; p) *Mastigoteuthis* sp (dorsal and ventral view) ML= 8.9 mm; q) *Liocranchia reinhardtii* (dorsal and ventral view) ML= 16.0 mm; r) (*r-v* on page 324) *Leachia* sp (dorsal and ventral view) ML= 23.1 mm, showing the left ventral tubercular strip; s) *Liguriella podophthalma* (dorsal and ventral view) ML= 9.2 mm; t) *Megalocranchia* sp (dorsal and ventral view) ML= 7.2 mm; u) and v) Cranchiidae unidentified (dorsal and ventral views) ML= 3.3 and 4.4 mm, respectively; w) (*w-z* on page 325) Bolitaenidae unidentified (dorsal and ventral view) ML= 3.4 mm; x) and y) Octopodidae unidentified (dorsal and ventral views) ML= 1.8 and 3.7 mm, respectively; z. *Argonauta* sp (dorsal and ventral view) ML= 2.8 mm.

*Abralia redfieldi* (n = 1; ML = 6.0 mm).—This specimen sampled at a station of the North Brazilian chain of seamounts was clearly identified by its relatively large fins, the arm tips with two rows of suckers, and five (large, small, large, small, large), round eye-ball light organs.

*Abralia* sp. (n = 16; ML = 2.1–5.0 mm).—All were characterized by the presence of three photophores forming a single row on the ventral surface of the eyes occurring at >3.0 mm ML and small photophores on the ventral side of the mantle (Fig. 2E).

*Abraliopsis* sp. (n = 5; ML = 3.5–6.0 mm).—It had arms longer than the mantle and possessed one photophore at the tip of the arm IV (Fig. 2F).

#### ANCISTROCHEIRIDAE

Six specimens of *Ancistrocheirus lesueurii* (ML = 3.0–5.0 mm), the only recognized species of this family were recorded in all three sampling regions. They were characterized by a wide body and paddle-shaped fins. Identification was based on the presence of photophores on the long and stout tentacles bearing large suckers on the manus. Photophores were recognised in some specimens also on the head between the eyes and on the ventral surface of the mantle (Fig. 2G).

#### OCTOPOTEUTHIDAE

*Octopoteuthis* sp. (n = 18; ML = 1.5–3.5 mm). These were mostly very small paralarvae that occurred in the area of the St. Peter and St. Paul Archipelago and along the Fernando de Noronha Chain, but not in the region of the North Brazilian Chain of seamounts. They were characterized by a broad and short mantle covered with numerous small chromatophores, a large head with prominent eyes, and a well-developed arm crown (arm formula T>2>3>1>4), and stout tentacles with up to eight large suckers of unequal size (Fig. 2H).

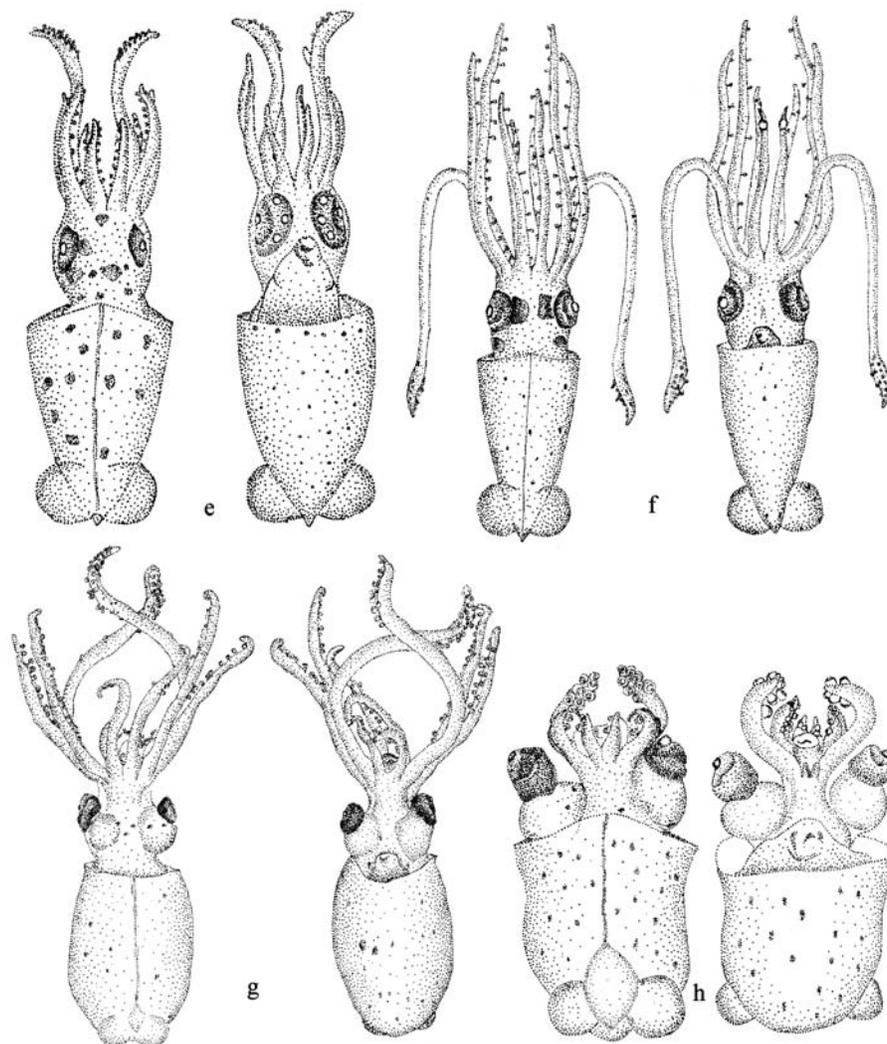
#### ONYCHOTEUTHIDAE

Paralarvae of this family were the most abundant forms in the samples. Fifty-eight specimens (ML = 1.7–8.5 mm) of three types were sampled. All had muscular mantles with one conspicuous chromatophore on the ventral side of the mantle at a midpoint of the basis of the fins, a gladius with a pointed rostrum, two rows of suckers on the arms, and one large photophore on the ventral surface of each eye, except in the smaller ones.

*Onychoteuthis* sp. type 1.—One single specimen (ML = 7.2 mm), caught at the Fernando de Noronha Chain, was identified as belonging to the *Onychoteuthis banksi* complex. It had an elongated mantle, small terminal fins, and the head was partly retracted into the mantle (Fig. 2I).

*Onychoteuthis* sp. type 2.—Most of the specimens of the Onychoteuthidae (n = 48; ML = 1.7–8.5 mm) had a wider mantle and larger fins and were allocated to the genus *Onychoteuthis* (Fig. 2J,K). These paralarvae occurred in all cruise legs, mostly at the Fernando de Noronha Chain.

*Onychoteuthis* sp. type 3.—Seven bullet-shaped paralarvae (ML = 2.1–6.0 mm) were collected in all three legs. They had a shorter and broader mantle, small paddle-like fins, and a less pointed gladius rostrum than the above two taxa, and large dark chromatophores along the mid-dorsal line of the mantle and on its antero-ventral margin (Fig. 2L,M).

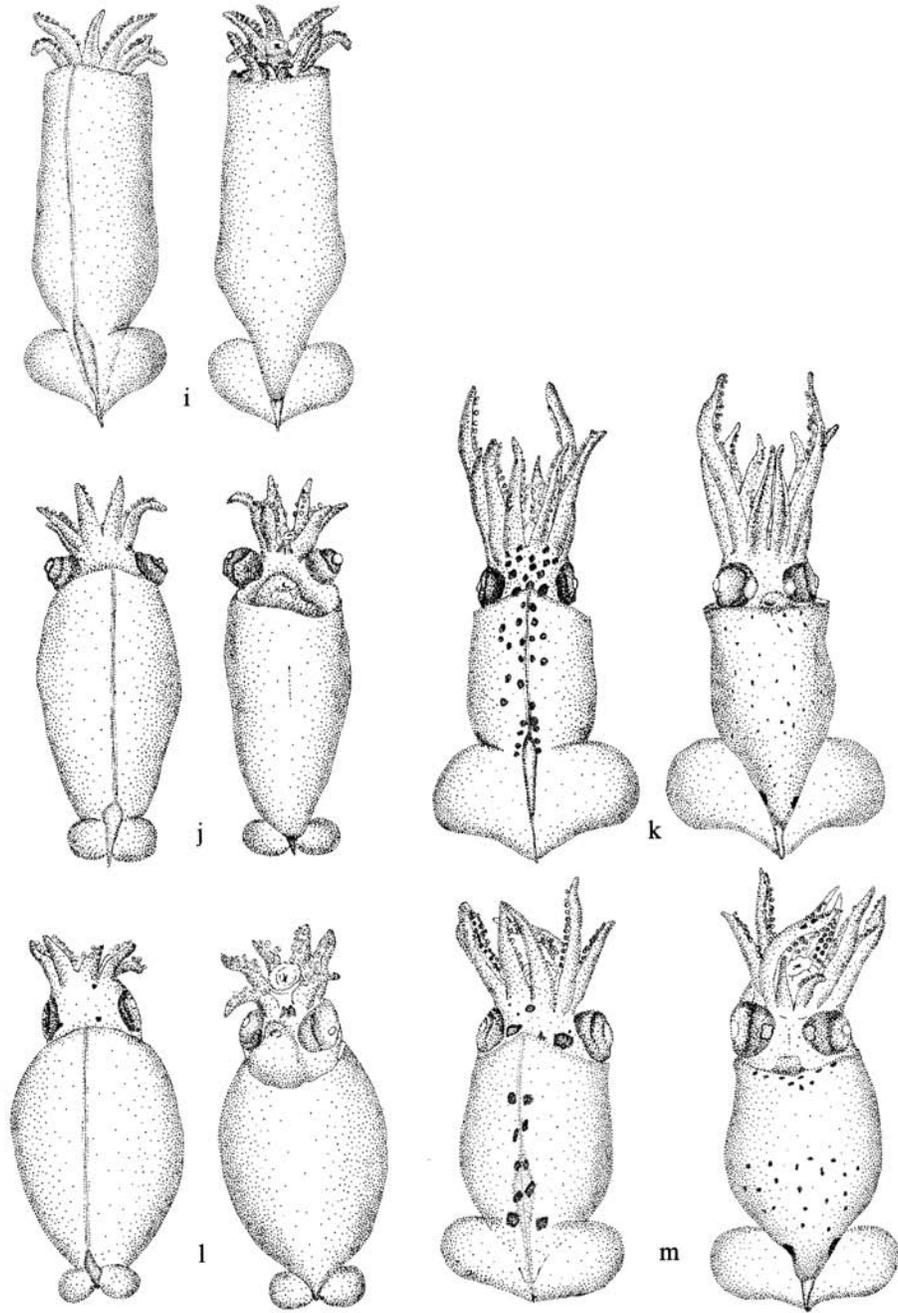


#### CHTENOPTERYGIDAE

Three specimens of *Chtenopteryx sicula* (ML = 2.5–6.0 mm) occurred in the area of the St. Peter and St. Paul Archipelago. They were characterized by a stout and blunt mantle, short elongated fins with trabeculae separated dorsally, lateral small eyes, short tentacles with oval clubs with suckers in a circular pad and the sucker surface directed towards the front (already visible in small specimens), (Fig. 2N).

#### OMMASTREPHIDAE

A total of 107 rhynchoteuthions (ML = 1.0–5.5 mm), the characteristic paralarvae of the Ommastrephidae were obtained. They were more abundant in the North Brazilian Chain and the Fernando de Noronha Chain. At the given size range, identification was based upon the presence/absence of photophores in the mantle cavity and on the ventral



surface of the eyes, on the relative length of the proboscis, and on the size of the two lateral proboscis suckers compared with the other six suckers of the proboscis.

*Ommastrephes bartramii* (n = 9; ML = 2.5–3.8 mm).—These paralarvae had a medium sized proboscis (38% of ML), enlarged (150–200%) lateral suckers on the proboscis tip and no photophores either on the eyes or on the viscera. They occurred in all three areas.

*Sthenoteuthis pteropus* (n = 32, ML = 0.8–5.5 mm).—It was easily identified by its long proboscis, on average reaching 104% of the mantle length, and the non-enlarged lateral suckers of the proboscis. Specimens of more than 4.5 mm ML showed a large single photophore developing on the ventral surface of each eye. The species was the most abundant ommastrephid in the North Brazilian Chain and the Fernando de Noronha Chain, but did not occur at the St. Peter and St. Paul Archipelago.

*Hyaloteuthis pelagica* (n = 1; ML = 2.5 mm).—The single specimen lacked the proboscis, but a large single visceral photophore and one photophore on the ventral surface of each eye were clearly visible.

Sixty-five rhynchoteuthion paralarvae measuring less than 3.8 mm ML had a short to medium-sized proboscis with enlarged lateral proboscis suckers. No photophores on the digestive glands or under the eyes were apparent. They could not be further classified, but the larger specimens were most likely *Ommastrephes bartramii*. Two rhynchoteuthions (ML = 2.4 and 4.2 mm) with photophores on the digestive gland and on each eye were considered to be either *Ornithoteuthis antillarum* or *Hyaloteuthis pelagica*.

#### THYSANOTEUTHIDAE

*Thysanoteuthis rhombus* (n = 8; ML = 1.7–8.0 mm).—The only species of this family, was identified by the short mantle covered with a large number of small chromatophores, rounded fins, which were short in the smaller specimens, stout tentacles and trabeculae on the protective membrane of the dorsal arms, and small laterally protruding eyes. These paralarvae occurred in all three areas.

#### CHIROTEUTHIDAE

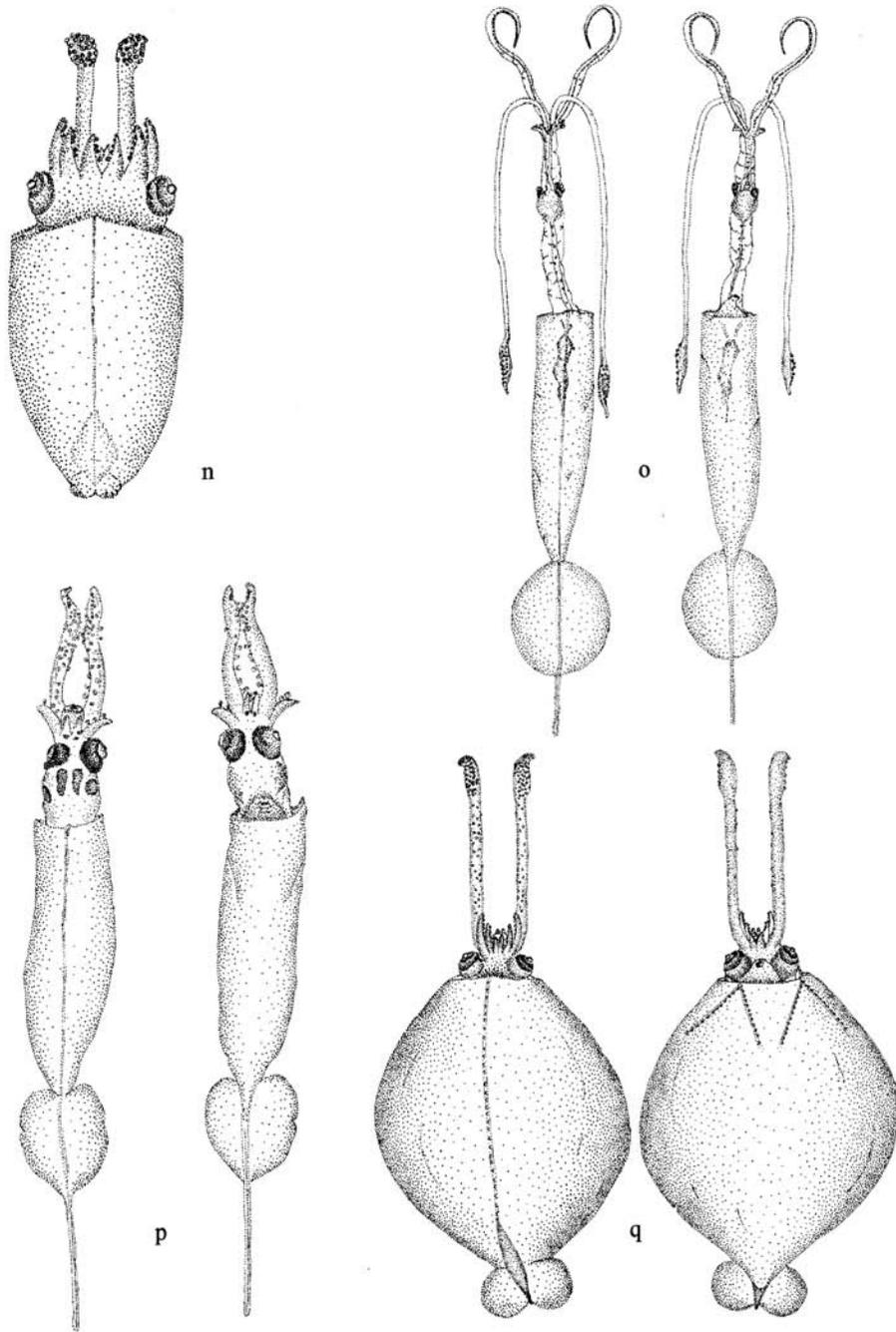
*Chiroteuthis* sp.—A single specimen (ML = 20.0 mm, without tail) was collected off the Fernando de Noronha Chain. It was characterized by a long and slender mantle, with the gladius extending well posterior to the round primary and secondary fins, the long vesiculated (columnar) neck, a short arm crown relative to the neck, long tentacles and the fourth arms much longer than the other arm pairs (Fig. 2O).

#### MASTIGOTEUTHIDAE

*Mastigoteuthis* sp.—Two specimens (ML = 8.9; 9.0 mm) were identified by their elongated mantle with a smooth surface and the gladius extending in a spike like tail, transversally oval, large eyes, and four large chromatophores observed on the dorsal surface of the head. Arms were short, particularly the third pair (arm formula T>2>1>4>>3), and tentacles were stout, with more than four rows of very small suckers on the club (Fig. 2P).

#### CRANCHIIDAE

This family is characterized by a thin-walled mantle which is fused to the head at the nuchal region and to the funnel at the postero-lateral corners. Fifty-three cranchiids (ML = 1.4–25.0 mm) belonging to at least four genera were caught.



*Liocranchia reinhardtii* (n = 5; ML = 7.2–20.0 mm).—This species was characterized by a stout spindle-shaped broad mantle with a smooth surface showing two ventral tubercular cartilaginous strips of equal length converging at each funnel-mantle fusion, small paddle-shaped fins, sessile eyes, short arm crown, and relatively short and stout tentacles (Fig. 2Q). It mainly occurred in the area of the St. Peter and St. Paul Archipelago.

*Leachia* sp. (n = 10; ML = 8.0–25.0 mm).—Characteristics of this genus were a moderately stout mantle with one ventral longitudinal tubercular cartilaginous strip extending to each funnel-mantle fusion with alternate rosette shaped and small unilobulated tubercles resembling those of *L. atlantica*, elliptical fins with the spine of the gladius projecting between them, long stalked and round eyes, a long arm crown with short arms and stout long tentacles. At the observed ML only a few photophores were beginning to form on the (Fig. 2R). It occurred in all three areas, but was abundant in Fernando de Noronha Chain.

*Liguriella podophthalma* (n = 6; ML = 7.0–17.0 mm).—This species was characterized by a stout spindle-shaped mantle, paddle-shaped fins and diamond-shaped lanceola, moderately stalked oval eyes, arm crowns with short arms and long stout tentacles, tentacles with two rows of suckers in the proximal half and four in the distal half (Fig. 2S). The species occurred mostly in the area of the St. Peter and St. Paul Archipelago.

*Megalocranchia* sp.—A single specimen of 7.2 mm ML occurred in the area of the St. Peter and St. Paul Archipelago. Its mantle was moderately stout with small fins, the arm crown was moderately long with stout and long tentacles possessing two rows of suckers in the proximal half and four on the distal half. In comparison with *Liguriella podophthalma* of similar size, it had a shorter mantle, longer stalked eyes and a shorter arm crown (Fig. 2T).

Thirty-one small cranchiids could only be classified to family level. Fifteen of them (ML = 1.4–4.2 mm) had elongated mantles with very small fins, very short arm crowns, relatively short arms and tentacles, and protruding eyes (Fig. 2U); the other 16 specimens (ML = 2.4–4.5 mm) had larger fins, elongated arm crowns and stalked eyes (Fig. 2V).

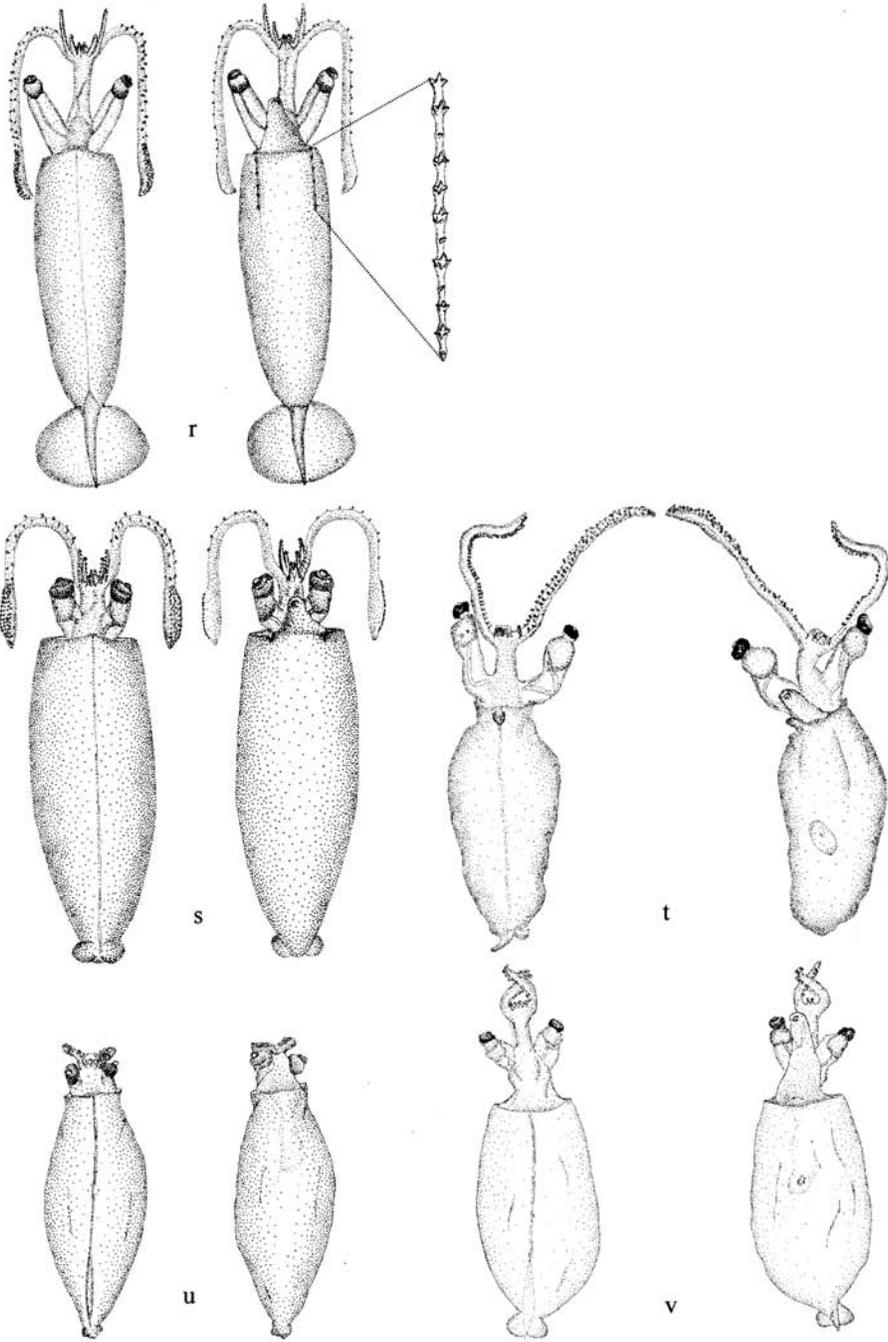
#### BOLITAENIDAE

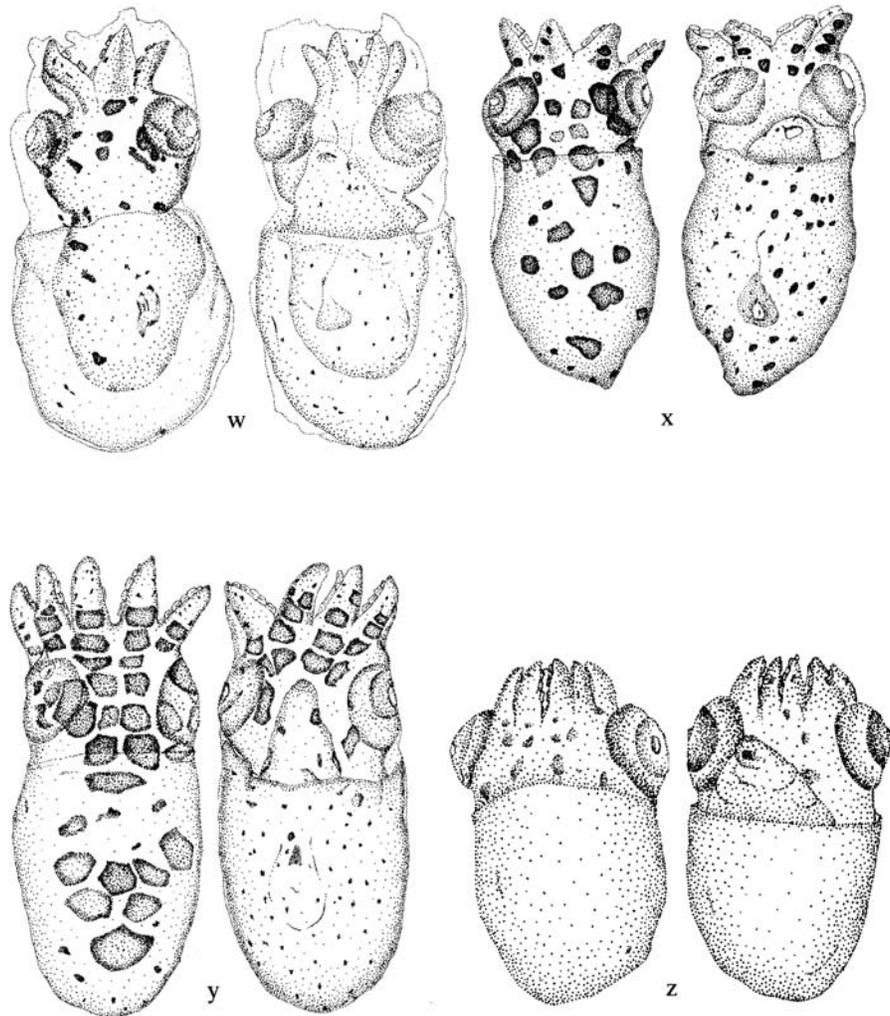
Two paralarvae of this family (ML = 2.5; 2.8 mm) were collected at the North Brazilian Chain of seamounts. They had an extremely soft and gelatinous body with a thick jelly-like outer coating (Fig. 2W). The mantle was covered with small chromatophores; eyes were small to medium in size and widely separated, arms short with uniserial suckers. A large oval digestive gland was visible.

#### OCTOPODIDAE

Forty-seven paralarval specimens of this group were found that consisted of muscular and gelatinous forms which lack fins and cirri, and which possess one or two series of arm suckers. Thirty-seven paralarvae (ML = 0.9–3.7 mm) could not be further identified. They had equally sized and relatively short arms with biserial suckers. The mantles were elongated and showed a chromatophore pattern very much resembling that of *Octopus vulgaris* (Fig. 2X, Y). With the exception of one specimen caught off the St. Peter and St. Paul Archipelago, all occurred along the Fernando de Noronha Chain and in the region of the North Brazilian Chain of seamounts.

*Octopus defilippi* (n = 10; ML = 1.0–3.8 mm).—These paralarvae had biserial arm suckers and showed the well-developed arm pair III.





## TREMECTOPODIDAE

*Tremoctopus violaceus* (ML = 2.0 mm).—A single specimen was found in the samples from the Fernando de Noronha Chain. This paralarvae had a firm muscular body, dorsal arms were the longest with large biserial suckers and a brachial membrane (arm formula 1>>2>4>>3).

## ARGONAUTIDAE

*Argonauta* sp. (ML = 2.2 mm).—One paralarvae of this genus occurred in the St. Peter and St. Paul Archipelago region. It had a gelatinous body completely covered with chromatophores, small eyes, and equally sized arms with biserial suckers (Fig. 2Z).

Table 1. Cephalopod paralarvae from the Bongo samples off the north-eastern Brazil during the expedition of the RV Victor Hensen in January/February 1995. Leg A (St. Peter and St. Paul Archipelago), 23 positive stations. Leg B (Fernando de Noronha Chain), 21 positive stations. Leg C (North Brazilian Chain) 13 positive stations.

Family	Species/Genus/Type	Leg A	Leg B	Leg C	All legs
Lycoteuthidae	<i>Selenoteuthis scintillans</i>	2	1		3
Enoploteuthidae	<i>Enoploteuthis</i> sp.	1			1
Enoploteuthidae	<i>Abralia redfieldi</i>			1	1
Enoploteuthidae	<i>Abralia</i> sp.	2	8	6	16
Enoploteuthidae	<i>Abraliopsis</i> sp.	2		3	5
Enoploteuthidae	unidentified	31	35	64	130
Enoploteuthidae Total		36	43	74	153
Ancistrocheiridae	<i>Ancistrocheirus lesueurii</i>	3	1	2	6
Octopoteuthidae	<i>Octopoteuthis</i> sp.	12	6		18
Onychoteuthidae	<i>Onychoteuthis</i> type 1		1		1
Onychoteuthidae	<i>Onychoteuthis</i> type 2	10	36	2	48
Onychoteuthidae	<i>Onychoteuthis</i> type 3	2	2	3	7
Onychoteuthidae	unidentified		1	1	1
Onychoteuthidae Total		12	40	6	58
Ctenopterygidae	<i>Ctenopteryx sicula</i>	3			3
Ommastrephidae	<i>Ommastrephes bartramii</i>	3	2	4	9
Ommastrephidae	<i>Sthenoteuthis pteropus</i>		14	18	32
Ommastrephidae	<i>Hyaloteuthis pelagica</i>			1	1
Ommastrephidae	unidentified	5	15	45	65
Ommastrephidae Total		8	31	68	107
Thysanoteuthidae	<i>Thysanoteuthis rhombus</i>	2	5	1	8
Chiroteuthidae	<i>Chiroteuthis</i> sp.		1		1
Mastigoteuthidae	<i>Mastigoteuthis</i> sp.	2			2
Cranchiidae	<i>Liocranchia reinhardti</i>	4	1		5
Cranchiidae	<i>Leachia</i> sp.	2	6		10
Cranchiidae	<i>Liguriella podophtalma</i>	5		1	6
Cranchiidae	<i>Megalocranchia</i> sp.			1	1
Cranchiidae	unidentified	8	16	7	31
Cranchiidae Total		19	23	11	53
Teuthida	unidentified	15	15	16	46
Bolitaenidae	unidentified			2	2
Octopodidae	<i>Octopus defilippi</i>	1	3	6	10
Octopodidae	unidentified	1	25	11	37
Octopodidae Total		2	28	17	47
Tremoctopodidae	<i>Tremoctopus violaceus</i>		1		1
Argonautidae	<i>Argonauta</i> sp.	1			1
Cephalopoda	unidentified	2			2
Total		119	195	197	511
Paralarvae/1000m <sup>3</sup>		13	34	31	24
Number of families		12	11	8	15
Number of genera		16	13	12	21
Number of species		8	8	8	11

## DISCUSSION

Due to the lower net avoidance which paralarvae perform in contrast to adult cephalopod, the sampling of paralarvae has become an important tool to study the distribution, recruitment patterns and stock assessment of cephalopods (Okutani and Watanabe, 1983; Wormuth and Roper, 1983; Piatkowski, 1998). Recently, several studies proved the high abundance of cephalopod paralarvae in tropical and sub-tropical seas. In a study on the distribution patterns of early life stages of pelagic cephalopods sampled with the MOCNESS system in various regions of the Arabian Sea, Piatkowski et al. (1993) recorded densities of enoploteuthids, which has also been the most abundant group in the present study, of up to 523 ind 1000 m<sup>-3</sup>. An extraordinary abundance of squid paralarvae in the tropical eastern Pacific Ocean was reported by Vecchione (1999). In his study a maximum abundance of >12,000 ommastrephid paralarvae which occurred in a 15-min tow in a band parallel to the coast, 740 to 900 km west off central America which was attributed to a warmed surface layer (29°C isotherm) in El Niño waters. Ommastrephid paralarvae were also the most abundant group in the cephalopod paralarvae assemblages in Hawaiian Islands waters that was sampled by 4 m<sup>2</sup> ring nets (Bower et al. 1999). They accounted for 2,144 of a total of 10,375 paralarval specimens, and a mean abundance of 8.1 ind 50 m<sup>-2</sup>. In a systematic study on cephalopod paralarvae from the sub-tropical Atlantic Ocean, Dawe and Stephen (1988) sampled 528 specimens with Bongo nets and 7045 specimens using midwater trawls in the Gulf Stream region east of 60°W. Again, Enoploteuthidae and Ommastrephidae as well as Cranchiidae constituted the bulk of cephalopod paralarvae.

Our samples yielded much lower numbers of cephalopod paralarvae (mean abundance 24 ind 1000 m<sup>-3</sup>), which may be attributed to (a) the lower effort of sampling with only 20447 m<sup>3</sup> filtered water volume, (b) the low abundance of cephalopod paralarvae in the investigated region, or (c) the underestimated ability of the cephalopod paralarvae to avoid the Bongo net. Another reason of the low abundances may be due to the pronounced variability of abundance encountered in consecutive tows (Okutani and McGowan, 1969). Such variability indicates spatial patchiness, a phenomenon difficult to overcome by sampling. This variability means that a large number of samples must be included in any detailed investigation of the distribution of cephalopod paralarvae. Here, we only can report on a snapshot taken of the cephalopod paralarvae assemblage off north-eastern Brazil. We feel that a greater effort in sampling is needed to draw meaningful conclusions about distribution patterns of cephalopod paralarvae in that region and to better quantify their abundance.

Our study, however, clearly confirms that Enoploteuthidae, Ommastrephidae and Cranchiidae are major groups dominating in tropical seas. Their early life stages as well as those of most other species and genera found in our investigation are typical epipelagic oceanic forms as they occur also in other tropical and sub-tropical regions of the Indian and Pacific Oceans (Yamamoto and Okutani, 1975; Piatkowski et al., 1993; Bower et al., 1999). The occurrence of small, recently hatched paralarvae of economically valuable ommastrephids such as *Ommastrephes bartramii* and *Sthenoteuthis pteropus* indicates that spawning of these squids occurs in or near the investigated area.

Some spatial segregation between frequently occurring families was evident. For example, Octopodidae and Cranchiidae tended to appear in different hauls. The former were more likely to be found near shallow banks where they spawn with small pelagic

paralarvae of the *Octopus vulgaris* form, whereas the latter spawned in offshore oceanic waters. It was striking though that we did not find any representatives of Brachioteuthidae and Histioteuthidae. These families are widely distributed in the surface layers of all oceans (Yamamoto and Okutani, 1975; Guerra et al., 1985; Young et al., 1985; Dawe and Stephen, 1988; Bower et al., 1999). This may be attributed to their daytime vertical distribution as they mostly occur in deeper layers than the maximum depth (150 m) sampled by the Bongo nets in our study.

No obvious differences were found among the cephalopod paralarvae assemblages recorded in the three areas that have been investigated. Mean abundance of paralarvae at the seamounts of the Fernando de Noronha Chain (34 ind 1000 m<sup>-3</sup>) and the North Brazilian Chain (31 ind 1000 m<sup>-3</sup>) were slightly higher than at the St. Peter and St. Paul Archipelago (13 ind 1000 m<sup>-3</sup>). We attribute this to the greater potential for enrichment of the surface layers in this region caused by seamount-induced perturbations, particularly in the North Brazilian Chain (Travassos et al., 1999). However, in all three regions strong thermoclines occurred at depths between 50 and 200 m suggesting a typical equatorial pattern of stable stratification. In the St. Peter and St. Paul Archipelago, Bröckel and Meyerhöfer (1999) reported an unexpected high variability of horizontal and vertical distribution of particulate organic carbon (POC) and nitrogen (PON) as well as chlorophyll *a* and pheopigments during the time of sampling. From their data no clear evidence arose for an enrichment of particulate organic material made available for higher trophic levels of the food chain. In fact, this region characterised by rocks reaching into the euphotic zone, showed the lowest mean abundance of cephalopod paralarvae (13 ind 1000 m<sup>-3</sup>). However, in this region some typical oceanic cephalopods occurred which were not abundant in the other regions, for example *Argonauta* sp., *Liguriella podophtalma*, *Chtenopteryx sicula*, *Mastigoteuthis* sp. It was surprising that octopod paralarvae showed the lowest abundances in this area, although the rocks should provide an important medium for settlement of later paralarval stages.

In conclusion, we can summarize that our data did not show the expected high concentrations of cephalopod paralarvae that could be related to an enhanced production along the sampled seamounts and rocks. However, our investigation provides a first account on the taxonomic composition and abundance of cephalopod paralarvae in the western part of the tropical Atlantic Ocean. Although, overall numbers of paralarvae collected from the zooplankton samples were relatively small, the study provides some new information on occurrence, relative abundance of tropical oceanic species.

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