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Bathymetric Distribution of Chaetognaths in the Indian Ocean

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Bathymetric distribution of chaetognaths in the Indian Ocean was studied based on stratified collections made on board of RV *Anton Bruun* from 2000 m to the surface during her cruises I to VII. Among the 25 species recorded 16 were epiplanktonic, 6 mesoplanktonic and 3 bathyplanktonic. *Sagitta enflata* and *S. decipiens* were the respective dominant species at the epiplanktonic and mesoplanktonic strata. *Eukrohnia fowleri* dominated the bathyplanktonic realm of the northern Indian Ocean and was replaced by *E. hamata* in the subtropical waters. Maximum density of chaetognaths was confined to the 125-0 m water column. Species diversity gradually decreased from epiplanktonic to bathyplanktonic domain. Maximum species diversity observed at 250-125 m was due to the mixing of the meso and epiplanktonic species at this stratum. Quantitative and qualitative variations along the latitudes indicated that the region north of the Equator sustained maximum diversity and a greater number of species than the other regions studied in the Indian Ocean. Epiplanktonic species were confined mainly to the upper 200 m with limited ingression into the lower strata. *Krohnitta subtilis*, *S. hexaptera* and *S. minima* were rare in the epiplanktonic realm of the north Indian Ocean and became common in that stratum towards the southern region. Species typical of southern Indian Ocean — *S. serratodentata* and *S. tasmanica* — were recorded up to 15° S lat. Most of the mesoplanktonic and bathyplanktonic species occupied their respective domain in the northern as well as central Indian Ocean and they emerged at the upper strata towards the subtropical convergence. Presence of 3 faunal zones with characteristic stratification of chaetognath species was recognized in the Indian Ocean: the tropical zone north of 10° S, the subtropical zone between 10° and 38° S and the transitional zone towards subtropical convergence.

INVESTIGATIONS on the chaetognaths from the Indian Ocean and adjacent seas have been reviewed[1-5]. Most of the earlier studies deal mainly with the horizontal distribution of different species. Studies on the vertical distribution of chaetognaths from the Indian Ocean are limited[6-8]. Alvariño[9] has tabulated the bathymetric disposition of different species in the Indian Ocean.

Zoogeography of chaetognaths in the entire Indian Ocean was investigated and based on the spatial extension of different species, distinct species assemblages along the tropical-subtropical regions are delineated[5]. At this stage, information on the stratification of chaetognath species is essential for complementing the above mentioned studies and also for evaluating the interaction between the species and varying environmental conditions in the vertical realm of the ocean. Stratified zooplankton samples collected on board of the US ship *Anton Bruun* during her cruises I to VII are useful in contributing data for this purpose. Vertical range of species inhabitingthe epi, meso and bathyplanktonic strata is studied in detail.

Materials and Methods

Collections studied were taken by the US ship *Anton Bruun* during IIOE. Station locations are shown in Fig. 1. The following cruises were made by *Anton Bruun* during 19.3.1963 to 7.9.1964: Cruise I — Bay of Bengal, 7° 27′ N to 20° 35′ N lat. and 80° 44′ to 97° 59′ E long.; cruise II — Central Indian Ocean, 17° 27′ N to 37° 12′ S lat. mainly along the 70° and 80° E meridian; cruise III — Western Indian Ocean, 11° 56′ N to 40° 54′ S lat. mainly along the 60° E meridian; cruise IVA — consisted for the most part sections from the central part of the Arabian Sea into and normal to the coast, 24° 48′ N to 19° 14′ S and 51° 02′ to 66° 21′ E long.; cruise V — Central and Western Indian Ocean, 16° 13′ N to 42° 23′ S lat. and 50° 22′ to 75° 20′ E long.; and cruise VII — area east of South Africa and south of Madagascar, 22° 34′ S to 35° 44′ S lat. and 32° 06′ to 43° 37′ E long.

Without taking aliquotes except in collections from cruise I, 905 samples were analysed. Most of the samples were oblique series collected using a Bé multiple plankton sampler[10] from the stratified depths 125-0 m, 250-125 m, 500-250 m, 1000-500 m and 2000-1000 m. Details of collections including particulars of net and hydrographical data are given in the station lists of the cruise reports published by the Woods Hole Oceanographic Institute[11]. Collections made by other nets like $75M_{25}$, NV70, $75M_3$, M-O were not utilised for quantitative evaluation since they were used for sampling depths different from those of Bé net samples. The 1548 standard samples[12] collected during IIOE Expedition (1960-65) were also considered for the vertical distribution of epiplanktonic chaetognath species.

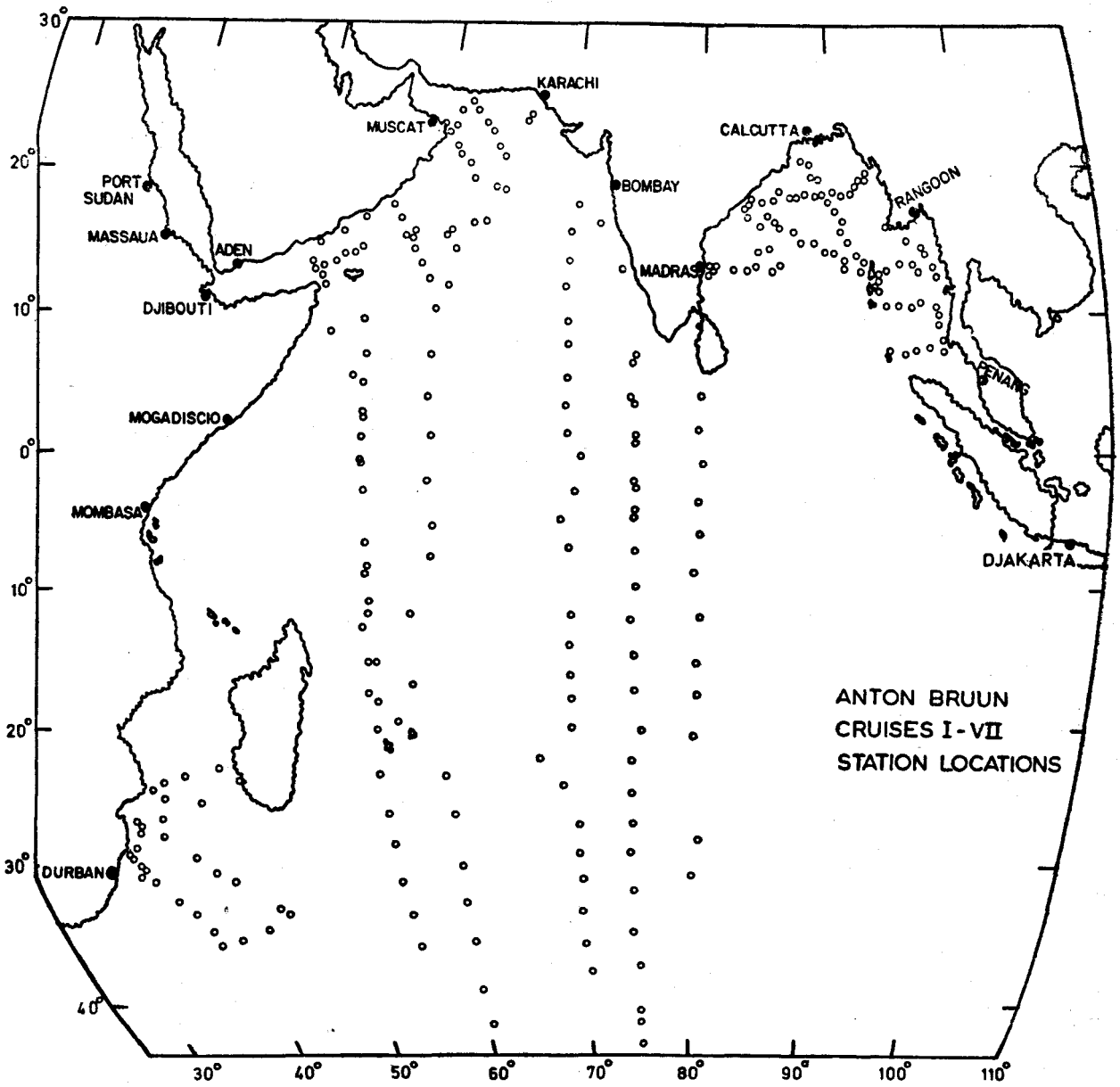


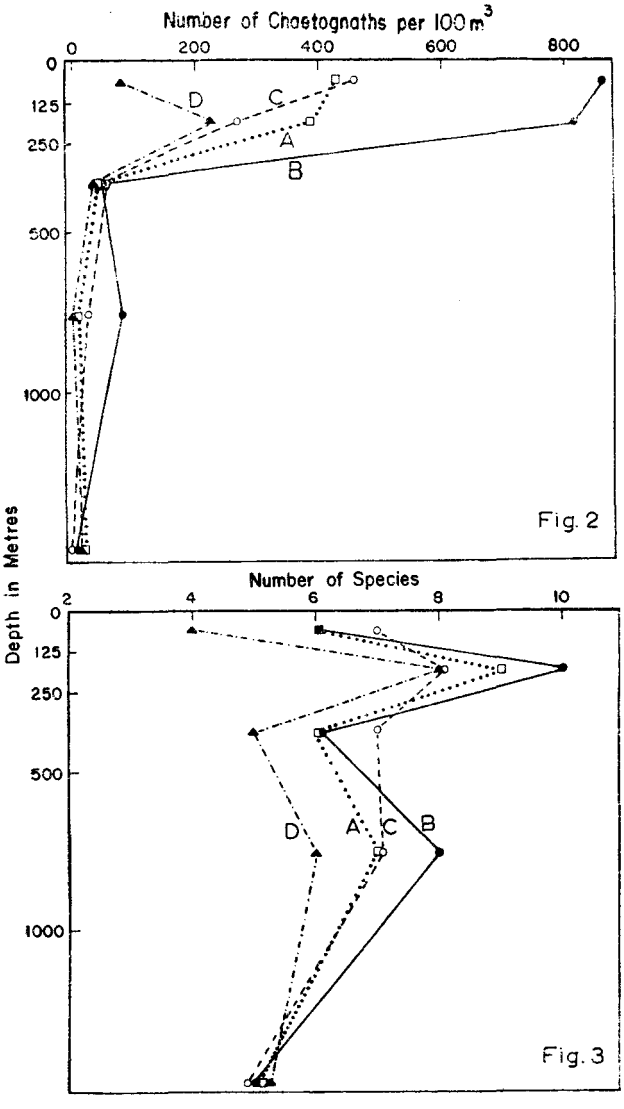
Fig. 1 — Stations occupied in the Indian Ocean during the various cruises of *RV Anton Bruun* during 19.3.1963 to 7.9.1964

Results and Discussion

Species of chaetognaths encountered in the samples in accordance with the strata they populate are: (i) Epiplanktonic (upper 200 m) — *Krohnitta pacifica* (Aida) 1897; *K. subtilis* (Grassi) 1881; *Pterosagitta draco* (Krohn) 1853; *Sagitta bedoti* Béraneck, 1895; *S. bipunctata* Quoy and Gaimard, 1827; *S. enflata* Grassi, 1881; *S. ferox* Doncaster, 1903; *S. hexaptera* d'Orbigny, 1843; *S. minima* Grassi, 1881; *S. neglecta* Aida, 1897; *S. pacifica* Tokioka, 1940; *S. pulchra* Doncaster, 1903; *S. regularis* Aida, 1897; *S. robusta* Doncaster, 1903; *S. serratodentata* Krohn, 1853; and *S. tasmanica* Thomson, 1947; (ii) Mesoplanktonic (200-1000 m) — *S. decipiens* Fowler, 1905; *S. gazellae* Ritter-Záhony, 1909; *S. lyra* Krohn, 1853; *S. macrocephala* Fowler, 1905; *S. maxima* (Conant) 1896; and *S. zetesios* Fowler, 1905; and (iii) Bathyplanktonic (below 1000 m) — *Eukrohnia bathypelagica* Alvariño, 1962; *E. Fowleri* Ritter-Záhony, 1909; and *E. hamata* Möbius, 1875.

Among the 25 species represented in the Indian Ocean, the epi, meso and bathyplanktonic realms were dominated respectively by *S. enflata, S. decipiens* and *E. Fowleri.* The last one was replaced by *E. hamata* in the subtropical region. Since the southern limit of sampling was restricted to 43° S lat., *S. gazellae* — the typical species of antarctic-subantarctic — was very sparsely represented. The vertical distribution of chaetognaths has to be considered under different sections for the elaboration of the many factors involved in the stratification.

Abundance and species diversity — Quantitative stratification of chaetognaths in the 2000-0 m water



Figs. 2 and 3 — Quantitative stratification of chaetognaths (2) and quantitative specific distribution in depth of chaetognaths (3) in the 2000-0 m water column [Mean values are represented. A — entire area; B — north of Equator; C — between Equator and 20° S lat.; D — south of 20° S lat.]

column is shown in Fig. 2. Maximum density was confined to the upper 250 m, particularly 125-0 m stratum. The 2000-1000 m sustained the lowest number and between the 2 depth intervals there was progressive reduction in numerical abundance. Previous studies also indicate a general decrease in the chaetognath population with increase in depth[8] and in the Indian Ocean Burfield and Harvey[6] found a more dense population in the upper 200 m.

Number of species and its relation to depth indicated (Fig. 3) that the former gradually decreased from the epipelagic zone to the deeper strata. The Maximum number of species was recorded between 250 and 125 m depth. Mixing of the mesoplanktonic with the epiplanktonic species at the 250-125 m stratum might have contributed to the maximum number of species found in this water column. This observation is contrary to the findings of Thiel[13] in the South Atlantic who found more species at 50 m depth. Possibly, difference in geographical location may account for such variation. The 1000 m to 500 m stratum also sustained a relatively higher number of species and it seems the extension of bathyplanktonic species into the mesoplanktonic domain might have contributed to this. In regions south of subtropical convergence, the upper 200 m water column maintained lesser number of species than the deeper strata, suggesting an inverse relationship to decrease in species number with increasing depth observed at the tropical-subtropical region. It was earlier observed by Alvarino[8] that in the north and south high latitudes, the layer below 200 m maintained a larger number of species of chaetognaths than the upper strata.

Latitudinal variation — Quantitative and qualitative variations were assessed along the latitudes for different depth intervals (Figs. 2 and 3). Results showed that the north Indian Ocean area, north of the Equator, harboured maximum density and a greater number of species than the other regions sampled in this ocean. The Indo-Pacific species are mainly confined to this zone[5] resulting in the aggregation of chaetognaths in this tropical zone. Towards the southern latitudes the population gradually decreased. South of 20° S, 250-125 m sustained maximum density of chaetognaths and presumably the surfacing of the mesoplanktonic species contributed to higher density. Latitudinal variations in species diversity influence mainly the epi and mesoplanktonic realms. Irrespective of latitudes the lowermost stratum sampled (2000-1000 m) supported a constant number of species. Merging of the species characteristic of different strata giving rise to prominent increase in species number in respective intermediate water column mentioned earlier was maintained along the different latitudes.

Epiplanktonic species — Detailed account on the epiplanktonic species in the upper 200 m of the Indian Ocean was reported by Nair[5]. Hence species showing significant change in the existing pattern of distribution alone was presented in the charts along with salinity and temperature profiles. The Indo-Pacific species *K. pacifica, S. bedoti, S. neglecta, S. pulchra* and *S. robusta* were confined mainly in the region north of 10° S[5] and were seldom represented in the 500-250 m hauls. *P. draco, K. subtilis, S. bipunctata, S. enflata, S. hexaptera, S. ferox, S. minima, S. pacifica* and *S. regularis* often extended below 250 m in regions north of 20° S and very rarrly encountered in samples below 500 m.

Even though *K. subtilis, S. hexaptera* and *S. minima* were reported to be epiplanktonic species in the Indian Ocean[9], they exhibited a different pattern of stratification other than that shown by the remaining epiplanktonic species. Latitudinal differences in the stratification of these species are shown in Figs. 4 and 5. *S. hexaptera* was sparsely represented in the upper 125 m and became more abundant below 200 m in regions north of 10° S and towards the southern part it became common in the epiplanktonic stratum (Fig. 4). Even though *K. subtilis* followed the same pattern of distribution as that of *S. hexaptera*, it occupied the epiplanktonic stratum only from area south of 22° S. North

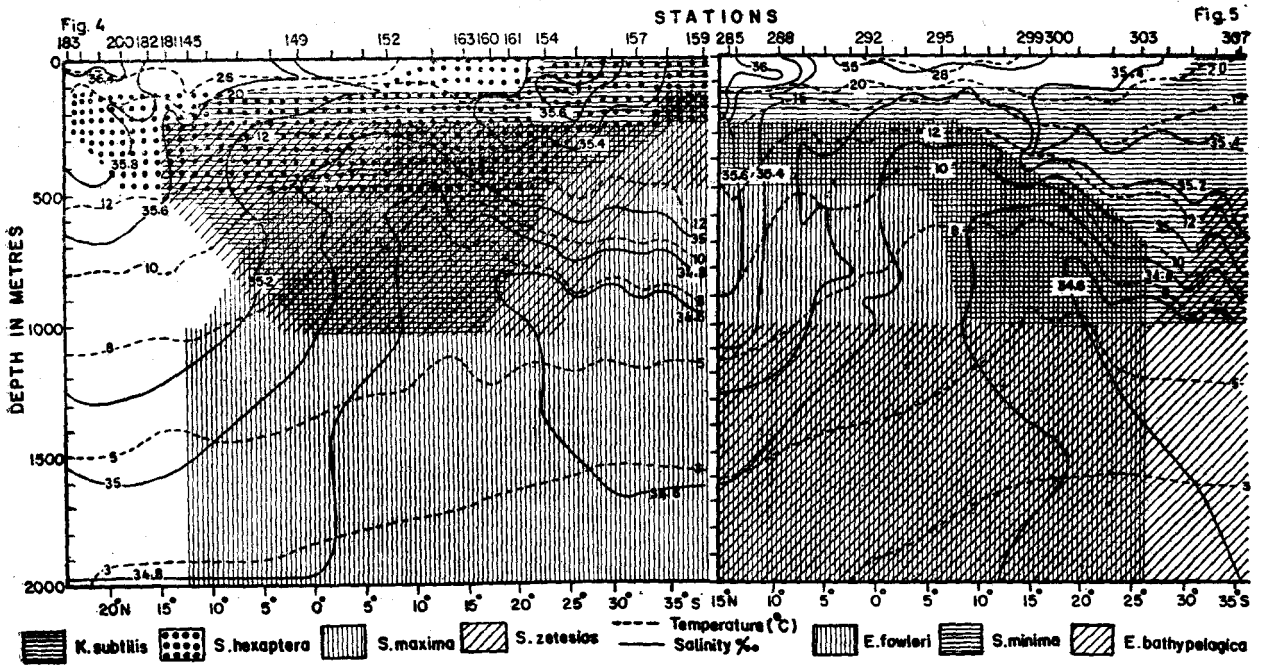


Fig. 4 — Hydrographic profile of *Anton Bruun* cruises III and IVA stations 145 to 163, 181 to 185 and 200, with distribution in depth of *K. subtilis*, *S. hexaptera*, *S. maxima* and *S. zetesios*

Fig. 5 — Hydrographic profile of *Anton Bruun* cruise V stations 285 to 307 with distribution in depth of *E. bathypelagica*, *E. fowleri* and *S. minima*

of the Equator *S. minima* was usually found in isolated areas in the upper 200 m (ref. 5). Towards south of the Equator it became more abundant in the epiplanktonic stratum and extended over a wide area (Fig. 5).

S. serratodentata, a typical species of temperate and warm Atlantic waters had been reported from the southern Indian Ocean[5,9]. This species was rarely obtained from stations located near 15° S from 1000-500 m and 2000-1000 m hauls. South of 25° S it was seen between 500 and 250 m and beyond 30° S in 250-125 m hauls. *S. tasmanica* is typical of the southern part of the Indian Ocean[5]. The northernmost record of *S. tasmanica* was 22° S in the east and 32° S in the west of the Indian Ocean[9]. In the present samples, they extended up to 15° S in layers below 250 m rising to the 250-125 m haul at locations south of 25° S. Near the subtropical convergence *S. tasmanica* was quite common in the 125-0 m hauls.

Mesoplanktonic species — S. decipiens: This was the dominant mesoplanktonic species in the Indian Ocean with maximum abundance between 1000-250 m (Fig. 6). The species quite often occupied layers below 1000 m in the northern and central Indian Ocean.

S. macrocephala: Vertical disposition of the species from north to south is presented in Fig. 7. In the northern Indian Ocean, the species was usually found between 1000-500 m level and south of the Equator reached the 500-250 m stratum. South of subtropical convergence it was encountered in samples from 250-125 m hauls.

S. maxima: This species exhibited an almost similar pattern of stratification as that of *S. macrocephala* (Fig. 4). However, numerically this species

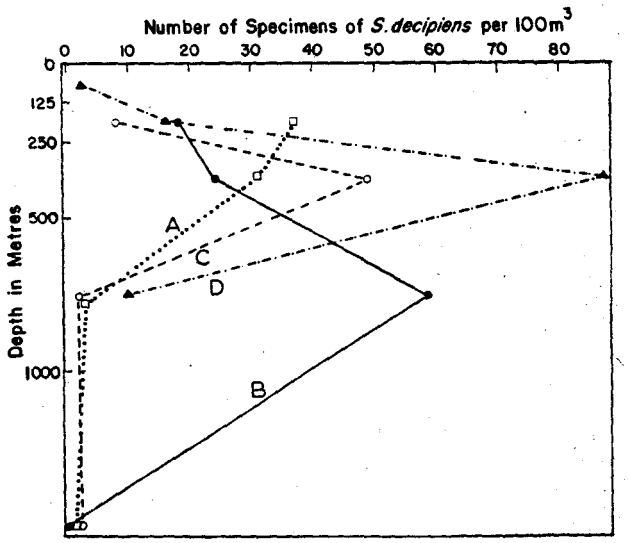


Fig. 6 — Quantitative vertical distribution of *S. decipiens* for *Anton Bruun* cruise V [A — station 284 (15° 22′ N 58° 12′ E); B — station 296 (8° 42′ S, 55° 07′ E); C — station 318 (16° 43′ S, 74° 53′ E) and D — station 307 (35° 42′ S, 55° 15′ E)]

was less abundant than *S. macrocephala*. North of 10° N *S. maxima* was usually absent or sparsely represented.

S. lyra: This species considered to be cosmopolitan in temperate and warm regions[9], was reported from the epiplanktonic realm of the Indian Ocean[8]. The present studies indicate that in the northern Indian Ocean, it was found below 200 m extending to 1000 m and up to 2000 m in the southern region, south of 30° S it reached the surface layers and often encountered in 125-0 m levels (Fig. 7).

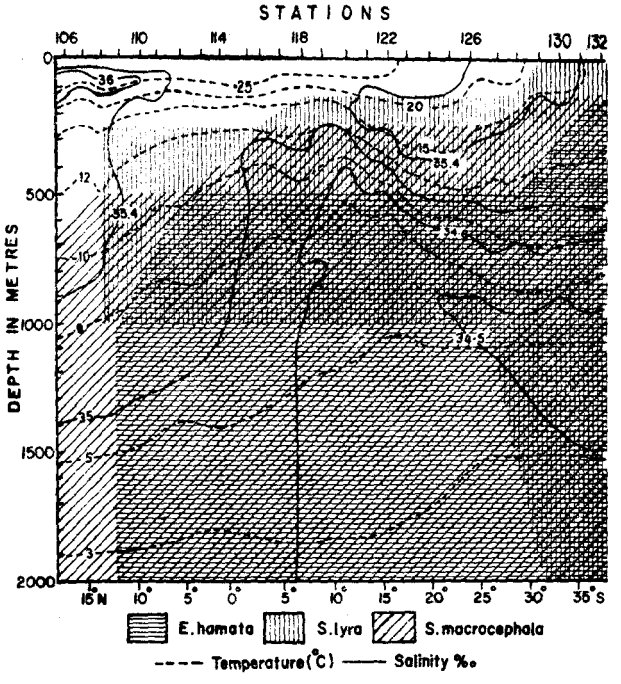


Fig. 7 — Hydrographic profile of *Anton Bruun* cruise II stations 106 to 132, with distribution in depth of *E. hamata*, *S. lyra* and *S. macrocephala*

S. zetesios: It was more common south of 10° N occupying the 1000-250 m level and slowly rising to the epiplanktonic stratum beyond 33° S (Fig. 4).

S. gazellae: This species was recorded from a single station located at 42° 23′ S and 74° 54′ E from 1000-500 m and 2000-1000 m depths. *S. gazellae* is characteristic of upper layers of Antarctic and Subantarctic waters[9,14,15]. Hence the present incidence of this species in deeper layers at subtropical convergence may indicate the presence of Antarctic waters.

Bathyplanktonic species — E. fowleri: In the northern Indian Ocean, *E. fowleri* was usually found below 500 m depth with the maximum abundance at layers below 1000 m (Fig. 5). *E. fowleri* was the dominant bathyplanktonic species in regions north of 20° S. The population was slowly decreasing towards the southern part of the Indian Ocean and it was not encountered in samples south of 25° S. South of 15° S wherever it was encountered in samples it was mostly from 2000-1000 m hauls.

E. hamata: This species was the dominant bathyplanktonic species in the southern Indian Ocean (south of 20° S). In the northern part it was less abundant and was often encountered in 2000-500 m water column. However, maximum density was noted below 1000 m. South of 28° S the species was quite often observed in 500-250 m hauls and beyond 34° S population was steadily spreading towards the 250-125 m stratum (Fig. 7). David[15] considered *E. hamata* as an abundant species in the Antarctic-Subantarctic region. Because of the lack of information it was considered scarce north of 30° S or inhabiting layers deeper than those sampled[9].

E. bathypelagica: The northernmost record of this species in the Indian Ocean was 11° 56′ S[2]. The present observation extends the distribution of the species to the northern part of the Indian Ocean indicating the species to be quite common even though quantitative representation was low. North of 26° S it was found in 2000-1000 m haul and south of this area it became more abundant entering the 1000-500 m stratum.

During the analyses it was noted that when these 3 bathyplanktonic species were found between 1000-500 m depth, the adults were seldom represented in the samples and they appeared in fair abundance in the 2000-1000 m stratum.

Sometimes the deep water species did not follow the normal distribution pattern as shown in Figs. 5 and 7 and appeared in the upper strata depending on the prevailing hydrographical conditions at the time of collection. In latitudes north of 3° N, *E. hamata* and *E. fowleri* were rarely encountered in 500-250 m hauls. However, during some other cruise of *Anton Bruun*, from a few stations *E. hamata* was obtained from 500-250 m hauls along with *E. fowleri* and this was reported as unusual incidence. At these stations temperature even at the surface was relatively low ranging from 24° to 25·5°C which may justify their incidence. At such stations *E. hamata* was numerically more abundant than *E. fowleri*.

Species Associated with Different Strata at Different Regions

Species observed at different depths in various parts of the Indian Ocean are given in Tables 1-2. The water masses found at the corresponding depths are also given in tables. The delineation of the different water masses in the Indian Ocean is in accordance with that of Wyrtki[16].

Species of the northwestern and northeastern Indian Ocean were almost similar at different strata. In the northern Indian Ocean, *K. pacifica*, *S. bedoti*, *S. neglecta* and *S. robusta* rarely extended beyond the 200 m depth (Table 1). The central and southern Indian Ocean sustained a different combination (Table 2) and here the absence of a few species — *K. pacifica*, *S. bedoti*, *S. neglecta* and *S. robusta* — was conspicuous during the present survey. *E. fowleri* and *E. hamata* which were seldom found at 500-250 m hauls at the northern Indian Ocean became more common along the same stratum towards the southern Indian Ocean.

The striking feature observed at subtropical convergence was the absence of epiplanktonic species excluding the *Serratodentata* group (Table 2). Incidence of mesoplanktonic species in the epiplanktonic and bathyplanktonic species in the mesoplanktonic strata was characteristic of this area. It was reported earlier that *E. hamata* lives at great depth in tropical and subtropical regions but in the subarctic and subantarctic it gradually rises to the surface[8,13]. In the present observation, *E. bathypelagica*, *E. hamata*, *S. macrocephala* and *S. maxima* exhibited this type of submergence at tropical waters.

General Remarks on Stratification of Chaetognaths

Apparent occurrence of mesoplanktonic and bathyplanktonic species in their respective strata in the

TABLE 1 — SPECIES OBSERVED AT DIFFERENT STRATA IN THE NORTHERN INDIAN OCEAN (NORTH OF 10° S LAT.)

Depth of haul (m)	Water masses found at particular stratum in the western side (west of 80°E long.)	Water masses found at particular stratum in the eastern side (east of 80°E long.)	Species
200-0	Arabian Sea surface water	Bay of Bengal surface water	*K. pacifica, K. subtilis, P. draco, S. bedoti, S. bipunctata, S. enflata, S. ferox, S. hexaptera, S. minima, S. neglecta, S. pacifica, S. pulchra, S. regularis, S. robusta.*
500-200	Persian Gulf water, Red Sea water	Bay of Bengal subsurface water, Persian Gulf water	*K. subtilis, P. draco, S. bipunctata, S. decipiens, S. enflata, S. ferox, S. hexaptera, S. lyra, S. macrocephala*, S. maxima, S. minima, S. pacifica, S. regularis, S. zetesios.*
1000-500	Arabian Sea intermediate water, Equatorial intermediate water, Pacific water, Antarctic intermediate water	Bay of Bengal subsurface water	*E. fowleri, E. hamata, S. decipiens, S. lyra, S. macrocephala, S. maxima, S. zetesios.*
2000-1000†	Arabian Sea intermediate water, Arabian Sea deep water		*E. bathypelagica, E: fowleri, E. hamata, S. decipiens, S. lyra, S. macrocephala, S. maxima, S. zetesios.*

*Found only in the northwestern Indian Ocean.
†For this stratum no data available from the northeastern Indian Ocean.

TABLE 2 — SPECIES OBSERVED AT DIFFERENT STRATA (i) IN THE CENTRAL AND SOUTHERN INDIAN OCEAN (BETWEEN 10° S AND 38° S LAT.) AND (ii) AT THE SUBTROPICAL CONVERGENCE (SOUTH OF 38° S LAT.)

Depth of haul (m)	Central and Southern Indian Ocean		Subtropical convergence	
	Water masses found at particular stratum	Species	Water masses found at particular stratum	Species
200-0	Surface water	*K. subtilis, P. draco, S. bipunctata, S. enflata, S. ferox, S. hexaptera, S. minima, S. pacifica, S. regularis*	Antarctic water	*S. decipiens, S. lyra, S. maxima, S. serratodentata, S. tasmanica*
500-200	Subsurface water	*E. hamata, E. fowleri, K. subtilis, P. draco, S. bipunctata, S. decipiens, S. enflata, S. lyra, S. macrocephala, S. maxima, S. minima, S. pacifica, S. serratodentata, S. tasmanica, S. zetesios*	Deep water	*E. bathypelagica, E. hamata, S. decipiens, S. lyra, S. maxima, S. serratodentata, S. tasmanica, S. zetesios*
1000-500	Antarctic water, Pacific water	*E. bathypelagica, E. hamata, E. fowleri, S. decipiens, S. lyra, S. macrocephala, S. tasmanica, S. zetesios*	do	*E. bathypelagica, E. hamata, S. decipiens, S. gazellae, S. lyra, S. macrocephala, S. maxima, S. zetesios*
2000-1000	Deep water	*E. bathypelagica, E. fowleri, E. hamata, S. macrocephala, S. tasmanica, S. zetesios*	do	*E. bathypelagica, E. hamata, S. gazellae, S. macrocephala, S. maxima, S. zetesios*

north as well as central Indian Ocean and their emergence at the upper strata towards the subtropical convergence were the most interesting aspects of the present study. Animals occur only with certain combinations of ranges of salinity and temperature. These combinations are represented by particular water mass which permits development and maintenance of its own characteristic fauna. A species bound to a water mass tends to follow the horizontal and vertical movement of that water mass[17]. If this approach for an understanding of the 3 dimensional distribution of zooplankton is acceptable, it may be presumed that movement of water masses is influencing the incidence of deep water chaetognath species at different levels in the Indian Ocean.

The hydrochemical front at 10° S and the subtropical convergence towards 40° S appear to deli-

neate the chaetognath fauna into 3 biogeographical provinces[5]. The stratification of different species also indicates the presence of 3 distinct faunal zones in the Indian Ocean: the tropical zone north of 10° S, the subtropical zone between 10° S to 38° S, and the transitional zone near subtropical convergence. The tropical zone is unique in maintaining the species in their respective bathymetric levels. At subtropical zone the Indo-Pacific species almost disappeared and the meso and bathyplanktonic species started penetrating into the strata just above the levels they are expected to occupy. Maximum faunistic contrasts were noticed at the transitional zone where the species of southern cold water and warm subtropical waters overlapped.

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