Plankton Biol. Ecol. 49 (1): 27–37, 2002

plankton
biology & ecology

Abundance and community structure of chaetognaths in the northern Indian Ocean

VIJAYALAKSHMI R. NAIR[1], MAKOTO TERAZAKI[2] & K. V. JAYALAKSHMY[3]

[1] *National Institute of Oceanography, Regional Centre, Lokhand wala Road, Four Bungalows, Mumbai-400 053, INDIA*
[2] *Ocean Research Institute, University of Tokyo, 1-15-1 Minamidai, Nakano-ku, Tokyo 164, Japan*
[3] *National Institute of Oceanography, Regional Centre, P.B. No. 1616, Dr. Salim Ali Road, Kochi-682 014, INDIA*

Received 20 December 1999; accepted 12 July 2001

Abstract: Abundance and community structure of chaetognaths in the northern Indian Ocean was investigated based on zooplankton samples collected during January to February 1990. Three types of sampling were done: from the upper 1100–1600 m water column, from discrete depths in the upper 1000 m covering day and night and from the upper 150 m water column using 0.33 mm (GG 54) and 0.1 mm (XX 13) mesh nets. In the first set of collections, population density of chaetognaths was higher in the Arabian Sea than in the Bay of Bengal. Nineteen species were found in the area of which the predominant species was *Sagitta enflata*. *S. decipiens* was the dominant mesopelagic species while *Eukrohnia fowleri* was the only bathypelagic species in the collections. In the vertical realm, the chaetognath population reached maximum abundance in the upper 100 m stratum and abruptly reduced on reaching the 1000 m stratum. In general, population density was higher in the night than in the day samples. Population density of chaetognaths caught by the 0.1 mm mesh net was higher than with the other nets and the community was predominated by *Krohnitta pacifica, Pterosagitta draco, Sagitta bipunctata, S. pacifica* and *S. regularis.* Stratification of chaetognaths in the 1000 m water column indicated variation within the community associated with the prevailing physico-chemical parameters. High species richness, high dominance/low evenness were obtained at low ambient temperature values. The relationship between dissolved oxygen concentration and community structure indices was negatively correlated , with lower DO values at higher community diversity indices. Data collected during the day revealed a high level of community similarity (>60% community coefficient values/similarity index values) between similar depths such as (50 m, 100 m), (300 m, 400 m), (500 m, 600 m), (600 m, 700 m) and (700 m, 800 m). At depths below 500 m, chaethognath species had narrower distributions, being confined to 100 m depth layers, centered around the depth of their maximum abundance. In the night collections similar trends were evident, in particular, the depth strata at 500 m and 600 m showed >80% similarity in the composition of species.

Key words: chaetognaths, species diversity, community structure, northern Indian Ocean.

Introduction

The northern Indian Ocean is rich in chaetognaths (Nair 1977; Pierrot Bults & Nair 1991) and this area is characterised by a seasonally changing monsoonal gyre (Wyrtki 1973) leading to distinct zoogeographic patterns in the distribution of chaetognaths (Nair 1978). Most of the reports on chaetognaths in the Indian Ocean are based on the collections taken during the International Indian Ocean Expedition (IIOE, 1960–65) and subsequent studies in the open ocean are limited to those for the Andaman Sea (Nair et al. 1981), the Western Indian Ocean along a transect between 9°N to 20°S (Nair & Madhupratap 1984), chaetognaths collected from the epipelagic realm of the Exclusive Economic Zone (EEZ) of India (Srinivasan 1990, 1996) and a mass occurrence of *Eukrohnia fowleri* in the northern Indian Ocean (Terazaki 1999). During the around the world expe-

Corresponding author: Vijayalakshmy R. Nair; e-mail, vijaya@hotmail.com

[1] Present address: National Institute of Oceanography, Regional Centre, P.B. No. 1616, Dr. Salim Ali Road, Kochi- 682 014, India.

dition of the RV *Hakuho Maru*, zooplankton samples were collected from the northern Indian Ocean and these were analyzed to determine the abundance and community structure of chaetognaths in the upper 1600 m. The stratified collection made from the Eastern Indian Ocean (Andaman Sea) during both day and night and the samples collected from the upper 150 m of the water column using nets of different mesh sizes provided additional information on the group.

Materials and Methods

Zooplankton samples collected from the northern Indian Ocean (Fig. 1) during the RV *Hakuho Maru* cruise KH–89–2 between January and February 1990 were used for the present study. Though the station locations are limited, the sampling covered the entire northern Indian Ocean. Three sets of samples were collected. (1) From Stns 17, 18, 20, 21 and SB4 oblique tows were made from depths between 1100 to 1600 m and the surface using an ORI net having a mouth area of 2 m^2 and a mesh aperture of 0.69 mm (Omori 1965). (2) At Stn 19 horizontal tows were made with an MTD net having a mouth diameter of 56 cm and mesh aperture of 0.33 mm (Motoda 1971). Twenty two tows were made from 11 depth layers between the surface and 1000 m during the day as well as at night. (3) The upper 150 m of the water column at Stns 17, 18, P13, 19, 20, 21 and SB4 was sampled using a twin NORPAC net with a 45 cm mouth diameter and mesh size of 0.33 mm (GG54) and 0.1 mm (XX13). A total of 14 samples were collected.

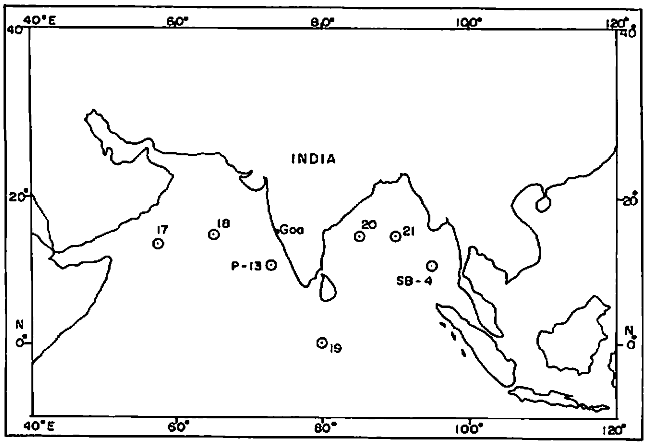

Fig. 1. Map indicating station locations.

Details of the collections are presented in Table 1 and the results are presented in Tables 2–10. Zooplankton samples were preserved in buffered 10% formalin seawater solution. Chaetognaths from the collections were sorted out and identified to species level. Population density was presented as number per 1000 m^3. The data were subjected to 3 way ANOVA for comparison between stations, depths, nets, species and interaction effects between any two of these variables (Snedecor & Cochran 1967). Factor analyses in two modes viz., R-mode for grouping of species and Q-mode for grouping of stations/depths was adopted. Using column (row) standardization and column (row) normalization for R-mode (Q-mode) and varimax rotation to simple structure for uniqueness of the factor groups obtained (Dagnelie 1960; Harman 1967; Morison 1978) the species and the stations/depths were grouped (Angel & Fasham 1973) into ecologically significant factor groups (eigen value $\lambda > 1$).

Community structure was described by concentration index (Simpson 1949), Shannon Weaver index (Shannon & Weaver 1963), richness index (Margalef 1968), dominance index (Pielou 1971) and evenness index (Heip 1974). Species niche breadth was calculated adopting the method of Ignatiades (1994). Prior to numerical analyses the population density data were transformed to log(x+1) for ob-

Table 1. Sampling details for zooplankton collections from the Indian Ocean used in this study.

Station	Date	Time (h)	Type of net	Towing method	Sampling layer (m)
17	23 Jan.1990	19:10–19:24	NORPAC	Vertical	0–150
17	24 Jan.1990	21:05–22:05	ORI-69	Oblique	0–1600
18	25 Jan.1990	18:28–18:37	NORPAC	Vertical	0–150
18	25 Jan.1990	22:14–23:18	ORI-69	Oblique	0–1150
19	3 Feb. 1990	12:30–14:35	MTD	Horizontal	Surface, 50, 100, 200, 300, 400, 500, 600, 700, 800, 1000
19	3–4 Feb. 1990	23:05–01:20	MTD	Horizontal	Surface, 50, 100, 200, 300, 400, 500, 600, 700, 800, 1000
20	7 Feb. 1990	02:12–02:21	NORPAC	Vertical	0–150
20	7 Feb. 1990	15:45–16:55	ORI-69	Oblique	0–1418
21	8 Feb. 1990	21:15–21:24	NORPAC	Vertical	0–150
21	8 Feb. 1990	11:58–13:08	ORI-69	Oblique	0–1117
SB4	11 Feb. 1990	04:38–04:47	NORPAC	Vertical	0–150
SB4	11 Feb. 1990	07:27–08:38	ORI-69	Oblique	0–1387

taining homogeneity and data was normalized for applying various statistical tests. Similarity between stations/depths with respect to chaethognath density was calculated using a community coefficient (Pearson & Rosenberg 1978).

Results

Ranges of various water quality parameters in the upper 1000 m are available only for Stns 17, 19 and 20 (Terazaki 1999). Temperature, salinity and dissolved oxygen varied respectively from 4.2 to 29°C, 34.8 to 36.8 PSU and 0.2 to 5.5 mg l^{-1}. Levels of phosphate and nitrate increased with depth and the ranges were 0.15 to 3.50 μM and 0.4 to 42.0 μM respectively. Levels of these chemical parameters for various depths in the upper 1000 m water column indicated decreases in temperature, salinity and dissolved oxygen towards 1000 m depth while the nutrient concentrations increased.

Distribution of chaetognaths in the surface to 1100–1600 m water column

Population density of chaetognaths was highest in the Arabian Sea (Stn 18) while relatively low numbers were found in the Bay of Bengal. Nineteen species belonging to four genera were present in the collections (Table 2). *Sagitta enflata* was the dominant species contributing 31 to 78% of the total chaetognath population. The other common epipelagic species in the area were *Pterosagitta draco*, *Sagitta bedoti*, *S. bipunctata*, *S. hexaptera* and *S. pacifica*. Among the mesopelagic species, *S. decipiens* predominated in the area, though *S. macrocephala* was also represented in all the samples. *Eukrohnia fowleri*, the only bathy pelagic chaetognath species represented in the collections, was fairly abundant with a percentage contribution of 0.4 to 11.5. Representation of species was marginally more in the Bay of Bengal as compared to the Arabian Sea with maximum diversity at Stn 20.

Factor analysis by Q mode (Morison 1978) for grouping of stations, based on absolute abundance of species when applied, divided the stations into 3 distinct groups: factor group 1 containing Stns 17, 18 and 20 and which contains 76.5% of the chaetognath population, group 2 containing Stn 21 and 16.9% of the total chaetognath population and group 3 containing Stn SB4 and only 6.7% of the total population. This classification shows greater similarity between Stns 17, 18 and 20 and differences between Stn 21 and those stations and also between the stn SB4 and the other stations (Table 3) as indicated by the 3 way ANOVA. About 43% of the variations in the spatial distribution of the chaetognath species is explained by the factor group 1. In this group, the numerically dominant species *S. enflata* (68.7%) is nearly 10 times as abundant as the next abundant species, *S. pacifica* (6.5%). The other species that contributed to the species composition of the group that clustered through factor group 1 comprised 3.3% or less numerically than the most abundant species, *S. enflata*. Factor group 2 (Stn 21) and factor group 3 (Stn SB4) explained almost equal amounts of variability, 28.5%. In these 2 factor groups the dominant species *S. enflata* is followed by different co-dominant species justifying the grouping.

Table 2. Total population and contribution of different species (no./1000 m^3) of chaetognaths species at various stations in the 0 to 1100–1600 m water column of the Indian Ocean collected using ORI net.

Species	Stations 17	18	20	21	SB4
Total population	1033	1625	1039	215	320
Eukrohnia fowleri	38	7	33	29	38
Krohnitta pacifica	16	2	4	9	2
K. subtilis	33	12	9	1	0
Pterosagitta draco	28	12	104	80	39
Sagitta bedoti	45	48	13	7	2
S. bipunctata	24	32	74	190	14
S. decipiens	2	8	75	56	64
S. enflata	756	1272	603	393	103
S. ferox	0	0	7	1	9
S. hexaptera	4	64	33	14	17
S. macrocephala	3	24	3	2	2
S. maxima	0	0	1	3	4
S. minima	12	28	4	0	0
S. neglecta	0	0	2	2	1
S. pacifica	69	112	61	19	22
S. pulchra	0	2	4	4	4
S. regularis	0	0	0	0	1
S. robusta	3	2	7	5	5
S. zetesios	0	0	2	0	2

Table 3. Q-mode factor analysis for grouping of Stns 17, 18, 20, 21, SB4 in 0 to 1100–1600 m water column.

Factor group	Stations identified by the factor group	Variability explained (%)	Closeness ratio (%)
1	17, 18, 20	43.1	94.3
2	21	28.3	97.4
3	SB4	28.5	99.8

R-mode factor analysis grouped the species based on absolute abundance into 4 significant factor groups (Table 5). Group 1 contained 9 species with high negative factor loadings explaining about 35.7% of the variations in the species distribution. The first 3 species included were moderately abundant at Stns 20, 21 and SB4 and others were very rare and showed only chance occurrence at Stn 18. Species included in the factor group 2 were either present in higher relative abundance or moderate relative abundance. Group 3 included species occurring relatively abundantly at Stn 17. Group 4 included species that were rare and appeared only at Stn SB4 (Table 5). The similarity relation between

Table 4. Q-mode factor analysis for grouping of day (D) and night (N) samples at Stn 19.

Factor group	Depth (m) identified by the factor group	Variability explained (%)	Closeness ratio (%)
1	600D, 600N, 700D, 700N, 800D, 800N	24.0	32.8
2	50D, 50N, 100D, 100N, 200D, 200N	24.9	59.8
3	400D, 400N, 500D, 500N	16.8	74.0
4	1000D, 1000N	5.1	80.5
5	Surface-D, Surface-N	7.5	86.7

Table 5. R-mode factor analysis for grouping of species based on the 5 Stns in the 0 to 1100–1600 m water column.

Factor group	Species identified by the factor group	Variability explained (%)	Closeness ratio (%)
1	*E. fowleri, P. draco, S. bipunctata, S. decipiens, S. maxima, S. neglecta, S. pulchra, S.robusta, S. zetesios*	35.7	57.0
2	*S. enflata, S. hexaptera, S. lyra, S. macrocephala, S. minima, S. pacifica*	30.1	81.6
3	*K. pacifica, K. subtilis*	15.8	90.8
4	*S. ferox, S. regularis, S. zetesios*	14.3	100.0

the stations in the 0 to 1100–1600 m water column, based on a community coefficient showed that only Stns 17, 18 and SB4 had community coefficients between 50 and 60% while all other pairs of stations had >70% association based on common occurrence of species.

Stratification and day/night variations in chaetognaths

In the vertical dimension the chaetognath population was most numerically abundant in the upper 100 m of the water column (average: 4569/1000 m^3), abruptly decreasing between 100–200 m and further decreasing gradually towards the 1000 m stratum. In the 700 m stratum the average population density of chaetognaths was 356/1000 m^3 showing a reduction of about 13 times from that of the surface values and this was further reduced by a factor of 54 at 1000 m compared to the 0–100 m water column. Day–night variation in chaetognath population density indicated that higher densities were invariably recorded at night rather than during the day at all locations except in the 500 m and 800 m stratum. The average population density for day and night in the 0 to 1100–1600 m water column were respectively 1021/1000 m^3 and 1991/1000 m^3 (Fig. 2).

A total of 19 species were represented in the collections. In accordance with bathymetric distribution of different species of chaetognaths Alvarino (1965) classified them to be epipelagic (upper 200 m), mesopelagic (200–1000 m) or bathypelagic (1000–4000 m). However, the present data showed variations in the stratification of species within these classification ranges. The distribution of the species was directly related to depth and the variables that change with depth. *S. enflata* continued to be the dominant epipelagic species in the upper 200 m of the water column with an average contribution to numerical abundance of 40% and was absent below 500 m. Epipelagic species like *K. pacifica*, *P. draco*, *S. bipunctata*, *S. ferox* and *S. regularis*, though common, were limited to the upper 400 m. *K. subtilis*, *S. hexaptera*, and *S. minima* were common below the epipelagic layer. *S. serratodentata* was represented only in a single sample from 800 m. The distributional range of *K. subtilis* extended down to 800 m while that for *S. hexaptera* and *S. minima* respectively extended down to 600 m and 700 m. The mesopelagic species *S. decipiens*, *S. lyra*, *S. macrocephala* and *S. zetesios* were abundant especially between 500 and 800 m. *S. maxima*, another mesopelagic species, was relatively low in abundance. Among the bathypelagic species *E. hamata* was the most common (13–36.5%) followed by *E. bathypelagica* (2.5–20.5%). *E. fowleri* was limited to depths between 700 to 1000 m. Species diversity between day and night samples showed irregular patterns (Table 7).

From the relation between richness factor and temperature it was observed that species richness decreased from a value of 8.00 to 4.00 as temperature increased from 12.5–30.0°C, i.e. as depth decreased from 300 m to the surface (Fig. 3). High species richness was observed at higher depths associated with lower temperatures. Species concentration increased from 0.72 to 0.83 as depth decreased from 800 m to 50 m. At the surface and at 1000 m, low concentrations of species were observed. Species diversity measured by Shannon Weaver index which gives weightage for the relative abundance of species, also followed the same trend as that of species concentration. High dominance/low evenness was obtained at low temperatures (Fig. 3).

The various community structure indices exhibited maximum values in the salinity range 34.9 to 35.5 PSU and a depth range of 1000 to 100 m. These indices also exhibited

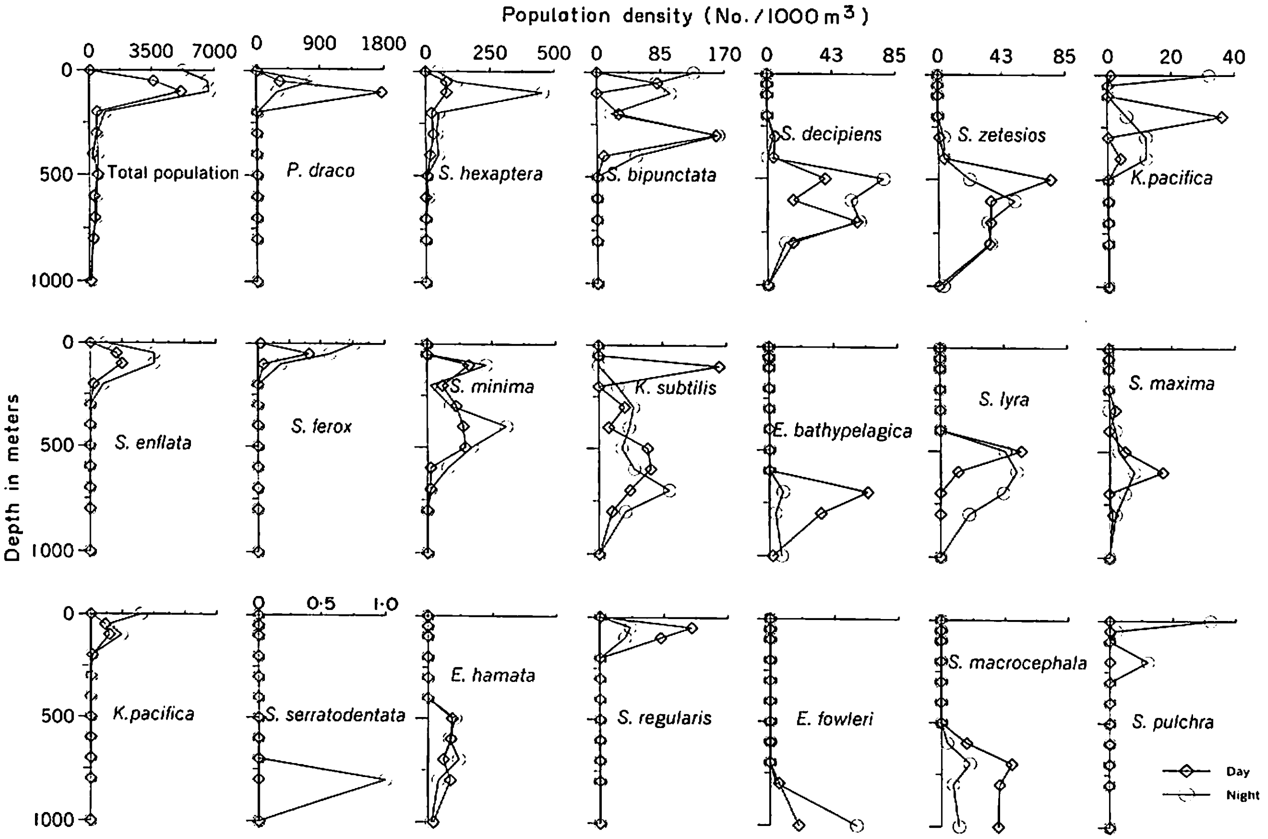

Fig. 2. Vertical distribution of total chaetognath population and the vertical abundance profiles of different species during day and night at Stn 19.

Table 6. R-mode factor analysis for grouping of species based on data from different depths in the 0 to 1000 m water column at Stn 19 during day and night.

Factor group	Species identified by the factor group	Variability explained (%)	Closeness ratio (%)
1	*S. ferox, S. pacifica, S. pulchra, S. regularis*	19.4	28.2
2	*E. hamata, S. decipiens, S. lyra, S. maxima, S. zetesios*	22.1	53.1
3	*S. enflata, S. hexaptera, S. minima*	11.9	63.2
4	*E. bathypelagica, S. macrocephala*	9.9	71.5
5	*S. serratodentata*	5.6	77.3
6	*K. pacifica*	5.9	82.5

higher values at lower dissolved oxygen concentrations, 1.0 to 2.0 ml l^{-1} in the depth range of 1000 to 200 m. With regard to the nutrients PO_4-P and NO_3-N, an increasing trend in the Margalef index with increasing nutrient concentrations was observed. Maximum values were reached in the 2.1 to 3.1 μM range for PO_4-P and the 25 to 35 μM range for NO_3-N (Fig. 3).

Three way ANOVA applied to compare between depths, species and day–night variation and the first order interaction effects between the above aspects showed significant depth-wise ($F_{(10,190)}=12.2309$, $P<0.05$) and species wise ($F_{(19,190)}=24.9219$, $P<0.05$) variations with a high species-depth interaction effect ($F_{(190,190)}=11.0088$, $P<0.05$). Vertical migration is also detected with specific depth preference for ($F_{(1,190)}=12.5650$, $P<0.05$) particular species.

Q mode factor analysis applied to study the influence of depth on the distribution of the species divided the depth-wise data into 5 distinct significant factor groups based on species abundance (Table 4). Factor group 1 contained the 600 to 800 m depth stratum, factor group 2 the 50 to 200 m depth stratum, factor group 3 the 400 to 500 m depth stratum and subsequent factor groups contained the 1000 m depth and surface stratum irrespective of the diel variation. In the 600 to 800 m depth stratum, the most abundant

Table 7. Species richness, concentration, diversity, evenness and dominance indices at different depths at Stn 19 during day and night (in parentheses).

Depth (m)	Margalef (Richness index)	Simpson (Concentration index)	Shannon (Diversity index)	Heips (Evenness index)	Pielou (Dominance index)	S (No. of species)	N (Total no. of chaetognaths)
0	3.90 (4.32)	0.45 (0.64)	1.10 (1.80)	0.66 (0.72)	0.53 (1.21)	4 (8)	59 (5276)
50	3.90 (3.61)	0.72 (0.64)	2.12 (1.92)	1.23 (0.97)	0.97 (1.01)	7 (7)	3605 (6619)
100	4.35 (3.61)	0.71 (0.65)	2.07 (1.93)	0.99 (0.98)	1.12 (0.94)	8 (7)	5154 (6699)
200	5.33 (6.23)	0.77 (0.34)	2.38 (1.22)	1.63 (0.30)	1.12 (1.33)	7 (9)	440 (905)
300	7.95 (6.97)	0.75 (0.78)	2.38 (2.55)	1.09 (1.47)	0.75 (0.94)	10 (9)	404 (444)
400	7.06 (6.87)	0.47 (0.56)	1.59 (1.81)	0.56 (0.64)	1.21 (1.22)	8 (9)	192 (479)
500	6.01 (6.07)	0.81 (0.75)	2.57 (2.35)	1.73 (1.35)	1.21 (1.45)	8 (8)	449 (452)
600	6.65 (7.12)	0.79 (0.84)	2.58 (2.79)	1.75 (1.91)	1.26 (1.38)	8 (9)	266 (385)
700	5.52 (7.09)	0.84 (0.81)	2.69 (2.66)	2.28 (1.66)	1.17 (1.24)	7 (9)	318 (395)
800	6.81 (8.87)	0.78 (0.74)	2.49 (2.39)	1.59 (1.10)	0.77 (0.87)	8 (10)	233 (159)
1000	3.65 (4.69)	0.64 (0.57)	1.63 (1.66)	1.37 (1.07)	0.32 (0.64)	4 (5)	78 (92)

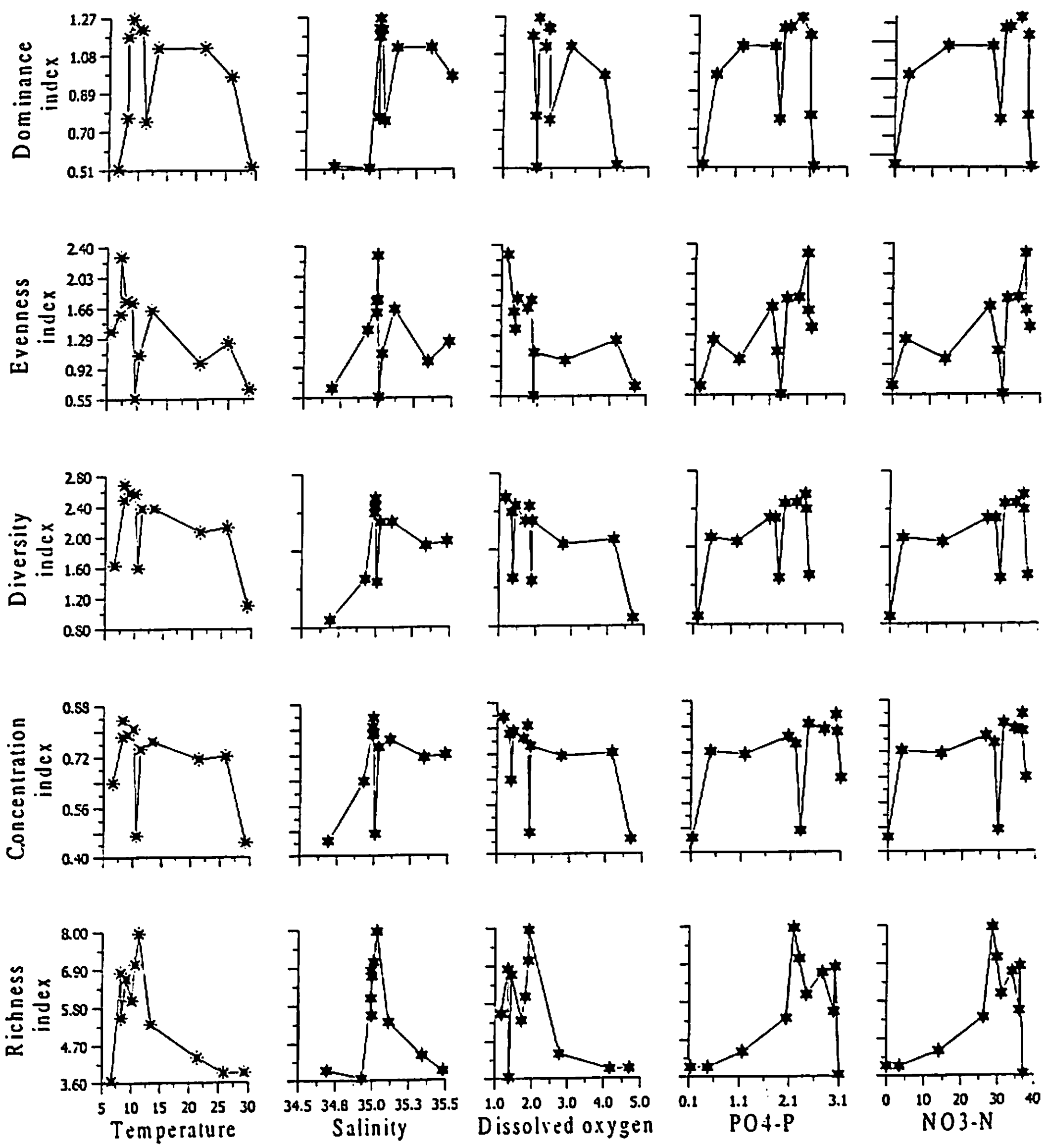

Fig. 3. The relationship between various community structure indices and water quality parameters at Stn 19.

species were *E. hamata* (relative abundance: 26.2%), *K. subtilis* (21.0%) and *S. decipiens* (11.6%). *P. bathypelagica* occurred only at 700 to 800 m depth but was not abundant. In the factor group 2 depth stratum (50 to 200 m), the dominant species were *S. enflata* (49.8%), *S. pacifica* (19.2%), *P. draco* (10.7%), *S. ferox* (7.1%) and *S. bipunctata* (2.1%). Maximum abundances of these species occurred between 50 to 100 m with marginal differences between day and night, except for *S. ferox* which was more abundant during the night (Fig. 2) and *S. enflata* which was nearly twice as abundant during the night as during the day. In the third factor group depth stratum (400 to 500 m), *E. hamata* (21.0%) and *S. lyra* (10.4%) were most abundant in the 500 m depth samples and were also present in deeper waters in almost the same proportions (Fig. 2). The third depth factor group also contained the species *S. minima* (50.8%), *K. subtilis* (8.8%), *S. decipiens* (6.8%) and *S. serratodentata*, the rarest species (Table 4, Fig. 2). In the fourth factor group depth stratum (1000 m), abundant species were *E. fowleri* (43.2%), the deep ocean species, *S. macrocephala* (30.9%) and *E. hamata* (18.7%), both mid depth to deep ocean species. In the fifth factor group, surface stratum, the dominant species were *S. ferox* (46.6%), *S. pacifica* (40.4%) and *S. enflata* (9.9%).

For these samples, R-mode analysis had clustered the species into 6 distinct factor groups containing 4, 5, 3, 2, 1 and 1 species respectively (Table 6). The first 3 factor groups accounted for >50% of the variation in the bathymetric distribution during both day and night with species clusters occupying the 0–200 m, 600–800 m, 50–500 m depth layers but most abundant in the 50–200 m water column, rare in the 300–600 m depth stratum and almost absent at depths >700 m, respectively. The fourth factor group contained 2 species (*E. bathypelagica* and *S. macrocephala*) occupying the depths between 700–1000 m (totally absent in the 700 m depth layer during the day and with a relative abundance of 12.1% in the 700–1000 m layer during the day, almost 3.8 times the abundance in that layer at night). The fifth factor group contained the rarest species (*S. serratodentata*). The sixth factor group contained a species (*K. pacifica*) occurring with a relative abundance of 32% on the average, in the lowest depth stratum (Fig. 2). R-mode and Q-mode analyses gave rise to a depth correlated zonation for the chaetognath species (Table 6). Samples collected during the day were highly similar (community coefficient: >60%) between near by depths such as (50 m, 100 m), (300 m, 400 m), (500 m, 600 m), (600 m, 700 m) and (700 m, 800 m). In particular, at depths exceeding 500 m, there were less pronounced vertical migrations of the chaetognath species and they migrated only within a column of 100 m depth from their depth of maximum daytime abundance (Fig. 4). During night collections, a similar result was obtained. In particular, the depth strata of 500 m and 600 m had more than 80% similarity in the species compositions (Fig. 5).

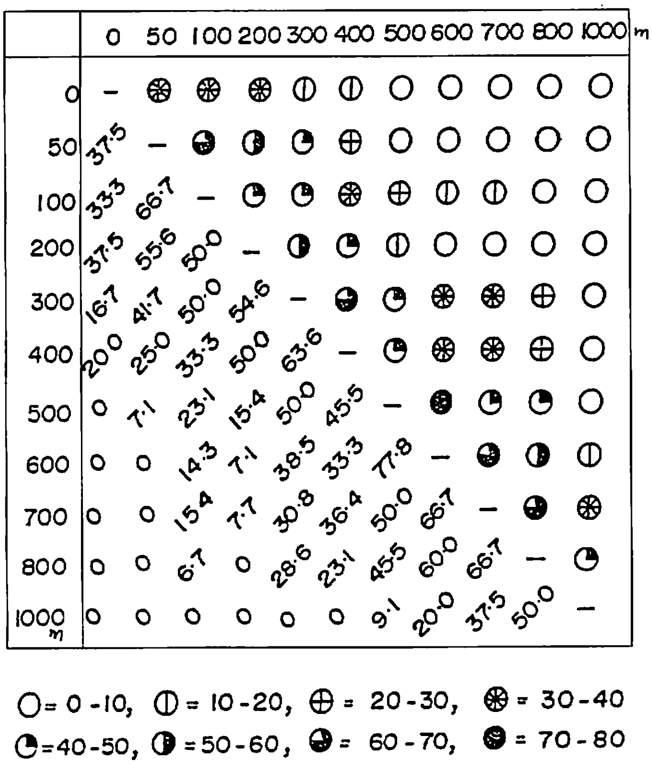

Fig. 4. Trellis diagram for community coefficient (%) between depths during day.

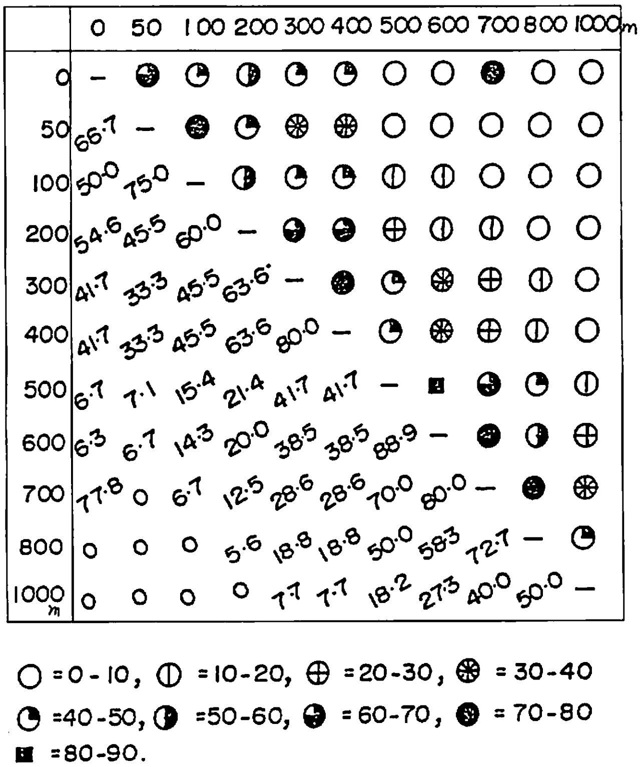

Fig. 5. Trellis diagram for community coefficient (%) between depths during night.

Table 8. Species richness, concentration, diversity, evenness and dominance at different stations.

Station	Type of net	Margalef (Richness index)	Simpson (Concentration index)	Shannon (Diversity index)	Heips (Evenness index)	Pielou (Dominance index)	S (No. of species)	N (Total no. of chaetognaths)
17	ORI-69	9.17	0.45	1.65	0.35	0.78	13	1033
	NORPAC-XX13	3.66	0.61	1.94	0.86	0.93	8	25629
	NORPAC-GG54	3.68	0.64	1.92	0.83	1.23	8	19652
18	ORI-69	10.03	0.39	1.43	0.23	1.38	13	1625
	NORPAC-XX13	3.66	0.70	2.16	1.09	0.92	8	25551
	NORPAC-GG54	4.83	0.51	1.70	0.50	1.19	10	23927
19	NORPAC-XX13	4.92	0.64	1.99	0.79	0.99	9	5534
	NORPAC-GG54	4.89	0.71	2.28	1.10	1.15	9	5856
P13	NORPAC-XX13	3.39	0.68	2.13	1.06	1.25	12	12771
	NORPAC-GG54	4.33	0.70	2.21	1.01	1.33	9	18140
20	ORI-69	12.98	0.64	2.29	0.52	1.39	18	1039
	NORPAC-XX13	5.92	0.80	2.70	1.27	1.23	12	18858
	NORPAC-GG54	4.72	0.78	2.56	1.45	1.26	9	7999
21	ORI-69	11.86	0.70	2.30	0.60	1.67	16	815
	NORPAC-XX13	4.85	0.79	2.65	1.46	1.17	10	18655
	NORPAC-GG54	4.95	0.74	2.42	1.14	1.44	10	15291
SB4	ORI-69	14.22	0.77	2.76	0.93	0.87	17	329
	NORPAC-XX13	3.58	0.81	2.52	1.91	1.23	7	7230
	NORPAC-GG54	5.54	0.82	2.76	1.65	0.89	10	5489

Community structure

At stns 17 to 20 and SB4 species richness varied between 9.17 (Stn 17) and 14.22 (Stn SB4). The species concentration varied between 0.39 (Stn 18) and 0.77 (Stn SB4) whereas diversity varied between 1.65 (Stn 17) and 2.77 (Stn SB4). The species evenness index showed a trend similar to that of species concentration recording a range from 0.23 (Stn 18) to 0.93 (Stn SB4). The dominance index was lowest at Stn 17 (0.78) and highest (1.61) at Stn 20 (Table 8). Species niche breadth, an index used to describe migration tendency, indicates that it is not a highly fluctuating factor but varied between 2.70 (*S. lyra*) and 5.00 (*S. regularis*). For the species *E. fowleri* (2.45%), *P. draco* (5.06%), *S. enflata* (66.73%), *S. maxima* (0.087%), *S. negleta* (0.087%), *S. pacifica* (5.82%) and for other rare species niche breadth varied between 4.02 and 5.00 showing that the relation between niche breadth and abundance is not very highly significant (Table 9). During the day, lowest species richness (~3.65) occurred at 0 m, 50 m and 1000 m depth and higher values (>7.05) were obtained at 300 m and 400 m depth (Table 7). The strata between 300 m and 800 m were more species rich than other depths. Species concentrations between 500 m and 1000 m and between 50 m and 300 m were denser, with a similar pattern of distribution for the diversity index also. Species abundance was more evenly distributed between 500 m and 700 m. The dominance index was found to be lowest at 0 m and 1000 m depth (Table 7).

Species niche breadth was highest (5.61) for *S. minima* (5.7%) which was present at all depths between 50 m and 700 m. For 5 of the species *P. draco* (19.1%), *S. enflata* (30.8%), *S. ferox* (7.7%), *S. pacifica* (18.2%) and *S. hexaptera* (2.13%), which were present at almost all depths, niche breadth ranged between 1.64–4.90 and indicated an inverse relationship between niche breadth and abundance in the daytime collections (Table 9).

Based on night samples, strata between 200 m and 800 m were found to be more species rich (>6.07) than other depth strata. Species concentration was >0.56 at all depths except 200 m. Species diversity was found to be >1.81 at all depths other than the surface and 1000 m depth. Species evenness was also generally high at depths >500 m. The dominance index was higher at depths between 400 m and 700 m (Table 7). Regarding niche breadth, distribution for the night-time collections, the highest value was 7.97, for *S. maxima* (0.1%; rarest species). Lowest values, (<2.69) were for *S. fowleri* (27.0%) and *S. ferox* (12.3%). For the abundant species, *S. enflata* (39.6%), *S. pacifica* (25.5%), niche breadth was <3.1 (Table 9). For the moderately abundant species, niche breadth was approximately 5.1, indicating an inverse relationship between niche breadth and species abundance in the night collections, as was also observed during the day (Table 9).

Average species richness and dominance were greater in the night samples (c.v.=23%) than in the day samples whereas species concentration, species diversity and species evenness were higher for day samples with less variability in the first two factors (c.v.=20%) and higher variation in the third factor (c.v.=37%) (Table 10).

For species collected with 0.33 mesh size, the number of

Table 9. Species niche breadth at different stations.

Species	ORI net (5 stations)	NORPAC-XX13 (7 stations)	Niche breadth values NORPAC-GG54 (7 stations)	MTD (Day)	MTD (Night)
Eukrohnia bathypelagica	—	—	—	2.97	6.82
E. fowleri	4.51	—	—	4.78	2.40
E. hamata	—	—	—	4.97	4.54
Krohnitta pacifica	3.67	4.85	5.00	3.15	4.90
K. subtilis	2.94	3.21	3.37	5.51	6.57
Pterosagitta draco	4.02	6.51	5.85	1.64	2.03
Sagitta bedoti	3.38	1.80	2.90	—	—
S. bipunctata	3.31	5.01	4.56	3.20	5.40
S. decipiens	3.52	2.09	1.38	4.98	4.24
S. enflata	4.19	5.34	5.57	2.45	3.31
S. ferox	3.28	1.53	2.26	1.76	2.69
S. hexaptera	3.69	3.12	3.47	4.90	3.96
S. lyra	2.70	—	—	2.85	4.65
S. macrocephala	2.74	—	—	4.71	5.77
S. maxima	4.13	—	—	5.29	7.97
S. minima	2.81	1.76	1.93	5.61	5.07
S. neglecta	4.71	3.20	2.69	—	—
S. pacifica	4.14	6.14	6.40	2.67	3.06
S. pulchra	4.51	—	2.65	—	5.24
S. regularis	5.00	5.09	5.14	3.41	3.49
S. robusta	4.61	—	1.81	—	—
S. zetesios	4.71	—	—	4.70	5.46

Table 10. The average values of the characteristics describing community structure of chaetognaths.

Community structure indices	ORI net (5 stations)	NORPAC-XX13 (7 stations)	NORPAC-GG54 (7 stations)	MTD (Day)	MTD (Night)
Margalef $\bar{X}$	11.65	4.36	4.71	5.56	5.95
σ	1.86	0.83	0.54	1.40	1.61
C.V. (%)	15.92	18.98	11.38	25.22	25.98
Simpson $\bar{X}$	0.59	0.72	0.70	0.70	0.66
σ	0.15	0.07	0.09	0.13	0.13
C.V. (%)	24.77	10.39	12.94	17.85	20.49
Shannon $\bar{X}$	2.09	2.30	2.26	2.15	2.10
σ	0.48	0.29	0.34	0.48	0.46
C.V. (%)	23.03	12.81	14.88	21.31	21.92
Heips $\bar{X}$	0.53	1.21	1.10	1.35	1.11
σ	0.24	0.36	0.36	0.49	0.45
C.V. (%)	45.47	29.79	32.39	36.05	40.37
Pielou $\bar{X}$	1.26	1.11	1.18	1.01	1.09
σ	0.29	0.13	0.18	0.23	0.24
C.V. (%)	23.04	11.53	14.89	22.52	21.92

$\bar{X}$=average value of the index over all stations/depths.
σ=Standard deviation of the index over all stations/depths.
C.V. (%)=Coefficient of the variation of the index over all stations/depths.

species obtained is almost homogeneous between all the stations. The richness factor was also similar at all stations (range from 3.68 at Stn 17 to 5.54 at Stn SB4) (Table 8). The species concentration factor was not a highly variable characteristic, ranging between 0.50 (Stn18) and 0.82 (Stn SB4). Species diversity was lowest (1.70) at Stn 18 and highest (2.76) at Stn SB4 with a similar pattern for species evenness. Species dominance was lowest (0.89) at Stn P13 and highest (1.44) at Stn 21, where *S. enflata* was the dominant species (51.2%). Regarding species niche breadth, it was high (>5.04) for *K. pacifica* (4.9%), *P. draco* (6.5%), *S. enflata* (51.2%), *S. pacifica* (12.2%) and *S. regularis* (4.4%) which were all distributed throughout the study area. Lower values (<1.93) were observed for *S. minima*, *S. robusta* and *S. decipiens*, which are relatively rare (Table. 9).

Community structure indices of the chaetognaths collected with a 0.1 mm mesh aperture NORPAC net in the upper 150 m (Table 8), showed that the average richness was 4.36, which was less than that calculated based on samples collected with 0.33 mm mesh size NORPAC nets. Species concentration, diversity and evenness were higher with 0.1 mm mesh size (0.72, 2.30 and 1.21 respectively) than with 0.33 mm mesh (0.70, 2.26 and 1.02 respectively) nets. Dominance however was higher with 0.33 mm mesh size nets (1.18) than with 0.10 mm mesh nets (1.11) (Table 10). Species niche breadth varied between 1.53 (*S. ferox*, 0.4%) and 6.14 (*S. pacifica*, 15.0%). Higher values (>5.01) were for *S. bipunctata* (16.2%), *S. enflata* (41.4%), *S. regularis* (5.8%) and *P. draco* (7.1%) (Table 9). These species were distributed throughout the study area and the results indicated linearity in the relationship between species abundance and niche breadth.

Discussion

Maximum density of chaetognaths was observed in the upper 100 m of the water column and 23 species were recorded from the present collections. The Indo–Pacific species, (Nair 1978) *K. pacifica*, *S. ferox*, *S. pacifica*, *S. pulchra* and *S. robusta* were confined mainly to the upper 100 m of the water column with limited incursion into the 400 m stratum. The epipelagic cosmopolitan species of the Atlantic, Indian and Pacific Oceans (Alvarino 1974; Nair 1977, 1978) like *P. draco*, *S. enflata* and *S. bipunctata* were observed down to the 400 m stratum.

The distribution and range of the epipelagic species *K. subtilis*, *S. hexaptera* and *S. minima* showed a different pattern, extending towards the deeper mesopelagic layers of the northern Indian Ocean up to depths of 600–800 m. *S. serratodentata*, a typical species in temperate and warm Atlantic waters (Alvarino 1965) has previously been reported from the southern Indian Ocean (Nair 1977). This species, which was recorded from a single day time collection at Stn 19 from the 800 m depth stratum, illustrates that the distributional range of this species extends further north. The most common mesopelagic species were *S. decipiens*, *S. lyra*, *S. zetesios* and *S. macrocephala* with low numbers of *S. maxima*. *E. fowleri* was the dominant bathypelagic species. *E. hamata* and *E. bathypelagica* were well represented at Stn 19.

The vertical distribution of species indicated the presence of 3 distinct distributional ranges: one where 73% of the population was confined to the surface to 400 m depth layer with the remainder of the population occurring above 800 m depth, a range containing mesopelagic species occurring between 300 m and 1000 m and a range containing bathypelagic species from 500 m to 1000 m depth. Even though *K. subtilis*, *S. hexaptera* and *S. minima* have been reported to be epipelagic species in the Indian Ocean (Alvarino 1965), they exhibited a different pattern of stratification to that shown by the other epipelagic species (Nair 1978). Due to their relatively higher abundance in the strata below 200 m, it would appear that the existing definition of epi, meso and bathypelagic species is arbitrary with glaring variations in the bathymetric distribution of chaetognaths.

Chaetognath population density was relatively low in the Andaman Sea compared with an earlier report (Nair et al. 1981). The present record of 4 indiv. m^{-3} in the upper 200 m of the water column is much lower than the IIOE data (20 indiv. m^{-3}) and subsequent data from the Andaman Sea (7 indiv. m^{-3}). Probably this is an artifact of the limited number of samples and differences in the sampling depths. Many chaetognath species undertake vertical migrations and this is illustrated by the higher abundance of chaetognaths in night rather than day samples from Station 19, with the community being dominated by *K. pacifica*, *P. draco*, *S. bipunctata*, *S. pacifica* and *S. regularis*.

In general, the northern Indian Ocean was rich in chaetognaths with a relatively higher abundance in the Arabian Sea than the Bay of Bengal (Nair 1977). However, species diversity was marginally greater along the eastern rather than the western part of the north Indian Ocean. *S. enflata* predominated in the epipelagic realm, while the meso and bathypelagic domains were dominated respectively by *S. decipiens* and *E. fowleri*. The relative contributions of epi, meso and bathypelagic species to the chaetognath community (0 to 1100–1600 m) were respectively 65, 22 and 13 percent. Statistically depth-wise, day–night and mesh size variations were significant with specific depth preferences for particular species.

The community structure of chaetognaths in the three sets of samples indicated representation by a higher proportion of species (80% of the total species number) when sampling depth was from 1000 m and below as compared to the upper 150 m of the water column (65% of the total species number). This trend appeared to be linked to the prevailing chemical parameters. In the upper 1000 m of the water column, high species richness, high dominance/low evenness were obtained at lower temperatures. The relationship of dissolved oxygen concentrations with the community structure values also showed higher values at lower levels of DO.

Acknowledgments

The first author is indebted to the University of Tokyo, Tokyo for awarding a Fellowship during the term the present work was carried out.

Literature Cited

Alvarino, A. 1965. Chaetognaths. Oceanogr. Mar. Biol. Ann. Rev.

3: 115–194.

Alvarino, A. 1974. The importance of the Indian Ocean as origin of the species and biological link uniting the Pacific and Atlantic Oceans. *J. Mar. Biol. Ass. India* **14**: 713–722.

Angel, M. V & M. J. R. Fasham 1973. Sond cruise 1965. Factor and cluster analysis of the plankton results. A general summary. *J. Mar. Biol. Ass.* (*U.K.*) **53**: 185–231.

Dagnelie, P. 1960. Contribution a Pe' tude des communaut'es ve' ge' tales par I'analyse factorielle. *Bull. Serv/Carte Phytogeogr.* **B5**: 7–71 and 93–195.

Harman, H. H. 1967. *Modern Factor Analysis*. Univ. of Chicago Press, Chicago, 474 pp.

Heip, C. 1974. A new index measuring evenness. *J. Mar. Biol. Ass.* (*U.K.*) **54**: 555–557.

Ignatiades, L. 1994. Species dominance and niche breadth in bloom and nonbloom phytoplankton populations. *Oceanol. Acta* **17**: 89–96.

Morisson, D. F. 1978. *Multivariate Statistical Methods*. McGraw-Hill International Book Company, 415 pp.

Margalef, R. 1968. *Perspectives in Ecological Theory*. Univ. Chicago Press, 111 pp.

Motoda, S. 1971. Devices of simple plankton apparatus *V. Bull. Faculty Fish. Hokkaido University* **22**: 101–106.

Nair, V. R. 1977. Chaetognaths of Indian Ocean. *Proc. Symp. Warm Water Zoopl.* Spl. Publ. UNESCO/ NIO. 168–195.

Nair, V. R. 1978. Bathymetric distribution of chaetognaths in the Indian Ocean. *Indian J. Mar. Sci.* **7**: 276–282.

Nair, V. R, Achuthankutty, C. T., Nair, S. R. S. & Madhupratap, M. 1981. Chaetognaths of the Andaman Sea. *Indian J. Mar. Sci.* **10**: 270–273.

Nair, V. R. & M. Madhupratap 1984. Latitudinal range of Chaetognatha and Ostracoda in the western tropical Indian Ocean. *Hydrobiologia*. **112**: 209–216.

Omori, M. 1965. A 160-cm opening–closing plankton net. 1. Description of the gear. *J. Oceanogr. Soc. Jpn.* **21**: 20–26.

Pearson, T. H. & R. Rosenberg 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Biol. Ann. Rev.* **16**: 229–311.

Pielou, E. C. 1971. Measurement of structure in animal communities, pp. 278. In: *Ecosystem Structures and Function* (ed. Wiens, J. A). Proc. 31st Annual Biology Colloquim. Oregon state U.P. Portland.

Pierrot-Bults, A. C. & V. R. Nair 1991. Distribution patterns in chaetognaths, p. 86–116. In *The Biology of Chaetognaths* (eds. Bone, Q, H. Kapp & A. C. Pierrot-Bults). Oxford Science Publications, Oxford, New York, Tokyo.

Shannon, G. E. & W. Weaver 1963. *Mathematical Theory of Communication*. Univ. of Illinois Press, Urbana, Illinois, pp. 117.

Simpson, E. H. 1949. Measurement of diversity. *Nature* **163**: 688.

Snedecor, G. W. & W. G. Cochran 1967. *Statistical Methods*. Oxford and IBH Publishing Company, New Delhi, 535 pp.

Srinivasan, M. 1990. Studies on the quantitative distribution of Chaetognatha from the Indian Seas, collected during the Cruise 1-44 of *FORV Sagar Sampada. Proc. First Workshop Scient. Result. FORV Sagar Sampada* (ed. Mathew, K.J.). **8**: 1–84.

Srinivasan, M. 1996. Spatial and temporal distribution of chaetognaths from the eastern Arabian Sea. *Proc. Second Workshop Scient. Result. Forv Sagar Sampada*, 139–148.

Terazaki, M. 1999. Mass occurrence of bathypelagic chaetognath *Eukrohnia fowleri* from the Arabian Sea and Bay of Bengal. *Indian J. Mar. Sci.* **28**: 163–168.

Wyrtki K. 1973. Physical Oceanography of the Indian ocean, p. 18–36. In *The Biology of the Indian Ocean* (ed. Zeitzschel, B.), Springer, Berlin, Heidelberg, New York.