

Bathymetric distribution of *Pleuromamma* (Copepoda, Calanoida) species in the Indian Ocean

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ABSTRACT

Based on the analysis of 204 zooplankton samples from the stratified depths in the Indian ocean collected during the International Indian Ocean Expedition (IIOE), the distribution of the genus *Pleuromamma*, a Calanoid Copepod, was studied. Seven species, viz. *Pleuromamma indica*, *P. gracilis*, *P. piseki*, *P. abdominalis*, *P. borealis*, *P. xipias* and *P. quadrangulata*, in the order of their abundance, and 1 variety of the genus *P. abdominalis abyssalis* were observed. Vertical distribution of species of *Pleuromamma* showed that they were inversely correlated with depth. Among the *Pleuromamma* species, *P. indica* could survive in an environment of low dissolved oxygen and lower depths of water column, whereas *P. xipias* and *P. abdominalis* could survive in an environment of high dissolved oxygen and at almost all depths of water column. Multiple regression analysis of the data suggested that light intensity, further depth stratification, seasonal variations, water currents and the interaction effects of temperature with dissolved oxygen and nutrients could provide a more pronounced prediction of the total abundance of the *Pleuromamma* species. Diversity function $H(s)$, in relation to latitude was a bell-shaped normal curve. $H(s)$ was linearly related to evenness index, e , and was a perfectly sloping up line. These relations were highly pronounced at lower depths of water column and in the highly productive regions.

Zooplankton samples collected during the International Indian Ocean Expedition (IIOE) have formed the basis of numerous studies on various planktonic groups including Copepoda (Saraswathy 1982). Distribution studies on Calanoid-Copepod genus *Pleuromamma* have presented very peculiar results such as isolation of *P. indica* in northern Indian ocean, latitudinal gradient for species coexistence, etc. in the upper 200 m water column. These results have necessitated further study of the species with respect to different depths. The present paper is concerned with the Calanoid-

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Copepod *Pleuromamma* collected during the IIOE. It particularly deals with the distribution of *Pleuromamma* species, at 3 main depths, viz. 500–250 m, 1000–500 m and 2000–1000 m, in the 4 regions defined by parallels of latitudes (1) north of 10°N, (2) equatorial region between 10°N and 10°S, (3) central Indian Ocean between 10° and 30°S and (4) the area of subtropical convergence between 30° and 40°S. The species of the genus *Pleuromamma* are noted for their diurnal vertical migration. Various references to *Pleuromamma* species from the Indian Ocean have been summarized earlier (Saraswathy 1986).

MATERIALS AND METHODS

Total 579 Zooplankton samples collected during IIOE formed the basis of this study. Of these, 204 samples were collected below 250 m water column in a uniform manner using the Indian Ocean standard net (Currie 1963). The details of sampling and mode of analysis were as per IOBC (1969). Sorted Copepods were again subsorted into different groups including the genus *Pleuromamma* which was then studied.

Zooplankton samples were collected from different depths during cruises 2,3,4A and 5 of R V Anton Bruun in the western Indian Ocean between 40° and 80° E and are available at the Smithsonian Oceanographic Sorting Centre, Washington, D C, USA. They were mainly an oblique series collected using a Be' multiple plankton sampler (Be' 1962), from stratified depths, viz. 21 samples from 500–250 m, 13 from 1000–500 m and 8 from 2000–1000 m in region 1; 23 samples from 500–250 m, 21 from 1000–500 m and 18 from 2000–1000 m in region 2; 25 samples from 500–250 m, 20 samples from 1000–500 m and 22 samples from 2000–1000 m in region 3; and 11 samples from each of the 3 depths in region 4. Total 7 species and 1 variety of the genus *Pleuromamma* were obtained. They were *Pleuromamma abdominalis* (Pa), *P. xipias* (Px), *P. quadrangulata* (Pq), *P. indica* (Pi), *P. gracilis* (Pg), *P. borealis* (Pb), *P. piseki* (Pp) and *P. abdominalis abyssalis* (Paa). Details of these samples are available in the cruise reports published by the Woods Hole Oceanographic Institute (Anonymous 1964–65).

Pleuromamma species were separated into males and females except for prediction. Environmental parameters like temperature, salinity, dissolved oxygen, phosphate

phosphorus and nitrate nitrogen were considered to determine the extent to which they control the total *Pleuromamma* species abundance in addition to depth in each region. All the analysis were carried out on the logarithmically transformed data to make use of the different statistical tests for interpretation (Colebrook 1960).

Following analysis were carried out : (1) Correlation coefficient (r) between species to study species association. (2) Cluster analysis to draw the dendrogram (Sanders 1978) to group the species into various clusters using the correlation coefficient as the similarity index. (3) r between species and environmental parameters to know the affinity of the species for the parameters. (4) Linear multiple regression model to formulate a predictive model for total abundance from the parameters. The model was $y = a_0 + a_1x_1 + a_2x_2 + a_3x_3 + a_4x_4 + a_5x_5$ and a_i where i is 1, 2, 3, 4, 5, regression coefficients; x_1 , temperature; x_2 , salinity; x_3 , dissolved oxygen; x_4 , phosphate phosphorus; x_5 , nitrate nitrogen; and Y , the total abundance of *Pleuromamma* species. Significance of the model fitted was tested using ANOVA technique (Snedecor and Cochran 1963). Variability explained by the significant models was also calculated to justify the confidence in the model. (5) Shannon Weaver information index, $H(s)$, and Mac Arthur's coefficient of equitability, e , were employed to determine the diversity, and evenness in the species distribution (Monte Lloyd and Ghelardi 1964). To study the influence of depth on species distribution pattern, $H(s)$ was plotted against latitude at each depth. (6) To determine depth region influence on $H(s)$ - e relationship, $H(s)$ - e plot was done at each depth in each region. (7) Trellis diagram showing the distribution of affinity between stations according to Sanders (1960) was drawn.

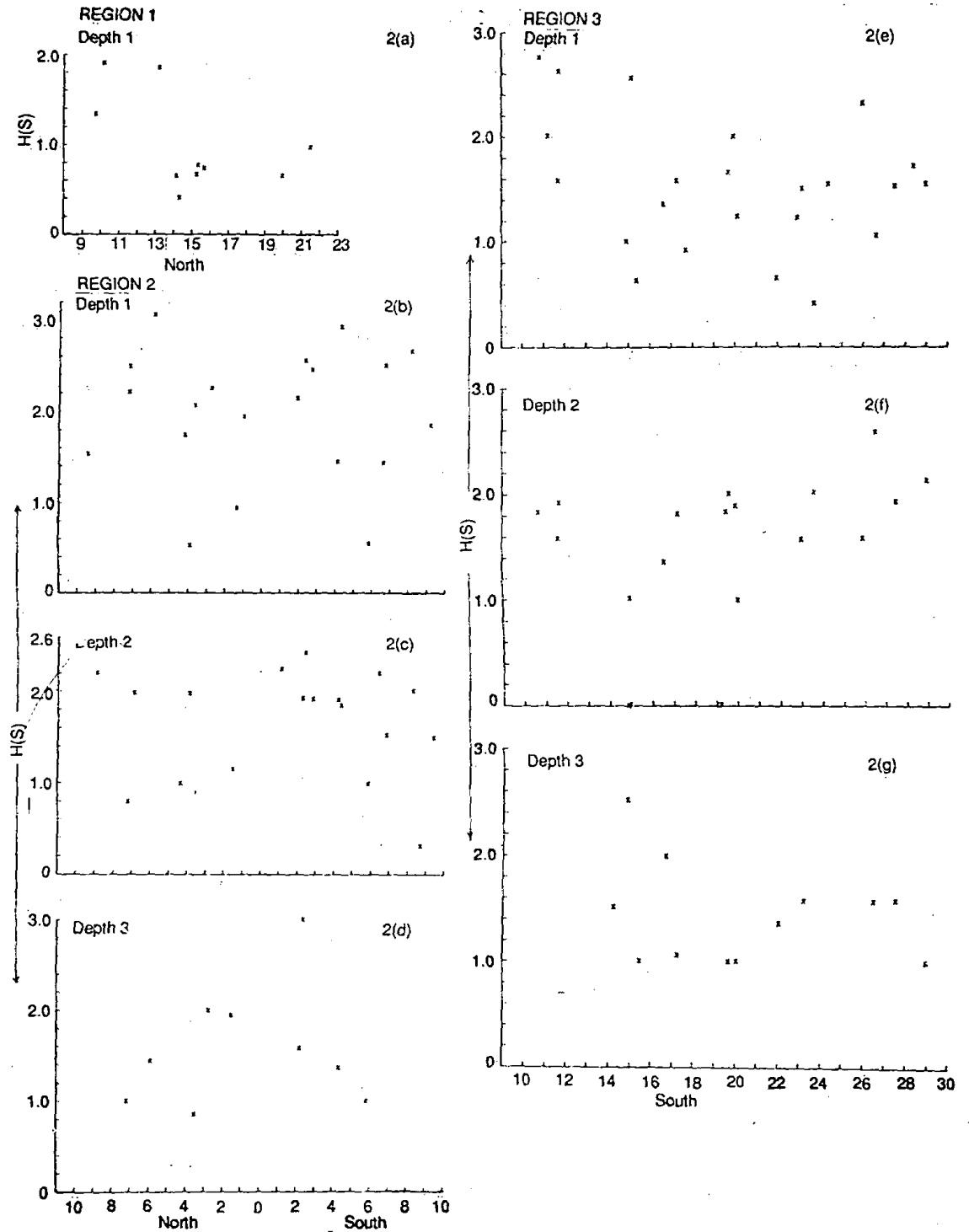
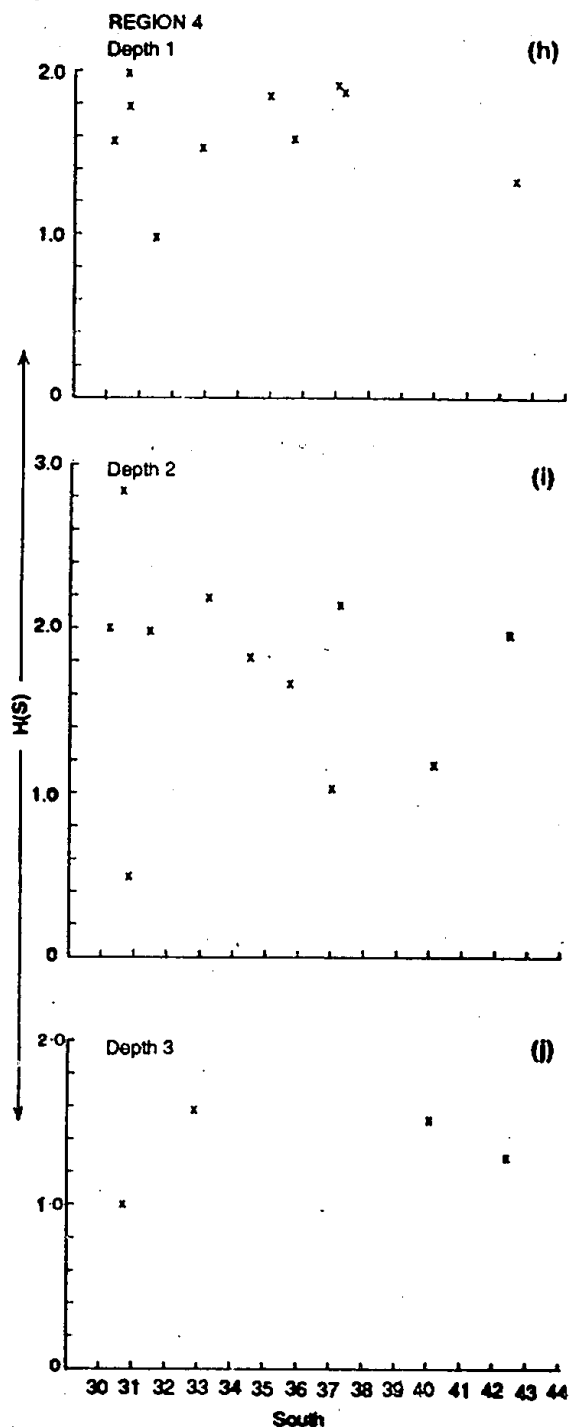


Fig. 2(a)-(j). Distribution of $H(s)$ with respect to latitude in region 1 at depth 1, in region 2 at depths 1, 2 and 3; in region 3 at depths 1, 2 and 3; and in region 4 at depths 1, 2 and 3 respectively.



former gradually increasing towards the south, maximum being in the area of subtropical convergence. *P. gracilis* and *P. piseki* preferred 500–250 m stratum and there was a gradual increase in their number

(h) towards the southern latitudes, maximum being at south of 30°S. *P. abdominalis abyssalis* was represented by fewer numbers at all depth zones while *P. borealis* only at surface in 30°S off.

Species association

From Table 2 and Fig. 1a–i it follows that coexistence of the species decreased with depth in regions 1, 2 and 3, but increased with depth in region 4. The percentage of coexistence was highest in the equatorial region (region 2) lying between 10° N and 10°S which comprised Somalia coast at its western boundary, with the majority of species having their maximum percentage of occurrence in this area. The lowest percentage of coexistence was in region 1, north of 10°N, where there was low dissolved oxygen and high nutrients, highly favourable conditions for *Pleuromamma indica* only. The subtropical gyre extends south of 10°S and the hydrochemical front at 10°S separates the low nutrient high oxygen waters of the subtropical gyre from the high nutrient low oxygen waters of the monsoon gyre in the northern Indian Ocean north of 10°S, thus acting as a barrier for the spread of the species dominant in the northern most areas. Thus there was an observable latitudinal gradient of increasing coexistence of species towards the south with decreasing abundance of *Pleuromamma indica*. There was a wide north-south range for the number of clusters in the different regions at different stratified depths also as observed in the upper 200 m water column (Jayalakshmy 1990).

Environmental variations

Regarding the variations in the average values of the parameters (Table 3), salinity remained almost constant without great variations at any depth in the 4 regions. Dissolved oxygen was very low in regions

Table 1. Various *Pleuromamma* species present and geometric mean and coefficient of variation of abundant species at different depths of the four regions

Region	Depth (m)	Species present	Abundant species	Geometric mean	Coefficient of variation (%)
1	500-250	Males and females of <i>Pa, Px, Pi, Pg, Pp</i>	<i>FPi</i>	17.7380	97.77
			<i>MPi</i>	4.6979	166.12
	1000-500	<i>MPx, FPa, FPx, FPi</i>	<i>MPx</i>	1.4832	170.15
	2000-1000	- do -	All species were rare	1.1893	162.00
2	500-250	All except <i>Paa</i> and <i>FPb</i>	<i>FPa</i>	3.5148	70.34
	1000-500	All except <i>Paa, FPb</i> and <i>MPp</i>	<i>Px</i>	2.2600	77.15
	2000-1000	All except <i>MPg, Paa, FPb, MPp</i>	<i>Px</i>	1.6900	167.03
3	500-250	All except <i>FPb</i>	<i>FPa</i>	4.0299	71.67
	1000-500	All except <i>Pg, Pi, Pp, Pb</i>	<i>FPx</i>	2.3988	96.97
	2000-1000	All except <i>Pi, FPp</i>	<i>FPa</i>	1.0517	122.31
4	500-250	All except <i>Pi, MPp</i>	<i>FPa</i>	4.9200	>70.32
	1000-500	All except <i>MPi, FPb, MPp</i>	<i>FPg</i>	3.6016	6.20
	2000-1000	<i>Px, Paa, FPa, FPg</i>	All were rare	1.2530	>165.00

Table 2. Significant clusters in different regions at different depths

Region	Depth (m)	Percentage of coexistence	Significant clusters	r
1	500-250	67.00	(<i>FPg, MPp, FPP, FPa</i>)	>> 0.65
		30.30*	(<i>MPx, FPx</i>), (<i>MPi, FPi</i>)	
	1000-500	50.00	—	1.0000
		50.00*		
2000-1000	16.00			
2	500-250	100.00*	(<i>MPx, FPa</i>)	>> 0.65
		84.80	(<i>MPx, FPi, FPa</i>), (<i>MPi, FPx</i>)	
	1000-500	23.20	(<i>MPp, FPP</i>)	>> 0.65
		76.4	(<i>MPa, FPx, FPq, MPi, FPi, FPg, FPP</i>)	
2000-1000	71.4*	(<i>MPx, FPx, FPa, MPa</i>)	>> 0.65	
	66.70	(<i>MPg, FPP</i>), (<i>MPg, FPi, FPq</i>)		
3	500-250	43.30*	(<i>FPq, FPi</i>), (<i>MPx, MPg</i>)	0.6874, 0.7467
		59.00	(<i>MPq, MPi</i>), (<i>FPg, FPP</i>)	0.6555, 0.5549
	1000-500	30.40*	(<i>MPa, MPx</i>), (<i>MPa, FPa</i>)	0.6632, 0.5756
		52.40	(<i>MPa, FPx</i>), (<i>MPx, FPa</i>)	0.7549, 0.5696
2000-1000	54.40*	(<i>MPx, FPx</i>)	0.8173	
	47.00	(<i>MPq, FPq</i>), (<i>MPq, FPi</i>)	r = 1 for	
	50.00*	(<i>MPq, FPP</i>), (<i>FPq, FPi</i>)	each group	
		(<i>FPq, FPP</i>)		
4	500-250	38.00	(<i>MPx, FPx</i>), (<i>FPq, FPx</i>)	>> 0.7715
		33.00*	(<i>MPa, MPx</i>)	
	1000-500	54.50	(<i>MPa, MPx</i>), (<i>MPa, FPx</i>)	0.6595, 0.6296
		23.30*	(<i>MPg, FPi</i>), (<i>MPq, FPP</i>)	0.6708, 0.6708
2000-1000	60.00	(<i>MPg, FPg</i>), (<i>Paa, FPi</i>)	0.9236, 0.8852	
	67.67*	(<i>MPx, FPx</i>), (<i>Paa, FPg</i>)	1.0000, 0.9999	
		(<i>Paa, FPa</i>), (<i>Pa, Pg</i>)	0.8714, 0.8506	

*Percentage of coexisting clusters significant at 5% level (P < 0.05)

1 and 2. Average value of phosphate phosphorus increased with depth in all the regions whereas it decreased towards the south at all the depths. At depth 2000–1000 m phosphate phosphorus values in all the regions were almost uniform. Nitrate nitrogen values increased moderately with depth at regions 1 and 2, but increased steadily at regions 3 and 4 except at 2000–1000 m depth in the equatorial region, where it increased only slightly. Average values of temperature decreased at all depths towards the south.

Relation with parameters

At depth 500–250 m some highly significant relations were found; in the north of 10°N, r of male (M) *Pa* with temperature ($r = 0.4611$), dissolved oxygen ($r = 0.4671$), nitrate nitrogen ($r = 0.4973$) and *MPi* ($r = 0.4508$) and female (F) *Pi* ($r = 0.4809$) with dissolved oxygen; in central Indian Ocean r of *MPa*, *MPq* and *MPi* with dissolved oxygen, phosphate phosphorus and nitrate nitrogen and *FPq* and *FPi* with temperature; and in the area of subtropical convergence, r of *MPq* ($r = 0.6357$), *FPb* ($r = -0.6194$) with dissolved oxygen, *Paa* ($r = -0.6086$) and *FPp* ($r = -0.6259$) with nitrate nitrogen, *FPb* with temperature ($r = -0.9054$), salinity ($r = -0.8211$) and phosphate phosphorus ($r = 0.8245$) were highly significant ($P < 0.05$) (Fisher and Yates 1963).

At depth 1000–500 m, only in north of 10°N, r of *MPx* ($r = 0.5691$) and *FPx* ($r = 0.6174$) with dissolved oxygen and *FPa* with temperature ($r = -0.8695$), salinity ($r = 0.6886$) and phosphate phosphorus ($r = 0.6996$) were high ($P < 0.05$), whereas in the other 3 regions at this depth no significant affinity could be obtained.

At depth 2000–1000 m, in equatorial region only r of *FPa* with salinity ($r = 0.5087$) and phosphate phosphorus ($r = 0.5201$) and *MPx* ($r = 0.5285$), *MPi* ($r =$

0.5761) and *FPx* ($r = -0.5383$) with dissolved oxygen; in central Indian Ocean, *FPa* with nitrate nitrogen ($r = 0.4790$); and in the area of subtropical convergence *Paa* ($r = -0.6488$), *FPg* ($r = 0.6488$) and *FPa* ($r = 0.7280$) with temperature were high ($P < 0.05$).

Species affinity with temperature and dissolved oxygen gradually diminished with depth and also from north to south. Multiple regression model formulated for predicting *Pleuromamma* species total abundance from the 5 parameters were not significant at any depth in any region except at depth 1000–500 m in central Indian Ocean (explained variability = 11.88%) and at depth 2000–1000 m in the area of subtropical convergence (explained variability = 27%) where relatively more number of species were highly correlated with these parameters.

Temperature was relatively the most important factor in regions 1 and 2 at depth 500–250 m, in regions 1, 3, 4 at depth 1000–500 m and in regions 1, 2, 3 at depth 2000–1000 m, whereas it was dissolved oxygen in region 3 at depth 500–250 m. The non-significance of the multiple regression model could be attributed to the factors such as interaction effects of temperature, dissolved oxygen and nutrients together with current effects and seasonal variations (Saraswathy 1986).

It was found that in upper 200 m water column also the 5 parameters could control the *Pleuromamma* species distribution precisely only in the presence of current effects and seasonal variations (Jayalakshmy 1990).

Species diversity and evenness

Shannon Weaver index of diversity $H(s)$ in north of 10°N at 500–250 m depth, ranged between 0.00 and 1.92, maximum being at 10°49' N 61°7' E. $H(s)$ plotted against latitude showed that generally $H(s)$ was very

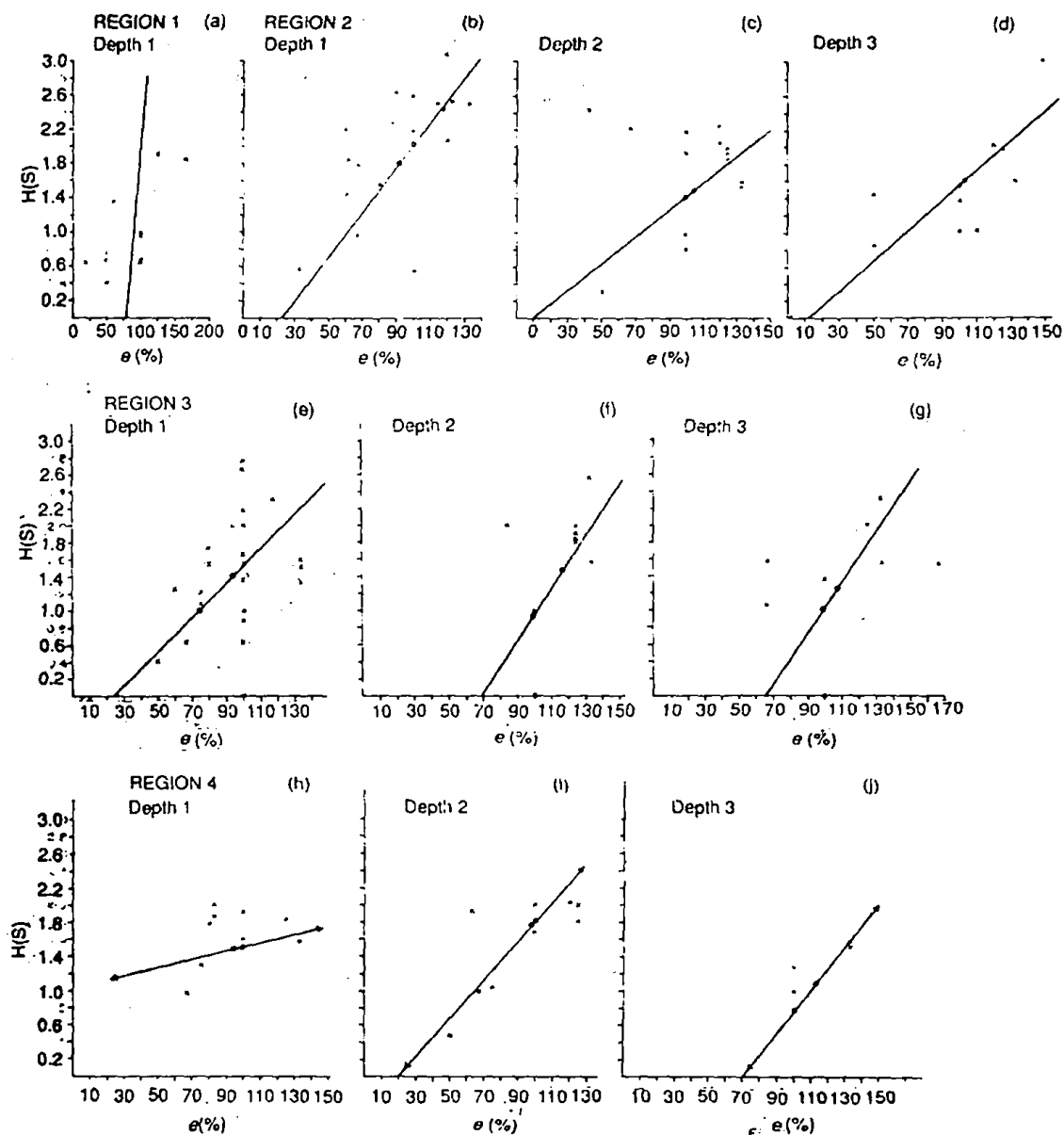


Fig. 3 (a)-(j). The linearity of relationship between $H(s)$ and e in region 1 at depth 1; in region 2 at depths 1, 2 and 3; in region 3 at depths 1, 2 and 3; and in region 4 at depths 1, 2 and 3 respectively.

small ($H(s) = 0.76$) in stations, between $13^{\circ} 30' N$ and $18^{\circ} 30' N$. It showed a decreasing gradient towards $30^{\circ} N$ latitude. The e was maximum, 166.67%, at $13^{\circ} 11' N$ $50^{\circ} 22' E$ (Fig. 2 a). $H(s)$ showed a good linear relationship ($r = 0.5830$) with e (Fig. 3a). At 1000–500 m depth, $H(s)$ varied between 0.86 and 1.30. Maximum $H(s)$ was at $13^{\circ} 11'$

$N 50^{\circ} 22' E$. Since the species were very rare e was 100% for almost all stations. Similarly at 2000–1000 m depth, maximum $H(s)$ was 1.59, at $15^{\circ} 18' N$ $57^{\circ} 43' E$ and 100% evenness was observed due to the few number of species with less abundance.

In the equatorial region between $10^{\circ} N$ and $10^{\circ} S$ at depth 500–250 m, $H(s)$ was

found to be between 0.00 and 3.09, maximum being at 5°48' N 70° 03' E. Nearly 85% of the considered stations have $H(s)$ more than 1.5. This area was rich in *Pleuromamma* species but not abundant. The e was ranging between 33.33% and 133.33%, maximum e was at 7°10' N 55° 05' E. $H(s)$ plotted against latitude (Fig. 2 b) showed that $H(s)$ was between 1.00 and 3.05 for those stations between 9°30' N and 9°30' S latitude, the highly productive area (Saraswathy 1986). $H(s)$ plot showed a decreasing trend from 10° N to equator and thereafter increased towards 10° S. $H(s)$ - e relationship was significantly linear ($r = 0.7593$) and sloping upwards (Fig. 3 b). But at depth 1000–500 m, $H(s)$ ranged between 0.00 and 2.43, maximum $H(s)$ was at 2°23' S 70°01' E. In these stations between 9°30' N and 9°30' S, $H(s)$ was between 0.8 and 2.5 with a normal distribution pattern (Fig. 2 c). $H(s)$ - e relationship was highly linear ($r = 0.5799$) (Fig. 3 c).

At depth 2000–1000 m, $H(s)$ varied between 0.67 and 3.00, the maximum being at 2°23' S 70°24' E where the species were equally distributed with high e ($e = 150\%$). $H(s)$ -latitude plot showed that $H(s)$ was normally distributed with respect to latitude

(Fig. 2d). $H(s)$ - e relationship was significantly linear ($r = 0.7116$) and sloping upwards (Fig. 3 d). The Arabian Sea intermediate waters, equatorial intermediate waters, the Pacific water and the Antarctic intermediate waters were present between 1000–500 m in the area north of 10° S. *P. xipias*, which appeared to be comparatively abundant in this stratum in this area was present along with stray specimens of *P. indica*, *P. abdominalis* and *P. quadrangulata*. In the 2000–1000 m stratum, to the north of 10°S, which was constituted by the Arabian Sea intermediate waters and the Arabian Sea deep waters, *P. xipias* and *P. abdominalis* were present.

In the Indian Ocean central waters at depth 500–250 m, $H(s)$ varied between 0 and 2.64, high value of $H(s)$ was at 11°47' S 74°42' E. The e was high (133%) at stations with less abundance. $H(s)$ was not found to have a normal pattern of distribution with latitude (Fig. 2 e). $H(s)$ - e relationship was linear (Fig. 3 e). At depth 1000–500 m, $H(s)$ ranged between 0.00 and 2.59, maximum being at 26°34' S 70°12' E. With high values, $H(s)$ followed a normal pattern of distribution with latitude (Fig. 2 f) and a linear relation with e ($r = 0.5980$) (Fig. 3

Table 3. Average values of temperature, salinity, dissolved oxygen, phosphate phosphorus and nitrate nitrogen

Region	Depth (m)	Temperature (°C)	Salinity (%)	Dissolved oxygen (ml/litre)	Phosphate phosphorus (μ mol/litre)	Nitrate nitrogen (μ mol/litre)
1	500-250	13.07	35.21	0.344	2.46	25.78
	1000-500	10.40	35.54	0.280	2.79	29.44
	2000-1000	5.60	35.09	1.162	2.93	34.20
2	500-250	13.16	35.00	1.901	2.01	30.44
	1000-500	7.98	34.97	1.385	2.52	35.69
	2000-1000	4.64	34.88	2.041	2.65	36.73
3	500-250	12.01	35.12	4.643	1.93	13.78
	1000-500	7.74	34.72	4.156	1.69	26.26
	2000-1000	3.84	34.66	3.220	2.42	35.86
4	500-250	11.71	35.09	5.420	0.81	09.81
	1000-500	8.34	34.72	5.087	1.41	18.97
	2000-1000	3.75	34.54	4.233	2.18	28.96

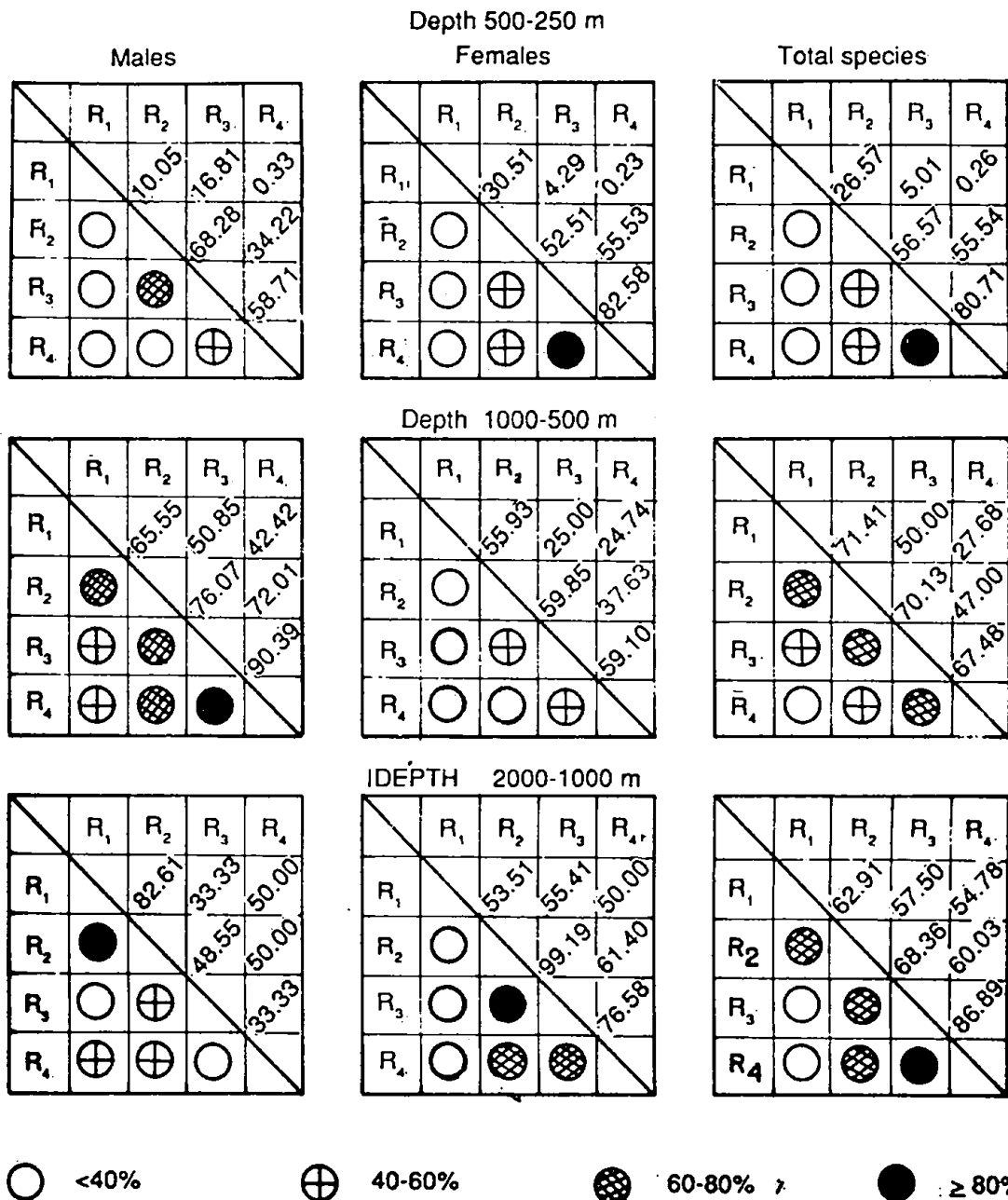


Fig. 4. Trellis diagram showing the affinity between regions with respect to males, females and total species abundance at depths 1, 2 and 3 respectively.

f). At depth 2000-1000 m, $H(s)$ ranged between 0.00 and 2.52 with no significant linearity with e but possessed a normal distribution pattern with respect to latitude (Figs 2g, 3g). Maximum $H(s)$ and e were observed at 14°53' S 55°02' E.

In the area of subtropical convergence $H(s)$ was small, maximum being 2.00 at 30°34' S 69°55' E at 500-250 m depth. (Fig. 2h). It exhibited a linear relation with e (Fig. 3 h). At 1000-500 m depth, $H(s)$ ranged between 0.00 and 2.85, high value

was at the above station with maximum e (125%). $H(s)$ showed a decreasing trend with latitude towards the south (Fig. 2 i). $H(s)$ - e relation was highly linear and sloping upwards ($r = 0.7784$) (Fig. 3 i). At depth 2000–1000 m, $H(s)$ was generally very small, 1.59 was the maximum value for $H(s)$ and 133% was the maximum evenness, observed at 32°58' S 69°52'E (Figs 2 j, 3 j), species being very rare.

Between 10°S and 35°S the stratum 500–250 m was formed by the Indian Ocean subsurface water and further south by the Indian Ocean deepwater. In the southernmost areas, *P. abdominalis*, *P. gracilis*, *P. piseki*, *P. borealis* and *P. adbominalis abyssalis*, and to a lesser extent *P. xipias* and *P. quadrungulata* were encountered. But *P. indica* was completely absent. So, diversity was naturally higher than that of region 1 at this depth. In all the regions, species diversity and equitability being higher at 500–250 m depth, it seem obvious that the genus *Pleuromamma* generally occupied the upper 500–250 m water column in the Indian Ocean.

Affinity between regions

Fig. 4 showed the distribution of affinity between regions according to Sanders (1960). This index is the percentage value of affinity between all possible pairs of regions, separately for males, females and total *Pleuromamma* species.

Depth 500–250m: Based on male *Pleuromamma* species distribution, region 2 had > 60% affinity with region 3 and region 3 had > 40% affinity with region 4. Based on females, regions (2, 3) and (2, 4) had > 40% affinity whereas regions 3 and 4 had > 80% affinity. Similar was the degree of relation based on total of males and females also.

Depth 1000–500 m : Male distribution showed > 60% affinity except regions (1, 3)

and (1, 4) whereas all pairs of regions had > 60% affinity for female *Pleuromamma* species distribution. Based on total of males and females, regions (1, 2), (2, 3) and (3, 4) had > 60% affinity.

Depth 2000–1000 m : All pairs of regions had only < 50% affinity except (1, 2) (> 80%) based on males distribution. Regions (2, 4) and (3, 4) had > 60%, while regions (2, 3) had > 80% affinity with respect to females. Generally > 60% affinity could be observed between regions based on total of males and females.

This study showed that the genus *Pleuromamma* generally occupied the upper 500 m water column in the Indian Ocean and the number of species and their abundance was inversely correlated with depth. *Pleuromamma indica* was the most abundant in region 1 where dissolved oxygen and the nutrients increased with depth while *P. xipias* and *P. abdominalis* dominated the regions 2, 3, and 4 where high variation was observed in the distribution of nutrients. *P. indica* could survive in an environment of low dissolved oxygen and high nutrients whereas *P. xipias* and *P. abdominalis* could tolerate high dissolved oxygen and low nutrients. *Pleuromamma* species distribution was similar in central Indian Ocean and the area of subtropical convergence. Species relation with parameters indicated that *Pleuromamma* species exhibited vertical segregation as Roe (1972) had observed in the Atlantic Ocean.

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