

Calanoid copepoda  
Distribution  
Zoogeography  
Structure  
Indian Ocean  
Copépode calanoïde  
Répartition  
Biogéographie  
Structure  
Océan Indien

# Epipelagic calanoid copepods of the northern Indian Ocean

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## ABSTRACT

Recent studies on the calanoid copepods of the northern Indian Ocean show that about 183 species occur frequently in the epipelagic realm. Fifteen more epipelagic species reported from this region occur only rarely. Another 45 species have been recorded which appear to be deep-water forms sporadically migrating to the upper layer and encountered there in low numbers. 40 species are fairly ubiquitous; many of them are often dominant components of the copepod community.

The present study shows more homogeneity between the Indian and Pacific fauna than between those of the Indian and Atlantic Oceans. Distributions, abundances and zoogeography of various calanoid species are discussed. Species assemblages are more or less homogeneous and the major zonation is the estuarine-neritic-oceanic ranges of the component species. Variations in the structure and niches of calanoid communities in oligotrophic and eutrophic waters are discussed.

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## RÉSUMÉ

### Copépodes calanoïdes épipélagiques du nord de l'Océan Indien

Des travaux récents sur les copépodes calanoïdes du nord de l'Océan Indien recensent 183 espèces fréquentes dans la zone épipélagique; 15 autres espèces épipélagiques de cette région n'y apparaissent que rarement; 45 autres sont signalées dans les profondeurs et ne migrent que sporadiquement vers la couche superficielle: 40 espèces se rencontrent à peu près partout, dont plusieurs sont souvent des formes dominantes de la communauté des copépodes.

Dans le présent travail, une homogénéité plus grande est observée entre les faunes des océans Indien et Pacifique qu'entre celles des océans Indien et Atlantique. La répartition, l'abondance et la biogéographie des différentes espèces de calanoïdes sont étudiées, ainsi que les assemblages d'espèces et la zonation des domaines estuarien-neritique-océanique pour les espèces composantes. Des variations de structures et de localisation des communautés calanoïdes dans les eaux oligotrophes et eutrophes sont discutées.

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## INTRODUCTION

The northern Indian Ocean (north of 10°S, west of 110°E with an area of ca 19.8 × 10<sup>6</sup> km<sup>2</sup>) has a unique physical setting which manifests itself in the seasonally reversing surface circulation and the monsoons. This area is also one of the better studied of the world oceans, especially through the concerted efforts of the International Indian Ocean Expedition (IIOE, 1960-

65). The calanoid copepods of the Indian Ocean, like its other fauna, are thought to have a predominantly Indo-Pacific lineage, fairly distinct from that of their Atlantic counterparts.

Studies on the copepods of the Indian Ocean date back to the beginning of this century (Cleve, 1901;

Thompson, Scott, 1903; Wolfenden, 1906); Sewell's work on taxonomy, systematics and distribution (1912; 1914; 1929; 1932; 1947; 1948) are particularly inspiring. There are many more recent studies on calanoid copepods from the Indian Ocean (see Zeitzchel, 1973; National Institute of Oceanography, 1977; Rao, 1979), most of which are discussed in this review.

While these studies outline the general geographic distributions of species, many do not consider abundances, which could be significant in ecosystem analysis. Information on distribution usually relates to a particular genus or family or is confined to a small area. Nevertheless, there have been considerable advances which have not been summarized for the last three and a half decades.

**MATERIALS AND METHODS**

Thirteen stations in the western Indian Ocean (8°49'N-19°48'S; 68°43'E-57°18'E) were sampled in January-February 1981 (Fig. 1). Vertical hauls from 200-0m were made with a Heron-Tranter net (mouth area 0.25 m<sup>2</sup>; mesh width 0.3mm) equipped with a flow meter. Vertical profiles of temperature, salinity and nutrients were also made at these stations. Zooplankton were enumerated. Adult calanoid copepods from whole samples or aliquots depending on sample volume were identified.

While these data are used as a springboard to identify species assemblages and abundances, information is also drawn from some earlier studies made in the Arabian Sea and the Bay of Bengal (Fig. 1). Copepoda of the Laccadive Sea were studied in December 1976 (Madhupratap *et al.*, 1977); oceanic and coastal waters of the western Bay of Bengal in June 1978 (Nair *et al.*, 1981); Andaman Sea in January-February 1979 (Madhupratap *et al.*, 1981); an annual cycle of zooplankton was studied in the offshore waters off Trivandrum (8°30'N; 76°55'E) during 1976-77 (Haridas *et al.*, 1980) and data were collected from estuaries of the southwest coast of India (Haridas, 1982; Madhupratap, Haridas, 1975). The mode of sampling in these studies was similar except that oblique hauls were taken at shallower stations in the Laccadive Sea, off Trivandrum and in the estuaries, and an Indian Ocean Standard Net was employed in the western Bay of Bengal.

Lists of calanoid copepod species recorded from the epipelagic realm (*ca.* upper 200m) of the northern Indian Ocean are given in Tables 1 and 2. Those species which occurred in more than 50% of our samples in coastal or oceanic areas (or both) are designated "common" (Tab. 1). A few more species were common in some restricted areas or seasons (L in Tab. 1). Some of the species listed are basically inhabitants of deeper waters (designated as "deep-dwelling"). Some of the deep dwelling as well as a few of the epipelagic species occurred only in very few samples (in less than 10% of the samples collected from neritic and/or oceanic areas) in low numbers or are reported to occur only rarely in

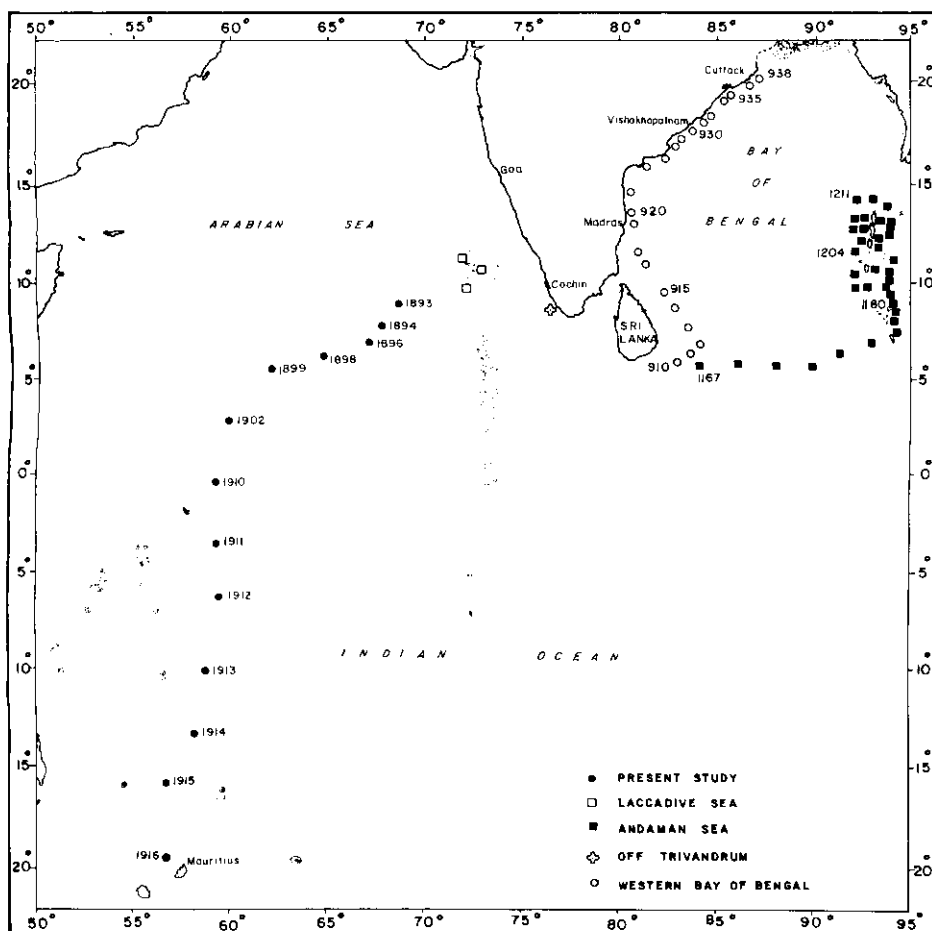


Figure 1  
Geographic locations of stations sampled.

this region (designated as "rare"). Species which occurred in 11 to 49% of our samples are marked by asterisks. However, many of the species listed did not occur in our samples and their frequencies of occurrence are not clear from the literature (designated as "frequency of occurrence unknown").

RESULTS

Observations in the present study were made during the NE monsoon (December-March) when the circulation in the northern Indian Ocean is anticyclonic. Unlike the SW monsoon, no striking upwelling areas develop during this period (Wyrtki, 1973). Details of hydrography, zooplankton standing stock and diversity were treated separately (Madhupratap, 1983).

Copepods comprised 83% of the total zooplankton counts in the samples; 27.2% of the copepods were cyclopoids and harpacticoids. Copepod numbers showed a considerable decrease south of 15°S. Low plankton standing crop and copepod counts and paucity of species have been reported earlier from the southern regions of the Indian Ocean (de Decker, Mombeck, 1964; Kasturirangan *et al.*, 1973). Total number of calanoids varied from 990/100m<sup>3</sup> at station 1916 to 15070/100m<sup>3</sup> at station 1894.

Sixty one species of calanoids belonging to 34 genera were identified from the present samples (Fig. 2-5). The number of species observed was highest at station 1913 (42 species) and decreased towards the south (20 species at station 1916).

Distribution

Calanidae

Species of this family contributed 5.9% of the total calanoid counts in the present study. *Undinula vulgaris* (2.6%) was the more abundant species. Earlier studies also showed that *U. vulgaris* was often a dominant component of neritic as well as oceanic waters (Fig. 6). *Cosmocalanus darwini* although frequent, occurred in lesser abundance. The former is a cosmopolitan species whereas *C. darwini* is an Indo-Pacific endemic.

*Canthocalanus pauper*, common in the Indo-Pacific (Fig. 2), appears to be absent from the North Atlantic. *Mesocalanus tenuicornis*, *Calanus minor* and *Neocalanus gracilis* have circumglobal distributions in the warm water belt. *N. robustior*, also widely distributed, is common in the surface waters of the subtropical eastern Indian Ocean (Tranter, 1977). This species does not appear to inhabit surface waters of the Arabian Sea and Bay of Bengal; Sewell's (1948) record from deeper waters in this area could well reflect extensions of subtropical populations and an example of tropical submergence.

*Calanoides carinatus* is common on the Agulhas Bank and in adjacent waters (de Decker, 1973) and occurs in fairly large numbers along the Somali coast during periods of upwelling. Its presence in this area is associated with lowering of temperature and this species exhibits ontogenetic migration as an annual life-history strategy (Smith, 1982).

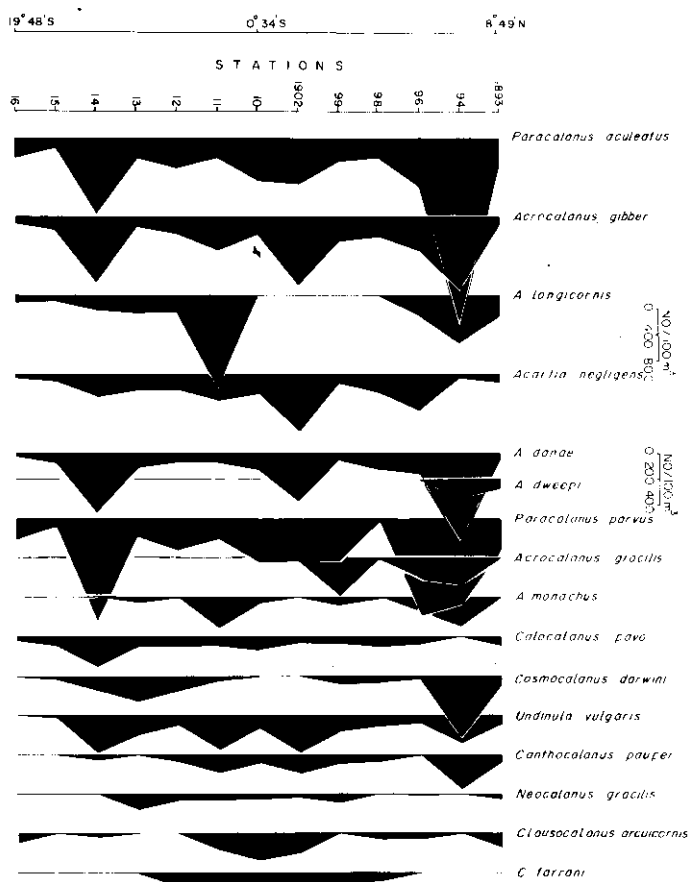


Figure 2  
Species observed (families Calanidae, Paracalanidae and Acartiidae) and their numerical abundance in the present study.

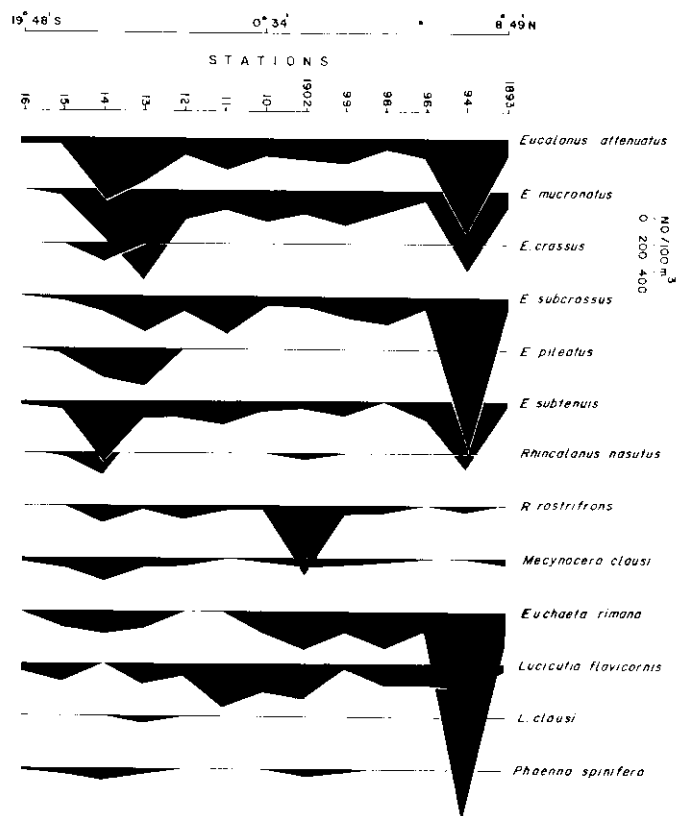


Figure 3  
Species observed (families Eucalanidae, Euchaetidae, Lucicutiidae and Phaenidae) and their numerical abundance in the present study.

Table 1

List of Calanoid copepod species (excluding Pseudodiaptomidae and Acartiidae) from epilanktonic realm of the northern Indian Ocean. Common species (c); rare species (r); deep-dwelling species (D); neritic species (N); species common in restricted areas or seasons (L); species whose frequency of occurrence is not determined (U); species which occurred in 11 to 49% of the samples are marked with asterisk.

CALANIDAE			
* 1. <i>Calanus minor</i> (Claus)	L	* 74. <i>E. russeli</i> Farran	r
2. <i>Cosmocalanus darwini</i> (Lubbock)	c	* 75. <i>E. acuta</i> Giesbrecht	
3. <i>Undinula vulgaris</i> (Dana)	c	76. <i>E. plana</i> Mori	r
4. <i>Canthocalanus pauper</i> (Giesbrecht)	c	77. <i>E. spinosa</i> Giesbrecht	r
5. <i>Neocalanus gracilis</i> (Dana)	c	PHAENNIDAE	
6. <i>N. robustior</i> (Giesbrecht)	L	78. <i>Phaenna spinifera</i> Claus	rD
* 7. <i>Mesocalanus tenuicornis</i> (Dana)		SCOLECITHRICIDAE	
8. <i>Calanoides carinatus</i> (Kroyer)	L	* 79. <i>Scolecithrix danae</i> (Lubbock)	c
EUCALANIDAE		* 80. <i>S. bradyi</i> Giesbrecht	
9. <i>Eucalanus attenuatus</i> (Dana)	c	* 81. <i>Scolecithricella nicobarica</i> Sewell	
10. <i>E. sewelli</i> Fleminger	U	* 82. <i>S. stenopus</i> (Giesbrecht)	
11. <i>E. mucronatus</i> Giesbrecht	c	83. <i>S. maritima</i> Grice and Hulsemann	r
* 12. <i>E. pileatus</i> Giesbrecht		84. <i>S. tenuiserrata</i> (Giesbrecht)	rD
13. <i>E. subtenis</i> Giesbrecht	c	85. <i>S. tropica</i> Grice	rD
14. <i>E. crassus</i> Giesbrecht	c	86. <i>S. dentata</i> (Giesbrecht)	rD
15. <i>E. subcrassus</i> Giesbrecht	c	87. <i>Scottocalanus securifrons</i> (T. Scott)	rD
* 16. <i>E. elongatus</i> (Dana)	L	88. <i>S. daughlihi</i> Sewell	rD
17. <i>E. hyalinus</i> (Claus)	U	89. <i>Amalothrix indica</i> Sewell	rD
18. <i>E. dentatus</i> A. Scott	r	90. <i>Macandrewella cochinchensis</i> Gopalakrishnan	rN
19. <i>Mecynocera clausi</i> Thompson	c	TEMORIDAE	
20. <i>Rhincalanus rostrifrons</i> Dana	c	91. <i>Temora turbinata</i> (Dana)	c
* 21. <i>R. nasutus</i> Giesbrecht		92. <i>T. discaudata</i> Giesbrecht	c
PARACALANIDAE		93. <i>Temoropia mayumbaensis</i> (T. Scott)	U
22. <i>Parvocalanus crassirostris</i> (Dahl)	cN	METRIDINIDAE	
23. <i>P. elegans</i> Andronov	U	94. <i>Gaussia princeps</i> (T. Scott)	rD
24. <i>P. latus</i> Andronov	U	95. <i>G. sewelli</i> Saraswathy	rD
25. <i>P. serratipes</i> (Sewell)	U	96. <i>Pleuromamma abdominalis</i> (Lubbock)	cD
26. <i>P. dubia</i> (Sewell)	U	97. <i>P. indica</i> Wolfenden	cD
27. <i>Paracalanus denudatus</i> Sewell	U	98. <i>P. xiphias</i> (Giesbrecht)	cD
28. <i>P. nanus</i> Sars	U	* 99. <i>P. piseki</i> Farran	D
29. <i>P. parvus</i> (Claus)	U	* 100. <i>P. gracilis</i> (Claus)	LD
30. <i>P. indicus</i> Wolfenden	c	101. <i>P. quadrungulata</i> (Dahl)	rD
31. <i>P. aculeatus</i> Giesbrecht	U	102. <i>P. borealis</i> (Dahl)	rD
32. <i>Delius nudus</i> (Sewell)	U	CENTROPAGIDAE	
* 33. <i>Acrocalanus gracilis</i> Giesbrecht		103. <i>Centropages furcatus</i> (Dana)	c
34. <i>A. longicornis</i> Giesbrecht	c	* 104. <i>C. gracilis</i> (Dana)	
35. <i>A. monachus</i> Giesbrecht	c	105. <i>C. calaninus</i> (Dana)	c
36. <i>A. gibber</i> Giesbrecht	c	* 106. <i>C. elongatus</i> Giesbrecht	L
37. <i>A. gardineri</i> Wolfenden	U	* 107. <i>C. tenuiremis</i> Thompson and Scott	N
38. <i>Bestiola similis</i> (Sewell)	cN	108. <i>C. alcocki</i> Sewell	cN
39. <i>B. inermis</i> (Sewell)	U	* 109. <i>C. orsinii</i> Giesbrecht	N
40. <i>Calocalanus pavo</i> (Dana)	c	* 110. <i>C. dorsispinatus</i> Thompson and Scott	N
41. <i>C. plumulosus</i> (Claus)	U	* 111. <i>C. trispinosus</i> Sewell	N
42. <i>C. minutus</i> Andronov	U	LUCICUTIIDAE	
43. <i>C. curtus</i> Andronov	U	112. <i>Lucicutia flavicornis</i> (Claus)	c
44. <i>C. pubes</i> Andronov	U	113. <i>L. clausi</i> (Giesbrecht)	rD
CLAUSOCALANIDAE		114. <i>L. ovalis</i> (Giesbrecht)	rD
* 45. <i>Clausocalanus arcuicornis</i> (Dana)	L	HETERORHABDIDAE	
46. <i>C. paululus</i> Farran	U	* 115. <i>Heterorhabdus papilliger</i> (Claus)	LD
47. <i>C. furcatus</i> (Brady)	U	116. <i>H. spinifrons</i> (Claus)	rD
* 48. <i>C. farrani</i> Sewell		AUGAPTILIDAE	
49. <i>C. mastigophorus</i> (Claus)	U	117. <i>Euaugaptilus hecticus</i> (Giesbrecht)	rD
50. <i>C. minor</i> Sewell	U	118. <i>Haloptilus longicornis</i> (Claus)	cD
51. <i>C. parapergens</i> Frost and Fleminger	U	* 119. <i>H. ornatus</i> (Giesbrecht)	LD
AETIDEIDAE		* 120. <i>H. spiniceps</i> (Giesbrecht)	LD
* 52. <i>Aetideus armatus</i> (Boeck)	LD	* 121. <i>H. paralongicirrus</i> Park	LD
53. <i>Chirundina streetsi</i> Giesbrecht	rD	122. <i>H. oxycephalus</i> (Giesbrecht)	rD
54. <i>Euaetideus acutus</i> (Farran)	rD	123. <i>H. austini</i> Grice	rD
* 55. <i>E. giesbrechti</i> (Cleve)	D	124. <i>H. mucronatus</i> (Claus)	rD
56. <i>Euchirella amoena</i> Giesbrecht	rD	125. <i>H. acutifrons</i> (Giesbrecht)	rD
57. <i>E. bella</i> Giesbrecht	rD	126. <i>H. chierchiai</i> (Giesbrecht)	rD
58. <i>E. messinensis</i> (Claus)	rD	127. <i>H. bulliceus</i> Farran	rD
59. <i>E. brevis</i> Sars	rD	128. <i>H. fertilis</i> Giesbrecht	rD
60. <i>E. curticauda</i> Giesbrecht	rD	129. <i>H. fons</i> Farran	rD
61. <i>Gaetanus armiger</i> Giesbrecht	rD	ARIETELLIDAE	
62. <i>G. miles</i> Giesbrecht	rD	130. <i>Metacalanus aurivilli</i> Cleve	LN
63. <i>G. pileatus</i> Farran	rD	131. <i>Arietellus giesbrechti</i> Sars	rD
64. <i>G. minor</i> Farran	rD	132. <i>A. plumifer</i> Sars	rD
65. <i>G. latifrons</i> Sars	rD	133. <i>A. setosus</i> Giesbrecht	rD
66. <i>Undeuchaeta major</i> Giesbrecht	rD	134. <i>A. simplex</i> Sars	rD
67. <i>U. plumosa</i> (Lubbock)	rD	135. <i>Paraugaptilus buchani</i> Wolfenden	rD
EUCHAETIDAE		136. <i>Phyllopus helgae</i> Farran	rD
68. <i>Euchaeta rimana</i> Bradford	c	137. <i>P. bidentatus</i> Brady	rD
* 69. <i>E. indica</i> Wolfenden	L	138. <i>P. muticus</i> Sars	rD
* 70. <i>E. concinna</i> Dana	L	CANDACIIDAE	
* 71. <i>E. tenuis</i> Esterly		* 139. <i>Candacia bradyi</i> A. Scott	N
* 72. <i>E. longicornis</i> Giesbrecht		* 140. <i>C. discaudata</i> A. Scott	N
73. <i>E. media</i> Giesbrecht	r	141. <i>C. pachydaetyla</i> (Dana)	c
		* 142. <i>C. catula</i> (Giesbrecht)	

* 143. <i>C. curta</i> (Dana)		171. <i>L. gangetica</i> Sewell	NU
144. <i>C. ethiopica</i> (Dana)	c	172. <i>L. euchaeta</i> Giesbrecht	NU
145. <i>C. longimana</i> (Claus)	U	173. <i>L. rotunda</i> Mori	r
* 146. <i>C. bipinnata</i> (Giesbrecht)		174. <i>L. laevidentata</i> (Brady)	NU
147. <i>C. caricans</i> (Giesbrecht)	U	175. <i>L. madurae</i> A. Scott	NU
148. <i>C. samassae</i> Pesta	U	176. <i>L. pseudacuta</i> Silas and Pillai	U
149. <i>C. guggenheimi</i> Grice and Jones	r	177. <i>Pontella investigatoris</i> Sewell	NU
150. <i>C. norvegica</i> (Boeck)	r	178. <i>P. princeps</i> Dana	NU
151. <i>C. tuberculata</i> (Wolfenden)	rN	179. <i>P. securifer</i> Brady	r
152. <i>C. tenuimana</i> (Giesbrecht)	r	* 180. <i>P. fera</i> Dana	
153. <i>Paracandacia truncata</i> (Dana)	c	* 181. <i>P. danae</i> Giesbrecht	N
154. <i>P. hispinosa</i> (Claus)	c	* 182. <i>P. spinipes</i> Giesbrecht	
155. <i>P. simplex</i> (Giesbrecht)	r	183. <i>P. andersoni</i> Sewell	NU
<b>PONTELLIDAE</b>			
* 156. <i>Calanopia minor</i> A. Scott		184. <i>P. atlantica</i> (H. Milne Edwards)	r
* 157. <i>C. elliptica</i> (Dana)	N	185. <i>P. denticauda</i> A. Scott	NU
158. <i>C. aurivilli</i> Cleve	NU	186. <i>P. diagonalis</i> Wilson	U
* 159. <i>C. thompsoni</i> A. Scott	N	* 187. <i>Pontellopsis macronyx</i> A. Scott	N
* 160. <i>C. herdmani</i> A. Scott	N	188. <i>P. krameri</i> (Giesbrecht)	NU
161. <i>C. seymouri</i> Pillai	U	189. <i>P. armata</i> (Giesbrecht)	U
162. <i>Labidocera pectinata</i> Thompson and Scott	cN	* 190. <i>P. herdmani</i> Thompson and Scott	N
* 163. <i>L. pavo</i> Giesbrecht	N	191. <i>P. scotti</i> Sewell	NU
* 164. <i>L. acuta</i> (Dana)	N	192. <i>P. villosa</i> Brady	r
* 165. <i>L. minuta</i> Giesbrecht		193. <i>P. regalis</i> (Dana)	r
* 166. <i>L. detruncata</i> (Dana)		* 194. <i>Pontellina plumata</i> (Dana)	L
* 167. <i>L. kroyeri</i> (Brady)	N	195. <i>P. morii</i> Fleminger and Hulsemann	U
168. <i>L. acutifrons</i> (Dana)	r	<b>TORTANIDAE</b>	
169. <i>L. bengalensis</i> Krishnaswamy	NU	196. <i>Tortanus forcipatus</i> (Giesbrecht)	cN
170. <i>L. bataviae</i> A. Scott	NU	197. <i>T. gracilis</i> (Brady)	NU
		198. <i>T. barbatus</i> (Brady)	NU

Collated from: Andronov (1972; 1973); Fleminger (1973); Fleminger and Hulsemann (1974); Fleminger et al. (1982); Frost and Fleminger (1968); Gopalakrishnan (1982); Haridas et al. (1980); Jones (1966a); Kasturirangan (1963); Lawson (1977); Madhupratap et al. (1977); Madhupratap et al. (1981); Nair et al. (1981); Pillai (1975); Saraladevi et al. (1979); Saraswathy (1966); Silas and Pillai (1973); Smith (1982); Stephen and Rao (1980); Tanaka (1973); Timonin (1971); Tranter (1977); Vinogradov and Voronina (1961); Present study.

**Eucalanidae**

Nine species of this family were observed in the present study and constituted 19.7% of the calanoids. Among the six *Eucalanus* species recorded in the present study (Fig. 3), *E. subcrassus*, *E. attenuatus* and *E. mucronatus*

plus *E. elongatus* are tropical Indo-Pacific forms (Fleminger, 1973). Apart from *E. pileatus*, *Eucalanus* species observed in the present study were often dominant components of the surface plankton (Fig. 6).

Among other species recorded from this family, *Mecy-*

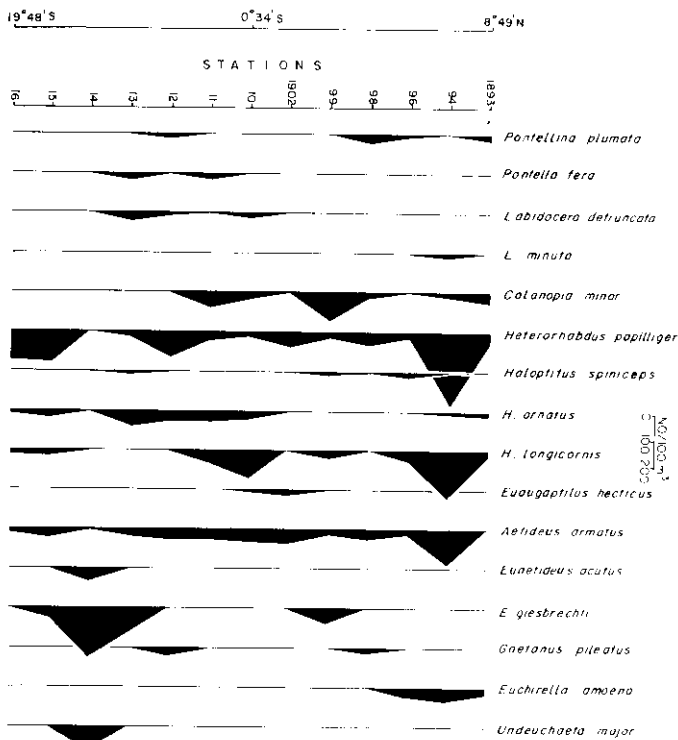
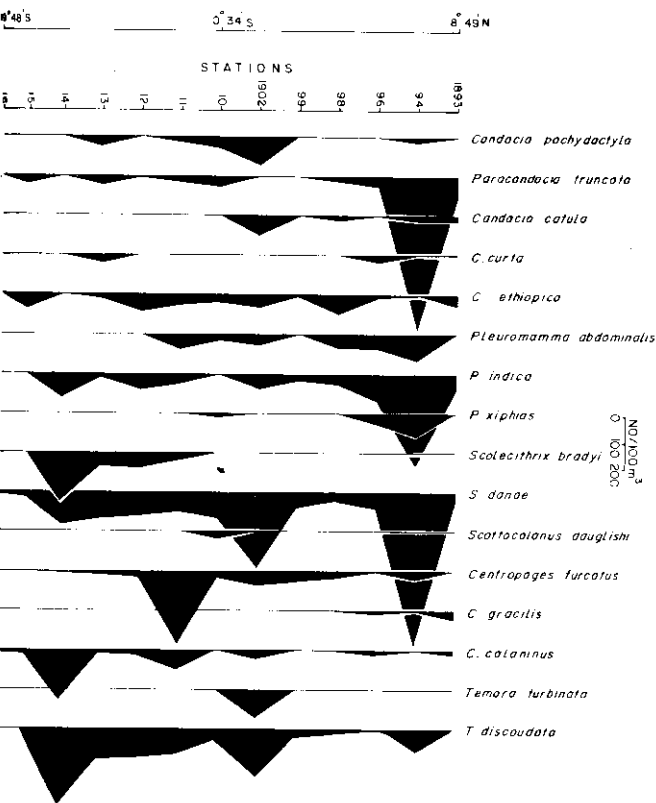


Figure 4  
Species observed (families Scolecithricidae, Temoridae, Metridinidae, Centropagidae and Candaciidae) and their numerical abundance in the present study.

Figure 5  
Species observed (families Aetideidae, Heterorhabdidae, Augaptilidae and Pontellidae) and their numerical abundance in the present study.

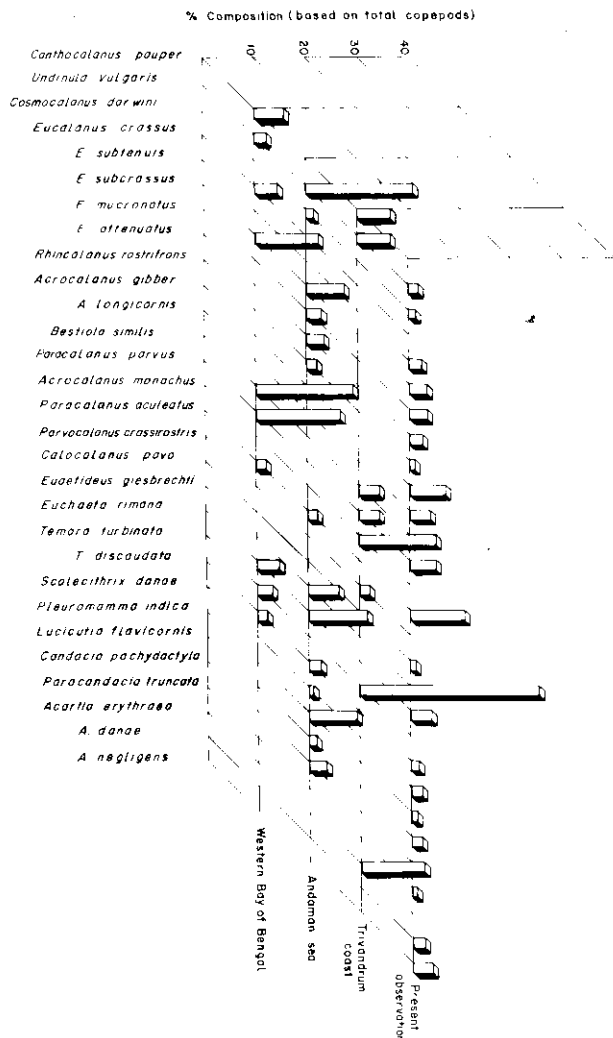


Figure 6  
Dominant species and their percentage of composition (based on total copepods) in various studies.

*nocera clausi* is a common circumglobal warm water species. *Rhincalanus rostrifrons* and *R. nasutus* have wide distributions and *R. nasutus* may occur as far as south as 65°S (Farran, 1936).

#### Paracalanidae

Species of this family are of considerable importance in the economy of tropical waters as they contribute a substantial fraction of calanoids (40.4% in the present study). Species belonging to the genera *Paracalanus*, *Parvocalanus*, *Acrocalanus* and *Bestiola* in particular are abundant in estuarine, coastal or oceanic waters (Fig. 2, 6).

*Paracalanus aculeatus* is a cosmopolitan species very common in coastal and oceanic waters. It is abundant in the Cochin Backwaters (salinity range 13.5–34.5, Madhupratap, 1979). *P. parvus* appears to have a distribution similar to that of *P. aculeatus*. *Paracalanus denu-datus* originally considered to be an Indian Ocean endemic (Sewell, 1948) was subsequently recorded from the Atlantic (Vervoort, 1963). *Parvocalanus serratipes* and *P. latus* appear to be endemic to the Indian Ocean while *P. elegans* occurs in the Pacific Ocean (Hiromi, 1981). *Delius nudus* appears to be widely distributed (Corral, 1972; Hiromi, 1981).

*Bestiola similis* is often a predominant component of estuarine zooplankton (salinity range 2–35.6, Madhupratap, 1979) and occurs in coastal waters. *Acrocalanus gracilis* and *A. longicornis* appear to be more common in oceanic waters while *A. gibber* and *A. monachus* occur both in coastal and oceanic waters.

Both *Calocalanus pavo* and *C. plumulosus* are cosmopolitan species, the former commonly occurred in the surface collections. Other species recorded from this area (Tab. 1) appear to be distributed only in the Indian Ocean. There are no recent records of *C. contractus* and *C. styliremis* from the northern Indian Ocean but a few records by Sewell (1929).

#### Clausocalanidae

Among the 13 species belonging to the genus *Clausocalanus* (Frost, Fleminger, 1968), 7 occur in the northern Indian Ocean (Tab. 1). Of these, all except *C. minor* enjoy circumglobal distribution. *C. arcuicornis* was widely distributed in the present samples and *C. farrani* was less frequent (Fig. 2). Although species of this genus are reported to be often abundant in surface waters (Frost, Fleminger, 1968; Bowman, 1971) they were not so common in our collections, probably due to the larger mesh size of the nets used.

#### Aetideidae

Most of the species belonging to this family are meso or bathypelagic forms. However, a few species like *Euaetideus giesbrechti* and *Aetideus armatus* frequently occurred in surface collections (Fig. 5,6). All the 6 species observed in the present study (Fig. 5) are widely distributed.

#### Euchaetidae

*Euchaeta rimana* occurred almost throughout the area of study and was often common (Fig. 3, 6). Five more species viz. *E. indica* (= *E. wolfendeni*), *E. concinna*, *E. tenuis*, *E. acuta* and *E. longicornis* occurred in our samples from the Bay of Bengal and the Arabian Sea, the first two being fairly common. Among the other species recorded from the northern Indian Ocean (Tab. 1), *E. plana* is confined to the Arabian Sea and Bay of Bengal (Tanaka, 1973) and *E. russeli* has a distribution similar to that of *Eucalanus dentatus* and is confined to the eastern Indian Ocean (Tranter, 1977). Tanaka (1973) observed that most species of this family from the Indian Ocean are Indo-Pacific forms. *E. acuta* and *E. media* have a wide distribution including the Atlantic.

#### Phaennidae

Species of this family are mostly deep-living forms but a few specimens of *Phaenna spinifera* occurred in the present samples (Fig. 1).

#### Scolecithricidae

27 species of this family occur in the Indian Ocean (Gopalakrishnan, 1982). Among the 12 species recorded from the epipelagic realm of the northern Indian Ocean (Tab. 1), *Scolecithrix danae* is very common, occurring in neritic as well as oceanic waters, and *S. bradyi* is also a frequently occurring species. *Sco-*

*Chricella ctenopus*, *S. tenuiserrata*, *S. nicobarica* and *S. dentata* are less common while others are rare in surface waters (Gopalakrishnan, 1982). Of the 12 species, *S. nicobarica* and *S. tropica* are Indo-Pacific forms whereas *Amallothrix indica*, *Scottocalanus daughlishi*, *Macandrewella cochinesis* and probably *Scolecichricella maritima* are endemic to the Indian Ocean.

#### Temoridae

Among the three epipelagic species of this family occurring in the northern Indian Ocean (Tab. 1), *Temora discaudata* is confined to the Indian and Pacific Oceans (Fleminger, Hulsemann, 1973). Along the south-west coast of India, *T. turbinata* is known to spurt into blooms during periods of upwelling (Haridas *et al.*, 1980).

#### Metridinidae

While species of this family are essentially deeper living forms, a few species belonging to the genus *Pleuromamma* are frequent in oceanic surface waters. *P. indica*, *P. abdominalis* and *P. xiphias* were frequent in our samples (Fig. 4). *P. gracilis* is also reported to be common in the surface and sub-surface waters (Vinogradov, Voronina, 1961). *P. indica* appears to be Indo-Pacific, but the other species (Tab. 1) occur in the Atlantic.

#### Centropagidae

All the three species, *Centropages gracilis*, *C. furcatus* and *C. calaninus* occurring in the present study (Fig. 4), and, to a lesser extent, *C. elongatus* are frequent in oceanic waters of the north Indian Ocean. Among these, *C. furcatus* and *C. elongatus* appear to be Indo-Pacific species. Other species (Tab. 1) are neritic and, with the exception of *C. dorsispinatus*, have been recorded inside estuaries (Madhupratap, Haridas, 1975). Among these, *C. tenuiremis*, *C. dorsispinatus* and *C. alcocki* are endemic to the Indian Ocean, whereas *C. orsinii* and *C. trispinosus* are Indo-Pacific forms.

#### Pseudodiaptomidae

Thirty species belonging to this family occur in the Indian Ocean and 22 species and one subspecies of these are recorded from the north Indian Ocean (Tab. 2). The list does not include *Pseudodiaptomus heterothrix* Brehm, the type locality of which is not known and which has not been recorded subsequently. It is doubtful if this species is extant (this seems to apply to *P. masoni* Sewell also, Pillai, 1976). Among the species occurring in the north Indian Ocean, only *P. serricaudatus* occurs in the Atlantic and others are confined to the Indian Ocean or Indo-Pacific region.

The distribution of some of the species of this family is unusual. There are no true oceanic species of pseudodiaptomids in the Indian Ocean but some species inhabit waters around oceanic islands. Among these, the geographical distribution of *P. marinus* is most peculiar. This species, originally described from coastal waters off Japan, now occurs near the islands of Mauritius and the Andamans in the Indian Ocean and Hawaii in the Pacific (Grindley, Grice, 1969; Jones, 1966c; Pillai, 1976). Grindley and Grice (1969) attributed this

curiously isolated distribution to the species being transported in ballast water tanks or having adhered to hulls of fishing vessels.

A large number of species of this family are estuarine and tolerate wide fluctuations of salinity. Those which are more numerous in comparatively higher salinities in the estuaries (like *P. mertoni*, *P. jonesi*, *P. serricaudatus*) are encountered in coastal waters, although not in abundance (Madhupratap, Haridas, 1975; Haridas *et al.*, 1980). Others frequent in lower salinity conditions in the estuaries (like *P. binghami*, *P. hickmani*) occur also in freshwater lakes (Reddy, Radhakrishna, 1982).

#### Lucicutiidae

*Lucicutia flavicornis*, although common in the surface waters (Fig. 3), is also known to occur at greater depths

Table 2

Distribution and habitat of species of the families Pseudodiaptomidae and Acartiidae occurring in northern Indian Ocean (c - common in the estuaries)

#### PSEUDODIAPTOMIDAE

Genus *Pseudodiaptomus* Herrick

<i>P. serricaudatus</i> (T. Scott)	estuarine & neritic	c
** <i>P. mertoni</i> Fruchtl	»	c
** <i>P. auriivilli</i> Cleve	»	c
* <i>P. jonesi</i> Pillai	»	c
* <i>P. annandalei</i> Sewell	»	c
* <i>P. ardjuna</i> Brehm	»	
* <i>P. salinus</i> Giesbrecht	»	
** <i>P. daughlishi</i> Sewell	»	
** <i>P. clevei</i> A. Scott	»	
* <i>P. compactus</i> Walter	»	
* <i>P. bowmani</i> Walter	»	
* <i>P. sewelli</i> Walter	»	
* <i>P. lobipes</i> Gurney	estuarine & limnetic	
* <i>P. binghami</i> Sewell	»	c
* <i>P. b. malayalus</i> Wellershaus	»	c
* <i>P. hickmani</i> Sewell	»	
* <i>P. tollingarae</i> Sewell	»	
* <i>P. burckhardti</i> Sewell	coastal waters of oceanic islands	
** <i>P. marinus</i> Sato	»	
* <i>P. nankauensis</i> Roy	»	
* <i>P. andamanensis</i> Pillai	»	
* <i>P. masoni</i> Sewell	»	

Genus *Archidiaptomus* Madhupratap & Haridas

* <i>A. aroorus</i> Madhupratap & Haridas	estuarine & limnetic	
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#### ACARTIIDAE

Genus *Acartia* Dana

<i>Acartia negligens</i> Dana	neritic & oceanic	
<i>A. danae</i> Giesbrecht	»	
** <i>A. amboinensis</i> Carl	»	
** <i>A. bispinosa</i> Carl	»	
** <i>A. pietschmani</i> Pesta	»	
<i>A. centrura</i> Giesbrecht	estuarine & neritic	c
** <i>A. spinicauda</i> Giesbrecht	»	c
** <i>A. erythraea</i> Giesbrecht	»	c
* <i>A. southwelli</i> Sewell	»	c
<i>A. pacifica</i> Steur	»	c
* <i>A. bilobata</i> Abraham	estuarine	c
* <i>A. bowmani</i> Abraham	»	c
* <i>A. plumosa</i> T. Scott	»	c
* <i>A. chilkaensis</i> Sewell	»	
* <i>A. dweepi</i> Haridas & Madhupratap	coastal waters of oceanic islands	
Subgenus <i>Acartiella</i> Sewell		
* <i>A. graveyi</i> Sewell	estuarine & limnetic	c
* <i>A. kempii</i> Sewell	estuarine	
* <i>A. major</i> Sewell	»	
* <i>A. minor</i> Sewell	»	
* <i>A. sewelli</i> Steur	»	
* <i>A. keralensis</i> Wellershaus	»	c
* <i>A. tortaniformis</i> Sewell	»	

Distribution: \* Indian Ocean; \*\* Indian and Pacific Oceans; others in Indian, Pacific and Atlantic Oceans.

(Hulsemann, 1966). Two more mesopelagic species *clausi* and *ovalis* were infrequently recorded from surface waters. All three species occur circumglobally.

#### Heterorhabdidae

Species of this family are generally deep-dwelling forms. However, *Heterorhabdus papilliger* frequently occurred in the present collections (Fig. 5). Grice and Hulsemann (1965) found this species from the surface to 3000 m depth in the north-east Atlantic.

#### Augaptilidae

*Haloptilus longicornis*, *H. ornatus*, and *H. spiniceps* occurred in the present samples. These, together with *H. paralongicirrus* form the commonest species of this genus encountered in surface waters of the Indian Ocean (Saraladevi *et al.*, 1979). Other species (Tab. 1) have a scattered distribution or are rare (Saraladevi *et al.*, 1979).

#### Arietellidae

The occurrence of 8 deep water species of this family in the surface waters of the Indian Ocean is given by Stephen and Rao (1980). No species of this family occurred in any of our collections. However, *Metacalanus aurivilli*, a small Indo-Pacific epipelagic copepod is reported to be common in plankton of the Gulf of Mannar (Kasturirangan, 1963) and inshore waters off Trivandrum (Saraswathy, 1966).

#### Candaciidae

Distribution of the species of this family in the Indian Ocean is given by Jones (1966 *a, b*) and Lawson (1977). Of the five species observed in the present study (Fig. 4), *Paracandacia truncata*, *Candacia ethiopica* and *C. pachydactyla* were commonest.

Among the 18 species that occur in the Indian Ocean, all but *C. cheirura* are present in the north Indian Ocean (Lawson, 1977). Species observed in the present study, together with *P. hispinosa*, are the most abundant. Of the species occurring in the north Indian Ocean (Tab. 1), *C. samassae* appear to be endemic (also present in the Red Sea) while *C. guggenheimi*, *C. catula*, *C. truncata*, *C. bradyi*, *C. discaudata* and *C. tuberculata* are Indo-Pacific forms.

#### Pontellidae

A large number of species from this family have been reported (Tab. 1) from surface waters of the Indian Ocean (Pillai, 1975; Silas, Pillai, 1973). Five species belonging to the genera *Calanopia*, *Labidocera*, *Pontella* and *Pontellina* occurred in the present samples (Fig. 5). Among the pontellids, *Labidocera pectinata* also occurs in estuaries and tolerates wide salinity fluctuations (Madhupratap, Haridas, 1975). Species of this family were never very abundant in our samples and the frequency of occurrence of many species is not clear. However, random analysis of neuston samples revealed large number of specimens belonging to this family, thus showing that vertical hauls do not give a true picture of their abundance. Many of the species appear to be chiefly neritic albeit also occurring rarely in oceanic waters.

Among the 40 species listed (Tab. 1) only 6 viz. *Labidocera acutifrons*, *Pontella spinipes*, *P. atlantica*, *Pontellopsis regalis*, *P. villosa*, and *Pontellina plumata* occur in the Atlantic. Six species, *Calanopia seymouri*, *Labidocera gangetica*, *L. pseudacuta*, *Pontella investigatoris*, *P. andersoni* and *Pontellopsis scotti* are endemic to the Indian Ocean. Twenty one of the species listed do not occur in the east Pacific region. Records of *L. acuta*, *L. detruncata*, *L. kroyeri*, *Pontella princeps* and *P. jera* from the Atlantic were based on wrong identifications and *Pontellopsis herdmanni*, considered to be endemic to the Indian Ocean, also occurs off eastern tropical Australia, New Guinea and across the Indo-Malayan Seas (Fleminger, pers. comm.).

#### Acartiidae

*Acartia danae* and *A. negligens* are common in the warm waters of all oceans. Both species were fairly abundant in the present collections (Fig. 2). *A. negligens*, together with the Indo-Pacific species *A. amboinensis*, often occurs in neritic waters also. There are no recent records of *A. tonsa* and *A. clausi* from the north Indian Ocean and Sewell's (1948) records of them from this area were probably erroneous. *A. dweepei* was present at a couple of stations in the Arabian Sea. A large number of species of this family, many of them endemic to the Indian Ocean, thrive in abundance in estuaries (Tab. 2) and a few of them periodically occur in inshore waters. Estuarine species belonging to the subgenus *Acartiella* often thrive in near freshwater conditions.

#### Tortanidae

*Tortanus forcipatus* is very common in the inshore waters off Goa (Madhupratap, Achuthankutty *et al.*, 1981). This species and *T. gracilis* have been recorded from the Lawson's Bay and off the Trivandrum coast (Ganapathi, Santhakumari, 1961; Saraswathy, 1966) and *T. barbatus* from coastal waters off Burma (Kyi Win, 1977). All three species are Indo-Pacific forms. Sewell (1948) recorded 3 more species from the northern Indian Ocean, viz. *T. murrayi* A. Scott, *T. brevipes* A. Scott and *T. tropicus* Sewell, but there are no recent records on these species from this area.

#### Zoogeography

The area under discussion falls within the warm water tropical belt and one would not expect drastic faunal transitions inside these limits. No marked temperature gradients nor water mass changes affect the epipelagic realm within it. The reduction in the number of species towards the southern regions observed in the present as well as some of the earlier studies is not easily explicable as most of the oceanic species listed have been recorded further south (de Decker, Mombeck, 1964; Gueredrat, 1972; Tranter, 1977). Along the African coast, the southward flowing Agulhas Current is a potential vehicle of dispersal.

The hydrochemical front at about 10°S from Timor extending to Madagascar (Wyrtki, 1973) forms a distributional barrier to the pteropod *Styliola subula* (Sakthivel, 1973), some euphausiids (Brinton, Gopalakrishnan,



1973) and some chaetognath species (Nair, Madhupratap, 1984). Lawson (1977) found that four species of candaciids: *Paracandacia truncata*, *Candacia catula*, *C. pachyactyla* and *C. curta*, decreased in abundance south of 10°S. In the present study a similar decrease was observed south of the equator or 10°S for species such as *Paracandacia truncata*, *Candacia catula*, *Pleuromamma abdominalis*, *Acrocalanus gracilis*, *A. monachus*, *Neocalanus gracilis*, *Canthocalanus pauper*, *Haloptilus spiniceps*, etc. However, many of these species, e.g. *Pleuromamma abdominalis*, *Paracandacia truncata*, *Candacia pachyactyla*, *Haloptilus spiniceps*, *Neocalanus gracilis* are common in the southern subtropical regions (Gueredrat, 1972; Tranter, 1977). On the other hand, a few species like *Haloptilus ornatus*, *Eucalanus pileatus*, *E. crassus*, *Scolecithrix bradyi*, *Pontella fera* and *Labidocera detruncata* were more common in the southern regions in the present study; of these, *Eucalanus pileatus* and *E. crassus* were reported to be not very common in the southeastern Indian Ocean (Tranter, 1977), and *Haloptilus ornatus* and *Scolecithrix bradyi* were common in the northern Indian Ocean in the IIOE samples (Saraladevi *et al.*, 1979; Gopalakrishnan, 1982). These inconsistencies show the spatial and temporal changes that can occur, and indicate that the data available are still inadequate to demarcate the zones of occurrence of most species. Thus, although a few species have restricted/specific areas of abundance, there is no evidence yet that the hydrochemical front restricts the distribution of any epipelagic calanoid species in this part of the Indian Ocean. The horizontal low salinity stretch of the front, separating the monsoon gyre from the subtropical gyre, shifts with seasons (Wyrski, 1971). Further, frontal characteristics in chemical properties are more pronounced in the sub-surface layers and would not radically affect the distribution of epipelagic organisms. The front is weakened by meridional circulation near Australia and NW of Madagascar. Species assemblages are vaguely homogeneous and apparently no major faunal boundary occurs north of the subtropical convergence. Timonin (1971) and Vinogradov and Voronina (1961) also came to similar conclusions on the calanoids of the Indian Ocean.

The 198 species listed (Tab. 1, 2; excluding rare deep species) include some not listed by Sewell (1948) since they were recorded or discovered later. However, some of the species listed by Sewell are omitted because they were later proven to be based on wrong identifications or erroneous records. Grice and Hulsemann (1967) showed that 92% of the deep living calanoid species present in the Arabian Sea occur in the North Atlantic, some 8000 nautical miles away. By comparison, about 60% of the surface living oceanic species in the north Indian Ocean appear in the Atlantic (91% in Pacific). 50% of the species which are not distributed in the Atlantic Ocean come from a few families such as the Eucalanidae, Euchaetidae, Candaciidae and Pontellidae. The percentage of species occurring in the Atlantic falls to 39 if the littoral and neritic species are also included (73% in Pacific).

Thus, there is more homogeneity in epipelagic calanoid species composition between the Indian and Pacific

Oceans than between the Indian and the Atlantic. The continuity of the Indian and Pacific Oceans through the Straits of Malacca and the Indonesian chain of islands is primarily instrumental in this consistency. On the other hand, the African continent separates the Atlantic and the Indian Oceans as far as 35°S. Moreover, the Agulhas Current is contiguous with the cold Benguela Current around the Cape of Good Hope (Veronis, 1973) which probably acts as a major barrier to the survival of many species. Nevertheless, a majority of warm water species enjoy a circumglobal disposition within 40°N and 40°S.

Recent studies (Fleminger, 1973; Fleminger, Hulsemann, 1973; 1974) have shown that some species which were originally considered to be circumglobal are not, but species may be replaced by closely allied cognates in different areas. Another interesting instance is the separation of two polytypic populations of *Candacia pachyactyla* in the Indian and Atlantic Ocean by 2000 miles of water (Jones, 1966b). Other examples are *Rhincalanus* spp. (*cornutus* and *rostrifons*) and *Eucheata* spp. (*marina* and *rimana*) of the Atlantic and Indian Oceans. These examples illustrate the importance of systematic biology as a tool in zoogeography.

There does appear to be a proliferation of species in the central western Pacific and the adjoining Indo-Malayan region. However van der Spoel and Pierrot-Bults (1979) maintain that holoplanktonic species endemic to this area are at least partly of secondary origin (established during a post glacial period) and do not reflect the presence of a primary speciation centre *sensu* Briggs (1974). A recent study by Fleminger *et al.*, (1982) shows that the Andaman Sea forms the eastern and western limits of distribution of *Labidocera rotunda* and *L. pectinata* respectively. In general, our studies did not discern any marked variations in the general composition of oceanic surface living calanoids between the Andaman Sea, the western Bay of Bengal and the Arabian Sea, despite lower salinity conditions prevailing in the northern bay. One striking feature, of course, is the reduction of the number of species in the Persian Gulf and Red Sea as pointed out by Sewell (1948) and evident from a later study of the Red Sea (Halim, 1969).

On the other hand, among species originally considered to be endemic to the Red Sea, *Candacia samassae* has been recorded from the Arabian Sea and Bay of Bengal (Jones, 1966a; Lawson, 1977). *Acartia fossae*, another species of this category, has now been recorded from the southwestern Australia (Haridas, Madhupratap, 1978) and the Pacific Ocean off the Philippines (Grice, 1964). This species probably occurs in the northern Indian Ocean as well. *A. dweepi*, a sibling species, occurs in the Laccadive waters (Haridas, Madhupratap, 1978).

Within the confines of the area under discussion the only major zonations are the oceanic-neritic-estuarine ranges of species. Many predominantly epiplanktonic oceanic species are frequent in neritic waters as well but the same is not true of deeper species. Autochthonous ranges of many neritic and a few oceanic species (e.g. *Eucalanus crassus*, *Calocalanus pavo*, *Labidocera*

spp., *Centropages* spp.) may extend to the mouths of estuaries. Expatriate populations of some neritic species could often be traced within estuaries when salinity conditions are favourable (Madhupratap, Haridas, 1975).

The adaptability of species belonging to the families Pseudodiaptomidae, Acartiidae and, to a large extent, Paracalanidae to estuarine conditions is remarkable. The Cochin Backwaters have the highest diversity within the Acartiidae (10 species) and Pseudodiaptomidae (10 species) so far recorded from any single environment (Madhupratap, 1979). A large number of species have evolved in the estuarine systems and coastal waters of the Indo-Malayan region (Tab. 2).

Sherman (1964) observed that 5 species of neritic pontellid copepods were restricted to within 40 km of islands in the central south Pacific. Similarly, among the pseudodiaptomids of the Indian Ocean, 5 species are known to occur only in the vicinities of oceanic islands (to some extent *Acartia dweepi* also shows this feature). Mechanisms which restrict these species to such narrow areas in the open ocean is not clear.

Most estuarine species of the families Pseudodiaptomidae and Acartiidae tolerate considerable salinity changes and many occur in near freshwater conditions. Sewell (1948, p. 326) discussed the distribution of the Pseudodiaptomidae and concluded that the genus *Pseudodiaptomus* was originally marine and that the ancestral forms must have been widely dispersed by currents before they invaded brackish and freshwater. Tokioka (1979) adopted a similar hypothesis for speciation among inlet chaetognaths. However there is no logical explanation for the selection mechanisms producing such a uniform *universal* dispersion as found in pseudodiaptomids. Moreover, the occurrence of *Archidiaptomus*, a genus exhibiting many primitive morphological features and showing close affinity to a more primitive freshwater calanoid family Diaptomidae, in near freshwater conditions (Madhupratap, Haridas, 1978) suggests a phylogeny where the evolution of this family could have taken place in the reverse direction.

### Structure

Tropical marine zooplankton communities are less influenced by seasonal changes than their counterparts in higher latitudes. Nevertheless, this stability is more characteristic of the central oligotrophic pool than coastal or equatorial areas where enrichment through seasonal upwelling or land run-off may alter the structure for brief periods. Although copepods generally form the bulk of the zooplankton standing crop, vast differences in abundance exist between estuarine, coastal and oceanic areas. Maximum counts of calanoid copepods were only 150/m<sup>3</sup> at station 1894 in the present study. Highest numbers in the Andaman Sea and the western Bay of Bengal were 55 and 1178 respectively (latter from a coastal station). The average population from slope and oceanic waters was less than 100/m<sup>3</sup>. On the other hand, the annual average counts from the inshore station located off Trivandrum (Fig. 1) was 700/m<sup>3</sup> with a peak value of 3290/m<sup>3</sup> in August associated with seasonal upwelling. These figures are relatively insignificant when compared with

peak values recorded from estuarine areas, e.g. 55390/m<sup>3</sup> in the Cochin Backwaters (Tranter, Abraham, 1971); 286,000/m<sup>3</sup> in the Vellar estuary (Subbaraju, Krishnamurthy, 1972). Such high densities result from a sequence of several discrete generations (Miller, 1983). The average numbers during the summer months from Cochin Backwaters ranged between 5000 to 10000/m<sup>3</sup> but drastic reductions to 1 to 200/m<sup>3</sup> occurred during the monsoon period when salinity approached zero (Madhupratap, 1979).

A few species of the family Acartiidae, Pseudodiaptomidae and Paracalanidae account for the majority of the standing stock of the copepod population during summer in the Cochin Backwaters (13 species form 90%). The diversity of copepod fauna in the estuaries is low. Only 34 calanoid copepod species occur in the Cochin Backwaters of which 11 are neritic and 4 are low saline species (Madhupratap, Haridas, 1975). Higher biomass is usually associated with low species diversity and equitability (Gueredrat, 1972; Haridas *et al.*, 1980; Madhupratap *et al.*, 1981; Nair *et al.*, 1981; Timonin, 1971; Tranter, 1977) since the increase is generally the result of the abundance of a single or a few species.

There is a progressively increasing gradient in species diversity from estuaries and lagoons to neritic and oceanic environments (Madhupratap, 1983). The oceanic environment, especially of the tropics, represents a relatively stable and mature system as implicated by the maintenance of higher diversity. Lawson's study (1977) on trophic adaptation and niche separation of Indian Ocean candaciids appears to be the only study of its kind from the oceanic environment of this area. He concluded that the candaciids appear to be in a state of biological equilibrium with minimum competition among themselves despite the perturbations caused by the monsoons. Presumably, this finding may be relevant to other copepods of oceanic oligotrophic areas.

In contrast, studies on the Acartiidae based on mandibular structure (Tranter, Abraham, 1971), and common calanoid copepods (Madhupratap, 1980) from the Cochin Backwaters indicate considerable niche overlap among the species. Biochemical composition indicates that the zooplankton of the Backwaters are continuous feeders with poor lipid storage (Madhupratap *et al.*, 1979). Peculiarities of this food rich system, such as the annual extinction of the competing species by monsoonal efflux and successional series with the ability to invade virgin areas with salinity incursions, probably allow them to survive as competitors (Madhupratap, 1980).

Dominance is often considered as a measure of successful evolution (Briggs, 1974). In our collections only 29 species comprised more than 1% of the total copepod population in the neritic and/or oceanic waters (Fig. 6). Among these, species like *Undinula vulgaris* and *Canthocalanus pauper* are dominant in inshore as well as oceanic areas whereas others like *Eucalanus* spp., *Euchaeta rimana* show ascendancy only in offshore areas. *Acartia erythraea*, *Parvocalanus crassirostris* and, to some extent, *Acrocalanus monachus* and

Table 3

Percentage of composition-species and counts (in parenthesis) of different trophic groups among calanoid copepods.

	Laccadive Sea	Andaman Sea	Western Bay of Bengal	Trivandrum coast	Present study
Source	Madhupratap <i>et al.</i> , 1977	Madhupratap <i>et al.</i> , 1981	Nair <i>et al.</i> , 1981	Haridas <i>et al.</i> , 1980	
Herbivores	52 (90.7)	33.3 (51.9)	33.4 (78)	28.6 (39.2)	38.7 (68.8)
Omnivores	36 (5.1)	42.9 (26.5)	33.3 (10.5)	42.8 (59.9)	33.8 (20)
Carnivores	12 (4.2)	23.8 (21.6)	33.3 (11.5)	28.6 (0.9)	27.5 (11.2)

*Bestiola similis* are typically more abundant in inshore waters and are also common in the estuaries.

While these 29 species were dominant at one time or other and fairly ubiquitous in the surface realm (with the exception of *Euaetideus giesbrechti*), a few others, the 12 additional species marked "common" in Table 1, were also frequent in our samples. Among the 16 species marked as "common in restricted areas" (Tab. 1), 13 species occurred fairly frequently in our surface collections in some areas (*Neocalanus robustior*, *Calanoides carinatus* and *Metacalanus aurivilli* were the three species which did not occur in our samples). 17 more species (belonging to families Pseudodiaptomidae and Acartiidae) are abundant and common in the estuarine waters of this region albeit seasonally (Haridas, 1982).

Analysis of species assemblages (Tab. 3) did not suggest much variation in the proportion of species belonging to herbivorous, omnivorous and carnivorous groups. The Laccadive Sea, where samples were taken from shallow waters adjoining the lagoons, is exceptional. However, there were invariably fewer carnivores of which *Euchaeta rimana* was usually the most abundant and common. While the number of carnivorous species present in the inshore waters was quite comparable (mostly neritic pontellids), low counts off Trivandrum (0.90%) clearly showed a reduction of their numbers towards inshore waters. The same is also applicable to estuaries. The only carnivorous calanoids in the Cochin Backwaters are extensions of the populations of a few neritic species (*Candacia bradyi*, *Labidocera pectinata*, *L. acuta*) which occur in low numbers during summer (Madhupratap, Haridas, 1975).

The general indications that emerged from the IIOE studies were that greater concentrations of copepods occurred near land masses and in the northern Indian Ocean as compared to southern and central oceanic areas (Kasturirangan *et al.*, 1973). Higher concentrations off Somali, the Arabian coast and the southwest coast of India during the SW monsoon correspond to the upwelling that occurs (Banse, 1968; Currie *et al.*, 1973) in these areas.

It is generally believed that a time-lag together with spatial dislocation occurs between upwelling and the development of phyto-zooplankton communities, and that carnivorous zooplankton are further displaced to the fringes of herbivorous populations (Rao, 1979; Vinogradov, Voronina, 1962). While these could be the patterns in areas where intense and prolonged upwelling occurs, our studies indicate that there is usually a simultaneous increase in both herbivores and carnivores in localities of mild upwelling or divergence (Fig. 7). The species which contributed to this were mainly a

few herbivores and omnivores of the genera *Eucalanus*, *Rhincalanus*, *Temora*, *Undinula*, *Scolecithrix*, *Paracalanus*, *Acrocalanus* and *Acartia* and carnivores like *Euchaeta rimana*, *E. concinna*, *E. indica*, *Candacia pachydaetyla*, *C. catula* and *C. discaudata*.

Upwelling in the Arabian Sea along land masses, and to some extent in the Bay of Bengal and equatorial regions, contributes to the abundance of copepods and other zooplankton organisms in the northern Indian Ocean when compared to southern areas. There is further evidence for this in the fact that the areas of high primary productivity coincide remarkably well with these areas and desert regions occur on both sides of the equator (Krey, 1973). Moreover the front at 10°S separates the monsoonal gyre, with high nutrient input, from the low nutrient content waters of the subtropical gyre (Wyrtki, 1973). Thus while the front might not limit the distribution of species, it might demarcate the areas of abundance for many species.

Fleminger and Hulsemann (1974) concluded that the three tropical species of the genus *Pontellina* viz. *morii*, *sobrina* and *platychela* occupy eutrophic waters characterized by equatorial upwelling, while the overall geographical range of *plumata* lies mostly in oligotrophic waters spreading across the tropics and subtropics; the abundance of these species tends to vary independently. There is also evidence for "centres of abundance" for

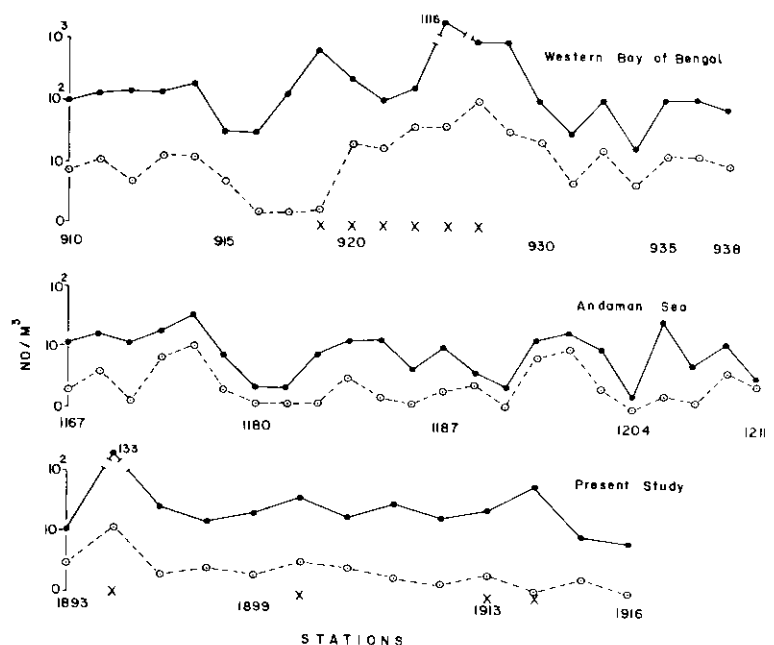


Figure 7

Numerical abundance of herbivores and omnivores (closed circle); carnivores (open circle) in various studies. Stations where mild upwelling or divergence was observed are marked by a cross.

some other calanoid species from a few other studies. Among the species of the genus *Haloptilus*, *H. paralongicirrus* and *H. oxycephalus* are more common in equatorial waters, while *H. longicornis* has a distribution similar to *Pontellina plumata* (Saraladevi *et al.*, 1979). Voronina (1962) reached similar conclusions on the pontellids of the Indian Ocean. *Scolecithrix danae*, the commonest species of the family Scolecithricidae, appears to be associated with eutrophic waters between 15°N and 15°S (Gopalakrishnan, 1982). Lawson (1977) identified *Paracandacia truncata*, *Candacia catula* and *C. pachydactyla* as the dominant forms of the equatorial gyre while *C. ethiopica* and *P. hispinosa* were more common in the central gyre with a broad zone of overlap centred on the equator.

The last two species, together with *C. tenuimana*, are generally infrequent north of 10°N. The spatial dislocation of centres of abundance of closely allied species probably minimizes niche overlap and competition among the congeners.

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### REFERENCES

- Andronov V. N., 1972. Some new species of the genus *Parvocalanus* (Copepoda, Paracalanidae). *Zool. Zh.*, **51**, 139-141.
- Andronov V. N., 1973. New species of *Calocalanus* (Copepoda, Paracalanidae) from the Atlantic and Indian Ocean. *Zool. Zh.*, **52**, 1405-1410.
- Banase K., 1968. Hydrography of the Arabian Sea shelf of India and Pakistan and effects on demersal fishes. *Deep-Sea Res.*, **15**, 45-79.
- Bowman T. E., 1971. The distribution of calanoid copepods off the southeastern United States between Cape Hatteras and Southern Florida. *Smithsonian Contr. Zool.*, **96**, 1-58.
- Briggs J. C., 1974. *Marine zoogeography*, McGraw-Hill Book Company, New York, 475 p.
- Brinton E., Gopalakrishnan K., 1973. The distribution of Indian Ocean euphausiids, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 357-382.
- Cleve P. T., 1901. Plankton from the Indian Ocean and the Malay Archipelago. *Kongol. Svenska. Vetenskaps-Akademiens. Handl.*, **35**, 5.
- Corral J., 1972. Copepoda, suborder: Calanoida, family: Calocalanidae (Paracalanidae part) genera *Calocalanus*, *Ischnocalanus*, *Mecynocera*. *Fiches Identif. Zooplanct. ICES*, sheet 138, 7 p.
- Currie R. I., Fisher A. E., Hargreaves P. M., 1973. Arabian Sea upwelling, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 37-52.
- de Decker A., 1973. Agulhas Bank plankton, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 189-219.
- de Decker A., Mombeck F. J., 1964. A preliminary report on the planktonic copepoda, South African contribution to the International Indian Ocean expedition, *Investigations and Reports, Division of Fisheries, South Africa*, **51**, 10-46.
- Farran G. P., 1936. Copepoda. Great Barrier reef expedition 1928-1929. *Sci. Rep.*, **5**, 3, 73-142.
- Fleminger A., 1973. Pattern, number, variability and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalanus* (Copepoda: Calanoida). *Fish. Bull. US*, **71**, 695-1010.
- Fleminger A., Hulsemann K., 1973. Relationship of Indian Ocean epiplanktonic calanoids to the world oceans, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 339-347.
- Fleminger A., Hulsemann K., 1974. Systematics and distribution of the four sibling species comprising the genus *Pontellina* Dana (Copepoda, Calanoida). *Fish. Bull. US*, **72**, 63-120.
- Fleminger A., Othman B. H. R., Greenwood J. G., 1982. The *Labidocera pectinata* group: an Indo-West Pacific lineage of planktonic copepods with description of two new species. *J. Plankton Res.*, **4**, 245-270.
- Frost B., Fleminger A., 1968. A revision of the genus *Clausocalanus* (Copepoda: Calanoida) with remarks on distributional patterns in diagnostic characters. *Bull. Scripps Inst. Oceanogr.*, **12**, 1-235.
- Ganapathi P. N., Santhakumari K., 1961. The systematics and distribution of planktonic copepods in the Lawson's Bay, Waltair, J. *Mar. Biol. Assoc. India*, **3**, 6-18.
- Gopalakrishnan T. C., 1982. Studies on the planktonic copepods-Calanoidea-Scolecithricidae of the Indian Ocean, *Ph. D. Thesis, Cochin Univ.*, 220 p.
- Grice G. D., 1964. Two new species of calanoid copepods from the Galapagos islands with remarks on the identity of three other species. *Crustaceana*, **4**, 255-264.
- Grice G. D., Hulsemann K., 1965. Abundance, vertical distribution and taxonomy of calanoid copepods at selected stations in the north-east Atlantic. *J. Zool.*, **146**, 213-262.
- Grice G. D., Hulsemann K., 1967. Bathypelagic calanoid copepods of the western Indian Ocean, *Proc. US Natl. Mus.*, **122**, 1-67.
- Grindley J. R., Grice G. D., 1969. A redescription of *Pseudodiaptomus marinus* Sato (Copepoda: Calanoida) and its occurrence in the island of Mauritius, *Crustaceana*, **16**, 125-134.
- Gueredrat J. A., 1972. Variations saisonnières de la diversité spécifique des copépodes de l'Océan Indien le long du 110°E. *J. Mar. Biol. Assoc. India*, **14**, 148-159.
- Halim Y., 1969. Plankton of the Red Sea, in: *Oceanography and marine biology. An annual review*, 7, edited by H. Barnes, George, Allen and Unwin Ltd., London, 231-276.
- Haridas P., 1982. Studies on the ecology of estuarine zooplankton of the Kerala coast, *Ph. D Thesis, Cochin Univ.*, 195 p.
- Haridas P., Gopala Menon P., Madhupratap M., 1980. Annual variations in zooplankton from a polluted coastal environment, *Mahastagar-Bull. Natl. Inst. Oceanogr.*, **13**, 239-248.
- Haridas P., Madhupratap M., 1978. *Acartia dweepi*, a new species of copepod (Acartiidae, Calanoida) from Lakshadweep, *Curr. Sci.*, **47**, 176-178.
- Hiromi J., 1981. Three species of paracalanid copepods in the neighbouring waters of Japan. *Bull. Plankton Soc. Jpn*, **28**, 153-164.
- Hulsemann K., 1966. A revision of the genus *Lucicutia* (Copepoda: Calanoida) with a key to its species, *Bull. Mar. Sci.*, **16**, 702-747.
- Jones E. C., 1966a. The distribution of species of the calanoid copepod family Candaciidae in the Indian Ocean with new records. *Proc. Symp. Crustacea Mar. Biol. Assoc. India*, **1**, 399-405.
- Jones E. C., 1966b. Evidence of isolation between populations of *Candacia Pachydactyla* (Dana)-(Copepoda, calanoida) in the Atlantic and Indo-Pacific Oceans, *Proc. Symp. Crustacea. Mar. Biol. Assoc. India*, **1**, 406-410.
- Jones E. C., 1966c. A new record of *Pseudodiaptomus marinus* Sato (Copepoda: Calanoida) from brackish waters of Hawaii, *Crustaceana*, **10**, 316-317.
- Kasturirangan L. R., 1963. A key for the identification of the more common planktonic Copepoda of Indian coastal waters, *INCOR Publ.*, **2**, C.S.I.R. New Delhi, 87 p.
- Kasturirangan L. R., Saraswathy M., Gopalakrishnan T. C., 1973. Distribution of Copepoda in the Indian Ocean, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin 331-333.
- Krey J., 1973. Primary production in the Indian Ocean I, *o* 115-126.

- Kyi Win., 1977. A species list of the zooplankton from the coastal waters of Burma. *Proc. Symp. Warm Water Zooplankton*, NIO/UNESCO, 93-99.
- Lawson T. J., 1977. Community interactions and zoogeography of the Indian Ocean Candaciidae (Copepoda : Calanoida). *Mar. Biol.*, **43**, 71-92.
- Madhupratap M., 1979. Distribution, community structure and species succession of copepods from Cochin backwaters. *Indian J. Mar. Sci.*, **8**, 1-8.
- Madhupratap M., 1980. Ecology of the coexisting copepod species in Cochin backwaters. *Mahasagar-Bull. Natl. Inst. Oceanogr.*, **13**, 45-52.
- Madhupratap M., 1983. Zooplankton standing stock and diversity along an oceanic track in the western Indian Ocean. *Mahasagar-Bull. Natl. Inst. Oceanogr.*, **16**, 463-467.
- Madhupratap M., Achuthankutty C. T., Nair S. R. S., 1981. Toxicity of some heavy metals to copepods *Acartia spinicauda* and *Tortanus forcipatus*. *Indian J. Mar. Sci.*, **10**, 266-269. 382-3
- Madhupratap M., Haridas P., 1975. Composition and variations in the abundance of zooplankton of backwaters from Cochin to Allepey. *Indian J. Mar. Sci.*, **4**, 77-85.
- Madhupratap M., Haridas P., 1978. *Archidiaptomus aroorus*, a new genus and new species of copepoda (Calanoida: Pseudodiaptomidae) from Cochin backwaters, India. *Crustaceana*, **3**, 253-258.
- Madhupratap M., Nair S. R. S., Achuthankutty C. T., Nair V. R., 1981. Major crustacean groups and total zooplankton diversity around Andaman-Nicobar islands. *Indian J. Mar. Sci.*, **10**, 266-269.
- Madhupratap M., Venugopal P., Haridas P., 1979. Biochemical studies on some tropical estuarine zooplankton species. *Indian J. Mar. Sci.*, **8**, 155-158.
- Madhupratap M., Wafar M. V. M., Haridas P., Narayanan B., Gopala Menon P., Sivadas P., 1977. Comparative studies on the abundance of zooplankton in the surrounding sea and lagoons in the Lakshadweep. *Indian J. Mar. Sci.*, **6**, 138-141.
- Miller C. B., 1983. The zooplankton of the estuaries, in: *Ecosystems of the world*, **26**, edited by B. H. Ketchum, Elsevier Sci. Publ. Comp., Amsterdam, 103-150.
- Nair S. R. S., Nair V. R., Achuthankutty C. T., Madhupratap M., 1981. Zooplankton composition and diversity in western Bay of Bengal. *J. Plankton Res.*, **3**, 493-508.
- Nair V. R., Madhupratap M., 1984. Latitudinal range of epiplanktonic Chaetognatha and Ostracoda in the western tropical Indian Ocean. *Hydrobiologia*, **112**, 209-216.
- National Institute of Oceanography, 1977. *Proceedings of the symposium on warm water zooplankton*, National Institute of Oceanography, Goa, 722 p.
- Pillai P. P., 1975. On the species of *Pontella* Dana and *Pontellopsis* Brady of the International Indian Ocean expedition collections (1960-1965). *J. Mar. Biol. Assoc. India*, **17**, 129-146.
- Pillai P. P., 1976. A review on the calanoid copepod family Pseudodiaptomidae with remarks on the taxonomy and distribution of the species from Indian Ocean. *J. Mar. Biol. Assoc. India*, **18**, 242-265.
- Rao T. S. S., 1979. Zoogeography of the Indian Ocean, in: *Zoogeography and diversity of plankton*, edited by S. van der Spoel and A. C. Pierrot-Bults, Bunge Sci. Publ., Utrecht, 254-292.
- Reddy Y. R., Radhakrishna Y., 1982. Redescription and/or remarks on four species of *Pseudodiaptomus* Herrick (Copepoda : Calanoida) from South India. *Hydrobiologia*, **87**, 255-271.
- Sakthivel M., 1973. Biogeographical change in the latitudinal boundary of a bisubtropical pteropod *Styliola subula* (Quoy et Gaimard) in the Indian Ocean, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 401-304.
- Saraladevi K., Stephen R., Rao T. S. S., 1979. Distribution of *Haloptilus* (Copepoda : Calanoida) in the Indian Ocean. *Indian J. Mar. Sci.*, **8**, 159-165.
- Saraswathy M., 1966. Pelagic copepods from the inshore waters off Trivandrum coast. *Proc. Symp. Crustacea. Mar. Biol. Assoc. India*, **1**, 74-106.
- Sewell R. B. S., 1912. Notes on the surface living copepoda of the Bay of Bengal. *Rec. Ind. Mus.*, **7**, 313.
- Sewell R. B. S., 1914. Notes on the surface Copepoda of the Gulf of Mannar. *Spol. Zeylan.*, **9**, 25, 191.
- Sewell R. B. S., 1929. The Copepoda of the Indian Seas. Calanoida. *Mem. Indian Mus.*, **10**, 1-221.
- Sewell R. B. S., 1932. The Copepoda of the Indian Seas. Calanoida. *Mem. Indian Mus.*, **10**, 223-407.
- Sewell R. B. S., 1947. The free swimming planktonic Copepoda. Systematic account. *Sci. Rep. John Murray Exped.*, **8**, 1-303.
- Sewell R. B. S., 1948. The free swimming planktonic Copepoda. Geographic distribution. *Sci. Rep. John Murray Exped.*, **8**, 317-579.
- Sherman K., 1964. Pontellid copepod occurrence in the Central South Pacific. *Limnol. Oceanogr.*, **9**, 476-484.
- Silas E. G., Pillai P. P., 1973. The calanoid copepod family Pontellidae from the Indian Ocean. *J. Mar. Biol. Assoc. India*, **15**, 771-858.
- Smith S. L., 1982. The northwestern Indian Ocean during the monsoons of 1979: distribution, abundance and feeding of zooplankton. *Deep-Sea Res.*, **29**, 1331-1353.
- Stephen R., Rao T. S. S., 1980. Distribution of the bathypelagic family Arietellidae (Copepoda : Calanoida) in the upper 200 m in the Indian Ocean. *J. Plank. Res.*, **2**, 239-247.
- Subbaraju R. C., Krishnamurthy K., 1972. Ecological aspects of plankton production. *Mar. Biol.*, **14**, 25-31.
- Tanaka O., 1973. On *Euchaeta* (Copepoda, Calanoida) of the Indian Ocean. *Indian Ocean Biol. Cent. Handbook.*, **4**, 126-149.
- Thompson I. C., Scott A., 1903. Report on Copepoda. *Ceylon Pearl cyster fisheries: Suppl. Rep.*, Part 1. 7. Royal Society, London, 227 p.
- Timonin A. G., 1971. The structure of plankton communities of the Indian Ocean. *Mar. Biol.*, **9**, 281-289.
- Tokioka T., 1979. Neritic and oceanic plankton, in: *Zoogeography and diversity of plankton*, edited by S. van der Spoel and A. C. Pierrot-Bults, Bunge Scientific Publ., Utrecht, 126-143.
- Tranter D. J., 1977. Further studies on plankton ecosystems in the eastern Indian Ocean. V: Ecology of the Copepoda. *Austr. J. Mar. Freshwater Res.*, **28**, 593-625.
- Tranter D. J., Abraham S., 1971. Coexistence of species of Acartiidae (Copepoda) in the Cochin Backwater, a monsoonal estuarine lagoon. *Mar. Biol.*, **11**, 222-241.
- van der Spoel S., Pierrot-Bults A. C., 1979. Zoogeography of the Pacific Ocean, in: *Zoogeography and diversity of plankton*, edited by S. van der Spoel and A. C. Pierrot-Bults, Bunge Scientific Publ., Utrecht, 293-327.
- Veronis G., 1973. Model of World Ocean circulation. I. Wind driven, two layer. *J. Mar. Res.*, **31**, 228-288.
- Vervoort W., 1963. Pelagic copepoda. Part I: Copepoda Calanoida of the families Calanidae upto and including Euchaetidae. *Atlant. Rep.*, **7**, 77-194.
- Vinogradov M. E., Voronina N. M., 1961. Distribution of some widespread species of copepods in the Indian Ocean. *Dokl. Acad. Nauk. SSSR*, **140**, 219-222.
- Vinogradov M. E., Voronina N. M., 1962. The distribution of different groups of plankton in accordance with their trophic level in the Indian Equatorial Current area. *Rapp. PV Cons. Inter. Explor. Mer.*, **153**, 200-204.
- Voronina N. M., 1962. On the surface plankton of the Indian Ocean. *Trudy Inst. Okeanol.*, **58**, 67-79.
- Wolfenden R. N., 1906. *Notes on the collection of copepoda. Fauna and geography of the Maldives and Laccadive Archipelagoes, vol. II*, edited by J. S. Gardiner, Cambridge Univ. Press, 989 p.
- Wyrtki K., 1971. Oceanographic atlas of the International Indian Ocean expedition, *National Science Foundation, US Government Printing Office*, Washington D.C.
- Wyrtki K., 1973. Physical oceanography of the Indian Ocean, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel, Springer-Verlag, Berlin, 18-36.
- Zeitzschel B., 1973. *The biology of Indian Ocean*. Springer-Verlag, Berlin, 549 p.