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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-néritique-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 $19.8 \times 10^6 \text{km}^2$) 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 200-0 m were made with a Heron-Tranter net (mouth area 0.25 m^2; mesh width 0.3 mm) 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 200 m) 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

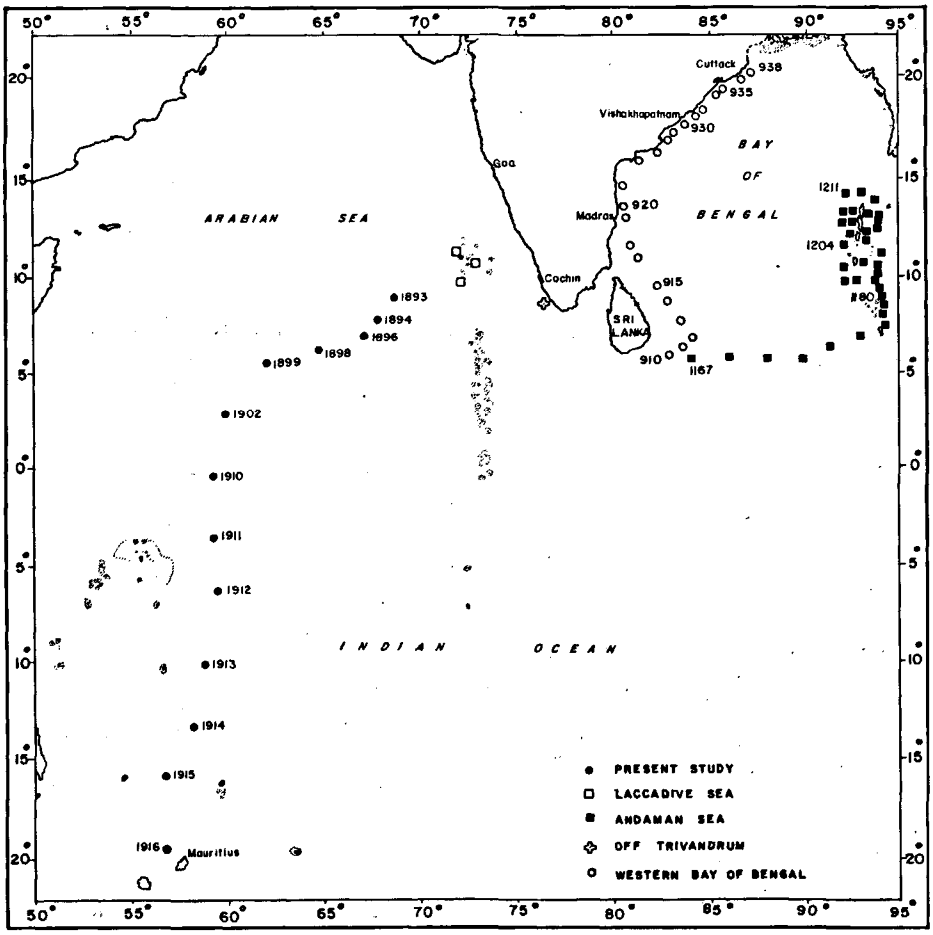

Figure 1
Geographic locations of stations sampled.

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 $990/100\,m^3$ at station 1916 to $15070/100\,m^3$ 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).

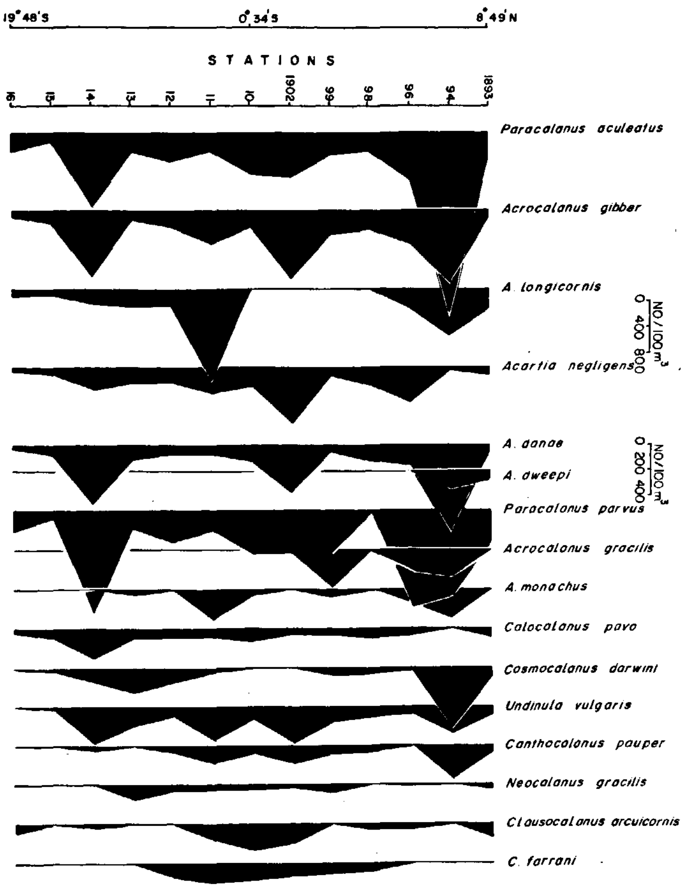

Figure 2

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

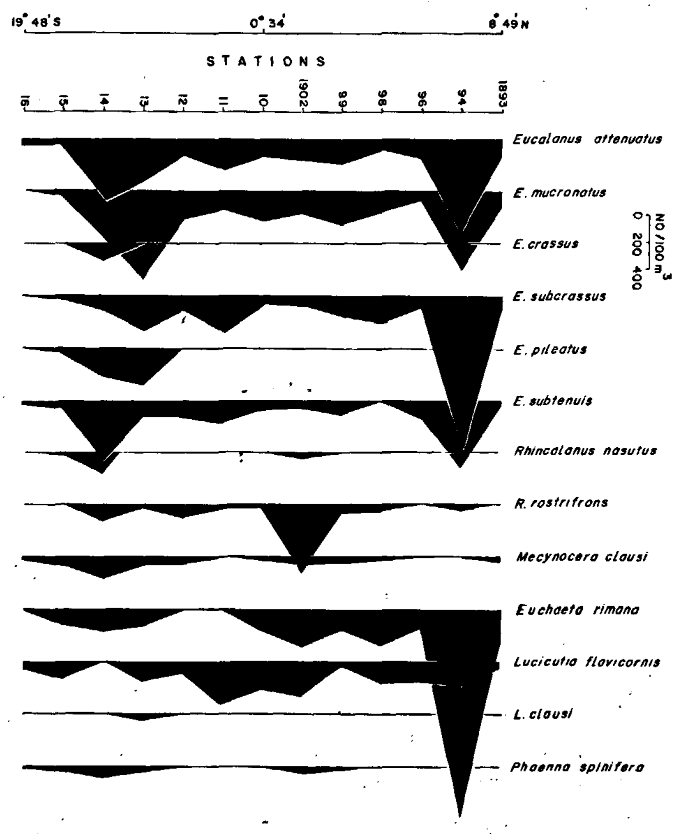

Figure 3

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

Table 1

List of Calanoid copepod species (excluding Pseudodiaptomidae *and* Acartiidae) *from epiplanktonic 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.*

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

* 143. *C. curta* (Dana)	
144. *C. ethiopica* (Dana)	c
145. *C. longimana* (Claus)	U
* 146. *C. bipinnata* (Giesbrecht)	
147. *C. varicans* (Giesbrecht)	U
148. *C. samassae* Pesta	U
149. *C. guggenheimi* Grice and Jones	r
150. *C. norvegica* (Boeck)	r
151. *C. tuberculata* (Wolfenden)	rN
152. *C. tenuimana* (Giesbrecht)	r
153. *Paracandacia truncata* (Dana)	c
154. *P. bispinosa* (Claus)	c
155. *P. simplex* (Giesbrecht)	r
PONTELLIDAE	
* 156. *Calanopia minor* A. Scott	
* 157. *C. elliptica* (Dana)	N
158. *C. aurivilli* Cleve	NU
* 159. *C. thompsoni* A. Scott	N
* 160. *C. herdmani* A. Scott	N
161. *C. seymouri* Pillai	U
162. *Labidocera pectinata* Thompson and Scott	cN
* 163. *L. pavo* Giesbrecht	N
* 164. *L. acuta* (Dana)	N
* 165. *L. minuta* Giesbrecht	
* 166. *L. detruncata* (Dana)	
* 167. *L. kroyeri* (Brady)	N
168. *L. acutifrons* (Dana)	r
169. *L. bengalensis* Krishnaswamy	NU
170. *L. bataviae* A. Scott	NU
171. *L. gangetica* Sewell	NU
172. *L. euchaeta* Giesbrecht	NU
173. *L. rotunda* Mori	r
174. *L. laevidentata* (Brady)	NU
175. *L. madurae* A. Scott	NU
176. *L. pseudacuta* Silas and Pillai	U
177. *Pontella investigatoris* Sewell	NU
178. *P. princeps* Dana	NU
179. *P. securifer* Brady	r
* 180. *P. fera* Dana	
* 181. *P. danae* Giesbrecht	N
* 182. *P. spinipes* Giesbrecht	
183. *P. andersoni* Sewell	NU
184. *P. atlantica* (H. Milne Edwards)	r
185. *P. denticauda* A. Scott	NU
186. *P. diagonalis* Wilson	U
* 187. *Pontellopsis macronyx* A. Scott	N
188. *P. krameri* (Giesbrecht)	NU
189. *P. armata* (Giesbrecht)	U
* 190. *P. herdmani* Thompson and Scott	N
191. *P. scotti* Sewell	NU
192. *P. villosa* Brady	r
193. *P. regalis* (Dana)	r
* 194. *Pontellina plumata* (Dana)	L
195. *P. morii* Fleminger and Hulsemann	U
TORTANIDAE	
196. *Tortanus forcipatus* (Giesbrecht)	cN
197. *T. gracilis* (Brady)	NU
198. *T. barbatus* (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* (1966*a*); *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-*

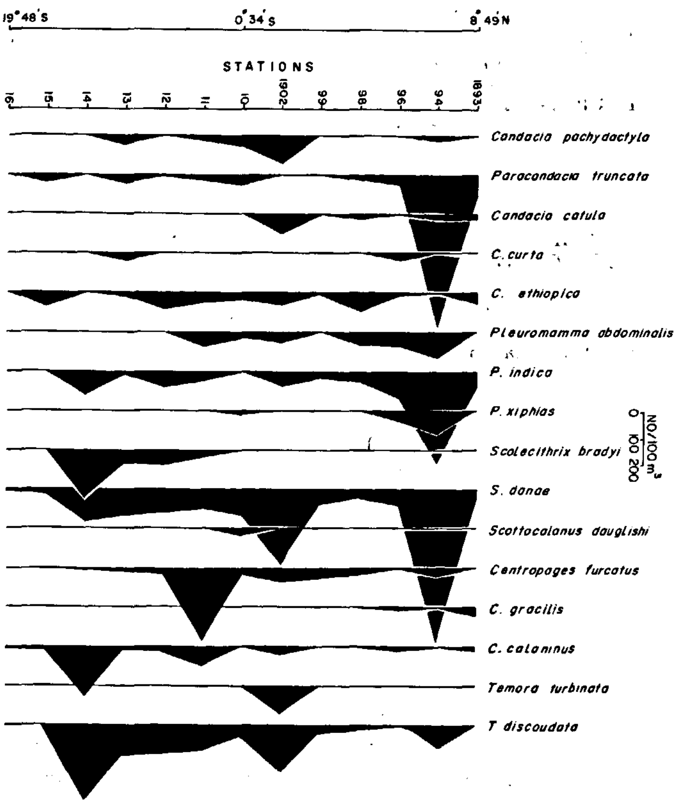

Figure 4

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

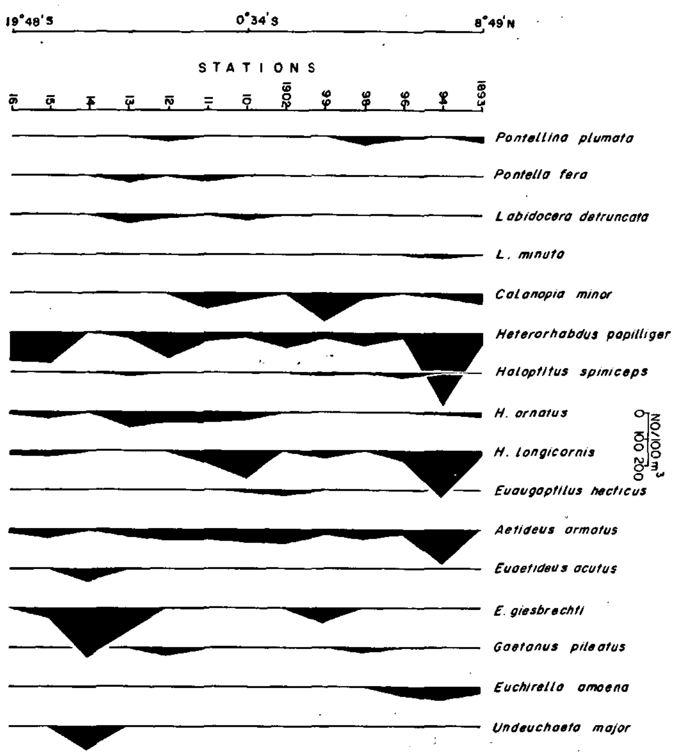

Figure 5

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

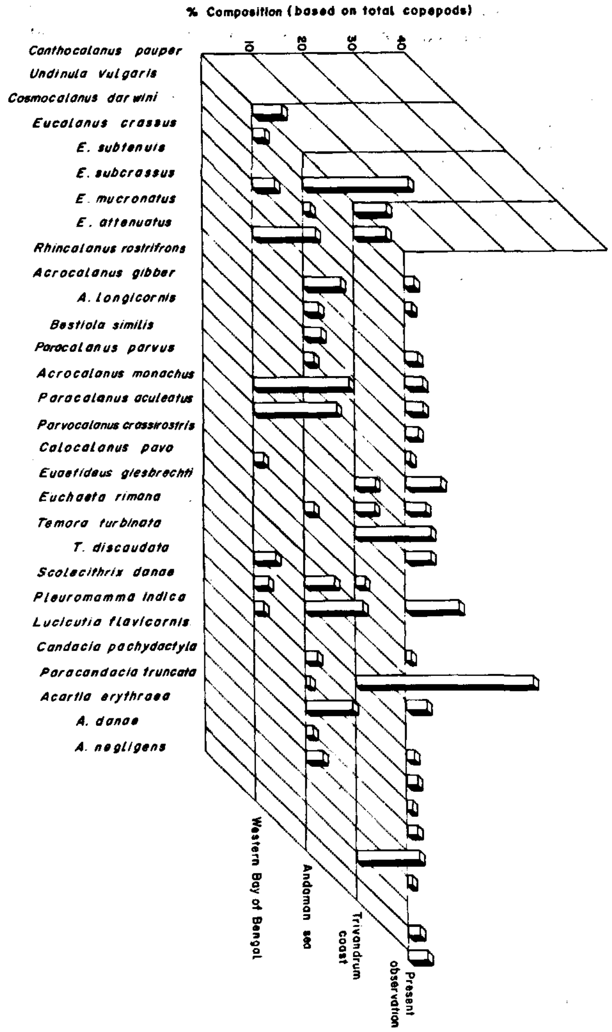

Figure 6

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 denudatus* 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. *Scole-*

cithricella 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 dauglishi, Macandrewella cochinesis* and probably *Scolecithricella 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, 1966*c*; 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		
P. serricaudatus (T. Scott)	estuarine & neritic	c
***P. mertoni* Fruchtl	»	c
***P. aurivilli* Cleve	»	c
**P. jonesi* Pillai	»	c
**P. annandalei* Sewell	»	c
**P. ardjuna* Brehm	»	
**P. salinus* Giesbrecht	»	
***P. daughlishi* Sewell	»	
***P. clevei* A. Scott	»	
**P. compactus* Walter	»	
**P. bowmani* Walter	»	
**P. sewelli* Walter	»	
**P. lobipes* Gurney	estuarine & limnetic	
**P. binghami* Sewell	»	c
**P. b. malayalus* Wellershaus	»	c
**P. hickmani* Sewell	»	
**P. tollingarae* Sewell	»	
**P. burckhardti* Sewell	coastal waters of oceanic islands	
***P. marinus* Sato	»	
**P. nankaurensis* Roy	»	
**P. andamanensis* Pillai	»	
**P. masoni* Sewell	»	
Genus *Archidiaptomus* Madhupratap & Haridas		
**A. aroorus* Madhupratap & Haridas	estuarine & limnetic	
ACARTIIDAE		
Genus *Acartia* Dana		
Acartia negligens Dana	neritic & oceanic	
A. danae Giesbrecht	»	
***A. amboinensis* Carl	»	
***A. bispinosa* Carl	»	
***A. pietschmani* Pesta	»	
A. centrura Giesbrecht	estuarine & neritic	c
***A. spinicauda* Giesbrecht	»	c
***A. erythraea* Giesbrecht	»	c
**A. southwelli* Sewell	»	c
A. pacifica Steur	»	c
**A. bilobata* Abraham	estuarine	c
**A. bowmani* Abraham	»	c
A. plumosa T. Scott	»	c
**A. chilkaensis* Sewell	»	
**A. dweepi* Haridas & Madhupratap	coastal waters of oceanic islands	
Subgenus *Acartiella* Sewell		
**A. gravelyi* Sewell	estuarine & limnetic	c
**A. kempi* Sewell	estuarine	
**A. major* Sewell	»	
**A. minor* Sewell	»	
**A. sewelli* Steür	»	
**A. keralensis* Wellershaus	»	c
**A. tortaniformis* 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. bispinosa*, 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. detruncuta, L. kroyeri, Pontella princeps* and *P. fera* from the Atlantic were based on wrong identifications and *Pontellopsis herdmani*, 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. dweepi* 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. pachydactyla* 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 pachydactyla*, *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 (Wyrtki, 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 pachydactyla* in the Indian and Atlantic Ocean by 2000 miles of water (Jones, 1966*b*). 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, 1966*a*; 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^3 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^3. On the other hand, the annual average counts from the inshore station located off Trivandrum (Fig. 1) was 700/m^3 with a peak value of 3290/m^3 in August associated with seasonal upwelling. These figures are relatively insignificant when compared with peak values recorded from estuarine areas, *e.g.* 55390/m^3 in the Cochin Backwaters (Tranter, Abraham, 1971); 286,000/m^3 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^3 but drastic reductions to 1 to 200/m^3 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 ascendency 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 *et al.*, 1977	Madhupratap *et al.*, 1981	Nair *et al.*, 1981	Haridas *et al.*, 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 pachydactyla, 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

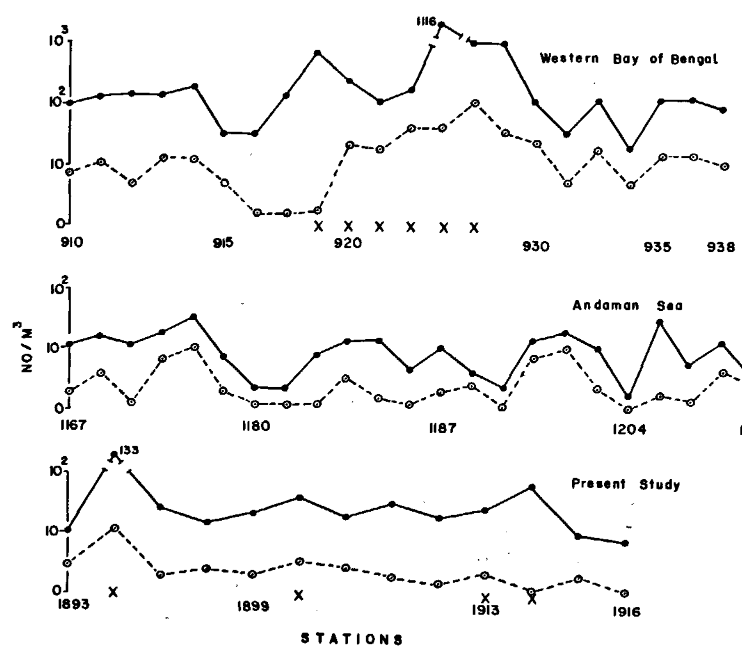

Figure 7
Numerical abundance of herbivores and omnivores (closed circle); carnivores (open circle) in various studies. Stations where mild upwelling or divergence was observed are marked by a cross.

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. bispinosa* 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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