

## Status and Strategy of Zooplankton of Tropical Indian Estuaries: A Review<sup>1), 2)</sup>

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### Abstract

Information on tropical estuarine zooplankton with particular reference to the Indian estuaries is presented. Large quantities of the primary and secondary production in these environments apparently contribute to the richness of organic content of bottom deposits. Among the estuarine species, a high saline and a medium saline component could be recognized. Immigrants from neritic waters and a few low saline forms complete the faunal spectrum. Copepods dominate, and among them species of the families Acartiidae, Pseudodiaptomidae and Paracalanidae are most common. Salinity changes induced by monsoonal rains have considerable effect on zooplankton abundance and distribution. High and medium saline species disappear during the rainy season and the mechanisms through which estuaries are repopulated after the rains remain poorly understood. Dominance by a few species and low species diversity characterize these estuaries. Availability of abundant resources and opportunity provided by salinity incursion to expand the width of niches probably allow the high saline species to coexist.

Tropical estuaries experience only limited fluctuations of temperature. However, the environment remains rigorous because of extreme changes in salinity. Species composition in these systems is fairly distinct from their counterparts in the temperate region. Studies on warm water estuarine systems, particularly on zooplankton, are few as pointed out by REEVE (1975). This is also reflected in two recent reviews on estuarine zooplankton (GRINDLEY 1981, MILLER 1983) which use very little tropical material.

Species composition and distribution of zooplankton are now well studied from some tropical estuaries of India. Nevertheless, certain aspects of biology, interaction of species and role of estuarine zooplankton in the ecosystem as a whole remain rather obscure. The present paper attempts to focus on some of these problems while recapitulating the available information. Whereas the aspects considered hereunder would in general pertain to any tropical estuarine system with a periodic flush-out, the presentation here is mainly based on studies conducted in the Cochin backwater system (HARIDAS et al. 1973, MADHUPRATAP & HARIDAS 1975, MADHUPRATAP 1976, 1979) and five other estuaries (Fig. 1) situated along the southwest coast of India (HARIDAS 1982). Available information from other estuaries situated along the east and west coasts of India are also incorporated.

### Environment

The Cochin backwater system is a large basin of brackish water (area--250 km<sup>2</sup>) into which

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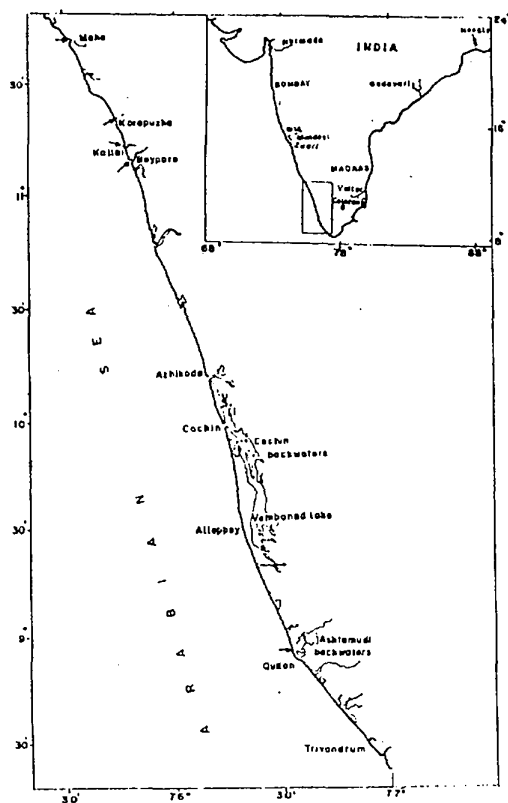


Fig. 1. Location of estuaries in India from where information on zooplankton was available. Arrows indicate estuaries on southwest coast of India which were investigated apart from the Cochin backwaters.

several rivers empty. It is a bar-built estuary with two openings to the Arabian Sea at Cochin and Azhikode and a tidal range of  $\sim 1$  m. The magnitude of tidal influence progressively decreases with increase in distance from the mouth.

Low salinity conditions occur in the estuary during monsoons (May-September) when large quantities of freshwater are brought into it through river discharge and land run-off (Fig. 2). Salinity remains at near zero values over a large portion of the estuary during this period. Precipitation on the estuary averages about  $300 \text{ cm yr}^{-1}$ . Residence time in the Cochin backwaters is not worked out. However, in the Mandovi estuary of Goa, which receives about two thirds precipitation compared to the Cochin backwaters, the residence time is about 5-6 days during monsoons and about 50 days during summer months (March-April) when precipitation is negligible (DAS & BHATTATHIRI unpubl.).

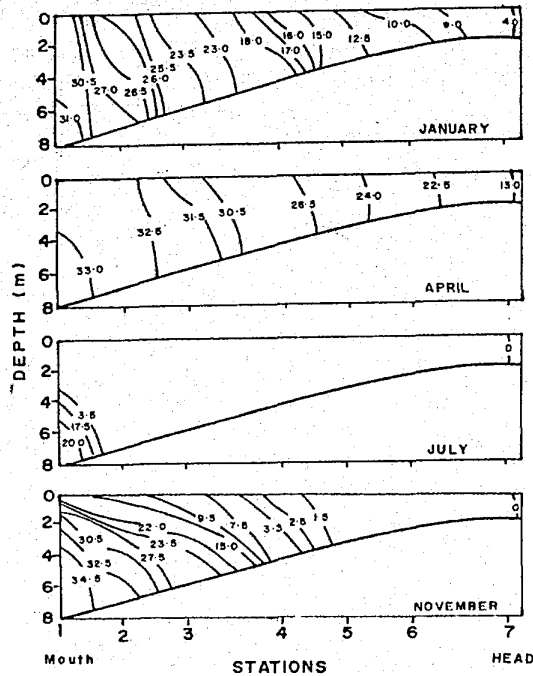


Fig. 2. Distribution of salinity from mouth to the head of the Cochin backwaters in representative months of the year 1972 (Modified from RAO et al. 1981).

During the rest of the year (postmonsoon, October–December; premonsoon, January–April), a gradual gradient develops in the distribution of salinity from mouth ( $\sim 34\text{‰}$ ) to head ( $\sim 13\text{‰}$ ). Length of seasons varies marginally from year to year, depending on the onset and duration of monsoons. Conditions never become hypersaline as experienced in some estuaries of South Africa (cf. GRINDLEY 1981). During the monsoon and postmonsoon seasons, the estuary becomes vertically stratified. Typical salt wedge develops along the bottom with interface sloping towards upstream. During summer, this condition gradually disappears and the estuary becomes more or less vertically homogeneous. While this is the pattern in the estuaries situated along the west coast of India which receive rainfall mainly from the southwest monsoon, in estuaries along the east coast such as the Vellar, salinity reduction occurs during northeast monsoon (October–November).

Surface temperature, on the other hand, varies only from  $\sim 28^{\circ}\text{C}$  during rainy season to  $\sim 30^{\circ}\text{C}$  in summer (26.5 to  $30^{\circ}\text{C}$ , respectively at bottom). Fluctuations of temperature and factors such as oxygen content are of minor importance to affect distribution of zooplankton (MADHUPRATAP 1978, MADHUPRATAP et al. 1977a). In the other five estuaries also the pattern was similar in relation to both hydrography and species distribution (HARIDAS 1982)

confirming the results obtained from the Cochin backwaters.

### Standing Stock and Productivity

Estuaries are generally recognized as highly productive systems both at primary and secondary levels. However, zooplankton biomass and counts are very poor during low saline period (Figs. 3 and 4). But, during the saline post and premonsoon seasons zooplankton thrives and proliferates. Standing stock (displacement volume) and counts per unit volume of water during this span often far exceed those observed in coastal waters and the open ocean. SUBBARAJU & KRISHNAMURTHY (1972) observed an average standing stock of  $2 \text{ ml m}^{-3}$  (maximum  $4 \text{ ml m}^{-3}$ ) and counts of  $92,000 \text{ m}^{-3}$  (maximum copepod counts  $286,000 \text{ m}^{-3}$ ) from the Vellar estuary during summer. Zooplankton standing stock reached  $1.9 \text{ ml m}^{-3}$  and counts  $18,000 \text{ m}^{-3}$  in the premonsoon period (Figs. 3 and 4) in the Cochin backwaters. TRANTER & ABRAHAM (1971) recorded copepod counts up to  $55,390 \text{ m}^{-3}$  in this estuary. In contrast, the coastal waters,

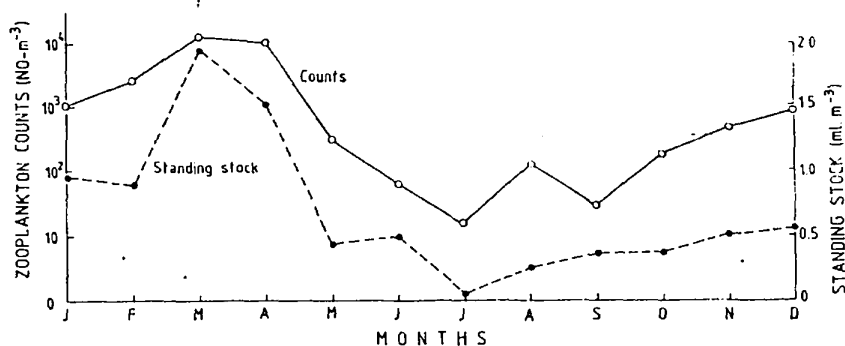


Fig. 3. Zooplankton standing stock and counts at a station 14 km away from mouth of the Cochin backwaters in 1972 (Data from MADHUPRATAP 1976).

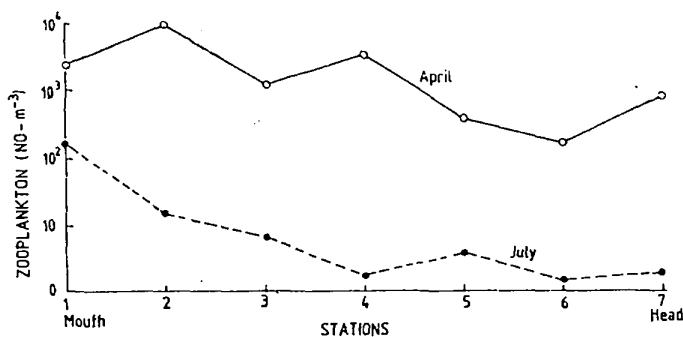


Fig. 4. Distribution of zooplankton from mouth to the head of the Cochin backwaters during saline (April) and low saline (July) months in 1972 (Data from MADHUPRATAP 1976).

let alone the open ocean, are far less productive. The average biomass was  $0.18 \text{ ml m}^{-3}$  and counts  $1,203 \text{ m}^{-3}$  in a nearshore environment in southwest coast of India (HARIDAS et al. 1980). However, sudden increases from zooplankton swarms resultant of upwelling could occur in coastal waters (HARIDAS et al. 1980, MADHUPRATAP et al. 1980). In general, average biomass ranged between  $0.07$  to  $0.08 \text{ ml m}^{-3}$  (NAIR et al. 1977) and  $0.09$  to  $0.3 \text{ ml m}^{-3}$  (NAIR et al. 1981) in the Bay of Bengal and  $0.09$  to  $0.1 \text{ ml m}^{-3}$  (NAIR et al. 1978) in the Arabian Sea. In the Andaman Sea the range was from  $0.02$  to  $0.1 \text{ ml m}^{-3}$  with zooplankton counts of 7 to  $140 \text{ m}^{-3}$  (MADHUPRATAP et al. 1981a).

MILLER (1983) estimates the secondary production in the temperate estuaries to be of the order of  $5$  to  $10 \text{ g C m}^{-2} \text{ yr}^{-1}$ . Rough estimates from the Mandovi-Zuari estuaries and the Cochin backwaters are to the magnitude of  $10.8$  and  $15.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ , respectively (MADHUPRATAP et al. 1977b, SELVAKUMAR et al. 1980). It must, however, be noted that the production rate is about 8 times higher during the saline period compared to the rainy season. Despite high zooplankton production, the coefficients of energy transfer from primary to secondary level was only  $7.4\%$  in the Cochin backwaters and  $6.6\%$  in Mandovi-Zuari estuaries (SELVAKUMAR et al. 1980). QASIM (1977) also arrived at similar conclusions regarding these two estuarine systems. In fact, these coefficients could be on the higher side considering that the estimates of primary production do not consider picoplankton which according to LONGHURST (1985) accounts for about  $50\%$  of primary production in tropical oceans. The role of the estuarine zooplankton in the food chain remains inconclusive because of the absence of large shoaling fishery (except *Acetes* spp.). A large quantity of the primary and secondary production in estuaries perhaps contributes to the productivity of coastal waters through tidal and monsoonal flush-outs or forms a major source for the organic matter in the bottom deposits. This could help the sustenance of a rich benthic life, and in fact, high benthic biomass has been reported from several of these estuaries (ANSARI 1974, PARULEKAR et al. 1980). Other bottom feeders like penaeid prawns which abound in the saline period are also major direct or indirect consumers. Analyzing the role of zooplankton of South African estuaries, DAY (1967) also came to a similar conclusion.

#### Composition of Zooplankton

As observed in the temperate regions, copepods usually form the dominant zooplankton component in the tropical estuaries. In the Cochin backwaters they constituted  $55$  to  $85\%$  (annual mean  $74.5\%$ ) of total zooplankton counts. Larvae of decapods, mainly comprising brachyuran zoeae, are next ( $\sim 13\%$ ) followed by other groups each of which usually contributes to less than  $1\%$ , such as hydromedusae, ctenophores, chaetognaths, amphipods, sergestids, other larvae, etc. (MADHUPRATAP 1978, 1979). Predominance of copepods is reported from estuaries along southwest coast of India (HARIDAS 1982), Mandovi-Zuari (GOSWAMI & SELVAKUMAR 1977), Narmada (GAJBHIYE et al. 1981) and Vellar (SUBBARAJU & KRISHNAMURTHY 1972).

Estuarine zooplankton usually has three components: (1) a marine component restricted

to the seaward parts, (2) estuarine endemics living in the brackish water and (3) fresh water species of the upper estuary (MILLER 1983). Although the design remains basically same, recognition of more subtle components is possible. Among copepods, some of the neritic forms like *Undinula vulgaris*, *Eucalanus crassus*, *Centropages tenuiremis*, *Labidocera kroeyeri*, etc. occur sporadically in very small numbers at the mouth (Fig. 5). These exotic species (cf. COX & WIEBE 1979), obviously, are brought in accidentally by tidal currents and have little impact on the estuarine biology or ecology. A few species like *Labidocera pectinata* and *Centropages alcocki* are able to withstand somewhat lower salinities (Fig. 6), and although expatriate, are able to penetrate up to the middle reaches. They do not occur in very large numbers and their centre of abundance is located around the lower reaches (Fig. 5). Yet other coastal forms are some species of the family Paracalanidae (e.g. *Bestiola similis*), which occur in considerable numbers and salinity range, and are able to breed in the lower and middle reaches of the estuary during summer.

Among the truly estuarine species, two groups could be recognized. One consists of 'high saline' species like *Acartia centrura*, *A. bowmani*, *A. bilobata*, etc. which virtually disappear during rainy season despite their wide salinity tolerance. They make their appearance near the mouth region in the postmonsoon months when salinity regains to threshold levels. As the premonsoon season progresses, and salinity increases towards the interior, these species are able to invade and dominate the lower and middle reaches (Figs. 5 and 7). Some of these species occur right up to the head of the estuary although never in large numbers. A second group consists of species like *Acartiella keralensis* and *Acartia plumosa* (the latter species of the Cochin backwaters is distinct from *A. plumosa* s. str. occurring in the Atlantic,

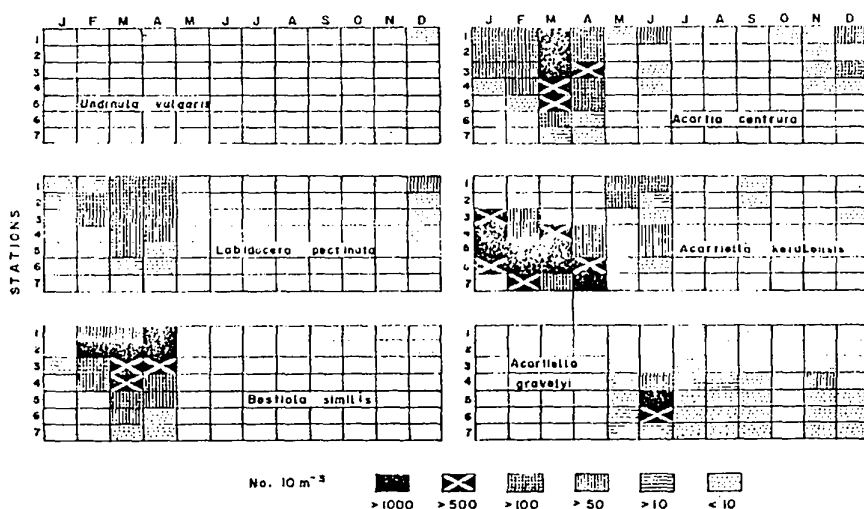


Fig. 5. Distribution of selected species in the Cochin backwaters in 1972. St. 1 is mouth and St. 7 is head (Data from MADHUPRATAP 1976).

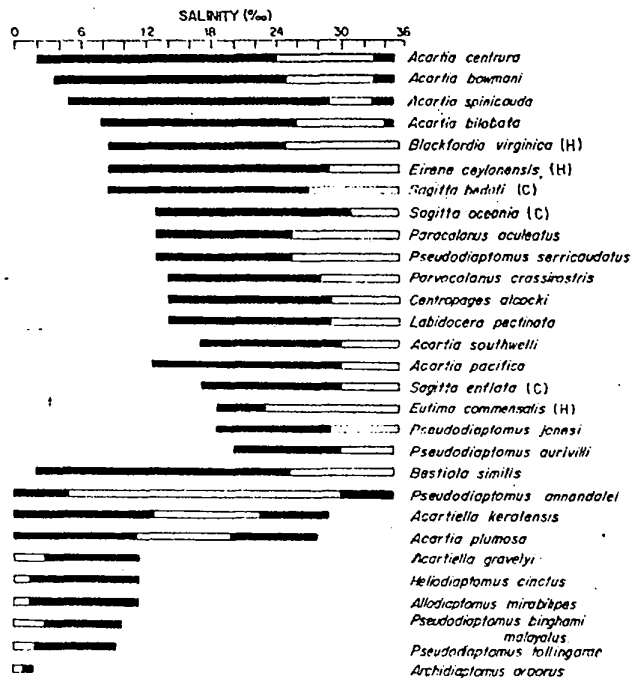


Fig. 6. Recorded salinity range (optimum unshaded) of common species occurring in the Cochin backwaters. (H)—Hydromedusae, (C)—Chaetognaths, rest are copepods (Data from MADHUPRATAP 1976).

UEDA pers. comm.) which thrive best in medium salinities. During peak summer, these 'medium saline' species occur in high abundance towards the upper reaches (Figs. 5 and 7), where salinity is optimal (~10-20‰). At the onset of rains, their populations shift towards the middle and lower reaches. Both the high saline and medium saline species are wiped out when salinity is reduced below the threshold. Presence of low saline water at the surface sometimes inhibits the vertical migration of high saline species during the initial stages of rainy season (MADHUPRATAP & RAO 1979).

About six copepod species occur in low salinities in the Cochin backwaters (Fig. 6). *Acartiella sewelli* is another 'low saline' species reported from the Mandovi-Zuari (GOSWAMI & SELVAKUMAR 1977) and the Hooghly (SARKAR et al. 1986) estuaries. However, all these species occur in very low abundance. *Acartiella graveleyi* is the most common species during rainy season, but the average abundance is only in the range of 5-15 indiv m<sup>-3</sup>. An abundant freshwater component like the cladoceran *Bosmina* sp. occurring in the St. Lawrence estuary (BOUSFIELD et al. 1975) is absent in the Indian estuaries.

Chaetognaths occur only during summer months and are merely extensions of their populations in inshore waters. However, the more common species are able to withstand some

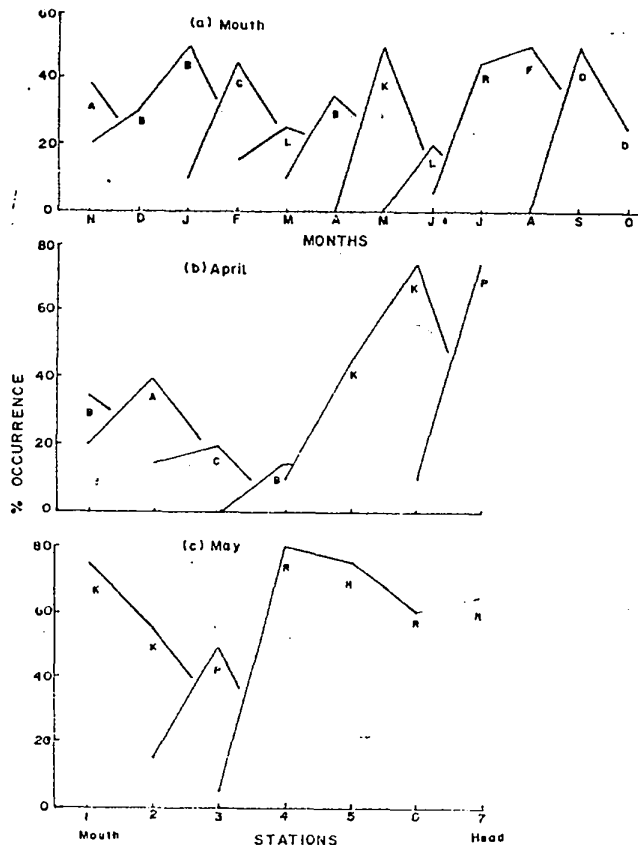


Fig. 7. Succession of dominant species of copepods at the mouth in 1971-'72 (a) and head to mouth in April and May 1972 (b and c) in the Cochin backwaters. A: *Bestiola similis*, B: *Acartia boromani*, C: *Acartia centrura*, D: *Acartia pacifica*, F: *Pseudodiaptomus amandalei*, L: *Acartia bilobata*, K: *Acartiella keralensis*, O: *Acartia plumosa*, R: *Acartiella gravelyi*. In 1972, rains started in May, there was a brief let up in June and again intensified in July (Modified from MADHUPRATAP 1979).

amount of salinity fluctuations (Fig. 6). Among these, *Sagitta bedoti* is common also in the Mandovi-Zuari, Narmada and Hooghly estuaries. This species appears to be capable of breeding in the estuaries during summer months (NAIR & SELVAKUMAR 1979). Of the three common species of hydromedusae which occur during high salinity period (Fig. 6), *Eutima commensalis* appears to be an estuarine endemic. The chaetognaths and hydromedusae plus the ctenophore *Pleurobrachia* sp. which also occur in fairly large numbers during summer form the main carnivorous component of the zooplankton.

The sergestid *Lucifer hanseni* occurs in a wide range of salinity (4-34.5‰) during the



premonsoon period albeit in small numbers. Among the coastal forms which penetrate into the estuary, the distribution of cladocerans does not jibe with the pattern. The two cladocerans *Evadne tergestina* and *Penilia avirostris* seem to tolerate wide salinity fluctuations. Curiously, these typically marine forms do not occur in the backwaters during saline premonsoon months. On the other hand, for reasons not easily explicable, these species occur in monsoon and post monsoon months often thriving in abundance in low salinities (MADHUPRATAP 1981). *Podon polyphemoides* has been recorded in low numbers from a few estuaries along southwest coast of India.

Most species of zooplankton which occur during saline period tolerate wide salinity fluctuations, but most of the estuarine species occur rarely in the inshore waters. GRINDLEY (1981) states that some species of the genus *Pseudodiaptomus* tolerate salinities from less than 1 to 75‰ in the South African estuaries but are seldom found in normal seawater. He attributes this exclusion to the possibility that they cannot compete with the wide range of species occurring in seawater. If the estuarine zooplankton species were commonly occurring in the inshore waters during monsoon period, it is conceivable that they would form the source of recruitment to repopulate the estuaries after the monsoonal wash-out. Their absence poses an interesting problem on the repopulation mechanisms. There is now conclusive evidence that some zooplankton produce resting eggs to overwinter adverse temperature conditions (see GRICE & MARCUS 1981, for review). A number of copepod species have been established to produce diapause eggs in the Inland Sea of Japan (KASAHARA & UYE 1979, UYE et al. 1979, UYE et al. 1984). Interestingly, these include a few species common in Indian estuaries such as *Acartia erythraea*, *A. pacifica* and *Tortanus forcipatus*. SANTHAKUMARI & VANNUCCI (1971) suggested that the hydroids of the hydromedusa *Eutima commensalis* encapsulate into resting stage during low saline period and bud off new medusae only when salinity regains to appropriate levels. It is possible that other high and medium saline estuarine species, especially copepods, may have resting stages/eggs to tide over the unfavorable low saline period.

Species belonging to the copepod families Acartiidae, Pseudodiaptomidae and Paracalanidae are common in the zooplankton of the Indian estuaries. While the number of species in Pseudodiaptomidae is comparable with that of Acartiidae, species belong to the latter attain much higher numerical proportions (1.7% and 70.6% respectively of the total annual copepod counts in the Cochin backwaters, MADHUPRATAP & HARIDAS 1975). In estuaries of colder regions of the northern hemisphere also, *Acartia* spp. are dominant components while both *Pseudodiaptomus* and *Acartia* spp. dominate the South African estuaries (cf. GRINDLEY 1981, MILLER 1983). However, the species composition among these families is different in different regions, and the reported occurrence of *Acartia clausi* and *A. longiremis* in the Godavari estuary of India (CHANDRAMOHAN 1977) is based on wrong identification. In the tropical estuaries of Texas and subtropical waters of South Florida, *Acartia tonsa* dominates (REEVE 1975, ARMSTRONG 1982) and this species does not occur in the Indian estuaries. Notably absent in the Indian estuaries are the genera *Eurytemora* common and often abundant in northern temperate estuaries and *Sulcalanus*, *Gladioferens*, *Boeckella*, *Calamocia*, etc. which

are characteristics of the Australian estuaries. The genus *Isias* is represented by a single species *I. uncipes* in Australian estuaries; *I. cochinesis* occurs in the Cochin backwaters albeit scantily.

The general composition of the zooplankton among the Indian estuaries is not very different. *Tortanus forcipatus*, very common in the Mandovi-Zuari during saline period, plus *Acartiella sewelli* does not occur in the Cochin backwaters. *Centropages alcocki* appears to be recorded only from the Cochin backwaters, the Rangoon River estuary (WELLERSHAUS 1970) and coastal waters of southwest coast of India (HARIDAS et al. 1980). *Pseudodiaptomus hickmani* occurs in the Hooghly estuary. However, records of *P. daughlishi* and *P. masoni* from this area (SARKAR et al. 1986) require confirmation (see WALTER 1986). Species like *Eutima commensalis*, *Acartia bilobata*, *A. bowmani*, *Acartiella keralensis*, *Pseudodiaptomus jonesi* and *Archidiaptomus aroorus* originally considered endemic to the Cochin backwaters occur in other estuaries along southwest coast of India (HARIDAS 1982). The apparent absence of these species in other Indian estuaries could be due to want of more intensive systematic studies.

#### Community Structure

In the Cochin backwaters, 10 out of the 56 copepod species recorded form 92.3% of the total copepod population (*Bestiola similis* 19.6%, *Paracalanus aculeatus* 2.6%, *Acartia centrura* plus *A. bowmani* 6.8%, *A. bilobata* 11.7%, *A. spinicauda* 2.4%, *A. plumosa* 14.2%, *Acartiella keralensis* 28.3%, *A. gravelyi* 4.1%, *Labidocera pectinata* 2.6%). HEINLE (1972) states a similar situation in the Chesapeake Bay where of the 73 species of copepods listed, only about 5 are abundant. Such dominance by a few species, although to a limited extent, also occurs in coastal and oceanic waters (MADHUPRATAP & HARIDAS 1986).

As mentioned earlier, copepods consisting mostly of herbivorous and omnivorous species, is the most abundant group. Nonetheless, no single species within copepods is able to maintain continuous dominance at the lower reaches during inter-monsoon period and the percentage of dominance achieved is also usually low (Fig. 7). Different species of the family Acartiidae are often dominant forms. However, this does not reflect any congeneric replacement and in fact they co-occur with other high saline species (of Acartiidae and other families) which also occur in fairly large numbers.

Most of the high saline species are opportunistic showing rapid population increase utilizing their adaptability to the variations occurring in the environment. While this is also true of the medium saline species, a few low saline species occurring in the monsoon period are present only in very low densities, thus leaving the estuaries virtually unexploited at secondary level during this time span. Primary production remains more or less stable throughout the year and the fluctuations in the production rate hardly exceed 3-4 times between seasons compared to 50 or more times between summer and winter in the higher latitudes (QASIM et al. 1969). The annual changes are recurrent and hence a fauna adapted to thrive in low salinities could be expected to have evolved under such predictable sequences. It may be that limnetic zooplankton are unable to withstand strong currents and turbidity experienced during rainy season.

The predatory zooplankton component mainly consisting of chaetognaths, hydromedusae and ctenophores, common during saline period, exert a certain amount of ecological dominance. Some observations (MADHUPRATAP unpubl.) in the Cochin backwaters showed that population of copepods could be drastically reduced when there is a teeming abundance of hydromedusae and ctenophores. Copepod densities were 1 and 38 indiv  $m^{-3}$  at two stations where the abundance of the predators were 195 and 203 indiv  $m^{-3}$  respectively whereas at a nearby station copepod density was 3,760 where the medusae/ctenophore population was only 4 indiv  $m^{-3}$ . The scyphozoan *Achrometes* sp. which occur in summer is a probable predator of hydromedusae and ctenophores. Analogous situation occurs in the Chesapeake Bay where a ctenophore controls the copepod population and a scyphozoan and another ctenophore control the population of the ctenophore (MILLER 1983). Ctenophore predation on other zooplankton has also been reported from the Narragansett Bay (DEASON & SMAYDA 1982)..

Species diversity in estuarine zooplankton is generally low. There is usually a progressive gradient in zooplankton diversity from estuaries and lagoons to nearshore and coastal environments, and oceanic regions maintain still higher diversity and evenness (Table 1). Out of about 87 holoplanktonic species recorded from the Cochin backwaters (Hydromedusae 19, Siphonophora 2, Chaetognatha 4, Copepoda 56, Cladocera 2, Sergestidae 2) only about 20 are true brackish water inhabitants (11 species of gammarid amphipods recorded from the estuary (NAIR et al. 1983) are essentially benthic and sporadically occur in the water column). Others are mostly coastal forms and a few are low saline forms. However, as typical of tropics, the number of estuarine species is higher compared to that of higher latitudes (cf. GRINDLEY 1981, MILLER 1983). Naturally, higher diversity occurs near the mouth and lower reaches because of the presence of neritic forms. The number of species in the environment shows a close relation to salinity (Fig. 8). An increase in diversity at very low salinities as observed in some

TABLE 1. RANGES OF ZOOPLANKTON DIVERSITY INDICES, AVERAGES IN PARENTHESIS (MODIFIED FROM MADHUPRATAP 1983).

Area	$D^*$	$E^{**}$	Source
<i>Estuaries and Lagoons</i>			
Cochin Backwaters	1.9-5.5(3.7)	0.11-0.59(0.32)	MADHUPRATAP 1983
Beypore Estuary	1.4-5.2(2.8)	0.22-0.47(0.34)	HARIDAS 1982
Lagoons (Laccadives)	2.0-3.7(2.9)		MADHUPRATAP et al. 1977c
<i>Nearshore Waters</i>			
Off southwest coast of India	3.1-7.7(5.9)	0.03-0.57(0.24)	HARIDAS et al. 1980
Inland Sea of Japan	0.9-2.4(1.4)	0.05-0.53(0.28)	MADHUPRATAP & ONBÉ 1986
<i>Distant Neritic and Open Ocean</i>			
Laccadive Sea	4.8-4.9		MADHUPRATAP et al. 1977c
Western Indian Ocean	6.4-8.6(7.3)	0.26-0.48(0.39)	MADHUPRATAP 1983
Andaman Sea	3.1-8.1(5.7)	0.25-0.72(0.50)	MADHUPRATAP et al. 1981b
Western Bay of Bengal	8.2-12.9(9.9)	0.17-0.82(0.48)	NAIR et al. 1981

\* Species richness index (MARGALEF 1968)

\*\* Equitability index (HIEP 1974)

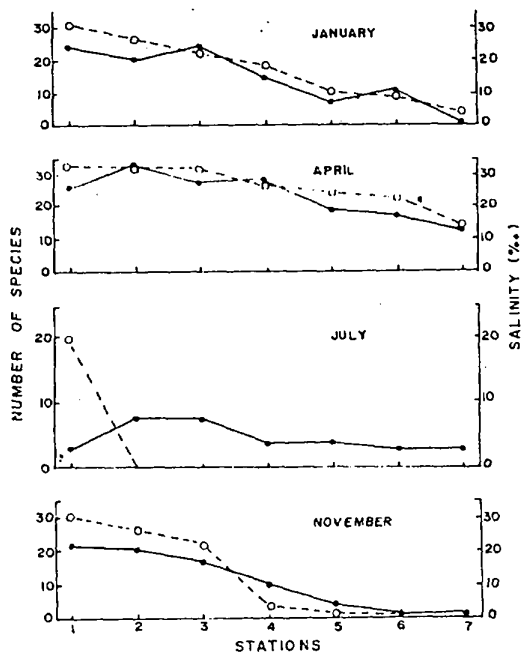


Fig. 8. Number of species of copepods that occurred from mouth to head of the estuary during representative months (solid line) and salinity (dotted line) (Data from MADHUPRATAP 1976).

of the South African estuaries does not happen.

Rigors of the environment certainly conduce to the paucity of a diverse estuarine fauna. Thus, among the several arguments advanced to explain low species diversities encountered in nature (see MACARTHUR 1955, RICKLEFS 1973), the more cogent reasoning with respect to the tropical estuaries pertains to the lack of stability. Only the inter-monsoon period allows some time for diversification, and even during this period, the environment is influenced by limited residence time, tidal flushings and turbulence and salinity gradient. Other hypotheses involving spatial heterogeneity, competition, predation, productivity, etc. do not appear to be compelling factors to affect the diversity. It should however be mentioned that the number of species in Pseudodiaptomidae and Acartiidae inhabiting estuarine and coastal waters is remarkably high. Ten species belonging to Pseudodiaptomidae (species in Fig. 6 plus *Pseudodiaptomus compactus*, *P. bowmani*, *P. sewelli*, WALTER 1984, 1986) and 10 species of Acartiidae (species in Fig. 6 plus *Acartia erythraea*) occur in the Cochin backwaters, perhaps the highest on record from a single locality (PILLAI 1971 recorded *Pseudodiaptomus ardjuna* and *Acartia chilkaensis* also from this estuary, but they appear to be misidentifications).

Logics leading to the evolution of such a high number of congeners in an *apparently*

unstable environment are difficult to postulate. It certainly reflects the adaptability of the species of these two families to the estuarine environment. On the other hand, it also perhaps indicates the diversity of the niches in the environment and adaptive radiation within these families and that factors other than stability are operative. A large number of coastal and brackish water species belonging to these two families have evolved in the Indo-Malayan region which appears to have been a primary speciation centre. The contention of VAN DER SPOEL & PIERROT-BULTS (1979) that this may not be the case for holoplankton appears to be more applicable to oceanic forms. Nonetheless, careful considerations of the zoogeographic and phylogenetic relationships of species, in a historical perspective, are necessary in order to conclude on the nature of processes leading to speciation in these families in different areas. Out of thirty four estuarine species of Pseudodiaptomidae and Acartiidae occurring in the northern Indian Ocean, twenty four are endemic, seven are Indo-Pacific and only three species, viz. *Pseudodiaptomus serricaudatus*, *Acartia centrura* and *Acartia pacifica*, are circumglobally distributed (MADHUPRATAP & HARIDAS 1986, excluding *A. plumosa*, vide supra). Monotypy of these circumglobal species, however, requires confirmation. Among the pseudodiaptomids,

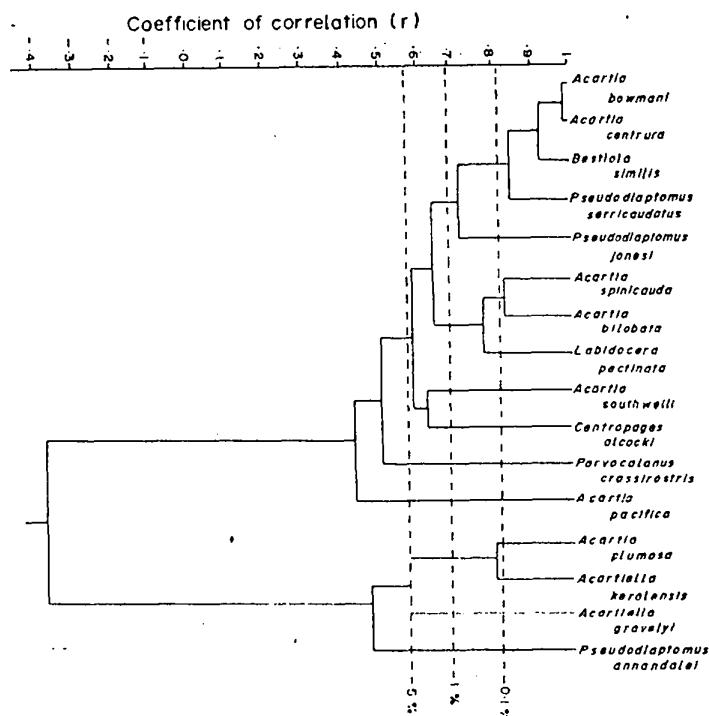


Fig. 9. Dendrogram showing the correlation among the common copepod species at the mouth of the Cochin backwaters and the level of significance of associations (dotted line) (Modified from MADHUPRATAP 1980).

the occurrence of *Archidiaptomus aroorus*, possessing both diaptomid and pseudodiaptomid characters, in low saline waters, is of particular interest in the evolution of this family (MADHUPRATAP & HARIDAS 1978).

The low saline and medium saline species are spatially and temporally separated from the high saline species. However, within the high saline species, they show considerable overlap in their co-occurrences (Fig. 9) indicating coexistence. This coexistence is not restricted to the mouth of the estuary alone, but over the entire space of the backwaters as well as over time (MADHUPRATAP 1980). A similar trend was discernible in other estuaries along the southwest coast (HARIDAS 1982). This leads to the possibility of considerable niche overlap or competition between them, especially among the congeneric species. Morphology of mouthparts of high saline species of Acartiidae occurring in the Cochin backwaters shows little variations to establish ecological differentiation or niche separation among them (TRANter & ABRAHAM 1971). There is not much size difference between the co-occurring estuarine copepods especially within the congeners. Analysis of gut contents also led to the conclusion that they exist as competitors. Some experimental evidence (POULET 1978) indicates that several coexisting species of copepods feed on the same size range of particles. FLEMINGER's (1975) conclusion that there is little or no evidence that body size and feeding appendage morphology may partition food resources among congeneric species of coastal-zone calanoid copepods having similar genetic and geographical heritages whereas a predominance of selection for the development of prezygotic mating barriers appears applicable for these copepod species also.

The high saline estuarine species tend to be more *r*-selected in the theoretical *r*-*K* continuum. The environment is characterized by high productivity, low stability and low species diversity and the inhabitant species appear to be opportunistic, exhibiting rapid increase of populations and catastrophic mortality rates. Under these circumstances, competition among species might appear to be a paradox.

The absolute validity of competitive exclusion theory, however, is under growing criticism (see SIMBERLOFF 1982 for review). Absolute niche separation/trophic specialization is not usually attained even in more stable communities (see SALE 1977, HULBURT 1977, HAYWARD 1980). Concept of a guild where a group of species avail themselves of a resource spectrum in a similar fashion (ROOT 1967) is gaining momentum. In view of the abundant food supply and rapid population increases, competition for food may not be as vital as competition for space. In these tropical estuaries an additional survival mechanism is possible—the species are able to disseminate towards the interior regions along with salinity incursion. More adapted species can exploit the situation better by being able to escape from severe competition at the lower reaches. The salinity incursion provides them the opportunity to utilize fresh resources and thereby expand their niches spatially. The periodic monsoon relieves them of the necessity to compete or coexist for long, until a situation where resources would be depleted.

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