

Species Associations of Calanoid Copepods in an Estuary

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Spatial and temporal changes in the species associations and species diversity of calanoid copepods in the estuary from Cochin to Alleppey are discussed. Mean diversity levels indicate higher α values at the mouth region of the estuary and during the high saline, relatively more stable premonsoon period. The index shows that the estuary is poorly inhabited during the low saline period and thus has a low efficiency in the utilization of the biotope. Complete co-existence is exhibited by some species while some are negatively correlated or correlated only either over space or time.

TROPICAL estuaries are subjected to wide fluctuations in environmental conditions, and so the biocoenosis appears to be largely controlled by physical factors. Calanoid copepods constitute a major component of the zooplankton numerically and also they account for a good part of the zooplankton biomass. Sequences of fluctuations in their abundance and ecological succession in the Cochin backwaters have been found to be closely associated with changes in salinity 1-3. Coexistence of some species of Acartidae in the backwater has been studied by Tranter and Abraham⁴, and diversity by Pillai et al.⁵. Spatial and temporal changes in the associations of copepod species and their diversity in the estuary are discussed in this paper.

Materials and Methods

Numerical abundance of calanoid copepod species in each sample taken in every month during 1972, from Cochin to Alleppey^{2,6}, was converted to numbers per 100 m³ of water filtered. Diversity index (α) was calculated using the formula of Fisher et al.⁷.

$S = \alpha \log_e (1 + N/\alpha)$, where S is the number of species present in a sample and N the number of individuals of all species taken together in a sample. For those samples, where the number of species present was one, diversity figures were not calculated. Variance of diversity index was calculated for comparison using the equation

$$V = \frac{\alpha^3 \left\{ (N + \alpha)^2 \log_e \frac{2N + \alpha}{N + \alpha} - \alpha N \right\}}{(SN + S\alpha - N\alpha)^2}$$

Coexistence of species within each family was studied by constructing correlation matrices.

Results

Total abundance of copepods did not show correlation with change in temperature. But it was significantly correlated with that of salinity except at station 1 (Table 1) where salinity exhibited considerable stratification throughout the monsoon⁶.

Variance of α was low (Legend, to Figs. 1 and 2) indicating that the estimated values of diversity are stable. The α values were analysed using the analysis of variance to study variations over months and stations. Significant variations existed between months ($F_{11,66} = 4.39$, $P \leq .001$) and between stations ($F_{6,66} = 12.77$, $P \leq .001$). Mean diversity levels at stations 1 and 2 which were nearer to the mouth of the estuary were higher and these decreased progressively towards the head. Diversity index values calculated, based on the occurrence of species at each station over the whole year, also showed a similar trend (Fig. 1). The α values were higher at the peak salinity months of March and April. They were lowest at the peak of the monsoon in July and gradually increased again showing another peak in December.

At stations near the mouth of the estuary α values exhibited an increase after being lowest during the monsoonal peak in July along with an increase of salinity (Fig. 2A). Number of species increased even though their total numbers were still low. By postmonsoon period their abundance increased and a lack of proportionate increase in number of species resulted in a fall of index values which fell to a level more or less equal to that of the premonsoon period. A similar trend was noticed at stations 2 and 3 also (Fig. 2, B and C).

TABLE --CORRELATION COEFFICIENTS BETWEEN ABUNDANCE AND TEMPERATURE (A) AND ABUNDANCE AND SALINITY (B) AT VARIOUS STATIONS

Station	A	B
1	0.49	0.35
2	0.41	0.66*
3	0.42	0.68*
4	0.25	0.87†
5	0.34	0.62*
6	0.06	0.70*
7	0.19	0.86†

Significant at * 5% level; † 0.1% level

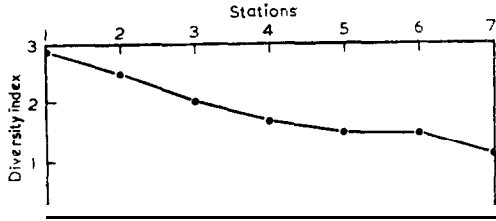


Fig. 1-Species diversity index (cc) over the whole year from mouth to head of the estuary [Range in variance of α , 0.007-0.021]

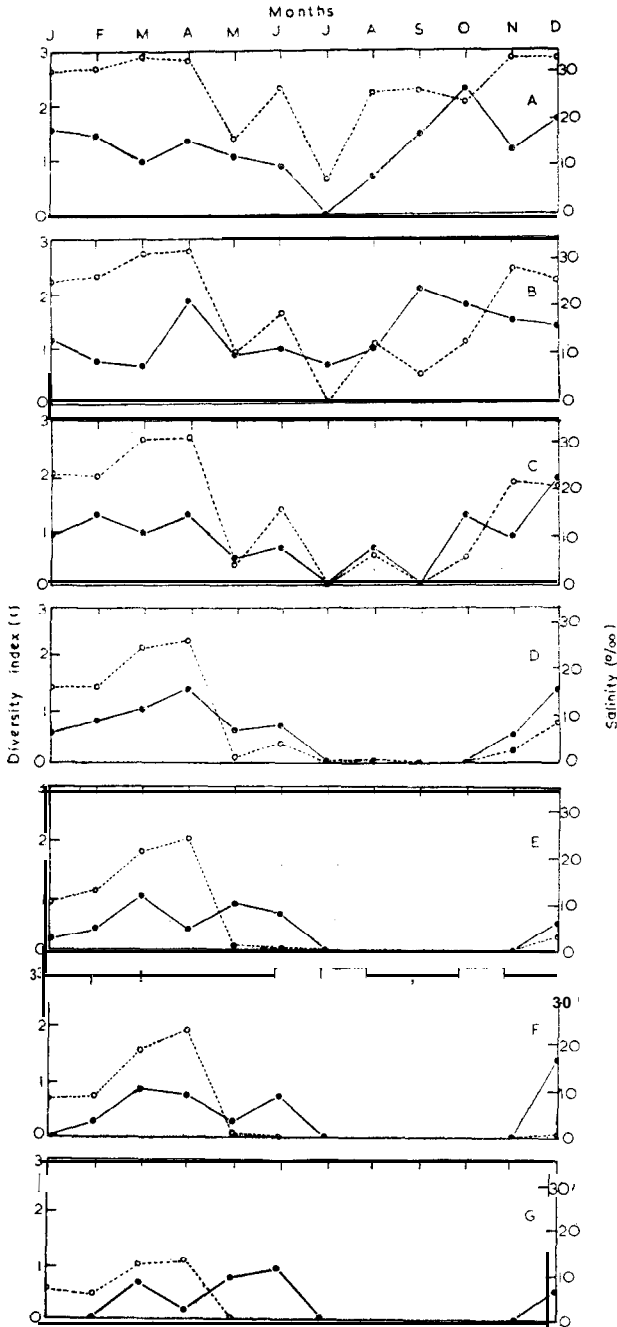


Fig. 2-Species diversity index (α , continuous line) and salinity (broken line) from the mouth to head of the estuary during 1972 [Range of variance of α , station 1 (A) 0.006-0.033; 2 (B) 0.001-0.032; 3 (C) 0.005-0.071; 4 (D) 0.008-0.041; 5 (E) 0.001-0.062; 6 (F) 0.002-0.103; and 7 (G) 0.001-0.005]

Towards the head of the estuary α values were low (Fig. 2, E-G) during late monsoon and early premonsoon (July-November). At the beginning of the monsoon low saline species accounted for the species composition at the upper reaches. As the monsoonal efflux gained momentum, the species diversity at the upper reaches became poor. A small increase observed by December was constituted by species like *Acartia plumosus* and *Acartiella keralensis* in the middle reaches and *Acartiella gravelyi* and Diaptomids at the head. The estuary at the middle and upper reaches is practically uninhabited even by low saline species of copepods at the peak of the monsoon. Apart from salinity or productivity (primary production in the estuary was more or less stable throughout the year*) there must be other reasons probably like high turbidity or strong currents which inhibit the inhabitation.

Analysis for coexistence showed that in Paracalanidae (Table 2) all the 3 species present in the estuary were significantly positively correlated over time. But complete coexistence — “any, appraisal of the completeness of coexistence must encompass both space and time”⁴ — was observed only between *Acrocalanus similis* and *Paracalanus aculeatus* f. *major*. *Centropages trispinosus*, *C. tenui-*

TABLE 2 — CORRELATION MATRIX FOR *Acrocalanus* AND *Paracalanus* SPECIES (PARACALANIDAE) OVER SPACE (MOUTH TO HEAD OF ESTUARY) AND TIME (JANUARY TO DECEMBER 1972)

	<i>similis</i>	<i>aculeatus</i>	<i>crassirostris</i>
SPACE			
<i>A. similis</i>	—	—	—
<i>P. aculeatus</i>	0.99*	—	—
<i>P. crassirostris</i>	0.75	0.68	—
TIME			
<i>A. similis</i>	—	—	—
<i>P. aculeatus</i>	0.96*	—	—
<i>P. crassirostris</i>	0.89*	0.90*	—

Significant at * 0.1% level.

TABLE 3 — CORRELATION MATRIX FOR *Centropages* SPECIES (CENTROPAGIDAE)

	<i>alcocki</i>	<i>trispinosus</i>	<i>tenuiremis</i>	<i>furcatus</i>
SPACE				
<i>alcocki</i>	—	—	—	—
<i>trispinosus</i>	0.78*	—	—	—
<i>tenuiremis</i>	0.98†	0.89†	—	—
<i>furcatus</i>	0.94†	0.83*	0.95‡	—
TIME				
<i>alcocki</i>	—	—	—	—
<i>trispinosus</i>	-0.01	—	—	—
<i>tenuiremis</i>	-0.08	0.72†	—	—
<i>furcatus</i>	0.29	0.59*	0.88‡	—

Significant at *. 5% level; † 1 % level; ‡ 0.1 % level.

remis and *C. furcatus* (Table 3) showed complete coexistence and *C. alcocki* though significantly correlated with other species over space did not correspond over time in family Centropagidae.

The two Diaptomids, *Heliodiaptomus cinctus* and *Allodiaptomus mirabilipes* occurring in the estuary were significantly correlated over time only ($r = 0.7523$, $P \leq 0.01$ over time, $r = 0.2108$, over space). Only two species, *Pseudodiaptomus mertoni* and *P. jonesi*, exhibited complete coexistence in the family Pseudodiaptomidae (Table 4). Many of them showed negative correlations, especially over time.

The species of the family Acartiidae constitute the majority of the copepods of the estuary. Of the 9 species (Table 5) *Acartia centrura*, *A. spinicauda*, *A. erythraea*, *A. bilobata*, *A. pacifica* and *A. southwelli* were positively correlated over space.

But significant correlation did not exist for *A. erythraea* with any other species and also between *A. spinicauda* and *A. southwelli*. *A. plumosa*, *Acartiella keralensis* and *A. gravelyi* were negatively correlated with most of the other species, though the latter 2 showed correlation between themselves. Over time all species except *Acartiella gravelyi* were positively correlated.

An assessment based on significant positive inter-correlation showed 2 groups : *Acartia centrura*-*Acartia spinicauda*-*Acartia pacifica* and *Acartia bilobata*-*Acartia southwelli* exhibiting complete coexistence over both space and time. Within these 2 groups *Acartia centrura* could be recognized to be coexisting with *Acartia bilobata*. *Acartia erythraea* which is a euryhaline marine species was not significantly correlated with any other species both over space

TABLE 4 -CORRELATION MATRIX FOR *Pseudodiaptomus* SPECIES (PSEUDODIAPATOMIDAE)

	<i>serricaudatus</i>	<i>annandalei</i>	<i>aurivillii</i>	<i>mertoni</i>	<i>binghami</i> malayalus	<i>tollingarae</i>	<i>jonesi</i>
SPACE							
<i>serricaudatus</i>							
<i>annandalei</i>	0.72						
<i>aurivillii</i>	0.10	0.45					
<i>mertoni</i>	0.59	0.62	0.13				
<i>binghami</i> malayalus	0.31	0.07	-0.16	-0.11			
<i>tollingarae</i>	0.35	-0.51	0.77*	0.55	-0.38		
<i>jonesi</i>	0.59	0.61	0.09	0.99:	-0.09	0.51	—

TIME

<i>serricaudatus</i>							
<i>annandalei</i>	-0.01						
<i>aurivillii</i>	-0.30	0.35					
<i>mertoni</i>	-0.01	0.46	0.88‡				
<i>binghami</i> malayalus	-0.06	-0.15	-0.23	-0.22			
<i>tollingarae</i>	-0.34	-0.46	-0.14	-0.13	-0.15		
<i>jonesi</i>	0.49	0.28	0.24	0.71 †	-0.18	-0.11	—

Significant at * 5% level; † 1% level; ‡ 0.1% level.

TABLE 5 -CORRELATION MATRIX FOR *Acartia* AND *Acartiella* SPECIES (ACARTIIDAE)

	<i>centrura</i>	<i>spinicauda</i>	<i>erythraea</i>	<i>bilobata</i>	<i>pacifica</i>	<i>southwelli</i>	<i>plumosa</i>	<i>keralensis</i>	<i>gravelyi</i>
SPACE									
<i>A. centrura</i>									
<i>A. spinicauda</i>	0.92*								
<i>A. erythraea</i>	0.74	0.53							
<i>A. bilobata</i>	0.95‡	0.95 †	0.52						
<i>A. pacifica</i>	0.97‡	0.95‡	0.59	0.96‡					
<i>A. southwelli</i>	0.85*	0.69	0.54	0.77*	0.87*				
<i>A. plumosa</i>	0.37	-0.32	-0.29	-0.37	-0.38	-0.46			
<i>Ac. keralensis</i>	0.48	-0.33	-0.90†	0.08	-0.31	-0.25	0.11		
<i>Ac. gravelyi</i>	-0.13	0.07	-0.72	0.14	0.01	-0.07	0.02	0.85*	—

TIME

<i>A. centrura</i>									
<i>A. spinicauda</i>	0.84‡								
<i>A. erythraea</i>	0.41	0.47							
<i>A. bilobata</i>	0.73‡	0.56	0.23						
<i>A. pacifica</i>	0.65*	0.87‡	0.47	0.29					
<i>A. southwelli</i>	0.56	0.55	0.38	0.73 †	0.45				
<i>A. plumosa</i>	0.77‡	0.69*	0.13	0.83‡	0.47	0.46			
<i>Ac. keralensis</i>	0.60*	0.41	0.14	0.94‡	0.11	0.64*	0.83‡		
<i>Ac. gravelyi</i>	-0.38	-0.24	-0.07	-0.71*	-0.06	-0.72‡	-0.30	-0.59*	—

Significant at * 5% level; † 1% level; ‡ 0.1% level.

or time. *Acartiella graveleyi*, the monsoonal species stood separate showing negative correlations with other species. A certain extent of coexistence can be recognized between *Acartia plumosa* and *Acartiella keralensis* the correlation though positive, was not significant over space.

Discussion

Assessment of the nature and causes of associations between species is hazardous in a complex system like an estuary. The number of species in an environment depends on the structure of the habitat⁹. Constant mixing of the fresh water and the sea water as a result of land runoff and tidal currents and the consequent, often unpredictable, changes in the hydrography renders the estuary far from being stable. Cold, dark, energy poor, but constant and predictable abyssal ocean floor is species rich while warm, energy-rich tropical estuaries with sporadic land runoff are species poor¹⁰.

At the peak of the monsoon the entire estuary is poorly inhabited. The species are limited by the environment, the severe changes in salinity acting as a physiological barrage in their survival.

When the force of the monsoonal efflux diminished, salinity began to recover at the mouth. This allowed the occupation of the niche by brackish and euryhaline marine species. This increase in diversity early in the succession is an approach to Set up equilibrium condition+. This increase will lead to habitat selections, at first within habitat and later between habitats⁹. But the occupation of the new niches by these species up the estuary and thus their dispersal is controlled by the extent and rate of salinity recovery.

After the monsoons the upper reaches of the estuary remain virtually unexploited, only a few species like *Acartia plumosa* and *Acartiella keralensis* were present here during early premonsoon period. As salinity recovered other species like *Acartia centrorura*, *A. spinicauda*, *A. bilobata*, *A. pacifica*, *A. southwelli*, *Acrocalanus similis*, *Paracalanus aculeatus* and *Labidocera pectinata* began to invade this area resulting in an increase in diversity. Short term stability depresses diversity and the mechanism for increasing diversity is the sudden access of unexploited resources¹². The relative stabler environment in the estuary is the period prior to the onset of the monsoons.

In Centropagidae, *Centropages alcoki* which did not show complete coexistence with the other species of the family appears to be the only one among them which is able to adapt to the estuarine conditions and breed in it since copepodites of only this species was present in the collections.

Coexistence pattern exhibited by the species of the family Acartiidae is more or less similar to the findings of Tranter and Abraham⁴. Ecological differentiation of the closely coexisting species

based on the mandibular structure is not lucid⁴. Morphological similarity may be deceptive for a total assessment. The degree of ecological differentiation required to permit coexistence is not clear¹³. On the other hand, are they competitors as their morphology would suggest managing to exist successfully because food is plenty? The final survival of the better adapted or the extinction of the other ("subtle differences can collectively culminate to make one species perform better than its competitor in a particular situation"¹⁴) is non-existent as the monsoon automatically averts it by flushing all of them out.

Barring the 'alternate pathways' that may exist, the efficiency of the system in the utilization of the biotope at secondary level appears to be low during the low saline period especially at the upper reaches, considering the low abundance of zooplankton during this season. Although this area remains freshwater for a considerable period of the year, surprisingly, only one species, *Acartiella graveleyi*, was dominant in the habitat. Other low saline species like *Heliodiaptomus cinctus*, *Allodiaptomus mirabilipes*, *Pseudodiaptomus binghami malayalus* and *P. tollingeriae* were of low abundance². Whether this is an adaptation against predation⁹ or a lack of adaptability to the environment is not known. Future studies on these species at the upper reaches of the estuary which will now be transformed into a completely fresh water lake by the Thanneermukkam barrier should be revealing.

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