

Coexistence of species of Acartiidae (Copepoda) in the Cochin Backwater, a monsoonal estuarine lagoon

D. J. TRANTER and S. ABRAHAM

Indian Ocean Biological Centre; Cochin, Kerala, India

Abstract

A study was made of copepods of the family Acartiidae which form the dominant component of the plankton in the Cochin Backwater (Kerala, India). At least nine species inhabit the backwater at one time or another, more than have been recorded for any other area. Reasons were sought for this diversity. The surface plankton was sampled from the head of the estuary to the mouth and from one season to another. There were large seasonal changes in salinity (0 to 35‰), due to monsoonal flooding, and associated changes in species composition. Species diversity was highest during the dry season and lowest in the wet. It is suggested that this annual catastrophic flooding leads, in the long run, to high

species diversity by imposing a regular check on interspecific competition.

Introduction

Habitats shared by closely related species are of considerable interest. "Their continued existence is a thing to wonder at and to study. . . every instance of apparent coexistence must be accounted for". (HARDIN, 1960). The Acartiidae of the Cochin Backwater constitute such a system. We have sought to

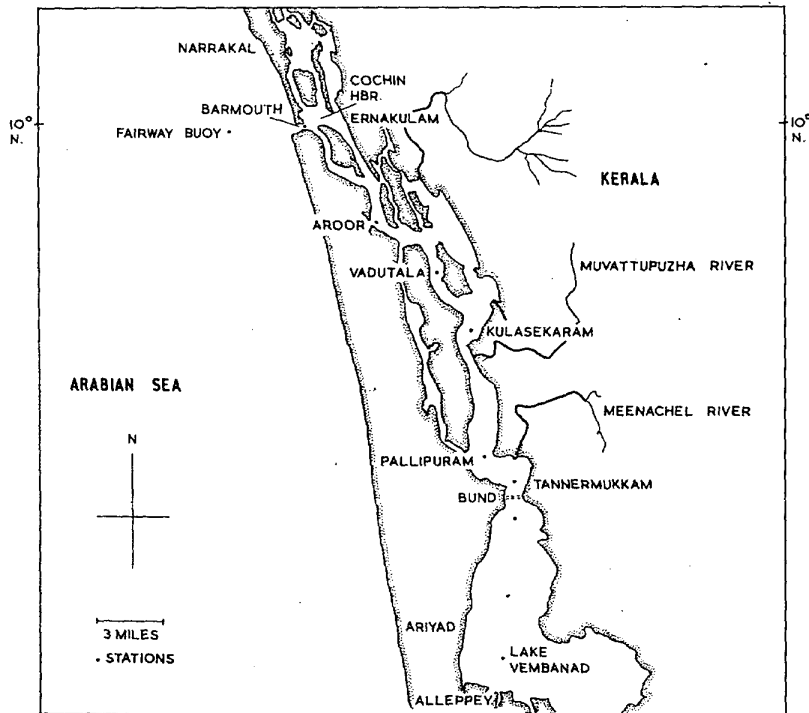


Fig. 1. Cochin Backwater and adjacent areas, showing positions of stations where collections were made

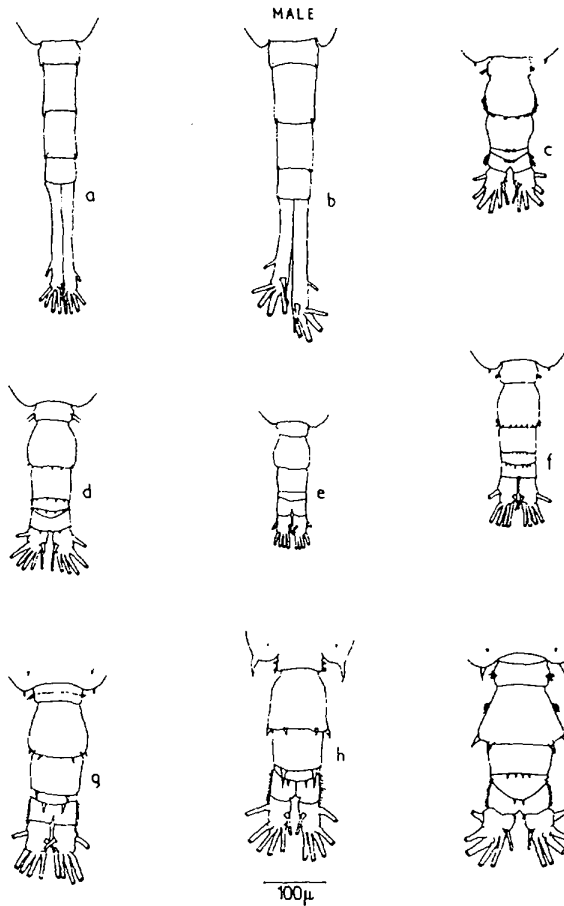


Fig. 2 A

Fig. 2. Acartiidae species from Cochin area which form basis of present study. (Fig. A) male; (Fig. B, p. 224) female. Abdominal structure of (a) *Acartiella gravelyi*; (b) *A. keralensis*; (c) *Acartia negligens*; (d) *A. bilobata*; (e) *A. southwelli*; (f) *A. plumosa*; (g) *A. centrura*; (h) *A. spinicauda*, (i) *A. erythraea*

discover and to describe some of the ways in which this habitat is shared.

The Cochin Backwater (Fig. 1) is a network of shallow, anastomosing waterways, parallel to the coast, forming a basin into which several large monsoonal rivers empty (QASIM and REDDY, 1967). Like most monsoonal estuaries, the backwater is saline during the dry season and fresh in the wet (monsoonal) season, except for a dense saline layer near the bottom (RAMAMIRTHAM and JAYARAMAN, 1963). At the height of the monsoon, a large volume of fresh water discharges through the bar-mouth into the sea, lowering salinities near the shore (DARBYSHIRE, 1967). The 1968 rainfall was 377 cm, with a maximum (130 mm) in July.

Nutrients are high during the monsoon season, due both to runoff from the land and to intrusion of cool, saline, upwelled water from the continental shelf (SANKARANARAYANAN and QASIM, 1969). Plankton production is limited not by nutrients, however, but by light, the waters being very turbid, especially during the monsoon; most of the plankton production takes place within a shallow surface stratum.

Seasonal changes in the plankton of the backwater have been described by GEORGE (1958), NAIR and TRANTER (1969), RAVINDRANATHA MENON et al. (1969) and VANNUCCI et al. (1970). The plankton is dominated by copepods which become very abundant at times (Table 1) equalling the highest densities recorded anywhere in the World Ocean (TRANTER, in

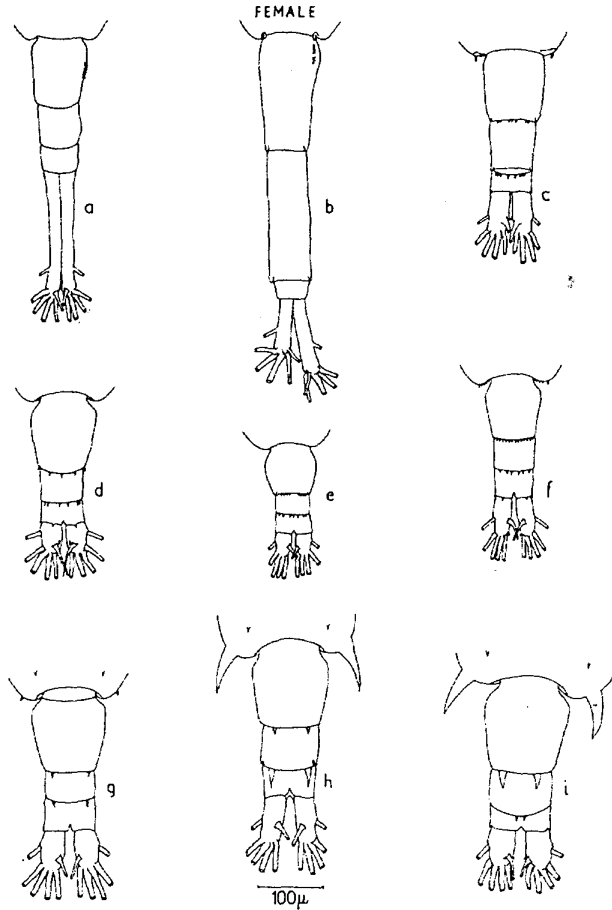


Fig. 2 B

press). These copepods are predominantly species of the families Acartiidae and Pseudodiaptomidae, the latter being more prevalent by night than by day.

ABRAHAM (1969) recorded 11 species of Acartiidae from the Cochin Backwater. Nine are relatively common and form the basis of the present study. They are as follows: *Acartiella keralensis* WELLERSHAUS, *A. gravelyi* SEWELL, *Acartia negligens* DANA, *A. bilobata* ABRAHAM, *A. southwelli* SEWELL, *A. plumosa* TH. SCOTT, *A. centrura* GIESBRECHT, *A. spinicauda* GIESBRECHT, and *A. erythraea* GIESBRECHT (Fig. 2). Six of these were previously recorded by WELLERSHAUS (1968). STEUER (1923) divided the family Acartiidae into 8 sub-genera, of which 5 are represented here, viz.: *Acartiella* (*keralensis* and *gravelyi*), *Euacartia* (*southwelli*), *Acanthacartia* (*plumosa*), *Odontacartia* (*centrura*, *spinicauda*, *erythraea*), and *Planctacartia* (*negligens*). These groupings have yet to be widely recognized.

Species of *Acartia* are among the few planktonic organisms cultivated successfully in the laboratory (ZILLIOUX, 1969; CORKETT, 1970; HEINLE, 1970; NASSOGNE, 1970), and the frontiers of knowledge about this group are rapidly expanding.

The estuarine habitat is considered to be ecologically severe and, as a result, species diversity is usually low (HEDGPETH, 1957). However, copepods of the family Acartiidae must be well adapted to the stresses of the estuarine environment — they are found in estuaries throughout the world. The communities which have been studied until now consist of not more than 3 or 4 species. On the northeast coast of the United States, the common species are *Acartia tonsa* and *A. clausi* (DEEVEY, 1948; CONOVER, 1956; JEFFRIES, 1962, 1967); on the south coast of Britain, *A. clausi*, *A. discaudata* and *A. bifilosa* (CONOVER, 1959); in the Black Sea and Mediterranean Sea, *A.*

clausi and *A. latisetosa* (PETIPA, 1958, 1959, 1966a, b; MATHURABY, 1964).

The Cochin Backwater, characterized as it is by the greatest species diversity of Acartiidae on record, is an area of unique interest. The present investigation is concerned with this diversity, and is the first study of its kind in the area.

Material and method

The material consists of two series of samples, one taken on a seasonal basis, the other on a spatial basis (see Tables 1 and 2). The first series consists of regular samples (usually every 2 weeks) from one station in the backwater (Aroor) and from one beyond the bar-mouth in the sea outside (Fairway Buoy). The

Table 1. *Acartiidae* species. Sampling Series 1: Fortnightly sampling at stations inside and outside Cochin Harbour

Date (1968)	Time (hrs)	Temperature (°C)	Salinity (‰)	Water filtered (m ³)	Copepod density (No/m ³)
Aroor (Inside)					
18 Jan.	13.25	30.5°	27.2	72.0	1,711
1 Feb.	12.13	31.0°	28.9	64.0	—
15 Feb.	11.48	31.4°	29.0	28.2	—
29 Feb.	14.13	32.6°	29.0	76.0	978
14 March	11.25	31.4°	29.0	76.0	4,574
28 March	11.45	31.6°	29.8	70.0	1,498
25 April	11.24	31.8°	32.8	104.0	418
9 May	11.59	31.9°	32.4	80.0	—
23 May	12.03	32.2°	30.0	76.0	558
6 June	11.08	31.2°	27.2	102.0	228
20 June	08.15	29.5°	32.9	82.0	174
4 July	10.32	27.8°	0.6	86.8	186
18 July	12.20	26.2°	0.8	8.2*	417
1 Aug.	10.45	28.4°	0.6	8.2*	166
14 Aug.	11.19	29.8°	0.4	8.2*	93
2 Sept.	15.52	31.0°	5.0	120.8	—
12 Sept.	11.58	28.6°	1.0	49.4	547
26 Sept.	11.14	30.3°	4.6	110.6	23
10 Oct.	11.35	32.6°	3.0	150.0	86
24 Oct.	12.30	32.8°	2.8	80.4	—
22 Nov.	13.06	32.4°	9.7	46.1	746
5 Dec.	12.13	31.8°	29.2	80.7	—
19 Dec.	11.57	30.4°	28.2	85.3	1,169
Fairway Buoy (Outside)					
18 Jan.	11.05	29.0°	31.6	67.0	902
1 Feb.	08.52	29.8°	31.5	60.0	994
15 Feb.	08.29	28.2°	32.3	61.0	148
29 Feb.	08.15	30.8°	32.1	60.0	245
14 March	08.16	30.6°	31.5	86.0	217
28 March	08.37	30.2°	32.0	85.6	—
25 April	08.26	31.8°	32.0	98.0	4,695
9 May	08.45	29.8°	33.0	79.0	—
23 May	09.04	29.9°	32.8	83.0	1,011
6 June	09.08	29.2°	21.5	104.0	459
11 July	09.45	25.4°	18.0	8.2*	1,329
9 Aug.	08.32	29.0°	16.8	220.0	3,514
12 Sept.	09.46	25.7°	13.4	120.7	1,816
26 Sept.	08.59	28.4°	11.6	39.0	6,171
10 Oct.	09.21	30.4°	19.9	103.7	502
24 Oct.	09.32	—	—	64.8	—
22 Nov.	10.32	30.0°	31.3	71.5	—
5 Dec.	10.07	29.8°	31.0	75.7	1,005
19 Dec.	09.49	29.4°	30.0	85.3	1,019

* Clarke-Bumpus sampler. Dashes: no data.

second series consists of samples taken from the headwaters of the estuary to Fairway Buoy, in November (immediately after the 1968 monsoon) and in April (immediately before the 1969 monsoon). All samples in the first series were taken by day, whereas in the second series samples were taken both by day and night. The general nature of the plankton in the

first series is described by RAVINDRANATHA MENON et al. (1969) and that in the second series by NAIR and TRANTER (1969). The hydromedusae from these collections were described by SANTHAKUMARI and VANNUCCI (1969) and VANNUCCI et al. (1970), and the chaetognaths by VIJAYALAKSHMI NAIR (1969). Samples were collected with the "Heron-Tranter net". This is

Table 2. *Acartiidae* species. Sampling Series 2: Head of estuary to Fairway Buoy

Station No.	Position	Time (hrs)	Temperature (°C)	Salinity (%)	Water filtered (m ³)	Copepod density (No/m ³)
Post-monsoon (November, 1968)						
1	Fairway Buoy	10.32	30.0°	31.3	72	253
1A	Fairway Buoy	11.00	—	—	56	—
2	Barmouth	11.45	30.9°	27.2	36	2,972
3	Aroor	13.06	32.4°	9.7	46	1,000
4	Vaduthala	14.05	32.6°	5.5	37	55,390
5	Kulasekharam	15.12	32.6°	0.7	31	295
6	Pallipuram	16.00	32.4°	0.1	37	32
7	Thaneermukkam (N)	16.26	32.0°	0.6	100	5
8	Thaneermukkam (S)	17.02	32.0°	0.4	158	2
9	Aryad (N)	—	—	—	—	—
10	Aryad (S)	18.40	31.0°	0.3	114	122
10	Aryad (S)	21.39	30.7°	0.3	141	82
9	Aryad (N)	—	—	—	—	—
8	Thaneermukkam (S)	22.43	30.8°	0.2	170	30
7	Thaneermukkam (N)	23.28	30.6°	0.4	136	50
6	Pallipuram	00.05	30.4°	0.2	46	144
5	Kulasekharam	01.13	30.8°	0.1	100	491
4	Vaduthala	03.33	30.2°	4.5	88	28,367
3	Aroor	04.27	29.9°	17.5	78	936
2	Barmouth	05.45	29.6°	30.0	43	1,534
1	Fairway Buoy	—	—	—	—	—
Pre-monsoon (April, 1969)						
1	Fairway Buoy	09.32	31.0°	33.4	38	2,370
2	Barmouth	10.40	33.0°	30.7	52	4,683
3	Aroor	11.58	32.8°	33.3	56	4,161
4	Vaduthala	12.51	33.5°	33.1	52	4,740
5	Kulasekharam	13.52	33.3°	31.5	36	1,139
6	Pallipuram	14.39	33.2°	30.2	40	1,181
7	Thaneermukkam (N)	15.12	33.6°	29.7	43	2,640
8	Thaneermukkam (S)	15.29	33.8°	29.7	26	1,096
9	Aryad (N)	16.33	34.1°	27.9	28	208
10	Aryad (S)	17.10	33.9°	25.4	38	478
10	Aryad (S)	20.03	33.8°	25.2	20	6,663
9	Aryad (N)	20.45	33.2°	28.0	30	18
8	Thaneermukkam (S)	22.02	33.0°	30.0	14	3,129
7	Thaneermukkam (N)	22.20	33.0°	30.0	13	2,908
6	Pallipuram	22.48	32.3°	29.6	32	4,063
5	Kulasekharam	23.49	33.2°	32.2	14	7,267
4	Vaduthala	01.19	32.4°	33.7	21	11,635
3	Aroor	02.03	32.3°	33.7	17	8,985
2	Barmouth	03.46	31.8°	34.4	39	12,377
1	Fairway Buoy	—	—	—	—	—

Dashes: — no data.

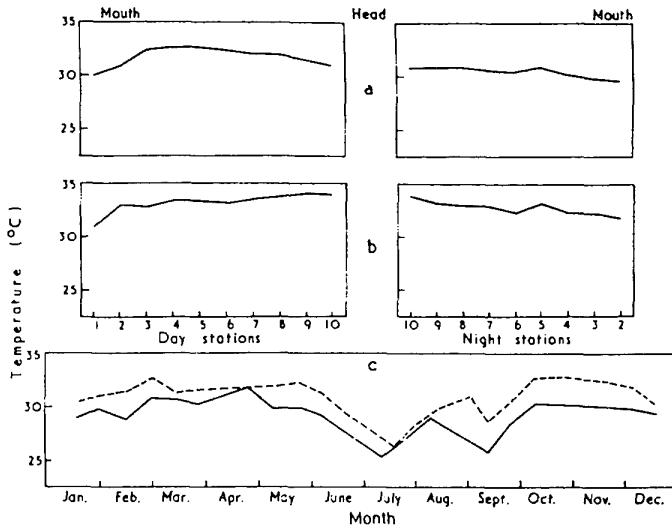


Fig. 3. Temperature regime. (a) From the head of the estuary to a point beyond the bar-mouth (Alleppey-Fairway Buoy), immediately after the monsoonal flood (November, 1968); (b) from Alleppey to Fairway Buoy immediately before the monsoonal flood (April, 1969); (c) seasonal variations at stations immediately inside (Aroor: broken line) and immediately outside (Fairway Buoy: continuous line) the backwater

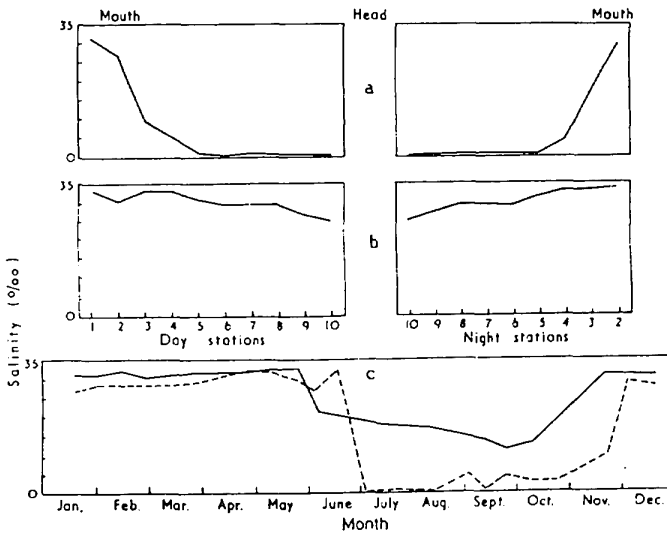


Fig. 4. Salinity regime. (a) Alleppey-Fairway Buoy, postmonsoon (November, 1968); (b) Alleppey-Fairway Buoy, pre-monsoon (April, 1969); (c) seasonal variations at Aroor (broken line) and Fairway Buoy (continuous line), January/December, 1968)

a light, square-mouth net (mouth area $\frac{1}{4}$ m²) with monofilament nylon gauze of mesh width 0.2 mm and open area ratio (TRANTER and SMITH, 1968) of 6. The net is towed from diagonally opposite pivots by a 2-leg bridle, a weight being suspended by a second

bridle from the same pivots. This system allows the net to stream freely, with little obstruction forward of the mouth. The net was towed horizontally, immediately beneath the surface, for a period of usually 5 min or so. No estimate was made of sampling error.

Associated measurements were made of surface temperature and salinity. On several occasions, the Clarke-Bumpus sampler (TRANTER, 1966) was used instead. Samples were fixed and preserved in 4% formaldehyde in sea water, buffered with 1% hexamine. Sub-sampling was made with a broadmouthed volumetric pipette.

Results

The temperature and salinity regimes in the study area are shown in Figs. 3 and 4. Variations in temperature were small (25° to 34°C) compared with

Series 1 (Fig. 5c) counts of adult Acartiidae only were available. The highest densities were found in November in the mixing zone of fresh and saline water towards the mouth of the estuary (Fig. 5a); further upstream, densities were low. By contrast, in April densities were uniformly high throughout the backwater system (Fig. 5b). The Acartiidae constituted the bulk of the copepods present. It is of considerable interest that the density of Acartiidae fell to zero during the monsoon (Fig. 5c). At Aroor, these copepods were absent during July when rains were heaviest; they were absent at Fairway Buoy throughout Sep-

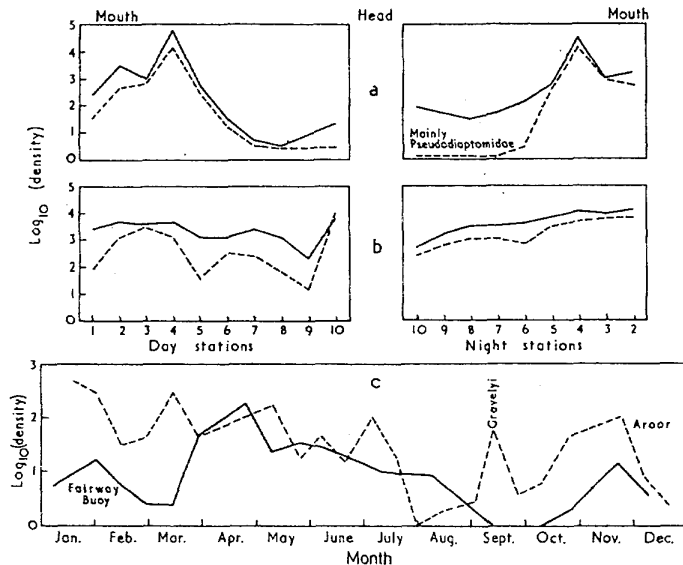


Fig. 5 (a) and (b). Density (No./m³) of total copepods (continuous line) and of Acartiidae (broken line) before and after monsoon (log values). (a) Alleppey-Fairway Buoy, November, 1968; (b) Alleppey-Fairway Buoy, April, 1969; (c) seasonal copepod density variations of adult Acartiidae at Aroor (broken line) and Fairway Buoy (continuous line)

variations in salinity (0 to 35‰). Temperatures were higher (Fig. 3c) and salinities were lower (Fig. 4c) at Aroor than at Fairway Buoy. With the onset of monsoonal rains in June, salinities were suddenly and substantially reduced. The subsequent low-salinity regime lasted until December, by which time the sea had gained dominance over the flood and had begun once again to enter the backwater. By April the sea had penetrated the entire backwater system and filled the large basin of Lake Vembanad (Fig. 1). The high-salinity regime persisted until the end of May, when the first monsoonal deluges began to flood the backwater.

The distribution and abundance of Acartiidae and total copepoda are shown in Fig. 5. For Sampling

tember and October. In November few were present towards the headwaters of the estuary; Pseudodiaptomidae, on the other hand, were relatively common, but only at night (Fig. 5a).

The main features of species distribution and abundance are summarized below:

Acartia bilobata (Fig. 6) appeared in the vicinity of the bar-mouth in November (Fig. 6a) and extended throughout the backwater with the salinity intrusion (Fig. 6b). The species was absent during the monsoon months, appearing and disappearing earlier at Aroor than at Fairway Buoy (Fig. 6c).

Acartia centrura (Fig. 7) penetrated and spread throughout the estuary between January and June with high salinity water from the shelf (Fig. 7b, c).

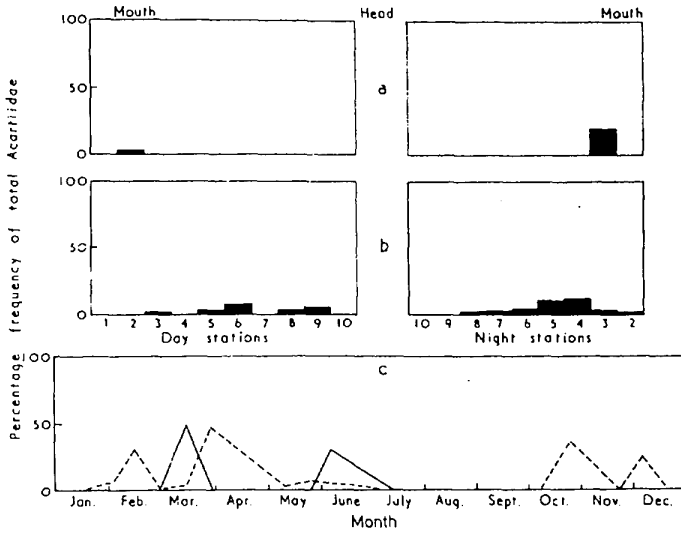


Fig. 6. Distribution of *Acartia bilobata*. (a) Alleppey-Fairway Buoy, November, 1968; (b) Alleppey-Fairway Buoy, April, 1969; (c) Seasonal variation (January/December, 1968) at Arroor (broken line) and Fairway Buoy (continuous line)

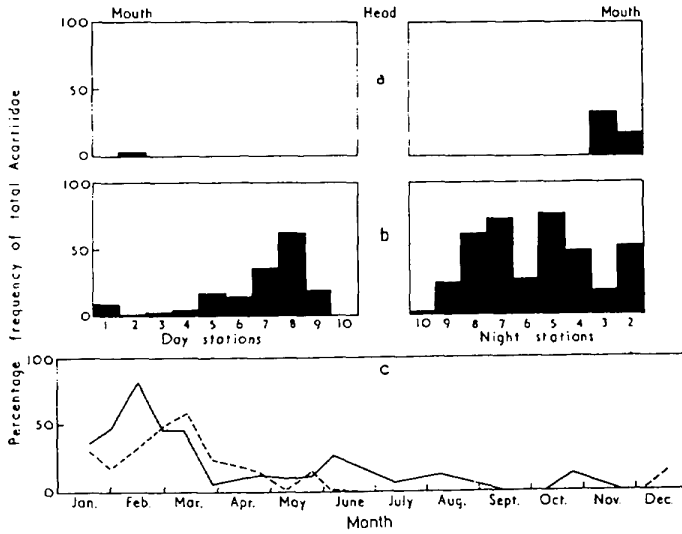


Fig. 7. Distribution of *Acartia centrura*. (a)-(c) as in legend to Fig. 6

During the low salinity regime (Fig. 7a, c), the species occurred only towards the mouth of the estuary.

Acartia erythraea (Fig. 8) was the first species to become established at Fairway Buoy at the end of the low salinity regime; it established dominance there on various occasions between November and May (Fig. 8c). The species penetrated the estuary in large

numbers only during the high salinity months, February/May, but there were curious isolated records well up the estuary in November when salinities were very low (Fig. 8a).

Acartia negligens (Fig. 9) is a well-known oceanic species (Fig. 20) and it is not surprising that it was rarely found within the study area. The species was

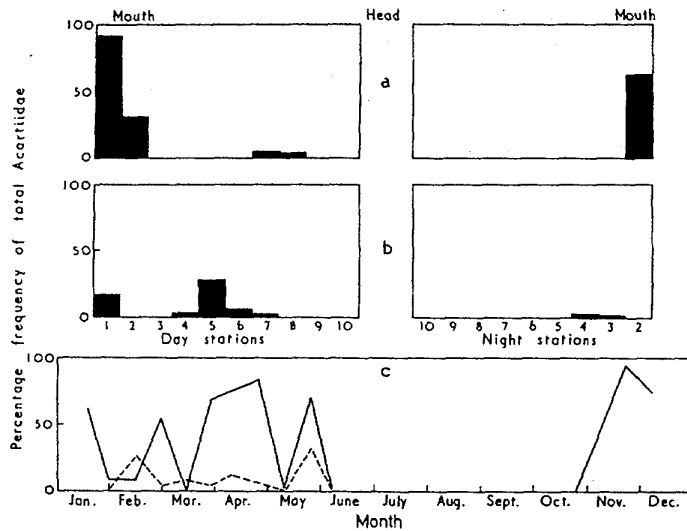


Fig. 8. Distribution of *Acartia erythraea* (a)—(c) as in legend to Fig. 6

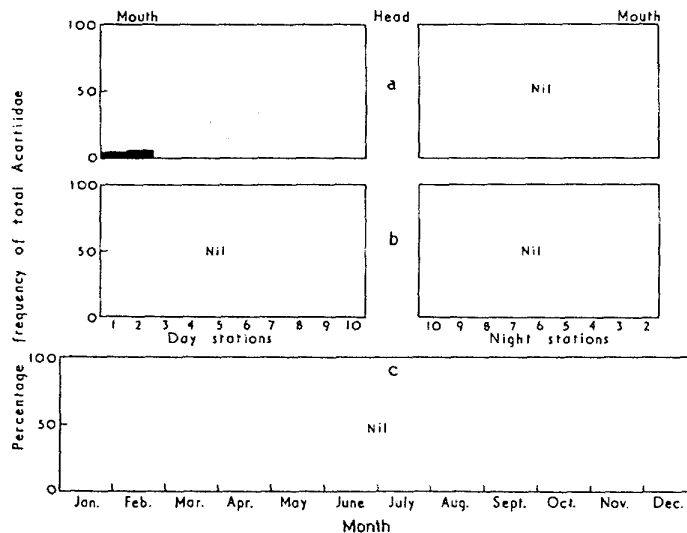


Fig. 9. Distribution of *Acartia negligens* (a)—(c) as in legend to Fig. 6

collected in November only, when Equatorial Surface Water is brought close to the coast (DARBYSHIRE, 1967).

Acartia plumosa (Fig. 10) was dominant throughout the estuary in November, when salinities were low (Fig. 10a), and towards the head of the estuary in April (Fig. 10b). The species was most common at Fairway Buoy, in July, at the height of the monsoon (Fig. 10c).

Acartia southwelli (Fig. 11) appeared near the bar-mouth rather suddenly, just before the monsoon, and by April it was dominant, almost to the exclusion of other species (Fig. 11b, c). The species died out during the low salinity regime, was still absent from the backwater in November, and was rarely found outside at Fairway Buoy (Fig. 11a, c).

Acartia spinicauda (Fig. 12) was widely distributed throughout the backwater in April (Fig. 12b)

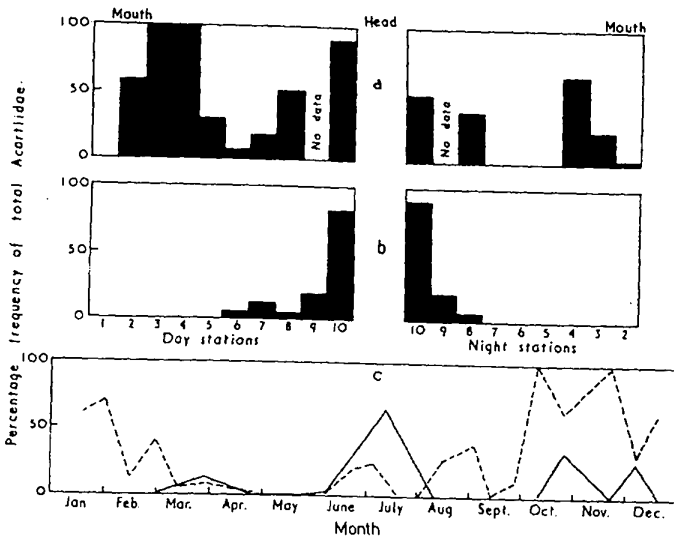


Fig. 10. Distribution of *Acartia plumosa* (a)–(c) as in legend to Fig. 6

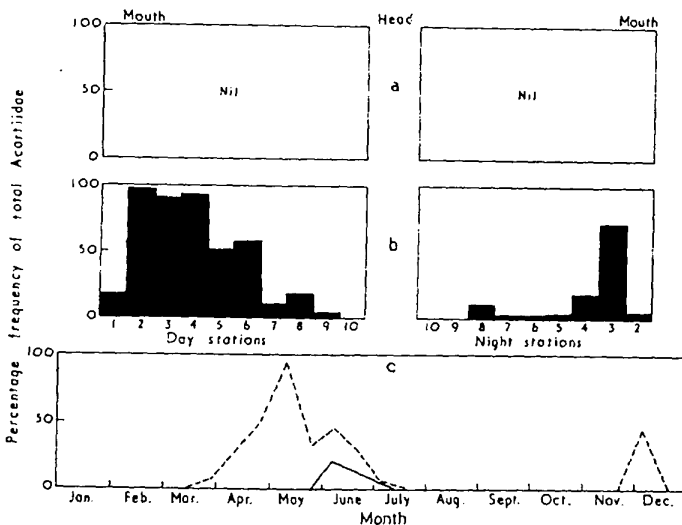


Fig. 11. Distribution of *Acartia southwelli* (a)–(c) as in legend to Fig. 6

and was dominant at Fairway Buoy on several occasions between May and October (Fig. 12c). Occasional specimens were, in November, found well upstream, where the waters were fresh (Fig. 12a).

Acartiella graveleyi (Fig. 13) is a monsoon species, absent from all stations during the high salinity regime (Fig. 13a, b). The species was dominant in the central part of the backwater in November, and absent at

higher salinities near the mouth (Fig. 13a). At Aroor, the species appeared first in July and became the dominant species in August and September (Fig. 13c). Few specimens were taken at Fairway Buoy, even during the monsoon months.

Acartiella keralensis (Fig. 14), like *A. graveleyi*, is a low-salinity species (WELLERSHAUS, 1968). At Aroor, the species became dominant in June and July, a

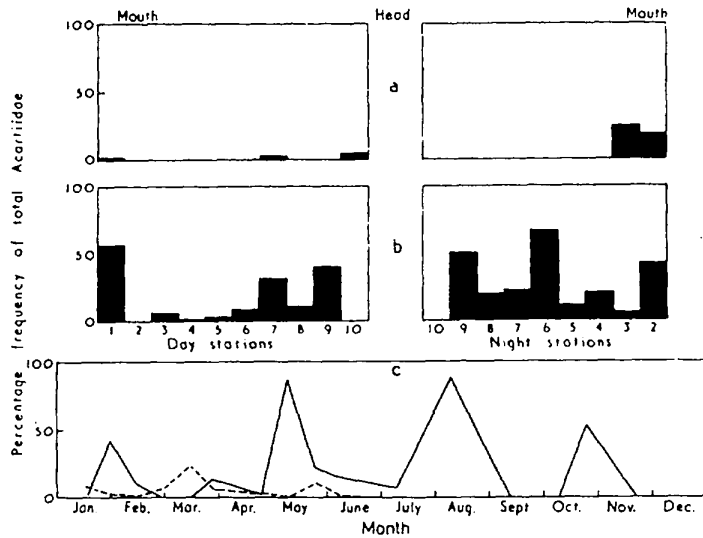


Fig. 12. Distribution of *Acartia spinicauda* (a)–(c) as in legend to Fig. 6

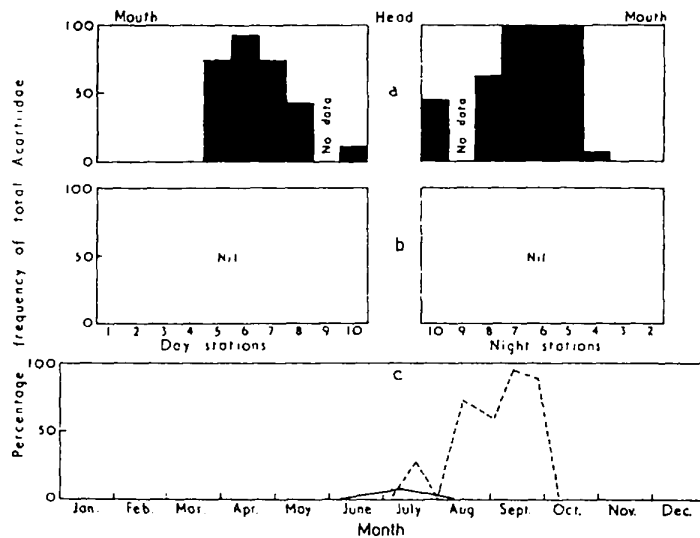


Fig. 13. Distribution of *Acartiella graveleyi* (a)–(c) as in legend to Fig. 6

little earlier than *A. graveleyi*, occasional specimens being found as far down as Fairway Buoy (Fig. 14c). The species was uncommon throughout the estuary both in November and April (Fig. 14a, b).

Fig. 15 shows the species diversity (MACARTHUR, 1965) of Acartiidae at each station, and Fig. 16 the succession of species dominance. Diversity varied with site, season, and time of day. On an average, diversity

was greater during the high salinity regime (January/June) than during the low salinity regime (June/December). *Acartia plumosa*, *A. southwelli*, *Acartiella keralensis*, and *A. graveleyi* were the main species responsible for seasonal reductions in diversity at Aroor (Fig. 16c). At Fairway Buoy, *Acartia erythraea*, *A. centrura* and *A. spinicauda* alternated in dominance (Fig. 16d). In November, diversity was low in the rich

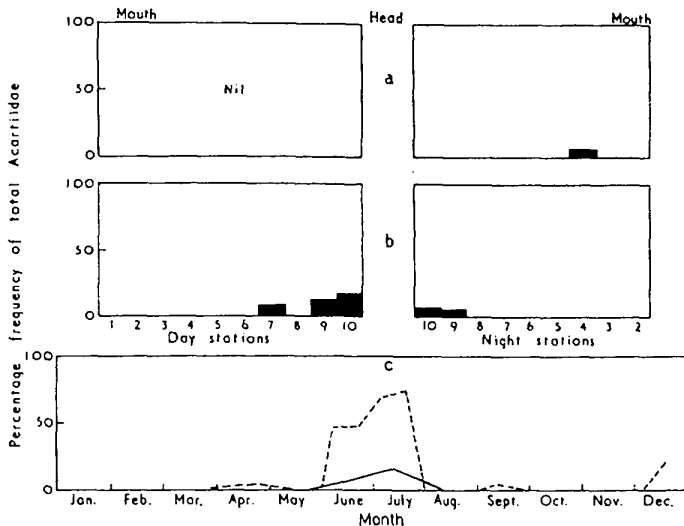


Fig. 14. Distribution of *Acartiella keralensis* (a)—(c) as in legend to Fig. 6

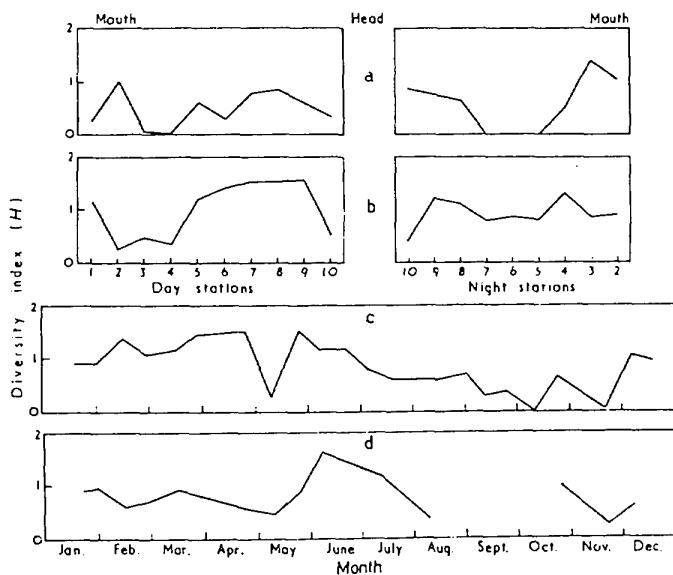


Fig. 15. Species diversity (H), in copepods of family Acartiidae ($H = -\sum_{i=1}^N p_i \log_e p_i$, where p_i is proportion of individuals belonging to i th species). (a) Alleppey-Fairway Buoy, November, 1968; (b) Alleppey-Fairway Buoy, April, 1969; (c) seasonal variation at Aroor, January/December, 1968; (d) seasonal variation at Fairway Buoy, January/December, 1968

copepod-area associated with the mixing zone toward the mouth of the estuary (Figs. 4a, 5a); here, the only species present was *Acartia plumosa* (Figs. 16a, 10), in densities as high as 5,000/m³. Further upstream,

Acartiella gravelyi was dominant, but at lower densities (Figs. 16a, 13). By April, *A. plumosa* had been replaced at the mouth of the estuary by *A. southwelli*, at densities in excess of 3,000/m³ (Figs. 16b, 11), and

had established dominance in the upper reaches, once again at the zone of mixing of fresh and saline water (Figs. 4b, 16b).

In summary, the nine species of Acartiidae in the backwater vary in their relative frequencies from site to site and season to season. Table 3 relates these species to the ecological classification of JEFFRIES (1967).

The Competitive Exclusion Principle states that "complete competitors cannot coexist" (HARDIN, 1960). Since our results show that at least eight related

estuary in only two seasons (Table 2) and throughout the year at only two stations (Table 1).

The coexistence between each pair of species, in space and time, is shown in Table 4 in the form of correlation matrices. Raw data were transformed to logs (base 10) before computation. Many correlations were significant. Most (15) were positive, indicating widespread coexistence. The greater number of significant negative correlations involved the species *Acartiella gravelyi*, which occurred during the monsoon months, usually alone.

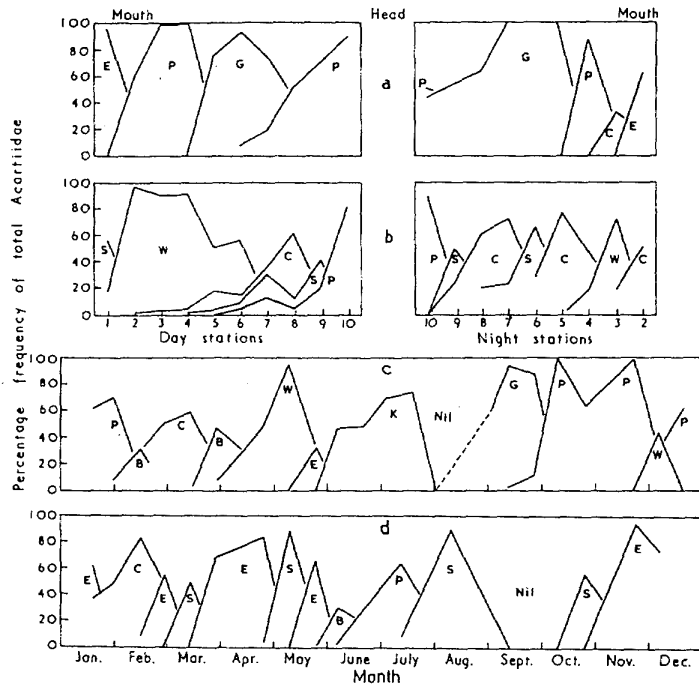


Fig. 16. Species succession of dominants (Acartiidae). (a) Alleppey-Fairway Buoy, November, 1968; (b) Alleppey-Fairway Buoy, April, 1969; (c) seasonal variation at Aroor, January/December, 1968; (d) seasonal variation at Fairway Buoy, January/December, 1968. B: *Acartia bilobata*; C: *A. centrura*; E: *A. erythraea*; G: *Acartiella gravelyi*; K: *A. keralensis*; N: *Acartia negligens*; P: *A. plumosa*; S: *A. spinicauda*; W: *A. southwelli*

species share the same habitat, it is of interest to determine in what ways they do not coexist or compete. We have directed correlation analysis toward the former question and a study of structural adaptations for gathering and handling food towards the latter question.

For a complete evaluation of coexistence, the entire estuary would need to be sampled at all depths throughout the year. Our evaluation is incomplete. In the first place we have explored only the surface layers. In the second place we have sampled throughout the

Any appraisal of the "completeness" of coexistence must encompass both space and time. Fig. 17 is a diagrammatic representation of the significant species correlations from the matrices of Table 4. The figure shows that matrix a (space) can be resolved into 4 species groups: *Acartia gravelyi* alone; *Acartia erythraea-Acartia negligens*; *Acartiella keralensis-Acartia plumosa*; *Acartia centrura-Acartia spinicauda-Acartia southwelli-Acartia bilobata*.

Matrix b (time) on the other hand is different. Here, only *gravelyi* is distinct, negatively correlated

with most species and positively correlated with none. The remainder are intercorrelated but polarized into two groups: *Acartia centrura*-*Acartia spinicauda*-*Acartia erythraea*, and *Acartia southwelli*-*Acartia bilobata*-*Acartiella keralensis*-*Acartia plumosa*.

We have concluded from this that, with two exceptions, coexistence of one species with another is not complete when considered in both space and time. The exceptions are *Acartia centrura*-*Acartia spinicauda* and *Acartia bilobata*-*Acartia southwelli*. These two species pairs are strongly correlated (99% significance level) both on a spatial and on a seasonal scale. Such coexistence is a source of special interest and will later be discussed at length.

Table 3. *Acartiidae*. Ecological classification of species studied, according to categories of JEFFRIES (1967)

Category	Species
Truly estuarine	<i>Acartiella keralensis</i> <i>Acartiella gravelyi</i> <i>Acartia plumosa</i> <i>Acartia bilobata</i> <i>Acartia southwelli</i>
Estuarine and marine	<i>Acartia centrura</i> <i>Acartia spinicauda</i>
Euryhaline marine	<i>Acartia erythraea</i>
Stenohaline marine	<i>Acartia negligens</i>

Table 4. Correlation matrix for *Acartiidae* species (*Acartia* and *Acartiella*) by space (mouth head of estuary, 2 seasons) and time (January/December, 1968, 2 stations)

(a) Space										
	<i>bilobata</i>	<i>centrura</i>	<i>erythraea</i>	<i>negligens</i>	<i>plumosa</i>	<i>southwelli</i>	<i>spinicauda</i>	<i>gravelyi</i>	<i>keralensis</i>	
<i>bilobata</i>										
<i>centrura</i>	.72 ^b									
<i>erythraea</i>	-.04	.04								
<i>negligens</i>	-.19	-.23	.70 ^b							
<i>plumosa</i>	-.22	-.30 ^a	-.28	-.09						
<i>southwelli</i>	.44 ^b	.54 ^b	.15	-.27	-.45 ^b					
<i>spinicauda</i>	.64 ^b	.89 ^b	.06	-.20	-.32	.43 ^a				
<i>gravelyi</i>	-.35 ^a	-.55 ^b	-.25	-.07	.22	-.42 ^a	-.51 ^b			
<i>keralensis</i>	-.11	.05	-.20	-.17	.60 ^b	-.16	.10	-.04		

(b) Time										
	<i>bilobata</i>	<i>centrura</i>	<i>erythraea</i>	<i>negligens</i>	<i>plumosa</i>	<i>southwelli</i>	<i>spinicauda</i>	<i>gravelyi</i>	<i>keralensis</i>	
<i>bilobata</i>										
<i>centrura</i>	.36 ^a									
<i>erythraea</i>	.05	.54 ^b								
<i>negligens</i>	No data									
<i>plumosa</i>	.35 ^a	.12	-.17							
<i>southwelli</i>	.60 ^b	.09	-.04		.20					
<i>spinicauda</i>	.17	.80 ^b	.44 ^b		.04	.09				
<i>gravelyi</i>	-.25	-.35 ^a	-.29	No data	-.04	-.19	-.29			
<i>keralensis</i>	.13	-.16	-.20	No data	.21	.50 ^b	-.12	.25		

^a 95% significance level.

^b 99% significance level.

We now proceed to examine one aspect of the competition between these species, namely their structural adaptations for feeding purposes.

ANRAKU and OMORI (1963) have shown that the feeding habits of copepods are reflected in the morphology of their mouthparts, the mandibles being adapted to handle that size of particle which the maxillary setules are able to sieve from the water.

Fig. 18 shows the mandibular structure of each of the nine species, ranked from blunt to sharp, together with a representation of the minimum mean size of particle which could be collected. There is a general relation between sharpness of teeth and minimum particle size. There is a striking difference between the mouthparts of *Acartia* and *Acartiella*. In *Acartiella* the setules on the maxillae are widely spaced, and the

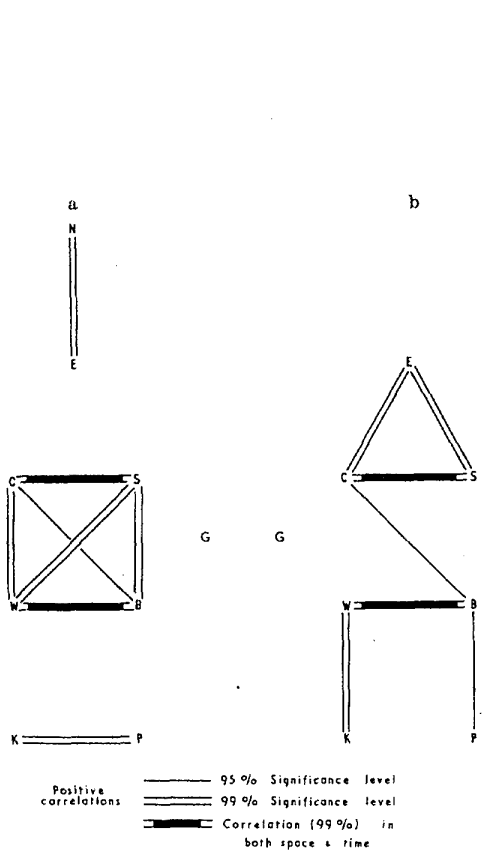


Fig. 17

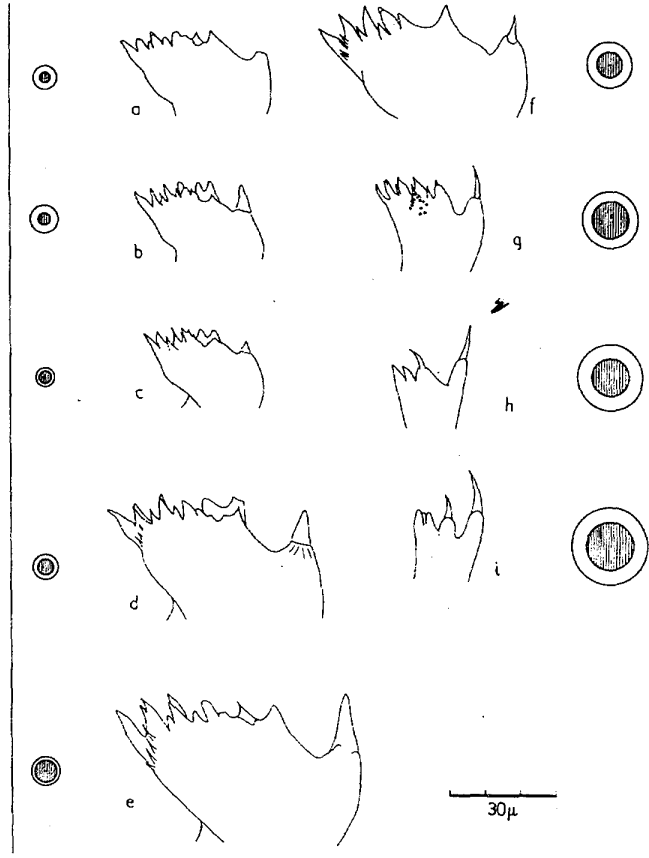


Fig. 18

Fig. 17. Diagram of species relationships considered by (a) space (mouth to head of estuary); (b) time (January/December). B: *Acartia bilobata*; C: *A. centrura*; E: *A. erythraea*; N: *A. negligens*; P: *A. plumosa*; S: *A. spinicauda*; W: *A. southwelli*; G: *Acartiella gravelyi*; K: *A. keralensis*

Fig. 18. Mandibular structure of Acartiidae species found in Cochin area, and representation of minimum mean size of particle which can be filtered out by setules of maxillae; smaller circles minimum, larger circles maximum, space between setules. (a) *Acartia plumosa*; (b) *A. southwelli*; (c) *A. bilobata*; (d) *A. centrura*; (e) *A. erythraea*; (f) *A. spinicauda*; (g) *A. negligens*; (h) *Acartiella gravelyi*; (i) *A. keralensis*

mandibular teeth are reduced in number and greatly elongated; these are adaptations for grasping and piercing rather than for grinding.

These differences have been expressed in quantitative terms using the analysis of MIRONOV (1963) for the mandibular structure of *Acartia clausi* in the Black Sea. The height and basal breadth of each tooth was measured and the ratio between the two used to indicate the tooth "acuteness" (Table 5). The mean acuteness of *Acartiella* teeth ranges from 2.0 to 2.2, whereas *Acartia* teeth fall within the range 0.7 to 1.6, *Acartia plumosa* having the bluntest teeth and *A.*

negligens the sharpest. The tooth acuteness of the other five species of *Acartia* falls within the narrow range 1.0 to 1.3, suggesting that they could use a common type of food; *A. bilobata* and *A. southwelli* are equipped by the finer spacing of the setules on the second maxilla to collect slightly smaller particles than can *A. centrura*, *A. erythraea* and *A. spinicauda*. The strongly correlated species pairs *Acartiella bilobata-Acartia southwelli*, and *Acartia centrura-Acartia spinicauda* are included in this interesting group of species with overlapping niches. The factors which permit their coexistence need now to be considered.

Table 5. *Acartiidae*. Acuteness of teeth (height/breadth) on mandibular plate of species from Cochin Backwater. Nomenclature of teeth after MIRONOV (1963): V: ventral, C: central, D: dorsal

Species	Teeth ratio									Overall Mean
	V	C	D1	D2	D3	D4	D5	D6	Mean D	
<i>Acartia plumosa</i>	0.5	0.4	0.6	1.1	1.6	1.3	1.3	2.0	1.3	0.7
<i>Acartia bilobata</i>	0.8	0.4	0.8	1.9	2.0	2.8	2.0	2.0	1.9	1.0
<i>Acartia centrura</i>	1.2	0.4	0.8	1.0	1.8	1.5	1.5	2.3	1.5	1.0
<i>Acartia southwelli</i>	1.5	0.5	0.9	2.0	2.0	1.6	2.1	2.4	1.8	1.3
<i>Acartia erythraea</i>	1.6	0.4	0.5	0.8	2.1	1.8	1.6	2.5	1.5	1.2
<i>Acartia spinicauda</i>	1.2	0.4	0.9	0.9	2.3	1.8	1.4	2.2	1.6	1.1
<i>Acartia negligens</i>	2.0	0.7	1.4	1.3	1.6	3.0	2.0	2.5	2.0	1.6
<i>Acartiella gravelyi</i>	3.3	1.1	1.6	—	1.5	—	—	1.6	1.6	2.0
<i>Acartiella keralensis</i>	3.0	2.3	—	—	1.1	—	—	1.8	1.4	2.2

Discussion and conclusions

The results we have described cannot be regarded as an exception to the Competitive Exclusion Principle, which is essentially a mathematical statement subject to mathematical proof. Rather, we must address our attention to the corollary of the Exclusion Principle — "Ecological differentiation is the necessary condition for coexistence" (HARDIN, 1960). Such studies throw new light upon the degree of ecological difference required to permit coexistence (SLOBODKIN, 1963). The plankton community provides a fertile field for such studies. For example, tropical epiplanktonic open-ocean communities contain many species of the same genus which appear, superficially, to have similar ecological requirements. Similarly, bathypelagic copepods living in what appears to be a singularly homogeneous and stable environment are remarkably diverse (VERVOORT, 1957).

In the discussion which follows, we have sought to identify some of the components of the "niche hypervolume" (HUTCHINSON, 1957) of the various species of Acartiidae in the Cochin Backwater.

Other species of *Acartia* have been shown to feed on phytoplankton and larval copepods (CONOVER, 1956; PETLPA, 1959; ANRAKU and OMORI, 1963). The seven species of *Acartia* from the Cochin Backwater have similar mouthparts and probably use the same sort of food. However, the two species of *Acartiella* are quite different. Their mouthparts are clearly adapted for carnivorous rather than herbivorous feeding (Fig. 18). In fact, the morphological differences between *Acartia* and *Acartiella*, in these and other respects (Fig. 2), are so striking that there is doubt whether the two genera are as closely related as their taxonomy would suggest.

We believe that the niches of *Acartiella* are defined in part by their special food requirements. For example, this component alone is sufficient to distinguish the separate niches of the coexisting species

Acartiella keralensis and *Acartia plumosa* (Fig. 18, Table 4).

Another component of the *Acartiella* niche is tolerance of low salinity. This alone is sufficient to account for the uniquely separate niche of *Acartiella gravelyi*, which is negatively correlated with several species and positively correlated with none (Table 4).

On the other hand, *Acartia erythraea* and *A. negligens* which are positively correlated (Table 4, Fig. 17), would appear to be more tolerant of high salinities or less tolerant of low salinities than any of the other species. *A. erythraea* is a neritic species which is sometimes carried into the open ocean (Fig. 19), whereas *A. negligens* is an open-ocean species (Fig. 20) which is sometimes carried into neritic regions. We conclude, therefore, that the salinity-influenced spatial distribution of these two species is an important component of their niches.

Whereas *Acartia plumosa* coexists with *Acartiella keralensis*, but occupies a separate trophic niche, *A. plumosa* occupies a similar trophic niche to *Acartia southwelli* and the two species do not coexist. The latter pair are small in size (less than 1 mm); their mouthparts are similarly adapted for dealing with food particles as small as 3 to 4 μ ; and both make a large contribution to plankton production in the backwater, their populations at times reaching densities as high as 2,000 to 5,000/m³. *A. plumosa* was widely distributed throughout the estuary in November when runoff was considerable (Fig. 10a), was quick to recover after the monsoon (Figs. 16c, 10c), and in April was predominant towards the headwaters (Fig. 10b). *A. southwelli*, on the other hand, was completely absent in November (Fig. 11a) and, except for a brief appearance in December (Fig. 11c), did not form a significant part of the plankton community until April, when it became the predominant species in the lower reaches of the estuary (Fig. 11b, c). Niche separation between these two species is not a simple

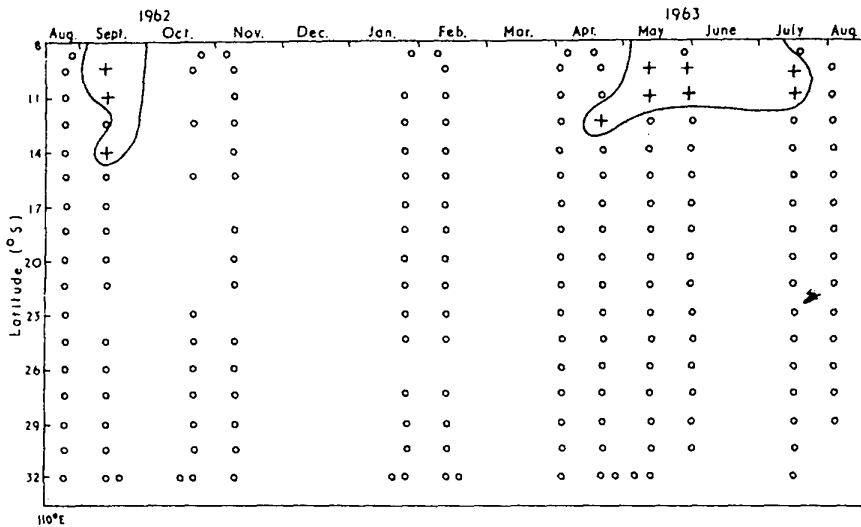


Fig. 19. Distribution of *Acartia erythraea* in eastern Indian Ocean (110° E) showing dispersal of species from shallows of Indonesian Archipelago (north of section line). +: present; o: absent; blank space: no data; displacements from section line: nearby reference stations

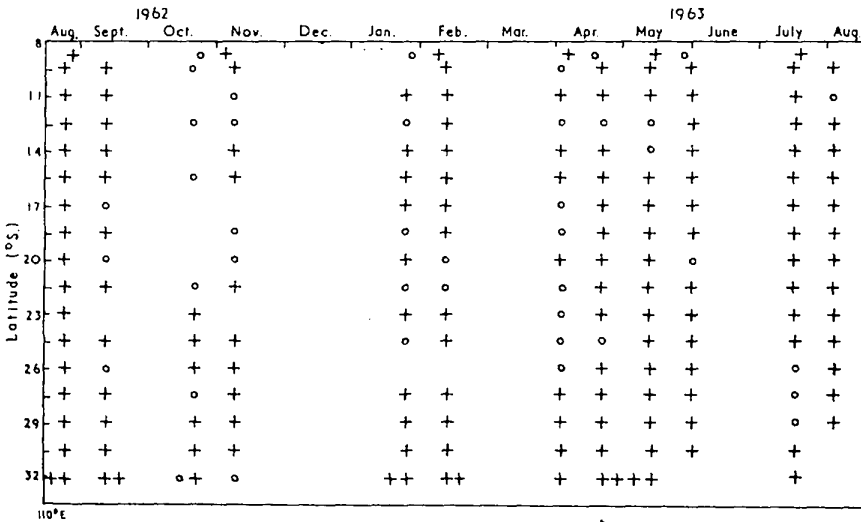


Fig. 20. Distribution of *Acartia negligens* in eastern Indian Ocean (110° E) by latitude and season, showing open-ocean character of species. +: present; o: absent; blank space: no data; displacements from section line: nearby reference stations

difference in salinity tolerance, because *A. southwelli* rarely occurred in the open sea where, on those grounds, it would be favoured. Some other factor is involved.

We now come to the two pairs of coexisting species: *Acartia bilobata*-*Acartia southwelli* and *Acartia centrura*-*Acartia spinicauda*. The species of each pair are

positively correlated, both in space and time (Table 4) and their trophic adaptations are similar (Fig. 18, Table 5). *A. bilobata* and *A. southwelli* are able to filter food particles as small as 3.5 to 4 μ , and *A. centrura* and *A. spinicauda* particles as small as 4.5 to 7.5 μ . In our opinion, the differences which do exist are not

efficient to establish niche separation. How then do these sympatric species pairs coexist? In what ways are they ecologically differentiated?

Before examining in further detail the fundamental niches of these two species pairs, one should consider the conditions which must be met before the exclusion principle would apply to any pair of sympatric populations (MULLIN, 1967): (a) There must be a single density-dependent limiting factor which controls both populations; (b) the environment must be stable enough to allow natural selection to favour one species for several generations. Of the many factors which are relevant to these two conditions, we shall consider only food sufficiency, generation length, salinity, and flow, which appear to us to be the most important.

According to CONOVER (1968) "The pelagic zone of the ocean or a large lake represents an essentially limitless food supply for the individual zooplanktonic animal, but, at the same time, this source of energy may be so thinly dispersed that the problem of getting enough to eat is still formidable". Presumably those species will compete whose feeding activities lead to further dilution of their common food supply. QASIM (1970) studied the plankton productivity of the Cochin Backwater and concluded that phytoplankton production was much greater than the consumption by zooplankton herbivores. However, our observations show that the copepod populations in this ecosystem are very large (TRANTER, in press) and it is possible that QASIM may have underestimated their food requirements. In our opinion, food may well be limiting.

Generation length is an inverse function of water temperature (MCLABEN, 1963). HEINLE (1970), for example, has showed that *Acartia tonsa* passes from one generation to the next in 4 to 5 days at a temperature of 30 °C. Nothing is known about the generation lengths of copepods in the Cochin Backwater; however, SUBBA RAJU (1967) has observed the life cycle of *Acartia erythraea* to take one week at Porto Novo on the east coast. Bearing in mind the high temperatures which prevail in the Cochin Backwater (Fig. 3), it seems likely that the life cycle of *Acartia* species in that environment would take no longer than at Porto Novo.

For 6 months of the year (June/December) the estuary is subject to drastic changes in the rate of flushing due to monsoonal runoff. For the other 6 months (December/May) the lower part of the estuary is relatively stable with respect to both temperature and salinity (Figs. 3, 4). There would be time for up to 20 generations or so to follow in succession. Although we have made no observations further up the estuary during this period, it seems likely that the salinity intrusion is a gradual process and that the period of stability would reduce progressively toward the headwaters of the estuary.

The stresses associated with salinity change place heavy demands on the tolerance of species which

inhabit estuarine environments. It is probably their behavioural and physiological adaptations to such stresses that have made the Acartiidae a characteristic and dominant feature of estuaries throughout the world. Not only salinity tolerance is involved. KETCHUM (1954) and BARLOW (1955) have shown that estuarine populations are limited in size by their rate of reproduction in relation to the rate of flushing in the estuary. Too great a flow results in a spectacular "washout" of the population as in laboratory chemostats (MALEK and FENCL, 1966). Such a washout took place in the backwater in July, and its effects were noted in the sea outside in August and September (Fig. 5).

It would seem, therefore, that the Acartiidae of the Cochin Backwater are a typical example of a "non-equilibrium population" (HUTCHINSON, 1953), where competition is terminated by a regular catastrophe before any one of the several competing species can be eliminated. Some may be what HUTCHINSON (1951) has termed "fugitive species". The fugitive "enjoys freedom from competition so long as small statistical fluctuations in the environment gives it a refuge into which it can run from competitors". Fugitive species are "forever on the move, always becoming extinct in one locality as they succumb to competition and always surviving by re-establishing themselves in some other locality as a new niche opens". They are incapable of surviving in competition with any other species entering the same niche, but manage to exist primarily by their efficient dispersal mechanisms.

It is of interest in this connection to enquire how populations are re-established in the backwater after the monsoonal washout. Does repopulation come from the waters of the continental shelf? Do residual populations persist in the deep pockets of more saline water that remain within the estuary during the flood? Do species have monsoonal resting stages in the bottom muds? There are no records of diapause in marine copepods, but ELMORK (1967) believes that this may be from want of observation.

So far this discussion has been concerned mainly with the question: How is diversity maintained? One can also ask: How does such diversity develop?

Unless a single species were to operate equally efficiently throughout the entire range of environmental conditions which characterises the monsoonal estuary, then unfilled niches would exist. The greater the diversity that develops, the greater the potential for ecosystem efficiency. The limit to diversity is set by the minimum width within this spectrum of environmental variation that would provide an adequate refuge from competition. JEFFRIES (1967) believes that congeneric species-complexes extract the raw materials of life from their environment with minimum waste "competing for common resources at times of the year when the biotope is least stable, wasting a minimum in acquiring the maximum". JEFFRIES'

reasoning suggests that selection pressures operating at the group (genus) level are the cause of this diversity.

Be that as it may, the species complex of Acartiidae which inhabits the Cochin Backwater would appear to be close to the limits of efficiency so far as utilization of the resources of their biotope is concerned. Whether this degree of efficiency is adequate to process the bulk of these resources, or whether a substantial part flows through the food web by "alternate pathways", as QASIM (1970) has suggested, is as yet unresolved. This is an interesting question for some future study.

Summary

1. The Cochin Backwater is a periodically unstable environment inhabited by many copepod species of the family Acartiidae, whose diversity forms the subject of the present study.

2. Species of the genus *Acartia* have feeding appendages which are similar, but adapted for dealing with food particles of slightly different size.

3. The feeding appendages of the genus *Acartiella* differ significantly from those of *Acartia*, suggesting that the two genera are not closely related and have distinctly different niches.

4. The nine species which were studied varied in relative frequency from site to site and season to season, in accordance with a definite pattern. Some, notably *Acartia plumosa* and *A. southwelli*, occurred at times in great abundance (2,000 to 5,000/m³).

5. Water temperatures were uniformly high throughout the year (25° to 34°C), whereas the water salinity varied from fresh to salt (0 to 35‰). The low salinity regime extended from June to December.

6. The occurrence of *Acartia negligens* and *A. erythraea*, together with evidence from other sources, showed that the former is characteristically an inhabitant of the open ocean (stenohaline marine) whereas the latter is principally neritic (euryhaline marine).

7. *Acartiella gravelyi*, *A. keralensis*, *Acartia plumosa*, *A. bilobata* and *A. southwelli* are true estuarine species, *Acartiella* and *Acartia plumosa* being particularly favoured by low salinity conditions. There is almost complete coexistence between *Acartia bilobata* and *A. southwelli*, and little obvious ecological differentiation.

8. *Acartia spinicauda* and *A. centrura* are characteristically both estuarine and marine. Here also the species coexist with considerable niche overlap.

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First author's address: Dr. D. J. TRANTER
CSIRO Division of Fisheries and
Oceanography
P.O. Box 21, Cronulla, N.S.W. 2230
Australia

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