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OBSERVATIONS ON THE BREEDING AND SEASONAL ABUNDANCE OF TEN
SPECIES OF PLANKTONIC COPEPODS OF THE GULF OF MANNAR*

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ABSTRACT

The quantitative biology of the following ten species of planktonic copepods is included in the present study: Pseudodiaptomus aurivili, Calanopia thompsoni, Acartia erythraea, Paracalanus aculeatus, P. parvus, Calanopia aurivili, Acrocalanus gibber, A. monachus, Euterpina acutirosa and Oithona rigida.

There have been three principal aims: (a) determination of the breeding seasons of different copepods; (b) estimation of quantitative seasonal distribution and (c) determination, if possible, of the number of broods in a year and the longevity of broods. The data obtained during the present studies on these subjects are presented, and compared with earlier works and points of interest are discussed.

Based upon the breeding habits, the planktonic copepods of the Gulf of Mannar are divided into three groups: those having a single, well-defined breeding season; those having more than one breeding season and those having irregular breeding periods. It may be added that this division is purely tentative for it is hard to explain why organisms living under similar environmental conditions should have different breeding habits.

INTRODUCTION

There have been three principal objectives for the present investigations: (a) determination of the breeding seasons of different copepods; (b) estimation of quantitative seasonal distribution of different species; and (c) determination, if possible, of the number of broods in a year and the longevity of broods. It may be stated that some useful informations have been obtained on the general pattern of breeding, quantitative variations of different species throughout the year and the succession of their life-cycles. The investigations were confined to adults and copepodites only. The correct identification of the naupliar stages is an extremely difficult task as the collections invariably contain various developmental stages.

Ten species which constitute the more common forms of the area investigated have been included in the present study. From the point of view of total abundance Acartia erythraea could be said to be the most important species though in tropical waters it is difficult to regard any single species as a dominant item of the plankton. Some species are found throughout the year without much seasonal variations while some others display great fluctuations. Digby (1950) in his excellent studies on the biology of small planktonic copepods off the Plymouth area derived his conclusions on following three types of evidences: (i) comparative abundance of different species; (ii) their percentage distribution; and (iii) the size of the adults. He has also pointed out the drawbacks of each of these considerations. Nevertheless, a study of these factors forms an important pre­requisite to an understanding of their biology as it reveals many important facts.

MATERIAL AND METHODS

The present study is based on the examination of eighty-eight horizontal surface plankton hauls collected in the Gulf of Mannar, each of fifteen minutes duration. These hauls were made

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from May 1959 to December 1960. All the collections were made between 5–30 and 6–30 A.M. Half-meter organdie nets with mesh size of 0.230 mm were employed in all the collections which were preserved immediately after the haul. On several occasions duplicate hauls were also made. These were used for comparing the two sets of readings. The routine collections were made at station A and the duplicate samples at station B, the details of which can be seen in Ummerkutty (1967).

For laboratory analysis the total catch was subsampled as follows: The entire quantity was transferred to a wide-mouthed bottle and diluted up to 250 c.c. by adding formalin. A subsample of 2 c.c. was taken out by means of a graduated pipette. All organisms contained in this example were counted under a binocular microscope by employing a plankton counting chamber.

**Breeding Periods**

*Pseudodiaptomus aurivilli* Cleve

Large numbers of adult males, females and copepodites swarmed the surface waters in the months of December-January 1959–60; this was to some extent accompanied and later on

![Graph 1](image1)

![Graph 2](image2)

*Fig. 1–2. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 1. *Pseudodiaptomus aurivilli*. Fig. 2. *Calanopia thompsonii*.**
followed by a large number of naupliar stages. The abundance was maintained in February though a steep reduction was noticed from the January level. A clear and gradual declination was observed during subsequent months and in July the species virtually disappeared. The data for next four months (August-November) display a gradual increase in the population. It is interesting to note that the level in December was almost the same as for the same month of the preceding year (Fig. 1).

A close study of the data available for 1959 revealed that in the month of May a fair number of individuals, more than half of which were adults, were caught. This was followed by a declination in June, July and August and in September the species was at its minimum of occurrence. The months of October and November witnessed an abrupt upward change in this species which compares well with the condition found in 1960.

![Graph 3](image3.png)
![Graph 4](image4.png)

FIGS 3-4. Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 3. *Acartia erythræa*. Fig. 4. *Paracalanus aculeatus*. 
The percentage distribution of adults throws more light on the breeding pattern of this species. August-September 1959 and July-August 1960 were the periods of lowest abundance of the species. During these periods only adults were caught. For the few months following this low peak the population consisted chiefly of adults. By the end of November both in 1959 and in 1960 good numbers of adult females were observed to carry eggs and this was followed by a sudden increase of early stages in the population in December and January. This suggests that intensive spawning takes place during the months of December-January. As young stages were also found during subsequent months, it appears that the breeding of stray individuals or isolated late spawners continue till about February.

*Calanopia thompsoni* A. Scott.

This species shows a great similarity to the earlier species in its distributional pattern except that during the non-peak period its abundance becomes very insignificant. It also has similar peaks during the months of September-January (Fig. 2), with, however, a fall in December. During May-June a fair number of first to third copepodites are present. In July and August these stages are replaced by fourth and fifth stages. The adults begin to appear in small numbers in August, and from September onwards they increase steadily and attain the maximum in January. The early copepodites of these species are seen in the months of September which signifies the commencement of breeding season. During subsequent months when intensive spawning recurs, the life-cycle passes in quick succession. In February and March the early stages begin to disappear, thus indicating the completion of breeding season. In these months the species is represented predominantly by late copepodites and adults.

Although occurring in relatively small numbers, *Calanopia thompsoni* appears to have some importance by virtue of its large size. If weight alone is taken as a criterion, the contribution of this species during the peak period to the total biomass will be found to be quite substantial.

*Acartia erythraea* Giesbrecht

This is one of the commonest species of this area and is found almost throughout the year. However, during the peaks of October and January, because of the swarming of so many other copepods, its comparative importance is reduced. There are two well-defined peak periods of abundance for this species, one in April-May and the other in October-January. During the latter peak, however, the population suffers a minor declination in November (Fig. 3). A study of the percentage distribution of the various stages show that the setback in November is due to a lower rate of recruitment of new copepodite population.

Kartha (1959) found two distinct peaks for this species first in March-April and the other in November-January, with an additional smaller peak in September. During the year 1960 these sequential changes appear to have shifted forward by one month. The first maximum is found in April-May, extending even up to first half of June. The smaller peak noticed by Kartha in September is found to occur in October and almost entirely merges with the second large peak of the year. The facts that during the year 1954 no such intermediate peak was noticed by Kartha and that even when present the peak is extremely small suggest that this smaller peak may better be considered in continuation of the all-round increase of the species during the colder months of the year.

*Paracalanus aculeatus* Giesbrecht

This species was found at its maximum during January-March whence it decreases gradually. The lowest number was observed in May. During June-July another peak was found to occur. But while in 1959 this latter peak was conspicuous it turned out to be quite insignificant in 1960 (Fig. 4). In September the species reached the second minimum and during this month the population consisted chiefly of the copepodites. By October, however, all the young stages have moulted.
either into fifth stage or adults. Incidentally this was the month when the adult population recorded its greatest percentage of abundance. This not only shows that the breeding has practically ceased a month or so earlier, but may also indicate that the next active breeding season of the species is in the offing.

Sewell (1929) has made the suggestion that it is probable that the abundance of this species and of the following is more or less mutually exclusive. He found that when *P. parvus* was dominant in a particular locality *P. aculeatus* was almost entirely absent or present only in small numbers. The reverse situation of abundance of *P. aculeatus* and an absence of *P. parvus* was also noticed.

**Paracalanus parvus** Claus

Kartha (loc. cit.) noted great variations in the trend of seasonal changes of this species. Both in 1952 and in 1953 he observed only a single prolonged breeding period with its maximum in December-January. In 1954 he found a second increase with breeding activity during April-May. This was, according to him, mainly responsible for the total copepod peak in May-June. The data available for 1960 present a picture almost intermediate to these two extremes (Fig. 5). The species reaches the maximum in November-January months. A second peak which comparatively is quite small and insignificant is found in May-June. A third increase occurs in September, just prior to the most intensive breeding period of the year. It is probable that active breeding starts early in September, and continues up to January or February. The steep reduction found in October is mainly due to a lesser percentage of adults.

Besides the main peak during the colder months, the presence of a second peak is reported for 1954 (Kartha, loc. cit.). Its occurrence in 1960 as well indicates that it is probably a regular feature of the species. Even in 1953 Kartha's figure shows a minor peak (Kartha, loc. cit., Fig. 3, b) which is not mentioned in the text and which resemble the second peak observed in 1960. The correspondence of the present data with these earlier reports thus is not a mere coincidence.

**Calanopia aurivili** Cleve

Generally the maximal occurrence of this species is during the months of October-December. The lowest numbers are found in May and August. There is a slight increase during the intervening months of June and July.

By September the species starts increasing in number. This process goes on steadily until November when the species attains its annual maximum (Fig. 6). That November is the most active breeding month is shown by the percentage distribution of the adults and copepodites. The latter which formed only forty-two per cent of the total population in September now swarm the water, constituting about seventy-eight per cent. Further while in September the early copepodites (I–III) were entirely absent, in subsequent months they contributed a major share in the total plankton.

Although small, the June-July peak also may indicate a clear breeding period. From April to June practically there was no new recruitment of early copepodites. But in July there is a sudden appearance of these stages, forming about sixty per cent of the total population of this species. By August all the young ones moult to higher stages and by September the population predominantly attains adulthood, and this marks the beginning of another active breeding period.

**Acrocalanus gibber** Giesbrecht

Kartha (loc. cit.) treated three species of this genus together and stated that in the Gulf of Mannar there was a fairly good population from June to August in 1952 with a peak in August;
and July-September in 1953". He further stated that "in 1954 there was a peak of short duration in May". The present observations differ from these records. It may be because of the fact that in the earlier account these different species were pooled and dealt with together.

![Graphs showing distribution of copepod population](image)

**Figs. 5-6**
Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 5. *P. parvus*. Fig. 6. *Calanopia aurivillii*.

**Figs. 7-8**
Distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960. Fig. 7. *Acrocalanus gibber*. Fig. 8. *A. momchus*.

*A. gibber* displays two major peaks in the year, the first in January-February, extending up to March and the second in June-July, extending up to August. There are clear gaps between the intervening periods (Fig. 7). However, a percentage distribution of different copepodites and adults reveals little information as to any change in the rate of breeding between different seasons. It is interesting to note that the peaks observed for this species correspond to those recorded for *Calanopia aurivillii* and *Pancalanus parvus*. The only difference being that the June-July peak is larger and the winter peak is shifted more towards the colder months.
The only definite thing that could be said about the distributional pattern of this species for the year 1960 is that there was an enormous increase of the population during the months of November-February, attaining the maximum in January (Fig. 8). After February there was a steep reduction, reaching the minimum in March. From then onwards small fluctuating peaks were observed, almost at intervals of two months until October when the species displayed a gradual increase. A study of the percentage distribution of various copepodites and adults does not reveal much except that in December the adult population reaches its maximum. The annual maximum population observed in February is due to active breeding of these adults.

*A. monachus* is a small species and it is possible that the sampling of the early copepodites is inadequate. It is also possible that during the laboratory analysis some of the copepodites could have been mixed up with those of a related species, *A. gracilis*. The latter is a large species and occurs only occasionally. However, when both species occur together, and especially when the population is dominated by the early copepodites, the correct identification becomes a difficult task.

![Graphs 9 and 10 showing distribution of total population (adults and copepodites) of different species of copepods in the Gulf of Mannar during 1960.](image)
Euterpinia acutifrons (Dana)

According to Kartha (loc. cit.) this species occurs throughout the year, with slight variations in its abundance and with an overall increase during the cold months. Only in 1954 he observed an additional peak during May-August. There is general agreement between the present data and the earlier accounts. The species started a steady increase in October and the tendency is continued upto January whence it takes a reverse direction. During March-October the species undergoes considerable fluctuations (Fig. 9), the yearly minimal level being recorded in the month of May. However, it is surprising that during this month the population was composed mainly by the copepodites especially the earlier ones and that the largest percentage of the adults was found to occur during the preceding month of April.

Oithona rigida Giesbrecht

Kartha (loc. cit.) found that the species of the genus Oithona showed irregularity in its distribution from year to year with, however, a constant peak in September. There is good agreement between the present findings and the earlier records. The present species attains its annual maximum during the months of December-January. Other peaks are observed almost at equal intervals in March-April, June-July and September-October (Fig. 10).

The four peaks observed in the present investigations correspond to those reported by Kartha, especially for the years 1953 and 1954. The present data differ from those of the year 1952 in that the peaks recorded in March-April and June-July in that year are considerably insignificant. It appears that this is a prolonged spawner, but with distinct periods of active breeding which are intercepted by short intervals of lesser reproductive activity.

Quantitative Distribution

The copepod population as represented by the ten species noted above in the Gulf of Mannar is the highest during the coldest months of the year, November-February (Figs. 11-19). By the end of February or March, almost all the species record varying degrees of declination (Figs. 20-21). In several species the decrease is constant during the summer months and a reversal towards the other direction is marked in the beginning of August or September whence the increase in their numbers becomes steady. By taking all species together it appears that the copepods show a unimodal pattern of distribution. However, this picture is obscured if we examine individual species separately. Not only do several of them show more than one peak in a year, but the peaks of different species are not often synchronised. In all species, however, one of the annual peaks corresponds with cold months of the year, thus resulting in an overall increase of the copepod population during that season. Prasad (1954 and 1956) found that although the copepod population showed an increase in October there was a reduction in November before attaining a subsequent increase resulting in a peak in December-February. Kartha (loc. cit.) obtained more or less similar informations. However, Prasad and Kartha (loc. cit.) have clearly demonstrated that a close relationship exists between the breeding of copepods and the diatom cycles and that treated in a general way "the maximum breeding in the Gulf of Mannar is during September to March". It is probable that the reduction of population obtained in November during certain years is not due to any complete break in the reproductive activities but may be due to a slowing down of the new recruitments of nauplii and copepodites after the completion of an initial generation. In several species (P. aurivilli, C. thompsoni, A. erythraea, P. parvus, A. gibber, O. rigida) this disjunction is seen in the winter peak. But in several others (P. aculeatus, C. aurivilli, A. monachus, E. acutifrons) the increase initiated during September or October is steady and continuous, attaining a single prolonged annual maximum. Prasad (1954) who first observed dicyclicity in the distribution of copepods in the Gulf of Mannar offered the following explanation: "It is possible that while in other localities the maximum occurrence of one or more species may overlap, there may be still others whose maxima fall in such a way as to fill the gaps and present an over-all unimodal distribution. A
similar phenomenon may not be taking place here thereby resulting in an apparent reduction in population level and a bimodal curve.

FIGS. 11-19. Percentage distribution of adult females in the different species of copepods in the Gulf of Mannar during 1960. Fig. 11. Pseudodiaptomus aurivilli. Fig. 12. Calanopia thompsoni. Fig. 13. Acartia erythraea. Fig. 14. Paracalanus aculeatus. Fig. 15. P. parvus. Fig. 16. Calanopia aurivilli. Fig. 17. Acrocalanus gibber. Fig. 18. A. monachus. Fig. 19. Oithona rigidia.
If individual species are considered separately it is found that the annual maximal peaks coincide with the most active breeding periods. It has been observed that the breeding activity is a continuous process in great many of the species and takes place almost throughout the year. Only in a few species (e.g., *P. aurivilli*) there is a cessation of spawning activities during the periods of minimal occurrence. However, in all the continuous spawners there is great reduction in the rate of production and the succession of broods during the non-peak periods. It appears that during these periods different nauplar and copepodite stages take longer durations than those during the peak periods when because of the highly favourable environmental conditions the reproductive activities are accelerated and that the life-cycles are spent in quicker succession.

The relative difference in the distribution of the two sexes of adult animals do not exhibit any particularly interesting trend except that in some species the females tend to dominate almost always while in others a fifty-fifty ratio is roughly maintained. In species with strongly defined annual peaks (e.g., *P. aurivilli*, *C. thompsoni*) the males slightly outnumber the females during the breeding periods. It is also interesting to note that in these species the females form a greater proportion of the adult population during the period of minimal occurrence. Among the late copepods, the ratio of sexes is monotonously uniform, each sex equaling the other. A sex-wise analysis of the earlier copepods is not possible as in these cases there is apparently no external character for sexual determination.
BREEDING AND SEASONAL ABUNDANCE OF PLANKTONIC COPEPODS

ANNUAL NUMBER OF BROODS AND THEIR LONGEVITY

*Pseudodiaptomus aurivilli* and *Labidocera bengalensis* have been reared in the laboratory for studying the stages of their life-cycles (Ummerkuty, 1965). The methods adopted for rearing was to select specimens of a particular stage and allow to moult to the next stage. In this way, by repeated observations on different stages a continuity of all stages could be established. In some cases the specimens survived longer than one moult, thus giving actual indication of the time required by the organism to moult from one stage to the other. However, the time taken by plankton organisms to moult in captivity to next higher stage may not be the same as in their natural environment. None of the nauplii and the early copepodites which underwent more than one consecutive moult in the laboratory took more than 2-3 or rarely 4 days for the process. The late copepodites hardly lived for four days after their first captive moult. Probably the duration required for the next moult is longer in these cases but may not exceed 6 or 7 days. Giving an average of three days for the naupliar and four or five days for the copepodite development it is found that a nauplius freshly hatched and reared under captive conditions could attain adulthood in five or six weeks. This could possibly depend on the optimum conditions of the environment.

There are many types of evidences to show that the period required for completion of the entire life-cycle is much shorter during the propitious colder months. It has been found both in the earlier studies (ch. Prasad, 1954 and 1956; Kartha, 1959) and also in the present investigations that for several species (*A. erythraea, P. parvus*, etc.) the winter increase is interrupted after a month or so before reaching the maximal peak. If this interruption is accepted as a break in the reproductive activity it can be seen that during the favourable periods of colder months the entire life-cycle requires four to five weeks for its completion.

During the non-peak periods the life activities in most of the species are slackened and although breeding takes place, the rate of production of new stocks appear to be at a much lower rate and the nauplii and the copepodites appear to last for longer durations. *Oithona rigida* which shows several peaks in a year provides a fine example. The breeding in this species is continuous. As noted earlier the species reaches its maximal abundance during December-January. Following this period there is a month of recuperation before the species launches on the next generation. The latter lasts exactly for two months before attaining maturity and for preparing the species to start on a new generation. The colder months, however, present a different picture. During this period two or more successful generations are completed in rather quick series within a period of three to four months, the generations sometimes being interrupted only by short periods of lesser reproductive activity.

It is possible that species with one annual maximum should have two or three broods during the entire active breeding period and one or two during the rest of the year. The species with two or more maximal periods would certainly have additional broods. Prasad and Kartha (loc. cit.) observed: “In the temperate waters the usual number of broods is three or four and in cold waters this appears to be reduced to one. It is not unlikely that in the tropical waters there are more number of broods than in the temperate and cold waters”.

GENERAL REMARKS

Breeding habits of copepods of the Gulf of Mannar appear to be divisible into three groups:

1. Those breeding throughout the year with irregular variations in the frequencies so that their population includes not only adults but also various copepodites. All these are caught irrespective of any seasons. *Acrocalanus monachus* and *Oithona rigida* exemplify this group.

2. Those breeding throughout the year but with distinct peaks during certain months so that although the various copepodites and the adults of the species are available in every month, yet their percentage abundance displays considerable differences. Several species fall into this group: *Acartia erythraea,*
Paracalanus aculeatus, *P. parvus*, Calanopia aurivilli, Acrocalanus gibber and possibly Euterpiна acutifrons. (3) Those breeding only during certain seasons. Among the species studied *Pseudo-*diaptomus aurivilli and *Calanopia thompsoni* come under this group.

This grouping of copepods on the basis of breeding habits is made with some reservations and should be regarded as tentative. In the first instance it is questionable why species residing under similar environmental conditions should have differential breeding seasons. It will not be out of place to suggest that the availability of food may serve as an important factor in controlling the breeding behaviour of copepods in tropical waters. The synchronisation of diatom outbursts and nauplial development of marine invertebrates has clearly been demonstrated (Ussing, 1938; Marshall and Orr, 1952; Barnes, 1957; Prasad and Kartha, 1959). Those species with clear seasonal spawning habits could be said to be under the strong influence of regular periodicities of phytoplankton. The breeding of other copepods, irrespective of the season, could be due to the fact that in tropical waters phytoplankton may be available almost throughout the year in varying quantities. This latter suggestion is, again, illustrated by *Tortanus gracilis* and *T. forcipatus* both of which are predatory and feed on nauplii and other minute creatures. These species are not very common in this area, but whenever present they are represented not only by adults but also by copepodites, indicating a continued breeding throughout the year. As the naupliar diet is invariably present throughout the year those copepods do not find any scarcity of food. They, therefore, breed all the year round.

The temperature variation in the Gulf of Mannar have recently been discussed by Prasad (1957) who noted that temperature is maintained more or less at a uniform level throughout the year except during some months corresponding to the calendar winter when there is an abrupt reduction. The earlier parts of these colder months represent the biological spring of this area with a great bloom of phytoplankton and the latter part the biological summer with the greatest number of zooplankton. The coincidence of the breeding of copepods with this part of the year is, therefore, natural. However, why several species should have another significant peak period during the months of June–July, extending even up to August is not clear. This is particularly interesting in view of the fact that during this period active breeding of copepods occurs in the Palk Bay (Prasad and Kartha, *loc. cit.*).

A final word may be added about the continuity of the species throughout the year. In temperate and cold waters several earlier workers have noticed (for a review see Digby, 1950 and Marshall and Orr, 1955) that species with well-defined seasonal breeding disappear almost altogether during the unfavourable periods. In such cases it is held that either these species migrate at lower depths during the unfavourable conditions or they never disappear completely from the water column, but merely are scarce enough to become noticed. In tropical waters the breeding appears to be a continuous process and only the intensity differs from season to season. The influence exerted by the immediate favourability or unfavourability of the environment is manifested in the breeding behaviour of the copepods in the form of seasonal rhythm.

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DISCUSSION

DR. B. RASMUESEN: There are no differences in the breeding period in most of the species of copepods mentioned, though in some there are these differences. Why?

Food can be said to be the important factor for abundance of some of the copepods and some relation can be established for these species while in some others there is no such relation.

DR. J. H. WICKSTEAD: The studies on Calanus have not been completed in Plymouth Lab.

DR. S. KRISHNASWAMY: I think we should stop thinking in terms of relating the phytoplankton bloom, etc. to the abundance of copepods, because Darwinian orthodoxy will not allow so many species to breed in one and same period.

DR. V. HANSEN: There are 3 species of copepods living in the North Atlantic and these species as they migrate up towards the surface from the depths as great as 600 meters they breed step by step (turn by turn), and I feel in such cases where the environment is more or less the same, we should look for other parameters or mechanisms for such kind of differential breeding seasons.

DR. V. H.: How isolated is this area, Gulf of Mannar?

DR. S. JONES: Beyond the islands, there is oceanic connection which ranges in depth up to about 1,000 fathoms.

DR. S. KRISHNASWAMY: The differential breeding season may be due to the liberation of certain amino-acids by the bloom of phytoplankton which may trigger the breeding, settling and growth of the larvae.

DR. B. RASMUESEN: It cannot be considered that all the animals should be influenced in same manner by the environmental factors. It may be that some animals may or do behave independently or differently.