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The annual reproductive cycles of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* (Decapoda: Crustacea) from the South-west coast of India

K. Krishna Pillay and N. Balakrishnan Nair

Department of Marine Biology and Oceanography, University of Kerala; Trivandrum, Kerala, India

Abstract

Employing the gonad index method, the reproductive cycles of three decapod crustaceans, *Uca annulipes* (Latreille), *Portunus pelagicus* (Linnaeus) and *Metapenaeus affinis* (Milne-Edwards) have been studied. In these crustaceans breeding is not continuous all the year round, but extends over several months of the year with distinct peak periods of gonadal activity. The male and female reproductive cycles are not concurrent. The peak of the reproductive cycle of males occurs slightly earlier in the breeding season than that of females. These studies indicate the possibility of production of successive broods of eggs during the same breeding season. In these species, the low saline conditions of the monsoon period are unfavourable for breeding. The medium and high saline conditions during the post-monsoon and pre-monsoon months, respectively, with plenty of planktonic food for the larvae, seem to be the favourable periods for breeding activity.

Introduction

The determination of the reproductive cycles of animals on the basis of the study of the gonad index has been successfully carried out by several investigators in recent years. The relationship of the ratio between gonad size and body weight and gonad development and gonad maturity during different times of the year has already been reliably established in fishes (Hickling, 1930; Chrzan, 1949; Bullough, 1951; Qasim, 1957). In invertebrates, the index has been obtained in different ways (see Moore, 1934, 1937; Giese, 1959). In recent years, similar studies have been also attempted in crustaceans (Subrahmanyam, 1963; Rahaman, 1967; Pillai and Nair, 1971).

The gonad index method involves the determination of the ratio of gonad weight to body weight and rests on the assumption that, in individuals large enough to be mature, a spent or immature gonad is small, whereas a ripe gonad is large and developed (Giese, 1959). The mean gonad index of the entire sample is considered to be a measure of the average reproductive condition of the population; the sweep of the reproductive cycle can thus be represented graphically when the gonad index values are plotted against time. A fact observed in all instances was that the breeding season was always indicated by high values for gonad index, a subsequent precipitous fall in the values suggesting a "spawn out" condition and a period of low gonad indices prior to the peak period denoting growth of the gonad. However, in such studies, continuous observation of the same sample of individuals is impossible, since the specimens have to be sacrificed for the study. Despite this disadvantage the method provides a reliable quantitative measure of the reproductive condition of the individuals of a population.

In crustaceans, the usual method (widely employed) to determine the breeding period was plotting of the percentage of ovigerous females against time; this provided only an incomplete picture of the sequence of events during the long and often drawn-out breeding season in these tropical habitats. It was, therefore, thought instructive and advantageous to follow closely, step by step, the activity of the gonad prior to berry formation, and also after deposition of eggs. When such data were examined simultaneously with observations on the incidence of ovigerous females in the case of crabs, a more accurate picture of the frequency of gonadal activity during the reproductive cycle of these animals would be achieved. Therefore, in this study, the gonad index method was employed with a view to following the reproductive cycles of three representative decapod crustaceans, *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis*.

Material and methods

Fortnightly samples of *Uca annulipes* were collected from selected localities along the shores of Cochin Backwaters, India, (latitude 9° 58′ N, longitude 76° 17′ E). The specimens were brought into the laboratory alive. Samples of *Portunus pelagicus* and *Metapenaeus affinis* were obtained chiefly from trawlers operating off Cochin in the shelf region and, in a few cases during the monsoon season, samples were also taken from either the shore seines or from the local fish markets where samples arrived from the inshore area. The specimens were thoroughly dried, first by towelling and later with filter paper. The measurements of size, carapace width in the crabs, and length from the tip of the rostrum to the tip of the telson in the case of prawns,

were noted. Random sampling was made. Specimens which were not in a healthy condition and those which had just moulted were not included in the samples. At least 10 individuals of each sex were thus examined every month, except in a few instances when the required number of specimens was not available. This number was chosen on the basis of MILLER's observation (see GIESE et al., 1958). However, larger sampling was made whenever possible. The individual weights were then determined to the nearest gram. The gonads were carefully dissected out and weighed in watch glasses to the nearest milligram. The wet weight of the gonad was then divided by the wet weight of the body and this factor was multiplied by 100; the resulting value was taken to represent the gonad index. The mean values for males as well as for females in each month were calculated to obtain the average reproductive condition of the population. Microscopic examination of the gonads revealed stage of development. The height of the breeding activity in these crustaceans during the annual cycle was determined by noting the variation in the values of the gonad index during the course of the year.

Results

In crabs, two types may be seen among females collected during the breeding season — berried and unberried. The berried forms are obviously in reproductive condition and these can be further differentiated into groups depending upon the stage of development of the eggs in the berry. The berry in a crab may be just formed, with eggs in early stages of development, or the eggs may be more advanced in development, or they may be in the final embryonic stages ready for liberation as zoeae. In berried crabs the ovary may also vary in size, colour and activity. If crabs in early berried stages are examined, two types of gonad appear — activated and non-activated. Similarly, two types of gonads occur in crabs with more advanced berries; in this category it may be possible to find crabs with either no activation of the gonad or with ripe gonads. In the case of non-ovigerous females, two types of gonad may be noted, especially during the breeding season, gonads showing no activation and those showing fair activity, the former probably represent forms which are in the resting phase, or which, due to factors as yet unknown, are not reproducing.

Thus, plots of the values of the gonad index of berried and unberried female crabs, both together and separately, facilitate a reliable assessment of the nature of the gonad and the frequency of its activity during different months. When the gonad indices of all the females in the samples are plotted, the values reflect the average reproductive condition of the population.

Since the data obtained from observations of males did not yield a reliable picture of the reproductive cycles, they were not continued for a second year. It was, however, found worthwhile to continue observations of females for a second year. This permitted comparison of the values for the respective months of the two years. The values for respective months differ in consecutive years in all species studied and, in certain months, the variation is quite considerable. Data collected for a period of 1 year or less may, therefore, lead to unsatisfactory conclusions; at least 2 years' data are necessary to arrive at fairly reliable conclusions.

The data on gonad indices of females and males of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* are presented in Tables 1 to 18 and in Figs. 1 to 11. In the latter figures the range of the gonad index and the mean values are plotted. The range of variation of the monthly gonad index values is divided into groups of 0.1 for males and 1 for females, and the frequency in each group is shown in the figures by horizontal divisions.

Uca annulipes

Table 1 and Fig. 1 present the yearly variations and the average gonad indices of females of *Uca annulipes* examined during the 2 year period from October, 1963 to September, 1965. It can be seen (Table 1, Fig. 1*A*) that the lowest mean gonad index was noticed during May (1.34). The gonad index thereafter showed an upward trend, reaching a high value during September (5.14). In October there was a fall, and in November the value further declined (3.6). Subsequent increase was remarkably rapid and the value touched a peak in December (5.51) representing the maximum; it remained at about this level in January. The values dropped steadily through February, March and April to reach the lowest value in May, completing the cycle.

Table 1. *Uca annulipes. Yearly variations and average gonad indices of females for different months of the year*

Month	Mean gonad index for 1963/1964	Mean gonad index for 1964/1965	Average gonad index for 1963/1965
October	4.16	4.27	4.22
November	1.88	5.33	3.60
December	8.60	2.41	5.51
January	6.44	4.23	5.34
February	3.80	2.24	3.02
March	3.29	2.00	2.64
April	2.10	2.15	2.13
May	1.64	1.05	1.34
June	1.91	1.71	1.54
July	2.03	6.34	4.18
August	3.31	5.63	4.47
September	5.36	4.92	5.14

In Table 1 and Fig. 1 the mean gonad indices for 1963/1964 (Figs. 1*B*, and 2) and 1964/1965 (Fig. 1*C*) are separately presented for comparison of the data during different years.

These conclusions are corroborated by the data obtained regarding the incidence of ovigerous females during the same period (Pillay and Nair, 1970). The

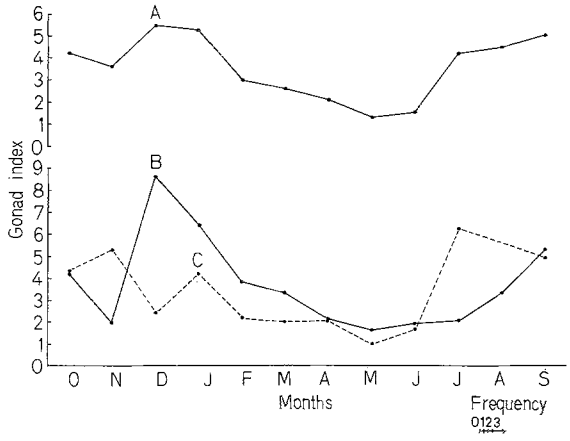

Fig. 1. *Uca annulipes*. Reproductive cycle. *A* Variations in mean gonad indices of females for 2 years, from October, 1963; *B* variations in mean gonad indices of females during first year, from October, 1963/September, 1964; *C* variations in mean gonad indices of females during second year, from October, 1964/September, 1965

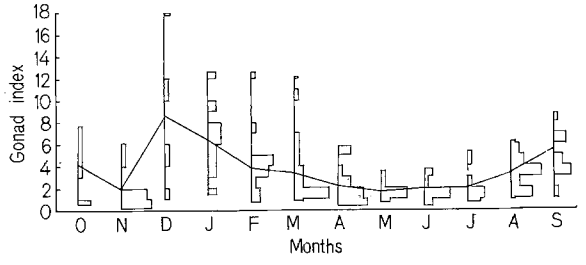

Fig. 2. *Uca annulipes*. Distribution graph illustrating inhomogenity of females throughout annual cycle during year 1963/1964. Range of gonad index in each month is divided into groups of 1; frequency in each group is shown by horizontal divisions

months showing high values in the incidence of ovigerous females are invariably preceded by months of high gonad indices. The period July to August may be regarded as the period when gonadal activity is resumed and the period September to February, as the period of egg deposition, as well as replenishment of the gonad. Laboratory observations indicated that a crab after one berry formation has normally a fully formed berry again within a period of 15 to 20 days. Instances were also noticed in which a crab after the liberation of the zoeae was found capable of reforming a new berry through fresh deposition of eggs within as brief a period as 4 days. This suggests the possibility of recuperation of the gonad even when the crab is in berried state, and that egg deposition and recuperation of the gonad may take place almost simultaneously,

Table 2. *Uca annulipes. Carapace-width range, range and mean gonad indices of females for different months of the years 1963/1965*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1963	October	13.0—16.5	0.59— 7.71	4.16
	November	12.0—17.5	0.24— 6.06	1.88
	December	12.2—15.8	0.99—17.94	8.6
1964	January	12.0—17.2	1.43—12.61	6.44
	February	11.2—15.5	0.67—12.55	3.8
	March	11.7—16.7	0.94—12.09	3.29
	April	12.2—17.5	0.3 — 5.83	2.1
	May	13.0—16.5	0.74— 3.49	1.64
	June	13.1—15.8	0.34— 3.73	1.91
	July	12.8—16.5	0.68— 5.29	2.03
	August	12.2—17.0	0.91— 6.2	3.31
	September	13.5—16.6	1.09— 8.66	5.36
	October	14.0—16.2	0.29—11.08	4.27
	November	13.0—16.0	0.22—18.73	5.33
	December	13.0—18.0	0.51— 8.84	2.41
1965	January	12.0—16.0	0.89— 8.44	4.23
	February	14.5—16.5	0.42— 6.87	2.24
	March	13.5—16.5	0.76— 8.57	2.0
	April	12.2—17.5	0.63— 7.41	2.15
	May	15.0—18.8	0.23— 2.64	1.05
	June	13.0—17.8	0.41— 3.13	1.71
	July	14.0—17.0	1.78—12.23	6.34
	August	14.2—17.0	1.71— 9.03	5.63
	September	12.2—16.0	1.44— 8.18	4.92

at least during a part of the breeding season in some members of the population. This is confirmed when we follow the gonad index values in the different individuals of the population.

These studies indicate that the reproductive activity of *Uca annulipes* along the coast of the Cochin Backwaters is not continuous, but extended over several months, i.e., from July to April, with 3 distinct phases of gonadal activity, a period of recuperation, followed successively by a period of intensive activity, and eventual recession of the gonad leading to an almost quiescent state.

Interesting points regarding the frequency of gonadal activity may be seen in Table 2, which gives the range of individual values for the respective months. The highest gonad index (18.73) noted during the present study for a female was in November, 1964.

Table 3. *Uca annulipes. Yearly variations and average gonad indices of non-ovigerous females for different months of the year*

Month	Mean gonad index for 1963/1964	Mean gonad index for 1964/1965	Average gonad index for 1963/1965
October	5.31	4.55	4.39
November	2.17	5.59	3.87
December	11.13	4.47	7.8
January	6.44	4.23	5.34
February	3.8	2.24	3.02
March	3.29	2.0	2.64
April	2.1	2.15	2.13
May	1.64	1.05	1.34
June	1.91	1.71	1.54
July	2.03	6.34	4.18
August	3.31	5.63	4.47
September	5.57	4.92	5.34

Table 4. *Uca annulipes. Carapace-width range, range and mean gonad indices of non-ovigerous females for different months of the years 1963/1965*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1963	October	13.5—16.5	0.59— 7.71	5.31
	November	12.0—17.5	0.46— 6.06	2.17
	December	12.2—15.8	4.34—17.94	11.13
1964	January	12.0—17.2	1.43—12.61	6.44
	February	11.2—15.5	0.67—12.55	3.8
	March	11.7—16.7	0.94—12.09	3.29
	April	12.2—17.5	0.3 — 5.83	2.1
	May	13.0—16.5	0.74— 3.49	1.64
	June	13.1—15.8	0.34— 3.73	1.91
	July	12.8—16.5	0.68— 5.29	2.03
	August	12.2—17.0	0.91— 6.2	3.31
	September	13.5—16.6	2.51— 8.66	5.75
	October	14.0—16.2	0.46—11.08	4.55
	November	14.0—16.0	1.56—18.73	5.59
	December	14.0—16.0	2.49— 8.84	4.47
1965	January	12.0—16.0	0.89— 8.44	4.23
	February	14.5—16.5	0.42— 6.87	2.24
	March	13.5—16.5	0.76— 8.57	2.0
	April	12.2—17.5	0.63— 7.41	2.15
	May	15.0— 8.8	0.23— 2.64	1.05
	June	13.0—17.5	0.41— 3.13	1.71
	July	14.0—17.0	1.78—12.23	6.34
	August	14.2—17.0	1.71— 9.03	5.63
	September	12.2—16.0	1.44— 8.18	4.92

The lowest value (0.22) was also in November, 1964, showing an increase in value by 85 times.

When the mean gonad indices of non-ovigerous females alone are considered (Tables 3 and 4, Fig. 3*B*) their mean values during September to December show an increase over the overall mean (Table 2) for the respective months, indicating that the ovigerous forms generally have low gonad indices. The lowest value for a non-ovigerous female during the breeding season (August to April) was 0.46 (November, 1963 and October, 1964) and the highest was 18.73 (November, 1964); the increase was, thus, about 41 times.

When the values for all months were taken together, the lowest gonad index for a non-ovigerous female was

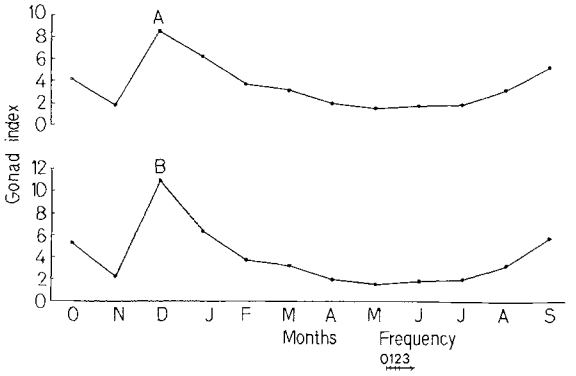

Fig. 3. *Uca annulipes.* Reproductive cycles of females (A), and of non-ovigerous females (B)

Table 5. *Uca annnlipes. Carapace-width range, range and mean gonad indices of ovigerous females for different months of the years 1963/1964*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1963	October	13.0—15.0	0.61—0.81	0.71
	November	14.0—15.0	0.24—0.85	0.61
	December	12.4—15.2	0.99—1.15	1.07
1964	September	14.5	1.09	1.09
	October	16.0	0.29	0.29
	November	14.0—16.0	0.22—0.57	0.39
	December	13.0—18.0	0.51—2.50	0.95

0.23 in May and the highest 18.73 in November; an increase of nearly 81 times. From this it is clear that a resting ovary in the month of May and the spent ovary (November, 1964) do not show significant difference in size.

From Table 5 it may be seen that the minimum (0.22) and the maximum (2.5) gonad indices for ovigerous females are found in November and December, respectively; the maximum mean value is in September (1.09). This gradual increase to nearly 11 times from the collapsed state takes place during a period of approximately 15 days. This suggests that, in some in-

dividuals, recuperation of the ovary occurs after the release of the larvae from the berry, but that in others a more rapid recuperation of the ovary can also be effected.

The yearly variations and average gonad indices of ovigerous females are presented in Table 6. It can be seen that, during September and December, the gonads of ovigerous females undergo rapid resumption of activity; October and November show only slow recovery of the gonad. This may be an indication that September and December are the two months of greater gonadal activity during the breeding season, one at the onset and the other before the termination of the season.

Table 6. *Uca annulipes. Yearly variations and average gonad indices of ovigerous females for different months of the year*

Month	Mean gonad index for 1963/1964	Mean gonad index for 1964/1965	Average gonad index for 1963/1965
September	—	1.09	1.09
October	0.71	0.29	0.5
November	0.61	0.39	0.50
December	1.07	0.95	1.00

Table 7. *Uca annulipes. Carapace-width range, range and mean gonad indices of males for different months of the years 1963/1964*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1963	October	15.0—19.5	0.80—0.55	0.26
	November	14.0—21.0	0.06—0.89	0.29
	December	11.0—22.2	0.10—0.5	0.31
1964	January	14.0—20.0	0.07—0.96	0.33
	February	15.8—19.5	0.15—0.66	0.32
	March	14.5—18.7	0.12—0.89	0.38
	April	15.0—19.0	0.13—0.31	0.23
	May	17.0—22.2	0.04—0.66	0.26
	June	15.1—19.9	0.15—0.47	0.31
	July	16.0—22.0	0.12—0.99	0.45
	August	16.0—20.0	0.09—0.59	0.30
	September	15.0—20.5	0.14—0.58	0.33

The data regarding the gonad index of the males for 1963/1964 are presented in Table 7 and Fig. 4.

The very low values for the males are presumably related to the small size of the testis. It is interesting that the testis does not seem to reach such a state of collapse through copulatory activity as that of the ovary after spawning. While the ovary remains inactive for a 3 month period, between May and July, with practically no oogenesis and egg laying, the testis shows evidence of more prolonged activity as may be seen from the data. The presence of spermatophores in the vas deferens during all the months suggests that males are sexually active throughout the year, irrespective of the restricted gonadal activity of the females.

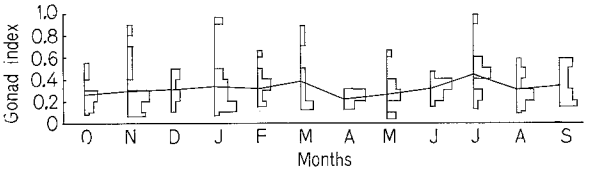

Fig. 4. *Uca annulipes.* Distribution graph and variations in mean gonad indices of males during October, 1963/September, 1964. Range of gonad index in each month is divided into groups of 0.1; frequency in each group is shown by horizontal divisions

Plots of the data on the gonad index of the males (Fig. 4) give a curve which suggests more prolonged and frequent activity of the testis than of the ovary. The highest value (0.99) was noted in a crab in July and the lowest (0.04) in May. Therefore, the increase in gonad size was only about 25-fold. The very low values noted during April and May are probably due to copulatory activity, which was frequently noticed in the field during this period.

During July, maximum value for the year was recorded not only with regard to mean value, but also for individuals. This might be preparatory to the next period of pairing before the active spawning period in females which extended from September to February. The trend suggested high gonadal activity before the period of frequent pairing. The data further showed that mating and egg deposition in these crabs need not necessarily be activities which are concurrent or consecutive, since these acts might be separated by wide intervals of time. This is not, however, unusual, since the spermatophores deposited within the spermathecae of the female crab during mating could remain viable for a long time (STEPHENSON, 1934).

Portunus pelagicus

The yearly variations and the average gonad indices of females of *Portunus pelagicus* examined during the two year period, February 1964 to January 1966, are presented in Tables 8 and 9 and Fig. 5. It will be seen (Fig. 5*A*) that low values are noted during the period April/July, with lowest values in April (0.23). Thereafter, the values showed a gradual increase to register a peak in January (5.33). Higher values are

Table 8. *Portunus pelagicus. Yearly variations and average gonad indices of females for different months of the year*

Month	Mean gonad index for 1964/1965	Mean gonad index for 1965/1966	Average gonad index for 1964/1966
February	1.76	2.96	2.36
March	2.30	2.01	2.15
April	0.29	0.18	0.23
May	0.33	—	0.33
June	0.31	0.17	0.24
July	0.71	—	0.71
August	1.39	0.73	1.06
September	0.95	1.93	1.44
October	0.62	2.69	1.66
November	0.92	2.68	1.8
December	3.90	2.71	3.31
January	5.44	5.24	5.33

Table 9. *Portunus pelagicus. Carapace-width range, range and mean gonad indices of females for different months of the years 1964/1966*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1964	February	100.0—154.0	0.55— 6.08	1.76
	March	98.0—134.0	0.51— 7.41	2.3
	April	106.0—130.0	0.06— 0.73	0.28
	May	116.5—140.0	0.09— 2.49	0.33
	June	111.5—157.0	0.14— 2.15	0.31
	July	118.5—161.0	0.27— 1.89	0.71
	August	126.0—161.0	0.28— 5.34	1.39
	September	122.0—151.0	0.38— 2.66	0.95
	October	113.5—145.0	0.03— 1.97	0.62
	November	122.0—150.0	0.59— 1.73	0.92
	December	139.0—154.0	0.55— 7.24	3.90
1965	January	95.0—143.0	0.67— 9.69	5.44
	February	95.0—164.0	0.17— 9.65	2.96
	March	107.5—143.0	0.07—10.62	2.01
	April	113.0—141.0	0.02— 0.75	0.18
	May	—	—	—
	June	106.0—141.0	0.07— 0.40	0.17
	July	—	—	—
	August	107.0—143.0	0.22— 1.86	0.73
	September	121.0—155.0	0.35— 9.27	1.93
	October	129.0—153.0	0.37—10.27	2.69
	November	124.0—151.0	0.83— 7.45	2.68
	December	101.0—153.5	0.60— 7.4	2.71
1966	January	137.0—160.0	1.47— 9.29	5.24

noted for the 4 month period from December to March. In Figs. 5 *B*, *C* and 6 and in Table 8, the mean gonad indices for the years 1964 and 1965 are presented for comparison.

The highest index for any female during the whole period of study is in March, 1965 (10.62) and the lowest is in April, 1965 (0.02; Table 9), the increase is about 531-fold.

Table 10 and Fig. 7 *B* present mean and yearly variations of gonad indices of non-ovigerous females. The maximum mean value was noted in January (6.66)

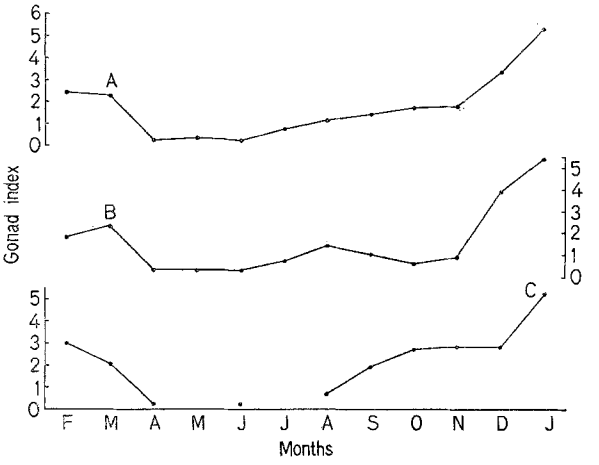

Fig. 5. *Portunus pelagicus.* Reproductive cycle. *A* Variations in mean gonad indices of females for 2 years from February, 1964; *B* variations in mean gonad indices of females during first year, from February, 1964/January, 1965; *C* variations in mean gonad indices of females during second year, from February, 1965/January, 1966

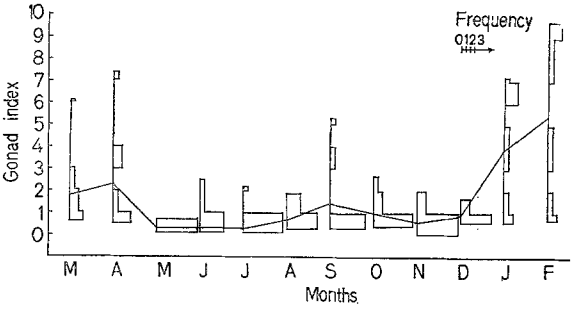

Fig. 6. *Portunus pelagicus.* Distribution graph illustrating inhomogeneity of females throughout annual cycle during year 1964/1965. Range of gonad index in each month is divided into groups of 1; frequency in each group is shown by horizontal divisions

and the minimum in April (0.22). The low values continued until August (1.05), with a gradual increase thereafter; the peak was attained in January, followed by a steady decline until the lowest value was recorded in April.

The lowest gonad index value noted in a non-ovigerous female during the course of the present investigation is 0.02 and the highest is 10.62 (Table 11); the increase amounts to about 531-fold. This confirms

that the gonad condition is not the same in all non-ovigerous females or recuperation of the ovary in these forms is not simultaneous, owing to the intervention of several factors which influence the complicated cycle of gonadal activity. Factors with high values during the non-breeding season need not necessarily be effective to result in berry formation. The probability of resorption of the gonad should not be forgotten when considering these values.

A separate determination of the gonad indices of ovigerous females alone has been made, and the data are presented in Tables 12 and 13. This helps us to arrive at a definite conclusion regarding the possibility of whether an already berried female can produce a subsequent brood during the same breeding season. A reliable conclusion regarding the frequency of gonad activation and berry formation can also be arrived at by separating the values for ovigerous females from those of the total females of each sample. The highest mean value (2.25) was recorded in December. During January, February, March and November, ovigerous females had fair mean values which suggest the production of more than one brood by an individual during the course of the breeding season.

Table 10. *Portunus pelagicus. Yearly variations and average gonad indices of non-ovigerous females for different months of the year*

Month	Mean gonad index for 1964/1965	Mean gonad index for 1965/1966	Average gonad index for 1964/1966
February	1.06	4.02	2.54
March	3.29	2.20	2.74
April	0.27	0.18	0.22
May	0.33	—	0.33
June	0.31	0.17	0.24
July	0.71	—	0.71
August	1.39	0.73	1.05
September	1.07	1.93	1.5
October	0.59	3.48	2.03
November	0.71	2.92	1.82
December	6.85	2.85	4.85
January	6.56	6.77	6.66

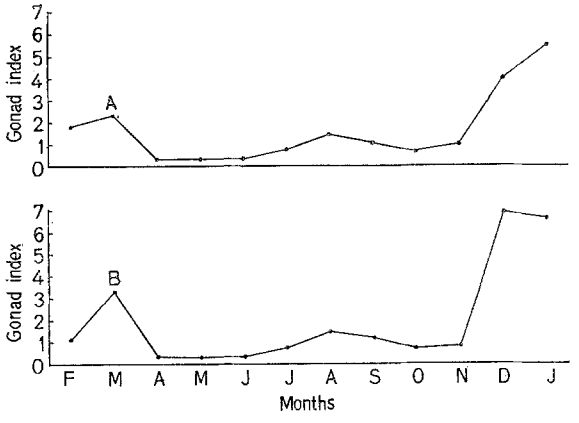

Fig. 7. *Portunus pelagicus.* Reproductive cycles of all females (A), and of non-ovigerous females (B)

Table 11. *Portunus pelagicus. Carapace-width range, range and mean gonad indices of non-ovigerous females for different months of the years 1964/1966*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1964	February	100.0—154.0	0.55— 1.43	1.06
	March	98.0—134.0	0.98— 7.41	3.29
	April	106.0—124.0	0.06— 0.73	0.27
	May	116.5—140.0	0.09— 2.49	0.33
	June	111.5—157.0	0.14— 2.15	0.31
	July	118.5—161.0	0.27— 1.89	0.71
	August	126.0—161.0	0.28— 5.43	1.39
	September	123.0—151.0	0.38— 2.66	1.07
	October	118.0—144.0	0.20— 1.06	0.59
	November	122.0—149.0	0.59— 0.85	0.71
	December	141.0—146.0	0.55— 7.24	6.85
1965	January	95.0—143.0	0.67— 9.69	6.56
	February	100.0—164.0	0.17— 9.65	4.02
	March	107.0—132.0	0.07—10.62	2.20
	April	113.0—141.0	0.02— 0.75	0.18
	May	—	—	—
	June	106.0—141.0	0.07— 0.40	0.17
	July	—	—	—
	August	107.0—143.0	0.22— 1.86	0.73
	September	121.0—155.0	0.35— 9.27	1.93
	October	129.0—155.0	0.37—10.27	3.48
	November	139.0—151.0	0.83— 7.45	2.92
	December	129.0—155.5	0.60— 7.4	2.85
1966	January	145.0—160.5	1.61— 9.29	6.77

Table 12. *Portunus pelagicus. Yearly variations and average gonad indices of ovigerous females for different months of the year*

Month	Mean gonad index for 1964/1965	Mean gonad index for 1965/1966	Average gonad index for 1964/1966
February	3.16	0.50	1.83
March	1.31	1.27	1.28
April	0.56	—	0.53
September	0.57	—	0.57
October	0.71	0.84	0.77
November	1.64	1.80	1.72
December	1.94	2.57	2.25
January	0.95	1.66	1.31

Table 13 shows the minimum individual value in October (0.03), the maximum in February (6.08), an increase of about 203 times; this increase occurs whilst the berry is still retained. This gonadal activity shown by ovigerous females, and extending from November to March, indicates protracted gonadal function.

From these considerations of gonad index studies on non-ovigerous and ovigerous females, it may also be concluded that the interval between successive broods in both categories in the breeding season may vary depending upon several factors yet to be determined.

Table 13. *Portunus pelagicus. Carapace-width range, range and mean gonad indices of berried females for different months of the years 1964/1966*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1964	February	112.0—124.0	0.66—6.08	3.16
	March	100.0—105.0	0.51—3.49	1.31
	April	109.0—130.0	0.56—0.57	0.56
	September	122.0—143.0	0.52—0.59	0.57
	October	113.5—145.0	0.03—1.97	0.71
	November	138.0—150.0	1.55—1.73	1.64
	December	139.0—154.0	0.55—4.19	1.94
1965	January	96.5— 99.0	0.70—1.2	0.95
	February	95.0—113.0	0.28—0.62	0.50
	March	112.0—143.0	1.04—1.50	1.27
	October	129.0—153.0	0.49—1.30	0.84
	November	139.0—151.0	0.93—3.39	1.80
	December	125.0—135.0	0.68—5.34	2.57
1966	January	145.0—160.0	1.47—1.89	1.66

Table 14. *Portunus pelagicus. Carapace-width range, range and mean gonad indices of males for different months of the years 1964/1965*

Year	Month	Carapace-width range (mm)	Range of gonad index	Mean gonad index
1964	February	68.0—132.0	0.05—0.89	0.30
	March	90.0—145.0	0.03—0.42	0.18
	April	73.5—123.5	0.04—0.72	0.24
	May	109.0—134.0	0.04—0.42	0.23
	June	115.5—155.0	0.17—0.72	0.47
	July	99.0—138.0	0.05—0.77	0.58
	August	107.0—157.0	0.11—0.58	0.29
	September	111.0—155.0	0.10—0.73	0.32
	October	125.0—144.0	0.36—0.82	0.43
	November	129.0—130.0	0.93—1.03	0.98
	December	—	—	—
1965	January	103.0—132.0	0.11—0.82	0.47

The gonad index values of males are given in Table 14 and in Fig. 8. As in *Uca annulipes*, the values of males are not clearly indicative of the duration of the breeding season. In males, the spermatophores are found throughout all months, and testicular activity is indicated by the presence of sperms in the testis. However, a low gonad index may mean a spawned-out condition and a high value is, no doubt, suggestive of increased testicular activity.

The lowest gonad index noted in a male was in March (0.03) and the highest in November (1.03). In December, no male was present in the sample. The increase from minimum to maximum gonad size was about 34 times. The lowest mean value was in March (0.18) and the highest in November (0.98) both coinciding with the months in which lowest and highest gonad index values were recorded for individuals.

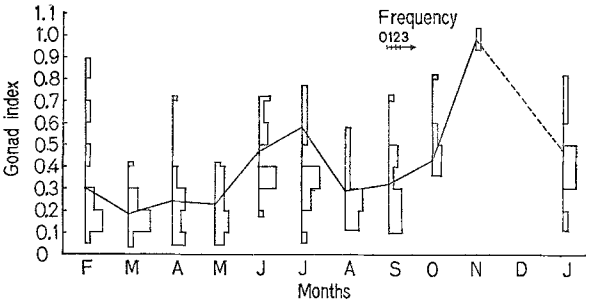

Fig. 8. *Portunus pelagicus.* Distribution graph and variations in mean gonad indices of males during February, 1964/January, 1965. Range of gonad index in each month is divided into groups of 0.1; frequency in each group is shown by horizontal divisions

The testicular cycle, as indicated by the male gonad index, is as follows. From the lowest mean in March (0.18) there is a gradual increase in subsequent months to 0.58 in July. The downward trend in August (0.29) may be due to copulative activity prior to ovarian activation in August (female gonad index showed an increase in August). From the low value of August there is a gradual rise until November (0.98); data for December could not be collected. This is followed by a gradual decline in January and February. Thus, in testicular development, two peaks are discernible, one in July and the other in November, preceding the initiation and peak periods, respectively, of ovarian activity.

Thus the breeding season in *Portunus pelagicus*, along the southwest coast of India seems, from a study of gonadal activity, to be an extended one of nearly 9 months, from August to April, with maximum gonadal activity during December/January.

Metapenaeus affinis

Table 15 and Fig. 9 give the yearly variations and mean gonad indices of female *Metapenaeus affinis* examined during the 2 year period, beginning March, 1964. The lowest average value (1.85) was noted in June (Table 15, Fig. 9*A*). Thereafter, a gradual increase is evident during the subsequent 6 months; the peak was attained in December (9.35). This was followed by a slight fall to 7.06 in January. February also registered a high value (9.26), but was followed by a fall in March and a slight rise in April. The same table provides, separately, the mean gonad indices for 1964/1965 and 1965/1966 (Figs. 10 and 9*B*, respectively). The period of breeding of this prawn along the south-west coast of India seems to be from August to April, with a major peak in December and a minor peak in April.

A study of the values of the gonad indices of individual specimens during different months is helpful

Table 15. *Metapenaeus affinis. Yearly variations and average gonad indices of females for different months of the year*

Month	Mean gonad index for 1964/1965	Mean gonad index for 1965/1966	Average gonad index for 1964/1966
March	3.97	6.38	5.17
April	4.62	7.62	6.12
May	2.89	3.27	3.08
June	1.84	1.87	1.85
July	1.30	2.73	2.02
August	2.84	4.67	3.76
September	2.25	4.77	3.51
October	4.49	4.74	4.62
November	4.15	5.94	5.04
December	11.73	6.96	9.35
January	5.67	8.94	7.06
February	10.19	8.33	9.26

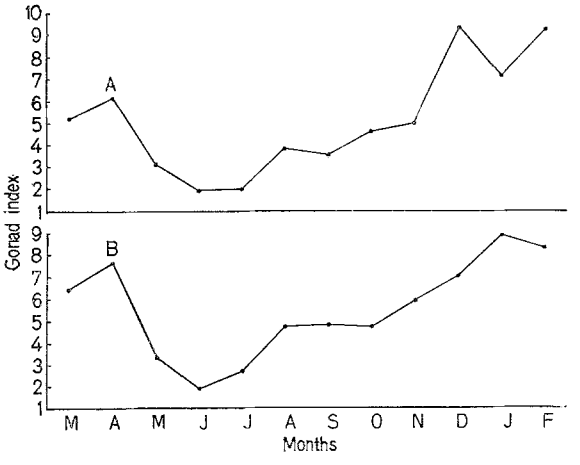

Fig. 9. *Metapenaeus affinis.* Reproductive cycle. *A* Variations in mean gonad indices of females for 2 years from March, 1964; *B* variations in mean gonad indices of females for second year, from March, 1965 to February, 1966

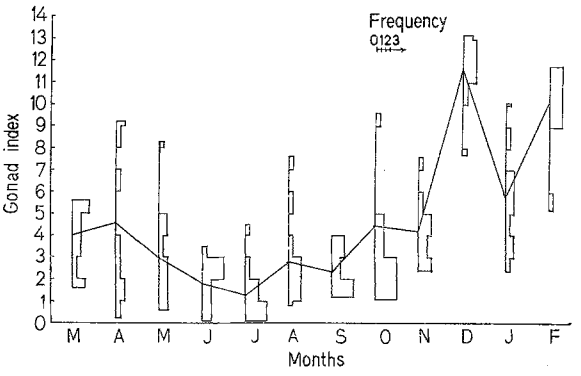

Fig. 10. *Metapenaeus affinis.* Distribution graph illustrating inhomogeneity of the population throughout annual cycle during first year, from March, 1964/February, 1965. Range of gonad index in each month is divided into groups of 1; frequency in each group is shown by horizontal divisions

Table 16. *Metapenaeus affinis. Length-range, range and mean gonad indices of females for different months of the years 1964/1966*

Year	Month	Length range (mm)	Range of gonad index	Mean gonad index
1964	March	120.0—150.0	1.57— 5.55	3.97
	April	107.0—149.0	0.21— 9.23	4.62
	May	108.0—131.5	0.60— 8.27	2.89
	June	118.0—167.0	0.11— 3.49	1.84
	July	112.5—171.0	0.12— 4.45	1.30
	August	130.5—170.0	0.80— 7.62	2.84
	September	128.0—142.0	1.20— 3.98	2.25
	October	119.0—149.0	1.09— 9.57	4.49
	November	133.0—157.0	2.42— 7.55	4.15
	December	135.0—163.0	7.71—13.21	11.73
1965	January	148.0—169.0	2.42—10.13	5.67
	February	130.0—171.0	5.23—11.81	10.19
	March	127.0—168.0	4.32—11.44	6.38
	April	125.0—160.0	1.87—12.03	7.62
	May	107.0—144.0	1.14— 6.0	3.27
	June	126.0—141.5	0.49— 3.81	1.87
	July	125.0—150.0	0.25— 5.64	2.73
	August	130.0—145.0	1.56— 9.46	4,67
	September	120.0—151.0	1.30— 7.95	4.77
	October	124.0—146.0	1.76— 8.23	4.74
	November	137.0—163.5	1.78—10.07	5.94
	December	125.0—157.0	3.46—10.58	6.96
1966	January	116.5—159.0	3.27—13.65	1.94
	February	130.0—162.0	2.95—14.09	8.33

in determining the rate of development of the gonad during the period concerned. Table 16 shows the highest gonad index for a female individual during this study to be 14.09 in February, 1966; the lowest to be 0.11 in June; an increase of about 128 times. A comparative study of the rate of change in the gonad weight during the breeding and the non-breeding season enables an idea of the condition of the gonad during these two periods to be formed. The lowest value noted during the breeding season indicates a spawned-out ovary, whereas a similar low value in non-breeding months denotes a resting gonad. The values noted during the present study are as follows. The lowest individual gonad index registered during the breeding season was in April, 1964 (0.21). In the non-breeding months, on the other hand, the lowest recorded value (0.11) was in June, 1964. Thus, a distinction between a spent gonad and a resting gonad may be noted, the former having a comparatively higher value, indicating the possibility of the production of successive broods in the breeding season.

Table 17. *Metapenaeus affinis. Length-range, range and mean gonad indices of males for different months of the years 1964/1966*

Year	Month	Length range (mm)	Range of gonad index	Mean gonad index
1964	March	112.5—135.0	0.58—1.35	0.94
	April	115.0—140.0	0.83—1.30	0.96
	May	100.0—133.0	0.58—1.17	0.93
	June	105.0—147.0	0.20—0.86	0.56
	July	118.0—165.0	0.57—1.30	0.96
	August	110.0—130.5	0.40—1.06	0.76
	September	114.5—129.5	0.60—1.14	0.88
	October	115.0—127.5	0.75—1.79	1.11
	November	124.0—140.0	0.65—1.37	1.05
	December	131.0—138.0	0.70—1.46	1.09
1965	January	119.0—141.0	0.54—1.71	0.99
	February	131.0—142.0	0.49—1.26	0.86

The range and mean gonad indices of males are presented in Table 17 and Fig. 11. The peak reproductive activity of males precedes that of females and, therefore, the reproductive cycles of the sexes are not concurrent. The presence of spermatophores in the terminal ampoule of at least some specimens almost throughout the year and the uniformly fair values (with the exception of June) of gonad indices during the year suggest prolonged activity in the testis.

The maximum value recorded for a male was 1.79 in October, the lowest, 0.2 in June; an increase of almost 9 times. The highest mean gonad index (1.11) was in October, coinciding with the highest individual value. The lowest mean was in June (0.56) indicating low activity during this period. Succeeding this period of low values, activity was initiated in July and reached a peak in October, a month prior to the female peak. Although the activities of both testis and ovary begin simultaneously in July/August, the peak is attained first by the former and the downward trend thereafter is suggestive of copulative activity. A similar, but less pronounced, peak precedes the minor peak for females noted in April.

At least some females carrying spermatophores in the thelycum may be found in almost all months of the year, indicating continuous testicular activity and the probability of copulation during a major part of the year.

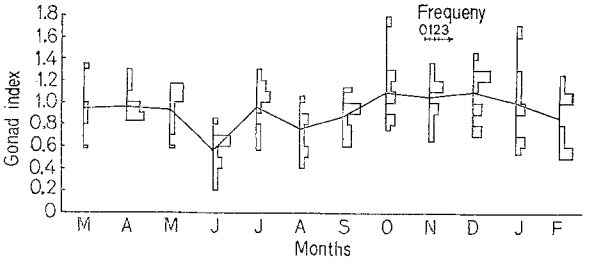

Fig. 11. *Metapenaeus affinis.* Distribution graph and variations in mean gonad indices of males during the year from March, 1964/February, 1965. Range of gonad index in each month is divided into groups of 0.1; frequency in each group is shown by horizontal divisions

Discussion

A reasonably reliable picture of the reproductive cycles of *Uca annulipes*, *Portunus pelagicus* and *Metapenaeus affinis* has been obtained during the present study by means of the gonad index method. The results furnish supplementary evidence to those obtained from a study of the incidence of ovigerous females. This method has additional advantages over the usual method of determining the breeding season of crabs by merely plotting the incidence of ovigerous females against different months, since it shows clearly, stage by stage, the changes undergone by the gonad during the annual cycle.

Several methods have been employed for determining the annual reproductive cycles of marine invertebrates (see GIESE, 1959). The gonad index method (1) provides accurate information of the breeding condition of the individual animal; (2) reveals the breeding activity of the individuals; (3) shows the sequence of events in the gonad between spawning seasons. Thus, the gonad index represents a measure of the reproductive condition of a population. A low value represents a quiescent, unripe, or spawned-out condition of the gonad, while a high index indicates the ripeness of the gonad; an immediate fall is suggestive of spawning

activity. Hence, the application of this method facilitates a quantitative assessment of the individual reproductive condition and enables us to obtain a graphic representation of the reproductive cycle of the species in question.

Employing this method, the annual reproductive cycles of a number of invertebrates have been studied from the west coast of America by GIESE (1959) and coworkers (1958). From the east coast of India reports, by investigators who have employed this method, are available on the reproductive cycle of the prawn *Penaeus indicus* (SUBRAHMANYAM, 1963), the sea star *Oreaster hedemanni* (RAO, 1965; RAHAMAN, 1966), the holothurian *Holothuria scabra* (KRISHNASWAMY and KRISHNAN, 1967) and the crab *Portunus pelagicus* (RAHAMAN, 1967).

months may not be suitable for the breeding of this species along the west coast. The monsoon months constitute the non-breeding season for this species along the west coast, whereas, on the east coast, similar changes in salinity do not occur and breeding might be continuous there. A similar discontinuity in the breeding season during the monsoon period has been noted in a variety of Crustacea from the west coast of India (MENON, 1952; GEORGE, 1961).

From Table 18, it can be seen that the increase in size of the ovary is greater than the increase in size of the testis in all the species investigated. In males the testis is very small in size. It is also evident from the tables that the fluctuations in the gonad index of males are not so pronounced as those in females and, therefore, the values of females alone have been taken to

Table 18. *The relative increase in the gonad index of females and males of three decapod crustaceans, Uca annulipes, Portunus pelagicus and Metapenaeus affinis*

Name of species	Sex and stage	Gonad	Minimum gonad index	Maximum gonad index	Relative increase
Uca annulipes	Female	Ovary	0.22	18.73	85
	Female (non-ovigerous)	Ovary	0.23	18.73	81
	Female (ovigerous)	Ovary	0.22	2.5	11
	Male	Testis	0.04	0.99	25
Portunus pelagicus	Female	Ovary	0.02	10.62	531
	Female (non-ovigerous)	Ovary	0.02	10.62	531
	Female (ovigerous)	Ovary	0.03	6.08	203
	Male	Testis	0.03	1.03	34
Metapenaeus affinis	Female	Ovary	0.11	14.09	128
	Male	Testis	0.19	1.79	9

From the data presented for the crabs *Uca annulipes* and *Portunus pelagicus*, and for the prawn *Metapenaeus affinis*, it is possible to arrive at interesting conclusions regarding the annual reproductive cycle of these species. It is evident that breeding in these crustaceans extends for several months of the year, with pronounced activity during certain months. The peak periods of gonad indices occur in December for *U. annulipes* and *M. affinis* and in December/January for *P. pelagicus*. Minor peaks of gonadal activity are also evident in all these cases. Similar data are available in the case of *P. pelagicus* from the east coast of India. Recently RAHAMAN (1967) concluded that *P. pelagicus* is a continuous breeder, with 3 periods of maximal gonad indices, November, January, and June, but with greatest activity in November/January. In *P. pelagicus*, the apparent differences in the breeding season on the east and west coasts may be due to the different hydrological conditions prevailing in the inshore waters of the west coast of India. The region is under the strong influence of the south-west monsoon, and the low salinity of the water during the monsoon depict the reproductive cycle. The females with high gonad index are potential spawners, and those with high index in the non-breeding season may be just stragglers which may either spawn or effect resorption of ova leading to a resting phase.

It is clear that, during certain months, individuals in different stages of maturity are present, representing a heterogenous population as seen from the range of variation in the gonad index and the frequency of individuals shown diagrammatically in horizontal histograms. This is also confirmed by the fact that the mean indices for the males and females representing these samples are markedly lower than those with ripe gonads.

From Table 18 it may be seen that the maximum value of the gonad index of females of *Uca annulipes* is greater than those of *Portunus pelagicus* or *Metapenaeus affinis*. This indicates that, during the breeding season, the ovary in *U. annulipes* assumes a relatively greater size in relation to the body, and is consequently capable of producing a larger number of gametes and thereby, a corresponding number of larvae, than the

other 2 species. This greater production of offspring in *U. annulipes* is probably due to its typical estuarine habitat, where water movement is considerable, with the possibility of the larvae drifting off from this special littoral habitat to the open areas where settlement is not possible.

Water movement provides an ideal means of scattering the larvae over a wide area, affording the maximum opportunity for the colonisation of suitable areas and, thereby, reducing overcrowding. However, forms such as *Uca annulipes*, which are restricted to special ecological niches in localised pockets of the environment such as sandy or muddy areas of estuarine habitats, demand a greater production of offspring, to compensate foi the pitfalls which may attend their planktonic existence, such as unfavourable transport to open ocean by water movement. Whereas, in a steady current, planktonic larvae are carried only in one direction, the oscillating tidal currents which prevail in the estuarine areas distribute the larvae in various directions from their original habitat. Large numbers of these larvae are likely to be drifted off the coast during the ebb tide. The mortality amongst the larvae which fail to find the requisite type of ground, together with the mortality from other causes, is considerable (THORSON, 1950). As there are chances of waste of larvae by dispersal as well as depredation by predators, the high value for the gonad index of *U. annulipes* compared to the other species studied seems to be reasonable, and the greater production of offspring in this species can thus be explained.

This fact is further confirmed from the same locality in another typical estuarine form, a shipworm *Nausitora hedlyi* with a high gonad index — 45.64 probably one of the highest recorded in any species studied so far (SARASWATHY, 1967). Similarly, GALTSOFF (1961) noted that, in *Crassostrea virginica*, where the highest gonad development is reached shortly before spawning, the ovary or the testis may form over 40% of the total body volume and weight.

Metapenaeus affinis shows a greater gonad index than *Portunus pelagicus*. This is probably due to the brooding habits of the latter, which sheds the eggs onto the pleopods and protects them in berry until the zoeae are liberated. In the case of *M. affinis*, planktonic life is protracted, and there is thus the likelihood of a much higher mortality due to predation than in *P. pelagicus*; therefore, a larger number of eggs is produced in the former species.

Studies on the gonad index have, hitherto, been performed chiefly on species where there is no sexual union, (sea urchins, sea stars, chitons, abalones). As external fertilisation is based on a chance-meeting of the reproductive elements, there is a considerable development of the testis as well as the ovary to compensate for the waste during spawning. The present study is based on species in which there is sexual union, which ensures effective fertilisation. This establishes an interesting correlation between the relative increase of the male and female sex organs and breeding habits (Table 18). Whereas the ovary and testis attain almost equal size in animals with external fertilisation (sea-urchin and sea stars), in these crustaceans the testis is proportionately small as may be seen from the values presented of the gonad index of males. It is noteworthy that, even in the three species under study, there are interesting differences. Despite sexual union, the testis of *Metapenaeus affinis* shows a comparatively much higher gonad index than that of the other two species of crabs, probably because the spermatophores in the former species are not inserted into the body, but deposited in the thelycum; they are thus exposed, and likely to be lost during the movements of the prawn. In the other 2 species the spermatophores are deposited into the spermathecae of the female crabs.

The reproductive cycles of males and females of these crustaceans are not concurrent. The gonad indices of males do not show significant increase, whereas those of females show a definite cycle indicative of growth, maturity and collapse through spawning and rest. In contra-distinction to this, in the tropical echinoderm *Holothuria scabra*, KRISHNASWAMY and KRISHNAN (1967) observed that both males and females breed almost simultaneously, even though gonadal activity is more intense in females than in males. However, in the present study, the gonad index of males shows an upward trend before the breeding season; similar cases of ill-defined male cycles have been reported by LASKER and GIESE (1954) in the purple sea urchin *Strongylocentrotus purpuratus*. FARMANFARMAIAN et al. (1958) recorded the presence of males with sperms throughout the year, but ripe females occurred only during certain seasons.

The evidence at hand indicates that these tropical crustaceans have an extended breeding season with periods of intensive activity. "An extended breeding season may mean that the individuals of a species are producing several successive broods during the year or that they are breeding asynchronously, i.e., some are in the earlier stages of maturation, some are spawning and still others are already spent" (GIESE, 1959). From the data based on the monthly samples of all these 3 species, it is seen that, although the breeding activities begin almost simultaneously, samples of different months contain crustaceans in different stages of reproductive activity. Some show high indices, others have low values; this is due to the inhomogeneous condition of the population, which consists of maturing forms, of spawners, and of individuals which are already spent. Therefore, the breeding season appears to be protracted, and several broods are produced during the season. As PANIKKAR and AIYAR (1939) have aptly pointed out, the individual reproductive rhythm of a species may not coincide, and this would result in asynchronous spawning.

Although it was believed that tropical animals breed throughout all the months of the year (SEMPER, 1881), recent research strongly suggests a definite periodicity in breeding in many species. STEPHENSON (1934) showed that the Great Barrier Reef invertebrates exhibit different patterns of breeding cycles, i.e., (a) a single breeding period in the year not lasting all the year round; (b) continuous breeding throughout the year with more activity in one part of the year than in the remaining months; (c) discontinuous breeding occurring in relation to lunar phases, during a larger or shorter portion of the year; (d) two spawning periods in the year, with a quiescent phase between them. Such differences have been noted by PANIKKAR and AIYAR (1939) in the brackish-water animals of Madras, and by PAUL (1942) in the sedentary fauna of Madras Harbour. Similar detailed data have not, hitherto, been collected from the west coast of India. As observed by STEPHENSON (1934) in *Thalamita stimpsoni*, the two crabs chosen for the present study also show an extended breeding season, with a well marked period of intensive gonadal activity. The prawn *Metapenaeus affinis* also has an extended breeding season, and shows periods of peak activity. In this connection it is interesting to note that, while it is generally believed that tropical animals breed continuously throughout the year, the crustaceans under investigation have a distinct breeding period as observed recently in a variety of other tropical marine invertebrates such as *Oreaster hedemanni* (RAO, 1965; RAHAMAN, 1967), *Penaeus indicus* (SUBRAHMANYAM, 1963), *Meretrix casta* (DURVE, 1964).

The factors which induce breeding in these marine invertebrates may be endogenous or exogenous or an interaction of both these factors. Since temperature has an important bearing on the breeding of marine animals, the tendency towards an extended breeding in the animals of tropical waters can be attributed to the uniformly high temperature (ORTON, 1920). However, the work of HORNELL (1910), MORTENSEN (1921), NICHOLLS (1931), MALPAS (1933), MOOREHOUSE (1933), GALTSOFF (1934), STEPHENSON (1934) and others point to the fact that temperature is not the sole factor influencing the breeding of marine animals in the tropics.

In the tropics, a number of workers have correlated breeding in marine animals with changes in salinity. MALPAS (1933) observed in the pearl oyster *Margaritifera vulgaris* of Ceylon, two spawning periods each year which reach their maxima in July, August and in December/January, coinciding with the south-west and north-east monsoons, respectively. This coincidence of the spawning maximum with maximum and minimum conditions of salinity suggests that oysters are stimulated to maximum spawning by salinity changes. In the Great Barrier Reef region, the summer months during which the vast majority of the species investigated was found to spawn, were the months of maximum rainfall, with consequent lowering of salinity (STEPHENSON, 1934). FOX (1924) showed that breeding was correlated with the phases of the moon in Red Sea echinoderms, molluscs and crabs. Similar correlation with moon phases and reproductive activity was not observed in the present study.

PANIKKAR and AIYAR (1939) concluded that the lowering of salinity consequent to the onset of the north-east monsoon influences the breeding of animals along the Madras Coast. The effects produced by the north-east monsoon along the Madras Coast are not comparable with those of the south-west monsoon along the west coast of India. The south-west monsoon commences some time in late May or early June, causing copious precipitation during the subsequent 4 months, during which time this area records more than half the total rainfall for the whole year. The inflow of large quantities of water through the major river systems into the Vembanad Lake, and their subsequent outflow through the Cochin Backwaters into the Arabian Sea, maintain the salinity of the area at a very low level for as long a period as 3 to 4 months. The intertidal animals such as *Uca annulipes* must, during this period, certainly experience prolonged stress due to very low salinity. In these circumstances those animals endowed with the ability to acclimatise to this condition may survive; others perish. It seems probable that, while a sudden change in salinity may act as a stimulus to trigger off reproductive activities in animals, as suggested by PANIKKAR and AIYAR (1939), continuous stress through low salinity may lead to mass mortality among many species, and those which survive seem to postpone their reproductive activity.

While the general hydrographic conditions prevailing along the east and west coasts vary, owing to the influence of the monsoon rains, it is interesting to note that the breeding period of *Uca annulipes* on both coasts is more or less the same. An explanation for this apparent similarity, despite hydrographic differences, is that during this period, in both these habitats, the ambient water has a medium salinity which probably may be the most suitable for the life and growth of the larvae. This fact was confirmed by laboratory experiments; zoeae of *U. annulipes* are unable to tolerate very low or very high salinity. Under both these conditions of salinity they are completely absent. It is also interesting to note that the liberation of the larvae occurs coincident with the presence of a lush plankton bloom during this time, both along the east and west coasts. This timing must have been accomplished through years of gradual acclimatisation and adaptation to the rhythms of meteorological, climatic and hydrographic conditions.

This timing of breeding is based on the fact that the planktotrophic larvae will have a better chance of finding an adequate food supply if liberated at a period when suitable types of planktonic food are available in the medium. This enables the larvae to exploit the

abundant food resources and grow rapidly before leaving the plankton. Thus, the breeding of this species seems to be influenced by the physico-chemical and biological conditions of the environment. It has been noticed in tropical waters that, when little seasonal variation in the quantity of phytoplankton occurs, breeding shows a tendency to be continuous throughout the year, although individuals may still have restricted breeding seasons.

In *Uca annulipes*, since the restricted peak breeding season coincides with the obvious plankton peaks in the inshore waters, there seems to be some justification in drawing a correlation between breeding and plankton peaks. The apparent similarity in the reproductive cycles of these crustaceans indicates that the factors controlling the reproductive cycles of the other two species, *Portunus pelagicus* and *Metapenaeus affinis*, may probably be the favourable salinity conditions of the environment and the availability of planktonic food for the larvae in this area. Since the larvae of these species are also planktotrophic, the liberation of the young at the most suitable time is, therefore, distinctly advantageous.

Summary

1. The annual reproductive cycles of two species of crabs, *Uca annulipes* (LATREILLE), *Portunus pelagicus* (LINNAEUS), and the prawn *Metapenaeus affinis* (MILNE-EDWARDS) have been studied employing the gonad index method. In these crustaceans, the breeding season is not continuous all the year round, but extends over several months of the year, with distinct peak periods of gonadal activity. In the female *U. annulipes*, the gonad index remains high during the months from July to March with a peak in December. *P. pelagicus* has a high gonad index for several months of the year from August to March, with a definite peak during December/January. In *M. affinis*, high gonad index values prevail from August to April, with a major peak in December and a minor peak in April.

2. The male and female reproductive cycles of these crustaceans are not concurrent. The peak of the reproductive cycle of males occurs slightly earlier in the breeding season than that of the female. In *U. annulipes* and *M. affinis*, fluctuation of the gonad index of the testis is not so conspicuous as that of the ovary; in males, sperms and spermatophores have been noticed throughout the year.

3. The ovigerous females of crabs with eggs in an advanced stage of development show a high gonad index and suggest the possibility of the production of a second brood during the same breeding season.

4. In the prawn *Metapenaeus affinis* also, the possibility of production of successive broods of eggs by an individual during a breeding season is indicated from the nature of the gonadal cycle.

5. In all three species, the low salinity period is unfavourable for breeding and the monsoon months are non-breeding months. The medium and high salinity conditions during the post-monsoon and premonsoon periods, respectively, with plenty of planktonic food for the larvae of these crustaceans, seem to be most favourable for breeding activity.

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First author's address: Dr. K. KRISHNA PILLAY
N. S. S. College
Mangeri
Kerala State
India

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