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Reproductive Biology of *Penaeus indicus* (H. Milne Edwards, 1837) from the Western Coastal Waters of Sri Lanka

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Abstract

The reproductive biology of *Penaeus indicus* (H. Milne Edwards, 1837) from the western coastal waters of Sri Lanka was studied during the period September 1998 to December 1999. Analysis of sex ratios of different size classes indicated that there was a significant deviation of sex ratio from unity for the size range studied. The predominance of males, especially in the size groups from 13.4 to 15.4 cm suggests that females may have a behavioral pattern of separating from males after reaching an age corresponding to size at first maturity. The sizes at 50% maturity for males and females were estimated as 12.83 and 14.86 cm, respectively. *P. indicus* spawns in the west coast of Sri Lanka throughout the year with peaks during the March/April and July/August periods. The estimated Type-I fecundity (total number of eggs that have been initially separated from the ovary in the reproductive stage I) of *P. indicus* varied between 1,165,660 to 1,411,406 eggs for the size range 11.03 to 16.93 cm. The estimated Type-II fecundity (total number of eggs which are ready to be shed in the reproductive stage IV) varied between 817,549 to 1,254,200 eggs for the size range 14.22 to 18.26 cm.

Introduction

The reproductive process of penaeids occurs in a continuous loop as a series of events from activation, through growth and gametogenesis in the gonads to the spawning of the gametes and recession of gonadal activity (Giese 1959). The reproductive process of penaeid shrimps involves attaining maturity, mating and spawning. Spawning usually occurs in open water of less than 50 m depth, often much shallower (Dall et al. 1990). The reproductive strategy of penaeids is iteroparity and they may spawn frequently, with only a short duration between successive spawnings and there may be several broods within a single year (Rao 1968).

The shrimp *P. indicus* (H. Milne Edwards, 1837) is a valuable penaeid shrimp found in the coastal waters of south and east Africa, Madagascar, India, Sri Lanka, South China, the Philippines and the northern Australia. It inhabits shelf areas from the coastline to depths of about 90 m, but is most abundant in shallow waters of less than 30 m depth, on sand or mud (Fischer and Bianchi 1984).

Thirty one species of penaeid shrimps have been recorded from Sri Lankan waters. Of these, the most important commercially is *P. indicus* (De Bruin 1970). It constitutes almost 50 to 70% of the total annual shrimp landings from Sri Lanka (Jayawickrema and Jayakody 1992). *P. indicus* is one of the major contributors to the shrimp catches from the Negombo lagoon and the associated coastal waters on the west coast of Sri Lanka (Jayawardane et al. in preparation).

Although some studies on the reproductive biology of *P. indicus* from the Western Indian Ocean have been conducted by Subrahmanyam (1965), Rao (1968), Subramanian (1987), Devi (1987), Hossain et al. (1991) and Mohan and Siddeek (1995), a detailed study on the reproductive biology of this species from the coastal waters off Sri Lanka has not been attempted so far. Inadequate knowledge on the reproductive biology of this species has restricted management of the shrimp fishery in this area.

The present paper is mainly focused on the vital aspects of the reproductive biology of *P. indicus* from the fisheries point of view. The objectives of the present study were to investigate the mean size at maturity, spatial and temporal variations in the sex ratio and the sexual dimorphism, spawning season, spawning frequency and the fecundity.

Materials and Methods

The sampling program commenced in September 1998 and continued for 16 consecutive months. For estimation of the mean size at maturity and the gonado somatic index (GSI) random samples of 40 to 50 shrimps were collected from trawl catches from the western coastal waters of Sri Lanka during the period September 1998 to August 1999 by making regular fortnightly field visits to the major fish landing centers in the west coast (Fig. 1). To determine the sex ratio and the sexual dimorphism, representative shrimp samples were collected from different gear types operating in the Negombo lagoon (trammel nets, cast nets, drag nets and stake-seine

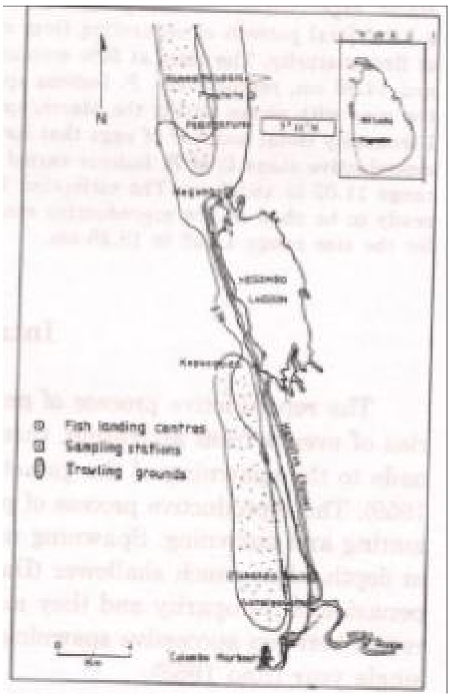

Fig. 1. Map of the study area

nets) and the associated coastal region (nonmechanised and mechanised trawls), at weekly intervals from September 1998 to August 1999 (Sample size varied from 659 to 24,396). These were then brought to the laboratory at the National Aquatic Resources Research and Development Agency (NARA), Colombo as rapidly as possible, for analysis.

Sex ratio and sexual dimorphism

In the laboratory all the shrimps were sorted to species and sexed. The total length of each specimen was measured to the nearest 0.1 cm using a measuring board. These samples were used to determine the overall sex ratio in all sites and the sex ratios specific to the lagoon and the associated coastal region. The estimated values for the sex ratios for each month were subjected to chi-square test (Zar, 1984) to determine whether these are significantly different from 1:1 ratio. In addition the same statistical test was used to investigate the size differences in the sex ratio.

Mean size at maturity and gonado somatic index (GSI)

Only the shrimps which are larger than the minimum size at maturity were used to determine GSI so as to avoid overestimation of immature stages and underestimation of GSI by including immature animals. In the laboratory the total length of each specimen was measured to the nearest 0.01 cm using a Vernier Caliper. The total weight of each individual was determined to the nearest 0.01 g. Shrimps were then dissected along the dorsal surface to expose the gonads and the stage of maturity was determined by macroscopic examination. Individual gonads were carefully removed and weighed to the nearest 0.0001 g to determine the GSI.

The GSI for each individual was estimated using the following equation described by Snyder, (1985) and monthly means were computed. All the shrimps in the samples were used in this analysis.

GSI = (Gonad weight x 100)/Body weight

Size at 50% maturity for the two sexes was estimated by plotting the percentage of mature shrimp in each size group against the mean length of the size class (Newman and Pollok 1974). All the shrimps in the samples were used in this analysis.

Fecundity and oocyte diameter frequency

Around 30 ovaries of reproductive stage IV and 20 ovaries of reproductive stages I, II, III and V of each species were preserved in Gilson's fluid (Bagenal and Braum 1978) for 10 to 12 weeks. They were shaken occasionally to separate eggs from the ovarian tissue. Fecundity was estimated volumetrically. Subsampling was carried out using a Stemple pipette (1 ml). The number of eggs in the ovaries of reproductive stages I to V was counted and the diameter of eggs in each ovary was measured using a graduated micrometer eye-piece. Oocyte diameter distribution for each reproductive stage was determined by pooling the results of all ovaries of the particular reproductive stage.

To estimate the batch fecundity, either as the number of eggs that are initially separated from the ovarian tissue (Type-I) (the mean number of eggs counted in the reproductive stage I) or as the number of eggs that are ready to be shed (Type-II) (mean number of eggs in the most advanced batches of the reproductive stage IV) (see Table 3), modes of the egg diameter distribution pattern of each reproductive stage were separated into their component batches using the method described by Bhattacharya (1967), which is widely used to separate the modes of frequency distributions. Once the batches were identified, the number of eggs initially separated from the ovarian tissue (Type-I) and the eggs that are ready to be shed (Type-II) were estimated (Table 3).

To estimate the relationship between the fecundity (Type-I) and body size a simple linear regression analysis (Zar 1984) was carried out between the number of eggs that are initially separated from the ovarian tissue (Type I fecundity) and the total length of the shrimp. Similarly the relationship between the Type II fecundity and the size of the shrimp was also determined. Knowing the proportion of eggs that are shed as the first batch and the number of eggs that initially separated from the ovarian tissue, the number of eggs that are shed in successive spawning acts was estimated.

Spawning season

The spawning season of *P. indicus* in the seas off the west coast of Sri Lanka was determined using the information on the occurrence of mature females in the population. To determine the spawning season, the percentage of mature shrimps (gravid and spent females) in the commercial shrimp catches (particularly in the trawl catches) was estimated on a monthly basis. This exercise was performed from February to December 1999 for males and September 1998 to February 2000 for females.

Results

Spatial and temporal variations in the sex ratio

The ratios of males to females in monthly catches within the lagoon were found not to be statistically different from unity ($P<0.05$) in the months October and December 1999 (Table 1). The deviations from unity in March and August 1999 were small (Fig. 2) and were found to be not different at the 99.9% level of significance. In the remaining six months the proportion of females exceeded males (November 1998 and January, February and from April until June 1999). It was only in September 1998 and July 1999 that the situation was reversed. However, it should be noted that the deviation from unity in the former month was not significant at the 99.9% level, which is a reflection of the relatively small sample size.

Similar statistical analysis of the offshore catches (Table 1; Fig. 2) revealed that sex ratios did not deviate significantly from unity (P<0.001) in eight of the twelve monthly samples. Only from May until August 1999 were the ratios significantly different from unity. In May, July and August the females were found to dominate catches whereas it was only in June that males outnumbered females. When the data from both locations were combined the overall sex ratios did not deviate from unity (P<0.001) in four months (September, October and December 1998 and March 1999). In the remaining months females dominated.

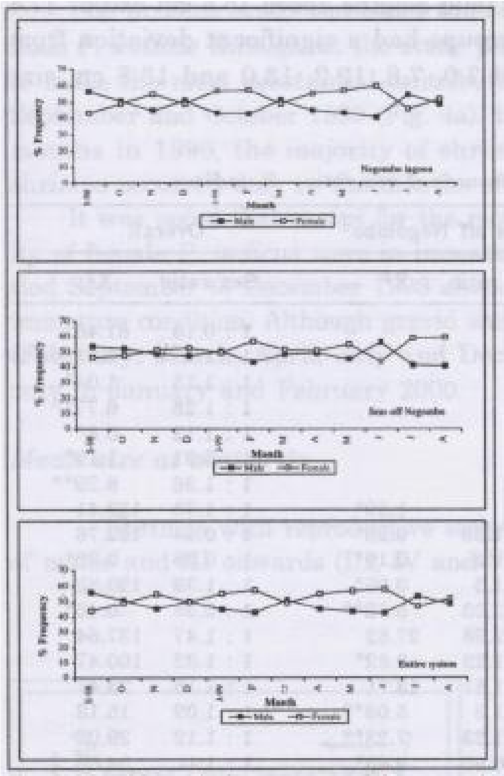

Fig. 2. Monthly variation patterns of the sex ratio of *P. indicus*

Size differences in the sex ratio

In lagoon catches, apart from the smaller sizes (3.4 to 5.8 cm total length) most of the other size groups had a significant deviation from unity (P<0.001 ; Table 2). Most of the uneven sex ratios had a predominance of females (Fig. 3), exceptions included 3.4 and 7.0 cm size groups.

Most size groups of *P. indicus* catches from offshore areas did not deviate significantly from unity

Table 1. Statistical analysis of the sex ratio of *P. indicus* on monthly basis

Month	Negombo lagoon		Seas off Negombo		Overall	
	Sex ratio	X^2	Sex ratio	X^2	Sex ratio	X^2
S - 98	1 : 0.77	9.31**	1 : 0.87	0.64*	1 : 0.79	9.53**
O	1 : 0.97	1.14*	1 : 0.92	0.3*	1 : 0.97	1.32*
N	1 : 1.22	53.55	1 : 1.05	0.13*	1 : 1.21	52.32
D	1 : 0.96	0.32*	1 : 1.10	0.58*	1 : 0.99	0.02*
J - 99	1 : 1.32	42.28	1 : 0.98	0.06*	1 : 1.23	31.58
F	1 : 1.34	227.57	1 : 1.31	8.18**	1 : 1.34	235.69
M	1 : 0.96	8.74**	1 : 1.05	0.52*	1 : 0.96	7.5**
A	1 : 1.23	248.33	1 : 1.03	0.28*	1 : 1.22	236.57
M	1 : 1.32	186.98	1 : 1.20	10.86	1 : 1.31	195.52
J	1 : 1.48	272.28	1 : 0.78	15.72	1 : 1.36	195.52
J	1 : 0.84	88.59	1 : 1.43	31.48	1 : 0.88	55.87
A	1 : 1.06	10.44**	1 : 1.45	22.54	1 : 1.07	17.5

X^2 0.05, 1 = 3.841
X^2 0.001, 1 = 10.828
*(P<0.05) **(P<0.001) Male : Female sex ratio is not statistically significantly different from 1:1

(P<0.001 ; Table 2). Of the ten remaining size groups the major cluster was in the larger size range (13.4 to 15.4 cm and 17.4 and 18.2 cm). For sizes between 13.4 and 15.4 cm males dominated whereas for the larger shrimps the ratios were reversed (Fig. 3).

When the data from both locations were combined, apart from the smaller (mid lengths up to 5.8 cm) and larger (mid lengths above 15.8 cm except 17.4 and 18.2 cm) sizes, most other size groups had a significant deviation from unity (P<0.001). Exceptions included 7.0, 7.8, 12.2, 13.0 and 13.8 cm size

Table 2. Statistical analysis of the size differences of sex ratio - *P. indicus*

TL (cm)	Negombo lagoon		Seas off Negombo		Overall	
	Sex ratio	X^2	Sex ratio	X^2	Sex ratio	X^2
3.4	1 : 0.15	61.45			1 : 0.15	61.45
3.8	1 : 1.2	0.81*			1 : 1.2	0.81*
4.2	1 : 1.15	1.04*			1 : 1.15	1.04*
4.6	1 : 1.28	6.77**			1 : 1.28	6.77**
5.0	1 : 1.12	0.8*			1 : 1.12	0.8*
5.4	1 : 0.91	1.19*			1 : 0.91	1.19*
5.8	1 : 1.26	8.29**			1 : 1.26	8.29**
6.2	1 : 1.74	134.38		1.59*	1 : 1.73	133.41
6.6	1 : 0.54	164.68	1 : 1.33	0.23*	1 : 0.54	162.76
7.0	1 : 0.98	0.32*	1 : 1.2	0.19*	1 : 0.98	0.28*
7.4	1 : 1.39	119.95	1 : 1.3	0.95*	1 : 1.39	120.83
7.8	1 : 0.97	0.87*	1 : 2.03	5.72**	1 : 0.98	0.46*
8.2	1 : 1.44	120.83	1 : 2.98	27.62	1 : 1.47	137.64
8.6	1 : 1.32	99.81	1 : 1.22	0.82*	1 : 1.32	100.47
9.0	1 : 1.13	16.71	1 : 1.61	13.71	1 : 1.15	23.47
9.4	1 : 1.08	12.50	1 : 1.3	5.08**	1 : 1.09	15.13
9.8	1 : 1.11	33.41	1 : 1.23	7.23**	1 : 1.12	39.02
10.2	1 : 1.12	39.94	1 : 0.95	0.63*	1 : 1.1	34.60
10.6	1 : 1.33	249.64	1 : 0.95	0.82*	1 : 1.28	217.76
11.0	1 : 1.16	60.51	1 : 0.86	8.37**	1 : 1.12	40.10
11.4	1 : 1.17	50.43	1 : 1.23	14.55	1 : 1.18	64.26
11.8	1 : 1.27	72.62	1 : 1.13	5.75**	1 : 1.24	74.73
12.2	1 : 1.07	3.26*	1 : 0.98	0.18*	1 : 1.04	1.44*
12.6	1 : 2.0	115.58	1 : 0.98	0.13*	1 : 1.3	43.28
13.0	1 : 1.08	0.44*	1 : 1.16	4.99**	1 : 1.14	5.15**
13.4		53.92	1 : 0.55	63.60	1 : 0.66	33.77
13.8			1 : 0.75	10.72**	1 : 0.75	10.72**
14.2			1 : 0.47	68.08	1 : 0.47	68.08
14.6			1 : 0.46	84.18	1 : 0.46	84.18
15.0			1 : 0.72	10.96	1 : 0.72	10.96
15.4			1 : 0.47	37.73	1 : 0.47	37.73
15.8			1 : 1.01	0.01*	1 : 1.01	0.01*
16.2			1 : 0.98	0.01*	1 : 0.98	0.01*
16.6			1 : 1.51	3.51*	1 : 1.51	3.51*
17.0			1 : 1.75	5.65**	1 : 1.75	5.65**
17.4				37.34		37.34
17.8			1 : 1.62	1.55*	1 : 1.62	1.55*
18.2				17.07		17.07
18.6				10.2**		10.2**

X^2 0.05, 1 = 3.841
X^2 0.001, 1 = 10.828
*(P<0.05) **(P<0.001) Male : Female sex ratio is not statistically significantly different from 1:1

groups. Females dominated most of the size groups with uneven sex ratios except for the mid lengths 3.4, 6.6 and 13.4 to 15.4 cm.

Monthly variation in the percentage occurrence of gonads

The present study indicated the occurrence of immature individuals of male *P. indicus* throughout the study period and that immature shrimps seem to make the most substantial contribution to the total catch in May, August, September and October 1999 (Fig. 4a). It was also revealed that outside these months in 1999, the majority of shrimps were mature. In addition, spent shrimps occurred only in the months of November and December 1999.

It was noted that except for the months March and April 1999 the majority of female *P. indicus* were in immature condition (Fig. 4b). During the period September to December 1998 almost all of the shrimps observed were in immature condition. Although gravid shrimps were observed in several months (February, March, April, July and December 1999) spent shrimps occurred only in January and February 2000.

Mean size at maturity

Shrimps with reproductive stages II onwards (II, III and IV) in terms of males and III onwards (III, IV and V) in terms of females were considered

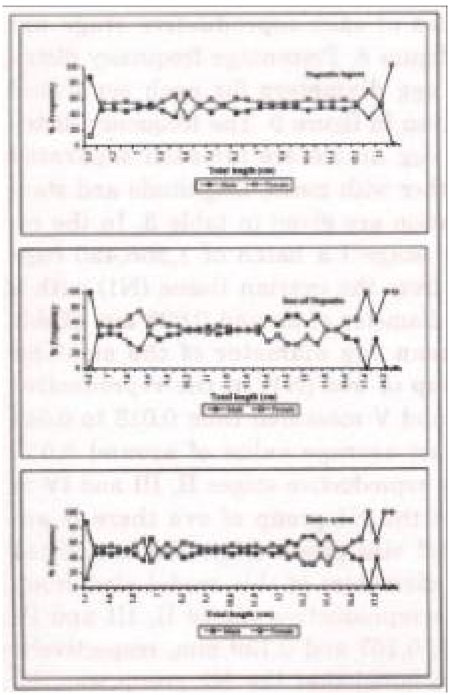

Fig. 3. The size differences in the sex raio of *P. indicus*

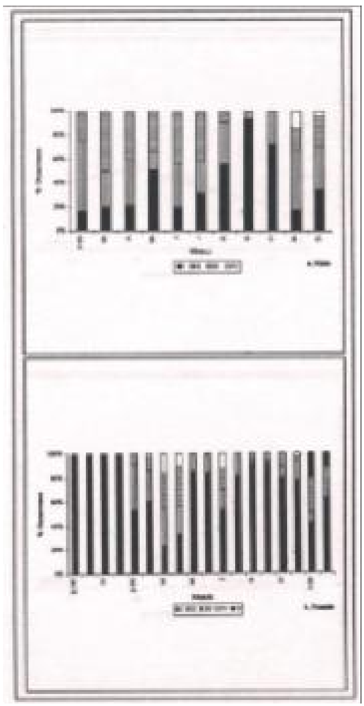

Fig. 4. Monthly variation of the percentage occurrence of gonads of different reproductive stages of *P. indicus*

as mature with respect to both species. The total lengths of the smallest mature male and female of *P. indicus* recorded during the present investigation were 10.44 and 13.16 cm respectively. The estimated values for the lengths at 50% maturity of *P. indicus* were 12.83 cm for males and 14.86 cm for females respectively (Fig. 5).

Gonado somatic index

The highest mean GSI recorded were 0.92 and 7.70 for the reproductive stages III for males and IV for females of *P. indicus* respectively (Figs. 6 a and b). The peak values for the mean GSI for *P. indicus* males (Fig. 7a) were recorded in the months March, August and November 1999 (0.86, 0.83 and 0.84, respectively) and for females in the months April and July 1999 (3.65 and 2.01, respectively) (Fig. 7b). The variation pattern of the mean GSI seems to follow a similar trend for both sexes over the study period.

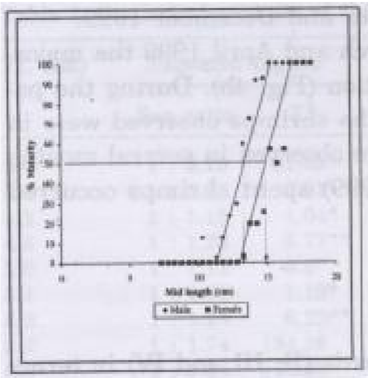

Fig. 5. Percentage of mature individuals in each length group of *P. indicus*

Oocyte diameter frequency

The mean frequencies of egg diameters for the reproductive stages II to V of *P. indicus* estimated by pooling data of all individuals in the samples of each reproductive stage are shown in figure 8. Percentage frequency distribution of egg diameters for each separated batch is given in figure 9. The frequency distribution of egg diameters for each separated batch together with mean, magnitude and standard deviation are given in table 3. In the reproductive stage I a batch of 1,256,420 eggs separated from the ovarian tissue (N1) with a mean egg diameter of around 0.028 mm (Table 3). The mean egg diameter of the smallest modal group of ova (N1) in the reproductive stages III and V measured from 0.018 to 0.045 mm with an average value of around 0.032 mm. In the reproductive stages II, III and IV in addition to the N1 group of ova there is another modal size group (N2). The estimated mean egg diameters of this modal size group (N2) in the reproductive stages II, III and IV were 0.129, 0.167 and 0.139 mm, respectively. It was also noted that the N2 group was the smallest modal size group in the reproductive

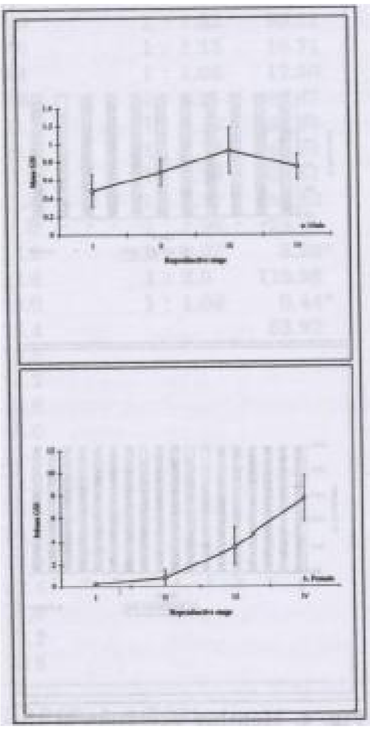

Fig. 6. Variation patern of the GSI of different reproductive stages of *P. indicus*

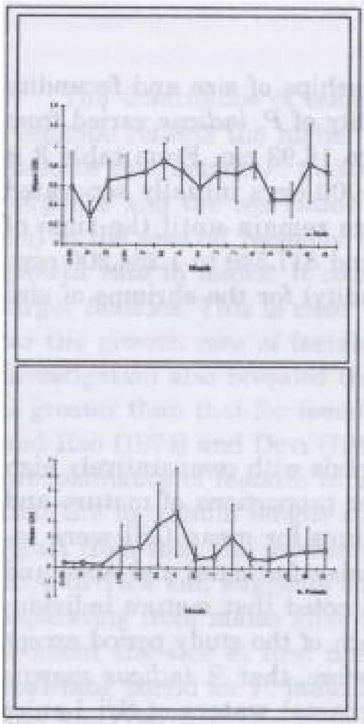

Fig. 7. Monthly variation of the mean gonado somatic index of *P. indicus*

stages II and IV. In addition to the above, in the reproductive stages II, III and IV another batch of ova (N3) also made an appearance and the mean egg diameter of this batch measured from 0.236 to 0.287 mm with an average of around 0.263 mm. The reproductive stage IV could be considered as the final stage before spawning. By the reproductive stage IV, a fourth batch of larger ova (N4) also made an appearance and the mean diameter of this ultimate batch was 0.444 mm.

The analysis of oocyte diameter frequency distribution of *P. indicus* indicated separation of a batch of around 1,250,000 eggs from the ovary at stage I, out of which around 985,179 (78.81%) are shed after stage IV (Table 3). At stage III, a secondary batch with a higher number of eggs, which amounts to around 1,337,000 made its appearance.

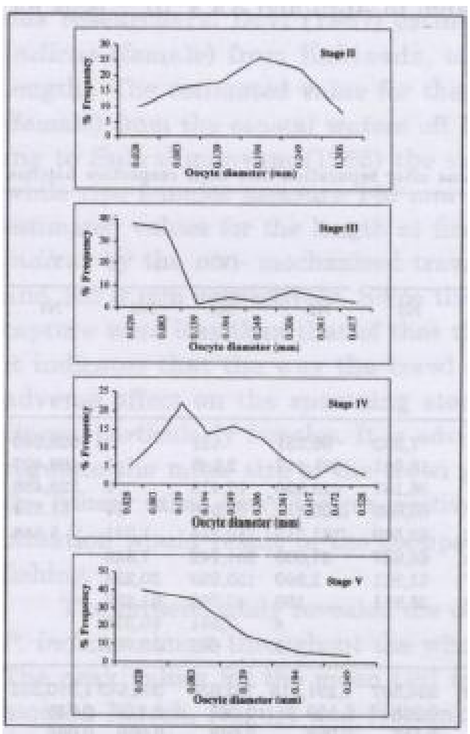

Fig. 8. Frequency distribution of egg diameters in different reproductive stages of *P. indicus*

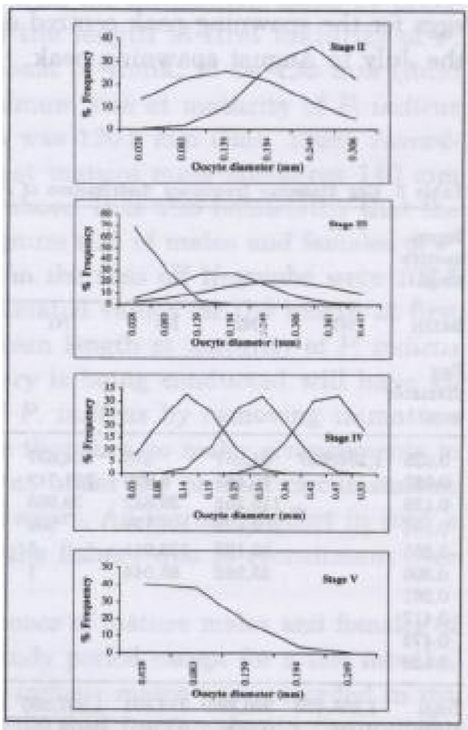

Fig. 9. Frequency distribution of egg diameters of *P. indicus* after separation into their respective batches

Fecundity

Using the statistically significant relationships of size and fecundity (Type–I), it was estimated that the Type–I fecundity of *P. indicus* varied from 1,165,660 to 1,411,406 for the size range 11.03 to 16.93 cm. From table 3 it was evident that out of a total of around 1,250,000 eggs initially separated from the ovary (in Stage I) around 985,179 eggs remain until the time of shedding. Therefore, it can be estimated that around 817,549 to 1,254,200 eggs remain until the time of shedding (Type-II fecundity) for the shrimps of size range 14.22 to 18.26 cm.

Spawning season

Spawning season was identified as the periods with comparatively high mean GSI for both sexes and occurrence of higher proportions of mature and spent shrimps among the catches. The peak values for mean GSI were recorded in the months of March, August and November for males and April and July 1999 for females (Figs. 7a and 7b). It is also noted that mature individuals are present in the commercial catches over much of the study period except for few months (Figs. 4a and 4b). It appears therefore, that *P. indicus* spawns in several months of the year in the western coastal waters of Sri Lanka with peaks around March to April and July to August. In addition the estimated seasonal egg productions of the population using the mean fecundity and the seasonal abundance of mature females in the west coast were 1.3×10^{13} eggs for the spawning peak centred on March to April and 3.4×10^{12} eggs for the July to August spawning peak.

Table 3. Egg diameter frequency distribution of *P. indicus* after separation into their respective batches

Reproductive stage	I	II		III			IV			V
Batch	N1	N2	N3	N1	N2	N3	N2	N3	N4	N1
Egg diameter (mm)										
0.028	1,256,420	64,851	573	904,667	10,355	7,592	96,231	121		528,240
0.083		10,481	6,920	391,742	29,442	18,581	281,477	2,145	1	496,407
0.139		125,252	39,632	39,983	50,896	36,137	423,956	19,413	3	228,486
0.194		102,629	107,721	962	53,493	55,849	328,811	89,518	77	51,511
0.250		59,127	138,941	5	34,182	65,589	131,317	210,314	1,071	5,688
0.306		23,952	85,044	1	13,280	66,937	27,005	251,742	7,845	
0.361					3,137	51,911	2,860	153,523	30,234	
0.417					450	31,911	156	47,700	61,292	
0.472							4	7,551	65,359	
0.528							1	609	36,661	
Total	1,256,420	386,292	378,831	1,337,360	195,235	334,507	1,291,818	782,636	202,543	1,310,332
Mean	0.028	0.129	0.236	0.018	0.167	0.266	0.139	0.287	0.444	0.045
SD		0.094	0.064	0.046	0.079	0.116	0.068	0.068	0.069	0.066
No. of samples	23	21		24			31			18

Discussion

The dominance of females in the lower size categories in the seas off Negombo reflects the higher incidence of females in the lagoon. It would also indicate that female *P. indicus* leave the lagoon earlier than males. The convergence and the sex ratios close to 1 : 1 in the middle size range (10 – 13 cm) in the seas off Negombo may indicate either differential mortality or faster growth rate in males. It could also be an indication of offshore migration of larger females. This is clear during the present study as the estimated value for the growth rate of females was greater than that for males. The present investigation also revealed that the estimated total mortality rate (Z) in males is greater than that for females. Similar observations were made by the Kurup and Rao (1974) and Devi (1987) in the coastal waters off India. In addition the predominance of females in larger length groups could also be due to the fact that the maximum length attained by females is greater than that of males. Apart from that, the predominance of males, especially in the size groups from 13.4 to 15.4 cm, suggests that females may have a behavioural pattern of separating from males after reaching an age corresponding to this size which is about the size at first maturity. Similar variation in the sex ratio in the spawning period for *P. indicus* was reported by George *et al.* (1963) and George and Rao (1967).

The estimated values for the mean sizes at maturity for males and females of *P. indicus* during the present investigation were 128.3 and 148.6 mm respectively. These values are comparable with the estimations made by previous researchers. Devi (1987) estimated the length at first maturity of *P. indicus* (female) from Kakinada, east coast of India, to be 125 mm (total length). The estimated value for the minimum size at maturity of *P. indicus* (female) from the coastal waters off India was 130.2 mm (Rao, 1968). According to Subrahmanyam (1965) the smallest mature male measures 140 mm while ripe females measure 140 mm and above. It is also noteworthy that the estimated values for the length at first capture (Lc) of males and females of *P. indicus* by the non- mechanised trawlers in the seas off Negombo were 102.5 and 102.0 mm respectively. Since the estimated values for the length at first capture were less than that of that the mean length at maturity of *P. indicus* it indicates that the way the trawl fishery is being conducted will have an adverse effect on the spawning stock of *P. indicus* by removing immature stages, particularly females. It is advisable therefore, to make arrangements to regulate the mesh size of the trawl gear as under the present circumstances the fishery takes away the prospective spawners. An increased effort in such a situation would result in the collapse of the fishery due to recruitment over fishing.

The present study revealed the occurrence of mature males and females of *P. indicus* almost throughout the whole study period except for a few months. The peak values for the mean GSI for *P. indicus* males were recorded in the months March, August and November 1999 and for females in the months April and July 1999. In addition, the contribution of mature females to the commercial shrimp catches was found to be insignificant over the study period.

During the present study, shrimp samples for biological investigations were frequently drawn from the commercial shrimp catches of nonmechanized trawlers but as the trawl operations by the nonmechanized trawlers are frequently conducted in the shallow coastal waters off Negombo, the poor representation of mature females in the commercial catches and the absence of synchronization between the spawning seasons of two sexes could probably be due to the spawning migration of females to deeper waters.

As revealed during the present investigation *P. indicus* spawns in the seas off the west coast of Sri Lanka in most months of the year with peaks around March/April and July/August periods. The study also indicated that both spawning peaks were equally responsible for the total egg productivity of the *P. indicus* population in the west coast. Continuous spawning behavior and the preference of deeper waters for spawning of *P. indicus* are reported frequently. According to Devi (1987) *P. indicus* spawns in the coastal waters off Kakinada in the east coast of India throughout the year with 2 to 3 peaks, the peaks being different in different years. George et al. (1963) report this species spawns in the coastal waters off Cochin throughout the year with peaks in December to January and May to June. Rao (1968) observed a prolonged spawning season of *P. indicus* in Cochin waters extending from October to April. As reported by Crosnier (1965), *P. indicus* has an extended spawning period in Madagascar waters with a peak in March/April. Based on the occurrence of postlarvae in the Cochin back waters, George (1962) determined the spawning season of *P. indicus* as from October to May with two peaks in November to December and February to April.

It is likely that the coastal penaeids move to deeper waters, whereas continental shelf living species move shoreward for suitable spawning grounds. According to Panikkar and Menon (1956) *P. indicus* preferred coastal waters not exceeding 18.3 to 22 m in depth for spawning. Hall (1962) demarcated the possible spawning area of *P. indicus* in the coastal waters off Malaya east of Singapore varying in depths from 18.3 to 36.6 m. Mohan and Siddeek (1995) observed a drastic fall in the proportion of females in the shrimp catches from the Gulf of Masira of Sultanate of Oman due to the spawning migration of females to deeper waters.

The highest value for mean GSI was observed for reproductive stages III and IV of males and females respectively. It is a common phenomenon for the eggs to become hydrated prior to spawning, increasing the total weight of the gonad (Picquelle and Stauffer 1985). Thus spawning would appear to commence from stages III and IV onwards for males and females, respectively.

The ova-diameter frequency distributions of reproductive stages III and IV indicate that (Table 3), in addition to the most advanced group of ova (N3 in stage III and N4 in stage IV), there was at least one group which had partially undergone the maturation process (N1 and N2 in reproductive stage III and N2 and N3 in reproductive stage IV). Therefore, the presence of such an intermediate group in the ova-diameter frequency curve of mature shrimp indicates either an occurrence of more than one spawning act or the serial spawning behavior of the shrimp. Since the mature group of ova are larger, the individuals are either in spawning condition or much closer to it. The presence of an intermediate group in addition to the mature and immature groups of ova indicates that spawning may occur over a long period. As the ovaries of spent recovering specimens (reproductive stage V) contain only small ova with a diameter of around 0.045 mm, all the mature ova present in the ovary may be released in a single spawning act.

The present study indicate that an estimated number (817,549 to 1,254,200) of eggs would be spawned by the shrimp of the size range 14.22 to 18.26 cm (Type-II fecundity or the total number of eggs, which are ready to be shed in the reproductive stage IV). The fecundity (Type-II) of this species in the size range 14.0 to 20.0 cm was estimated to be varying between 68,000 and 731,000 by Rao (1968). In addition as reported by Jayakody (1984) fecundity of *P. indicus* in the size range 15.0 to 18.0 cm varied between 50,000 and 700,000. Although the estimations made on the fecundity of *P. indicus* by Rao (1968) and Jayakody (1984) seem to be slightly lower when compared with the fecundity estimations made during the present investigation, these values are more or less comparable. The wide variation in fecundity observed during the study conducted by Rao (1968) and Jayakody (1984) could be associated with the serial spawning behavior of this species, where the eggs are shed in batches rather than all at once. The high fecundity estimate at one end probably represents the number of eggs at the onset of spawning. The low fecundity estimate at the other end indicates that some of the eggs are released in subsequent batches.

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