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Reproductive Biology of *Metapenaeus dobsoni* (Miers, 1878) from the Western Coastal Waters of Sri Lanka

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Abstract

The reproductive biology of *Metapenaeus dobsoni* (Miers, 1878) from the western coastal waters of Sri Lanka has been studied during the period September 1998 to December 1999. The ratios of males to females in monthly catches from lagoon and offshore areas were found to be significantly different in certain months. There is a significant deviation of sex ratio from unity for the size range studied except for the smaller and larger length groups. Sizes at 50% maturity for males and females were estimated as 6.36 and 7.31 cm (total length), respectively. The estimated values for reproductive load were 0.55 and 0.54 for males and females, respectively. *M. dobsoni* spawns in the west coast of Sri Lanka throughout the year with peaks in March, September, October and November. An offshore migration of females for spawning was also evident. The estimated Type-I fecundity (total number of eggs that have been initially separated from the ovary in the reproductive stage I) of *M. dobsoni* varied between 178,098 to 404,564 eggs for the size range 7.91 to 11.15 cm. The estimated Type-II fecundity (total number of eggs, which are ready to be shed in the reproductive stage IV) varied between 91,652 to 225,679 eggs for the size range 6.96 to 11.72 cm. The estimated probability of an egg developing into recruit varied from 3.3×10^{-4} to 8.1×10^{-4}.

Introduction

The reproductive process of penaeid shrimps involves attaining maturity, mating and spawning. After fertilization, the eggs are not retained by the females, but are released directly into the water. For all known members of this family, the sequence of development is similar to a progression after hatching from planktonic larvae, with several naupliar, protozoeal, mysis through post larval stages followed by juvenile and adult stages, which may require both oceanic and brackish waters (Fischer and Bianchi 1984).

The shrimp, *Metapenaeus dobsoni* (Miers 1878), is a valuable shrimp found in the coastal waters off India, Sri Lanka, Thailand, Indonesia, Malaysia and the Philippines (Fischer and Bianchi 1984). *M. dobsoni* lives at sea in mud down to 37 m depth while their juveniles inhabit estuaries, backwaters and paddy fields. It tolerates salinity ranging from 3 to 43 psu and is abundant in low saline lagoons and adjacent marine areas, but rather rare in high salinity lagoons (Fischer and Bianchi 1984).

M. dobsoni is the most abundant shrimp in the penaeid fauna of Sri Lanka. It supports commercial shrimp trawl fisheries along the west coast and the traditional prawn fishery in estuaries, lagoons and shallow coastal waters. In backwaters it is mainly caught by trammel nets, drag nets, cast nets, traps and stake-seine nets (De Bruin 1970; Siddeek 1978).

The present paper describes the reproductive biology of *M. dobsoni* from the western coastal waters of Sri Lanka where this species makes a substantial contribution to shrimp catches from the Negombo lagoon and the associated coastal ecosystem in the west coast. Inadequate knowledge on the reproductive biology of *M. dobsoni* has restricted management of the shrimp fishery in the west coast. Therefore, the present paper is mainly focused on the vital aspects of the reproductive biology of this species from the fisheries point of view. The prime objectives of the present study were to investigate the mean size at maturity, spatial and temporal variation in sex ratio and sexual dimorphism, spawning season, spawning frequency and fecundity or reproductive potential.

Materials and Methods

The sampling programme 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 (drag nets and stake-seine nets) and the associated coastal region (nonmechanized and mechanized trawls), at weekly intervals from September 1998 to August 1999 (Sample size varied from

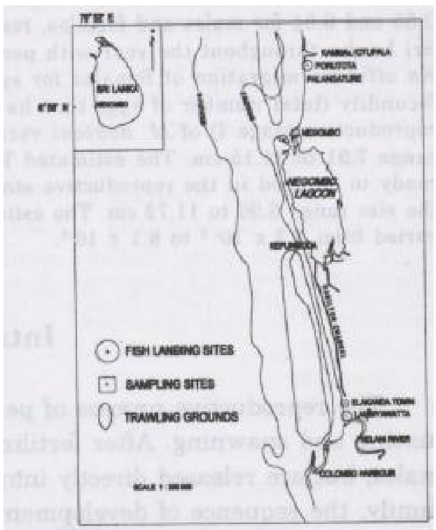

Fig. 1. Map of the study area

322 to 5,242). These were then immediately brought to the laboratory at the National Aquatic Resources Research and Development Agency (NARA), Colombo, for analysis.

Sex ratio and sexual dimorphism

At 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 (by pooling the shrimp samples collected from all sites in the study area) and the sex ratios specific to the lagoon and the associated coastal region (by pooling the shrimp samples collected at fish landing centers inside the lagoon and the coastal region, respectively). The estimated values for the sex ratio 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 sex ratio by size.

Mean size at maturity and gonado somatic index (GSI)

Only the shrimps, which are larger than the minimum size at maturity (6.1 cm for males and 6.03 cm for females), were used to determine GSI so as to avoid overestimation of immature stages and underestimation of GSI by including immature animals. 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 using an electronic balance. Shrimps were then dissected along the dorsal surface to expose the gonads; the stage of maturity was then determined through macroscopic examination (Table 1). Individual gonads were carefully removed and weighed to the nearest 0.0001 g to determine the GSI.

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

$$GSI = (\text{Gonad weight} \times 100)/(\text{Body weight}-\text{Gonad weight})$$

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). The probability curve was smoothed using the logistic model incorporated into the FiSAT software (Gayanilo and Pauly 1997) to estimate the mean length at 50% maturity. All the shrimps in the samples were used in this analysis.

Reproductive load

The reproductive load, expressing the proportion of the potential growth span of the species covered before maturation (Beverton 1992) was estimated using the following formula described by Cushing (1981).

Reproductive load = Lm/L_∞

where,

Lm = length at 50% maturity

L_∞ = asymptotic length (the values of L_∞, 11.56 and 13.54 cm for males and females respectively were obtained from Jayawardane et al., unpublished)

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

Table 1. Classification of the reproductive stages of gonads

Reproductive stage	State (male)	State (female)	Description	
			Male	Female
I	Inactive	Immature	Minute and thread-like testes. Vasa deferentia are not visible. Testes confined to the posterior half of the carapace.	Ovaries are thin, translucent, unpigmented and confined to the abdomen. They contain oocytes and small spherical ova with clear cytoplasm and conspicuous nuclei.
II	Active	Maturing	Gonads extend up to the posterior end of the cardiac stomach. Vasa deferentia are slightly visible.	The ovaries increase in size and the anterior and middle lobes are formed. The dorsal surface is light yellow to yellowish green. Opaque yolk granules are formed in the oocyte or ovarian cytoplasm and partly obscure the nuclei. The developing ova are clearly larger than the immature ones.
III	Mature	Late maturing	Vasa deferentia are well developed. Gonads extend halfway or full way on the cardiac stomach. Gonads are filled with seminal fluid.	The ovary is light green and visible through exoskeleton. The anterior and middle lobes are fully developed. The accumulation of yolk in maturing ova turns them opaque.
IV	Spent	Mature	Vasa deferentia are flaccid and shrunken	The ovary is dark green and clearly visible through the exoskeleton. The ova are larger than in the preceding stage and the peripheral region of ova becomes transparent.
V		Spent-recovering		Ovarian lobes are flaccid and much convoluted. The gonad revert almost immediately to the immature condition.

(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) (Table 4), 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 normal 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 4).

To estimate the relationship between Type I fecundity 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, a linear relationship between the Type II fecundity and the size of the shrimp was also determined. Knowing the proportion of eggs that were shed as the first batch and the number of eggs that were initially separated from the ovarian tissue, the number of eggs shed in successive spawning acts was estimated.

Probability of an egg developing into recruit

Using the following equation, an approximate estimate of probability of an egg developing into recruit (P) of *M. dobsoni* in the seas off west coast of Sri Lanka was obtained. The equation used is as follows:

$$P = R_1 /(R_2-(C+NL)) \times F$$

Where

R_1 = mean annual recruitment number of males and females
R_2 = mean annual recruitment number of females
C = mean annual catch of females
NL = female natural losses
F = total annual fecundity

Note – For the above analysis the information on mean annual recruitment numbers, mean annual catch of females and the natural losses of female *M. dobsoni* were obtained from Jayawardane et al. (unpublished).

Spawning season

The spawning season of *M. dobsoni* 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 December 1999 for females.

Results

Spatial and temporal variations in the sex ratio

The ratios of males to females in monthly catches within the lagoon were statistically different from unity (P<0.05) in September 1998 and from February to July 1999 (Table 2). The deviation from unity in February 1999 was (P<0.05) somewhat large, but was found to be not different at the 0.1% level of significance. In September, October and December 1998 and from March until July 1999 the proportion of females exceeded the males in the Negombo lagoon. It was only in November 1998 and January, February and August 1999 that the situation was reversed. It should be noted that the deviations from unity in the latter months were not significant at the 0.1% level.

Similar statistical analyses of the offshore catches (Table 2; Fig. 2) revealed that sex ratios did not deviate significantly from unity (P<0.001) in eight of the twelve monthly samples. Only in September 1998 and February, March and August 1999 were the ratios highly significantly different from unity. In October and December 1998 and January, April and August 1999 the females were found to dominate catches whereas in the remaining months the males outnumbered

Table 2. Statistical analysis of the sex ratio of *M. dobsoni* on monthly basis

Month	Negombo lagoon			Seas off Negombo			Overall		
	Male	Female	X^2	Male	Female	X^2	Male	Female	X^2
Sep-98	170	238	11.29	268	194	11.89	438	432	0.05*,**
Oct	124	127	0.04*,**	128	133	0.1*,**	254	260	0.07*,**
Nov	215	198	0.73*,**	230	205	1.46*,**	449	403	2.47*,**
Dec	164	187	1.56*,**	348	358	0.16*,**	529	545	0.23*,**
Jan-99	71	63	0.49*,**	78	108	5.07**	150	171	1.39*,**
Feb	108	76	5.42**	146	85	16.11	254	161	20.69
Mar	320	530	51.65	278	203	11.44	603	733	12.59
Apr	125	189	12.84	352	382	1.21*,**	488	571	6.44**
May	789	1366	154.85	334	294	2.52*,**	1125	1661	102.88
Jun	663	934	45.94	514	429	7.54**	1178	1363	13.50
Jul	84	139	13.83	799	679	9.71**	887	818	2.76*,**
Aug	1865	1772	2.36*,**	681	920	35.66	2550	2692	3.87**

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

the females. When data from both locations were combined the overall sex ratios deviated from unity (P<0.001) in four months (February, March, May and June 1999). In *M. dobsoni* catches from the entire system, males dominated only in the months of September and November 1998 and February and July 1999. In the remaining months the females outnumbered the males.

Size differences in the sex ratio

In the Negombo lagoon, most of the size groups of *M. dobsoni* did not deviate significantly from unity (P<0.001; Table 3). From the six remaining size groups, major cluster was in the intermediate size range (4.1 to 4.7 cm and 5.1 and 5.7 cm). All the uneven sex ratios had a predominance of females (Fig. 3). Apart from a few size groups (2.9, 3.1, 3.5, 6.3 and 6.5 cm) *M. dobsoni* females dominated catches from Negombo lagoon over the entire size range.

Apart from the smaller and the larger sizes (mid lengths up to 6.1 and above 10.9 cm) most other size groups of *M. dobsoni* from offshore areas had a significant deviation from unity (P<0.001; Table 3). Exceptions included 8.3, 8.7 and 8.9 cm size groups. The percentage of females was greater compared to males up to the mid length 5.3 and beyond 8.7 cm, while males dominated between 5.3 and 8.7 cm. Most of the uneven sex ratios had a predominance of females (Fig. 3).

When 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 mid lengths from 4.9 - 6.1 and 8.3, 8.7 and 8.9 cm. Generally *M. dobsoni* catches from the system were dominated by females in smaller and larger length groups whereas for the size range from 6.1 to 8.3 cm the ratio was reversed.

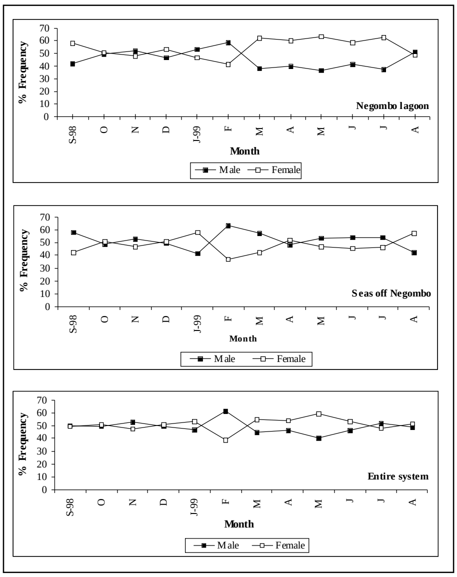

Fig. 2. Monthly variation of sex ratio of *M. dobsoni*

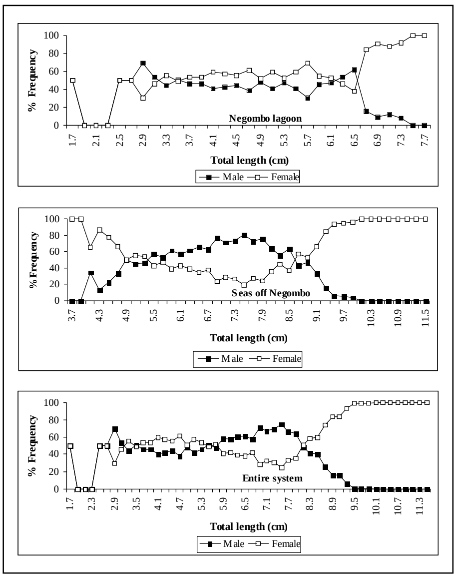

Fig. 3. The variation in the sex ratio of *M. dobsoni* by size

Size ranges for individuals of different reproductive stages

In *M. dobsoni* the total lengths of shrimps up to stage II ranged from 5.89 to 8.95 cm and from 6.43 to 9.0 cm for males and females respectively. From stage III onwards, individuals ranging from 6.72 to 9.11 cm in males and 6.03 to 11.04 cm in females were observed among the samples.

Table 3. Statistical analysis of size differences of sex ratio - *M. dobsoni*

TL (cm)	Negombo Lagoon			Seas off Negombo			Overall		
	Male	Female	X^2	Male	Female	X^2	Male	Female	X^2
2.9	16	7	3.64*,**				16	7	3.64*,**
3.1	27	23	0.32*,**				27	23	0.32*,**
3.3	106	133	3.02*,**				106	133	3.02*,**
3.5	752	732	0.26*,**				752	732	0.26*,**
3.7	439	510	5.32**				439	510	5.37**
3.9	785	903	8.28**				785	903	8.32**
4.1	523	766	45.80	2	5	0.68*,**	526	771	46.38
4.3	479	648	25.18	1	9	5.6**	481	655	26.85
4.5	636	802	19.18	6	22	8.86**	641	822	22.46
4.7	297	463	36.26	18	35	5.44**	315	495	39.88
4.9	203	218	0.53*,**	28	28	0*,**	231	243	0.33*,**
5.1	156	223	12.01	49	62	1.36*,**	201	272	10.51**
5.3	101	113	0.74*,**	75	90	1.35*,**	165	191	1.87*,**
5.5	61	88	5.06**	150	111	5.73**	174	171	0.04*,**
5.7	24	54	11.75	154	138	0.92*,**	160	171	0.35*,**
5.9	17	20	0.27*,**	152	97	12.04	155	109	8.14**
6.1	25	28	0.16*,**	226	173	7.13**	203	149	8.23**
6.3	18	15	0.19*,**	232	145	20.26	213	136	16.90
6.5	24	15	2.24*,**	295	160	40.06	227	144	18.57
6.7	4	19	10.56**	291	179	26.86	234	174	8.83**
6.9	1	12	8.9**	353	107	130.88	303	125	73.93
7.1	2	13	8.78**	410	162	107.99	301	147	52.74
7.3	1	6	4.79**	424	155	125.23	341	153	71.90
7.5	0	3	3.01*,**	694	171	315.17	531	176	178.01
7.7	0	1	1.27*,**	445	169	123.72	334	172	51.71
7.9	0	0		428	139	147.89	338	190	41.70
8.1	0	0		370	206	46.37	197	203	0.1*,**
8.3	0	0		250	203	4.75**	160	222	10.31**
8.5	0	0		350	207	36.46	191	286	18.72
8.7	0	0		113	150	5.13**	69	195	60.04
8.9	0	0		75	85	0.53*,**	48	254	140.22
9.1	0	0		55	110	18.30	25	126	68.24
9.3	0	0		18	97	54.67	12	176	142.44
9.5	0	0		9	124	100.28	2	216	208.45
9.7	0	0		2	51	43.83	1	102	100.20
9.9	0	0		1	37	33.28	1	100	97.71
10.1	0	0		0	41	41.18	0	56	55.57
10.3	0	0		0	21	20.91	0	31	31.37
10.5	0	0		0	25	25.38	0	36	35.98
10.7	0	0		0	15	14.66	0	17	16.99
10.9	0	0		0	9	9.06**	0	11	10.52**
11.1	0	0		0	1	1.43*,**	0	1	0.85*,**
11.3	0	0		0	3	2.5*,**	0	2	1.51*,**
11.5	0	0		0	1	1.02*,**	0	2	2.01*,**

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

Monthly variation in percentage occurrence of gonads

The majority of male *M. dobsoni* were in mature (stages II and III) condition almost throughout all the study period (Fig. 4a). The presence of immature shrimps was also noted in the months of April, June, August, September, October and December, 1999. In addition, except for the months March, April, July and August, spent shrimps occurred throughout the study period and their contribution was substantial in the months of June, October, November and December.

Spent shrimps of female *M. dobsoni* were observed throughout the study period and gravid shrimps were present in seven months in 1999, but absent in April, May, June, August and December (Fig. 4b). Spent shrimps made a substantial contribution to catches during the periods October 1998 to February 1999. Also in the period August to November 1999 spent stages represented >30% of the catch. Gravid shrimps on the other hand were prominent among the catches in the months of October and November 1998 and March 1999. It was noted that except for the month of April 1999 the majority of shrimps were in mature condition throughout the study period.

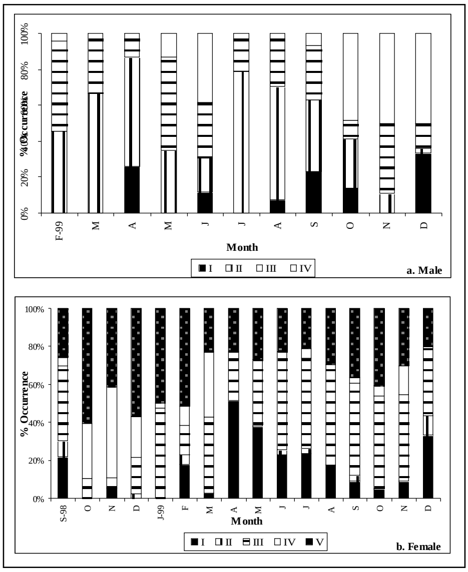

Fig. 4. Monthly variation in the percentage occurrence of gonads of different reproductive stages of *M. dobsoni*

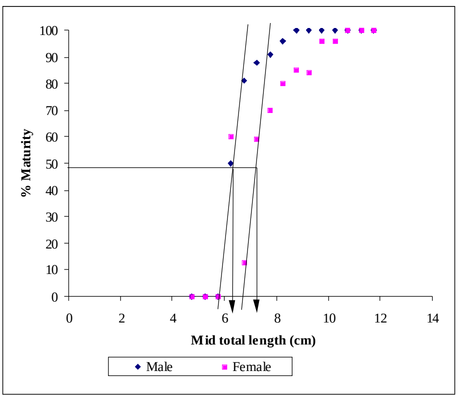

Fig. 5. Percentage of mature individuals in each length group of *M. dobsoni*

Mean size at maturity

Shrimps with reproductive stages II onwards (II, III and IV) for males and III onwards (III, IV and V) for females were considered as mature. The total lengths of the smallest mature male and female *M. dobsoni* recorded during the present investigation were 6.1 and 6.03 cm, respectively. The lengths at 50% maturity of *M. dobsoni* were estimated at 6.36 and 7.31 cm for males and females, respectively (Fig. 5).

Reproductive load

The estimated values for the reproductive load (Lm/L_{∞}) of *M. dobsoni* were 0.55 and 0.54 for males and females respectively.

Gonado somatic index (GSI)

The peak values for mean GSI (3.1 and 4.55) were recorded for the reproductive stages III and IV for males and females, respectively (Fig. 6a & b). Relatively higher values for GSI were observed in the months January, March and May (3.15, 3.15 and 3.19, respectively) for males (Fig. 7a). For females however, except for the month of March 1999 (3.71) no great variation in terms of mean GSI was observed over the study period (Fig. 7b).

Oocyte diameter frequency

A batch of around 298,540 eggs were initially separated from the ovarian tissue in the reproductive stage I. The mean egg diameter of this batch (N1) was 0.028 mm (Table 4). The mean egg diameters of the smallest modal group of ova (N1) in the reproductive stages III and V measured from 0.017 to 0.021 mm with an average value of 0.019 mm. There is another modal size group of ova (N2) in the reproductive stages II, III and IV. The mean egg diameter of this group measured from 0.137 to 0.198 mm with an average value of 0.167 mm. By the reproductive stage IV a third batch of ova (N3) made appearance with mean egg diameter of 0.222 mm. In addition to the reproductive stages III and IV, a fourth batch of larger ova (N4) was also appeared and the mean egg diameter of this ultimate batch was 0.333 mm. Stage IV can be considered as the ultimate stage before spawning. Through reproductive stage V, another new batch (N1) made an appearance and the mean diameter of this batch was around 0.021 mm.

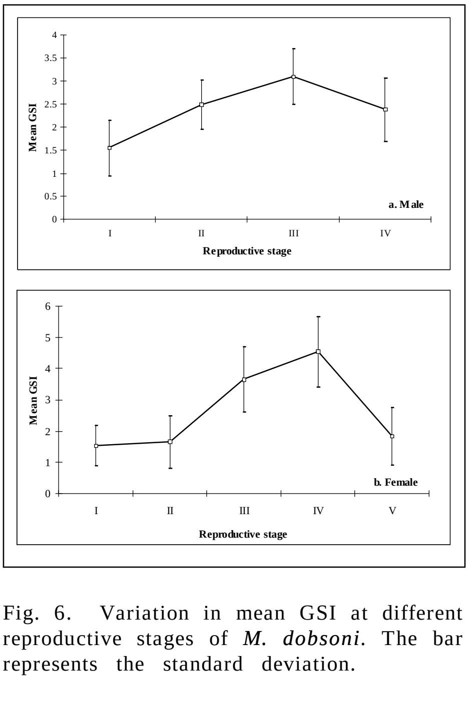

Fig. 6. Variation in mean GSI at different reproductive stages of *M. dobsoni*. The bar represents the standard deviation.

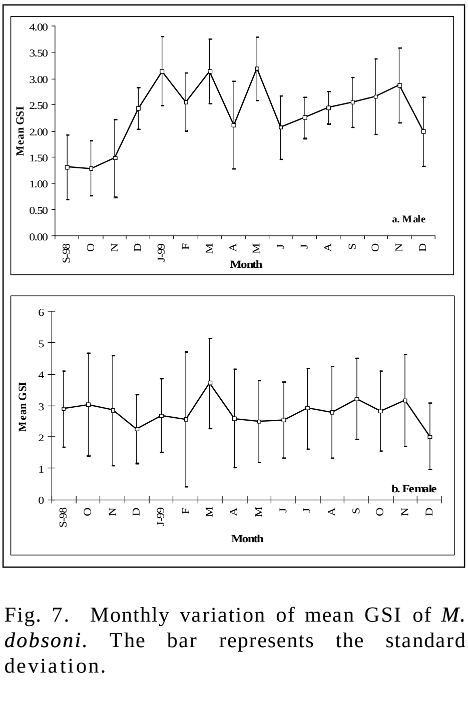

Fig. 7. Monthly variation of mean GSI of *M. dobsoni*. The bar represents the standard deviation.

As revealed during the present investigation a batch of around 298,500 eggs separates from the ovary at stage I, out of which around 163,300 (54.71%) (mean number of eggs in the most advanced batches of the reproductive stage IV) remain until stage IV (Table 4). At stage III, a secondary batch with a slightly low magnitude, which amounts to a little over 281,000 eggs, made an appearance.

Fecundity

Using the statistically significant relationship of size and fecundity (Type–I) (F = 69,897 TL – 374,787, $r^2 = 0.678$, n = 22), it was estimated that the Type–I fecundity of *M. dobsoni* vary from 178,098 to 404,564 for the size range 7.91 to 11.15 cm. From Table 4, it was evident that out of a total of 298,500 eggs initially separated from the ovary (in Stage I) around 163,300 eggs remained until the time of shedding. Therefore, it can be estimated that around 91,652 to 225,679 eggs remain until the time of shedding (Type-II fecundity) (F = 28,157 TL – 104,321, $r^2 = 0.85$, n = 33) for the shrimps of size range 6.96 to 11.72 cm.

Probability of an egg developing into recruit

Based on the approximations of mean annual recruitment number of females and total individuals (330, 474, 200 and 630, 359, 250 respectively), natural losses (198, 781, 957) and the mean annual catch of females (123, 204, 529) (Jayawardane et al., unpublished) the probability of an egg developing into a recruit in the seas off west coast of Sri Lanka was estimated to vary from 3.3×10^{-4} to 8.1×10^{-4}.

Table 4. Egg diameter frequency distribution of *M. dobsoni* after separation into their respective batches

Reproductive stage	I	II	III			IV			V
Batch	N1	N2	N1	N2	N4	N2	N3	N4	N1
Egg diameter (mm)									
0.028	298,540	1,843	191,805	2,114		9,375	386		42,862
0.083		12,422	80,980	6,020		58,797	3,234		35,027
0.139		40,942	8,059	10,414		114,553	13,656	1	19,354
0.194		65,969	189	10946		69,332	29,042	98	7,230
0.250		51,966	1	6991		13,035	31,104	3,687	1,826
0.306				2712	6,922	761	16,777	24,659	
0.361				639	23,989	14	4,557	29,309	
0.417						1	623	6,191	
0.472									
0.528									
Total	298,540	173,142	281,034	39,837	30,911	265,868	99,380	63,945	106,299
Mean	0.028	0.198	0.017	0.167	0.332	0.137	0.222	0.333	0.021
SD		0.066	0.046	0.079	0.014	0.051	0.067	0.042	0.089
No. of samples	17	24		21			33		14

Spawning season

Relatively higher values of GSI of *M. dobsoni* were recorded in the months of January, March and May for males, while for females no great variation in mean GSI was observed over the study period (Figs. 7 a and b). It was also evident that mature shrimps made a substantial contribution to the commercial catches and occurrence of spent shrimps in most months of the study period (Figs 4 a and b). This may be an indication of continuous spawning behaviour of *M. dobsoni* in the western coastal waters of Sri Lanka.

Discussion

The ratios of males to females in monthly catches within the lagoon were found to be statistically different from unity in September 1998 and from March to July 1999. Similar statistical analyses of the offshore catches revealed that sex ratio did not deviate from unity in eight of the twelve monthly samples. When data from both locations were combined overall sex ratios significantly deviated from unity in February, March, May and June 1999. The analysis of sex ratios of different size classes indicated that there is a significant deviation of sex ratio from unity for the size range studied except for smaller and larger size groups. In Negombo lagoon, except for a few length groups, females outnumbered the males over the entire size range studied. However, in the seas off Negombo, the percentage of females was greater compared to males up to the mid length 5.3 and beyond 8.7 cm, while between the size groups 5.3 and 8.7 cm, males outnumbered the females. In addition both sexes were not represented in all length groups, with the larger length groups entirely represented by females.

The predominance of females in certain months and in the larger length groups suggests either a faster growth rate in females or differential mortality. The fisheries study conducted in the Negombo lagoon and the associated coastal waters indicated (Jayawardane et al., unpublished) that females do grow faster than males and the estimated total mortality rate for males was greater than that for females (the estimated growth rates and the total mortality coefficients were 1.02 and 4.14 for males and 1.73 and 4.36 females respectively). Early attainment of sexual maturity in males may be responsible for impairing growth in males, which could also be a reason for the early mortality in males. The predominance of males between the length groups 5.5 and 8.5 cm suggests that females may have a behavioural pattern of separating from males after attaining the age corresponding to this size (5.5 cm – total length). Similar variation in sex ratio was reported by Menon (1957). According to Menon (1957) predominance of males in the size group 80 to 100 mm in the commercial catches from the seas off southwest coast of India could probably be due to migration of females towards deeper waters.

The peak values for mean GSI of *M. dobsoni* (males) were recorded in January, March and May 1999 and for females, a prominent peak was recorded in the month of March 1999 while minor peaks were recorded in October 1998 and September and November 1999. The present study also revealed the occurrence of mature males and females in shrimp catches from the seas off Negombo throughout the study period. It was also noted that the contribution of mature shrimps (both males and females) to the commercial catches was substantial and that spent shrimps were also present in catches throughout the study period. It is reasonable therefore, to conclude that *M. dobsoni* spawns in the seas off west coast of Sri Lanka throughout the year with peaks around March, September, October and November and that the spawning population is well exploited by the trawl gear.

The continuous spawning behaviour of this species is well documented. George (1962) and George et al. (1963) reported that *M. dobsoni* spawns in the coastal waters off Cochin throughout the year with peaks in November and June to August. Kesteven and Job (1957) also recorded the year round spawning of this species. Rao (1968) observed continuous spawning of *M. dobsoni* in the coastal waters off Cochin.

A substantial contribution of mature shrimps to the catches from the shrimp trawlers indicates that spawning of *M. dobsoni* takes place in relatively shallow areas off the west coast of Sri Lanka where trawling is conducted in varying depths from 7 to 12 m. According to De Bruin (1965), *M. dobsoni* spawns in shallow muddy regions at depths of 9 to 14 m in the coastal waters off Ceylon. George et al. (1963) observed in the coastal waters off Cochin, India that *M. dobsoni* may move from the regular trawl fishing zone of 10 to 30 m to the very near shore for spawning. However, a preference for relatively deeper waters for spawning of this species has also been reported by Menon (1952, 1965). Many females liberate their eggs in the depths varying from 22 to 23 m.

The estimated values for the mean sizes at maturity for males and females of *M. dobsoni* during the present investigation were 6.36 and 7.31 cm, respectively. This compares favourably with the mean size of 6.41 cm at maturity for female *M. dobsoni* estimated by Rao (1968) during the study conducted off the southwest coast of India. In addition, the estimated values for the length at first capture (Lc) of males and females of *M. dobsoni* by the nonmechanised and mechanised trawlers operating in the seas off the west coast of Sri Lanka were 6.69 and 7.23 cm and 7.37 and 9.26 cm respectively (Jayawardane et al., unpublished). As the estimated values for the length at first capture of males and females by the nonmechanised and mechanised trawlers were mostly greater than that of mean sizes at maturity of *M. dobsoni*, it is understood that the way the trawl fishery is carried out has no adverse effect on the spawning population of *M. dobsoni*.

The occurrence of *M. dobsoni* (female) between 6.8 to 9.0 cm up to reproductive stage II and between 6.03 to 11.72 cm from stage III onwards indicates that the shrimp passes through more than one spawning period. They initially move through reproductive stages I, II, III, IV and V. After completion of the first spawning act shrimps seem to rest for a while in stage II before going through the maturation cycle again. In addition the highest values for mean GSI were observed for reproductive stages III and IV for 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 mature ovaries indicate that there have been three batches of ova representing the immature, maturing and mature stocks (Table 4). These three groups are sharply separated from each other in size. As the mature group of ova is larger, the individuals are either in spawning condition or very 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 contain only small ova of less than 0.021 mm in diameter, all the mature ova present in the ovary may be released in a single spawning act. The determination of the spawning period and its duration becomes difficult owing to the fact that spawning is rather protracted in the population as a whole. This suggests either the presence of different spawning times for younger and older specimens within the parent stock or that shrimp may spawn frequently with only a short duration between successive spawning. The former has been reported to occur in other decapods *Palaemon elegans* and *Carcinus maenas* by Thorson (1946). Presumably recruitment is continuous from the lagoon, so that there could be a succession of new spawners to the parent stock.

The present study indicates the occurrence of shrimps of various sizes in different reproductive stages in most months. It is reasonable therefore, to conclude that *M. dobsoni* spawns several times during their lifetime. The frequent spawning of individuals of various sizes and the short time between successive spawning would result in the occurrence of all reproductive stages in the fishery, and thereby show a prolonged spawning period in the population as a whole.

The estimated value for the Type-I fecundity (total number of eggs that have been initially separated from the ovary in the reproductive stage I) (Table 4) of *M. dobsoni* varied between 178,098 to 404,564 for the size range 7.91 to 11.15 cm. Using the proportion of eggs that are shed from an initial batch, the number of eggs that could be spawned during secondary spawning act could be estimated as 153,735. Therefore, an estimated number of 91,652 to 225,679 eggs would be spawned by the shrimp of the size range 6.96 to 11.72 cm (Type-II fecundity or the total number of eggs that are ready to be shed in the reproductive stage IV). However, the fecundity (Type-II) of this species in the size range 7.0 to 12.0 cm was estimated to vary between 34,500 and 160,000 by Rao (1968). Although the estimated value for the fecundity of *M. dobsoni* by Rao (1968) seems to be slightly lower when compared with the fecundity estimations made during the present investigation, these values are almost comparable. In addition it was also noted that the variation in fecundity in similar proportions was also observed during the present investigation and this may be due to the serial-spawning behaviour of this species.

The estimated values for the reproductive load (Lm/L_∞) of *M. dobsoni* during the present study (0.55 and 0.54 for males and females respectively) are well within the estimated range of reproductive load for fish (0.4 to 0.9) by

Froese and Binohlan (2000). Jensen (1996) suggested that fish generally optimise their mean length at maturity to coincide with the length class of maximum fecundity, proposing an average reproductive load of around 0.66. If this is applied to the shrimp fishery in the west coast of Sri Lanka, then the length of maximum fecundity should be approximately 8.7 cm, which is greater than the estimated value for the length at first capture (Lc) of female *M. dobsoni* by the non-mechanised trawlers operating in the seas off the west coast of Sri Lanka (7.23 cm) (Jayawardane et al., unpublished).

It has been observed for many fish stocks around the world that the mean recruitment level is almost constant in a large intermediate range of variation of the parental stock (Sparre and Venema 1992). The estimated probability of an egg developing into a recruit during the present study varied from 3.3×10^{-4} to 8.1×10^{-4}. This low rate of survival has very little to do with fishing, as we are considering the mortality in the pre-exploited phase of the life history. According to Beverton and Holt (1957) the recruitment is affected only when the rate of fishing is increased beyond a certain level. The effect of fishing is a reduction of the spawning potential (growth over fishing), but not the recruitment, except in situations where fishing pressure is substantially high. In spite of heavy exploitation of juveniles (shrimp catches from the system comprised of around 65 and 76% of under sized males and females respectively) the recently concluded resource evaluation exercise indicated that the fisheries are performing satisfactorily in terms of *M. dobsoni* in the Negombo lagoon and the associated coastal ecosystem (Jayawardane et al., unpublished). Therefore, it is understood that the manner in which the shrimp fishery is conducted could still be justified by the existence of the *M. dobsoni* stocks in the seas off west coast of Sri Lanka.

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