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Reproductive Characteristics of Squid *Sepioteuthis lessoniana* (Lesson, 1830) from the Northern Coast of Sri Lanka

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Abstract: The present study was carried out to understand some reproductive characteristics such as spawning season, variation in maturation indices with months, fecundity, sperm count and relationships between various measurements and mantle length of tropical *Sepioteuthis lessoniana* from the Northern coastal waters of Sri Lanka. A total of 797 specimens of *S. lessoniana* (404 males and 394 females) were collected from commercial catches of squid fishery and analyzed. The dorsal mantle length of male *S. lessoniana* ranged from 4 to 26 cm while females ranged from 3.8 to 24.3 cm. According to the morphological appearance of gonads males were categorized into immature, maturing and fully mature whereas females were categorized into immature, maturing and spawning. High occurrence of spawning stage in squids was observed in August, October, November and March. Fecundity increased exponentially with mantle length from 20 (7 cm mantle length) to 793 (26 cm mantle length). The least square linear regression analysis expressed that there are positive, significant ($p<0.001$) relationships for ovary weight, nidamental gland weight and oviducal gland weight with the mantle length in females and for total weight, testis weight and spermatophoric complex weight with mantle length in males. It was concluded that *S. lessoniana* spawns more than once, exhibits group-synchronous ovulation and intermittent terminal spawning. Peak or intense spawning of this squid in Northern coast of Sri Lanka is during March, August and October to November.

Key words: Fecundity, spawning, group-synchronous, *Sepioteuthis lessoniana*, nidamental gland weight

INTRODUCTION

Sepioteuthis lessoniana is a neritic species most widely distributed throughout the Indo-west pacific (Lee *et al*., 1994) and it has a major commercial value in Northwestern, Northern and Northeastern waters around Sri Lanka. Squids are important components of food webs in most marine ecosystems, too (O'Dor *et al*., 2005; Clarke, 1996). They are organism with a fast metabolic rate and growth and they play an important role in the transfer of energy to higher trophic levels (Jackson and Domeier, 2003).

The squid giant axon is a valuable preparation in biomedical research. Squids have been used as research models not only for neuroscience, but also for physiology (cardiac, circulatory, sensory and muscle), immunology, molecular biochemistry, nutritional biochemistry, oncology, aging and ethology (Gilbert *et al*., 1990). Squids also have commercial importance since they are eaten regularly in many regions of the world, especially in the orient and Southern Europe (Asian Development Bank/Infofish, 1991).

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The knowledge on reproductive biology of this species is essential for proper management and its conservation. Ovulation may be distinguished as synchronous, group-synchronous and asynchronous ovulation according to oocyte formation and development in cephalopods (Rocha *et al*., 2001).

Mode of reproduction in fishes can be expressed as two major types, iteroparous and semelparous. Iteroparous organisms have more than one reproductive event in their life-time whereas, semelparous organisms reproduce only once (Rocha *et al*., 2001; Stearns, 1992). The present study attempts to identify the mode of reproduction in *S. lessoniana* from the Northern waters of Sri Lanka.

Little is known about the spawning seasonality of tropical and subtropical squid and cuttlefish (Jackson and Moltschaniwskyj, 2001). In several loliginids mature females and eggs are found year-round. In the Gulf of Mexico *Loligo peali* spawns throughout the year. *Sepioteuthis sepioidea* in the Western tropical Atlantic and *S. lessoniana* in the Western Pacific also spawn year-around (Costa and Fernandes, 1993). However, the greater abundance of recruits during certain periods of the year suggests that some seasonality exists.

The present study was carried out to understand some reproductive characteristics such as spawning season, variation in maturation indices with months, fecundity, sperm count and relationships between various measurements and mantle length of tropical *S. lessoniana* from the Northern coastal waters of Sri Lanka. Such information provides detailed understanding about *S. lessoniana* and knowledge to formulate management measurements in the squid fishery in order to maintain sustainable squid fishery in Sri Lanka.

MATERIALS AND METHODS

Random samples of *Sepioteuthis lessoniana* were collected weekly from Kurunagar, Ponnalai, Navanthurai and Point pedro coast (Fig. 1) from June 2007 to May 2008. Jaffna lagoon is one of the largest shallow water body located in the Northern Province of Sri Lanka with an area of 412.8 km^2 (Somasekaram, 1997). It is situated between 79° 52' E to 80° 38' E longitude and 9° 26' N to 9° 46' N latitudes (Somasundarampillai, 2002).

In Jaffna, fishermen use various techniques to capture squids. Mainly they capture squids by Sirahu valai. Being a small scale fishery, some fishermen use jiggers and pots to capture squids. Usually, they are caught incidentally along with other food fishes in trawl nets, boat seines and cast nets (Sivashanthini *et al*., 2009).

A total number of 797 squids, covering a size range of 2.1 to 26.0 cm dorsal mantle length were analyzed. Measurements of dorsal Mantle Length (ML) and total Body Weight (BW) were recorded. Length measurements were measured to the nearest cm using measuring board and vernier caliper and weight was measured to the nearest 0.001 g by using top loading electronic balance (AND FY 300). Sexes were confirmed after dissecting the squid specimens; for each specimen maturity stage was categorized by macroscopic observation of the gonads.

Various morphometric measurements were taken for males and females. For males, the Weight of Testis (TEW) and Spermatophoric Complex Weight (SCW) were measured; then the spermatophoric complex was dissected to separate the spermatophores and the total numbers of macroscopic spermatophores were counted. Various reproductive indices such as the Gonado Somatic Index (GSI), Spermatophoric Complex Index (SCI) and Maturity Coefficient (MCO) for males were computed using the following equations (Durward *et al.,* 1979; Lipinski, 1979; Juanico, 1983; Gabr *et al*., 1998):

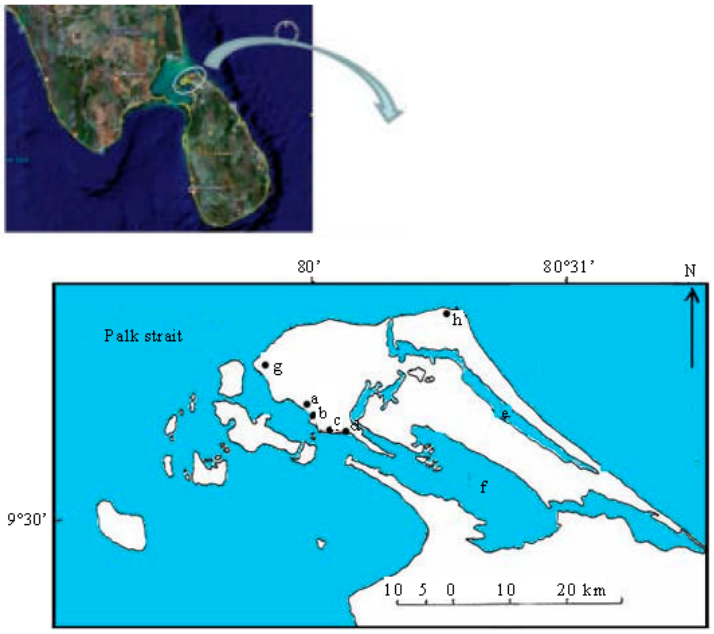

Fig. 1: Sampling sites (b, c, g and h) of *Sepioteuthis lessoniana* form the Northern coast of Sri Lanka; a: Kakkaithevu, b: Navanthurai, c: Kurunagar, d: Pasaioor, e: Thodaimannar lagoon, f: Jaffna lagoon, g: Ponnalai and h: Point pedro

$$\text{Gonado Somatic Index (GSI)} = \frac{\text{TEW}}{\text{BW}} \times 100$$

$$\text{Spermatophoric Complex Index (SCI)} = \frac{\text{SCW}}{\text{BW}} \times 100$$

$$\text{Maturity COefficient (MCO)} = \frac{\text{TEW} + \text{SCW}}{\text{BW}} \times 100$$

where, BW is the body weight. The spermatophoric complex includes the spermatophoric organ, vas deference, spermatophoric sac or Needam's sac, sperm duct and penis.

For females, the total Weight of Ovary (OW), Weight of OViducal gland (OVW), Nidamental Gland Weight (NGW) and colour of accessory nidamental gland were recorded. Various reproductive indices such as the Gonado Somatic Index (GSI), Nidamental Gland Index (NGI) and Maturity COefficient (MCO) for females were computed using the following equations (Durward *et al.*, 1979; Lipinski, 1979; Juanico, 1983; Gabr *et al.*, 1998):

$$\text{Gonado Somatic Index (GSI)} = \frac{\text{OW}}{\text{BW}} \times 100$$

$$\text{Nidamental Gland Index (NGI)} = \frac{\text{NGW}}{\text{BW}} \times 100$$

$$\text{Maturity COefficient (MCO)} = \frac{\text{OW} + \text{OVW}}{\text{BW}} \times 100$$

where, BW is the body weight.

The percentage occurrence of various maturity stages of ovaries in different months was computed by pooling the data for one year and represented graphically. Maturity stages recognized macroscopically were categorized in to different stages.

Fecundity was defined as the total number of maturing ova (with striation) and mature ova (large smooth ova) in the ovary and the number of ova in the oviducal glands, proximal and distal gland (Gabr *et al*., 1998). Collected eggs were preserved in Gilson's fluid for at least 48 h in order to count the total number of eggs, the fecundity. Fecundity was counted in 116 females ranged from 7.0 to 26.0 cm mantle length. In the ovaries, there were different stages of ova; striation was used to group ova into small (without striation and milky in appearance), maturing (with striation) or mature (large and smooth-transparent) (Gabr *et al*., 1998).

Length at maturity were analyzed for squids collected from July to November to reduce the possibility of classifying resting, mature fish as immature. Length at maturity was based on 165 females and 159 males (9.7 to 26.0 cm TL). The maturity data were grouped into 2.5 cm size groups and the percentage occurrence of the specimens in each size group was calculated. Size at first maturity was arrived by plotting the percentage occurrence of mature specimens against total length and by obtaining the length at 50% maturity (L_{50}).

For male squids, relationships of total Body Weight (BW)-Mantle Length (ML), Weight of TEstis (TEW)-Mantle Length (ML), Spermatophoric Complex Weight (SCW)-Mantle Length (ML) and Total Sperm Count (TSC)-Mantle Length (ML) were fitted by the logarithmic transformation of Log Y = log a + b log X (Bagenal and Tesch, 1978), where, Y is the dependant variable and X is the independent variable.

Similarly for females, relationships of total Body Weight (BW)-Mantle Length (ML), the total Weight of Ovary (OW)-Mantle Length (ML), Weight of OViducal gland (OVW)-Mantle Length (ML), Nidamental Gland Weight (NGW)-Mantle Length (ML), Fecundity (F)-Mantle Length (ML), Fecundity (F)-total Body Weight (BW) and the total Weight of Ovary (OW)-total Body Weight (BW) were fitted by the least square regression analysis.

Sex ratio was determined from the number of specimens of each sex sampled every month to test the significant deviations from an expected 1:1 sex ratio for all male and female fishes. The sex ratio values obtained every month were subjected to chi-square test (Sokal and Rohlf, 1981) employing the formula:

$$\chi^2 = \sum [(o-e)^2/e]$$

where, o is observed number and e is expected number.

RESULTS

A total of 797 specimens of *S. lessoniana* (404 males and 394 females) were collected from commercial catches of squid fishery from the Northern coast of Sri Lanka. The size (dorsal mantle length, ML) of male *S. lessoniana* ranged from 4 to 26 cm ML while females ranged from 3.8 to 24.3 cm ML. From the collected data it was apparent that males are heavier than the females. Eleven unsexed specimens which range from 2.1-4.3 cm ML were also collected.

Unlike most fin fishes, external sex differentiation is possible in *S. lessoniana*. In fresh female specimens, whitish colour mass (Nidamental gland) and pale colored ovary were able to observe through the ventral side of the transparent mantle. In fresh male *S. lessoniana* chromatophore arrangements create transverse bars in the dorsal side of the mantle and fourth left arm is hectocotylized. External appearance (dorsal view) of fresh female and male *S. lessoniana* is shown in Fig. 2a and b. In comparison, matured males were narrow and longer than matured females. Dissection through mid ventral axis clearly defined the sexes. Interestingly some females had bunches of spermatophores at the buccal funnel region and a photograph of it is shown in Fig. 3.

According to the morphological appearance of gonads males were categorized into immature, maturing and fully mature as described in Table 1 while females were categorized into immature, maturing and spawning as described in Table 2 and Fig 4a and b. In freshly dissected ovaries the matured eggs were observed in the peripheral region whereas immature and maturing eggs were observed as the central mass. Extrusion of matured eggs to the exterior through the oviduct was also observed in females and it is shown in Fig. 4c.

Monthly variation of various maturity indices of males and females are shown in Fig. 5 and 6. For males, the MCO values varied from 1.09 to 4.02 with an average of 1.87±0.21; GSI values varied from 0.65 to 1.5 with an average of 1.02±0.08; SCI values varied from 0.44 to 3.36 with an average of 1.00±0.23. For females, the MCO values varied from 7.70 to 11.70 with an average of 9.92±0.37; GSI values varied from 3.44 to 7.11 with an average of 5.39±0.31; NGI values varied from 1.52 to 4.55 with an average of 3.49±0.27.

Monthly distribution of maturity stages of ovaries of *S. lessoniana* is shown in Fig. 7. In female *S. lessoniana*, spawning stage was recorded throughout the year except in May (Fig. 8). High percentages i.e., 65 and 60% of immature squids recorded in September and May, respectively. Lowest percentage (20%) of immature squids was recorded in July. Maturing squids were recorded throughout the year except in August and September. High

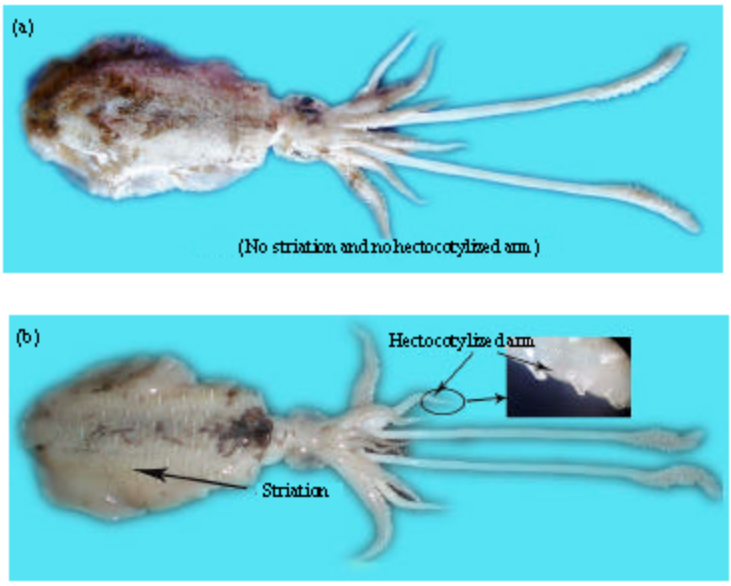

Fig. 2: (a) External appearance of fresh female *S. lessoniana*. (b) External appearance of fresh male *S. lessoniana*

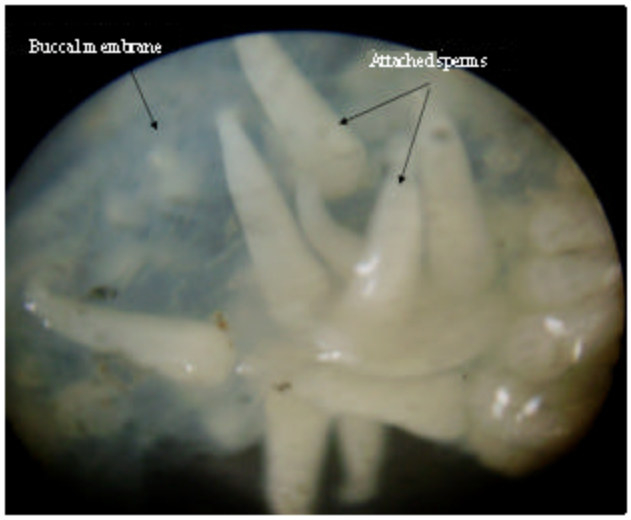

Fig. 3: Sperms attached to the female's buccal membrane

Table 1: Male maturation scale in *Sepioteuthis lessoniana*

Maturity stage	Morphological characters
Immature	Small, thin, transparent testis; very small, transparent spermatophoric complex; Needham's sac without sperms.
Maturing	Testis is white and large, Spermatophoric complex and Needham's sac clearly visible. Needham's sac contains few spermatophores.
Fully mature	Needham's sac is filled with tightly packed spermatophores, which are well developed with distinct spiral filament cement body

Table 2: Female maturation scale in *Sepioteuthis lessoniana*

Maturity stage	Morphological characters
Immature	Nidamental gland (NG) thin transparent or translucent, Accessory Nidamental (ANG) gland transparent or translucent with white or light brown patches. Ovary very small, no ova apparent
Maturing	NG thicker, creamy white and clearly visible, ANG translucent with light orange patches. Ovary with small to striated eggs
Spawning	NG swollen, thick and white colour in appearance, ANG pale yellow with dark orange patches. Ovary has small ova, medium ova, large yellow reticulated ova and large smooth transparent ova. Proximal oviduct is filled with mature eggs

occurrence of spawning stage in squids was observed in August, October, November and March. This suggests that the peak spawning period of *S. lessoniana* is in August, March, October and November even though it spawns throughout the year. Presence of all three stages of macroscopic eggs in the same ovaries confirms that the spawning of *S. lessoniana* in the Northern coastal waters should be more than once and said to be asynchronous or group synchronous.

Fecundity increased exponentially with Mantle Length (ML) from 20 (7 cm) to 793 (26 cm TL) but a weak correlation was obtained with mantle length ($r = 0.59$, $p<0.01$). A weak relationship ($r = 0.59$, $p<0.01$) was also obtained for fecundity with total body weight. However a correlation ($r = 0.77$, $p<0.01$) between ovary weight and total body weight was obtained in the present study. In males, number of sperm varies from 5 to 568 for individuals of 9.8 to 24.3 cm dorsal mantle length.

Plots obtained for percentage occurrence of mature squids against mantle length class interval indicates that *S. lessoniana* male reached maturity at 15 cm mantle length, while

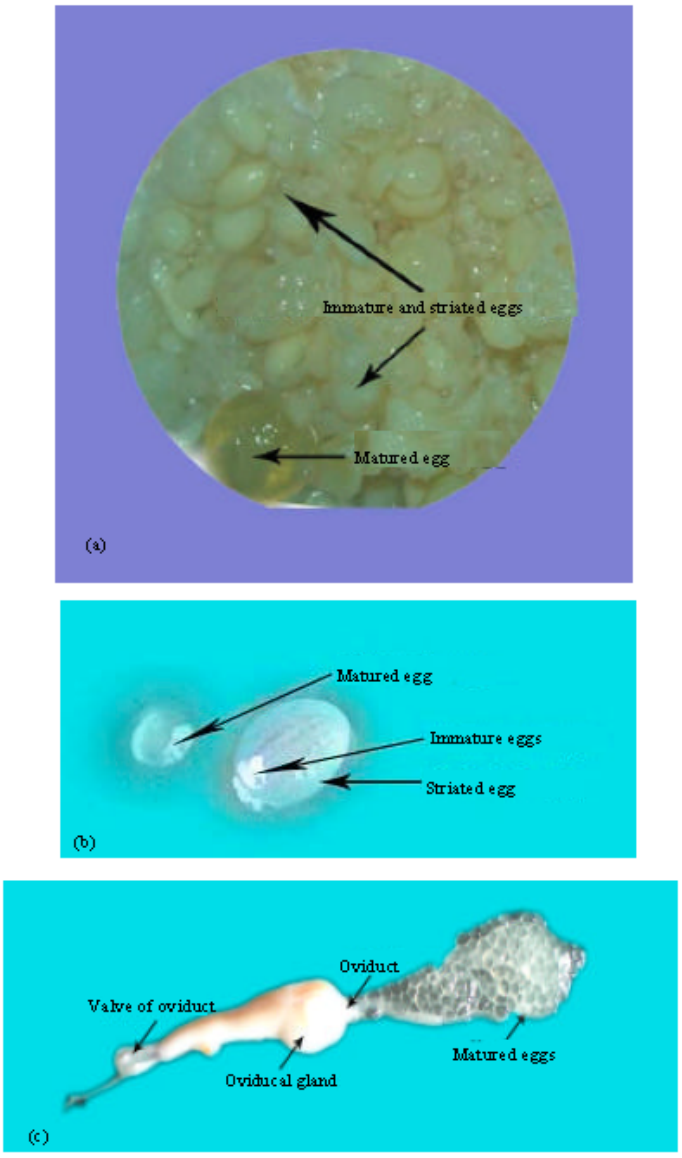

Fig. 4: (a, b) Immature, maturing and matured stages of ova in female *S. lessoniana* ovary. (c) Extrusion of matured eggs to the exterior through the oviduct in female *S. lessoniana*

female reached maturity at 17.5 cm mantle length. All males and females were matured at 20.0 cm mantle length.

The least square linear regression analysis expressed that there are highly significant ($p<0.001$) relationships for OW, NGW and OvW with the mantle length in females. That is OW, NGW and OvW proportionately increased with increasing mantle length in females. Similarly highly significant ($p<0.001$) relationships for TW, TEW and SCW with mantle length

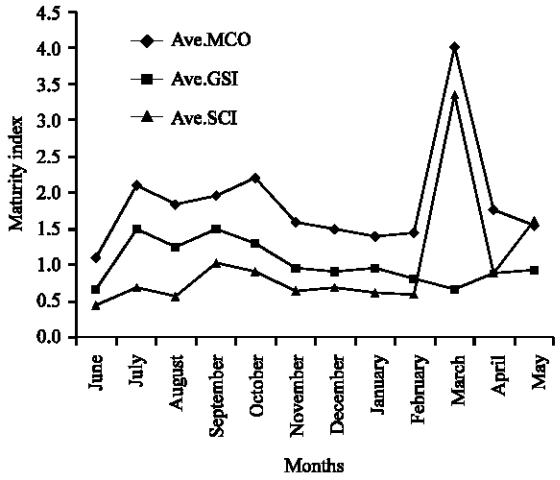

Fig. 5: Indices of reproductive status for male *S. lessoniana* against months

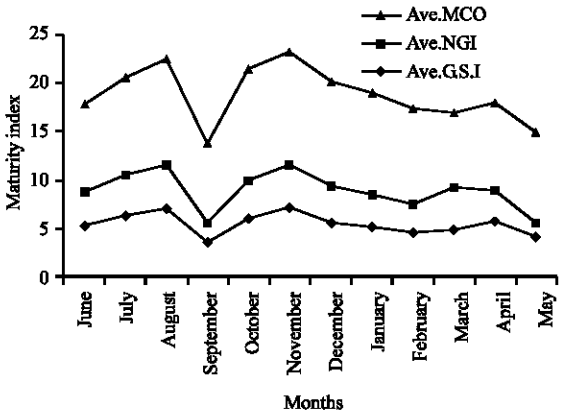

Fig. 6: Indices of reproductive status for female *S. lessoniana* against months

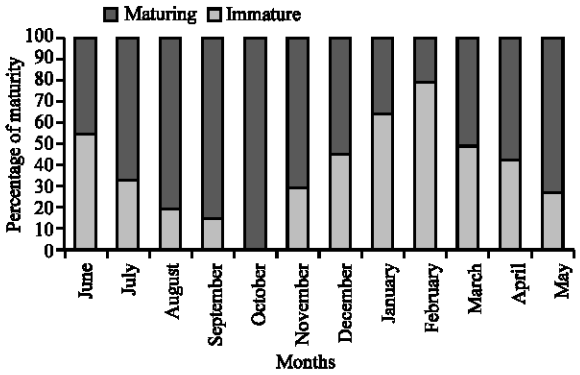

Fig. 7: Monthly distribution of maturity stages of male *S. lessoniana*

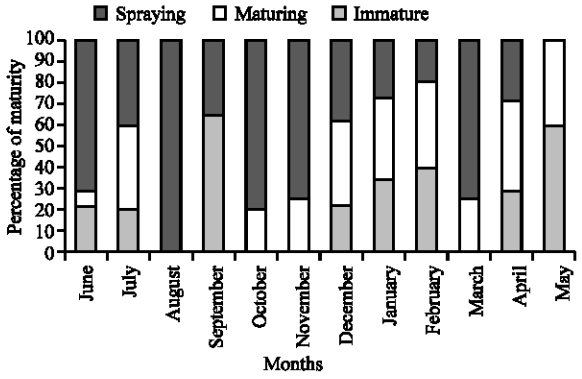

Fig. 8: Monthly distribution of maturity stages of female *S. lessoniana*

Table 3: Correlations of reproductive parameters of *Sepioteuthis lessoniana*

Sex	Correlation	N	R	p-value	Equations
Female	TW versus ML	404	0.98	<0.001	$TW = (0.18)\ ML^{2.491}$
	OW versus ML	404	0.77	<0.001	$OW = (2.38\times10^{-7})\ ML^{6.447}$
	NGW versus ML	404	0.88	<0.001	$NGW = (4.06\times10^{-7})\ ML^{6.162}$
	OvW versus ML	404	0.83	<0.001	$OvW = (1.00\times10^{-6})\ ML^{5.492}$
	Fecundity versus ML	116	0.59	<0.001	$Fecundity = (0.05)\times ML^{3.234}$
	Fecundity versus BW	116	0.59	<0.001	$Fecundity = (0.48)\times ML^{1.298}$
	OW versus BW	404	0.77	<0.001	$OW = (7.81) \times BW^{0.233}$
Male	TW versus ML	393	0.98	<0.001	$TW = (0.18) \times ML^{2.512}$
	TEW versus ML	393	0.77	<0.001	$TEW = (5.67\times10^{-4})\ ML^{2.947}$
	SCW versus ML	393	0.85	<0.001	$SCW= (6.06\times10^{-5})\ ML^{3.639}$
	Sperm count versus ML	108	0.76	<0.001	$Sperm\ count = (6.78\times10^{-3})\ ML^{3.437}$

were obtained for males. Parabolic equations for relationships of various morphometric measurements versus mantle length, R^2 and p-values of above relationships for both male and female squids are presented in Table 3.

Of the 797 *S. lessoniana* sexed, 404 were females and 393 were males. Chi-square value calculated for overall sex ratio conformed to the expected 1:1 ratio ($p>0.05$).

DISCUSSION

Sexual differences in length - weight relationship in *S. lessoniana* was not evident in the present study. It tallies with the earlier findings of the researchers. Comparison of length-weight regression lines for both sexes showed no significant difference ($p>0.05$) between males and females (Sivashanthini *et al.*, 2009). Length weight relationship of *S. arctipinnis* males were reported as $W = 0.0005\ L^{2.449}$ and females as $W = 0.0003\ L^{2.659}$ by Rao (1954). Segawa (1987) reported on the length-weight relationship of wild and cultured *S. lessoniana* and obtained the regression equations $W = 0.0003\ L^{2.675}$ and $W = 0.0004\ L^{2.553}$, respectively. The exponential value 'b' obtained for *S. lessoniana* male and female in the present study 2.5119 for males and 2.491 for females are in consistent with the earlier studies. The slight deviation may be due to food supply and water condition.

Some females had bunches of spermatophores on both sides of the mantle wall at the base of the gill near the opening of the oviduct suggests that the fertilization in this species occur at the buccal funnel region. Sometimes more than two bunches of spermatophores were observed and it infers that females may mate more than once. Egg clusters of

S. lessoniana were frequently found attached to hard substrate from August to January near the coasts further confirms the spawning period.

Fecundity of *S. lessoniana* found to be lesser than that of *S. pharaonis* for example, number of ova in 14 cm ML *S. dollfusi* and *S. lessoniana* was 730 (Gabr *et al*., 1998) and 700, respectively. Fecundity of *S. pharaonis* ranged between 517 and 1525 ova for females of 11-24 cm ML (Gabr *et al*., 1998) whereas for *S. lessoniana* ranged between 20 and 793 for females of 7-26 cm ML. Fecundity for *S. lessoniana* in the Zanzibar coastal waters ranged from 180 to 1180 eggs for individuals of size range 14.0-24.9 cm ML (Mhitu *et al*., 2001) which is higher than the present results. The variation for the same species may have been attributed due to varying environmental factors, food availability and so on in different habitats.

The weak correlation between fecundity and mantle length may have been resulted as some females of similar size have already been laid different number of eggs. Therefore all these individuals appeared to be in spawning condition and it is an evidence of continuous egg production throughout the adult life confirming the multiple spawning. A similar result was also observed in *S. lessoniana* and *S. australis* of Australian waters by Peel (2001). Multiple spawning strategy can also be explained by the fact that large eggs in the ovary causing the oviduct volume to be insufficient to accommodate all eggs. Therefore, number of egg masses must be spawned in several batches (Rocha *et al*., 2001).

Maturation in female *S. lessoniana* individuals was a size-related process, because weight of ovary, nidamental gland and oviducal gland were all highly correlated with mantle length. Maturation in male *S. lessoniana* individuals was also a size-related process, because testis weight was highly correlated with mantle length.

Finally, it can be concluded that squid *S. lessoniana* exhibits reproductive pattern of spawning more than once, group-synchronous ovulation and reproductive strategy of intermittent terminal spawning. Peak or intense spawning of this squid in Northern coast of Sri Lanka is in March, August and October to November. In a squid population an exploited stock can be renewed through recruitment. If overexploitation occurs, matured squids could be reduced and subsequently reproductive capacity of the population diminished. Such situation can be managed by setting restrictions on mesh sizes of the gears used to catch squids. Further, breeding females should be protected during the peak spawning period in order to maintain sustainability. Findings of the present study would definitely lead to formulate a management strategy and ensure a long term sustainability of *S. lessoniana* in coastal waters of Sri Lanka.

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REFERENCES

Asian Development Bank/ Infofish, 1991. Cephalopods AOB infofish global industry update. Infofish, Kaula Lumpur, Malaysia, pp: 127.

Bagenal, T.E. and F.W. Tesch, 1978. Age and Growth. In: Methods for Assessment of Fish Production in Freshwater. IBP Handbook No. 3, Bagenal, T. (Ed.). Blackwell Scientific Publications, Oxford and Edinburgh, pp: 101-136.

Clarke, M.R., 1996. The role of cephalopods in the world's ceans. Phil. Trans. R. Soc. Lond., 351: 977-1112.

Costa, P.A.S. and F.C. Fernandes, 1993. Reproductive cycle of *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in the Cabo Frio region, Brazil. Mar. Ecol. Prog. Ser., 101: 91-97.

Durward, R.D., T. Amaratunga and R.K. O'Dor, 1979. Maturity index and fecundity for female squid *Illex illecebrosus* (Le Sueur, 1821). ICNAF Res. Bull., 14: 67-72.

Gabr, H.R., R.T. Hanlon, M.H. Hanafy and S.G. Etreby, 1998. Maturation, fecundity and seasonality of reproduction of two commercially valuable cuttlefish. *Sepia pharaonis* and *Sepia dollfusi* in the Suez Canal. Fish. Res., 36: 99-115.

Gilbert, D.L., W.J. Jr. Adelman and J.M. Arnold, 1990. Squid as Experimental Animals. Plenum Press, New York, pp: 516.

Jackson, G.D. and N.A. Moltschaniwskyj, 2001. The influence of ration level on growth and statolith increment width of the tropical squid *Sepioteuthis lessoniana* (Cephalopoda: Loliginidae): An experimental approach. Mar. Biol., 138: 819-825.

Jackson, G. D. and M.L. Domeier, 2003. The effects of an extraordinary El Nino/ La nina event on the size and growth of the squid *Loligo opalescens* off Southern California. Mar. Biol., 142: 925-935.

Juanico, M., 1983. Squid Maturity Scale for Population Analysis. In: Advances in Assessment of World Cephalopod Resources, Caddy, J.F. (Ed.). FAO., Rome, Italy, pp: 341-378.

Lee, P.G., P.E. Turk, W.T. Yang and R.T. Hanlon, 1994. Biological characteristics and biomedical applications of the squid *Sepioteuthis lessoniaana* cultures through multiple generaions. Biol. Bull., 186: 328-341.

Lipinski, M., 1979. Universal maturity scale for the commercial important squids. The results of maturity classification of *Illex illecebrosus* (Lesueur, 1821) population for years 1973-1 977. Res. Doc. 79/11/38. Serial No.5364. Int. Comm. Northwest Atl. Fish., 40.

Mhitu, H., Y. Mgaya and M. Ngoile, 2001. Western Indian Ocean Marine Science Association, Zanzibar (Tanzania) and Institute of Marine Sciences, Zanzibar (Tanzania) University of Dar es Salaam. In: Growth and Reproduction of the Big Fin Squid, *Sepioteuthis lessoniana*, in the Coastal Waters of Zanzibar, Richmond M.D. and J. Francis (Eds.). IMS/WIOMSA, Zanzibar, pp: 289-300.

O'Dor, R., J. Aitken and G.D. Jackson, 2005. Energy balance growth models: Applications to cephalopods. Phuket mar. Biol. Cent. Res. Bull., 66: 329-336.

Peel, G., 2001. Flexible reproductive strategies in tropical and temperate *Sepioteuthis* squids. Marine Biol., 138: 93-101.

Rao, K.V., 1954. Biology and fishery of the Palk-bay squid, *Sepioteuthis arctipinnis* gould. Ind. J. Fish., 1: 37-67.

Rocha, F., A. Guerra and F.A. Gonzalez, 2001. A review of reproductive strategies in Cephalopods. Biol. Rev., 76: 291-304.

Segawa, S., 1987. *Sepioteuthis lessoniana* in Kominato and adjacent waters, Central Honshu, Japan. J. Tokyo. Univ. Fish., 74: 67-105.

Sivashanthini, K., G.A. Charles and W.S. Thulasitha, 2009. Length-weight relationship and growth pattern of *Sepioteuthis lessoniana* lesson 1830 (Cephalopoda: Teuthida) from the Jaffna Lagoon, Sri Lanka. J. Biol. Sci., 9: 357-361.

Sokal, R.R. and F.J. Rohlf, 1981. Biometry: The Principles and Practice of Statistics in Biological Research. W.H. Freeman and Company, San Francisco, pp: 706.

Somasekaram, T., 1997. Arjuna's Atlas of Sri Lanka. Arjuna Consulting Co. Ldt., Dehiwela, Sri Lanka, pp: 220.

Somasundarampillai, A., 2002.. Introduction of Sri Lanka Fisheries Exploitation and Development. Ampalam Publications, Wattala, pp: 1-2.

Stearns, S.C., 1992. The Evolution of Life History. Oxford University Press, Oxford.