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Reproductive strategy uniqueness of *Littoraria scabra* (Gastropoda: Littorinidae), in Tombariri mangrove, North Sulawesi, Indonesia

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Key words: *Littoraria scabra,* Reproductive strategy, Ovovivipar, Sex ratio, Gonad.

Abstract

This study used *Littoraria scabra* as a research model of reproductive strategy and attempted to understand how the species optimize their survival in mangrove area. It was aimed at investigating the reproductive strategy of ovoviviparous *L. scabra* in order to maintain their survival in mangrove ecosystem. Reproductive strategy observations of *L. scabra* were done by looking at mating, gonad maturity index, and sex ratio**.** Results showed that the reproductive strategy of *L. scabra* was as follows: a) there were 64.58% of mating pairs on the stem of *S. ovata* and b) sex ratio was globally significant different, but it was generally nonsignificant on monthly basis. Specific strategy of ovoviviparous species *L. scabra* with reproductive patterns, i.e mating, gonad maturity, and sex ratio was to optimize their reproductive success in extreme three-dimensional mangrove habitat**.** This study concluded that the reproductive strategy uniqueness of male *L. scabra* possessed fertilized eggs and very rare brooding system in male body and quickly released larvae.

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Introduction

Concept of reproductive strategy has become a main component in life history theory (Todd, 1985). Comprehension on reproductive strategy diversity reflected by living organisms and their interaction with environment is central issue in ecology (Hart and Begon, 1982; Todd, 1985). Reproductive strategies are an adaptation and response to complex environmental factors and physiological characteristics of a species (Thorp and Covich, 1999). Reproductive strategy of gastropods is possibly affected by environmental factors, such as environmental variability, major production and physico-chemical factors. Reproductive efforts and strategies are important indicators of the life history strategy (Grahame and Branch, 1985).

Reproductive strategy of tropical snails, littorinid, is relatively lack of information since the biological studies on *littorinid* are largely limited to stony beaches (genus *Littorina*) in temperate regions (Sanpanic *et al.,* 2008).

The reproductive study of *littorinid* (Littorinidae) in mangrove ecosystem, especially genus *Littoraria,* is very limited (Gallagher and Reid, 1974; Sanpanic *et al.,* 2008; Ng, 2013). According to Ng (2013), various adaptive reproductive characteristic has evolved in genus *Littoraria* in which it represents species specific strategies to optimize the reproductive success. Reproductive success is an adaptive capability of exploiting mangrove habitats for ovoviviparous species development (Reid, 1992). Family Littorinidae is the best group to study the reproductive strategy, patterns and larval development, because the species occurs in all intertidal habitats (including supraintertidal) in the world (Mileikovsky, 1975).

According to Ng (2013), the importances of *Littoraria spp*. reproduction are: (1) female's role in controlling male mate selection (Edward and Chapman, 2011), holding the sperms (Reid, 1989; Buckland-Nicks *et al*., 1999), and as a consequence, it creates sperm competition potential; (2) phylogenetic role succeeds avoiding taxonomic ambiguity of genera *Littoraria* and subfamily Littorininae through morphological and molecular data (Reid *et al.,* 2010 and 2012) that enable to reconstruct the evolutionary history of reproductive characteristics in family Littorinidae, and (3) *Littoraria spp* shows relatively simple behavioral patterns, such as complex courtship behaviors", as recorded in terrestrial gastropods (Gallagher and Reid, 1974). Considering few information on reproductive strategy of *Littoraria scabra*, a study on reproductive strategy of ovoviviparous *L. scabra* needs to do in order to sustain the survivorship in mangrove ecosystem.

Materials and methods

Reproductive strategy method of *L.scabra* is to assess mating, gonad maturity index (Gonadosomatic Index, GSI), and sex ratio. Ten individuals of each males and females collected were mature.

The collection was done 4 days before new moon and full moon period from February to December 2014. Sampling of 10 mating pairs were collected. The males and females were put in different plastic containers. Gonad weight and body weight ratio were used to estimate gonad maturity (Blonk *et al*., 2013). GSI is a quantitative indicator of gonad condition and represents the simplest way to measure changes in size and weight of this organ in relation to total weight of the organism (Rodriguez-Gonzalez, 2006).

Data were randomized for both 10 mature males and 10 mature females. Gonad maturity was observed in individual males and females and in mating males and females. Sex ratio is a ratio between total number of males and females in a population. Traditional sex ratio model was introduced by Fisher (1930) that male and female ratio of 1:1 indicated a stable evolution. The sex ratio of *L.scabra* was determined by looking at the ratio of male and female frequencies using Chi-Square test. Map of Research Location in Mangrove Tombariri, North Sulawesi Indonesia (Figure.1 A and 1B).

Fig. 1 A. Map of Research Location in Mangrove Tombariri, North Sulawesi Indonesia.

Fig. 1 B. Map of North Sulawesi, Indonesi.

Results and discussion

Sex Ratio

Total number of *L. scabra* found in this study was 562 individuals, 243 (43.24 %) males and 319 (56.76 %) females. These data shows that sex ratio was 1:1.31 indicating that number females are higher than that of males (Table 1).

Table 1. Number and percent of males and females of *Littoraria scabra* at 2 month intervals from February 2014 to December 2014 in the coastal mangrove of Tombariri.

Month	No.Samples	No.Males	Males (%)	No.Females	Females (%)
February	84	33	39.29	51	60.71
April	72	32	44.44	40	55.56
June	111	43	38.74	68	61.26
August	96	42	43.75	54	56.25
October	94	37	39.36	57	60.64
December	105	56	53.33	49	46.67
Total	562	243	43.24	319	56.76

Sex ratio = 1 :1.31

Overall sex ratio showed difference between number of males and females. The significant difference was recorded in February, June and October (Table 2).

Table 2. Sex ratio and Chi-Square value of *Littoraria scabra* in different months from February to December 2014, in the coastal mangrove of Tombariri.

Month	Male : Female	Chi-Square value	P = 0.05
February	1 : 1.55	$3.86 > 3.84$	Significant
April	1 : 1.25	$0.88 < 3.84$	Nonsignificant
June	1 : 1.58	$5.64 > 3.84$	Significant
August	1 : 1.29	$1.50 < 3.84$	Nonsignificant
October	1 : 1.54	$4.26 > 3.84$	Significant
December	1 : 0.88	$0.46 < 3.84$	Nonsignificant
Global	1 : 1,31	$16.60 > 11.07$	Significant

Study in inner mangrove found a total of 505 individuals of *L. scabra*, 202 males (40 %) and 303 females (60 %). Descriptive sex ratio analysis shows that male and female ratio is 1 :1.50 indicating that females outnumber the males as shown in Table 3.

Table 3. Number and percent of males and females of *L.scabra* at 2 month intervals from February to December 2014 inner mangrove Tombariri.

Month	Sample Size	No. Males	Males (%)	No.Females	Females (%)
February	72	30	41.67	42	58.33
April	76	33	43.42	43	56.58
June	87	31	35.63	56	64.37
August	81	35	43.21	46	56.79
October	91	40	43.96	51	56.04
December	98	33	33.67	65	66.33
Total	505	202	40.00	303	60.00

Sex ratio = 1 : 1.50.

In general the statistical tests were nonsignificant, except in June and global . Although global the sex ratio is descriptively 1 : 1.5 reflecting higher number of females than males (Table 4).

Table 4. Sex ratio and Chi-Square value of *L. scabra* in different months from February to December 2014, in inner mangrove of Tombariri.

Month	Male : Female	Chi-Square Test	P = 0.05
February	1 : 1.40	$2.00 < 3.84$	Nonsignificant
April	1 : 1.30	$1.32 < 3.84$	Nonsignificant
June	1 : 1.81	$7.18 > 3.84$	Significant
August	1 : 1.31	$1.50 < 3.84$	Nonsignificant
October	1 : 1.28	$1.32 < 3.84$	Nonsignificant
December	1 : 1.97	$0.66 < 3.84$	Nonsignificant
Global	1 : 1.50	$13.98 > 11.07$	Significant

In Tombariri mangrove, both coastal mangrove and inner mangrove globally show significantly different sex ratio, but there are significantly different and non significantly different sex ratio in different months. According Hamilton (1967), sex ratio is not always balanced**.** In some animals, parents can control the brood sex ratio according to their own physiological or environmental conditions (Yusa, 2004). Other environmental conditions, such as density, and food availabilty also influence the sex ratio and mating pairs. It seems unlikely that parental conditions affect the brood sex ratio in this snail (Yusa, 2004); this condition can be occurred in *Littoraria scabra*.

Table 5. Occurrence of *Littoraria scabra* mating pairs on 3 parts of the mangrove tree.

Mangrove Species	No.Mating pairs (%) on the root	No. Mating pairs (%) on the branch	No. Mating pairs (%) on the stem	(n)
Sonneratia ovata	0	85 (34.15 %)	155 (64.58 %)	240
Avicennia marina	0	31 (38.27 %)	50 (61.73 %)	81
Rhizophora apiculata	17 (73.71 %)	0	6 (26.09 %)	23

Observations on operational sex ratio (OSR) of *L. scabra* on *Sonnerratia ovata* showed that mating was not as agressive as on *Rhizophora apiculata* due to relatively low number of females. As a consequence, competition occurs between males over the same females for mating, and therefore, mating males needs additional cost. This condition is brought about by unbalanced OSR of *L. scabra* on *Rhizophora* that influences their mating behavior, and thus, sex selection intensity is limited (Emlen and Oring, 1977). In relation with reproductive level, number of larvae released by *L. scabra* are higher than number of eggs delivered by *L. melanostoma* during the mating season. Hence, *L. melanostoma* has possibly lower reproductive level (Ng, 2013). In general, *L. scabra* had OSR equilibrium on *S. ovata*. The sex ratio is available in a population in certain time, and therefore, this sex ratio could possess higher level of competion for sex selection (Allsop *et al.,* 2006).

Unbalanced sex ratio of *L. scabra* on mangrove tree, *Rhizophora*, could result from higher predation intensity by crabs than on mangrove *Avecinnia* and *Sonneratio*. The unbalanced OSR will usually result in increased competition between mating individuals and more abundant individual sexes, and the extent of unbalanced OSR will determine the competition level and sex selection interaction (Clutton-Brock and Parker, 1992). *L. scabra* population has balanced sex ratio of mature individuals. Unbalanced male OSR could still tend to occur because of different reproductive investment between both sexes (Emlen and Oring, 1977). In general, females invest more on egg production as in males producing sperms (Trivers, 1972). Therefore, females need longer time to fill the egg cost (for instance, females will have lower potential reproductive level) reducing a number of females to receive active male sexuality (Clutton-Brock, 2007).

The OSR gives impacts on mating competition and competitive selection (Kvarnemo and Ahnesjo, 1996). The unbalanced OSR will usually increase the competition of mating individuals; the resources of excessive sex competition and broad OSR deviation will need the level of mating competition and sex selection intensity (Clutton-Brock and Parker, 1992). For example, male spider mite (*Tetranychus urticae*) whose mating competition rises as the OSR changes due to lower number of males, and consequently sex selection causes increased body size of the male relative to female body size (Enders, 1993).

Sex allocation theory predicts that if the OSR is disturbed from its unity (in time or space), the facultative sex ratio adjustment will occur (Allsop *et al.,* 2006). Perhaps this principle could occur in the OSR of *L. scabra*. In this way, female spawners could reduce the competition from sex dominance, and therefore, maximize the survival of the youngsters (Allsop *et al*., 2006). *Littoraria* species living in the lower mangrove canopy (where marine predators are more abundant), in general, possess thicker shell than those occurring in the higher mangrove canopy (Reid, 1992). Shell thickness has an adaptive value in relation with intensive predation pressure in mangrove habitat (Reid, 1992). This condition perhaps gives clear information on how the natural selection controller, predation in this regard, that might affect the operational sex ratio and sex selection intensity of *L. scabra*.

Table 6. Bilunar periodicity of mating in *Littoraria scabra*. Total population was counted every day during this August; percentage are based on this number in mangrove.

Date August 2014	Total population	No. of individual Snails pairing	Snails Pairing (%)	Moon phase
1	156	1	0.64	
2	166	1	0.60	
3	183	12	6.56	
4	161	16	9.94	
5	175	26	14.86	
6	190	34	17.89	
7	182	41	22.53	
8	240	72	30.00	Fullmoon
9	160	30	18.75	
10	175	26	14.86	
11	131	8	6.11	
12	203	11	5.42	
13	178	5	2.81	
14	187	4	2.14	
15	192	3	1.56	
16	195	1	0.51	
17	204	5	2.45	
18	218	11	5.05	
19	231	18	7.79	
20	171	16	9.36	
21	178	20	11.20	
22	186	24	12.90	
23	165	26	15,76	
24	187	32	17.11	
25	220	60	27.27	Newmoon
26	182	26	14.29	
27	166	17	10.24	
28	143	11	7.69	
29	130	6	4.69	
30	136	4	2.94	
31	152	2	1.32	

Mating pairs of L. scabra

The present investigation showed mating pairs found on mangrove tree *Sonneratia ovata* were 155 (64.58 %) on the stem and 85 (34.15 %) on the branch, respectively (Table 5) and 6). Most mating pairs were found in three canopies (roots, branches, stems) where mate search would appear to be extremely difficult due to low number (26.09 %), especially on stem part of mangrove tree *Rhizophora apiculata* (Table 5).

According to (Ng, 2013), this success of mate location (substrate of root, branch and stem) may be achieved by the male's ability to discriminate, and follow mucus trails laid by conspecific females during the mating season (Erlandsson and Kostylev, 1995). In a complex three-diensional habitat like the mangrove tree canopy, evolution of a successful mate-finding strategy is likely under strong selection pressure and mucus trail tracing is likely a behavioral trait selected to optimize reproductive success of these mangrove snail (Ng, 2013). This condition could also occur in *L. scabra*. Males encounter potential mating pairs within a population is limited by ecological factors, such the spatiotemporal distribution of the individuals and the operasional sex ratio (OSR) of population, i.e. the average ratio of sexually active males to sexually active females (Emlen and Oring, 1977). Because of the differential investment in reproduction between the sexes, females are the limiting sex for which males generally compete (Trivers, 1972). Reproductive success is largely predicted by the number of mating pairs obtained.

Table 7. Mean gonad maturity index of *L.scabra* on *Sonneratio ovata* during the study In Tombariri mangrove.

Month	Mokupa St		Elu St		Tambala St	
	Male	Female	Male	Female	Male	Female
Feb'2014	8.08	7.58	8.07	7.98	7.89	7.95
Sea margin	7.77	7.49	6.99	7.82	7.94	7.36
Full moon						
New moon						
Inner mangrove	8.64	7.30	7.74	7.66	7.88	8.49
Full moon	7.82	7.89	7.89	7.91	7.62	7.53
New moon						
Apr'2014	7.69	7.75	7.54	7.96	7.80	7.84
Sea margin	8.30	8.84	7.08	8.58	7.72	8.54
Full moon						
New moon						
Inner mangrove						
Full moon	7.81	7.68	7.24	7.58	7.29	8.37
New moon	7.93	8.63	7.92	8.43	7.28	8.29
Jun'2014	6.87	7.73	7.29	7.63	7.45	7.81
Sea margin	7.39	7.92	7.52	7.91	7.42	7.38
Full moon						
New moon						
Inner mangrove	7.27	7.94	7.25	7.74	7.14	7.43
Full moon	7.63	7.87	7.53	7.91	7.29	7.66
New moon						
Aug'2014	7.21	7.69	7.54	7.71	7.46	7.58
Sea margin	7.29	7.66	7.10	7.89	7.44	7.85
Full moon						
New moon	7.64	7.70	7.76	7.92	7.42	7.72
	7.29	7.66	7.10	7.89	7.44	7.85
Inner Mangrove						
Full moon						
New moon						

Oct'2014	7.32	7.88	7.37	7.63	7.35	7.66
Sea margin	7.40	7.77	7.54	7.60	7.45	7.82
Full moon						
New moon	7.48	7.77	7.15	7.77	7.18	7.42
Inner Mangrove	7.43	7.92	7.44	7.74	7.26	7.59
Full moon						
New moon						
Dec'2014	7.40	7.54	7.19	7.49	7.10	7.89
Sea margin	7.47	7.76	7.49	7.79	7.30	7.79
Full moon						
New moon	7.42	7.60	7.40	7.62	7.41	7.74
	7.47	7.76	7.38	7.98	7.33	7.87
Inner Mangrove						
Full moon						
New moon						

Based on table 6 shows the percentage of snailing and the numbers at different days during August 2014. This specie s pairing of snails reached a peak 5 day before the fullmoon and newmoon days. On 8 August 2014 snail pairing was observed 30 % (fullmoon) and 27.27 % pairing was observed on 25 August 2014. Therefore, *L.scabra* would that mating exhibits a bilunar periodicity that follow tide cycle.

(Bateman, 1948)._Males generally suffer from higher mortality rates because of the costs associated with searching for a mate, such as predation risks and energetic expenses (Kokko and Wong, 2007). Hence, biases in the operational sex ratio should create the adopted male mating strategy (Emlen and Oring, 1977).

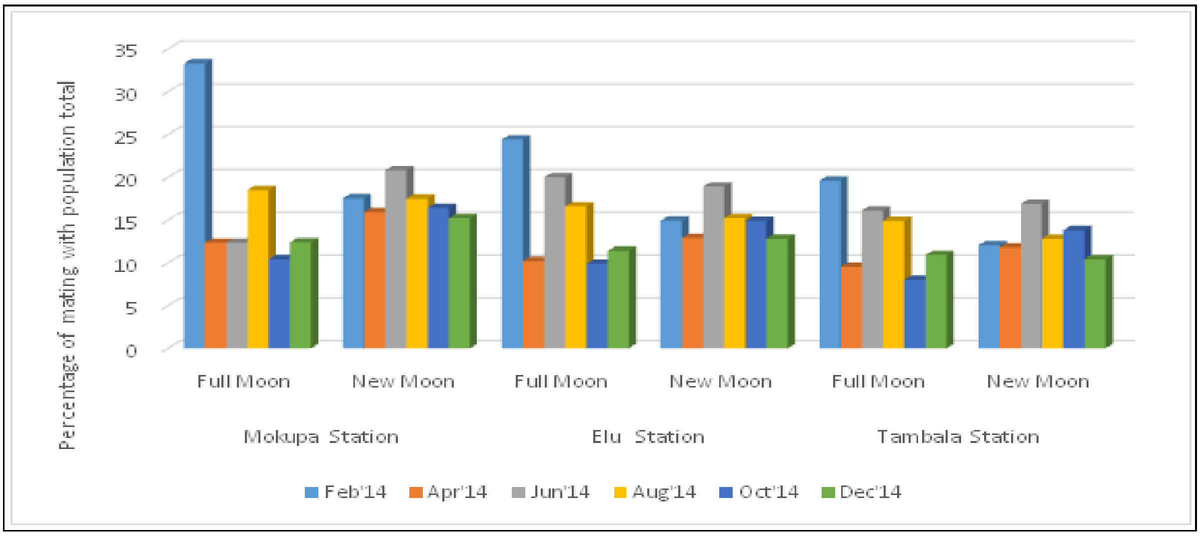

Fig. 1. Mating pairs of individual ratio in population total during the study in Tombariri mangrove.

During mating, males quickly move to the right side of the females, while females strongly attached on the substrate. Penis was inserted into female's mantlecavity from the right side of the aperture.

Duringmales released the sperms, the flat part serves to hold the penis on site. Copulation of *L. scabra* occurred for under humid condition or on wet habitat.

One-year observations, February 2014 to December 2014, at two-month intervals in station Tambala showed that the highest mating occurred in the full moon of February 2014, (Figure 1) with 10 mating pairs of total 51 individuals due to high rain to increase to change for mating, while the lowest occurred in the full moon of October, with 10 mating pairs of total 125 individuals.

Gonad Development Index of Littoraria scabra

In the present investigation, maximum mean Gonadosomatic Index (GSI) value (8,44 %) of mating individuals was found in February at full moon indicating the period of maximum growth in female *L. scabra* in station Mokupa. The minimum mean GSI value (5,60 %) was found in February in station Elu. Reproductive process of *Littoraria scabra* before larval release is mostly metabolism outcomes directed to gonad development (Reid, 1984). At that time, the gonad will increasingly develop simultaneous with increased gonad development. The gonad of *L. scabra* reaches maximum when the snail will release the larvae. After the snail released the larvae, their gonad development usually declined, but *L. scabra* has its unique in which their gonad did not recede. Other uniqueness was also found that in *L. scabra*, both mating males and females released the larvae.

GSI is percent of gonad weight against body weight of *L. scabra*. The index value is in lined with gonad development. GSI is a quantitative gonad development. The index value is dependent upon the snail size and the gonad maturity level. Based on the present findings, this study showed that the uniqueness of mating *L. scabra* is both sexes release the larvae (Figure 2).

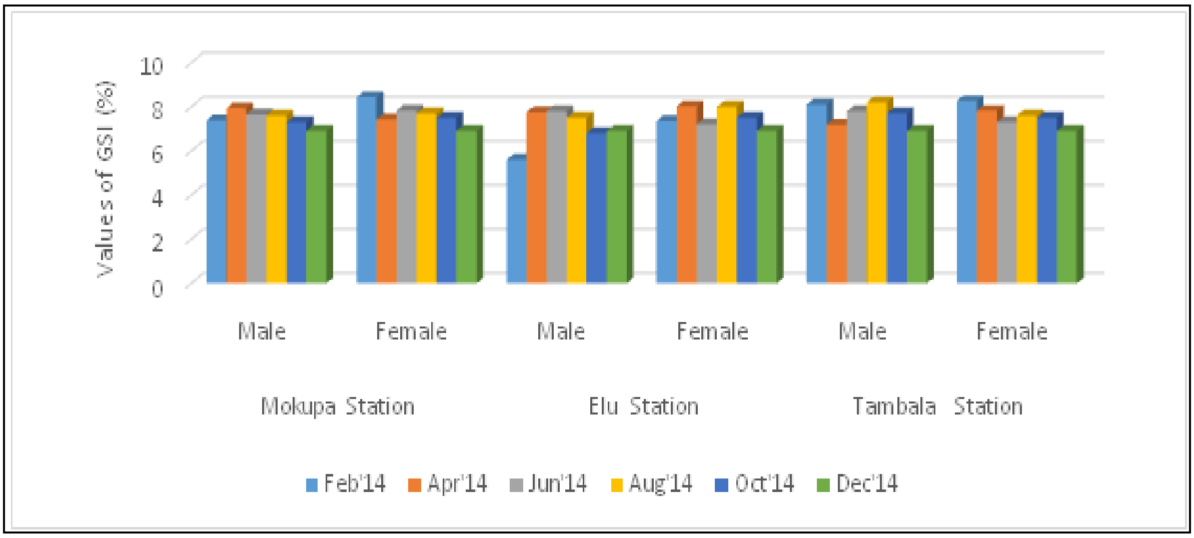

Fig. 2. Mean Gonadosomatic index (GSI) of mating individuals in full moon on mangrove *Sonneratio ovata* amongs station during the study Tombariri mangrove.

Mean gonad maturity index of either male or female in station Mokupa of sea margin mangrove and inner mangrove shows relatively small variations relative to those sites in Tombariri. Mean gonad maturity index along the year, particularly February to December 2014 (Figure 3).

Gonad development index of *Littoraria scabra* is summarized in Table 7. In this researched showed little variation of gonad development was observed between full moon and new moon and also between mangrove of sea margin and inner mangrove.

Ng (2013) stated that gonad development in many invertebrates, including littorinid snails, is strongly correlated with seasonal environmental variables such as critical temperatures (Berry 1961; Borkowski 1971 and Giesel 1976) in Malaysia where warm weather (air temperature > 25 °C) persists throughout the year, females of *L. melanostoma* spawn year-round (Berry & Chew 1973).

In the present investigation, reproductive development, especially mean gonadosomatic index of *L.scabra* on *Sonneratio ovata* in Tombariri mangrove, showed little variation of gonadosomatic index. Variations of the reproductive development patterns, especially gonad maturity, are different along the intertidal due to selection, distribution, and habit of the ancestor (Jablonski and Ludtz, 1983). Chambers (1994) stated that gonad development in invertebrates is non-random distribution along the intertidal including mangrove. Gonad development in many invertebrates, including littorinid snails, is strongly correlated with seasonal environmental variables, such as critical temperatures and variations in food availability (Borkowski, 1971).

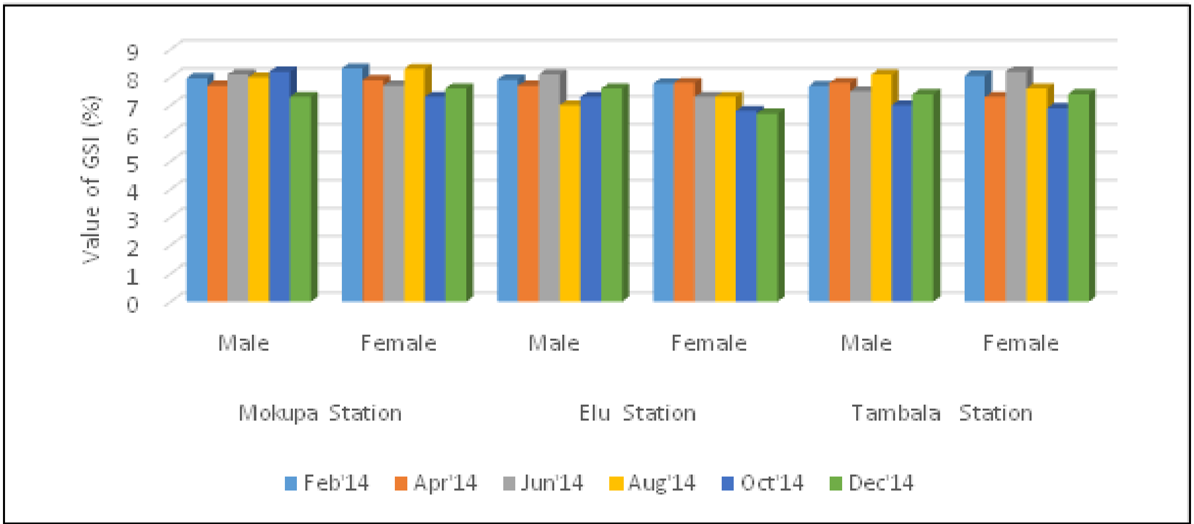

Fig. 3. Mean Gonadosomatic index (GSI) of mating individuals in new moon on mangrove *Sonneratio ovata* amongs station during the study Tombariri mangrove.

Littorinids living high on the shore are only reached by new or full moon spring tides, and hence most release their eggs or larvae during these periods. Both *L. ardouiniana* and *L. melanostoma* live in the upper zone of the mangrove trees (Yipp 1985; Lee and Williams 2002; Reid 1986), and their bi-lunar periodicities of egg or larval release, associated with spring tides, matches those of many other rocky shore and mangrove littorinids (Gallagher and Reid 1974; Alifierakis and Berry 1980). In Malaysia, however, *L. melanostoma* mainly spawns during full moon spring tides, as tidal heights during this phase of the moon are higher than during the new moon phase (Berry and Chew 1973), but this is not the case in Hong Kong '*Littoraria melanostoma*' in Hong Kong has, however, been suggested to be an unnamed, cryptic species, genetically distinct from *L. melanostoma* in Singapore (Reid *et al.*, 2010 & 2012). As such, if the '*L. melanostoma*' in Malaysia belong to the Singapore type, the differences in reproductive traits between members of this 'species

In general, invertebrates, including *L. scabra,* have developed their strategy along the intertidal, and even those living in the upper supralittoral reached by the water only in new moon or full moon. Therefore, *L. scabra* has very developed strategy to overcome the three-dimensional mangrove habitat, and the animals have the ability to hold the embryo in the mantle cavity to keep the fertilized eggs before they release the larvae. This result is supported (Strusaker, 1966; Gallagher and Reid 1974; Muggeridge, 1979; Reid, 1984; Reid *et al.,* 2010; Ng, 2013). This reproductive strategy to overcome mangrove habitat is an adaptive significance. The adaptive significance of development in the mantle cavity *L. scabra* that eggs were fertilized up to hatching as larvae remain safe. Female and male reproductive systems have probably evolved in genus *Littoraria*, including *L. scabra*. The reproductive characteristics are specific strategy of *L. scabra* to optimize the reproductive success. Egg incubation period of *L. scabra* is short with fast larval release**.** Fast larval release is a strategy to minimize the exposure to aquatic predators in mangrove habitat.

Reproductive strategy of male *L. scabra* is an adaptation and response to a complex three-dimensional mangrove environmental factors and high predation intensity. The power of natural selection and sex selection in mangrove environment is believed to change the pattern of male reproductive organ as larvae holder.

According to Arngvist and Rowe (1995), both sexes have evolved to respond to common natural selection regimes. Reproductive development of the invertebrates, including *L. scabra,* is influenced by habitat, distribution and balanced between various size, number of youngster, optimal solution on animal ecological enviroment (Grahame and Branch, 1985), and intertidal zonation (Mileikovsky, 1975). In *Littoraria*, the development pattern is not only ecologically significant, but also evolutionarily significant, and it affects the extinction rate of the species and species speciation (Jablonski and Lutz, 1983).

Eberhard (1985) stated that the spectacular genital morphological diversification was very wide among species of internal fertilization**.** According to Ebert (1993), sex selection hypothesis, is contrary to hipotesis evolution of genitalia divergent, results from variations in post-mating paternity among males (Arnqvist, 1997*)*. Post-mating sex selection hypothesis is male genital selection resulted from mechanisms causing variations in post-insemination paternity success among males. Such a mechanism covers: *first,* several processes in which female influences male paternity success, cryptic female selection (Eberhard, 1985*); second,* competition among male gametes for fertilization, sperm competition (Waage, 1979) and *third,* generation evolution between male and female, sex conflict (Arnqvist and Rowe, 1995). Invertebrate reproductive strategy including *L. scabra* is correlated with various ecological aspects, such as habitat isolation, latitude, depth, level of inntertidal, and various size (Chambers, 1994).

The reproductive organ of this mangrove snail has probably evolved fast in male sexual function; as a consequence, male *L. scabra* has ability to hold the fertilized eggs in the body up to hatching as veligers; and thus, the male is capable of releasing the larvae. Males obtained fertilized eggs while mating; during the copulation males release the sperms to fertilize eggs in female body, and then the fertilized eggs are sucked in as part by 'penial glandular disc' for storing in mantle of male *L. scabra*.

The eggs then hatched in the male body that are released in full and new moon at high tide. Kamel and Grosberg (2012) stated that males would become main target of egg laying soon during the copulation. Jones *et al*. (1999) gave the best example of 'male pregnancy' in sygnathid fish, in which males are consistent with father's gen from children. Ovoviviparous species with internal fertilization and development patern in male reproduction system possible had evolved in *Littoraria scabra.*

Reproductive characteristics represent the specific strategy of *L. scabra* to optimize the reproductive success. Short incubation process of mating *L. scabra* quickly releasing the larvae reflects a strategy to minimize the exposure to aquatic predators in mangrove habitats.

The reproductive pattern, mating, gonad maturity, larvae releasing rate are spesific strategy from *L. scabra for* optimizing their survival in mangrove area. As conclusion, this study found that reproductive strategy of male *L. scabra* possessed a unique larvae storing system in male body, and the reproductive strategy of *mating L. scabra* showed that both sexes released the larvae with bi-lunar and tidal cycles.

Conclusion

1.Specific strategy of the ovoviviparous *L. scabra* was indicated by reproductive patterns, mating, maturity index, larval release rate, and sex ratio to optimize reproductive success in extreme three-dimensional mangrove habitat.

2. Males had unique and very rare larvae storing system and quickly released the larvae during research period.

3. Mating individuals, both males and females, released their larvae following bi-lunar and tidal cycles during research period.

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