

**Signifikansi Reproduksi Kawin Dan Pelepasan Larva *Littoraria scabra* (Gastropoda: Littorinidae), di Mangrove Tombariri, Sulawesi Utara, Indonesia**

**(Significance Of Reproduction Especially Mating and Larval Releasing of *Littoraria scabra* (Gastropoda: Littorinidae), In Tombariri Mangrove, North Sulawesi, Indonesia)**

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**ABSTRACT**

This study used *Littoraria scabra* as a model of research that attempted to understand how the species optimize their survival in mangrove area. It was aimed at investigating the reproductive significance of oviparous *L. scabra* and larval release periodicity in order to maintain their survival in mangrove ecosystem. Reproductive observations of *L. scabra* were done by looking at mating, larvae releasing rate. Results showed that the reproductive significance of *L. scabra* was observed as follows: a) there were 64.58% of mating pairs on the stem of *S. ovata*; b) Mating *L. scabra* releasing the larvae did not have gonad reduction; c) *L. scabra* released significantly larger female larvae than male. Specific significance of ovoviviparous species *L. scabra* with reproductive patterns, i.e mating, larvae releasing rate, was to optimize their reproductive significance in extreme three-dimensional mangrove habitat. This study concluded that the reproductive significance of male *L. scabra* possessed a uniqueness and very rare in nature larva storing system and quickly released larvae. This study support research 2016, also found the reproductive significance in which males and females, while mating, released larvae with bi-lunar and tidal cycles.

**Keyword** : *Littoraria scabra*, reproductive strategy, ovovivipar, larval periodicity

**ABSTRAK**

Penelitian ini menggunakan sebagai model penelitian yang mencoba untuk memahami sepsis mengoptimalkan survivalnya di Kawasan mangrove. Penelitian ini bertujuan menyelidiki signifikansi reproduksi ovovivipar *Littoraria scabra* dan periodisitas pelepasan larva agar mempertahankan survivalnya di ekosistem mangrove. Observasi reproduksi *L. scabra* dikerjakan dengan pengamatan kawin dan tingkat pelepasan larva. Hasil menunjukkan bahwa signifikansi reproduksi *L. scabra* diamati, sebagai berikut : a) ada 64.58 % dari pasangan kawin pada batang mangrove *Sonneratia ovata*; b).Pasangan *L. scabra* melepaskan larva yang tidak mengalami reduksi gonad, c) *L. scabra* melepaskan larva secara signifikan dari induk betina daripada induk jantan. Signifikansi spesifik sepsis ovovivipar *L. scabra* dengan pola reproduksi, contoh kawin, tingkat pelepasan larva adalah memanfaatkan signifikansi reproduksi di habitat mangrove tiga dimensi yang ekstrim. Penelitian ini menyimpulkan bahwa signifikansi reproduksi dari jantan *L. scabra* yang memiliki keunikan dan sangat jarang di alam jantan (induk jantan) yang memiliki sistem penyimpanan dan dengan cepat melepaskan larva. Penelitian ini juga memperkuat penemuan tahun 2016 bahwa signifikansi jantan-jantan dan betina-betina sementara kawin, melepaskan larva dengan mengikuti siklus bulan dan siklus pasang.

**Kata kunci** : *Littoraria scabra*, Ovovivipar, Periodisitas Larva, Strategi Reproduksi

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## INTRODUCTION

Concept of reproductive significance has become a main component in life history theory (Stearns, 1976). Comprehension on reproductive strategy diversity selected by living organisms and their interaction with environment is central issue in ecology (Todd, 1985). Reproductive strategies are an adaptation and response to complex environmental factors and physiological characteristics of a species (Thorp dan 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, 1977).

Reproductive significance 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 (Ng, 2013). According to Ng (2013), various adaptive reproductive significance 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 oviparous species development (Reid, 1992). Family *Littorinidae* is the best group to study the reproductive significance patterns and larval development, because the species occurs in all intertidal habitats (including supralittoral) in the world (Mileikovsky, 1975).

According to Ng (2013), the importances of *Littoraria* spp., reproduction are: (1) female role in controlling male mate selection (Bonduriansky, 2001), female role in holding the sperms (Reid, 1989), 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, 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 significance of *Littoraria scabra* is available, a study on reproductive strategy of ovoviviparous *L. scabra* and its larval periodicity needs to do in order to sustain the survivorship on extreme mangrove ecosystem.

## MATERIALS AND METHODS

Reproductive significance of *L. scabra* is to assess mating and larval release rate. Ten individuals of each males and females collected were matured. The collection was done 4 days before new moon and full moon to avoid missing larvae release period from February to December 2020. Male and female spawners were separated in different plastic container. Males and females released larvae in the plastic bottle, and they were counted using a dissecting microscope/binocular. Also, 10 mating pairs were collected. The males and females were put in different plastic container. They released larvae as well, and the larvae were counted.

Larvae releasing rate is number of larvae released per second (Ng, 2013). Number of larvae released was counted using a hand tally counter. Ten individuals of each males and females releasing the larvae were randomly selected. *L. scabra* larvae were released by withdrawing their snout and tentacle inside mantle cavity. Difference in larval release between male and female was estimated using t-test. The same test was also used for difference in the larvae released by mating male and females.

## RESULTS AND DISCUSSION

### **Mating of *L. scabra***

Based on the Table 1 mating pairs found on mangrove tree *Sonneratia ovata* were 155 (64.58 %) on the stem and 85 (34.15 %) on the branch, respectively (Table 1). 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 mantle cavity from the right side of the aperture. During males 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. It remained going on for several hours after the copulation. Mating data were recorded in the morning on mangrove tree *Sonneratio ovata* when the

tree was slightly humid or wet from the dew. Since humid and wet condition and cool air from the wave sprinkle dewing the substrate gave opportunities for *L. scabra* to mate, so that mating could occur not only along the year but everyday (Lalita, pers.obs).

**Table 1.** 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)
<i>Sonneratia ovata</i>	0	85 (34.15 %)	155 (64.58 %)	240
<i>Avicennia marina</i>	0	31 (38.27 %)	50 (61.73 %)	81
<i>Rhizophora apiculata</i>	17 (73.71 %)	0	6 (26.09 %)	23

Observations on operational sex ratio (OSR) of *L. scabra* on *Sonneratia ovata* showed that mating was not as aggressive 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 operational sex ratio 'OSR' of *L. scabra* on *Rhizophora* that influences their mating behavior, and thus, sex selection intensity is limited (Emlen dan 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 mating season. Hence, *L. melanostoma* has possibly lower reproductive level (Clutton-Brock and Vincent 1991; Ng, 2013). In general, *L. scabra* had sex ratio equilibrium on *S. ovata*, OSR (The Operational sex ratio). The sex ratio is available in a population in certain time, and therefore, this sex ratio could possess higher level of competition for occurring sexes 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 *Avicennia* 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). For instance, the sex ratio of adult males, OSR (the Operational sex ratio), is one of main factors determination OSR (Clutton-Brock dan Vincent 1991), spatial distribution, and migration period, also affect the OSR (the Operational sex ratio).

*L. scabra* population is an equilibrium in 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 received active male sexuality (Vincent et al., 1992). The OSR gives impacts on mating competition and competitive selection (Kvarnemo and Ahnesjo, 1996,2002). Unbalanced OSR will usually increase competition of mating individuals; the resources of excessive sex competition and broad OSR disequilibrium will need the level of mating competition and sex selection intensity (Clutton-Brock and Parker, 1992).

Sex allocation theory predicts that if the OSR is disturbed from its unity (in time or space), the facultative sex ratio adjustment (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 1989, 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*.

### Larval Periodicity of mating *L. scabra*

The present findings in station Mokupa demonstrated that *L. scabra* spawned along the year with the highest in the full moon of February 2021, 10 mating pairs of total 30 individuals encountered and the lowest in the full moon of October 2021, 10 mating pairs of total 98 individuals. In new moon, the highest mating pairs occurred in June 2021, 10 mating pairs of total 96 individuals the lowest, can be seen in Table 2.

The highest larvae release of mating male *L. scabra* was found in station Mokupa in April 2020, 259.4 per individuals in full moon and 267.1 per individuals in new moon. The lowest was recorded in June 2021, 182.1 per individuals in full moon and 148.4 per individuals in new moon of December 2021. In Station Elu, males released the highest number of larvae in new moon, 229.2 per individuals, in April 2021 and in new moon, 290.5 per

individuals, in February 2021. The lowest number of larvae was recorded in full moon of August 2020, 100.6 per individuals, and in new moon of the same month, 155.8 per individual. Station Tambala has the highest number in full moon of April 2021, 256.4 per individuals and in new moon of October 2020, 268.4 per individuals. The lowest number occurred in full moon of June 2021, 108.7 larvae per individuals and in new moon of August 2021, 189.2 per individuals (Table 2).

One-year observations, February 2021 to December 2021, at two-month intervals in station Tambala showed that the highest mating occurred in the full moon of February 2020, with 10 mating pairs of total 51 individuals, while the lowest occurred in the full moon of October, with 10 mating pairs of total 125 individuals.

**Table 2.** Mean larval periodicity of mating individuals on *Sonneratio ovata* during the study in Tombariri Mangrove

Month		St Mokupa		St Elu		St Tambal	
		Male	Female	Male	Female	Male	Female
Feb'2021	Full moon	241.9	175.3	235.5	249.2	180.2	244.7
	New moon	184.2	213.7	258.4	290.5	195.8	251.6
Apr'2021	Full moon	259.4	275.7	229.2	289.0	256.4	283.6
	New moon	267.1	321.4	225.4	273.5	233.1	310.2
Jun'2021	Full moon	182.1	169.8	163.2	141.4	108.7	150.7
	New moon	225.6	309.8	225.8	246.6	60.5	246.0
Aug'2021	Full moon	183.0	196.8	189.0	194.3	135.5	168.5
	New moon	150.6	190.1	100.6	155.8	189.2	158.4
Oct'2021	Full moon	211.2	207.7	138.3	296.5	196.7	189.7
	New moon	170.4	169.7	189.9	215.5	268.4	286.2
Dec'2021	Full moon	189.0	221.4	214.6	349.1	255.3	350.8
	New moon	94.8	148.4	159.2	163.9	179.3	122.7

#### Larval Periodicity of non-mating *L. scabra*

This study found that both males and females released their larvae. Larval periodicity occurred along the year for either females or males. Rare finding was male *L. scabra* released their larvae along the year with the highest mean periodicity in Mokupa station of the sea margin and it was achieved in the full moon of December, 2021, 257.4 per individuals. The lowest larval periodicity occurred in August 2021, 174.9 per individuals in April 2021 and the lowest occurred in June 2021, 126 per individuals (Table 3).

In new moon, the highest mean number of larvae released by males was 291.7 individuals. Elu station of sea margin and inner mangrove, the highest mean number of larvae released occurred in full moon, 433 per individuals in October 2021 and new moon, 249.2 per individuals in February, 2021. The lowest larval release occurred in full moon, 184.1 per individuals, in August 2021 and in new moon, 159.3 per individuals, in June 2021. In Elu station of inner mangrove, the highest mean number of larvae released by males occurred in full moon, 310 per individuals, in February 2021 and in new moon, 285.2 per individuals, in April 2021. The lowest larval release, 181.4 per individuals, occurred in full moon of April 2020 and in new moon, 149.6 per individuals, in December 2021 (Table 3).

**Table 3.** Mean larval periodicity on *Sonneratio ovata* during the study in Tombariri mangrove

Month	St Mokupa		St Elu		St Tambala	
	Male	Female	Male	Female	Male	Female
<b>Feb'2021</b>						
<u>Sea margin</u>						
Full moon	247.8	244.49	210.2	194.8	289.1	357.9
New moon	250.8	224.6	197	249.2	195	255.3
<u>Inner mangrove</u>						
Full moon	252.6	248.12	72.7	310	182.1	194.9
New moon	228.1	207.1	222.5	250.2	287.4	326.6

<b>Apr'2021</b>						
<u>Sea margin</u>						
Full moon	180.4	206.5	212.1	255.5	248.4	243.1
New moon	291.7	217.6	241.8	245.7	268.9	279.8
<u>Inner mangrove</u>						
Full moon	232.2	258.51	81.4	303.3	232	305.2
New moon	227.2	295	256.8	285.2	248.9	331.8
<b>Jun'2021</b>						
<u>Sea margin</u>						
Full moon	185.6	247.52	55.3	219.2	252.6	232.3
New moon	126	124.31	63.3	15.3	109.4	92.7
<u>Inner mangrove</u>						
Full month	200.31	88.4	181.4	158.5	116.1	189.3
New moon	97.4	72.8	256.8	180.9	237.6	172.9
<b>Aug'2021</b>						
<u>Sea margin</u>						
Full month	174.9	338.9	184.1	158.5	116.1	189.3
New month	141.7	224.4	236.6	180.5	237.6	172.9
<u>Inner mangrove</u>						
Full month	138.3	175.1	201.2	151.2	194.7	242.2
New month	208.4	166.1	296.7	208.8	174.4	106.8
<b>Oct'2021</b>						
<u>Sea margin</u>						
Full moon	254.5	618.5	433.5	533.5	252.7	205.9
New moon	202.8	186.2	491.1	18.7	217.1	330.6
<u>Inner mangrove</u>						
Full moon	318.2	320.1	355.4	256	206.4	405.5
New moon	290.3	271.9	268.2	246.1	254.7	393.1
<b>Dec'2021</b>						
<u>Sea margin</u>						
Full moon	257.4	275.7	204.4	198	152.4	161.3
New moon	209	159.9	195.3	203.9	182.5	219.2
<u>Inner mangrove</u>						
Full moon	197.5	221.2	190.1	208.4	145.1	183.1
New moon	164.2	144	177.9	149.6	273.3	230.7

In Tambala station of sea margin mangrove, males released the highest number of larvae in full moon, 289.1 per individuals in February 2021 and in new moon, 268.9 per individuals, in April 2021. The lowest was found in full moon, 109.4 per individuals, in June 2021 and in new moon, 92.7 per individuals, in June 2021 (Table 3).

**Table 4.** Larval releasing mean of *L. scabra* while mating that delivering larvae on mangrove tree *Sonneratio ovata* that combined during one year with confidence interval 95%

Larval releasing while mating Station	Confidence interval (%) $\bar{x} \pm SD$			
	Full moon		New moon	
	Male	Female	Male	Female
Mokupa	211.10 $\pm$ 92.33	207.00 $\pm$ 98.92	182.12 $\pm$ 140.06	225.00 $\pm$ 187.61
Elu	192.97 $\pm$ 145.97	253.25 $\pm$ 193.47	193.22 $\pm$ 145.79	224.63 $\pm$ 155.84
Tambala	188.80 $\pm$ 155.84	231.33 $\pm$ 153.43	221.05 $\pm$ 76.70	229.18 $\pm$ 146.98
<b>Larval releasing</b>				
Coastal Mokupa	216.77 $\pm$ 80.46	322.03 $\pm$ 95.04	203.67 $\pm$ 126.11	89.50 $\pm$ 81.91
Inner Mokpula	223.18 $\pm$ 121.27	235.23 $\pm$ 105.56	206.60 $\pm$ 131.28	192.82 $\pm$ 135.9
Coastal Elu	249.93 $\pm$ 185.87	259.87 $\pm$ 123.17	254.18 $\pm$ 107.08	203.88 $\pm$ 73.28

Inner Elu	249.93±185.87	236.28±128.39	229.40±108.43	215.08 ±110.93
Coastal Tambala	218.38±135.71	231.63±137.11	201.75±109.51	225.08 ±168.18
Inner Tambala	182.58±73.97	238.50±144.05	236.60±95.43	261.75±96.20

Based on Table 4, mean larval periodicity rate released by male *L. scabra* was 211.10± 92.33 mangrove while females averagely released was 207.00± 98.92 per sec at full moon in Mokupa mangrove. In Elu mangrove mean larval periodicity rate released by male *L. scabra* was by male 192.97 ± 145.97 while females averagely was 253.25±193.47 per sec at full moon. Tambala mangrove, mean larval periodicity rate released by male was 188.80±155.84 per sec at full moon while females averagely was 231.33±153.43 per sec at full moon.

Based on the t-test, mean rate of larval release was significantly different between males and females. Total duration of larval release was 2.2 – 5.0 min or 132 -300 sec. This study found very rare and unique phenomenon in the nature where mating males and females release their larvae along the year in full and new moon following the tidal cycle. They had mean larval release rate of 88.65 ± 11.25 per sec. (95 % confidence level), n = 20, for males, and 138 ± 14.18 per sec., n = 20, for females. The t-test on mating individuals shows significantly higher number of larvae released by females than males. The combination of ovovivipar and their planktotrophic development is uncommon in molluscs was not found in other genera, but it becomes typical characteristic of all *Littoraria*, including *L. scabra*, particularly subgenus *Littorinopsis*. It is believed that they have adapted to quickly release the larvae, and thus, minimized the time needed on the surface vulnerable to aquatic predators (Reid, 1984).

The synchronised release of larvae has been argued to minimise the risks of predation and unfavourable environmental factors (Forward, 1987; Morgan, 1995). An error in timing of larval release could have fatal results for progeny and significant implications for local population. Timing errors of larval release could occur if adults did not have an adaption of endogenous release rhythms, or if entrainment to a cycle, on rare occurrences, increased the risk of mortality (Ricardo, 2011).

Larval release occurs more in reproduction season along the year, in which male and female *L. scabra* probably spend less time submerging in the seawater, and therefore, reduce time exposed to the predators. Larval release season occurs along the year (Whipple, 1966) indicated with (1) Male and female *L. scabra* mature all the year; (2) the continuous presence of mature oocytes in the ovary and the gonadal oviduct; (3) no evidence of gonad decrease period (gonadal regression), as found in the littorinid in spawning season (Borkowski, 1971; Muggeridgeridge, 1979); (4) Spawning peak occurrence due to effect of tide (Borowski, 1971), water temperature (Muggeridgeridge, 1979), and phytoplankton abundance (Underwood, 1979), and (5) prolonged spawning period of *L. scabra* as response to high predation for small and new settled individuals.

Chambers (1994) stated that reproductive development in invertebrates is non-random distribution along the intertidal including mangrove. It also occurs in *Littoraria* and *Littorina* that are distributed in the upper intertidal, while the planktotrophic development occurred in the middle and upper intertidal. The reproductive development patterns are different along the intertidal due to selection, distribution, and habit of the ancestor (Jablonski and Lutz, 1983).

The reproductive significance 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 (2002), both sexes have evolved to respond to common natural selection regimes. Reproductive development of invertebrate, included *L. scabra* was influenced by habitat, distribution and balanced between various size, number of youngster, optimal solution on animal ecological environment (Grahame and Branch, 1985), and intertidal zonation (Mileikovsky, 1975). In *Littoraria* included *L. scabra*, the development pattern shows 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. A number of hypotheses suggested for animal genital evolution, but empirical data needed is very rare. According to Ebert (1993), sex selection hypothesis, is contrary to hipotesis evolution of genitalia divergent, results from variations in post-mating paternity among males (Arngvist, 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 coivers: first, several processes in which female influences male paternity success, cryptic female selection (Eberhard, 1985); second, competition among male gamets 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. Male was 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 syngnathid 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. Specific strategy of ovoviviparous *L. scabra* with reproduction pattern, mating, gonad mature, quickly releasing the larvae, sex rasio is to optimize the reproductive success in extreme three-dimensional mangrove habitat. As conclusion, this study found that reproductive strategy of male *L. scabra* possessed a unique larvae storing system, and the reproductive strategy of mating *L. scabra* showed that both sexes released the larvae with bi-lunar and tidal cycles.

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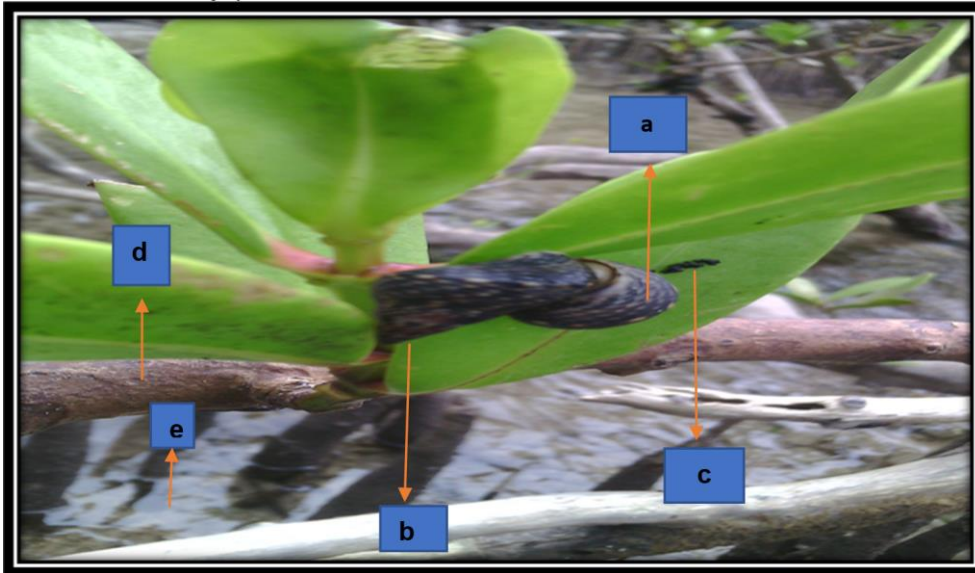
**Appendix 1.** Mangrove Tombariri Research Map, North Sulawesi



**Appendix 2.** Map of North Sulawesi



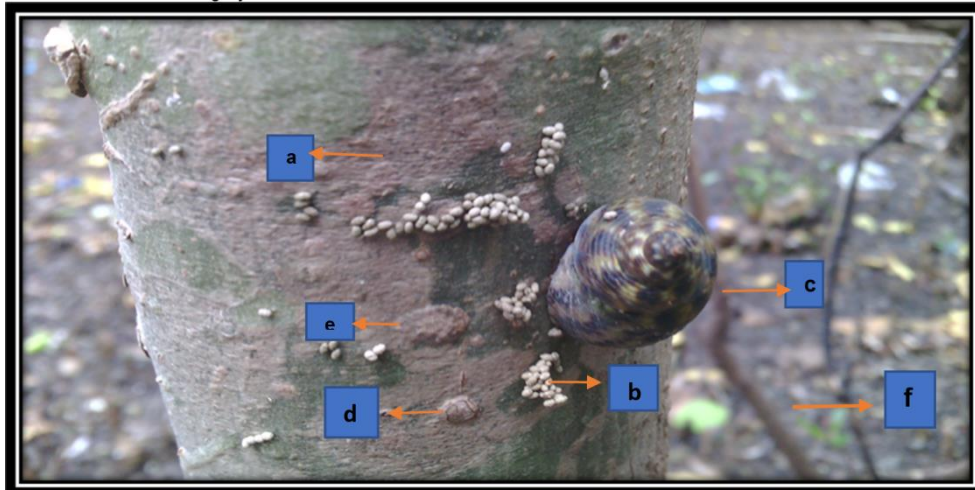
**Appendix 3.** Rare found (a) two pairs of *Littoraria scabra* mating side by side on microhabitat (b) stem of mangrove *Sonneratio ovata*, (c) Pneumatophora (d) *Balanus* sp, and (e) While copulation, releasing larva. (f) branch and (g) leaf of *S.ovata*. Photo with S-6 Samsung by Jans Lalita.



**Appendix 4.** Generally *L. scabra* on stem microhabitat batang, branch, and root; that is why, very rare larval releasing while mating *L.scabra* on leaf microhabitat of *S.ovata*. a. Female and b. Male copulation. c. Larval releasing while mating d.Branch and e. Below canopy of mangrove.  
 Photo with S-6 Samsung by Jans Lalita



**Appendix 5.** Male of *L. scabra* with orange penis while larva releasing by male and female. (a) orange penis, (b) larvae in the body of male, (c) larvae, (d) tentacle  
 Photo with S-6 Samsung by Jans Lalita



**Appendix 6.** *L. scabra* releasing larvae on highest tides, if not delivering larvae on stem of mangrove *Avicennia marina* while *L. scabra* walking. (a) Stem of *A.marina*, (b) Larvae,(c) *L.scabra*, (d) *Balanus* sp. (e) *Onchidium* sp, and (f) below of mangrove canopy.

Photo S-6 Samsung by Jans Lalita



**Appendix 7.** (a) Number code of sampling , on Mokupa mangrove Sonnaratio (coastal mangrove,CM), male inner of mangrove( MI).(b) Larvae already releasing by male parent (c) receptacle of aqua glass for accommodating larvae that already releasing (d) male parent and female of *L.scabra*. (e) Female sampling code. (f) Aquarium for keeping high humidity.

Photo S-6 Samsung by Jans Lalita