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Reproductive cycle and size at maturity of wild mud crab, *Scylla tranquebarica* (Fabricus, 1798) in Marudu Bay, Sabah

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Abstract

This study was conducted to investigate the reproductive cycle and size at maturity of wild mud crab, *Scylla tranquebarica*, in the mangrove forest of Marudu Bay. The sampling was conducted for 12-month consecutively with the assistance of local fishermen. Each sampling was carried out for 2 days, and baited crab traps were deployed in the river. During the sampling period, a total of 1459 crab specimens were caught. The different maturation stages of crab can be found throughout the year. The percentage of mature female crabs (Stage III to V) was relatively higher in February (38.5%) and May (50.5%), and lower in March (17.6%) and June (17.4%). A similar trend was observed in the male crab. Recruitment of crabs into the mangrove forest was observed after the breeding season. It was observed through histological observations that when 50% of the crabs were sexually mature, the size at maturity was in the range of 94.0 to 96.1 mm and 97.0 to 99.5 mm carapace width for female and male, respectively. This study suggests that *S. tranquebarica* breeds throughout the year and shows two peak breeding seasons and recruitment in Marudu Bay. This information can be used as baseline for mud crab fisheries management in Sabah.

Keywords: Gonad maturation, Maturity stages, Breeding season, Population recruitment, *Scylla tranquebarica*

Introduction

Purple mud crab, also known as mangrove crab, *Scylla tranquebarica*, is among the four species of mud crabs that are commonly exploited by coastal fishermen as a source of food and income. This species can be found living together with other species of mud crabs at the mudflats of the littoral zones, supralittoral zones until the intertidal zones of mangrove forests and coastline that are inundated with reduced salinity seawater (Keenan et al., 1998). *S. tranquebarica* is a widespread species that known to be distributed from the Indian Ocean towards the Pacific Ocean and the South China Sea including Sabah and Sarawak waters (Keenan et al., 1998; Mohd Sharif et al., 2019).

The knowledge on gonad maturation is one of the important aspects to understand the reproductive potential of the animal in the wild. This information is needed to monitor the biological characteristics of exploited population stocks and to gain insights into the population dynamics of the animal (Rasheed and Mustaquim, 2010) particularly resulting from breeding (Shinkafi et al. 2011). Mud crabs are known to breed throughout the year with identified peak seasons. However, the peak of the breeding season may vary due to the various geographical areas, species, and environmental factors (Prasad and Neelakantan, 1989; Ali et al., 2004; Ali et al., 2020; Paul et al., 2021). In Bangladesh, a similar peak breeding season was observed even within two different districts. A study on *S. olivacea* done in the district of Satkhira found March to April and August to September periods as the first and second peak breeding time (Ali et al., 2020). In addition, a study conducted in the district of Khulna also reported the peak breeding season in September for the same species (Paul et al., 2021). While for *S. serrata*, two distinct peaks were observed: December to March and September to November in Karwar, India (Prasad and Neelakantan, 1989). Therefore, it is essential to identify the peak breeding season to implement a more efficient ecosystem-based fisheries management of the species. For example, with the information on the breeding season, regulations can be imposed to protect the crabs, especially berried females, during the breeding period to allow population renewal. Besides, a minimum legal landing size based on the size at first maturity of the species can also be obtained through the study on maturation stages of mud crabs. The implementation of regulation based on minimum harvesting size can allow the crabs to mate and spawn at least once before being captured (Ali et al., 2020; Paul et al., 2021). In decapods, the most common applied method to define size at first maturity is based on the estimation when 50% of the population is mature. This method of estimation is based on the body size of crabs when there is 50% chance of mature specimens in the population (Corgos and Freire, 2006; Paul et al., 2021).

Reproductive information on the wild population is required to manage the fisheries resources on a more sustainable basis and for the implementation of fishery legislation consistent with the conservation policies (Goncalves et al., 2007; Ali et al., 2020). Besides, this information is also vital for the development of aquaculture industry, especially broodstock management. Currently, mud crabs are exploited on a large scale for export and aquaculture industry. The current practices of mud crab farming are capture-based where various sizes of wild crabs are caught for fattening in grow-out culture systems (Overton et al., 1997; Nandi et al., 2016; Lalramchhani et al., 2019). The increasing demand of soft-shell crab production in many Asian countries also depends on the seedstock from the wild (Ikhwanuddin et al., 2011; Ganesh et al., 2015). Without regulated fisheries management, many places had reported the catch of smaller size of mud crabs, lower catch per unit effort and poor harvest (Ewel, 2008; Mohd Sharif et al., 2019).

Sabah is one of the main seafood exporters in Malaysia. The export includes mud crabs among several other species. Many studies on mud crabs had been documented in Sabah including the species diversity and distribution (Mohd Sharif et al., 2019), genetic diversity (Mohd Sharif et al., 2016; Hassan and Mustapah, 2019), infection by parasitic barnacle (Shaiful Kahar, 2016; Waiho et al., 2017a) and growth in aquaculture facilities (Lee et al., 2017; Thien et al., 2022a,b; Sanudin et al., 2022). These studies provided vital information for the fishery management and aquaculture development of the mud crabs. However, there is still a lack of reproductive information on the purple mud crab, *S. tranquebarica*, which is a dominant species in Sabah. This study was carried out to obtain information on reproductive biology of mud crab, *S. tranquebarica*, particularly on the gonad maturation stages, size at first maturity and breeding season. The main novelty of the present work is the assessment on the breeding season of *S. tranquebarica* based on a year-round data of wild mud crabs from Sabah. The findings can possibly be used in formulating policies or regulations regarding conservation and management of fisheries in Sabah coastal waters.

Materials and Methods

Study area and crab sampling

The present study was conducted at Marudu Bay located in the northern region of Sabah, Malaysia (06°42’N, 116°54’E) (Figure 1). The samplings were carried out for 12 consecutive months from October 2012 until September 2013 with the assistance of local fishermen.

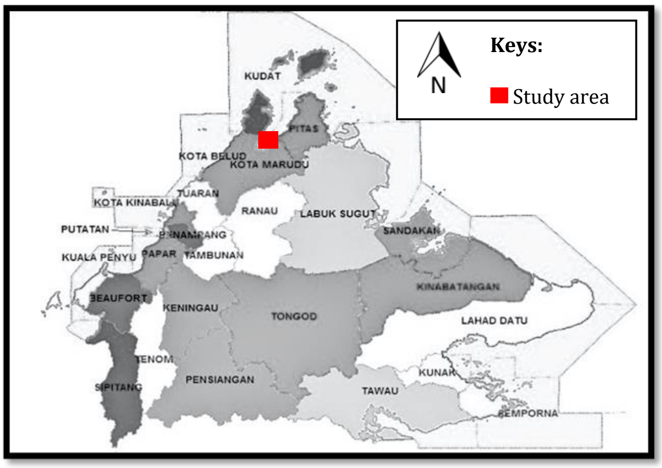


Figure 1. The geographical map of the sampling area in Marudu Bay, Sabah.
Source : Jabatan Tanah dan Ukur (2016)

Samplings were conducted along the mangrove river channel using collapsible baited crab traps commonly used by the local fishermen (dimension of 50cm x 25cm, with entrance width 15cm). Each of the traps was tied with a buoy using polyethylene rope. Bigeye fish (*Priacanthus blochii*) was used as bait. In each sampling, 50 baited traps were used. These traps were deployed along the river at about 15-20 m apart and left for approximately 1 hour before these traps were collected and the catches were recorded. The traps were deployed 2 to 3 times daily depending on the tidal condition. In each month, sampling was conducted for 2 days. After the sampling, the crabs were brought to Borneo Marine Research Institute, Universiti Malaysia Sabah, for further measurements and observations. Smaller crabs with carapace width (CW) less than 60 mm were species identified, measured and released at the sampling sites.

Gonad maturation stages and reproductive cycle

Mud crab species were identified according to Keenan et al. (1998). The carapace width (CW) and body weight (BW) were measured using Vernier callipers to the nearest 0.1 cm and digital electronic balance to the nearest 0.1 g, respectively.

The crabs were then separated into different sex group based on the shape of the abdominal flap (Islam et al., 2010a; Ikhwanuddin et al., 2011). At intervals of 10 mm CW, 3-5 crab specimens were taken out for dissection and histological observations. For females, the body weight and gonad weight were recorded to estimate the gonadosomatic index (GSI). Small portions of the dissected ovary and testis were preserved in Bouin’s solution and subjected to histological preparation following El-Halfawy et al. (2007). The samples were sectioned to 6 µm thickness and stained with haematoxylin and eosin. Histological examination and maturation stages for both sexes were determined according to the scheme suggested by Islam et al. (2010a), Islam et al. (2010b), Islam and Kurokura (2012), Islam and Kurokura (2013). For female crabs, the diameter of oocytes was also measured. Based on these observations, the stages of maturation in each sampling were classified.

Identification of peak breeding season

The data was further analysed on a monthly basis from October 2012 to September 2013 to observe the possible peak breeding seasons in Marudu Bay. Observations also included small crabs with CW <60mm.

Estimation of size at maturity

Size at maturity of crabs in the population was determined when 50% of the specimens caught was sexually mature (SMy-50). Following formula was used for calculation and presentation of data through a sigmoid curve (Robertson and Kruger, 1994; Koolkalya et al., 2006; Islam et al., 2010b; Ikhwanuddin et al., 2011; Islam and Kurokura, 2012; Islam and Kurokura, 2013).

$$P_{CW} = \frac{1}{1+e^{(M1-M2\times CW)}}$$

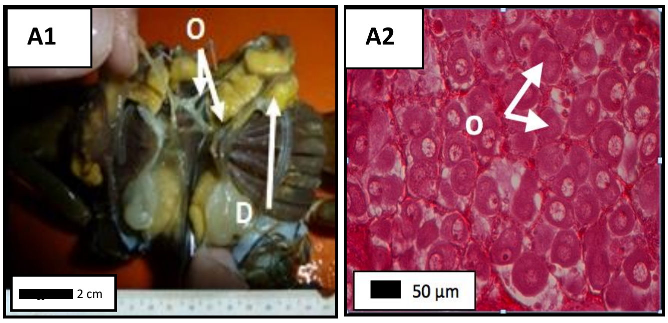
Where, the P_{ICW} is the proportion of mature to immature crabs in each CW class (10 mm interval), and M_1 and M_2 are the parameter estimates. M_1 and M_2 were estimated using the logistic regression through application of Statistical Package of Social Sciences (SPSS) version 18.0. The fitted curve was estimated by using the Microsoft Excel version 2011. The data on gonado- somatic index was calculated using one-way analysis of variance and Tukey's post hoc test (SPSS) to determine the difference between the mean values of each gonadal stage at 95% level of significance.

Results

In the present study, a total of 1459 of *S. tranquebarica* were caught during the 12-month samplings. Overall, there were more male (981 crabs) compared to the females (478 crabs). Samples of 880 male and 396 female specimens were taken out for examining the maturation of gonads.

Gonadal maturation stages

In female crabs, ovarian development was classified into 5 stages based on the maturation stage. Stage I ovary was transparent in colour (Figure 2: A1). Histologically, the ovary consisted of oogonia that were abundant towards the outer part of the ovary (Figure 2: A2). Stage II was creamy to off-white in colour (Figure 2: B1). The primary oocytes started to form with the presence of vacuolated globules in the cytoplasm (Figure 2: B2). Stage III ovary appeared to be of light-yellow colour and with small yolk globules at the outer layer of the cytoplasm (Figure 2: C1&C2). Stage IV appeared to be of orange colour. Few nuclei of the oocyte were visible, yolk globules were distinct and the cytoplasm and follicle cells around the oocytes could hardly be observed (Figure 2: D1&D2). Stage V ovary was red orange in colour, contained the yolk globules in the oocyte that were fused to one another and the nucleus was not easily visible (Figure 2: E1&E2). Based on the appearance of yolk globules, female of stage III - V ovarian stages were grouped as mature females, while females with stage I and II ovarian developmental stages were classified as immature females.



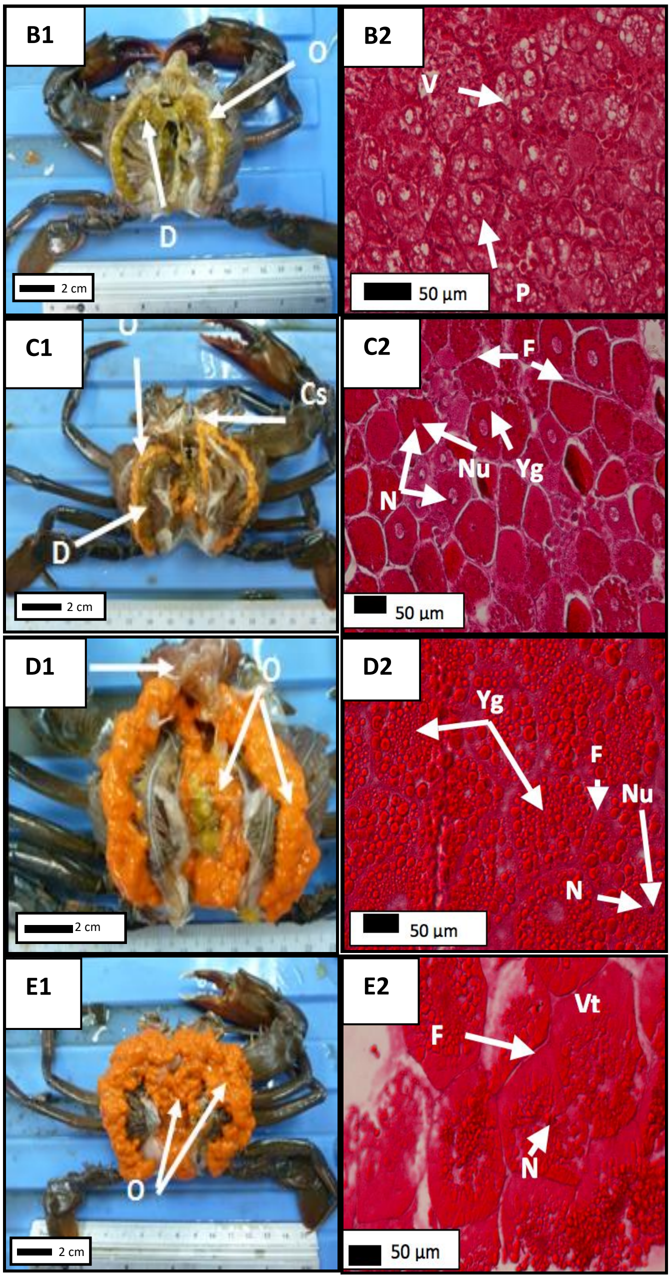


Figure 2. Five ovarian developmental stages classified based on the morphological (A1,B1, C1,D1,E1,F1) and histological observations (A2,B2,C2,D2,E2). **A1&A2**: Stage I immature ovary in proliferation stage; **B1&B2**: Stage II developing ovary in previtellogenesis stage**; C1&C2**: Stage III early maturing ovary in primary vitellogenesis stage; **D1&D2**: Stage IV late maturing ovary in secondary vitellogenesis stage; **E1&E2**: Stage V mature ovary in tertiary vitellogenesis stage.
O: ovary; Cs: cardiac stomach; D: digestive gland; F: follicle cell; N: nucleus; Nu: nucleolus; O: oogonium; P: primary oocytes; Yg: yolk globule; V: vacuolated globule; Vt: vitellus.

In the male crabs, three developmental stages were identified. Stage I testis was immature and not clearly visible. The vas deferens resembles translucent filaments (Figure 3: A1). Under histological observation, spermatogonia were observed in the testis (Figure 3: A2). Stage II or maturing testis was easily noticeable. The vas deferens was thin (Figure 3: B1). Secondary spermatocytes were predominantly observed although some primary spermatocytes were also present (Figure 3: B2). In stage III, the mature testis was dintinctly large in size compared to the previous stage (Figure 3: C1) and spermatozoa were dominated by spermatids (Figure 3: C2).

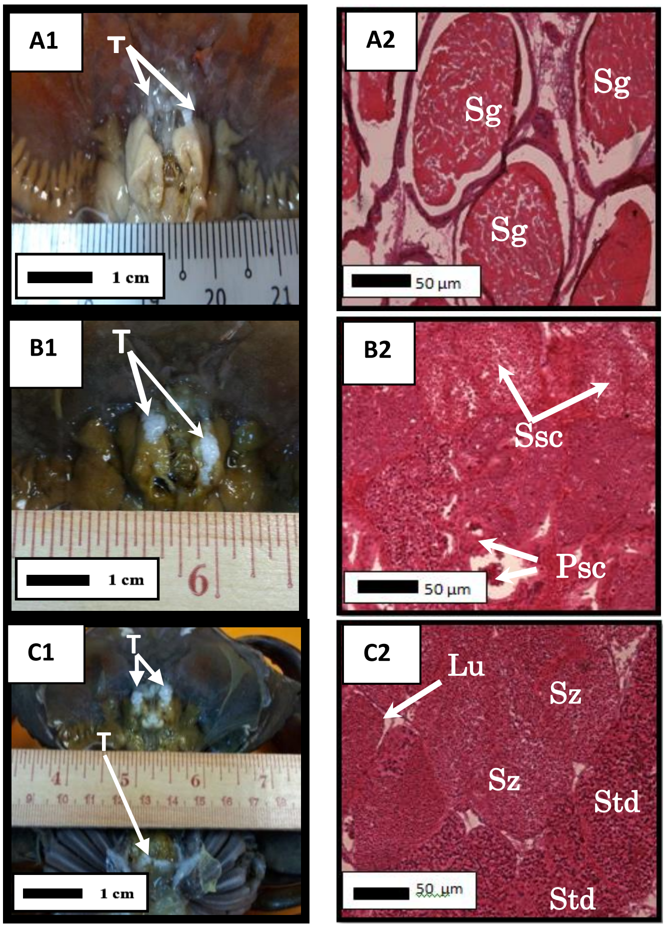


Figure 3. Three testicular developmental stages classified based on the morphological (A1, B1, C1) and histological observations (A2, B2, C2). **A1 & A2** : Stage I immature testes; **B1 & B2**: Stage II maturing testes; **C1 & C2** : Stage III mature testes.
Sg, spermatogonia; Psc, primary spermatocytes; Ssc, secondary spermatocytes; Sz, spermatozoa; Std, spermatids; Lu, lumen.

Relationship between oocytes diameter, gonado- somatic index and carapace width with maturation stages

a) Female

The oocytes diameter, GSI and CW of female mud crab at different maturation stages are presented in Table 1. The oocytes diameter, GSI and CW of the female increased with the gonadal maturation stages. The average oocytes diameter was below 76µm at stage I and II, and increased to 89.4µm at stage III, markedly increased to 121.8µm at stage IV and reached 190.2µm at stage V. A similar trend was observed in GSI where it was low with an average of 0.64% at stage I ovary, then increased significantly to 3.19% at stage III, 7.66% at stage IV and attained GSI 9.89% at Stage V.

Likewise, the CW also increased from 65mm in stage I to 142.9mm in stage V where value was significantly higher than the previous stage ($P<0.05$). The CW of female crab was increased proportionately with the ovarian developmental stages; stage I female recorded CW in the range of 65-90.4 mm to Stage V females where it ranged from 119.8-142.9 mm.

Table 1. Oocytes diameter, GSI and CW for each ovarian developmental stage of female mud crab, *Scylla tranquebarica*.

Ovarian developmental stages	Stage I	Stage II	Stage III	Stage IV	Stage V
Average oocytes diameter (µm)	34.4±1.5	76.0±8.1	89.4±14.0	121.8±15.7	190.2±21.0
Range of oocytes diameter (µm)	30 - 50	45 – 70	70 - 120	135 - 180	175 - 260
Gonad somatic index (%)	0.64± 0.22[a]	1.08± 0.25[b]	3.19± 0.51[c]	7.66± 0.84[d]	9.89± 0.92[e]
Carapace width (mm)	65.0 – 90.4	88.4 – 111.5	96.1 – 121.3	105.1 – 134.7	119.8 – 142.9
No. of samples (n)	174	58	68	83	13

Values are presented as mean ± standard deviation. Different superscript letters within the same row indicate a significant difference ($P < 0.05$).

b) Male

Similar to females, the CW of male also increased with the testicular development stage (Table 2). The smallest size of immature male crab with the presence of gonads was 62.5 mm CW while the largest of immature male crab was 123.8 mm CW (stage I and II). The smallest mature male crabs were recorded at 97.0 mm CW and the largest mature male crab recorded was 142.8 mm CW.

Table 2. Carapace width range for each testicular development stage of male mud crabs, *Scylla tranquebarica*.

Testicular developmental stages	Stage I	Stage II	Stage III
Carapace width, CW (mm)	62.5 – 100.9	79.8 – 123.8	97.0 – 142.8
No of sample (n)	240	253	387

Monthly data on female gonadal maturation stages
Based on the gonadal maturation stages of the mud crab, the percentage of different maturation stages of females in the population in each sampling was calculated and presented in Figure 4. Female crabs with ovarian maturation stages I and II were grouped as immature while females with ovarian maturation stage III - V were categorized as mature females. The data also included the percentage of smaller sized immature females with CW less than 60mm.

The different maturation stages of the female crab can be found year-round. The percentage of mature females ranged from 17.4% to 50.5% on a monthly basis. On an average, 28.7% out of the total females caught was a mature specimen. The percentage of mature female crabs increased gradually from October (27.1%) to February (38.5%) followed by a sharp decrease in March (17.6%). The percentage of mature females then continued to increase in the following 2 months and reached the highest percentage in May (47.4%) before it plunged drastically in June (17.4%) similar to the condition observed during February-March. In the following months in July to September, the percentage of mature females remained in the range of 26.5% to 28.6%.

The percentage of immature females ranged from 5.0% to 49.2%, with an average of 31.4% immature crabs caught yearly. The percentage of immature females did not show a similar pattern with the mature specimens. However, two peaks of immature females were recorded in December-January and April-June where their percentage was higher than the mature female. The highest percentage of immature females was recorded in January while lowest in August.

The percentage of smaller size immature females with CW less than 60mm ranged from 10.8% to 69.1%, with an average of 39.9% of the crabs caught monthly. For these smaller crabs, a higher percentage was observed in October (58.3%) and November (59.4%) followed by a sharp decrease in December and January before it gradually increased to 43.1% in March. Another drastic decrease was observed again in the following months until it reached the lowest percentage of 10.8% in May. The percentage of the small crab thereafter increased gradually to the highest percentage of 69.1% in August. Subsequently, it decreased again in September to 47.1%. Overall, these smaller size immature females showed a different trend with the mature female and/or immature female, where appearance of a higher percentage of this smaller size immature female and a lower percentage of the mature female and/or immature female can be observed.

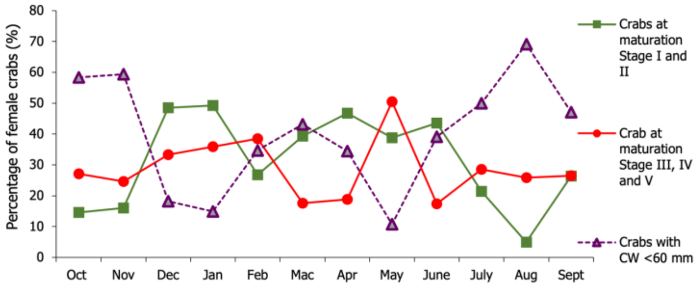


Figure 4. Percentage of different maturation stages of *S. tranquebarica* female caught during the period October 2012 to September 2013.

Monthly data on male gonadal maturation stages
The percentage of different maturation stages of male in each sampling was determined (Figure 5) using the similar methods as for the female crabs. Male crabs in testicular maturation stages I and II were classified as immature and male with testicular maturation, and stage III were classified as mature male. The percentage of smaller size immature male with CW less than 60mm also included in the dataset.

The results showed that different gonadal maturation stages of male crabs can be found throughout the year. On an average, 35.0% of the total male crabs caught were mature and their percentage ranged from 21.3% to 47.4% on a monthly basis. A similar reproductive pattern as seen in the mature female crabs was observed for the mature male crabs. The percentage of male crabs increased progressively from October (27.3%) to February (45.8%), and then decreased substantially in March (31.4%). The percentage of adult males steadily increased over the next two months, reaching its highest point in May (47.4%) before plummeting precipitously in June (22.5%), mirroring the trend observed in February and March. In the following months, July through September, the percentage of mature male crabs remained between 21.3% and 37.7%.

The percentage of immature male ranged from 18.9% to 48.9%, with an average of 39.4% caught monthly. Higher percentage of immature male crabs was recorded in December to February (42.1% to 47.0%), April (45.7%) and September (48.9%) where the percentage was higher than the mature male crabs.

The percentage of smaller size immature male crabs with CW less than 60mm ranged from 7.2% to 43.7% (average of 25.6%) were noticed in the monthly samplings. For these smaller size immature crabs, a higher percentage was recorded in October (33.7%) followed by a gradual decline to its lowest point in February (7.2%) before increasing in March (30.5%). Subsequently, another noticeable decrease was observed in the following months until May (9.7%). Thereafter, the percentage of these small immature crabs started to increase, 43.7% in June and 43.4% in July. In August and September, the percentage decreased again to 29.7 and 29.8, respectively. Overall, this smaller size immature male exhibited a similar trend with the smaller size immature females.

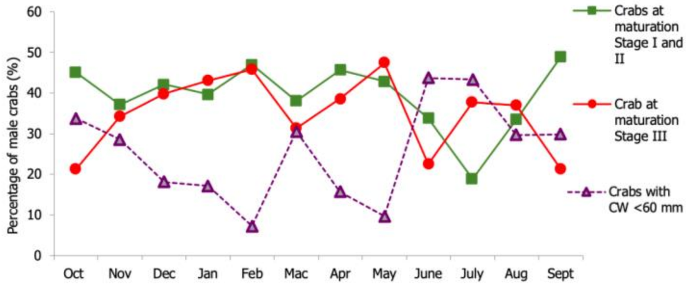


Figure 5. Percentage of male *S. tranquebarica* caught during the period of October 2012 to September 2013 based on the maturity stages.

Comparison of the mature female and male

A comparison of the percentage of mature females and males during the sampling period showed that both mature crabs maintained an almost similar pattern (Figure 6). The percentage of mature females and males gradually increased from October to February followed by sudden decrease in March. The percentage of these mature crabs increased gradually again from March and peaked in May then showed the same trend of decline in June.

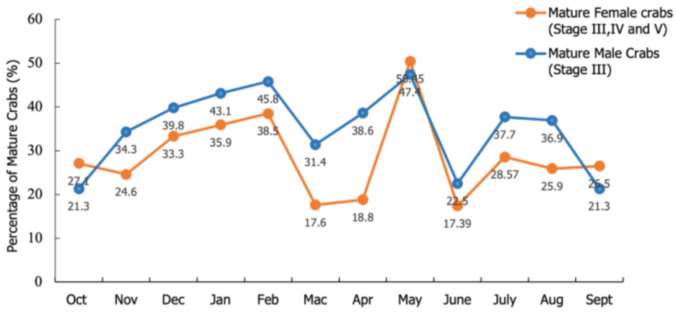


Figure 6. Percentage of mature female and male *S. tranquebarica* caught during the period of October 2012 to September 2013.

Estimation of size at maturity

Based on the SMy-50 method, the size at maturity when 50% of the female crabs sexually mature was estimated at 94.0 mm CW (Figure 7). Meanwhile, for male crab, the size at maturity was 99.5 mm CW (Figure 8).

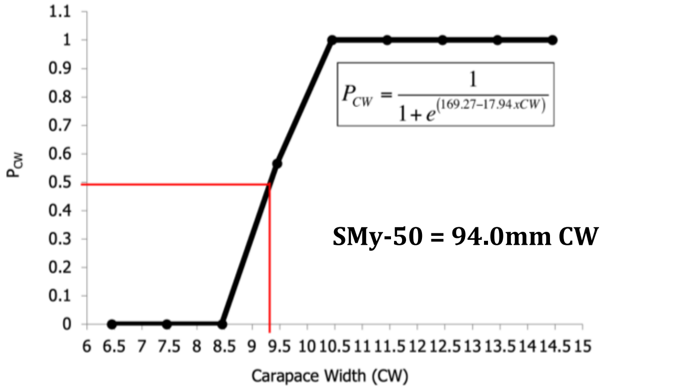


Figure 7. Estimation of size at maturity (SMy-50) for *S. tranquebarica* from fitted sigmoid curve where SMy-50 = 94.0 mm CW.

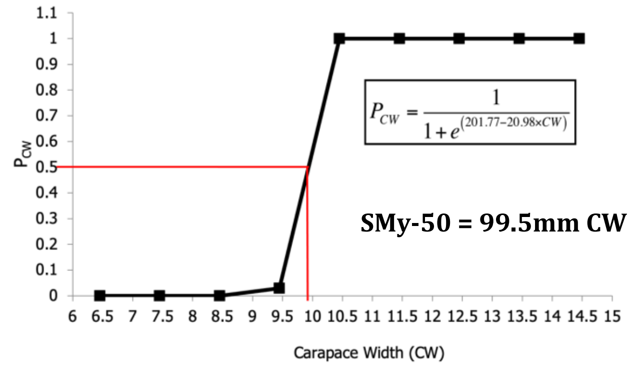


Figure 8. Estimation of size at maturity (SMy-50) for *S.tranquebarica* from fitted sigmoid curve where SMy-50 = 99.5mm CW.

Discussion

In the present study, the ovarian developmental stages of *S. tranquebarica* were seen to be identical to those of other *Scylla* species, including *S. serrata* (Quinitio et al., 2007), *S. olivacea* (Islam et al., 2010a; Ghazali et al., 2017) and *S. paramamosain* (Islam et al., 2010b). Five ovarian stages were classified in the present study based on the histological features which was similar with previous study on *S. serrata*, *S. olivacea* and *S. paramamosain* (Quinitio et al., 2007; Islam et al., 2010a, Islam et al., 2010b; Ghazali et al., 2017). However, some studies on *S. olivacea* classified ovarian development into 4 stages where ovarian stage I and II were grouped into one category (Ghazali et al., 2017; Muhd-Farouk et al., 2019). In general, the ovarian developmental stages or the oogenesis can be divided into two phases which are the previtellogenic phase as immature stage with stage I and II ovaries that contain mostly primary oocytes. Further development leads to vitellogenic phase that is characteristic of mature stage that includes the stages III, IV and V. In this phase, the oocytes increased in size as yolk globules started to appear in the cytoplasm (Islam et al., 2010a; Islam et al., 2010b; Ikhwanuddin et al., 2014; Muhd-Farouk et al., 2016). Due to this change, the oocytes diameter was observed to increase gradually from stage I to stage V with significant increase between stage IV and V. Increase in the oocytes diameter with the progress of ovarian development results in an increase in the volume of ovary as shown by the GSI value. At the previtellogenic phases, GSI recorded the highest value (1.08%). The GSI later started to rise significantly in the vitellogenic phases until it reached 9.89% at stage V. Similar pattern of increment in GSI was observed during previtellogenic and vitellogenic phases in S. *paramamosain* and *S. olivacea* in Thailand (0.7%, 1.1%, 3.2%, 8.3%, 10.7% and 0.9%, 1.3%, 5.3%, 8.6%, 11.3%, respectively) (Islam et al., 2010a; Islam et al., 2010b). Thus, the oocyte diameter and GSI were closely related with the ovarian development and provide a reliable basis for classification of maturity stages. Besides, the progressive ovarian developmental also demonstrated colour changes on the ovary. The ovary changed colour from translucent in stage I to red orange colour at stage V in the wild caught females. The changes in colour were due to the accumulation of yolk in the oocytes that also involves accumulation of carotenoid in the higher ovarian developmental stages (Quinitio et al., 2007; Islam et al., 2010a; Ikhwanuddin et al., 2014; Tantikitti et al., 2015; Ghazali et al., 2017; Aaqillah-Amr et al., 2018). Carotenoids work as antioxidants to protect developing tissue from peroxidative damage caused by free radicals (Surai and Speake, 1998; Tantikitti et al., 2015). Tantikkiti et al. (2015) and Aaqillah-Amr et al. (2018) also reported that the levels of carotenoid increased with ovarian maturation during embryonic development. Thus, a brighter orange or red colour also reflects higher maturation stage.

In the present study, three stages of testicular development were observed in male crabs. These stages appeared to be the same as reported for *S. olivacea* (Islam and Kurokura, 2012; Waiho, et al., 2017b), *S. paramamosain* (Islam and Kurokura, 2013; Islam et al., 2018) and other portunid crabs, including blue swimming crab, *Portunus pelagicus* (De lestang et al., 2003). Male crabs with the presence or absence of testes are the features that were used to differentiate morphologically between stage I and stage II. Besides, stage I testes were difficult to differentiate from other internal organs particularly the hepatopancreas due to lucid-watery external appearance (Islam et al., 2018). For stage II, the testes were immediately discernible due to their coiled shape and watery white appearance. In accordance with the findings of the previous study, at stage III, the gonadal development was characterized as swollen, opaque and white (Islam and Kurokura, 2012; Waiho et al., 2017b; Islam et al., 2018).

During the 12-month samplings in the mangrove area in Marudu Bay, different maturation stages of female and male crabs, including the mature crabs, were found to occur in each collection. This indicates that breeding of the mud crab can occur year-round. Besides, a higher percentage of mature females and males were recorded in May followed by a sudden decrease in June. It was then followed by a gradual increase of the smaller size crabs (<60mm CW) marking the process of recruitment of the young crabs in the mangrove area in June - September. A similar pattern was also observed during February-April, however, with lower values. This indicates the occurrence of a major breeding peak in the months of May and June and another minor breeding peak in February-April. Obviously, this reflects population renewal that follows the breeding cycle. This is consistent with previous research by Koolkalya et al. (2006) suggesting that *Scylla* species are continuous breeder with peak breeding season. Mud crab, *S. olivacea*, in Bangladesh was reported to breed throughout the year and also showed two peaks of breeding season: March-April and August-September (Ali et al., 2020). On the other hand, in Andaman Sea, female *S. olivacea* was also reported to spawn throughout the year but spawning peak was reported to occur with the onset of rainy season in early June (Koolkalya et al., 2006). For *S. serrata* in India, two breeding peaks were observed in December and March and the other peak occurred between September and November (Prasad and Neelakantan, 1989). These studies suggest that the breeding season of mud crabs may vary with different species and geographical conditions and is consistent with earlier investigations showing that reproductive biology of a species differs with seasons and environmental conditions (Martinelli et al., 2002; Ali et al., 2004; Ali et al., 2020).

During the sampling period, decrease of the proportion of mature female and male crabs happened in March and June after a peak in the previous months. The occurrence of mature female crabs from stages I to V at the sampling sites indicates that gonadal maturation and mating of the mud crabs take place in the mangrove area. Besides, throughout the study, no berried females were found in the mangrove forest. This suggests that spawning does not occur in the mangrove area. These findings supported previous studies on the migration of mature female crabs from the mangrove area to offshore to release their eggs during the spawning season. Females of *S. olivacea*, *S. serrata* and *S. paramamosain* have been reported to migrate offshore for spawning after mating (Overton and Macintosh, 2002; Islam et al., 2010a; Islam et al., 2010b; Ikhwanuddin et al., 2011; Ali et al., 2020). Besides, mature males were also found to show a similar pattern with the mature females marked by a sudden decrease in the number of male crabs in the mangrove area during the breeding season. This reflects that the mature male crabs may also migrate out of the mangrove area during the breeding season. However, no previous research has indicated that male crabs leave the mangrove during the season. In a study done in Kota Marudu by Mohd Sharif et al (2019), it was reported that this species (*S. tranquebarica*) was abundantly distributed in the two rivers near the open sea or mangrove area dominated by *Rhizophora* sp. with higher water salinity. Research carried out by Ikhwanuddin et al. (2012) and Fazhan et al. (2022) stated that *S. tranquebarica* is a free ranging crab, with a non-territorial existence and is not restricted to home site unlike other *Scylla* species. The data have shown that *S. tranquebarica* was found concentrated in mangrove forest and estuaries. Since *S. tranquebarica* exhibited a preference for areas with a higher salinity, it is possible that male crabs would migrate out of the breeding area, which would explain the dramatic decline in male crabs in the samples collected during the breeding season. Further investigations are required to shed light on the movement of male crabs particularly during the breeding season.

Earlier studies considered the size when 50% of the female population attained ovarian maturity to determine female maturation in an area (Islam et al., 2010b; Ikhwanuddin et al., 2011; Ali et al., 2020). In the present study, the SMy-50 of female crabs was estimated at 94.0 mm CW. This SMy-50 is slightly larger compared to a study conducted in Sarawak waters which reported SMy-50 at 92.0 mm CW for the same species (Ikhwanuddin et al., 2011). Meanwhile, based on the morphological and histological observations, the size of maturity of female *S. tranquebarica* was recorded as 96.1 mm CW in this observation. On the other hand, the SMy-50 of male crab was estimated at 99.4 mm CW while 97.0 mm CW was based on the histological observation of stage III testis. Variations in the results between these different methods were also reported for other mud crab species. For *S. olivacea* female crab, the SMy-50 was 90.8mm CW while based on the morphological and histological observations the size at maturity was 81.8mm CW in Kedah, Malaysia (Ikhwanuddin et al., 2014). In Thailand, the SMy-50 for *S. olivacea* female crab was 99.1mm CW compared to 89.8 mm CW based on morphological and histological observations (Islam et al., 2010b). For male crabs, the SMy-50 estimated in the present study was slightly larger compared to other *Scylla* species. For *S. olivacea* male crab, the size at maturity was recorded at 84.0mm CW in Thailand (Islam & Kurokura, 2012), 80.0mm CW in Terengganu, Malaysia (Ikhwanuddin et al., 2010) and 67.0mm CW in Sarawak, Malaysia (Ikhwanuddin et al., 2011). For *S. paramamosain*, the size at maturity was 82.0mm CW in Penang, Malaysia (Islam et al., 2018) and 84.0mm CW in Thailand (Islam & Kurokura, 2012). These studies also indicate that differences in size may be related to different methods used as there is no standard method to determine the size at maturity. The methods used include shape of abdominal flaps of the female crab (Ikhwanuddin et al., 2011), color and the size of the gonad (Quinn and Kojis, 1987), and morphological and histological features of the gonad during various stages of its development (Quinitio et al., 2007; Islam et al., 2010a; Islam et al., 2010b). Besides, the variation of these results might be due to the different species size among the *Scylla* spp. *S. tranquebarica* was reported to be larger in size than *S. olivacea* followed by *S. paramamosain*. However, all the three species were smaller compared to *S. serrata* (Ikhwanuddin et al., 2010). SMy-50 for *S. serrata* female crabs was reported to be 100mm CW in Ranong (Macintosh et al., 2002). Apart from that, the variations are also caused by the latitude of the location (Quinn and Kojis, 1987; Poovachiranon, 1992; Ikhwanuddin et al., 2010b; Ikhwanuddin et al., 2011; Ali et al., 2020). Environmental factors such as temperature are also suggested to influence the size at first maturity (Sukumaran and Neelakantan, 1996; Fisher, 1999; Jirapunpipat, 2008). Fishing pressure has been reported as yet another factor influencing the size at maturity. In spiny lobster, *Panulirus marginatus*, fishing pressure from commercial or recreational fishing has led to a reduction in SMy-50 (Polovina, 1989).

In ecosystem-based fisheries management, information on biology of a species especially the breeding system, provides crucial information for the management wild populations. Regulation on the fishing activities, especially the protection of mature females during closed season or no-take months can be implemented on a knowledge-based basis. During the closed or no-take periods, fishing of mature crabs could be restricted to enable more mature crabs to breed. In the present study, a major breeding peak was recorded in the months of May-June and a minor one in February-April where fishing restriction can be implemented in Sabah, Malaysia. Besides, based on the size at first maturity, the implementation of the minimum legal harvesting size of mud crabs can also be considered. In the present study, mature females and males were seen in the range of 94.0 to 96.1 mm CW and 97.0 to 99.4 mm CW, respectively. This information can be the reference point to regulate the minimum legal landing size of mud crabs to prevent overexploitation. The positive effect of such regulations has been witnessed in Queensland (Brown, 1993) and Western Australia (Department of Fisheries of Western Australia, 2013). After a decade of implementation of the prohibition of harvesting female specimens and enforcement of regulated minimum landing size of the mud crabs in Queensland, the catch per unit effort (CPUE) had significantly increased. The State of Queensland, Department of Employment, Economic Development and Innovation (2011) suggested that the implementation also protected the spawning capacity of the mud crab population in that area. Besides, this approach also allows the adult stock to mate and spawn at least once before being captured (Stevens et al., 1993).

In the present study, more immature crabs were recorded compared to the mature specimens. On an average, 71.3% and 65.0% of immature females and males were observed compared to 28.7% and 35.0% of mature females and males, respectively. The purple mud crab (*S. tranquebarica*) is the dominant species in Marudu Bay and can be found together with *S. paramamosain* and *S. olivacea* and (Mohd Sharif et al., 2019). A higher abundance of immature crabs of *S. paramamosain* (72.6%) compared to the mature crabs (27.4%) during the same sampling period was noticed although *S. olivacea* recorded a lower percentage of immature crabs at 55.7% in comparison with mature crabs, 44.3% (Shaiful Kahar, 2016). Based on the estimates generated by FiSAT (FAO-ICLARM Stock Assessment Tool) software, the recruitment of *S. tranquebarica* was reported to occur throughout the year with two peaks - a major one in May - September and a minor one in January - March (Mohd Sharif, 2016). This may indicate that the mangrove forest in Marudu Bay is a nursery and grow-out area for the mud crabs. The low percentage of mature crabs in this area may be an indication of overfishing of the larger sized crabs or else it could be due to the natural behaviour of mature crabs to migrate out from the mangrove. Marudu Bay is a common fishing ground for the local community. Increase in the market price and demand of the mud crabs has triggered more harvesting pressure to fulfil the demand especially for the export market and intensified interest in soft-shell crab production. In Marudu Bay, Mohd Sharif et al. (2019) reported a decreasing trend of CPUE in the same study site in 2012 to 2013. Therefore, further research is also required to reinvestigate the current fisheries status of mud crabs in Marudu Bay.

Conclusion

The mud crabs (*Scylla* spp.) form an economically important component of small-scale coastal fisheries in many countries including Malaysia. Fundamental information on biology is vitally important for sustainable management of crab populations. There is a paucity data on aspects such as the cycle of maturation and spawning. Efforts were made in this study to generate scientific data of practical value in sustainable management of capture fisheries of mud crabs. It was noticed that February-April and May-June are peak breeding seasons for *S. tranquebarica* in Marudu Bay, Sabah. Besides, based on the estimated size at first maturity, minimum landing size can be considered in the implementation of knowledge-based regulations in mud crab fishery.

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