

Oceanic Influences on Mud Crab (*Scylla olivacea*) Reproductive Traits: A Comparative Study Across the Indian and Pacific Oceans

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Scylla olivacea is a commercially important species in the Indo-Pacific region, currently facing growing pressures from anthropogenic stressors. This study compares populations from the Indian Ocean (Andaman Sea) and the Pacific Ocean (Gulf of Thailand) to assess how different oceanic region and seasonal conditions influence key reproductive traits. By examining parameters such as sex ratio, size at first maturity, fecundity, and gonadosomatic index (GSI), the study aims to identify the differences that can inform targeted and sustainable management strategies. Crab samples were collected monthly from five sampling sites along the coast of the Indian Ocean (Ranong, Satun and Trang provinces) and the Pacific Ocean (Pattani and Surat Thani provinces) using traditional crab

traps by local fishermen from April 2022 to May 2023 and subsequently analyzed in the laboratory. Results indicated that crabs from Ranong province, the Indian Ocean, exhibited smaller body sizes and values of most reproductive parameters ($p < 0.01$). The fecundities were 1.03×10^6 and 1.49×10^6 for crabs from Ranong and Pattani provinces, respectively. Positive relationships were found between internal carapace width (ICW), carapace length (CL), abdomen width (AW), and body weight (BW) with ovary weight (OW). Mature females, based on gonad development stages III and IV, were present year-round at both oceanic coasts. Peak abundances were found in November at both sites. High GSI levels were recorded in April and June for Ranong province (3.05 ± 1.97 to 10.97 ± 1.96) and February and June for Pattani province (3.19 ± 1.72 to 10.52 ± 1.71). The estimated sizes at maturity (M_{50}) for female/male of *S. olivacea* varied across locations with smaller sizes observed from the Indian Ocean viz., 78.0/83.1 mm, 64.0/79.2 mm and 81.9/80.6 mm in the provinces of Ranong, Satun and Trang, respectively and 92.3/93.2 mm and 96.9/96.8 mm in Pattani and Suratthani, respectively. The sex ratio also indicated variations across region, with male:female ratios of 1:0.92, 1:0.78, 1:0.77 and 1:1 in the provinces of Pattani, Ranong, Satun and Trang. It is thus concluded that the oceanic region affects reproductive characteristics of *S. olivacea* and these findings can be applied to highlight the importance of localized management strategy for a sustainable use of mud crab resources.

Keywords: Mud crab, Size at 50% Maturity, Fecundity, Gonadosomatic Index, Andaman Sea, Gulf of Thailand

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BACKGROUND

Understanding reproductive biology of aquatic animals is crucial for sustainable resources management and aquaculture development (Reynolds et al. 2005; Fontoura et al. 2009; Trindade-Santos and Freire 2015; Fazrul et al. 2018; Soe et al. 2022; Soe et al. 2023; Hajisamae et al. 2025). Parameters such as sex ratio, gonadosomatic index, maturity stage, fecundity, size at first maturity, spawning season and relationships between various parameters with reproductive traits are commonly employed in the management of many aquatic animals (Koolkalya et al. 2006; Fontoura et al. 2009; Mora et al. 2011; Hajisamae et al. 2015). Collections of these data spatially and

temporally are essential to support sustainable management practices (Trindade-Santos and Freire 2015).

Mud crabs, *Scylla* spp., are recognized as highly economic species, are found along coastal areas of the Indo-Pacific region such as the Philippines, Indonesia, Vietnam, China, Taiwan, India, Sri Lanka, Bangladesh, and Malaysia (MacNae 1969; Bir et al. 2020; Soe et al. 2023). They are high potential aquatic animal to be domesticated for as aquaculture species due to fast growth rate, large size, high reproductive capacity, high disease resistance, and adaptability to farming condition (Viswanathan and Raffi 2015). In Thailand, four species of mud crabs have been reported viz., *Scylla paramamosain*, *S. transquebarica*, *S. olivacea*, and *S. serrata*. Notably, it was dominated by *S. olivacea* with seldom report of *S. serrata* (Pradissan 2006; Sodsuk 2006). Its fisheries contribute significantly to Thailand's economy by providing livelihoods for coastal community, employment opportunity and aquaculture sectors. An increasing demand for mud crabs locally and internationally has been leading to an overexploitation of the resources in many parts of the world. Loss of mangrove habitat, geographical changes and degradation of coastal ecosystem are considered negative factors for the decline of natural mud crab populations (Paul et al. 2021). Moreover, it was also reported in Bangladesh that most of the crab populations were caught before reaching the first size of maturity (Islam et al. 2013). To sustain mud crab population accurate and up to date scientific data related to reproductive characteristic of specific locality is thus highly required. Oceanographic conditions play a crucial role in shaping the dispersal patterns of marine species. For mud crab, it is reported that these factors significantly influencing the timing of larval metamorphosis, especially impact of temperature variations on the incubation period of larvae (Hamasaki 2002; Nurdiani and Zeng 2007; He et al. 2010), thereby impacting their dispersal potential and, ultimately, their ability to successfully colonize new habitats. These may lead to affect reproductive activities of mud crabs. Many studies have reported ecological, biological and fisheries aspects of *S. olivacea* including growth, abundance, recruitment and mortality (Moser et al. 2002), capture size, reproductive biology (Koolkalya et al. 2016; Islam et al. 2010), and sexual maturity (Ikwanuddin et al. 2014) in different parts of the world. However, all are conducted in a specific habitat during different period of time. Reproductive characteristics of mud crab from different oceanic regions, especially in the Indian and Pacific coasts, have not been simultaneously investigated. These knowledges can provide valuable biological status and characteristics of mud crab resources based specifically on reproductive traits investigated within the same period of time in different oceans. The southern peninsula of Thailand is located between the Andaman Sea, part of the Indian Ocean, in the west and the Gulf of Thailand, part of the Pacific Ocean, in the east. It is thus appropriate to use these coasts as representatives of the two major oceans to comparatively investigate reproductive aspects of different populations of *S. olivacea*.

This study represents the first attempt to simultaneously investigate and compare key reproductive traits, such as sex ratio, size at first maturity, fecundity, and gonadosomatic index (GSI), of *S. olivacea* populations from the Indian and Pacific Oceans. By examining the relationships between these traits, it is aimed to gain a deeper understanding of the reproductive ecology of this species across different oceanic regions.

MATERIALS AND METHODS

Study area

The study was conducted in coastal waters of the Indian and Pacific Oceans along the southern peninsular of Thailand. Sampling sites were selected from the Andaman Sea (Ranong, Satun, and Trang provinces) to represent the Indian Ocean and the Gulf of Thailand or the GoT (Pattani and Suratthani provinces) to represent the Pacific Ocean (Fig. 1). These regions are recognized for their diverse habitats and significant fisheries (Satapoomin 2011; Wattayakorn 2006). The Pacific coast experiences three distinct seasons: dry (January–April), southwest monsoon (May–August), and northeast monsoon (September–December) (Chaiwanawut et al. 2005). In contrast, the Indian Ocean coast has two primary monsoon seasons: northeast monsoon (November–February) and southwest monsoon (May–September) (Koolkalya et al. 2006).



Fig. 1. Sampling sites across five locations. Pattani and Suratthani represent the Gulf of Thailand in the Pacific Ocean, while Ranong, Satun, and Trang represent the Andaman Sea in the Indian Ocean.

Sample collection and analysis

Both male and female specimens of *S. olivacea* from all five study sites were collected monthly between June 2022 and May 2023 using traditional crab traps operated by local fishermen to assess sex ratio, size at sexual maturity (SM_{50}), and seasonal variation in gonad maturity stages. Sample coverage and parameter assessments by site are summarized in table 1. Specimens were anesthetized, preserved, and measured for internal carapace width (ICW) using digital vernier calipers (Fig. 2).

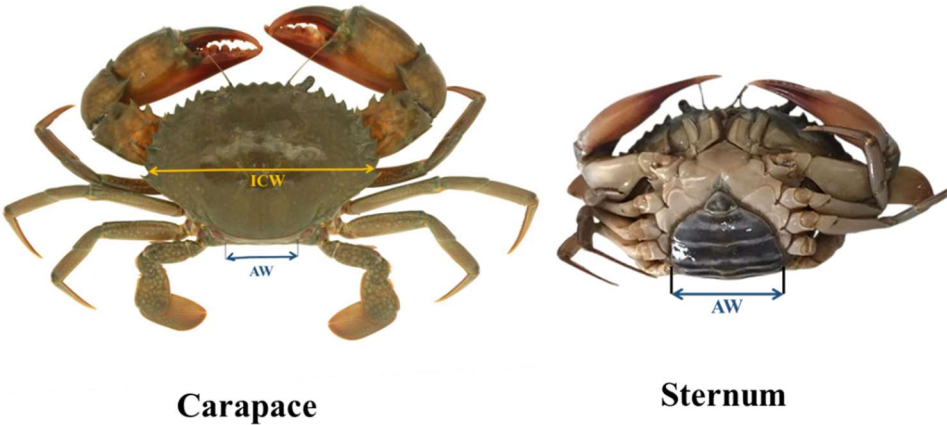


Fig. 2. Morphological characters for measurement by consist internal carapace width (ICW), and abdomen width (AW). Source: Jirapunpipat et al. (2008).

Table 1. Summary of sample collection based on study sites and the assessment of reproductive parameters

Study sites	Reproductive parameters					
	GSI	Fecundity	Regression	Sex ratio	SM ₅₀	Seasonal variation in GMS
Indian Ocean						
Ranong	✓	✓	✓	✓	✓	✓
Satun				✓	✓	✓
Trang				✓	✓	✓
Pacific Ocean						
Pattani	✓	✓	✓	✓	✓	✓
Surat Thani				✓	✓	✓

Remark: 1. GSI, fecundity, and morphometric regression analyses were conducted on Stage. IV female *S. olivacea* collected from Ranong and Pattani provinces between April 2022 and March 2023. 2. Sex ratio, size at sexual maturity (SM₅₀), and seasonal variation in gonad maturity stages (GMS) were assessed using male and female *S. olivacea* samples collected from all study sites between June 2022 and May 2023.

Additional specimens of female *S. olivacea*, up to 50 crabs for each site, with fully mature ovaries (Stage IV) were obtained monthly from Ranong province (Indian Ocean) and Pattani province (Pacific Ocean) between April 2022 and March 2023. These ovaries were characterized by a deep orange color, occupying more than 75% of the body cavity and covering major internal organs. Yolk globules were fused into a dense mass, and oocytes ranged from 190–220 μ m in diameter (Ikhwanuddin et al. 2014). The specimens were used to measure abdominal width (AW), body weight (BW) and ovary weight (OW). The differences of body weight, ICW, AW and OW between crabs from Ranong and Pattani provinces were assessed by t-test using PAST software (Hammer et al. 2001).

Sex ratio

Sex ratio was determined by calculating the proportion of male individuals to female individuals (Oliveira et al. 2015). A chi-square test (χ^2) was employed to assess the statistical

significance of monthly and total variations in sex ratio. It is noted that data on sex ratio from Surat Thani province was excluded from the analysis due to limited sample availability.

Size at first maturity

The analysis of inter-carapace width (ICW) data was performed to estimate the size at which 50% of male and female crabs reach sexual maturity (SM_{50}). Female crabs were classified as either mature or immature based on abdominal morphology, following Islam et al. (2010), in which a wide, globular, and darkened U-shaped abdomen indicates maturity. Male crabs were classified as mature or immature based on external morphological characteristics. Males were considered mature if they exhibited fully developed gonopods and broadened abdominal flaps that fit tightly against the sternum, following the criteria described by Islam et al. (2010) and Ikhwanuddin et al. (2011).

The proportion of mature individuals in each 10 mm ICW size class was calculated and fitted to a logistic regression model, as described by Robertson and Kruger (1994), using the following equation:

$$P_{lm} = (1 + \exp^{-\ln 19(M - M_{50})/(M_{95} - M_{50})})^{-1}$$

where, P_{lm} is the proportion of mature crabs at 10 mm ICW size class M , M_{50} and M_{95} represent the sizes at which 50% and 95% of females are mature, respectively.

Fecundity

Altogether, 237 specimens from Ranong province and 63 specimens Pattani province with ovaries at developmental stage IV were used to assess fecundity. Ovaries were carefully removed from the carapace, washed with freshwater, and preserved in modified Gilson's fluid. This preservative solution consisted of 100 mL of 60% ethanol, 880 mL of water, 15 mL of 80% nitric acid, 18 mL of glacial acetic acid, and 20 g of mercuric chloride. To ensure effective preservation and egg separation, samples were vigorously shaken for 24 hours (Ikhwanuddin et al. 2014). A subsample of eggs was counted under a stereoscopic microscope. To estimate fecundity, a gravimetric method was employed (Laevastu 1971; Tresierra and Culquichicón 1993 1995). A subsample of eggs was counted under a stereoscopic microscope. The average count from three subsamples was then extrapolated to the total egg weight per crab to determine the total number of eggs. The following formula was applied.

$$F = nG/g$$

where, n is the number of eggs in the sample; G is the weight of all the eggs; and g is the weight of the subsample (0.01 g).

Gonadosomatic Index (GSI)

To define a monthly reproductive phase of *S. olivacea*, the GSI of female with mature ovaries (Stage III and IV) was calculated with the following equation:

$$GSI = \left(\frac{GW}{BW} \right) \times 100$$

where; GW is weight of crab ovary and BW is crab body weight (Azmie et al. 2012). A one-way analysis of variance (ANOVA) was performed to examine variation between month of GSI, following by Tukey HSD test for post-hoc analysis once monthly different was detected. The analysis was conducted by PAST software (Hammer et al. 2001).

Morphometric regression analyses

Female crabs with fully mature ovaries (Stage IV) from Ranong and Pattani provinces were used to analyze relationship between fecundity (F) and morphometric parameters, including body weight (BW), ovary weight (OW), inter-carapace width (ICW), and abdominal width (AW). All observed values were transformed using the base 10 logarithm ($\log_{10}$). Linear regression analysis (Gulland 1983) was subsequently performed on the log-transformed data using PAST software (Hammer et al. 2001) by the following equation:

$$\log(F) = \log(a) + b \cdot \log(X)$$

which corresponds to the power function:

$$F = a \cdot X^b$$

where, F is fecundity, X is the morphometric parameter (e.g., BW , OW , ICW , or AW), and a and b are constants derived from the regression model.

RESULTS

Body size, ovary weight, GSI and fecundity

The average $\pm$ S.D. size of BW, ICW, AW, OW, GSI and fecundity from Ranong province, the Andaman Sea and Pattani province, the GoT, were shown in table 2. The results indicate that in Ranong, the observed size ranges for various parameters, with the exception of ovary weight, were significantly smaller ($p < 0.001$) than those recorded in Pattani. Despite their smaller body size, the Ranong specimens demonstrated significantly higher fecundity ($p < 0.001$).

Table 2. Average $\pm$ S.D. values of body weight, inter-carapace width, abdominal width, ovary weight, gonadosomatic index and fecundity of mature female (stage IV) *Scylla olivacea* in Pattani province, the Pacific Ocean and Ranong province, the Indian Ocean

	Ranong province (Indian Ocean) $n = 237$	Pattani province (Pacific Ocean) $N = 63$
Body weight (g)	219.96 ± 40.33	$256.76 \pm 79.41^*$
Inter-carapace width (mm)	95.47 ± 8.65	$106.82 \pm 10.47^*$
Abdominal width (mm)	39.29 ± 4.01	$44.60 \pm 5.50^*$
Ovary weight (g)	18.93 ± 5.91	18.89 ± 4.74
Gonadosomatic index	$8.61 \pm 2.15^*$	$7.54 \pm 0.99^*$
Fecundity	$1.49 \times 10^6 (\pm 8.00 \times 10^5)^*$	$1.03 \times 10^6 (\pm 3.48 \times 10^5)$

n = number of samples, *Significantly different at $p = 0.001$ (two tail).

Size at first maturity

Logistic regression analysis of *S. olivacea* revealed variation in SM_{50} across different oceanic. In the Andaman Sea, SM_{50} values for females/males were 78.0/83.1 mm (Ranong), 64.0/79.2 mm (Satun), and 81.9/80.6 mm (Trang). In the GoT, values were 92.3/93.2 mm (Pattani) and 96.9/96.8 mm (Suratthani). By comparing among all study sites, results from logistic regressions indicated that ICW_{50} for both female and males from the Andaman Sea matured earlier than the GoT (Fig. 3).

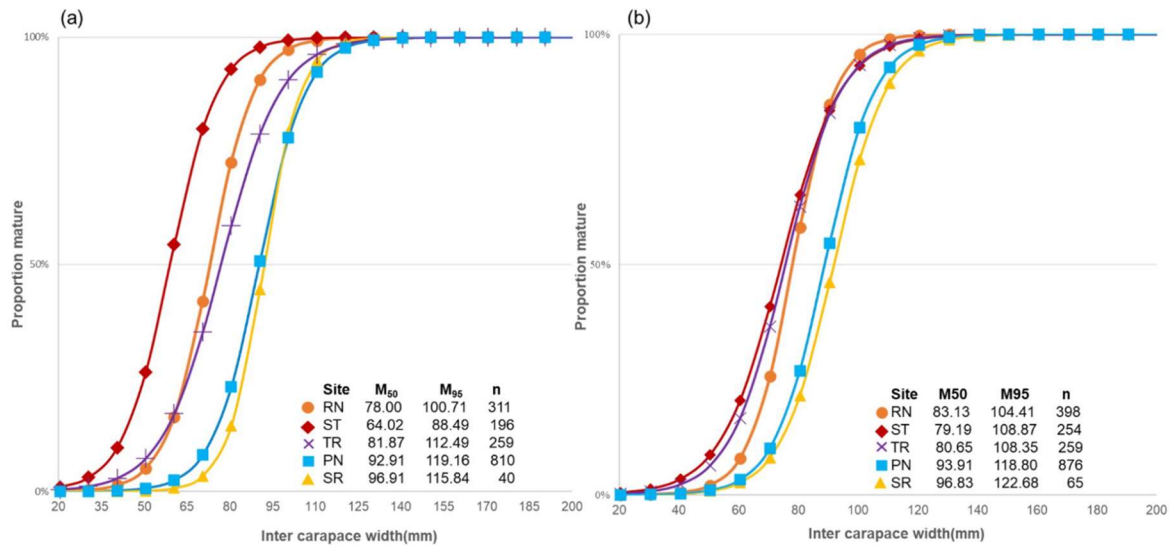
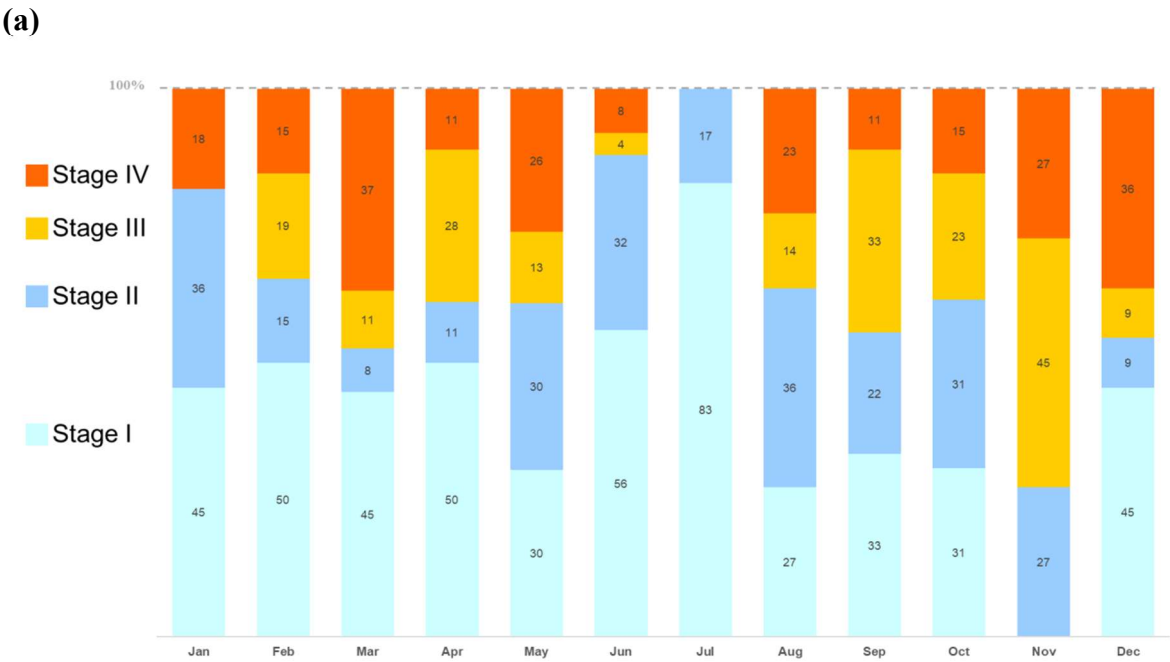


Fig. 3. Percentage of mature (a) female and (b) male of size at first maturity (ICW₅₀) of *Scylla olivacea* collected from five sites during June 2022 to May 2023. Cut-off 50% indicated crab was first mature. RN = Ranong, ST = Satun, TR=Trang (Andaman Sea) and PN = Pattani, SR= Suratthani (Gulf of Thailand).

Seasonal changes of gonadal maturity stages in females

Mature females (Gonad Development Stages III and IV) were present the whole year-round at both the Andaman Sea and the GoT coasts. Peak abundances were observed in November at both sites (Fig. 4a and 4b). A notable decline in mature females was observed in July, particularly absence along the Andaman Sea coast, with the lowest abundance recorded in the GoT during this month. Seasonal patterns in gonad maturity stages were evident at both oceanic regions.



(b)

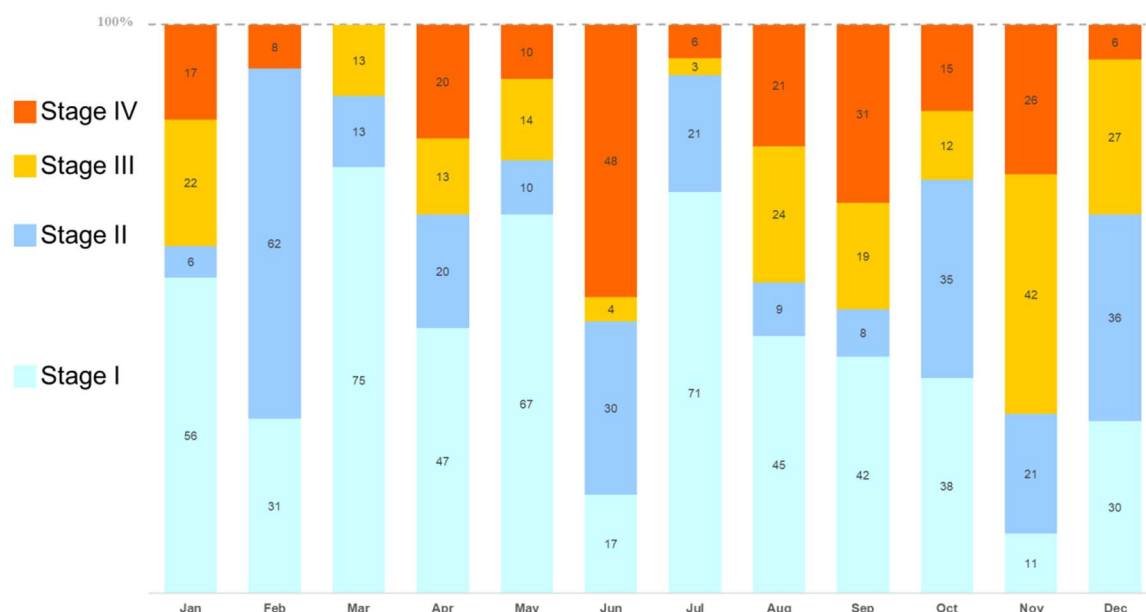


Fig. 4. Seasonal changes in gonad maturity stages of *Scylla olivacea* for female from, (a) Andaman Sea (Ranong, Satun and Trang provinces) and (b) Gulf of Thailand (Pattani and Surat Thani provinces) during June 2022 to May 2023.

Sex ratio

The sex ratio of *S. olivacea* varied between four sites (Table 3). The overall male: female ratios were estimated as follows; Ranong (1:0.78; $\chi^2 = 10.68$, $p < 0.005$), Satun (1:0.77; $\chi^2 = 7.48$, $p < 0.05$), Trang (1:1; $p > 0.05$), and Pattani (1:0.92; $\chi^2 = 2.74$, $p > 0.05$). These findings indicate that the sex ratio differs both spatially and temporally, suggesting potential influences from environmental or biological factors. In the GoT (Pattani Province), a male-biased sex ratio was observed in January and February, with a lower proportion of females during these months. Similarly, in the Northern Andaman Sea (Ranong Province), male-biased sex ratios were detected in multiple months, including April, August, October, November, and December, indicating a seasonal decline in the female population. Conversely, in the Southern Andaman Sea (Satun and Trang Provinces), a higher proportion of females was captured during specific months, particularly in March. This suggests that traditional fishing methods used in these regions may be more effective in capturing females during certain periods. These spatial and seasonal variations in sex ratios may reflect behavioral patterns such as migration, mating, or spawning activities, which influence the distribution and availability of males and females. Detailed sex ratio values and statistical results for each site and month are provided in table 2.

Table 3. Monthly variation in sex ratio of *S. olivacea* collected in Pattani, Ranong, Satun and Trang from June 2022 to May 2023

Month	Ranong		Satun		Trang		Pattani	
	Ratio (M:F)	<i>p</i> value	Ratio (M:F)	<i>p</i> value	Ratio (M:F)	<i>p</i> value	Ratio (M:F)	<i>p</i> value
January	1:0.96	> 0.05	1:0.71	> 0.05	1:0.92	> 0.05	1:0.65	< 0.05
February	1:0.97	> 0.05	1:1.06	> 0.05	1:0.86	> 0.05	1:0.6	< 0.05
March	1:1.35	> 0.05	1:2.8	< 0.05	1:1.95	< 0.05	1:0.74	> 0.05
April	1:0.53	< 0.05	1:1.07	> 0.05	1:0.78	> 0.05	1:0.9	> 0.05
May	1:0.83	> 0.05	1:0.6	< 0.05	1:2.11	> 0.05	1:0.93	> 0.05
June	1:1.08	> 0.05	1:0.73	> 0.05	1:1.2	> 0.05	1:1.08	> 0.05
July	1:1.07	> 0.05	1:0.77	> 0.05	1:0.83	> 0.05	1:1.11	> 0.05
August	1:0.44	< 0.005	1:1	> 0.05	1:1.23	> 0.05	1:1.16	> 0.05
September	1:0.94	> 0.05	1:0.77	> 0.05	1:0.45	< 0.05	1:1.18	> 0.05
October	1:0.5	< 0.05	1:0.77	> 0.05	1:0.65	> 0.05	1:1.02	> 0.05
November	1:0.23	< 0.001	1:0.48	< 0.05	1:1.2	> 0.05	1:0.72	> 0.05
December	1:0.5	< 0.05	1:0.68	> 0.05	1:0.5	> 0.05	1:0.76	> 0.05
Over all	1:0.78	< 0.005	1:0.77	< 0.05	1:1	> 0.05	1:0.92	> 0.05

Gonadosomatic index (GSI) of females having stage III and Stage IV

Different trends of monthly pattern for mean GSI of *S. olivacea* between two oceanic regions, Ranong province in the Indian Ocean, and Pattani province in the Pacific Ocean, were reported (Fig. 5), and significant differences of GSI among months from each region were found ($p < 0.05$). The GSI values ranged from $3.05 (\pm 1.97)$ to $10.97 (\pm 1.96)$ in Ranong province and $3.19 (\pm 1.72)$ to $10.52 (\pm 1.71)$ in Pattani province throughout the year, suggesting the possibility of multiple spawning events, with peaks observed during specific months. In Ranong province, the GSI exhibited a clear bimodal pattern, with lower values observed in January and March. The GSI remained consistently elevated from April to December with peak in June (10.97 ± 1.96) and April (9.08 ± 0.29). In Pattani province, the GSI exhibited a trimodal pattern, with peaks recorded in February (8.47 ± 0.44), June (8.48 ± 0.38), and August to November. These peaks were interspersed with declines observed in March (6.50 ± 0.40), July (5.50 ± 0.50), and December (5.24 ± 0.60). Notably, from August to November, the GSI showed a trend of increase, with no statistically differences among these months ($p > 0.05$).

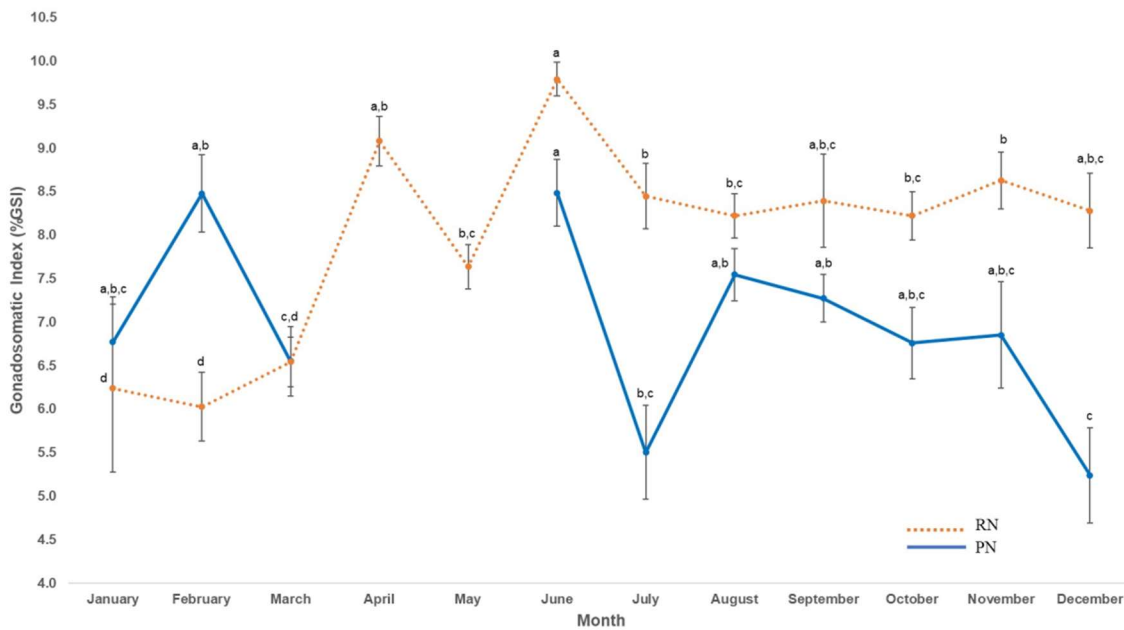


Fig. 5. Monthly variation of gonadosomatic index (mean $\pm$ SE) of *Scylla olivacea* collected from Ranong and Pattani during April 2022 to March 2023. Different letters (a, b, c) indicate significant differences between months as determined by a post hoc test ($p < 0.05$).

Relationship between BW, ICW, AW and OW with fecundity

The logarithmic relationship between body weight (BW), inter-carapace width (ICW), abdominal width (AW), and ovary weight (OW) with fecundity in female *S. Olivacea* from Ranong. Log-log regression revealed positive and significant relationships between fecundity and all morphometric traits ($p < 0.001$). Ovary weight showed the strongest correlation ($R^2 = 0.8905$; $n = 237$), with the equation: $\log(F) = -1.9865 + 0.5307 \cdot \log(OW)$ corresponding to $F = 0.0103 \cdot OW^{0.5307}$. Body weight showed a moderate relationship ($R^2 = 0.3898$; $n = 237$), while ICW and AW showed weaker correlations $R^2 = 0.1428$ and 0.1176 , respectively. Though all relationships remained statistically significant (Fig. 6).

The logarithmic relationship between body weight (BW), inter-carapace width (ICW), abdominal width (AW), and ovary weight (OW) with fecundity in female *S. Olivacea* from Pattani province. Log-log regression analysis revealed significant positive relationships between fecundity and all morphometric traits ($p < 0.001$). The strongest correlation was observed with body weight, described by the equation: $\log(F) = -0.9301 + 0.5473 \cdot \log(BW)$ ($R^2 = 0.7162$), corresponding to the power function $F = 0.117 \cdot BW^{0.5473}$. Ovary weight also showed a strong relationship ($R^2 = 0.6789$), with the equation: $\log(F) = -1.3039 + 0.4229 \cdot \log(OW)$, or $F = 0.0498 \cdot OW^{0.4229}$. Similarly, AW and ICW width exhibited moderately strong correlations $R^2 = 0.6579$ and 0.6059 respectively. (Fig. 7).

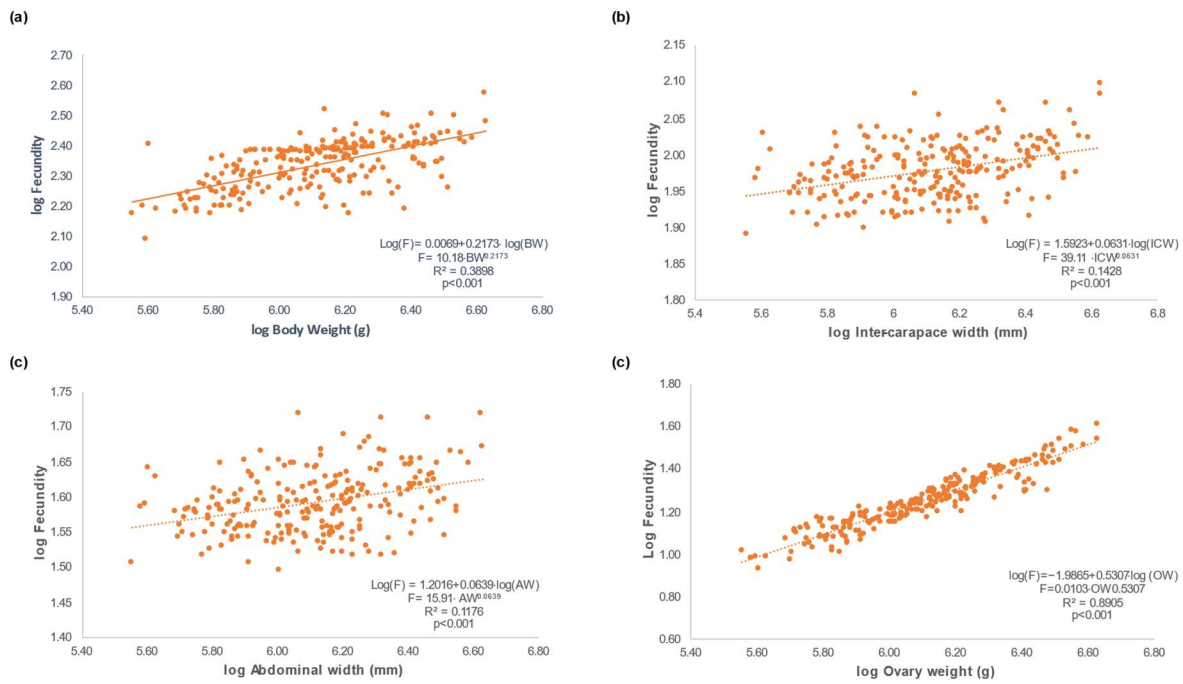


Fig. 6. The logarithmic relationship between (a) body weight, (b) inter-carapace width, (c) abdominal width and (d) ovary weight, and fecundity of female stage IV *S. olivacea* collected from Ranong during April 2022 to March 2023.

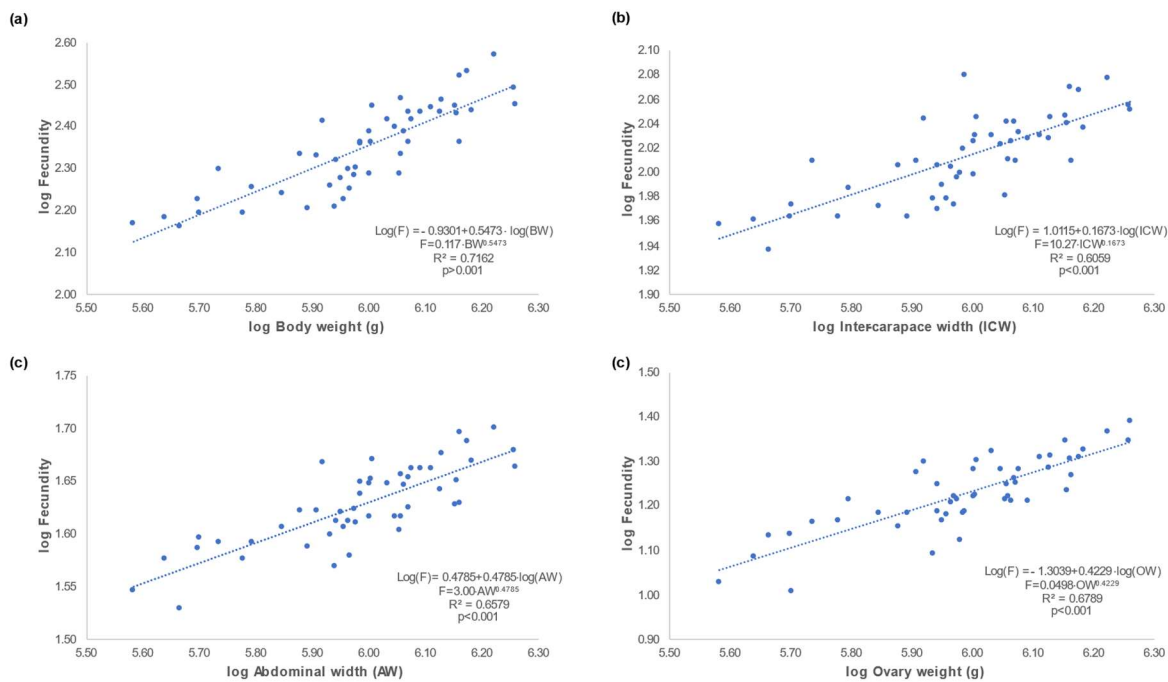


Fig. 7. The logarithmic relationship between (a) body weight, (b) inter-carapace width, (c) abdominal width and (d) ovary weight, and fecundity of female stage IV *S. olivacea* collected from Pattani during April 2022 to March 2023.

DISCUSSION

This study proved that the *S. olivacea* population from Ranong province, representing the Indian Ocean, exhibited smaller body sizes than those from the GoT, representing the Pacific

Ocean, yet demonstrated greater reproductive capacity. This is evidenced by their lower body weight but higher gonadosomatic index (GSI) and fecundity, indicating higher reproductive potential despite smaller physical dimensions. This finding aligns with previous reports on *S. olivacea* size variation across different oceanic regions. Female *S. olivacea* from Klong Ngao mangrove swamp, Ranong Province, Thailand, was earlier reported to have an average size of 79 mm (Jirapunpipat 2008), with carapace width range between 45–140 mm (Viswanathan et al. 2019). In contrast, studies from the Pacific Ocean indicated larger size ranges. For instance, female crabs from Sarawak, Malaysia, had a carapace width of 94.1 mm (Ikwanuddin et al. 2011), and those in Urado Bay, Japan was found between 70–140 mm (Ogawa et al. 2012). Similarly, Hamasaki et al. (2011) reported size ranges of 86–129 mm in the GoT.

Variation of size among populations is common in brachyuran crabs and normally influenced by a range of factors, including sex ratio, food availability, population health, fishing pressure, and genetic diversity (Waiho et al. 2016; Araujo and Lira 2012). The variation is also influenced by genetic factors and local environmental conditions, including food availability, habitat productivity, and fishing pressure (Araujo and Lira 2012; Fazhan et al. 2020), which may differ between regions. Additionally, smaller body size in certain species may be associated with other factors. A smaller crab tends to reach sexual maturity more rapidly and reproduce earlier, which can confer ecological advantages under specific environmental conditions (Fazhan et al. 2020). The observed size difference of *S. olivacea* population in this study may be linked to variation in fishing activities and the associated fishing pressure across different regions. Increased fishing intensity, particularly in heavily exploited areas, results in the selective removal of larger individuals, leading to a decrease in the average size of the population over time. This phenomenon is well documented in fisheries targeting brachyuran crabs, where high fishing pressure can cause a shift in size distribution towards smaller individuals (Walton et al. 2006). Thus, the region with intense fishing activity as in Ranong province, overharvesting of larger crabs may contribute to the smaller average sizes observed in the present study. There was a report on an intensive small-scale fishing with year-round activities such as crab gill netting and trap fishing in this province. The area has been recognized for high fishing intensity due to commercial and artisanal exploitation of coastal and estuarine resources (Moser et al. 2005). Food and Agriculture Organization (FAO 2020) categorized Ranong province in the Coastal Zone V of Thailand, predominantly occupied by small scale fisherman, and marine capture fisheries expanded rapidly in this region. The FAO also reported that resource depletion in this area is driven by factors such as declining seawater quality, increased use of more efficient fishing gear, and illegal fishing practices. These conditions may contribute to the overharvesting of larger individuals, leading to a shift in size structure toward smaller crabs in the population. This phenomenon has been documented in various crustacean

fisheries where size selective harvesting exerts evolutionary and ecological pressure, resulting in reduced average body size over time (Heino and Godø 2002; Sharpe and Hendry 2009). Therefore, the size differences observed in this study may reflect regional variation in ecological pressures and fishing intensity, which in turn influence growth patterns and reproductive strategies within *S. olivacea* populations.

Size at first maturity (SM_{50}) of female and male *S. olivacea* exhibits oceanic variation, with the larger individuals observed in the Pacific Ocean compared to the Indian Ocean. Specifically, SM_{50} values of female/male for *S. olivacea* in Pattani and Suratthani provinces within the GoT are 92.3/93.2 mm and 96.9/96.8 mm, respectively. These findings are consistent with the 91.2 mm ICW_{50} of *S. olivacea* reported by Overton and Macintosh (2002). Although Koolkalya et al. (2016) recorded a slightly larger ICW_{50} of 99.35 mm for *S. olivacea* in Trat province (GoT), this value remained smaller than those observed for *S. paramamosain* (111.67 mm) and *S. tranquebarica* (110.97 mm). Conversely, the present study's ICW_{50} values surpass those reported for female *S. olivacea* from the west coast of Peninsular Malaysia (89.0 mm; Ikwanuddin et al. 2014) and the Terengganu coastal waters, east coast of Peninsular Malaysia (90.6 mm; Ikhanuddin et al. 2010). For males, Waiho et al. (2016) documented a CW_{50} of 87.78 mm for *S. olivacea* in Malaysia's Setiu Wetlands, while Islam and Kurokura (2013) found an ICW_{50} of 108.2 mm for mature *S. paramamosain* males in Thailand's Pak Phanang mangroves. Such differences highlight size variations at maturity across habitats and species. Notably, *S. serrata* from Iriomote Island, Japan, reached sexual maturity at larger sizes, with female and male ECW_{50} values of 132.4 mm and 150.7 mm, respectively (Ogawa et al. 2011). In the Andaman coast, results from the investigation of *S. olivacea* populations from Ranong, Satun, and Trang provinces indicated the ICW_{50} of female/male were 78.0/83.1 mm, 64.0/79.2 mm, and 81.9/80.6 mm, respectively. These values are not only smaller than the individual from the GoT but also notably smaller than those previously reported for female *S. olivacea* in the Klong Ngoa Mangrove area, Ranong province, 94.00 mm (Koolkalya et al. 2006) and 95.5 mm (Jirapunpipat 2008). This finding thus suggests a substantial decline of approximately 17% in the size at first maturity for female *S. olivacea* from the Andaman Sea, Ranong province, between 2006 and 2023. Variations of size at first sexual maturity among aquatic organism populations can be attributed to differences in molting patterns and resource accessibility, as previously documented by Rasheed and Mustaqim (2010) and Jirapunpipat (2008). The timing of maturation is characterized by a plasticity, responding to fluctuations in environmental parameters. Factors such as temperature, salinity, and habitat quality have been identified as potential drivers of differences in maturation schedules (Roff 1983; Hunter 2005). While elevated temperatures can accelerate growth and consequently reduce size at first maturity, conversely, lower temperatures may decelerate growth, resulting in larger individuals at sexual maturation (Alberts-

Hubatsch 2015). Furthermore, the heightened vulnerability of smaller individuals to predation suggests that predation pressure can exert a significant influence on maturation patterns (Roff 1983). In the case of this study, given the minimal temperature difference between the Andaman Sea (27.4°C) and the GoT (27.5°C) as reported by the Thai Meteorological Department (2022), temperature is unlikely to be a primary determinant of the observed size disparities between these regions. Food availability is another critical factor influencing the size at first maturity in *Scylla* species. Abundant food resources can accelerate growth rates, leading to earlier attainment of reproductive maturity, while food scarcity can delay maturation and result in smaller adult sizes (Shelley and Lovatelli 2011; Djunaidah et al. 2003). However, those reports are based on captive studies and may not fully represent the complexities of natural populations as investigated by this present study.

Fishing pressure has been implicated in the evolution of earlier maturation at smaller sizes in several crustacean species, including mud crabs (Lestang et al. 2003; Moser et al. 2005; Hamasaki 2011; Ikhwanuddin et al. 2011; Olson et al. 2018; Mullowney and Baker 2021). This phenomenon is attributed to the disproportionate removal of larger, older individuals, thereby conferring a reproductive advantage to those maturing at smaller sizes (Hunter 2005). The theory of top-down intraspecific competition posits that reduced predation on smaller males, resulting from the removal of larger competitors through fishing, can further accelerate maturation at smaller sizes (Mullowney and Baker 2021). While smaller individuals are generally more susceptible to predation and competition, their reduced vulnerability to size selective fishing gear can contribute to the observed trend toward early maturation. The combined effects of fishing pressure and decreased abundance of large male can induce alterations in molting pattern and growth dynamics, including increased skip molting, which can ultimately lead to earlier and smaller male maturation (Mullowney and Baker 2021). Given the Andaman Sea's reputation as a significant mud crab fishing ground, it is plausible that these processes are contributing to smaller size at first maturity of *S. olivacea* population trends in the region. Consequently, implementing effective management strategies, such as size restrictions for female mud crabs during the spawning season, is imperative. It is suggested that different minimum allowable sizes of *S. olivacea* for each area shall be proposed viz., the ICW of 92.26 and 96.91 mm for Surat Thani and Pattani provinces, respectively and 78.0 mm, 64.02 mm, and 80.65 mm for Ranong, Satun, and Trang provinces, respectively. A comprehensive understanding of the regional variations in *Scylla* maturation is crucial for the development of robust conservation and management plans. Future research should focus on elucidating the ecological and genetic underpinnings of these differences to inform more effective conservation strategies. Sex ratio is a critical indicator of population structure and reproductive potential (Trindade-Santos and Freire 2015). Moreover, a skewed sex ratio may affect size structure

indirectly by altering competition dynamics or reflecting selective harvesting patterns (Pinheiro and Fransozo 2002; Hines 1982). This study revealed significant spatial temporal variation, with male-biased ratios in Ranong (1:0.78) and Satun (1:0.77), and more balanced ratios in Trang (1:1) and Pattani (1:0.92). In Ranong, male-biased ratios were especially pronounced in April, August, October, November, and December, likely reflecting offshore migration of gravid females during the monsoon season as a response to spawning needs and larval dispersal (Tongdee 2001; Koolkalya et al. 2006; Ikhwanuddin 2011; Moser and Macintosh, 2001). Female crabs may migrate away from estuarine environments due to their sensitivity to low salinity or to enhance larval survival (Hill 1994). This region experiences a pronounced Southwest Monsoon (May–October), which generates strong upwelling, increased freshwater input, and variable salinity in coastal waters (Kiran 2012). These factors could drive gravid females to migrate offshore to seek more stable salinity and temperature conditions for spawning. In contrast, the more stable and stratified environment of the GoT (Yanagi and Takao 2008) may reduce the need for such movement, contributing to the more balanced sex ratios in Pattani province. These findings align with similar observations from Setiu Wetlands, Malaysia (Ikhwanuddin et al. 2010 2011).

The gonadosomatic index (GSI) further illustrates regional reproductive differences. In the Andaman Sea, particularly Ranong, GSI values remained elevated from April to December, peaking in June, August, and September (> 9.5). This prolonged reproductive period aligns with the Southwest Monsoon season (May–October), characterized by enhanced rainfall, nutrient rich upwelling, and stable high salinity (31.5–33.0‰) (FAO 2003; DMR 2023). The year-round presence of all ovarian developmental stages further supports continuous reproductive activity in this region.

In contrast, reproductive activity in Pattani province (GoT) followed a more seasonally restricted pattern, with peaks in April–May and again from October to January. These periods coincide with transitional and Northeast Monsoon phases, during which significant freshwater influx reduces salinity (often to 25–30‰), increases turbidity, and enhances temperature variability (Pongtippatee et al. 2012; World Bank 2021). Continuous presence of all ovarian stages suggests prolonged spawning. In contrast, GSI of crab from Pattani province (GoT) displayed bimodal peaks (April–May, October–January), with greater sensitivity to environmental fluctuations such as freshwater influx and turbidity during the Northeast Monsoon season (Pongtippatee et al. 2012; World Bank 2021). These findings are in line with previous studies reporting regional variation in GSI trends of *S. olivacea*. Koolkalya et al. (2006) noted two reproductive peaks in the Andaman Sea (June and November), while Viswanathan et al. (2019) and Ali et al. (2020) reported bimodal peaks in southeast India and Bangladesh, respectively. However, the more extended reproductive season observed in Ranong province is likely supported by its relatively stable marine environment, in

contrast to the estuarine dominated GoT, which is heavily influenced by monsoon driven riverine discharge. The consistent salinity and ecological richness in the Andaman Sea promote more stable reproductive conditions, while the GoT's shallower, variable environment imposes constraints on reproductive success. Salinity, temperature, and food availability are key environmental drivers influencing reproductive rhythms, larval development, and physiology in *Scylla* spp. (Zohar and Mylonas 2001; Hamasaki 2002; He et al. 2010; Nurdiani and Zeng 2007). These oceanographic differences likely account for the spatial variability in reproductive traits observed between the two regions.

In Thailand, wild mud crab landings have fluctuated over the past decade, dropping from 2,905 tonnes in 2012 to only 282 tonnes in 2018, before recovering to 2,871 tonnes in 2021 (Lovatelli et al. 2025). Even though with shorter coastline compared to the GoT, the catch of wild mud crab from the Andaman Sea contributed larger proportion to the national catch accounting 57%, 61% and 55% of total catch in 2016, 2017 and 2021, respectively. These data suggest that fishing effort in the Andaman is persistently high, particularly in provinces such as Ranong and Satun. The predominance by artisanal fisheries in the Andaman coast where fishers relying on small scale gear such as crab gillnets, drift nets, and light purse seines (FAO 2020) may influence the catch of nearshore mud crab resources. Artisanal fishing practices, with less mechanized, can still exert considerable pressure on reproductive segments of the population. For instance, gravid females aggregating in mangrove channels during spawning seasons may be disproportionately captured by crab traps, potentially leading to shifts toward smaller body size and earlier reproductive maturation. These contrasting fishing practices may underlie the observed reproductive divergence with the population of *S. olivacea* in the Andaman Sea exhibit smaller body size and SM_{50} but comparable or higher fecundity and GSI. It supports the hypothesis that size selective harvesting and fishing intensity shape life history traits in mud crabs (Walton et al. 2006; Mullowney and Baker 2021).

It is obvious by this study that the fecundity found is approximately 1.4 million eggs per crab, slightly lower than the findings by Shelley and Lovatelli (2011) who have reported fecundity levels of around 2.0 million eggs for three *Scylla* spp. Koolkalya et al. (2006) documented pre-spawning fecundity of *S. olivacea* from the Andaman Sea, ranging from 1,229,472 to 4,787,967 eggs, with significant correlations between fecundity and ICW.

Pre-spawning fecundity of *S. olivacea* examined in this study was positively correlated with body weight (BW), internal carapace width (ICW), abdominal width (AW), and ovarian weight (OW). Viswanathan et al. (2019) further confirmed that fecundity of this species was related to ICW, CW, BW, and OW, highlighting the strong influence of these morphological variables on reproductive output.

A year-round presence of mature female *S. olivacea* in both the GoT and the Andaman Sea, with a minor exception in July, indicates a continuous breeding pattern for this species. This data provides a clear insight into the variations in gonad maturity across different regions and highlights the differences in maturity stages observed in each location. This finding aligns with prior research that similarly documented year-round reproductive activity in *S. olivacea* (Koolkalya et al. 2016; Jirapunpipat 2018; Paul et al. 2021; Islam et al. 2022). Furthermore, *S. paramamosain* and *S. tranquebarica* have also been observed to spawn throughout the year with two distinct peaks (Koolkalya et al. 2016). Similar reproductive patterns have been reported in other brachyuran crabs, such as *Leptodius exaratus* and *Portunus segnis*, where ovigerous or egg carrying females have been observed year-round (Fahimi et al. 2017; Rasheed and Mustaqim 2010; Safaie et al. 2013). The occurrence of mature crab throughout the year is considered continuous breeding, while the presence of mature crabs during only a few months is regarded as discontinuous or seasonal breeding, which is influenced by favorable environmental conditions during that period (Rasheed and Mustaqim 2010).

CONCLUSIONS

This study represents the first simultaneous assessment of reproductive traits of *S. olivacea* populations across both coasts of the Indian and Pacific oceans. The results revealed clear regional differences in body size, reproductive parameters, and seasonal reproductive patterns likely shaped by distinct oceanographic conditions and varying fishing pressures. Notably, crabs from the Andaman Sea, particularly in Ranong Province, had smaller body sizes but higher reproductive indices, including gonadosomatic index (GSI) and fecundity, compared to those from the GoT. These findings suggest that the minimum legal size for capturing female mud crabs be set above the highest observed size at maturity (SM_{50}) in the Andaman populations ideally at or above 82 mm to ensure that individuals have the opportunity to reproduce before harvest. Furthermore, seasonal fluctuations in the abundance of mature females indicate a pronounced reproductive peak in November and a significant decline in July, particularly along the Andaman coast. To enhance reproductive success and protect spawning stocks, seasonal closures or fishing effort reductions in July, coupled with targeted protection during peak reproductive months, are advised. Together, these recommendations highlight the importance of implementing spatially adaptive, ecosystem-specific management strategies. Establishing region specific minimum size limits and temporal protection measures will be essential to ensuring the long term sustainability of *S. olivacea* fisheries in Thailand.

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