



The reproductive biology of mangrove crab (*Neosarmatium smithi*) in Xuan Thuy National Park, Nam Dinh, Vietnam

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ABSTRACT

The results of the analysis of 458 samples of mangrove crab (*Neosarmatium smithi*) collected in areas where mangrove crab is distributed in the tidal zone with mangrove forests in Xuan Thuy Nam Dinh National Park from October 2022 to September 2023 showed that the spawning season of mangrove crab is from mid - April to early September, and is concentrated from early June to early August. In all months, the ratio of females to males is always dominant. The female/male ratio in the mangrove crab population averages 1.36 and ranges from 1.25–1.46. The onset of sexual maturity occurs when the carapace width (CW) of females exceeds 21 mm and that of males exceeds 24 mm. Absolute fecundity (Fa) ranged from 17,580–25,733 eggs/individual, averaging 21,571 eggs/individual. The larvae of the mangrove crab develop from zoea larvae with 5 sub - stages, and megalop larvae with 3 sub - stages. Our findings contribute information to the planning of the artificial seed production, conservation and sustainable development of the mangrove crab native resource.

Keywords: Mangrove crab, reproductive biology, spawning.

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Introduction

The mangrove crab (*Neosarmatium smithi*) is a species distributed in the intertidal mangrove forests. Studies have highlighted the ecological value of this species. Beyond its value as a food source, *N. smithi* plays a crucial role in mangroves through its burrowing activities, which aerate and loosen sediment, improve oxygen circulation, reshape topography, and influence particle-size distribution while trapping energy in the mangrove forest [1, 2]. Additionally, its burrowing creates microhabitats for other organisms, contributes to secondary production, increases nutrient availability, and reduces sediment sulfide concentrations [3, 4].

Due to their important role in mangroves, burrowing crabs are considered indicator species for the “health” of mangrove ecosystems [3]. Research has also shown that *N. smithi* is one of the key taxa contributing to species diversity and total biomass in mangrove systems. These crabs account for over 50% of the biomass of large animals [4, 5], giving them significant conservation value.

Xuan Thuy National Park features diverse ecosystems with distinct natural conditions, including intertidal mudflats with mangrove forests, intertidal mudflats without mangroves, and sand dunes [6]. Among these, the intertidal zones with mangrove forests exhibit high biodiversity, hosting various species, including *N. smithi*, which is considered endemic to this region. However, studies on *N. smithi* in Vietnam remain limited, even though wild populations are increasingly depleted due to overexploitation, often involving destructive harvesting methods. Therefore, a deeper understanding of this species is necessary to support conservation and resource management efforts.

Research methods

Materials, time, and research location

A total of 458 *N. smithi* individuals were collected across five size groups based on carapace width (CW): < 10, 10–20, 21–30, 31–40, and > 40 mm. Samples were gathered monthly during spring tides at sites where the species

naturally occurred, with 30 to 50 individuals collected per sampling event.

Egg-carrying females were separated and preserved in plastic containers containing 10% formalin solution. Non-ovigerous individuals were packed in labeled polyethylene bags and stored in iceboxes for transport to the laboratory for analysis. The collected crabs were classified, identified to species level, and sexed. Biological parameters were measured, and species composition ratios within the samples were calculated. Sampling for reproductive biology analysis took place from October 2022 to September 2023. The sampling sites were located in the intertidal zones with mangrove forests at Xuan Thuy National Park, at 20°10'–20°18'N and 106°28'–106°37'E.

Research methods

Identification: Specimens were identified based on the classification documents of Carpenter et al. [5]. Individual size was measured with a Vernier caliper with an accuracy of 0.05 mm. Body weight and gonads were determined using an electronic scale (Adam/AQT - 200 of England with an accuracy of 0.1 g).

Sex: Determined based on the morphological characteristics of the gonads in the abdomen. Males have 2 genital openings located at the base of the 5th pair of legs and a short penis attached to them. Females have 2 genital openings located at the base of the 3rd pair of legs. In pre - sexually mature females, the abdomen (plaque) is slightly square in shape. When mature, the plaque becomes wide with 6 normal segments; males have a narrow V - shaped plaque, with only segments 1, 2 and 6 clearly visible, while segments 3, 4 and 5 are connected to each other.

Determination of fecundity: Fecundity is determined by the method of removing all the eggs of the crab from the abdomen (bib) and then weighing (weighing accurately to 0.01 g) and counting under a microscope (Nikon Eclipse E 400) [7, 8]. The fecundity absolute of crab is calculated as follows:

$F_a = n(W/\bar{w})$, in which F_a is the fecundity absolute, n is the number of eggs in the sample, and W is the total weight of the eggs of the individual and \bar{w} is the average weight of the eggs.

Fecundity relative (Frg): is the ratio between fecundity absolute and total body weight or ovarian mass calculated by:

$Frg1 = Fa/Wtt$; $Frg2 = Fa/Wbt$, in which $Frg1$ = Fecundity relative calculated by total body weight, $Frg2$ = Fecundity relative calculated by ovarian mass, and Wtt = Whole body weight and Wb = Ovary weight. Determination of reproductive season stages, sex ratio, size at first sexual maturity, and fecundity was conducted based on references on other crustacean species. Stages of gonadal development in males and females according to M. A. A. Pinheiro & A. Fransozo (1998); F. L. M. Mantelatto & A. Fransozo (1996); R. B. Ituarte, E. D. Spivak & T. A. Luppi (2004) [8–11].

Reproductive season: The gonadal development of *N. smithi* was observed through monthly sampling to determine the occurrence and quantity of sexually mature individuals.

Sex ratio: The sex ratio was determined by observing gonadal morphology and counting male and female individuals from random samples collected during each sampling event.

Size at first sexual maturity: This parameter was determined for the smallest size group (CW) in which over 50% of individuals in the population had gonads at stage III or higher, based on graphical analysis [10].

Morphological studies were conducted using a stereomicroscope. High - resolution digital photographs were taken to provide clearer visual evidence of external morphological characteristics. Carapace width (CW) was measured at the widest point from the anterior to the posterior margins, while carapace length was measured from the front to the most posterior point of the carapace. Measurements were taken with calipers to an accuracy of 0.01 mm.

Data processing

Data are expressed as mean \pm standard error using the Descriptive Statistics tool to analyze data on Microsoft Office EXCEL 2007.

Results

*Male and Female Morphology and Sex Ratio of *N. smithi* in the Study Area*

*Male and Female Morphology of *N. smithi**

Male and female *N. smithi* can be easily distinguished by several external morphological characteristics (Fig. 1):



Figure 1. Morphology of male and female *Neosarmatium smithi*

Characteristics of the male's mating legs: The male gonopods (copulatory appendages) are slender, densely covered with setae at the tip, and the chitinous terminal end is not pointed. The sixth abdominal segment is longer than its width. The second and third pairs of walking legs are equal in length and longer than the other pairs. The longest gonopod is approximately 1.7 times the carapace width. The third leg segment is 2.2–2.5 times longer than its width.

Characteristics of the female abdomen: The female abdomen consists of seven segments and has four pairs of pleopods, each divided into an inner and outer branch. The inner branch functions to hold the eggs, which attach to setae on this branch. Each inner branch has two rows of setae extending from the base to the tip, with about 24 to 25 rows

per branch and 5 to 7 setae per row. Each setae can carry approximately 100 to 110 eggs.

In females, there are four pairs of abdominal appendages, each with a biramous structure consisting of a basal segment and two branches. The inner branch serves to hold the eggs, while the outer branch provides protection. In males, the first and second pairs of abdominal appendages are modified into copulatory appendages, while the remaining appendages are reduced.

Sex Ratio of *N. smithi*

Observations of the sex ratio of *N. smithi* showed that the female - to - male ratio across months averaged 1.36 and ranged from 1.25 to 1.46. The monthly sex ratio of the population throughout the year is presented in Figure 2.

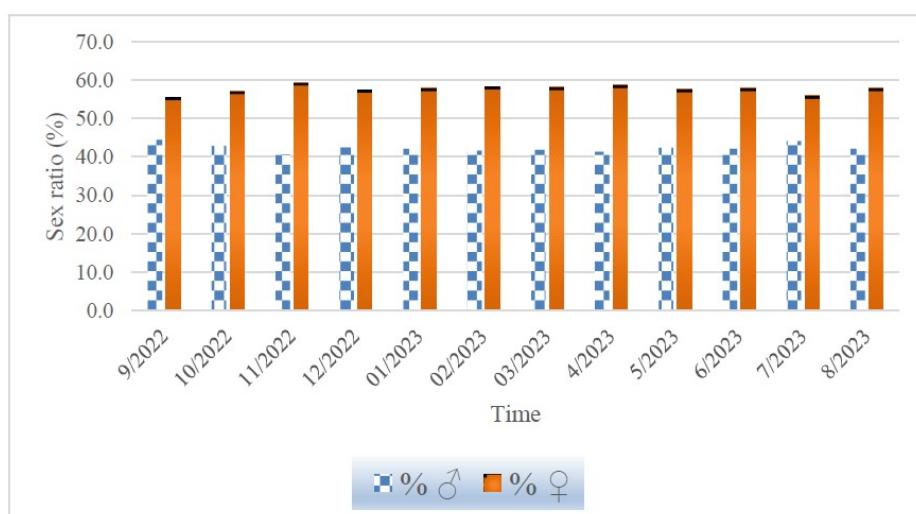


Figure 2. Sex ratio of *Neosarmatium smithi*

Throughout the year, females predominated in the population. In all size groups, the female

proportion consistently exceeded that of males, particularly in the smaller size groups.

Table 1. Sex ratio of *Neosarmatium smithi* in size groups

| Size group (mm) | TotalInd | Males | | Females | |
|-----------------|----------|-----------------|-----------|-----------------|-----------|
| | | Quantity of ind | Ratio (%) | Quantity of ind | Ratio (%) |
| < 10 | 89 | 41 | 46.07 | 48 | 53.93 |
| 10–20 | 114 | 48 | 42.11 | 66 | 57.89 |
| 21–30 | 114 | 45 | 39.47 | 69 | 60.53 |
| 31–40 | 85 | 38 | 44.71 | 47 | 55.29 |
| > 40 | 56 | 22 | 39.29 | 34 | 60.71 |

The sex ratio in different size groups showed a persistent trend of female dominance. Smaller - sized groups exhibited a higher female - to - male ratio, indicating potential sex - based differences in growth, survival, or sampling bias (Table 1).

The carapace width (CW) of female *N. smithi* ranged from 9.2 to 44.5 mm, while males ranged from 8.1 to 42.3 mm. In the smaller size groups, females were less frequently encountered compared to larger size groups. These findings differ significantly from the results reported by Conde et al. (2000) [12] in a study of *Aratus*

pisonii populations in the Bertioga estuary, São Paulo, Brazil, where the female - to - male ratio ranged from 1.15 to 1.168.

Reproductive season and size at first maturity of *Neosarmatium smithi*

Reproductive season

Based on descriptions by Ituarte et al. (2004) [10] and observations of gonadal morphology, the gonadal development of *N. smithi* progresses through five stages:

| Stages | Description | |
|--------|--|---|
| | Females | Male |
| I | Undeveloped, not visible | Undeveloped, not visible |
| II | Filamentous and transparent | The sas deferens very thin and orange - yellow in color |
| III | Ovaries still small, bright orange, eggs begin to appear | The vas deferens is clearly visible, color ranges from brown to transparent |
| IV | Ovaries occupy a large space, reddish-brown with distinct oocytes | Partially twisted testes ,white |
| V | Gonads dark red to brown; occupy larger volume than hepatopancreas | Testes enlarged and become bright white |

The reproductive season of *N. smithi* was determined by observing the number of sexually mature individuals (at stage III or higher).

The proportion of *N. smithi* individuals with mature gonads increased from March, reached its peak in June, and then gradually declined in the following months. In November and December, the proportion of sexually mature individuals was relatively low. The development of gonads appeared to be strongly influenced by temperature and nutrient availability. As temperatures began to rise in March, *N. smithi* accumulated energy and initiated sexual maturation. From April onwards, the percentage of sexually mature individuals reached 72.1% (Fig. 3).

These observations indicate that *N. smithi* is capable of reproducing year - round, with a primary breeding season at Xuan Thuy National Park occurring from April to September. The peak reproductive period spans from early June to late July, after which the proportion of mature individuals rapidly declines from August onwards. These findings provide critical insights

for establishing artificial breeding programs, as well as for conservation and resource management. Limiting the harvest of *N. smithi* during the peak reproductive season would allow natural reproduction to sustain the population, contributing to long-term ecological balance and resource preservation.

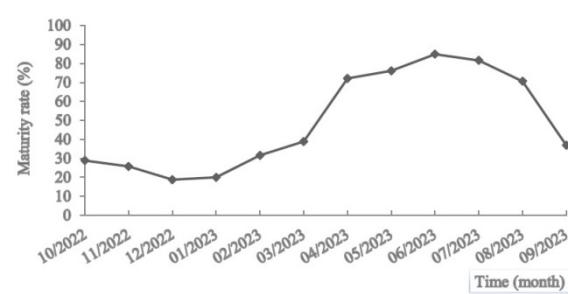


Figure 3. Maturity rate of *Neosarmatium smithi*

Size at first maturity

The size at first maturity was determined as the smallest size group in which over 50% of

individuals reach maturity (gonads at stage III or higher) during the reproductive season (Fig. 4).

The results showed that the first maturity size for male *N. smithi* was observed in individuals with a carapace width (CW) of 24 mm or larger. In contrast, females reached maturity at a smaller size, with the first mature individuals found in the 21 mm or larger size group. These findings differ significantly from those reported by Carlos Lutilo (2005) [13] in a study on *N. meinerti* in the mangrove forests of Inhaca Island, northern Mozambique, where

males reached maturity at a CW greater than 17 mm, and females at a CW greater than 15 mm. In the studied population, females also reached maturity at a smaller size than males. This result provides a scientific basis for rational exploitation and sustainable use of *N. smithi* populations. To support conservation and natural stock replenishment, harvesting individuals with a CW smaller than 20 mm should be avoided, allowing them to participate in reproduction and contribute to population regeneration in the wild.

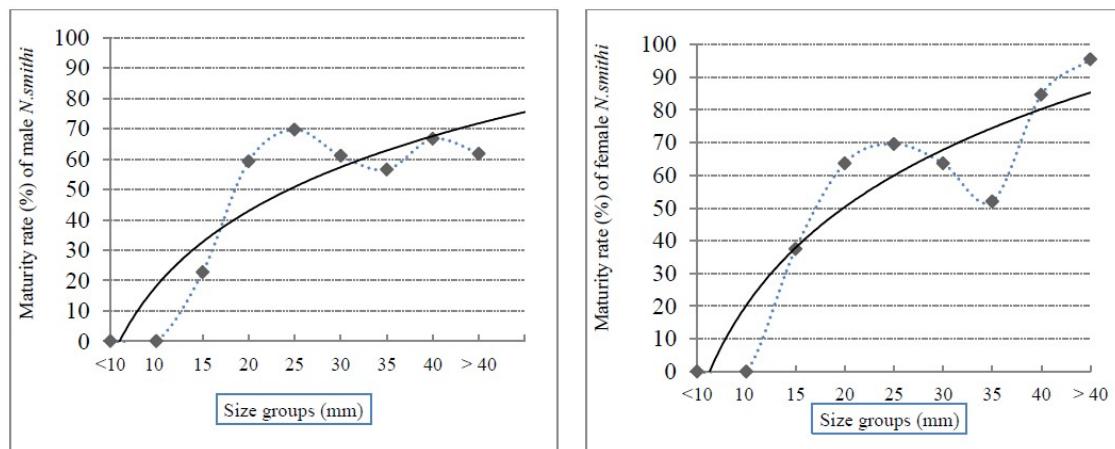


Figure 4. Size at first maturity of *Neosarmatium smithi*

Fecundity of *Neosarmatium smithi*

Fecundity of *N. smithi* is shown in Table 2.

Table 2. Fecundity of *Neosarmatium smithi*

| Value | Size (mm) | Fecundity | | |
|----------------|-----------|--------------------------------|-----------------------------|-------|
| | | Fecundity absolute - Fa (eggs) | Fecundity relative (eggs/g) | |
| | | | Frg1 | Frg2 |
| Mean | 35.7 | 21,571 | 1,173 | 3,915 |
| Standard error | 9.1 | 4,079 | 215 | 733 |
| Min | 25.8 | 17,580 | 1,038 | 3,388 |
| Max | 43.8 | 25,733 | 1,421 | 4,752 |

Fecundity absolute (Fa) of *N. smithi* ranged from 17,580 to 25,733 eggs per individual, with an average of 21,571 eggs per individual. Fecundity relative calculated based on total body weight (Frg1), averaged 1,173 eggs per gram. Meanwhile, fecundity relative based on ovary weight (Frg2) averaged 3,915 eggs per gram. These findings provide essential insights for artificial breeding programs, helping to

optimize broodstock selection and manage the number of berried females required according to hatchery capacity.

Larval development stages of *Neosarmatium smithi*

Neosarmatium smithi undergoes a series of larval metamorphoses, beginning with the zoea

stage, which consists of five substages (Zoea 1 to Zoea 5). This is followed by the megalopa stage, which has three substages (Megalopa 1 to Megalopa 3), before transitioning into the juvenile crab stage. Figure 5 illustrates several key stages of *N. smithi* larval development.

Similar to most species in the infraorder Brachyura, the mating process of *N. smithi* occurs immediately after the female molts, while her exoskeleton is still soft. During this time, the male copulates with the female, transferring sperm for fertilization. The female

has the ability to store sperm for extended periods before using it to fertilize her eggs. After fertilization, the eggs are carried under the female's abdomen, protected by the abdominal flap. Embryonic development takes place while the eggs are attached to the mother's abdomen, ensuring the offspring are well-guarded until hatching. Upon hatching, the larvae emerge as free-swimming Zoea, which drift with currents. At this stage, they begin feeding externally, marking the start of their independent development in the aquatic environment.

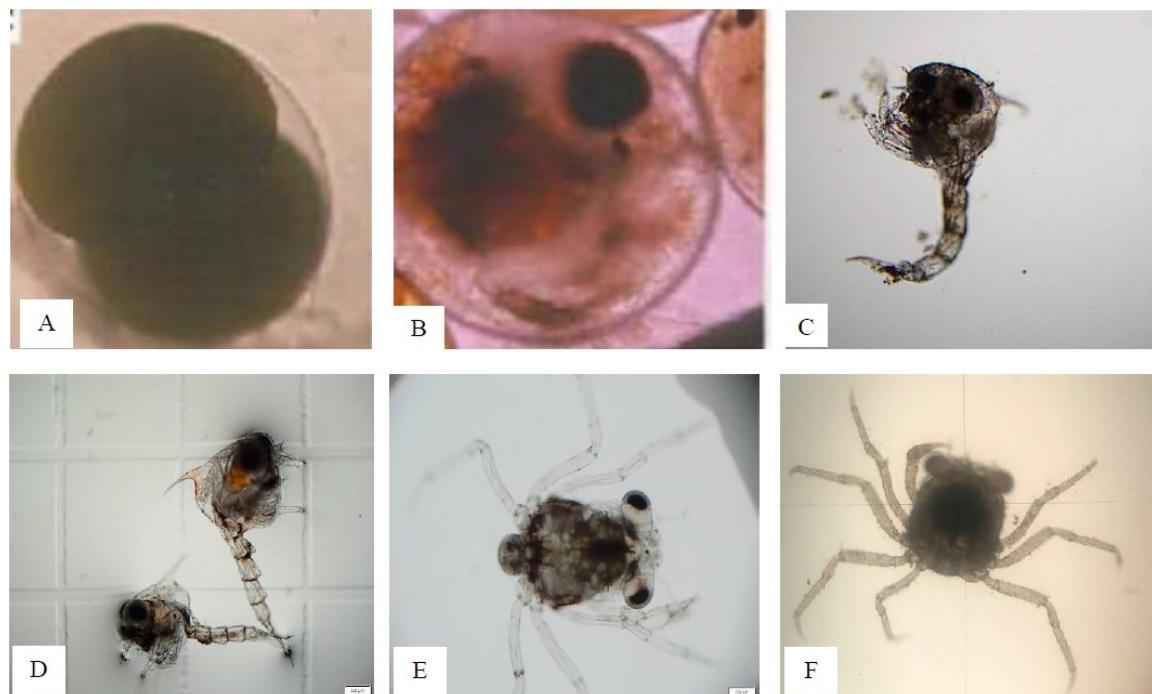


Figure 5. Developmental Stages of *Neosarmatium smithi* Larvae. Notes: A: Fertilized egg; B: Egg ready to hatch; C: Zoea 1 stage; D: Zoea 5 stage; E: Megalopa stage; F: Juvenile stage

Discussion

The results showed that the sex ratio of *N. smithi* in Xuan Thuy National Park consistently favored females, which aligns with the general pattern observed in many Sesarmidae species inhabiting mangrove ecosystems, where environmental factors and habitat-related behavioral differences may affect the two sexes differently [14, 15]. The predominance of females, particularly in the smaller size classes, suggests a strong potential for population

replenishment and may reflect a high recruitment rate during early life stages [16–18].

The reproductive season extending from April to September, with a peak between June and July, corresponds well with observations in other tropical mangrove crabs whose reproductive activities are largely driven by temperature, salinity, and tidal cycles [19]. The increase in the proportion of mature individuals from March onward indicates early energy accumulation, which is characteristic of seasonal reproductive patterns reported in

Grapsidae species [20–23]. This highlights the adaptive capacity of *N. smithi* to the pronounced seasonal hydro-environmental fluctuations typical of Xuan Thuy National Park.

The size at first maturity recorded for females (≥ 21 mm CW) and males (≥ 24 mm CW) was higher than that reported for closely related species in Mozambique [24]. Such differences may be associated with variations in food availability, population density, and fishing pressure between regions. These findings provide a scientific basis for establishing minimum harvestable sizes to ensure reproductive capacity, particularly given the increasing exploitation of mangrove crab resources [25–27].

The absolute fecundity of *N. smithi*, ranging from 17,580 to 25,733 eggs per female, is comparable to that of medium-sized mangrove crabs [28]. The relatively stable fecundity values within the population suggest an efficient reproductive output that supports natural recruitment even under seasonally fluctuating nutrient conditions. The similarity of relative fecundity (based on body and ovary weight) to that of other Sesarmidae species further indicates that *N. smithi* is a suitable candidate for broodstock selection in artificial seed production programs.

Larval development through five *Zoea* stages and three *Megalopa* stages conforms to the typical life-history pattern of Brachyuran crabs [29]. Each developmental stage is associated with specific ecological requirements, particularly regarding salinity and food availability. This underscores the need for hatchery protocols to account for environmental fluctuations when rearing larvae under artificial conditions.

Overall, the findings demonstrate that *N. smithi* exhibits adaptive reproductive characteristics and strong population renewal potential under natural conditions in Xuan Thuy National Park. These results provide an essential basis for recommending restrictions on harvesting during the peak breeding season, establishing minimum harvest sizes, and selecting appropriately sized broodstock for seed production. The dataset also contributes valuable information for designing conservation measures and sustainable management strategies for the local mangrove crab resources [30].

Conclusion

Throughout the year, the female *N. smithi* population consistently outnumbered the males, with an average female - to - male ratio of 1.36, ranging from 1.25 to 1.46 across different months. The first maturity was observed when the carapace width (CW) reached: Females: Over 21 mm; Males: Over 24mm. Fecundity parameters were recorded as follows: Fecundity absolute (Fa) ranged from 17,580 to 25,733 eggs per individual, with an average of 21,571 eggs per individual. Fecundity relative by body weight (Frg1) averaged 1,173 eggs per gram of body weight. Fecundity relative by ovary weight (Frg2) averaged 3,915 eggs per gram of ovary weight.

The larval development of *N. smithi* progresses through distinct stages: The *Zoea* stage consists of five sub-stages. The *Megalopa* stage consists of three sub - stages, eventually transitioning into juvenile crabs. These findings provide a scientific foundation for developing artificial breeding programs, protecting, and ensuring the sustainable management of *N. smithi* populations in the local mangrove system.

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References

- [1] T. J. Smith III, K. G. Boto, S. D. Frusher, and R. L. Giddins, “Keystone species and mangrove forest dynamics: The influence of burrowing by crabs on soil nutrient status and forest productivity,” *Estuarine, Coastal and Shelf Science*, vol. 33, no. 5, pp. 419–432, 1991. DOI: 10.1016/0272-7714(91)90081-L.

[2] S. Y. Lee, "Ecological role of grapsid crabs in mangrove ecosystems: A review," *Marine and Freshwater Research*, vol. 49, no. 4, pp. 335–343, 1998. DOI: 10.1071/mf97179.

[3] M. W. Skov and R. G. Hartnoll, "Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves?," *Oecologia*, vol. 131, no. 1, pp. 1–7, 2002. DOI: 10.1007/s00442-001-0847-7.

[4] E. C. Ashton, "Mangrove sesarmid crab feeding experiments in Peninsular Malaysia," *Journal of Experimental Marine Biology and Ecology*, vol. 273, no. 1, pp. 97–119, 2002. DOI: 10.1016/s0022-0981(02)00140-5.

[5] K. E. Carpenter and V. H. Niem, *The living marine resources of the Western Central Pacific: 2. Cephalopods, crustaceans, holothurians and sharks*, 1998.

[6] N. X. Thanh, "The reproductive biology of hard clam (*Meretrix meretrix*) in the intertidal zone of Nam Dinh Province," *Vietnam Journal of Marine Science and Technology*, vol. 13, no. 4, pp. 357–364, 2013. [in Vietnamese].

[7] M. H. de Arruda Leme, "A comparative analysis of the population biology of the mangrove crabs *Aratus pisonii* and *Sesarma rectum* (Brachyura, Grapsidae) from the north coast of São Paulo State, Brazil," *Journal of Crustacean Biology*, vol. 22, no. 3, pp. 553–557, 2002. DOI: 10.1651/0278-0372(2002)022[0553:ACAOTP]2.0.CO;2.

[8] M. A. A. Pinheiro and A. Fransozo, "Sexual maturity of the speckled swimming crab *Arenaeus cribrarius* (Lamarck, 1818) (Decapoda, Brachyura, Portunidae), in the Ubatuba littoral, São Paulo State, Brazil," *Crustaceana*, vol. 71, no. 4, pp. 434–452, 1998.

[9] F. L. M. Mantelatto and A. Fransozo, "Size at sexual maturity in *Callinectes ornatus* (Brachyura, Portunidae) from the Ubatuba region (SP), Brazil," *Nauplius*, vol. 4, pp. 29–38, 1996.

[10] R. B. Ituarte, E. D. Spivak, and T. A. Luppi, "Female reproductive cycle of the Southwestern Atlantic estuarine crab *Chasmagnathus granulatus* (Brachyura, Grapoidea, Varunidae)," *Scientia Marina*, vol. 68, no. 1, pp. 127–137, 2004.

[11] N. X. Thanh and D. C. Thung, "The reproductive biology of lyrate Asiatic hard clam (*Meretrix lyrata*) in the intertidal zone of Nam Dinh Province," *Vietnam Journal of Marine Science and Technology*, vol. 14, no. 2, pp. 163–169, 2014. [in Vietnamese].

[12] H. Díaz and J. E. Conde, "Population dynamics and life history of the mangrove crab *Aratus pisonii* (Brachyura, Grapsidae) in a marine environment," *Bulletin of Marine Science*, vol. 45, no. 1, pp. 148–163, 1989.

[13] C. Litulo, "Size at sexual maturity in the red mangrove crab *Neosarmatium meinerti* (De Man, 1887) (Brachyura: Grapsidae)," *Western Indian Ocean Journal of Marine Science*, vol. 4, no. 2, pp. 207–210, 2005. DOI: 10.4314/wiojms.v4i2.28489.

[14] F. Dahdouh-Guebas, M. Verneirt, J. F. Tack, and N. Koedam, "Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves," *Hydrobiologia*, vol. 347, no. 1, pp. 83–89, 1997. DOI: 10.1023/A:1003015201186.

[15] J. E. Conde, M. M. P. Tognella, E. T. Paes, M. L. G. Soares, I. A. Louro, and Y. S. Novelli, "Population and life history features of the crab *Aratus pisonii* (Decapoda: Grapsidae) in a subtropical estuary," *Interciencia*, vol. 25, no. 3, pp. 151–158, 2000.

[16] R. L. Giddins, J. S. Lucas, M. J. Neilson, and G. N. Richards, "Feeding ecology of the mangrove crab *Neosarmatium smithi* (Crustacea: Decapoda: Sesarmidae)," *Marine Ecology Progress Series*, vol. 33, pp. 147–155, 1986.

[17] S. Baklouti, O. Hamida, and O. Jarboui, "Reproductive biology of the spider crab *Maja squinado* (Herbst, 1788) (Decapoda: Majidae) in the Gulf of Gabès (Tunisia, Central Mediterranean)," *Cahiers de Biologie Marine*, vol. 56, no. 4, pp. 337–347, 2015.

[18] D. P. Gillikin, S. De Grave, and J. F. Tack, "The occurrence of the semi-terrestrial shrimp *Merguia oligodon* (De Man, 1888) in *Neosarmatium smithi* H. Milne Edwards, 1853 burrows in Kenyan mangroves," *Crustaceana*, vol. 74, no. 5, pp. 505–507, 2001.

[19] S. Fratini, S. Cannicci, and M. Vannini, "Competition and interaction between *Neosarmatium smithi* (Crustacea: Grapsidae) and *Terebralia palustris* (Mollusca: Gastropoda) in a Kenyan mangrove," *Marine Biology*, vol. 137, no. 2, pp. 309–316, 2000. DOI: 10.1007/s002270000344.

[20] E. C. Ashton, P. J. Hogarth, and R. Ormond, "Breakdown of mangrove leaf litter in a managed mangrove forest in Peninsular Malaysia," *Hydrobiologia*, vol. 413, pp. 77–88, 1999. DOI: 10.1023/A:1003842910811.

[21] T. Luppi, E. Spivak, and K. Anger, "Postsettlement growth of two estuarine crab species, *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Crustacea, Decapoda, Grapsidae): laboratory and field investigations," *Helgoland Marine Research*, vol. 55, no. 4, pp. 293–305, 2002. DOI: 10.1007/s10152-001-0088-5.

[22] M. A. A. Pinheiro and A. Fransozo, "Reproduction of the speckled swimming crab *Arenaeus cribrarius* (Brachyura: Portunidae) on the Brazilian coast near 23°30' S," *Journal of Crustacean Biology*, vol. 22, no. 2, pp. 416–428, 2002. DOI: 10.1651/0278-0372(2002)022[0416:ROTSSC]2.0.CO;2.

[23] M. L. Negreiros-Fransozo, A. Fransozo, and G. Bertini, "Reproductive cycle and recruitment period of *Ocypode quadrata* (Decapoda, Ocypodidae) at a sandy beach in southeastern Brazil," *Journal of Crustacean Biology*, vol. 22, no. 1, pp. 157–161, 2002. DOI: 10.1651/0278-0372(2002)022[0157:RCARPO]2.0.CO;2.

[24] S. Sarker, M. Hossain, and H. Takeoka, "Seed production and restocking potential of mangrove crabs in Okinawa," *Journal of Crustacean Research*, vol. 31, no. 3, pp. 225–233, 2012.

[25] M. A. A. Pinheiro and A. G. Ficarelli, "Length-weight relationship and condition factor of the mangrove crab *Ucides cordatus* (Linnaeus, 1763) (Crustacea, Brachyura, Ucididae)," *Brazilian Archives of Biology and Technology*, vol. 52, pp. 397–406, 2009. DOI: 10.1590/s1516-8913200900200017.

[26] M. S. Islam and S. Shokita, "Effects of salinity and temperature on larval development of *Neosarmatium trispinosum*," *Fisheries Science*, vol. 68, no. 2, pp. 409–412, 2002.

[27] D. Mann, T. Asakawa, and M. Pizzutto, "Development of a hatchery system for larvae of the mud crab *Scylla serrata* at the Bribie Island Aquaculture Research Center," in *Mud Crab Aquaculture and Biology*, C. P. Keenan and A. W. Blackshaw, Eds., ACIAR Proceedings No. 78, Brisbane: Watson Ferguson & Co., pp. 153–158, 2023.

[28] Y. Nakanishi, T. Matsutani, K. Hinokidani, T. Nagai, and M. Irie, "A role of a herbivorous crab, *Neosarmatium smithi*, in dissolved iron elution from mangrove ecosystems," *Tropics*, vol. 28, no. 4, pp. 91–97, 2020. DOI: 10.3759/tropics.ms19-06.

[29] D. P. Gillikin, S. De Grave, and J. F. Tack, "The occurrence of the semi-terrestrial shrimp *Merguia oligodon* in *Neosarmatium smithi* burrows," *Crustaceana*, vol. 74, no. 5, pp. 505–507, 2001.

[30] E. Kristensen, S. Bouillon, T. Dittmar, and C. Marchand, "Organic carbon dynamics in mangrove ecosystems: A review," *Aquatic Botany*, vol. 89, no. 2, pp. 201–219, 2008. DOI: 10.1016/j.aquabot.2007.12.005.