Mangrove Clam Genus *Geloina*: A Comprehensive Review of Biology

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ABSTRACT

The mangrove clam or mud clam genus *Geloina* is a vital component of tropical mangrove ecosystems, significantly contributing to their biodiversity. *Geloina* species display remarkable tolerance, enabling them to thrive across a broad spectrum of salinity levels. They are found in muddy, brackish, and even nearly freshwater regions within mangrove swamps. Mangrove clam *Geloina* possesses favorable characteristics for marine culture, as they are easy to cultivate. Due to their unique ecological attributes, *Geloina* clams emerge as objective species for fostering eco-friendly aquaculture. However, environmental factors affecting *Geloina* species must be considered at all time. The spawning activities of *Geloina* clams occure almost year around in tropical countries. With broodstock shell lengths of 68.61 and 58.63 mm, the estimated fecundity of *Geloina* clams ranged from 0.3185×10^6 to 4.416×10^6 oocytes. However, larval survival rate is compromised due to many environmental factors. Therefore, the life cycle and growth performance of mangrove clams should be focal points in upcoming studies to explore efficient techniques for seed production and aquaculture practices. This article also addresses these ecological challenges by comprehensively examining the natural science related to *Geloina* species, focusing on Southeast Asia with Vietnam as a primary focal point. Furthermore, in the strategy towards sustainable resource management, this review also discusses the incorporation of the biological characteristics of *Geloina* species into extractive aquaculture practices. The information regarding maturation, spawning of broodstock, and specific biological conditions for mangrove clams from this review is valuable for the resource management and aquaculture practices.

Keywords: Biology, Distribution, Environment, *Geloina*, Mud clam

INTRODUCTION

Mangrove clams, also known as mud clams, belong to the genus *Polymesoda* or *Geloina* and are widely distributed in the Indo-Pacific region (Idris *et al*., 2017). This species is collected through both commercial and artisanal means by inhabitants of tropical and subtropical regions. It serves as a significant protein source and is highly regarded as a delicacy within numerous communities (Clemente and Ingole, 2009; Argente *et al*., 2014; Sarong *et al*., 2015). Studies have shown that *Geloina* species are deep-burrowing bivalves, living semi-infaunally in soft sediments, with adults are usually occupying the landward side and being most abundant during high tides. Juveniles are available throughout tides and when algae are present (Clemente and Ingole, 2011; Idris *et al*., 2017). These clams feed by filtering suspended particles from the water, thereby cleaning the system (Elvira and Jumawan, 2017). The availability of food and other significant parameters in the water column corresponds with physiological process that trigger growth in this species (Sahin *et al*., 2006). Moreover, research has indicated a connection between the condition index and gonadal somatic index, which directly responds to the availability of algae for mangrove clams (Clemente and Ingole, 2009; Rahim *et al*., 2012).

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The sex of both young spats and adult clams *Geloina coaxans*, is easily distinguishable based on the well-developed features of their gonads (Quach and Ngo, 2011; Ngo *et al*., 2019b). There is no outward organ that differentiates the genders; instead, differentiation is typically based on visual and color distinctions of the gonads, especially in specimens under 34 mm in length within *G. erosa* (Clemente and Ingole, 2011). *Geloina* species display remarkable tolerance, enabling them to thrive across a broad spectrum of salinity levels. They are found in muddy, brackish, and even nearly freshwater regions within mangrove swamps, however, their habitat is threatened by large-scale destruction (Morton, 1976). In Vietnam, they are also found in estuarine tidal flats in the Mekong Delta, where they can tolerate water salinity fluctuations. For instance, *Geloina* sp., is found in the U Minh Thuong district of Kien Giang province in the southern region of Vietnam's Mekong Delta (Ngo *et al*., 2019b).

Globally, mangrove ecosystems are undergoing functional alterations due to factors such as diminishing forest coverage, shifts in land use, sediment accumulation, and unauthorized logging (Redjeki *et al*., 2020). This has impacted the population structure of benthic organisms, especially *Geloina* sp. and other economically important species (Clemente and Ingole, 2011). Historically, mangrove forests have been destroyed at a rate of 3.6% yearly (Valiela *et al*., 2001), but the rate has recently been reduced to 0.2–0.7% annually (Hamilton and Casey, 2016; Friess *et al*., 2019). However, about 50% of the global mangrove forest area is in Southeast Asia (Friess *et al*., 2019), where more than half of the mangrove habitat has been lost due to the transformation of forests into aquaculture and rice fields (Bryan-Brown *et al*., 2020). In Vietnam, mangrove habitat destruction continues at a rate of 0.25% (Clemente and Ingole, 2011). The diminishing mangrove forest expanse in Indonesia significantly impacts the populations of diverse benthic organisms, notably *Geloina* sp. and other economically significant species (Redjeki *et al*., 2020). In the Philippines, the distribution and composition of *G. erosa* are altered by human activities (Elvira and Jumawan, 2017). Restricted data exists regarding the population structure and biomass of *Geloina* in Southeast Asian countries. This data is crucial for determining sustainable utilization levels and the potential for aquaculture advancement. Therefore, understanding the natural science of this species is necessary for management and conservation purposes. In Malaysia, local communities have initiated a collaborative effort to cultivate mangrove clams within cages positioned in mangrove zones near their settlements. This initiative underscores the potential of the fisheries sector or aquafarming to enhance the socioeconomic well-being of indigenous populations residing near mangrove ecosystems (Thomas *et al*., 2017).

BIOLOGICAL ASPECTS OF GENUS *GELOINA*

According to the World Register of Marine Species (WORMS, 2024), the *Geloina* genus has been classified as follows: Mollusca (Phylum), Bivalvia (Class), Venerida (Order), Cyrenoididae (Family). Argente (2016) reported that within the Corbiculidae family (are accepted as Cyrenoididae), there are three genera with a global distribution: *Batissa, Polymesoda* (now accepted as *Geloina*), and *Corbicula*. These clams have successfully colonized aquatic environments such as estuaries and rivers across the globe, establishing their dominance within the Corbiculidae family. The genus *Geloina* includes three species of mangrove clams found in the Indo-Pacific region; *Geloina bengalensis, Geloina erosa* and *Geloina expansa* (Ingole *et al*., 1994). *G. expansa* is also known as *G. erosa* auct. Lightfoot (Peralta and Serrano, 2014; Sarong *et al*., 2015), *Geloina* genus are prevalent inhabitants of tropical and subtropical mangrove ecosystems worldwide. Notably, *Geloina coaxans*, a mangrove clam belonging to the Corbiculidae family (accepted as Cyrenoididae), represents a quintessential example of a mangrove-dwelling bivalve (Idris *et al*., 2017; Yahya *et al*., 2018).

Shell characters and size of Geloina

According to Morton (1976), the shell of *Geloina erosa* (now accepted as *Geloina expansa*) exhibits considerable size, thickness, and a color spectrum spanning from dark green to yellowish.

Young shells tend to be dark green; however, this hue tends to fade with age, eventually darkening to black in older specimens (Morton, 1976). The largest specimen (dead) recorded in Singapore measured 102 mm in length, 91 mm in height, and 54 mm in width. The mangrove clam boasts an elliptical, dome-shaped shell, a pair of which is also referred to as a graft or valve. The shell's inner portion is coated in a robust periostracum that exhibits a white coloration. This periostracum is initially yellow with green markings in young spat and transitions to a dark brown shade in adult clams, as reported by Dwiono (2003). Internally, *Geloina* species consist of organs like gonads, foot, cardinal teeth, heart, kidney, stomach, and anus, as indicated by Morton (1976) and Tumisem and Ramadhan (2020). Their circulatory system operates in an open manner due to the absence of blood vessels. Instead, oxygen-rich and nutrient-dense blood envelops the organs, serving as a fluid supply source (Morton, 1976). The mangrove clam, *Geloina coaxans*, is often distributed in the mangrove areas, south of Vietnam. The shell is large, triangle-shaped with smooth growth lines and closely arranged, and in mature individuals the shell is 75 mm in length, 60 mm in height, and 40 mm in width.

Hamli *et al*. (2015) reported that shell measurements and their ratios were significantly different ($p<0.05$) between *G. expansa*, and *G. bengalensis*. The ratio on cardinal tooth length to standard length (LCT/SL) for *G. bengalensis* was higher than *G. expansa*. *Geloina bengalensis* is the only species that presents ventral posterior margin length (VPM) characters and that therefore was available for VPM/SL. In terms of morphology, *G. expansa* that has shell expand posteriorly and *G. bengalensis* with sub-trigonal shell shape. Nguyen (1996) described *Geloina coaxans* has trigonal shell sharp with three cardinal middle teeth and the two small and thin teeth divide into branches (Figure 1).

Life cycle

The life cycle of the clam consists of four distinct phases: larval stage, spat, juvenile and adult clam (Sarong *et al*., 2015). Different reproduction and fertilization strategies have been reported by Hedtke *et al*. (2008) and Lydeard and Cummings (2019) observed sexual and primarily asexual reproduction with androgenesis in some *Corbicula* organisms where, polyploid individuals were capable of self-fertilization, hence the hermaphroditism trait (Qiu *et al*., 2001). On the contrary, Pigneur *et al*.

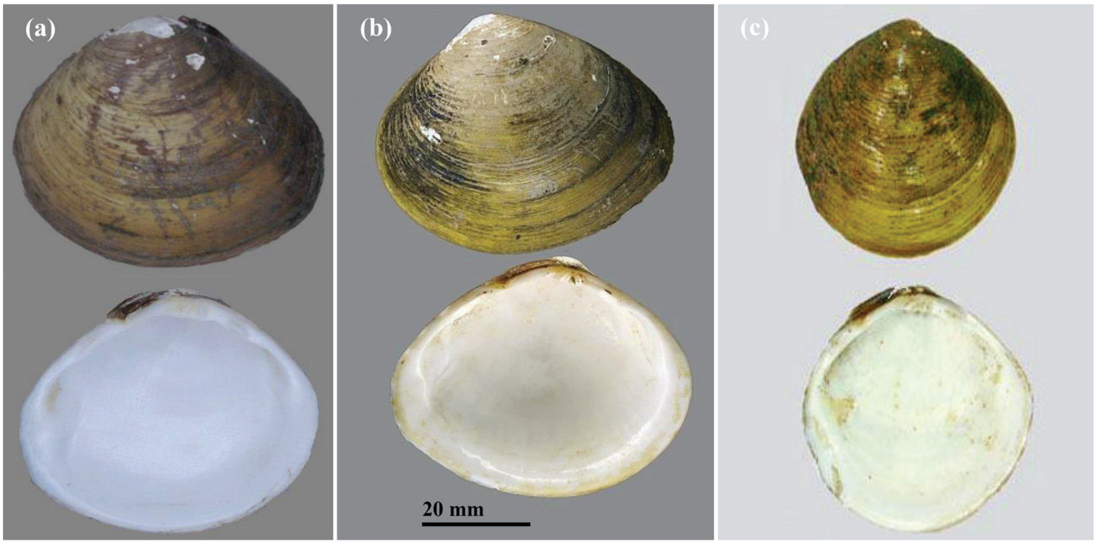

Figure 1. External and internal view of shell valves from three *Geloina* species: (a) *Geloina bengalensis* (Lamarck, 1818); (b) *Geloina expansa* (Mouson, 1849); (c) *Geloina coaxans* (Gmelin, 1791) (Source: Hamli *et al*. (2015); https://www.gbif.org/species/5855561; https://www.gbif.org/species/9575290)

(2012) suggested that exclusive androgenesis is a rare phenomenon observed in a limited number of organisms among several clam species within the *Corbicula* genus. Hermaphroditic lineages within *Corbicula* exhibit global distribution and appear to reproduce through androgenesis, while their sexual counterparts are geographically confined. Similarly, Morton (1984) observed that the clams can be dioecious, and iteroparous with external fertilization, and also a small percentage of hermaphroditism was seen. This could be due to the depth at which mangrove clams burrow, resulting in a low probability of sperm fertilizing the egg. This behavior can be explained as a predation control mechanism, and it can also reduce number of recruits.

Lifespan

The projected lifespan of *Geloina expansa* in Malaysia was determined to be approximately 4.3 years, as indicated by Yahya *et al*. (2018). This finding aligns with the recorded longevity of *G. expansa* in India, which was estimated at 4.0 years by Clemente and Ingole (2011). In contrast, the estimated lifespan for *G. erosa* in the Philippines was shorter, totaling 3.0 years as reported by Dolorosa and Dangan-Galon (2014). However, Ransangan *et al*. (2019) obtained contrasting results, with a maximum life span of 1.32 years for *G. erosa* and 1.22 years for *G. expansa*. In essence, these findings collectively emphasize the extended longevity of *G. expansa* compared to other species. This is notably exemplified by its 4.3–year lifespan, surpassing the 2.7 years of the blood cockle *Anadara granosa* (Mirzaei *et al*., 2015).

Morphology

Most related studies on mangrove clams in the Southeast Asia were conducted in the Philippines, Malaysia, and India. The study in Malaysia recorded a maximum length of 72.5 mm of *G. expansa* (Yahya *et al*., 2018). In contrast, the study by Ransangan *et al*. (2019) documented the dimensions of *G. expansa* to be 92.4 mm. These variations in the sizes of *G. expansa* are attributable to diverse environmental factors within mangrove habitats, including parameters such as salinity, pH, and sediment composition. These factors potentially exert an influence on growth and reproduction dynamics, as suggested by Dolorosa and Dangan-Galon (2014).

Feeding behavior

Clam *Geloina erosa* is a filter-feeding species, primarily active during low-tide immersion stages characterized by frequent inundation (Elvira and Jumawan, 2017). During such periods, these clams rely solely on the natural productivity of marine phytoplankton. This sustenance arrives in the form of either living algae or detritus, conveyed to the bivalves via water currents (Wijsman *et al*., 2019). Notably, these clams play a role in reducing phytoplankton and chlorophyll-*a* concentrations, causing a decline of 20–75% in the Potomac River (Cohen *et al*., 1984). Findings by Kusunoki *et al*. (2004) denote *Polymesoda* (*Geloina*) species as both suspensive and saprophytic, positioning them as potential K-strategists, an idea postulated by Morton (1988). *G. expansa*, recognized for its filter-feeding behavior, has additionally emerged as a bio-indicator species employed for monitoring heavy metal pollution within Malaysian waters (Edward *et al*., 2009). This distinct trait underscores its value within aquaculture, where the clam contributes to the purification of ponds. However, it has been reported that, the mangrove clam harbors symbiotic bacteria (Sulphur Oxidizing Bacteria) in its gills from which it derives most of its nutrition (Adan, 2000), hence an applicable organism for extractive aquaculture.

Distribution of mangrove clam in South-East Asia

Idris *et al*. (2017) reported the widespread occurrence and harvest of the mangrove clam, *G. expansa* (Mousson, 1849), within mangrove forests of the Indo-West Pacific region. This clam, valued for its high protein content, holds a prominent place among shellfish (Gimin *et al*., 2004; Clemente and Ingole, 2009; Hamli *et al*., 2012; Argente *et al*., 2014; Sarong *et al*., 2015; Idris *et al*., 2017). Within the Indo-Pacific region, three marsh clam species have been documented: *G. erosa, G. bengalensis,* and *G. expansa*. However, Ransangan *et al*. (2019) suggested that *G. bengalensis* is confined to the

Bay of Bengal, while *G. erosa* and *G. expansa* boast broader, partially overlapping distributions spanning from India to Vanuatu and extending from northern Vietnam to Eastern Java in the south. Notably, there's speculation that *G. expansa* might exhibit reduced tolerance to colder waters at the extremities of its distribution. Numerous factors can influence the spatial spread of these clams.

Dispersion

The erosion and subsequent transport of juvenile benthic invertebrates, including bivalves, have the potential to bring about shifts in distribution and abundance patterns during the initial post-settlement phase. It's worth noting that substantial spatial discrepancies in the transport rates of juvenile bivalves are often observed (Widianingsih *et al*., 2020). These disparities in transport between different sites can stem from both physical and biological factors. These factors include variations in water flow, sediment granule size, and the local biological community (Hunt, 2005). The dispersal of macrofauna post-larval stage assumes particular significance in habitats characterized by soft bottoms. This importance arises due to the close proximity of juvenile organisms to the sediment surface, rendering them susceptible to displacement by currents and waves (Hunt, 2005).

Locations of mangrove clam populations in wild environment

Geloina clam inhabits regions where estuaries, mangrove forests, and expansive rivers converge, creating an interface between saltwater and freshwater realms (Tumisem and Ramdhan, 2020). This species adopts a semi-infaunal lifestyle within soft sediments that accumulate around the bases of mangrove trees and spends a major portion of its life exposed to air in mangroves swamps (Idris *et al*., 2017). Hiong *et al*. (2004) reported that *G. expansa* is commonly found in channels and pools formed by small streams running between the roots of mangrove plants. Positioned mainly on the landward side of the high intertidal zones within mangrove forests, the presence of *G. erosa* is notably documented (Clemente and Ingole, 2011). These bivalves burrow into muddy substrates, flourishing in the context of mangrove ecosystems and the upper intertidal regions (Gimin *et al*., 2004; Clemente and Ingole; 2011). It's noteworthy that these clams exhibit adaptability to environments characterized by high turbidity as well (Argente *et al*., 2014).

Natural spawning period in wild environment

The reproductive cycles of marine bivalves encompass distinct phases, namely gametogenesis, spawning, larval development, and subsequent growth stages (Clemente and Ingole, 2009). This cycle's duration varies based on species and location, with possibilities including annual, semiannual, or continuous cycles (Clemente and Ingole, 2009; Idris *et al*., 2017). Idris *et al*. (2017) identified five stages of gonad development applicable to both males and females: resting, developing, mature, spawning, and spent stages in *G. expansa*. Their research observed that gametogenesis initiated in November, with mature clams appearing by January. Additionally, it was noted that mature gametes were under 25% in March and October, while January exhibited active maturation but with gradual gametogenesis. Popovic *et al*. (2013) highlighted that the mature stage in *G. erosa* is characterized by over 90% gonad volume occupied by mature follicles. In May, 90% of gonads showed maturity, while partial to complete depletion was seen in 17–76% of gonads during August and September. The spawning season was noted year-round, with gonad index values of 2.0 for females in September and 1.7 for males in both March and November (Idris *et al*., 2017). This contrasts with findings by Clemente and Ingole (2011) that indicate a spawning period lasting about 4 months, from June to early October, with peaks in August and September. Moreover, research has unveiled a link between the condition index and gonadal somatic index, directly influenced by algal availability. This connection is particularly apparent during the low-values spawning season (Clemente and Ingole, 2011; Rahim *et al*., 2012). Ngo *et al*. (2019b) indicated that *Geloina coaxans* gametogenesis was a year-round occurrence, exhibiting varying gonadal index values, ranging from 2.75 (June) to 3.70 (December). Clemente and Ingole (2011) suggested the gametogenic cycle of *G. erosa* commences in October to November, accompanied by oocyte diameters ranging from 50 to 140 µm. Fecundity estimates for *G. erosa* ranged from 0.3185×10^6 to 4.416×10^6 oocytes, with shell lengths of 68.61 and 58.63 mm. Despite this high fecundity, larval survival is compromised due to vulnerability to water currents. Sarong *et al.* (2015) revealed that late-stage growing oocytes prevailed in clams ranging from 36.37 to 49.09 mm, whereas mature oocytes were more common in clams measuring 49.09 to 61.81 mm. These findings showed that the proportion of mature oocytes is in accordance with higher length size. Additionally, while some studies showed a positive correlation between environmental factors and gonadal maturation, but other studies contradicted these findings. Warmer summer months were found to be the beginning of maturation and high GSI values (Clemente and Ingole, 2011), flow-through water system and reduced temperature triggered spawning in *Geloina coaxans* (Quach and Ngo, 2011). Contrary, Rahim *et al.* (2012) and Idris *et al.* (2017), observed no correlation with physiochemical parameters in *G. expansa* as the species spawned all year regardless of water parameters. This could be due to the different geographical regions and mangrove clam species.

Recruitment pattern

Geloina expansa becomes sexually mature upon reaching 40–46 mm shell length (Clemente and Ingole, 2011; Dolorosa and Dangan-Galon, 2014) which is attainable within six months (Dolorosa and Dangan-Galon, 2014). Contrary to the observation made by Clemente and Ingole (2009) as color of gonads were seen at the shell length of less than 34 mm in *G. erosa*. Nonetheless, the yearly pattern of *G. expansa's* recruitment exhibited a singular seasonal pinnacle, marked by the highest recruitment rates in July (20.71%) and August (19.95%), which coincided with the southwest monsoon, according to Yahya *et al.* (2018). This discovery mirrors those noted by Dolorosa and Dangan-Galon (2014), who observed peaks in April (14.41%) and September (12.18%), and by Clemente and Ingole (2009), whose findings pointed to recruitment concentrated in the August to September period, aligning with the southwest monsoon. In contrast, Rahim *et al.* (2012) and Idris *et al.* (2017) indicated that recruitment transpired from the conclusion of the southwest monsoon through to the onset of the northeast monsoon, spanning September to December. Notably, both *G. erosa* and *G. expansa* demonstrated ongoing recruitment, peaking in June and November, respectively, within Malaysia (Ransangan *et al.*, 2019). Consequently, substantial recruitment peaks potentially serve as indicators of major spawning seasons for *G. expansa* (Yahya *et al.*, 2018). Though recruitment could be reduced due to the deep burrowing of adult clams, the larvae feed on algae found in the water column.

ARTIFICIAL PROPAGATION

Inducing spawning plays a pivotal role in the successful operation of bivalve hatcheries, encompassing strategies aimed at regulating reproductive timing to optimize fertilization rates. Chemical methods for induction include the utilization of hydrogen peroxide in giant clams (20–30 mL of a 3% solution), serotonin (0.4 mL of 2 mM) in species like surf clam, oyster, and bay scallop (Gibbons and Castagna, 1984; Lucas and Southgate, 2003). Additionally, sex steroids like testosterone, estradiol, and progesterone (in aliquots of 200 µL) have been employed in sea scallops through injection into the gonad or mantle of the broodstock (Wang, 2006). Biological stimulation techniques involve the application of microalgae, such as *Pseudoisochrysis paradoxa*, at concentrations ranging from 2 to 2.5 million cells·mL^{-1}. This dietary approach is used for the conditioning of adult bivalves, particularly razor clams (*Siliqua patula*, Breese and Robinson, 1981). Physical shock can be administered by rapidly altering salinity or temperature, either increasing or decreasing, to stimulate the spawning response in mature bivalves. The method of decreasing temperature and then using flow through water system was suitable for inducing spawning with females spawning rate reaching 22% in *Geloina coaxans* (Quach and Ngo, 2011; Ngo *et al.*, 2018). Junelyn (2004) reported that, in mangrove clam the use of serotonin was the most successful with 94.38% spawns for both males and females. Overall, it's evident that diverse bivalve species exhibit distinct responses contingent on the employed spawning method (Gibbons and Castagna, 1984).

EFFECTS OF ENVIRONMENTAL PARAMETERS

The growth and morphology of bivalve shells are subject to the impact of both internal physiological factors and external environmental factors (Elvira and Jumawan, 2017). Various aspects influence this interplay; for instance, the nature and quality of phytoplankton and water quality play significant roles. Additionally, water depth, along with factors like currents and water turbulence, contributes to the intricate equation (Grizzle *et al*., 1992). Furthermore, Meysick *et al*. (2022) mentioned variables including sediment type, bottom composition, wave exposure, collectively shape the complex dynamic that affect bivalve shell growth and form.

Salinity and temperature

Ngo *et al*. (2023) reported that the best weight and size growth of juvenile *Geloina coaxans* presented at 5‰ and 10‰ and were significantly higher than in 1‰ and 15‰. As reported by Nybakken (1992), normal temperature of *Geloina erosa* ranged between 20.0–35.0 °C. Similarly, a swifter process of gonadal maturation was noted within the temperature range of 25–30 °C compared to the condition of 20 °C. This phenomenon could be attributed to heightened metabolic rates (Idris *et al*., 2017) and water temperature at 24 °C had a low threshold for gonad development. Salinity changes after heavy rainfall acted as a cue for spawning in *P. erosa* (accepted as *Geloina expansa*) (Clemente and Ingole, 2009). On the other hand, Idris *et al*. (2017) argued that water temperature (27.7 °C) did not affect spawning of this species as the organism spawns annually, so if there is a variation it is not significant. This was strengthened by Ngo *et al*. (2019b), who found that temperature variations had no effect on mangrove clam *G. coaxans*.

In *Polymesoda erosa* (accepted as *Geloina expansa*), it was observed that gonadal maturation proceeded more rapidly within the temperature range of 25–30 °C compared to 20 °C. This discrepancy is likely attributable to the increased metabolic rates at the higher temperatures (Idris *et al*., 2017), and water temperature at 24 °C had a low threshold for gonad development. This entails that annual spawning activities of this species varies by geographical region, environment, and species. Modassir (2000) identified *G. erosa* as a euryhaline species, capable of tolerating salinity levels ranging from 7 to 22‰.

Corbicula species exhibit a capacity to endure a temperature spectrum ranging from 2 to 34 °C (Janech and Hunter, 1995). Similarly, their tolerance for salinity spans from 5 to 14‰ (Morton and Tong, 1985). In the study of Widianingsih *et al*. (2020), it was noted that the temperature in the Panikel area waters, inhabited by *G. expansa*, oscillated between 29 and 31.5 °C. This finding correlated with the temperature measurements taken from the waters of Kendari Bay, the habitat of the mangrove clam, which fluctuated between 28 and 32 °C (Akbar and Bahtiar, 2014). Likewise, congruent results were echoed in research focused on the Segara Anakan region, revealing a temperature range of approximately 27 to 30.3 °C as habitat for mangrove clam populations (Irwani and Suryono, 2006).

pH

The level of acidity significantly impacts aquatic organisms, including shellfish, some of which are linked to primary productivity. Unfavorable conditions linked with reduced pH often have detrimental effects on bivalves during their early life stages (Gazeau *et al*., 2010). Such conditions diminish the saturation state of biominerals used by organisms to form shells and skeletons (Feely *et al*., 2004; Doney *et al*., 2009). However, as individuals grow in size, their resilience to fluctuations in carbonate chemistry increases (Green *et al*., 2009; Waldbusser *et al*., 2010).

Oxygen

The oxygen content of waters is crucial for the growth and sustainability of shellfish (Rizal, 2012), especially *Geloina* larvae. When exposed to air, *Geloina* engages in aerial respiration through its mantle (Clemente and Ingole, 2011). Lebata (2001) reported that clams can burrow to depths of 28 to 50 cm in mangrove mud, where oxygen is limited. According to Setyobudiandi (2004), a temporary decrease in oxygen for several days usually does not significantly impact mussels, as they can close their shell valves. However, the quantity and vitality of mangrove clams depend on the characteristics of substrates that promote aerial respiration (Clemente and Ingole, 2011). *Corbicula* clams can endure weeks of exposure to air but are sensitive to diminished oxygen levels (McMahon and Williams, 1984). These clams colonize habitats ranging from nutrient-poor to nutrient-rich flowing streams, rivers, and lakes, typically favoring oxygenated muddy to sandy sediment substrates (McMahon and Williams, 1984). Therefore, oxygen is essential for the larval development stage.

Effects of sediments

Tumisem and Ramadan (2020) documented that an appropriate substrate for *Geloina* sp. contains approximately 80–90% coarse sandy mud with a diameter exceeding 40 µm and a pH ranging between 5.35 and 6.40. Finer-grained sediment tends to be unproductive and may create unfavorable conditions for juvenile clams to survive or remain in the sediment (Green *et al*., 2009), given that juvenile clams primarily inhabit the upper centimeter of sediment (Hunt, 2004). Alexander *et al*. (1993) found that bivalves tend to occupy areas with a high proportion of sandy substrate and a lower percentage of silt and clay.

The influence of physico-chemical factors of the water and sediments on population densities of bivalves varies across geographical areas (Hunt, 2004). This is due to the pH concentration affecting the absorption and loss of calcium in the bottom sediment. Calcium is crucial for functions like muscular contractions, cellular cohesion, nervous activities in bivalves, and maintaining acid-base balance (Chetail and Krampitz, 1982). A soil pH below 6.8–6.9 triggers excessive calcium loss to the external environment, surpassing calcium gains by sediments (Vindograv *et al*., 1993). Consequently, the essential calcium required for normal metabolic functions of bivalves (Bamber, 1990). Low pH could also hinder ion exchange (Byrne and Dietz, 1997) and affect glutamate catabolism in the mitochondria of the bivalve mantle (Moyes *et al*., 1985). Thus, pH beyond the optimum range in riverbeds might indirectly influence bivalve population density.

Previous studies have demonstrated that an low pH is unfavorable for mollusks which tend to thrive in slightly alkaline environments (Silva and Barros, 2001). The acidity and alkalinity of aquatic ecosystems are crucial for bivalve shellfish, which rely on pH-sensitive calcification processes to construct their calcareous shells (Gazeau *et al*., 2007). An elevated metabolic acid load caused by respiratory or acid stress can completely inhibit shell formation (Pynnonen, 1995).

RECOMMENDATIONS

Clams of the *Geloina* genus are distributed within mangrove forests of the Indo-West Pacific regions. The substrate suitable for *Geloina* sp. comprises approximately 80–90% coarse sandy mud with a diameter exceeding 40 µm and a pH ranging between 5.35 and 6.40. Mangrove clams are euryhaline species, capable of tolerating salinity levels ranging from 4 to 22‰. Due to their unique ecological attributes, *Geloina* clams emerge as objective species for fostering eco-friendly aquaculture.

Mangrove clam *Geloina* possesses favorable characteristics for marine culture, as they are easy to cultivate (Morton, 1976; Gimin *et al*., 2004). Additionally, mangrove clams can withstand a broad spectrum of environmental circumstances. Therefore, environmental factors affecting *Geloina* species must be considered at all time. It is also well-known that mangrove clams are marketed locally and cultured in some areas (Ransangan and Soon, 2018; Ngo *et al*., 2019b; Ransangan *et al*., 2019; Widianingsih *et al*., 2020). The life cycle and growth performance of mangrove clams should be focal points in upcoming studies to explore efficient techniques for seed production and aquaculture practices. Recently, Ngo *et al*. (2019) successfully reared mangrove clam larvae from veliger to umbo stage over 17 days, achieving a survival rate of 10.3%. It is imperative to improve rearing techniques to produce clam seeds for farming requirements. The information regarding maturation, spawning of broodstock, and specific biological conditions for mangrove clams from this review is valuable for the resource management and aquaculture practices.

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