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# Strategi reproduksi dan karakteristik gonad kerang hijau *Perna viridis* di Teluk Banyuurip: pengaruh faktor lingkungan dan musim
# [Reproductive strategies and gonadal characteristics of indonesian green mussel *Perna viridis* in Banyuurip Bay: environmental and seasonal influences]

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**ABSTRACT |** This study aimed to examine the gonadal characteristics and reproductive strategies of the green mussel *Perna viridis* in Banyuurip Bay, Java Sea, Gresik Regency, Indonesia, with a focus on oocyte size, gonad morphology, and seasonal variations in reproductive activities. Micromorphological and field observations analysis revealed that the gonad, the site of gametogenesis in female mussels, is characterized by an orange colour. In contrast, in males, it is creamy white. During gametogenesis, the diameter of the oocyte increases from 0.28 to 0.60 µm at the oogonia stage and to 1.17 to 3.19 µm when it becomes a vitellogenic oocyte. Significant daily and seasonal variations are observed, which may contribute to high environmental pressure on the population. The green mussel population continues to grow despite ecological disturbances, including food scarcity and high levels of pollution, which are exerting pressure on the population. The significantly smaller oocyte size compared to other populations was identified as a potential adaptation to these challenges. These findings underscore the importance of understanding reproductive strategies to support sustainable mussel cultivation and effective management, particularly in areas characterized by fluctuating environmental conditions.

**Key words |** *P. viridis*, gonadal characteristics, reproductive strategy, oocyte size

**ABSTRAK |** Penelitian ini bertujuan untuk mengeksplorasi karakteristik gonad dan strategi reproduksi populasi kerang hijau *P. viridis* di Teluk Banyuurip, Kabupaten Gresik berfokus pada ukuran oosit, morfologi gonad, dan variasi musiman dalam aktivitas reproduksi. Observasi lapangan dan analisis mikromorfologi mengungkapkan bahwa gonad sebagai tempat berlangsungnya gametogenesis pada kerang betina ditandai oleh warna orens sedangkan pada jantan berwarna putih krem. Selama gametogenesis, oosit berkembang dengan diameter makin membesar, dari ukuran 0,28 hingga 0,60 µm pada stadium oogonia menjadi 1,17 hingga 3,19 µm pada stadium oosit vitelogenik. Variasi lingkungan yang signifikan baik harian maupun musiman diduga berkontribusi pada tingginya tekanan terhadap populasi. Namun demikian, kerang hijau tetap berkembang meskipun menghadapi tekanan lingkungan yang tinggi. Ukuran oosit yang jauh lebih kecil dari populasi lainnya diidentifikasi sebagai adaptasi potensial terhadap tantangan tersebut. Temuan ini menegaskan pentingnya pemahaman strategi reproduksi untuk mendukung budidaya kerang hijau yang berkelanjutan dan pengelolaan yang efektif, khususnya di wilayah yang menghadapi kondisi lingkungan fluktuatif.

**Kata kunci |** *P. viridis*, karakteristik gonad, strategi reproduksi, ukuran oosit

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## INTRODUCTION

Bivalves are a significant global food source, contributing to national food security and economic independence through fisheries and aquaculture an increasingly vital role in the context of a growing global population (Kapranov *et al.*, 2021; Rittenschober *et al.*, 2016). One of the commercially important mussels, the green mussel (*P. viridis*) (Cheng *et al.*, 2018), is significant due to its contribution to food security and the livelihoods of coastal communities (Asrum & Morkoyunlu, 2025). To date, the green mussel remains a pivotal component in coastal livelihoods and is widely cultivated (Putra, *et al.*, 2022a; Rejeki *et al.*, 2021). In Banyuurip Bay, Ujungpangkah Regency, East Java, green mussel fisheries and cultivation become an important part of the local economy. The productive mussel fields in this bay support traditional farming practices, which help small-scale fishermen's families earn additional income. Mussel cultivation not only supports household income but also contributes to the socio-economic resilience of the Banyuurip Bay community, a resilience that has long been integral to the community (Farikhah *et al.*, 2023; Setiahadi, 2021).

However, the sustainability of green mussel cultivation in Banyuurip Bay faces many challenges. The decline in green mussel harvest and catch has an impact on the declining income of traditional fishermen. Spats attached to the collection ropes experience many disturbances that prevent the population from growing until harvest due to attacks by competitors and parasites. The condition (CI) states that Banyuurip green mussels are thin (Allaf *et al*., 2025; Fauzi *et al*., 2022), which has implications for low selling prices. Fishermen also often cancel the harvest of green mussels even though the shell size is relatively large (>60 mm) because thin mussels are less in demand by consumers. To overcome these problems, the reproductive aspect is a crucial factor that needs to be studied to find solutions to the issues faced in green mussel cultivation amidst the threat of the severe decline in the quality of the marine ecosystem. The anthropogenic, industrial, and climate change factors that disturb populations make a study of population reproduction strategies increasingly necessary. Increased total suspended solids (TSS), agricultural runoff, and urban pollution have been shown to interfere with the reproductive cycles in mussels (Gascho Landis & Stoeckel, 2016; Richard *et al*., 2024).

Identifying reproductive status based on macroscopic examination remains difficult due to the unclear separation of internal organs in soft-bodied bivalves. Therefore, histological techniques are crucial for accurately assessing reproductive development (Galimany *et al*., 2015). The species is increasingly threatened by water pollution, which compromises population quality. However, scientific descriptions of *P. viridis* reproductive biology remain limited, and gonadal structures are often inaccurately generalized based on non-mussel bivalves. Previous studies have primarily focused on the influence of the lunar cycle and water physicochemical on gonadal maturation of *P. viridis* (Baldevieso *et al.,* 2021), cultivation techniques (Parappurathu *et al*., 2021; Rusydi *et al*., 2022), parasitic infections and heavy metal accumulation (Amirah Hamzah *et al*., 2023; Salsabila *et al*., 2024). This gap underscores the need for validated anatomical references. Accordingly, this study aims to provide a more accurate histological description of green mussel gonads based on credible scientific literature, thereby offering a reliable foundation for future reproductive biology research in this species.

## MATERIAL AND METHODS

### Research Location and Time

The research was conducted in Banyuurip Bay, located in the Java Sea, approximately 2.5 km from the mouth of the Bengawan Solo River, within the Banyuurip Mangrove Center (BMC) in Ujungpangkah District, Gresik Regency. This site is adjacent to a 3.5-hectare mangrove forest that remains well-conserved. The sampling site featured traditional *Bagan tancap* farming structures, where dozens of hanging ropes were observed, each densely colonized by adult green mussels (*P. viridis*) with varying shell lengths. One hanging rope was cut from the bamboo in Bagan tancap using a sharp knife, and then it was carefully placed into a clear plastic bag to prevent the green mussel colony attached to the rope from detaching. The green mussel colony in the plastic was then transported to the Aquaculture Laboratory of the Faculty of Agriculture, Muhammadiyah University of Gresik.

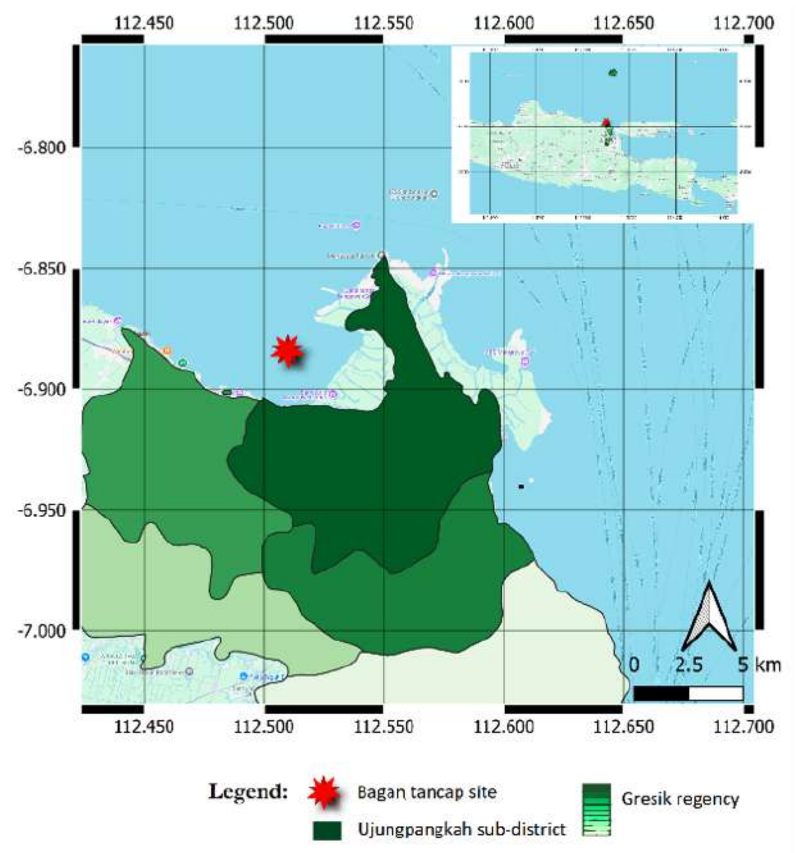


**Figure 1.** Sampling site (red asterisk) of green mussels (*P. viridis*) from a population in Banyuurip Bay, Java Sea, Ujungpangkah District, Gresik Regency, East Java, Indonesia.

**Research design and data collection**

This study employed a descriptive research design to investigate the reproductive system of green mussels (*P. viridis*) through anatomical and histological analysis. Mussels were sorted based on shell length, and individuals exceeding 40 mm were selected for further analysis. One male and one female were randomly selected based on visual criteria, specifically mantle colouration, after careful dissection with a sharp knife. Limited sample numbers are permitted for the initial description or preliminary study of gonadal structure and gametogenesis using descriptive morphological or histological methods (Gosling, 2015; Lima *et al.*, 2012).

The right-side mantle was excised and preserved for histological preparation. Tissue sections were examined to assess the structure of gonadal acini, focusing on parameters such as acinus wall integrity, epithelial cell type and thickness, lumen size, presence and type of oocytes, and connective tissue characteristics. A total of 25 acini per specimen were analyzed across eight visual fields using the Olympus microscope (BX series), and oocytes in each acinus were counted. Reproductive stages were classified based on microscopic observations, and oocyte quality was quantified by measuring oocyte diameter using *ImageJ* software for Windows.

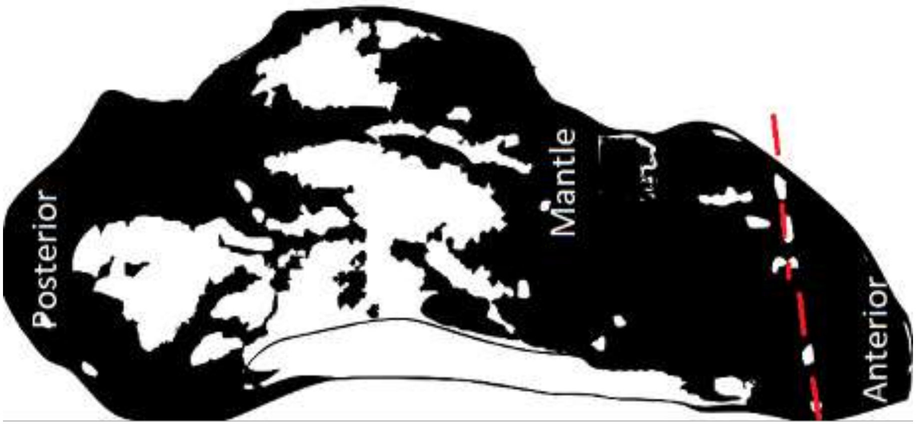


**Figure 2**. Transverse cutting position of green mussel (*P. viridis*) tissue near the hinge region to obtain gonadal tissue for histological analysis (Rapalini *et al.*, 2022). The dotted red line indicates the precise location of the tissue sectioning used for preparing histological slides.

**Histology procedure**

The histological procedure involved several systematic steps to prepare tissue samples for microscopic analysis, as previously reported (Mellisa *et al.*, 2019; Putra *et al.*, 2021; Rahimi *et al.*, 2019). First, the mussels are dissected to extract the gonadal tissue, and then they are carefully trimmed into small pieces to ensure optimal fixation. The samples are immediately fixed in 10% buffered formalin for 24–48 hours to preserve cellular structure and prevent degradation. After fixation, the tissues are washed in running tap water to remove excess fixative and then dehydrated through a graded ethanol series, typically starting from 70% ethanol and progressing to absolute alcohol. Following dehydration, the samples are cleared using a clearing agent such as xylene to replace the alcohol and prepare the tissues for embedding. The cleared tissues are then embedded in paraffin wax to form solid blocks. Using a microtome, the paraffin-embedded tissues are sectioned at a thickness of 5–7 µm and mounted onto glass slides. These sections are then deparaffinized, rehydrated through a descending alcohol series, and stained commonly using Hematoxylin and Eosin (H&E) to highlight cellular and tissue structures (Iqbal *et al.*, 2024; Putra *et al.*, 2012; Putra *et al.*, 2024). Finally, the slides are dehydrated, cleared, and mounted with a coverslip for microscopic examination (Putra *et al.*, 2022b), allowing for the determination of gonadal development stages and reproductive status.

**Data analysis**

The data obtained were analyzed descriptively in relation to relevant scientific literature, focusing on gonadal location, reproductive stages, and associated histological characteristics. Morphological aspects of the gonads were assessed following the criteria established by Lima *et al.* (2012) (Table 1).

**Table 1.** Micromorphology of gonadal aspects (Lima *et al.*, 2012).

| Aspects | Description |
|---|---|
| *Acini* | Regular, irregular, continuous *acini* wall, discontinuous |
| Germinal | Continuous, discontinuous, thick+thin, thin, |
| Lumen | There is no lumen, small lumen, medium lumen, large lumen, no epithelium, atresia oocytes, total *acini* with |
| Connective | No oocytes/no hemocytes, oocytes, oocytes+hemocytes, |

Oocyte differentiation was conducted according to the methodology described by Tos *et al.* (2016). Reproductive staging was determined based on the classification system by Kim *et al.* (2006), and visual assessment of reproductive status was guided by Buchanan (2010). Quantitative data were processed and presented using Microsoft Excel 2013.

## RESULTS

**Macroscopic gonadal morphology**

The reproductive system of the green mussel (*P. viridis*) includes the gonads and gonoducts located in the posterior part of the visceral cavity, just beneath the inner shell surface. These organs are closely connected to the digestive glands, forming an integrated internal structure. The gonoduct is a short canal that channels reproductive cells from the gonads to the gonopores, which are paired openings through which eggs or sperm are released. Although the gonopores are positioned near the renopore (excretory opening), they are anatomically separate.

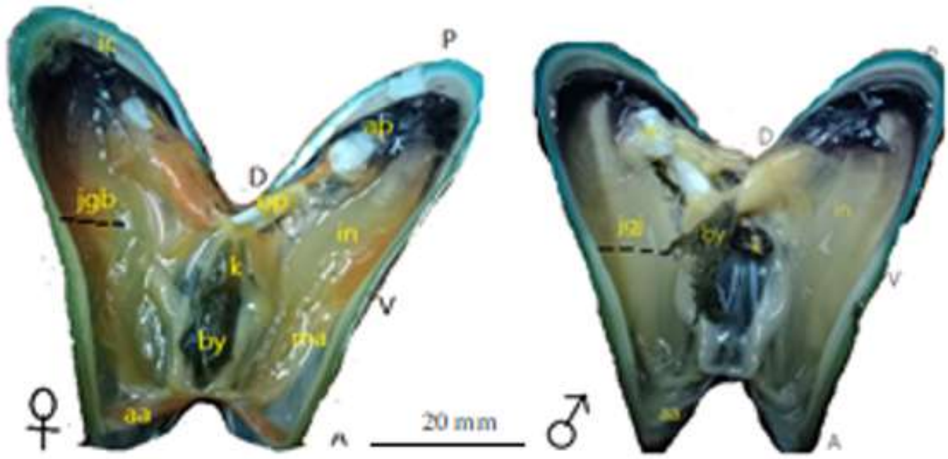


**Figure 3**. Internal morphology of the green mussel P. viridis from the Banyuurip Bay, Java Sea, Gresik Regency, taken in November (caption: Left: female species; Right: male species; A: anterior part; P: posterior part; V: part ventral; D: dorsal part; ap: posterior adductor muscle; op: pedal muscle; aa: anterior adductor muscle; in the internal shell; in: gills; k: foot; by: byssus; jgb: female gonad tissue; jgj: tissue male gonads; determining the name of the organ refers to several literatures (Eggermont *et al*., 2020; Gerdol *et al*., 2017; Gosling, 2015; Oyarzún *et al*., 2020).

In females, the gonadal tissue branches out and spreads into the mantle membrane and can be visually identified by its distinct orange colouration, which lines the inner lateral part of the shell (Figure 3, left). This colour varies in intensity, with deeper orange or yellowish tones appearing around the dorsal side, ventrolateral areas, and near the tip of the anterior adductor muscle. In contrast, paler orange colouration may indicate a lower concentration of eggs, particularly in areas such as the gills, foot, or muscle tissues, where the gonad may not have fully developed.

In contrast, the creamy white color (Figure 3, right) indicates that spermatozoa are suspended in the seminal plasma, filling the internal mantle cavity of the male mussel and giving it a thickened appearance. The milt extends from the dorsal-lateral to the ventral side and from the anterior to the posterior, including the regions around the anterior and posterior adductor muscles, as well as the pedal muscle. It is widely distributed throughout the soft body. Despite similar gonad morphology between male and female green mussels *P. viridis*, a key difference lies in the type of gametes produced. These findings support the notion that green mussel *P. viridis* is gonochoric. This term is characterized by separate sexes with distinct male and female individuals.

**Microhistological structure of green mussel *P. viridis* gonad**

The green mussel *P. viridis* possesses follicles or sacs that serve as sites for gametogenesis. These structures, known as acini or germinal lobes, are small compartments where gametes differentiate—through oogenesis in females and spermatogenesis in males. Each acinus is lined by germinal epithelium and enclosed by an acinar wall composed of follicular cells, housing oocytes at various developmental stages. The acini are interspersed within connective tissue, forming a lobular network.

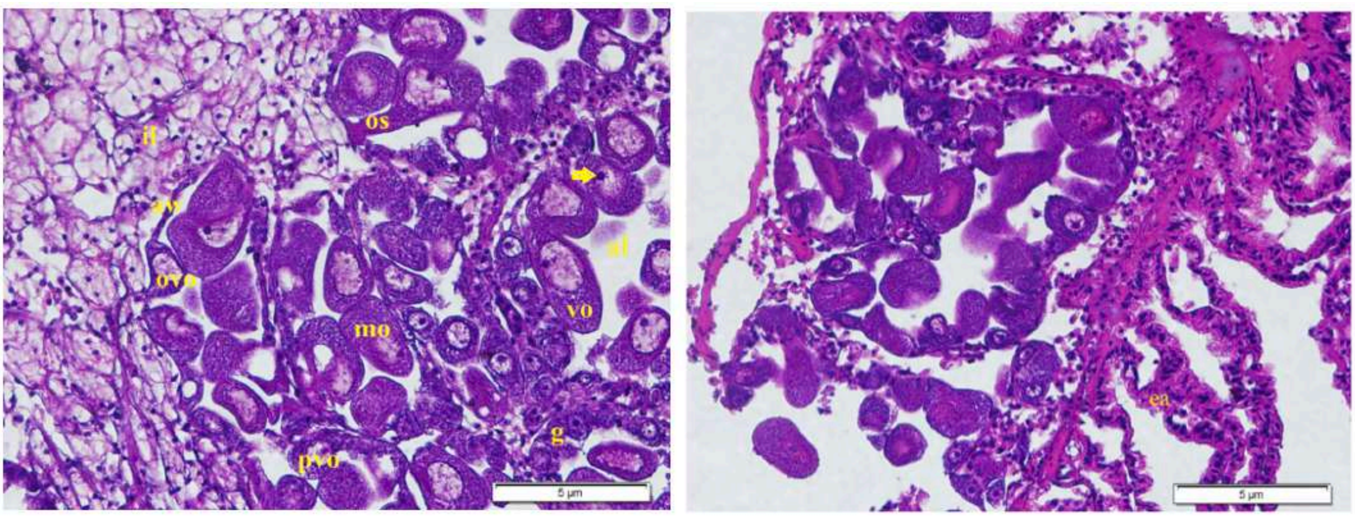


**Figure 4.** Micro-anatomy of the female gonad of the green mussel *P. viridis* from the Banyuurip Bay, Java Sea, Gresik Regency, taken in November (M=400x) (abbreviation: os: oocyte stalk; g: oogonia; pvo: oocyte in vitellogenesis 1; vo: oocyte in late vitellogenesis; om: mature oocyte; aw: acini wall; il: germinal lobule interconnection; al: acini lumen; n: nucleus; black arrow: nucleolus; ea: empty acini).

In partially spawned females, prominent connective tissue and enlarged acinar lumens are observed. The presence of a large lumen and predominance of vitellogenic oocytes are marked by a shift in cytoplasmic staining—from basophilic to increasingly acidophilic—indicating progression beyond the previtellogenic phase. Many oocytes appear prominent; some are attached via stalks to the follicular wall, while others float freely within the lumen. The germinal epithelium also contains numerous oogonia, suggesting active redevelopment and ongoing gametogenic cycles. However, some acini appear undeveloped, lacking visible oocytes and signs of differentiation, indicating asynchronous gonadal activity.

**Table 2**. Quantification of the micrograph in one individual female gonad from acini characteristics (n=25).

| **Variables** | **Characteristics** | ***Acini* number** |
|---|---|---|
| *Acini* | Regular | 10 |
| | Irregular | 15 |
| | Continuing walls | 15 |
| | Discontinuing walls | 10 |
| Germinal | Continue | 15 |
| | Discontinue | 10 |
| | Thick | 1 |
| | Thick+ thin | 19 |
| | Thin | 5 |
| | Undifferentiated | 13 |
| | Oogonia | 24 |
| | Oocyte | 25 |
| | Stalked oocyte | 11 |
| Lumen | Without lumen | 1 |
| | Small lumen | 13 |
| | Medium lumen | 6 |
| | Big/wide lumen | 6 |
| | Without epithelium | 12 |
| | Atretic oocyte | 0 |
| | Total *acini* with | 0 |
| | Mature oocyte | 14 |
| | Mature oocyte + | 0 |
| Connective | Oocyte + haemocyte | Present |

In green mussels (*P. viridis*), gonadal tissue develops by extending into the connective tissue between internal organs, particularly over the surface of the digestive glands. This tissue is primarily composed of adipogranular (ADG) and vesicular connective tissue (VCT) cells, which function to support the acini—the primary sites of gametogenesis structurally. As gametes mature and accumulate within the acini, the gonads expand and progressively infiltrate the mantle tissue. The degree of infiltration varies depending on the reproductive stage of the individual. Gonadal extensions are also observed within the pallial muscles of the mantle. The quantitative evaluation of acinar development is summarized in Table 2. Most acini appeared irregular in shape, and in several instances (n = 10), discontinuous acinar walls were noted—an indication of more advanced gonadal maturation.

In contrast, acini with regular, continuous walls are considered immature. The acini walls varied in thickness; many were uneven, with some areas thick and others thin (19). This observation corresponds with the maturation of oocytes, with vitellogenic oocytes predominating. However, the presence of growing oogonia in the acinar walls suggests that the acini examined are undergoing ongoing maturation. Most contained oocytes, with the majority (24) also showing the presence of oogonia, confirming the active maturation process in the ovaries. Primary oogonia were embedded in the acinar walls. Additionally, the acini exhibited lumens of varying sizes: 13 were small, six were medium, and six were large, while 14 acini contained mature oocytes, indicating different stages of reproductive development.

Most of the acini in the gonads are populated by oogonia and dense previtellogenic oocytes. In certain acini, vitellogenic oocytes dominate, and some have already matured into oocytes within the lumen. Other acini appeared empty but contained a few late-stage oocytes, while some showed no oocytes at all. However, all acini exhibited vitellogenic oocytes and oogonia, indicating active oocyte development. Some acini contained lumens filled with mature oocytes, suggesting that spawning is actively occurring (Figure 5).

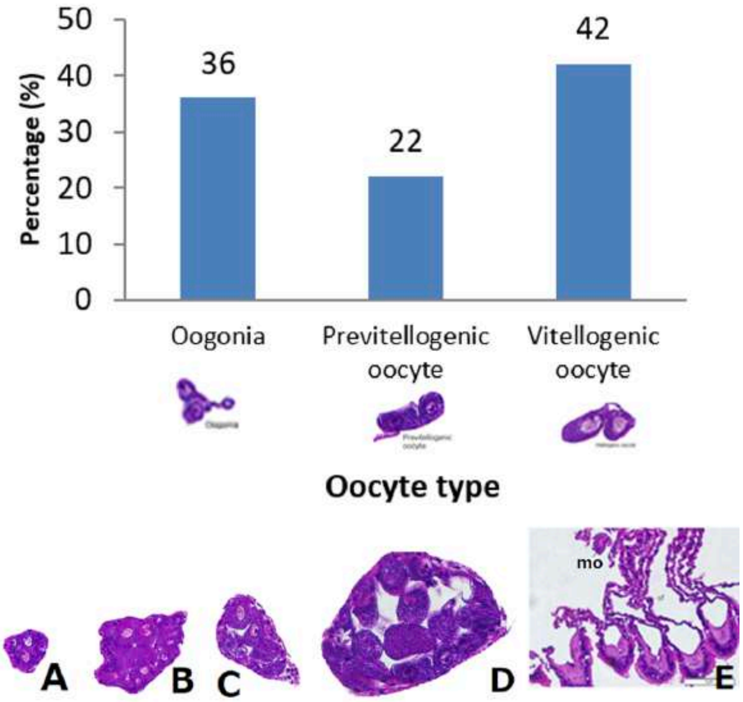


**Figure 5**. The oocytes of different types in the acinus of a female green mussel originating from the Banyuurip Bay, Java Sea, Gresik Regency, in November. A description of each oocyte type is explained below the bar chart. A. Immature acini; B. Small lumen and mature oocyte; C. Medium lumen, oocyte in vitellogenesis stage; D. Large lumen containing mature oocyte; E. The remaining oocytes are in the empty acinus (M=400x) (description: mo: mature oocytes).

Oogonia attached to the acinar lobes signify that the maturation process is underway, with future spawning anticipated alongside the current spawning cycle. No resorbed oocytes were observed in any of the acini. Some empty acini displayed a continuous band-like germinal epithelium, indicating they had not yet resumed oogenesis for the next reproductive cycle. The mature oocytes present in the empty acini are likely remnants from a previous spawning event. These acini, while empty, have not yet undergone further maturation, signalling that the female mussels are transitioning through the spawning and development stages, preparing for subsequent reproductive events. The diameter of oocytes at different developmental stages showed significant variation ($p<0.05$), as presented in Table 3. The size of oogonia starts at 0.45 ± 0.10 µm and increases approximately threefold to 1.51 ± 0.34 µm upon entering the previtellogenesis phase. At the peak of vitellogenesis, when yolk granules in the oocyte reach their maximum, the oocyte size increases to 2.28 ± 0.50 µm. Once vitellogenesis concludes, the oocyte is released from the acinar wall, allowing the released cells to gather within the acini lumen.

**Table 3**. Oocyte diameter in the acinus of a female green mussel originating from the Banyuurip Bay, Java Sea, Gresik Regency, in November month.

| Oocyte type | n (cells) | Diameter (µm) | | |
|---|---|---|---|---|
| | | Min. | Max. | Mean±SD |
| Oogonia | 20 | 0,28 | 0,60 | 0,45±0,10 |
| Previtellogenic | 20 | 1,07 | 2,63 | 1,51±0,34 |
| Vitellogenic | 20 | 1,17 | 3,19 | 2,28±0,50 |
| Mature (in lumen) | 6 | 1,90 | 2,41 | 2,15±0,28 |

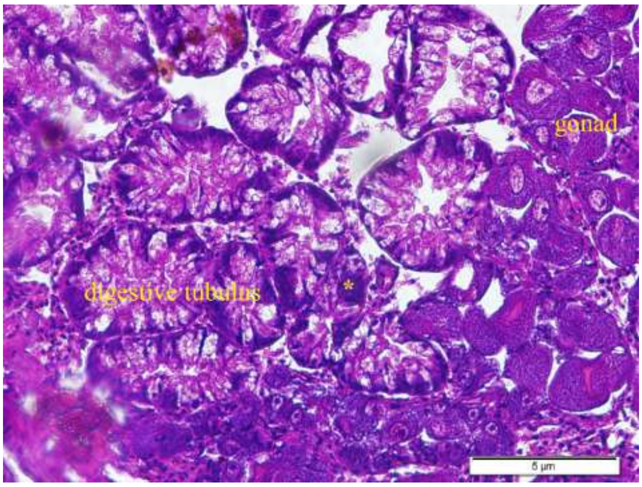


**Figure 6.** Gonad tissue adjacent to the digestive glands (caption: yellow star (*): basophilic; black arrowhead: single layer digestive (ltd); l: lumen; determination of labeling of this tissue refers to (Cuevas *et al*., 2015; Gosling, 2015)

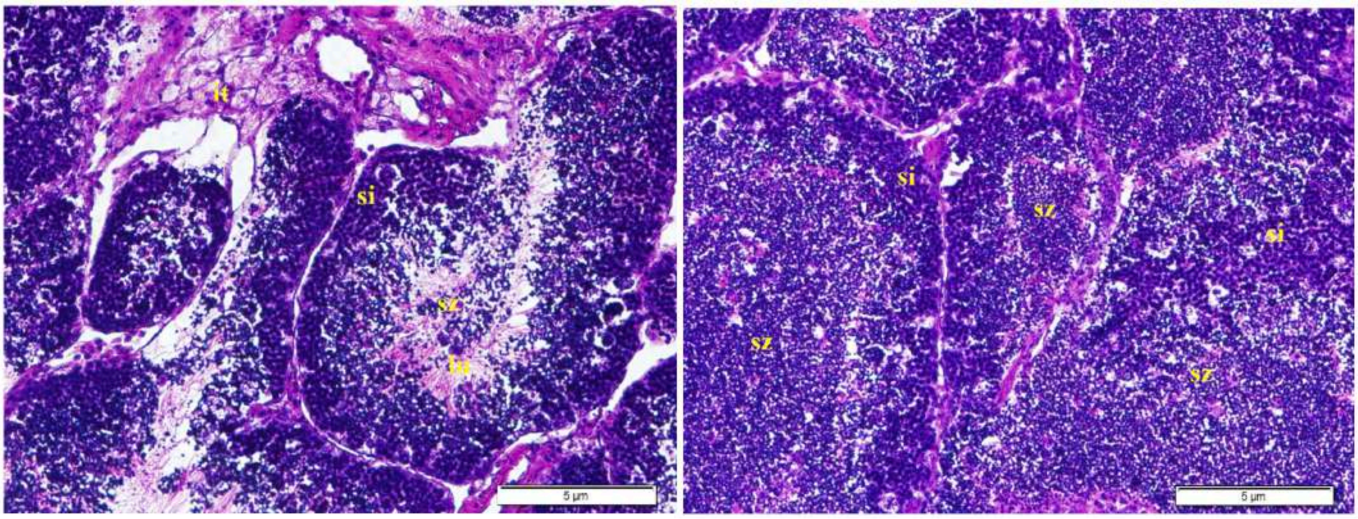


**Figure 7**. (Left) Micrograph of male acinus in the spawning stage on green mussel *P. viridis* from the Java Sea, Banyuurip Bay, Gresik Regency during sampling in November; (Right) Acini without have lumen (caption: dotted black line: testicular follicles; it: interlobular tissue; si: immature sperm in the form of spermatogonia & spermatocytes; sz: spermatozoa; lu: lumen lobules; Labeling of this tissue refers to references (Cuevas *et al*., 2015; Khafage *et al*., 2019)

The gonads are anatomically adjacent to the digestive glands and intestines, as shown in Figure 6. These organs are not easily separable, reflecting their functional interdependence. The digestive glands consist of basophilic cells and digestive cells that produce digestive enzymes essential for synthesizing lipids and proteins. The micrograph of the digestive glands indicates a healthy and normal state, with primary and secondary tubules containing vacuoles. Notably, the tubules are free from parasites or invading organisms that might otherwise inhabit the acini or digestive tubules.

The developmental variation in male green mussel gonads observed in this study revealed that several mature spermatozoa were successfully released from the gonads, as evidenced by the presence of a lumen space in some acini. Some acini lack a central lumen, indicating that spermatozoa have not yet been released during the spawning process. In two of the eight visual fields examined under the microscope, late-stage testicular development was noted, but mature gametes had not been released into the surrounding water (Figure 7).

## DISCUSSION

This study describes an in-depth characterization of the reproductive system of *P. viridis* in Banyuurip Bay, integrating macroscopic and histological observations. Several critical findings emerged, offering insights into the reproductive strategies employed by this species in response to environmental stressors. The reproductive strategy of an organism plays a significant role in population dynamics, biogeography, and the long-term survival of the species within its habitat, despite significant challenges (Llodra, 2002). One of the most notable findings was the small oocyte diameter, averaging 2.15 ± 0.28 µm, which is significantly smaller than those reported in other populations (e.g., 12.8–55.5 µm in Bangladesh). This deviation suggests a potential adaptive mechanism in response to environmental pressures, such as high turbidity, heavy metal contamination, and food scarcity. Similar patterns have been observed in *Brachidontes rodriguezii* and *Mytilus edulis*, where energy constraints due to stress lead to the production of smaller gametes (Bayne *et al*., 1983; Rapalini *et al*., 2022).


**Figure 9.** High water turbidity appears dark brown and cloudy in images A and B while decreasing turbidity makes the water highly transparent (Image C). However, the trash between the hanging ropes is always present for nearly a day (Image D)

Smaller oocytes represent a common reproductive strategy in a stressful environment, helping organisms conserve energy while maintaining reproductive continuity. In high-stress environments, such as those with extreme turbidity and heavy metal contamination, the energy available for the reproductive process becomes limited. Small oocytes require lower energy investment per cell, allowing the organism to maintain continuous gametogenesis activity. Although fecundity measurements were not conducted in this study, it is known from the literature that *P. viridis* has a naturally high fecundity, with the potential to produce millions of eggs in a single cycle (Gosling, 2015). Without increasing the number of eggs, small oocyte sizes still support reproductive success by maintaining metabolic efficiency and allowing the continuation of the reproductive cycle in challenging environmental conditions, such as in Banyuurip Bay. The study by Liu *et al*. (2010) supports the argument that the small diameter of oocytes is not due to other factors, such as starvation because starvation would stop the spawning stage. However, gonad development continues to occur. The presence of lumens in both female and male gonads demonstrates that the Banyuurip green mussels maintain spawning activity.

The absence of atretic oocytes in female gonad samples observed in this study indicates that the oogenesis process in *P. viridis* in Banyuurip Bay is active and efficient. In many studies, the presence of atretic oocytes is often associated with severe environmental stress or physiological disturbances, such as exposure to heavy metals or nutrient deficiencies (Cuevas *et al*., 2015). Therefore, the reduced oocyte diameter does not indicate reproductive failure but rather illustrates the individual's success in completing the gamete maturation cycle. In the context of the very high natural fecundity of *P. viridis*, the small size of the oocytes and the absence of atresia support the interpretation that this species employs an energy-efficient strategy that remains effective in ensuring reproductive continuity despite stressful environmental conditions.

The size variations in the oocytes of *P. viridis*, noting diameters ranging from 0.28 to 0.60 µm for oogonia, 1.07 to 2.63 µm for previtellogenic oocytes, and 1.17 to 3.19 µm for vitellogenic oocytes. Notably, previously unreported size differences within a single developmental stage were observed, suggesting maternal effects that can influence oocyte size, similar to the 57% size variation seen in *Mytilus californianus* egg cells (Phillips, 2007). These variations could be influenced by genetic or environmental factors (Diz *et al*., 2009).

Histological analysis revealed various oocyte stages coexisting within a single acinus, indicating asynchronous gametogenesis. This finding suggests that *P. viridis* maintains continuous reproductive capability throughout the year. Such a strategy aligns with patterns observed in other tropical mussel populations, including those in Florida Bay and the Bay of Bengal (McFarland *et al*., 2016; Noor *et al*., 2021). The ability to spawn intermittently may help ensure recruitment despite unpredictable environmental fluctuations.

Water quality is one of the main factors that affect the reproductive success of aquatic organisms, including *P. viridis*. One of the most prominent environmental pressures in Banyuurip Bay is the high level of water turbidity, which is caused by the mixing of water masses from the Bengawan Solo River with those from the open sea. According to Dewi (2023), the turbidity value at the estuary of this river ranges from 5.84 to 947.00 NTU, far exceeding the standard threshold for estuary waters, which is around <25–50 NTU. In fact, according to the Minister of Environment's Decree No. 51 of 2004, the maximum threshold for estuaries is 25 NTU, indicating the potential for extreme pressure due to high Total Suspended Solids (TSS) levels. Previous research also showed that more than 58% of the Bengawan Solo estuary area was classified as heavily polluted based on the STORET classification (Aidi *et al*., 2021), and the TSS content was stated to exceed the quality standard (Sahid & Zainab, 2024). The source of TSS comes from agricultural runoff, sedimentation from upstream, mining activities, deforestation, and domestic and industrial waste. Suspended particles not only contain heavy metals such as Cu and Pb but also inhibit the penetration of light into the water column, thus disrupting the photosynthesis process of phytoplankton.

Field observations (Figure 9) indicate that water clarity in Banyuurip Bay varies significantly, ranging from 5 to 70 cm. During the west monsoon, increased water discharge leads to a significant spike in turbidity, which directly reduces primary productivity and plankton biomass. Since plankton is the primary food source for *P. viridis*, a decline in plankton quality and quantity can negatively impact the nutritional status of mussels and their gametogenic processes.

Seasonality significantly influences the reproductive status of many bivalves (Buchanan, 2010), primarily due to variations in water temperature, food availability, and dynamics of hydrographic factors. While the annual reproductive cycle of *P. viridis* in the East Java Sea is not well-documented in the scientific literature, local fishermen provide a general overview. They report that spat abundance in Banyuurip Bay occurs year-round, with peak recruitment from March to June. With an estimated gonad maturity period from stage 0 to maturity of 60 days (Noor *et al*., 2021), the recruitment in Banyuurip Bay is similar to that in the Bay of Bengal, Bangladesh, which undergoes five-stage gametogenesis from January to April (Asaduzzaman *et al*., 2019). Recruitment continues through to the end of the year, as evidenced by Farikhah *et al*. (2023), who found approximately 16,000–19,000 spat/m² attached to the hanging rope of floating cages in November.

Nevertheless, the main physicochemical parameters, such as temperature, salinity, pH, and dissolved oxygen, are still within the optimal range for green mussel growth (Allaf *et al*., 2025; Firdaus *et al*., 2023; Mazida *et al*., 2023; Rudianto *et al*., 2024; Shofiyah *et al*., 2022). However, the dissolved copper content reaching 0.3 mg/L (Risjani *et al*., 2023) exceeds the regulatory threshold and can interfere with the reproductive process. Research by Lettieri *et al*. (2019) demonstrated that copper could interfere with the formation of protamine protein, which is crucial for sperm integrity in blue mussels (*Mytilus galloprovincialis*). In addition to Cu, the high presence of Pb in the Bengawan Solo estuary (Setiyowati *et al*., 2024) also contributes to the decline in recruitment rates of green mussels.

Gonadal anatomy was clarified through comparisons with previous studies, noting variability in anatomical descriptions due to complex internal structures. Consistent withthe gonads are located in the mantle and consist of branched tubules opening into the gonoduct.

Together, these findings demonstrate how *P. viridis* in Banyuurip Bay has evolved and maintained flexible and efficient reproductive strategies to adapt to environmental challenges. The integration of visual, anatomical, and histological data provides a robust framework for future studies on bivalve reproduction under stress while also offering practical insights for sustainable mussel aquaculture development. According to these findings, this paper explains a comprehensive characterization of the gonads of the green mussel *P. viridis*, both macroscopically and microscopically, for both male and female individuals, incorporating insights from previous research.

## CONCLUSION

This study provides a detailed analysis of the reproductive system of the green mussel *P. viridis*, with a focus on the gonads and gonoducts, which are crucial for gametogenesis. The gonads, located in the posterior region of the visceral cavity, are adjacent to the digestive glands, reflecting their close functional relationship. The gonadal structure was found to be gonochoric, with distinct male and female individuals, contrary to some prior studies that suggested hermaphroditism. Female mussels displayed a characteristic orange gonadal tissue infiltrating the mantle, while males exhibited creamy white gonads, indicative of mature spermatozoa. Histological examinations revealed that gametogenesis occurs within the acini, with gonadal tissue extending into connective tissues and the mantle. The size of the oocyte increased significantly during the reproductive cycle, with peak vitellogenesis marked by large oocytes rich in yolk granules. These findings enhance our understanding of the reproductive biology of *P. viridis*, particularly its gonadal development and gamete maturation processes. Future research should explore the environmental factors, such as water temperature, salinity, and food availability, that influence the reproductive cycle of *P. viridis*.

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