Egyptian Journal of Aquatic Biology & Fisheries
Zoology Department, Faculty of Science,
Ain Shams University, Cairo, Egypt.
ISSN 1110 – 6131
Vol. 29(5): 609 – 637 (2025)
www.ejabf.journals.ekb.eg

Aquaculture Perspectives on the Reproductive Biology of the Asian Moon Scallop (*Amusium pleuronectes*) from Two Indonesian Waters

Budiyati[1], Sharifuddin Bin Andy Omar[2], Andi Niartiningsih[2], Ita Widowati[3], Rina[4], Nurdin Kasim[1], Maria Goreti Eny Kristiany[5], Sinar Pagi Sektiana[5]

[1]Marine and Fisheries Polytechnic of Bone, Jl. Sungai Musi KM 9 Pallete, Bone Regency, South Sulawesi, 92719 Indonesia.
[2]Department of Fisheries Science, Faculty of Marine Sciences and Fisheries, Hasanuddin University, Jl. Perintis Kemerdekaan Km.10, Tamalanrea, Makassar, South Sulawesi 90245, Indonesia.
[3]Department of Marine Science, Faculty of Fisheries and Marine Science, Universitas Diponegoro, Semarang, Central Java 50275, Indonesia.
[4]Fisheries Resource Utilization Study Program, Fisheries Business Expert Polytechnic (AUP), Jl. AUP No. 1, Pasar Minggu, South Jakarta 12520, Indonesia.
[5]Aquaculture Technology Study Program, Fisheries Business Expert Polytechnic (AUP), Jl. AUP No. 1, Pasar Minggu, South Jakarta 12520, Indonesia.

[*]Corresponding author: budiyati343@gmail.com

ARTICLE INFO

Article History:
Received: June 5, 2025
Accepted: Aug. 29, 2025
Online: Sep. 13, 2025

Keywords:
Amusium pleuronectes,
Gonadosomatic index,
Gonadal maturity stages,
Size at first gonadal Maturity,
Makassar Strait,
Bone Bay

ABSTRACT

The scallop *Amusium pleuronectes* is a highly economically and ecologically valuable bivalve species. This study examined biometric parameters, gonadal maturity stages (GMS), size at first gonadal maturity, and the gonadosomatic index (GSI) to evaluate their implications for broodstock management, hatchery seed production, and the broader development of sustainable scallop aquaculture in Indonesia. Sampling was conducted at Teluk Bone and Makassar Strait in January, May, July, September, and October 2021. Analyses included morphological and histological assessments of gonadal maturity and the determination of size at first gonadal maturity using the Spearman–Karber method. The results revealed significant differences in GMS, size at first gonadal maturity, and oocyte diameter between the two locations. In Teluk Bone, scallops exhibited greater variability in GMS, with the highest mean value recorded in September (25.99 ± 18.36%), whereas in Makassar Strait, GMS peaked in October (47.84 ± 35.61%). The size at first gonadal maturity was 52.69 mm in Teluk Bone and 45.77 mm in Makassar Strait. These findings indicate that environmental conditions in the two locations significantly influence the reproductive characteristics of *A. pleuronectes*. Teluk Bone, with more variable conditions, may provide a more favorable environment for reproduction and aquaculture potential than the Makassar Strait. This study provides critical insights for the sustainable management, aquaculture development, and conservation of *A. pleuronectes* populations in Indonesian waters.

INTRODUCTION

The development of aquaculture for bivalves has increasingly gained attention as global demand for sustainable seafood production continues to rise **(Wijsman *et al.*, 2018)**. In line with international commitments to the United Nations Sustainable

Development Goals, which emphasize the sustainable use and conservation of marine resources **(United Nations, 2015)**. Among commercially valuable bivalves, scallops (family Pectinidae) are a promising aquaculture candidate due to their rapid growth, high market value, and consumer preference **(Danilov *et al.*, 2024)**. The Asian moon scallop (*Amusium pleuronectes*) is widely distributed in Indo-Pacific waters and has become one of Southeast Asia's most exploited scallop species **(Soffa *et al.*, 2024)**. Despite its potential, cultivation of *A. pleuronectes* in Indonesia remains underdeveloped, mainly due to limited knowledge of its reproductive biology, a fundamental prerequisite for hatchery seed production and sustainable aquaculture practices.

Reproduction plays a central role in the life cycle of scallops, encompassing gonadal development, maturation, spawning, and fecundity. Gonadal maturity stages provide essential information for understanding reproductive cycles, including the size and age at first maturity, spawning frequency, and reproductive seasonality **(Belda & Norte, 1988; Son & Chung, 2009)**. These parameters are critical in aquaculture because they determine the timing of broodstock conditioning, spawning induction, and larval rearing in hatchery systems. Moreover, the ability of scallops to exhibit hermaphroditic characteristics, producing both male and female gametes within the same gonad **(Gosling, 2003)**, highlights their reproductive plasticity, which has direct implications for seed production strategies.

Globally, scallop aquaculture has been widely practiced. In Japan, *Mizuhopecten yessoensis* (hotate) has been cultured since the mid-20th century using ear hanging, bottom, and net cage methods (Shumway and Parson, 2006). In Australia, research has focused on *Amusium balloti*, *Chlamys australis*, and *Pecten fumatus* **(Williams & Dredge, 1981; Cropp, 1993; O'Connor *et al.*, 1999)**. On the other hand, experimental culture of *Pecten maximus* was initiated in Scotland **(Mason, 1958)**. Studies on *A. pleuronectes* have been reported in Australia, the Philippines, and Indonesia, covering aspects such as growth, reproduction, recruitment, habitat conditions, and initial hatchery trials **(Belda & Del Norte, 1988; Del Norte, 1988; Widowati *et al.*, 1999; Prasetya *et al.*, 2010; Taufani *et al.*, 2016; Cabacaba *et al.*, 2020; Satriawan *et al.*, 2024)**.

Moreover, previous studies on related scallop species have established gonadal development stages and fecundity rates as essential indicators of reproductive potential **(Dredge, 1981; Arendse *et al.*, 2008; Williams & Babcock, 2005)**. However, information on the reproductive biology of *A. pleuronectes* in Indonesian waters remains scarce, particularly regarding the size at first maturity, gonadosomatic index (GSI), and fecundity under various environmental conditions. Such information is indispensable for establishing broodstock management protocols, determining minimum catch sizes to prevent recruitment overfishing, and developing hatchery-based aquaculture programs. Without these data, the sustainable utilization and cultivation of *A. pleuronectes* cannot be effectively achieved, potentially undermining both national aquaculture development and broader sustainability targets established under the SDGs **(FAO, 2020)**.

The Makassar Strait and Bone Bay represent two of Indonesia's most significant fishing grounds for *A. pleuronectes*, where natural populations are abundant and subject to intense harvesting **(Budiyati *et al.*, 2025)**. Despite their ecological and economic importance, the reproductive biology of these populations remains poorly understood, particularly regarding potential variations in gonadal development, fecundity, and size at first maturity across different environmental conditions. Such knowledge gaps limit the capacity to implement effective management measures for conserving wild stocks and developing sustainable aquaculture programs. Environmental factors such as water temperature, salinity, food availability, and local hydrodynamics can influence reproductive performance, potentially leading to population-specific adaptations that are critical to recognize for site-specific broodstock selection and hatchery operations **(Satriawan *et al.*, 2024; Soffa *et al.*, 2024)**.

Comparative studies of reproductive traits between populations in distinct habitats can provide valuable insights into the species' adaptive responses to local environmental conditions, informing fisheries management and aquaculture planning **(Farhadi *et al.*, 2024)**. Understanding these differences is particularly relevant for designing broodstock conditioning protocols, optimizing spawning induction, and maximizing seed production efficiency in hatchery systems. Moreover, such information supports the development of site-specific aquaculture strategies that balance production objectives with the ecological sustainability of natural populations. This ensures that aquaculture growth contributes not only to local food security but also to global commitments for ocean conservation and sustainable fisheries **(FAO, 2022)**.

Beyond national aquaculture priorities, this research also aligns with global sustainability agendas. Strengthening scallop aquaculture contributes directly to the United Nations Sustainable Development Goals (SDGs), particularly SDG 14 (Life Below Water), which emphasizes the sustainable use of marine resources **(United Nations, 2015)**. By enhancing knowledge of the reproductive biology of *A. pleuronectes*, this study supports evidence-based management of natural populations, reduces reliance on wild harvests, and promotes sustainable aquaculture systems that can mitigate fishing pressure on coastal ecosystems **(FAO, 2020; FAO, 2022)**. In this way, the findings extend beyond local contexts, offering insights relevant to regional and global efforts aimed at responsible aquaculture and biodiversity conservation.

In this context, the present study was conducted to investigate the reproductive biology of *A. pleuronectes* from the Makassar Strait and Bone Bay with an aquaculture-oriented perspective. We specifically examined biometric parameters, gonadal maturity stages, size at first maturity, and gonadosomatic index to evaluate their implications for broodstock management, hatchery seed production, and the broader development of sustainable scallop aquaculture in Indonesia. The outcomes of this research are expected to provide a scientific foundation for the cultivation and conservation of *A. pleuronectes*, contributing to the establishment of economically viable aquaculture systems while ensuring the long-term ecological integrity of natural populations.

MATERIALS AND METHODS

1. Study duration and sampling sites

This study was conducted over one year, from January 2021 to December 2021, to capture the complete reproductive cycle of *A. pleuronectes*. Monthly sampling was carried out to monitor gonadal development and reproductive patterns. Samples were collected during the first week of each month from Bone Bay and during the third week from the Makassar Strait. This sampling schedule was designed to provide temporal comparability between the two locations and to capture potential seasonal variations in reproductive activity. Sampling was conducted in two geographically distinct coastal regions of Indonesia. In the Makassar Strait, sites near the Cambaya District, Maros Regency, were selected to represent typical environmental conditions of the area. In Bone Bay, sampling occurred in the waters around Cappa Ujung, Bone Regency, reflecting the bay's general hydrographic and ecological characteristics (Fig. 1). These sites were chosen due to abundant *A. pleuronectes* populations and their importance for local fisheries, ensuring that the samples collected are representative of natural populations in both regions.

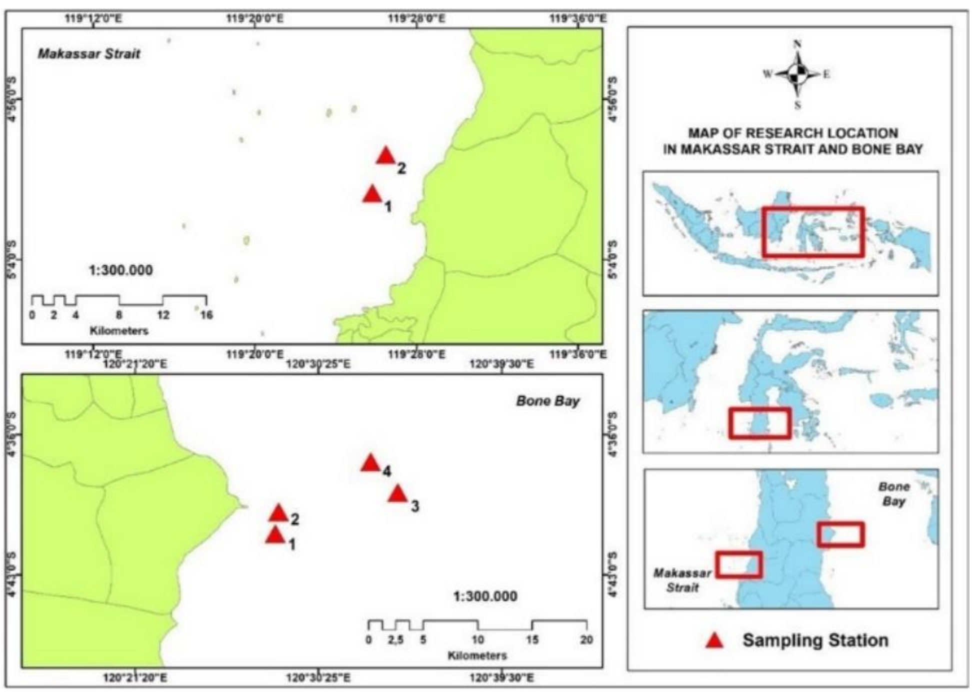

Fig. 1. Map of study site

2. Research procedure

Sampling of *A. pleuronectes* was conducted using a small-scale trawl operated by local shrimp fishers. All collected scallops were measured and weighed according to the sampling time. The specimens were immediately placed in cool boxes with ice to maintain freshness during transport to the Fisheries Aquaculture Laboratory, Polytechnic of Marine and Fisheries, Bone Regency. For gonad analysis, samples were stored in a freezer until further analysis. Whereas for shell length, scallops were removed from the freezer for laboratory processing and placed in basins with running water to thaw the ice. Shell length was measured using a Mitutoyo Vernier caliper (0–300 mm) with a precision of ±0.03 mm, and body weight was recorded using a digital balance with 0.001 g accuracy. Then, the scallop shells were carefully opened using a surgical knife, and the adductor muscle was dissected to expose the internal organs. Sex determination and gonadal maturity stage (GMS) were conducted using both macroscopic (morphological) and microscopic (histological) observations. Histological preparations were performed at the Maros Veterinary Center. The *A. pleuronectes* is known to reproduce as a simultaneous hermaphrodite, with both testicular and ovarian tissues developing within the same gonad during the reproductive cycle **(Del Norte, 1988)**. Morphological classification of gonadal maturity followed the criteria described by **Barber and Blake (2016)** (Table 1).

Table 1. GMS of Asian Moon Scallop (*A. pleuronectes*) – macroscopic and microscopic characteristics

Stage	Macroscopic Characteristics	Microscopic Characteristics
0 – Immature	Small, flat, transparent, colorless	Few connective tissues; narrow tubules with primary germ cells forming follicles
I – Developing	Follicles visible; light brown to yellowish; no sexual differentiation	Growing follicles; male follicles are lined with spermatogonia; female follicles contain oogonia and small oocytes (≤30 µm)
II – Differentiating	Clear differentiation into testis (white) and ovary (yellowish)	Spermatozoa appear in male follicles; many developing oocytes in female follicles (30–60 µm)
III – Recovering	Larger, thicker, soft, watery; testis white, ovary orange	Male follicles with more spermatozoa, not dense; most oocytes are developing in female follicles
IV – Maturing	Larger, thicker, brighter (testis white, ovary orange–pink)	Spermatogonia, spermatocytes, a few spermatids; partly grown and some larger oocytes (60–80 µm); minimal connective tissue
V – Half-full	Thicker, firm, bright (testis white, ovary pink)	Lumina filled with spermatozoa and nearly mature oocytes; few oogonia; minor connective tissue
VI – Full	Large, thick, firm, highly colored (testis cream, ovary dark red)	Maximum follicle size; male follicles packed with spermatozoa; female follicles filled with polygonal oocytes (80–90 µm)
VII – Spawning/Spent	Dull, thin, collapsed; watery; follicles empty; sexual differentiation may disappear	Smaller follicles with large empty spaces; few remaining spermatocytes and oocytes

Gonads were then separated from other internal organs and weighed to determine gonad weight. Female gonads at advanced maturity stages (GMS IV, V, VI, and VII) were placed in Rol bottles containing Gilson solution to cover the entire gonad. After several days of treatment, the gonads were transferred to Petri dishes for fecundity assessment. Oocytes were counted using a hand tally counter, pins, and a magnifying glass. Subsequently, egg diameters were measured by randomly selecting 300 oocytes, placing them on a desk glass, and observing under a microscope equipped with a calibrated ocular micrometer. This procedure allowed for the precise determination of gonadal development, fecundity, and egg size, providing essential data for reproductive biology assessment and aquaculture applications.

3. Data analysis

a) Biometric parameters

Biometric analysis of *Amusium pleuronectes* involved measuring and analyzing physical and biological characteristics to assess condition, health, and population dynamics. Parameters included total body weight, soft tissue weight, and shell weight. Differences in biometric parameters between the two study sites were evaluated using an independent-samples t-test in SPSS version 29 for Windows. The t-test formula is expressed as follows:

$$t = \frac{\overline{X_1} - \overline{X_2}}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

Where, $\overline{X_1}$ and $\overline{X_2}$ are the mean values of the two groups, s_1^2 and s_2^2 are the sample variances, n_1 and n_2 are the sample sizes.

b) Gonadosomatic index (GSI) and size at first gonadal maturity

The gonadosomatic index (GSI) was calculated following **Barber and Blake (2016)** using the formula:

$$\text{GSI}\ (\%) = \frac{\text{Gonad weight (g)}}{\text{Total tissue weight (g)}} \times 100$$

The average size at first gonadal maturity was estimated using the Spearman–Karber method **(Udupa, 1986)**:

$$m = Xk + \frac{x}{2} - X.\Sigma Pi$$

With a 95% confidence interval:

$$Antilog\ m = \left[m \pm 1,96 \sqrt{X^{2\Sigma}\left(\frac{p_i - q_i}{n_i - 1}\right)} \right]$$

In this method, m represents the logarithm of the shell length at which scallops first reach gonadal maturity. Xk is the midpoint logarithm corresponding to 100% gonadal maturity, while X indicates the difference between successive midpoints. For each size class, Pi is calculated as the proportion of mature scallops (ri) relative to the total number of scallops in that class (ni), and qi represents the proportion of immature scallops, calculated as 1 – Pi. This approach allows for a statistically robust estimation of the mean size at first maturity along with its confidence interval.

RESULTS AND DISCUSSION

1. Biometric parameters

The biometric analysis of *A. pleuronectes* from the Makassar Strait and Bone Bay revealed marked seasonal and spatial variations in gonadal development. Descriptive statistics indicated significant differences in tissue, gonad, testis, and ovary weights between the sites, particularly during January, May, September, and October ($P < 0.05$). For example, scallops from Bone Bay exhibited higher tissue and gonad weights in January and October. In contrast, individuals from the Makassar Strait showed comparatively higher values for specific parameters in May and July. Ovarian weights also varied, with Bone Bay generally exhibiting higher values, except in September, when Makassar Strait scallops displayed more advanced ovarian development.

Table 2. Biometric characteristics of Asian Moon Scallop (*A. pleuronectes*) at Makassar Strait and Bone Bay

Month	Parameter	Bone Bay (Mean g)	Makassar Strait (Mean g)	*P*-value
January	Soft tissue weight	11.04	6.33	0.001
	Gonad weight	1.52	0.58	0.001
May	Soft tissue weight	13.45	17.17	0.001
	Gonad weight	1.9	2.86	0.001
July	Soft tissue weight	8.42	8.82	0.301
	Gonad weight	1.78	3.09	0.004

These findings suggest that scallop populations in the two sites do not follow identical reproductive cycles, reflecting localized environmental conditions that differentially influence gonadal growth. Such site-specific differences in biometric parameters are critical for determining broodstock conditioning strategies, as they highlight the need to align hatchery seed production schedules with natural peaks in gonadal development.

2. Gonad maturity stage (GMS) based on morphological characteristics

The reproductive cycle of *A. pleuronectes* was categorized into six gonadal maturity stages (GMS phase 1–6), each reflecting distinct morphological, physiological, and functional characteristics of the gonads (Fig. 2 and Table 3). These stages illustrate the transition from immature gonads to complete spawning and subsequent recovery, providing valuable information for understanding reproductive biology and guiding broodstock management in aquaculture.

At this initial stage (Fig. 2A), the gonads were very small, translucent, and often indistinguishable from surrounding tissues. No gametogenesis was observed, and histological sections confirmed the absence of germ cells. The pale appearance of the gonad indicates minimal reproductive activity, consistent with an early somatic growth phase **(Freites *et al.*, 2010)**. Physiologically, energy is allocated primarily to tissue development and resource accumulation rather than reproduction. Such immaturity is typical of young scallops and is strongly influenced by environmental factors such as temperature, food supply, and habitat quality, all of which regulate the timing of gonadal activation **(Croll & Wang, 2007)**. Other bivalves note that this early stage represents a preparatory period during which energy reserves are built to sustain later reproductive investment **(Teaniniuraitemoana *et al.*, 2014)**. Identifying scallops in GMS-1 for aquaculture is important, as these individuals are unsuitable for broodstock conditioning and should be maintained under growth-enhancing conditions.

Table 3. Gonadal development stages of the scallop (*A. pleuronectes*) based on morphological characteristics

GSI Stage	Maturity Phase	Description
Stage 1	Immature	Very small, pale gonads; no visible gametes; non-functional for reproduction..
Stage 2	Developing	Enlarged gonads, early gametogenesis visible; gametes immature.
Stage 3	Nearly Mature	Gonads enlarged, dense, gametogenesis nearly complete; close to spawning.
Stage 4	Fully Mature	Gonads are fully developed with mature gametes; peak reproductive condition.
Stage 5	Spawning	Active release of gametes; gonads shrink post-release.
Stage 6	Post-spawning (Spent)	Shrunken, pale gonads; recovery and regeneration phase.

During the GMS-2 stage (Fig. 2B), the gonads increased in size and became more opaque, exhibiting noticeable shifts in pigmentation from translucent to whitish or pale cream. The darker coloration indicates the initiation of gametogenesis and elevated metabolic activity **(Wu *et al.*, 2017)**. Biochemically, this phase corresponds to lipid and protein accumulation in gonadal tissues, fueling gamete development and contributing to pigmentation changes **(Li *et al.*, 2000)**. Pigments like melanin accumulate as a protective mechanism against oxidative stress generated during rapid cellular proliferation **(Hurtado *et al.*, 2012)**. Histological analysis shows early differentiation of germ cells, with spermatogonia and oogonia beginning to proliferate **(Kapranova *et al.*, 2019)**. Environmental influences, including fluctuations in temperature and food availability, can accelerate or delay entry into GMS-2 **(Kalinina *et al.*, 2009)**. This stage represents the onset of reproductive activity, providing hatchery managers with an indication that individuals are beginning to invest in gamete production, though not yet ready for spawning.

At near-maturity (GMS-3, Fig. 2C), gonads became significantly enlarged, firmer in texture, and darker in color compared to earlier stages. Gametogenesis was advanced, with oocytes and spermatocytes fully formed, indicating fertilization readiness **(Freites *et al.*, 2010)**. Nutrient accumulation was especially evident, with high levels of lipids and glycogen supporting the energetically demanding processes of gamete maturation **(Hong-liu, 2004)**. The hormonal regulation of this stage is critical, with reproductive hormones such as estradiol and testosterone playing central roles in gametogenesis and sexual differentiation **(Croll & Wang, 2007)**. From a reproductive standpoint, this stage is pivotal because scallops are approaching peak spawning readiness. For aquaculture, individuals in GMS-3 are ideal candidates for broodstock selection, as they contain nearly mature gametes but have not yet released them. Conditioning broodstock during this stage ensures high-quality gametes for hatchery seed production.

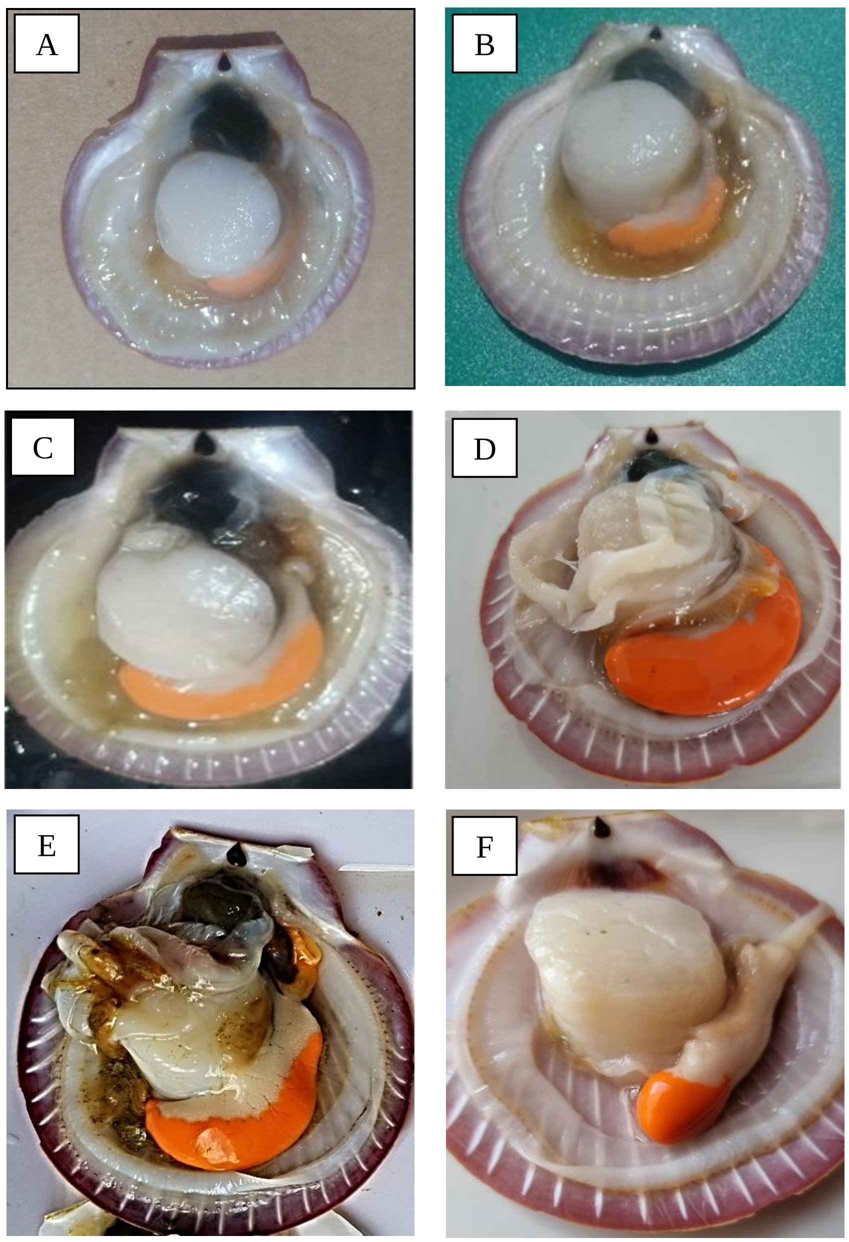

Fig. 2. Morphology of *A. pleuronectes* gonads at A) GMS-1; B) GMS-2; C) GMS-3; D) GMS-4; E) GMS-5; and E) GMS-6

The stage of GMS-4 represented full gonadal maturity (Fig. 2D), where scallops were entirely prepared for spawning. Morphologically, gonads reached their maximum size, were firm, and exhibited deep coloration due to dense gamete concentration. Both testes and ovaries were filled with mature gametes, with histological observations confirming full development of oocytes and spermatozoa **(Hong-liu, 2004)**. Biochemically, gonads exhibited peak levels of fatty acids and glycogen reserves, which are crucial for embryogenesis and larval growth **(Joaquim *et al.*, 2008; Freites *et al.*, 2010)**. Structural adaptations, such as expanded follicular tissues and efficient gamete release channels, ensured readiness for synchronized spawning **(Awaji & Hamano, 2004)**. Environmental stimuli, particularly temperature and food availability, are known to act as spawning cues **(Croll & Wang, 2007)**. In aquaculture, GMS-4 individuals are most valuable as broodstock, since gametes are of the highest quality and fertilization success is maximized when spawning is induced under controlled hatchery conditions.

Spawning occurred at GMS-5 (Fig. 2E), marked by the release of gametes into the water column. Externally, gonads appeared smaller and lighter in color due to gamete depletion. Histological analysis revealed residual gametes and the onset of gonadal regression. This stage is associated with a reduced condition index, as scallops experience high energetic costs from gamete release **(Deudero *et al.*, 2017)**. Cellular processes such as leukocyte infiltration and phagocytosis of remaining germ cells have been reported in related species, indicating gonadal remodeling **(Rouabhi *et al.*, 2019)**. In Mytilus and other bivalves, gonadal resorption at this stage has been linked to reduced physiological condition **(Besseau & Faliex, 1994)**. For aquaculture, scallops at GMS-5 are unsuitable for broodstock use, as spawning has already occurred and gamete quality is compromised. However, identifying this stage is important for timing broodstock replacement and understanding natural spawning windows.

The final stage (GMS-6, Figure 2F) corresponds to post-spawning recovery. Gonads were flaccid, pale, and markedly reduced in volume, reflecting exhaustion of reproductive reserves. At this point, scallops undergo tissue reorganization and begin regenerating gonadal structures in preparation for the next reproductive cycle **(Deudero *et al.*, 2017)**. Physiologically, glycogen and protein stores are severely depleted, reducing muscle strength and immune capacity **(Li *et al.*, 2010)**. This stage is vulnerable, with scallops exhibiting lower resistance to environmental stress and predation. Recovery depends on food quality and availability, as nutritional intake replenishes energy reserves required for gonadal redevelopment. In aquaculture, recognition of GMS-6 is important because broodstock in this phase require extended conditioning before re-entering the reproductive cycle. Effective management of this stage ensures recovery and long-term reproductive sustainability in cultured populations.

The sequential progression from GMS-1 to GMS-6 underscores the dynamic balance between growth, energy storage, gametogenesis, spawning, and recovery in *A. pleuronectes*. Understanding these stages provides a robust framework for optimizing broodstock management, synchronizing hatchery seed production with natural reproductive peaks, and ensuring the sustainable exploitation and conservation of wild scallop populations.

3. Gonad maturity stage (GMS) based on histology analysis

The histological section presented in Fig. (3) illustrates the GMS-2 (early developing stage) in female *A. pleuronectes*. The connective tissue (CT) is visible at this stage, forming a prominent structural component within the gonad. This tissue serves as both a physical framework and a metabolic matrix, facilitating the transport and allocation of nutrients to developing oocytes. Such dual functionality has been widely reported in bivalves. For instance, in the American oyster Crassostrea virginica, the vesicular connective tissue (VCT) functions as a temporary reservoir for nutrients that are subsequently mobilized during vitellogenesis, thereby supporting oocyte growth through the provision of lipids, proteins, and glycogen **(Eckelbarger & Davis, 1996)**. A similar role can be inferred in *A. pleuronectes*, as well-developed connective tissue at this stage strongly suggests active preparation for gametogenic development.

Within the gonadal lumen, oocytes at different stages of growth are conspicuously distributed, with a predominance of early oocytes (ot) and more advanced oocytes (oc). Their abundance reflects an intense cellular activity, marking the transition from an undifferentiated gonad towards a more specialized reproductive tissue. This proliferation of oocytes indicates that the gonad is actively entering a reproductive trajectory, although it has not yet reached full maturity. Notably, the increase in oocyte density is accompanied by the progressive organization of germinal and somatic cell components, suggesting the initiation of sexual differentiation pathways as observed in other mollusks **(Guerrero-Estévez & Mendoza, 2012; Silva *et al.*, 2012)**.

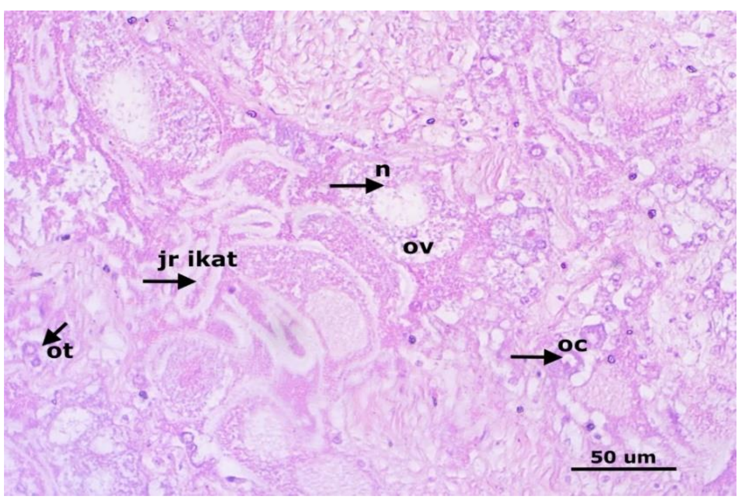

Fig. 3. Histology of GMS-2 from female *A. pleuronectes*. jr ikat = connective tissue; oc = Oocyt; and ot = ootid

Follicle cells surrounding the oocytes are another key feature during GMS-2. These cells maintain close structural and functional interactions with the oocytes, playing a fundamental role in nutrient transfer and possibly in the local regulation of gametogenesis. Evidence from deep-sea mussels, such as Bathymodiolus childressi, shows that follicle cells actively participate in yolk precursor synthesis and transport, directly contributing to vitellogenesis **(Eckelbarger & Young, 1999)**. Similarly, in several molluscan species, follicle and connective tissue cells have been reported to facilitate nutrient translocation via endocytic mechanisms, ensuring the continuous supply of materials for yolk formation and cytoplasmic growth **(Richter, 1986)**. In *A. pleuronectes*, the proximity of follicle cells to the developing oocytes supports the hypothesis that these cells act as a mediating interface between the nutrient reservoirs of the connective tissue and the metabolically demanding oocytes.

The compact and organized cellular structure of the gonad at this stage reflects a clear onset of differentiation within the germinal epithelium. However, despite the advanced histological organization, the oocytes remain in a preparatory phase, not yet reaching their optimal maturity required for spawning. The microscopic evidence presented in Fig. (3), therefore, highlights a gonad that is physiologically active and in transition, characterized by ongoing gametogenesis, but still far from achieving the cytoplasmic and nuclear conditions typical of fully mature, fertilization-ready oocytes. This stage thus represents a critical developmental window in which the scallop's gonadal tissue is intensively engaged in building the cellular foundation for subsequent reproductive success.

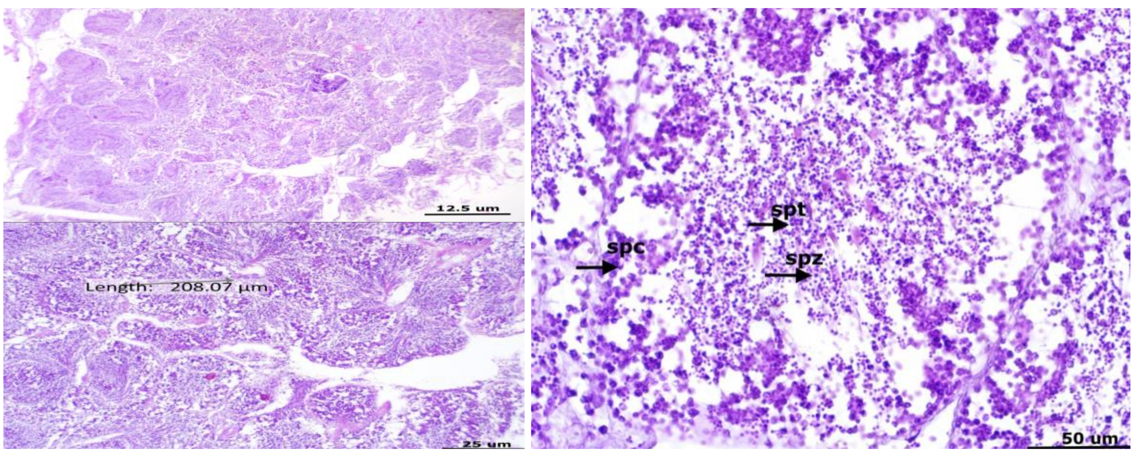

Fig. 4. Histology of GMS-2 from male *A. pleuronectes*. spc = spermatocysts; spt = spermatids; and spz = spermatozoa

Fig. (4) illustrates the gonadal tissue of male *A. pleuronectes* at Gonadal Maturity Stage 2 (GMS-2). At this stage, spermatocytes (spd) were clearly dominant compared to spermatids (spt) and spermatozoa (spz). The prevalence of spermatocytes indicates that the gonad is undergoing an active proliferative phase of spermatogenesis, in which spermatogenic cells are engaged in continuous division and differentiation. This stage is characterized by the mitotic division of spermatogonia, which gives rise to primary spermatocytes. These subsequently undergo meiotic processes to form secondary spermatocytes and, eventually, spermatids, as reported in other invertebrates such as Macrobrachium rosenbergii **(Poljaroen *et al.*, 2010)**.

Although spermatids were observed, their abundance remained relatively lower than that of spermatocytes at GMS-2. This suggests that differentiation into spermatozoa had already begun, but spermiogenesis was still in its early stages. Spermiogenesis involves profound morphological transformations of spermatids, including chromatin condensation, nuclear reshaping, and acrosome formation, which ultimately yield functional spermatozoa **(Ge *et al.*, 2011)**. The relatively limited presence of spermatids compared to spermatocytes thus highlights the transitional character of this stage, where spermatogenic activity is shifting from proliferation to differentiation.

Spermatozoa were observed in only small numbers at this stage, reinforcing the interpretation that the gonads were not yet fully mature and therefore not ready for active spawning. The scarcity of spermatozoa proves that spermatogenesis in *A. pleuronectes* proceeds progressively, with spermatozoa only becoming dominant in the later gonadal stages. Similar developmental trajectories have been documented in other marine species, including the Atlantic halibut *Hippoglossus hippoglossus*, where spermatocytes and spermatids predominate during the earlier stages of gonadal development. At the same time, spermatozoa become more abundant at advanced stages before spawning **(Weltzien *et al.*, 2002)**. The histological features of GMS-2 in male *A. pleuronectes* highlight a phase of intense spermatogenic proliferation coupled with the early onset of differentiation. From an aquaculture perspective, understanding this transitional stage is essential for determining the timing of broodstock conditioning and optimizing the capture of gametes at their most viable state for hatchery seed production.

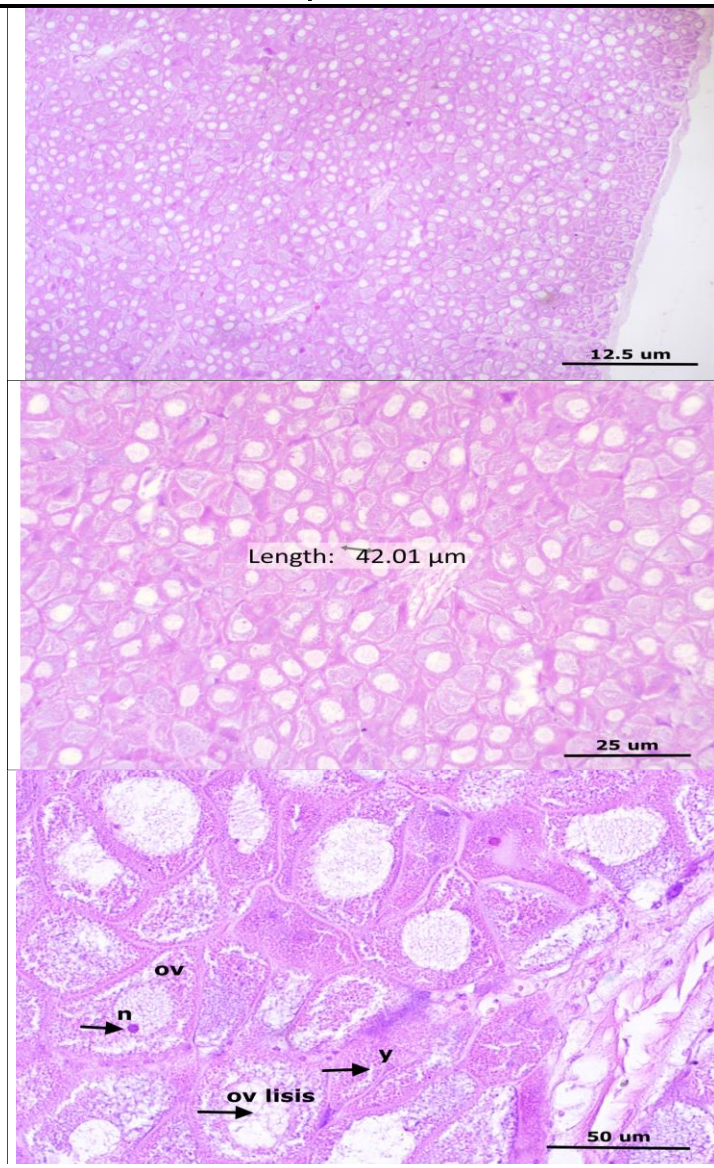

Fig. 5. Histology of GMS-3 from female *A. pleuronectes*. y= yolk; ov lysis= tertiary oocytes lysis .

The female gonads at GMS-3 (Fig. 5) exhibited advanced oogenic activity, with several features characteristic of the transition toward reproductive readiness. At this stage, tertiary oocytes (ot) were dominant compared to secondary oocytes (os), reflecting a substantial progression in gonadal development. The predominance of tertiary oocytes indicates that the scallops are approaching the final phase of gametogenesis, when the oocytes become competent for fertilization. This stage is typically associated with significant morphological and biochemical changes in mollusks, including cytoplasmic enlargement and nuclear migration, which collectively prepare the gametes for ovulation and subsequent spawning. Such dominance of tertiary oocytes is widely recognized as a reliable marker of reproductive capacity, highlighting that individuals in this stage are close to contributing to the spawning population.

A critical feature observed during this stage was the vitellogenesis (vt) process, which represents one of the most essential steps in oocyte maturation. Vitellogenesis is characterized by the intensive accumulation of yolk reserves in the cytoplasm, consisting mainly of lipids, proteins, and carbohydrates, which provide the necessary energy and structural materials to sustain embryonic development after fertilization. In Rapana venosa, vitellogenesis has been shown to involve both endogenous autosynthetic activity within the oocyte (mediated by the Golgi complex and endoplasmic reticulum) and exogenous nutrient uptake from surrounding follicle cells, resulting in the deposition of yolk granules and protein vesicles **(Son *et al.*, 2015)**. The presence of active vitellogenic oocytes in *A. pleuronectes* at stage III demonstrates that the species invests heavily in providing its gametes. This strategy maximizes larval survival in the planktonic phase and enhances recruitment success in natural populations and hatchery conditions.

Another notable feature of this stage is the prominent presence of germinal cells (gs), which play a supportive and regulatory role in oocyte maturation. Germinal cells provide trophic support, regulate the microenvironment surrounding the developing oocytes, and facilitate both vitellogenic and maturational processes. In species such as Patinopecten yessoensis, germinal cells have been shown to contribute through nutrient transfer and mediating signaling pathways that coordinate the timing of yolk accumulation and nuclear maturation **(Chung *et al.*, 2009)**. Their conspicuous presence in *A. pleuronectes* stage III gonads suggests that a similar mechanism may work, ensuring that oocytes develop synchronously and nutritionally adequate. This highlights the physiological complexity of reproductive processes in scallops and underscores the importance of maintaining optimal broodstock conditioning to support these cellular interactions in aquaculture.

The features of stage III gonads, namely the dominance of tertiary oocytes, the onset of intensive vitellogenesis, and the active involvement of germinal cells, represent a pivotal transitional point in the reproductive cycle of *A. pleuronectes*. These findings provide insights into the species' reproductive biology and have practical implications for broodstock management. Ensuring that broodstock reach this stage under controlled conditions is critical for optimizing gamete quality and hatchery seed production, thereby supporting the sustainable development of scallop aquaculture in Indonesia.

Fig. (6) illustrates the gonadal tissue of male *Amusium pleuronectes* at gonadal maturity stage 3 (GMS-3), where spermatids (spt) are visibly dominant compared with spermatocytes (spd) and spermatogonia (spg). This histological profile reflects an advanced phase of spermatogenesis, indicating that males at this stage have undergone substantial reproductive development toward sexual maturity. The prevalence of spermatids suggests that cellular differentiation has reached a critical point at which most germ cells are progressing toward functional spermatozoa. At this stage, spermatids, which arise after completing meiotic divisions, undergo spermiogenesis, characterized by profound morphological transformations. These include chromatin condensation, acrosome formation, and restructuring of cytoplasmic components, ultimately producing highly specialized spermatozoa optimized for fertilization **(Papah *et al.*, 2013)**. The dominance of spermatids in the gonadal tissue indicates that the testes primarily engage in terminal differentiation rather than early proliferative phases. Accordingly, the proportion of spermatogonia is reduced, reflecting a shift in gonadal activity from the generation of precursor cells to the maturation of gametes ready for spawning.

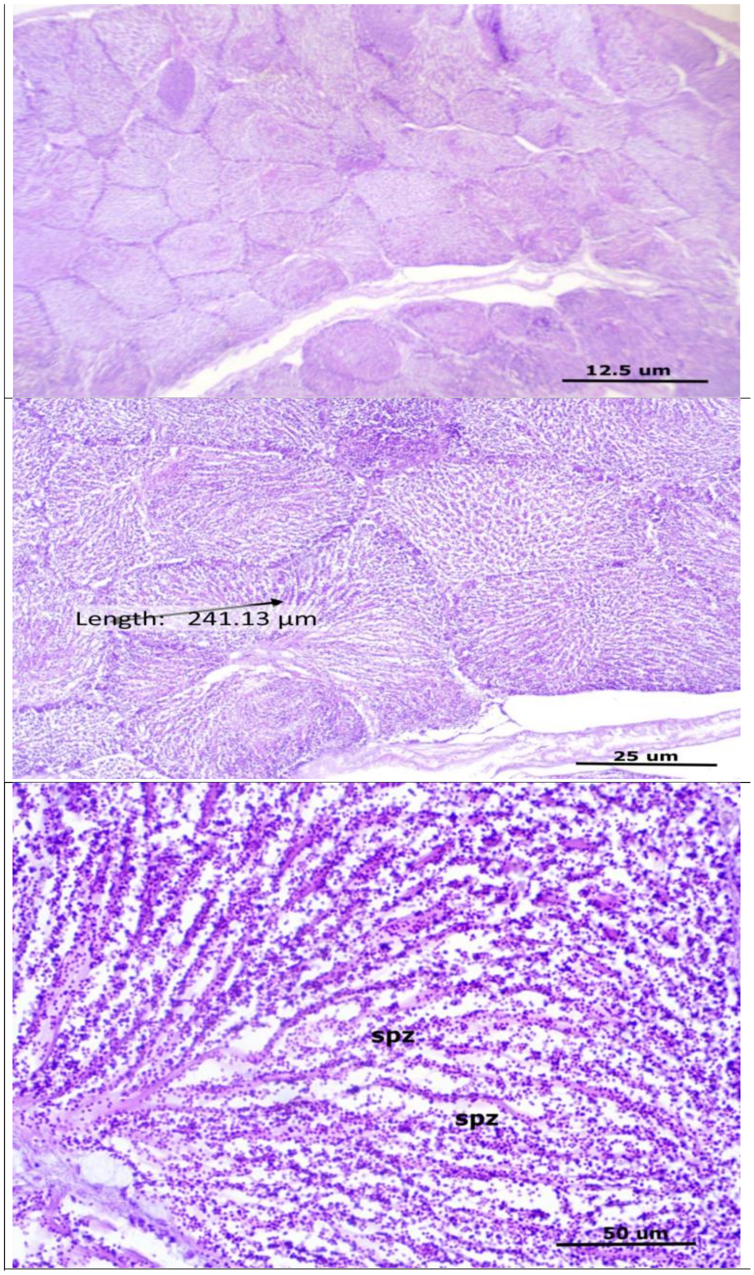

Fig. 6. Histology of GMS-3 from male *A. pleuronectes*. spt= spermatids; spz= spermatozoids; and spg= spermatogonium

Spermatocytes, the intermediate stage between spermatogonia and spermatids, are present but less abundant, as most have already completed meiotic division. Through this process, diploid spermatocytes undergo two successive meiotic divisions to form haploid spermatids **(Guraya, 1987)**. The transition from spermatocytes to spermatids marks a crucial point in gametogenesis, as it ensures genetic recombination and reduction in chromosome number, both essential for maintaining genetic stability across generations. The spermatids then proceed through spermiogenesis, involving nuclear elongation, mitochondrial migration, and the rearrangement of other organelles, ultimately producing mature spermatozoa capable of successful fertilization **(Bruslé, 2004)**. Thus, the histological profile of male gonads at GMS-3 highlights a stage of reproductive readiness in which spermatid differentiation predominates, while spermatogonial proliferation has declined. This transition reflects the physiological strategy of scallops to maximize sperm production during the peak of reproductive activity, ensuring reproductive success in natural spawning events and providing a valuable reference point for aquaculture broodstock management.

Fig. (7) illustrates the histological structure of female gonads at GMS-4, providing detailed insights into the internal cellular processes at this advanced stage of the reproductive cycle. The most prominent feature observed is the extensive lysis of mature oocytes (oc), accompanied by clear signs of degradation within the ovarian tissue (ov lysis). This condition reflects the post-spawning phase, in which the scallop has already passed the peak of reproductive readiness. At this point, unfertilized oocytes undergo structural breakdown, marking the onset of gonadal regression and resorption.

The process of oocyte lysis is closely linked to increased enzymatic activity within the gonadal tissue. Lysosomal proteases, such as cathepsins, play a fundamental role in breaking down cellular components that are no longer needed after spawning. Previous studies in marine organisms, including the gilthead seabream (*Sparus aurata*), have demonstrated that cathepsin B and L are key enzymes responsible for degrading vitellogenin-derived yolk proteins during oocyte maturation and subsequent resorption **(Carnevali *et al.*, 1999)**. Such enzymatic processes are essential for recycling nutrients stored within the oocytes, ensuring their availability for metabolic demands or future gametogenic cycles.

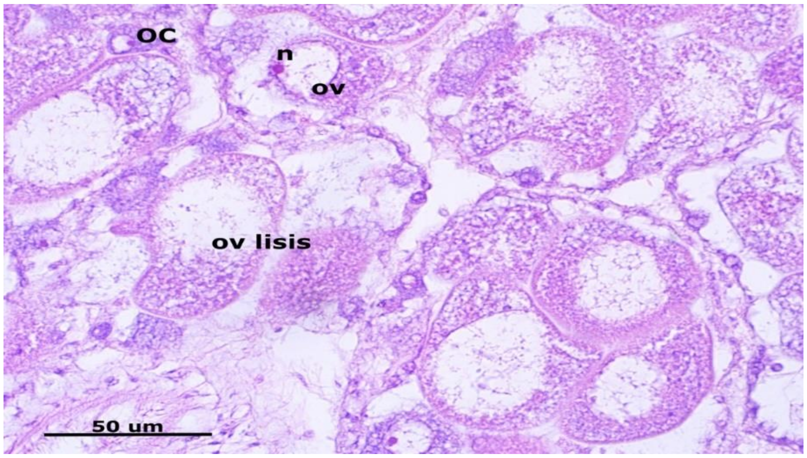

Fig. 7. Histology of GMS-4 from female *A. pleuronectes*. OC= oocytes; ov lysis= ovary lysis

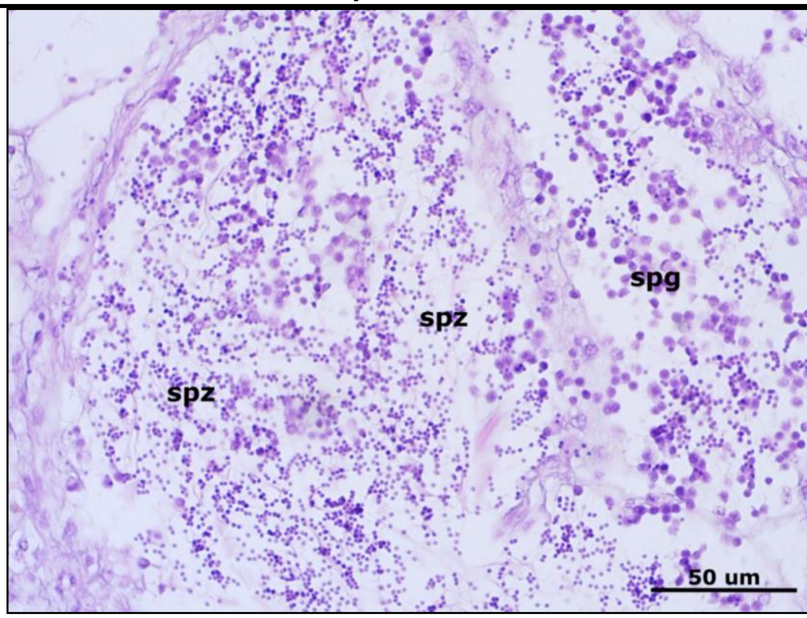

Fig. 8. Histology of GMS-4 from male *A. pleuronectes*. spz= spermatozoa; spg= spermatogonia

Additionally, histological observations suggest that oocyte resorption is supported by phagocytic activity of somatic cells within the gonads. These cells actively engulf and digest the remnants of lysed oocytes, forming phagosomes that facilitate the removal of degraded cellular material. This phenomenon has also been reported in other marine invertebrates, such as the starfish Asterina gibbosa, where phagocytic activity intensifies during winter due to temperature-induced mass oocyte lysis **(Ferrand, 1983)**. These processes collectively highlight that GMS-4 in female *A. pleuronectes* represents a transition into gonadal recovery, during which tissue remodeling and nutrient recycling dominate gametogenic activity.

Fig. (8) depicts the histological condition of male gonads at GMS-4, which similarly represents the terminal phase of the reproductive cycle. The testes at this stage are characterized by residual spermatozoa (spz) remaining in partially emptied follicles. Most spermatozoa have already been released during spawning, leaving behind follicles with a loose and vacated structure. The presence of a few remaining spermatozoa suggests that the gonad is completing its reproductive function, with unused gametes either undergoing resorption or being expelled in the final stages. This histological pattern corresponds to a marked reduction in spermatogenic activity, as the testes gradually shift from a densely packed state to one of depletion. The disintegration of spermatogenic tissue and follicular collapse are consistent with gonadal regression following spawning. Similar processes have been documented in other bivalves, where testicular regression involves not only the cessation of sperm production but also the catabolism of residual gametes to recycle energy reserves.

Thus, in both sexes, GMS-4 reflects the completion of the reproductive cycle in *A. pleuronectes*. For females, the stage is dominated by enzymatic degradation and phagocytic clearance of unfertilized oocytes, while in males, it is characterized by the resorption and elimination of remaining spermatozoa. These findings emphasize the cyclical nature of reproductive activity in scallops and provide crucial biological evidence for determining spawning seasonality, broodstock conditioning, and the timing of seed collection in aquaculture operations.

3. Gonadosomatic index (GSI)

The Gonadosomatic Index (GSI), also referred to as the Index of Maturity (IM) or Gonad Index (GI), is a percentage ratio representing the weight of gonads relative to the total body weight (including gonads) multiplied by 100 **(Bongers *et al.*, 1997; Guillena, 2018; Retnoaji *et al.*, 2023)**. This index has been widely employed to indicate aquatic organisms' gonadal development and reproductive readiness. In bivalves such as scallops, GSI is particularly valuable for assessing gametogenic cycles and seasonal reproductive patterns **(Barber & Blake, 2006)**.

Table 4. Comparison of gonadosomatic index (GSI) *P*-value between two locations

Month	Bone Bay (Mean ± SD)	Makassar Strait (Mean ± SD)	*P*-value
January	14.11 ± 8.72	9.50 ± 3.97	<0.001
May	13.88 ± 3.99	16.13 ± 5.44	0.027
July	18.58 ± 10.46	37.60 ± 31.55	<0.001
September	25.99 ± 18.36	23.11 ± 22.10	0.46
October	15.08 ± 7.67	47.84 ± 35.61	<0.001

GSI measurements can be based on either wet or dry tissue weights. However, dry weights are often preferred to reduce variability arising from differences in water content, which may fluctuate seasonally or across tissues **(Sastry, 1966)**. Changes directly influence the GSI in gonadal mass relative to somatic tissue, providing a reliable quantitative measure of reproductive activity and gonadal investment **(Mallet & Carver, 2009)**. In addition, GSI analysis is commonly integrated with histological observations to validate the timing of gametogenesis and spawning events across species **(Williams & Babcock, 2005)**.

Table (4) presents the seasonal variation in the GSI of *Amusium pleuronectes* collected from two distinct locations: Teluk Bone and the Makassar Strait. These data provide insight into the reproductive dynamics of scallops in relation to environmental conditions across both sites. In Teluk Bone, GSI values exhibited pronounced fluctuations throughout the year, with the highest mean recorded in September (25.99 ± 18.36%). This sharp increase may suggest that environmental factors, such as optimal seawater temperature, salinity, and food availability, created favorable conditions for gonadal development **(Bergeron & Buestel, 1979; Williams & Babcock, 2005)**. The broad range of GSI values across months indicates significant variability, reflecting the influence of seasonal nutrient availability and physical habitat conditions, including water currents and sedimentation rates **(Sastry, 1966)**. Such variability suggests possible adaptive strategies, including migration or microhabitat selection, to optimize reproductive success **(Beninger, 1987)**.

In contrast, the Makassar Strait exhibited a more consistent and progressive increase in GSI, particularly from January through October, with the highest mean value observed in October (47.84 ± 35.61%). This trend suggests the presence of relatively stable environmental conditions supportive of continuous gametogenic activity, such as steady temperature, salinity, and plankton availability **(Williams & Babcock, 2005)**. Notably, high variability in July (37.61 ± 31.55%) and October (47.84 ± 35.61%) indicates intra-population differences in gonadal maturation, possibly due to individual-level adaptive strategies in response to ecological pressures, including predation and competition **(Ali, 2019)**.

A statistical comparison using t-tests confirmed significant differences in GSI between Teluk Bone and the Makassar Strait during most months. In January, the mean GSI was significantly higher in Teluk Bone (14.11) compared to Makassar Strait (9.5) (t = 3.358, $P < 0.001$). In May, the trend reversed, with higher values in Makassar Strait (16.13) compared to Teluk Bone (13.88), yielding a significant difference (t = –2.255, $P = 0.027$). A more pronounced difference was observed in July, where Makassar Strait exhibited nearly double the GSI (37.61) compared to Teluk Bone (18.58) (t = –3.436, $P < 0.001$). Interestingly, in September, the difference between the two locations was not statistically significant (t = 0.742, $P = 0.460$), despite mean values of 25.99 (Teluk Bone) and 23.11 (Makassar Strait). This convergence suggests that environmental conditions in both sites may have aligned during this period, leading to similar reproductive outputs. Finally, in October, a significant difference was again detected, with Makassar Strait (47.84) showing markedly higher GSI values compared to Teluk Bone (15.08) (t = –5.102, $P < 0.001$).

These findings highlight that scallop reproductive patterns in Teluk Bone and the Makassar Strait are subject to considerable spatiotemporal variability. While Teluk Bone populations display sharp seasonal peaks in gonadal maturity, Makassar Strait scallops demonstrate a more sustained reproductive investment with markedly higher GSI values in the year's later months. Such differences may reflect localized environmental influences, including food availability, hydrographic conditions, and habitat stability, which drive reproductive strategies and gametogenic timing **(Son & Chung, 2009)**.

From a management perspective, understanding these site-specific reproductive cycles is crucial. Identifying periods of peak gonadal maturity enables more effective scheduling of conservation measures, such as seasonal closures during spawning peaks, as well as optimization of broodstock collection for hatchery purposes. These insights contribute to sustainable fisheries management and aquaculture development of *A. pleuronectes* in both regions..

4. Size at first gonadal maturity

Based on the analysis of 327 specimens from Bone Bay (Table 5), the size at first gonadal maturity for *A. pleuronectes* was estimated at 52.69 mm (logarithmic value 1.722). Among these, 217 individuals (66.4%) were found to have mature gonads, indicating that most of the population reaches sexual maturity at this size. In contrast, data from 257 specimens from the Makassar Strait (Table 6) revealed a smaller size at first gonadal maturity of 45.77 mm (logarithmic value 1.661), with 165 individuals (64.2%) being sexually mature. This indicates that individuals in the Makassar Strait population reach reproductive capability at a smaller size compared to those in Bone Bay.

Table 5. Estimation of the size at first gonadal maturity of *A. pleuronectes* in Bone Bay

Length Class (mm)	Class Midpoint (mm)	Log Midpoint (Xi)	Immature (Σ)	Mature (ri)	Total Samples (ni)	Proportion of Gonadal Maturity (pi)	(Xi+1 – Xi) = (X)	qi = 1 – pi	(pi × qi) / (ni – 1)
30.1 – 35.0	32.55	1.51	6	0	6	0.00	0.06	1.00	0.00
35.1 – 40.0	37.55	1.57	5	0	5	0.00	0.05	1.00	0.00
40.1 – 45.0	42.55	1.63	6	1	7	0.14	0.05	0.86	0.02
45.1 – 50.0	47.55	1.68	6	7	13	0.54	0.04	0.46	0.02
50.1 – 55.0	52.55	1.72	8	13	21	0.62	0.04	0.38	0.01
55.1 – 60.0	57.55	1.76	3	24	27	0.89	0.04	0.11	0.00
60.1 – 65.0	62.55	1.80	4	27	31	0.87	0.03	0.13	0.00
65.1 – 70.0	67.55	1.83	19	39	58	0.67	0.03	0.33	0.00
70.1 – 75.0	72.55	1.86	32	76	108	0.70	0.03	0.30	0.00
75.1 – 80.0	77.55	1.89	8	18	26	0.69	0.03	0.31	0.01
80.1 – 85.0	82.55	1.92	10	8	18	0.44	0.03	0.56	0.01
85.1 – 90.0	87.55	1.94	3	4	7	0.57	–	0.43	–

Note: Nilai m = 1.722; Estimasion size (Antilog m) = 52.69; Confidence level 95%; Minimum value = 55.54; Maximum value = 49.99

Table 6. Estimation of the size at first gonadal maturity of *A. pleuronectes* in the Makassar Strait

Shell Length Class (mm)	Class Midpoint (mm)	Log Midpoint (Xi)	Immature (Σ)	Mature (ri)	Total Sample (ni)	Proportion Mature (pi)	(Xi+1 – Xi) = (X)	qi = 1 – pi	(pi × qi)/(ni – 1)
30.1 – 35.0	32.55	1.51	27	3	30	0.10	0.06	0.90	0.00
35.1 – 40.0	37.55	1.57	3	4	7	0.57	0.05	0.43	0.04
40.1 – 45.0	42.55	1.63	1	5	6	0.83	0.05	0.17	0.03
45.1 – 50.0	47.55	1.68	3	3	6	0.50	0.04	0.50	0.05
50.1 – 55.0	52.55	1.72	5	13	18	0.72	0.04	0.28	0.01
55.1 – 60.0	57.55	1.76	5	27	32	0.84	0.04	0.16	0.00
60.1 – 65.0	62.55	1.80	15	12	27	0.44	0.03	0.56	0.01
65.1 – 70.0	67.55	1.83	10	25	35	0.71	0.03	0.29	0.01
70.1 – 75.0	72.55	1.86	11	24	35	0.69	0.03	0.31	0.01
75.1 – 80.0	77.55	1.89	7	16	23	0.70	0.03	0.30	0.01
80.1 – 85.0	82.55	1.92	1	26	27	0.96	0.03	0.04	0.00
85.1 – 90.0	87.55	1.94	4	7	11	0.64	0.02	0.36	0.02
Total	–	–	92	165	257	7.71	0.04	–	0.19

Note: m = 1.661; Estimasion size (Antilog m) = 45.77; Confidence level 95 %; Minimum value = 49.46; Maximum value = 48.67

The observed disparity between the two locations reflects the influence of both environmental and biological factors on gonadal development. In Teluk Bone, larger size at first maturity may be associated with favorable environmental conditions, including optimal water temperature, salinity, and food availability, which promote growth and allow individuals to reach gonadal maturity at larger sizes **(Williams & Babcock, 2005; Hold *et al.*, 2013)**. Conversely, the smaller size at first maturity in the Makassar Strait population may reflect adaptive responses to local ecological pressures, such as higher predation risk or competition, which favor earlier maturation at smaller sizes to ensure reproductive success **(Ali, 2019)**.

Histological observations support these findings, showing that individuals approaching exhibit well-developed gonadal structures, confirming sexual readiness. Genetic differentiation may also influence the variation between the two populations, as local adaptation has been documented to affect reproductive traits, including size at maturity **(Mahidol *et al.*, 2007)**. These findings have important implications for resource management. Minimum catch sizes should be tailored to the local values to ensure that individuals can reproduce before harvest. For example, enforcing a size limit above 52 mm in Teluk Bone and above 45 mm in the Makassar Strait would allow populations to maintain reproductive capacity, promoting sustainable aquaculture management of *A. pleuronectes* populations in both regions.

CONCLUSION

The reproductive biology of *Amusium pleuronectes* demonstrates distinct spatial and seasonal differences between Bone Bay and the Makassar Strait. Scallops in Bone Bay mature at larger sizes and show pronounced seasonal peaks, while those in the Makassar Strait reach maturity earlier and maintain more continuous reproductive activity. Histological and GSI analyses confirm the full reproductive cycles of both populations, emphasizing the importance of aligning broodstock selection with peak gametogenic stages for optimal hatchery performance. These findings also indicate that minimum harvest sizes should be adapted to local maturity thresholds to maintain population sustainability. Understanding these patterns supports site-specific management and sustainable development of scallop aquaculture in Indonesia.

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