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Color characteristics and histology of the ovarian development in the sesarmid crab, *Episesarma versicolor* (Tweedie, 1940) from Thailand

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ABSTRACT: The female reproductive histology of crabs has been widely observed but not for the sesarmid crab, *Episesarma versicolor* (Tweedie, 1940), an economically important crab in Thailand. This study determined how oocyte development related to the gonadosomatic index (GSI). The ovaries of the collected specimens were morphologically and histologically examined. The germination of the ovary commenced at the center of the ovarian tissue, consisting of oogonia proliferation as the primary growth phase, referred to as the previtellogenic stage (OcI). The secondary growth phase was divided into the early vitellogenic stage (OcII) and the late vitellogenic stage (OcIII) with the mature stage (OcIV) formed within the germinal zone. Four distinct stages of ovary development were identified. Stage I ovary (immature stage; GSI $= 0.32 \pm 0.13$, $n = 69$) appeared as the smallest organ with a translucent color and most oogonia proliferation in the primary growth phases. Stage II ovary (developing stage; GSI $= 0.70 \pm 0.10$, $n = 52$) was characterized by the appearance of a creamy white color and mainly contained OcII oocytes. In Stage III (developed stage; GSI $= 1.23 \pm 0.37$, $n = 46$), a bright orange ovary developed with the proliferation of OcIII/OcIV oocytes, while Stage IV ovary (mature stage; GSI $= 2.63 \pm 0.43$, $n = 49$) presented as a deep yellow to red-brown/orange color and dominantly consisted of OcIV. The information obtained is beneficial for successful broodstock development as the initial step toward realizing large-scale production of this species.

KEYWORDS: mangrove habitat, sesarmid crab, reproductive system, ovary development, vitellogenesis, gonadosomatic index

INTRODUCTION

Oogenesis is commonly recognized as a vital element of breeding and fecundity in crustaceans [1, 2]. Several studies have investigated the process of oocyte development, and the reproductive cycle in decapod crustaceans has also been documented by many authors [1–4]. Historically, oocyte development has been categorized into maturity stages using 2 criteria as cellular characteristics such as size, form, nucleus-cytoplasm ratio and staining features, and the degree of vitellogenesis or yolk formation [2, 5, 6]. Based on the cellular feature, the oocytes are typically characterized into 4 to 6 stages, ranging from stage I oocytes (OcI) to stage VI oocytes (OcVI) [3, 4, 6], while for yolk formation, the oocytes are usually classified into 6 stages: primary oocytes; early previtellogenic oocytes; late previtellogenic oocytes; early vitellogenic oocytes; late vitellogenic oocytes; and mature oocytes [2–4, 6]. Events in the process of oogenesis are similar for most decapods, but the time relationship between certain events as well as the period and frequency of these events vary greatly in different species [5, 6]. Studies on the morphological differentiation of ovaries and oocytes relating to the oogenetic process are crucial keys to understanding reproductive mechanisms and ecology of different species to promote the sustainability of stocks in their natural habitats.

The sesarmid crab *Episesarma versicolor* (Tweedie, 1940) is highly diverged in the family Sesarmidae and is widely distributed in marine and estuarine waters throughout the Indo-West Pacific region [7, 8]. This species feeds mainly on mangrove leaves and detritus and is typically recognized as a decomposer that recycles organic matter within the ecosystem [9, 10]. In Thailand, *E. versicolor* inhabits mangrove ecosystems, living in burrows excavated at tree bases in mangrove habitats along the Andaman Sea Coast and the Gulf of Thailand [9, 11]. This crab is also widely exploited as a major source of protein-rich food [9, 12]. However, commercial hatcheries for this species are limited, with utilization mainly relying on wild stocks [12]. Therefore, this species is considered a potential candidate for aquaculture and stock enhancement programs. Previous studies have detailed the reproductive systems of both male and female sesarmid crabs [13, 14], but little information is available for the reproduction of *E. versicolor* [15]. This study provides a holistic description of oocyte development and reproductive cycles in *E. versicolor*. The results will improve the understanding of the regulatory mechanisms of oogenesis and embryogenesis in this species.

MATERIALS AND METHODS

Crab collection and study site

Two hundred and sixteen specimens of female *E. versicolor* (mean carapace width = 3.170 ± 2.12 cm and mean total weight = 25.16 ± 3.87 g) were collected monthly from mangrove habitats in Palian district, Trang Province, Thailand (7° 08′ 58.12″ N, 99° 40′ 10.11″ E) between December 2021 and September 2022. The study site was a large 32 km^2 mangrove forest with temperature and salinity varying from 23 to 28 °C and 20 to 45 ppt, respectively, during the study period. The samples were transported to the Marine Crab Research Laboratory, Faculty of Science and Technology, Rajamangala University of Technology Srivijaya, Trang Campus, and identified following the taxonomic guidelines of Lee et al [7]. Ethical approval for this study was granted by the Animal Care and Use Committee of Rajamangala University of Technology Srivijaya (ID#IAC 13-01-64).

Sample preparation and morphological analysis

Healthy crabs were sorted, packed in labeled plastic bags, and anesthetized using a rapid cooling method for 30 min [16]. The body weight (BW) and carapace width (CW) of each specimen were measured using a digital balance and calipers, respectively. The dorsal portion of the carapace was removed, and the ovaries were examined under a light microscope and photographed using a digital camera, Canon EOS 550D (Canon Inc., Tokyo, Japan). The reproductive stages of the ovaries were classified based on morphological characteristics such as color, texture, and the volume occupied inside the carapace [17, 18]. The ovaries were then collected and weighed using a standard electric balance with an accuracy of 0.0001 g. The gonadosomatic index (GSI) values were calculated using the formula: % GSI = ovary weight/body weight × 100.

Histological analysis

A whole ovary of each crab was quickly dissected and fixed in Davidson's fixative for 48 h at ambient temperature [19]. The ovary specimens were then processed using a standard histological technique [20, 21] with the fixed samples dehydrated through an alcohol series ranging from 70% to 100%. The ovaries were then infiltrated with xylene and embedded in paraffin. Tissue sections at 4-µm thickness were prepared using a rotary microtome, mounted on slides, and stained using various histochemical staining techniques such as Masson's trichrome (MT) and the periodic acid-Schiff reaction (PAS). The ovarian structure, cell types found in the ovary, and their development were determined and described using a light microscope, following the standard histological criteria [13, 22]. Three sections of each sample were used for measuring the size of the germinative cells. Diameters of the oogonia and oocytes were measured from around 50 cells per section using a micrometric ocular lens with sizes of the germinative cells at each development stage recorded as mean ± SD.

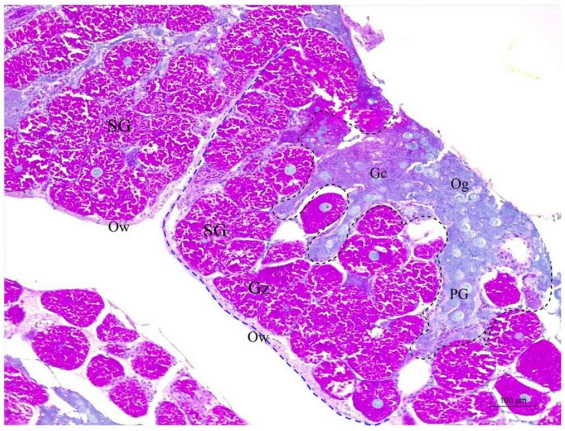

Fig. 1 Light photomicrographs of developed ovary of the sesarmid crab *E. versicolor*. Ovarian lobe (Ol, blue line) was divided into germinal center (Gc, black line) and germinal zone (Gz), which was surrounded by a thin layer of ovarian wall (Ow). Within the ovarian parenchyma, it consisted of the differentiating of oocytes including oogonia (Og), primary growth phase (PG), and secondary growth phase (SG). Staining method: Periodic acid-Schiff staining method.

RESULTS

Ovaries of *E. versicolor* were typically located above the hepatopancreas with H-like shapes and histologically composed of several ovarian lobes. The ovarian lobe was surrounded by the ovarian wall (Fig. 1). Each lobe was divided into 2 distinct zones: the germinal center (sometimes called germinative center) and the germinative zone. The germinal center comprised an inner layer of irregularly shaped epithelial cells with differentiating stages of oocytes including oogonium to primary growth phase, while the secondary growth phase was in the germinal zone. The female germ cells were assembled in an increased order of maturity from the germinal center toward the germinal ovarian wall. The commissure and some changes in oocytes and ovarian structure were observed with the progress of maturity.

Differentiation of oocytes during oogenesis

The developmental process of oocytes in the ovaries was asynchronous with each ovarian lobe composed of germ cells at various developmental stages such as the formation and accumulation of yolk granules as well as the nucleus-cytoplasm ratio. The developing germ cells of *E. versicolor* were categorized based on the shape and size of the oocytes into 3 distinct phases: oogonial phase (oogonia (Og)), primary growth phase

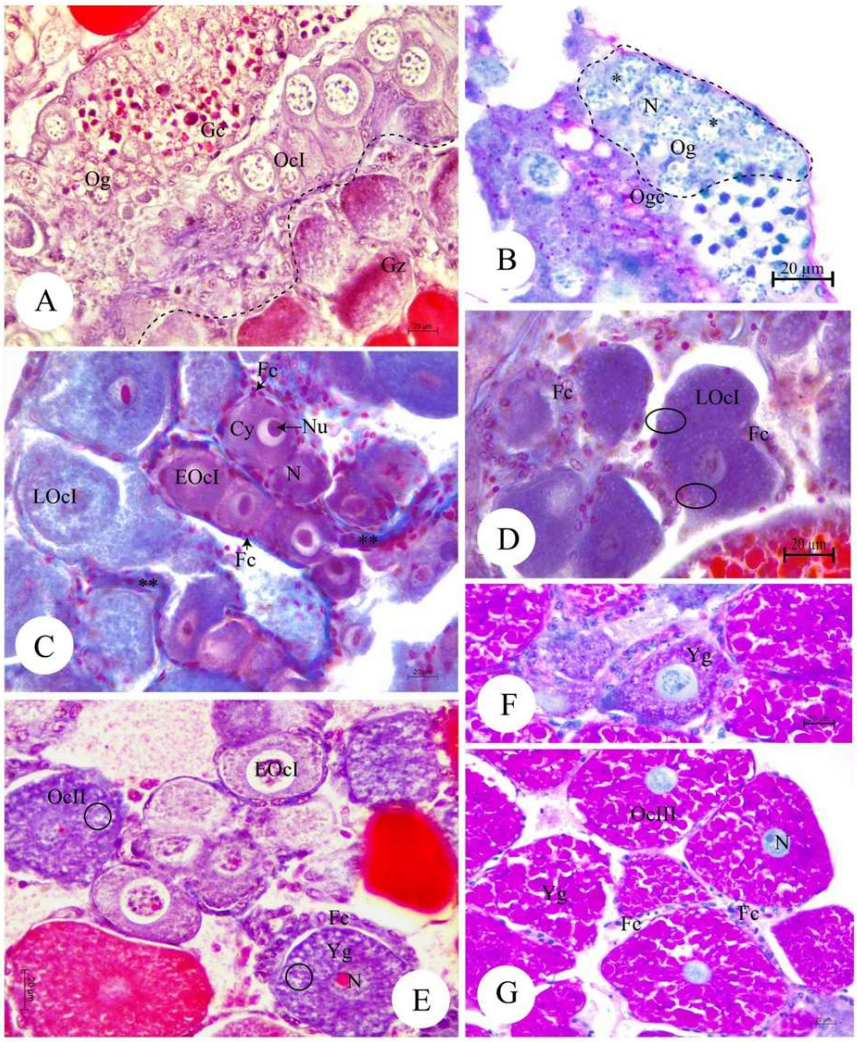

Fig. 2 Light photomicrographs of oogenesis in the sesarmid crab *E. versicolor*. Enlarged views of differentiating oocytes including oogonium (Og) within the oogonial cyst (Ogc) [A,B], early previtellognic (EOcI) and late previtellogenic (LOcI) stages [C,D], early vitellogenic stage [E,F], and late vitellogenic stage [G]. Atrerisks = connective tissue, Cy = cytoplasm, Fc = follicular cells, Gc = germinal center, Gz = germinative zone, Circles = lipid droplets, N = nucleus, Nu = nucleolus, and Yg = yolk granules. Staining method: A, C, D, E = Masson's trichrome staining method and B, F, G = Periodic acid-Schiff staining method.

(previtellogenic oocytes (OcI)) and secondary growth phase (early vitellogenic oocytes (OcII), late vitellogenic oocytes (OcIII), and mature oocytes (OcIV)) (Fig. 2 and Fig. 3).

Oogonium (Og) stage

The oogonia in the germinal center of the ovaries were differentiated from the primordial germ cells. The shapes of the oogonia were spherical or slightly oval with an average diameter of 10.23 ± 0.98 µm (Fig. 2A,B) and commonly found in the oogonial cyst (Fig. 2B). The nucleus was large and contained heterochromatin as a blue-purple color with PAS staining. The cytoplasm was thin and basophilic, resulting in a high nucleus-cytoplasm ratio.

Previtellogenic oocyte (OcI) stage

The developing Og became the previtellogenic primary oocytes (OcI) during the primary growth phase and exhibited evidence of mitotic division. They were classified into early OcI and late OcI stages (Fig. 2C,D). The onset of early OcI was round or slightly oval and increased in size with a mean diameter of 25.09 ± 0.72 µm (Fig. 2C) and penetrated among the connective tissue. The nucleus was oval and basophilic with a single large nucleolus. The cytoplasm

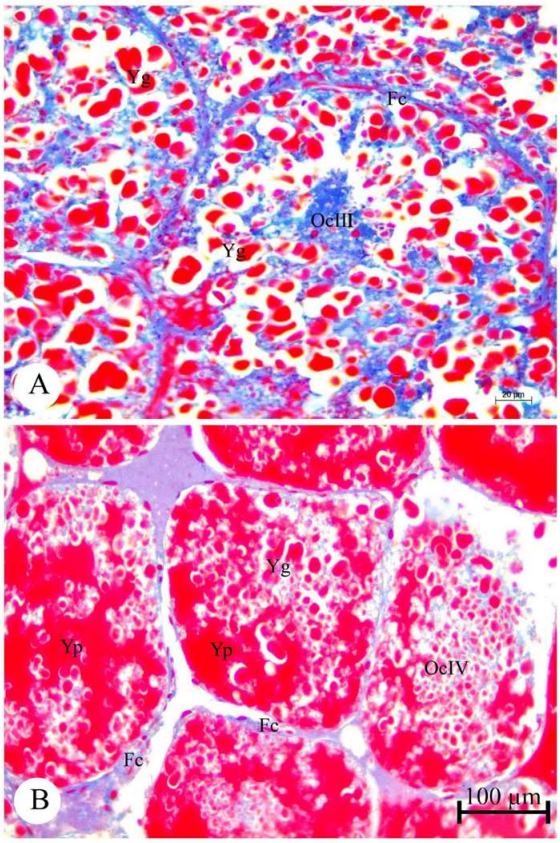

Fig. 3 Light photomicrographs of late vitellogenic stage (OcIII) [A] and mature ovary containing mature oocyte (OcIV) [B] of the sesarmid crab *E. versicolor*. Fc = follicular cell, Yg = yolk granule, and Yp = yolk plate. Staining method: A,B = Masson's trichrome staining method.

was homogeneous and basophilic and exhibited even purple staining using the MT method. The follicular cells began to develop but did not completely surround the oocytes. The late OcI stage continuously developed and increased in size to 56.02 ± 0.82 µm. Lipid droplets were observed in the cytoplasm, and follicular cells were identified (Fig. 2D).

Early vitellogenic oocyte (OcII) stage

The OcI grew rapidly and turned into early vitellogenic oocytes (OcII) in the secondary growth phase, which were initially characterized by the formation and accumulation of yolk granules. The shape of OcII was oval, and the size increased drastically to an average diameter of 86.09 ± 0.77 µm. The nucleus was irregularly shaped and located in the center of the oocytes (Fig. 2E,F). The cytoplasm became acidophilic with an even distribution of yolk granules (Fig. 2E). These yolks reacted positively to the PAS method (Fig. 2F) with numerous lipid droplets accumulating at the outer zone of the cytoplasm (Fig. 2E). The follicular cells became round-shaped and increased in number and size, resulting in a multilayer arrangement surrounding the oocytes (Fig. 2E).

Late vitellogenic oocyte (OcIII) stage

The OcII changed into late vitellogenic oocytes (OcIII) with significant increases in mean diameter to 151.20 ± 0.98 µm. The OcIII stage was defined by a high content of yolk granules (Fig. 2G). The nucleus decreased in size and presented as an irregular shape, moving towards the eccentric pole of the oocytes. The cytoplasm became robustly acidophilic, indicated by the pinkish color with the PAS method and red staining with the MT method (Fig. 3A). The nucleus cytoplasm ratio was low. The follicular cells had flat nuclei and formed a well-developed layer surrounding the oocytes (Fig. 2G).

Mature oocyte (OcIV) stage

This stage was the full development of the secondary growth phase. The mature oocytes (OcIV) were round and attained an average diameter of 165.43 ± 1.23 µm. The nucleus was presented at the animal hemisphere of the oocytes with no nucleolus and high condensation of chromatin. The cytoplasm was a strong reddish color (MT staining method) due to the complete integration of yolk granules (Fig. 3B). Some areas showed yolk platelets. The follicular cells had flat nuclei and formed a thin single layer with most detached from the surface of the oocytes.

Color characterization and histological changes in ovaries during the reproductive cycle

Based on the ovarian shape, the proportion of oocytes at each developing stage, and the histological characteristics, the ovaries were classified into 4 distinct stages: (I) immature stage; (II) developing stage; (III) developed stage; and (IV) mature stage (Fig. 4 and Fig. 5).

Stage I: Immature stage of ovary

The ovaries were small and a semi-transparent whitish color (Fig. 4A), making them difficult to distinguish from the digestive tract. Histological examination showed that the ovaries were composed of numerous Og and OcI, which were clearly evident in the germinative center of the ovarian lobes (Fig. 4B).

Stage II: Developing stage of ovary

The ovaries developed rapidly, becoming rod-like shaped with a creamy-white color (Fig. 4C). The thickness and width of the ovaries also increased. Histological observations revealed that the ovaries comprised a small number of Og and OcI with large amounts of OcII (Fig. 4D).

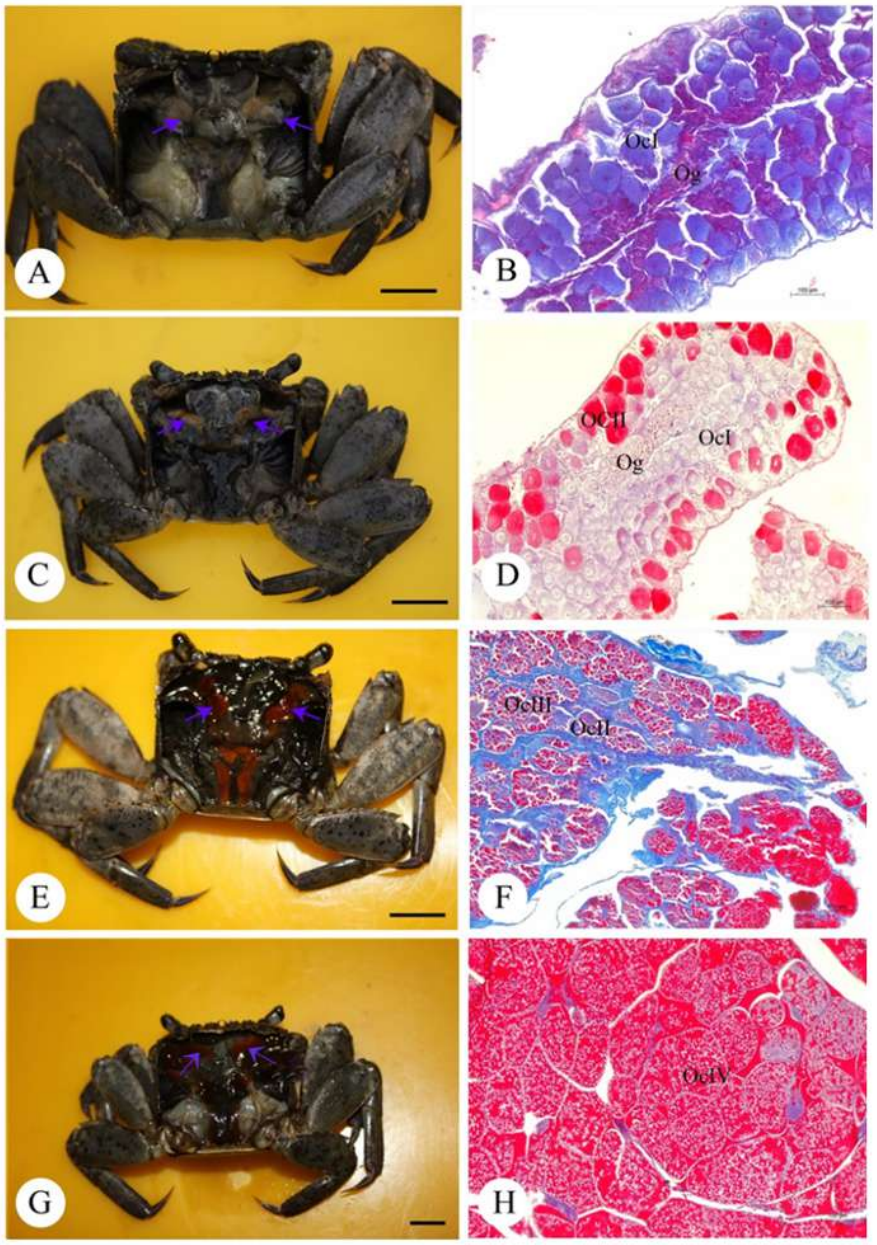

Fig. 4 Light photomicrographs of the ovarian development in the sesarmid crab *E. versicolor*. A,B: Immature stage, C,D: Developing stage, E,F: Developed stage, and G,H: Mature stage. Og = oogonia, OcI = pre-vitellogenic stage, OcII = early vitellogenic stage, OcIII = late vitellogenic stage, and OcIV = mature oocyte stage. Staining method: B, D, F, H = Masson's trichrome staining method.

Stage III: Developed stage of ovary

The ovaries grew rapidly, resulting in a substantial increase in volume, and turned bright orange (Fig. 4E), covering more than half of the hepatopancreas. Microscopic examination revealed that the ovaries were composed of OcII with OcIII as the most common oocytes (Fig. 4F).

Stage IV: Mature stage of ovary

The ovaries developed rapidly and reached full maturity. They were grape-like in shape and deep orange to red (Fig. 4G). Histological examination showed that mature oocytes (OcIV) were found in the germinal zone of the ovaries (Fig. 4H) of the crab.

Unfortunately, we noted that very few samples

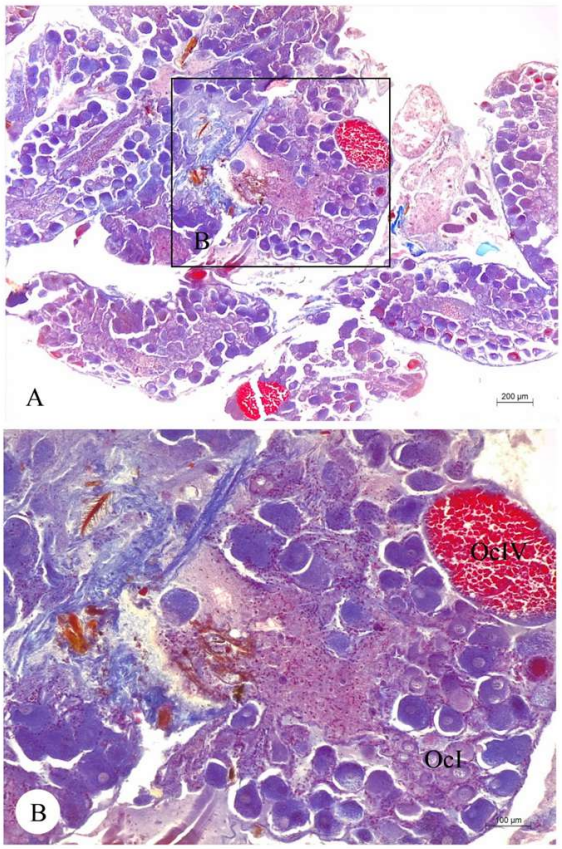

Fig. 5 Light photomicrographs of the immature stage (A,B) with the presence of mature stage (OcIV) among the previtellogenic stage (OcI) of the sesarmid crab *E. versicolor*.

of immature ovary stages ($n = 5$ from 20 individual samples) were found (Fig. 5A,B). Some oocyte stages may progress more rapidly, and this hypothesis should be tested in future studies.

Changes in the GSI values and the relationships between GSI and ovarian cycles observed in this study were considered important characteristics of ovary growth and development. The GSI values changed with the seasons, with the lowest value (0.32 ± 0.13) for ovaries at the immature stage I. For ovaries in the developing stage II, the GSI values did not change significantly (0.70 ± 0.10), while at the developed stage III, the GSI values increased (1.23 ± 0.37). At the mature stage IV, the GSI reached maximum value (1.95–4.21), and the ovaries reached maturation.

DISCUSSION

The oocytes in different regions of the ovary exhibited similar morphological characteristics and degrees of development, as previously described in many crustaceans [23, 24], for example the freshwater crab *Travancoriana schirnerae* [1], the spider crab *Libinia spinosa* [23], the freshwater crab *Paratelphusa lamellifrons* [25], and the deep-water shrimp *Aristeus antennatus* [26]. However, this information is not included in the sesarmid crab *E. versicolor*; this is the first report.

Several classifications of ovarian development in decapods have been documented following a broad range of criteria including both histological and microscopic features [5, 6, 27, 28] and ultrastructural characteristics [2, 24]. Unfortunately, these ovarian features and oocytes were similar to those reported in the ovaries of *E. versicolor*. The oogonia were present as the first oocyte differentiation in the germinal center of the ovaries. Similarly, Krol et al [29] reported that oogonia were found in the periphery of ovarian tissue in decapod crustaceans. During the OcII, the shift from basophilic to acidophilic ooplasm was congruent with many observations in crustaceans [30–32].

The follicular cells changed between OcII and OcIII in both number and size, resulting in a multilayer arrangement surrounding the oocytes, associated with significant changes to the uptake of yolk granules during vitellogenesis [13, 24, 33]. These changes were also recorded in other decapods including the sesarmid crab *E. singaporense* [13], the blue swimmer crab *Portunus pelagicus*, the mud crab *Scylla serrata* [22], and the giant river prawn *Macrobrachium rosenbergii* [34].

The developmental stages of *E. versicolor* oocytes and ovaries based on their gross morphology closely followed the spider crab *Libinia emarginata* [3], the sesarmid crab *E. singaporense* [13], the giant river prawn *M. rosenbergii* [34], the snow crab *Chionoecetes opilio* [35], the blue swimmer crab *P. pelagicus* [36], and the mud crab *S. paramamosain* [37]. A similar color pattern was also observed in *Uca rapax* [5] and *Portunus sanguinolentus* [17].

CONCLUSION

The morphological and histological changes observed in this study first elucidated the sequential developmental patterns of oocyte and ovarian maturations of *E. versicolor*. A pronounced macroscopic differentiation in size, coloration, and histology was observed during the ovary maturation process. To investigate the gonadal differentiation of the life cycle, relationships between the accurate reproductive cycle and environmental factors should be observed in-depth in future studies, thereby allowing adequate protection of the reproductive process and safeguarding the reproductive health status of *E. versicolor* populations in estuarine regions in Thailand.

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