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Original Article

Ovarian development of *Xiphopenaeus kroyeri* (Crustacea: Penaeidae) from Espírito Santo, southeastern Brazil

Desenvolvimento ovariano de *Xiphopenaeus kroyeri* (Crustacea: Penaeidae) no Espírito Santo, sudeste do Brasil

C. V. Bernabé[a], C. F. F. Craveiro[b], D. C. Mattos[a], P. H. R. Aride[c], A. B. Souza[a], L. A. Bassul[a], M. F. Polese[a], L. D. Cardoso[a], M. A. Silva[d] and H. D. Lavander[a*]

[a]Instituto Federal de Educação, Ciência e Tecnologia do Espírito Santo – IFES, Piúma, ES, Brasil
[b]Universidade Federal Rural de Pernambuco – UFRPE, Departamento de Pesca e Aquicultura, Recife, PE, Brasil
[c]Instituto Federal de Educação, Ciência e Tecnologia do Amazonas – IFAM, Manaus, AM, Brasil
[d]Universidade Federal do Espírito Santo – UFES, Alegre, ES, Brasil

Abstract

This study aimed to describe and characterize the stages of gonadal development of females of *Xiphopenaeus kroyeri* caught by artisanal fishers in Espírito Santo state, southeastern region of Brazil. All females (n= 1,831) were subjected to macroscopic and microscopic morphological analysis (n= 333) of the ovaries. From the morphology, coloration and degree of turgidity of the fresh ovary, macroscopic analysis determined five stages of gonadal development. The macroscopic analysis showed difficulties in differentiating the immature and spawning stages due to the similarity between the colors of the ovaries, which confirms the need to perform the macroscopic and histological analysis simultaneously for fisheries management studies. Microscopic observations allowed us to analyze the following six stages of cell development: oogonia, previtellogenic oocytes, primary vitellogenic oocytes, secondary vitellogenic oocytes, mature oocytes and atretic oocytes. From this, five stages of gonadal development were defined, i.e., immature, early development, advanced development, mature and spawned. The presence of peripheral bodies was not observed in this species. These results help to clarify and better understand the reproductive and population aspects of the Atlantic Seabob, which are fundamental for the establishment of management and conservation measures of this resource.

Keywords: reproduction, gonadal development, maturation stages, histology, germ cells.

Resumo

Este estudo teve como objetivo descrever e caracterizar os estágios de desenvolvimento gonadal de fêmeas de *Xiphopenaeus kroyeri* capturado por pescadores artesanais no Estado do Espírito Santo, região sudeste (Região sudeste = Rio de Janeiro, São Paulo, Minas Gerais e Espírito Santo) do Brasil. Todas as fêmeas (n= 1.831) foram submetidas à análise morfológica macroscópica e microscópica (n= 333) dos ovários. A partir da morfologia, coloração e grau de turgidez do ovário fresco, a análise macroscópica determinou cinco estágios de desenvolvimento gonadal. A análise macroscópica mostrou dificuldades em diferenciar os estágios imaturo e reprodutivo devido à semelhança entre as cores dos ovários, o que confirma a necessidade de realizar a análise macroscópica e histológica simultaneamente para estudos de manejo pesqueiro. As observações microscópicas permitiram analisar os seguintes seis estágios de desenvolvimento celular: oogônias, ovócitos previtelogênicos, ovócitos em vitelogênese primária, ovócitos em vitelogênese secundária, ovócitos maduros e ovócitos atrésicos. A partir disso, foram definidos cinco estágios de desenvolvimento gonadal, ou seja, imaturo, desenvolvimento inicial, desenvolvimento avançado, maduro e desovado. A presença de corpos periféricos não foi observada nesta espécie. Estes resultados ajudam a esclarecer e compreender melhor os aspetos reprodutivos e populacionais do camarão do Atlântico, que são fundamentais para o estabelecimento de medidas de gestão e conservação deste recurso.

Palavras-chave: reprodução, desenvolvimento gonadal, estágios de maturação, histologia, células germinativas.

1. Introduction

Penaeids shrimp are one of the most commercially captured and valued resources in the world (Pérez-Farfante and Kensley, 1997; FAO, 2022). Fishing for this resource is carried out on a large scale along the Brazilian coast and plays an important social, cultural, and especially economic role in fishing communities (Branco, 2005; Knox

*e-mail: henrique.lavander@ifes.edu.br
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and Trigueiro, 2015). According to the Ministry of Fisheries and Aquaculture (MPA), in 2011, 38.7 thousand tonnes (t) of marine shrimp were captured in Brazil. Among the most caught species in fisheries are the Atlantic Seabob *Xiphopenaeus kroyeri* (Heller, 1862), the pink shrimp (*Penaeus* spp.) and the white shrimp *Penaeus schmitti* (Burkenroad, 1936), with the Atlantic Seabob being responsible for 39.8% (15.4 thousand t) of the country's total marine shrimp production (Brasil, 2012).

The *X. kroyeri* or Atlantic Seabob as popularly known, is distributed in Venezuela, Guyana, Suriname, French Guyana and Brazil (Maranhão, Rio Grande do Norte, Alagoas, Sergipe, Bahia, Espírito Santo, Rio de Janeiro, São Paulo e Santa Catarina states), and in the Eastern Pacific, in Colombia (Carvalho-Batista et al., 2019). They inhabit coastal areas and regions with greater depths but are more abundant in shallower depths close to the coast, which have sandy or muddy bottoms (Costa et al., 2003; Costa et al., 2007; Boos et al., 2016). The life cycle occurs exclusively in the marine environment, and it is common to find juveniles and adults inhabiting the same environment (Branco, 2005; Santos and Freitas, 2006), preferentially inhabiting shallow zones of up to 30 meters (D'Incao, 1999; Costa et al., 2003).

The fishing of *X. kroyeri* is carried out either by the artisanal fleet, which acts mainly in the coastal and estuarine environments, or by the industrial fleet, which acts exclusively in oceanic regions (D'Incao et al., 2002; Boos et al., 2016). The artisanal fleet involved in this activity is composed basically of wooden vessels, small (6 to 10 meters long) and low power, resulting in short trips (Basilio et al., 2015; Musiello-Fernandes et al., 2017). The trawl net is the most used fishing gear in this type of fishing (Hostim-Silva and Soares, 2013). Despite the wide use of trawling, this activity causes significant negative impacts on marine ecosystems (Dias-Neto, 2011; Hiddink et al., 2017), since it is responsible for capturing a high percentage of bycatch, i.e., accompanying fauna (non-target species) and young specimens (Pérez-Roda et al., 2019) that have not reached sexual maturity and/or that have not yet contributed to the maintenance of the species (D'Incao et al., 2002; Castilho et al., 2015). Studies have indicated a significant reduction in natural stocks over the years due to trawl fishery activities in coastal environments (D'Incao et al., 2002; Simpson and Watling, 2006; Pérez-Roda et al., 2019) since this high effort negatively interferes with the recruitment and reproduction of the species (D'Incao et al., 2002; Boos et al., 2016).

Understanding of the reproductive aspects of a species is one of the factors that most contributes to good fishery management (Martins et al., 2013; Bolognini et al., 2017). In this sense, obtaining information on the reproductive processes of shrimps can help in the development of management policies that minimize the impacts caused by trawling. Among the main studies used is the classification of the stages of gonadal development of the species (Quintero and Gracia, 1998; Peixoto et al., 2003; Simpson and Watling, 2006; Lopes et al., 2014; Bolognini et al., 2017; Garcia et al., 2021; Craveiro et al., 2022).

The macroscopic and histological classification of the gonadal development stages is one of the most used methods in the description of the reproductive processes of penaeid shrimps (Quintero and Gracia, 1998; Bolognini et al., 2017). The microscopic classification of the ovaries aims to describe the stages of gonadal maturation at the cellular level and is increasingly used to confirm and validate the color scales determined in the macroscopic analysis (Quintero and Gracia, 1998; Lopes et al., 2014; Rios et al., 2022). The joint use of these analyzes guarantees a more reliable and complete description of maturation stages than estimates based only on macroscopic observations (Peixoto et al., 2003). These analyses are considered important tools for the definition of maturational stages, which serve as a basis for population and reproductive parameters and are fundamental for the establishment of management and conservation policies for penaeid shrimps (Peixoto et al., 2003; Simpson and Watling, 2006; Garcia et al., 2021).

The gonadal development of the species *X. kroyeri* was previously described by many authors, for different regions of Brazil (Campos et al., 2009; Martins et al., 2013; Lopes et al., 2017). Martins et al. (2013) used only macroscopic analysis to classify the stages, while Campos et al. (2009) and Lopes et al. (2017) used macroscopic and microscopic analyzes together. These studies classified the development of the ovary into four stages of maturation, namely: immature, developing, mature and spawned. However, several authors classified the ovarian development of other penaeid species into five different stages: immature, early maturation, advanced maturation, mature and spawning such as Vogt et al. (1989), Castille and Lawrence (1991), Tan-Fermin (1991), Medina et al. (1996); Quintero and Gracia (1998), Palacios et al. (1999), Ayub and Ahmed (2002), and recent studies as those by Bolognini et al. (2017), Craveiro et al. (2019) and Garcia et al. (2021). This difference is due to the lack of standardization in the maturation classification stages in shrimp, which so far does not have a solid/well-detailed basis to follow, making it difficult to take measures to manage these resources.

In this context, the present study aimed to describe and characterize in detail the stages of ovarian development of the Atlantic Seabob (*X. kroyeri*) caught in Espírito Santo state, southeastern Brazil, in order to obtain relevant information on the reproductive aspects of the species and contribute to a better management of this resource of great economic importance.

2. Material and Methods

2.1. Study area and sample processing

Shrimps were caught for 12 months (March 2019 to February 2020) by artisanal fishers in the municipalities of Anchieta (20° 48' 21" S 40° 38' 44" W), Piúma (20° 50' 7" S 40° 43' 42" W) and Itapemirim (21° 0' 42" S 40° 50' 2" W), located in the southern region of the state of Espírito Santo, southeastern Brazil (Figure 1).

Sampling was carried out with the authorization of the SISBIO Biodiversity Information and Authorization System No. 67056-1 and 67056-2, based on ICMBio Normative

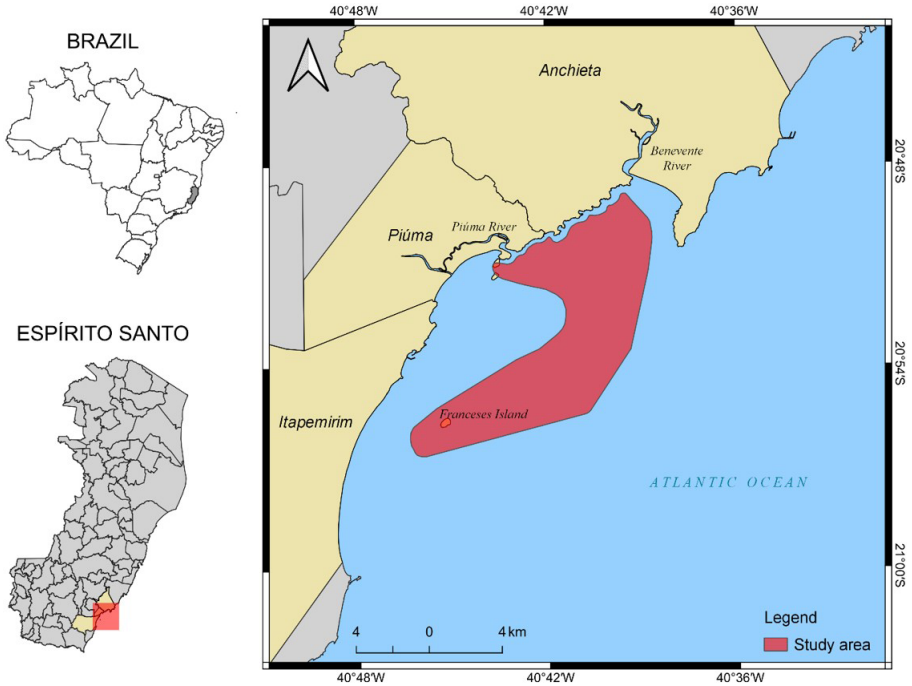

Figure 1. Geographical location of the study area on the southern coast of the state of Espírito Santo, southeastern region of Brazil.

Instruction Nº. 03/2014 (Brasil, 2014). The specimens were captured by a local motorized vessel 10 meters long, operating with double bottom trawl nets with wooden trawl doors. The net was 12 m long, with a 2.5 m wide mouth, 30 mm meshes (between knots) on the wings and body of the net, and 15 mm (between knots) on the bagger. The trawls were carried out in typical areas of shrimp fisheries, in a range of 4 to 20 meters in depth, lasting 60 minutes each at an approximate speed of 1.5 to 2 knots.

After each trawl, the captured shrimps were separated from the bycatch, then packed in plastic bags and stored in a thermal box with ice. Subsequently, the samples were transported to the laboratory, where individuals were identified as to species according to the Illustrated Key for Dendrobranchiata Shrimp Identification of Costa et al. (2003), taking into consideration the genetic studies conducted by Carvalho-Batista et al. (2019) in the state of Espírito Santo, Brazil. After the identification of the species, they were separated by sex according to their external characters (presence of petasma in males and thelycum in females).

Then, the females were measured for total length (TL: from the tip of the rostrum to the tip of the telson) and the length of the cephalothorax (CL: from the base of the rostrum to the upper margin of the carapace) with analog calipers (0.05 mm).

2.2. Macroscopic and microscopic description of the ovaries

All females were subjected to macroscopic evaluation of the ovaries through morphology (n= 1,831), and the degree of turgidity and coloration of the fresh gonads were compared with a widely available color catalog (Pantone Matching System, Coated Simulation, Pantone, Carlstadt, NJ, USA).

For histological analysis, 333 ovaries were used (approximately 25 females randomly sampled per month), which were dissected, weighed and pre-classified as to their macroscopic maturational stage (adapted from Craveiro et al., 2019; Craveiro et al., 2022). The samples were fixed in Davidson's solution for 24 hours, then transferred and stored in 70% ethanol (Bell and Lightner, 1988).

For the microscopic description, fragments of the median portion of each ovary were subjected to dehydration in increasing series of ethanol (70-100%), diaphanized in xylol, impregnated and set in paraffin at 55 °C. After embedding in paraffin, the tissues were sectioned (5 µm) in a rotating microtome and stained using the Haematoxylin(H)/Eosin-phloxine(E-P) method (adapted from Junqueira and Junqueira, 1983). All slides were photographed through the optical microscope equipped with a digital camera, using the *Leica LAS EZ 3.4 software* for the characterization of gonadal development at the cellular level. The photomicrographs of the slides were digitized with Leica software with objectives from 4x to 100x of magnification.

Oocytes were classified according to the histological characteristics described for penaeids (adapted from Craveiro et al., 2019; Craveiro et al., 2022) and about 100 oocytes (or total number available per category) presenting sectioned nucleus were measured using the *Image Tool software version* 2.0 for Windows (University of Texas Health Science Center in San Antonio, TX, USA). The mean and standard deviation were obtained for the diameter of the oocytes and were subsequently subjected to analysis of variance (ANOVA) at a 5% confidence interval,

considering the necessary assumptions of normality and homoscedasticity, which was followed by the Tukey test ($p<0.05$) for the separation of means in case of significant differences.

3. Results

Over 12 months, 1,831 females were captured (approximately 153±49 females per month), which varied in total length from 42 to 146 mm (mean: 101.4±19 mm), cephalothorax length from 8 to 35 mm (mean: 21.2±5 mm) and total wet weight ranging from 0.7 to 18.2 g (mean: 6.4±3.3 g).

3.1. Macroscopic description of the ovaries

The ovary of the female of *X. kroyeri* is a symmetrical organ and presents bilateral symmetry. It has a tubular shape and is fused in the cephalothorax region all the way to the final portion of the abdomen. They have two anterior lobes, seven short lateral lobes and two long posterior lobes, which undergo changes in coloration, consistency, and turgidity as they develop. It has two oviducts located in the dorsal-ventral portion, which connect to the genital pores located at the base of the third pair of pereiopods. From the macroscopic analysis of the ovaries, it was possible to determine five distinct maturational stages for the species *X. kroyeri*, as described below:

Stage I (immature) – the ovaries are extremely small and thin. They have a smooth, inconsistent surface and translucent coloration (without Pantone code catalog), and they cannot be visualized through the exoskeleton (Figure 2a). The average weight of the ovaries at this stage is 0.01±0.04 g.

Stage II (initial maturation) – the ovaries are at the beginning of maturation, with the gonad increasing in size and weight (average weight: 0.28±0.20 g) when compared to Stage I. They have little coloration in the anterior and lateral lobes, and it is possible to visualize them with a light green coloration (Pantone code catalog 375 PC) through the exoskeleton, though only in the cephalothorax region (Figure 2b).

Stage III (advanced maturation) – the ovaries are more developed, larger, and heavier (average weight: 0.34±0.25 g) compared to the previous stage. They have a more pronounced medium green coloration in all lobes (Pantone code catalog 377 PC) and are less evident in the abdominal region (Figure 2c).

Stage IV (mature) – the ovaries are at the maximum level of maturation, and present a rough, consistent surface and more intense dark green coloration (Pantone code catalog 5753 PC) throughout the dorsal cavity (Fig 2d). The average weight of the ovaries at this stage is 0.42±0.27 g.

Stage V (spawned) – the females have already spawned, that is, the mature oocytes have been expelled into the environment. Currently, the ovaries are flabby, with a slightly rough surface and have a very discreet coloration (Pantone code catalog 585 PC) or are translucent (Figure 2e). The average weight of the ovaries at this stage is 0.08±0.07 g.

3.2. Microscopic description of the ovaries

In the microscopic analysis, it was possible to identify six phases of cell development, namely, oogonia (OO), previtellogenic oocytes (PVTG), primary vitellogenic oocytes (VTG_1), secondary vitellogenic oocytes (VTG_2), mature oocytes (MO) and atretic oocytes (AO). From the macroscopic and histological analysis, it was possible

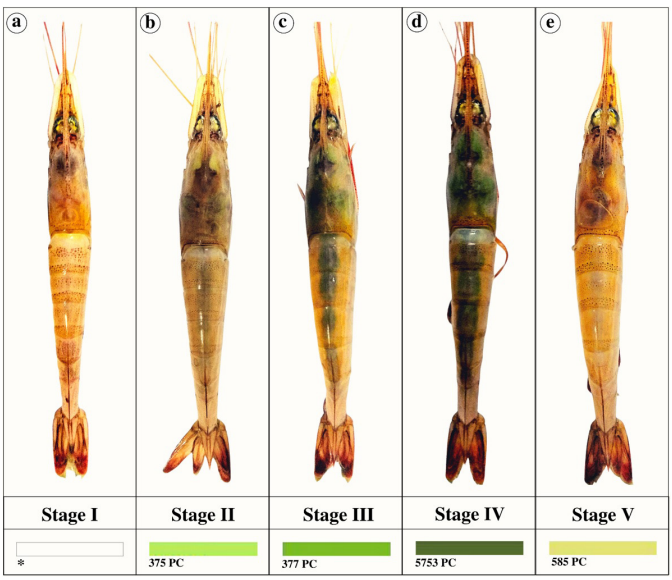

Figure 2. Schematic representation of the different stages of ovarian development of the Atlantic Seabob *Xiphopenaeus kroyeri* (Heller, 1862) caught in southeastern Brazil. Key: (a) Stage I – immature (translucent coloring), (b) Stage II – initial maturation (Pantone code catalog: 375 PC), (c) Stage III – advanced maturation (Pantone code catalog: 377 PC), (d) stage IV – mature (Pantone code catalog: 5753 PC), and (e) Stage V – spawned (Pantone code catalog: 585 PC or translucent coloring).

to determine five stages of gonadal development at the cellular level (Figure 3), as described below:

Stage I (immature) (Figure 3a, 3b) – there is a predominance of basophilic cells oogonia (OO) and previtellogenic oocytes (PVTG), i.e., cells evidenced by blue-purple staining (H). OO have a nucleus (n) that is proportionally larger than the cytoplasm, which is a spherical shape and is organized in the germinative zone (gz; Figure 3c), located in the central region of the ovary. The PVTG have an oval shape, cytoplasm that is more developed compared to OO and have nucleoli on the periphery of the nucleus. Follicular cells (fc) are cubic in shape and are dispersed throughout the ovary. The gonadal wall (gw; Figure 3b) is thinner compared to the other stages of gonadal development.

Stage II (initial maturation) (Figure 3c, 3d) – there is a dominance of acidophilic cells, which are the primary vitellogenic oocytes (VTG_1), i.e., cells evidenced by pink coloring (E-P). In addition, it is possible to visualize the presence of three to six nucleoli that are strongly stained by Haematoxylin, evidencing the basophilic characteristic in the nucleus. The VTG_1 has the most developed cytoplasm when compared to the OO and PVTG, this is due to the initial deposit of lipid droplets in the cell cytoplasm. OO and PVTG are also found at this stage, but in smaller quantities. Follicular cells (fc) have a cubic shape and are better organized, forming clusters around VTG_1.

Stage III (advanced maturation) (Figure 3e, 3f) – there is a predominance of secondary vitellogenic oocytes (VTG_2), evidenced by pink staining (E-P) of the cytoplasm and purple staining of the nucleus (H). In addition, it is possible to visualize the presence of acidophilic globules in the periphery of the nucleus and large droplets of yolk along the cytoplasm of the cell, giving it a granular appearance. OO and PVTG are found in smaller amounts. Follicular cells (fc) have a scaly shape and form clusters around VTG_2.

Stage IV (mature) (Figure 3g, 3h) – there is a predominance of mature oocytes (MO), which have highly acidophilic cytoplasm (E-P) and the basophilic nucleus (H), and are evidenced by the pink and purple coloration, respectively. At this stage, it is possible to observe yolk granules throughout the cell cytoplasm. They present basophilic cells (OO and PVTG) in a lower quantity when compared to stages I, II and III. Follicular cells (fc) form an outer layer of MO.

Stage V (spawned) (Figure 3i, 3j) – The OO and PVTG are dominant at this stage, which is evidenced by the blue-purple coloration (Haematoxylin). Oocytes in atresia (AO) have acidophilic nature (Eosin-phloxine) and, due to the rupture of the cell membrane, the shape of this cell is not well defined. This process is the result of resorption of mature oocytes that were not released during spawning or may even be due to environmental stress. Follicular cells (fc) are cubic in shape and are dispersed throughout the ovary. The gonadal wall is thick and has a loose/disorganized appearance (Figure 3i). As the gonads develop and undergo reproductive events, the gonadal wall tends to get thicker and loose, and does not return to its initial state, which is the main characteristic that differentiates the spawned stage from the immature stage.

Germ cells (OO and PVTG) were found in all stages of gonad development and showed greater frequency in the immature and spawned stages. As the gonad develops, the concentration of OO and PVTG decreases, giving way to vitellogenic oocytes (VTG_1, VTG_2 and MO) (Table 1). As the germ cells develop, the cytoplasm increases in size, with OO having the smallest diameter (5.97±1.88 µm), followed by PVTG (32.82±9.55 µm), VTG_1 (95.71±14.94 µm), VTG_2 (138.64±16.01 µm) and MO (185.32±22.09 µm) (Table 1).

4. Discussion

Females of penaeid shrimps have different stages of gonadal maturation throughout the reproductive cycle (Dall et al., 1990; Bolognini et al., 2017); however, there is still no standardization of the classification of maturational stages. In the present study, the ovarian development of the species *X. kroyeri* was classified into five different maturational stages, which have also been described for other shrimp species belonging to the genus *Penaeus* (Bolognini et al., 2017; Craveiro et al., 2019; Garcia et al., 2021). Notwithstanding, other studies have classified gonad development into only four stages, condensing the early maturation and advanced maturation stages into a single stage, which is named as "in development"

Table 1. Diameter for each oocyte phase (mean±SD) and cell composition observed at each gonadal maturity stage of *Xiphopenaeus kroyeri* (Heller, 1862) captured off the coast of Espírito Santo, Brazil.

Oocyte	Diameter (µm)	Stages of ovarian maturation				
Type	(Mean±SD)	I	II	III	IV	V
Oogonia	5.97±1.88[a]	++	+	+	+	++
Previtellogenic	32.82±9.55[b]	++	+	+	+	++
Primary vitellogenic	95.71±14.94[c]	-	++	-	-	-
Secondary vitellogenic	138.64±16.01[d]	-	-	++	-	-
Mature	185.32±22.09[e]	-	-	-	++	-
Atretic	*	-	-	-	-	+

Key: (+) present; (++) abundant; (-) absent; (*) not present. Immature (I); initial maturation (II); advanced maturation (III); mature (IV); spawned (V). Values in the same column with different letters are significantly different ($p < 0.05$).

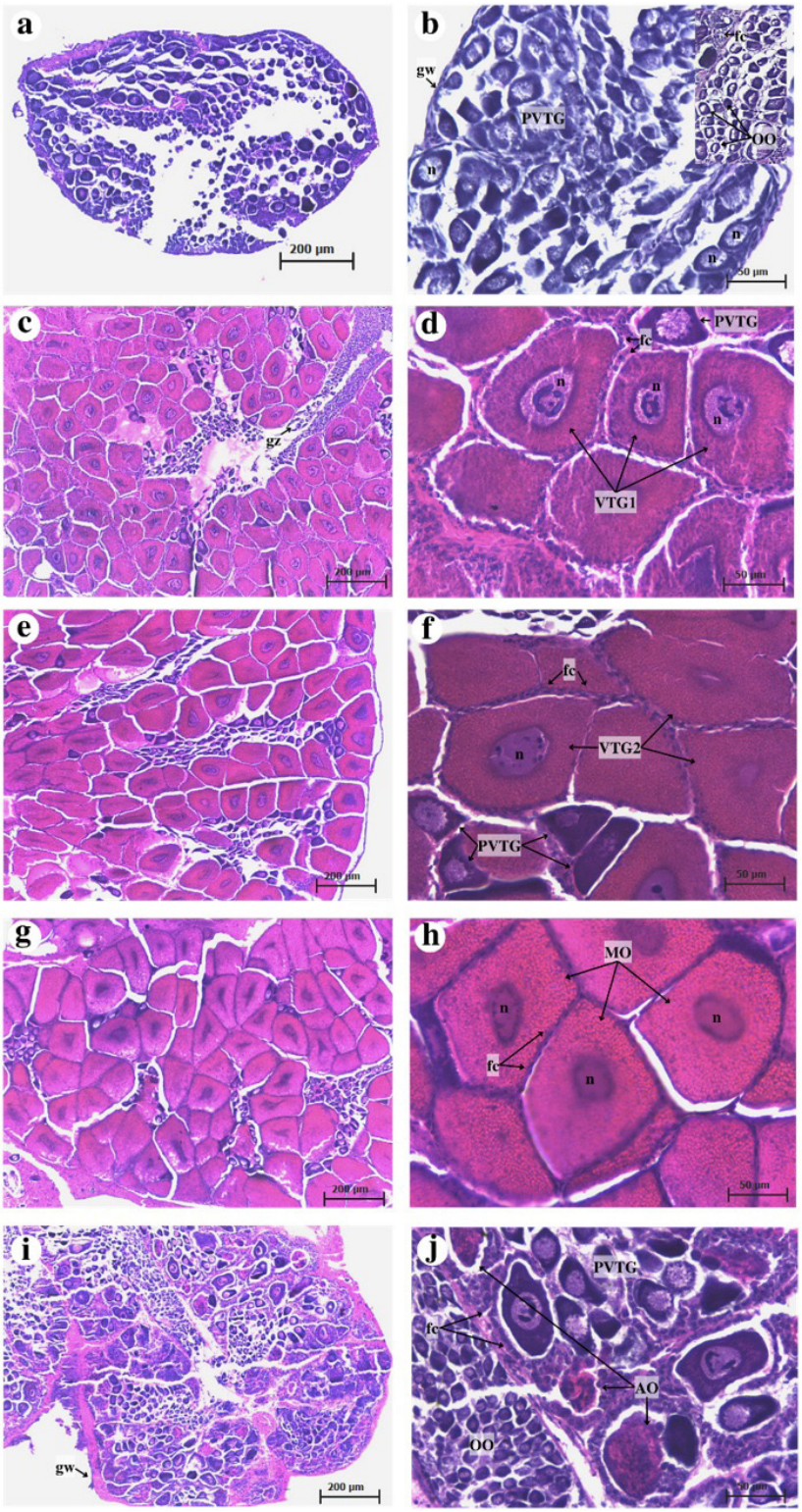

Figure 3. Microphotographs of the stages of ovarian development of the shrimp *Xiphopenaeus kroyeri* (Heller, 1862) caught off the coast of Espírito Santo, Brazil. (a, b) immature [translucent coloring (Figure 2a)]; (c, d) initial maturation [Pantone code catalog: 375 PC (Figure 2b)]; (e, f) advanced maturation [Pantone code catalog: 377 PC (Figure 2c)]; (g, h) mature [Pantone code catalog: 5753 PC (Figure 2d)]; and (i, j) spawned [Pantone code catalog: 585 PC (Figure 2e)]. (OO) oogonia; (PVTG) previtellogenic oocyte; (VTG_1) primary vitellogenic oocyte; (VTG_2) secondary vitellogenic oocyte; (OM) mature oocyte; (OA) atretic oocyte; (gw) gonadal wall; (gz) germinative zone; (n) nucleus; (fc) follicular cells. [10x objective (a, c, e, g, i) 40x objective (b, d, f, h, j)].

(Peixoto et al., 2003; Campos et al., 2009; Martins et al., 2013; Lopes et al., 2017). The differentiation in a greater number of stages implies the ability to define maturation with more precision and detail the differences in and phases of cell development, which can assist studies of population and reproductive dynamics (Garcia et al., 2021).

In relation to the macroscopic ovarian coloration pattern found in this study, the initial maturation stage was characterized by light green coloration that intensified as the gonads developed until they reached the mature stage, which is characterized by a more intense dark green coloration. The same pattern was found for the same species in other regions of Brazil, such as in the south (Campos et al., 2009), southeast (Martins et al., 2013) and northeast (Lopes et al., 2017). The coloring of the ovary may be due to the type of carotenoid pigment assimilated by the body during feeding (Liñán-Cabello et al., 2002). In these organisms, the intensification of the green color occurs due to the constant accumulation of carotenoid pigments during the vitellogenic phase (Liñán-Cabello et al., 2002), which are important components for the embryonic development and reproductive success of these species (Bolognini et al., 2017; Souza et al., 2017).

The stages of gonadal development in penaeid shrimps are basically determined by the presence of basophilic, vitellogenic and/or atretic oocytes (Quintero and Gracia, 1998; Peixoto et al., 2003). Previtellogenic oogonia and oocytes develop from the proliferation zone (germinative zone) and, as they mature, they give rise to vitellogenic oocytes (Peixoto et al., 2003; Abraham and Manisseri, 2012). In the present study, basophilic oocytes (OO and PVTG) were found in all stages of development; however, in stages I and V they were more frequent. In addition, it was also possible to visualize the increase in the diameter of oocytes throughout the maturation process (Table 1), which occurs due to the constant accumulation of yolk granules (reserve substances) deposited in the cell cytoplasm. The frequency and increase in the size of *X. kroyeri* oocytes showed similarity to results found in studies with the same species (Lopes et al., 2017), as well as other species of penaeids (Quintero and Gracia, 1998; Bolognini et al., 2017; Peixoto et al., 2018; Craveiro et al., 2019).

In addition to germ cells, other components were also considered essential in stage differentiation, such as gonadal wall thickness and follicular cells (Craveiro et al., 2022). The thickness of the gonadal wall changes in size and arrangement as females undergo reproductive events (Craveiro et al. 2022). As a result, the ovary wall tends to become thicker and looser, unlike immature ovaries which have a thin, consistent wall. Therefore, these characteristics have become fundamental in identifying immature females from females that have already spawned at least once. Follicular cells were also considered key components in differentiating the stages of maturation, because their shape and arrangement changed as the oocytes increased in size (Worsmann et al., 1976; Chang and Shih, 1995; Craveiro et al., 2022). Contributing to the differentiation of stages into early, advanced and mature maturation, confirmed from the significant difference in the diameter of the oocyte in these different stages. Studies such as Campos et al. (2009) and Lopes et al. (2017), probably did not consider the behavior of follicular cells in their descriptions, which ended up grouping the early and advanced maturation stages into a single stage, the developmental stage.

The immature and spawned stages are similar in relation to their (transparent) coloring, which makes it difficult to observe the gonads through the exoskeleton during the macroscopic classification of the ovaries (Dumont and D'Incao, 2004; Campos et al., 2009; Lopes et al., 2017). However, histological analysis helps to differentiate these stages with greater precision due to the visualization being at the cellular level, thus allowing us to observe characteristics such as the presence of atretic oocytes, which is considered one of the main characteristics used to differentiate the immature gonads from the spawned stage (Quintero and Gracia, 1998; Peixoto et al., 2003; Lopes et al., 2017). Oocytes in atresia are the result of resorption of mature oocytes that were not released during spawning (Peixoto et al., 2005). Although atretic oocytes were only observed at the spawning stage in the present study, oocyte resorption can also be triggered by environmental impacts, such as pesticide contamination, for example (Rodríguez et al., 2021); and they should only be used as the main classification characteristic when one has full knowledge of the local environmental parameters. In this case, we also used the differentiation of the stages according to the thickness of the gonadal wall, which tends to become thicker, and looser as new reproductive events occur.

Macroscopic analysis is widely used to classify ovarian development in shrimp due to the practicality of differentiating the stages from the color pattern of the gonads (Bolognini et al., 2017; Garcia et al., 2021). However, we found it difficult to differentiate the immature and spawned stages due to the similarity between the colors of the ovaries (translucent) visualized through the exoskeleton. This same difficulty was reported by Campos et al. (2009) and Lopes et al. (2017) for *X. kroyeri*, and also for other penaeid species, such as *Artemesia longinaris* (Spence Bate, 1888) (Dumont and D'Incao, 2004), *Penaeus brasiliensis* (Latreille, 1817) (Quintero and Gracia, 1998), *Penaeus paulensis* (Pérez Fartante, 1967) (Peixoto et al., 2003; 2018), *Penaeus kerathurus* (Forskal, 1775) (Bolognini et al., 2017) and *Penaeus schmitti* (Craveiro et al., 2019; Garcia et al., 2021).

In this study, the macroscopic analysis proved to be inefficient in differentiating these stages, and with the aim of reducing classification errors, we decided to intensify our histological sampling. Histology was therefore used to confirm or correct the macroscopic pre-classification, resulting in a more detailed and accurate description of the ovarian development stages of the species under study. Therefore, in view of the subjectivity and doubts generated by the macroscopic analysis, we emphasize the need to carry out the macroscopic and microscopic analysis simultaneously, mainly for studies with the purpose of conservation and fisheries management, which need accurate information and that demonstrate the real situation that the stock meets.

Regarding the maturation of oocytes, it was possible to observe a difference in the final stage of development of

germinative cells of the species under study. The presence of peripheral bodies (cortical rods) is a very common feature during the final stage of oocyte maturation for different species of penaeids, e.g., *P. brasiliensis* (Quintero and Gracia, 1998), *P. paulensis* (Peixoto et al., 2003), *P. kerathurus* (Bolognini et al., 2017), *P. schmitti* (Craveiro et al., 2019; Garcia et al., 2021) and *X. kroyeri* (Campos et al., 2009; Lopes et al., 2017). The peripheral bodies are formed after the complete accumulation of vitellogenin in the cell cytoplasm, which indicates the final phase of oocyte maturation; however, in the present study, this characteristic was not found in any of the individuals analyzed, thus diverging from the result found by the authors cited above.

The study by Campos et al. (2009) mention that previous investigations on ovarian maturation did not report the presence of peripheral bodies in *X. kroyeri*, and that according to Clark Junior et al. (1980), the absence of this structure may be related to the water temperature. Campos et al. (2009) and Lopes et al. (2017) developed their studies in the South and Northeast of Brazil, respectively, regions with different environmental conditions in the Southeast region studied. Santa Catarina is the limit coastal zone for the occurrence of the species *X. kroyeri* in the south of the country, which is a region characterized by its low temperature waters (Campos et al., 2009). Low temperatures can slow down gonadal development (Campos et al., 2009), while higher temperatures can accelerate this process and trigger the spawning of marine invertebrates (Bauer, 1992).

In Northeastern Brazil, the annual temperature variation is very small, Lopes et al. (2017) found a variation of only 2 °C between the maximum (28 °C) and minimum values (~26.5 °C) during the period from August 2011 to July 2012, showing that in this region the waters remain warm throughout the year. Different from what was found by Heckler et al. (2013) in the Southeast region of the country, where the temperature range was much higher throughout the year (~10 °C between the maximum and minimum values), with a water temperature of approximately 18.5 °C in the spring to a maximum temperature of 28.0 °C in the summer. These same authors reported a significant and positive relationship between water temperature and the abundance of mature females of *X. kroyeri*. The climatic conditions along the Brazilian coast and the results found in the literature mentioned above indicate that ovarian development may have different characteristics between regions, even when dealing with the same species.

The absence of peripheral bodies in this study hindered the differentiation of the advanced maturation stages and mature stages since this characteristic facilitates the classification of these stages. However, this differentiation was characterized by an increase in the size of yolk granules and their displacement to the cell end, and these characteristics were also observed for the species *A. longinaris* (Dumont and D'Incao, 2004) due to the absence of cortical rods. Other studies of penaeid shrimps also did not observe the presence of this structure, such as *Metapenaeopsis dalei* (Rathbun, 1902) (Sakaji et al., 2000) and *Metapenaeus monoceros* (Fabricius, 1798) (Abraham and Manisseri, 2012). The absence of peripheral bodies in the present study and in the other studies cited above, allows us to state that this type of structure is not mandatory in the final phase of maturation of penaeid shrimps.

The results presented in this study contribute to a greater understanding of the reproductive aspects of the species *X. kroyeri*. The detailed classification of the stages of gonadal development was fundamental in order to provide relevant information, which in the future will assist in studies on the population and reproductive dynamics of the species. These studies are considered essential for the development of adequate guidelines for the sustainable management of fishing activity. We suggest that further analyzes be carried out to better investigate the absence of peripheral bodies in the final stage of maturation of *X. kroyeri*, since this structure seems to be predominant in the species of penaeids captured in Brazil.

5. Conclusion

Five stages of ovarian development were identified for females of the Atlantic Seabob (*X. kroyeri*) found in southeastern Brazil, which is important since the stages of early and advanced maturation had not been previously described for this species. In addition, no peripheral bodies were found at the final stage of oocyte maturation, which differs from the results found in the literature for the same species in other regions of the country. These results can help us to better understand the reproductive characteristics of the species *X. kroyeri* and generate important information that serves as a basis for the development of conservation and management measures that ensure the sustainable use of this resource.

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