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Histological description of hepatopancreas in spiny lobster (*Panulirus penicillatus*) and bamboo lobster (*Panulirus versicolor*) in Sabang Waters, Aceh, Indonesia

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Abstract. *Abbas MA, Iqbal M, Firdus F, Sari W, Putra DF. 2024. Histological description of hepatopancreas in spiny lobster (*Panulirus penicillatus*) and bamboo lobster (*Panulirus versicolor*) in Sabang Waters, Aceh, Indonesia. Biodiversitas 25: 3739-3749.* This study aimed to analyze the histology of the hepatopancreas in two lobster species, *Panulirus penicillatus* (Olivier, 1791) and *Panulirus versicolor* (Latreille, 1804), originating from Sabang waters. The primary objectives were to identify and compare the cellular composition and structural differences within the hepatopancreas of both species and to understand how these differences might reflect adaptations to their distinct local environments and dietary conditions. The histological analysis was conducted on the hepatopancreas of 10 specimens from each species using the paraffin section method and Hematoxylin-Eosin (H&E) staining. The results showed striking differences in the tubule cells between the two species. In *P. penicillatus*, B-cells were found to be more dominant, whereas in *P. versicolor*, F-cells were more prevalent. Additionally, the study observed significant variations in the size and arrangement of the Tubules, as well as the distribution of different cell types within the hepatopancreas. These differences likely reflect adaptations to their distinct local environments and dietary conditions in Sabang waters. The hepatopancreas, a vital organ for digestion, nutrient absorption, and detoxification, showed distinct histological features in the two lobster species. Understanding these variations provides valuable insights into their biological and physiological adaptations. The research highlights the importance of species-specific studies to comprehend the ecological and physiological adaptations of marine organisms. Furthermore, these findings have significant practical implications for the management and cultivation of these lobster species. By understanding the histological differences and their underlying causes, better strategies can be developed for the conservation and sustainable exploitation of these valuable marine resources. The study underscores the role of histological analysis in assessing the health and condition of lobster populations, which is crucial for effective management.

Keywords: Digestive system, hepatopancreas, histology, *Panulirus penicillatus*, *Panulirus versicolor*

INTRODUCTION

Indonesia, as the largest archipelagic nation with over 17,000 islands, possesses immense potential in marine fisheries, significantly contributing to the global seafood market. This sector not only supports millions of livelihoods but also presents substantial export opportunities, particularly for high-demand species such as tuna, shrimp, and lobster (Rahmizal 2022).

In Sabang, located in Aceh Province, the fisheries sector is vital to the local economy. Its strategic position near the Malacca Strait enhances the richness of its marine resources, especially spiny and bamboo lobsters (Indriani and Nugroho 2023). These species are in high demand both domestically and internationally, making them crucial for the region's economic growth. To ensure the sustainability of these resources and protect the area's biodiversity, effective management practices are essential for long-term viability (Edwarsyah 2017).

Sabang waters stand out as a unique location for ecotourism development, particularly in the fisheries sector due to the abundance of diverse lobster species that serve as a livelihood for local fishermen (Sutaman et al. 2023). The area's abundant diversity of lobster species not only provides a livelihood for local fishermen but also offers a unique attraction for ecotourists. The presence of small islands surrounding Sabang waters further supports lobster cultivation (Kurniasari et al. 2019; Salmarika et al. 2022). Currently, Indonesia has five major lobster production areas: Cilacap, Yogyakarta, Gresik, Lombok, and Aceh (Tjoeng 2015; Hajad and Aripin 2023). Based on this, Aceh, including Sabang waters, has the potential to become a new center for fisheries and aquaculture development. Previous studies have recorded the presence of six lobster species in this area, such as *Panulirus ornatus* (Fabricius, 1798), *Panulirus versicolor* (Latreille, 1804), *Panulirus penicillatus* (Olivier, 1791), *Panulirus homarus* (Linnaeus, 1758), *Panulirus longipes* (A.Milne-Edwards, 1868), and

Panulirus polyphagus (Herbst, 1793) (Damora et al. 2021; Akmal et al. 2023; Nurdin et al. 2024).

Understanding the lobster's digestive system is of paramount importance. Lobster has become a high-value commodity, with more than half of the global production volume being processed to meet the increasing demand for various lobster-based products (Setyanto et al. 2019; Putra et al. 2022). The processing of the commodity typically generates large quantities of by-products, including heads, shells, liver, and eggs, which constitute approximately 50-70% of the raw material (Wijaya et al. 2018; Pane et al. 2021; Safir et al. 2024). This underscores the importance of understanding lobster's digestive system. In addition, several key components have been reported to play vital roles, such as hepatopancreas, which is a vital organ for digestion, nutrient absorption, and detoxification (Perera and Simon 2015; Munian et al. 2021). Histological analysis of this organ can provide valuable information regarding lobster adaptation and health in facing environmental variations in Sabang waters (Wahle 2015; Hoenig et al. 2017; Konecny et al. 2024).

The digestive system typically follows a sequential pathway from the mouth, esophagus, stomach, hepatopancreas, intestine, to the anus, with metabolic waste being excreted through flame cells (Putra et al. 2012; Setyanto et al. 2019; Putra et al. 2024). According to previous studies, lobster digestive system consists of three distinct sections, namely the foregut, midgut, and hindgut. These sections are formed separately at the nauplius stage and later merge at the final embryo phase with abbreviated development (Kropielnicka-Kruk et al. 2022; Kawirian et al. 2023). During this phase, the embryo lives with abundant yolk reserves (Vogt 2019). Several studies have shown that the pyloric stomach is a triangular structure consisting of a central tooth with rows of denticle-like teeth on each side (lateral teeth) (Vogt 2021). The structure is known as the gastric grinding mill and functions similarly to the gizzard in turkeys used to grind food into fine particles. After grinding, these particles enter the pyloric stomach where sieving is carried out based on their size by indentations consisting of dense, hair-like structures. Small particles typically proceed to the midgut gland (tomalley), and digestion occurs in the hemolymph (Štrus et al.2019; Zhang et al. 2023). Meanwhile, large food is expelled from the sieve and returns to the pyloric stomach, where it enters the straight and tubular parts of the midgut gland. The food then passes through the cephalothorax and abdomen (Vogt 2021; Xu et al. 2023).

Histologically, in lobsters, the size of hepatopancreas organ varies and has a positive correlation with body growth. Additionally, for the aquaculture industry, a better understanding of lobster histology can help optimize cultivation conditions, enhance lobster health, and ultimately improve the quality and quantity of production (Davies et al. 2014; Rowley and Coates 2023). Therefore, integrating histological studies into lobster management and production can bring significant benefits to the sustainability of fisheries resources and the fishing industry as a whole. This phenomenon is mainly caused by the activity of E-cells in the organ. During molting, the mitotic activity of E-cells becomes more active, leading to accelerated tubule elongation (Ihsan and Istriyati 2017; Sukenda et al. 2024). It is hoped that the results of this study will provide insights into the health of lobster populations in Sabang waters. This study aimed to observe the histological features of the digestive system, specifically the hepatopancreas, in *P. penicillatus* and *P. versicolor* lobster species in the waters of Sabang.

MATERIALS AND METHODS

Study area and sample collection

This study was conducted in the coastal areas of Sabang City (Tabel 1, Figure 1) using the purposive sampling method, with samples obtained from the catch of local fishermen; sampling was carried out at three stations: Lhok Krueng Raya, Teupin Sirui, and Lhok Weng in Sabang waters (Table 1). Each station had different criteria, but all were suitable for the lobster sampling process (WWF Indonesia 2015).

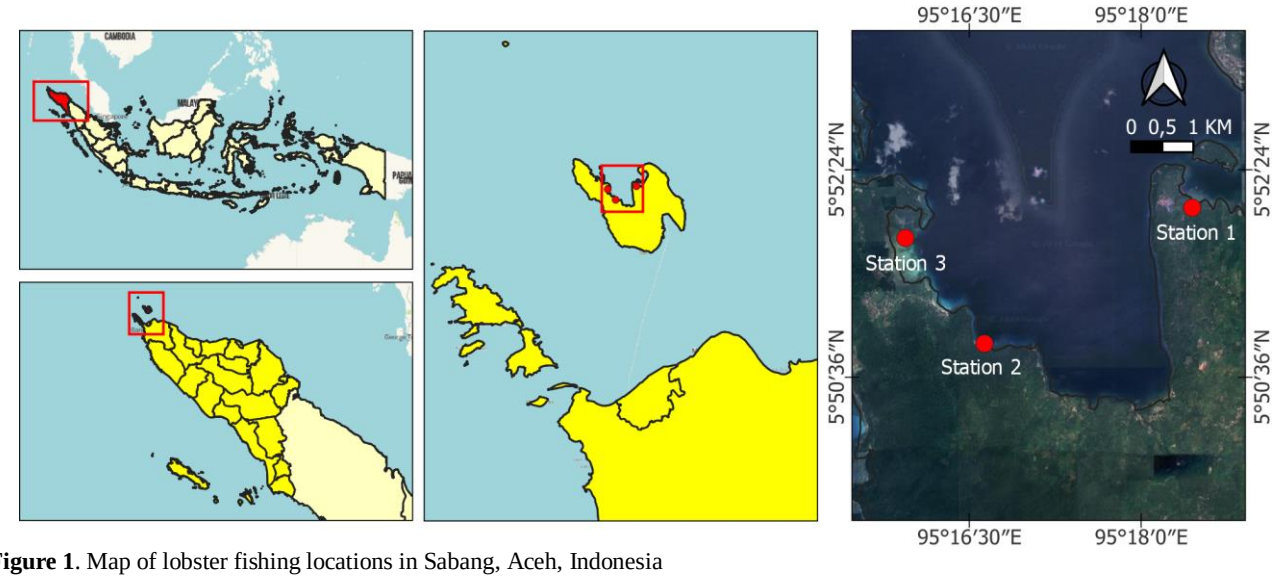

Figure 1. Map of lobster fishing locations in Sabang, Aceh, Indonesia

Table 1. Characteristics of the research site

Station	Location name	Coordinates	Characteristics
1	Lhok Krueng Raya (Teupin Cireuek)	5.8679° N, 95.3074° E	Located near Sabang City Harbor, influenced by port and fishing activities, but relatively sheltered.
2	Teupin Sirui	5.8482° N, 95.2772° E	Far from fishing activities, well-preserved habitat, highly suitable for lobster presence.
3	Lhok Weng	5.8635° N, 95.2657° E	The most sheltered and protected station with good water input from sea waves, allowing rapid lobster development.

The study procedures were carried out from February to July 2023, using samples of each species, which were collected for histological analysis of the digestive system. A total of 10 samples from each species of adult lobster (*P. penicillatus* and *P. versicolor*) were examined, specifically focusing on the hepatopancreas. The analysis was conducted at the Structure and Development Laboratory, Department of Biology, Faculty of Mathematics and Natural Sciences, Syiah Kuala University.

In this case, the study team collaborated with local fishermen regarding lobster stocks caught, particularly *P. penicillatus* and *P. versicolor* in Sabang Waters. The sizes of samples taken were randomly selected following Regulation Minister Fisheries No. 12 of 2020 (Ministry of Marine Affairs and Fisheries 2020). The lobster samples for identification were previously placed in polystyrene boxes that were coated with dry sea sand to ensure the lobster arrived at the location alive and then taken to the Laboratory of Marine Biology, Faculty of Marine and Fisheries Sciences, Syiah Kuala University, for collection of digestive organs (Lopeztegui-Castillo 2021).

Sample storage and preparation

The surgical procedure for the digestive system involved several steps, including dissection, fixation, washing, dehydration, de-alcoholization, infiltration, and embedding. The process began with the dissection of the hepatopancreas, which was a combined digestive gland consisting of the liver and pancreas (Wang et al. 2022). The entire digestive tract, from the mouth cavity to the anus, was stored in a 4% formalin solution (Ruiz et al. 2020). The fixation process involved soaking the samples for 17.5 hours in a fixative solution without being washed with physiological saline, as their blood was hemolymph-containing hemocyanin (Feldman and Wolfe 2014). Next, a thorough washing step was carried out to remove the fixative effect on the tissue by replacing the solution with 70% alcohol, followed by soaking for 5 hours (Ihsan et al. 2019).

The dehydration process involved soaking the samples in a series of graded ethanol solutions, including 70%, 80%, 90%, and absolute ethanol. Each ethanol solution was applied for 2 hours, with 2 repetitions at each ethanol concentration (Shield and Boyd 2014). The de-alcoholization process involved transferring the tissues to an xylene solution, and they were allowed to soak for 16.5 hours. The infiltration process involved dipping the samples in a series of increasingly concentrated alcohol solutions, including 80%, 90%, 96%, and absolute alcohol (Leland et al. 2015); each ethanol solution was applied for 1 hour and two repetitions. The embedding process was conducted by placing the preserved organs in a bottle containing paraffin and xylene mixture (bottle IV) in a heating chamber. Embedding boxes previously coated with glycerin were used to hold the paraffin as a preparatory step, which was then carefully poured into the boxes before embedding the impregnated organs (Smolowitz 2021).

Histology data analysis

The trimming process ensured optimal positioning of organ samples for accurate sectioning (Atherley et al. 2021). The sectioning process involved cutting paraffin blocks into 6-µm thin sections using a microtome facilitated by frozen blocks for precise cutting (Frischer et al. 2022). The mounting process included applying Entellan, covering with a coverslip, and drying for 24 hours to prepare the sections for microscopic examination (Gurina and Simms 2023). Histological staining, such as H & E, was employed to clarify tissue structures for better identification (Suherman et al. 2023). The samples were then examined under a microscope at various magnifications, documented through photography or detailed recording, and processed using Zen 12 software (Shield and Boyd 2014; Ross et al. 2019). Zeiss Zen 12 plays a crucial role in the examination of hepatopancreas organ samples in lobsters. This software is used to visualize and analyze microscopic images of hepatopancreas tissue. With Zen 12, researchers can accurately measure and identify cellular structures, assess morphological changes, and evaluate pathological indicators within the tissue. Additionally, Zen 12 enables image segmentation, allowing specific tissue areas to be isolated and further analyzed. This capability is particularly valuable for assessing the health condition of the lobster's hepatopancreas, understanding its response to various environmental conditions, or examining the effects of experimental treatments (Jonkman et al. 2020).

RESULTS AND DISCUSSION

The lobster's hepatopancreas is a complex organ composed of several key histological components, each playing a crucial role in the digestive process. At its core are B-cells, which are responsible for absorbing and storing essential nutrients like lipids and glycogen, ensuring the lobster has the necessary energy reserves. F-cells complement this process by secreting digestive enzymes that break down food particles, making nutrients available for absorption (Ruiz et al. 2020).

The hepatopancreas in lobsters is located in the cephalothorax and is a crucial organ in the digestive process. This organ functions as the primary digestive gland, producing enzymes to digest food and absorbing and storing nutrients. Its strategic location and critical function make the hepatopancreas a central focus in histological analysis to understand lobsters' physiological adaptations to their environment (Vogt 2019). The following is an overview of the initial dissection process carried out to view and extract the hepatopancreas from each lobster.

The cells that form the basic structure of the hepatopancreas are located in the tubules. These tubules not only support cells but also play a crucial role in overall organ function. Inside the tubule is the lumen, the central cavity where digestion takes place. It serves as the channel through which digestive enzymes act on food and where nutrients are subsequently absorbed and transported throughout the body. Together, these components work to ensure productive absorption, assimilation, and capacity of supplements, as well as detoxification, which forms fundamental for the lobster's survival (de Melo 2019).

The histological results of the hepatopancreas of *P. penicillatus* in various lobster samples indicated striking differences between the two images (Figures 2. A and 2.B). The most significant difference was the large number of Tubules in Figure 3.A, which were more numerous and orderly arranged compared to Figure 3.B. In addition, in Figure 3.A, each Tubule was closely packed with no space for separation from each other.

In the histological samples, it could be observed that hepatopancreatic tubules consisted of digestive epithelium attached to the basal membrane. The inner wall was similar to a brush border, and the interior of the Tubules comprised a Lumen. This characteristic is clearly seen in Figure 3.A.

Furthermore, Figure 3.B illustrated that the central portion tended to enlarge, pushing several cells, specifically F-cells and B-cells, to shrink and be located on the outer skin of the tubules. Based on a magnification of 100x or 200 µm on histological cells of *P. penicillatus*, it was found that the distance between each Lumen was narrow, showing tightly packed tubules. Partial arrangements of lumens were visible in some areas in the histology of *P. penicillatus* only, while the similarity of both images was observed in the still-forming Tubules.

When the density of Tubules in Figure 3.C was evaluated, the lobster appeared to be in good condition, as the arrangement of Tubules was very tight, and the extra tubular connective tissue was not thickened. It was observed in both Figures 3.C and 3.D at a magnification of 400x or 50 µm in histological cells of *P. penicillatus* that its shape could still be recognized as pouch-shaped. Some structures that were still clearly visible included the Tubules, Lumen, F-cells, and B-cells.

The results of the histological examination of hepatopancreas in *P. versicolor* across different samples revealed striking differences between the two images. In Figures 3.A and 3.B, the most notable difference was the large number of tubules in Figure 3.A compared to Figure 3.B

Hepatopancreatic Tubules consisted of digestive epithelium attached to the basal membrane as observed in this image. The inner wall of the Tubules was similar to the brush border of the intestine, and the tubules' interior consisted of Lumen. This is visible in Figure 4.A. Based on the magnification of 100x or 200 µm on the histological cells of *P. versicolor*, it was revealed that the distance between each Tubule was close to each other, as indicated by the very narrow and small Hemolymph Sinus (HS). Only a few parts showed glimpses of some arrangements of Tubules in the histology of *P. versicolor*.

It was evident that the Lumen was enlarged in the section of both samples, particularly in Figure 4.A, where their shapes appeared regular. However, in Figure 4.B, the Lumen section was not visible and had already begun to break in some Tubules. It was observed in one of the Tubules between Figure 4.C; D when magnified to 400x or 50 µm on the histological cells of *P. versicolor*. In Figure 4.C, The Tubule's shape still appeared pouch-like and was easily identified. Some parts that remained visible included the Tubule, Lumen, B-Cells, Vacuola, and Microvilli.

The most significant difference between *P. penicillatus* and *P. versicolor* was observed in Figure 5; a comparison of their histology revealed differences in the shape of the Tubules between the two species. In Figure 5.A, there was a visible spacing between each tubule in *P. penicillatus.* It had a rounded shape with a significant presence of B-cells and was slightly different from Figure 5.B, which depicts histological results from *P. versicolor*. The most striking difference was the saturation level of the color and the predominance of B-cells.

In Figure 5.B, the tubules did not appear fully rounded compared to those in Figure 5.A. This section also seemed to provide no gaps for the F-cells, which were only visible at the edge of the tubule. The density level between the tubules was significantly different, as observed in Figure 5.A, where the spacing was sparse, marked by the Hemolymph Sinus (HS), also the Lumen was wider compared to Figure 5.B. Another difference was the number of Tubules, with Figure 5.A showing more compared to Figure 5.B when observed at a magnification of 100x. This indicated that the size of the Tubules in Figure 5.A was much smaller than in Figure 5.B.

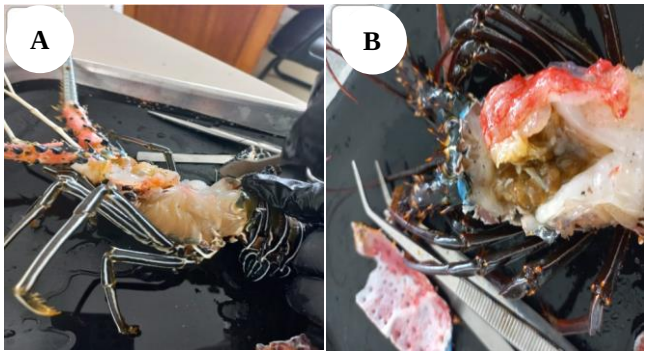

Figure 2. A. Dissection of the stomach contents in the lobster after opening the cephalothorax. B. Arrangement of the lobster's hepatopancreas components after the dissection process

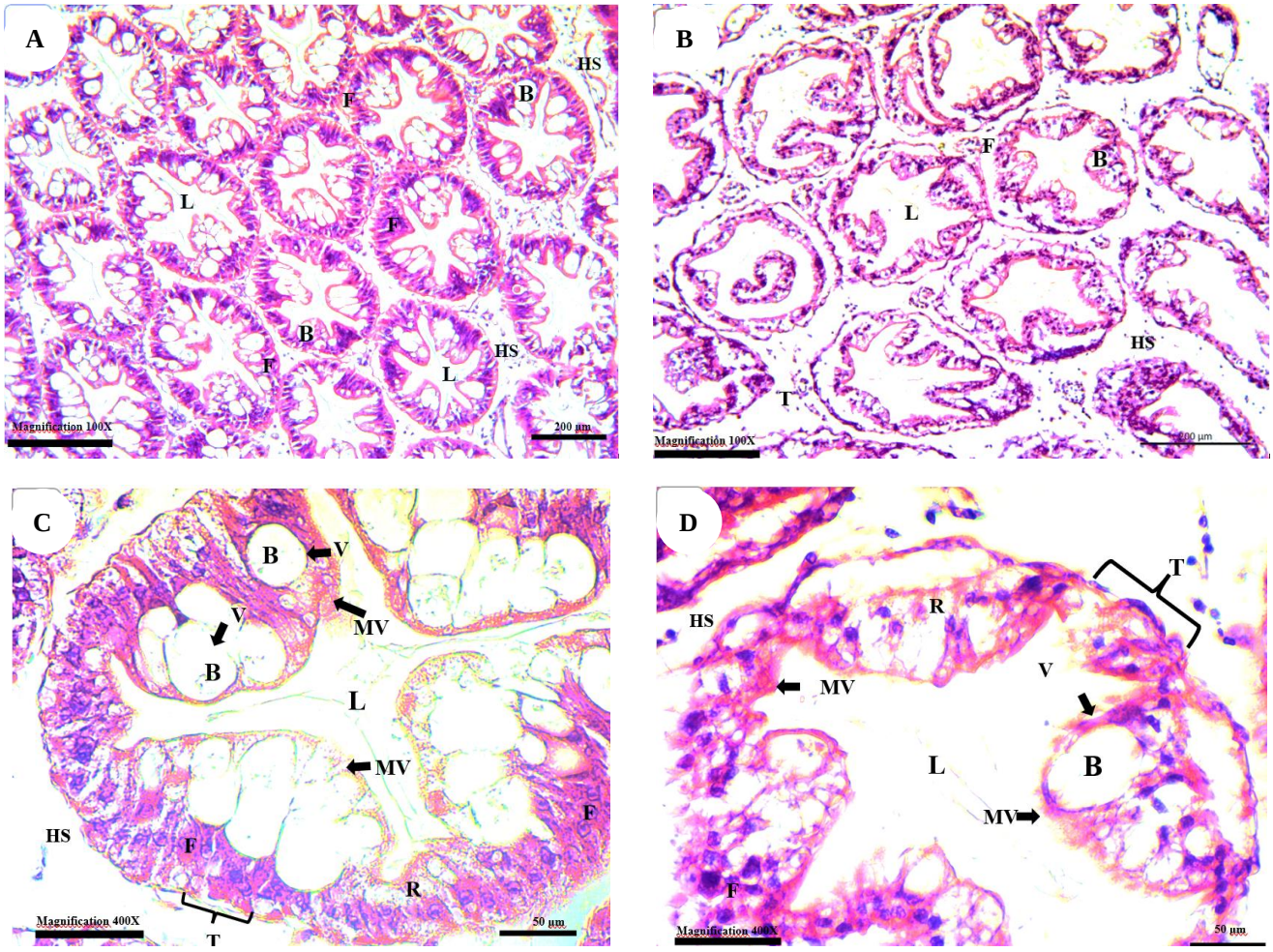

Figure 3. A. Histology of the hepatopancreas of *P. penicillatus* at 100x magnification. Individual I. Note: (B) B-cells, (F) F-cells, (T) Tubules, (L) Lumen, and (HS) Hemolymph Sinus (scale bar 200 µM); B. Histology of the hepatopancreas of *P. penicillatus* at 100x magnification. Individual II. Note: (B) B-cells, (F) F-cells, (R) R-cells, (T) Tubules, (L) Lumen, and (HS) Hemolymph Sinus (scale bar 200 µM). C. Histology of the hepatopancreas of *P. penicillatus* at 400x magnification in Individual I. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubule, (L) Lumen, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus. (scale bar 200 µM). D. Histology of the hepatopancreas of *P. penicillatus* at 400x magnification in Individual II. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubule, (L) Lumen, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus. (scale bar 200 µM)

Following this, a detailed comparison between *P. penicillatus* and *P. versicolor* was conducted using a microscope at a magnification of 400x. This comparison was to identify significant differences in the lobster's tubule cores. Several main parts were the primary focus at this magnification, providing a clearer view of the various vacuole shapes associated with the B-cells. Another focus was on examining the core of the lumen, which is surrounded by microvilli, and comparing these features across different lobster samples.

The histological images of the hepatopancreas of *P. penicillatus* and *P. versicolor* showed clear differences in the cells present. In Figure 5.C, it was evident that the most dominant cells were the B-cells, which surrounded the Lumen. Meanwhile, the number of F-cells was not as dominant and appeared compressed at the edges. This contrasted with Figure 5.D, where the F-cells were quite dominant, indicated by their purple color near the Tubules. The number of B-cells was fewer and outnumbered by the F-cells.

Each tubule of hepatopancreas in *P. penicillatus* was surrounded by muscle tissue composed of longitudinal and circular fibers, as well as muscle cell bodies protruding into the Hemolymph Sinus (HS). These cell bodies were comprised of nuclei, myofilaments, mitochondria, rough Endoplasmic Reticulum (rER), and free ribosomes. Additionally, this was observed in the HS between lobster Tubules that were closely situated due to favorable nutritional factors and healthy food in the lobster's digestive system (Strus et al. 2019). A characteristic feature of hepatopancreas in *P. penicillatus* was its full-rounded shape, with the most dominant part being the Lumen, which was closed-packed together. The tubules were narrow and small, but the large lumen indicated a digestive gland that secreted enzymes into the digestive tract for extracellular digestion and the thinning of lipid content within cells (Bennett et al. 2023).

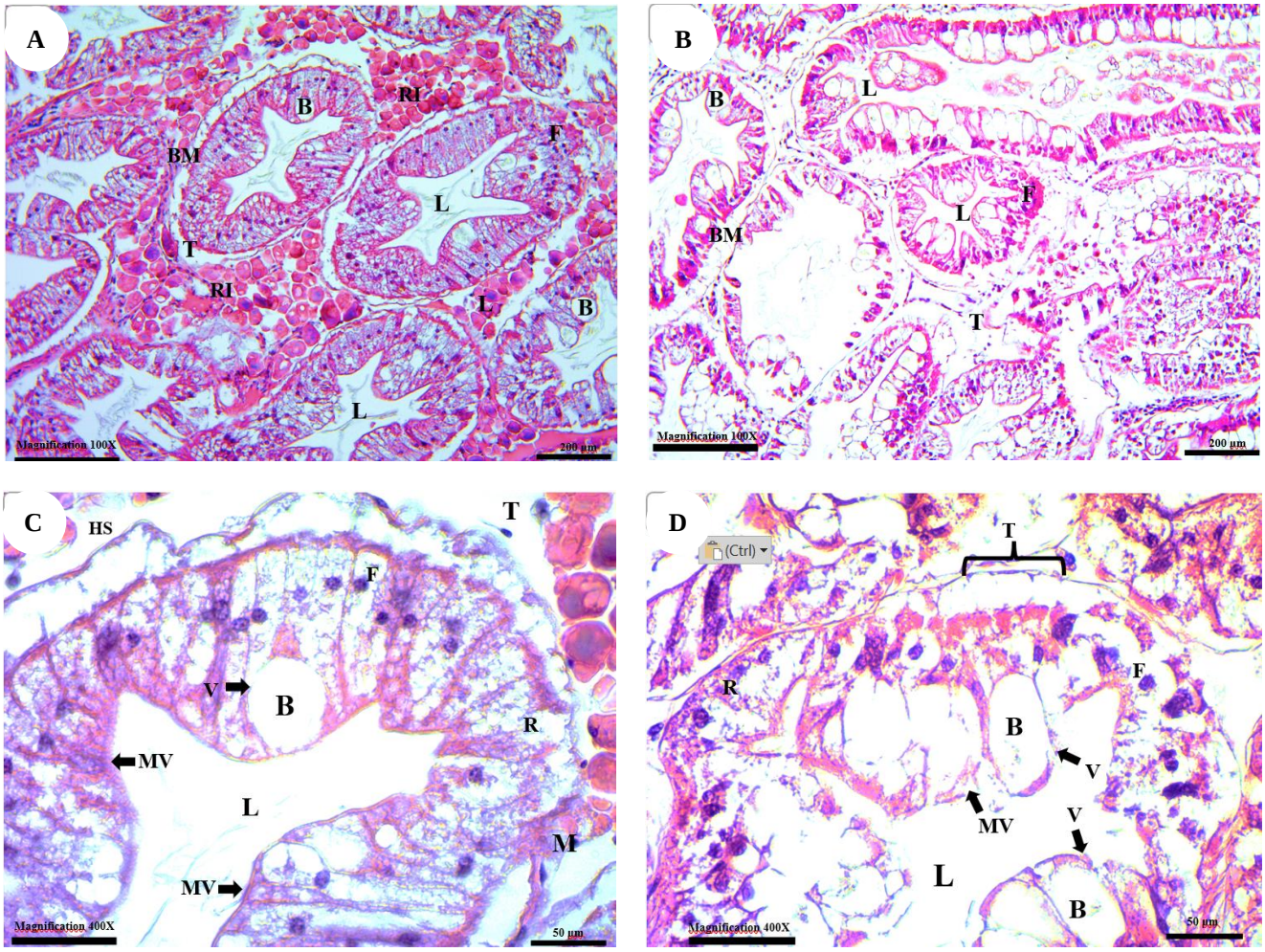

Figure 4. A. Histology of the hepatopancreas of *P. versicolor* individual I (B) Description: (T) Tubules, (L) Lumen, (F) F-Cell, (B) B-Cell. Magnification 100x (scale bar 50 µM). B. Histology of the hepatopancreas of *P. versicolor* individual II (B) Description: (T) Tubules, (L) Lumen, (F) F-Cell, (B) B-Cell. Magnification 100x (scale bar 50 µM). C. Histology of the hepatopancreas of *P. versicolor* at 400x magnification. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubules, (L) Lumen, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus. Magnification at 400x (scale bar 200 µM); D. Histology of the hepatopancreas of *P. versicolor* at 400x magnification. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubules, (L) Lumen, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus. Magnification at 400x (scale bar 200 µM)

Hepatopancreas, also known as the midgut gland, is vital for several cellular processes, such as digestion, metabolism, detoxification, storage of organic and inorganic compounds, and nutrient absorption (Wang et al. 2014). Structurally, the hepatopancreas consists of three lobes, each containing numerous Tubules as primary components (Hartenstein et al. 2019). These Tubules house different cell types, including B-cells, which are involved in nutrient absorption and storage, and F-cells, which are responsible for enzyme secretion for digestion.

In the Tubules of each species, the most dominant parts were the F-cells and B-cells, particularly in *P. penicillatus*. B-cells functioned in nutrient absorption through pinocytosis, intracellular digestion processes, and the excretion of metabolic waste. Mature B-cells were characterized by the presence of large central vacuoles (Strus et al. 2019). These vacuoles were extruded from the epithelium at the end of the B-cell zone through holocrine secretion, related to an unknown digestive process. Previously, B-cells were considered mature F-cells, and their central vacuoles were interpreted as large zymogen storage compartments.

Structurally, the hepatopancreas consisted of three lobes, each comprising numerous Tubules (Martínez-Alarcón et al. 2018). In the hepatopancreas of *P. versicolor*, the optimal size of the tubules was identified, characterized by several tubules that were well-sized and regularly arranged. The Tubules increased in size without Lumens, and the number of small vacuoles, including the cuticle, separated from the large hemal space between the liver tubules in the lobster (Sakhare and Kamble 2014; Nur 2018).

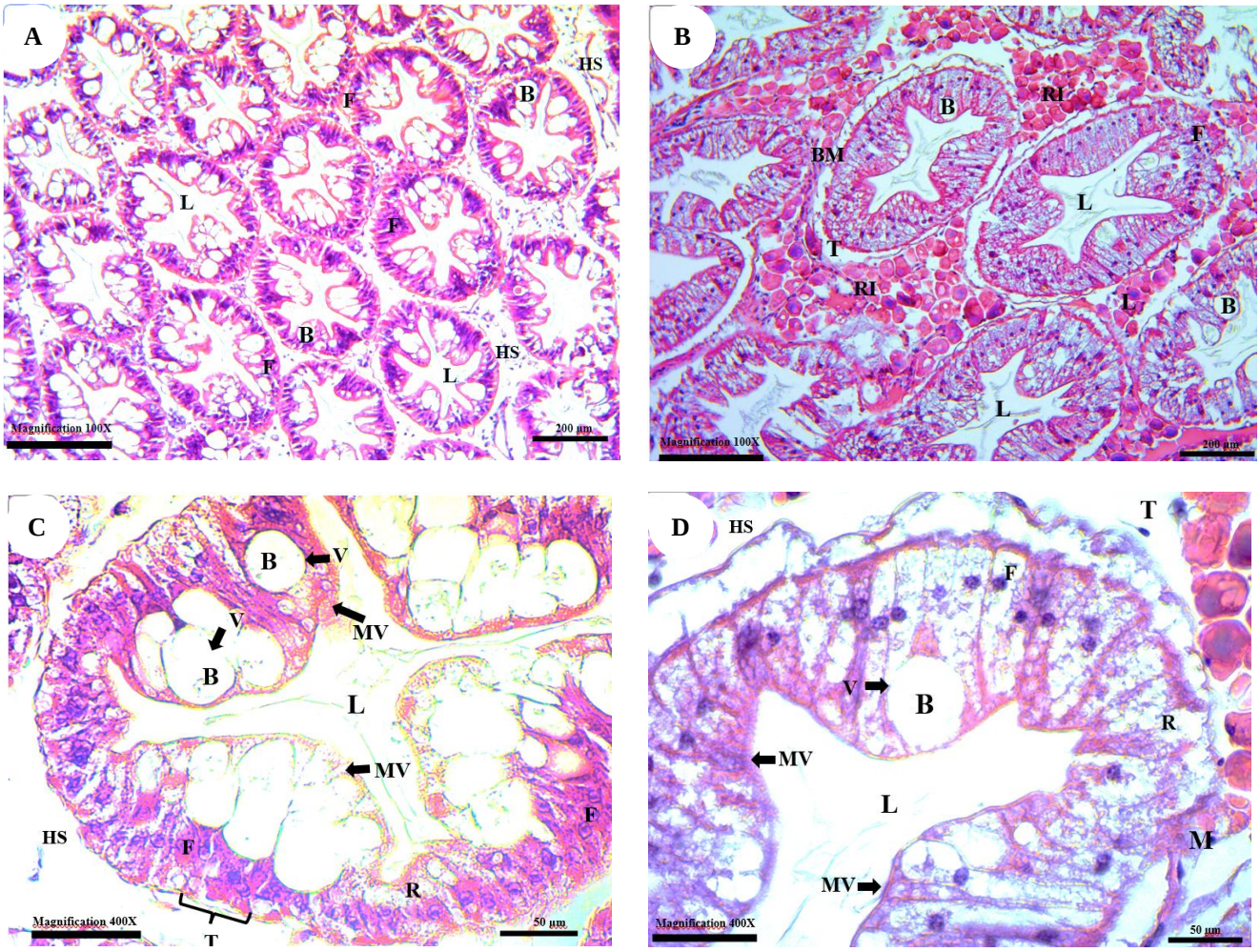

Figure 5. A. Histology of hepatopancreas in *P. penicillatus* with a magnification of 100x. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubule, (L) Lumen, and (HS) Hemolymph Sinus (scale bar 200 µM). B. Histology of hepatopancreas in *P. versicolor* with a magnification of 100x. Note: (B) B-cell, (F) F-cell, (R) R-cell, (T) Tubule, (L) Lumen, and (HS) Hemolymph Sinus (scale bar 200 µM). C. Hepatopancreas of *P. penicillatus* at 400x magnification (bar 200 µM). Note: (T) Tubules, (L) Lumen, (F) F-cells, (B) B-cells, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus. D. Hepatopancreas of *P. penicillatus* at 400x magnification (bar 200 µM). Note: (T) Tubules, (L) Lumen, (F) F-cells, (B) B-cells, (V) Vacuole, (MV) Microvilli, and (HS) Hemolymph Sinus

Discussion

The most significant difference was in the size of the Tubules in Figure 3.D, which were larger and pushed F-cells and B-cells to the periphery. In Figure 3.C, B-cells and F-cells were visible compared to Figure 3.D. This difference was further emphasized by the presence of lumens and epithelial cells with different functions based on cell types, namely E-cells, F-cells, B-cells, and R-cells. E-cells played a role in molting intensity, while F-cells were involved in the synthesis of digestive enzymes. Additionally, B-cells formed vacuoles adjacent to the F-cells, and R-cells were responsible for nutrient absorption from the lumen through active transport, as well as maintaining and metabolizing glycogen and lipid content in the hepatopancreas (Ihsan and Istriyati 2017).

In Figure 3.C, there was a tendency for a dominant number of B-cells surrounding the Tubule. On the edge of the Tubules, there were clustered F-cells, clearly visible by their reddish-purple color, which was different from the adjacent R-cells. The functions of R-cells and F-cells were to secrete from the epithelium at the proximal end of the Tubule. However, F-cells also performed protein synthesis while R-cells absorbed nutrients (Sousa 2007). On the outermost part of the Lumen, Microvilli were visible on each cell, which elongated parallel to the outer part of the Lumen in Figure 3.C. In contrast, Figure 3.D showed a widened lumen and a larger number of F-cells compared to R-cells, which were basophilic with nuclei located at the basal part and cytoplasm containing numerous lipid channels (Lewis et al. 2023).

The primary nutrients are stored in the hepatopancreas, and various studies have shown that lipids are preferentially used during periods of starvation or to support the molting process in lobsters. Total lipid accumulation has been shown to follow a cyclical pattern throughout a molting cycle. Some studies have indicated that starved lobsters have empty lipid vacuoles and reduced lipid content in their digestive glands. The larger area of

these cells suggests excessive intracellular digestion and the elimination of waste products, such as digestive enzymes and undigested particles (Factor 2020).

In B-cells, a large vacuole compressed the basal nucleus, nearly penetrating the Lumen. As the B-cells enlarged and continued to develop, the vacuole also grew larger, which was similar to the thinning of lipid layers on the cell walls. In the core of the lumen of both samples, numerous lines of microvilli were observed surrounding the fibrous core of the lumen. Additionally, around the B-cells, large vacuoles formed through enlargement, pushing against the F-cells. The presence of vacuoles in each B-cell was visible in both samples used in this study. During periods of reduced intake, the size of the B-cells increased in a manner similar to the enlargement of the vacuoles.

Histology analysis of lobster hepatopancreas concerning reduced metabolic rates in exposed groups showed measurements for B-cells and R-cells. The results indicated that the total area of B-cells per tubule for the exposed group was smaller compared to the control group (Daoud et al. 2014). The significant difference between the two tubules from each sample was not particularly dominant. However, the most notable characteristic in the images was the presence of F-cells surrounding the B-cells and the nucleus of the lumen. This was evidenced by the purple-colored dots around the edge of the tubule, representing F-cells. At this magnification, the distinct shape of microvilli inside the lumen was visible, resembling fine hair-like structures along the length of the lumen. Meanwhile, in the B-cell section, vacuoles were visible at the edge of the cell, with their size increasing as the lipid layer of the B-cells became depleted.

The size of the hepatopancreas varied among lobsters, depending on their growth (Mirzaei et al. 2021). Generally, larger lobsters have a larger hepatopancreas. This is consistent with the activity of E-cells in the hepatopancreas. The mitotic activity of E-cells becomes more active during molting, leading to a more rapid elongation of the tubules (Ciaramella et al. 2014; Gutzler and Butler 2017). Hepatopancreatic ducts have a columnar epithelium consisting of R-cells and F-cells, with a clear brush border for absorption and storage (Ruiz et al. 2020). Although R-cells are found in relatively small numbers, their primary function is to store large amounts of lipids and glycogen. Additionally, these cells serve as the site for nutrients and reserved energy that are mobilized during molting (Deyashi et al. 2024).

Organelles within all hepatopancreatic cells undergo the catabolism process (Vogt 2019). Another factor contributing to the reduced number of R-cells was the lobster trapping process conducted during brighter months, a period when lobsters tend to molt. Many samples of *P. penicillatus* were in the molting stage, indicated by dark red color signals, which showed that the number of R-cells in the tissue began to decrease due to several influencing factors. One primary factor was the molting process, where the number of R-cells significantly decreased (Wei et al. 2017; Massucci 2019). Additionally, the increase in lipid inclusion within R-cells was correlated with a decrease in lipid content in the lobster's body during molting (Nashida et al. 2013). This phenomenon illustrated a complex dynamic associated with structural changes and cellular composition in the context of the lobster's life cycle as well as their development.

In samples of *P. penicillatus*, M-cells, the smallest and rarest cells in the epithelium, were not found. These cells were located individually on the basal lamina with close contact with the Hemolymph Sinus (HS) and did not have contact with the Tubules Lumen. M-cells were believed to regulate the function and dynamics of neighboring epithelial cells or muscle tissue activities that lack neuromotor connections (Vogt 2019). In the hepatopancreas of *P. versicolor*, purplish dots along the edges of the tubules, representing F-cells, were easily observed. F-cells generally function to release digestive enzymes into the Lumen of the digestive gland, which are then secreted into the digestive tract for extracellular digestion. B-cells, characterized by large vacuoles, play a role in intracellular digestion and the elimination of undigested waste (Nur 2018; Bennett et al. 2023). The most common cell type found was the F-cells, which contained numerous rough endoplasmic reticulum, stained blue to dark purple in H & E preparations, and had a fibrillar appearance in cross-section.

Another characteristic was the varying shape of the Microvilli inside the Lumen, which appeared as fine hairs along the length of the Lumen. Meanwhile, in the B-cells, vacuoles were visible at the edge of the cell. The size increased as the lipid layer of the B-cell became depleted. The Tubules began from the Lumen and extended to the peripheral part, with each digestive Tubules including digestive epithelium, basement membrane, contractile cells, and tunica propria (Strus 2019).

In the tubules of *P. versicolor*, a very minor process of vacuolization occurred, as observed in the infected hepatopancreas, which was at a lower level compared to the uninfected hepatopancreas (Sun et al. 2015; Smedbold 2024). The main components were the Lumen, B-cells, R-cells, and F-cells (Vogt 2019). Furthermore, in *P. versicolor*, the hepatopancreas shape was normal, indicating that its habitat was still intact and uncontaminated. A normal hepatopancreas in lobsters, as observed in *P. versicolor*, suggests that the organ is functioning well without signs of infection or damage. This condition suggests that the lobster lives in a healthy, uncontaminated habitat and is able to meet its nutritional needs effectively (Butler et al. 2022; Lopeztegui-Castillo et al. 2023). Ecologically, a normal hepatopancreas reflects good environmental quality, including clean water, sufficient food availability, and minimal or no pollutants or harmful pathogens. This implies that the ecosystem where the lobster resides is balanced and optimally supports marine life. The ecological impact of a normal hepatopancreas is significant because lobsters play a role in the food chain and the balance of marine ecosystems. Beside of water condition, pathogen attacks are a significant cause of hepatopancreas degradation in lobsters (Shield 2011). These pathogens may weaken the lobster's immune system and directly damage the organ's structure and function, resulting in various clinical symptoms that

can range from inflammation to severe tissue necrosis (Davies and Wootton 2018; Nur and Yusnaini 2018). Therefore, healthy lobsters significantly contribute to a stable population, which in turn supports biodiversity and the overall functioning of the ecosystem (van Putten et al. 2016; Ruiz-Salmón et al. 2021). If these conditions are maintained, the sustainability of fisheries resources can be ensured, benefiting both the fishing industry and local economies that rely on marine resources (Hai and Speelman 2020).

In conclusion, the histological analysis of hepatopancreas in *P. penicillatus* and *P. versicolor* revealed significant differences in tubule size, arrangement, and cell distribution. These differences suggest adaptations to distinct environmental conditions and dietary habits between the two species, providing valuable insights into their biological and physiological variations. Furthermore, these findings emphasize the importance of understanding histological differences among species to deepen our knowledge of their biology and physiology.

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REFERENCES

Akmal Y, Irfannur I, Muliari M, Batubara AS, Yunus M, Plumeriastuti H, Dhamayanti Y. 2023. A comprehensive description of the exoskeleton of six lobster species (Genus *Panulirus*) in Aceh Province, Indonesia. Fish Res 264: 106731. DOI: 10.1016/j.fishres.2023.106731.

Atherley NA, Dennis MM, Behringer DC, Freeman MA. 2021. Size at sexual maturity and seasonal reproductive activity of the Caribbean spiny lobster *Panulirus argus*. Mar Ecol Prog Ser 671: 129-145. DOI: 10.3354/meps13762.

Bennett HM, Griffin M, Francis-Floyd R, Baker S, Camus A, Pelton C, Dill-Okubo J. 2023. *Vibrio harveyi* in a Caribbean spiny lobster (*Panulirus argus*) with hepatopancreas necrosis. Vet Pathol 60 (5): 618-623. DOI: 10.1177/03009858231164754.

Butler CB, Butler J, Ross EP, Matthews TR. 2022. Seasonal and fishery impacts on the nutritional condition of the Caribbean spiny lobster Panulirus argus in Florida, USA. Mar Ecol Prog Ser 696: 43-56. DOI: 10.3354/meps14139.

Ciaramella MA, Battison AL, Horney B. 2014. Measurement of tissue lipid reserves in the American lobster (*Homarus americanus*): hemolymph metabolites as potential biomarkers of nutritional status. J Crustac Biol 34 (5): 629-638. DOI: 10.1163/1937240X-00002262.

Damora A, Fadli N, Andriyono S, Suman A. 2021. The potential of the spiny lobster fishery in Aceh waters: A short review. IOP Conf Ser: Earth Environ Sci 869 (1): 012049. DOI: 10.1088/1755-1315/869/1/012049.

Daoud D, Fairchild WL, Comeau M, Bruneau B, Mallet MD, Jackman PM, Benhalima K, Berillis P, Mente E. 2014. Impact of an acute sublethal exposure of endosulfan on early juvenile lobster (*Homarus americanus*). Aquat Sci Technol 2 (2): 14-40.

Davies CE, Whitten MMA, Kim A, Wootton EC, Maffeis TGG, M, Vogan CL, Rowley AF. 2014. A comparison of the structure of American (*Homarus americanus*) and European (*Homarus gammarus*) lobster cuticle with particular reference to shell disease susceptibility. J Invertebr Pathol 117: 33-41. DOI: 10.1016/j.jip.2014.01.001.

Davies CE, Wootton EC. 2018. Current and emerging diseases of the European lobster (*Homarus gammarus*): A review. Bull Mar Sci 94 (3): 959-978. DOI: 10.5343/bms.2017.1142.

de Melo MS, Dos Santos TPG, Jaramillo M, Nezzi L, Muller YMR, Nazari EM 2019. Histopathological and ultrastructural indices for the assessment of glyphosate-based herbicide cytotoxicity in decapod crustacean hepatopancreas. Aquat Toxicol 210: 207-214. DOI: 10.1016/j.aquatox.2019.03.007.

Deyashi M, Chakraborty SB. 2024. Histomorphology and ultrastructure of the hepatopancreas of a brachyuran crab, *Varuna litterata* (Fabricius, 1798). Zoomorphology 2024: 1-15.

Edwarsyah E. 2017. Lobster fishery management in the marine ecosystem approach at Simeulue Island waters (WPP-NRI 572). Elektronik Jurnal Ilmu dan Teknologi Kelautan Tropis 9 (2): 795-804. DOI: 10.29244/jitkt.v9i2.19311. [Indonesian]

Factor JR. 2020. Development of the feeding apparatus in decapod crustaceans. In Functional Morphology of Feeding and Grooming in Crustacea. CRC Press, London.

Feldman AT, Wolfe D. 2014. Tissue processing and hematoxylin and eosin staining. Methods Mol Biol 1180: 31-43. DOI: 10.1007/978-1-4939-1050-2_3.

Frischer ME, Landers SC, Walker AN, Powell SA, Lee RF. 2022. Black gill in marine decapod crustaceans: A review. Rev Fish Sci Aquac 30 (4): 498-519. DOI: 10.1080/23308249.2022.2047153.

Gurina TS, Simms L. 2023. Histology, Staining. In: StatPearls. Treasure Island (FL): StatPearls Publishing; 2024 Jan.

Gutzler BC, Butler MJ. 2017. Comparison of methods for determining nutritional condition in spiny lobsters. J Shellfish Res 36 (1): 175-179. DOI: 10.2983/035.036.0118.

Hai ATN, Speelman S. 2020. Economic-environmental trade-offs in marine aquaculture: The case of lobster farming in Vietnam. Aquaculture 516: 734593. DOI: 10.1016/j.aquaculture.2019.734593.

Hajad V, Aripin N. 2023. Evaluation of pro-fishermen lobster trade policies in Aceh Province. J Government Polit 5 (1): 32-49. [Indonesian]

Hartenstein V, Martinez P. 2019. Structure, development and evolution of the digestive system. Cell Tissue Res 377 (3): 289-292. DOI: 10.1007/s00441- 019-03102-x.

Hoenig JM, Groner ML, Smith MW, Vogelbein WK, Taylor DM, Landers Jr DF, Swenarton JT, Gauthier DT, Sadler P, Matsche MA, Haines AN, Small HJ, Pradel R, Choquet R, Shields JD. 2017. Impact of disease on the survival of three commercially fished species. Ecol Appl 27 (7): 2116-2127. DOI: 10.1002/eap.1595.

Ihsan M, Istriyati, Muliasari H. 2017. Morphology and histology of the hepatopancreas (midgut gland) of the green spiny lobster (*Panulirus Homarus L.*). Jurnal Ilmu Biologi 3: 125-129. [Indonesian]

Ihsan M, Suhirman, Jayadi EM, Sagista R, Hardianti YE, Muliasari H, Tantilar LA, Ilahi WB. 2019. Analysis of natural food in the stomach and microhabitat of the puerulus phase of the sand lobster (*Panulirus homarus*) in Awang Bay. Jurnal Riset Akuakultur 14 (3): 183-191. [Indonesian]

Indriani RD, Nugroho BH. 2023. The role of floating net cages in supporting grouper fish in Sabang Bay Waters, Aceh. Komunitas: Hasil Kegiatan Pengabdian Masyarakat Indonesia 1 (1): 31-45. [Indonesian]

Jonkman J, Brown CM, Wright GD, Anderson KI, North AJ. 2020. Tutorial: Guidance for quantitative confocal microscopy. Nat Protoc 15 (5): 1585-1611. DOI: 10.1038/s41596-020-0313-9.

Kawirian RR, Affandi R, Mashar A, Effendi I. 2023. Food preferences of early juvenile scalloped spiny lobster in Ekas Bay, Lombok, Indonesia. Indones Aquac J 18 (1): 61-69. DOI: 10.15578/iaj.18.1.2023.61-69.

Konecny CA, Cote D, Broome J, Nicolas JM, Regular PM, Cook AM, Hatefi F. 2024. Influences of environmental and individual-level covariates on movement behaviour in American lobster *Homarus americanus*. Mar Ecol Prog Ser 729: 151-166. DOI: 10.3354/meps14519.

Kropielnicka-Kruk K, Fitzgibbon QP, Codabaccus BM, Trotter AJ, Giosio JR, Carter CG, Smith GG. 2022. The effect of feed frequency on growth, survival and behaviour of juvenile spiny lobster (*Panulirus ornatus*). Animals 12 (17): 2241. DOI: 10.3390/ani12172241.

Kurniasari N, Rosidah L, Erlina MD. 2019. Development strategy for the marine and fisheries sector in Sabang City. Jurnal Kebijakan Sosial Ekonomi Kelautan dan Perikanan 8 (2): 125-135. [Indonesian]

Leland J, Bucher D, 2017. Direct age determination with validation for commercially important Australian lobster and crab species: Western, Eastern, Southern and Ornate Rock Lobsters and Crystal, Giant and Mud Crabs. Fisheries Research and Development Corporation and Southern Cross University.

Lewis CL, Fitzgibbon QP, Smith GG, Elizur A, Ventura T. 2023. Ontogeny of the Cytochrome P450 superfamily in the ornate spiny lobster (*Panulirus ornatus*). Intl J Mol Sci 25 (2): 1070. DOI: 10.3390/ijms25021070.

Lopeztegui-Castillo A, Olivera-Espinosa Y, Abitia-Cárdenas LA. 2023. Influence of environmental factors on nutritional condition of spiny lobster *Panulirus argus* (Decapoda: Palinuridae). Thalassas 39: 1003-1014. DOI: 10.1007/s41208-023-00546-5.

Lopeztegui-Castillo A. 2021. Assessment of nutritional condition in crustaceans: A review of methodologies and guidelines for applying inexpensive and wide-ranging indices to the spiny lobster *Panulirus argus* (Latreille, 1804) (Decapoda: Achelata: Palinuridae). J Crustac Biol 41 (4): ruab067. DOI: 10.1093/jcbiol/ruab067.

Martínez-Alarcón D, Saborowski R, Rojo-Arreola L, García-Carreño F. 2018. Is digestive cathepsin D the rule in decapod crustaceans? Comp Biochem Physiol B Biochem Mol Biol 215: 31-38. DOI: 10.1016/j.cbpb.2017.09.006.

Massucci Toledo, T. 2019. Effect of dietary lipid on the molecular and metabolic profile of a freshwater crayfish [Dissertation]. Queensland University of Technology, Brisbane.

Ministry of Marine Affairs and Fisheries. 2020. Minister of Marine Affairs and Fisheries Regulation No. 12 of 2020, concerning the capture of lobsters (*Panulirus* spp.), crabs (*Scylla* spp.), and blue swimming crabs (*Portunus pelagicus* spp.) 4-5.

Mirzaei MR, Ajdari A, Chakeri A. 2021. Review on aquaculture of different spiny lobster species. Adv Aquac Sci J 4 (4): 25-38.

Munian A, Cockcroft A, Hoffman LC, Auerswald L. 2021. Analysis of biological and biochemical parameters of adult male spiny lobsters *Jasus lalandii* for identification of possible growth predictors. Fish Res 243: 106061. DOI: 10.1016/j.fishres.2021.106061.

Nashida T, Sato R, Haga-Tsujimura M, Yoshie S, Yoshimura K, Imai A, Shimomura H. 2013. Antigen-presenting cells in parotid glands contain cystatin D originating from acinar cells. Arch Biochem Biophys 530 (1): 32-39.

Nur I, Yusnaini. 2018. Parasites and histopathology of infected spiny lobster *Panulirus* spp. cultured in outer of Kendari Bay, Indonesia. Aquacult Aquarium Conserv Legis 11 (1): 108-117.

Nurdin MS, Hasanah N, Serdiati N, Putra AE. 2024. Reproductive biology of two species spiny lobster in Donggala Waters Central Sulawesi. Biosaintifika 16 (1): 63-72. DOI: 10.15294/biosaintifika.v15i1.3504.

Pane AR, Alnand R, Marasabessy I, Suman A. 2021. Biological aspects and utilization status of bamboo lobster (*Panulirus versicolor*) in the Aru Islands Waters, Maluku. BAWAL Widya Riset Perikanan Tangkap 13 (2): 85-94. [Indonesian]

Perera E, Simon C. 2015. Digestive physiology of spiny lobsters: Implications for formulated diet development. Rev Aquacult 7 (4): 243-261. DOI: 10.1111/raq.12066.

Putra A, Finasthi D, Putri SY, Aini S. 2022. Economically important aquaculture commodities in Indonesia. Warta Iktiologi 6 (3): 23-28. [Indonesian]

Putra DF, Abol-Munafi AB, Muchlisin ZA, Chen J-C. 2012. Preliminary studies on morphology and digestive tract development of Tomato Clownfish, *Amphiprion frenatus* under captive condition. AACL Bioflux 5 (1): 29-35.

Putra DF, Salsabila F, Dewiyanti I, Batubara AS, Nasir M. 2024. The morphological and histological developmental study of the gastrointestinal tract of peres fish (*Osteochilus kappenii*) larvae. Jordan J Biol Sci 17 (2): 269-275. DOI: 10.54319/jjbs/170206.

Rahmizal M. 2022. Analysis of Indonesia marine fisheries with economic growth, population and effort effectiveness. Eur J Formal Sci Eng 5 (1): 53-61. DOI: 10.26417/ejef.v1i1.p17-22.

Ross EP, Behringer DC, Muñoz A, Díaz D, Bojko J. 2019. A histological atlas for the Palinuridae (Crustacea: Decapoda: Achelata): A guide to parasite discovery and spotting the abnormal in spiny lobsters. J Invertebr Pathol 163: 21-33. DOI: 10.1016/j.jip.2019.03.001.

Rowley AF, Coates CJ. 2023. Shell disease syndromes of decapod crustaceans. Environ Microbiol 25 (5): 931-947. DOI: 10.1111/1462-2920.16344.

Ruiz TFR, Vidal MR, Ribeiro K, Vicentini CA, Vicentini IB. 2020. Histology of the hepatopancreas and anterior intestine in the freshwater prawn *Macrobrachium carcinus* (Crustacea, Decapoda). Nauplius 28: e2020023. DOI: 10.1590/2358-2936e2020023.

Ruiz-Salmón I, Laso J, Margallo M, Villanueva-Rey P, Rodríguez E, Quinteiro P, Dias AC, Almeida C, Nunes ML, Marques A, Cortés A, Moreira MT, Feijoo G, Loubet P, Sonnemann G, Morse AP, Cooney R, Clifford E, Regueiro L, Méndez D, Anglada C, Noirot C, Rowan N, Vázquez-Rowe I, Aldaco R. 2021. Life cycle assessment of fish and seafood processed products – A review of methodologies and new challenges. Sci Total Environ 761: 144094. DOI: 10.1016/j.scitotenv.2020.144094.

Safir M, Maasily IS, Serdiati N, Islamy RA. 2024. Growth of bamboo lobster (*Panulirus versicolor*; Latreille, 1804) fed with feed made from sosodek fish meal (*Atherinomorus lacunosus*). Jurnal Penelitian Pendidikan IPA 10: 100-106. DOI: 10.29303/jppipa.v10iSpecialIssue.7884.

Sakhare SS, Kamble NA. 2014. Impact of environmental pollution on hepatopancreas of freshwater crab *Barytelphusa cunicularis* (Westwood, 1836). Intl J Curr Microbiol Appl Sci 3 (5): 1009-1018.

Salmarika S, Shadiqin I, Irham M, Agustina I, Rahayu R, Aprilla RM, Rahmah A. 2022. Performance analysis of catch fisheries in Sabang Waters. Depik 11 (3): 265-270.

Setyanto A, Rachman NA. Yulianto ES. 2019. Distribution and composition of lobster species caught in Java Sea of East Java, Indonesia. Jurnal Perikanan Universitas Gadjah Mada 20 (2): 49-55. DOI: 10.22146/jfs.36151. [Indonesian]

Shields JD, Boyd RA. 2014. Atlas of lobster anatomy and histology. Special Papers in Marine Science No. 9 Virginia Institute of Marine Science. The Collage of William & Mary. DOI: 10.21220/V5001R.

Shields JD. 2011. Diseases of spiny lobsters: A review. J Invertebr Pathol 106 (1): 79-91. DOI: 10.1016/j.jip.2010.09.015.

Smedbold E. 2024. Fatty acid composition in the hepatopancreas of the Norwegian lobster *(Nephrops norvegicus)* in Romsdalsfjord, a Norwegian fjord effected by intensive aquaculture [Thesis]. Institutt for Biologiske fag Ålesund, Besøksadresse.

Smolowitz R. 2021. Mollusca: Bivalvia. Invertebrate Histology. Wiley Online Library. DOI: 10.1002/9781119507697.ch6.

Sousa MEC, Santos FA, Wanderley-Teixeira V, Teixeira AA, de Siqueira HAA, Alves LC, Torres JB. 2010. Histopathology and ultrastructure of midgut of *Alabama argillacea* (Hübner) (Lepidoptera: *Noctuidae*) fed Bt-cotton. J Insect Physiol 56 (12): 1913-1919.

Štrus J, Žnidaršič N, Mrak P, Bogataj U, Vogt G. 2019. Structure, function and development of the digestive system in malacostracan crustaceans and adaptation to different lifestyles. Cell Tissue Res 377 (3): 415-443. DOI: 10.1007/s00441-019-03056-0.

Suherman A, Santosa MA, Ihsan YN, Wijayanto D, Juwana S. 2020. The eradication of IUU fishing in Indonesia for fisheries resources sustainability by the Task Force 115. AACL Bioflux 13 (5): 2522-2537. DOI: 10.5555/20203600135.

Sukenda S, Lastriliah M, Widanarni W, Effendi I, Hidayatullah D. 2024. The presence of disease in growing spiny lobster *Panulirus* spp. in floating net cages at Tanjung Putus Island, Lampung Indonesia. Jurnal Akuakultur Indonesia 23 (1): 24-35. DOI: 10.19027/jai.23.1.24-35.

Sun S, Xuan F, Fu H, Zhu J, Ge X, Gu Z. 2015. Transciptomic and histological analysis of hepatopancreas, muscle and gill tissues of oriental river prawn (*Macrobrachium nipponense*) in response to chronic hypoxia. BMC Genomics 16 (1): 491. DOI: 10.1186/s12864-015-1701-3.

Sutaman, Dina KF, Nurjanah, Mulatsih S. 2023. Study of compatibility level of waters in the bay of Sabang for the development of marine cultivation. IOP Conf Ser: Earth Environ Sci 1147: 012008. DOI: 10.1088/1755-1315/1147/1/012008.

Tjoneng A. 2015. Realizing Indonesia as the World's Maritime Axis. Dialogia Iuridica 7 (1): 47-55. [Indonesian]

van Putten IE, Farmery AK, Green BS, Hobday AJ, Lim-Camacho L, Norman-López A, Parker RW. 2016. The environmental impact of two Australian rock lobster fishery supply chains under a changing climate. J Ind Ecol 20 (6): 1384-1398. DOI: 10.1111/jiec.12382.

Vogt G, 2019. Functional cytology of the hepatopancreas of decapod crustaceans. J Morphol 280 (9): 1405-1444. DOI: 10.1002/jmor.21040.

Vogt G. 2021. Synthesis of digestive enzymes, food processing, and nutrient absorption in decapod crustaceans: A comparison to the mammalian model of digestion. Zoology 147: 125945. DOI: 10.1016/j.zool.2021.125945.

Wahle RA, Dellinger L, Olszewski S, Jekielek P. 2015. American lobster nurseries of southern New England receding in the face of climate change. ICES J Mar Sci 72 (suppl 1): i69-i78. DOI: 10.1093/icesjms/fsv093.

Wang W, Wu X, Liu Z, Zheng H, Cheng Y. 2014. Insights into hepatopancreatic functions for nutrition metabolism and ovarian development in the crab *Portunus trituberculatus*: gene discovery in the comparative transcriptome of different hepatopancreas stages. PloS One 9 (1): e84921. DOI: 10.1371/journal.pone.0084921.

Wang X, Jin M, Cheng X, Hu X, Zhao M, Yuan Y, Sun P, Jiao L, Tocher DR, Zhou Q. 2022. Hepatopancreas transcriptomic and lipidomic analyses reveal the molecular responses of mud crab (*Scylla paramamosain*) to dietary ratio of docosahexaenoic acid to eicosapentaenoic acid. Aquaculture 551: 737903. DOI: 10.1016/j.aquaculture.2022.737903.

Wei B, Yang Z, Wang J, Chen A, Shi Q, Cheng Y. 2017. Effects of dietary lipids on the hepatopancreas transcriptome of Chinese mitten crab (*Eriocheir sinensis*). PLoS One 12 (7): e0182087. DOI: 10.1371/journal.pone.0182087.

Wijaya D, Nurfiarini A, Nastiti AS, Riswanto R. 2018. Food habits, niche breadth, and overlap of some spiny lobsters from Gulf of Prigi, Trenggalek. BAWAL Widya Riset Perikanan Tangkap 9 (3): 153-161. [Indonesian]

WWF Indonesia. 2015. Deep Sea Lobster Fisheries: Catching and Handling Guidelines.

XuY, Zhang B, Yu C, Hung Z, Hu N, Cai Y, Li Y. 2023. Comparative transcriptome analysis reveals the effects of different feeding times on the hepatopancreas of Chinese mitten crabs. Chronobiol Intl 40 (5): 569-580. DOI: 10.1080/07420528.2023.2189481.

Zhang Z, Jiang H, Liu Y, Wu X, Chen X. 2023. Histological observations and gene expression of the digestive system of the Chinses mitten crab (*Eriocheir sinensis*). Aquaculture and Fisheries. DOI: 10.1016/j.aaf.2023.12.003.