Int Aquat Res (2024) 16:271–292
https://doi.org/10.22034/iar.2024.2008690.1686

ORIGINAL RESEARCH

Growth, health and tail muscle composition of marron *(Cherax cainii)*: a comparison of animal and plant protein dietary ingredients

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Received: 20 May 2024 / Accepted: 11 September 2024 / Published online: 22 September 2024

Abstract A 110-day feeding trial on marron *(Cherax cainii)* evaluated the effects different protein sources on the growth, immunocompetence, and tail muscles amino acid profile. Four animal-protein-based diets—poultry by-product meal (PBM), black soldier fly meal (BSFM), tuna hydrolysate (TH), and fishmeal (FM)—and two plant-derived protein diets—lupin meal (LM) and soybean meal (SBM)—were tested. A total of 450 marron were individually placed in containers and distributed into 18 tanks, representing six dietary treatments in three replicates. The results demonstrated that marron fed BSFM and FM diets obtained significantly higher ($P<0.05$) weight gain (WG) and specific growth rate (SGR) values (73.18–81.86% and 0.65–0.67%/day, respectively) than other diets. There were no significant differences in survival or net biomass increment. Marron fed BSFM showed the highest moult increments (MI) and the shortest intermoult periods (Tim), while TH and LM resulted in the lowest. The BSFM diet also led to the lowest hepatopancreatic moisture. The total haemocyte count and granular cells proportion in marron fed TH were lower than those in marron fed other diets. Protease activity was lower in marron fed TH and LM than other protein sources. Except for methionine, amino acid profiles in the tail muscle of SBM-fed marron were similar to those in FM, PBM, and TH groups. Marron fed TH and LM showed an enlargement of tubular and intertubular spaces within epithelium in the hepatopancreas, myodegeneration in tail muscles, and shorter fold height and width in the marron intestine. In conclusion, FM, PBM, and BSFM protein-based diets promoted the growth, immunity, and hepatopancreatic health of marron, while TH and LM diet resulted in decreased growth. SBM did not significant impact growth. The results would contribute to using local protein ingredients as replacement for fishmeal protein for the development of marron industry in Western Australia.

Keywords Black soldier fly larvae . Poultry by-product meal . Tuna hydrolysate . Lupin meal . Growth performance . Immunity . Hepatopancreas histology

Introduction

Marron (*Cherax cainii*) an iconic aquaculture species, is the largest farmed freshwater crayfish species in Western Australia. Marron can grow up to a large size (up to 2.5 kg) and has a simple life cycle that is free from any diseases. Marron, can be transported alive, thereby attracting a high market demand (Duarte Alonso 2010; Lawrence 1998). The production of yabbies (*Cherax destructor*), marron, and red claw (*C.*

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quadricarinatus) in Australia was 17.3 tonnes, 55.8 tonnes and 31.2 tonnes, respectively (Tuynman et al. 2023), valued at $615,000, $2,266,000 and $850,000, respectively, in 2021-22. In Western Australia, the value of the marron was $2,070,000 from a total production of 52.0 tonnes in 2021-22.

Protein requirements in crayfish are affected by several dietary, biological and environmental variables (Guillaume 1997; Gutiérrez-Yurrita and Montes 2001; Manomaitis 2001). Marron are omnivores and can eat anything, including microbial-enriched detritus, phytoplankton, zooplankton, insects, and other small aquatic animals (Duarte Alonso 2009). Marron constitute an important freshwater aquatic ecosystem by converting plant and algae matter into valuable animal protein (Beatty et al. 2019). Marron can go for weeks without food in natural aquaculture, but they require a regular and good quality diet for optimal growth and can be commercially viable (Fotedar 2015). Marron's feeding habits are complex and multi-trophic. The marron often ignored the remains of disintegrated pieces of the formulated pellets, therefore, the pellets need to be stable and last a sufficient period for the marron to feed before they start disintegrating (Jussila and Evans 1996b).

Fishmeal (FM) has been the primary source of protein in aquafeeds due to its excellent amino acid profile and high digestibility (Saleh et al. 2022). However, as the aquaculture industry has grown, the demand for FM has also increased, leading to concerns about its limited availability and sustainability. Plant-based protein sources have been a common replacement for FM in aquafeeds due to their acceptable protein levels, availability, lower cost and consistent quality (Watanabe 2002), however, plant-based proteins possess some negative attributes like deficiency in methionine and lysine (Gatlin III et al. 2007) and anti-nutritional factors (ANFs) such as trypsin inhibitors, lectins, oligosaccharides and saponins that may affect digestion and reduce nutrient availability, for example in shrimp (Dersjant-Li 2021) while animal-based proteins have a balanced dietary amino acids protein, similar to FM. Poultry by-product meal (PBM) is derived from various parts of poultry that humans do not commonly consume and can be processed and incorporated into aquafeed to provide valuable protein and nutrients to aquatic animals (Chaklader et al. 2019). PBM generally contains high protein and essential amino acids, similar to FM. Studies on PBM with promising results have been carried out on the American signal crayfish (*Pacifastacus leniusculus)* (Fuertes et al. 2013), marron (Saoud et al. 2008, Saputra et al. 2019, Saputra and Fotedar 2021; Siddik et al. 2020), and red swamp crayfish (*Procambarus clarkii)* (Yang et al. 2022). In a previous study, Saputra et al. (2019) found that PBM can replace FM protein in marron with a higher total haemocyte count and longer microvilli in the intestine.

Like PBM, fish protein hydrolysates (FPHs) are seafood by-products of skin, fins, heads, trimming, frames, and roe (Benhabiles et al. 2012). FPHs contain short-chain peptides rich in biological activity and free amino acids (Chalamaiah et al. 2012), which help to increase feed intake and nutrient absorption. In their study, Refstie et al. (2004) reported increased feed intake of Atlantic salmon (*Salmo salar)* when fed a diet containing 10% and 15% FPHs. When used to replace up to 15% protein in diets, FPHs enhanced growth in juvenile pike silverside (*Chirostoma estor)* (Ospina-Salazar et al. 2016), whereas the inclusion of 50 and 75% of tuna hydrolysate (TH) reduced the growth performance of barramundi (*Lates calcarifer)* (Siddik et al. 2018). Regarding crustaceans, Pacific white shrimp *(Litopenaeus vannamei)* postlarvae fed diets supplemented with FPHs between 21.22 and 26.35% exhibited maximal growth performance (Niu et al. 2014).

Insects represent an emerging and sustainable animal protein source in aquaculture feeds (Surendra et al. 2016; Tran et al. 2015). One of the most promising insect species is black soldier fly larvae (*Hermetia illucens*) which can convert low-value by-products and waste into proteins and fat suitable for feeding livestock animals and fish (Spranghers et al. 2017). Black soldier fly meal (BSFM) is high in protein (42.1%) and lipids (10–30%) and has a well-balanced amino acid profile, similar to that in FM (Henry et al. 2015; Makkar et al. 2014; Tran et al. 2015). There is limited research on the potential of including BSFM in decapod crustacean diets. A study by Cummins et al. (2017) found acceptable growth performance in *L. vannamei* when fed 7–36% of BSFM. In marron, supplementation of low levels of BSFM, along with FM, enhances immune-relevant gene expression and intestinal microbiota (Foysal et al. 2021).

Soybean meal (SBM) is one of the most favoured plant protein sources in aquaculture diet formulations due to its global availability, well-balanced amino acid profile, and relatively reasonable price (Allen Davis and Arnold 2000; Amaya et al. 2007a, b; Daniel 2018; Divakaran et al. 2000). The use of SBM as a

dietary protein source has been extensively studied and applied in aquaculture in various species, including Southern white shrimp *(Litopenaeus schmitti)* (Alvarez et al. 2007), kuruma shrimp (*Marsupenaeus japonicus)* (Bulbul et al. 2015), *L. vannamei* (Hulefeld et al. 2018; Lim and Dominy 1990), *C. destructor* (Jones et al. 1996), *P. clarkii* (Wan et al. 2017), *C. quadricarinatus* (García-Ulloa et al. 2003; Qian et al. 2021; Thompson et al. 2005), and *P. leniusculus* (Fuertes et al. 2012). However, the cultivation of soybeans causes environmental deterioration such as deforestation, the widespread use of genetically modified (GM) soybean seeds, and the heavy use of fertiliser and pesticides (Sánchez-Muros et al. 2014; Sánchez-Muros et al. 2020). Lupin meal (LM) is being considered as an appealing alternative to SBM due to its relatively favourable composition and regional availability (Szczepański et al. 2022). The nitrogen-fixing properties of lupins can benefit subsequent crops in a rotation system (Sulieman and Tran 2016), reducing overall fertilisation requirements (Weiss et al. 2020). Australia is the world's largest lupin producer, and Western Australia's wheat belt area contributes about 80% of the country's lupin production. Plant-derived nutrient sources contain ANFs such as protease inhibitors, lectins, phytic acid, saponins, tannins, and alkaloids (Francis et al. 2001; Small 2022). These ANFs can inhibit digestion or interfere with nutrient absorption, which can result in reduced growth (Makkar 1993). Various treatments, such as heating, soaking, and fermenting, are employed to mitigate the impact of ANFs in diets (Vikas et al. 2012). A few studies on using protein from LM have been reported in the shrimp species *L. vannamei* (Molina-Poveda et al. 2013; Weiss et al. 2020) and black tiger prawn (*Penaeus monodon)* (Smith et al. 2007a; Smith et al. 2007b; Smith et al. 2007c; Sudaryono et al. 1999a; Sudaryono et al. 1999b; Sudaryono et al. 1999c; Sudaryono 2003), but research on using LM as a protein source in marron diet is limited.

A study by Fotedar (2004) reported that protein sources are not important for marron growth in commercial, semi-intensive culture, as the natural productivity of the complementing pond ecosystem is characterised by a lack of amino acids from diverse protein sources. Similarly, Saputra and Fotedar (2021) and Saputra et al. (2019) stated that different protein sources did not affect marron growth, only their immune responses and gut micrographs under laboratory conditions. The information on moult increment and moult intermoult, as well as digestibility from dietary various protein sources, is limited. Therefore, in this study, growth parameters such as moult increment, amino acid composition, immune responses, and the microstructure of the hepatopancreas and intestine of marron were used as physiological tools to compare the effectiveness of animal proteins such as FM, PBM, BSFM, and TH with plant protein sources such as LM and SBM in the marron diet. The outcomes of this study would significantly provide nutritional knowledge on using alternative protein sources in marron formulated diets to maintain the sustainable development of the marron industry.

Materials and methods

Ethical statement

All experimental protocols were carried out according to the standard operating procedure of Curtin Aquatic Research Laboratory (CARL) at Curtin University, Perth, Western Australia. Though animal ethics approval is not required for experimentation with marron, all experimental protocols were carried out in strict compliance with the Australian Code for the Care and Use of Animals for Scientific Purposes (2013) to minimize the pain and discomfort of the experimental animals.

Feed composition and preparation

All dry ingredients of the experimental test diets were purchased from Specialty Feeds Company, Glen Forrest, Western Australia. The dried black soldier fly larvae were from Future Green Solution, Western Australia. Dried black soldier fly larvae were ground with Sunbeam Grind Fresh Coffee Grinder EMO440 to prepare BSFM. Southern bluefin tuna *Thunnus maccoyii* hydrolysate was provided by SAMPI, Port Lincoln, Australia. All dry ingredients were mixed before adding fish oil and distilled water to form a dough. The dough was passed through a pelletiser to obtain 2 mm diameter pellets. The pellets were then dried in an oven at 60°C for 24 h until a constant dry weight was achieved, and then stored in a cool room at 4°C until use. Formulation and proximate composition of the test diets were given in Table 1.

Feed proximate composition analysis, amino acids and fatty acid analysis

Feed proximate composition were analysed according to AOAC (2005). Crude protein was determined using the Kjeldahl method. Crude lipids were determined via Soxhlet extraction. To estimate their moisture content, the samples were dried in an oven at 105°C for 24 h (until constant dry weight was achieved). The ash contents were determined by placing samples in a muffle furnace at 550°C for 24 h followed by weighing. Determination of the amino acid composition of experimental diets was performed as per the Australian Proteome Analysis Facility (APAF) SOP AAA-001 method, following the laboratory procedure described by (Chaklader et al. 2020a). The fatty acid profile of test diets was carried out following the protocol of O'Fallon et al. (2007) and Siddik et al. (2019a).

Experiment design

The feeding trial was conducted at the Curtin Aquatic Research Laboratory (CARL), Technology Park, Curtin University, Western Australia. 450 marron with an average initial weight of 1.61 ± 0.05 g were purchased from Blue Ridge Marron Farm, Manjimup, Western Australia (-34° 14'27.60''S, 116°08'45.60''E) and acclimated for two weeks in experimental facilities.

After the acclimation period, dead and weak marron were removed. The remaining marron were randomly distributed at a density of 25 per tank into 18 circular polyethylene tanks (approximately 300 L in capacity, 100 cm in diameter and 40 cm in height), each fitted with a biological filter and with continuous aeration. Each marron was individually stocked in a 1,000 mL plastic container to avoid cannibalism, and the containers were labelled for identification. Marron were fed six test diets, in replicates of three tanks, by inserting the pellets into each container. Thus, three randomly assigned tanks represented one test diet. The marron were fed 3% of their total biomass once a day for 110 days during the dark hours. The natural photocycle of the marron was reversed by employing artificial lights in the dark laboratory to maintain 12 h of darkness through the day. The marron containers were cleaned, and the uneaten feed and faeces were siphoned out daily before the next feeding commenced. Water exchange at a rate of 70–100% of the total water volume was performed in all tanks every two weeks to maintain suitable water quality. Water quality

Table 1 Proportion of different ingredients in the formulated feeds (g/kg)

Ingredients *	Experimental diets					
	FM	PBM	BSFM	TH	LM	SBM
FM	46.00	0.00	0.00	0.00	0.00	0.00
PBM	0.00	42.00	0.00	0.00	0.00	0.00
BSFM	0.00	0.00	33.60	0.00	0.00	0.00
TH	0.00	0.00	0.00	27.00	0.00	0.00
LM	0.00	0.00	0.00	0.00	70.00	0.00
SBM	0.00	0.00	0.00	0.00	0.00	62.00
Wheat	30.00	34.50	33.40	35.00	7.00	12.00
Corn/wheat starch	11.00	11.00	11.00	11.00	11.00	10.00
Cholesterol	0.50	0.50	0.50	0.50	0.50	0.50
Canola oil	2.00	1.50	0.00	0.00	2.00	4.00
Cod liver oil	3.00	2.00	0.00	0.00	2.50	5.00
Vitamin premix	0.30	0.30	0.30	0.30	0.30	0.30
Vitamin C	0.10	0.10	0.10	0.10	0.10	0.10
Dicalcium phosphate	0.10	0.10	0.10	0.10	0.10	0.10
Lecithin – soy	3.00	3.00	3.00	3.00	3.00	3.00
Barley	4.00	5.00	5.00	4.00	3.50	3.00
Casein	0.00	0.00	13.00	19.00	0.00	0.00
Proximate composition (%dry weight)						
Crude protein (%)	30.81	31.06	30.25	31.04	30.06	31.17
Crude lipid (%)	12.99	13.75	13.27	12.32	12.95	12.21
Moisture (%)	8.31	8.23	8.58	7.86	8.50	8.04
Ash (%)	11.07	6.52	4.22	5.17	3.18	5.47

*Fishmeal (FM): crude protein 58.55%, crude lipid 9.46%; Black soldier fly meal (BSFM): crude protein 44.04%, crude lipid 28.3%; Soybean meal (SBM) crude protein 46.41%, crude lipid 2.51%; Lupin meal (LM): crude protein 41.47%, crude lipid 9.01%; Poultry by-product meal (PBM): crude protein 62.75%, crude lipid 15.1% and Tuna hydrolysate (TH): crude protein 37.91% and crude lipid 35.50%.

parameters, including temperature, pH, and dissolved oxygen (DO) were measured once a week using a portable multi-parameter meter (YSI, United States) and total ammonia was measured weekly with chemical test kits (Aquarium Pharmaceuticals™ API).

Growth and moulting

The mortality and weight of the moulted marron were recorded for each tank to calculate the survival and moult increment. At the end of the feeding trial, individual marron weight was determined using electronic scales after excess moisture was removed with a paper towel to calculate overall growth performance. Moult increment and intermoult period were determined by counting the number of moults marron in each tank. Weight gain (WG), specific growth rate (SGR), biomass increment (BI), survival rate (SR), moult increment (MI), intermoult period (Tim), and moulting rate (MR) were calculated using the following formulas as proposed by Jussila and Evans (1998).

$$\text{WG (\%)} = 100 \times \frac{(\text{Final weight} - \text{Initial weight})}{\text{Initial weight}}$$

$$\text{SGR (\%/day)} = 100 \times \frac{(\ln \text{Final weight} - \ln \text{Initial weight})}{\text{Number days}}$$

$$\text{BI (\%)} = 100 \times \frac{(\text{Final biomass} - \text{Initial biomass})}{\text{Initial biomass}}$$

$$\text{SR (\%)} = 100 \times \frac{\text{Final number of marron}}{\text{Initial number of marron}}$$

$$\text{MI (g)} = \text{Weight of moult}_{n+1} - \text{Weight of moult}_{n}$$

where n = the number of moults

$$\text{MI (\%)} = 100 \times \frac{(\text{Weight of moult}_{n+1} - \text{Weight of moult}_{n})}{\text{Weight of moult}_{n}}$$

$$\text{Tim (day)} = T_{n+1} - T_{n}$$

where T_{n+1} = date of n+1 moult; T_{n} = date of n moult

$$\text{MR (\%)} = 100 \times \frac{\text{Number of moulted marron}}{\text{Total number ofmarron}}$$

Organosomatic indices

Organosomatic indices of marron were measured following the methods described by Mai and Fotedar (2018). One marron from each tank was dissected to remove the tail muscle and hepatopancreas, which were placed in an aluminium cup to calculate their wet weight. The same tail muscle and hepatopancreas were then dried in oven at 80°C for 24 h to record their dry weight. The wet hepatosomatic index (Hiw), wet tail muscle index (Tiw), dry hepatosomatic index (Hid), dry tail muscle index (Tid), moisture of hepatopancreas (HM), and moisture of tail muscle (TM) were calculated using the following formula:

$$\text{HM (\%)} = 100 \times \frac{\text{Weight of wet hepatopancreas}}{\text{Total weight of marron}}$$

$$\text{Tiw (\%)} = 100 \times \frac{\text{Weight of wet tail muscle}}{\text{Total weight of marron}}$$

$$\text{Hid (\%)} = 100 \times \frac{\text{Weight of dry hepatopancreas}}{\text{Total weight of marron}}$$

$$\text{Tid (\%)} = 100 \times \frac{\text{Weight of dry tail mucles}}{\text{Total weight of marron}}$$

$$\text{HM (\%)} = 100 \times \frac{(\text{Weight of wet hepatopancreas} - \text{Weight of dry hepatopancreas})}{\text{Weight of wet hepatopancreas}}$$

$$\text{TM (\%)} = 100 \times \frac{(\text{Weight of wet tail muscle} - \text{Weight of dry tail muscle})}{\text{Weight of wet tail muscle}}$$

Immune parameters

Three marron from each tank were randomly chosen to collect haemolymph from the fifth pereopod into a 1 mL sterile syringe (27 gauge) containing 0.2 mL anticoagulant solution (100 mM glucose, 30 mM trisodium citrate, 26 mM citric acid, 15.5 mM NaCl, and 10 mM EDTA) and transferred into 1.5 mL Eppendorf tubes (haemolymph–anticoagulant ratio = 1:1). The haemolymph samples were kept in an ice bag at 5°C for further analysis.

Total haemocyte count (THC) and differential haemocyte count (DHC)

To calculate THC, a 50 µL of the haemolymph–anticoagulant mixture (diluted haemolymph) was placed on a haemocytometer (Improved Neubauer, MarienFeld, Germany) (Sang et al. 2009). The cells were counted in both grids under a microscope at 40X magnification.

$$\text{THC} = \frac{\text{Cells counted}}{\text{Volume of grid}} \times 1.000$$

To calculate the DHC, a drop of diluted haemolymph was smeared onto a glass slide and air-dried before fixing in 70% methanol for 5 min. The slides were placed in May–Grunwald stain and then Giemsa stain solution for 10 min in each stain solution. Identification of the hyaline cells (HC), semi-granular cells (SGC) and granular cells (GC) was carried out as described by Sang et al. (2009).

$$\text{HC} = 100 \times \frac{\text{Number of hyaline cells}}{\text{Total haemocyte cells counted}}$$

$$\text{SGC} = 100 \times \frac{\text{Number of semi} - \text{granular cells}}{\text{Total haemocyte cells counted}}$$

$$\text{GC} = 100 \times \frac{\text{Number of granular cells}}{\text{Total haemocyte cells counted}}$$

Lysozyme activity assay

The lysozyme activity in marron haemolymph was assessed using the turbidimetric assay by Tulsankar et al. (2022) with some modifications. In summary, 5 mg of *Micrococcus lysodeikticus* (Sigma-Aldrich, St. Louis, MO, USA) was mixed with 20 mL of phosphate-buffered saline (PBS) at pH 7.4 to prepare a bacterial suspension. Then, 100 µL haemolymph samples were pipetted and placed into a 96-well plate in duplicate. After incubation for 15 min at 25°C, 100 µL of bacterial suspension was added to the wells and mixed. The plate was placed in a MS212 reader (Titertek Plus, Tecan, Grodig, Austria), and absorbance at 450 nm was monitored every 2 min for a total of 20 min. The results are expressed as EU/ml.

Protease activity assay

The same three marron were dissected and their hepatopancreas removed and stored at -80°C for the protease assay. A sample of 0.3 g hepatopancreas was weighed and homogenised in PBS buffer at 1:10 (tissue: buffer). The samples were centrifuged at 10,000 x g for 10 min at 4°C to eliminate the distinct layers of lipids and tissue debris that settled at the bottom. Only the supernatant was used for protease activity measurement. The protease activity in the hepatopancreas was assayed using a commercial kit and following the manufacturer's instructions (Thermo Scientific TM Pierce TM Protease Assay Kit), with succinylated casein as substrate. To summary, 10 mg of lyophilised succinylated casein was dissolved in 5 mL BupHTM borate buffer to prepare succinylated casein solution. Then, 100 µL of the succinylated casein solution was placed in a 96-well microplate, and 50 µL of sample was then added to the wells containing succinylated

casein in duplicate. The microplate was incubated for 20 min at room temperature, and 50 µL TNBSA (2,4,6-trinitrobenzene sulfonic acid) working solution was then added to each well. The plate was further incubated for 20 min at room temperature. The plate was placed in a MS212 reader (Titertek Plus, Tecan, Grodig, Austria), and the absorbance at 450 nm was recorded. The results are expressed as specific activity (U/mg protein).

Marron proximate composition analysis and amino acids analysis

Six marron from each tank were dissected to collect tail muscles. Marron tail muscle samples were wrapped in aluminium foil, freeze dried for 3 days, and then stored at -80°C for further analysis. Crude protein, crude lipid, crude ash, and moisture were determined according to the standard methods of AOAC (2005). Determination of the amino acid composition of tail muscles was performed as per the Australian Proteome Analysis Facility (APAF) SOP AAA-001 method, following laboratory producer (Chaklader et al. 2020a).

Histology of hepatopancreas, muscle, and intestine

Six marron per tank were collected, and their hepatopancreas, gut and tail muscles were immediately fixed in a 10% formalin solution for later histological examination. Preparation of samples for histological analysis was undertaken by the Animal Health Laboratories, Department of Primary Industries and Regional Development (DPIRD). Dehydration of the tissue was performed by passing through a series of 70%, 85%, and 98% alcohol solutions. The samples were vacuum embedded in paraffin. Histological sections of 4–5µm were cut and stained with haematoxylin and eosin (H&E). The sections were examined and photographed using a microscope BX40F4, Olympus, Tokyo, Japan (Chaklader et al. 2020b). The fold height, fold width, and muscular thickness of the intestine of marron fed test diets were measured in micrometer using digital imaging software (Adobe Photoshop version 22.4.3, Adobe System Incorporated, USA).

Feed stability test

Four grams of pelleted feed from each diet was weighed and put in glass beakers containing 50 mL of water in triplicate. The immersion times examined were 30 min, 60 min, 2 h, 8 h and 24 h. After the selected immersion time, the water was siphoned off, and the pellets were dried at 60°C for 24 h and then cooled in a desiccator until constant weights were achieved. The water stability of test diets was determined by measuring the dry matter weight of the pellets before and after the selected immersion time in water. The percentage dry matter loss was calculated using the following equation:

$$\text{Dry matter loss} = 100 \times \frac{\text{DMt0} - \text{DMtn}}{\text{DMt0}}$$

where DMt_0 = weight dry matter of the diet at the start of the test
DMt_n = weight of dry matter of the diet after immersion at t = n minutes.

Statistical analysis

SPSS version 25.0 was used to analyse the data. The results were presented as the mean ± SE. The normality of data was assessed using the Shapiro–Wilk test and Levene test prior to analysis. One-way ANOVA followed by Tukey HSD post hoc tests were used to determine significant differences among treatment groups. In addition, a paired t-test was used to compare the moult parameters between two successive moult increments.

Results

Diet amino acids and fatty acids composition

All test diets showed approximately similar values of essential amino acids, except in the case of methi-

onine, lysine, and arginine (Table 2). Plant-derived protein diets (LM and SBM) had lower methionine and lysine compared to animal-based protein diets (FM, PBM, BSFM and TH). LM had the lowest lysine and methionine. Conversely, LM contained the highest arginine among any test diets. Glutamic acid was the most prominent non-essential amino acid in the diets. BSFM had high lauric and myristic acid contents (Table 3). Saturated fatty acid (SFA) was most abundant in BSFM, followed by the TH diet. The FM diet was rich in eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) compared to other diets, and the highest amount of polyunsaturated fatty acid (PUFA) was observed in the FM diet.

Growth performance, intermoult period, and survival rate

During the experiment, the water temperature ranged from 19.00 to 20.30°C, the pH from 6.50 to 7.75, and the DO from 7.37 to 7.71. After 110 days of feeding, final marron body weight differed significantly ($P < 0.05$) among test diets. The growth of marron was similar when fed PBM and SBM compared to other diets, whereas FM and BSFM diets resulted in significantly higher ($P < 0.05$) WG and SGR than diets containing TH and LM. The biomass increment and survival rate of the marron were independent ($P > 0.05$) of the protein source (Table 4).

For all diets, there was a significant difference ($T = -6.553$, $P = 0.000$) in moult increment between the first and second MI (g) (Table 5). Moult increments were significantly longer at the second moult than at the first moult. Similarly, Tim was significantly different between the first and second moults ($T= -8.780$, $P = 0.000$). However, there was no significant difference in MI (%) between the first and second moult of marron fed any test diets ($T= 8.97$, $P= 3.82$).

Marron fed TH and LM had the lowest MI (g), whereas the highest MI (g) was recorded in marron fed BSFM, followed by marron fed SBM, FM, and PBM ($P < 0.05$). Marron fed BSFM diet showed lower first and second Tim (29 and 40 days, respectively), whereas those fed TH and LM had significantly higher Tim ($P < 0.05$). Marron receiving PBM and SBM diets had similar Tim (32 and 34 days, respectively) (Table 5).

There were significant differences ($P < 0.05$) in moulting rate at the second moult among marron fed different protein sources. Only marron fed FM and BSFM recorded a fourth moult (Table 6).

Organosomatic indices

Organosomatic indices values for marron fed various protein source diets are presented in Table 7. There were no significant differences ($P > 0.05$) in Hiw and TM among marron fed any of the test diets. A healthier condition was observed in marron fed BSFM, as demonstrated by the highest Hid and lowest HM, whereas marron fed TH had the lowest Hid and highest HM. Marron fed FM, PBM, LM, and SBM had similar Tiw

Table 2 Amino acid composition (g/100g dry matter basis) of the experimental diets.

	FM	PBM	BSFM	TH	LM	SBM
Essential amino acids (g/100g on dry matter basis)						
Histidine	2.95	2.27	2.90	2.82	2.96	2.76
Threonine	4.63	4.03	4.19	4.28	3.98	4.23
Lysine	6.95	5.68	6.61	6.87	4.21	5.61
Arginine	6.25	6.85	4.33	4.35	11.60	7.15
Methionine	2.70	2.05	2.15	2.46	0.61	1.09
Valine	5.51	5.09	6.24	6.04	4.59	5.26
Isoleucine	4.70	4.25	4.98	4.88	4.77	5.04
Leucine	8.18	7.73	8.42	8.53	7.88	8.53
Phenylalanine	4.67	4.36	4.98	4.88	4.62	5.52
Non-essential amino acids (g/100g on dry matter basis)						
Serine	4.56	4.43	5.11	5.34	5.53	5.45
Glutamic acid	16.00	17.66	20.04	20.60	22.58	20.21
Glycine	8.14	10.40	3.99	4.41	4.81	4.56
Aspartic acid	9.02	8.06	8.04	7.37	10.16	11.36
Alanine	6.56	6.74	4.70	4.31	3.56	4.52
Proline	6.56	8.02	9.00	9.46	4.96	5.84
Tyrosine	2.63	2.38	4.33	3.42	3.18	2.86

FM: fish meal; PBM: poultry by-product meal; BSFM: black soldier fly meal; TH: tuna hydrolysate; LM: lupin meal; SBM: soybean meal.

and Tid that were significantly (P < 0.05) lower than in marron fed BSFM.

Immune responses and digestive enzymatic activity

Marron fed TH had significantly lower (P < 0.05) THC (Figure 1B) and the percentage of granular cells (Figure 1C), while the hyaline cells (Figure 1D) proportion were not affected by any test diets ($P > 0.05$). The lysozyme (Figure 1A) and protease (Figure 1F) activity of marron fed LM were significantly lower than that of marron fed PBM and BSFM.

Table 3 Fatty acid composition (g/100g on dry matter basis) of the experimental diets.

Fatty acid profile	Experimental diets					
	FM	PBM	BSFM	TH	LM	SBM
C12:0 (lauric acid)	0.03	0.06	27.68	2.76	0.12	0.20
C14:0 (myristic acid)	2.03	1.13	4.87	3.79	1.12	2.48
C14:1n5	0.04	0.10	0.07	0.04	0.03	0.06
C15:0	0.41	0.16	0.33	0.60	0.14	0.24
C16:0 (palmitic acid)	15.24	17.31	15.15	24.01	12.59	14.31
C16:1n7	2.99	3.74	3.13	3.67	1.76	4.08
C17:0	0.70	0.26	0.44	0.89	0.19	0.33
C17:1	0.34	0.20	0.31	0.44	0.15	0.27
C18:0 (stearic acid)	4.50	5.07	3.19	7.68	4.22	3.22
C18:1cis+trans	25.52	36.91	15.89	23.89	34.97	29.55
C18:2 cis	18.01	21.85	17.74	14.24	30.52	22.25
C18:3n6	0.09	0.10	0.08	0.09	0.03	0.05
C18:3n3 (linolenic acid)	3.96	3.92	3.85	2.07	4.28	3.98
C18:4n3	0.59	0.33	0.94	0.70	0.30	0.65
C20:0	0.32	0.21	0.12	0.34	0.49	0.29
C20:1	3.61	2.60	0.85	2.07	3.21	7.30
C20:2	0.20	0.16	0.07	0.20	0.10	0.16
C20:3n6	0.12	0.17	0.08	0.12	-	0.06
C20:4n6	1.09	0.70	0.65	0.55	0.08	0.18
C20:3n3	0.10	0.04	0.05	0.09	-	0.07
C22:0	0.22	0.15	0.08	0.18	0.96	0.22
C20:5n3 (EPA)	3.96	1.56	2.09	2.98	1.48	3.40
C22:1n9	0.28	0.21	-	0.24	0.26	0.69
C22:4n6	0.98	-	-	0.27	-	-
C22:5n3 (DPA)	1.01	0.44	0.14	0.82	0.28	0.69
C24:1	0.33	0.11	-	0.53	0.13	0.30
C22:6n3 (DHA)	13.29	2.44	0.74	6.34	2.25	4.92
∑SFA	23.51	24.41	53.33	40.63	20.19	21.34
∑MUFA	33.10	43.87	20.24	30.89	40.50	42.25
∑PUFA	43.39	31.72	26.42	28.48	39.31	36.41
∑n-3 PUFA	22.90	8.74	7.81	13.01	8.58	13.72
∑n-6 PUFA	2.27	0.96	0.81	1.04	0.11	0.29
∑n-3/∑n-6	10.09	9.07	9.67	12.57	78.85	47.55

EPA: eicosapentaenoic acid; DPA: docosapentaenoic acid; DHA: docosahexaenoic acid; ∑SFA: sum of saturated fatty acids; ∑MUFA: sum of monosaturated fatty acids; ∑PUFA: sum of polyunsaturated fatty acids; ∑n-3 PUFA: sum of omega-3 polyunsaturated fatty acids; ∑n-6 PUFA: sum of omega-6 polyunsaturated fatty acids.

Table 4 Weight gain, specific growth rate, biomass increment, and survival rate of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days.

	FM	PBM	BSFM	TH	LM	SBM
IBW (g)	1.56±0.12	1.55±0.11	1.65±0.10	1.73±0.175	1.60±0.11	1.57±0.12
FBW (g)	3.09±0.17^{ab}	2.82±0.13^{ab}	3.29±0.15^{a}	2.74±0.17^{ab}	2.55±0.10^{b}	2.92±0.16^{ab}
WG (%)	81.86±3.21^{a}	66.84±2.57^{ab}	73.18±2.77^{a}	51.14±7.20^{b}	48.55±5.54^{b}	66.93±4.05^{ab}
SGR(%/day)	0.67±0.03^{a}	0.57±0.03^{ab}	0.65±0.01^{a}	0.47±0.05^{b}	0.43±0.05^{b}	0.55±0.02^{ab}
BI (%)	62.26±10.49	56.01±6.12	55.14±6.06	44.06±5.93	45.74±7.48	45.55±2.64
SR (%)	95.83±4.17	91.23±1.87	89.01±1.94	93.70±3.42	97.78±2.23	87.73±3.17

Mean value (±SE) of three replicates. Values in the same row sharing different superscript letters denote significant difference as determined by one-way ANOVA and Tukey HSD post hoc test (P < 0.05). IBW: initial body weight; FBW: final body weight; WG: weight gain; SGR: specific growth rate, BI: biomass increment; and SR: survival rate.

Marron tail muscles: composition and amino acid profile

The different protein-based diets did not affect ($P > 0.05$) the crude protein, moisture, and ash contents in the tail muscles. Tail muscle crude lipid content differed significantly ($P < 0.05$), with the highest lipid level in the marron fed PBM diet followed by the marron fed FM, SBM, and LM group, and the lowest fat content was for the BSFM and TH diet (Table 8).

With the exception of glutamic acid, lysine, and tyrosine, the remaining amino acids exhibited different concentrations in marron tail muscles when fed the various protein sources (Table 8). Marron fed the BSFM diet had significantly higher ($P < 0.05$) levels of essential amino acids (EAAs), except for arginine, compared to marron fed LM. Methionine had the lowest concentration in tail muscles of marron fed LM and the highest in FM-marron ($P < 0.05$). However, BSFM-fed marron had the lowest percentages of serine and glycine (non-essential amino acids). Marron showed higher amounts of amino acids when fed with SBM compared to LM, comparable to marron fed FM, with the exception of methionine. Marron fed FM, PBM, LM, and SBM had the lowest levels of alanine and proline.

Histopathology of hepatopancreas and tail muscle

The histopathological changes in response to TH and LM protein sources in the hepatopancreas are shown in Fig. 2. Marron fed FM, SBM, BSFM, and PBM showed normal hepatopancreas structure with a regular tubular lumen and intertubular spaces and normal R, E, and B-cells, whereas an enlargement of the tubular lumen and intertubular spaces with thin epithelium was observed in the hepatopancreas of marron fed LM

Table 5 The first and second moult increments and intermoult periods of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days.

Moult parameters	FM	PBM	BSFM	TH	LM	SBM
First MI (g)	0.66±0.04^{a}	0.46±0.03^{ab}	0.65±0.06^{a}	0.43±0.08^{ab}	0.36±0.03^{b}	0.67±0.07^{a}
Second MI (g)	0.74±0.06^{ab}	0.58±0.01^{bc}	0.81±0.04^{a}	0.50±0.06^{c}	0.51±0.01^{c}	0.76±0.03^{ab}
First MI (%)	29.42±2.98^{ab}	27.32±0.99^{ab}	34.46±3.82^{a}	17.83±2.28^{b}	26.51±2.97^{ab}	36.66±3.90^{a}
Second MI (%)	30.10±3.02	23.70±2.74	27.68±4.65	22.03±4.86	23.25±6.17	26.00±2.27
First Tim (days)	30.00±2.14^{b}	32.86±2.40^{ab}	29.25±0.81^{b}	41.80±1.38^{a}	34.50±4.37^{ab}	30.95±0.83^{ab}
Second Tim (days)	42.10±1.35^{ab}	43.36±1.08^{ab}	40.84±2.76^{b}	46.37±1.08^{ab}	50.73±2.46^{a}	44.56±1.73^{ab}

Mean value (±SE) of three replicates. Values in the same row sharing different superscript letters denote significant difference as determined by one-way ANOVA and Tukey HSD post hoc test ($P < 0.05$). The mean moult increment of first and second was compared by paired t-test. MI: moult increment; Tim: intermoult period.

Table 6 Moulting rate ((MR (%)) of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days.

	FM	PBM	BSFM	TH	LM	SBM
1st moult	84.44±5.87	77.77±2.22	73.33±3.84	80.00±3.85	73.33±3.84	80.00±3.85
2nd moult	46.66±6.66^{a}	35.55±2.22^{ab}	40.00±3.85^{ab}	42.22±2.22^{ab}	24.44±4.44^{b}	28.89±5.87^{ab}
3rd moult	11.11±11.11	11.11±5.87	15.55±2.22	8.89±8.89	6.66±3.84	15.55±5.87
4th moult	2.22±2.22	0.00±0.00	4.44±2.22	0.00±0.00	0.00±0.00	0.00±0.00

Mean value (±SE) of three replicates. Values in the same row sharing different superscript letters denote significant difference as determined by one-way ANOVA and Tukey HSD post hoc test ($P < 0.05$).

Table 7 Organosomatic indices of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days.

	FM	PBM	BSFM	TH	LM	SBM
Hiw	6.66±0.26	6.30±0.20	5.77±0.13	6.82±0.51	6.40±0.26	6.53±0.32
Hid	2.32±0.09^{a}	1.86±0.05^{ab}	2.35±0.10^{a}	1.62±0.14^{b}	1.87±0.21^{ab}	2.21±0.09^{a}
HM	65.09±2.25^{bc}	70.45±0.98^{ab}	59.20±2.14^{c}	76.00±2.71^{a}	70.89±2.81^{ab}	66.07±1.32^{abc}
Tiw	26.79±0.52^{ab}	27.96±0.96^{ab}	29.82±0.86^{a}	25.68±0.93^{b}	27.93±0.98^{ab}	27.79±0.61^{ab}
Tid	5.20±0.14^{ab}	5.23±0.07^{ab}	6.10±0.06^{a}	4.92±0.36^{b}	5.62±0.22^{ab}	5.30±0.25^{ab}
TM	80.60±0.52	81.26±0.52	79.52±0.66	80.91±0.89	79.89±0.60	80.95±0.47

Mean value (±SE) of three replicates. Values in the same row sharing different superscript letters denote significant difference as determined by one-way ANOVA and Tukey HSD post hoc test ($P<0.05$). Hiw: wet hepatosomatic index; Hid: dry hepatosomatic index; HM: moisture of hepatopancreas; Tiw: wet tail muscle index; Tid: dry tail muscle index; TM: moisture of tail muscle.

and TH. Similarly, in terms of the tail muscle histological structure (Fig. 3), normal muscle structure was observed in marron fed FM, whereas myodegeneration was observed in marron fed LM and TH.

Gut mucosal barrier function

The tight lamina propria and orderly lamina epithelial cells exhibited normal palisade arrangements, and regular nuclei were observed in fed marron in all cases of the test diets (Fig. 4). However, the mucosal morphological measurements showed that the fold height and width of the intestine decreased significantly ($P < 0.05$) in marron fed TH, LM, and SBM (Fig. 4A-B), whereas muscular thickness was not affected by any of the test diets (Fig. 4C).

Water stability of pellets

The percentage of dry matter weight loss in the diets varied from 8.16% to 13.51% after 60 min and from 10.26% to 18.12% after 8 h. After 24 h, the FM diet was more stable compared to the other diets, with a loss of 13.26% dry weight for the FM diet, whereas over 20% dry matter loss was recorded for LM and TH. Dry matter loss significantly increased in all test diets after 24 h (Table 9).

Discussion

Marron exhibited higher growth performance when fed animal protein sources rather than plant-based diets, except in the case of the TH and SBM diets, for which performance like plant and animal protein diets. It is in contrast with the findings of Saputra and Fotedar (2021), and Saputra et al. (2019) who reported that an LM-based diet resulted in similar growth rates to dietary animal protein in marron. The difference

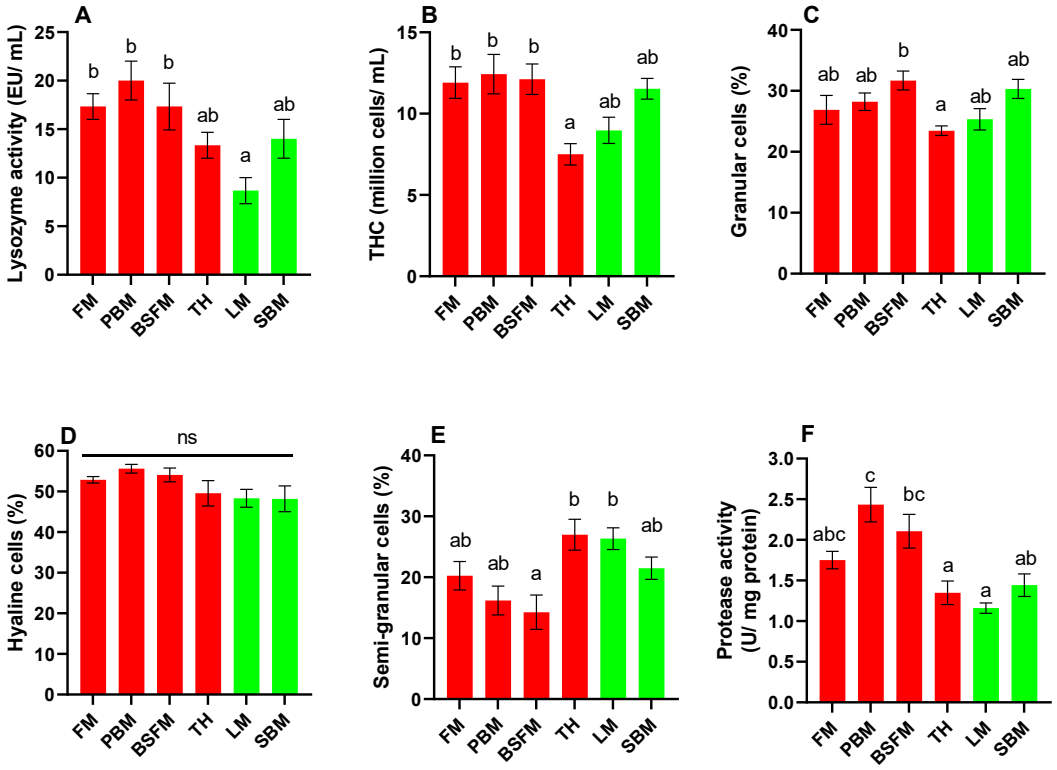

Fig. 1 Immune responses lysozyme (A), THC total haemocyte count (B), granular cells (C), hyaline cells (D), semi granular cells (E) and protease activity (F) of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days. The mean value (± SE) of three replicates is given. Bars with different letters denote significant differences ($P < 0.05$) as determined by one-way ANOVA and Tukey HSD post hoc test.

may be due to differences in the duration of the growth trials and the sizes of the experimental marron. The present study was conducted on smaller marron of 1.61 g for 110 days, whereas the feeding trials conducted by Saputra and Fotedar (2021), and Saputra et al. (2019) were on marron of 9.09 g for 90 days. This is consistent with the fact that smaller marron can grow at a faster rate than their larger counterparts (Barki and Karplus 2004). The present study is also a follow up of the studies by Siddik et al. (2020), Saputra and Fotedar (2021), Saputra et al. (2019) that further investigates underlying factors for the growth

Table 8 Proximate composition (% dry weight) and the amino acid composition (g/100g) of marron tail muscles when fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources over a period of 110 days.

	Experimental diets					
	FM	PBM	BSFM	TH	LM	SBM
Proximate composition						
Crude protein	88.78±0.43	90.76±1.27	86.27±0.28	86.77±1.31	88.10±1.77	88.93±1.21
Crude lipid	2.99±0.26^{ab}	4.10±0.51^{a}	2.09±0.79^{b}	1.74±0.06^{b}	3.07±0.15^{ab}	2.80±0.04^{ab}
Moisture	78.81±0.25	80.39±0.79	81.28±1.25	80.36±0.81	80.73±0.69	79.42±1.42
Ash	6.95±0.17	7.28±0.43	6.30±0.21	6.59±0.19	7.27±0.21	6.93±0.19
Essential amino acid						
Histidine	2.23±0.02^{ab}	2.19±0.02^{b}	2.30±0.01^{a}	2.19±0.02^{b}	2.19±0.03^{b}	2.22±0.02^{ab}
Threonine	3.92±0.03^{ab}	3.91±0.02^{ab}	4.00±0.02^{a}	3.91±0.01^{ab}	3.86±0.01^{b}	3.90±0.05^{b}
Lysine	8.27±0.03	8.21±0.06	8.31±0.03	8.28±0.06	8.14±0.02	8.20±0.04
Arginine	10.76±0.23^{b}	11.22±0.11^{ab}	9.39±0.15^{c}	10.76±0.11^{b}	11.64±0.01^{a}	11.22±0.14^{ab}
Methionine	2.59±0.02^{a}	2.54±0.02^{ab}	2.57±0.01^{ab}	2.54±0.03^{abc}	2.44±0.02^{c}	2.50±0.03^{bc}
Valine	4.62±0.02^{b}	4.61±0.01^{b}	4.77±0.02^{a}	4.64±0.02^{b}	4.50±0.02^{c}	4.65±0.02^{b}
Isoleucine	4.64±0.02^{a}	4.63±0.01^{ab}	4.68±0.01^{a}	4.62±0.02^{ab}	4.56±0.02^{b}	4.66±0.02^{a}
Leucine	8.03±0.04^{a}	8.01±0.02^{a}	8.09±0.04^{a}	8.00±0.02^{ab}	7.88±0.01^{b}	8.05±0.03^{a}
Phenylalanine	4.30±0.03^{a}	4.28±0.02^{ab}	4.34±0.03^{a}	4.27±0.01^{ab}	4.20±0.02^{b}	4.32±0.01^{a}
Non-essential amino acid						
Serine	4.30±0.02^{a}	4.22±0.03^{ab}	4.08±0.02^{c}	4.18±0.04^{abc}	4.11±0.04^{bc}	4.24±0.01^{a}
Glutamic acid	15.45±0.09	15.34±0.09	15.78±0.14	15.36±0.14	15.46±0.09	15.31±0.10
Glycine	8.52±0.04^{abc}	8.74±0.15^{ab}	7.98±0.15^{c}	8.52±0.13^{acb}	8.84±0.16^{a}	8.10±0.21^{bc}
Aspartic acid	10.18±0.05^{a}	9.93±0.03^{b}	10.22±0.04^{a}	10.18±0.05^{a}	10.09±0.02^{ab}	10.18±0.08^{a}
Alanine	5.26±0.03^{b}	5.13±0.01^{b}	5.60±0.15^{a}	5.41±0.02^{ab}	5.17±0.03^{b}	5.21±0.03^{b}
Proline	3.34±0.09^{b}	3.45±0.09^{b}	4.43±0.14^{a}	3.70±0.15^{b}	3.42±0.09^{b}	3.70±0.08^{b}
Tyrosine	3.64±0.03	3.55±0.00	3.62±0.02	3.50±0.02	3.57±0.02	3.60±0.06

Mean value (±SE) of three replicates. Values in the same row sharing different superscript letters denote significant differences ($P < 0.05$) as determined by one-way ANOVA and Tukey HSD post hoc test.

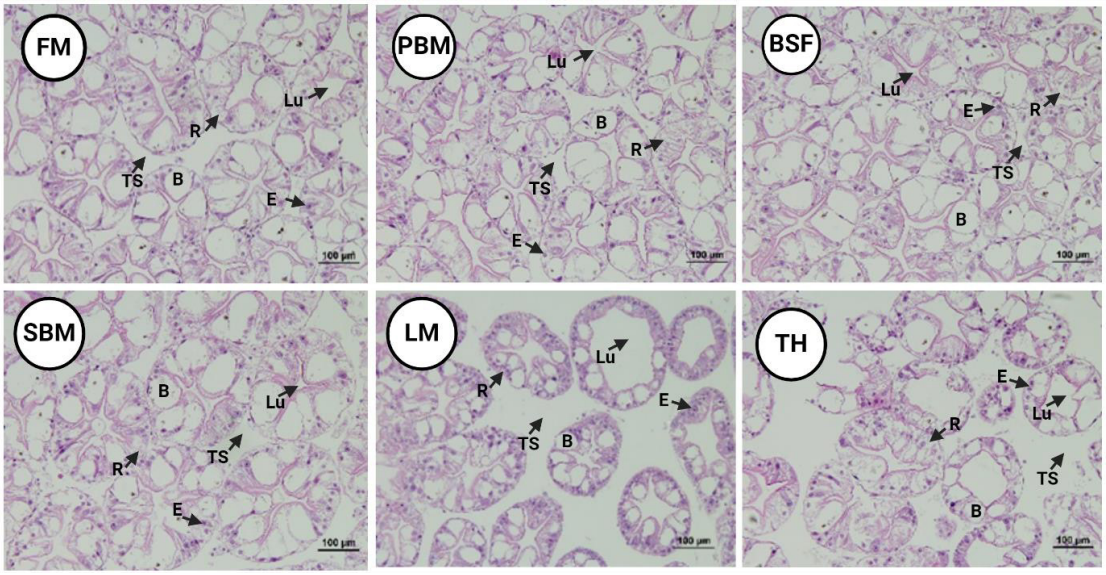

Fig. 2 Histopathological changes in the micrograph of hepatopancreas of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources. Abbreviations: B: blister cell, E: embryonic cell, R: reabsorption cell, Lu: lumen, TS: tubular spaces.

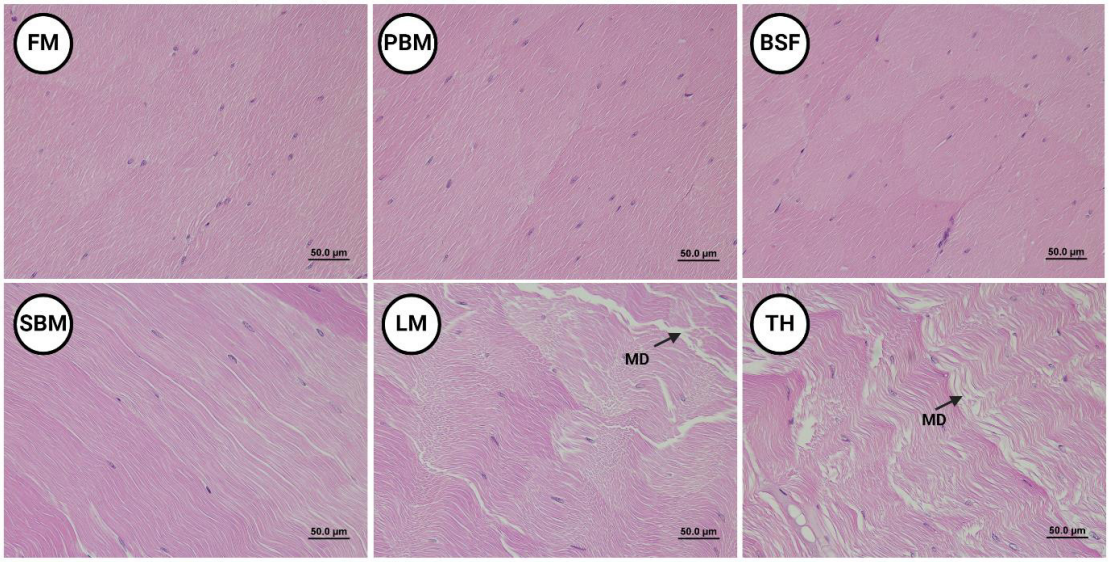

Fig. 3 Histopathological changes in the micrograph of tail muscle of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources. MD: myodegeneration

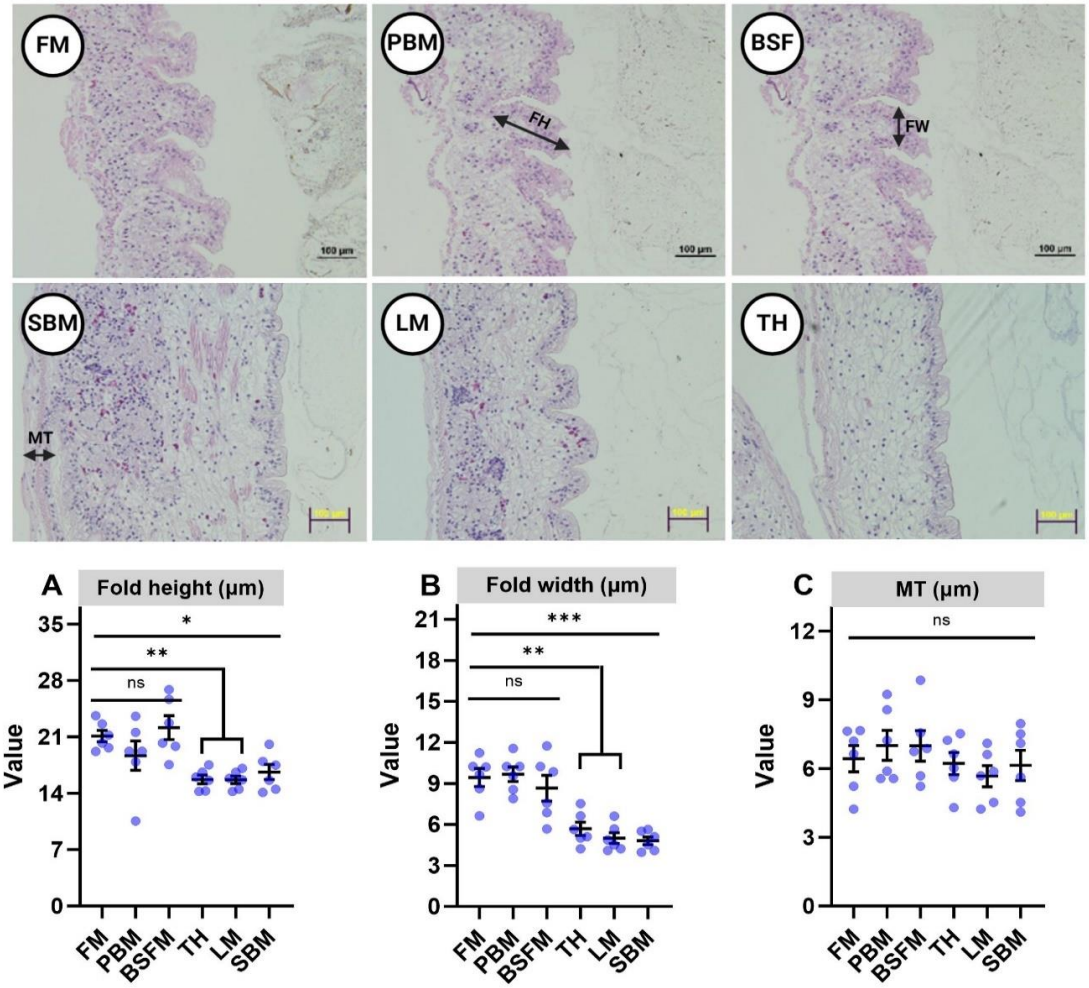

Fig. 4 Representative light microscopy of micrograph of intestine of marron fed various animal (FM, PBM, BSFM, and TH) and plant protein (LM and SBM) sources. Measurement of the fold height (A), fold width (B), and muscular thickness (C) of the intestine of marron fed test diets. Mean ±SE (n=6). ns denotes not significant, * P< 0.05, **P< 0.01 ***P< 0.001. FM: fishmeal diet; PBM: poultry by-product meal diet; BSFM: black solider fly meal diet; TH: tuna hydrolysate diet; LM: lupin meal diet; SBM: soybean meal diet; FH: fold height; FW: fold width; MT: muscular thickness.

and physiology of larger sized marron while focussing on comparative effectiveness of dietary animal and plant protein ingredients. Hence, the present study represents a step forward by incorporating more protein ingredients and investigating comparative growth based on moult-based data, analysis of amino and fatty acid profiles, and digestive enzyme comparisons. In contrast, the study of Siddik et al. (2020) focussed on the role of dietary fermented PBM on the health status and intestinal microbiota of marron and showed no significant differences in growth performance between marron fed FM and marron fed fermented PBM. The corresponding SGR values in the study by Siddik et al. (2020) were 0.19 and 0.21, respectively, lower than those in the present study.

Crustacean growth is governed by moult frequencies and moult increments (Jussila and Evans 1996a; Li et al. 2021; Reynolds 2002). In the present study, the improvement in growth performance of marron fed BSFM and FM is explained by an increase in moult increments, the higher number of moults, and the shorter intermoult periods. A possible reason for the improved growth of BSFM-fed marron may also be attributed to the chitin present in BSFM, a structure comparable to crustacean exuviae. The efficacy of BSFM in improving growth has already been reported in different studies; for example, significant increases in FBW, WG, and SGR were observed in *L. vannamei* when <25% BSFM feed was added at the expense of FM (Cummins et al. 2017). Positive growth effect results were also achieved in juvenile *L. vannamei* fed diets containing 15% BSFM (Hu et al. 2019) and *L. vannamei* fed defatted BSFM with a replacement of 60% FM (Wang et al. 2021). Similarly, Shin and Lee (2021) also reported a significantly higher growth in *L. vannamei* fed a diet in which 10% of tuna by-product meal was substituted with BSFM.

The digestive tract of *L. vannamei* contains several chitinase-secreting bacteria to facilitate the partial breakdown of dietary insect chitin provided in the feed (Tzuc et al. 2014). In addition, our results also showed there was higher protease activity in BSFM-fed marron, potentially supporting marron in digesting dietary insect chitin, which is reflected in improved growth. Similarly, the immune system of shrimp and fish can be modulated by the presence of chitin and antimicrobial peptides (AMPs) (Elhag et al. 2017; Esteban et al. 2000; Wang and Chen 2005) which may have positive effects on health and disease resistance. For example, increased survival, non-specific immune responses, and improved antioxidant enzyme activity were reported in *L. vannamei* fed with dietary supplementation of insect meal (Shin and Lee 2021). All these results support the theory of the positive impact of dietary chitin in BSFM on marron growth and health.

Another factor that could have resulted in the improved growth of marron fed animal-based diets is the higher water stability of the FM, PBM, and BSFM pellets. Due to the slow feeding behaviour of crustaceans, including marron, it is important to consider pellet stability during feed formulation, ensuring minimum nutrient leaching and disintegration to optimise feed intake and reduce wastage (Holdich 2002; Volpe et al. 2012). This argument is also supported by Jussila (1996), who concluded that marron fed stable pellets grow faster than those fed unstable commercial diets in both intensive and semi-intensive culture systems. The reason provided by Jussila (1996), and applicable to the results presented here, is the supposition that marron do not favour ingesting the remains of disintegrated pellets in the tanks, and reduced growth could therefore occur due to the poor ingestion rate (Jussila and Evans 1998).

The PBM diet promoted similar growth to the FM and BSFM diets in fed marron, which is in harmony with the previous findings on the same species by Saputra and Fotedar (2021) and Saputra et al. (2019) who concluded that substitution of FM with various protein sources did not affect marron growth and survival. PBM can replace up to 75% FM without any adverse effects on the growth and intestinal morphology of

Table 9 Dry matter weight loss (%) of treatment diets at different immersion time points

Period	FM	PBM	BSFM	TH	LM	SBM
30 min	$_{1}6.74\pm0.22^{d}$	$_{1}8.39\pm0.07^{c}$	$_{1}7.92\pm0.38^{cd}$	$_{1}9.08\pm0.23^{bc}$	$_{1}10.97\pm0.59^{a2}$	$_{1}10.64\pm0.27^{ab}$
60 min	$_{2}8.16\pm0.42^{c}$	$_{1,2}9.37\pm0.44^{bc}$	$_{2}9.88\pm0.24^{bc}$	$_{2}11.49\pm0.45^{ab}$	$_{1}13.51\pm0.80^{a}$	$_{1,2}12.56\pm0.71^{a}$
2 h	$_{2}8.97\pm0.13^{c}$	$_{2}10.81\pm0.45^{c}$	$_{2}10.41\pm0.20^{c}$	$_{3}14.78\pm0.52^{b}$	$_{2}16.70\pm0.23^{a}$	$_{2,3}14.75\pm0.60^{b}$
8 h	$_{3}10.26\pm0.16^{d}$	$_{3}15.37\pm0.09^{bc}$	$_{3}14.14\pm0.39^{c}$	$_{4}17.73\pm0.54^{a}$	$_{2,3}18.12\pm0.58^{a}$	$_{3,4}16.76\pm0.61^{ab}$
24 h	$_{4}13.26\pm0.15^{c}$	$_{4}17.89\pm0.37^{b}$	$_{4}17.89\pm0.48^{b}$	$_{5}20.04\pm0.55^{a}$	$_{3}20.48\pm0.41^{a}$	$_{4}19.28\pm0.61^{ab}$

Values represented as (mean ± SE) of three replicates. Superscript letters (a, b, c) denote significantly different means for different test diets ($P < 0.05$) as determined by one-way ANOVA and Tukey HSD post hoc test. Superscript numerical (1,2,3,4) indicate significantly different means at different time periods ($P < 0.05$). FM: fishmeal diet; PBM: poultry by-product meal diet; BSFM: black solider fly meal diet; TH: tuna hydrolysate diet; LM: lupin meal diet; SBM: soybean meal diet.

P. clarkii (Yang et al. 2022). The growth of *P. leniusculus* fed a diet with 45% replacement of FM protein is comparable to those fed an FM diet (Fuertes et al. 2013). In crayfish *C. quadricarinatus*, replacement of FM by PBM without impairing growth performance has been reported (Saoud et al. 2008). The enhanced growth of marron can also reflect the similarity of total amino acids between PBM-fed marron and FM-fed marron. Several studies showing increased growth due to the inclusion of dietary PBM have been reported in oriental river prawn (*Macrobrachium nipponense)* (Yang et al. 2004), and *L. vannamei* (Cheng et al. 2002; Cruz-Suárez et al. 2007).

The fact that marron fed LM had the lowest growth is like the results of Sudaryono et al. (1999a, 1999b), who demonstrated that growth performance decreased in *P. monodon* receiving LM-based diets. It has been shown in *P. monodon* that 40% of FM can be replaced by LM as a source of protein in a diet without adversely impacting on the growth (Smith et al. 2007a). It has been previously reported in *L. vannamei* that diets with 10% LM inclusion resulted in no adverse effects on survival and growth, but that high LM inclusion (30%) reduces growth (Molina-Poveda et al. 2013; Weiss et al. 2020). In addition, high fibre content, ANFs (alkaloids), poor digestibility, and low lysine and methionine amino acids in the LM (Glencross 2001) can result in poorer growth in marron fed LM diet. Most plant proteins are deficient in methionine and lysine (Nunes et al. 2014). The methionine content of LM diet (0.61 g/100g) is below the requirements determined for *P. mondon* (Millamena et al. 1996), and it might also be lower than the requirement of marron. In addition, the low amounts of most amino acids in tail muscles in marron fed LM could have partially contributed to depressed growth. The beneficial effects of dietary lysine and methionine supplementation on growth have been demonstrated in previous studies in *P. monodon* (Biswas et al. 2007) and *M. japonicus* (Alam et al. 2005). Nwanna et al. (2019) reported that the methionine requirement ranges from 6.2 to 6.8 g/kg, which results in maximum growth of *P. monodon*, and supplementation of lysine and methionine can prevent the negative growth induced by the inclusion of high levels of vegetable protein in the diet of *P. clarkii* (Tan et al. 2018). The exact methionine requirement in marron diets awaits further investigations.

Marron fed SBM obtained high MI and low Tim, comparable to marron fed BSFM. In the present study, the values of MI among test diets ranged from 17.83 to 36.66%, which is similar to findings of Pattikawa and Wenno (2014) and Saputra and Fotedar (2021) on the same species. LM-fed marron had lower MI than SBM-fed marron, which could be partially related to the reduced growth of marron fed LM. Moreover, at least 73.33% of moulted marron were observed in each group, and some marron had moulted two, three, or four times during the experiment. Only marron fed FM and BSFM moulted four times, with moulting rates of 2.22 and 4.44%, respectively, indicating that marron fed FM and BSFM moulted frequently, resulting in higher growth. Except for methionine, SBM-fed marron had the same total amino acid content in tail muscle as FM-fed marron, which can possibly explain the better growth performance of marron fed SBM. SBM can be used to replace up to 45% of FM protein in the diets of *L. vannamei* (Lim and Dominy 1990), speckled shrimp (*Metapenaeus monoceros)* (Abdel Rahman et al. 2010), and *M. japonicus* (Bulbul et al. 2015). Substitution of up to 75% SBM protein showed a higher final weight and protein efficiency ratio in *L. schmitti* (Alvarez et al. 2007). Replacement of 25% FM protein by SBM in diets was recommended for *P. leniusculus* (Fuertes et al. 2012). However, García-Ulloa et al. (2003) reported dietary inclusion of 25% SBM replacement reduced growth in *C. quadricarinatus*, and 20% SBM replacement caused decreased growth of giant freshwater prawn (*Macrobrachium rosenbergii)* (Du and Niu 2003). Based on these above studies, it was concluded that the capability of SBM utilisation in diet varies among species.

The detrimental growth effect on marron when fed TH could be due to an excessive amount of low-molecular-weight peptides and free amino acids that have been reported to work as ANFs (Carvalho et al. 2004; Ospina-Salazar et al. 2016). The present results are in agreement with those of Li et al. (2018), who concluded that the increased rates of inclusion of low-molecular weight FPHs in the diet decreased the growth of *L. vannamei.* Moderate dietary inclusion levels of between 3% and 20% FPHs have been suggested to enhance growth and survival in *P. monodon* (Anggawati et al. 1990) and *L. vannamei* (Hlordzi et al. 2022; Nguyen et al. 2012, Niu et al. 2014). In the present study, TH and LM protein diets resulted in lower protease activity, suggesting that marron may not be able to effectively digest protein from LM and TH, which may also explain the poor immunity and growth performance in marron fed these diets. The protease activity is influenced by the nutrient quality and quantity, and a high digestive enzymatic activity has been reported to contribute to effective digestion, resulting in improved growth and immunity and thereby the health of marron (Nugroho and Fotedar 2015). In addition, the free amino acids and small polypeptides

in TH can reduce the substrate area for the enzymes, which may explain the lower activity observed in the hepatopancreas of *L. vannamei* fed with high quantities of TH (Córdova-Murueta and García-Carreño 2002). A study by Lopez-Lopez et al. (2005) demonstrated a higher protease activity in juvenile *C. quadricarinatus* fed diets with FM and soy paste protein sources than squid meal, red crab, and sardines. Pavasovic et al. (2007) also demonstrated that *C. quadricarinatus* can utilise nutrients from a wide range of sources, including animals, plants, and single cells. The above studies suggest that digestive enzyme activity may be species- and/or size-dependent.

Various protein sources have previously been reported to influence the immune responses of marron (Saputra et al. 2019), where the authors found that PBM-fed marron had the highest THC, and the proportion of HC did not differ among dietary protein sources, which is similar to the response in the present study. High THC, GC, and lysozyme activity were observed in marron fed PBM and BSFM diets, suggesting that PBM and BSFM do not compromise the immune function of marron. This is supported by the findings of Foysal et al. (2019), where the effects of dietary PBM were found to be like FM in terms of marron health and immunity. The previous study on *P. clarkii* reported that PBM replacing up to 75% of FM did not decrease lysozyme activity in haemolymph (Yang et al. 2022). THC in the haemolymph of juvenile *M. nipponense* were not significantly different when fed diets with 50% of PBM than FM diet (Yang et al. 2004). This might be due to the presence of adequate levels of EAAs (methionine, arginine, and leucine) in PBM, which are required for marron growth (Saputra et al. 2019). However, the negative impact of TH and LM on lysozyme, THC, and GC supports reduced growth, cellular changes in hepatopancreas and tail muscle, and alterations in intestinal barrier function. The observed results of LM on marron immunity are aligned with Saputra et al. (2019), who found an elevated bacterial load in haemolymph with a consequent THC decrease in marron. As mentioned earlier, exclusive inclusion levels of TH have been reported to result in excessive levels of free amino acids, which work as ANFs, consequently affecting the immune response of marron. Similarly, the inclusion of 50 and 75% of TH significantly reduced FBW, WG, and SGR and increased lipid accumulation in *L. calcarifer* liver (Siddik et al. 2018). Hence, further studies are needed with the inclusion of TH in smaller quantities (5–10%) in marron diets also considered, as low inclusion levels in diets are already shown to function as an immunostimulant in finfish (Chaklader et al. 2020a; Chaklader et al. 2021; Gupta et al. 2020; Siddik et al. 2019b).

In the present study, the high percentage of pellet dry matter loss, around 20% in TH- and LM-based pellets, is due to the low binding strength of the particles in these ingredients. This was confirmed by Sudaryono (2001), who reported the least water stability in LM-based diets. It is known that fibre levels, not analysed in the present study, can also affect the water stability of diets (Akiyama et al. 1992). These authors found the least retention of dry matter in diets containing 40% whole lupin, *Lupinus albus,* seed meal with 6.3% fibre, and 35% dehulled lupin with 4.1% fibre. In addition, wheat flour in the feed formulation may partially contribute to water stability, as wheat flour contains 30% starch (Sudaryono et al. 1995). In contrast, in the study of Molina-Poveda et al. (2013) on *L. vannamei*, the pellet water stability was reportedly more sTable with increasing LM inclusion in the diet after 2 h of immersion. In the present study, the high dry matter loss in TH- and LM-based diets caused poor ingestion and thus nutrient deprivation, contributing to the depression in marron growth.

In previous studies on the same species, condition indices have been used to evaluate the nutritional status of the dietary supplementation and health status (Fotedar 2004, Jussila 1999; Saputra et al. 2019). The present study showed that marron fed BSFM diet had significantly higher Hid with a low HM, suggesting the reservation of higher total energy. This is in agreement with Mai and Fotedar (2017), who stated that the higher wet and dry hepatosomatic indices with low hepatopancreas moisture are indicators of well-conditioned animals, whereas TH-fed marron presented the opposite trend on the condition indices with a higher HM and low Hid. The present results contrast with the findings of Saputra et al. (2019), who concluded different dietary protein sources have no effects on condition indices. Previous researchers have also used similar health condition parameters to evaluate the health status of different species. For example, juvenile tropical spiny lobsters (*Panulirus ornatus*) fed mannan oligosaccharide were reported as nutritionally healthier, as demonstrated by lower HM and higher Hiw and Hid (Sang and Fotedar 2010), and in western king prawn (*Penaeus latisulcatus)* reared at optimum salinity of 22 to 34 ppt (Sang and Fotedar 2004). However, knowledge about the effects of hydrolysate protein on marron immune responses and the aligned relationship with health indices is limited and deserves further study.

Various protein sources did not affect the protein, moisture, and ash levels in the tail muscles of marron, similar to the results of studies by Fotedar (2004) on marron, Thompson et al. (2004) on *C. quadricarinatus*, and Fuertes et al. (2013) on *P. leniusculus*. Marron fed BSFM and TH had the lowest lipid concentrations in the tail muscles, similar to the low lipid content (6.95%) in *L. vannamei* when graded levels of dietary TH were used to replace FM (Hlordzi et al. 2022) or as reported with increased BSFM inclusion levels (Chen et al. 2022). Moreover, the BSFM diet also has high amounts of lauric acid and myristic acid and is rich in SFA, similarly to the review of Lu et al. (2022). Previous studies with *L. vannamei* (Lim et al. 1997, Soller et al. 2019) and *P. monodon* (Kumaraguru vasagam et al. 2005) reported that high SFA content, especially lauric acid, in the diet leads to a reduction in the crude lipid content in the shrimp. However, in *P. clarkii*, the lipid content of the whole body increases with an increase in dietary lipid level (Xu et al. 2013) due to the presence of SFA and PUFA in dietary BSFM (Chen et al. 2022). Another factor potentially contributing to lipid content is the type of BSFM, both normal or defatted, used as a dietary inclusion which affected the lipid deposition in juvenile Jian carp (*Cyprinus carpio* var. Jian*)* (Li et al. 2016). In the current study, full-fatted BSFM with 44% protein and 28% fat was used to formulate marron feeds. Therefore, it is recommended that future research should compare the nutritional effects of dietary full-fat and defatted black soldier fly larvae.

Marron fed LM- and TH-based diets showed increased intertubular spacing and an enlarged tubular lumen resulting from the thinned epithelial layer in the hepatopancreas, the major site of digestion, nutrient absorption, reserve storage, and synthesis and secretion of digestive enzymes in crustaceans (Ceccaldi 1989). Hlordzi et al. (2022) observed a similar damaged hepatopancreas morphology in *L. vannamei* fed dietary FPHs, reflecting the poorer condition and nutritional status of the marron (Jussila 1997, Parrillo et al. 2017). The histopathological changes in the hepatopancreas and tail muscle of marron fed LM can be hypothesised to be due to the presence of ANFs or lack of biological available minerals such as organic selenium (Ilham et al. 2016). Previous research has shown that the exclusive dietary inclusion of plant proteins, including LM or SBM, or animal-based (PBM) protein sources, can cause histopathological alterations in the hepatic and muscle health of finfish. For example, Ilham et al. (2016) found that the inclusion of 25 and 75% of LM induced the proliferation of lipid deposition in the liver and necrosis in the muscle tissues of *L. calcarifer,* but selenium supplementation abolished these negative effects. Similarly, Siddik et al. (2018) reported the inclusion of 50 and 75% of TH and fermented TH resulted in the presence of necrotic foci and nucleus disappearance in hepatic cells of *L. calcarifer*. There are no studies on freshwater crayfish, including marron; hence, further investigation should consider supplementing the selected micronutrient with TH at an appropriate level to minimise the negative effects of full TH inclusion.

Conclusions

In this study, it was shown that marron fed with TH and LM exhibited lower growth, enzymatic activity, and immunity in addition to histopathological changes in hepatopancreas and intestine, whereas marron fed with BSFM, PBM, FM, and SBM showed relatively higher growth. Marron fed with BSFM showed the highest moult increments together with the shortest intermoult periods, whereas the lowest MI and the longest Tim were observed in marron fed TH. BSFM-fed marron showed high growth with an improved amino acid profile and immune response, and no histopathological changes in the hepatopancreas. Further complementing research is warranted, focused on low-quality LM with functional ingredients and incorporating smaller inclusion levels of TH to further understand the effect of TH in marron diet.

Competing interests The authors declare that they have no competing interest.

Author Contributions Conceptualization, R.F and T.T.T.D.; methodology, T.T.T.D. and R.F.; software, T.T.T.D. and Md R.C; validation, R.F.; formal analysis, T.T.T.D. and Md R.C.; investingation, T.T.T.D. and Md R.C; resources, R.F. and J.H; data curation, T.T.T.D.; writing—original draft preparation, T.T.T.D.; writing—review and editing, R.F.; J.H and Md R.C; visualization, T.T.T.D.; supervision, R.F. and J.H; project administration, R.F. and J.H; funding acquisition, R.F and J.H. All authors have read and agreed to the published version of the manuscript.

Acknowledgments The authors would like to thank to all the staff of CARL for rendering technical assistance during the wet laboratory work and the staff of Blue Ridge Marron farm, Manjimup, Western Australia, for providing live marron.

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