Int. J. Aquat. Biol. (2025) 13(3): 109-134
ISSN: 2322-5270; P-ISSN: 2383-0956
Journal homepage: www.ij-aquaticbiology.com

Review Article

Development of "red head" in shrimp: Analysis of possible causes and product appearance quality

Mohammadali Khanlar*[1], Seyed Mahdi Ojagh*[2], Bahareh Shabanpour[1], Alireza Alishahi[1], Seyed Vali Hosseini[2], Seyedeh Zahra Mirhosseini Roudbaraki[2]

[1]Department of Fisheries, Faculty of Fisheries and Environment, Gorgan University of Agricultural Sciences and Natural Resources, Gorgan, Iran.
[2]Fisheries Department, Faculty of Natural Resources, University of Tehran, Karaj, Iran.

Abstract: The development of red coloration in the hepatopancreas of shrimp is a complex issue in the industry that is often linked to poor culture and harvest management, particularly in relation to inefficient temperature settings during harvesting and processing. Despite strict adherence to temperature management protocols, the introduction of *Litopenaeus vannamei* to marine shrimp farms has resulted in red discoloration in the hepatopancreas, known as discolored or ruptured hepatopancreas (RDHP). This condition is caused by the oxidation of carotenoids in protein compounds, resulting in the formation of a multi-macromolecular complex, crustacyanin, in the hepatopancreas and cephalothorax regions. Although RDHP is harmless to consumers and has no direct correlation with microbial spoilage, it negatively affects the sensory aspects and visual quality of the product. To avoid such issues, various options are available, including different storage and processing techniques, as well as keeping the product cold using ice, which is the most commonly used method. Understanding the causes, processes, and consequences of red head is crucial for preventing such problems and preserving the product's good appearance. Accordingly, the current review aims to gather and present the most up-to-date information on red head in a concise and comprehensible manner.

Article history:
Received 29 December 2024
Accepted 24 June 2025
Available online 25 June 2025

Keywords:
Pacific white shrimp
Hepatopancreas
Carotenoid
Astaxanthin

Introduction

The quality and acceptability of commercial crustacean species, such as *Litopenaeus vannamei*, are affected by product color (Erickson et al., 2007), which is affected by food, genetic, and environmental factors (Sathapondecha et al., 2014). Environmental factors, such as water temperature, light, water quality, substrate color, dietary astaxanthin levels, and rearing tank color schemes, can affect shrimp color (Tume et al., 2009; Luchiari et al., 2012; Martínez et al., 2014; Bernal Rodríguez et al., 2017; Wade, Cheers et al., 2017). Improving the darkness or redness of shrimp can enhance product quality and consumer acceptance, resulting in higher economic returns for producers (Tume et al., 2009). Additionally, the color of cooked prawns is considered an indicator of product quality for consumers, incentivizing them to pay higher prices (Wade et al., 2014).

The hepatopancreas of *P. vannamei*, which fulfills several metabolic functions, can have different colors depending on the pigments such as zeaxanthin, carotene, and astaxanthin (Ceccaldi). Damaged or ruptured hepatopancreas in shrimp, which can lead to discolored or ruptured hepatopancreas (RDHP), can affect the appearance of shrimp, particularly after cooking. The problem is more evident in species with lighter colors, like the Pacific white shrimp, as the contrast between the body and the darker head increases. The issue has been referred to by different names in various countries, such as black head or red head; however, this paper will use the term RDHP. Shrimp farms have experienced poor color in their products supplied to the European market due to RDHP in the animals, resulting in orange, red, green, or black discoloration in the head of affected animals. However, no information on RDHP has been reported

---

*Correspondence: Mohammadali Khanlar and Seyed Mahdi Ojagh
E-mail: khanlar2012@yahoo.com; ojagh@ut.ac.ir
DOI: https://doi.org/10.22034/ijab.v13i12.2405

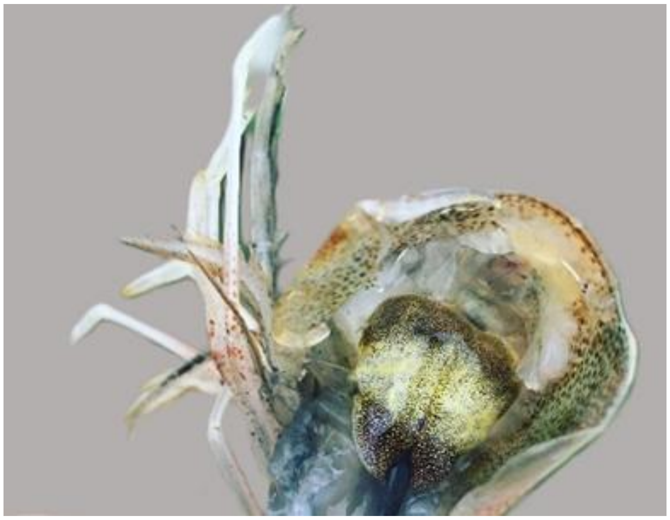

Figure 1. View of fresh Vannamei shrimp hepatopancreas in cephalothorax

in Pacific white shrimp during storage and handling. This study aims to examine the reasons for the changes in RDHP in Pacific white shrimp during storage and handling.

Functions of hepatopancreas: The largest functional organ in a shrimp is the hepatopancreas, which is also referred to as the midgut or digestive gland. The health of the hepatopancreas is crucial for the success of shrimp farming. This organ is unique to shrimps and crabs because it is incapable of secreting bile; instead, it performs digestive and nutrient storage functions, primarily for oils. These functions are different from the liver cell structure found in higher animals, as reported by Liang et al. (2016), Zhu et al. (2013), and Qiu et al. (2018) (Fig. 1).

The hepatopancreas performs multiple functions, including the secretion of digestive enzymes, the absorption and storage of nutrients, and the detoxification of harmful substances, as reported by Ren et al. (2020). It also plays a role in defense by producing clotting factors (Gross et al., 2001) and in metabolizing various vitamins, fats, proteins, and hormones (Wang et al., 2014; Ning et al., 2019; An et al., 2020; Chien et al., 2020). Damage to the hepatopancreas can lead to the collapse of shrimp organs. Additionally, the hepatopancreas is responsible for the digestion, absorption, and storage of oil in shrimps and crabs, with 90% of the feed being processed in this organ (Wang et al., 2020) (Fig. 2).

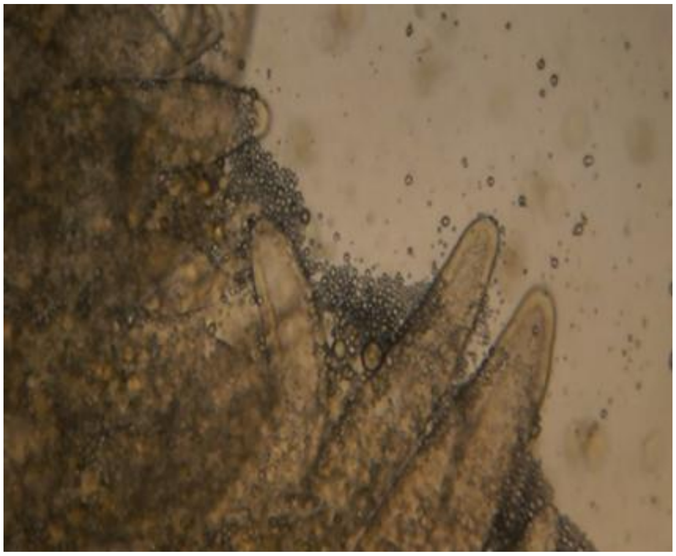

Figure 2. Shrimp hepatopancreatic tissue in contact with fat cells, and protein.

Figure 3. Soft shell with yellow gills and orange hepatopancreas compared to a hard shell and healthy gills.

According to Wilder et al. (2009), the energy required for normal activities in shrimps comes from the absorption of essential elements such as calcium, magnesium, and phosphorus. A decrease in the number of lipid droplets indicates that the shrimp is at risk of developing diseases. As shrimps undergo breeding, their bodies become softer, suggesting that they have exhausted their oil reserves and have started consuming protein. Saving shrimps at this stage is challenging (Cervellione et al., 2017) (Fig. 3). As

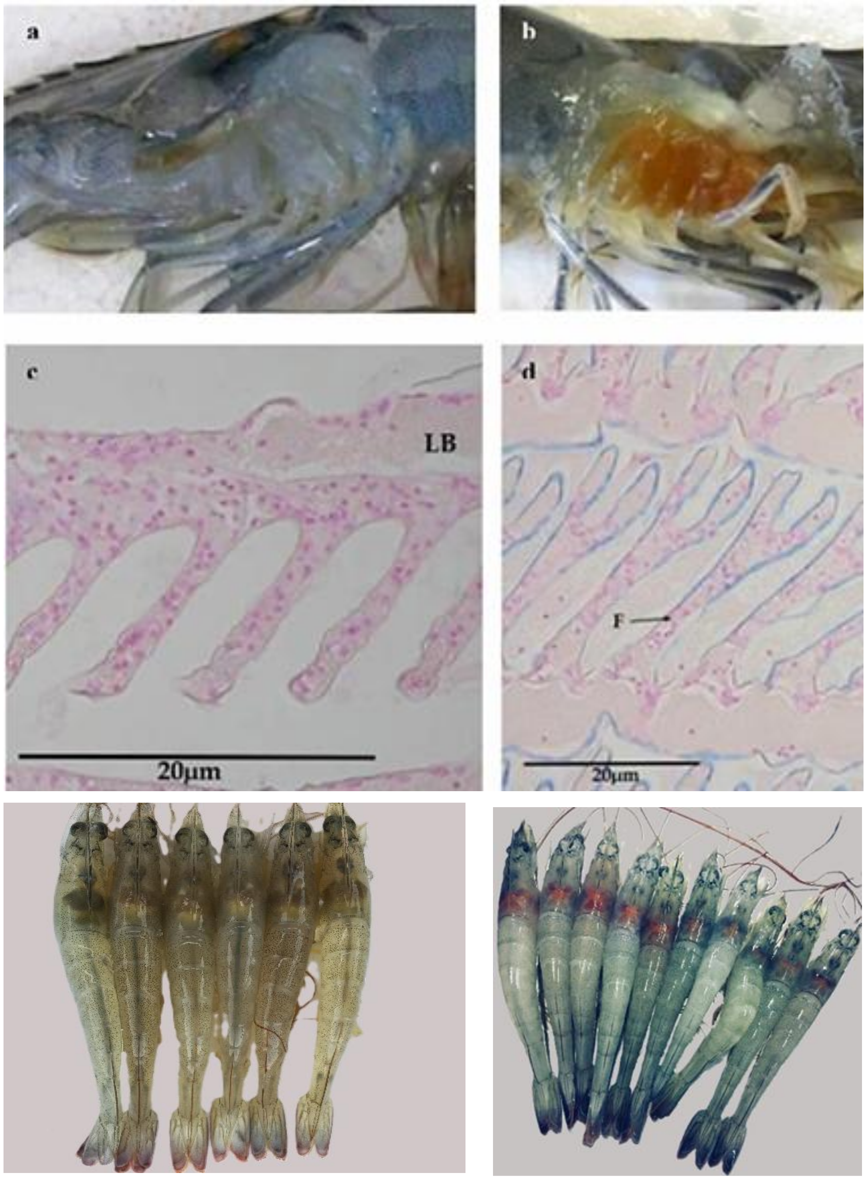

Figure 4. Macroscopic images of the cephalothorax of animals (a) without and (b) with dark orange gills (DOG). Based on the histological analysis using the Perls Prussian blue staining technique, iron on gill surfaces (blue color) was supported. (c) white gills (WG) and (d) DOG are located on the left and right, respectively. LB: lamella, F: filament. (Interested readers can visit the web version of the articles for interpretation of the references to color.) (Restrepo et al., 2018), (E) *Litopenaeus vannamei* from harvest in Iran, showing normal (acceptable) colored hepatopancreas on the left and (F) different levels of red head on the right.

reported by Xu et al. (2018), the number, size, and proportion of fat granules in a shrimp can indicate its health status. This information can be used to predict the health of the hepatopancreas and minimize the occurrence of diseases during the breeding process. The hepatopancreas plays a crucial role in the absorption and biometabolism of elements such as Cu, Fe, Mn, Zn, and Se, which contribute to detoxification and antioxidant defense (Jiao et al., 2021). When faced with sudden changes in external weather, such as a drop in temperature, a poor antioxidant capacity can result in the reddening of the hepatopancreas and intestines, leading to a loss of appetite. This situation can worsen in the presence of algae (Davis, 1990) (Fig. 4).

Ammonia: Ammonia is a major environmental factor that poses a serious threat to the survival of shrimp in aquaculture systems. It is caused by excess food, decomposing organic solids, animal excrement, and surplus ammonia from agricultural production. Ammonia is found in ionized (NH_4) and un-ionized (NH_3) states in water, with NH_3 easily diffusing into the hemolymph and across the cell membrane. The ratio of NH_4/NH_3 is affected by pH, salinity, and temperature. Studies have shown that high levels of ammonia can reduce the growth rate of shrimp, increase the frequency of molting, and increase the mortality rate. Ammonia also affects the osmoregulatory capacity and physiological condition of the gills and hepatopancreas, and can suppress the shrimp's immune system, making them more susceptible to pathogens. Ammonia stress causes nucleotide and amino acid disorders, attributed to apoptosis induced by ammonia and functional damage of the hepatopancreas. Lower serum levels of amino acids can also influence normal growth rates and slow down shrimp growth. Therefore, understanding the molecular mechanism by which *L. vannamei* responds to ammonia stress is crucial for managing shrimp aquaculture.

When the level of ammonia in shrimp exceeds their tolerance limit, it becomes toxic and can cause direct damage to their tissues, including the hepatopancreas and gills. This toxicity can also impact various physiological processes, including metabolism, respiration, osmotic regulation, immunity, molting, excretion, and growth, thereby reducing the shrimp's resistance to pathogens and increasing their mortality rate. In addition to harming the organs and tissues of aquatic animals, ammonia toxicity or stress can lead to oxidative damage and an increase in reactive oxygen species levels in shrimp. Changes in environmental factors such as pH, salinity, and temperature can alter the ammonia levels in water, which can, in turn, reduce feeding and growth rates, degrade the immune function of aquatic organisms, and increase the risk of diseases (Corbo et al., 2005; Zhang et al., 2015; Liang et al., 2016; Cui et al., 2017; Li et al., 2018; Qiu et al., 2018). When water quality is abnormal, such as in the presence of high levels of ammonia, nitrous acid, or algae, with low detoxification ability, the food intake of shrimp decreases, and their shells become softer, leading to the death of a small number of seedlings. To promote molting, shrimp use sterols stored in the hepatopancreas to synthesize chitin, lipids stored in the hepatopancreas to provide energy for molting, and store calcium, magnesium, phosphorus, and other elements in the hepatopancreas before molting. However, excessive ammonia levels affect the molting process, as chitinase secreted by the epidermis degrades the inner layers of the old exoskeleton and synthesizes a new skeleton in the molting process (ecdysis). Shrimp exposed to ammonia stress treatments have shown a significant decrease in the molting process.

Higher levels of ammonia can lower the immunity of shrimp and intensify their susceptibility to pathogens. Additionally, elevated levels of ammonia can reduce the capacity of hemocyanin to carry oxygen, which is one of the key mechanisms by which ammonia causes toxic effects in shrimp. The latest transcriptional analyses on shrimp hepatopancreas cases have also indicated a decline in the expression of genes related to prophenoloxidase in response to the stress caused by ammonia. Ammonia can also perturb amino acid metabolism by heightening the expression of some genes related to ammonia excretion and detoxification. Extreme levels of ammonia can also affect metabolism and osmotic regulation in crustaceans. For example, in the case of *L. vannamei*, NH^{+4} influences ammonia-metabolizing enzyme activity and the excretion of ammonia (Zou and Bonvillain, 2004; Chand and Sahoo, 2006; Romano and Zeng, 2010; Spriggs et al., 2010; Salma et al., 2012; Liang et al., 2016; Lu et al., 2016, 2018; Pinto et al., 2016; Cui et al., 2017; Zhou et al., 2017; Li et al., 2018; Qiu et al., 2018; Xiao et al., 2019).

Ammonia stress can have a significant impact on the health and well-being of shrimp, including reduced food intake, softer shells, and decreased immune function. However, different species of shrimp exhibit varying levels of tolerance to ammonia stress, suggesting that distinct adaptation strategies can be employed to mitigate this stressor. Selective breeding for ammonia tolerance and disease resistance traits can be a faster and more reliable method for improving the health and yield of shrimp compared to traditional methods of selection. The success of breeding new varieties of shrimp with higher

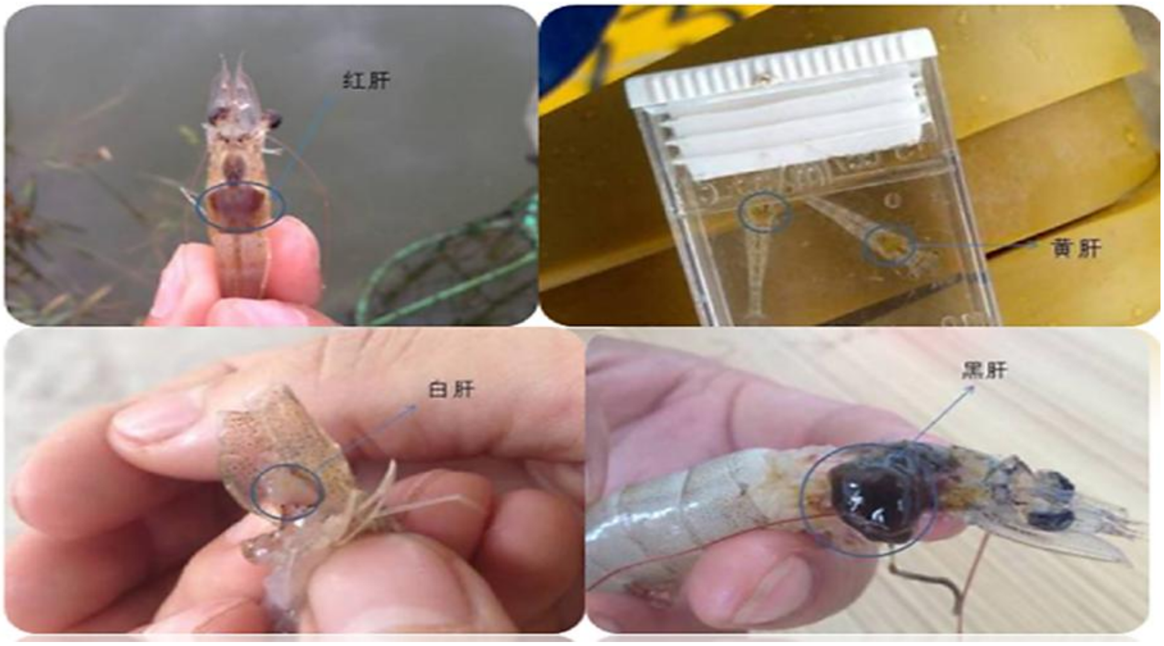

Figure 5. The external symptoms of environmental hepatopancreatic diseases in aquatic animals include red hepatopancreas, gut and body, unsuccessful molting and soft shell, black hepatopancreas, and hepatopancreas atrophy.

resistance to stress and disease highlights the potential of this approach to improve the shrimp breeding industry. However, more research is needed to fully understand the molecular mechanisms of stress resistance in shrimp, including the transfer and heritability of tolerance to ammonia and the potential extra benefits of stress resistance. By gaining a better understanding of these mechanisms, researchers can develop more effective strategies for improving the health and well-being of shrimp in aquaculture.

Hepatopancreatic diseases: Aquatic animal diseases pose a major challenge to the sustainability and profitability of the aquaculture industry. The emergence and spread of diseases can lead to significant economic losses, especially in regions heavily reliant on aquaculture. Viruses such as IHHNV, TSV, HPV, WSSV, MBV, and YHV have caused significant losses to shrimp farming in recent years. The discovery of new viruses, such as SHIV, highlights the ongoing risk of disease outbreaks. In addition to viruses, bacterial and fungal infections also pose a threat to aquaculture. AHPND is a bacterial disease that has caused significant losses in shrimp farms worldwide. Efforts to combat aquatic animal diseases involve a combination of prevention and treatment measures. Prevention measures include strict biosecurity protocols, disease surveillance and monitoring, and selective breeding for disease resistance. Treatment measures may include the use of antibiotics, antivirals, and vaccines. However, the use of antibiotics in aquaculture has been a subject of concern due to the potential development of antibiotic resistance in bacteria. Therefore, alternative disease control strategies such as probiotics, immunostimulants, and herbal medicines are being explored.

In addition, research efforts are focused on understanding the molecular mechanisms of disease resistance in aquatic animals, which can provide new targets for the development of effective treatments and vaccines. Overall, managing aquatic animal diseases remains a significant challenge for the aquaculture industry. A concerted effort is necessary to address this issue and ensure the industry's sustainable growth (Fig. 5). These symptoms can indicate the presence of diseases such as acute hepatopancreatic necrosis disease (AHPND), *Enterocytozoon hepatopenaei* (EHP), and other viral, bacterial, and fungal infections that can affect the health and productivity of aquaculture farms. The emergence of diseases like EMS/AHPND and EHP has had a significant impact on the shrimp farming industry in Southeast Asia and other regions. These diseases have caused significant financial losses for shrimp farmers and have led to reduced shrimp production. Farmers must monitor the health of their shrimp and take preventive measures to minimize the risk of disease outbreaks. This may involve maintaining good water quality, providing adequate nutrition, and implementing biosecurity measures to prevent the introduction and spread of pathogens. Effective disease management strategies may include the use of probiotics, immunostimulants, or other treatments to support shrimp health and reduce the risk of disease. Ongoing research in aquaculture focuses on developing new methods for disease prevention and management to support sustainable shrimp farming practices (Fig. 6).

Shrimp nutritional hepatopancreatic diseases manifest in slow molting and growth, unsuccessful molting, soft shells, and slow hard-shell formation. These symptoms are often overlooked and considered to require calcium supplementation. However, environmental and pathogenic hepatopancreatic diseases are the actual causes of these diseases. Environmental factors, including dissolved oxygen, ammonia nitrogen, nitrite, and algal toxins, mainly influence the health of shrimp and their hepatopancreas. Microsporidia multiplication causes the lysis of hepatopancreatic epithelial cells, the release of spores into the lumen, and the destruction of the digestive function of the hepatopancreas (Edgerton et al., 2002). A healthy cultured shrimp's hepatopancreas is brownish-black, with a clear outline and a white covering on the ventral surface. If the cover is peeled off, the hepatopancreas tissue should be reddish-brown (Lio-Po et al., 2001). When the color of the hepatopancreas turns red, yellow, dark, or white (Muthukrishnan et al., 2019), it indicates the initiation of the disease. This is the best time to protect the hepatopancreas using bile acids (Kuhn et al., 2010).

Hepatopancreas-transferring period: Generally, when shrimp seedlings are taken care of properly for over 20 days or reach a size of 4-6 cm, a white covering appears around the hepatopancreas. After the white covering vanishes, the hepatopancreas becomes brown, marking the period of hepatopancreas transfer. During this period, the hepatopancreas tissue of the shrimp is full and has a clear outline. Additionally, the shrimp's feed intake increases, which can cause toxins to accumulate and put a heavy burden on the hepatopancreas. If the hepatopancreas is in poor health and fails to develop correctly, it can lead to a decline in the survival rate of shrimp seeds. Therefore, it is important to focus on protecting and caring for the hepatopancreas during this period, as well as ensuring good pond bottom quality.

Figure 6. Shrimp infected with BA55 strain with PirVP genes pertinent to AHPND and healthy *Litopenaeus vannamei*. (A) Left shrimp view. Gross signs of AHPND-infected shrimp (left): pale, atrophied hepatopancreas surrounded by a white membrane with smooth consistency (black arrow). Normal shrimp (right): normal size hepatopancreas with brownish color. (B) Right shrimp view. Gross signs of AHPND-infected shrimp (left): complete hepatopancreas destruction (black arrow). Normal shrimp (right): normal size hepatopancreas with brownish color.

The transfer of hepatopancreas occurs during a period when the temperature is already relatively high and the water temperature exceeds 25°C. Poor control of pond quality can lead to the release of toxic and harmful substances, such as hydrogen sulfide and methane, from the pond bottom, which can directly harm the health of *vannamei's* hepatopancreas (Silvestre et al., 2010). To address this issue, an oxidative base should be used to oxidize the organic matter at the bottom of the pond during the hepatopancreas transfer period, thereby reducing the generation of harmful substances and preventing bottom heating (Xiao et al., 2019).

In addition, it is crucial to cultivate beneficial algae during this period, stabilize the water, prevent algae blooms, and inhibit the growth of harmful algae. When harmful algae such as dinoflagellates dominate in the pond, they can produce large amounts of toxins that can cause irreversible damage to the hepatopancreas and nervous system of Vannamei Shrimp (Cen et al., 2019). Therefore, it is crucial to cultivate high-quality algae in ponds to prevent the accumulation of harmful algae. *Chlorella* and diatoms are excellent examples of algae, with *Chlorella* being the most widely used and effective in algae cultivation. The development of hepatopancreas occurs in three stages: the homogeneous period (2-4 cm in length), the turn liver period (25 days), and the envelop period (6-7 cm in length) (Kanazawa, 1985). During the homogeneous period, also known as the start feeding period, the shrimp seed is approximately 2-4 cm in length, and metabolism is the main concern, with only a few cases of bacterial infection. The turn-liver period begins 25 days after the shrimp are fed in the pools. It is characterized by high-speed growth in shrimp length and weight, but weak organic development, especially in the hepatopancreas. The envelop period is the mature phase of hepatopancreas function, during which the shrimp are 6-8 cm in length. At this stage, the white protective envelope turns into a normal dark chocolate brown color, resulting in a consistently darkened body color, intestinal microbiota homeostasis, and changed hepatopancreas metabolism in *L. vannamei* (Leiner and MacKenzie, 2001; Li et al., 2021). After being kept in constant darkness for eight weeks, the genes involved in regulating diurnal rhythms, immune function, body color formation, nutrient metabolism, hormone levels, and post-translational modifications were downregulated. Follow-up analysis of intestinal microbiota revealed that dark treatment-induced alterations in intestinal bacterial abundances and circadian rhythms led to a higher susceptibility to pathogens and reduced nutrient metabolism (Jiao et al., 2021) (Fig. 7).

Figure 7. Formation of a white protective envelope, which turns into a normal dark chocolate brown color.

Cyanobacteria: The RDHP issue is commonly caused by cyanobacteria, which are also known as cyanoprokaryota or blue-green algae. Cyanobacteria possess several competitive advantages over eukaryotic taxa, including enhanced nutrient sequestration, resistance to grazing, and improved light utilization. This allows them to survive under conditions of high herbivory and excessive nutrients or light. Moreover, aquaculture species are at risk of cyanobacterial metabolites through the aquatic food chain. The metabolites, which include cytotoxins, hepatotoxins, dermatoxins, neurotoxins, and odorous metabolites, can accumulate in the consumer's body and facilitate their transfer through the food chain. Hepatotoxins can enter Atlantic salmon through the consumption of toxins in biofouling organisms and crab larvae, resulting in net-pen liver disease (Andersen et al., 1993; Kent et al., 1996). Shrimp/prawns and tilapia that feed on plankton can withstand high levels of cyanobacterial toxins and accumulate them in their liver/hepatopancreas in natural and aquaculture settings. No studies have been conducted on the histopathological effects of hepatotoxins on other aquaculture species, such as bivalves, snails, or shrimp/prawns. However, immersion studies have shown that marine and freshwater bivalves can survive exposure to high concentrations of toxic cyanobacteria for several days, indicating their ability to tolerate ecologically acceptable concentrations for a brief period. The signal crayfish, *Pacifastacus leniusculus*, also exhibits tolerance to hepatotoxins, as evidenced by the fact that ingestion of microcystins for 14 days did not result in changes in behavior, feeding, glucose levels, or hepatopancreas weight (Lirås et al., 1998). Based on these studies, two primary conclusions can be drawn: (1) younger life stages are more sensitive to CYL

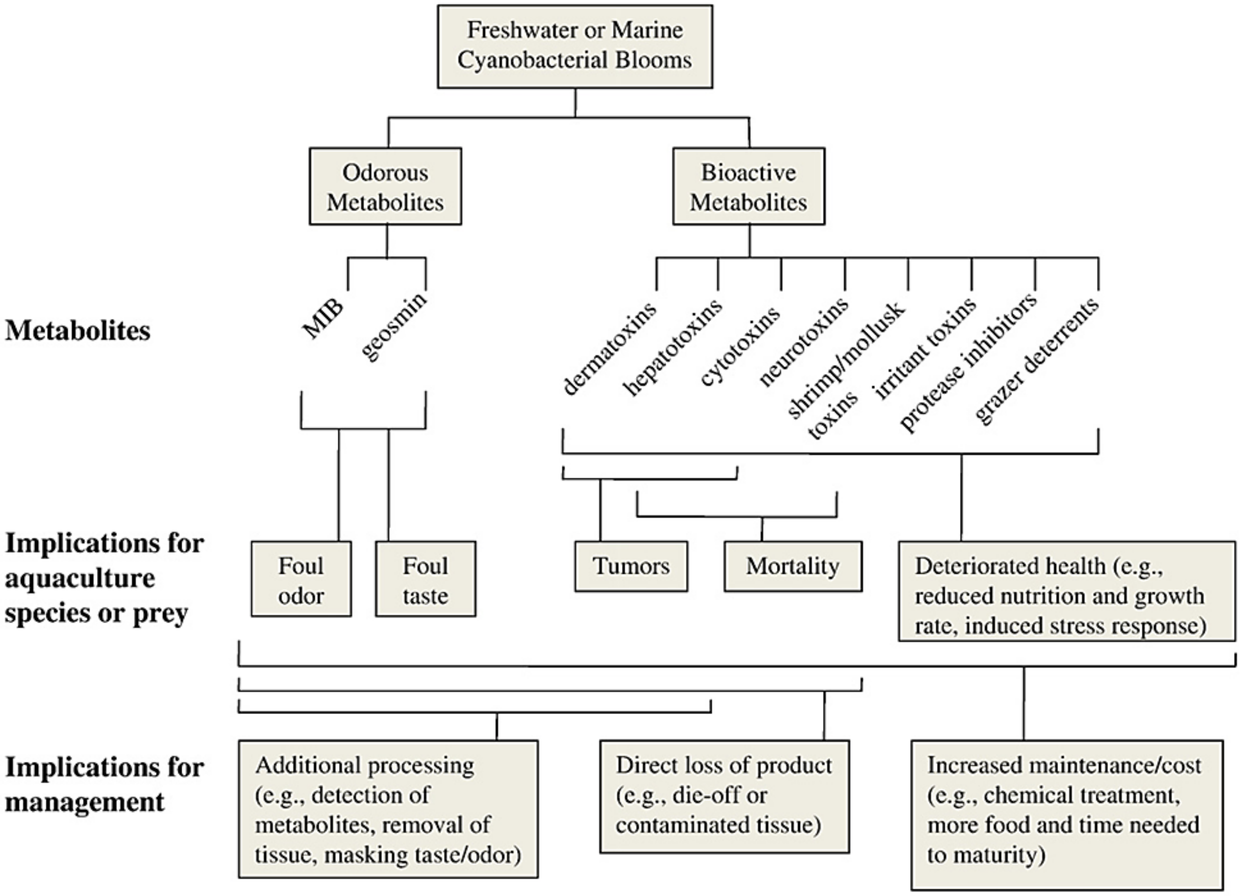

Figure 8. Possible implications of cyanobacterial secondary metabolites for aquaculture species (cultured crustaceans, mollusks, and fish) and management.

exposure compared to adults, and (2) species that rely on cyanobacteria, such as freshwater mussels, crayfish, and adult snails, exhibit tolerance to CYL, but further research is needed to confirm these conclusions. Future research can investigate the impact of CYL and its analogs accumulation on other species, including shrimp and fish. *Lyngbya majuscula* contains potent toxins that can harm various organisms, such as *Biomphalaria glabrata* (barbamide), mollusks, and snails (taveuniamides and curacins). These toxins have different structures, including taveuniamides (LC_{50} = 1.7-4.2 µg ml^{-1}) (Williamson et al., 2004), chlorinated lipids and lipids curacin A and D (LC_{50} = 0.003-0.03 µg ml^{-1}), the chlorinated lipopeptide barbamide (LC_{100} = 10 µg ml^{-1}) (Gerwick et al., 1994; Orjala et al., 1995; Márquez et al., 1998). All of these cyanobacterial secondary metabolites can reduce productivity in aquaculture systems and, therefore, require intervention (Fig. 8).

Losing revenue and production is a consequence of mortality in target organisms. Additionally, nutritional intake may decline due to grazer deterrents and protease inhibitors, leading to a reduction in the growth rate of the target species. Furthermore, energy may be expended on repair or detoxification processes as a result of cytotoxins, neurotoxins, hepatotoxins, irritant toxins, and dermatoxins. Crowded aquaculture sites are more susceptible to bioactive metabolites due to hypoxia and high stocking densities, which are known stressors. Unfavorable odors (geosmin, MIB) or disfigured or malformed shapes (hepatotoxins, and saxitoxin) caused by lesions or tumors (microcystins) reduce the value of a product due to the costs of addressing the problem. Removing toxin-laden tissue or organs imposes additional costs (cytotoxins, neurotoxins, hepatotoxins, and dermatoxins). Hepatotoxins, in particular, may persist in the flesh of aquatic animals for weeks or months after being transferred to a clean environment (Eriksson et al., 1989; Yokoyama and Park, 2003). In intensive aquaculture, controlling cyanobacteria is a significant challenge. However, RDHP can occur in newly opened ponds and well-managed ponds with good water quality. This occurs when the pond bottom is contaminated or the water exchange rate is insufficient, resulting in the replacement of the pond ecosystem's phytoplankton with a bacterial system that promotes the growth of cyanobacteria. Increasing the water exchange rate or enhancing aeration can help avoid dead areas and reduce the cyanobacteria population.

Feed quality problems: *Litopenaeus* is a genus of Pacific white shrimp cultured worldwide (Cheng et al., 2006). The cultivation of *L. vannamei* in inland saline water has become increasingly popular due to its tolerance to salinity levels ranging from 0.5 to 50 ppt (Saoud et al., 2003). Although culturing *L. vannamei* in low salinity inland water can lead to high economic yield, it can also pose potential risks and problems that can degrade commercial production, including low immunity (Ponce-Palafox et al., 1997), low survival rate, slow growth (Li et al., 2007), and low resistance to stress caused by certain water-borne toxins (Li et al., 2007). As a result of low salinity, salt diffusion from the blood to the ambient environment or body tissues may decline, leading to increased water absorption in the environment and swollen cells. In the case of salinity stress, aquatic animals must adapt to the changing water environment through osmoregulation and changes in various enzymes and transporters, which consume a considerable amount of energy (Tseng and Hwang, 2008). Therefore, it is reasonable to find a practical and appropriate method to address shrimp production issues at low salinity by modulating various aspects of dietary nutrition, as osmoregulation is highly energy-consuming in several decapod species (Tseng and Hwang, 2008).

The problem of ruptured hepatopancreas is highly prevalent and should be addressed by members in the supply chain, including feed millers, farmers, and packers. Consumers continue to demand and reject shrimp with dark hepatopancreas, which is due to a combination of various factors at different levels in the production chain, with nutritional factors being the most significant element. Shrimp cultivation is highly dependent on quality feed. Recently, the cost of raw materials for animal feed has increased rapidly, leading to a corresponding rise in feed prices. Consequently, several farmers have resorted to using inferior-quality feed or storing feed improperly to save expenses, which has resulted in the development of numerous mycotoxins. Shrimps that consume low-quality or contaminated feed are more susceptible to developing hepatitis, which, when coupled with external environmental factors, can result in high mortality rates. To achieve a balance between feed quality and costs, given the increasing prices of raw materials and feed, the only viable solution is to have a better feed formulation. Cuzon (1999) and the AQUACOP Team from IFREMER in Tahiti analyzed this challenge in *Penaeus stylirostris* in New Caledonia. Cuzon et al. (2004) found that the use of low-quality fish meal and fish oil has a direct impact on the hepatopancreas.

To determine whether a fish is consumable, European regulations rely on the measurement of TVBN (Total volatile Basic Nitrogen) and TMA (Trimethylamine). The level of TMA in a fish indicates its freshness, as it is produced by specific bacteria that use trimethylamine oxide as a hydrogen acceptor. Quality control criteria for fish are based on chemical analysis (TVBN + report/ratio TVBN /TMA) and organoleptic tests (grid of standard quotation of the EEC). While feed producers in Asia have improved the quality of food given to *P. monodon* in recent years, the raw materials used for *L. vannamei* are of low quality. This is due to lower demand for protein in *L. vannamei* compared to the *monodon* shrimp. However, both species require the same quality feed. In practice, *L. vannamei* feed is made using locally produced meals and oils without quality control, resulting in high levels of oxidation, low pH, and lipid peroxidation. Mycotoxin contamination is also a common issue in feed, especially in tropical countries with hot and humid climates. Aflatoxins, which are highly resistant to high temperatures and not destroyed during the extrusion and pelleting process, are a particular concern for shrimp growth. Even low concentrations of mycotoxins can cause heavy losses, as experienced by poultry feed producers (Cuzon et al., 1994). At low concentrations of 25 ppb, aflatoxin B1 has been found to cause damage to the hepatopancreas. The most effective way to prevent mycotoxin contamination in feed is to avoid using materials that are contaminated. Feed additives that absorb and deactivate mycotoxins are an economical and effective way to mitigate the risks associated with mycotoxins. These additives should be used during pelleting so that mycotoxins are absorbed onto the surface of the additive particles, preventing their absorption by animals. As a result, mycotoxins are excreted in the feces without any negative effect on shrimp (Browdy, 1998).

Carotenoid sources in crustacean aquaculture: Aquatic species obtain their red, orange, and yellow coloring from carotenoids, which are beneficial for their survival, growth, reproductive ability, and resistance to disease and stress. Photosynthetic plants and certain types of algae provide carotenoids, which are crucial for crustaceans and other animals. The specific types and amounts of carotenoids required vary among species and even within different stages of their life cycle, including their molt stage and various tissues and organs. Crustaceans with high concentrations of specific carotenoids can interconvert them and use them for particular functions in specific tissues. During early maturation, carotenoids are stored in the hepatopancreas in esterified and free forms, and then transported to the ovaries via the hemolymph during secondary vitellogenesis. The type and amount of carotenoids present in crustaceans change notably during ovarian development (Katayama et al., 1971; Lenel et al., 1978; Goodwin, 1984; Valin et al., 1987; Okada et al., 1994; Liñán-Cabello and Paniagua-Michel, 2004; Sachindra et al., 2005; Wade, Gabaudan, et al., 2017).

In the past, shrimp with low pigmentation were considered diseased; however, this issue was resolved by supplementing their diet with carotenoids. Recent research has shown that pigmentation in banana shrimp can be inherited, suggesting a genetic basis for the retention of carotenoid pigments. Changes in crustacean color are not always due to dietary carotenoids, as differences in the expression and sequence pattern of pigment genes, such as crustacyanin, can cause color changes. A protein called carotenoprotein complex stabilizes pigments like astaxanthin and the tertiary and quaternary structures of proteins. The level of expression of crustacyanin subunit A and C is lower in dark shrimp than in light shrimp. The effect of pigment and chromatophores on crustacean color appears in the exoskeleton or in the underlying hypodermal substrate, which is called chromatophores. Chromatophores can change pigment content when exposed to different substrates, and this process can happen quickly and often rhythmically in some crustaceans.

The hormones responsible for the contraction and expansion of crustaceans' pigments are the red pigment-concentrating hormone (RPCH) and the pigment-dispersing hormone (PDH), which are secreted by the eyestalks. Various physiological cues trigger these color changes and can affect the background color, light source, and photoperiod. Short-term exposure to a black substrate can expand the hypodermal chromatophores in prawns and enhance their pigmentation. Shrimp body color can fade, and chromatophores lose their diurnal rhythm under constant exposure to light. Exposure to hypoxic and thermal stress has been shown to cause the color of *P. monodon* to become redder, but this effect can be reversed by removing the stress. However, hypoosmotic stress does not affect color. When cooked, the color of *L. vannamei* becomes redder after exposure to 1 mg L^{-1} of copper over nine days (Martínez et al., 2014). Although color changes were not investigated after stress was removed, there is a strong likelihood that color response is related to stress. The darkening caused by accumulation is the foundation for determining the stage of ovarian maturation in female shrimp (Wouters et al., 2001). During ovarian maturation, esterified and free astaxanthin accumulate in the hepatopancreas, while their levels remain constant in the integument (Dall,

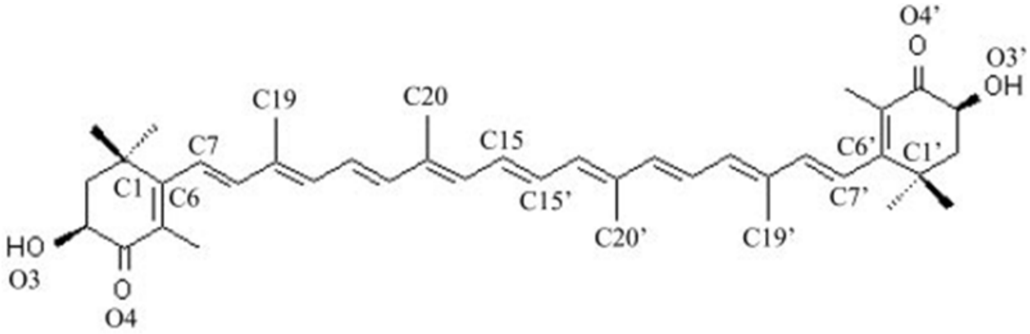

Figure 9. The chemical scheme of the carotenoid AXT. The molecule is centrosymmetric.

1995). Shrimp kept in captivity typically have lower carotenoid levels, especially in the IV ovarian stage, than those caught in the wild (Liñán-Cabello et al., 2003), indicating a deficiency in broodstock nutrition. For Penaeid shrimp, a carotenoid level of 30-50 mg/kg body weight is required in the tissue for optimal coloration. However, this amount does not necessarily result in the same overall coloration level for all species, with *L. vannamei* having lighter coloration than *P. monodon* at the same body astaxanthin level. In some cases, a much higher body astaxanthin level may be necessary. The reddish coloration, which is considered a sign of quality, is primarily attributed to astaxanthin, a carotenoid found in salmonids (Boonyaratpalin et al., 2001). Crustaceans in both the wild and captivity exhibit tissue distribution and various types of carotenoids, including astaxanthin, which is present in both esterified and free forms (García-Chavarría and Lara-Flores, 2013). Camouflage is a crucial biological mechanism for avoiding predators, and changes in shell color play a significant role in this regard. Depending on their species, diet, and carotenoid accumulation level, shrimp in their natural habitats display a range of colors (Erickson et al., 2015). Research has indicated that adding carotenoid supplements to their diet can cause crustaceans to become darker (brown) or reddish in color when cooked, unlike those specimens that do not receive these supplements in their feed. The interaction between astaxanthin and cooking changes the color from red to blue, but cooking shrimp disrupts this interaction, resulting in a distinct red color in cooked crustaceans.

Astaxanthin (3,3'-dihydroxy-β, β-carotene-4,4'-dione) is a primary carotenoid pigment that is present in numerous aquatic species and is responsible for the pink or red color of Salmonidae (salmon and rainbow trout) and Crustacea (shrimp and krill). Studies have demonstrated that astaxanthin has 80% anti-lipid peroxidation activity in rats with gastric ulcers and skin cancer caused by ethanol. Additionally, other studies have shown that astaxanthin can have a positive impact on human health, including enhanced lipid metabolism, anti-aging effects, and anti-inflammatory properties (Fig. 9). Research has examined the color preferences of consumers for both cooked and raw shrimp. The findings suggest that a higher concentration of astaxanthin in shrimp results in a darker color. When shrimp is cooked, the complex breaks down, causing the free astaxanthin to produce hues of red, orange, and yellow with a wavelength ranging from 470 to 472 nm (Cianci et al., 2002). According to Katayama et al. (1971), the primary reason for the coloration in crustaceans is the presence of astaxanthin in their exoskeleton and hypodermal tissue (Fig. 10).

In *P. monodon* and Black Tiger Prawn, as with all crustaceans, pigmentation is caused by the interaction between a protein called crustacyanin (CRCN) and astaxanthin (Zagalsky, 1985). This interaction causes the color of astaxanthin to change to blue. However, when cooked, the interaction is disrupted, and red color is produced, resulting in the characteristic red color of cooked crustaceans. This color change, caused by the formation or disruption of the complex, is known as a bathochromic shift, referring to the shift in wavelength that occurs with compounds (Cianci et al., 2002).

Figure 10. The development of red heads could be delayed, but not prevented, if the shrimp farmer stops feeding approximately 24 hours before harvest. Properly handled, Shell-on shrimp treated with ever-fresh have a potential shelf-life of 16-17 days. Loose heads limit the shelf-life of whole, head-on freshwater shrimp to 7-8 days in ice storage.

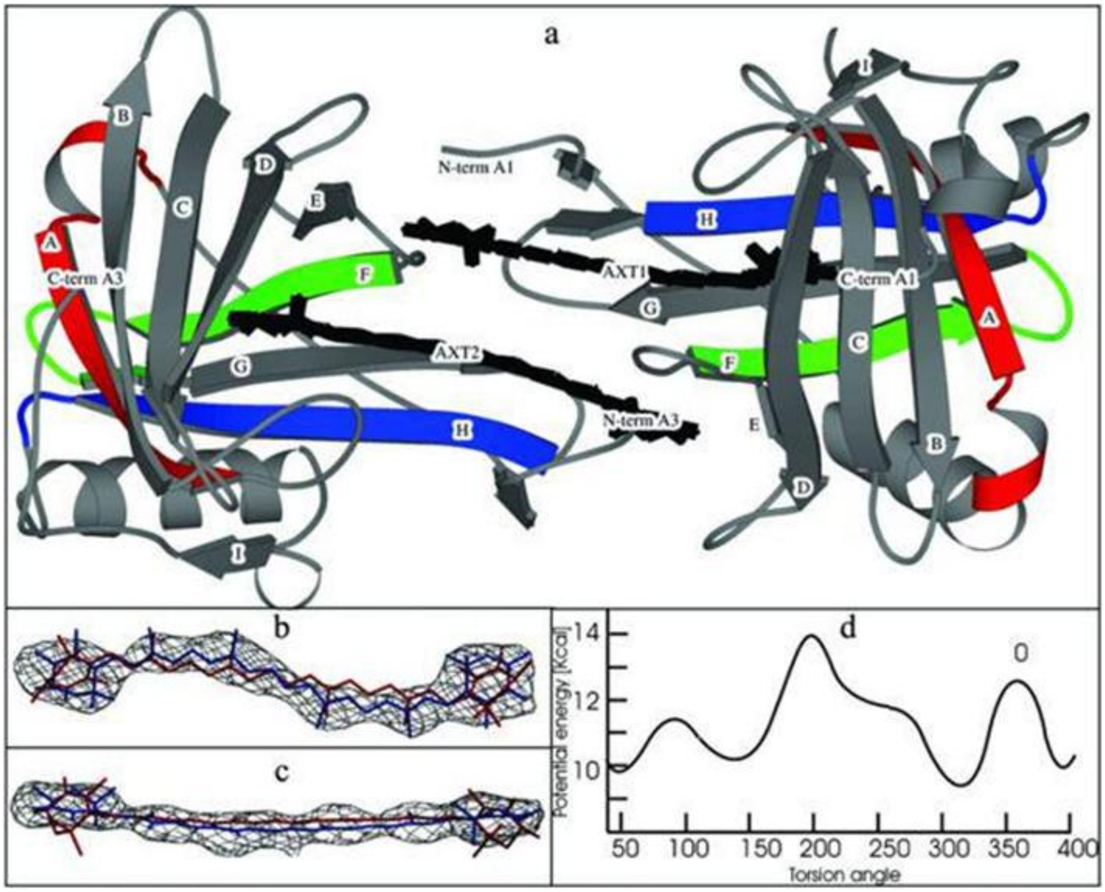

Figure 11. The A1-A3 dimer assembly (as ribbon) containing the two bound carotenoids (in “stick” format, colored black). Each strand is coded by color based on the consensus regions. (b) Superposition of AXT1 starting (red) and refined (blue) models on (Fo - Fc) difference density. (c) Edge view of b.(d) Graphical result of the obtained potential energy in AXT, which depends on the torsion angle, the end ring, and the polyene chain. [Re+produced with permission from ref. 31 (Copyright 1994, Birkhauser Basel)] (Cianci et al., 2002).

The astaxanthin molecule comprises two ionone rings linked through a chain of conjugated double bonds, resulting in various geometrical isomers (Fig. 11). However, astaxanthin is highly unstable when free and prone to oxidation (Etoh et al., 2012), so it is either found esterified with one or two fatty acids (monoester and diester forms) (Fig. 12), conjugated with proteins in nature to stabilize the molecule (Lorenz and Cysewski, 2000). In *Haematococcus pluvialis* microalgae, astaxanthin occurs in three forms: free (5%), diesters (25%), and monoesters (70%) (Miao et al., 2006). Red yeast *Phaffia rhodozuma* and salmon only contain free astaxanthin (Hussein et al., 2006). Arctic shrimp (*Pandalus borealis*) contains both astaxanthin monoesters and diesters, where diesters are predominant, and lauric

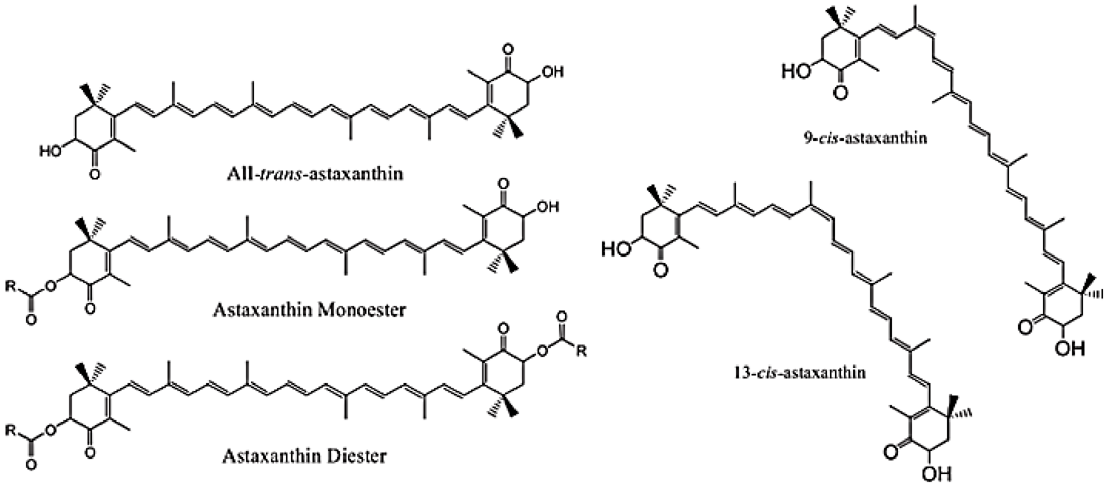

Figure 12. Structures of all-trans-, 9-cis-, 13-astaxanthinesters.

acid is one of the prevalent fatty acids (Naguib, 2000; Kamath et al., 2008; Etoh et al., 2012). Astaxanthin diesters constitute about 70% of the carotenoid extract in krill (Grynbaum et al., 2005), and astaxanthin esters contain fatty acids such as C16:0, C14:0, C18:1, C20:0, C16:1, C20:5, and C22:6, with PUFAs (C20:5 and C22:6) only present in astaxanthin diesters. Unfortunately, our understanding of astaxanthin composition, esters, and fatty acids is limited. Astaxanthin exists in its all-trans isomeric forms and can easily convert to its 9-cis and 13-cis isomers upon exposure to light, heat, and oxygen.

The isomerization of astaxanthin has the potential to alter its nutritional function and reduce its bioavailability. The red color that is observed in processed shrimp products is highly desirable and considered a key indicator of quality by consumers. Pacific white shrimp is the preferred choice for shrimp farming due to its high level of environmental stability, availability of healthy post-larvae throughout the year, and strong return on investment (Ju et al., 2011). Astaxanthin diesters are more stable in storage compared to the monoester form because they have a longer chain that requires more energy to break up, and they are more lipophilic and less polar, which facilitates their incorporation into biological tissues (Miao et al., 2013). The lipophilic property of esterified astaxanthin allows for better integration with membranes, which helps to prevent their thermal degradation (Cervantes-Paz et al., 2014).

Astaxanthin esters that have been esterified with saturated fatty acids possess greater stability and are less prone to degradation and enzyme-assisted decomposition due to photo/thermos-oxidation (Fukami et al., 2006; Cervantes-Paz et al., 2014). When compared to zeaxanthin esters without saturated fatty acids, those containing unsaturated fatty acids display less stability. Nonetheless, astaxanthin diesters such as Asta-C22:6/C22:6 and Asta-C22:5/C20:5 exhibit a lower degradation rate during thermal treatment in shrimp when compared to other diester molecules (Fig. 12). The lower rate of degradation of these diesters suggests that they are more thermostable, likely due to their high relative content in shrimps and smaller molecular polarity, which enhances their binding to biological tissues and protects them. When free astaxanthin is subjected to heat, it undergoes conversion to cis forms, primarily 9-cis-astaxanthin and 13-cis-astaxanthin, along with degradation. When subjected to thermal processing, esterified astaxanthin is less stable than free astaxanthin, as it undergoes hydrolysis and degradation. Astaxanthin diesters are more stable than the monoester form under these conditions. In addition, astaxanthin esters that contain DHA or EPA are less stable during thermal processing than those containing saturated fatty acids. A recent study utilized LC-(APCI)-MS/MS to measure and identify oxy/cis-isomers and molecular species of astaxanthin esters in both raw and thermally processed shrimp.

The study found a significant volume of EPA and DHA esterified astaxanthin in Pacific white shrimps, highlighting their potential value in developing functional foods that incorporate these fatty acids. Astaxanthin is present in both esterified and free forms, such as mono/di-ester with fatty acids, and can also be seen as caroteno-proteins in exoskeletons, which change color from blue/green to red during the cooking process (Okada et al., 1994; Britton and Goodwin, 2013).

Reports indicate the presence of small amounts of other carotenoids, such as zeaxanthin and lutein (Hooshmand et al., 2017). In crustaceans, carotenoids not only contribute to pigmentation but also serve as a source of provitamin A activity (Miki et al., 1982), enhance tolerance to stress (Chien and Shiau, 2005), and play important roles in differentiation and development processes (Liñán-Cabello et al., 2002). Crustaceans are capable of undergoing physiological and morphological color changes, which can occur rapidly or slowly due to hormonal or environmental factors (Rao, 1980; Stoner, 2012). Additionally, studies have shown that a higher abundance of epithelial CRCN protein is associated with improved pigment (Wade et al., 2012; Drozdova et al., 2020). The color of prawns is evaluated commercially based on a subjective assessment by consumers using either the SalmoFan color scale (DSM Nutritional Products) or the Australian Tiger Prawn Color Chart (Aqua Marine Marketing).

Harvesting and cooking change color blackening: There is a variety of shrimp products available in the market. Among them, pre-cooked shrimp is widely favored due to its reddish color (Hassoun et al., 2020). The pre-cooking process is used to extend the product's shelf life and enhance its color appeal. This process deactivates some enzymes that can degrade quality and eliminates microorganisms, resulting in a more stable product. Gökoğlu (2021) suggests that boiling the shrimp for two minutes is sufficient to deactivate PPO. Triyannanto and Lee (2015) found that vacuum-packaged shrimp before cooking had lower melanosis during chilled storage. When pre-cooking shrimp using traditional or steam oven methods and spraying them with a 4-hexylresorcinol formula beforehand, there was minimal melanosis in the final product. Pre-cooked shrimp products are commonly available in frozen (Triyannanto and Lee, 2015). However, melanosis is a frequent issue with pre-cooked shrimp due to residual PPO, which is the main cause. Melanosis can occur during pre-cooking or when the product is handled or stored in a refrigerated retail environment. The carapace is the first area to show signs of melanosis, which can then spread to other parts of the shrimp, resulting in a lower-quality product. One solution to prevent melanosis is to use a sufficiently high temperature during pre-cooking to inactivate PPO completely. Additionally, adequate heat can stop proteases, mainly located in the cephalothorax, from triggering PPO activity. However, creating harsh conditions may reduce the yield of pre-cooked shrimp.

There is limited information available on melanosis in pre-cooked shrimp, as well as the impact of pre-cooking on both melanosis and yield. Figure 13 displays data on melanosis in pre-cooked Pacific white shrimp stored for seven days in a refrigerator at various core temperatures. On the first day of storage, no melanosis was observed (score = 0), but as storage time increased, melanosis scores increased in all samples. However, samples cooked at 85 and 90℃ showed no signs of melanosis on the fourth and fifth days of storage, respectively. Increasing the core temperature was found to retard melanosis to a greater extent, indicating that higher temperatures likely deactivated the endogenous PPO through thermal denaturation. After 7 days of storage, melanosis was observed in the cephalothoraxes and pleopods due to the action of endogenous PPO (Manheem et al., 2012). The highest level of melanosis was seen in the sample with the lowest core temperature, and the least amount was found at higher temperatures, with no melanosis observed in samples cooked at 90°C. The yield and loss of the cooking process of pre-cooked Pacific white shrimp at different temperatures are illustrated in Figure 13. There were no differences in yield and loss of cooking at core temperatures between 50 and 65°C. However, an increase in core temperature led to

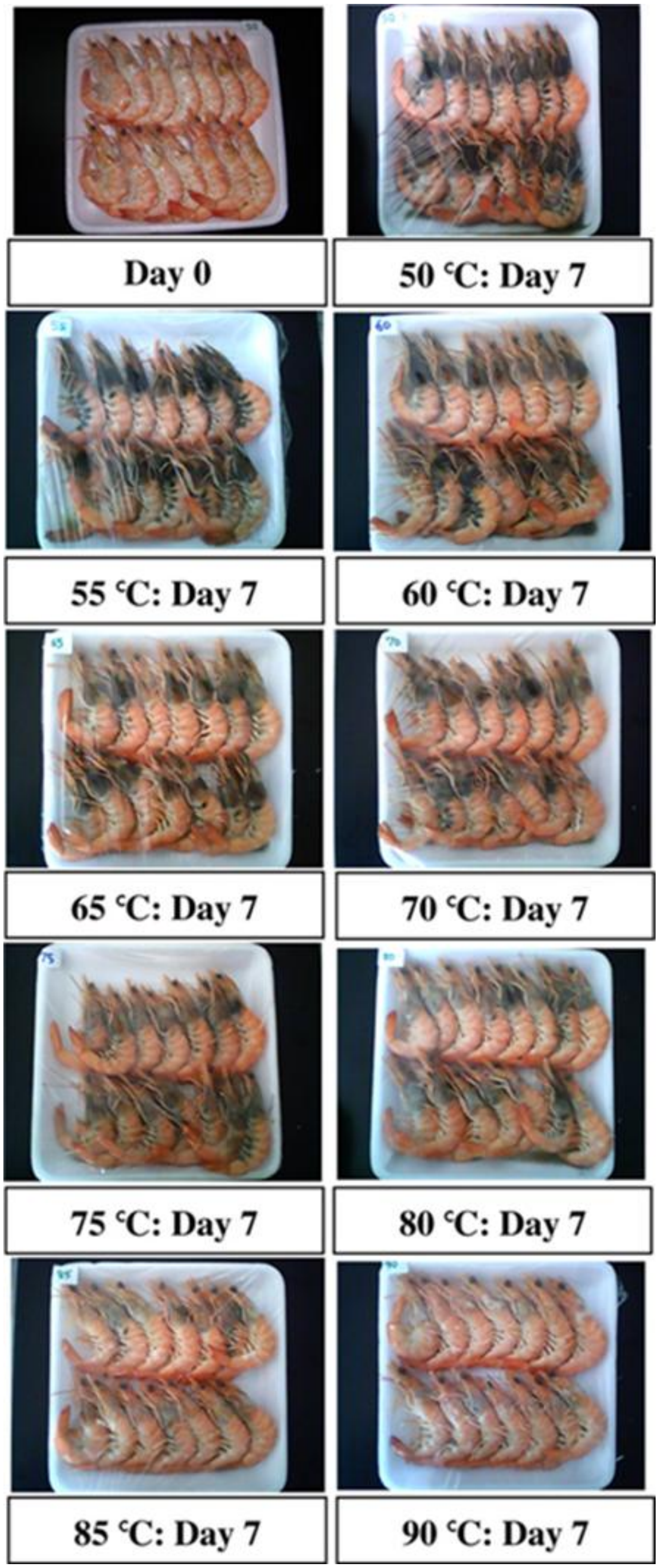

Figure 13. Pacific white shrimp pre-cooked at diverse core temperatures in zero and seven days of being stored in the refrigerator (Manheem et al., 2012).

a decrease in water content in the shrimp, along with an increase in protein and fat (Benjakul et al., 2008). This decrease in water was due to heat-induced protein denaturation, resulting in less water being present within the protein structures (Aaslyng et al., 2003).

Although we cannot accurately predict the effect of raw Lab value on cooked color, we can make inferences based on the negative correlation observed between the two. Higher raw L values indicated a lighter color before cooking and a lower cooked value after pre-cooking, resulting in less pigmented prawns. The uncooked prawns, which were kept on ice for more than 4 hours, or those that were frozen and then thawed, had significantly paler colors. Freeze-thawed raw products had a similar effect to those stored on ice for 8 hours, resulting in less pigmented products with lower color grades and prices. There is a lack of research in this area, although a study on *Macrobrachium rosenbergii* has shown that taste can be improved through salt acclimation after harvesting (Schilling, 2013). However, there have been no studies on the potential effects of ice storage on color.

Leon et al. (2006) demonstrated that digital images or colorimeters can be used to detect quantitative differences in prawn color. Improvements in the accuracy of converting RBG values to Lab values can be achieved using neural network models. In addition, Wade et al. (2014) observed significant differences in prawn color between farms and ponds within the same farm. Variations in prawn color can be attributed to a range of factors, including the type of ponds (lined or earthen), pigmentation regimes in feeds, and pond algal densities. Higher concentrations of total axanthin were observed in *P. monodon* postlarvae under constant light conditions compared to those in constant darkness, possibly due to higher generation and accumulation of axanthin in algae inside the tank that was ingested by the animals (Wade et al., 2014). Studies have also shown that prawn color can change rapidly in response to exposure to dark-colored substrates (Tume et al., 2009; Parisenti et al., 2011). However, in the case of *P. monodon*, no association was found with a change in axanthin concentration (Tume et al., 2009). Although potential changes in color of substrates in the pond cannot be determined, they can affect the color of the cooked product

Figure 14. Cooked prawns cultured in a black tank (left) or a white tank (right) for 28 days.

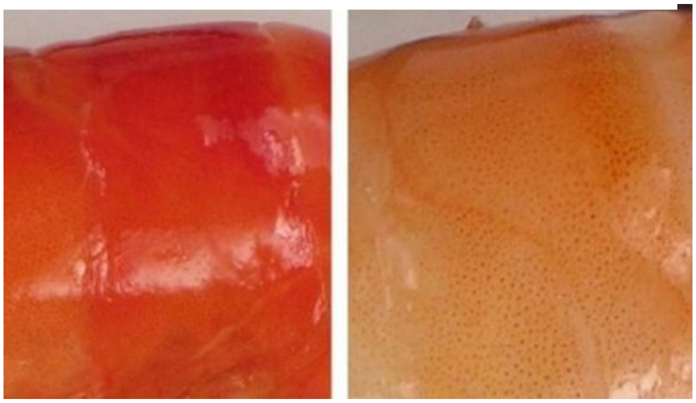

Figure 15. The first abdominal segment of prawns cultured in black (left) or white (right) tanks for 28 days. In comparison with dispersed pigment from the prawns grown in dark tanks, there are densely packed chromatophores on the right.

(Altmann et al., 2018) (Figs. 14, 15, 16).

According to Näslund and Johnsson (2016), most reports discussing the impact of harvest stress on pigmentation are brief and lack scientific methods to investigate potential effects. In the study by Phuthaworn et al. (2016), variations in color between farms were primarily attributable to changes resulting from specific harvesting conditions at a particular time, rather than differences between farms. The findings of Pan et al. (2021) demonstrate that uncooked prawns kept in ice for more than 4 hours, or those that were frozen and then thawed, exhibited a paler color.

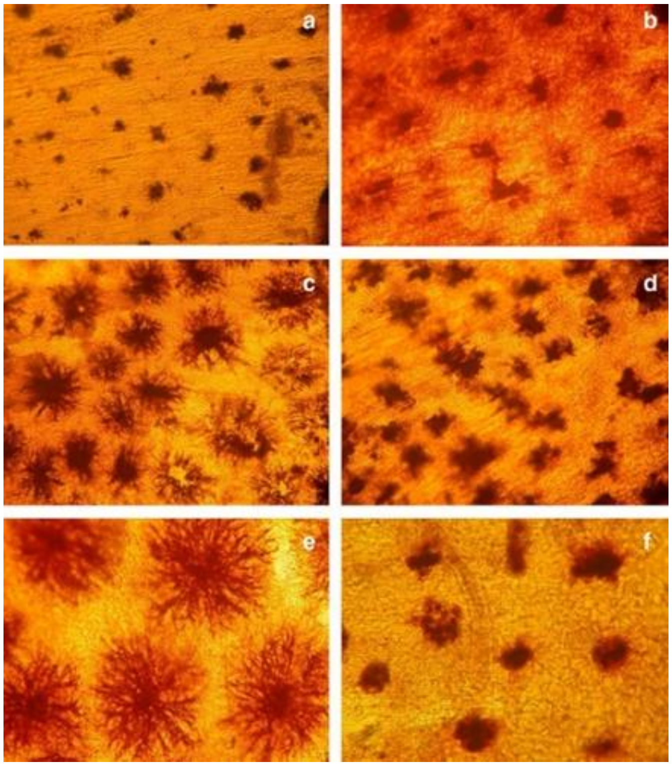

Figure 16. Light microscopic images of separated epidermal layer of the first abdominal segment of prawns. Chromatophores are seen at different moments following transfer between tanks (white to black; a, 0 h, c, 3 h, e, 7 days and black to white; b, 0 h, d, 3 h and f, 7 days). In general, images have different magnification; still, the mean distance between centers of chromatophores is about 380 μm.

Da Silva Campelo et al. (2019) reported that salt brining after cooking can enhance flavor and color, and the duration of cooking can impact the appearance of dark spots during frozen storage of *P. vannamei*. However, there has not been a comprehensive evaluation of the overall effects on color. *Litopenaeus vannamei* is another highly valued and popular species due to its characteristic quality. The handling of aquatic animals, such as during harvesting, can significantly impact the quality of the product. However, there is limited information on how the slaughter method affects the quality of farmed white leg shrimp. Killing marine animals by melting ice is not advisable, as it leads to osmotic shock, dilutes the water's salinity, and affects the quality of the product (Fig. 17). The process of killing shrimp causes stress, which negatively impacts the quality of their flesh. Instead, it is suggested to use ice water immersion for

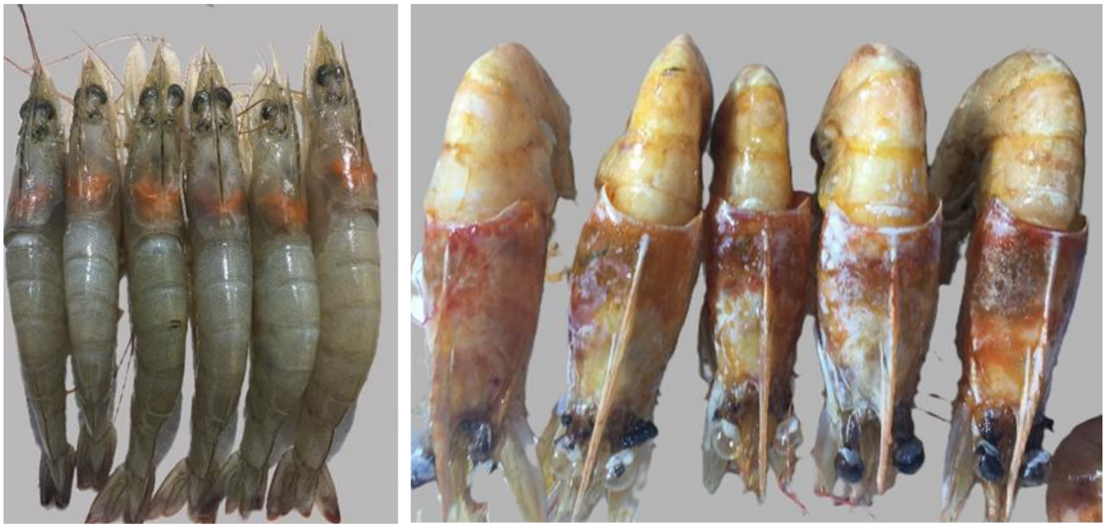

Figure 17. Shrimp during chilling storage, B2: flake-iced samples, 4 days, Cooked Shrimp for 4 days.

white leg shrimp, as they have a higher tolerance to cold water than ice temperature. The use of ice water immersion for killing shrimp results in lower TVC, and any differences in the quality of white leg shrimp due to different slaughter methods are primarily attributed to changes in the structure of fat and protein. When the hepatopancreas of harvested shrimp develops red or pink coloration, it is often associated with poor harvest management and temperature abuse during harvest and processing. This discoloration occurs due to damage or rupture of the hepatopancreas (RDHP), and it has a significant impact on the appearance of cooked shrimp. In the case of raw shrimp with RDHP, the hepatopancreas appears red and turns black after cooking, which diminishes the market value of the product, especially for lighter-colored species like Pacific white shrimp.

Handling and processing: Although using ice is the preferred method for preserving shrimp during harvesting and handling, it is worth noting that fishery products stored in cold or refrigerated conditions can undergo significant chemical and enzymatic autolytic reactions. While many studies have investigated the effects of treatment on the shelf-life and quality of Pacific white shrimp, there is limited research on the spoilage progression in untreated shrimp. Pacific white shrimp stored in ice for up to ten days after harvest experienced an increase in total color difference (TCD) and metric chroma (C), indicating that shrimp color can change with longer storage in ice (Okpala et al., 2014). However, the initial color changes observed in Pacific white shrimp were attributed to the shrimp carapace. Samples cooled with flake ice had the highest initial color score, while those in the liquid ice batch had a lower score (Okpala et al., 2014). This finding appears to contradict the results regarding the color of deep-water pink shrimp processed using ice (Huidobro et al., 2002). A recent report indicated that after four days, the color of shrimp chilled using liquid ice decreased significantly compared to the control group chilled using flaked ice. Sensory examination revealed that the quality of the color decreased due to higher whiteness and a loss of orange/pink color, which could decrease the product's market value (Okpala et al., 2014). It is believed that freezing can also affect the overall color of Brown shrimps (Althomali, 2019).

To determine color changes during chilling storage, studies have used L* (lightness), a* (redness), and b* (yellowness) values. Typically, L* values decrease, while a* and b* values increase during storage, resulting in a darker, more yellow, and red product. Zhang et al. (2015) found that melanosis (a dark and yellow pigmentation) in shrimp increased with storage time and was a significant factor in color changes during chilling storage. They observed that in all treatments, the L value decreased and the b value increased with longer storage time due to the decay of astaxanthin and lipid oxidation. However, the shrimp samples treated with slurry ice had higher L values and lower b values in the second segment, and showed less color change than the control and flake-iced samples. According to Wade et al. (2014), direct immersion in ice slurry and raw product freezing are not common methods for storing prawns because they can adversely affect the color of cooked prawns. However, the findings showed that storing prawns in an ice slurry led to a small but significant decrease in L value, but a significant increase in a and b values, indicating higher levels of yellow and red hues and a positive effect on prawn color.

Oxygen is also a crucial factor in the development of melanosis in shrimp, contributing to the change in color. The presence of endogenous proteases can enhance hydrolysis, causing the release of free carotenoids from the proteinaceous matrix and leading to an increase in carotenoid levels. Exogenous proteases, mainly from microorganisms, can also facilitate the hydrolysis of the proteinaceous matrix, especially during prolonged storage periods, leading to a decrease in carotenoid content. This decline is likely due to the increased oxidation of carotenoids, which have numerous conjugated double bonds that are susceptible to oxidation. As a result, oxidation can lead to discoloration (Butnariu, 2016). The carotenoid present in shrimp is vulnerable to oxidation due to its unsaturated structure, which makes it sensitive to heat, oxygen, and light. Consequently, during storage, the carotenoid undergoes gradual oxidation. Zhang et al. (2015) and Benjakul et al. (2008) have discussed the slurry ice treatment, which involves the use of small ice particles that flow around the shrimp and fill all oxygen pockets, creating uniform direct contact and resulting in a significant improvement in appearance quality.

Carotenoids, particularly astaxanthin, are the primary pigments responsible for the reddish-orange color in crustaceans and salmonids (Gulzar and Benjakul, 2018; Martínez-Cámara et al., 2021). The decline in carotenoid pigment astaxanthin, caused by lipid oxidation, leads to further color changes in shrimp. However, the use of slurry ice slows down lipid degradation during chilling storage, as evidenced by the TBARS findings, which suggests that it can improve the sensory aspect of the product with extended storage. According to Takeungwongtrakul et al. (2012), the lipid content of carotenoids in hepatopancreas and cephalothorax increased during the first 2-4 days of iced storage, with astaxanthin and its esters being the primary pigments (Núñez-Gastélum et al., 2016), suggesting that the protein matrix of both portions can release free carotenoids, including astaxanthin. However, the color of the portions faded and became yellowish during storage, which is partially attributed to the photooxidation of astaxanthin induced by high partial pressure of oxygen (Brotosudarmo et al., 2020; Maoka, 2020). In ice storage, approximately 20% of fish lipids are hydrolyzed, releasing free fatty acids that are susceptible to oxidation and thereby accelerating lipid oxidation (Sikorski, 1990). Therefore, longer storage times lead to faster and more extensive hydrolysis of lipids, making them more prone to deterioration and oxidation, as reported for the hepatopancreas and cephalothorax in Pacific white shrimp (Okpala et al., 2014).

The breakdown of hydroperoxides resulted in the generation of aldehydes and other secondary oxidation products. Over the storage period, a decrease in the formation of triacylglycerol (TG) and free fatty acids (FFA) is observed, indicating high hydrolysis, resulting in an improvement in peroxide value (PV) along with an increase in anisidine value (AnV), consistent with previous studies (Senphan and Benjakul, 2012). However, the gradual decrease in AnV suggests that PV may not significantly impact the extensive increase in AnV, which tends to approach peak values. Studies have shown that AnV can alter the levels of non-volatile aldehydes, 2-alkenals, and 2,4-alkadienals in lipids. In acidic environments, aldehydes react with the p-anisidine reagent, forming yellow-colored products. An increase in AnV coincides with aldehyde production, which can also undergo condensation or dimerization reactions and decrease at a specific level of aldehyde (Senphan and Benjakul, 2012; Takeungwongtrakul et al., 2012). Temporal PV/AnV rates can be used to demonstrate the primary to secondary lipid oxidation

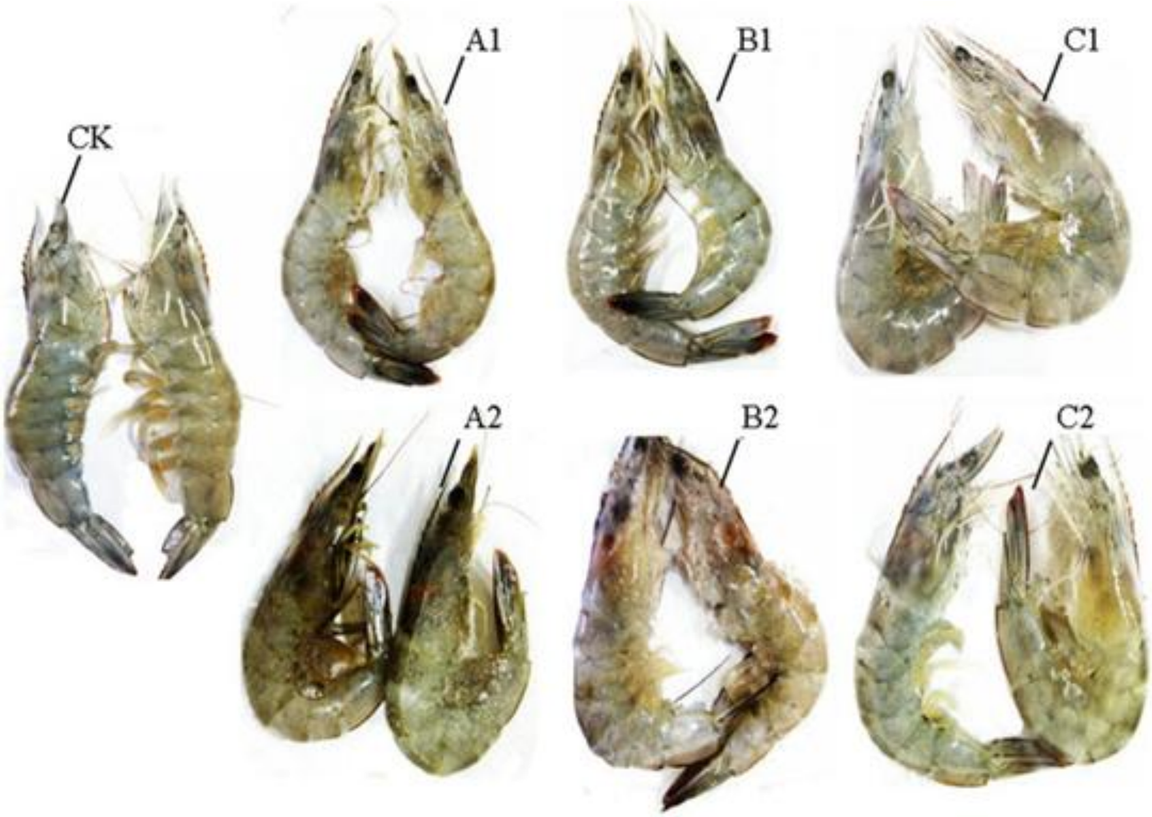

Figure 18. Shrimp in chilling storage in control (A), flake ice (B) and slurry ice (C) ck: control samples, 0 day; A1 and A2: control samples, 4 and 12 days; B1 and B2: flake-iced samples, 4 and 12 days; C1 and C2: slurry-iced samples, 4 and 12 days.

behavior of fresh *L. vannamei* shrimp, in addition to the high PV content relative to AnV observed during the early days of storage in ice.

Acidic electrolyzed water (AEW) ice is a new and effective technology for preserving food freshness and inactivating bacteria. Previous studies have focused on evaluating the microbiological (total viable count), physical (texture, color difference), and chemical (pH, TVB-N, and TBA) changes that occur in aquatic products preserved with AEW ice (Phuvasate and Su, 2010; Lin et al., 2013; Wang et al., 2014). These studies have demonstrated that AEW ice can significantly inhibit bacterial proliferation, resulting in changes in pH, color, and TVB-N formation. The degradation of aquatic animals after death follows a series of processes, including rigor mortis, degradation, autolysis, and bacterial spoilage, which are mainly caused by endogenous enzymes and bacterial actions (Lin et al., 2013). Lipase has been identified as a potentially important determinant of the specific fatty acids released from the storage depots in the hepatopancreas of crustaceans, as reported by Pasquevich et al. (2013) in *Macrobrachium borellii*. Their results indicate that previous studies have primarily focused on investigating the impact of AEW ice on the preservation of aquatic products by analyzing changes in physical characteristics, such as color and texture, as well as microbiological factors, including the total viable count, and chemical properties, including TVB-N, pH, and TBA (Pasquevich et al., 2013). From the above analysis, it can be concluded that the previous studies have mainly concentrated on evaluating the effect of AEW ice on aquatic product preservation by measuring the changes in the microbiological (total viable count), physical (texture, color difference, etc.), and chemical (pH, TVB-N, TBA, etc.) properties (Phuvasate and Su, 2010; Lin et al., 2013; Wang et al., 2014). These processes are responsible for the structural and ultrastructural disorders associated with postmortem degradation in aquatic animals, which is mainly caused by endogenous enzymes and bacterial actions (Anacleto et al., 2011; Manheem et al., 2012; Chen et al., 2022).

According to Wang et al. (2015), AEW ice can prevent changes in total bacterial count, pH, muscle fiber shrinkage, and bacterial flora in shrimp when compared to TW ice. Moreover, AEW ice is effective in reducing the activity of cathepsin B and PPO, but it has no effect on acid phosphatase, lipase, and cathepsin D. The use of SDS-PAGE and AEW ice does not have a negative impact on sarcoplasmic proteins. The reduction in Ca^{2+}-ATPase activity can be attributed to the conformational changes in the myosin globular head and the aggregation of the portion. The protein reorganization that occurs due to the interaction among proteins during freeze-thawing may also contribute to the decrease in ATPase activity. The study found no significant difference in CA ATPase between species, suggesting that the stability of muscle proteins, especially myosin, is likely the same. However, the research also shows that the protein in the muscle undergoes a considerable degree of denaturation as the freeze-thaw cycle increases (Fig. 18).

Acknowledgment

This research was funded by the Iran National Science Foundation (INSF, Grant Number: 96016303).

References

Aaslyng M.D., Bejerholm C., Ertbjerg P., Bertram H.C., Andersen H.J. (2003). Cooking loss and juiciness of pork in relation to raw meat quality and cooking procedure. Food quality and preference, 14(4): 277-288.

Althomali A.W. (2019). Behavioural ecotoxicology of the brown shrimp, Crangon crangon: changing colour in polluted environments.University of Salford (United Kingdom).

Altmann B.A., Neumann C., Velten S., Liebert F., Mörlein D. (2018). Meat quality derived from high inclusion of a micro-alga or insect meal as an alternative protein source in poultry diets: A pilot study. Foods, 7(3): 34.

An W., He H., Dong X., Tan B., Yang Q., Chi S., Zhang S., Liu H., Yang Y. (2020). Regulation of growth, fatty acid profiles, hematological characteristics and hepatopancreatic histology by different dietary n-3 highly unsaturated fatty acids levels in the first stages of juvenile Pacific white shrimp (*Litopenaeus vannamei*). Aquaculture Reports, 17: 100321.

Anacleto P., Teixeira B., Marques P., Pedro S., Nunes M.L., Marques A. (2011). Shelf-life of cooked edible crab (*Cancer pagurus*) stored under refrigerated conditions. LWT-Food Science and Technology, 44(6): 1376-1382.

Andersen R.J., Luu H.A., Chen D.Z.X., Holmes C.F.B., Kent M.L., Le Blanc M., Williams D.E. (1993). Chemical and biological evidence links microcystins to salmon ‘netpen liver disease’. Toxicon, 31(10): 1315-1323.

Benjakul S., Visessanguan W., Kijroongrojana K., Sriket P. (2008). Effect of heating on physical properties and microstructure of black tiger shrimp (*Penaeus monodon*) and white shrimp (*Penaeus vannamei*) meats. International Journal of Food Science and Technology, 43(6): 1066-1072.

Bernal Rodríguez C.E., Garcia A., Ponce-Palafox J., Spanopoulos-Hernández M., Puga-López D. (2017). The color of marine shrimps and its role in the aquaculture. International Journal of Aquaculture and Fishery Sciences, 3(3): 062-065.

Boonyaratpalin M., Thongrod S., Supamattaya K., Britton G., Schlipalius L.E. (2001). Effects of β-carotene source, Dunaliella salina, and astaxanthin on pigmentation, growth, survival and health of *Penaeus monodon*. Aquaculture Research, 32: 182-190.

Britton G., Goodwin T.W. (2013). Carotenoid chemistry and biochemistry: Proceedings of the 6th International Symposium on Carotenoids, Liverpool, UK: 26-31 July 1981. Elsevier.

Brotosudarmo T.H.P., Limantara L., Setiyono E., Heriyanto. (2020). Structures of astaxanthin and their consequences for therapeutic application. International Journal of Food Science, 2020(1): 2156582.

Browdy C.L. (1998). Recent developments in penaeid broodstock and seed production technologies: improving the outlook for superior captive stocks. Aquaculture, 164(1-4): 3-21.

Butnariu M. (2016). Methods of analysis (extraction, separation, identification and quantification) of carotenoids from natural products. Journal of Ecosystem and Ecography Open Access, 6(2): 1-19.

Ceccaldi H. (1989). Anatomy and physiology of digestive tract of Crustaceans Decapods reared in aquaculture. Advances in Tropical Aquaculture, Workshop at Tahiti, French Polynesia, 20 Feb - 4 Mar 1989. pp: 243-259.

Cen J., Cui L., Duan Y., Zhang H., Lin Y., Zheng J., Lu S. (2019). Effects of palytoxins extracted from Ostreopsis ovata on the oxidative stress and immune responses in Pacific white shrimp *Litopenaeus vannamei*. Fish and

Shellfish Immunology, 95: 670-678.

Cervantes-Paz B., Yahia E.M., de Jesús Ornelas-Paz J., Victoria-Campos C.I., Ibarra-Junquera V., Pérez-Martínez J.D., Escalante-Minakata P. (2014). Antioxidant activity and content of chlorophylls and carotenoids in raw and heat-processed Jalapeño peppers at intermediate stages of ripening. Food chemistry, 146: 188-196.

Cervellione F., McGurk C., Berger Eriksen T., Van Den Broeck W. (2017). Effect of starvation and refeeding on the hepatopancreas of whiteleg shrimp *Penaeus vannamei* (Boone) using computer-assisted image analysis. Journal of Fish Diseases, 40(11): 1707-1715.

Chand R.K., Sahoo P.K. (2006). Effect of nitrite on the immune response of freshwater prawn Macrobrachium malcolmsonii and its susceptibility to *Aeromonas hydrophila*. Aquaculture, 258(1-4): 150-156.

Chen L., Jiao D., Liu H., Zhu C., Sun Y., Wu J., Zheng M., Zhang D. (2022). Effects of water distribution and protein degradation on the texture of high pressure-treated shrimp (*Penaeus monodon*) during chilled storage. Food Control, 132: 108555.

Cheng W., Chieu H.-T., Ho M.-C., Chen J.-C. (2006). Noradrenaline modulates the immunity of white shrimp *Litopenaeus vannamei*. Fish and Shellfish Immunology, 21(1): 11-19.

Chien C.-C., Lin T.-Y., Chi C.-C., Liu C.-H. (2020). Probiotic, Bacillus subtilis E20 alters the immunity of white shrimp, *Litopenaeus vannamei* via glutamine metabolism and hexosamine biosynthetic pathway. Fish and Shellfish Immunology, 98: 176-185.

Chien Y.-H., Shiau W.-C. (2005). The effects of dietary supplementation of algae and synthetic astaxanthin on body astaxanthin, survival, growth, and low dissolved oxygen stress resistance of kuruma prawn, *Marsupenaeus japonicus* Bate. Journal of Experimental Marine Biology and Ecology, 318(2): 201-211.

Cianci M., Rizkallah P.J., Olczak A., Raftery J., Chayen N.E., Zagalsky P.F., Helliwell J.R. (2002). The molecular basis of the coloration mechanism in lobster shell: β-crustacyanin at 3.2-Å resolution. Proceedings of the National Academy of Sciences, 99(15): 9795-9800.

Corbo M.R., Altieri C., Bevilacqua A., Campaniello D., D'Amato D., Sinigaglia M. (2005). Estimating packaging atmosphere–temperature effects on the shelf life of cod fillets. European Food Research and Technology, 220: 509-513.

Cui Y., Ren X., Li J., Zhai Q., Feng Y., Xu Y., Ma L. (2017). Effects of ammonia-N stress on metabolic and immune function via the neuroendocrine system in *Litopenaeus vannamei*. Fish and Shellfish Immunology, 64: 270-275.

Cuzon G., Guillaume J., Cahu C. (1994). Composition, preparation and utilization of feeds for Crustacea. Aquaculture, 124(1-4): 253-267.

Cuzon G., Lawrence A., Gaxiola G., Rosas C., Guillaume J. (2004). Nutrition of *Litopenaeus vannamei* reared in tanks or in ponds. Aquaculture, 235(1-4): 513-551.

da Silva Campelo M.C., Rebouças L.d.O.S., de Oliveira Vitoriano J., Junior C.A., da Silva J.B.A., de Oliveira Lima P. (2019). Use of cold atmospheric plasma to preserve the quality of white shrimp (*Litopenaeus vannamei*). Journal of Food Protection, 82(7): 1217-1223.

Dall W. (1995). Carotenoids versus retinoids (vitamin A) as essential growth factors in penaeid prawns (*Penaeus semisulcatus*). Marine Biology, 124(2): 209-213.

Davis D.A. (1990). Dietary mineral requirements of *Penaeus vannamei*: evaluation of the essentiality for thirteen minerals and the requirements for calcium, phosphorus, copper, iron, zinc, and selenium. In: The Shrimp Book.Texas A&M University. pp: 485-490.

Drozdova P., Saranchina A., Morgunova M., Kizenko A., Lubyaga Y., Baduev B., Timofeyev M. (2020). The level of putative carotenoid-binding proteins determines the body color in two species of endemic Lake Baikal amphipods. PeerJ, 8: e9387.

Edgerton B.F., Evans L.H., Stephens F.J., Overstreet R.M. (2002). Synopsis of freshwater crayfish diseases and commensal organisms. Aquaculture, 206(1-2): 57-135.

Erickson E., Wakao S., Niyogi K.K. (2015). Light stress and photoprotection in *Chlamydomonas reinhardtii*. The Plant Journal, 82(3): 449-465.

Erickson M.C., Bulgarelil M.A., Resurreccion A.V.A., Vendetti R.A., Gates K.A. (2007). Consumer differentiation, acceptance, and demographic patterns to consumption of six varieties of shrimp. Journal of Aquatic Food Product Technology, 15(4): 35-51.

Eriksson J.E., Meriluoto J.A.O., Lindholm T. (1989). Accumulation of a peptide toxin from the cyanobacterium *Oscillatoria agardhii* in the freshwater mussel Anadonta cygnea. Hydrobiologia, 183: 211-216.

Etoh H., Suhara M., Tokuyama S., Kato H., Nakahigashi R., Maejima Y., Ishikura M., Terada Y., Maoka T. (2012). Auto-oxidation products of astaxanthin. Journal of Oleo Science, 61(1): 17-21.

Fukami H., Namikawa K., Sugiura-Tomimori N., Sumida M., Katano K., Nakao M. (2006). Chemical synthesis of astaxanthin n-octanoic acid monoester and diester and evaluation of their oral absorbability. Journal of Oleo Science, 55(12): 653-656.

García-Chavarría M., Lara-Flores M. (2013). The use of carotenoid in aquaculture. Research Journal of Fisheries and Hydrobiology, 8(2): 38-49.

Gerwick W.H., Proteau P.J., Nagle D.G., Hamel E., Blokhin A., Slate D.L. (1994). Structure of curacin A, a novel antimitotic, antiproliferative and brine shrimp toxic natural product from the marine cyanobacterium *Lyngbya majuscula*. The Journal of Organic Chemistry, 59(6): 1243-1245.

Gökoğlu N. (2021). Shellfish processing and preservation. Springer. 336 p.

Goodwin T.W. (1984). The biochemistry of the carotenoids. II. Animals. Chapmann and Hall, London. 224 p.

Gross P.S., Bartlett T.C., Browdy C.L., Chapman R.W., Warr G.W. (2001). Immune gene discovery by expressed sequence tag analysis of hemocytes and hepatopancreas in the Pacific White Shrimp, *Litopenaeus vannamei*, and the Atlantic White Shrimp, L. setiferus. Developmental and Comparative Immunology, 25(7): 565-577.

Grynbaum M.D., Hentschel P., Putzbach K., Rehbein J., Krucker M., Nicholson G., Albert K. (2005). Unambiguous detection of astaxanthin and astaxanthin fatty acid esters in krill (*Euphausia superba Dana*). Journal of Separation Science, 28(14): 1685-1693.

Gulzar S., Benjakul S. (2018). Ultrasound waves increase the yield and carotenoid content of lipid extracted from cephalothorax of Pacific white shrimp (*Litopenaeus vannamei*). European Journal of Lipid Science and Technology, 120(5): 1700495.

Hassoun A., Ojha S., Tiwari B., Rustad T., Nilsen H., Heia K., Cozzolino D., Bekhit A.E.-D., Biancolillo A., Wold J.P. (2020). Monitoring thermal and non-thermal treatments during processing of muscle foods: A comprehensive review of recent technological advances. Applied Sciences, 10(19): 6802.

Hooshmand H., Shabanpour B., Moosavi-Nasab M., Golmakani M.T. (2017). Optimization of carotenoids extraction from blue crab (*Portunus pelagicus*) and shrimp (*Penaeus semisulcatus*) wastes using organic solvents and vegetable oils. Journal of Food Processing and Preservation, 41(5): e13171.

Huidobro A., López-Caballero M., Mendes R. (2002). Onboard processing of deepwater pink shrimp (*Parapenaeus longirostris*) with liquid ice: effect on quality. European Food Research and Technology, 214: 469-475.

Hussein G., Sankawa U., Goto H., Matsumoto K., Watanabe H. (2006). Astaxanthin, a carotenoid with potential in human health and nutrition. Journal of Natural Products, 69(3): 443-449.

Jiao L., Dai T., Lu J., Tao X., Jin M., Sun P., Zhou Q. (2021). Effects of dietary manganese supplementation on growth performance, antioxidant capacity, immune function and intestinal microbiota in Pacific white shrimp *Litopenaeus vannamei*. Aquaculture Nutrition, 27(6): 1972-1982.

Jiao L., Dai T., Tao X., Lu J., Zhou Q. (2021). Influence of light/dark cycles on body color, hepatopancreas metabolism, and intestinal microbiota homeostasis in *Litopenaeus vannamei*. Frontiers in Marine Science, 8: 750384.

Jiao L., Dai T., Zhong S., Jin M., Sun P., Zhou Q. (2021). *Vibrio parahaemolyticus* infection influenced trace element homeostasis, impaired antioxidant function, and induced inflammation response in *Litopenaeus vannamei*. Biological Trace Element Research, 199: 329-337.

Ju Z.Y., Deng D.F., Dominy W.G., Forster I.P. (2011). Pigmentation of Pacific white shrimp, *Litopenaeus vannamei*, by dietary astaxanthin extracted from Haematococcus pluvialis. Journal of the World Aquaculture Society, 42(5): 633-644.

Kamath B.S., Srikanta B.M., Dharmesh S.M., Sarada R., Ravishankar G.A. (2008). Ulcer preventive and antioxidative properties of astaxanthin from *Haematococcus pluvialis*. European Journal of Pharmacology, 590(1-3): 387-395.

Kanazawa A. (1985). Nutrition of penaeid prawns and shrimps. In: Taki Y., Primavera J.H. and Llobrera J.A. (Eds.). Proceedings of the First International Conference on the Culture of Penaeid Prawns/Shrimps, 4-7 December 1984, Iloilo City, Philippines. Iloilo City, Philippines: Aquaculture Department, Southeast Asian Fisheries Development Center. pp: 123-130.

Katayama T., Hirata K., Chichester C.O. (1971). The biosynthesis of astaxanthin-IV. The carotenoids in the prawn, *Penaeus japonicus* Bate (Part I). Bulletin of the Japanese Society of Scientific Fisheries, 37(7): 614-620.

Kent M.L., Dawe S.C., St. Hilaire S., Andersen R.J. (1996). Effects of feeding rate, seawater entry, and exposure to natural biota on the severity of net-pen liver disease among pen-reared Atlantic salmon. The Progressive Fish-Culturist, 58(1): 43-46.

Kuhn D.D., Lawrence A.L., Boardman G.D., Patnaik S., Marsh L., Flick Jr G.J. (2010). Evaluation of two types of bioflocs derived from biological treatment of fish effluent as feed ingredients for Pacific white shrimp, *Litopenaeus vannamei*. Aquaculture, 303(1-4): 28-33.

Leiner K.A., MacKenzie D.S. (2001). The effects of photoperiod on growth rate and circulating thyroid hormone levels in the red drum, Sciaenops ocellatus: evidence for a free-running circadian rhythm of T4 secretion. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology, 130(1): 141-149.

Lenel R., Castillo R., Negre-Sadargues G. (1978). The presence of α-doradexanthin in crustacea and its possible metabolic fate. Biochemical Systematics and Ecology, 6(3): 251-253.

Leon K., Mery D., Pedreschi F., Leon J. (2006). Color measurement in L∗ a∗ b∗ units from RGB digital images. Food Research International, 39(10): 1084-1091.

Li P., Lawrence A.L., Castille F.L., Iii D.M.G. (2007). *Litopenaeus vannamei* (Boone). Aquaculture Research, 38: 887-890.

Li X., Han T., Zheng S., Wu G. (2021). Nutrition and functions of amino acids in aquatic crustaceans. amino acids in nutrition and health: Amino acids in the nutrition of companion. Zoo and Farm Animals, 169-198.

Li Y., Zhou F., Huang J., Yang L., Jiang S., Yang Q., He J., Jiang S. (2018). Transcriptome reveals involvement of immune defense, oxidative imbalance, and apoptosis in ammonia-stress response of the black tiger shrimp (*Penaeus monodon*). Fish and Shellfish Immunology, 83: 162-170.

Liang Z., Liu R., Zhao D., Wang L., Sun M., Wang M., Song L. (2016). Ammonia exposure induces oxidative stress, endoplasmic reticulum stress and apoptosis in hepatopancreas of pacific white shrimp (*Litopenaeus vannamei*). Fish & shellfish immunology, 54: 523-528.

Lin T., Wang J.J., Li J.B., Liao C., Pan Y.J., Zhao Y. (2013). Use of acidic electrolyzed water ice for preserving the quality of shrimp. Journal of Agricultural and Food Chemistry, 61(36): 8695-8702.

Lin Y.-C., Chen J.-C., Morni W.Z.W., Putra D.F., Huang C.-L., Li C.-C., Hsieh J.-F. (2013). Vaccination enhances early immune responses in white shrimp *Litopenaeus vannamei* after secondary exposure to Vibrio alginolyticus. PloS one, 8(7): e69722.

Liñán-Cabello M.A., Paniagua-Michel J. (2004). Induction factors derived from carotenoids and vitamin A during the ovarian maturation of *Litopenaeus vannamei*. Aquaculture International, 12: 583-592.

LiÑÁN-Cabello M.A., Paniagua-Michel J., Hopkins P.M. (2002). Bioactive roles of carotenoids and retinoids in crustaceans. Aquaculture Nutrition, 8(4): 299-309.

Liñán-Cabello M.A., Paniagua-Michel J., Zenteno-Savín T. (2003). Carotenoids and retinal levels in captive and wild shrimp, *Litopenaeus vannamei*. Aquaculture Nutrition, 9(6): 383-389.

Lio-Po G.D., Lavilla C.R., Cruz-Lacierda E.R. (2001). Health management in aquaculture. Aquaculture Department, Southeast Asian Fisheries Development Center.

Lirås V., Lindberg M., Nyström P., Annadotter H., Lawton L.A., Graf B. (1998). Can ingested cyanobacteria be harmful to the signal crayfish (*Pacifastacus leniusculus*). Freshwater Biology, 39(2): 233-242.

Lorenz R.T., Cysewski G.R. (2000). Commercial potential for Haematococcus microalgae as a natural source of astaxanthin. Trends in Biotechnology, 18(4): 160-167.

Lu X., Kong J., Luan S., Dai P., Meng X., Cao B., Luo K. (2016). Transcriptome analysis of the hepatopancreas in the Pacific white shrimp (*Litopenaeus vannamei*) under acute ammonia stress. PloS one, 11(10): e0164396.

Lu X., Luan S., Dai P., Meng X., Cao B., Luo K., Kong J. (2018). iTRAQ-based comparative proteome analysis for molecular mechanism of defense against acute ammonia toxicity in Pacific White shrimp *Litopenaeus vannamei*. Fish and Shellfish Immunology, 74: 52-61.

Luchiari A.C., Marques A.O., Freire F.A.M. (2012). Effects of substrate colour preference on growth of the shrimp *Litopenaeus vannamei* (Boone, 1931)(Decapoda, Penaeoidea). Crustaceana, 789-800.

Manheem K., Benjakul S., Kijroongrojana K., Visessanguan W. (2012). The effect of heating conditions on polyphenol oxidase, proteases and melanosis in pre-cooked Pacific white shrimp during refrigerated storage. Food Chemistry, 131(4): 1370-1375.

Maoka T. (2020). Carotenoids as natural functional pigments. Journal of natural medicines, 74(1), 1-16.

Márquez B., Verdier-Pinard P., Hamel E., Gerwick W.H. (1998). Curacin D, an antimitotic agent from the marine cyanobacterium Lyngbya majuscula. Phytochemistry, 49(8): 2387-2389.

Martínez-Cámara S., Ibañez A., Rubio S., Barreiro C., Barredo J.-L. (2021). Main carotenoids produced by microorganisms. Encyclopedia, 1(4): 1223-1245.

Martínez A., Romero Y., Castillo T., Mascaro M., Lopez-Rull I., Simoes N., Arcega-Cabrera F., Gaxiola G., Barbosa A. (2014). The effect of copper on the color of shrimps: redder is not always healthier. PloS one, 9(9):

e107673.

Miao F., Geng Y., Lu D., Zuo J., Li Y. (2013). Stability and changes in astaxanthin ester composition from Haematococcus pluvialis during storage. Chinese Journal of Oceanology and Limnology, 31(6): 1181-1189.

Miao F., Lu D., Li Y., Zeng M. (2006). Characterization of astaxanthin esters in Haematococcus pluvialis by liquid chromatography–atmospheric pressure chemical ionization mass spectrometry. Analytical Biochemistry, 352(2): 176-181.

Miki W., Yamaguchi K., Konosu S. (1982). Comparison of carotenoids in the ovaries of marine fish and shellfish. Comparative Biochemistry and Physiology. B, Comparative Biochemistry, 71(1): 7-11.

Muthukrishnan S., Defoirdt T., Ina-Salwany M.Y., Yusoff F.M., Shariff M., Ismail S.I., Natrah I. (2019). *Vibrio parahaemolyticus* and *Vibrio harveyi* causing acute hepatopancreatic necrosis disease (AHPND) in *Penaeus vannamei* (Boone, 1931) isolated from Malaysian shrimp ponds. Aquaculture, 511: 734227.

Naguib Y.M.A. (2000). Antioxidant activities of astaxanthin and related carotenoids. Journal of Agricultural and Food Chemistry, 48(4): 1150-1154.

Näslund J., Johnsson J.I. (2016). Environmental enrichment for fish in captive environments: effects of physical structures and substrates. Fish and Fisheries, 17(1): 1-30.

Ning M., Wei P., Shen H., Wan X., Jin M., Li X., Shi H., Qiao Y., Jiang G., Gu W. (2019). Proteomic and metabolomic responses in hepatopancreas of whiteleg shrimp *Litopenaeus vannamei* infected by microsporidian Enterocytozoon hepatopenaei. Fish and Shellfish Immunology, 87: 534-545.

Núñez-Gastélum J.A., Sánchez-Machado D.I., López-Cervantes J., Rodríguez-Núñez J.R., Correa-Murrieta M.A., Sánchez-Duarte R.G., Campas-Baypoli O.N. (2016). Astaxanthin and its esters in pigmented oil from fermented shrimp by-products. Journal of Aquatic Food Product Technology, 25(3): 334-343.

Okada S., Nur-E-Borhan S.A., Yamaguchi K. (1994). Carotenoid composition in the exoskeleton of commercial black tiger prawns. Fisheries Science, 60(2): 213-215.

Okpala C.O.R., Choo W.S., Dykes G.A. (2014). Quality and shelf life assessment of Pacific white shrimp (*Litopenaeus vannamei*) freshly harvested and stored on ice. LWT-Food Science and Technology, 55(1): 110-116.

Orjala J., Nagle D.G., Hsu V., Gerwick W.H. (1995). Antillatoxin: an exceptionally ichthyotoxic cyclic lipopeptide from the tropical cyanobacterium *Lyngbya majuscula*. Journal of the American Chemical Society, 117(31): 8281-8282.

Pan N., Dong C., Du X., Kong B., Sun J., Xia X. (2021). Effect of freeze-thaw cycles on the quality of quick-frozen pork patty with different fat content by consumer assessment and instrument-based detection. Meat Science, 172: 108313.

Parisenti J., Beirão L.H., Tramonte V.L.C.G., Ourique F., da Silveira Brito C.C., Moreira C.C. (2011). Preference ranking of colour in raw and cooked shrimps. International Journal of Food Science and Technology, 46(12): 2558-2561.

Pasquevich M.Y., Dreon M.S., Rivera J.N.G., Boucard C.V., Heras H. (2013). Effect of crude oil petroleum hydrocarbons on protein expression of the prawn *Macrobrachium borellii*. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology, 157(4): 390-396.

Pauly D., Zeller D. (2019). Agreeing with FAO: Comments on SOFIA 2018. Marine Policy, 100: 332-333.

Phuthaworn C., Nguyen N.H., Quinn J., Knibb W. (2016). Moderate heritability of hepatopancreatic parvovirus titre suggests a new option for selection against viral diseases in banana shrimp (*Fenneropenaeus merguiensis*) and other aquaculture species. Genetics Selection Evolution, 48: 1-10.

Phuvasate S., Su Y.-C. (2010). Effects of electrolyzed oxidizing water and ice treatments on reducing histamine-producing bacteria on fish skin and food contact surface. Food Control, 21(3): 286-291.

Pinto M.R., Lucena M.N., Faleiros R.O., Almeida E.A., McNamara J.C., Leone F.A. (2016). Effects of ammonia stress in the Amazon river shrimp *Macrobrachium amazonicum* (Decapoda, Palaemonidae). Aquatic Toxicology, 170: 13-23.

Ponce-Palafox J., Martinez-Palacios C.A., Ross L.G. (1997). The effects of salinity and temperature on the growth and survival rates of juvenile white shrimp, *Penaeus vannamei*, Boone, 1931. Aquaculture, 157(1-2): 107-115.

Qiu L., Shi X., Yu S., Han Q., Diao X., Zhou H. (2018). Changes of ammonia-metabolizing enzyme activity and gene expression of two strains in shrimp *Litopenaeus vannamei* under ammonia stress. Frontiers in Physiology, 9: 211.

Rao T.A. (1980). Food and feeding habits of *Pennahia macrophthalmus* Bleeker at Visakhapatnam. Indian Journal of Fisheries, 27(1&2): 61-65.

Ren Y., Li J., Guo L., Liu J.N., Wan H., Meng Q., Wang H., Wang Z., Lv L., Dong X. (2020). Full-length transcriptome and long non-coding RNA profiling of whiteleg shrimp *Penaeus vannamei* hemocytes in response to Spiroplasma eriocheiris infection. Fish and Shellfish Immunology, 106: 876-886.

Restrepo L., Bayot B., Arciniegas S., Bajaña L., Betancourt I., Panchana F., Reyes Munoz A. (2018). PirVP genes causing AHPND identified in a new Vibrio species (*Vibrio punensis*) within the commensal Orientalis clade. Scientific Reports, 8(1): 1-14.

Romano N., Zeng C. (2010). Survival, osmoregulation and ammonia-N excretion of blue swimmer crab, *Portunus pelagicus*, juveniles exposed to different ammonia-N and salinity combinations. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology, 151(2): 222-228.

Sachindra N.M., Bhaskar N., Mahendrakar N.S. (2005). Carotenoids in different body components of Indian shrimps. Journal of the Science of Food and Agriculture, 85(1): 167-172.

Salma U., Uddowla M.H., Kim M., Kim J.M., Kim B.K., Baek H.-J., Park H., Mykles D.L., Kim H.-W. (2012). Five hepatopancreatic and one epidermal chitinases from a pandalid shrimp (*Pandalopsis japonica*): cloning and effects of eyestalk ablation on gene expression. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 161(3): 197-207.

Saoud I.P., Davis D.A., Rouse D.B. (2003). Suitability studies of inland well waters for *Litopenaeus vannamei* culture. Aquaculture, 217(1-4): 373-383.

Sathapondecha P., Panyim S., Udomkit A. (2014). Molecular characterization of a cDNA encoding red pigment-concentrating hormone in black tiger shrimp *Penaeus monodon*: Implication of its function in molt and osmoregulation. Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology, 175: 124-130.

Schilling N. (2013). Sociolinguistic fieldwork. Cambridge University Press. 313 p.

Senphan T., Benjakul S. (2012). Compositions and yield of lipids extracted from hepatopancreas of Pacific white shrimp (*Litopenaeus vannamei*) as affected by prior autolysis. Food chemistry, 134(2): 829-835.

Sikorski Z.E. (1990). Seafood: resources, nutritional composition, and preservation (Vol. 1). CRC Press, Boca Raton, FL.

Silvestre F., Tu H.T., Bernard A., Dorts J., Dieu M., Raes M., Phuong N.T., Kestemont P. (2010). A differential proteomic approach to assess the effects of chemotherapeutics and production management strategy on giant tiger shrimp *Penaeus monodon*. Comparative Biochemistry and Physiology Part D: Genomics and Proteomics, 5(3): 227-233.

Spriggs K.A., Bushell M., Willis A.E. (2010). Translational regulation of gene expression during conditions of cell stress. Molecular Cell, 40(2): 228-237.

Stoner A.W. (2012). Assessing stress and predicting mortality in economically significant crustaceans. Reviews in Fisheries Science, 20(3): 111-135.

Takeungwongtrakul S., Benjakul S., Aran H. (2012). Lipids from cephalothorax and hepatopancreas of Pacific white shrimp (*Litopenaeus vannamei*): Compositions and deterioration as affected by iced storage. Food Chemistry, 134(4): 2066-2074.

Triyannanto E., Lee K.T. (2015). Effect of pre-cooking conditions on the quality characteristics of ready-to-eat Samgyetang. Korean Journal for Food Science of Animal Resources, 35(4): 494.

Tseng Y.-C., Hwang P.-P. (2008). Some insights into energy metabolism for osmoregulation in fish. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology, 148(4): 419-429.

Tume R.K., Sikes A.L., Tabrett S., Smith D.M. (2009). Effect of background colour on the distribution of astaxanthin in black tiger prawn (*Penaeus monodon*): Effective method for improvement of cooked colour. Aquaculture, 296(1-2): 129-135.

Valin A., Castillo R., Negre-Sadargues G., Lenel R. (1987). Quantitative aspects of carotenoid pigment circadian variations in the crayfish *Astacus leptodactylus*. Biochemical Systematics and Ecology, 15(5): 607-610.

Wade N.M., Anderson M., Sellars M.J., Tume R.K., Preston N.P., Glencross B.D. (2012). Mechanisms of colour adaptation in the prawn *Penaeus monodon*. Journal of Experimental Biology, 215(2): 343-350.

Wade N.M., Cheers S., Bourne N., Irvin S., Blyth D., Glencross B.D. (2017). Dietary astaxanthin levels affect colour, growth, carotenoid digestibility and the accumulation of specific carotenoid esters in the Giant Tiger Shrimp, *Penaeus monodon*. Aquaculture Research, 48(2): 395-406.

Wade N.M., Gabaudan J., Glencross B.D. (2017). A review of carotenoid utilisation and function in crustacean aquaculture. Reviews in Aquaculture, 9(2): 141-156.

Wade N.M., Paulo C., Goodall J., Fischer M., Poole S., Glencross B.D. (2014). Quantitative methods to measure pigmentation variation in farmed Giant Tiger Prawns, *Penaeus monodon*, and the effects of different harvest methods on cooked colour. Aquaculture, 433: 513-519.

Wang J.J., Lin T., Li J.B., Liao C., Pan Y.J., Zhao Y. (2014). Effect of acidic electrolyzed water ice on quality of shrimp in dark condition. Food Control, 35(1): 207-212.

Wang M., Wang J.J., Sun X.H., Pan Y.J., Zhao Y. (2015). Preliminary mechanism of acidic electrolyzed water ice on improving the quality and safety of shrimp. Food Chemistry, 176: 333-341.

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.

Wang Y., Wang B., Liu M., Jiang K., Wang M., Wang L. (2020). Comparative transcriptome analysis reveals the potential influencing mechanism of dietary astaxanthin on growth and metabolism in *Litopenaeus vannamei*. Aquaculture Reports, 16: 100259.

Wilder M.N., Jasmani S., Jayasankar V., Kaneko T., Aida K., Hatta T., Nemoto S., Wigginton A. (2009). Hemolymph osmolality, ion concentrations and calcium in the structural organization of the cuticle of the giant freshwater prawn *Macrobrachium rosenbergii*: changes with the molt cycle. Aquaculture, 292(1-2): 104-110.

Williamson R.T., Singh I.P., Gerwick W.H. (2004). Taveuniamides: new chlorinated toxins from a mixed assemblage of marine cyanobacteria. Tetrahedron, 60(33): 7025-7033.

Wouters R., Molina C., Lavens P., Calderón J. (2001). Lipid composition and vitamin content of wild female *Litopenaeus vannamei* in different stages of sexual maturation. Aquaculture, 198(3-4): 307-323.

Xiao J., Li Q.-Y., Tu J.-P., Chen X.-L., Chen X.-H., Liu Q.-Y., Liu H., Zhou X.-Y., Zhao Y.-Z., Wang H.-L. (2019). Stress response and tolerance mechanisms of ammonia exposure based on transcriptomics and metabolomics in *Litopenaeus vannamei*. Ecotoxicology and Environmental Safety, 180: 491-500.

Xu C., Li E., Liu Y., Wang S., Wang X., Chen K., Qin J.G., Chen L. (2018). Effect of dietary lipid level on growth, lipid metabolism and health status of the Pacific white shrimp *Litopenaeus vannamei* at two salinities. Aquaculture Nutrition, 24(1): 204-214.

Yokoyama A., Park H.D. (2003). Depuration kinetics and persistence of the cyanobacterial toxin microcystin-LR in the freshwater bivalve *Unio douglasiae*. Environmental Toxicology: An International Journal, 18(1): 61-67.

Zagalsky P.F. (1985). Invertebrate carotenoproteins. Methods in Enzymology, 111: 216-247.

Zhang B., Deng S.G., Wang Q. (2015). Chemical changes related to loss of quality in Pacific White Shrimp (*Litopenaeus vannamei*) during Chilled Storage under Slurry Ice Conditions. Journal of Food Processing and Preservation, 39(6): 2507-2515.

Zhang B., Ma L.-k., Deng S.-g., Xie C., Qiu X.-h. (2015). Shelf-life of Pacific white shrimp (*Litopenaeus vannamei*) as affected by weakly acidic electrolyzed water ice-glazing and modified atmosphere packaging. Food Control, 51: 114-121.

Zhou K., Zhou F., Huang J., Yang Q., Jiang S., Qiu L., Yang L., Zhu C., Jiang S. (2017). Characterization and expression analysis of a chitinase gene (PmChi-4) from black tiger shrimp (*Penaeus monodon*) under pathogen infection and ambient ammonia nitrogen stress. Fish and Shellfish Immunology, 62: 31-40.

Zhu L., Wang Z., Shu Q., Takala J., Hiltunen E., Feng P., Yuan Z. (2013). Nutrient removal and biodiesel production by integration of freshwater algae cultivation with piggery wastewater treatment. Water Research, 47(13): 4294-4302.

Zou E., Bonvillain R. (2004). Chitinase activity in the epidermis of the fiddler crab, *Uca pugilator*, as an in vivo screen for molt-interfering xenobiotics. Comparative Biochemistry and Physiology Part C: Toxicology and Pharmacology, 139(4): 225-230.