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Research Article

Role of antioxidants in the pigmentation of ornamental fishes

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Abstract

Beyond aesthetics, the varied pigmentation in fish serves as evidence of manifold functions and has ecological importance. Fish pigmentation is an adaptive feature and critical to their survival. Despite their evolved pigmentation for survival and adaptation, fish are not immune to biochemical challenges presented by their surroundings. Harmful free radicals generated by various factors can lead to oxidative stress, impacting cellular components like pigments. Oxidative stress arises from an imbalance between the production of reactive oxygen species and cellular antioxidant defense mechanisms. Nevertheless, antioxidants play a role as crucial protectors, coordinating the defense of cells against oxidative damages. This review aims to elucidate the relationship between antioxidants and fish pigmentation by examining the sources of antioxidants in fish diets and their specific effects on pigmentation. The use of antioxidant compounds offers a promising avenue to mitigate pigmentation loss, enhance carotenoids production, and improve overall fish coloration, contributing to both aesthetic and physiological aspects in the aquaculture industry.

Introduction

More than just a spectacle of aesthetics, the varied pigmentation seen in fish stands as evidence of the manifold functions and ecological importance associated with their vibrant hues. In aquatic environments, where camouflage is a critical strategy for survival, fish pigmentation is an adaptive feature (Reebs, 2008; Maan and Sefc, 2013; Alonso, 2016). Fish pigmentation is affected by several factors including nutrition, genetic, physiological, and environmental factors (Luo *et al.*, 2021; Siahkalroodi *et al.*, 2023). The ability to blend seamlessly with the surrounding environment through coloration enables fish to evade predators and ambush prey (Heathcote *et al.*, 2020; Encel and Ward, 2021). Furthermore, the vibrant colors exhibited by fish contribute to complex communication mechanisms within and between species (Price *et al.*, 2008). Intricate patterns and chromatic displays serve as visual signals for courtship, aggression, and territorial demarcation.

In addition, fish pigmentation is an important factor for physiological adaptation (Vissio *et al.*, 2021). There are different pigments found in fish, such as melanins that are responsible for dark colors, and carotenoids that contribute to reds, oranges, and yellows (Kaur and Shah, 2017; Andriani *et al.*, 2021). These pigments serve as a protective shield against the harmful effects of ultraviolet (UV) radiation, which is a common prevalent factor in aquatic environments (Häder *et al.*, 2014). By absorbing and dissipating UV radiation, pigments help prevent cellular damage and maintain the overall health of fish. Fish are exposed to factors generating harmful free radicals, leading to oxidative stress. This can impact cellular components, compromising their stability and functionality, including pigments (Cahn, *et al.*, 2015). Thus, while fish have evolved remarkable pigmentation for survival and adaptation, they are not immune to the biochemical challenges presented by their surroundings. Oxidative stress occurs when there is an imbalance between the production of reactive oxygen species and the cellular antioxidant defense mechanisms. Antioxidants play a crucial role in this balance by protecting cells against oxidative damage.

The purpose of this review is to clarify complex link between antioxidants and fish pigmentation. This review aims to examine the sources of antioxidants in the fish's diet and evaluate the particular impacts of these substances on pigmentation.

Fish pigments

The vibrant color of fish scales originates from the presence of pigments. These pigments rang from the profound blacks and browns attributed to melanins to the vivid reds, oranges, and yellows contributed by carotenoids. Each pigment plays a significant role in creating distinct and captivating color patterns that define various fish species. Beyond serving as a visual spectacle, the diverse colors of fish offer valuable insights into their adaptations and ecological dynamics.

Types of pigments

Fish species have distinct color patterns which are defined by different pigments. Melanin, divided into eumelanin and pheomelanin, primarily contributes to dark and earthy tones, enhancing camouflage in deeper waters or protection from sunlight (Solano, 2014). However, fish melanophores do not generate pheomelanin, but only eumelanin (Cal *et al.,* 2017). Carotenoids, acquired through dietary intake, produce red, orange, and yellow hues, serving as pigments and essential nutrients for aquatic organisms' health (de Carvalho and Caramujo, 2017; Galasso *et al*., 2017; Maoka, 2020; Andriani *et al.,* 2021; Joy *et al*., 2021; Lim *et al.,* 2023). Synthetic carotenoids have negative effects on the environment, so there has been increased demand for natural carotenoids in aqua feed. This article has discussed some naturally available carotenoid-rich ingredients, such as microalgal pigments, yeast extract, marigold, and capsicum (Nakano and Wiegertjes, 2020). Chromatophores, including xanthophores, erythrophores, and iridophores, contribute to yellow, red, and reflective qualities, respectively (Fujii, 1993; Ligon and Mccartney, 2016; Huang *et al.,* 2021). Guanine crystals provide a metallic sheen, while bilins contribute to blue and green colors, which are often associated with the breakdown of hemoglobin (Levy-Lior *et al.,* 2008). Fluorescent proteins, notably in coral reef fish, emit light (Stepanenko *et al.,* 2008). Pteridines are responsible for the bright red and orange colors seen in fish. These colors are acquired through their diet or synthesized internally, demonstrating the adaptability of fish to different environments and diets (Andrade and Carneiro, 2021; Stuart-Fox *et al.,* 2021).

The role of pigments

Protection

Pigments in fish serve a crucial role beyond just being ornamental features. They act as important elements of protection (Price *et al.,* 2008). For instance, guanine crystals, not only contribute to the visual attractiveness of fish but also play a functional role in their underwater habitats (Miyashita and Iwaasaka, 2014). The reflective nature of guanine crystals helps fish to blend in seamlessly with their surroundings, serving as a valuable tool for camouflage. This adaptive advantage is a strategic asset in their natural habitats, enhancing their ability to remain undetected by predators or potential prey.

Communication and attracting mate

Besides their role in protection, pigments in fish serve vital functions in communication and mate attraction (Maan *et al.,* 2006; Price *et al.,* 2008; Johnson and Fuller, 2014). Studies have shown that changes in pigment patterns in zebrafish and pearl danio are linked to cellular communication mechanisms involving pigments. In zebrafish, the stripes on pigments require specific cellular projections to promote Delta-Notch signaling, which involves interactions between xanthophore and melanophore cells. Conversely, pearl danio with uniform pigment patterns does not exhibit such cellular projections, leading to changes in xanthophore differentiation that are likely to influence the signaling available to melanophores (Eom *et al.,* 2015). Fish use pigments as visual signals to attract mates, especially during the transition from juvenile to adult stages. As fish reach reproductive maturity, they undergo a remarkable color change, displaying vibrant hues to indicate their readiness for mating (Sargent *et al.*, 1998; Amundsen and Forsgren, 2001; Sköld *et al.*, 2016; Camargo-dos-Santos *et al.*, 2021).

Reduction of pigment in fish

Fish pigmentation can decline due to various factors such as internal and external influences. Inadequate or imbalanced nutrition, particularly deficiencies in essential pigmentation-related nutrients like carotenoids, can lead to faded or less vibrant colors (Gupta *et al.*, 2007; Ranjan, 2016). Stressful conditions, such as poor water quality, overcrowding, or changes in environmental parameters, can disrupt the hormonal balance and biochemical processes that are involved in pigmentation. This disturbance can result in a decrease in color intensity. Additionally, diseases and infections may directly affect pigment-producing cells or interfere with pigment synthesis and distribution (Raman and Marappan, 2013). Genetic factors may also contribute to variations in pigmentation, including seasonal changes or alterations during specific life stages (Felice *et al.*, 2008). Exposure to an environment with inadequate lighting conditions can also lead to a loss of pigmentation in fish (Filho *et al.*, 2001; Sugimoto, 2002). A decrease in pigmentation can harm fish by increasing oxidative stress (Chowdhury and Saikia, 2020). Diminished pigmentation compromises the fish's ability to effectively camouflage itself, increasing its vulnerability to predation. Social communication, especially during courtship and mating behaviors, relies on vibrant colors. Therefore, a decrease in pigmentation may impede these crucial interactions and ultimately affect the fish ability to reproduce successfully. Additionally, weak pigmentation can be a sign of oxidative stress or poor health, leading to a weakened immune response and increased vulnerability to diseases (Stien *et al.*, 2005; Kittilsen *et al.*, 2009). The attractiveness of fish is often linked to their vibrant colors, and a loss of pigmentation may affect their appeal as potential mates and impact their reproductive fitness. Reduced pigmentation may lead to changes in behavior, such as altered feeding patterns or reduced activity levels, which may indicate potential distress that can be exacerbated by oxidative stress. In commercial aquaculture, the value of fish is often linked to their colorful pigmentation, making any decrease in their pigmentation a significant economic concern. In aquariums, where the visual appeal of fish is paramount, a loss of pigmentation may be aesthetically undesirable. Therefore, it is crucial to address oxidative stress and other factors that contribute to maintain the health and vibrancy of fish.

Antioxidant role in fish diet

The role of antioxidants is important for maintaining the health and well-being of fish. Antioxidants play a crucial role in neutralizing reactive oxygen species, which are natural byproducts of metabolic processes. If not neutralized, they can lead to cellular damage and contribute to various health issues. In the aquatic environment, fish are constantly exposed to various factors such as pollution, fluctuating water conditions, and pathogenic challenges, which can elevate oxidative stress (Filho *et al.,* 2001). Therefore, antioxidants are essential in maintaining the health of fish.

Source of antioxidant

To combat this oxidative stress and maintain the health of fish, it is crucial to provide them with a source of antioxidants in their diet. Antioxidants play a vital role in protecting fish cells and tissues from damage caused by free radicals (Sukhovskaya *et al.,* 2023). Adding antioxidant-rich ingredients such as vitamins, plant extract, and natural antioxidants in their diet can help bolster their antioxidant status and enhance their immune response (Asimi and Sahu, 2013; Armenta López *et al.,* 2015; Rahimnejad *et al.,* 2021; Ponomarev *et al.,* 2022). Selenium nanoparticles (SeNPs) are an important source of antioxidants for fish, playing a pivotal role in improving the antioxidant status of aquatic organisms. Any potent substances are capable of countering oxidative stress. Antioxidants work by neutralizing harmful free radicals. SeNPs serve a dual purpose as both food additives and therapeutic agents, actively contributing to the regulation of antioxidant enzymes in fish (Çiçek and Özoğul, 2021).

A study conducted by Wangkahart *et al.* (2022) has revealed notable impacts of selenium supplementation on antioxidant enzyme activities and growth performance in juvenile Nile tilapia. The two forms of selenium, SeMet (L-selenomethionine) and Na_2SeO_3 were found to enhance the activities of key antioxidant enzymes such as lysozyme, catalase, myeloperoxidase, superoxide dismutase, and glutathione peroxidase. Moreover, the inclusion of SeMet at a concentration of 1 mg Se/kg in the diet resulted in a substantial improvement in growth performance compared to the basal diet. Intriguingly, while SeMet had a positive effect on growth, Na_2SeO_3 supplementation did not exhibit a significant impact on growth parameters (Wangkahart *et al.,* 2022). A study also found that the dietary inclusion of curcumin boosted the antioxidant parameters in Nile tilapia (Amer *et al.,* 2022).

In a study conducted by Lizárraga-Velázquez *et al.* (2019) the impact of dietary phenolic compounds (PCs), specifically derived from mango peel extract (MPE), on the activities of antioxidant enzyme in the liver of zebrafish was investigated. The results revealed that there was a notable increase in catalase activity which was dose-dependent in response to MPE PCs. This indicates that there is a possibility of an increase in hydrogen peroxide concentrations, particularly within peroxisomes. This finding suggests a regulatory role of MPE PCs in the antioxidant defense system, specifically by enhancing catalase activity. Interestingly, despite this observed effect on catalase, no significant alterations were observed in the activities of superoxide dismutase and glutathione peroxidase. This lack of effect on superoxide dismutase and glutathione peroxidase activities may be attributed to the non-occurrence of oxidative stress conditions during the study. This highlights the nuanced and context-dependent nature of the interactions between dietary PCs and the endogenous antioxidant defense mechanisms in zebrafish liver.

Extracts derived from the Bryophyllum plant are rich in bioactive compounds with substantial antioxidant activity. The total phenolic content in these extracts, quantified between 3.4 to 5.9 mM and expressed in gallic acid equivalents (GAE), underscores their rich phenolic composition. The abundance of phenolic compounds found in Bryophyllum plant extracts is directly related to their antioxidant activity. This can be evidenced in their ability to safeguard fish oil-in-water emulsions from lipid peroxidation. It’s worth noting that the level of antioxidant efficiency is directly proportional to the concentration of phenolic compounds, with a linear correlation up to 500 µM GAE (García-Pérez *et al.*, 2020).

The addition of Echinacea roots to the fish feed resulted in a notable augmentation in both phenolic compounds and antioxidant activity. Specifically, the fish feed enriched with 60 g/kg of Echinacea roots exhibited a remarkable increase in antioxidant activity (Oniszczuk *et al.*, 2019).

A recent study discovered that a dietary supplement comprising multi-probiotic compounds, namely *Bacillus velezensis* V4 and *Rhodotorula mucilaginosa*, had numerous benefits for juvenile Atlantic salmon. The study revealed a spectrum of positive effects, encompassing improvements in growth, immune responses, antioxidant capability, and disease resistance. Notably, the probiotic compound played a pivotal role in enhancing the overall growth performance of the salmon population. Moreover, its impact on disease resistance was particularly noteworthy, as the supplement contributed to a heightened ability to combat challenges, showcasing the potential for immunomodulation (Wang *et al.*, 2019).

Nile tilapia which was subjected to a diet enriched with 10 g/kg of *Silybum marianum*, demonstrated notable improvements in their physiological condition. It exhibited the highest activity of total antioxidant enzyme, particularly in superoxide dismutase and catalase, indicating stronger antioxidant defenses. Additionally, a significant upsurge in the accumulation of transcripts growth hormone was identified (Hassaan *et al.*, 2019). In the convict cichlid species (*Amatitlania nigrofasciata*), administering a polyphenol mixture (PMIX) composed of chestnut wood and olive mill wastewater at a dose of 2 g/kg resulted in a substantial increase in serum radical scavenging activity and peroxidase activity. This treatment demonstrated notable antioxidant responses when compared to other treatments. The group that received this treatment also exhibited significantly higher serum catalase activity which suggests that it can potentially enhance antioxidant mechanisms. Furthermore, even at a lower concentration, the 1 g/kg PMIX treatment displayed significantly higher serum catalase activity in comparison to the control group. These findings highlight the positive impact of PMIX supplementation, particularly at higher concentrations, on the convict cichlid's antioxidant defenses (Hoseinifar *et al.*, 2020).

The inclusion of *Hypnea flagelliformis* and *Sargassum boveanum* in rainbow trout diets, specifically GP5 with 5% *G. persica* and HF10 with 10% *H. flagelliformis*, demonstrated significant benefits for the fish. These diets effectively enhanced serum immune indices, contributing to improved fish health. Notably, extended feeding on GP5 and HF10 resulted in elevated levels of superoxide dismutase and peroxidase, indicating a bolstered antioxidant status in the head kidney. These findings underscore the positive impact of adding specific types of seaweeds to the diet of rainbow trout (Vazirzadeh *et al.*, 2020). Furthermore, orally administered *Phaffia rhodozyma* at a concentration of 47 g/kg in the rainbow trout diet demonstrates notable advantages, including better overall performance, heightened antioxidant activities, and enhanced pigmentation of the fillet as compared to a control diet supplemented with synthetic astaxanthin (Kheirabadi *et al.*, 2022).

The effects of adding *Moringa oleifera* leaves to the diet of gilthead seabream were investigated to determine its impact on the antioxidant activity of gilthead seabream. The study by Jiménez-Monreal *et al.* (2021) revealed that gilthead seabream specimens fed diets enriched with higher percentages of Moringa exhibited a notable increase in antioxidant activity. This observed enhancement in antioxidant potential is ascribed to the rich presence of polyphenolic compounds in Moringa leaves. These findings underscore the potential of Moringa as a valuable dietary supplement in aquaculture, suggesting its ability to improve the antioxidant status of gilthead seabream. Polyphenols are renowned for their free radical-scavenging properties (Jiménez-Monreal *et al.*, 2021). Extracts from red seaweed (*Gracilaria gracilis*) may have the potential to enhance the immune response and reduce stress in fish. The bioactive compounds in the extract showed antioxidant and antibacterial properties, indicating the seaweed's potential as a beneficial additive in fish diets for promoting overall health in fish (Afonso *et al.*, 2021).

Dietary supplementation with β-carotene and phycocyanin extracted from *Spirulina* (*Arthrospira platensis*) is a promising strategy to augment antioxidant enzyme activities and shield Nile tilapia, mullet, and rainbow trout from oxidative stress. This is possible through several mechanisms, including the ability of natural antioxidants to efficiently scavenge free radicals within the internal antioxidant system. Another possible mechanism was the supplementation regimen demonstrates an inhibitory effect on lipid peroxidation, which is a crucial process implicated in cellular damage. These compounds may also contribute to the cleansing of reactive oxygen species, acting as a countermeasure against oxidative stress (Rosas *et al.*, 2019; Sheikhzadeh *et al.*, 2019; Teimouri *et al.*, 2019; Hassaan *et al.*, 2021).

The dietary supplementation of fish with dihydroquercetin (a) and arabinogalactan (b) has been demonstrated to have a positive impact on fish health. This supplementation not only enhances antioxidant defenses but also affects the lipid and fatty acid profiles of the fish. The supplemented diet results in higher rates of molecular antioxidants, including reduced glutathione and alpha-tocopherol, indicating a bolstered antioxidant status in the fish. Moreover, the enzyme activities associated with antioxidant defense mechanisms, such as peroxidase, catalase, and glutathione-S-transferase, exhibit increased rates in the group that is receiving the supplemented diet (Sukhovskaya *et al.*, 2023).

A study on channel catfish (*Ictalurus punctatus*) found that supplementing their diet with chlorogenic acid (c) demonstrated a significant alleviation of hepatic oxidative stress. Notably, chlorogenic acid exhibited a pronounced ability to mitigate the adverse effects of oxidative stress induced by oxidized fish oil (Zhang *et al.*, 2023) (Fig. 1).

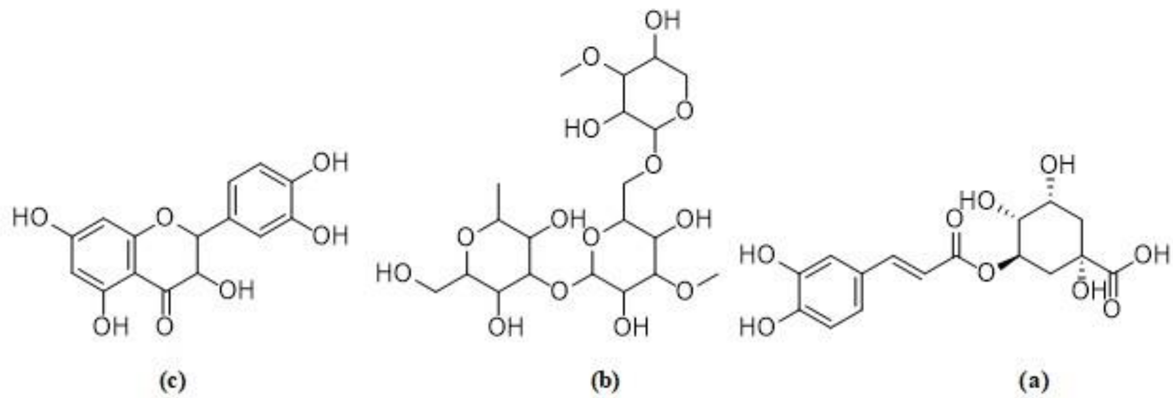

Figure 1: Structure of dihydroquercetin (a), arabinogalactan (b), chlorogenic acid (c).

Antioxidant role in pigmentation of fish

Fish pigmentation loss poses a significant challenge in aquaculture, impacting the visual appeal and market value of fish (Mansour *et al.*, 2020). The coloration of fish can change due to physiological and morphological factors, such as changes in pigment organelle aggregation, dispersion within skin chromatophores, and apoptosis of skin chromatophores. These changes are influenced by variations in underwater light and darkness conditions, which are crucial for adaptive responses in the number of melanophores (Fujii, 2000; Sugimoto *et al.*, 2005; van der Salm *et al.*, 2005; Camargo-dos-Santos *et al.*, 2021). In order to prevent pigmentation loss in fish, scientists have explored the use of antioxidant compounds. These compounds have the ability to protect against oxidative stress and damage, which are known to contribute to pigmentation loss. By reducing the toxic effects of reactive oxygen species, antioxidants can prevent the degradation of carotenoids, which are responsible for enhancing the color of fish (Wagde *et al.*, 2018). Incorporating antioxidant compounds into fish diets holds the potential to mitigate their pigmentation loss, ensuring ornamental fish maintain their vibrant colors (Sathyaruban *et al.*, 2021).

According to the research by Liu *et al.* (2019) incorporating *Arthrospira platensis* (Spirulina) in the diet of juvenile yellow catfish yielded noteworthy antioxidative benefits. The groups that were given *A. platensis* exhibited notable enhancements in glutathione concentrations and glutathione peroxidase activities, particularly in the plasma and liver of the fish. Significantly, these antioxidative effects displayed a dose-dependent relationship, emphasizing the positive correlation between the amount of *A. platensis* supplementation and the observed antioxidant response. Moreover, the introduction of *A. platensis* to the diet resulted in a distinct increase in skin yellowness among the yellow catfish. This dual impact on antioxidant parameters and skin pigmentation highlights the potential of *A. platensis* as a valuable dietary supplement, showcasing its ability to promote physiological parameters and the appearance of juvenile yellow catfish.

Utilizing controlled stress-induced algae as a valuable antioxidant source in aquaculture exhibited noteworthy effects on fish, influencing not only their skin pigmentation but also enhancing antioxidant properties and fostering overall growth (Mukherjee *et al.*, 2020). Butylated hydroxytoluene (a), ethoxyquin (b) in the Figure 2, and different extracts of *Ginkgo biloba* leaves (EGbs) exhibited a dual impact on carp erythrocytes treated with hydroxyl radicals. They reduce the generation of reactive oxygen species (ROS) and impede the oxidation of cellular components. Additionally, these compounds demonstrated a capacity to restore the activities of enzymatic antioxidants in carp erythrocytes treated with hydroxyl radicals. The observed antioxidative and anti-apoptotic effects of EGbs have been positively associated with their flavonoid content. This correlation suggests that the presence of flavonoids in EGbs may contribute significantly to their ability to inhibit lipid oxidation and apoptosis (Li *et al.*, 2016).

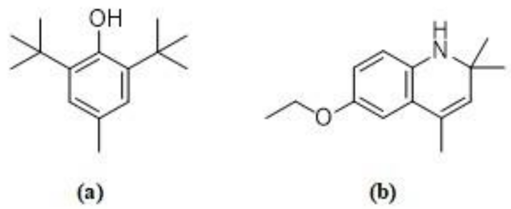

Figure 2: Structure of butylated hydroxytoluene (a) and ethoxyquin (b).

Antioxidants can enhance the production and uptake of carotenoids in fish, leading to increased their pigmentation and improve their coloration (Gupta *et al.*, 2007; Parolini *et al.*, 2018; Sánchez *et al.*, 2020; Castro-Castellón *et al.*, 2023). However, carotenoids may produce reactive species, including free radicals, through one-electron oxidations or reductions, under specific conditions. These reactive species can act as prooxidants, promoting oxidative stress within cells and potentially contributing to oxidative damage. These compounds play a crucial role in maintaining the stability and functionality of carotenoids, which are responsible for the vibrant colors in fish (Castro-Castellón *et al.*, 2023).

Fish diets that are enriched with microalgae have been found to be very effective in intensifying yellow pigmentation and imparting a vibrant hue to the skin of fish. Conversely, poultry by-product meal was found to be associated with the least yellow pigmentation. It is noteworthy to note that the observed yellow color is linked to carotenoids, which are compounds known for their antioxidant properties. It has been found that diets high in yellow pigmentation not only enhance the color of fish but also provide antioxidant effects to the fish. This dual benefit highlights the intricate relationship between dietary components, pigmentation, and potential health benefits of gilthead seabream (Pulcini *et al.,* 2020). Furthermore, a study on microalgae in Atlantic salmon also showed it increased their growth, immunity, and pigment deposition (Mueller *et al.,* 2023).

Haematococcus pluvialis, a green microalgae recognized for its ability to synthesize astaxanthin under stress conditions, has been demonstrated to be effective in pigmenting various species, including red sea bream and ornamental fish. Beyond its pigmentation attributes, *H. pluvialis* plays a pivotal role in enhancing the antioxidant activity of extruded fish feed. Studies have revealed a substantial increase in the inhibition of the DPPH radical, ranging from 49% to 57%, in feeds containing *H. pluvialis*. This is significantly higher than the antioxidant efficacy observed in control feeds without microalgae which was between 25-27%. Notably, the antioxidant activity of feeds enriched with *H. pluvialis* far exceeds that of commercial trout feed (Martinez-Delgado *et al.,* 2020).

In study Liu *et al.* (2022) demonstrated that incorporating *A. platensis* into the diet of yellow catfish enhanced their antioxidant defenses, including increased activities of superoxide dismutase and glutathione peroxidase, along with higher levels of glutathione in the plasma. This indicates that *A. plantesis* supplementation has the potential to protect the fish against oxidative stress induced by air exposure. Additionally, *A. platensis* supplementation in the catfish diet led to higher levels of lutein in the skin which improved skin redness, yellowness, and chroma. This suggests that *A. plantesis* supplementation has a positive impact on fish pigmentation and the potential to alleviate body color abnormalities caused by oxidative stress from air exposure (Liu *et al.,* 2022).

Astaxanthin supplementation exerted a pronounced influence on the pigmentation of juvenile giant grouper (*Epinephelus lanceolatus*), enhancing key color parameters such as redness, yellowness, chroma, and hue values in their fins. It was observed that regardless of the dosage, fish receiving astaxanthin-enriched diets exhibited a remarkable intensification of yellow coloring. Those fed at 75 and 150 mg/kg demonstrate three times higher values compared to counterparts on non-supplemented diets. Moreover, this dietary intervention significantly elevated the total antioxidant capacity in the liver tissues of giant grouper, indicating a bolstered antioxidant defense mechanism (Fernando *et al.,* 2022).

Research also indicates that some antioxidant compounds are able to stimulate the expression of genes related to carotenoid metabolisms in fish, such as CSF1R, BCDO2, SR-B1, MLN64, STAR5, GSTA2, and PLIN2, resulting in higher carotenoid production and improved pigmentation (Tripathy *et al.,* 2019; Du *et al.,* 2021; Teixeira *et al.,* 2022; Awad *et al.,* 2023). Carotenoids are stored in special skin cells called xanthophores. They are primarily controlled by the CSF1R gene, which facilitates their movement for pattern formation. Increased activity of csf1r is associated with longer feeding periods and higher carotenoid levels in diets, underscoring its role in xanthophore migration. Once broken down, carotenoids are deposited in muscles and intestine. The BCDO2 gene encodes an enzyme that helps break down carotenoids and increasing the activity of this gene in the skin is linked to better absorption of carotenoids. Moreover, the MLN64 and STAR5 genes contribute to the binding and deposition of lutein in the skin. Their increased activity is linked to extended feeding periods and higher concentrations of carotenoids. Since carotenoids are hydrophobic compounds, they travel through lipoproteins, particularly high-density lipoproteins. The STAR5 gene plays a vital role in lipid and lipoprotein transport. A study by Teixeira *et al.* (2022) showed that dietary curcumin on gilthead seabream (*Sparus aurata*) increased mRNA levels of CSF1R, TNFα, and HEP genes (Teixeira *et al.,* 2022). It also revealed that xanthophyll can act as antioxidant compounds (Lim *et al.,* 1992) and upregulated BCDO2 gene (Gao *et al.*, 2016).

Conclusions

The loss of pigmentation in fish presents a significant challenge in aquaculture that impacts the visual appeal and market value. To address pigmentation loss, the use of antioxidant compounds has been explored due to their ability to protect against oxidative stress and damage, which are the factors that contribute to pigmentation loss in fish. Incorporating antioxidant compounds in fish diets not only mitigates pigmentation loss but also enhances the production and uptake of carotenoids, leading to increase pigmentation and improve the coloration of ornamental fishes. Furthermore, studies have indicated that antioxidant compounds stimulate the expression of genes related to carotenoid metabolism in fish, resulting in higher carotenoid production and improved pigmentation.

Conflicts of interest

The authors declare no conflict of interest.

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