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Astaxanthin: A Powerful Antioxidant Used in Aquaculture for Coloration with Aquatic Animal Health Implications

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ABSTRACT

Astaxanthin is a xanthophyll with unique properties that make it a potent antioxidant and photoreceptor. It is synthesized in lower trophic level organisms, such as microalgae, yeast, and some other microbes. It is also synthetically manufactured. The use of astaxanthin for pigmentation in aquaculture is well documented, as are the numerous benefits for humans from the consumption of astaxanthin. However, little research has been conducted on its potential health benefits to aquatic species. Astaxanthin has recently been identified as a semi-essential nutrient for some common aquaculture species, such as crustaceans and salmonids, but its effectiveness as a health supplement in aquatic species is unclear. This review aims to summarize the varied current uses of astaxanthin in aquaculture, as well as the potential effects of astaxanthin on the aquatic animal species which receive it.

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Introduction

Aquaculture has become a major producer of food for human consumption. In 2020, 56% of the seafood eaten by people was grown; 44% was obtained via wild capture [1]. In addition, aquaculture accounted for 83% of the freshwater aquatic animals consumed, with both freshwater and saltwater production split approximately equally between aquaculture and the harvest of wild stocks [1]. Feed ingredients that maximize growth, maintain health, and improve the appearance of aquatic animals are essential to the continued growth of aquaculture. One important ingredient is astaxanthin, which is a xanthophyll, an oxidized form of β-carotene naturally synthesized by lower trophic level organisms such as microalgae, yeast, and some microbes [2-4]. It is also synthetically manufactured [5,6]. Astaxanthin has historically and widely been used in aquaculture as a pigment to color fish flesh [7-10]. However, fish and shellfish grown in aquaculture cannot synthesize astaxanthin de novo [2,11,12]. It must be included in their diets [13,14].

While considerable initial research has examined the astaxanthin dosages and feeding durations required to produce the desired coloration in cultured aquatic animals, additional benefits have begun to appear. Astaxanthin is a potent antioxidant [11,15], with likely positive effects on the immune function and overall health of fish and shellfish, as well as their survival during hatchery rearing [2,16]. Improvements in the growth of fish and crustaceans receiving dietary astaxanthin have also been observed, although these results are somewhat inconsistent [17]. Astaxanthin also appears to positively impact reproduction and subsequent egg survival in some fish species [18].

This review article describes astaxanthin from an aquaculture perspective. The chemical properties and characteristics of astaxanthin are described first, followed by a discussion of natural and artificial astaxanthin sources. A review of the effects of astaxanthin on oxidative stress and immune responses occurs next, followed by a review of those studies examining astaxanthin effects on aquatic animal growth and reproduction. Lastly, the use of astaxanthin as a pigment source for fish and shellfish is reviewed, including the dosages, feeding durations, and retention times.

Chemical Formula and Properties

Carotenoids are a group of naturally occurring pigments [11]. There are two classes of carotenoids, xanthophylls and carotenes, whose chemical formulas differ. Xanthophylls are distinguishable by the presence of oxygen in addition to a double-bonded polyene carbon chain, whereas carotenes do not have oxygen. Astaxanthin (3,3’-dihydroxy-β, β’carotene-4, 4’-dione) is a xanthophyll [19-21]. It contains hydroxyl and keto moieties on either side of the ionone ring at either end of the polyene chain which give the molecule both lipophilic and hydrophilic properties. It is generally naturally occurring in esterified forms, with many different isomers [2,19-24]. Esterified astaxanthin is found primarily in the skin of fish [25,26], however, most, if not all, astaxanthin found in the muscle of salmonid fish is unesterified or free [27-29].

Unlike crustaceans, fish and other higher trophic level animals are unable to synthesize astaxanthin and must acquire it through food [2,11,12]. For example, salmonid fish cannot epimerize 3-hydroxy groups, but 3S,3’S astaxanthin isomer is in the muscle tissue, indicating that astaxanthin must have a dietary source [30,31]. Higuera-Ciapara et al. [14] reported that salmonids obtain astaxanthin from zooplankton, which in turn accumulate astaxanthin primarily by ingesting Spirulina and Haematococcus algae (green microalgae). Storebakken et al. [32] isolated the chiral isomer of astaxanthin in crustaceans consumed by wild salmonids.

Sources

Natural astaxanthin is produced mainly at the primary trophic level by higher plants, microalgae, bacteria, and some fungi. Examples of astaxanthin-producing species include some microalgae (*Haematococcuslacustriss*, *Chromochloriszofingiensis*, *Scenedesmus obliquus*), red yeast (*Phaffiarhodozyma*), and many other algal species [33].

Astaxanthin was first discovered in lobster (Homerusgammarus) in 1938 and was extracted from *Haematococcus* algae in 1944. Naturally sourced astaxanthin has traditionally been from crustacean by-products [2,3]. Recently, extraction of astaxanthin is possible from red yeast, [34-36] and microalgae [6,18,22,23,37-39] which are emerging as a sustainable natural source [4].

Astaxanthin is harvested from microalgae in one of two ways. The first process involves two steps. Microalgae are cultured to produce biomass, and then the microalgae are exposed to ultra-violet light or stressed. The stress can be applied by using chemicals, temperature, or lack of nutrients. The second method uses a one-step process where the microalgae are grown at a low level of stress for simultaneous biomass and astaxanthin production. The microalgae respond to the stressful environmental conditions by becoming dormant and forming cysts full of astaxanthin as protection against oxidative stress. The microalgal cysts are surrounded by a tough sporopollenin or algaenan cell wall which requires either mechanical or chemical processes for astaxanthin extraction. Extraction makes up about 20-to-30% of the production cost of astaxanthin [4,19,40]. The two-step process is the most widely used and is likely the most efficient process because the production of the algal biomass is not ideal under any stress conditions [41]. Synthetic astaxanthin is commonly used [8,15,36,39,42-49] and is much less expensive to produce than natural forms [5,6]. Approximate costs for synthetic astaxanthin range from $1,000-to-$2,000 USD per kg, while natural sources are approximately $7,000 USD per kg [40,50].

Oxidative Stress and Organism Health

Mitochondrial metabolic activity constantly produces free radicals, reactive oxygen, and nitrogen species that can cause oxidative damage to proteins and genetic material. While a small amount of reactive oxygen species is necessary for cell signaling and homeostasis, an over-abundance is known to contribute to genomic mutations and oxidative stress, such as the irreversible modification of a number of biologically-important molecules such as proteins and lipids [15,16,38,49]. Carotenoids protect against chronic stress by preventing lipid peroxidation and reducing oxidative stress, thereby reducing the inflammatory response [3,7,30]. Part of the initial stress response of an organism is mild inflammation, which involves the generation of oxidants. While this immediate oxidative response is necessary for fighting infectious agents, it can be damaging if it becomes chronic. Carotenoids help prevent chronic inflammation because they are potent antioxidants [11]. Astaxanthin is a multifaceted molecule with 100 to 500 times the potency of other carotenoids and antioxidant vitamins [15,48]. Its unique polar structure allows it to embed in cell membranes, providing protection against lipid peroxidation inside the cell membrane and allowing it to scavenge free radicals outside the cell membrane. Because of these unique properties, it is highly anti-carcinogenic, anti-diabetic, anti-ageing, anti-inflammatory, anti-tumor, anti-bacterial, ultra-violet light protective, cardio-protective, ocular-protective, neuro-protective, hepato-protective, and gastro-protective, with positive effects on athletic performance, fertility, immune response, and disease resistance in humans [2,3,16,20,21,38,51-55].

Although astaxanthin is a well-known pigment in fish and crustaceans, relatively few studies have investigated the potential health benefits of astaxanthin to these organisms [2,38,53]. Just as in mammals, astaxanthin is likely important for various functions other than coloration, such as immune function, antioxidant capacity, and reproductive performance [56-58]. Although focusing on astaxanthin use for pigmentation, Pham et al. [6] did investigate its antioxidant properties. More recent studies have focused on the health effects of astaxanthin on cultured crustaceans [15,37,39,59,60]. Yu et al. [60] reported that in Pacific white shrimp (*Litopenaeusvannamei*), astaxanthin supplementation was associated with increased survival and hepatopancreatic health. In juvenile red king crab (*Paralithodes camtschaticus*) in Alaska, astaxanthin supplementation enhanced survival [37]. Wang et al. [47] found that dietary astaxanthin increased immune response and tolerance against freshwater shock stress in kuruma shrimp (*Marsupenaeus japonicus*). Adult Chinese mitten crab (*Eriocheir sinensis*) showed a marked decrease in antioxidant enzyme activity [59]. These results are in contrast to some aquatic species as well as mammalian studies, which observed increased antioxidant enzyme activity [3,51,52].

Long et al. [39] studied green microalgae powder in Chinese mitten crabs and found no significant difference in hepatosomatic index between treatments. However, this index is a relatively crude indicator of antioxidant activity, and the old age of the crabs may have negatively influenced the results [39]. Lastly, astaxanthin mitigates the oxidative stress caused by microplastics in fish, but this occurs at the expense of skin pigmentation [61].

Growth

The impact of astaxanthin on crustacean growth is uncertain, likely because of species-specific nutritional differences, differences in study durations, and differences in diet compositions among the studies. Wu et al. [59], Long et al. [39], Wang et al. [15], and Ma et al. [62] found no significant effect on the growth. However, Daly et al. [37], Zhang et al. [56], and Wang et al. [49] both reported improved growth with the use of astaxanthin. These studies either used juvenile crabs or crabs that molted during the experiment. Wang et al. [49] used two levels of astaxanthin and three levels of vitamin E in kuruma shrimp and found the treatment with high levels of astaxanthin and medium levels of vitamin E outperformed the other treatments. Zhang et al. [56] found Pacific white shrimp had similar growth and survival as controls when fed only 25 mg/kg astaxanthin when stressed with low oxygen levels. However, there was increased survival with fish fed 75-125 mg/kg astaxanthin.

Just as with crustaceans, the effect of astaxanthin on fish growth is also uncertain. Similar to the studies involving invertebrates, the studies evaluating astaxanthin in fish are not uniform. Not only are the astaxanthin effects likely influenced by species-specific nutritional differences, the studies also have different study durations and use diets with different ingredients, many of which could potentially influence astaxanthin absorption or utilization. Some studies have shown a positive relationship between astaxanthin and fish growth [18,43,47,48,63,64] while others have found no relationship [6,37,48,56,65]. Palma et al. [48] found increased egg quality and juvenile growth and survival when astaxanthin was fed to parental females in long snout seahorses (*Hippocampus guttulatus*). Hansen et al. [47] found female spawning age Atlantic cod (*Gadus morhua*) to have increased egg production and efficiency, with higher fertilization success, egg survival, and larval growth when fed a diet with astaxanthin included. Feeding astaxanthin for six weeks improved the growth of red tilapia (*Oreochromis* spp.), and also improved skin coloration [66].

Reproduction

Little research has been conducted on the effects of astaxanthin consumption on aquatic animal reproduction. In salmonids, studies examining the possible relationship between astaxanthin consumption and reproductive success have produced mixed results. Christiansen and Torrissen [67] reported no significant effects on egg fertilization or survival when Atlantic salmon (*Salmo salar*) broodstock diets were supplemented with synthetic astaxanthin. Choubert et al. [68] also did not observe any relationship among astaxanthin and several reproduction parameters in rainbow trout (*Oncorhynchus mykiss*). In contrast, Ahmadi et al. [17] found a positive correlation between synthetic astaxanthin and fertilization, eyed-egg percentage, and percent hatch in rainbow trout, and suggested that astaxanthin supplementation of brood stock diets are necessary for optimal reproductive performance in rainbow trout. Sawanboonchun et al. [45] and Hansen et al. [47] found an increase in egg quality and larval production in Atlantic cod.

Pigmentation

Carotenoids are one of four main pigment groups (melanins, purines, pteridiums, and carotenoids) that produce yellow, red, and orange pigments in fish and crustaceans [69]. Carotenoids in the skin of fish are deposited in xanthophores and erythrophores. Astaxanthin is generally the most efficiently absorbed carotenoid pigment, although this may vary by species [69].

Astaxanthin is most widely known for its role in the pigmentation of salmonid muscle [14,70]. Increased pigmentation in food fish increases market demand and customer satisfaction [2,10,38,53,71]. Astaxanthin is also an important pigment for crustaceans [2,6,38], because coloration is also a key component of customer satisfaction and market demand [39,59].

Tissue Integration

Astaxanthin cannot be synthesized de novo by salmonids and therefore must be ingested as part of their diet [14]. Once ingested, the food undergoes enzymatic digestion and then enters the intestine where any astaxanthin esters are hydrolyzed by lipases. They are then absorbed into the blood serum through the intestinal lumen as the free form of astaxanthin and deposited in the muscle tissue [72-74]. Most salmonids fed supplemental astaxanthins receive it in the synthetic free form because it is more readily absorbed than the naturally occurring esterified forms; the degree of esterification influences absorption [23,24].

Once ingested and dependent on temperature, astaxanthin typically begins to appear in blood serum three hours after feeding with levels increasing rapidly from that point. When astaxanthin is conveyed across the lumen wall it enters the blood stream where it is transported in high density lipoproteins and very high-density lipid proteins [26,31,75-77]. Once astaxanthin-containing lipoproteins reach muscle tissue, attachment to the cells is dependent upon specific binding sites. Astaxanthin binds to actomyosin using one ionone ring. Depending upon the developmental stage of the fish, lipoproteins carrying astaxanthin can vary in size and density, with high density lipoproteins dominating in early life stages and very low-density lipoproteins increasing dramatically with age. Some transport pigment from the intestine to the liver and others transport pigment from the liver to other tissues. Astaxanthin distribution and deposition changes throughout the salmonid life cycle, with younger fish depositing more esterified form in their skin and maturing fish depositing more free form in their muscle tissue [9,78-81]. With the onset of sexual maturity astaxanthin, originally obtained from the diet, begins transference from the flesh to reproductive organs and eggs.

At all fish ages, the esterified form of astaxanthin is more likely to be deposited in the skin with the free form being deposited in the muscle tissue [82]. Once consumed, astaxanthin deposition is dependent on several factors including the rate of absorption, transport, metabolism, and excretion [29,83]. Considerable research has focused on the effects of these variables on pigmentation in the muscle of food fish such as rainbow trout [9,35], Atlantic salmon [36], coho salmon (*Oncorhynchus kisutch*) [8,84], Australian snapper (*Pagrus auratus*) [46], and red porgy (*Pagruspagrus*) [61]. Iwamoto et al. [84] suggested that pigmentation may be mostly determined by genetics. In addition, March and MacMillan [44] also concluded that the genetics has a large influence on astaxanthin absorption and deposition in Atlantic salmon. Micah et al. [85] documented 4,250 differently expressed genes affecting numerous metabolic and physiological pathways in blood parrotfish (*Viejamelanurus* x *Amphilopuscitrinellus*) fed astaxanthin,

Feed composition contributes to astaxanthin deposition efficiency. Increased dietary fat concentrations in rainbow trout increases astaxanthin digestibility, transport [86], absorption [87] and retention efficiency [88]. If higher lipid levels lead to changes in fish growth or feed conversion ratios, dietary astaxanthin must be adjusted to obtain desired pigment levels [89]. Lipid type and quality play an important role in the absorption of carotenoids and flesh pigmentation. Atlantic salmon fed diets containing animal fats had lower levels of astaxanthin in their muscle tissue than those receiving fish oil [90]. Compared to more-highly-saturated fats, polyunsaturated fatty acids increase astaxanthin retention in the muscles of salmonids in diets with high levels of vitamin E [91].

The source and type (astaxanthin or canthaxanthin) of carotenoids also influences pigmentation. Pham et al. [6] fed juvenile olive flounder (*Paralichthysolivaceus*) either synthetic astaxanthin, green algae extract, whole green algae, or paprika extract to assess the effects of each treatment on flesh color. Both paprika and whole green algae had a significantly better effect on the flesh pigmentation than the other treatments [6]. Teimouri and Amirkolaie [68] investigated feeding synthetic astaxanthin and canthaxanthin to an aquarium species. After supplementation with five different astaxanthin or canthaxanthin concentrations, carotenoid concentrations and coloration parameters were consistently higher in fish fed astaxanthin than in those fed canthaxanthin. Red porgy fed astaxanthin from shrimp meal also had significantly better coloration than those fed either a control diet or one with canthaxanthin [63]. March and MacMillan [44] looked at the effects of feeding different astaxanthin concentrations on carotenoid absorption and deposition in rainbow trout, Chinook salmon (*Oncorhynchus tschawytscha*), and Atlantic salmon. They found rainbow trout had the highest astaxanthin concentration in muscle tissue and the most visible pigmentation, chinook salmon and rainbow trout were equally variable in pigmentation, and Atlantic salmon had the lowest muscle astaxanthin concentrations and the lowest visible pigmentation.

The coloration of ornamental fish can be safely enhanced using astaxanthin [92]. Song et al. [93] observed improved skin pigmentation in discus fish (*Symphysodon spp.*) receiving at least 200 mg/kg of dietary astaxanthin for four weeks. The external coloration of goldfish (*Carassius auratus*) was also improved with relatively low levels of dietary astaxanthin [85] while considerable higher levels were used with blood parrotfish to achieve changes in skin coloration [94]. Both natural and synthetic sources of astaxanthin improved the coloration of orchid dottyback (*Pseudochromisfridmani*) with natural source astaxanthin deemed a more effective colorant [95]. Clown anemonefish (*Amphiprionocellaris*) skin pigmentation was positively related to the dietary astaxanthin concentrations and the duration of feeding astaxanthin-containing diets [96]. In spinecheek anemonefish (*Premnasbiaculeatus*), external coloration was achieved after feeding 214 mg/l astaxanthin for 115 days [97]. Supplemental astaxanthin improved the external orange-red coloration of red zebra cichlid (*Maylandiaesterae*) [98], while differing levels of carotenoids in commercial diets influenced the external color of goldfish (*Carassius auratus*) [99].

Astaxanthin is extremely sensitive to light, heat, moisture, and oxygen exposure and can be damaged during feed manufacturing [100,101]. Storage in sealed dark packaging at cold temperatures and even vacuum-packaging is recommended. Decreased efficiency of pigmentation could be caused by any milling processes or storage practices of feed that contain astaxanthin, which would lead to premature decomposition [101,102].

Dosages and Retention

There is an inverse relationship between dietary astaxanthin dose and deposition rate in the flesh of salmonids. Bjerkeng et al. [103] reported pigment concentration in muscle directly increased with increasing dietary doses of astaxanthin. However, increasing dietary astaxanthin reduced retention rates. Feeding lower doses of astaxanthin over an extended period produces the best pigment retention [8]. In rainbow trout, astaxanthin inclusion levels of 50-to-70 mg/kg astaxanthin appear to be optimal [44,103,104]. March and MacMillan [44] reported the highest levels of rainbow trout pigmentation were achieved at 27 weeks with 40 mg/kg of dietary astaxanthin or 22 weeks with 70 or 100 mg/kg astaxanthin. Storebakken and No [69] stated that little extra flesh pigmentation can be gained in rainbow trout at dietary astaxanthin levels higher than 50-to-60 mg/kg.

There is very little information on retention duration after the cessation of feeding astaxanthin. However, astaxanthin levels do not decrease even after several months of starvation in fish [28,105,106]. Brown et al. [107] reported no decrease in muscle coloration in rainbow trout after the elimination of dietary astaxanthin. A compilation of astaxanthin studies in fish and invertebrates are provided in Tables 1 and 2, respectively.

Conclusion

The carotenoid astaxanthin is a potent antioxidant available from both natural and synthesized sources. It has documented benefits to mammalian health that have yet to be fully investigated and described for aquatic animals. Its underlying physiological mechanisms of action, which have been researched in mammals, also need to be further detailed for fish and crustaceans. Study results are likely influenced by species and genetic differences in the ability to absorb and utilize astaxanthin, as well as the source of astaxanthin used. The stability of astaxanthin also likely influences study results. In its most bioavailable form, astaxanthin is the least stable, and even in the more stable forms it is highly susceptible to oxidation. Feed manufacturing, shipment, and storage could be exerting a substantial influence on astaxanthin potency.

Sustainable astaxanthin sourced from microalgae is promising if production and processing can be streamlined. With recirculating aquaculture systems expanding rapidly in commercial aquaculture, the use of astaxanthin has tremendous potential. It could provide a buffer against various stressors inherent to fish and shellfish rearing, potentially improving growth, and decreasing the likelihood of catastrophic disease outbreaks.

Table 1. A compilation of published research on astaxanthin in fish.

Species	Source[1]	Dose (mg/kg)	Duration (days)	Results	Reference
Asian seabass (*Lates calcarifer*)	Green microalgae (*Haematococcus Pluvialis*)	50 100 150	90	Linear increase in specific growth rate, feed utilization efficiency, and survival with increasing astaxanthin (algae) levels	[64]
Atlantic cod (*Gadus morhua*)	Astaxanthin	73.7	60	Increased egg quality and larval production	[45]
		100	90	Increased egg production and efficiency, fertilization success, egg survival, and larval growth	[47]
Atlantic salmon (*Salmo salar*)	Astaxanthin	0.2	77	Marginal growth Decreased survival	[43]
		0.4	77	Marginal growth Decreased survival	[43]
		0.7	77	Marginal growth Decreased survival	[43]
		1.0	77	Marginal growth Increased survival	[43]
		5.3	77	Increased growth and survival Minimum dietary concentration needed for maximum growth and survival	[43]
		13.7	77	Increased growth and survival	[43]
		36.0	77	Increased growth and survival	[44]
		40	86	Decreased caratenoid concentration and retention compared to red yeast diet	[36]

			186	Slower response to pigmentation than rainbow trout	[44]
		70	186	Slower response to pigmentation than rainbow trout	[44]
		81.4	77	Increased growth and survival	[43]
		100	0 – 1,265	Astaxanthin levels in eggs of little value measurement of egg quality	[62]
			186	Slower response to pigmentation than rainbow trout	[44]
		190.1	77	Increased growth and survival	[43]
		317.3	77	Increased growth and survival	[43]
	Red yeast (*Phaffiarhodozyma*)	40	86	Increased caratenoid concentration and retention (more efficient) compared to astaxanthin diet	[36]
Australian snapper (*Pagrus auratus*)	Astaxanthin	13	63	Increase redness linearly with dosage after 21 days Plateau redness after 63 days Highest retention while obtaining maximum pigmentation	[46]
		26	63	Increase redness linearly with dosage after 21 days Plateau redness after 63 days	[46]
		39	63	Increase redness plateau with dosage after 21 days: astaxanthin not efficiently used Plateau redness after 63 days	[46]
		52	63	Increase redness plateau with dosage after 21 days: astaxanthin not efficiently used	[46]
		65	63	Increase redness plateau with dosage after 21 days: astaxanthin not efficiently used	[46]
		78	63	Increase redness plateau with dosage after 21 days: astaxanthin not efficiently used	[46]
Blood parrotfish (*Viejamelanurus* x *Amphilophus citrinellus*)	Astaxanthin	450	74	Increased skin redness and yellowness Specific genes up and down regulated	[85]
Brown trout	Canthaxanthin +	30 + 30		Rainbow trout better coloration than brown trout	[42]

(*Salmo trutta*)	Astaxanthin				
Chinook salmon (*Oncorhynchus tshawytscha*)	Astaxanthin	40	186	Slower response to pigmentation than rainbow trout	[44]
		70	186	Slower response to pigmentation than rainbow trout	[44]
		100	186	Slower response to pigmentation than rainbow trout	[44]
Coho salmon (*Oncorhynchus kisutch*)	Astaxanthin*(oil extract from Antarctic krill (*Euphausia superba*)	72	56	Retained color throughout next 168 days being fed non-carotenoid diet	[80]
		144	56	Retained color throughout next 168 days being fed non-carotenoid diet	[80]
	Astaxanthin	15	196	Linear relationship between dietary and flesh carotenoid concentrations Diet of 15 mg/kg most economical	[8]
		30	196	Linear relationship between dietary and flesh carotenoid concentrations	[8]
		45	196	Linear relationship between dietary and flesh carotenoid concentrations	[8]
		60	196	Linear relationship between dietary and flesh carotenoid concentrations	[8]
Clown anemone fish (*Amphironocellaris*)	Astaxanthin	40	90	No significant effect on skin color	[96]
		60	90	No significant effect on skin color	[96]
		80	90	Significant skin coloration improvement	[96]
		100	90	Significant skin coloration improvement	[96]
Discus fish (*Symphysodon* spp.)	Astaxanthin	50	56	No growth effects, improved skin redness	[93]
		100	56	No growth effects, improved skin redness	[93]
		200	56	No growth effects, stable skin redness	[93]
		300	56	Reduced weight gain, stable skin redness	[93]
		400	56	Reduced weight gain, stable skin redness	[93]
Goldfish (*Carassius auratus*)	Astaxanthin	25	28	Improved skin coloration, increased survival, no weight gain effect	[94]
		50	28	Improved skin coloration, increased survival, no weight gain effect	[94]
		75	28	Improved skin coloration, increased survival,	[94]

		100	28	no weight gain effect Improved skin coloration, increased survival, no weight gain effect	[94]
Longsnout seahorse (*Hippocampus reidi*)	Astaxanthin	75	210	Increased egg quality and juvenile growth and survival	[48]
		100	210	Increased egg quality and juvenile growth and survival	[48]
		125	210	Increased egg quality and juvenile growth and survival	[48]
Olive flounder (*Paralichthysolivaceus*)	Astaxanthin	100	56	Increased carotenoid and redness Survival, gain, and feed intake not different	[6]
		200	56	Increased carotenoid and redness Survival, gain, and feed intake not different	[6]
	Green microalgae (raw)	100	56	Increased carotenoid and redness As efficient as synthetic astaxanthin Survival, gain, and feed intake not different	[6]
	(extract)	100	56	Increased carotenoid and redness Survival, gain, and feed intake not different	[6]
		200	56	Increased carotenoid and redness Survival, gain, and feed intake not different	[6]
	Paprika	100	56	Increased carotenoid and redness As efficient as synthetic astaxanthin Survival, gain, and feed intake not different	[6]
		200	56	Increased carotenoid and redness Survival, gain, and feed intake not different	[6]
Orchid dottyback (*Pseudochromis fridmani*)	Astaxanthin	25	70	Color improved with increasing concentration	[95][95] [95] [95]
		50	70	Color improved with increasing concentration	
		75	70	Color improved with increasing concentration	
		100	70	Color improved with increasing concentration	[95] [95] [95] [95]
	Green algae (*Haematococcus*	25	70	Color improved with increasing concentration	

	pluvialis)	50	70	Color improved with increasing concentration	
		75	70	Color improved with increasing concentration	
		100	70	Most effective concentration and astaxanthin source for coloration	
Rainbow trout (*Oncorhynchus mykiss*)	Astaxanthin$^{\text{*raw calanus}}$ (*Calanus finmarchicus*)	9	53	Best pigment retention of diets fed free astaxanthin	[72]
		12	53	Best pigment retention of diets fed free astaxanthin	[72]
		26	53	Best pigment retention of diets fed free astaxanthin	[72]
		61	53	Best pigment retention of diets fed free astaxanthin	[72]
	Astaxanthin$^{\text{*shrimp}}$ (*Pandalus borealis*) byproducts)	3.4	225	Increase of astaxanthin in flesh throughout experiment Increase redness linearly with dosage	[88]
		6.0	225	Increase of astaxanthin in flesh throughout experiment Increase redness linearly with dosage	[88]
		12.1	225	Increase of astaxanthin in flesh throughout experiment Highest redness	[88]
	Astaxanthin$^{\text{*Red beat}}$ (*Calanus finmarchicus*)	20	37	Increase astaxanthin in flesh from 21 to 37 days	[88]
	Astaxanthin	0.07	42	Linear relationship on dosage of astaxanthin and amount of astaxanthin content in eggs Positive relationship between egg astaxanthin content and fertilization rate, eyed, and hatch success	[17]
		12.5	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			42	Linear relationship on dosage of astaxanthin and amount of astaxanthin content in eggs Positive relationship between egg astaxanthin content and fertilization rate, eyed, and hatch success	[17]
		25	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			56	Increased carotenoids by 1.5x and retention of color than canthaxanthin	[7]

			112	Increased redness and utilization of astaxanthin than canthaxanthin	[103]
		30	0 – 467	Duration of feeding pigmented feed did not matter for overall flesh color	[9]
			54	Growth similar to green microalgae	[23]
		33.3	42	Linear relationship on dosage of astaxanthin and amount of astaxanthin content in eggs Positive relationship between egg astaxanthin content and fertilization rate, eyed, and hatch success	[17]
		35.4	69	Increased redness with all-E-astaxanthin compared to mixture of all-E- and Z-astaxanthin Increased digestibility	[89]
		36.9	69	Decreased redness with mixture of all-E- and Z-astaxanthin compared to all-E-astaxanthin Decreased digestibility	[89]
		40	139	Some fed non-astaxanthin diet, some fed astaxanthin for 84 days then fend non-astaxanthin diet, and some fed astaxanthin diet for 139 days Increased redness in fillets of fish either fed for 84 days or 139 days compared to control Fish will retain coloration for at least 55 days after stocking	[107]
			186	Quickest response to pigmentation than Atlantic or Chinook salmon	[44]
		50	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			56	Increased carotenoids by 1.5x and retention of color canthaxanthin	[7]
				Anterior intestine use in carotenoid absorption	[22]
			112	Increased redness and utilization of astaxanthin than canthaxanthin	[103]
			180	No effect of number of eggs produced, egg survival, or larval survival compared to control	[68]
		65.1	42	Linear relationship on dosage of astaxanthin and amount of astaxanthin content in eggs Positive relationship between egg astaxanthin content and fertilization rate, eyed, and hatch success	[17]

		70	186	Quickest response to pigmentation than Atlantic or Chinook salmon	[44]
		92.9	42	Linear relationship on dosage of astaxanthin and amount of astaxanthin content in eggs Positive relationship between egg astaxanthin content and fertilization rate, eyed, and hatch success	[17]
		96	39	Females had higher hue angle	[13]
		100	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			28	Increased carotenoids and retention compared to canthaxanthin and yeast	[35]
			112	Increased redness and utilization of astaxanthin than canthaxanthin	[102]
			180	No effect of number of eggs produced, egg survival, or larval survival compared to control	[68]
			186	Quickest response to pigmentation than Atlantic or Chinook salmon	[44]
			980	Efficiently utilized from week 23 to 56 with astaxanthin compared to canthaxanthin Increased carotenoid concentration in skin with astaxanthin compared to canthaxanthin	[103]
		200	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
	Canthaxanthin	12.5	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
		25	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			56	Decreased carotenoids by 1.5x and retention of color astaxanthin	[7]
			112	Decreased redness and utilization with canthaxanthin than astaxanthin	[103]
		50	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			56	Decreased carotenoids by 1.5x and retention of color astaxanthin	[7]
			112	Decreased redness and utilization with canthaxanthin than astaxanthin Increased carotenoid concentration from 25 to 50	[94]
		100	10	Carotenoid absorption maximum up to 25 mg/kg	[83]
			28	Decreased carotenoids and retention compared to astaxanthin	[35]

			112	Decreased redness and utilization with canthaxanthin than astaxanthin Minimal increase carotenoid concentration from 50 to 100	[94]
			980	Not efficiently utilized from week 23 to 56 with canthaxanthin compared to astaxanthin Decreased carotenoid concentration in skin with canthaxanthin compared to astaxanthin	[92]
		200	10	Carotenoid absorption maximum up to 25 mg/kg	[82]
			90	No effect of number of eggs produced, egg survival, or larval survival compared to control	[68]
			180	No effect of number of eggs produced, egg survival, or larval survival compared to control	[68]
	Canthaxanthin + Astaxanthin	30 + 30	?	Rainbow trout better coloration than brown trout	[42]
		0 + 200	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
		40 + 160	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
		80 + 120	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
		120 + 80	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
		160 + 40	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
		200 + 0	57	Synthetic astaxanthin deposited more efficiently Combination gave higher total carotenoid deposition	[29]
	Green microalgae	30	54	Growth similar to synthetic astaxanthin	[23]
		50	56	Anterior intestine use in carotenoid absorption	[22]
	Yeast	50	28	Decreased carotenoids and retention compared to astaxanthin	[35]

		100	28	Decreased carotenoids and retention compared to astaxanthin	[35]
Red porgy (*Pargus major*)	Astaxanthin* (Shrimp shell meal)	20	105	Slight improvement of reddish coloration Increased commercial value	[63]
		40	105	Better utilization, only diet to give reddish coloration overall Increased commercial value	[63]
	Canthaxanthin	40	105	No overall reddish coloration	[63]
		100	105	No overall reddish coloration	[63]
Red tilapia (*Oreochromis* spp.)	Green algae (powder)	40,000	42	Increased weight gain, protein efficiency ratio, higher redness	[66]
		80,000	42	Increased weight gain, protein efficiency ratio, higher redness	[66]
		120,000	42	Increased weight gain, protein efficiency ratio, higher redness	[66]
Red zebra cichlid (*Maylandiaestherae*)	Astaxanthin	3,000	70	Produced acceptable skin coloration	[98]
Rosy barb (*Pethiaconchonius*)	Astaxanthin	20	56	Increased carotenoid and retention compared to canthaxanthin	[69]
		40	56	Increased carotenoid and retention compared to canthaxanthin	[69]
		60	56	Increased carotenoid and retention compared to canthaxanthin	[69]
		80	56	Increased carotenoid and retention compared to canthaxanthin Increased market value	[69]
		100	56	Increased carotenoid and retention compared to canthaxanthin Increased market value	[69]
	Canthaxanthin	20	56	Decreased carotenoid and retention compared to astaxanthin Not suitable replacement of astaxanthin	[69]
		40	56	Decreased carotenoid and retention compared to astaxanthin Not suitable replacement of astaxanthin	[69]

		60	56	Decreased carotenoid and retention compared to astaxanthin Not suitable replacement of astaxanthin	[69]
		80	56	Decreased carotenoid and retention compared to astaxanthin Not suitable replacement of astaxanthin	[69]
		100	56	Decreased carotenoid and retention compared to astaxanthin Not suitable replacement of astaxanthin	[69]
Spinecheek anenomefish (*Premnasbiaculeatus*)	Astaxanthin	23 214 2,350	115 115 115	Increasing coloration with increasing astaxanthin concentration and increasing feeding duration. Recommended 214 mg/l for 115 days to provide adequate coloration.	[97]
Yellow croaker (*Larimichthyspolyactis*)	Astaxanthin	37.5	63	Similar growth Effective carotenoid sources for skin color improvement	[65]
		75	63	Similar growth Effective carotenoid sources for skin color improvement	[65]
	Green microalgae	20	30	Similar results as control diet	[18]
		40	30	Supplementation increases growth, antioxidant capacity	[18]
		80	30	Supplementation increases growth, antioxidant capacity	[18]
	Xanthophylls	37.5	63	Similar growth Effective carotenoid sources for skin color improvement	[65]
		75	63	Similar growth Effective carotenoid sources for skin color improvement	[65]

[a] Astaxanthin is synthetic, unless otherwise noted.

Table 2. A compilation of published research on astaxanthin in invertebrates.

Species	**Source**^{1}	**Dose (mg/kg)**	**Duration (days)**	**Results**	**Reference**
Abalone (*Haoliotis discus*)	Astaxanthin	80	120	No growth effect Improved anti-oxidant capacity	[62]
Chinese mitten crab (*Eriocheir sinensis*)	Astaxanthin	68	28	Increased ability to handle high pH environment Increased redness	[15]
	Green microalgae	28.5	60	No effect on survival, gonadosomatic index, and hepatosomatic index (ovary development) Increased coloration, antioxidation capacity, and protein content in ovaries	[39]
		43.9	60	No effect on survival, gonadosomatic index, and hepatosomatic index (ovary development) Increased coloration, antioxidation capacity, and protein content in ovaries	[39]
		82.6	60	No effect on survival, gonadosomatic index, and hepatosomatic index (ovary development) Increased coloration, antioxidation capacity, and protein content in ovaries	[39]
Kuruma shrimp (*Marsupenaeus japonicus*)	Astaxanthin	600	56	Interaction between astaxanthin and vitamin E Pigmentation better when fed astaxanthin	[49]
Pacific white shrimp (*Litopenaeusvannamei*)	Astaxanthin	25	56	Similar growth and survival as control	[56]
		75	56	Increased survival after low dissolved oxygen stress for 1 hour	[56]
		100	56	Increased survival after low dissolved oxygen stress for 1 hour	[56]
		125	56	Increased gain, specific growth rate, and total antioxidant status Increased survival after low dissolved oxygen stress for 1 hour	[56]
		150	50	Dose-dependent protection against oxidized fish oil damage to oxidation and hepatopancreatic	[60]
			56	Increased gain, specific growth rate, and total antioxidant status Increased survival after low dissolved oxygen stress for 1 hour	[56]
		250	50	Dose-dependent protection against oxidized fish oil damage to oxidation and hepatopancreatic	[60]

		450	50	Dose-dependent protection against oxidized fish oil damage to oxidation and hepatopancreatic	[60]
	Green microalgae	60	30	Increased astaxanthin content Protective antioxidant effect	[38]
Red king crab (*Paralithodes camtschaticus*)	Green microalgae	380	56	Increased survival, saturation, and lower brightness	[36]

[a] Astaxanthin is synthetic, unless otherwise noted.

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Conflicts of interest

The authors declare no conflict of interest.

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