

The essential role of vitamin C and E supplementation in enhancing growth, health, and body composition of aquaculture species

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ABSTRACT

Vitamins C (L-ascorbic acid) and E (α -tocopherol) are essential micronutrients and antioxidants in feeds for various aquatic animals. This review compiles and analyzes the studies that focus on the effects and interactions between vitamins C and E on the growth, health, and body composition of different aquaculture species. As can be seen, vitamins C and E are indispensable nutrients for almost all aquaculture species. Information on their nutritional requirements and effects on aquatic animals has been examined and limited to several aquaculture species. Numerous studies have shown the vital roles of vitamins C and E in antioxidative functions. However, many other studies have also indicated that supplementing vitamins C and E in diets positively affects the growth performance, health, and body composition of aquaculture species. The review summarizes the documented findings related to the roles of dietary vitamins C and E in aquaculture. This study provides valuable information for nutritionists, feed mills, and other related institutions, as well as the effective use of these vitamins in the aquafeed industry.

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1. Introduction

Vitamins are essential components in sustaining aquaculture species' physiological functions and growth. They are categorized into two groups: water-soluble and fat-soluble vitamins. Among these, vitamin C (VC) is a water-soluble vitamin and a vital antioxidant involved in many physiological processes such as growth, lipid metabolism, stress response, and immune function of aquatic animals (Shahkar et al., 2015; Ibrahim et al., 2020). Despite extensive research on the dietary VC requirements of various farmed fish species, information on VC requirements for fish still needs to be investigated. The results from the previous studies showed that the recommended dietary level of VC varies widely depending on species, fish sizes, environmental conditions, and nutrient interactions, necessitating species-specific analyses (Kong et al., 2021; Yusuf et al., 2021; Xu et al., 2022).

Playing an equally vital role as VC, vitamin E (VE) is a fat-soluble micronutrient and indispensable in fish nutrition due to its critical role in numerous physiological and biochemical processes (Hamre, 2010; Lu et al., 2016). As fish cannot synthesize VE endogenously, they rely entirely on dietary intake to meet their requirements. VE exists in various natural forms, comprising four tocotrienols and four tocopherols, with α -tocopherol being the most biologically active. Among the α -tocopherols, DL- α -tocopherol acetate is the most stable and commonly used in animal feed (NRC, 1993).

Co-supplementation of VC and VE in diets for aquaculture species has shown positive effects on growth, feed utilization, health, immune function, and nutrient deposition. The interactions between VC and VE have demonstrated potential benefits for fish growth, health, body composition, antioxidant activity,

and disease resistance (Lee & Dabrowski, 2004; Harsij et al., 2020; Rahimnejad et al., 2021).

The effects of VC and VE on fish and shrimp growth performance, antioxidant activities, immune responses, and other biological activities and metabolic functions were well documented (Yildirim-Aksoy et al., 2008; Gao et al., 2014; Anzabi et al., 2023). However, information on the functional roles and interactive effects of VC and VE in aquaculture species still remains limited. Thus, this review analyses and summarizes the results collected from numerous studies to elucidate the roles and interactive effects of VC and VE on the growth, feed utilization, immune function, health, and body composition of aquaculture species.

2. Effects of Vitamins C and E on Aquaculture Species

2.1. Effects of vitamins C and E on growth and feed utilization

The supplementation of VC has shown significantly positive effects on the growth performance and feed efficiency of various aquaculture species. In marine species, the optimal dietary doses of VC were reported; for example, juvenile red sea bream (*Pagrus major*) with higher than 400 mg/kg to maintain specific growth rate (SGR) and feed conversion ratio (FCR) regardless of being fed the oxidized lipid diet (Gao et al., 2012b); parrot fish (*Oplegnathus fasciatus*) with 118 mg/kg in the form of L-ascorbyl-2-monophosphate to maximize weight gain (WG) (Wang et al., 2003); Coho salmon (*Oncorhynchus kisutch*) with 188.10 mg/kg to maximize SGR and 190.68 mg/kg to minimize FCR (Xu et al., 2022); coral trout (*Plectropomus leopardus*) with VC doses ranging from 255.25 to 273.84 mg/kg to improve growth performance (based on SGR and WG) (Zhu et al., 2022); walleye pollock (*Gadus chalcogrammus*) with VC doses ranged from 145.46 to 202.51 mg/

kg to achieve significantly higher growth (FBW, WG, and SGR) and improve feed utilization and protein efficiency ratio (FE and PER) (Lee et al., 2024); and hybrid grouper (*Epinephelus fuscoguttatus* ♀ × *Epinephelus lanceolatus* ♂) with 47.2 mg/kg to achieve minimum FCR and 156.2 mg/kg to attain the highest FBW and SGR (Ebi et al., 2018). In freshwater fish, the positive effects of VC were demonstrated with 1,200 mg/kg VC to obtain the best FCR, along with improved growth, PER in stinging catfish (*Heteropneustes fossilis*) (Alam et al., 2009). A co-supplementation of 300 mg/kg VC and 0.68 mg/kg nano-selenium generated synergistic effects on WG, SGR, and FCR improvement in juvenile mahseer (*Tor putitora*) (Khan et al., 2017). Similarly, the VC and nano-selenium combination was reported to maximize growth-related parameters (FBW, WG, and SGR) and reduced FCR with 500 mg/kg of VC and 1 mg/kg of nano-selenium in Nile tilapia (*Oreochromis niloticus*) (Dawood et al., 2020b). Furthermore, optimal doses of VC were reported to improve growth performance and feed utilization in various freshwater species. For example, 150 mg/kg was effective for freshwater prawn (*Macrobrachium rosenbergii*) (Asaikkutti et al., 2016), while 250.12 mg/kg was optimal for red swamp crayfish (*Procambarus clarkii*) (Kong et al., 2021). In channel catfish (*Ictalurus punctatus*), the effective range was reported to be between 143 and 573 mg/kg (Yadav et al., 2020), and for fingerling *Channa punctatus* (Bloch), 40 mg/kg was sufficient (Zehra & Khan, 2021). A summary of dietary VC recommendations for different fish species is presented in Table 1.

The published results indicated that the recommended dosages varied significantly among species, including freshwater, marine, brackish, and diadromous, highlighting the diversity in VC requirements. Freshwater fish had VC requirements ranging from 150 - 1,200 mg/kg LAA, 38.2 - 600 mg/kg LAPP, and 19.5 - 599 mg/kg LAMP. Similarly, marine

and blackish species had requirements of VC including 156 - 259.09 mg/kg LAA, 54.4 - 150 mg/kg LAMP, and 400 - 800 mg/kg of LAMP-Na/Ca. In diadromous species, VC requirements ranged from 79 mg/kg in Atlantic salmon (Li et al., 2007) to 1,000 mg/kg in Caspian roach (Nikjoo et al., 2023). Some freshwater species, such as Nile tilapia, require a much higher dose (400 - 500 mg/kg) compared to marine species like hybrid grouper, which require lower levels (148 - 156 mg/kg). Additionally, the inclusion of three different types of VC (e.g., LAA, LAMP, LAPP) highlighted the author's attention to the stability and bioavailability of VC. By identifying which forms of VC were used in studies, the role of vitamin form and its effectiveness were demonstrated in feed manufacturing in terms of shelf life and nutrient retention.

Similar to the variation observed in VC requirements, VE requirements also show species-specific and even sex-specific differences in aquaculture species. For example, Liang et al. (2021) recommended the optimal VE level at approximately 133.45 mg/kg for improved WG and PER in hybrid grouper (*Epinephelus fuscoguttatus* ♀ × *Epinephelus lanceolatus* ♂). Zhang et al. (2021) reported sex-specific differences in VE requirements in Nile tilapia. The optimal VE level for females was 120 mg/kg, resulting in the highest SGR and reproductive performance, whereas males required 160 mg/kg to achieve similar outcomes. While dietary VE content recommended less than 50 mg/kg for parrot fish (*Oplegnathus fasciatus*) (Galaz et al., 2010) and juvenile yellow catfish (*Pelteobagrus fulvidraco*) (Lu et al., 2016), higher than 100 mg/kg of VE was required to optimize growth and feed efficiency in grouper (*Epinephelus malabaricus*) (Lin & Shiau, 2005) and juvenile red sea bream (*Pagrus major*) (Gao et al., 2012a). Many studies on the dietary VE requirement of various aquaculture species are summarized in Table 2.

Table 1. Recommended dietary vitamin C levels for various aquaculture species

	Average IBW (g)	Average FBW (g)	Vitamin source ¹	Recommended dosage (mg/kg)	References
Freshwater species					
Channel catfish (<i>Ictalurus punctatus</i>)	22.5	33.55	LAPP	143	Yadav et al., 2020
Stinging catfish (<i>Heteropneustes fossilis</i>)	7.77	18.97	LAA	1,200	Alam et al., 2009
Nile tilapia (<i>Oreochromis niloticus</i>)	14.13	53.39	LAA	500	Dawood et al., 2020b
Nile tilapia (<i>Oreochromis niloticus</i>)	14.73	40.87	LAAP	400	Ibrahim et al., 2020
Mahseer fish (<i>Tor putitora</i>)	2.3	4.56	LAPP	300	Khan et al., 2017
Golden shiners (<i>Notemigonus crysoleucas</i>)	1.04	11.88	LAMP	19.5 - 218.5	Chen et al., 2003
Largemouth bass (<i>Micropterus salmoides</i>)	10.87	58.42	LAMP	120.46 - 145.35	Yusuf et al., 2021
Fingerling <i>Channa punctatus</i> (Bloch)	5.68	39.85	LAPP	38.2 - 47.9	Zehra & Khan, 2021
Red swamp crayfish (<i>Procambarus clarkii</i>)	7	14.39	LAA	265.67	Kong et al., 2021
Freshwater prawn (<i>Macrobrachium rosenbergii</i> .)	0.745	0.858	LAA	150	Asaikkutti et al., 2016
Marine and brackish species					
Hybrid grouper (<i>Epinephelus fuscoguttatus</i> ♀ × <i>Epinephelus lanceolatus</i> ♂)	7.71	66.78	LAA	156	Ebi et al., 2018
Hybrid grouper (<i>Epinephelus fuscoguttatus</i> ♀ × <i>Epinephelus lanceolatus</i> ♂)	15	N/A	LAPP	148	Cai et al., 2022
Red sea bream (<i>Pagrus major</i>)	3.4	786	LAMP- Na/Ca	400 - 800	Gao et al., 2012b
Parrot fish (<i>Oplegnathus fasciatus</i>)	3.9	12.8	LAMP	118	Wang et al., 2003
Large yellow croaker (<i>Larimichthys crocea</i>)	150.83	233.6	LAMP	150	Wei et al., 2020
Cobia (<i>Rachycentron canadum</i>)	5.5	56.34	LAMP	54.4 - 96.6	Zhou et al., 2012a
Cobia (<i>Rachycentron canadum</i>)	6.95	25.6	LAPP	400	Le et al., 2025
Coral trout (<i>Plectropomus leopardus</i>)	17.43	50.2	LAA	259.09	Zhu et al., 2022
Walleye pollock (<i>Gadus chalcogrammus</i>)	173.5	232.58	LAMP	156.42	Lee et al., 2024
Snubnose pompano (<i>Trachinotus blochii</i>)	81.23	234.23	LAPP	450	Ho et al., 2024
Pacific white shrimp (<i>Penaeus vannamei</i>)	0.0391	0.0821	LAPP	80.2	Ko & Lee, 2024
Ivory shell (<i>Babylonia areolata</i>)	0.11	0.45	LAMP	800	Li et al., 2024
Diadromous species					
Atlantic salmon (<i>Salmo salar</i>)	161.75	674	LAPP	79	Li et al., 2007
Coho salmon (<i>Oncorhynchus kisutch</i>)	183.19	420.36	LAAP	93.08 - 224.68	Xu et al., 2022
Caspian roach (<i>Rutilus rutilus caspicus</i>)	1.115	2.2525	LAA	1,000	Nikjoo et al., 2023

¹LAA, L-ascorbic acid; LAMP, L-ascorbyl-2-monophosphate; LAPP, L-ascorbyl-2-polyphosphate; LATP-Ca, L-ascorbate 2-Triphosphate Calcium; LAAP, L-ascorbic acid 2 phosphate; IBW, initial body weight; FBW, final body weight; N/A, not available.

Table 2. Recommended dietary vitamin E levels for various aquaculture species

	Average IBW (g)	Average FBW (g)	Vitamin source ¹	Recommended dosage (mg/kg)	References
Freshwater species					
Nile tilapia (<i>Oreochromis niloticus</i>)	14.15	52.01	DL-ATA	100	Dawood et al., 2020a
Nile tilapia (<i>Oreochromis niloticus</i>)	46.13	99.93	DL-ATA	100	Bazina et al., 2025
Female hybrid red tilapia (<i>O. niloticus</i> × <i>O. mossambicus</i>)	272.56	352.54	AT	50	Griesh et al., 2024
Grass carp (<i>Ctenopharyngodon idella</i>)	266.39	345.53	DL-ATA	116.2	Pan et al., 2017
Grass carp (<i>Ctenopharyngodon idella</i>)	9.78	67.24	DL-ATA	160	Xia et al., 2025
Crucian carp (<i>Carassius auratus</i>)	280	N/A	AT	100	Tang et al., 2024
Yellow catfish (<i>Pelteobagrus fulvidraco</i>)	2.01	37.75	DL-ATA	33	Lu et al., 2016
Sunshine bass (<i>Morone chrysops</i> ♀ × <i>Morone saxatilis</i> ♂)	25.1	112.06	DL-ATA (synthetic)	30	Trushenski & Kohler, 2006
Rohu fry (<i>Labeo rohita</i>)	0.58	7.72	DL-ATA	131.91	Sau et al., 2004
Marine and brackish species					
Gilthead seabream (<i>Sparus aurata</i> L.)	150	163.75	ATA	1200	Ortuño et al., 2003
Red sea bream (<i>Pagrus major</i>)	1.8	21.1	AT	100 - 200	Gao et al., 2012a
Black sea bream (<i>Acanthopagrus schlegeli</i>)	18.49	58.05	DL-ATA	150	Peng et al., 2009
Grouper (<i>Epinephelus malabaricus</i>)	7.8	N/A	DL-ATA	61 - 68 (4% lipid diet)	Wang et al., 2003
Hybrid grouper (<i>Epinephelus fuscoguttatus</i> ♀ × <i>Epinephelus lanceolatus</i> ♂)	8.79	N/A	DL-ATA	150	Wei et al., 2020
Hybrid grouper (<i>Epinephelus fuscoguttatus</i> ♀ × <i>Epinephelus lanceolatus</i> ♂)	20.48	N/A	DL-ATA	130.12 - 156.52	Xu et al., 2023
Parrot fish (<i>Oplegnathus fasciatus</i>)	20.15	53.7	DL-ATA	38	Galaz et al., 2010
Large yellow croaker (<i>Larimichthys crocea</i>)	3.01	22.08	DL-ATA	120	Yi et al., 2017
Snubnose pompano (<i>Trachinotus blochii</i>)	5.22	45.60	ATA	117.25 - 189.03	Pham et al., 2025
Juvenile cobia (<i>Rachycentron canadum</i>)	6.1	62.07	DL-ATA	78	Zhou et al., 2012b
Milkfish - <i>Chanos chanos</i> larvae	0.048	0.372	AT	205 - 243	Sivaramakrishnan et al., 2023

¹AT, α -tocopherol; ATA, α -tocopherol acetate; AAT, 2-ambo- α -tocopherol; D-ATA, D- α -tocopherol acetate; DL-ATA, DL- α -tocopheryl acetate; RRR-ATA, RRR- α -tocopheryl acetate, DLAR-ATA, DL-all-rac- α -tocopherol acetate.

The studies demonstrated the varying requirements for VE among various fish species. It was noted that species-specific supplementation is necessary for effective aquaculture nutrition. By specifying the VE sources, mainly DL-ATA (DL- α -tocopheryl acetate) and ATA (α -tocopheryl acetate), the studies provided insights into the bioavailability and stability of

each VE type, which is valuable for formulating feeds that retain vitamin efficacy and duration. Additionally, VE dosages should be adjusted based on dietary composition. For instance, in species like grouper, the recommended VE dosage varies with lipid content: 61 - 68 mg/kg for a 4% lipid diet and 104 - 115 mg/kg for a 9% lipid diet (Lin & Shiau, 2005).

2.2. Effects of vitamins C and E on fish health, immunity, and disease resistance

Dietary VC contributes significantly to enhancing fish health by supporting hematological functions, nutrient metabolism, and oxidative stability. The positive effects of dietary VC on hematological and immunological parameters have been shown for various aquaculture species. Generally, hematocrit (Hct), hemoglobin (Hb), and red blood cell (RBC) count increased significantly in fish fed with dietary VC levels, thereby improving oxygen transport and systemic resilience to stress in mahseer fish (Khan et al., 2017), channel catfish (Yadav et al., 2020), fingerling *Channa punctatus* (Zehra & Khan, 2021), and Nile tilapia (Sherif et al., 2024). Additionally, dietary VC stimulated digestive enzyme activity (protease, lipase, and trypsin), enhancing FCR and PER in species like whiteleg shrimp (Ko & Lee, 2024), coral trout (Zhu et al., 2022), and Caspian roach (Nikjoo et al., 2023). It also modulated stress biomarkers (cortisol and glucose) and maintained tissue integrity via increased collagen synthesis and reduced lipid peroxidation (Ibrahim et al., 2020; Le et al., 2025).

In terms of disease resistance, dietary VC enhances antioxidant defenses by increasing antioxidant enzyme activities in fish serum, such as glutathione peroxidase (GPx), catalase (CAT), superoxide dismutase (SOD), and total antioxidant capacity (TAC). Simultaneously, it reduced malondialdehyde (MDA) levels, indicating protection against lipid peroxidation (Sherif et al., 2024). Dietary VC reduced histological damage in organs such as gills, liver, and intestine under chemical stress (e.g., diazinon pesticide in Caspian roach) (Nikjoo et al., 2023) as well as under bacterial and viral challenges (e.g., *Aeromonas sobria* in Nile tilapia) (Ibrahim et al., 2020); white spot syndrome virus in red swamp crayfish (Kong et al., 2021); *Vibrio harveyi* in coral trout (Zhu et al., 2022); and *Vibrio*

parahaemolyticus in whiteleg shrimp (Ko & Lee, 2024). Particularly, activities of immune-related enzymes in fish serum have been widely studied, including lysozyme activity, a key indicator of immune response (Khan et al., 2017; Ibrahim et al., 2020; Kong et al., 2021), alkaline phosphatase (AKP) activity associates with improved immune function (Xu et al., 2022; Zhu et al., 2022; Nikjoo et al., 2023). In addition, higher dietary VC levels boosted lysozyme activity, phenoloxidase (PO), and nitric oxide synthase (NOS) in Nile tilapia (Ibrahim et al., 2020), in red swamp crayfish (Kong et al., 2021).

In addition to the roles of VC, VE contributes to maintaining fish health by stabilizing cell membranes, mitigating oxidative damage, and enhancing immunophysiological responses in various aquaculture species. Hematologically, VE supplementation raised RBC, Hb, and WBC levels, and immunoglobulin concentrations in experimental fish, indicating enhanced oxygen-carrying capacity and physiological resilience (Lin & Shiau, 2005; Zhou et al., 2012b; Griesh et al., 2024). Immunologically, VE stimulated non-specific defense mechanisms, such as enhanced lysozyme activity, IgM concentrations, phagocytic activity, and immune-related gene expression (Xu et al., 2023; Bazina et al., 2025). The VE also upregulated antioxidant-related genes and improved the activity of enzymes like GPx and CAT, leading to reduced oxidative stress and better membrane integrity. Additionally, histological analysis revealed that fish fed with higher dietary VE levels exhibited longer intestinal villi and higher lymphoid cell concentration in the lamina propria, contributing to enhanced digestive and absorptive function as well as mucosal barrier protection (Sivaramakrishnan et al., 2023; Bazina et al., 2025). These benefits enhanced disease resistance, as shown by reduced mortality and improved tissue histology in fish challenged with *Streptococcus agalactiae* and *Aspergillus flavus* (Bazina et al., 2025; Pham et al., 2025).

2.3. Effects of vitamins C and E on body composition and nutrient deposition

Dietary VC levels have shown important effects on improving nutrient deposition and body composition in fish by supporting protein metabolism, digestive function, collagen synthesis, and growth-related hormonal regulation. Studies in species like seaperch, pollock, tilapia, and murrel reported higher muscle or whole-body protein levels and improved PER when fish were fed VC-supplemented diets, PER rose to 2.44 in seaperch (Luc et al., 2021), to 2.09 in tilapia (Eid et al., 2020), and protein content reached 172 g/kg in murrel (Zehra & Khan, 2021). These effects were mechanistically linked to upregulation of anabolic genes such as IGF-I, IGF-II, and growth hormone, enhancing muscle protein synthesis, as shown in largemouth bass (Yusuf et al., 2021). Additionally, VC enhanced digestive capacity through increased protease, lipase, and amylase activities, which improved nutrient breakdown and absorption efficiency. Protease activity peaked at 6.16 U/mg in Caspian roach (Nikjoo et al., 2023), and similar improvements were seen in coral trout (Zhu et al., 2022), tilapia (Ibrahim et al., 2020), and shrimp (Ko & Lee, 2024). In carp, intestinal absorption was further supported by taller villi and more goblet cells (Labh, 2024). These physiological changes led to improved FCR across various fish species, such as 1.50 in carp (Labh, 2024), 1.60 in tilapia (Eid et al., 2020), and 1.76 in pompano (Ho et al., 2024). In large yellow croaker, VC and proline co-supplementation also elevated muscle collagen crosslinking, contributing to improved muscle integrity and retention of structural protein (Wei et al., 2020).

In addition to promoting growth and digestion, VC plays a important role in preserving deposited nutrients by enhancing antioxidant defense, modulating lipid metabolism, and stabilizing tissue structure. Under oxidative stress, VC upregulated antioxidant enzymes

such as superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPx) while lowering malondialdehyde (MDA) levels, thus protecting lipids and proteins from degradation. This effect was seen in catfish (Yadav et al., 2020), silver catfish (Gomes et al., 2022), and abalone (Li et al., 2020). Moreover, in yellow croaker and abalone, VC decreased saturated fatty acids and increased beneficial polyunsaturated fatty acids (PUFAs) like DHA and EPA, leading to improved muscle quality and lean tissue development (Li et al., 2020; Wei et al., 2020). In coho salmon, hepatic VC concentrations reached 83.4 µg/g at optimal VC doses, showing strong retention and systemic availability (Xu et al., 2022). In shrimp, broodstock fed VC showed reduced triglycerides and cholesterol while upregulating GPx and CAT gene expression, maintaining metabolic stability and antioxidant homeostasis (Montalvo et al., 2022). Furthermore, VC has been shown to enhance collagen synthesis via enzymes, such as prolyl hydroxylase and lysyl oxidase, reinforcing tissue structure and contributing to better muscle texture and water-holding capacity (Wei et al., 2020). In general, these mechanisms show that VC not only facilitates efficient nutrient absorption and protein synthesis but also protects and stabilizes the tissue deposition, enhancing body composition in various aquaculture species.

In addition to VC, dietary VE has been widely recognized for its role in improving body composition and nutrient retention in farmed fish through its antioxidant and metabolic functions. According to Bera et al. (2022), dietary VE supported protein retention, reduced lipid oxidation, and protected essential fatty acids by interacting with VC. Bazina et al. (2025) found that VE combined with selenium improved protein and lipid deposition, digestive enzyme activity, and intestinal structure in Nile tilapia. Zhang et al. (2021) also reported improved feed efficiency and growth performance at optimal VE levels in Nile tilapia, reflecting better nutrient utilization.

Additional studies confirmed VE's role in preserving nutrients during growth and storage. Yadollahi et al. (2023) showed that VE helped maintain protein content and fatty acid stability in rainbow trout fillets during freezing. In hybrid grouper, Liang et al. (2021) and Huang et al. (2022) demonstrated that VE improved lipid metabolism, and reduced fat accumulation in the liver, and increased tissue α -tocopherol levels, supporting more efficient nutrient deposition.

3. Synergistic Interactions between Vitamins C and E

3.1. Synergistic interactions in fish growth and health

The synergistic effects of VC and VE supplementation on growth performance have been demonstrated in various fish species. In rainbow trout, the co-supplementation of dietary VC and VE significantly improved growth performance (FBW, WG, and SGR) and feed utilization (FCR, PER, and LER). These results were observed with the combined supplementation of 0.2 mg/kg nano-selenium, 200 mg/kg VC, and 60 mg/kg VE (Harsij et al., 2020), as well as with dietary levels of 400 mg/kg VC and 200 mg/kg VE (Anzabi et al., 2023). In Nile tilapia, Sherif et al. (2024) reported that dietary supplementation with nanoencapsulated VC (420 mg/kg) and VE (100 mg/kg), administered at 1 g/kg of fish feed, significantly improved growth performance, feed efficiency, and overall health status. Furthermore, previous studies investigated optimal VC and VE levels for enhancing growth and feed utilization in a variety of freshwater species, such as juvenile yellow perch (Lee & Dabrowski, 2004), Nile tilapia (Lim et al., 2010), juvenile discus fish (Liu et al., 2018), and hybrid catfish (Pitaksong et al., 2012), as summarized in Table 3.

In addition, numerous studies have investigated the synergistic interactions of VC and VE on fish growth, health, and immunity, aiming to determine optimal and balanced dosages for different fish species. Notable findings include co-supplementation of 600 mg/kg VC and 600 mg/kg VE in African catfish (Oginni et al., 2020), 40 mg/kg VC and 80 mg/kg VE in juvenile discus fish (Liu et al., 2018), 500 mg/kg VC and 125 mg/kg VE in hybrid catfish (Pitaksong et al., 2012), and 250 mg/kg VC and 160 mg/kg VE in juvenile yellow perch (Lee & Dabrowski, 2004). The optimal and balanced dosages of dietary VC and VE for co-supplementation in various aquaculture species are summarized in Table 3.

The studies provided synergistic benefits of VC and VE supplementation with practical dosages, serving as a guideline for feed formulation to enhance growth, health, and immunity. The combined vitamin dosages varied considerably, influenced by different factors such as fish species and stages, dietary lipid contents, applied vitamin forms, experimental rearing systems, and specific physiological functions that the vitamins are intended to support. For species-specific dosages, each species had distinct recommended dosages for VC and VE, ranging from lower levels (e.g., 25 mg/kg of VC for hybrid striped bass) (Sealey & Gatlin, 2002) to higher levels (e.g., 1,000 mg/kg of VC for Kuruma shrimp) (Nguyen et al., 2012), emphasizing the need for tailored supplementation. According to El-Sayed & Izquierdo (2022), several freshwater species exhibit relatively lower VE needs for improving growth performance, likely due to the low lipid content typically present in their diets (e.g., 50 mg/kg of VE for 6% lipid of Nile tilapia diet) (Lim et al., 2010), as compared with higher VE requirements of some marine species (e.g., 100 mg/kg of VE for 18.7% lipid of Japanese flounder diet) (Gao et al., 2014). In rainbow trout fed oxidized lipid diets, for example, higher doses of stable forms, L-ascorbyl-2-monophosphate

Table 3. Synergistic interaction and co-supplementation of VC and VE on growth, health, and immunity in various aquaculture species

Aquaculture species	Average IBW (g)	Average FBW (g)	Vitamin source ¹	Recommended dosage (mg/kg)	References
Freshwater aquaculture species					
African catfish (<i>Clarias gariepinus</i>)	14.03	N/A	VC:LAMP VE:DL-ATA	600 600	Oginni et al., 2020
Channel catfish (<i>Ictalurus punctatus</i>)	8.19	29.1	VC:LAPP VE:DL-ATA	100 50	Yildirim-Aksoy et al., 2008
Hybrid catfish	25.12	107.85	VC:LAMP VE:DL-ATA	500 125	Pitaksong et al., 2012
Nile tilapia (<i>Oreochromis niloticus</i>)	6.73	63.95	VC:LAAP-Na VE:D-ATA	100 50	Lim et al., 2010
Nile tilapia (<i>Oreochromis niloticus</i>)	31.0	83.8	VC:LAA VE:DL-ATA	420 100	Sherif et al., 2024
Rainbow trout (<i>Oncorhynchus mykiss</i>)	12.75	87.23	VC:LAA VE:DL-ATA	400 200	Anzabi et al., 2023
Rainbow trout (<i>Oncorhynchus mykiss</i>)	46.93	151.25	VC:LAMP VE:DL-ATA	500 400	Rahimnejad et al., 2021
Rainbow trout (<i>Oncorhynchus mykiss</i>)	11.89	44.14	VC:LAA VE:ATA VC:LAMP-Mg	200 60 250	Harsij et al., 2020
Yellow perch (<i>Perca flavescens</i>)	2.25	28.9	VE:DLAR-ATA-Na	160	Lee & Dabrowski, 2004
Discus fish (<i>Symphysodon haraldi</i>)	7.96	17.35	VC:LAAP-Mg	40 80	Liu et al., 2018
Golden shiners (<i>Notemigonus crysoleucas</i>)	0.79	3.71	VC:LAMP VE:DL-ATA	98 38	Chen et al., 2004
Marine and brackish aquaculture species					
Hybrid striped bass (<i>Morone chrysops</i> × <i>M. saxatilis</i>)	12	33.44	VC:LAPP VE:AAT	25 30	Sealey & Gatlin, 2002
Gilthead sea bream (<i>Sparus aurata</i>)	0.121	N/A	VC:LAA VE:AT	1,800 1,500	Izquierdo et al., 2019
Japanese flounder (<i>Paralichthys olivaceus</i>)	1.1	9.64	VC:LAA VE:AT	500 100	Gao et al., 2014
Milkfish (<i>Chanos chanos</i>) (Forsskal)	0.96	1.61	VC:LAMP VE:ATA	1,500 50	Azad et al., 2007
Kuruma shrimp (<i>Marsupenaeus japonicus</i>)	50	N/A	VC:LAPP VE:DL-ATA	1,000 600	Nguyen et al., 2012
Diadromous aquaculture species					
Atlantic salmon (<i>Salmo salar</i>)	18.3	82.95	VC:LAA VE:AT	190 150	Hamre et al., 2016

VC, vitamin C; VE, vitamin E; AT, α -tocopherol; ATA, α -tocopherol acetate; AAT, 2-ambo- α -tocopherol; D-ATA, D- α -tocopherol acetate; DL-ATA, DL- α -tocopheryl acetate; RRR-ATA, RRR- α -tocopheryl acetate, DLAR-ATA, DL-all-rac- α -tocopherol acetate.

(500 mg/kg) and DL- α -tocopheryl acetate (400 mg/kg), were effective in grow-out trout for enhancing immune and antioxidant responses (Rahimnejad et al., 2021), while lower doses of L-ascorbic acid (400 mg/kg) and DL- α -tocopheryl acetate (200 mg/kg) improved hematological parameters in juveniles (Anzabi et al., 2023). When combined with nano-selenium, lower doses of L-ascorbic acid (200 mg/kg) and α -tocopherol acetate (60 mg/kg) were sufficient to enhance growth, antioxidant capacity, and immune responses in juvenile rainbow trout under ammonia stress (Harsij et al., 2020).

3.2. Synergistic interactions in body composition and nutrient deposition

The co-supplementation of VC and VE in fish diets has been studied for its synergistic effects on body composition and nutrient deposition. Oginni et al. (2020) found that African catfish fed VC and VE in fumonisin B1-contaminated diets had improved crude protein and fat content in the flesh. The synergistic effects of VC and VE were attributed to their complementary antioxidant functions, which protect muscle cells from oxidative damage induced by fumonisin B1. The VE helps stabilize membrane lipids, while VC regenerates VE and scavenges aqueous radicals. Together, they preserve protein synthesis, reduce cellular stress, and promote nutrient retention in muscle. In rainbow trout, supplementing 500 mg/kg VC and 400 mg/kg VE in oxidized fish oil diets resulted in the highest DHA (22:6n-3) to EPA (20:5n-3) ratio in muscle tissue (Rahimnejad et al., 2021). Similarly, in meagre larvae, higher levels of VC and VE in diets containing 3% HUFA significantly increased body weight, total lipid, DHA, and total n-3 fatty acid contents (Kertaoui et al., 2015). These results demonstrated that co-supplementation of VC and VE enhanced lipid absorption, preserved polyunsaturated fatty acids (PUFA/HUFA), such as DHA and EPA, from oxidation, and improved

body composition. Mechanistically, VE acted as a membrane protector by scavenging lipid radicals, while VC regenerated VE to its active form, highlighting a synergistic antioxidant role (Rahimnejad et al., 2021). Moreover, the synergistic interaction between VC and VE also influenced tissue vitamin deposition in a dose-dependent manner. Sealey & Gatlin (2002) reported that increasing dietary levels of VC and VE significantly elevated their concentrations in the plasma and liver of hybrid striped bass. In yellow perch, dietary VC increased its levels in the liver and testis and enhanced VE content in sperm, suggesting a sparing effect (Lee & Dabrowski, 2004). Similarly, Nguyen et al. (2012) observed that co-supplementation of VC and VE in kuruma shrimp resulted in dose-dependent increases in tissue and egg concentrations of both vitamins. VE deposition was enhanced by increasing dietary VE and, notably, by high VC levels, while VC retention was also influenced by dietary VE, confirming a mutual sparing interaction. These findings confirm that tissue deposition of VC and VE is closely regulated by their dietary levels and mutual interaction.

3.3. Sparing effects of both vitamins affecting vitamin accumulation in fish tissues

Protective effects between both vitamins

Numerous studies have explored the sparing effects between VC and VE in various fish species, demonstrating how these vitamins could protect against each of their deficiencies. Chen et al. (2004) observed that higher levels of VC mitigated some VE deficiency signs in golden shiners, such as darkened skin and muscular atrophy. In yellow perch, Lee & Dabrowski (2004) reported that VC supplementation improved health and reproductive performance, even in the absence of sufficient dietary VE levels. The sparing effect between VC and VE is attributed to their complementary antioxidant roles. VE

protects membrane lipids by neutralizing peroxy radicals, while VC regenerates oxidized VE, sustaining its activity. This interaction allows each vitamin to partially compensate for the other's deficiency. Lim et al. (2010) found that dietary VC levels maintained liver VE levels in Nile tilapia when dietary VE was low, though VE primarily protected against mortality under *Streptococcus iniae* challenge. Yildirim-Aksoy et al. (2008) found that in catfish, VE supplementation at 23.1 mg/kg prevented VC deficiency symptoms, such as vertebral deformities, while VC enhanced liver α -tocopherol levels, suggesting a mutual protective effect.

Vitamin C sparing effect on vitamin E

Several studies have demonstrated the impact of dietary VC and VE supplementation on the accumulation of these vitamins in fish tissues. In channel catfish, higher levels of VC (2000 mg/kg) improved growth and feed efficiency even with low VE (23.1 mg/kg), and increased liver VE concentrations, suggesting a role for VC in preserving VE levels (Yildirim-Aksoy et al., 2008). Similarly, Lee & Dabrowski (2004) found that VC supplementation enhanced the accumulation of VE in fish tissues, particularly in the liver and sperm of yellow perch, supporting the idea that VC can regenerate VE in vivo. Further studies by Lim et al. (2010), Nguyen et al. (2012), and Pitaksong et al. (2012) confirmed that increased dietary VC enhanced the retention and accumulation of VE in various fish species, including in the liver, plasma, and reproductive tissues. Gao et al. (2014) also reported that higher dietary VC levels led to increased liver VE concentrations, while Hamre et al. (1997) found that VC deficiency significantly reduced liver VE levels in juvenile Atlantic salmon, highlighting the interdependence of these vitamins in tissue accumulation. Harsij et al. (2020) observed that VC supplementation increased tissue VE levels, especially in the liver and muscle, further

demonstrating its sparing effect by preventing VE depletion under stress. Lee & Dabrowski (2004) stated that in yellow perch, VC supplementation at 250 mg/kg significantly elevated liver VE levels, particularly in groups under low dietary VE (160 mg/kg), showing a clear sparing effect. Lim et al. (2010) reported that in Nile tilapia, high dietary VC (2000 mg/kg) increased liver VE concentrations, even with low VE levels, suggesting that VC helps maintain or enhance VE levels. Liu et al. (2018) and Pitaksong et al. (2012) observed similar effects in discus fish and hybrid catfish, respectively, where VC supplementation helped conserve VE, improving antioxidant capacity and reducing oxidative stress.

Vitamin E sparing effect on vitamin C

Yildirim-Aksoy et al. (2008) observed that in channel catfish, VE supplementation at 23.1 mg/kg prevented VC deficiency symptoms, such as vertebral deformities, even in the absence of dietary VC. However, optimal growth was achieved only when both vitamins were adequately supplied. Chen et al. (2004) also found that VE supplementation helped conserve VC, as evidenced by higher tissue concentrations of total ascorbic acid (TAA) and dehydroascorbic acid (DHAA) in fish fed VE-supplemented diets, indicating that VE helps conserve VC in fish tissues. Gao et al. (2014) demonstrated in red sea bream that increasing dietary levels of both VC and VE led to higher liver and plasma concentrations of these vitamins, showing their ability to regenerate one another under oxidative stress, thereby reducing tissue damage.

3.4. Pro-oxidant effects of excessive vitamin C and E supplementation

Pro-oxidant effects were reported to be caused by high doses of VC and VE, especially under certain conditions. Gao et al. (2014) found that excessive supplementation of VC and VE led to increased lipid peroxidation in fish

tissues, as evidenced by elevated TBARS values in the liver, suggesting a pro-oxidant response. Hamre et al. (1997) observed similar effects in juvenile Atlantic salmon, where high tissue levels of VE combined with low VC resulted in increased lipid peroxidation, indicating a pro-oxidant effect of VE in the absence of adequate VC. Excessive dietary VC and VE in fish have been associated with pro-oxidant effects, primarily due to disruptions in antioxidant balance. Mechanistically, high VE levels may lead to the accumulation of α -tocopheroxyl radicals, which, if not fully reduced by VC or glutathione, can initiate lipid peroxidation and cellular damage (El-Sayed & Izquierdo, 2022). Similarly, excessive VC may act as a pro-oxidant by over-reducing metal ions, generating reactive oxygen species (Poljšak & Ionescu, 2011). Izquierdo et al. (2019) noted that in marine larvae, excessive supplementation of VC and VE (exceeding 3,000 mg/kg) caused an imbalance, leading to the accumulation of pro-oxidant tocopheroxyl radicals and a reduction in VC storage, contributing to oxidative stress and skeletal anomalies. Rahimnejad et al. (2021) reported that high doses of these vitamins could function as pro-oxidants rather than antioxidants, with increased TBARS levels and decreased antioxidant enzyme activities (SOD, CAT). Whereas Wang et al. (2023) found that excessive VE supplementation (above 100 mg/kg) could result in growth retardation due to possible pro-oxidant activities. These findings emphasize the importance of balanced VC and VE supplementation to avoid oxidative stress and ensure optimal health outcomes in aquaculture species.

4. Conclusions

This review has provided beneficial values and a comprehensive analysis of the functional roles and effects of VC and VE on the growth, health, and body indices of aquaculture species. Exploiting the functional values of these vitamins in fish nutrition will lead to a better understanding of their role in the aquafeed industry. Despite many studies on the individual and combined effects of VC and VE for fish, there remain gaps in our knowledge of their precise functional roles, underlying mechanisms, and interactions among different aquaculture species. Thus, further investigations are needed to elucidate the long-term impacts of vitamin supplementation on growth performance, immune response, and product quality in diverse aquaculture systems. Furthermore, novel approaches and innovations in this field will be the key to advancing fish nutrition and health.

Conflict of interest

The authors declare no conflict of interest.

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