

REVIEW

The importance of vitamin E for farmed fish—A review

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Abstract

Vitamin E (VE) is composed of a group of fat-soluble molecules, from which the most active homologous is α -tocopherol. VE is a structural component of cell membranes with a potent chain-breaking antioxidant action, which plays a main role in several biological processes. In cultured fish, VE can prevent peroxidation of cellular and sub-cellular membrane phospholipids and also red blood cells, leading to maintaining the structural and functional integrity of animal cells. VE performs several other biological and metabolic functions, including improvement of the immune response, enhancing growth performance and feed efficiency, preventing muscle degeneration, reducing the risk of atherosclerosis, improving reproductive efficiency and larval performance, meat quality and shelf life of seafood. Besides, VE interacts with other micronutrients, especially vitamin C and selenium. Fish feed and fish flesh generally contain high concentrations of lipids, especially polyunsaturated fatty acids, which renders these lipids more susceptible to lipid peroxidation. Supplemental VE may, therefore, become necessary to prevent this peroxidation. However, the VE requirement of farmed aquatic animals varies significantly, depending on dietary contents of VC, selenium and lipid (unsaturated fatty acids). This review summarizes the current knowledge on the physiological functions of VE in farmed fish and shrimp, and the effects of supplemental VE on fish performance, reproduction, health and product quality. The future considerations of VE requirements of farmed fish in light of the predicted climate change have also been discussed, especially with regard to feed input supplies (fish meal and fish oil vs. plant proteins and oils) and weather temperature.

KEYWORDS

antioxidant, fish, lipids, selenium, vitamin E, vitamin E/vitamin C interaction

1 | INTRODUCTION

Vitamin E (VE) is a term that includes a group of fat-soluble molecules, from which the most active homologous is α -tocopherol. Thus, VE comprises at least ten homologous derivatives of a 6-chromanol ring with a phytol side chain, including tocopherols, tocotrienols and tocmonoenols. Among them, α -tocopherol (5, 7, 8-trimethyl tocol) (α -TOH) is the most widely distributed form of VE, with the highest biological activity and biopotency, in relation to its selective uptake and transport.^{1,2} VE is a structural component of cell membranes with a potent chain-breaking antioxidant action, which plays a main

role in several biological processes. In cultured fish and shrimps, VE improves growth and feed utilization; promotes health status and contributes to regulate the immune system and selenium (Se) metabolism; enhances reproductive performance and larval development and improves fillet quality and shelf life.³ Therefore, VE has always been added in aquafeeds, for almost all studied fish and crustacean species.⁴

In recent years, a large bulk of research has been devoted to determining the effects of VE on fish and shrimp performance, antioxidation, immunity, quality, and other biological activities and metabolic functions. These issues have been comprehensively

reviewed by Hamre,³ who deeply analysed and interpreted the published works on the role of VE in aquaculture. However, during the last decade, over 200 documents have been published on the role of VE in aquaculture and its effects on the quality of produced fish. Bringing all this diverse and scattered information to the target readers in a single review becomes necessary and timely. Nonetheless, a comprehensive review on this role is missing from current literature. A better understanding of the functions and applications of VE in aquaculture and its interactions with other nutrients is also lacking.

Therefore, this review analyses and discusses the published studies on the importance of VE for cultured finfish, with emphasis on the information published during recent years. The review was organized into five major sections: (1) role of VE in antioxidant protection; (2) interaction of VE with other dietary elements (namely vitamin C, lipids and selenium); (3) dietary VE requirements for growth, health and flesh quality of freshwater fish and marine fish; (4) dietary VE requirements for reproduction; and (5) future considerations. Other specific aspects of VE metabolism, such as absorption or transport, have been previously reviewed and are beyond the scope of this study.³⁻⁵

2 | ROLE OF VITAMIN E IN ANTIOXIDANT PROTECTION

Vitamin E is particularly important for fish and shrimps, since they are high in polyunsaturated fatty acids (PUFA), which are very susceptible to oxidation. Oxidation of PUFA results in the formation of a number of primary and secondary toxic products that can cause a wide range of problems in fish and shrimps, including oxidative stress, decrease in growth rates, reduction in immune response, loss of nutritive value, unpleasant flavour, or reduction of quality and shelf life.^{3,6-8} The peroxidation of fatty acid reduces membrane fluidity, increases the permeability of the membrane and inactivates membrane-bound enzymes.⁹ The antioxidant effects of VE have been widely investigated in several marine and freshwater fish. For instance, lipid peroxidation in liver and muscle was significantly reduced in juvenile Coho salmon (*Oncorhynchus kisutch*) fed high VE (≥ 50 IU VE kg^{-1} diet) compared to those fed a VE-free diet.¹⁰

Microcystins (MCs), which are a group of cyclic, water-soluble cyanotoxins produced by cyanobacteria and released into the water column can accumulate along the ecological food chain, resulting in animal poisoning.¹¹ MCs modulate antioxidant enzymes, leading to the formation of reactive oxygen species (ROS), which may cause oxidative damages to animal tissues.^{12,13} The protective effect of VE on MCs-induced oxidative damage in aquatic organisms has been demonstrated in Nile tilapia (*Oreochromis niloticus*).¹⁴ In this species, lipid peroxidation (LPO) increased when fish was exposed to MCs, whereas VE supplementation protected the fish from MCs-induced oxidative damage in a dose-response manner. Thus, VE supplementation enhances the activities of antioxidant enzymes, such as catalase (CAT), superoxide dismutase (SOD), glutathione peroxidase (GPX) and glutathione reductase (GR).

The accumulation of heavy metals, such as copper and cadmium, in the aquatic environment also promotes ROS production and inhibits antioxidant enzymes activities, leading to oxidative stress and impairment of antioxidant defence in fish.¹⁵ VE supplementation may counteract this oxidative damage and improve the performance of farmed fish. For instance, supplemental VE enhanced antioxidant defences in Nile tilapia fingerlings exposed to copper-oxychloride.¹⁶ Dietary VE supplementation has also similar protective effects and enhancement of immune response in Nile tilapia,¹⁷ grass carp (*Ctenopharyngodon idellus*),¹⁸ yellow catfish (*Pelteobagrus fulvidraco*)¹⁹ and largemouth bass (*Micropterus salmoides*).²⁰

In contrast with the above results, the protective role of VE supplementation against oxidative stress was not observed in other studies. This fact may be related to a series of factors such as fish species and size, water temperature, dietary lipid source or the interaction with other nutrients, which may affect VE efficiency as an antioxidant and also VE requirements.^{4,21-24} For example, feeding halibut (*Hippoglossus hippoglossus*) with oxidized oil does not increase the activity of antioxidant defence enzymes (GPX, GST and GR) and VE supplementation only reduced SOD.²² Similarly, dietary VE supplementation did not affect liver antioxidant enzymes activities, liver glutathione content, total mercaptans or phagocytic chemiluminescent response in Atlantic salmon smolt reared in freshwater, under normoxic and moderate oxidative stress.^{25,26} In salmonids, this moderate protective effect of VE against lipid peroxidation may be related to the presence of another antioxidant: astaxanthin. Astaxanthin can prevent VE from oxidation and in turn exhibit a vitamin-E-sparing effect.^{27,28} In addition, the high lipid contents in salmon diets may provide sufficient amount of VE, which may meet the VE requirement of these fish.²⁵ This suggests that in diets for salmonids, it would be unnecessary to supplement VE to promote antioxidant defences, overall health and growth, if sufficient amounts of astaxanthin and VE are provided by the raw materials used in feed formulation.

The antioxidant efficacy of VE supplementation may also be dependent on the dietary lipid content or fish size and developmental stage. Thus, fish that require low dietary lipid levels (such as tilapia) need also low levels of VE compared with fish that require high dietary lipids.^{17,29} Moreover, the increase in dietary PUFA also raises the VE requirements for antioxidant protection, particularly in fast growing species and young fish.³⁰⁻³² For instance, when gilthead seabream (*Sparus aurata*) larvae were fed increased dietary PUFA levels, elevation of VE supplementation improved growth, survival and PUFA contents in fish polar lipids.³⁰ Early life stages also require more VE than older stages as has been shown in gilthead seabream,^{29,33} meagre (*Argyrosomus regius*)³⁴⁻³⁶ and European seabass (*Dicentrarchus labrax*).³¹

The relationship between VE requirement and water temperature is also evident. At low temperatures, fish must regulate membrane bilayer fluidity, which is essential for cellular function under cold stress.^{37,38} Under such conditions, membrane homeostasis is secured by the production of high levels of low molecular weight, unsaturated fatty acids in cellular membrane lipids.^{37,39} However,

excessive production of unsaturated lipid makes cellular membranes more vulnerable to oxidative damage, which can impair cellular functions. Therefore, supplemental antioxidants such as VE can play a significant role in combating the fish cellular damage. This suggests that the VE requirement for fish increases with decreasing water temperature, as suggested by Cowey, Degener, Tacon, Youngson and Bell⁴⁰ who reported that VE requirement of rainbow trout may increase with decreasing water temperature. VE supplementation also improved blood parameters, ACH50 and survival of golden shiner (*Notemigonus crysoleucas*) exposed to heat stress, compared with VE-deficient fish.⁴¹ Besides, dietary lipid levels and sources modulate the response of Nile tilapia to cold stress,^{42,43} supporting the adaptive role of VE against cold stress in aquatic organisms.³⁸

The dietary levels of other antioxidants, or pro-oxidants, such as VC or selenium (Se) may also affect the VE requirements.^{3,29,36,44} In addition, the degree of lipid oxidation may affect the capability of fish to ingest these lipids and modulate their VE antioxidant response. For example, secondary lipid oxidation products (such as thiobarbituric acid-reactive substances; TBARS) have been reported to affect sensory characteristics of the oil, while primary lipid oxidation products (hydroperoxides) are odourless and tasteless.⁴⁵ Therefore, some fish can ingest oxidized lipids, whereas other fish cannot.

3 | INTERACTION OF VITAMIN E WITH OTHER DIETARY ELEMENTS

3.1 | Interaction of vitamin E with vitamin C

Vitamin C (VC) (ascorbic acid) is a water-soluble vitamin, which has an antioxidant potential, can reduce the oxidative stress in animals and inactivate oxidative free radicals produced by cellular activities or other stressors.^{46–48} Most of these radicals are reactive oxygen species (ROS), including hydrogen peroxide, hydroxyl radical and superoxide anion, which can damage cellular membrane components, such as lipids, carbohydrates, proteins and DNA.⁴⁹ Thus, VC is considered a reducing agent (ie electron donor), playing a significant role as an antioxidant, which can scavenge the free radicals and ROS, and in turn, prevent cellular radical damage, protect cell membrane and cytosol substances and restore VE when both vitamins are available. The ability of VC to restore or spare VE from membrane α -tocopherol radicals is necessary for its antioxidant function.⁵⁰ This means that both VC and VE work synergistically as major antioxidants, growth promoters and immune response stimulators. They also perform many other physiological functions in farmed aquatic animals.^{1,47,51} However, VC cannot be synthesized in vivo, because fish lack L-gulonolactone oxidase enzyme, which is required for VC biosynthesis.⁵² Therefore, exogenous VC is essential for fish performance and physiological functions.

The VE-VC interaction has been investigated in several fish species, including gilthead sea bream,^{53–55} channel catfish (*Ictalurus punctatus*),^{56,57} red sea bream (*Pagrus major*),⁵⁸ Atlantic

salmon,^{59,60} rainbow trout,⁶¹ Nile tilapia,⁶² yellow perch (*Perca flavescens*),⁶³ sturgeon (*Acipenser fulvescens*),⁶⁴ meagre (*Argyrosomus regius*),³⁵ Japanese flounder (*Paralichthys olivaceus*)⁶⁵ and discus fish (*Symphysodon haraldi*).⁴⁴ The interactive effects of these two vitamins on these fish species can lead to the following benefits.

3.1.1 | Prevention of lipid peroxidation

Malondialdehyde (MDA) is a highly reactive compound, formed as one of the products of lipid peroxidation, leading to cellular damage and dysfunction; therefore, it is considered a strong biomarker for oxidative stress.⁶⁶ The activity of antioxidant enzymes, such as SOD, CAT or GPX, is also an indicator of lipid peroxidation and cellular damage.⁴⁷ Increased secretion of these enzymes prevents lipid peroxidation and cellular damage.

The coexistence of VE and VC at appropriate ratios can exert synergistic antioxidant effects, leading to modulation of the above-mentioned oxidative stress indicators, avoidance of cellular radical damage and prevention of lipid peroxidation.⁶⁷ For example, high supplemental VC and VE in discus fish (*Symphysodon haraldi*) diets led to increasing total antioxidant capacity and decreasing total SOD activity.⁴⁴ Also, high dietary VC concentration significantly reduced the levels of secondary lipid oxidation products (TBARS) in hybrid tilapia (*Oreochromis niloticus* × *O. aureus*) fed a VE-deficient diet.⁶⁸ This finding suggests that VC can suppress lipid peroxidation and protect the cells against oxidative stress. Similar results were also reported on Atlantic salmon,⁶⁰ channel catfish^{56,69,70} or European seabass,⁷¹ where dietary VC protected these fish from VE deficiency and increased their tissue concentrations of α -tocopherol. The interactive effect of dietary VC and VE on lipid metabolism in red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegelii*) has also been confirmed by Ji, Om, Yoshimatsu, Hayashi, Umino and Nakagawa.⁷²

Both VC and VE are also involved in the hypothalamic-sympathetic-chromaffin cell axis and interfere in stress responses, where they protect the leucocyte functions.⁵⁴ VC is also able to spare VE from membrane α -tocopherol radicals, inducing an antioxidant function.⁵⁰ Thus, VC interaction affects lipid metabolism by accelerating VE retention and/or preventing VE oxidation; suggesting the strong lipid antioxidant effect of VC, which acts synergistically with VE to improve fish health and vitality.

The VC-VE interaction mechanism has been related to the varying sensitivity to VE deficiency in farmed fish species.^{70,73} When channel catfish were fed VC-deficient diets, they exhibited reduced growth performance, regardless of VE supplementation. Also, symptoms of VE deficiency were not detected in fish fed a VE-deficient diet with supplemental VC.^{56,70} Similarly, the protective role of VC in the absence or deficiency of VE has been demonstrated in rainbow trout and Atlantic salmon.^{74,75}

On the other hand, vitamins C and E can act as pro-oxidants in vivo when given in excess, causing oxidative stress. Excessive amounts of both vitamins may lead to a significant reduction and

imbalance in the VC/VE ratio, and in turn, impair the amount of VC required for VE restoration, as demonstrated in Atlantic salmon.⁵⁹ This would lead to the accumulation of pro-oxidant tocopheroxyl radicals, which would promote irreversible oxidation of VC³ and reduce the VC content in fish body.²⁹ The pro-oxidant effect of VC and VE has been demonstrated in sturgeon⁶⁴; where excessive doses of VC or VE led to increased phospholipid peroxidation of dehydroascorbic acid reductase activity; causing adverse effects on physiological functions, including the pro-oxidative effects. Similarly, when gilthead seabream larvae were fed high levels of VC and VE (up to 3000 mg kg⁻¹), the expression of antioxidant enzymes genes was up-regulated, bone anomalies were increased and survival was reduced, indicating a strong pro-oxidant effect.²⁹ Moreover, dietary supplementation with taurine, another nutrient with antioxidant properties, mitigated these symptoms.²⁹ These studies suggest that appropriate levels of VC and VE, and the ratio between them, are necessary for exerting their antioxidant effects and optimizing their metabolism.^{73,75} Meanwhile, the antioxidant synergism between VE and VC is expected to be more evident when high contents of PUFA are included in fish diets, as demonstrated in seabass larvae.⁷¹

3.1.2 | Role of VE/VC ratio in improving fish growth and health status

The ratio between vitamins C and E in fish feeds is essential for optimum growth, immune response and disease resistance. As mentioned above, both vitamins have synergistic effect on growth performance and health status of farmed aquatic animals. Earlier researches suggested a sparing effect of VC on VE when high levels of VC are supplemented to VE-deficient feeds. VE sparing has been reported in Atlantic salmon,⁶⁰ hybrid tilapia⁶⁸ and channel catfish.⁵⁶ About 100 mg dietary VC kg⁻¹ sufficiently improved growth and feed efficiency of Nile tilapia, whereas the amount of VE contained in the basal diet was sufficient to support fish performance.⁷⁶ However, 50 mg VE kg⁻¹ was necessary for optimum survival when dietary VC was deficient. Increasing dietary VC increased liver VE concentration, while supplemental VE did not affect liver VC. On the other hand, excessive dietary VC or VE did not improve the immune response. Supplemental VC at 100 mg kg⁻¹ feed improved growth, feed efficiency, survival and haematological parameters, and prevented vertebral deformity in channel catfish fed diets with different VC.⁵⁶ Increasing dietary VC increased liver α -tocopherol, supporting the assumption of sparing effect of VC on VE. The growth of darkbarbel catfish (*Pelteobagrus vachelli*) also increased with increasing both dietary linolenic acid and VC levels, whereas a VC-deficient diet inhibited the activities of antioxidant enzymes, immunity and disease resistance.⁷⁷ Meanwhile, higher VE levels improved immune responses against *Aeromonas hydrophila* challenge.⁷⁸ This finding suggests that high dietary linolenic acid, VC and VE can enhance the immune response and resistance in darkbarbel catfish challenged with *A. hydrophila*.

3.2 | Interaction of VE with dietary fatty acids and oxidized oils

As mentioned above (Role of VE in antioxidant protection), fish diets and tissues containing large amounts of highly unsaturated fatty acids (HUFA) are susceptible to lipid oxidation, releasing a number of toxic products, and causing several problems to animals.^{3,6-8,79,80} The presence of VE in fish body, as an antioxidant, prevents lipid oxidation, while decreased VE concentration decreases the VE/PUFA ratio.⁸¹ In addition, VE plays a significant role in the desaturation process of n-3 and n-6 PUFA, through the regulation of the microsomal electron chain, which is a part of the desaturase complex.⁸² This means that increasing dietary HUFA contents increases the requirement for VE in farmed fish.^{1,57,83,84} In support, vitamin E requirement of common carp (*Cyprinus carpio*),⁸⁵ blue tilapia (*Oreochromis aureus*),⁸³ grouper (*Epinephelus malabaricus*)⁸⁴ increased with increasing dietary lipid (PUFA) levels. In addition, Lim, Yildirim-Aksoy, Shelby, Li and Klesius⁵⁷ found that VE concentration in channel catfish liver was related to dietary levels of VE, but was negatively correlated with dietary lipid (fish oil) levels. High supplementation of VE (200 mg kg⁻¹ diet) significantly reduced liver VE at increasing dietary fish oil. These results support the role of VE as an antioxidant, preventing lipid oxidation.

Fish oils rich in PUFAs, especially n-3 HUFA such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), are highly susceptible to peroxidation during processing and storage.^{9,22} This process generally leads to several negative impacts, including cell biomembrane damage,^{86,87} deterioration in animal health, growth and feed efficiency^{3,88} and product quality.⁷ The use of oxidized oil in fish feeds has also been reported to cause skeletal abnormalities,⁸⁹ reduce blood glucose,⁹⁰ increase haemoglobin level and glycolytic activity,⁹¹ and reduce VE concentration in fish tissues.^{92,93} These symptoms can be partially or totally alleviated when α -tocopherol is supplemented at appropriate levels.

On the other hand, progression of lipid peroxidation of frozen seafood products leads to a decrease in α -tocopherol concentrations in these products.⁹⁴ This, in turn, leads to deterioration in the quality of seafood. Therefore, supplementation of VE to oxidized lipid in aquaculture feed has been shown to reduce lipid peroxidation and improve fish performance, health status and product quality, as demonstrated in sea bream (*Acanthopagrus schlegelii*),⁸⁸ hybrid tilapia (*Oreochromis niloticus* \times *O. aureus*)⁹⁵ and turbot (*Scophthalmus maximus*) and gilthead sea bream (*S. aurata*).^{22,96}

3.3 | Interaction of VE with dietary selenium

Selenium (Se) is an indispensable trace element for living animals, due to the role it plays as an antioxidant. It is incorporated in glutathione peroxidases (GPX), which is an important defence wall against peroxidation, by oxidizing and destroying the free radicals (peroxides), and saving glutathione (GSH) in a reduced form.³ Both Se and VE are biological antioxidants, used to prevent the damage of

cell membranes, caused by PUFA peroxidation.⁹⁷ The presence of Se can reduce the VE requirement for maintenance and can also help in retention of VE in animal tissues and in blood plasma lipoproteins. Similarly, VE has the ability to reduce Se requirement by preventing loss of Se from the body, or by maintaining its active form. This interaction leads to the reduction of the amount of GPX needed for peroxides destruction.

The interaction between VE and Se has been well investigated in many fish species, including rainbow trout (*Oncorhynchus mykiss*),^{98–101} grouper (*Epinephelus malabaricus*),¹⁰² yellowtail kingfish (*Seriola lalandi*),^{103,104} Nile tilapia (*Oreochromis niloticus*),¹⁰⁵ largemouth bass (*Micropterus salmoide*)⁴⁵ and hybrid striped bass (*Morone chrysops* × *M. saxatilis*).¹⁰⁶ These studies demonstrated that VE and Se act synergistically and can spare the metabolic requirements of one another. Also, deficiency of dietary Se may result in reduced concentrations of tissue VE, whereas the deficiency of both micronutrients leads to anaemia, muscular dystrophy and proteins in plasma.^{70,107–109} This means that sufficient supplementation of either VE or Se can meet the deficiency of the other.

The positive interactive sparing effects between dietary Se and VE were demonstrated in grouper (*E. malabaricus*)¹⁰² and yellowtail kingfish (*S. lalandi*).¹⁰³ Increasing supplemental Se improved growth rates of fish fed diets containing low levels of (or deficient in) VE, whereas simultaneous application of both Se and VE improved growth and health indices. Also, dietary supplementation of Nano Se and/or VE improved the growth, intestinal health, blood parameters, oxidative status, and immune-related gene expression of Nile tilapia (*O. niloticus*)¹⁰⁵ and rainbow trout.⁹⁸ The combination of both micronutrients also provides synergistic effects in modulating the high density stress-related haematological responses. This can prevent the effects of oxidative stress and improve antioxidant status and innate immune responses, as reported in rainbow trout.¹⁰¹ A combination of Nano Se, VC and VE also increased growth performance, antioxidant capacity and immunity in rainbow trout juveniles exposed to ammonia stress.¹¹⁰

Dietary supplementation of both VE and Se has also been found to protect fish from the oxidative damage against dietary oil oxidation. This effect has been attributed to the reduction of glutathione and liver and muscle malondialdehyde (MDA) contents, and suppression of hepatic catalase activities.^{45,105} For example, largemouth bass (*M. salmoide*) fed oxidized oil suffer from increased CAT activity, poor growth and impaired feed utilization, whereas Se supplementation increased liver and muscle lipid contents and VE lead to reduced hepatic catalase activities.⁴⁵

On the contrary, studies on hybrid bass (*Morone chrysops* × *M. saxatilis*) revealed that Se supplementation neither affects growth performance nor has any interaction with dietary VE.^{106,111} These studies suggested that the basal diets may have contained sufficient amount of Se to meet the fish requirement, as supported by the lack of Se deficiency signs in fish fed the basal diets without additional Se supplementation. The lack of synergistic effects of dietary VC, VE and Se on growth performance of Nile tilapia and their disease resistance to *Edwardsiella tarda* has also been documented.²¹ However,

sufficient dietary supplementation of VE or VC (separately) significantly improved tilapia performance. It seems from these discussions that the metabolic response of fish to dietary VE and Se is species specific, depending on fish species and size, form and concentration of supplemental VE and Se, and the contents of these micronutrients in basal diets.

4 | DIETARY VITAMIN E REQUIREMENTS FOR GROWTH, HEALTH AND FLESH QUALITY

It is known that animals neither biosynthesize tocopherols nor store them in large amounts in their bodies.¹¹² Therefore, continuous supply of dietary VE is essential for animals' maintenance, growth and physiological functions. In this regard, several research papers have been published on the beneficial effects of dietary VE for growth, survival, feed efficiency, reproduction, antioxidant activity, and immune response of different farmed fish. Studied fish groups comprised several freshwater fish species, such as tilapia,^{62,95} channel catfish,^{56,57,113} African catfish,^{92,114} carps^{18,115,116} and rainbow trout.^{98–100,117,118} Marine species included sea breams,^{58,96,119,120} sea bass,^{20,45,71,121} salmon,^{26,122–124} cobia,¹²⁵ meagre^{34,35} and flounder.^{126–128}

This section overviews and analyses these publications. For facilitating the topic and assisting the readers extract the necessary information on VE requirements, the major findings of these studies are summarized in a comprehensive table (Table 1). Most of the recorded results were obtained by broken line regression. It should be emphasized, however, that there is a number of interactions of VE with other nutrients, such as VC, selenium and dietary lipid levels and composition, which affect fish performance and health status (as reviewed in the above sections). Therefore, it is necessary to consider these interactions when determining the VE requirement of farmed fish. In addition, the VE requirement may differ from one response variable to another. In other words, the amount of VE required for growth, antioxidant capacity, immunity response, meat quality or reproductive efficiency can vary significantly among species, and even among different sizes in the same species.

4.1 | Vitamin E requirements for freshwater fish

As mentioned above, the VE requirement of farmed fish varies significantly, depending on farmed species and size, dietary lipid sources and levels, and culture conditions (see Table 1 for details). The function for which VE is supplied also has a significant effect on its dietary requirement. Relatively low VE requirements were reported for a number of freshwater fish species, presumably due to the relatively low lipid contents in their diets. For example, about 40–66 mg VE kg⁻¹ feed was sufficient for improving growth performance of sub-adult Nile tilapia,^{17,129} whereas higher amounts (100–200 mg VE kg⁻¹) were required for fingerlings.⁶² More than 10-fold increase

TABLE 1 A summary of the effects of vitamin E on performance and health status of different farmed fish species

	VE level (mg kg ⁻¹ feed)			
Species (wt. g fish ⁻¹)	Tested	Required	Remarks	Reference
Freshwater fish				
Nile tilapia (<i>O. niloticus</i>) (79.37)	0–1000	>40	Higher levels (574–582 mg kg ⁻¹) were required for optimum fillet texture	17
GIFT Nile tilapia (<i>O. niloticus</i>) (80.3)	0–240	43.2–45.8 (6% lipid) 66–76 (13% lipid)	Requirement increased with increasing dietary lipids	129
GIFT Nile tilapia (<i>O. niloticus</i>) (0.66)	0–320	80 (growth) 160–320 (VER)	VE deficiency reduced growth, fat metabolism and disrupted the inflammatory response. Optimum VE improved growth and the inflammatory response and AC in fish exposed to <i>S. iniae</i>	130
Nile tilapia (<i>O. niloticus</i>) (7.16)	0–200	100–200	Increasing dietary lipid to 14% decreased liver VE. Immune response decreased in fish fed 10 or 14% lipids, but increased at 100 or 200 mg VE kg ⁻¹	62
Hybrid (<i>O. niloticus</i> × <i>O. aureus</i>) (1.45)	0–300 IU kg ⁻¹	62.5 IU kg ⁻¹	Tissue VE and liver glutathione increased with increasing VE	95
Grass carp (<i>C. idella</i>) (11.2)	0–400	100.36	VE supplementation improved growth rates and enhanced AC	18
Grass carp (<i>C. idella</i>) (266.4)	0–225	116.2–130.9	VE deficiency depressed GR and immune response, and disturbed structural integrity of the skin, spleen and Kidney	116
Rohu (<i>L. rohita</i>) (0.58)	0–200	131.91	Fish fed diets containing <100 mg VE kg ⁻¹ had lower GR	132
Yellow catfish (<i>P. fulvidraco</i>) (2.01)	19.6–156.9	33 (growth) 46 (lysozyme)	Dietary VE improved GR, FE, antioxidant activity and cumulative survival following challenge with <i>A. hydrophila</i>	19
Darkbarbel catfish (<i>P. vachelli</i>) (0.99)	50–400	400	Fish were fed 2, 4 and 6% linseed oil. At 2% dietary linseed oil and 400 mg VE kg ⁻¹ , negative effects of ammonia mitigated	78
Channel catfish (<i>I. punctatus</i>) (3.18)	50–200	50	The diets contained 6, 10 and 14 fish oil. Liver VE increased with increasing dietary VE, but decreased with increasing dietary fish oil	57
Channel catfish (<i>I. punctatus</i>) (5.2)	0–1000	50–100	Dietary VE improved GR, digestive enzymes activity and intestinal structure and function	133
Japanese eel ^a (<i>A. japonica</i>) (15)	0–120	>21.2–<21.6	VE improved GR and FE. GR was better at 15 mg VE kg ⁻¹ than at other VE levels	137
Japanese eel (<i>A. japonica</i>) (360)	0–428	212.9 (VER) 428 (immunity)	VE levels in liver, kidney, muscles and gonads were positively correlated with dietary VE	24
Snout bream (<i>M. amblycephala</i>) (0.59)	0–500	55.5	Supplementation of VE improved GR and increased EPA, DHA and total liver n-3 HUFA	131
Largemouth bass (<i>M. salmoides</i>) (7.54)	14.24–225.32	73 (growth) 108 (VER)	VE deficiency reduced GR, feed utilization, antioxidant and immunity states	20
Marine fish				
Gilthead seabream (<i>S. aurata</i>) (150)	100–1800	1200	At 1200 mg VE kg ⁻¹ , non-specific immune system was stimulated. Lower or higher dietary VE caused an imbalance in VE ratio with other antioxidants	140
Gilthead seabream (<i>S. aurata</i>) (5.66 mm TL)	128–3281	1783	Highest survival and GR and lowest incidence of bone anomalies were achieved at 1783, 1921 and 7000 mg kg ⁻¹ VE, VC and taurine, respectively. Increasing dietary VE and VC to 3000 mg kg ⁻¹ led to unbalanced body VC/VE ratio and highest bone anomalies	29

TABLE 1 (Continued)

Species (wt. g fish ⁻¹)	VE level (mg kg ⁻¹ feed)		Remarks	Reference
	Tested	Required		
Gilthead seabream (<i>S. aurata</i>) (5.2 mm TL)	540 and 2900	2900	Increasing VE improved larval growth, especially at lower HUFA levels. 2900 mg VE kg ⁻¹ feed required only at the highest HUFA	30
European sea bass (<i>D. labrax</i>) (208)	139–942	>98	Tissue VE content increased with increasing dietary VE	138
Grouper (<i>E. Malabaricus</i>) (7.8)	0–800	61–68 (4% lipid) 104–115 (9% lipid)	Higher VE was required at high dietary lipid. Body VE was directly correlated with dietary VE. VE improved blood parameters and immune response	84
Japanese flounder (<i>P. olivaceus</i>) (40.5)	20–213	213	The highest non-specific immune responses were obtained at 213 mg VE kg ⁻¹ and 2.0% n-3 HUFA	128
Japanese flounder (<i>P. olivaceus</i>) (8.8)	0–1000	100	The diets contained high levels (10%) of FO or mixed VO. The lowest GR was obtained at VO with low VE. VO and too high or too low VE may affect inflammatory and oxidative stress	21
Coho salmon (<i>O. kisutch</i>) (385)	11–105 IU kg ⁻¹	>50	GR, FE and BC were not affected by dietary VE. Liver and muscle VE contents increased with increasing dietary VE	10
Black sea bream (<i>A. schlegelii</i>) (18.5)	150–800	>150	OFO reduced GR and survival. Supplemental VE improved GR and increased liver VE content	88
Meagre (<i>A. regius</i>) (62.9)	0–1500	451	Muscle HUFA increased, while SFA decreased, with increasing dietary VE. VE deficiency or excess may deteriorate fish health	34
Meagre (<i>A. regius</i>) larvae (30 dph)	40–800	800	Low levels of VE and VC (40 and 100 mg kg ⁻¹) improved larval growth, but did not prevent appearance of granulomas. Granulomatosis disappeared at 800 mg kg ⁻¹ VE and 2000 mg kg ⁻¹ VC	36
Cobia (<i>R. canadum</i>) (6.1)	10–120	78 (growth) 111 (lysozyme)	Liver VE increased with increasing dietary VE levels. VE enhanced GR, antioxidant status and non-specific immunity	125
Parrot Fish (<i>O. fasciatus</i>) (20.15)	0–500	38 (growth) >500 (immunity)	Liver VE increased with increasing dietary VE. No clinical signs or mortality of VE deficiency occurred	139
Northern whiting (<i>S. sihama</i>) (2.14)	4–198	100.37	Dietary VE improved GR, FE, immunity and oxidation resistance at genetic and enzymatic levels	49

Abbreviations: ARA, arachidonic acid; AC, antioxidant capacity; ACA, alternative complement activity; ATPase, adenosine triphosphatase; BC, body composition; CA, catalase activity; DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid; FT, fillet texture; FCR, feed conversion ratio; FE, feed efficiency; GIFT, genetically improved farmed tilapia; GR, growth rates; HUFA, highly unsaturated fatty acids; MDA, malondialdehyde; OFO, oxidized fish oil; RBA, respiratory burst activity; SFA, saturated fatty acids; SOD, superoxide dismutase; TAN, total ammonia nitrogen; TBARS, thiobarbituric acid-reactive substance; VC, vitamin C; VE, vitamin E; VER, vitamin E retention; VO, vegetable oils; WBC, white blood cells.

^a *Anguilla Japonica* are catadromous fish; spawning in the sea, but live parts of their life in fresh water. They are farmed mainly in freshwater and brackish water environments.

in VE was needed for fillet texture and serum antioxidant capacity¹⁷ and for VE retention in fish flesh and activation of the immune system response and antioxidant capacity in fish challenged with *Streptococcus iniae*.¹³⁰ A low dietary VE concentration (55.5 mg kg⁻¹) was also required for optimum performance of a cyprinid fish, the Blunt snout bream (*Megalobrama amblycephala*) larvae (0.59 g).¹³¹ However, early life stages of grass carp (*Ctenopharyngodon idellus*)^{18,116} and rohu (*Labeo rohita*)¹³² require more VE than older stages.

A wide discrepancy in VE requirements of catfish has been reported by different authors. Small amounts of VE supported growth rates, feed efficiency and antioxidant activity of yellow catfish (*Pelteobagrus fulvidraco*) (33–45 mg kg⁻¹)¹⁹ and channel catfish (*Ictalurus punctatus*) (50–100 mg VE kg⁻¹).¹³³ On the other hand, significantly higher amount of VE was required for optimum performance of darkbarbel catfish (*Pelteobagrus vachelli*).⁷⁸ These discrepancies have been attributed to the differences in fish sizes and

developmental stages, dietary lipid levels and sources, fatty acid composition and water temperature. For example, yellow catfish require much lower dietary lipid level (about 8–11%) (Han et al.¹³⁰; than darkbarbel catfish (about 20%),²³ which may justify the higher VE requirement of the later species. In addition, dietary lipid sources (coconut oil, perilla oil, sunflower oil and fish oil + sunflower oil) and fatty acid profiles significantly influenced antioxidant activities and immune response in yellow catfish.¹³⁴ Ma, Jin, Zhu, Li, Lu, Yuan, Xiong and Zhou¹³⁵ found also that moderate levels of dietary arachidonic acid (ARA) improved growth performance and antioxidant response of yellow catfish. The optimum combination of lipid level and water temperature (7.7% and 26.9°C) has also optimized growth performance, antioxidative activity and immune response of these fish.¹³⁶

The vitamin E requirement may also vary from one developmental stage to the other in the same species. Juvenile eel (15 g), for instance, require very little amount of VE (21 mg kg⁻¹) for optimum growth,¹³⁷ whereas sub-adult fish require much higher VE concentration in their diets for improving non-specific immune responses and high VE retention in the liver, kidney, muscles and gonads.²⁴ It is obvious from these findings that several factors affect the VE requirements of farmed fish. These factors should be considered during the evaluation of VE requirements of farmed fish, in order to achieve reliable results, and to make sound comparisons.

4.2 | Marine fish

One may assume that the VE requirements for marine fish are higher than those reported for freshwater fish, due to the high lipid and n-3 HUFA levels in marine fish diets. However, this assumption may not be always true, since some marine fish require low levels of dietary VE for optimum performance. For example, grouper (*Epinephelus Malabaricus*),⁸⁴ European sea bass,¹³⁸ coho salmon¹⁰ and cobia (*Rachycentron canadum*)¹²⁵ require less than 100 mg VE kg⁻¹ feed for optimum performance. Moreover, only 38 mg VE kg⁻¹ were sufficient to support the growth of parrotfish (*Oplegnathus fasciatus*), despite that >500 mg kg⁻¹ was required for optimum immune response.¹³⁹

On the contrary, some other marine fish species require much higher dietary VE levels for growth and health status. Sub-adult gilthead sea bream, for example, require 1200 mg kg⁻¹ feed for optimum health status and non-specific immune response.¹⁴⁰ In addition, much higher dietary VE supplementation is reported for larval sea bream.^{29,30} When the larvae were fed diets containing different levels of VC, VE and taurine, the highest survival, growth and osteocalcin gene expression and lowest incidence of bone anomalies were achieved at 1783, 1921 and 7000 mg kg⁻¹ VE, VC and taurine, respectively.²⁹ Moreover, when gilthead seabream larvae are fed extremely high dietary HUFA, even higher dietary VE levels seem to be needed for optimum performance.³⁰ This particular study also shows the antioxidant effect of VE and suggests a higher protection value when HUFA are limiting.³⁰ However, increasing dietary VE and

VC to 3000 mg kg⁻¹ results in unbalanced body VC/VE ratio, up-regulation of antioxidant enzymes genes, the highest incidence of bone anomalies and the lowest survival rates.²⁹

The above-mentioned factors (fish sizes and growth stages, dietary lipid and fatty acid profiles, other micronutrients, water temperature, etc.) which affect the VE requirement of freshwater fish (see the above section) may also affect the response of marine fish to dietary VE. It has been documented that when marine fish larvae are fed on inert diets, they become highly susceptible to oxidative stress, due to the high dietary content of LC-PUFA and pro-oxidants such as minerals.^{3,30,71} Therefore, the inclusion of high dietary antioxidants such as VE becomes necessary to prevent oxidative damage and improve larval survival and performance, as reported in sea bass larvae.⁷¹ These studies also showed that the presence of other dietary nutrients such as VC, Se or taurine (and their ratios with VE) also modulates VE requirements for marine fish.^{29,71} Also in meagre, VE requirement (800 mg kg⁻¹) is higher during early life stages than during later grow-out stages.³⁶

4.3 | Effects of vitamin E on seafood quality

It is well known that seafood is more susceptible to spoilage and oxidation during processing and storage than other food classes. This has been attributed to their high moisture contents, the presence of several volatile nitrogenous compounds with low molecular weights, the high contents of n-3 HUFA, especially in fatty fish, and the presence of psychrophilic bacteria, which can significantly reduce the quality of these products.^{7,141} As mentioned earlier, lipid peroxidation leads to the production of peroxy radicals, free fatty acids and product rancidity. As lipid peroxidation continues, VE concentration in seafood decreases,^{94,142} which may further deteriorate the quality of seafood products. This means that seafood should contain sufficient amounts of α -tocopherol to protect them against lipid oxidation.^{143–145}

A number of studies indicated that supplemental dietary VE significantly improved product quality of different fish products. When Coho salmon was fed different types of antioxidants, a VE-supplemented diet resulted in the best sensory and physical properties of the long-term frozen salmon product.¹⁴⁵ Fillet textural parameters, cohesiveness, resilience and chewiness of GIFT Nile tilapia were also significantly higher in fish fed VE-supplemented diets than in those offered a VE-deficient diet.¹⁷ The addition of VE also increased serum and muscle SOD and serum CAT activities, and decreased serum and muscle MDA levels, supporting the role of VE in antioxidant protection. Also, muscle HUFA in meagre (*Argyrosomus regius*) increased, and saturated fatty acids and TBARS values decreased, with increasing dietary VE.³⁴ Similarly, a positive correlation was also found between dietary VE levels and the concentrations of α -tocopherol in turbot (*S. maximus*) and Atlantic halibut (*H. hippoglossus*)¹⁴⁶ and rainbow trout fillet.¹⁴² Prolonged feeding with high VE diets also increased the proportion of total USFAs, PUFAs and n-3 FAs, and decreased the proportion of saturated fatty acids (SFAs)

and n-6 FAs. In addition, supplementation of tocopherols significantly reduced TBARS values in carp (*Ciprinus carpio*) fillets stored at 5°C, compared with tocopherol-deficient samples.¹⁴⁷

Vitamin E may also improve the fillet quality of fish fed oxidized fish oil (OFO), as has been demonstrated in red sea bream (*Pagrus major*).¹²⁰ The OFO-fed fish had high fillet TBARS values, and low VC and VE concentrations during storage, compared with fish fed fresh oil. Also, increasing supplemental VE increased fillet VE levels and reduced fillet TBARS values, whereas VC supplementation did not affect fillet quality parameters. Thus, the positive effects of VE on fillet quality of fish fed OFO have been related to the reduction of lipid peroxidation, saturated fatty acids and TBARS values, in addition to increasing body VE contents.^{88,95,138} The dietary and tissue contents of other antioxidants such as VC and Se may also contribute the quality of fish fed OFO.

5 | EFFECTS OF VITAMIN E ON REPRODUCTIVE PERFORMANCE

The metabolic rates in rapidly growing tissues are high, which may result in the production of high concentrations of free radicals, as suggested by Rudneva II.¹⁴⁸ This author found that the activity of antioxidant enzymes (lipoygenase, SOD, CAT, peroxidase and glutathione reductase) in five Black Sea fish species increased during

eggs development and in hatched larvae. This suggests that the presence of antioxidants is necessary for tissues protection against peroxidation, and therefore, VE may play a significant role in these metabolic processes. In this regard, high levels of VE were found in eggs and seminal fluid of European sea bass (*Dicentrarchus labrax*) before and after egg fertilization, and in embryos during development and at hatching, while low levels were observed in dead eggs and in embryos with low survival rates.¹⁴⁹ These findings suggest that VE is vital for egg and larval development in these fish. In addition, dietary supplementation of VE and arachidonic acid (ARA) had synergistic effects on non-specific immune responses in Japanese eel (*Anguilla japonica*) broodstock.¹⁵⁰ A linear correlation was also found between dietary VE and VE content in the ovarian tissue.

Consequently, the role of dietary VE in supporting gonadal development, reproductive processes, spawning performance and larval growth and survival has received considerable attention during the past two decades. The results of these researches are summarized in Table 2. These studies indicated that high dietary supplementation of VE can reduce egg deformity and abnormality and improve fish fecundity, egg development and larval quality, and also protect eggs from oxidation.^{151–155} VE can also improve sperm quality and protect sperm cells from oxidation.^{156,157}

On the other hand, VE-deficient diets may produce immature gonads and decrease egg fertilization and hatchability and larval survival.^{153,156,158,159} When zebrafish (*Danio rerio*)^{159,160} and goldfish

TABLE 2 Vitamin E requirement for optimum reproductive performance of farmed fish

Species	Dietary vitamin E levels (mg kg ⁻¹ feed)		Remarks	Reference
	Tested	Required		
Gilthead sea bream (<i>S. aurata</i>)	22–2010	2010	The diets contained different levels of HUFA (1.4–2.2%). Egg VE content increased only at very high dietary VE levels (2020 mg kg ⁻¹) at 1.4% HUFA	153
Turbot (<i>S. maximus</i>).	65.14–721.60	721.60	Dietary VE increased sperm concentration, size, motility, uniformity of mitochondrial size, integrity of mitochondria cristae and plasma membrane and VE contents in testis and liver	157
Swordtail (<i>X. helleri</i>)	0–1000	500	Gonad weight and GSI increased with increasing dietary VE up to 500 mg kg ⁻¹ , and declined thereafter. Early embryo stages were dominant in fish fed 250 and 1000 mg VE, whereas late stages were dominant at 500 mg VE kg ⁻¹ diet	158
Rainbow trout (<i>O. mykiss</i>)	300 and 500	300	Sperm numbers, motility and spermatocrit increased with the addition of VE, whereas fertilization rate was not affected	156
Nile tilapia (<i>O. niloticus</i>)	200–500	400	VE supplementation improved fecundity, spawning frequency, hatchability, larval production and survival. Fertilization rates, egg weight and diameter were not affected by dietary VE	154
Pindani (<i>P. socolofi</i>)	121.3–270.0	219.3	Reproductive performance, hatching rates and larval survival increased with increasing dietary VE levels up to 219.3 mg kg ⁻¹ , then levelled off or declined	155
Goldfish (<i>C. auratus</i>)	0–600	300	VE-lacking diet resulted in delayed spawning. Higher fecundity and better hatchability were obtained at 300 mg VE kg ⁻¹ feed	161

(*Carassius auratus*) broodstock¹⁶¹ were fed VE-deficient diets, they exhibited low fecundity and delayed spawning, and produced viable embryos with depleted VE concentrations, with higher malformation and mortality than embryos from broodstock fed VE-supplemented diets.

Vitamin E has been reported to mobilize (mainly via lipoproteins) from peripheral tissues during vitellogenesis in different fish species.^{162–164} When Japanese flounder *Paralichthys olivaceus* broodstock were fed a VE-supplemented diet (1000 mg kg⁻¹), α -tocopherol was associated with vitellogenesis and transported to, and preserved in, the gonads during the reproduction season.¹⁶⁴ After spawning, serum α -tocopherol was combined with the increasing lipoprotein. Besides, providing VE through primary pituitary cells in vitro stimulates the expression of gonadotropin hormones (follicle-stimulating hormone (FSH) and luteinizing hormone (LH)) in the pituitary of turbot (*S. maximus*).¹⁶⁵

6 | FUTURE CONSIDERATIONS

Despite aquaculture's rapid expansion, its sustainability faces some menaces related to climate change, including sea-level rise, global warming, changes in rainfall patterns, changes in water salinity and uncertainty of feed inputs supplies.¹⁶⁶ The expected impacts of climate change on aquaculture production include direct changes (physical, behavioural and physiological changes of farmed species in the production systems) and indirect changes (altering wind and water circulation, the primary and secondary productivity, structure of the ecosystems, input supplies, availability and prices, and product prices).^{167–169} However, the uncertainty of external input supplies and global warming will probably be the most determining parameters on the future of aquaculture. In this regard, the sustainability of aquaculture industry will likely require an adaptation to predicted climate change, in addition to appropriate mitigation measures.

6.1 | Uncertainty of external input supplies

The impact of climate change on capture fisheries will significantly affect fishmeal (FM) and fish oil (FO) supplies, prices and sustainability. In fact, the supply of FM and FO has already been declining in recent years, whereas their prices have sharply increased. FM and FO have traditionally been used as major nutritional inputs in aquaculture, especially for marine species, which require high levels of these two sources. However, the global shortage in their supply and continuous increase in their prices are a serious challenge facing aquaculture industry worldwide. As a result, the potential of plant proteins and oils (mainly oilseeds) in aquafeeds has been accelerating. Substantial amounts of research have been carried out on partial or total substitution of FM and FO with plant-based sources.^{170,171}

It is likely from the above prediction that the use of FM and FO in fish feeds will decline significantly. Consequently, the requirements

for VE will likely change. It is well documented that VE requirements increase at high levels of dietary n-3 PUFA (eg fish oil). In light of the expected heavy inclusion of plant proteins and oils (n-6 PUFA) in fish feeds, possibly lower dietary VE levels would be required to optimize fish performance and prevent lipid peroxidation.²⁵ The fish requirements for other micronutrients which are interacting with VE, such as Se and VC, may also change. This simply means that considerable attention in the future research must be directed to reevaluation of these micronutrients, in light of the expected plant-based aquafeed formulations.

6.2 | Impact of climate change

The increase or decrease in water temperature, as a result of climate change, may also affect the VE requirement and metabolism in farmed fish. Fish can adapt to cold temperatures by biochemical regulation of membrane bilayer fluidity, which is essential for cellular function at low temperatures.^{37,38} Under such conditions, membrane homeostasis is secured by the production of high levels of low molecular weight, unsaturated fatty acids in cellular membrane lipids.^{37,39} High lipid unsaturation would render cellular membranes vulnerable to oxidative damage, which can impair cellular functions. This means that VE may play a significant role as an antioxidant, to combat the expected cellular damage at low temperature. In support, Gieseg, Cuddihy, Hill and Davison¹⁷² found that Antarctic fish had plasma VE concentrations five to six times higher than in temperate water fish species, suggesting that Antarctic fish may be exposed to greater metabolic stress than temperate species. This indicates that VE may be required at greater amounts in cold-exposed fish species than in tropical or temperate species. However, these requirements will likely be species-specific and will also depend on the degree of coldness. Further research is needed to explore and clarify the relationship between dietary VE and cold stress.

Similarly, increasing environmental temperatures may modulate the VE requirements and metabolism. In land animals, for example, high temperature reduces the serum concentrations of vitamins, including VE and micro minerals.¹⁷³ Since VE is considered the first defence line against lipid peroxidation caused by heat stress, higher dietary levels of this micronutrient, together with other vitamins and minerals, are recommended under heat stress.^{173,174} Nonetheless, the VE requirements and the metabolism of farmed fish in response to heat stress are not well investigated. Only Chen, Lochmann, Goodwin, Praveen, Dabrowski and Lee⁴¹ reported that dietary VC and VE significantly affected the response of juvenile golden shiner (*Notemigonus crysoleucas*) to heat stress. When the fish were fed a VE-deficient diet and exposed to stressful water temperatures (36–37.8°C), they exhibited lower visceral VE concentrations, haematological parameters, alternative complement activity (ACH50) and survival than those fed VE-supplemented diets. This particular study suggests that fish, like land animals, may require higher dietary VE when exposed to heat stress. However, further research is needed to support this assumption. It is evident from the above

discussion that future research will have to reconsider the VE requirements of farmed fish under the expected heat or cold stresses, resulting from the changes in weather temperature.

7 | CONCLUSION

Vitamin E (VE) is composed of a group of fat-soluble molecules, from which α -tocopherol is the most active homologous. It is a structural component of cell membranes with a potent chain-breaking antioxidant action, which plays a main role in several biological processes. VE performs many functions in farmed fish, including prevention of peroxidation of cellular and subcellular membrane phospholipids and leading to maintaining the structural and functional integrity of animal cells, improvement of the immune response, enhancing growth performance and feed efficiency, preventing muscle degeneration, reducing the risk of atherosclerosis, interaction with a number of micronutrients especially VC and Se, improving reproductive efficiency and larval performance, and improving meat quality and shelf life of seafood. However, the role of VE as strong, fat-soluble antioxidant against lipid peroxidation remains the most investigated function.

The effects of VE depend on fish species and size, VE dose, lipid composition (polyunsaturated fatty acids; PUFA), presence or absence of other micronutrients, such as VC and Se. Generally speaking, marine fish require higher VE for lipid peroxidation protection and growth promotion than freshwater fish. Also, early life stages may require higher VE levels than latter grow-out stages. VE, VC and Se also act synergistically and can spare the metabolic requirements of one another.

The aquaculture sustainability, especially the certainty of external feed input supplies and environmental conditions (such as water temperature and salinity), will likely be affected by climate change. For example, fish meal (FM) and fish oil (FO), which have traditionally been used as major nutritional inputs in aquaculture, will be (and have already been) seriously affected by climate change, leading to global shortage in their supply and increase in their prices. Therefore, the requirements of farmed fish for dietary FM and FO should be reconsidered, whereas searching for FM and FO potential replacers must be encouraged. Plant protein and oil sources (such as oilseeds) are an ideal candidate to fill this predicted gap. The use of these sources in aquafeeds has already been escalating. Consequently, the requirements for VE will have to be reevaluated. The fish requirements for other micronutrients which act synergistically with VE, such as Se and VC, should also be reconsidered. In light of the expected heavy inclusion of these plant protein and oil sources in fish feeds, lower dietary VE levels may possibly be required to optimize fish performance and prevent lipid peroxidation. However, more research is needed to support this assumption.

Heat and cold stresses, resulting from climate change, affect the VE metabolism and, in turn modulate the VE requirement, in land animals. Higher levels of dietary VE (and other vitamins and minerals) have been recommended under heat stress. However, the VE requirement and metabolism of farmed fish in response to high or low temperatures are not well investigated. Farmed fish may require higher dietary VE when exposed to heat or cold stresses, but this

assumption requires further investigations. Generally speaking, future research should reconsider the VE requirements of farmed fish under the uncertainty of feed input supplies and the expected heat or cold stresses, resulting from the impacts of climate changes.


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