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Review Article

Vitamin A in crustaceans: a review of the actual knowledge and research perspectives

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ABSTRACT. Vitamin A is an indispensable nutrient in feeds for crustaceans and plays an important role in several metabolic aspects of this group of organisms. This work reviews current knowledge of vitamin A and its role in vision, systemic functions, reproduction, larval development, and the immunological response of crustaceans, as well as the dietary requirements of species of commercial importance.

Keywords: larval development; reproduction; retinoic acid; growth; retinol; retinal

INTRODUCTION

Vitamin A (vitA) is a nutrient that plays an important role in several metabolic functions in vertebrates, including vision, normal growth, reproduction, epithelial maintenance, mucus secretion and embryonic development (Hernández-Hernández & Hardy 2020). In crustaceans, however, information is still scarce. For several years, it was believed that its main role was related to vision (Cronin & Jinks 2001) as retinoids (mainly retinal) are not distributed throughout the body of crustaceans as in vertebrates but are rather concentrated in the eyes of the studied species (Dall 1995). However, recent evidence shows that vitA has a role in growth (Shiau & Chen 2000, Hernandez-Hernandez et al. 2009), larval development (Castillo et al. 2025), and sexual maturation (Liñan-Cabello & Paniagua 2004, Liñan-Cabello et al. 2004, Mengqing et al. 2004) of different species of decapod crustaceans. The mechanisms of vitA in crustaceans are not fully elucidated, except for vision (Goldsmith & Cronin 1993, Suzuki et al. 1993), and according to Albalat (2009), vitA could act as it does in vertebrates. However, crustaceans may have more efficient mechanisms in retinoid homeostasis. For this reason and considering the importance of this micronutrient in the different life stages of crustaceans, the present work reviews the actual knowledge of the role of vitA in vision, systemic functions, reproduction, larval development and immunological responses for this group of organisms, as well as the reported dietary requirements in species of commercial importance.

Vitamin A description

The term vitamin A (vitA) describes all molecules with biological activity of all-*trans*-retinol. Chemically, the parental structure of retinol (Rol) comprises a ring β-ionone (4-{2,6,6-trimethyl-2-cyclo-hexen-1-y1}-3-buten-2-one) that joins in the 6th position to a chain of three isoprenoid units (Eitenmiller & Landen 1999). The molecules with vitA activity and derived from Rol are known as retinoids and include Rol itself, retinal (Ral) and esters of retinol (Erol) (Combs 1998). Ral maintains the same chemical structure as Rol, but at the end of the isoprenoid chain the group alcohol (-CH_2OH) is substituted by an aldehyde group (-CHO).

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The Erol and Rol molecules are joined to a fatty acid (among the commonest are the palmitic acid $C_{16}H_{32}O_2$, and oleic acid, $C_{18}H_{34}O_2$).

There is another retinoid derived from Rol that plays an important role in the systemic functions of vitA, the retinoic acid (ARE). This molecule represents the most oxidized form of Rol, with a carboxyl group (COOH) at the end of the isoprenoid chain (Albalat 2009). For the synthesis of ARE from Rol, two oxidative reactions are necessary: first, the alcohol group of Rol is oxidized to produce Ral (-CH_2OH → -CHO), and a subsequent reaction of oxidation of the Ral finally produces ARE (-CHO → -COOH) (Eitenmiller & Landen 1999). The first reaction (from Rol to Ral) is reversible, but once the molecule is converted to ARE, it is metabolically impossible to produce Ral. Due to this, ARE is not considered vitA, as it does not fulfill the biological activity of Rol (Combs 1998). In Figure 1, the chemical structure of some retinoids is shown.

Besides retinoids, there is another group of molecules that might be converted into Rol by oxidative reactions: carotenoids or provitA (Ball 1988). Carotenoids are yellow and red pigments, and their prototypical chemical structure is a chain of eight isoprenoid units joined head-to-tail, which produces a 40-carbon skeleton known as lycopene (Fig. 2). Structural modification of lycopene has led to the diversity of carotenoids, with nearly 600 different types that have been described. β-carotene (βc) is the carotenoid with higher provitA activity, as it presents two β-ionone groups at the end of the hydrocarbon chain (Fig. 3) and represents, in theory, two molecules of Ral. Besides βc, other 50 carotenoids present more or less provitA activity, and the α-carotene, γ-carotene and β-criptoxanthin are among the highest (Fig. 3). These molecules have at least one β-ionone ring at the end of the isoprenoid chain, which is essential for the conversion into vitA.

Metabolism of dietary vitamin A

VitA is not synthesized in animal tissues, and thus, it must be obtained from feed. Most of the dietary vitA is found as Erol and βc, but small quantities of Rol and Ral may also be detected. The activity of vitA in food is regularly expressed as international units (IU), and 1 IU is equivalent to 0.3 μg of all-*trans*-Rol and 0.6 μg of βc. Also, it can be expressed as retinol equivalents (RE), and 1 RE represents 1 μg of all-t*rans*-Rol and 6 μg of βc (Combs 1998).

The information on vitA absorption and metabolism has been extensively documented in terrestrial vertebrates, especially in mammals. However, information in crustaceans and other invertebrates is limited and is very similar to that observed in mammals. The following description is based on vertebrate information.

The Erol are hydrolyzed in the gut lumen by two enzymes, the carboxyl ester lipase and the pancreatic triglyceraldehyde lipase, which produce Rol. Rol is absorbed by enterocytes by diffusion at physiological concentrations or by passive diffusion at pharmacological concentrations (Harrison & Hussain 2001). However, some findings suggest the presence of specific proteins to transport Rol in the membrane border of enterocytes (Dew & Ong 1994). On the other hand, βc is absorbed intact by passive diffusion in the enterocytes of the small intestine, and once inside, is cleaved through the action of the carotene 15-15′-dioxygenase to yield Ral (Vogel et al. 1999). Ral is subsequently reduced to Rol by Ral reductase or can be oxidized to ARE (Van het Hof et al. 2000).

The obtained Rol from Erol and βc is esterified with long-chain fatty acids, such as palmitic acid (50% of the total esterified Rol) or stearic acid (near 25% of esterified Rol). This reaction is dependent on the lecithin: retinol acyltransferase (LRAT) and the acyl: CoA retinol acyltransferase (ARAT). It has been suggested that LRAT works when Rol concentrations available for esterification are low, while ARAT activates when cellular retinol binding protein type II is saturated (Combs 1998). Both CRBPII and cellular retinol binding protein (CRBP) are responsible for binding free Rol in the cytoplasm. CRBPII is found exclusively in enterocytes, while CRBP is found in different tissues. CRBPII plays a fundamental role in Rol absorption into enterocytes and also acts in the reaction that produces Ral from Rol (Napoli 1999).

The Erol synthesized in the enterocytes, and the βc that did not undergo cleavage, are incorporated into chylomicrons, proteins that mobilize lipids, and are transferred from the enterocytes to the lymphatic system by exocytosis. Chylomicrons are subjected to hydrolysis to produce the chylomicron remnants, and their main role is to distribute retinoids and βc to the different tissues (Silveira & Moreno 1998, Harrison & Hussain 2001).

The liver takes most of the Erol from the remnants, and once inside, it is quickly hydrolyzed to Rol again, which is then mobilized to the endoplasmic reticulum. In this organelle, Rol binds to the retinol-binding protein (RBP) and forms the complex Rol-RBP. The Rol-RBP complex is responsible for distributing Rol to the tissues that require it. Rol that is not used is stored

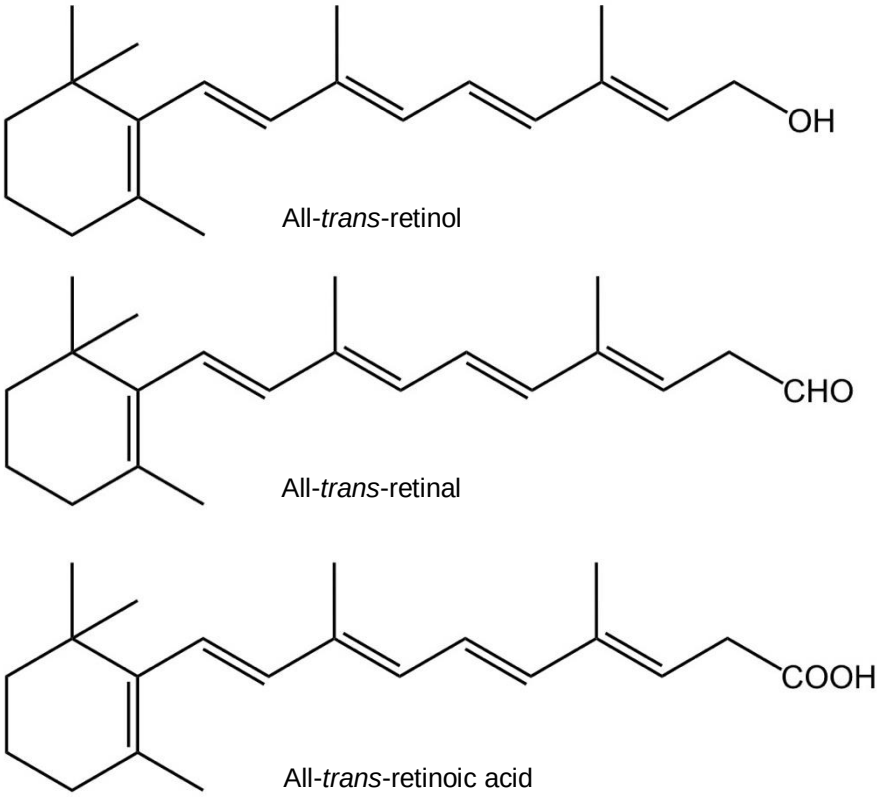

Figure 1. Chemical structures of the active retinoids involved in the vitamin A functions.

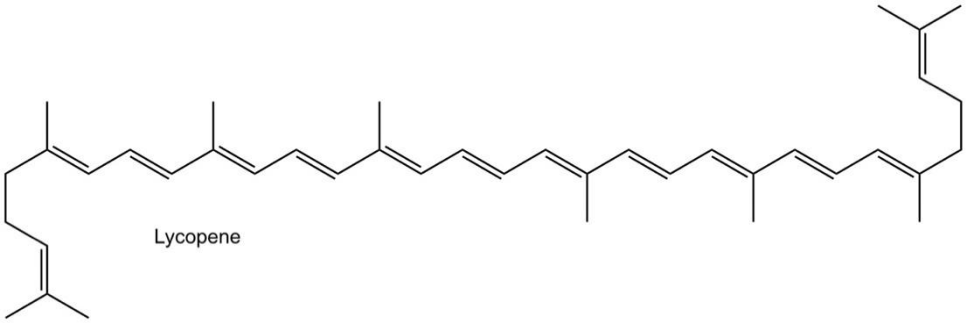

Figure 2. Chemical structure of lycopene, the prototypic molecule of carotenoids.

as Erol in the stellate cells of the liver (Silveira & Moreno 1998, Vogel et al. 1999).

The Rol-RBP complex associates with the protein transthyretin (TTR) inside the hepatic cell and then is liberated to the circulation, where the complex is taken up by the target cells (Napoli 1999). Some evidence shows that a receptor for RBP is present in the membrane of the target cells. Still, it is also possible that Rol crosses the cellular membrane by a "flip-flop" mechanism in the presence of high concentrations of intracellular CRBP (Noy & Xu 1990).

Once in the target cells, Rol might follow several metabolic pathways: it can be stored as an Erol, can be metabolized to ARE, or be recycled and sent back to the systemic circulation (Ross 1993). The conversion of Rol to ARE (both of its isomers, the all-*trans*-ARE and the 9-*cis*-ARE) starts with the oxidation of Rol to Ral, a reaction mediated by alcohol dehydrogenase and the Rol dehydrogenase. Afterward, Ral dehydrogenase and a member of the P450 family participate in the reactions to produce all-*trans*-ARE (Silveira & Moreno 1998). The ARE binds to cellular retinoic acid-binding protein

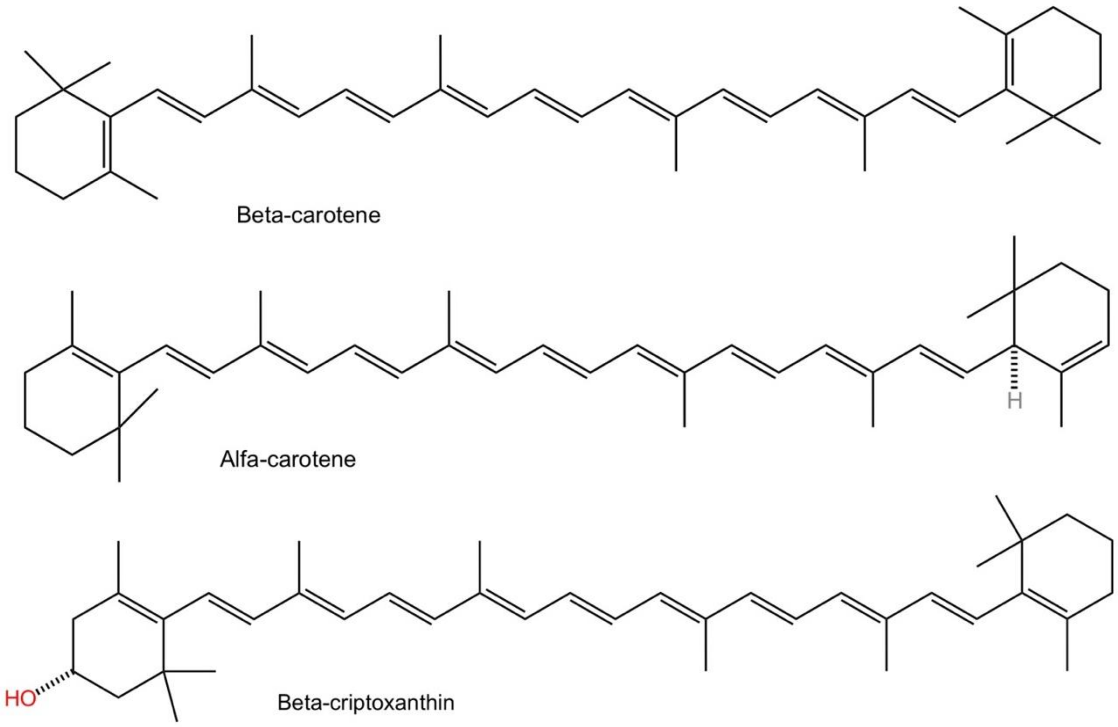

Figure 3. Chemical structure of carotenoids with the higher activity of provitamin A.

(CRABP) and is transported from the cytosol to the nucleus. CRABP is also responsible for ARE homeostasis inside the cell by limiting its distribution and biological effects (Ross 1993).

So far, the findings among crustaceans include the work of Lindohorst et al. (2009), which reported that the hepatopancreas of *Procambarus clarkii* presents activity of the enzyme ARAT but was unable to determine activity of LRAT. Gu et al. (2002), on the other hand, showed the presence of a CRABP-like enzyme in the ovaries and eyes of the shrimp *Metapenaeus ensis*, which binds to both ARE and Ral with similar affinity. According to Alabat (2009), mechanisms of vitA metabolism in crustaceans might be similar to those observed in vertebrates. However, crustaceans show some metabolic novelties, such as the presence of enzymes that help control the effects of retinoids.

Vitamin A functions in crustaceans

Vision

The role of vitA in vision is one of the best-described functions in animals, and for a long time it has been known that working animals require certain foods to avoid night blindness (Hernández & Hardy 2020). These foods (such as carrots, alfalfa, and other vegetables) are a rich source of carotenoids that serve as provitA.

The main molecule of vitA involved in the vision process is 11-*cis*-RAL, which binds to a group of proteins collectively known as opsins and is found in retinal cells, the rods and cones. The 11-*cis*-RAL binds to a specific opsin in each cellular type: in the rods it forms rhodopsin, while in the cones it binds to three different types of iodopsins (Combs 1998). The iodopsins and rhodopsins differ among them in amino acid sequences and allow them to absorb different wavelengths during light stimulation (Temple et al. 2006).

For crustaceans, early works reported that vitA was mainly stored in the eyes and not in the rest of the body, as has been observed in vertebrates (Table 1). Furthermore, these studies identified an isomer of vitA that was the most abundant in eye samples and called it neo-*b* vitA. This neo-*b* form of vitA was identified as a *cis* isomer. Still, with the analytical techniques available at the time, it was impossible to separate it from the all-*trans*-Rol and determine its chemical structure. It was not until the late 1960s that neo-*b*-vitA was finally identified as the 9-*cis*-Ral (Wald 1967). Interestingly, some of these works used extracts containing the vitA isomers to test them in rats and determine isomer biopotency (activity). In most cases, such extracts showed activities between 50 and 75% of the Rol.

Table 1. Early works with vitA and its role in vision of crustaceans.

Authors	Species	Findings
Fisher et al. (1954)	Five species of Euphausiacea and *Homarus americanus*	Astaxanthin is considered a vitA precursor. VitA content is seasonal, particularly in the eyes.
Fisher et al. (1955)	Eleven species of Euphausiacea	Conversion of carotenoids into vitA in all the species analyzed.
Fisher et al. (1957a)	Six species of Penaeidae and seven of Sergestidea	Higher content of vitA in Sergestidea than Penaeidae, probably due to the pelagic habitat of the sergestids.
Fisher et al. (1957b)	Two species of Euphausiacea and three of Decapoda	Near 90% of vitA is found in eyes and not distributed in the rest of the body. Described different vitA *cis* isomers associated with vision.
Lambertsen & Brækkan (1955)	*Pandalus borealis*	Possible presence of a new isomer in the eyes of this species, l Δ-3-5-di-*cis*-retinol.
Wald & Burg (1957)	*Homarus americanus*	VitA is found exclusively in the eye, and the most abundant isomer was neo-*b* vitA.
Wald & Brown (1957)	*Meganycliphanes norvegica*	The isomer neo-*b* vitA was the most abundant in the eyes.
Goldsmith & Cronin (1993)	Seven species of Stomatopoda	Retinol and retinal as isomers 11-*cis* and all-*trans* in eyes of these species.

Suzuki et al. (1984) reported that eyes of *P. clarkii* showed two Ral isomers, the 11-*cis*-Ral and the 11-*cis*-dehydroretinal, also known as vitA_2 aldehyde. The combination of the opsin and the vitA_2 aldehyde forms the prophyropsin. Suzuki et al. (1988) reported, as well, that temperature influences the presence of prophyropsin as photoreceptor in the eye of *P. clarkii*. According to Cronin & Jinks (2001), the conformation of the eyes and photopigments of some species changes according to the stage of development and the ecological niche that particular stage occupies.

The visual process starts with 11-*cis*-Ral binding to the respective opsin available in the rods and cones. With the light stimulus, 11-*cis*-Ral is quickly isomerized to all-*trans*-Ral, and the opsin-Ral complex dissociates due to the molecule's instability, a process known as bleaching. All-*trans*-Ral is reduced to all-*trans*-Rol, transported to the epithelial cells of the retina, where it is esterified and isomerized to the 11-*cis* form, and stored in lipidic deposits of such cells. The process of formation of the 11-*cis*-Ral implies the hydrolysis of the 11-*cis*-Rol esters, transportation of 11-*cis*-Rol to the photoreceptor cells, and once in place, the oxidation to 11-*cis*-Ral, which joins to the respective opsin as mentioned before (Saari 1999). In insects, the isomerization of 11-*trans* to the configuration 11-*cis* occurs under light conditions, but according to Srivastava et al. (1996), in some species of decapods, such as *Homarus* and *Procambarus*, the process of isomerization is enzymatic. Srivastava & Goldsmith (1997) reported that in *Procambarus*, the isomerization of 11-*trans*-Rol to 11-*cis*-Rol occurs just after Rol esterification by LRAT, providing the necessary energy for the reaction.

The role of vitA in vision of crustaceans (particularly in decapods) seems to be very similar to that described in vertebrates, showing that an enzymatic pathway enables retinoid isomerization and differs from that reported for other arthropods.

Systemic functions

The systemic functions of vitA are mediated by the ARE, as this retinoid can regulate gene expression through nuclear receptors. The all-*trans*-ARE and the isomer 9-*cis*-ARE bind to two members of the family of hormone nuclear receptors, ARE receptor (RAR) and the retinoid X receptor (RXR). RAR can bind both all-*trans*-ARE and 9-*cis*-ARE, while RXR recognizes only 9-*cis*-ARE. Once the ARE has joined the respective receptor, a dimer is formed, which can be a homodimer RXR-RXR or a heterodimer RXRs-RAR (Kam et al. 2012). Dimers start the transcription of the target gene when they bind to a promoter sequence that consists of three or more repetitions of the sequence AGGTCA and is known as a response to ARE element (RARE) and a response to homodimer element (RXRE) (Underhill & Weston 1998). ARE not only acts on the target genes, but also on transcription factors that activate other genes.

The information about the role of vitA in systemic functions in crustaceans is still limited. Findings show different mechanisms than those observed in vertebrates: Hopkins & Durica (1995) reported that the crab *Uca pugilator* presents a nuclear receptor homologous to the vertebrate nuclear receptor RXR and can form a heterodimer with another nuclear receptor, the ecdysteroid receptor (EcR), during limb regeneration. Ecdysteroids are steroid hormones related to

several physiological processes in arthropods, such as molting and growth (Benrabaa et al. 2024). Durica & Hopkins (1996) reported that heterodimer RXRs-EcR are expressed similarly during the first days of the limb regeneration of *U. pugilator*. The heterodimer RXR-EcR has been determined in several crustaceans, such as the shrimps *Crangon crangon* (Verhaegen et al. 2011) and *Neomysis integer* (De Wilde et al. 2013), as well as in the cladoceran *Daphnia magna* (Ito-Harashima et al. 2023). This information suggests that the heterodimer RXR-EcR might be equivalent to the vertebrate dimers RXR-RXR and RAR-RXR. Recently, Benrabaa et al. (2024) showed that the RXR-EcR heterodimer initiates several processes: molting, growth, tissue regeneration, and reproduction. Until now, a RAR has not been described for invertebrates, nor for crustaceans, so it seems that RAR is a novelty in the retinoid metabolic pathway of vertebrates.

Regarding molting and growth, ecdysone (molting hormone) activates the RXR-EcR dimer (De Wilde et al. 2013, Shen et al. 2013). However, ARE may play a role in dimer activation, as it has been reported in other processes, such as limb regeneration (Hopkins & Durica 1995, Durica & Hopkins 1996) or reproduction (Huang et al. 2022c). More information is necessary to conclude, but the mechanism may be as follows: ARE binds to RXR in the RXR-EcR dimer and improves the binding of ecdysone to EcR. This allows the dimer to initiate the transcription of the target gene.

Another function related to the ARE and the 9-*cis*-ARE in vertebrates is glucose homeostasis, as both molecules promote insulin secretion and the expression of glucose transport proteins. For crustaceans, Zou & Bonvillain (2003) reported that injection of all-*trans*-ARE causes hyperglycemia in the crab *U. pugilator*, and the authors consider that ARA affects the absorption of glucose from hemolymph. Reddy & Sainath (2008) found that 9-*cis*-ARE regulates the secretion of the crustacean hyperglycemic hormone in the eyestalk of the crab *Oziotelphusa senex senex*. However, no further information is available regarding this subject.

Although more information is necessary, it appears that the nuclear receptors involved in the regulation of gene expression in crustaceans by vitA are different from those reported in vertebrates (RXR-EcR *vs*. RXR-RXR and RXR-RAR, respectively). The mechanisms of dimer activation and later binding to the promoter sequence (tentatively similar to the vertebrate RARE) look very similar in both groups, which indicates that ARE gene expression regulation is highly conserved throughout evolution from crustaceans to mammals.

Reproduction

As in the case of vertebrates, vitA inclusion has a positive effect on sexual maturation and reproduction of crustaceans. According to Alava et al. (1993), inclusion of 15,000 UI kg^{-1} vitA palmitate had a positive effect on ovary maturation, with higher values of gonad-somatic index in *Marsupenaeus japonicus* females. Mengqing et al. (2004) reported that females of *Penaeus chinensis* fed with 60 mg kg^{-1} vitA acetate showed higher fecundity and improved the survival rate of the larvae produced. On the other hand, Liñan-Cabello et al. (2004) showed that three injections of vitA palmitate (16.3 μg per g of weight) improved the gonad-somatic index and ovary maturation. Liñan-Cabello & Paniagua-Michel (2004) reported similar results in *Penaeus vannamei* females injected with vitA palmitate (133 μg per g of weight). The authors of these two reports considered that use of vitA might be an alternative to eye stalk ablation. As well, Barim-Oz & Sahin (2016) reported that 240 mg kg^{-1} of vitA improved the number and size of the eggs in the ovary of *Astacus leptodactylus* females.

Vitellogenesis is the most significant process during the sexual maturation of crustacean females, as it consists of vitellogenin (*vtg*) synthesis in the hepatopancreas, transportation to the ovaries, and chemical modification to produce vitellin and incorporate it into oocytes (Kluensoongnoen et al. 2021). Vitellin is a lipoprotein that provides energy and nutrients to the embryos during the first stage of development (Subramoniam 2011). In several species of crustaceans, such as *Scylla paramamosain* (Gong et al. 2016), *Penaeus monodon* (Kluensoongnoen et al. 2021), and *Carcinus maenas* (Nagaraju et al. 2011), expression of the gene RXR generates positive expression of the *vtg* gene during ovary development. As previously described, Girish et al. (2015) and Kluensoongnoen et al. (2021) showed that RXR forms a heterodimer with EcR and is related to positive expression of the *vtg* gene. According to Huang et al. (2022c), inclusion of 8,000 UI kg^{-1} vitA positively regulates the *rxr*, *ecr*, and the early responsive to ecdysteroids (*e75*) in females of crab *Eriocheir sinensis*. Thus, the mechanism might be as follows: ARE binds to the RXR of the heterodimer RXR-EcR and allows increased binding of ecdysteroids to EcR. One of the targets of the active RXR-EcR is E75, a nuclear receptor that mediates ecdysone responses and has been associated with oogenesis among other responses (Gong et al. 2016). It may also initiate a pathway that includes the positive expression of *vtg* in the hepatopancreas, and it probably plays an important

role in the absorption of *vtg* from hemolymph to the ovary by regulating the *vtg* receptor (Girish et al. 2015).

These findings show the importance of vitA during the reproductive process of crustacean females. However, the quantitative requirements of dietary vitA for females have not been reported. There is also no information available about the effects of vitA on male maturation and spermatogenesis.

Larval development

The larval stage of crustaceans is often complex and includes several morphological and physiological changes that require energy and nutrients to reach the juvenile stage. Little information is available regarding the role of vitA during this stage. Pakdeenarong & Damrongphol (2006) reported that *Macrobrachium rosenbergii* embryos showed greater development of germinal cells and gonads when receiving treatments of 10 and 50 g mL^{-1} of all-*trans*-ARE. On the other hand, Castillo et al. (2025) reported that larvae of *Macrobrachium acanthurus* fed with *Artemia* nauplii enriched with 5 and 10 mg of vitA palmitate showed better survival and faster larval development.

The effect of vitA during larval development requires further research, but evidence suggests that ARE is strongly involved in this process.

Immunological response

VitA has been associated with a normal immune response, as its deficiency results in immunodepression. It is well known that mammals show increased humoral and cell-mediated responses when fed high vitA doses, but knowledge in crustaceans is still developing.

The crustacean immunological system is considered almost exclusively non-specific, as they do not possess adaptive antibodies, such as immunoglobulins (Rowley 2016). For this reason, their antioxidant system is considered vital for defense against diseases (Frías-Gómez et al. 2023), and most of the available information focuses on these types of responses.

Wong et al. (1999) reported that inclusion of 54,000 UI kg^{-1} vitA in juvenile *P. chinesis* improved the phenoloxidase and resistance to infections caused by *Vibrio parahaemolyticus* and *V. alginolyticus*. Females of *Astacus leptodactylus* might require at least 240 mg kg^{-1} vitA to improve the antioxidant response during their gonadal development (Barim-Oz & Yilmaz 2016). Feng et al. (2019) reported that inclusion of 24,000 UI kg^{-1} improved the total count of hemocytes and the phenoloxidase in the serum of the crab *E. sinensis* when exposed to polychlorinated biphenyls. Also, 8,000 UI kg^{-1} vitA in a diet with palm oil increased antioxidant metabolism gene expression in the hepatopancreas of *E. sinensis* and reduced inflammation. Thus, vitA may positively affect the toll2/myD88/relish signaling pathway, which is involved in the production of inflammatory interleukins (Huang et al. 2022b). Huang et al. (2023) reported that vitA positively affected the proinflammatory response of the crab *E. sinensis* when fed plant-origin oils, in addition to reducing lipid peroxidation. Tang et al. (2025) recently reported that inclusion of 5.4 mg kg^{-1} vitA improved the antioxidant capacity of juvenile crabs *Scylla paramamosain*.

Available information to date indicates the essential role of vitA in performing suitable immunological responses. However, the mechanisms involved and whether high doses may help improve the immune and antioxidant systems are still unclear.

Vitamin A requirements

The requirements of vitA in feds for aquatic organisms are relatively well described in several fish species (Hernández & Hardy 2020). In crustaceans, however, vitA requirements have been reported only for a few species of the Penaeidae and Palaemonidae families (Table 2).

Early work on vitA requirements focused on including this nutrient in diets. Still, no formal quantitative studies were performed: Kanazawa (1985) reported that *Marsupenaeus japonicus* requires inclusion of the vitamin in the diet. In the same species, Alava et al. (1993) found that adults presented a higher gonadosomatic index when fed 15 mg vitA palmitate kg^{-1} (equivalent to 15,000 UI). Akiyama et al. (1992) showed that 10,000 UI kg^{-1} is necessary in diets for penaeids of commercial importance. He et al. (1992) reported that *P. vannamei* showed improved growth performance when fed 4,500 UI kg^{-1}. Finally, Reedy et al. (1999) reported that *P. monodon* also required vitA in diets. More recently, quantitative requirements have been reported for several crustacean species (Table 2), using broken-line regression analysis (Robbins et al. 1979) with weight gain (%) and/or specific growth rate (% d^{-1}) as response variables. Other authors have used hepatopancreas integrity in juveniles of *Pleoticus muelleri* (Fernández-Gimenez et al. 2008), as well as survival rate and larval development (Castillo et al. 2025). This information indicates that requirements for juveniles vary between 5,000 and 10,000 UI kg^{-1}, though requirements for *P. chinesis* range from 12,000 to 17,000 UI 100 g^{-1} for juveniles of 7 and 1 g, respectively (Chen 1994).

Table 2. Reported quantitative requirements for different species of crustaceans. [1]Broken-line model was used.

Species	Common name	Stage	Requirement (units kg^{-1})	Source of vitA	Response variable	Reference
Penaeus chinesis	Chinese shrimp	Juvenile (1 g) Juvenile (7 g)	18,000 UI 100 g^{-1} 12,000 UI 100 g^{-1}	N/A	Growth and feed conversion rate	Chen & Li (1994)
Penaeus monodon	Tiger shrimp	Juvenile	8,400 UI	Retinyl acetate	Weigh gain (%)[1]	Shiau & Chen (2000)
Pleoticus muelleri	Red shrimp	Juvenile	180 mg	Rovomix A 500	Hepatopancreas morphology	Fernández-Gimenez et al. (2008)
Marsupenaenus japonicus	Kuruma prawn	Juvenile	7,500 UI	Retinyl palmitate	Weight gain (%)[1]	Hernandez-Hernandez et al. (2009)
Pacifastacus leniusculus	Crayfish	Juvenile	5,000 UI	Retinyl acetate	Growth	Fuertes et al. (2014)
Eriocheir sinensis	Mitten crab	Juvenile	5,340-5,540 UI	Retinyl esters	Weight gain (%) and specific growth rate (% d^{-1})[1]	Huang et al. (2022a)
Scylla paramamosian	Mud crab	Juvenile	8,605 UI	Retinyl acetate	Weigh gain (%)[1]	Tang et al. (2025)
Macrobrachium acanthurus	Cinnamon fresh-water prawn	Larvae	10,000 UI	Retinyl palmitate	Survival and larval development	Castillo et al. (2025)

Deficiency signs of vitA at the macroscopic level have been reported as reduced growth rates and increased mortality (Kanazawa 1985, Reddy et al. 1999). At the microscopic level, deficiency has been associated with cellular damage in the hepatopancreas (Fernández-Gimenez et al. 2008). On the other hand, toxic concentrations of vitA may be above 20,000 UI kg^{-1}, as hypervitaminosis A negatively affects growth performance (Shiau & Chen 2000) and leads to higher mortality during the larval stage (Castillo et al. 2025). Signs of vitA excess appear to manifest earlier than those of deficiency, though this requires further confirmation.

Besides the negative effects on growth performance and increased mortality, other signs of vitA deficiency or excess have not been observed, unlike what has been reported for other aquatic organisms (Hernández & Hardy 2020).

CONCLUSIONS

VitA is an important nutrient for crustaceans as it is involved in several metabolic processes such as vision, growth, normal development, reproduction, and larval development. The mechanisms are still to be fully understood; but in the last decade some advances have been made regarding growth and reproduction.

For the larval stage, knowledge is still very limited, and the findings show that deficiency and excess have negative effects on survival and larval development. Regarding the immune system, it is well known that vitA is necessary for an optimal response, but the mechanisms are mainly unknown.

New technologies help us better understand the role of vitA in several metabolic processes of crustaceans and the possible interactions with hormones such as ecdysone and other ecdysteroids. Regarding crustacean species of aquaculture importance, most do not have quantitative vitA requirements determined. A full understanding of vitA requirements and their functions across all stages of development is an important step for further development of sustainable aquaculture.

Credit author contribution

J. Morales-Aravena: conceptualization, validation, methodology, formal analysis, writing-original draft; S. García: Funding acquisition, project administration, supervision, review, and editing; D.E. Avaria & R. Juárez: methodology, validation, supervision, review, and editing; M. Urrutia: methodology, data curation, formal analysis, review, and editing; C.B. de Oliveira: methodology, formal analysis, review and editing; M. Zárate: formal analysis, review and editing. All authors have read and accepted the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

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