Vitamin A: Requirements and Functions on Aquatic Organisms

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Abstract

Vitamin A (vitA) plays an important role in several physiological processes including vision, reproduction, embryogenesis, growth and differentiation and maintenance of epithelial cells. The knowledge of vitA on aquatic organisms is still limited, but growing in the last years. For this reason, the aim of the present review is to present an overview of state of the art of the requirements and functions of vitA on aquatic species. Along the review, it is presented the effects of vitA on reproduction, the early embryonic development and actual dietary requirements of several species of fish and crustaceans. As well, are discussed new trends on research to understand completely the role and the actual requirements of this nutrient along the life stages of fish and crustaceans of commercial importance, which might be helping in a further and better development of intensive aquaculture.

Key words: crustaceans, fish, functions, growth, reproduction, requirements, vitamin A

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1. Introduction

The term vitamin A (vitA) has been defined as the generic descriptor for all C_{20}-β-ionone derivatives with the qualitative biological activity of all-*trans*-retinol (Bearer-Rogers, Diefferbacher, & Holm 2001; Combs 1998). The retinol (ROL) molecule comprises an β-ionone ring (4-(266-trimethyl-2-cyclo-hexen-1-yl)-3-buten-2-one) with a side chain of three isoprenoid units linked at the 6-position of the β-ionone (Figure 1) (Eitenmiller & Landen 1999). VitA active compounds can fall into two basic groups: vitA (retinoids) and provitamin A, the carotenoids (Ball 1988).

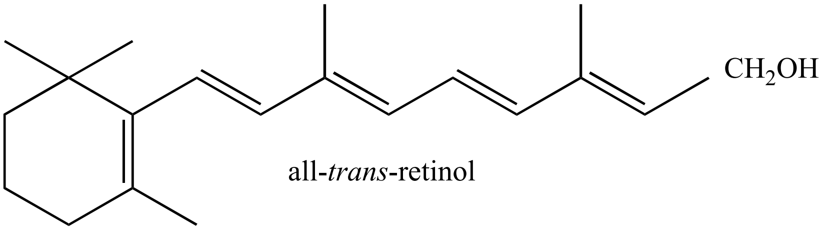

Figure 1. Chemical structure of the retinol

Owing to their close structural similarities to ROL, the retinoids are formally derive from a monocyclic parent compound containing five carbon-carbon double bonds and a functional group at the terminus of the acyclic portion (Combs 1998). The vitA-active retinoids are ROL, retinal (RAL) and retinyl esters (RNE) and some examples are show in Figure 2.

The oxidized form of ROL, retinoic acid (RA) is another important retinoid with several isomers (particularly several *cis* forms) involved in the control of cell differentiation (Figure 2). However, RA is unable to be metabolic converted to ROL and not fulfill the ROL functions and thus is not consider as a vitA (Bearer-Rogers *et al.* 2001).

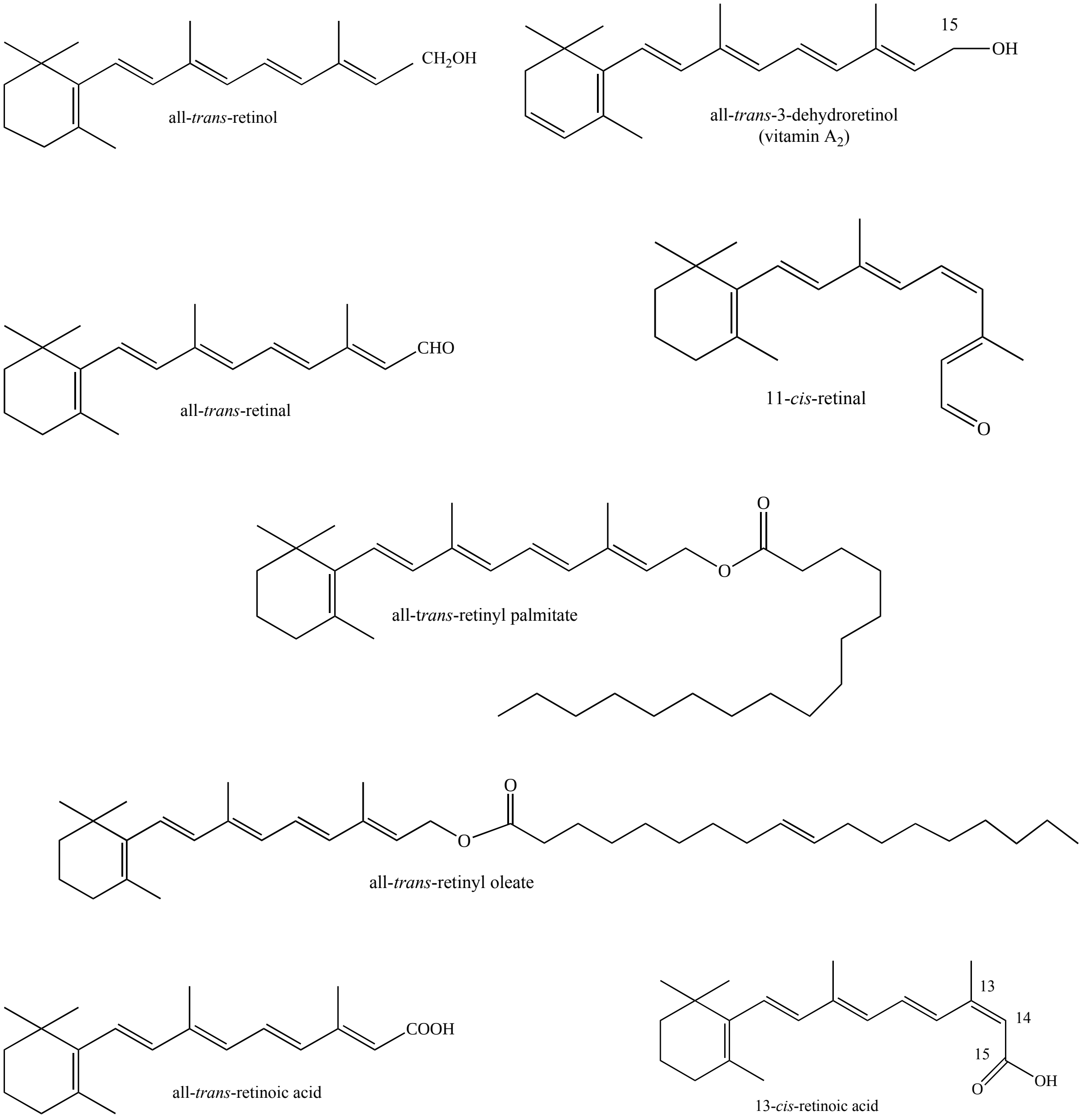

Figure 2. The chemical structure of retinoids

Carotenoids are the yellow to red pigments responsible for the color of many vegetables and fruits and might be convert into ROL by oxidative reactions (Ball 1988). The carotenoid structure is based on a lycopene molecule, and lycopene shows the acyclic hydrocarbon backbone chain and is regard as the prototype of the family. Structural modifications of lycopene lead to the

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diverse nature of carotenoids (Eitenmiller & Landen 1999). Of 500 naturally occurring carotenoids, about 60 possess vitA activity in varying degrees (Figure 3).

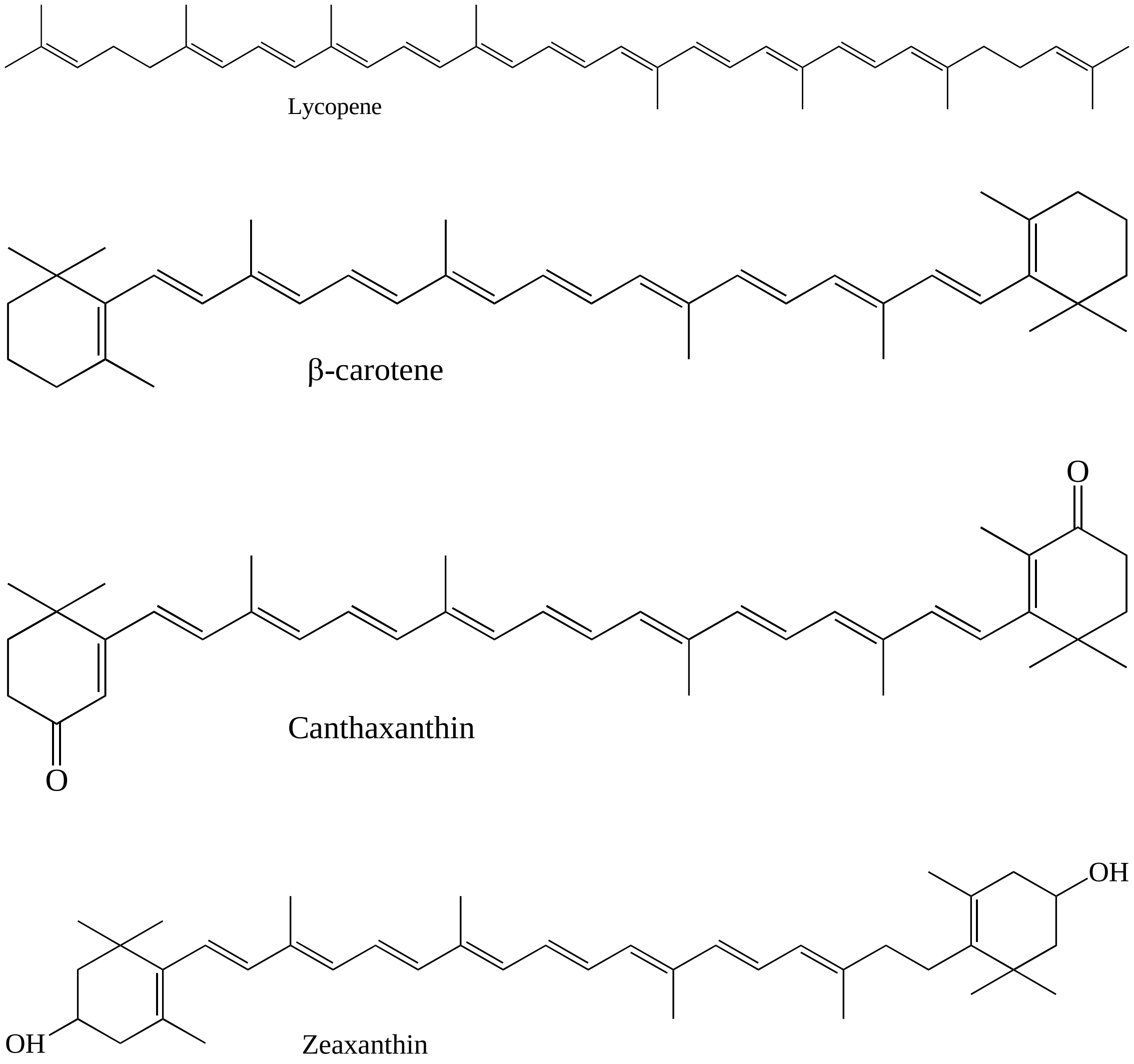

Figure 3. The chemical structure of some carotenids

The vitA and its active metabolites play several roles along the vertebrate life: vision, proper growth, reproduction, maintenance of differentiate epithelia, mucus secretions and embryonic development. The 11-cis-RAL supports the vision process, while other functions are mainly maintained by RA.

So far, the best-elucidated function of vitA is in the visual process: 11-*cis*-RAL serves as photosensitive chromophoric group of the visual pigments of the rod and cone cells of retina in eye. The rod cells contain the pigment rhodopsin and the cone cells contain one of three possible iodopsins. In both cases, 11-*cis*-RAL is bound to a specific lysyl residue of the respective protein collectively know as opsins (Combs 1998).

VitA have several functions referred as systemic functions: proper growth by the differentiation and growth of epithelial cells, mucus secretions and embryonic development, in those the functions of vitA resembles that of a hormone (Combs 1998). The all-*trans*-RA and 9-*cis*-RA are in charge of those systemic functions by the regulation of gene expression, which is receptor mediated These receptors are believed to act as activators of gene transcription, binding as dimmers to specific nucleotides sequences present in the response elements of their target genes.

VitA seems to be necessary for reproduction, but the biochemical basis is still unclear. RA seems to be necessary for the gonad cell proliferation, but animal maintained with this retinoid grow well and appear healthy, but lose reproductive ability: males show impaired spermatogenesis and females abort and reabsorb their fetuses. Injections of ROL restore the spermatogenesis and it has been propose that these effects are secondary to lesions in cellular differentiation and/or hormonal sensitivity (Combs 1998).

Due to the importance of dietary vitA, the aim of the present review is to present an overview of the actual knowledge of the requirements and functions of vitA on aquatic organisms, as well the new trends necessary on research to understand completely the role of this nutrient along the life of fish and crustaceans of commercial importance.

2. VitA on fish

a. Metabolic functions of vitA on fish

The research with vitA and fish started in the late 50's, when Halver in 1958 reported that fish fed on a vitA-deficient diet showed xerophthalmia and cataracts (Halver 2002). Later, it was reported that vitA had a growth-promoting effect in Japanese eel (*Anguilla japonica*). Since then, is believed that metabolic functions of vitA in fish are the same than those reported for other vertebrates, particularly those of mammals, by far the most studied group (Halver 2002). The visual process is one the best understood process on fish and now is clear that freshwater species have 2 different types of photopigments, the rhodopsin (opsin conjugated with all-*trans*-RAL) and porphyropsin, a molecule formed with the opsin and the 3,4-didehydroretinal, an isomer of all-*trans*-RAL, which is found mainly in freshwater fish (Tsin, Gentles & Castillo 1989). Other metabolic roles of vitA are less understood (Lovell 1989), but is clear that is an important factor for growth, as vitA-deficient diets often caused growth depress (Gouillou-Coustans & Guillaume 2001), particularly in young and rapid growth organisms (Woodward 1994; NRC 1993).

As mentioned before, vitA is necessary for reproduction in vertebrates and research in fish indicates a similar trend: Alsop, Matsumoto, Brown & Van Der Krak (2008) reported that adults of zebra fish have the enzymes and the receptors involved in the RA signaling at the cells of gonads, which seems to be related to cell proliferation. On other hand, the lack of vitA on diet seems to affect the reproduction: broodstock of Japanese flounder *Paralicthys olivaceus* fed on a diet with less than 2,000 International Units of vitA (IU kg^{-1}, 1 IU = 0.3 μg all-*trans*-ROL) showed short spawning period than organisms fed with more 50,000 IU kg^{-1} (Furuita, Tanaka, Yamamoto, Suzuki & Takeuchi 2003). A same trend is reported for bighead carp *Aristichthys nobiles* (Santiago & Gonzal 2000). Alsop *et al.* (2008) reported that reproduction is affected when RAL, ROL or RA are depleted from the body storages. Fontagné-Dicharry, Lataillade, Surget, Brèque, Zambonino & Kaushik (2010) found that rainbow trout brookstock requires high levels of dietary vitA (from 60,000 to 200,000 IU kg^{-1}) to sustain reproduction performance.

As well, vitA is not only necessary to sustain normal reproduction, as several reports indicates that retinoids must be supplemented to the eggs from female brookstock: Samar, Levi, Hurvitz & Lubenz (2005) suggested that besides the retinol binding protein (RBP), the vitellogenin is involved in the transport of retinoids to the eggs on rainbow trout, during the vitollegenesis. Santiago & Gonzal (2000) reported that inclusion of vitA on the diet of brookstock improved the egg hatchability and the survival of fry. Furuita *et al.* (2003) reported that Japanese flounder showed a higher percentage of normal larvae when brookstock was fed 50,000 IU kg^{-1}. Furuita, Unuma, Nomura, Tanaka, Sugita & Yamamoto (2009) also reported that inclusion of vitA on the diet of Japanese eel improved the egg hatchability and the survival rate of larvae. In other hand, Fontagné-Dicharry *et al.* (2010) reported that high levels of vitA on the diet of rainbow trout brookstock induced high mortalities at embryonic stages. So far and despite the importance of vitA on reproduction, egg production, egg hatchability and early larvae survival, not real requirements has been determined for brookstock of any species of fish and the requirements reported for juveniles might not be enough to meet such requirements.

As see before, vitA it is an important compound for the larvae development and survival during the first days after hatching and much of this vitamin comes from the females. However, once larvae finish their reserves from the yolk sac, must to start exogenous feeding and consumption of vitA might disrupt the organism normal development. During embryonic stages, vitA through all-*trans*-RA and some its isomers regulate the activity of homeobox genes, which have fundamental roles in the organization of developmental pattern of central body axis and the limbs of vertebrates (Ross, McCaffery, Drager & De Luca 2000). VitA excess alters the formation of vertebra through alterations in gene expression, by extending the time of normal expression (Means & Gudas 1995) and several works have been published on the effect of this nutrient on the fish larvae body deformities. Dedi, Takeuchi, Sekai & Watanabe (1995) reported that Japanese flounder larvae presented 100 % of occurrence of bone deformities when fed on *Artemia* enriched with more that 40 mg of vitA palmitate in 10 l of enrichment medium. They found the principal deformities in vertebra, which were compressed. Takeuchi, Dedi, Ebisawa, Watanabe, Seikai, Hososya & Nakazoe (1995) found that Japanese flounder larvae fed on *Artemia* enriched with several carotenoids (β-carotene, astaxanthin, and cantaxanthin) showed low frequency of vertebral deformity when compared with larvae fed on *Artemia* enriched with 100 mg of vitA palmitate. Dedi, Takeuchi, Seikai, Watanabe & Hosoya (1997) reported that larvae of Japanese flounder fed on *Artemia* enriched with 100 mg of vitA palmitate per 10 l of enrichment medium during the period of notochord segmentation showed a high incidence of vertebral deformities and that long exposure to vitA also caused a high frequency of deformity. Takeuchi, Dedi, Haga, Seikai & Watanabe (1998) reported that ROL, retinyl palmitate, retinyl acetate and RA caused high incidence of deformities in vertebra of Japanese flounder larvae. Haga, Takeuchi & Sekai (1999) fed *Artemia* enriched with several concentrations of RA to Japanese flounder larvae and found that RA induces vertebral deformity in a dose dependent manner. In other hand, Ørnsrud & Waagbø (2004a) reported that Atlantic salmon *Salmo salar* larvae showed a slightly higher incidence of incorrect position of liver when eggs contain more ROL (3.4 μg/g of dry mass) and incubated at high temperature (14 °C) than those with a lower content of ROL (2.2 μg/g of dry mass) and incubated at lower temperature (8 °C). Ørnsrud, Wargelius, Sæle§, Pittman§ & Waagbø (2004b) also reported that Atlantic salmon eggs showed higher relative expression of the sonic hedgehog genes when initial ROL was 3.3 μg/g of dry mass than eggs with initial ROL of 2.2 μg/g of dry mass. The hedgehog genes are homoebox genes, which are in charge of the organization of developmental pattern of central body axis and the limbs of vertebrates (Ross *et al.* 2000). Hernandez, Teshima, Koshio, Ishikawa, Gallardo-Cigarroa, Alam & Uyan (2006) showed that larvae of red sea bream (*Chrysophrys major*) have a lower degree of vertebral deformities when fed vitA palmitate than larvae fed RA. Larvae fed RA also presented lower growth and survival rates. Fernández, Hontoria, Ortiz-Delgado, Kotzamanis, Estévez, Zambonino-Infante & Gisbert (2008) reported that larvae of gilthead sea bream (*Sparus aurata*) showed an acceleration of the intramembranous ossification of vertebral centrums, which led to supranumerary vertebrae and high incidence of fused and compressed vertebrae when fed rotifers enriched with more than 109.2 ng of vitA/mg of dry weight. Similar patterns of deformities were observed on larvae of Senegalese sole (*Solea senegalensis*) when fed *Artemia* nauplii enriched with more that 2.1 mg of vitA/mg of dry weight (Fernández, Pimentel, Ortiz-Delgado, Hontoria, Sarasquete, Estévez, Zambonino-Infante & Gisbert, 2009). As in mentioned for fish brookstock, vitA requirements in larvae are still unclear: use micro diets during the first days of exogenous feeding or different live feds (such as rotifers or *Artemia* nauplii and the different techniques of enrichment) make difficult to obtain constant concentrations of the vitamin delivered to the larvae.

In juvenile stage fish fed vitA excess might cause also deformities, but concentrations on the diet must be really high: Hilton (1983) reported that juvenile rainbow trout fed 8,104,000 IU/kg for 16 weeks caused some spinal deformities. Saleh, Elaraky & Gropp (1995) reported that tilapia fingerlings fed for 18 weeks on a diet with 40,000 IU/kg showed vertebra fusion.

b. Dietary vitA requirements on fish

The vitA requirements for species of commercial interest fish are listed in Table 1. Most of these requirements have been determined for juveniles and are low as 1,000 IU kg^{-1} and as high as 20,000 IU kg^{-1}. It looks like freshwater species of fish have requirements between 5,000 and 10,000 IU kg^{-1} of vitA in diet, while marine species have a tendency of higher dietary requirements (Table 1). So far, there is no an explanation to this observations.

Growth performance was used to assess those levels, but also deficiency and excess sings. In salmonids (rainbow trout *Oncorhynchus mykiss* and Pacific salmon *Oncorhynchus* sp.) vitA deficiency sings are reduce growth, exophthalmia, body de-pigmentation, clouding and thickening of corneal epithelium, degeneration of the retina (NRC 1993). Other freshwater species, show similar signs, but also is reported anorexia for common carp *Cyprinus carpio* (Aoe, Masuda, Mimura, Saito & Komo 1968) atrophy of kidney and increased mortality in channel fish and poor feed efficiency and high mortality in common guppy *Poecilia reticulata* (Shim & Tan 1990). The deficiency of vitA symptoms in yellowtail *Seriola quinqueradiata* are dark coloration, anorexia, hemorrhage in fins, eyes, and in liver, anemia, and poor growth of opercula (Shimeno 1991). Symptoms of hypervitaminosis are reported for several species of fish, the rainbow trout fed on more than 2,704,000 IU kg^{-1} showed growth depression, increased mortalities, abnormal and necrotic anal, caudal, pectoral and pelvic fins, and pale and fragile livers; while those fed on 8,104,000 IU kg^{-1} presented also scoliosis and lordosis (Hilton 1983). Tilapia *Oreochromis* *niloticus* showed reduced growth, hemorrhages in skin, necrosis of the caudal fin, enlargement of liver and spleen, and impaired skeletal formation, especially in vertebrae (Saleh *et al.* 1995). Grisdale-Helland, Helland & Åsgård (1991) reported that Atlantic salmon fed on diets with supplementation of 5,000 and 50,000 IU kg^{-1} resulted in high mortality. Larvae of Japanese flounder presented high incidence of vertebral deformities when fed *Artemia* enriched with more than 20 mg 10 L^{-1} of enrich medium (Dedi *et al.* 1995). Furuita, Tanaka, Yamamoto, Shiraishi & Takeuchi (2001) reported that Japanese flounder presents darker coloration and some skin lesions when fed 337,000 IU 100 g^{-1} of diet for about 8 months.

Table 1**.** Reported requirements of dietary vitA for some species of fish

Species	IU* kg^{-1}	Reference
Rainbow trout *Oncorhynchus mykiss*	2,500-3,500	Kitamura *et al.* 1967
Common carp *Cyprinus carpio*	4,000-20,000	Aoe *et al.* 1968
Guppy *Poecilia reticulata*	2,000-4,000	Shim & Tan 1990
Tilapia *Oreochromis niloticus*	5,000-10,000	Saleh *et al.* 1995
Tilapia *O. niloticus*	5,400	Ferraz *et al.* 2009
Hybrid tilapia *O. niloticus* x *O. aureus*	5,870-6,970	Hu *et al.* 2006
Channel catfish *Ictulurus punctatus*	1,000-2,000	NRC 1993
Yellowtail *Seriola quinqueradiata*	10,500-12,500	Shimeno 1991
Greasy grouper *Ephinephelus tauvina*	3,101	Mohamed *et al.* 2003
Atlantic halibut *Hippoglossus hippoglossus*	8,333	Moren *et al.* 2004
Red sea bream *Chrysophrys major*	5,000-20,000	Hernandez *et al.* 2004
Japanese flounder *Paralichthys olivaceus*	9,000	Hernandez *et al.* 2005
Amur sturgeon *Acipenser schrenckii*	923	Wen *et al.* 2008

* 1 IU = 0.3 μg all-*trans*-ROL

3. VitA on crustaceans

a. Metabolic functions of vitA on crustaceans

The knowledge of the role of vitA in crustaceans is still scare and by far conclusive. Early studies conducted by Fisher *et al.* (1952 and 1957) found that several species of euphausiid and some species of penaeids have large quantities of vitA in the eyes (more that 90%), and not distributed in throughout the body as in vertebrates. These findings lead to believe that the main role of vitA in crustaceans was the production of pigments for vision (Dall 1995; Conklin 1997). Indeed, the eyes of some species of crustaceans have substantial stores of RNE (Goldsmith & Cronin 1993). The mechanism of isomerization of the all-*trans*-RNE to their 11-*cis*-form seems to be very similar to that present in the vertebrates (Srivastava & Goldsmith 1997). As explained before, the ROL in the *all*-trans-form needs to be isomeraze to the 11-*cis*-form and then metabolize to 11-*cis*-RAL, the molecule in charge of forming the photopigments.

In other hand, recently, it has been found that vitA may have another functions in crustaceans. Several authors (He, Lawrence & Liu 1992; Reedy, Ganapathi & Annappaswamy 1999; Shiau & Chen 2000; Hernandez, Teshima, Ishikawa, Koshio, Gallardo-Cigarroa, Uyan & Alam 2009) have reported that vitA is essential for optimal growth in some penaeid species. The growth is mainly regulated by RA and the fiddler crab *Uca pugilator* (Chung, Durica, Clifton, Roe & Hopkins 1998a; Chung, Durica & Hopkins 1998b) and the zoea and mysis stages of *Metapenaeus ensis* (Gu, Silva, Chow, He & Chan 2002) had been found to have different isomers of RA, ROL receptors of the type RXR and CRBP, suggesting that vitA may play a similar role to that of the vertebrates (Liñan-Cabello, Paniagua-Michel & Hopkins 2002). As well, Shiau & Chen (2000) suggested that vitA might has a role in the homeostasis of body lipids, as they found that *Penaeus monodon* fed on high concentrations of vitA presented high body fat content and low levels of triglyceride in blood.

As in vertebrates, vitA seems to be also related to the reproduction: Alava, Kanazawa, Teshima & Koshio (1993) found that adult *Marsupenaeus japonicus* fed on diet with supplemental vitA presented a higher gonado-somatic index than those fed on a vitA-deficient diet. Similar findings have been reported for *Litopenaeus vannamei* (Liñan-Cabello, Paniagua-Michel & Zenteno-Savín 2003), *Penaeus chinesis* (Mengqing, Wenjuan, Qing & Jialin 2004) and *Cherax quadrucarinatus* (Liñan-Cabello, Medina-Zendejas, Sánchez-Barajas & Mena 2004). Alava *et al.* (1993) reported that during the gonad maturation, exist a mobilization of vitA from eyes to gonad, suggested that this vitamin might has an active role in the embryonic development of crustacean, as is reported in vertebrates (Combs 1998). Mengqing *et al.* (2004) reported that increasing levels of dietary vitA of the brookstock of *P. chinesis*, improved the survival rates of the larvae.

b. Dietary vitA requirements on crustaceans

The dietary requirements of vitA in crustaceans have been focused on the penaeid shrimps and prawns, because of their commercial importance (Table 2). Besides, the study of the requirements of vitA in penaeid shrimps (and in other crustaceans) presents several problems: the slow growth and the access to natural sources of nutrients makes difficult to assess deficiency sings, if these are present as in vertebrates. Also the use of marine oils (rich in these vitamins) as sources in lipids, make difficult to produce a complete deficient diet.

Early works showed that juveniles *M. japonicus* required a source of vitA in the diet (Kanazawa 1985), but no quantitative requirements were estimated. Later, Alava *et al.* (1995) reported that adults of *M japonicus* have a better gonado-somatic index that those fed on a deficient diet, but no provide formal estimates of dietary requirements. Akiyama, Dominy & Lawrence (1992) reported that a supplementation of 10,000 IU kg^{-1} is necessary in commercial diets for penaeids. The requirements for *L. vannamei* had not been determined, but He *et al.* (1992) reported that this vitamin is required for growth, as juveniles fed on vitamin A deficient diet has a poor growth compared with those fed on diet with a supplement of 4500 IU kg^{-1}. Reddy *et al.* (1999) showed that vitA is essential for *P monodon* and Shiau & Chen (2000) reported that this species requires about 8,400 IU kg^{-1}. Recently, Hernandez *et al.* (2009) determined that juveniles of *M. japonicus* required 7,500 IU kg^{-1} for optimal growth.

Reports of sings of deficiency of dietary vitA for penaeids had been reported as a retarded growth and low survival rates (Kanazawa 1985; Reddy *et al.* 1999). As for excess, Shiau & Chen (2000) reported a decrease in the weight gain and in the blood triglyceride of *P monodon* juveniles fed with more that 150,000 IU kg^{-1}

Table 2. Reported requirements of dietary vitA for some species of crustaceans

Species	IU* kg^{-1}	Reference
Litopenaeus vannamei (juveniles)	4,500	He *et al.* 1992
Penaeus spp. (commercial diet)	10,000	Akiyama *et al.* 1992
Penaeus monodon (juveniles)	8,400	Shiau & Chen 2000
Marsupenaenus japonicus	15,000	Alava *et al.* 1993
(broodstock)	7,500	Hernandez *et al.* 2009
M. japonicus (juvenile)		
L. vannamei (broodstock)	16,000	Liñan-Caballero *et al.* 2002

*1 IU = 0.3 μg all-*trans*-ROL

4. New trends on vitA research

The requirements of vitA to sustain normal development of gonads of brookstock and reproduction are unknown, so it is necessary to try several levels of dietary vitA on the adults to assess the requirements by evaluating the gonad maturation, production of eggs and sperm. Moreover, only a few steps have been took to understand how parental vitA is involving in the normal development of eggs, embryos and larvae after hatching. With the new molecular techniques, as RT-PCR, might be possible to understand how homeobox genes are expressed at different concentration of parental vitA and how could affect the normal development of larvae. Regarding larvae, it is necessary to understand how dietary vitamin is affecting the expression of such genes and thus, the normal development of axial pattern. Again, by using RT-PCR, might be easy to understand how such genes are expressed on different concentration of dietary vitA and establish a maximum requirement. Another important way to decreased deformities in larvae (which lead to high mortalities rates) could be the use of carotenoids as provitamin A. Takeuchi *et al.* 1995 and Hernandez *et al.* (2006) reported a lower percentage of deformities on larvae of Japanese flounder and red sea bream, respectively, by using β-carotene, astaxanthin, and cantaxanthin, than the observed on larvae fed with ROL or RA. Several species of fish are able to transform carotenoids (Yamashita *et al.* 1996), but activity depends of species, size, age and vitA status (Choubert, 2001; Torrissen & Christiansen, 1995). Then, it could be an interesting option the use of carotenoids on larvae as provitamin A and see how does affect the normal development and how the organism are able to transform into vitA at different ages.

Another important aspect in fish is how vitA interacts with other nutrients, particularly with lipids. Some of our data (unpublished) shows that vitA has a differential effect of lipid deposition on body. Swordtail fish (*Xiphophorus helleri*) showed a tendency of higher content of lipids on viscera as vitA increased on diet, while contents of lipids from muscle were similar, despite the level of dietary vitA. This phenomenon might be related to sexual maturation of the organism and should be considered as another aspect for the optimization of reproduction.

As for crustaceans, the knowledge of vitA shows a similar trend to that observed on fish, as much information has been reported for exclusively for juveniles. Now, it is clear that vitA is not only related to the visual process, but it is involved on reproduction and normal growth. Only two species of shrimp (*Marsupenaenus japonicus* and *Litopenaeus vannamei*) and have reports regarding the inclusion of dietary vitA during reproduction, so might be necessary to obtain more accurate requirements for these and other commercial species. As well, there are no reports on how vitA might affects the development, growth and survival of larval stages of crustaceans.

5. Conclusions

VitA is an essential nutrient for normal growth, development and reproduction of fish and crustaceans. As seen before, the knowledge of functions and requirements for aquatic organisms is growing during the last years, but still fragmented. Much of the available information has been published on the juvenile stage, as is easily to work with. With the development of the new molecular techniques, now is possible to get deeper on brookstock and larvae and understand clearly the requirements and functions of vitA. The complete understand of the different functions of this nutrient along the all life stages of aquatic organisms, is clearly important for a further and better development of intensive aquaculture.

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