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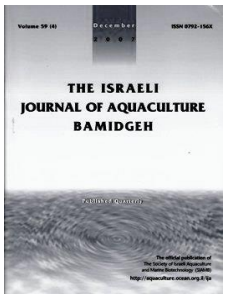

Eyestalk Ablation, a Prerequisite for Crustacean Reproduction: A review

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Keywords: crustacean; eyestalk; eyestalk ablation; neuroendocrine; reproduction; crustacean hyperglycemic hormone; molt-inhibiting hormone; vitellogenesis-inhibiting hormone; mandibular organ- inhibiting hormone

Abstract

Reproduction in crustaceans is a process which demands critical study in order to help improve productivity in aquaculture. In recent years, many studies have been geared towards studying how eyestalk ablation affects the reproduction of crustaceans. This review highlights many of the various neuroendocrine groups found in the crustacean eyestalks, their importance, and their contribution to crustacean reproduction. This review also provides a description of the eyestalk, eyestalk ablation, and how it affects crustacean reproduction. Conclusions and perspectives have also been made to aid further studies.

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Introduction

Crustaceans are a broad, distinct group with important potential in aquaculture. The reproductive patterns of commercially important species are a significant part of crustacean management. The crustacean eyestalk stores an important neuroendocrine center which produces and releases molt- and gonad-inhibiting hormones. Hormonal control of molt and gonad development were examined by Adiyodi & Adiyodi (1970), Cooke & Sullivan (1982), Kleinholz (1984), Passano (1960); however, the exact form of action is still contentious. As a result of increased awareness of reproductive endocrinology in crustaceans, the approach of removing eyestalk has become known as a method used to promote ovary maturation and breeding in confinement. This is a significant approach towards improved seed production in aquaculture (Kuo *et al*., 2009). Eyestalk ablated females of *Penaeus canaliculatus* spawn more times than non-ablated ones, but the latter produce more eggs that hatched successfully (Choy 1987). Eggs most often do not develop very well after eyestalk ablation (Anilkumar and Adiyodi 1985).

In white shrimp *Litopenaeus vannamei*, *Macrobrachium rosenbergii*, *Farfantepenaeus aztecus* AQUACOP (1977), and *Farfantepenaeus duorarum*, the removal of eyestalks promoted several metabolic activities that enhanced reproductive performance (Caillouet 1972). The main neuroendocrine gland found in the eyestalk of crustaceans is the X Organ Sinus Gland (XOSG), (Beltz 1988; Chang 1992). The XOSG is responsible for synthesizing, storing and secreting hormones to the hemolymph in order for metabolism to occur (Chang, 1992) including vitellogenesis, (Subramoniam 2011; Fingerman 1995; and Palacios *et al.,* 1999), intake of food (Taylor *et al.,* 2004), digestion and conveying nutrients (Rosas *et al.,* 1995), molting (Chang and O`Connor 1988), metabolizing lipids (Teshima *et al*., 1988; Santos *et al.,* 1997), and regulating glucose and proteins (Teshima *et al*., 1988; Santos and Keller 1993a; Santos and Keller 1993b; Chen and Cheng 1995). The occurrence of these different metabolic processes is vital to ensure normal gonad maturation, copulation, fecundity, and larvae development.
Removal of the eyestalk elevated the growth of female gonads akin to transporting reserves from the hepatopancreas to the ovaries through the hemolymph (Arcos et al., 2003; Meera et al., 2006). Removal of eyestalk improves spawning numbers and comparably the number of eggs and nauplii produced per female as compared to non-ablated females (Aktas and M. Kumlu 1999). This is assumed to be due to decreasing levels of gonad- and molt-inhibiting hormone (GIH/MIH) in the hemolymph of the eyestalk ablated females, (Dall *et al.*, 1990). Studies have shown that the functions of GIH on ovarian development in diverse crustaceans have been firmly established and that removing the eyestalk increases premature gonad development (Longyant *et al*., 1996; Sithigorngul *et al*., 1996). Gonad- and molt- inhibiting hormones are members of the multifunctional family of hormones associated with the crustacean hyperglycemic hormone (CHH) that has been investigated to a great extent in various species (Marco *et al*., 2002).

Ablation of eyestalks in crustaceans is known to also affect the regular feeding, metabolism, and behavior of prawns negatively, which leads to increased death, (Arnstein & Beard 1975; AQUACOP, 1975, 1977, 1979; Marchiori 1983; Primavera & Borlongan 1977). Research has shown that unilateral eye ablation, which destroys only one eyestalk is enough to promote molting and growth of the reproductive gland and also minimize the damaging effects (Arnstein & Beard 1975; AQUACOP, 1975, 1977, 1979; Marchiori 1983; Primavera & Borlongan 1977).
Reproduction in decapods is regulated by two antagonistic peptide hormones which emerge from varying origins. The X-organ-sinus gland (XO/SG) complex, found in the eyestalks secretes gonad-inhibiting hormones (Quackenbush 1989), and impedes growth of the ovary, whereas the brain and thoracic ganglia secrete gonad-stimulating hormone (GSH), (Otsu 1963), which stimulates ovarian growth through it chemical state, mode, and field of action of GIH, (Huberman 2000), but the actual role of GSH has yet not been clearly defined. A study showed that, ovarian development accelerates the stimulatory consequence of brain and thoracic ganglia, (Fingerman 1997). Hence, a collaboration of GIH and GSH is critical in eventual ovary development.

Reproduction and molting are two significant processes which control a considerable period of the lifetime of most crustaceans (Van Herp 1992). Though they are sometimes separated, their roles are intimately integrated (Adiyodi & Adiyodi 1970).

The relation and interdependence of GIH and GSH are a result of coordinated roles of the stimulatory and inhibitory principle. The function of molt- and gonad-inhibiting hormone in promoting ecdysis and reproduction has been demonstrated in past studies (Okumura and Aida 2001; Okumura 2004; Tamone *et al*., 2005; Nazari *et al*., 2007; Sudha and Anilkumar 2007; Zmora *et al*., 2009; Uawisetwathana *et al*., 2011). Nevertheless, the removal of gonad- and molt- inhibiting hormones through extirpation of eyestalk improves reproduction and molting respectively, and it is dependent on the conditions at the period of eyestalk ablation (Anilkumar and Adiyodi 1980; Adiyodi 1988; Laufer *et al*., 2002; and Sudha and Anilkumar 2007).

Reproduction in crustaceans is an essential process which demands a critical study in order to help improve productivity in aquaculture. This makes the study of eyestalk ablation an important issue. This review discusses the various neuroendocrine hormones found in the eyestalk of crustaceans that aid in reproduction, eyestalks of crustaceans and the effect of eyestalk ablations on reproduction in crustaceans.

Crustacean reproductive system and its regulation

The sex of decapod crustaceans can be differentiated by appendages on the posterior section of the body behind the thorax called pleopods. The male has a more extensive first pair of pleopods than the female. The pleopods metamorphose into the mating organ which aid the transport of sperm sac from spermatophore to the female thylecum during copulation. The females store the sperm sac for some time, and the eggs are not laid right after copulation. The sperms fertilize the eggs only as they are laid.

Control of reproduction in crustaceans varies. Destruction of the eyestalk is a widely known procedure for inducing gonad development and spawning in crustaceans, presumably as a result of the disposal of endogenous gonad inhibiting hormones (Brown and Jones 1949). Reproduction in decapod crustaceans is affected by both external and internal factors. Figure 1 shows the internal and external regulators of crustacean reproduction.

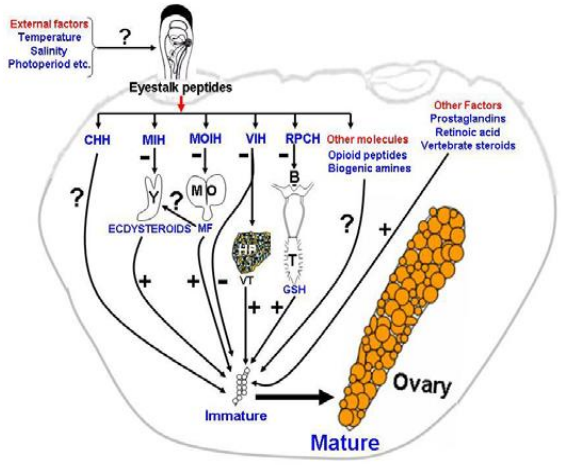

Figure 1: An illustration of factors and hormone regulating reproduction in crustaceans. Swetha *et al*., (2011).
CHH= Crustacean Hyperglycemic Hormone,
MIH= Molt-Inhibiting Hormone,
MOIH= Mandibular Organ-Inhibiting Hormone,
VIH= Vitellogenesis-Inhibiting Hormone,
RCPH= Red Pigment Concentrating Hormone

The male reproductive system

The male crustacean reproductive system is comprised of vas deferens (carrying-away vessel), genital aperture, seminal vesicles, and a pair of testes. The testis also has an H-like structure just like that of the ovary. The vas deferens emerges from the testis and stretches to the gonophores located at the base of the fifth pair of pereiopods. There are three unique and minute regions of the vas deferens and sperms are found in them during the different stages of maturation. The testis of crustaceans houses 10–15 lobes with each made up of several seminiferous tubules, which changes shape conforming to the stage of spermatogenesis. It is in the undifferentiated seminiferous tubules (porcini) on top of each lobe that spermatogenesis begins. Meiosis happens in the acini that carve

out proacini somehow situated close to the top of the lobes. Lobules contain many primary spermatocytes at this level. The regulation of spermatogenesis by hormonal activities in crustaceans is not entirely understood. Figure 2 shows the control of reproduction in male decapod crustaceans.

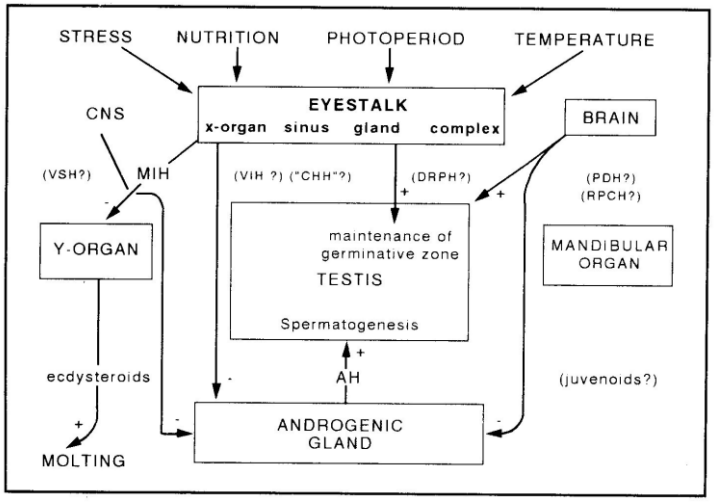

Figure 2. An illustration of the hormonal regulation of reproduction in male decapod Crustacean: the process of spermatogenesis. Herp and Payen (1991).

The female reproductive system

The female crustacean has a pair of ovaries, oviduct, gonophore, and an outer sperm chamber, thylecum. The ovaries are identified at the maturation stages and found in the cephalothorax. The oviduct consists of an ovary laterally beside where the heart is positioned and opens in the abdomen through a gonophore. The ovary fills up the cephalothoracic region at maturity. Ovarian color is transparent at the immature stage and changes to pale yellow or orange when vitellogenesis starts, but at the stages of spawning the color of the ovary becomes dark brown. Due to rapid growth, the oocyte diameter increases as a result of the yolk deposition (Ganji and Nagaraju, 2011). In crustaceans, large quantities of yolk accumulation are the underlying requisite of embryonic and larval development within the developing oocytes during maturation. These type of changes occurs by the settling of yolk material in the oocytes, which causes oocytes diameter to increase rapidly. In each new maturation stages the color of oocytes changes due to the presence of an element called, carotenoid. Hemolymph vitellogenin concentration is a good indicator of the start of vitellogenesis during early maturation. In crustaceans, this a complex physiological phenomenon (Adiyodi and Adiyodi 1970; Nagabhushanam *et al.,* 1985; Subramoniam 1999b). It is with this process that the yolk protein, Vitellin (vn) and Vitellogenin (Vg) which are linked with the lipid and carbohydrate, are formed. Crustacean eggs are mostly full of yolk (Adiyodi and Adiyodi 1970; Nagabhushanam *et al*., 1985). Giant freshwater prawns are perennial breeders and attain maturity at the length 14cm (Rajyalakshmi 1961; Rao 1991). *Macrobrachium rosenbergii* also attains four maturity stages (Rao and Tripathi 1993). Figure 3 shows the control of reproduction in female crustaceans;

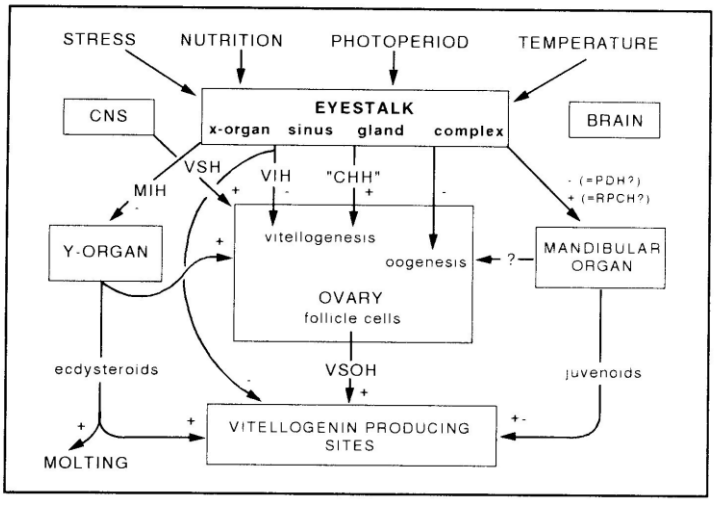

Figure 3. An illustration of hormonal regulation of reproduction in female decapod Crustacean: the process of vitellogenesis. Van Herp and Payen (1991).

The crustacean eyestalk

The significant endocrine regulatory region is the medulla terminalis ganglionic X-organ-sinus gland complex which can be found in eyestalks of most stalk-eyed crustaceans (Reddy and Ramamurthi 1999). The X-organ consists of a bunch of neurosecretory somata. The axons of the X-organ cells were reported to make up the majority of nerves in each eyestalk that cluster on a lateral hemolymph sinus where their dilated axon terminals form a detached depository and releasing site, thus, sinus gland (Spaziani et al., 1994). The sinus gland stores hormones produced by X-organ, to be secreted under the relevant stimuli. Molt-inhibiting hormone (MIH), Vitellogenesis inhibiting hormone (VIH), Mandibular organ inhibiting hormone (MOIH), and Crustacean hyperglycemic hormone (CHH); are the main peptide hormones produced by sinus gland, and they are together called CHH-family peptides. The biological activities of these peptide hormones are overlapped (Keller 1992; Webster 1998; Chan *et al.,* 2003; Nagaraju 2011). In addition to CHH-family peptides, the following are also produced and released by the crustacean eyestalk; the chromatophore regulating peptides namely, pigment-dispersing hormone (PDH) and red pigment concentrating hormone (RPCH), and the neurotransmitters like serotonin, melatonin, and dopamine. The reality of the ovarian growth inhibitory agent in eyestalks was first discovered by the use of *Leander serratus* (Panouse 1943). Gorell and Gilbert (1971) further confirmed this using *Orconectes virulis* and Eastman-Reks and Fingerman (1984) used *Uca pugilator* some years later.

The role of Vitellogenesis-Inhibiting Hormone in the reproduction

Vitellogenesis is a significant process of reproduction in a female crustacean. Vitellogenin (VG) which is the antecedent of the main egg yolk protein, vitellin (VT). It is produced mainly at the hepatopancreas and ovary in decapods and deposited into the hemolymph, and then built up in the growing oocytes. Levels of vitellogenin in hemolymph or of VG mRNA expression at the vitellogenin synthetic regions may most probably be used as markers of ovarian development, as vitellogenin levels change with the cycle of reproduction (Mesuy and Payen 1998; Wilder *et al*., 2002; Wilder *et al*., 2010).

Gonad- or vitellogenesis-inhibiting hormone (GIH/VIH), located in the eyestalk is the primary inhibiting hormone of reproduction. In 1943, Panouse was the first to demonstrate the function of GIH in prawn *Leander serratus*, where the destruction of the eyestalk during sexual inactivity led to constant rise in ovarian size and premature deposit of eggs, presumably because of the removal of GIH. Panouse's work led to several works demonstrating the VIH-induced inhibition of ovarian development in most crustaceans (De Kleijn *et al.*, 1998; Edomi *et al*., 2002; Ohira et al., 2006; Ollivaux *et al*., 2006; Treerattrakool *et al*., 2008; Treerattrakool *et al*., 2011; Tsutsui et al., 2007).

Primary and secondary vitellogenesis are the two phases of ovarian development (Charniaux-Cotton 1985; Quakenbush 1986). Meusy and Charniaux-Cotton (1984) and Van Herp and Soyez (1998) explained primary vitellogenesis as the preparatory stage of oocyte development. During this stage, the oocytes grow slowly and start to build up yolk; ribosomes accrue in the cells, and the rough endoplasmic reticulum prepares for the boosting of yolk by multiplying and producing glycoproteins internally. On the outer layer of the oocyte, the follicle cells tightly embrace the oocyte and will help in the uptake of proteins for accumulation within the cell (Adiyodi and Subramoniam 1983; Van Herp and Soyez 1998). The oocytes then undergo a resting period before secondary vitellogenesis occurs (Meusy and Charniaux-Cotton 1984).

The role of Molt- Inhibiting Hormone in reproduction

The main function of MIH is to inhibit ecdysteroid synthesis from Y-organs. There are not many reports on MIH controlling crustacean reproduction. An account of the inhibiting activity of MIH on vitellogenesis in *M. ensis* shrimps have been investigated (Tiu and Chan 2007). They incubated recombinant MeMIH-B, hepatopancreas and ovary explants and observed the up-regulation of vitellogenin gene in the explants in a dose-dependent manner. The role of MIH in regulating vitellogenesis is predicted to be through tissue specific receptors with variable kinetics and signal transduction. Chang (1985),

reported that MIH adversary conducts molt hormone synthesis through the Y organ and serve as a bridge between neurological signaling and steroidal direction of progressions such as molting and embryo development. Though most researchers in the area of crustacean endocrinology imply that the chemical identity of the active factor is demonstrated, little is known on the biochemistry of Molt-inhibiting hormone. The basic signs are that MIH is either a protein or a peptide that are based on the knowledge that neurosecretory neurons produce it and thus, make trypsin-sensitive (Rangarao 1965).

The role of the Crustacean Hyperglycemic Hormone in reproduction

In the X Organ Sinus Gland, the first polypeptide hormone found in the crustacean neuroendocrine system is the Crustacean hyperglycemic hormone (CHH). Members of the CHH family promote important physiological circuits such as metabolizing energy via mobilization of glucose, ecdysis, regulation of osmotic pressure and reproduction in decapod crustaceans (Bocking *et al*., 2002; Chan *et al*., 2003; Chang *et al*., 2001; Chung *et al*., 2010; Webster *et al*., 2012). The constituents of the CHH- peptides group primarily consists of 70-80 amino acid residues with six conserver cysteine residues that form three intramolecular disulfide bonds (Gorgels-Kallen and Vooter 1985; Mattson and Spanziani 1985).

The start of vitellogenesis is also promoted by CHH hence reproduction; aside regulating carbohydrate metabolism. The role of CHH in promoting vitellogenesis has also been explained by Van Herp (1998).

The role of Mandibular Organ Inhibiting Hormone in reproduction

Methyl farnesoate (MF) is produced in the mandibular organs, and it is involved in the regulating reproduction in crustaceans. There was an increase in the size of the mandibular organ during ovarian growth in the female American lobster, *Homarus americanus* as reported by Byard (1975) and Waddy *et al*., (1995). Eyestalk neuropeptide mandibular organ-inhibiting hormone (MOIH) negatively controls the mandibular organ by inhibiting the production of Methyl farnesoate (Wainwright *et al.*, 1996b; Reddy *et al*., 2004).

There is a chemical similarity between the methyl farnesoate and the insect juvenile hormone III (Laufer *et al.,* 1987b). In recent years, there has been a debate on the physiological function of methyl farnesoate (Laufer *et al*., 2002; Olmstead and LeBlanc 2002). The regulation of molting is partly controlled by Methyl farnesoate (Yudin *et al*., 1980; Chang *et al*., 1993; Tamone and Chang 1993; Wilder *et al*., 1995). Methyl farnesoate also known to regulate reproduction (Borst *et al*., 1987; Laufer and Biggers 2001; Sagi *et al*., 1993; Reddy and Ramamurthi 1998; Kalavathy *et al*., 1999), morphogenesis (Laufer *et al*., 1997; Laufer and Biggers 2001; Abdu *et al*., 1998; Rotllant *et al*., 2000), and general protein synthesis (Paulson and Skinner 1988).

Eyestalk ablation

Since 1970, removal of eyestalk is considered a method to promote the production of *Penaeus spp.* Larvae in aquaculture, Bray W and Lawrence A (1992) and Subramoniam T (2011). In the white shrimp *Litopenaeus vannamei*, *Macrobrachium rosenbergii*, *Farfantepenaeus aztecus,* AQUACOP (1977) and *Farfantepenaeus duorarum*, Caillouet WC (1972), eyestalk ablation promotes several metabolic changes that improve reproductive performance.

Shortening of intermolting and interbreeding periods by eyestalk removal is now a reality in most crustaceans. The significance of eyestalk ablation in promoting ecdysis and/or reproduction by enhancing molting is mostly dependent on season during which this process occurs (Adiyodi and Subramoniam 1983).

Enucleating eyestalk has been used by aquaculturists to promote ovarian maturation in many prawns. This approach is most useful to bring about ovarian development and spawning in prawns that are incapable of maturing in confinement. Idyll (1971) was the first to carry out bilateral eyestalk ablation successfully on *Penaeus duorarum* to induce ovarian growth in about two weeks. Following Idyll's work, many penaeid species have been induced to mature and spawn in confinement; removal of just one eyestalk was most effective (Alikunhi *et al*., 1975; Primavera 1978; Lumare (1979; Muthu and Lakshminarayana, 1981).

Effects of eyestalk ablation on reproduction

In most juveniles and adults of some decapods, eyestalk ablation or specifically destroying the pars ganglionaris X-organ results in premature molt, presumably linked to the disposal of MIH and coherent activation of the Y-organ which produces the molting hormone (MH) (Bliss 1966; Passano 1960; Passano & Jyssum 1963). In adult females of various species, eyestalk ablation does not lead to molting, but precocious release of yolk in the ovary, during both non-breeding and breeding seasons and in some other species such as *Paratelphusa*, *hydrodromous Herbst,* Gomez (1965) and *Scylla serrata Forskal* (Rangneker & Deshmukh 1968; it happens during the prepubescent stages too.

Eyestalk removal destroys the neuroendocrine system of prawns found in the eyestalk which promotes various life activities such as growth, metabolism, and reproduction (Venkitraman et al., 2010). Also, eyestalk removal increased the development of the gonads of females, corresponding with transporting reserves from the hepatopancreas to the ovaries through the hemolymph (Arcos *et al.,* 2003; Meera *et al.,* 2006). An accelerated ovarian growth following eyestalk removal has been revealed in the crayfish; *Procambarus clarkii* by Chaves in 2000. Removing just one or the two eyestalks (both unilateral and bilateral eyestalk ablations) promoted premature ovarian growth in *Penaeus indicus* (Mohamed and Diwan 1991). Okumura and Aida investigated the effect of removing both eyestalks on ovarian growth in the *Macrobrachium rosenbergii* and noticed the cycles of reproduction in the eye -stalked female prawns was shortened.

Okumura and Sakiyama also discovered that the induced ovarian growth in *Marsupenaeus japonicus* after the removal the eyestalks in their non-reproductive seasons and calculated their gonadosomatic index as a reproductive endpoint. Pre-pubertal stages were induced in crabs, *Paratelphusa hydrodromous* and *Scylla serrata* after eyestalk ablation (Gomez 1965; Ragneker and Deshmukh 1968). Also, an increase in gonadosomatic index and levels of vitellogenin mRNA in the ovary of juvenile *M. japonicus* after removal of both eyestalks has been reported (Tsutsui *et al.,* 2005). Significant induction of ovarian growth and rise in ovarian weight, hemolymph vitellogenin levels, and vitellogenin mRNA were observed in young female *M. japonicas* after both eyestalks were removed (Okumura 2007). The above-stated studies also show that eyestalk ablation speeds up ovarian development in crustaceans.

Conclusions and perspectives.

Reproduction in decapods, under the control of neuroendocrine and non-neuroendocrine systems, has become a key topic for investigation and deliberations for the past sixty years because of its importance in crustacean aquaculture. Most neurohormones transmitted by X-organ are said to affect several physiological events, in addition to peripheral endocrine gland activities, vitellogenin production, which precedes the main yolk protein, gonad maturation and hence reproduction. The area of reproductive endocrinology of crustaceans is becoming highly practiced, and modern approaches which allow elaborate investigations on the intricacy of endocrine regulation of reproduction have been introduced. Current approaches such as immunohistochemistry, molecular biology, and biochemical methods must be expanded to cover crustaceans in order to clarify the cellular dynamics of the neuroendocrine cell systems producing Vitellogenesis inducing hormone, Molt-inhibiting hormone, Mandibular organ inhibiting hormone and Crustacean hyperglycemic hormone. Though modern studies have shown a high ability of unilateral eyestalk ablation for inducing growth and ovarian development in crustaceans, other studies have reported high mortality during eyestalk ablation due to the disregard to the nutritional demands of the crustaceans. Therefore, further investigations should be conducted on how to meet the nutrient demands of eyestalk ablated crustaceans that undergo gonad maturation.

Acknowledgments

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