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Reproductive Biology of the Calanoid Copepod *Eucalanus monachus*

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Abstract: Copepods are vital key components of marine and freshwater ecosystems and play vital role in the energy transfer from primary producers to secondary consumers. Their traits like high diversity, different life cycle strategies, sexual reproduction and nutritive value are unique among different zooplankton. In nature, copepods constitute most preferred food of many commercially important marine finfish larvae. Mass culture of copepods is a requisite considering their various applications in aquaculture, environmental monitoring, and pharmaceutical usage. For sustained production of copepods in culture systems there should be proper understanding of their reproductive aspects. In the present study, reproductive biological aspects such as oogenesis, spermatogenesis, spermatophore formation and its transfer to the female of a calanoid copepod, *Eucalanus monachus* are described. Considering the reproductive features, fecundity, egg size and direct broadcasting of eggs to the medium, *E. monachus* could be a potential candidate for mass culture and use as live feed in marine finfish larval rearing.

Keywords: Copepod, reproduction, *Eucalanus monachus,* Live feed, Zooplankton

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Introduction

Copepods constitute an important biotic component of aquatic ecosystem and they are vital links of the freshwater and marine food chain and food webs. Most commercially exploited fishes feed on copepods directly during their larval development and many continue to feed as adults. Copepods are directly collected from nature and used as live food for rearing the larvae of ornamental fishes (Barnabe, 1980; Altaff *et. al.,* 2002). Their high nutritive value makes them potential live food in mass production of commercially important fishes. The nutritional value of copepods is higher than *Artemia* nauplii for fish larvae. The levels of eicosapentaenoic acid, docosahexaenoic acid and (n-3) highly unsaturated fatty acids are high in copepod nauplii

than their adults.

Reproductive biology of copepods constituted one of the important areas of research and many aspects such as maturation, fecundity, nature of egg broadcasting and variation in fecundity were reported for many species (Kiorboe and Sabatini, 1995; Uye, 1981; Peterson and Kimmerer, 1994). It is stated that despite growing knowledge of copepods fauna of meso and bathypelagic region of the ocean, many elements of the life history of these species such as measures of reproductive investments by adult females, egg size, clutch size, mode of reproduction, rate of release of egg and development of ova remain incompletely described (Ohman and Townshend, 1998). Kiørboe (2006) reported that the sex-ratio of copepods communities was affected by their reproduction systems. Copepods such as *Temora longicornis*, lacking sperm storage organs, tend to be closer to an equal gender based ratio (Harris and Paffenhofer, 1976). Though reproductive biology of many calanoid copepod species from temperate regions have been reported, only few species were studied from tropical waters. Importance of the basic knowledge of copepod physiological process, food and feeding habits, breeding biology and population dynamics is essential for developing mass culture techniques (Stottrup, 2000). It has been pointed out that basic research on copepod has been limited to few species only (Marcus, 2005). As copepods are highly suitable live feed for rearing marine finfish larvae their mass culture might augment finfish larval production. In this regard, knowledge of calanoid copepods reproductive biology is essential for their sustained production and use in mariculture. The present study describes the reproductive biology of one of the potential calanoid copepod, *Eucalanus monachus*.

Materials and Methods

Zooplankton samples were collected from offshore of the Kovalam (13.0827° N, 80.2707° E) station, Chennai using 170 µm mesh size plankton net and preserved in 5% buffered formalin. From the plankton sample the calanoid copepod, *E. monachus* was separated and identified to species level following the taxonomic descriptions of Kasturirangan (1963) and Conway *et al.* (2003). To view *in situ*, reproductive system of *E. monachus,* borax–carmine staining method of Pantin (1964) was followed. To view reproductive system of female and male, *E. monachus* were stained overnight with borax–carmine stain and destained with acetic acid till the exoskeleton become transparent. These differentiated specimens were dissected in a glycerol–ethanol mixture medium to describe the parts of the reproductive system following the terminology of Hopkins (1978) and Dussart and Defaye (1995).

For histology, specimens were fixed in aqueous Blouin's fluid, dehydrated in ethanol, cleared in xylene and embedded in paraffin wax. Serial sections of 8 µm were cut and stained with haematoxylin and counter stained with alcoholic eosin (Patki *et al*., 1987). The different parts of reproductive system were observed under compound microscope and photomicrographed at magnification of 100x and 400x.

Results

Anatomy of female reproductive system:

The female reproductive system of *E. monachus* consists of a median ovary, a pair of oviducts and a pair of seminal receptacles. The pear-shaped ovary occurs dorsally on the anterior region of the midgut. The central part of the ovary is dilated compared to anterior and posterior regions. The length of the ovary of this species is 342 µm and width at broadest point is 124 µm. A pair of oviducts after originating from the anterior part of the ovary, take a short course anteriorly, then take a ventro posterior course up to the end of the prosome somites. The oviducts have wide lumen up to the end of the cephalosome and thereafter run as narrow tubes to enter vaginal cavity in the genital segment. A pair of spherical seminal receptacles are located antero-laterally and connected to the vaginal canal (Fig.1a).

Histology of female reproductive system:

The ovary of *Eucalanus monachus* has a thin wall

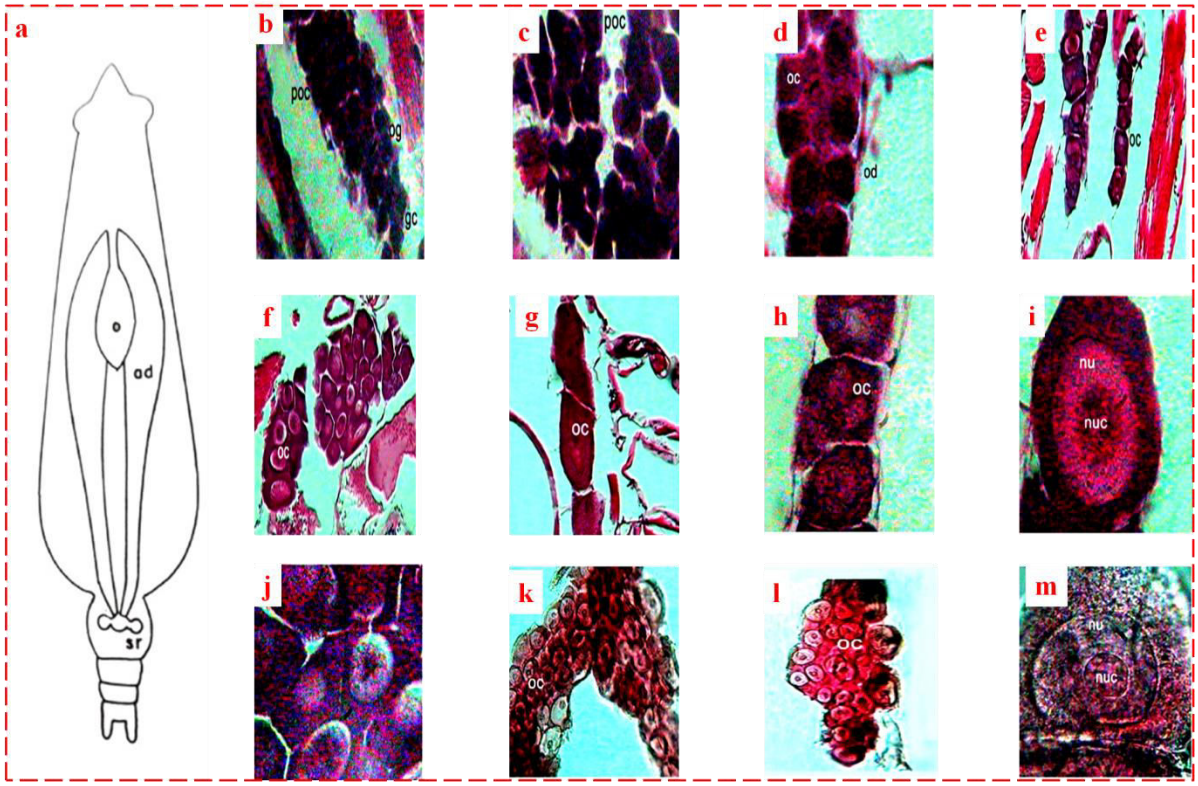

Fig. 1: Female Reproductive System of *Eucalanus monachus* and its Histology. (a) Female reproductive system; (b) L.S. of Ovary; (c) Previtellogenic oocytes; (d-f) Oocytes in oviduct; (g-m) Oocytes in different stages of vitellogenesis. (ov - ovary; od – oviduct; oc- oocytes; poc – primary oocytes; og – oogonial cells; gc – germinal cells; nu – nucleus; nuc – nucleolus).

consisting of an external connective tissue and an internal epithelial layer. The germarium of the ovary located at the posterior end is formed of spherical cells deeply stained with haematoxylin. The oogonial cells are spherical and are derived from the germinal cells by mitosis. They are smaller in diameter than the germinal cells. The different stages of oogenetic cells are arranged in ascending series form posterior to the anterior end of the ovary (Fig. 1b). The primary oocytes and secondary oocytes occupy as successive layers of cells after oogonial cells. The anterior most part of the ovary contains previtellogenic oocytes mostly in the germinal vesicle stage.

The anterior and middle part of the oviduct occupy most of the perivisceral cavity of the cephalosome and holds layers of vitellogenic oocytes. A bigger nucleus with a mono or bi-nucleoli occurs in the previtellogenic oocytes. The nucleus is chromophobic while nucleoli are deeply stained with haematoxylin (Fig. 1c). The cytoplasm of these cells is haematoxylin positive indicating their acidophilic nature. Vitellogenesis commences with the deposition of small granules of yolk in the cytoplasm. The oocytes become basophilic at the onset of vitellogenesis (Fig. 1d). During vitellogenesis oocytes changes their shape from spherical to rectangular. The size of the yolk granule increases during the active vitellogenic process leading to the increase in the volume of the cytoplasm of the oocytes (Figs. 1e-g). In the mature oocytes, the yolk granules are compactly arranged and the cytoplasm is more intensively stained with eosin. In this species, it appears that there is no deposition of yolk globules. Examination of oocytes in different stages of vitellogenesis indicates that high proportion of the nucleus to the cytoplasm is evident in this

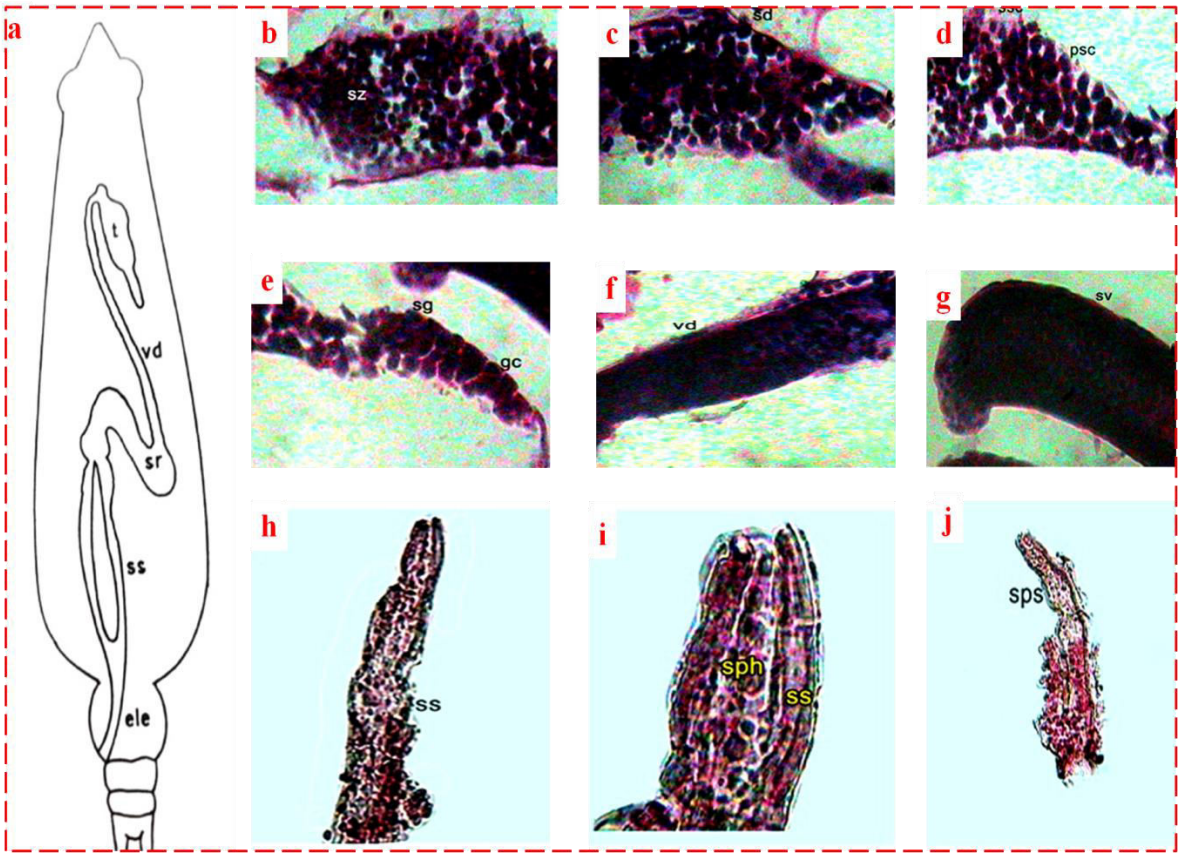

Fig. 2: Male Reproductive System of *Eucalanus monachus* and its Histology.(a) Male Reproductive System; (b-e) L. S. of different regions of testis; (f) Vas deferens; (g) Seminal vesicle; (h) Spermatophore sac; (i). Anterior region of spermatophoresac; (j) Spermatophore in spermatophore sac. (sz – spermatozoa; sd – spermatids; psc – primary spermatocytes; ssc – secondary spermatocytes; gc – germinal cells; vd – vas deferens; sv – seminal vesicle; ss – spermatophore sac; sg – spermatogonial cells).

species (Figs. 1h-m). The seminal receptacles communicate with the vaginal canal through a narrow thin walled duct. In this species many layers of oocytes undergo vitellogenesis and maturation in the oviducts. After maturation the oocytes descend through the vaginal canal and get fertilized. The fertilized eggs are spawned directly into the medium where they undergo embryonic development to hatch out into a nauplii. The size of the mature oocytes of *E. monachus* is 124±10 µm and number of eggs produced in a clutch is 100±12 µm.

Anatomy of male reproductive system:

The male reproductive system of *E. monachus* consists of a median testis and a single genital duct, which passes through the central region of the perivisceral cavity and communicates to the exterior in the genital segment. The testis is an elongate organ with broad anterior and narrow posterior regions. Vas deference originates from the anterior end of the testis and takes a posterior course centrally up to the end of cephalosome and then proceeds laterally to transform into the seminal vesicle. The seminal vesicle is broader than the vas deference and opens into spermatophore sac. The spermatophore sac is an elaborate structure which molds the spermatophore. It leads to a narrow ductus ejaculatorius which passes through the genital segment and opens to the exterior through a lateral slit (Fig. 2a).

Histology of male reproductive system:

The posterior most region of the testis contains spherical germinal cells which are deeply stained

with haematoxylin. The germinal cells give rise to spermatogonial cells which are less intensively stained with haematoxylin. Anterior to the spermatogonial cells primary spermatocytes occur in the testis. The primary spermatocytes transform into secondary spermatocytes when they enter reduction division. The secondary spermatocytes are smaller than the primary spermatocytes. These cells become spermatids at the end of the reduction division. The spermatids are smaller than other spermatogenic stages. These cells undergo spermiogenesis in order to become spherical spermatozoa which occur at the anterior most part of the testis (Figs. 2b-e). The spermatozoa of this species measure 11.5 µm in diameter. The anterior most part of the testis has a small triangular mass of tissue composed of glandular cells which produce secretory material in which spermatozoa are blended.

Histologically the vas deference of *E. monachus* is a prominent tube composed of a thick wall and large lumen. The wall of the vas deference has thick layer of epithelial cells which produces large quantity of eosin positive secretory material. The spermatozoa get suspended in the secretory material of the vas deferens (Fig. 2f). The seminal vesicle of *E. monachus* is a thick and prominent structure of the genital duct. It has a narrow proximal region which communicates with the vas deferens and a curved distal region which opens into the spermatophore sac. The wall of the seminal vesicle is thick and formed of highly glandular epithelial cells. These cells occur in many rows and produce large quantity of secretory material. The lumen of seminal vesicle is very large and stores spermatozoa and other secretory material meant for the formation of spermatophore (Fig. 2g).

The spermatophore sac has a thick wall consisting of spongy cells and less glandular in nature. However, it produces secretory material which occur as small droplets. The lumen has a tripartite structure with a narrow proximal and intermediate middle and broad distal regions. Spermatophore is formed in this sac (Figs. 2h, i). The spermatophore has a tubular form with a narrow anterior region, a long and tubular posterior region and a middle region with constricted posterior end (Fig. 2j). The wall of the spermatophore is formed of a chitinous material. The spermatophore contains secretory material in its lumen in which spermatozoa occur as a layer of cells suspended peripheral to the core secretory material. There is a thin layer of secretory material in between the spermatozoa and wall of the spermatophore. The ductus ejaculatorius is thin walled structure and formed of non-glandular cells.

Discussion

The reproductive system of female calanoid copepod species shows a generalized pattern of having a single median ovary, paired oviducts originating from antero-lateral part of the ovary which leads to the genital segment through the sides of the digestive tract and open into a single chamber, the genital antrum. Though such a generalized female reproductive system is reported in many calanoid species there is considerable species specific variations (Park, 1966; Marshall and Orr, 1972; Corkett and McLaren, 1978; Blades-Eckelbarger and Youngbluth, 1984; Razouls *et al.,* 1986, 1987; Norrbin, 1994; Altaff, 2003, 2020; Dharani and Altaff, 2004a). The genital antrum has paired dorso-laterally directed pouches, the seminal receptacles in which spermatozoa are stored. Such an organization of female reproductive system is observed in the *E. monachus*. However, in this species variation is observed about the size and shape of the ovary, wide lumen of the oviducts without any distinct diverticula, structure of the antrum and seminal receptacles.

The common feature of oogenesis of copepod is occurrence of germinal cells at the posterior most narrow part of the ovary and oogonial cells proliferate from them and occupy the next anterior region. The oogonial cells give rise to primary oocytes and then secondary oocytes which in rows occupy the mid part of the ovary. The secondary oocytes give rise to previtellogenic

oocytes containing a prominent nucleus and nucleolus. These cells occupy the anterior part of the ovary and then transferred to the oviducts. The oogenesis of *E. monachus* also follow the same order of arrangement of ovarian cells however, size of the ovarian cells of this species is smaller than the other calanoid copepods. The size of the eggs and number of eggs produced in a clutch of female calanoid copepods shows considerable variations in different species. In the present study mean size of egg diameter recorded in *E. monachus* is 124 µm and a clutch contained about 100 eggs. Variation in the egg size and number produced by the copepods depends on the physico-chemical parameters and depth of their inhabitation. Pertaining to reproductive strategies of the four congeneric and sympatric calanoid copepods *Paraeuchaeta glacialis, P. norvegica, P. barbata,* and *P. polaris*, Auel (2004) reported females of all species produce egg sacs and carry their brood attached to the genital opening until the offspring hatch. However, egg size and lipid content as well as clutch size and the fraction of females carrying egg masses show characteristic differences among the four species. *P. glacialis* and *P. norvegica* produce large numbers (37 to more than 50) of relatively small eggs, whereas *P. barbata* and *P. polaris* rely on small numbers (10 to 19 and 4 to 6, respectively) of large eggs with a high energy content. There is no correlation between female body size and egg size or clutch size, respectively. Females of the smallest species, *P. polaris*, produce relatively large eggs and show the highest energetic investment per egg.

According to Kosobokova *et al.* (2007) out of nine Calanoida families, females of seven species released eggs freely into the water and females of three species produced membrane-bound egg sacs while *Aetideopsis rostrata*, produced a mass of eggs. In calanoid copepods broadcast spawning is predominant in the benthopelagic species, and both broadcast spawning and egg brooding in the planktonic species. Clutch size and egg diameter varied widely between species in both broadcast spawners and egg-brooders. In broadcast spawners, the clutch size varied from 1 to 95 eggs /female, while the average egg diameter ranged from 152 to 440 µm. The clutch size for egg brooders varied between 3 and 82, while average egg diameter varied from 258 to 732 µm (Kosobokova *et al.*, 2007). Such diverse nature of egg production and spawning facilitates production of either subitaneous or diapausing eggs (Dharani and Altaff, 2004b).

Variation is observed in the oviducts of calanoid copepods, in species like *Pseudodiaptomus annandalei* and *Pseudodiaptomus serricaudatus* -- lateral diverticulae are absent (Altaff, 2020) while in the case of *Euchaeta marina* and *Pleuromamma xiphias* extensively developed diverticulae are reported (Blades-Eckelbarger and Youngbluth, 1991). In many fresh water diaptomids like *Hemidiaptomus ingens provinciae* and *Mixodiaptomus kupelwieseri,* (Cuoc *et al.*, 1989 a,b) and *Heliodiaptomus viduus* (Altaff and Chandran, 1994; Altaff, 2003) there is no internal seminal receptacle to store spermatozoa and they form temporary sperm receptacle attached to the genital cavity to store sperms.

The reproductive system of marine male calanoids consists of a single testis and a genital duct that take posterior course either laterally or centrally and open at a gonopore on the first urosomal segment. The genital duct is morphologically divided into the vas deferens, seminal vesicle, spermatophore sac, and ductus ejaculatorius. As immature spermatozoa pass from the testis through these regions, the various components of the seminal fluid, spermatophore wall, and material associated with fixing to the female gonopore are produced and secreted into the lumen (Blades-Eckelbarger, 1991). The male reproductive system of *E. monachus* shows generalized pattern of calanoid copepods. Nevertheless, testis of this species is an elongate organ with broad anterior and narrow posterior regions. Vas deference after originating from the anterior end of the testis takes a posterior course centrally up to the end of cephalosome and then proceeds laterally to transform into the seminal

vesicle. The seminal vesicle is broader than the vas deference and opens into spermatophore sac. The spermatophore sac is an elaborate structure which molds the spermatophore.

Pochon-Masson (1983) described two kinds of testicular cells in crustaceans i.e., germinal and somatic cells. The germinal cells are smaller in size with a large nucleus and are deeply stained with haematoxylin. The somatic cells are large, rich in organic resource and also have a large nucleus. Contrary to the other crustaceans, the testis of the calanoids copepods have only germinal cells and somatic cells are totally absent such a condition is also reported in the freshwater *Diaptomids* such as *Sinodiaptomus* (*Rhinediaptomus*) *indicus* (Dharani and Altaff, 2004 a)), *Heliodiaptomus viduus* (Altaff, 2003) The testicular cells of *E. monachus* are arranged in an ascending pattern from posterior to anterior end. The spermatogonial cells proliferate to produce primary spermatocytes which transform into secondary spermatocytes. The smaller secondary spermatocytes become spermatids at the end of the reduction division. The spermatids are smaller than other spermatogenic stages. These cells undergo spermiogenesis to become spherical spermatozoa which occur at the anterior most party of the testis

Histologically the vas deference of *E. monachus* composed of a thick wall and large lumen. The wall of the vas deference has thick layer of epithelial cells which produces large quantity of eosin positive secretory material. The spermatozoa are glued in the secretory material of the vas deferens. The vas deferens of *Heliodiaptomus viduus* is histologically distinguished into anterior vas deferens and posterior vas deferens showing multiple epithelial layers in the posterior regions which can produce large quantity of secretory material (Altaff, 2003). The vasa differentia of *E. monachus* presently studied did not show any such differentiation. The seminal vesicle is the prominent region of the genital duct and show considerable variation in many calanoids copepods (Blades-Eckelbarger and Youngbluth, 1991). Basically, the seminal vesicle is formed of ascending and descending limb. These limbs are wider than the vas deferens and show species specific variations. The seminal vesicle of *E. monachus* is a thick and prominent structure of the genital duct and has a short descending and long ascending limb. The wall of the seminal vesicle is thick and form many rows of highly glandular epithelial cells which produce large quantity of secretory material. The lumen of seminal vesicle is very large and stores spermatozoa and other secretory material meant for the formation of spermatophore. It is apparent that the seminal vesicle apart from producing secretory material for the formation of spermatophore it also acts as an organ of storage of seminal material. Such functions of seminal vesicle are reported in many calanoids copepods (Mauchline *et al.*, 1998; Altaff, 2003, 2020).

In the calanoid copepods the spermatophore sac is the largest part of the male genital duct. It is large, elongate, highly glandular and divided into two morphologically distinct regions which mold the spermatophore. Depending on the species, simple adhesive secretions or more complex plates of a coupling apparatus are produced within the anterior spermatophore sac and connected to the neck region of a mature spermatophore flask that lies in the lumen of the sac proper. The size and cellular composition of the anterior spermatophore sac is related to the final configuration and complexity of the coupling apparatus. The *Euchaeta norvegica* produces a spermatophore without coupling plates therefore the anterior spermatophore sac is a simple gland that secretes an adhesive substance onto the spermatophore neck (Hopkins, 1978). With complex coupling plates in *Undinula vulgaris* the anterior spermatophore sac is composed of 4 to 6 distinct secretion types (Blades-Eckelbarger, 1991). The glandular region of spermatophore sac in the pontellids *Epilabidocera amphitrites* (Park 1966) and *Labidocera aestiva* (Blades-Eckelbarger and Youngbluth 1981) produces 7 to 8 different secretion types that are molded by the shape of the lumen into the highly complex plates of the coupling apparatus. *E. monachus* produces a

simple spermatophore without coupling plates therefore the anterior spermatophore sac is a simple gland that secretes an adhesive substance at the anterior region of the spermatophore which denote simplified copulatory process and spermatophore transfer to the female. The spermatophores of *E. monachus* are simple, elongate tube-like structure that store the spermatozoa and associated seminal secretions. It narrows toward open end of the tube into a spermatophore neck. As in the case of many calanoid copepods, the spermatophore of *E. monachus* adheres to the female by a cement like secretion extruded from the spermatophore.

Conclusion

The reproductive biology of *E. monachus* illustrates many interesting features like well-developed female and male reproductive system, high fecundity, smaller eggs and egg broadcasting type of spawning. These traits are vital for considering this species for mass culture and application as live feed in aquaculture. The diapausing eggs produced could be developed as dry live food which can be highly desirable development for marine finfish larval rearing. Further studies on better understanding of diapause eggs of this species and processing them as dry cysts is necessary for use in marine finfish larval rearing hatcheries.

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