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FECUNDITY, EMBRYONIC AND LARVAL DEVELOPMENT OF THE MARINE SNAIL *Linatella caudata* (MOLLUSCA: GASTROPODA)

FECUNDIDAD, DESARROLLO EMBRIONARIO Y LARVARIO DEL CARACOL MARINO *Linatella caudata* (MOLLUSCA: GASTROPODA)

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ABSTRACT**.** The marine gastropod *Linatella caudata* (Gmelin, 1791) represents a serious threat to bivalve aquaculture facilities as a consequence of its intensive predatory behaviour on these mollusks of commercial interest. We study the fecundity and embryonary development of this snail species. The developmental sequences of the ovigerous capsule including the "immature", early mature and advanced mature or final stages. Regarding fecundity, six ovigerous capsules masses (eggs mass) were studied and showed a variable number of ovigerous capsules (101-203) and eggs per capsule (83-198). This may correspond to a different total number of eggs in each ovigerous capsule mass, within the range of ca. 8 400 to 40 200 eggs. In the embriogenesis, the blastula, gastrula, trochophore and veliger stages occurred on days 2, 4, 6 and 18 of their embryonic development, respectively, whereas larval hatching was observed at day 26. *Linatella caudata* hatches from the ovigerous capsule as apelagic larvae (being a planktotrophic larvae).

Key words: snail, ovigerous capsule, larvae culture, trochophere larvae, veliger larvae.

RESUMEN**.** El gasterópodo marino *Linatella caudata* (Gmelin, 1791) presenta una seria amenaza para los cultivos de bivalvos como consecuencia de su intenso comportamiento depredador sobre estos moluscos de interés comercial. En este estudio fueron investigados varios aspectos relacionados con la fecundidad y el ciclo de vida temprano de esta especie de caracol. Las secuencias de desarrollo de la cápsula ovigera incluyeron las etapas inmaduras, maduras tempranas y maduras avanzadas o finales. Con respecto a la fecundidad, se estudiaron seis masas de capsulas ovígeras (masa de huevos) que mostraron diferencias en el número de cápsulas ovigeras (101-203) y el número de huevos por cápsula (83-198). Esto correspondería con un número total muy diferente de huevos en cada masa de cápsulas ovigeras, que varió entre 8 400 a 40 200 huevos. En la embriogénesis, las etapas de blástula, gástrula, trocófora y veliger ocurrieron en los días 2, 4, 6 y 18 de su desarrollo embrionario, respectivamente, mientras que la eclosión de las larvas se observó en el día 26. *Linatella caudata* eclosiona de la cápsula ovígera como larva pelágica (siendo larvas planctotróficas).

Palabras clave: caracol, capsulas ovígeras, cultivo de larvas, larva trocófora, larva veliger.

INTRODUCTION

In the northeastern region of Venezuela, snails of the Family Ranellidae (= Cymatidae) are commonly present in natural banks of bivalves, which in turn represent one of the main food resources for some species of this gastropods family such as members of the genera *Linatella*, *Monoplex* or *Cymatium*. Small individuals were frequently observed in the brown mussel P*erna perna,* cultivation platforms whose trophic relationships were confirmed experimentally by Urosa (1972). Narváez *et al.* (2000) observed a decrease in the survival rates of the bivalve *Pinna carnea* under suspended cultivation conditions that was associated with the presence of *Cymatium poulsenii.* This observation was also made during the suspended cultivation of the pectinid *Euvola ziczac* (Vélez *et al*.1995; Freites *et al.* 1995). Freites *et al*. (2000) noted that C. *poulsenii* was present in the 48% of the cultivation baskets, with a predation rate of

0.84 individuals d^{-1}. More recently, Malavé *et al*. (2012) showed that the survival of the pearl oyster *Pintada imbricata* was significantly smaller during the intense recruitment period of *L. caudata*. According to Beu & Cernohorsky (1986), *Linatella caudata* is synonymous with *C. poulsenii* and *C. cingulatum*, consequently, this species has been implicated in the predation of marine bivalves at Pantropical level, in places as distant as the Gulf of Mannar, India (Thangavelu & Muthiah 1983); Hong Kong (Morton 1990); Hainan Island, China (Zhou & Pan 1999); Viet Nam (Ching 2001); Tuléar, Madagascar (Beu & Zibrowius 2007); Santa Catarina, Brasil (Figueiredo & Rosso 2011); Arakan Waters, North Sulawesi (Toreh *et al*. 2018) and Santa Elena Province, Ecuador (Freites *et al*. 2019).

Ramón (1991) observed the egg mass and larval development of *Cymatium cutaceum* and *C. corrugatum*; species which inhabit in the Mediterranean Sea and western Africa. This author observed free larvae 27 days after the spawning. Govan (1995) reported free larvae of *C. muricinum*, *C. aquatile* and *C. nicobaricum* hatching in less time, that is, at days 22, 19, and 17 days, respectively. Scheltema (1966, 1971) studied the behaviour of *C. parthenopeum* and *C. nicobaricum* larvae with regard to their probable transoceanic transport by marine currents. However, there are no studies in the Caribbean Sea and adjacent areas regarding the fecundity of different *Cymatium* species, having only literature related to predation exerted on cultivated marine animals (Littlewood 1988, 1989; Freites *et al*. 2000; Núñez 2010).

Individuals of the genus *Cymatium* (Ranellidae) transfer sperm through the copula and fertilization occurs internally. After the copula, eggs are layed in the proteinaceus mass of eggs capsules (Webber 1977). Egg capsules are characterised by relatively thin walls in comparison with that of neo-gastropods and an exit orifice is lacking (Houbrick & Fretter 1969; Laxton 1969). Egg capsules of various species of the genus *Cymatium* spp. have been described with a spherical concave mass that corresponds to the helicoidally ordering of the eggs capsules. These eggs capsules are cemented to the substrate by a gelatinous mass, with the central egg capsules located deeper than the external ones and with their apical zone directed towards the exterior. These egg masses have been described for *C. muricinum* (Boullaire 1953), *C. nicobaricum* (Houbrick & Fretter 1969), *C. parthenopeum* (Laxton 1969) and *C. corrugatum* (Ramón 1991).

On the other hand, studies focusing on the fecundity of the genus *Cymatium* are scarce. Approximately 100 egg capsules were deposited by individuals of *C. nicobaricum*, *C. gemmatum* (Houbrick & Fretter 1969) and *C. muricinum* (Boullaire 1953) although the number of eggs per capsule varied widely for inter and intra-specific comparisons. Indeed, the amount of egg capsules may vary between 518 400 (Muthiah & Sampath 2000) and 587 050 (Zhou *et al*. 2000) for *C. pileare*; values representing high fecundity.

From the taxonomic and physiological point of view, the larval and post-larval developments in prosobranch gastropods are of high interest and may contribute to the knowledge of numerous aspects of their biology which is, in turn, important for the cultivation of aquatic organisms (Butman 1987). Accordingly, the protoconch larva has been interpreted in different ways, for example as an ancestral characteristic (Marwick 1957; Marshall 1978, 1983; Allmon 1988, Kowalke 1998a, 1998b; Nützel 1998; Hickman 1999, 2001), or an adaptation to planktonic life or as a result of early bio-mineralization (Hickman 2001). The ornamentation of the larval shell is recognizable as a great taxonomic value and the identification of gastropod larvae has been achieved through observations of cultivated larvae from known parental individuals (Lebour 1945; Fretter & Graham 1962; Scheltema 1962; Thorson 1965; Thiriot-Quiévreux 1967a, b, 1969; Struhsaker & Costlow 1968; Robertson 1974; Thiriot-Quiévreux & Scheltema 1982; Scheltema & Williams 1983; Romero *et al*. 2004).

Considering the scarcity of studies on aspects related to fecundity and the early life cycle of *L. caudata*, and that Freites *et al.* (2000) showed that this gastropod caused high mortality rates in the commercial culture of marine bivalves, we consider it necessary to know its biology, as a contribution to the optimization of the commercial production of marine bivalves. Therefore, the present study was carried out to investigate some aspects of the early development of this species as a fundamental contribution to understand part of its biology.

MATERIALS AND METHODS

Sampling of individuals

In August were collected six individuals of *L. caudata* from cultivation baskets (Pearl nets, 6 mm mesh) of the pearl oyster *Pinctada imbricata* hung on a long-line located at the Turpialito Hidrobiológical Station associated to Instituto Oceanográfico de Venezuela of

Universidad de Oriente, Gulf of Cariaco (10º27'30"N; 64º01'52"W). These were then transferred to the humid laboratory and placed in 6 40-L aquariums, containing 10 individuals of *Pinctada imbricata* offered as prey. The seawater was prefiltered and irradiated with UV, at a temperature of 27 ± 1 °C. Sea water was totally replaced daily to eliminate excretion metabolites, rests of the oysters dead and excedents of surplus food offered to them. The latter consisted of a 1: 1 mixed diet of *Isochrysis galbana* (T-Iso clone) and *Chaetoceros gracilis,* at a concentration of 70 000-80 000 cells per oyster d^{-1}. Once the laying of the ovigera mass began, the oysters were removed because the snail stopped consuming them. Of the last ovigera capsules layed, corresponding to the outer part of the ovigera mass, some of these capsules were removed with a dissecting forceps. By removing freshly layed capsules, we made sure to obtain early developing embryos. Once the ovigera capsule was opened, the sample was taken with a syringe and placed in an 5 ml eppendorf test tube, and preserbed with 2 ml of 3% formalin.

Embryonic and larval development of the gastropod *L. caudata*

Four embryonic and larval developments were followed by a photographic register that was performed using optic microscopy, with a stereomicroscope LEICA, MZ75; ZOOM 2000 and a DM 1000 microscope. Biological material (eggs and larvae) was collected every four hours during the first four days and preserved with 3% formalin, and then they were collected daily until hatching of larvae. Sigma Scam Pro software was used for size measurement of the different embryo stages and the larvae development. Five embryos or larvae from each female were measured. The size shown in the description of the different stages of the ovigera capsule, embryonic, and larval development are expressed in their mean and standard deviation (n=20).

Is the methodology used for the cultivation of *L. caudata* veliger larvae was developed as detailed by Romero *et al*. (2004). Maturing egg masses from cultivation cages were placed in 4 L containers in the laboratory at temperature and salinity levels of 22 ± 2 °C and 35 PSU, respectively (similar to the natural conditions), for a period of 1-5 days until hatching occurred. After the larvae hatched, food consisting of the microalgae *Isochrysis galbana* and *Chaethoceros gracilis* suspended in seawater was added *ad libitum* in a 1:1 proportion and a final concentration of 30 000 cells microalgae mL^{-1} over the entire development stage. The seawater was first filtered under vacuum with 0.7 µm fiberglass Whatman GFF filters using Millipore equipment.

The shell ornamentation was described in detail so that it can be used in future identifications of these larvae, observed in planktonic sampling of seawater.

RESULTS

Fecundity

Oviposited ovigerous capsules masses from six individuals (mean size of 6.0 ± 0.34 cm) were incubated under laboratory conditions at 22 ± 2 °C and a salinity of 35 PSU and where viable complete embryonic and larval developments were obtained, although the timing of each stage of the process varied. The number of ovigerous capsules and eggs per capsule showed high variability. The six ovigerous capsules masses studied also showed large differences in the number of egg capsules (101-203) and the number of eggs per capsule (83-198) which represented a very different total number of egg per ovigerous capsules mass within the range of ca. 8 400 to 40 200 eggs. At the beginning of the spawning, some egg capsules (<20 %) presented a dark purple colour and were generally empty or had a decomposed content.

Adults spawning was a frequent observation in the field (Fig. 1A). Figures 1B, C and D show the sequence of the development of the immature, early mature and advanced mature or final egg capsules, respectively. Egg capsules in the mature stage can be observed in Figure 1E and the advanced or final stage with the beginning of the larval hatching is illustrated in Figure 1F. The time between the oviposition process of spawning of the egg masses at the larval hatching was of 26 days in the laboratory, in all of the several spawning and hatching bioassays.

Encapsulated development: embryonic and larval stage

Fertilised oocytes were observed in the inner space of the ovigerous capsules (Fig. 2A), embedded in a white and opaque capsular albumin (this characteristic depends on the quantity of vitellus). The segmentation corresponded to the spiral type and with the formation of the polar lobule, eggs obtained a diameter value of 130 ± 5.3 µm. The eggs became rounded again and the first division started, resulting in the formation of the blastomeres AB and CD. The polar body formed rapidly and was discharged within 10-20 min (Fig. 2B), with the thinnest portion located in the vegetal hemisphere of the

egg. It is important to note that we tried to isolate the egg capsules in this phase to observe whether segmentation may continue outside of the capsule. However, after 30 min the egg capsules ruptured and turned purple which indicated the death of the embryos.

A polar view an of 8-cells embryo showed the highest length of 130 µm (Fig. 2C). As development proceeded, the gastrula became elongate and acquired an ovoid shape. This condition is called post-gastrula. In the dorsal region, the ciliated band originated during the blastula stage and developed to form a densely ciliated band that corresponded to the vesicle of the head. Under light microscopy, the embryo was spherical with a diameter value of 140 µm ±20 µm. The lateral

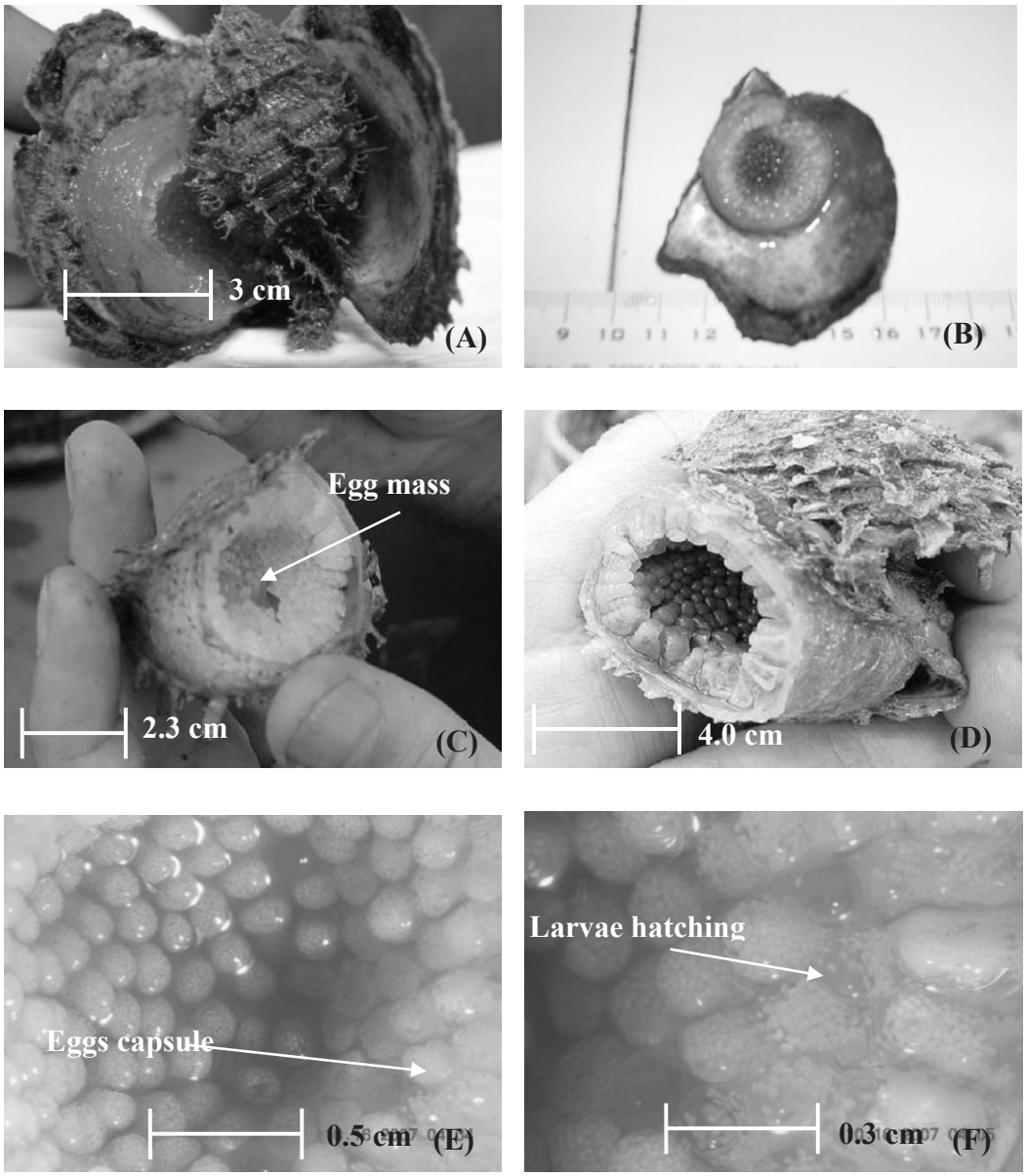

Figure 1 A) Adult individual incubating ovigerous capsule mass; B) ovigerous capsule masses; C and D) ovigerous capsule in different developmental stages; E) ovigerous capsule filled with eggs, and F) ovigerous capsule in the larvae hatching process.

areas of the embryo were covered with microvilli and had two hemispherical protuberances with diameters of 20 and 22 µm. The embryonic process continued until the formation of a post-gastrula, which appeared after 6 days in a trochophore state. In the dorsal zone of the prototroch, small cilia was observed that extendeding to the apical region and to the sides (Fig. 2D). From day 7 to 8, the early trochophore stage measured a length of 230 ± 7.8 µm, and presented an elongated cylindrical shape. Late trocophere stage was observed in that same eighth day (Fig. 2E).

The prototroch was visualized with a band of cilia in constant activity (Fig. 3A, C), and two eye spots were observed (Fig. 3B). The ciliated area under the stomodeum projected forward initiating the formation of the foot. The initial development of the bilobed velum was also observed (Fig. 3A-C). On day 18, there was a noticeable change in the dorse of the larvae, which had a more developed protoconch forming a conic in the dorsal direction which, in the following 24 h, was oriented toward the right side showing the onset of swirl. The initial development of the bilobed velum was also observable.

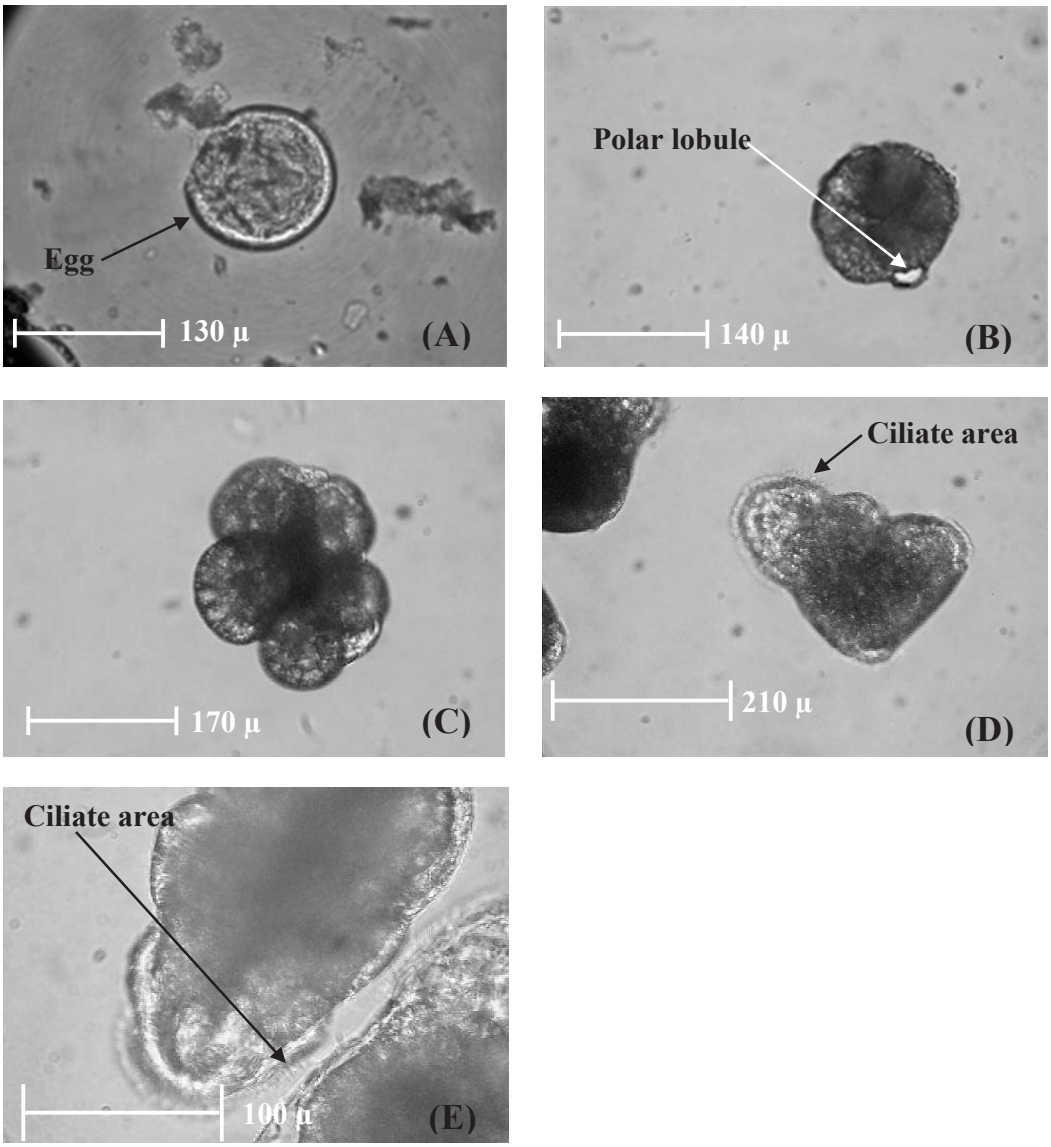

Figure 2. Larval development stages of *Linatella. caudata*; A) egg; B) expulsion of the first polar lobe (20X); C) Cellular divisions (20X), and D) Trochophore larvae.

After 22 days the velum of the larvae developed and was symmetrically bilobed with a band of 11 to 13 cilia closely associated and arranged perpendicularly to its margin with a length of about 20 µm. A feeding channel can also be observed along the edge of each wing of the velum. The lower half of the larva had a rounded shape and simple cilia were present dorsally on the mantle edge (Fig. 3C). The larvae were observed to be actively swimming in the capsule, but the soft tissues within the protoconch were not retracted. Some of these had consumed much of their yolk reserves which helped to distinguish the stomach. The colunmela became an increasingly dark suture located at the lower end of the protoconch aperture.

The intracapsular period ended with the emergence of the first larvae throughout the perforations in the apex of the capsule, with a length of about 220 ± 8.5 µm (Fig. 4). The larvae hatched by the apical perforation without evident cap or lid (Fig. 2F), in a process for all eggs masses that lasted from 2 to 3 d, after which they actively swam to the surface inside the velum forming clusters.

In the inferior part of the velum of the larvae, as opposed to the inner preoral band, there was a band of simple cilia of approximately 110 µm in length (Fig. 4A and B). The operculum completely covered the back of the foot and the opening of the shell when the larva was retracted (Fig. 5B). Immediately after hatching, the postlarvae were fed with *Isochrisys galbana* "*ad libitum*", and after 20 min the larval intestine showed a dark green colour, indicating the ability to ingest this microalga. Dotted shell-type ornaments were found on the surface of the shell (Fig. 4B).

DISCUSSION

In the present study, blastula and gastrula stages were observed as well as the trochophore with its cylindric and long form with a ciliated area, the protoconch and the formation of the foot. All these stages and characteristics mentioned, especially the cylindrical form and the development of structures such as sensorial and cephalic plaques, the stomodeum, arquenteron, protoconch, statocysts and the cilia are typical of the trochophore

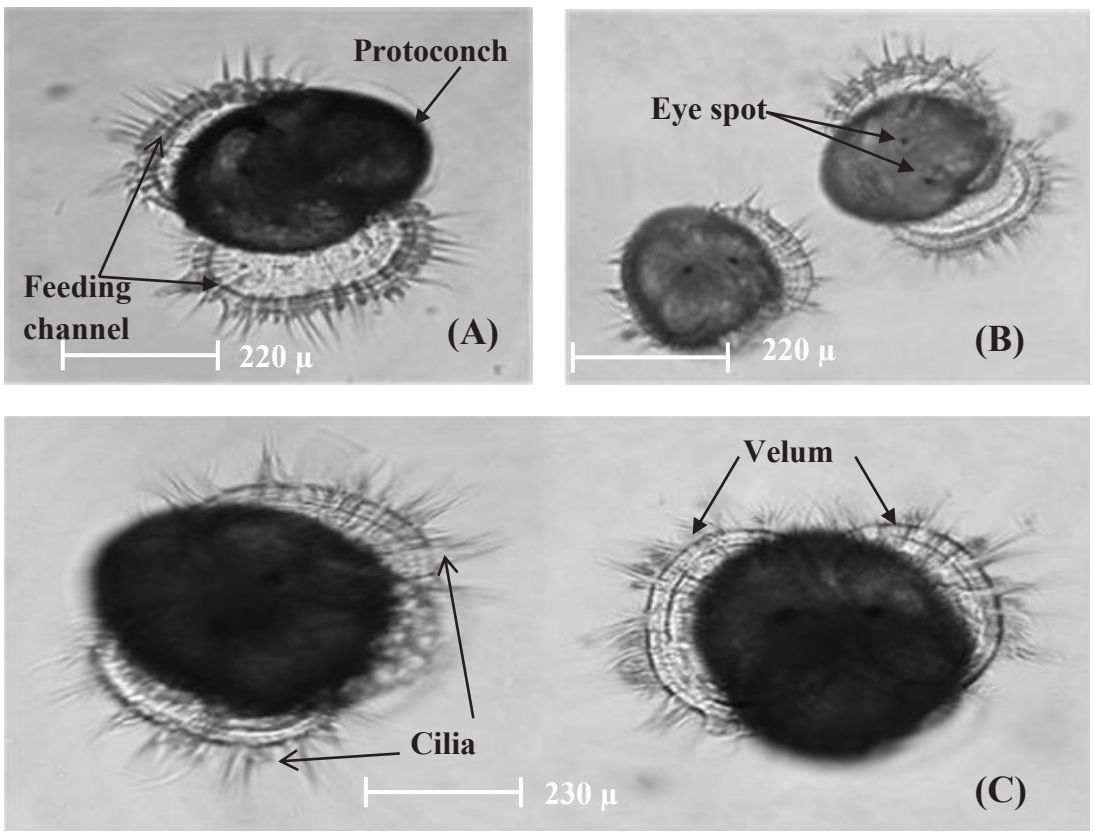

Figure 3. Larvae veliger stage of *Linatella caudata*; A) feeding channels cilia, B) eye spot; C) velum and simple cilia.

larvae of the neo-gastropod (Raven 1958; Hyman 1967). Moreover, the trochophore stage presented a ciliate area (see Fig. 3D), in agreement with Raven (1958). This author described that trochophore of the Prosobranchia as having a ciliated crown, or troch, around its body.

The absence of a cap at the time of hatching and lack of perforations observed in the inner housing in pre-hatching capsules (Fig. 5E), suggest that the emergence of this species depends on enzymes that dissolve the capsule operculum, allowing that water enter and exit of the larvae. In this sense, the environmental influence on the hatching process was rejected by D'Asaro (1966), with the observation that this always occurs at the same stage of larval development of *L. caudata*. Thus, species with indirect development such as *L. caudata*, whose larvae do not perform mechanical actions to exit the capsules, suggests that other forms of hatching should be considered. These include collapse of the capsular walls due to the increase in osmotic pressure of the intracapsular content, such as for *Littorina littorea* and *Lacuna* sp (Webber 1977). This author suggested that the opening of the capsules would be produced by a substance secreted by the larvae. Subsequent studies have confirmed this idea and determined that the substance acts as an enzyme and softens the capsule operculum. This substance is inactive at low temperatures and is species-specific (Pechenik 1975; Sullivan & Bonar 1984). In contrast, hatching of larvae in species with direct development such as *Thais hippocastanea* occurs because juveniles scrape or cut the walls of the capsules (Thorson, 1935, 1940).

With regard to the size of the veliger larva of *L. caudata*, length of 220 µm reported here agree with values by Zhou *et al*. (2000) for *C. pileare*. However, these differed with those for veliger larvae of other species of the same genus, which ranged from 230 µm for *C. aquatile* and *C. nicobaricum* (Govan 1995) to 290 µm for *C. corrugatum* (Ramón 1991). On the other hand, there was agreement on the characteristics of the velum of *L. caudata* (bilaterally symmetrical, bilobed, ciliated bands pre-and post-oral and food groove), which is shared by most prosobranch species in planktotrophic larval stage. These bands of cilia collaborate in swimming and feeding, contributing to the uptake of phytoplankton (Fretter & Graham 1962).

In laboratory tests *L. caudata* presented a planktotrophic larva using the terminology reported by Jablonski and Lutz (1980, 1983) and Jablonski (1986). The existence of the planktonic larvae in the development of *L. caudata* may be explained from an evolutionary point of view as a mechanism of geographical species distribution. In this sense, the larvae of many species belonging to the family Ranellidae are characterized by a long planktonic stage, as has been described for teleplanic-type larvae that remain as plankton for over two months (Scheltema 1971). These larvae have been described for *Cymatium gracile*, *C. labiosum*, *C. martinianum* and *C. parthenopeum* (Scheltema 1989). This planktonic life allows them to drift over long distances in the ocean and thus facilitates a wider geographical distribution. This would explain the pan-tropical distribution for species like *C. muricinum* whose

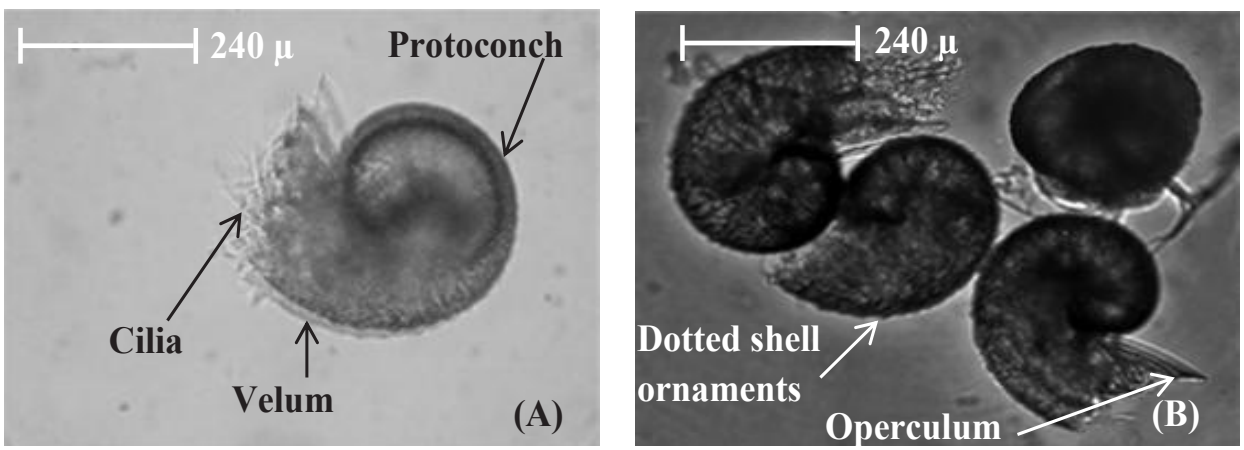

Figure 4. Selected protoconch stages of *Linatella caudata* from its formation up to the juvenile stage (A-B) and formation of the protoconch.

Table 1. Species of the Ranellidae family studied and their biometric and fecundity parameters.

Species	Size, culture and eclosion time						Diameter of ovigerous capsule mass (mm)	Eggs number		Reference
	Snail size (mm)	Egg (µm)	Egg capsules (mm)	Free larvae (µm)	Culture temp. (ºC)	Hatching time (day)		Ovigerous capsules	Ovigerous capsules mass	
C. cingulatum (= *L. caudata)*	55-60	NI	10.9	NI	NI	NI	47.2	1 278	346 338	Thangavelu & Muthia (1983)
C. cutaceum	NI	NI	6.97	240	16-19	27	40	NI	NI	Ramón (1991)
C. cutaceum	48-76	95.2	NI	265	27.2	14	NI	NI	197 925	Muthiah & Sampath (2000)
C. pileare	46.2	NI	3-5	250	NI	12	33	NI	NI	Govan (1995)
C. pileare	31-93	125-150	6	252	24.8	12	33	2 880	518 400	Muthiah & Sampath (2000)
C. pileare	56-71	108-121	3.9-5.4	220-240	24.8	15-20	27-37	1420-2966	174 660-587 050	Zhou *et al.* (2000)
C. corrugatum	NI	NI	7.80	290	20-23	18	35	NI	NI	Ramón (1991)
*C. aquatil*e	50.6	NI	3-5	230	NI	19	NI	200 000	NI	Govan (1995)
C. muricinum	48.4	NI	3-5	240	NI	22	NI	28 000-30 000	NI	Govan (1995)
C. nicobaricum	39.3	NI	3-5	230	NI	12-17	NI	65 000	NI	Govan (1995)
C. felipponei	NI	115-121	NI	NI	14.8	18	NI	1 150	126 000	Penchaszadeh & De Mahieu (1975)
Fusitriton magellanicus	90	180	9.6	296.2	8-9	55	NI	179	436 664	Cañete *et al.* 2012
L. caudata	60.0	130	9.7-10.7	220	22	26	20-24	83-198	8 383 – 40 194	Present study

NI: It does not indicate, no indica

presence was reported in almost all tropical seas, from the Solomon Islands (Govan 1995) to Jamaica (Littlewood 1988) and *C. pileare* with similar distribution, including the coast of Israel (Hughes-Games 1977).

As described previously, *L. caudata* has an indirect development (planktotrophic larvae), with an embryology that lasted for about 18 days and the whole process until the hatching of the larvae was achieved in 26 days. This duration can be considered to be relatively long compared other reports. The longest period reported for other gastropods of the genus *Cymatium*, such as *C. cutaneum* was 27 days (Ramón, 1991), followed by *C. pileare* ranging between 15 and 20 days (Zhou *et al*., 2000) and *C. aquatile* with 19 days (Govan, 1995). The shortest period of development until hatching was only 12 days for *C. pileare* (Muthiah & Sampath, 2000). However, is inconvinient to establish comparisons since, Zhou *et al*. (2000) reported a development of *C. pileare* between 15 and 20 days, depending on the culture temperature, while Muthiah & Sampath (2000) reported only 12 days for the same species.

The egg mass of *L. caudata* corresponds to type circular and concave (Fig. 1B, C and D), with the apical holes of the egg capsules orientated toward the central concavity (Fig. 1E and F). such has been described for *Cymatilesta spenglery* (Anderson, 1959), *Cymatium nicobaricum* and *C. gemmatum* (Houbrick & Fretter 1969) and *C. cutaceum* and *C. corrugatum* (Ramón, 1991).

Although individuals in this study were exposed to the same experimental conditions and identical amounts of *Pinctada imbricata* individuals as preys, their spawning showed differences in the number of capsules and eggs. This suggests that the number of egg capsules in the egg mass most likely dependent on intraspecific variability that could be determined, on one hand, by endogenous processes such as an individual's condition, age, energy reserves, stress, etc. Furthermore, there is a direct relationship between the size of the individual and the egg mass in terms of numbers of egg capsules and egg per capsule, as demonstrated by Zhou *et al*. (2000). In this study before mentioned, the smallest individuals of *C. pileare* (56.8 mm) deposited 123 capsules and a total of about 174 660 eggs, while the largest individuals (71.4 mm) deposited 198 capsules and about 587 050 eggs; a difference of 412 390 eggs. This illustrates the difficulty in making comparisons between different species of the genus *Cymatium* spp. This indicates a capacity for greater production of capsules and eggs on the size of the snail.

Ornamentation of the shell of *L. caudata* larvae consisting of smalls dots which gives the surface of the shell a dotted appearance when observed by light microscopy. This ornamentation of the *L. caudata* shell is very different from that described by Govan (1995) who detailed that the shell of the veliger larvae of *C. nicobaricum* and *C. muricinum* showed a surface covered with an interlaced network of sinuous ridges that formed small irregular polygons.

Concluding, *L. caudata* showed high fertility with values reaching up to 40 194 eggs. With regard to its early developmental stages, trocophera and veliger stages occurred after 6-8 and 18 days, respectively, while hatching of larvae was observed after 26 days. The egg mass corresponds to the circular and concave type, with the apical holes of the egg capsules orientated toward the central concavity. This period of development was relatively longer than those reported in the literature, (surpassed only by the 27 d of *C. cutaceum*). Therefore, further studies under the same and different culture conditions are required to confirm these results and make further comparisons.

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