

the material that remained inside the capsules. Some egg masses collected in the field had polychaete tubes attached.

The oviposition of egg capsules lasted for about 8 days; females did not eat until spawning was completed. Communal spawning was not observed in the laboratory.

Discussion

The spawning season of *Pugilina morio* in the estuary of the Ceará River determined in the present study, July to November, may be related to the occurrence of the dry season in the region during this time of the year, when the salinity in the estuary is higher. According to Matthews-Cascon et al. (1990), the time of reproduction of *Pugilina morio* at Salinas Beach, Pará State in the north of Brazil, was mainly during the months of September and October.

Hatching as free veliger larvae has also been reported in *Pugilina cochlidium* by Natarajan (1958). Most of the other members of the family studied (*Melongena*, *Hemifusus*, *Busycon*, and *Busycotypus*) have direct development (Clench & Turner, 1956; Robertson, 1974; D'Asaro, 1997); however, *Melongena melongena* from the southern Caribbean also hatches as a veliger larva (Bandel, 1975).

We did not observe nurse eggs inside the egg capsules, and Clench & Turner (1956) observed the same thing for *Melongena corona*. D'Asaro (1997) estimated the presence of 52 to 74 eggs per capsule in *Pugilina morio* from Sierra Leone, west Africa, whereas in the present study we found a wider range of 50 to 167 eggs per capsule.

The same author compared the egg capsules of populations of *Pugilina morio* from Sierra Leone, west Africa and from Gambia, west Africa and Brazil and found that in the first population the exit aperture is located in the middle of the upper side of the capsule and in the second and third population (Gambia and Brazil), the exit aperture is displaced laterally, which is consistent with our own observations.

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Embryonic Development of *Crepidula aculeata* (Gmelin, 1791) (Caenogastropoda: Calyptraeidae) from the Venezuelan Caribbean

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Introduction

The genus *Crepidula* Lamarck, 1799, is widely distributed in South and North America, with about 20 species in the Pacific and Atlantic coast of North America (Abbott, 1974; Hoagland, 1986), at least seven species in the Caribbean (Díaz & Puyana, 1994; De Jong & Coomans, 1988; Warmke & Abbott, 1961), and at least five species



Figure 1. Dorsal and ventral view of the adult shell of *Crepidula aculeata*.

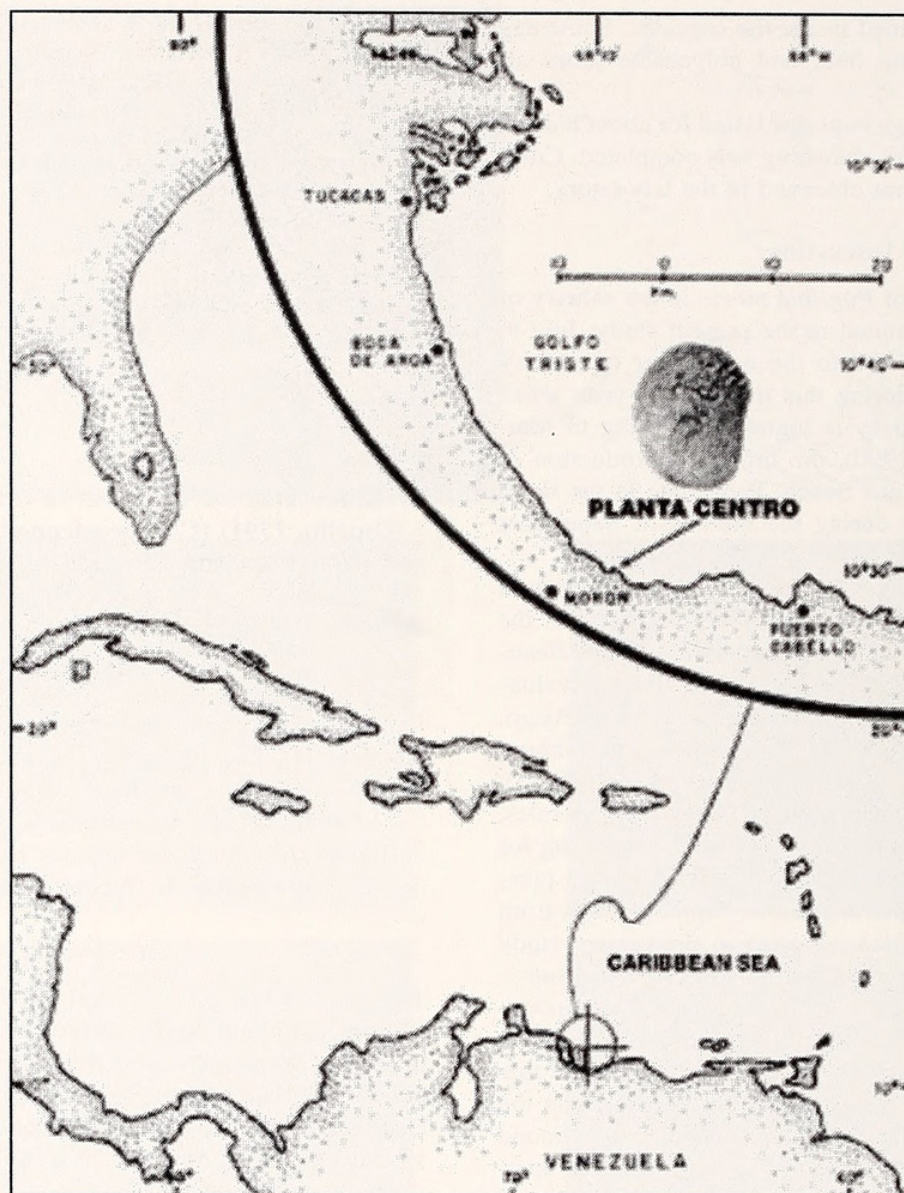



Figure 2. Map of the Caribbean showing the collecting site on the coast of Venezuela.

Table 1

Egg capsule dimensions of *Crepidula aculeata*. Values represent mean \pm SD, numbers in parentheses indicate range. (n = number of egg capsules measured).

Species	Egg capsule shape	Width (A) mm	Length (B) mm	Stalk (C) mm
<i>Crepidula aculeata</i>		3.1 \pm 0.8 (1.6–5.3) n = 361	3.2 \pm 0.6 (1.6–5.3) n = 361	3.2 \pm 0.7 (1.7–5.3) n = 175

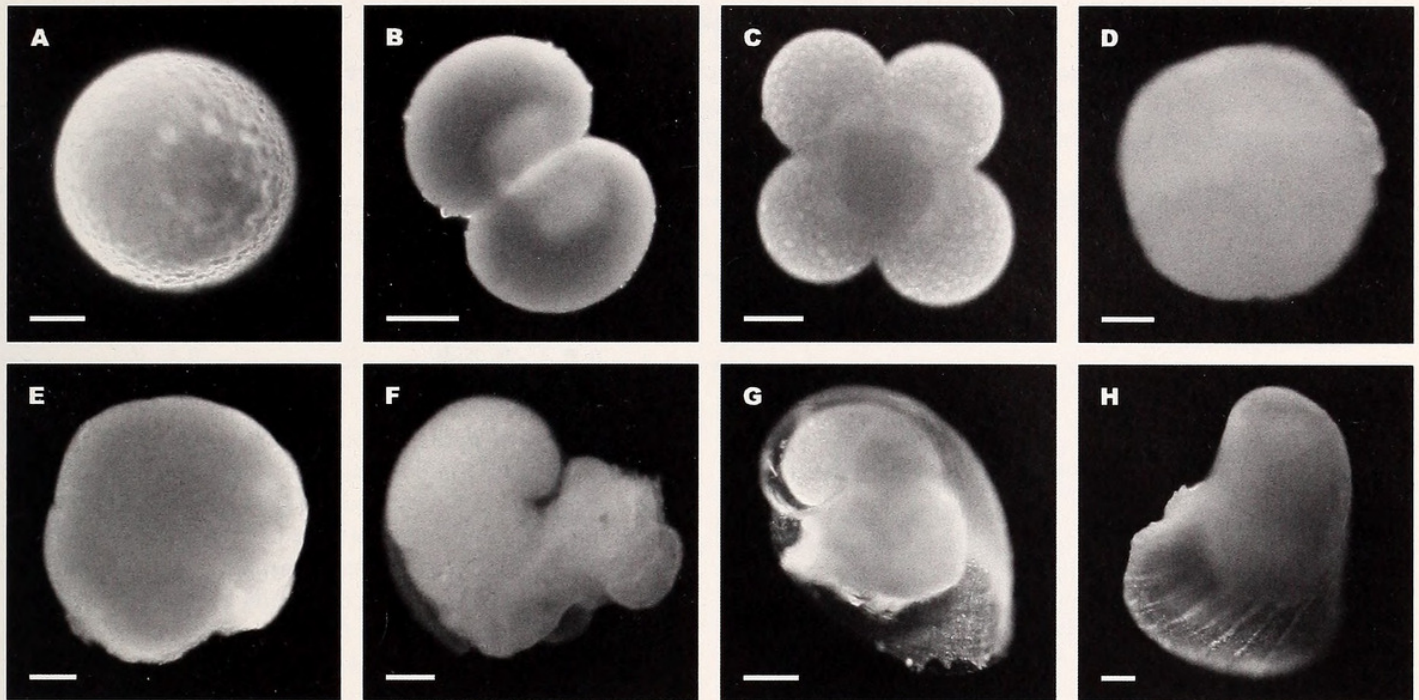


Figure 3. Embryonic development of *Crepidula aculeata*. A. Uncleaved egg. B. First cleavage. C. Four blastomeres. D. Gastrula. E. Trochophore. F. Early veliger. G. Late veliger. H. Pre-hatching. Scale bar 100 μ m. (All photos taken from preserved material).

in southern South America (Cledón & Penchaszadeh, 2001). The reproduction of several species has been described (Hoagland, 1986; Stone Ament, 1979; Collin, 2000a,b; Cledón & Penchaszadeh, 2001; Gallardo, 1977, 1996); however, the developmental mode is still unknown for about half of the currently recognized species (Collin, 2000b). A common feature among the genus and other members of the family is the pattern of encapsulation and brooding. The egg capsules have a similar shape but variable sizes and numbers and are all attached to the substrate by a common point. The brooding chamber, between the female and the substrate, is well oxygenated due to a continuous inhalant current from the female gills while brooding (Hoagland, 1979). *Crepidula* species have a great diversity in developmental modes. Some species hatch as planktonic veligers, and others hatch as pediveligers or as crawling juveniles. Development is completed in many species by the ingestion of extraembryonic food sources such as nurse eggs and/or sibling embryos within the same capsule (Hoagland, 1986; Collin, 2000b; Miloslavich & Penchaszadeh, 2001).

In this paper, we describe the egg capsules, embryonic development, and hatching mode of *Crepidula aculeata* (Gmelin, 1791) from Puerto Cabello, Venezuela, on the northwestern coast of Golfo Triste, Venezuela. We also study the relationship between female size and some reproductive parameters such as number and size of egg capsules, number and size of eggs, number and size of hatchlings and hatching mode and, finally, determine if

the embryos benefit from extraembryonic food sources such as nurse eggs or cannibalism.

Materials and Methods

A total of 62 brooding females of *Crepidula aculeata* (Figure 1) were collected during 1986 at the intake channel of the Planta Centro power plant in Puerto Cabello, Venezuela, between 1 and 3 m depth. They were attached to flat, large rocks at both sides of the channel entrance. Planta Centro is located on the coast of Golfo Triste on the central west coast of Venezuela between 10°29'48" and 10°30'6"N and 68°9'12" and 68°9'36"W (Figure 2). The samples were observed alive and then were fixed in 7% formalin, preserved in 70% ethanol, and stored in the egg and capsule collection of the Marine Biology Laboratory, Universidad Simón Bolívar for further measurements. Voucher adult material was deposited at the Academy of Natural Sciences, Philadelphia, USA, number A11990.

The following reproductive aspects were studied: (1) number and size of egg capsules brooded per female, (2) number and size of eggs and developing embryos within the capsule, (3) observation of the different stages of development, and (4) hatching mode and size of hatchling. We also calculated the relationship between female size in terms of shell length and the following reproductive parameters: number of capsules, number of eggs per capsule, and capsule size with a Pearson correlation coefficient.

Table 2

Crepidula aculeata. Description of the embryos during intracapsular development. Values represent mean \pm SD, numbers in parentheses represent range, n represents number of observations. All measurements taken from preserved material. (n = number of embryos measured at each stage, n' = number of females with embryos at each of the developmental stages)

Stage	Description	Number of embryos per capsule	Size of embryos (μm)
Egg	Round, yellow, uncleaved egg.	38 \pm 11 (12–65) n = 57, n' = 10	417 \pm 43 (300–630) n = 263
First cleavages	Yellow embryo with 4 blastomeres.	38 \pm 5 (34–43) n = 3, n' = 1	413 \pm 23 (360–450) n = 30
Gastrula	Roundish yellow embryo with yolk at the vegetal pole.	30 \pm 5 (20–43) n = 16, n' = 5	486 \pm 52 (420–630) n = 101
Trochophore	Elongated yellow embryo, yolk in the posterior end. Development of velum begins.	17 \pm 6 (8–23) n = 5, n' = 3	587 \pm 48 (450–720) n = 88
Early veliger	Yellow embryos with eyes, organic matrix of shell, yolk in the posterior end and small velum.	23 \pm 6 (9–30) n = 21, n' = 9	618 \pm 63 (480–810) n = 239
Late veliger	Development of the foot with an operculum (227 \pm 55 μm in diameter). Velum with black spots. Calcified shell, transparent and very fragile.	17 \pm 3 (12–21) n = 5, n' = 3	687 \pm 62 (570–750) n = 36
Pre-hatching	Crawling juvenile with calcified white shell with vertical lines, foot with operculum. Yolk reserves in the posterior end.	14 \pm 6 (4–20) n = 5, n' = 2	858 \pm 102 (660–1080) n = 54
Hatching	Crawling juvenile with calcified white shell with vertical lines, foot with operculum and black pigmentation.	Live observations from different females in the laboratory	1181 \pm 337 (900–1170) n = 8

Results and Discussion

Brooding females of *C. aculeata* measured between 15 and 36 mm in shell length, between 12 and 23 mm in shell width, and between 4.5 and 6.6 mm in shell height. A significant relationship between female size and some reproductive parameters such as size and number of egg capsules per brood, as well as the number of eggs per capsule is a common feature in calyptraeid species (Hoagland, 1986; Chaparro et al., 1999) but in *C. aculeata* we found no relationship between female size and any reproductive parameter (Pearson correlation coefficient, $p > 0.05$ for all parameters). Each female brooded between four and 19 egg capsules. The egg capsules were thin and transparent and had the typical shape among calyptraeids, triangular, with one corner extending to form a stalk by which all the egg capsules were attached to the substrate at a common point. Egg capsules measured between 1.5 and 5.3 mm both lengthwise (without the stalk) and in width. The stalk measured between 1.7 and 5.3 mm in length (Table 1). Each capsule contained between

12 and 65 uncleaved eggs measuring about 417 μm in diameter (Figure 3A). Adelphophagy of nurse eggs was not directly observed, and all eggs underwent cleavage (Figures 3B, C); however, a significant difference between the number of eggs and the number of gastrulas was obtained (Kruskal-Wallis between all stages, $p < 0.01$ followed by non-parametric T for multiple comparisons between egg and gastrula stages). The gastrula (Figure 3D) measures almost the same size as the uncleaved egg and it develops to a trochophore (Figure 3E). Between the trochophore stage and the pre-hatching stage, the mean number of embryos per capsule also decreased significantly, possibly due to cannibalism among sibling embryos. We observed 47 egg capsules in the pre-hatching stage containing a total number of 898 pre-hatching embryos. Of these, 20 egg capsules had empty embryonic shells (42.5%) with a total count of 38 empty shells (4.2%). In calyptraeids, sources of extraembryonic nutrition are usually nurse eggs or sibling embryos, not both as could be the case here. The only way to be accurate

Table 3

Summary of the reproductive aspects of *Crepidula aculeata*. Values represent mean \pm SD, numbers in parentheses indicate range. (n = represents number of measurements).

Species shell length (mm)	Number of capsules per female	Capsule length (mm)	Eggs per capsule	Egg diameter (μ m)	Hatchlings per capsule	Hatchling length (μ m)
<i>C. aculeata</i> 22.8 \pm 3.9 (15–36) n = 62	9 \pm 2 (4–19) n = 51	3 \pm 1 (2–5) n = 361	38 \pm 11 (12–65) n = 57	417 \pm 43 (300–630) n = 263	13 \pm 6 (4–20) n = 5	1181 \pm 337 (900–1170) n = 8 Crawling juvenile

about these observations (besides collecting egg capsules at all stages of development and comparing the number of embryos per capsule between them) is to monitor live egg capsules throughout development, witnessing the ingestion of one or both sources of food by the embryos. Another calyptraeid known to have both strategies (adelphophagy and cannibalism) is *Crucibulum auricula* (Gmelin, 1791), reported by Miloslavich & Penchaszadeh (2001).

The intracapsular veliger (Figure 3F) has a velum with black spots. It measures about 620 μ m in shell length, and by the time the foot develops, it measures about 690 μ m in shell length (Figure 3G). This foot has a round and transparent operculum that measures about 227 μ m in diameter. The pre-hatching embryo had no velum, a crawling foot, and measured about 860 μ m in shell length. This shell is calcified, white, and has smooth radial ribs (Figure 3H; Tables 2 and 3 for summary of development and reproductive aspects, respectively). Hatching embryos were observed live. These were crawling juveniles with a shell measuring between 900 and 1170 μ m, which had less yolk reserves than the prehatching embryos; the foot had black pigmentation. Hoagland (1986) also reported that *C. aculeata* from Florida (Key Biscayne, Fort Pierce) hatches as a crawling veliger; however, an interesting fact is that this author did not report nurse eggs or cannibalism in the Florida population. Other than this important difference and the fact that the Venezuelan population has a larger adult and hatchling shell length than the Florida population, the rest of the reproductive aspects are very similar (number of egg capsules per female, developing embryos per capsule, and egg diameter).

Regarding the development of the operculum, a feature which is completely absent in all adult calyptraeids, Collin (2000b) mentioned that in the genus *Crepidula* direct developers do not develop this structure, which we clearly observed in the second veliger and hatching stages of *C. aculeata*, but most of the papers dealing with development in calyptraeids are very unspecific about this point. In this sense, direct and indirect developers have a very similar early development while encapsulated, and the fact that they have extraembryonic food sources allows

the embryos to develop more structures while still in the egg capsule, and to reach larger sizes.

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World Congress of Malacology
Perth, Western Australia
11-16 July 2004

The next World Congress of Malacology will be held on the campus of The University of Western Australia, in Perth, Western Australia, the first such Congress in the Southern Hemisphere. The UWA campus, on the banks of the Swan River, is one of the most beautiful in Australia. The Congress will adopt the style of the last two highly acclaimed Congresses in Washington, D.C., USA (1998) and Vienna, Austria (2000).

All aspects of the study of mollusks will be included. There will be contributed paper sessions and a special poster session with posters on display throughout the conference. Several major symposia are planned: Phylogeny

of mollusks; molluscan aquaculture and fisheries; ecology of mollusks; and special sessions on particular groups (such as bivalves) and other topics (such as conservation) are also planned or can be included. In addition, smaller symposia are being planned on nudibranchs, nonmarine mollusks, and laval development. There will also be a curators' meeting.

Three-star motel units and student accommodation will be available on the university campus, a walk of only a few minutes from the conference venue. Three star and higher accommodation is available in hotels 5 km or a 10 minute taxi trip away from the conference venue. The university accommodation includes breakfast. Lunches will be at the conference on session days. There are a variety of restaurants just off campus.

The registration fee for students will be substantially reduced. In addition, both *Unitas Malacologica* and the Malacological Society of Australasia will be offering travel support and student prizes.

A choice of marine, nonmarine, and cultural excursions will be available during the conference. The Western Australian Museum's collections will be available for examination. Perth is served by nearly 20 international airlines.

Further information will be available on the websites of *Unitas Malacologica* (interim address) <http://www.inter.nl.net/users/Meijer.T/UM/um.html> and the Malacological Society of Australasia <http://www.amonline.new/au/malsoc> as it becomes available. Alternatively, information can be obtained from

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