Pacific Science (1975), Vol. 29, No. 4, p. 353–359 Printed in Great Britain

On the Reproductive Biology of Cerithium moniliferum Kiener (Gastropoda, Cerithiidae) at Heron Island, Great Barrier Reef¹

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AT HERON ISLAND, Great Barrier Reef, Cerithium moniliferum Kiener occurs abundantly on the beach rock platform along the southern side of the island. At low tide, clusters of up to "a few thousand" may be seen (Moulton 1962), but nothing appears to be known of their reproductive biology. In 1960 Anderson urged a study in tropical Australia of the reproductive biology of coral reef cerithiid prosobranchs, notably Cerithium, as so little was known about these snails, which are found commonly throughout the shallow tropics. Contributions to the knowledge of the anatomy of the reproductive systems of Cerithium have been made by Risbec (1943), Johannson (1953), Marcus and Marcus (1964), and Houbrick (1971). It is known that the male lacks a penis and that the pallial ducts are open. Houbrick (1971) listed several brief reports of spawn and early development in Cerithium which indicate eggs are attached to the substratum, generally in coiled filaments from which planktotrophic veligers emerge within a few days. The following observations on the reproductive biology of Cerithium moniliferum at Heron Island are presented as a contribution to the study of this large and seemingly diverse group.

Thanks are extended to Professor J. F. A. Sprent, University of Queensland, for provision of facilities in Brisbane and to the Great Barrier Reef Committee for the use of facilities at the Heron Island Research Station.

MATERIALS AND METHODS

Snails were fixed for sectioning in Bouin's fluid, 10 percent formal-saline, Zenker's and

Helly's fluids, embedded in 60° C paraffin wax, sectioned at 5–7 μ , and stained with hemalum and eosin, Mann's methyl blue eosin, PAS (periodic acid Schiff), and Feulgen. Drawings of reproductive structures are based on sections of three males and five females as well as on dissections, made specifically to study reproductive anatomy, of at least 20 mature individuals of both sexes during parasitological studies on over 2000 snails.

Observations in the field were made both at high tide (snorkeling) and low tide. In the laboratory, snails were kept in recycling seawater aquaria in which they fed on naturally growing algae. Hatching and behavior of young snails were observed in finger bowls of sea water with the aid of a stereoscopic microscope.

RESULTS

Mature male *Cerithium moniliferum* measure (length by breadth in mm) $\overline{x} \pm s = 12.8 \pm 4.1 \times 5.9 \pm 1.7$ (range, 6.2 to 23.4×3.0 to 10.2; N = 25), and mature females, $\overline{x} \pm s = 12.7 \pm 2.8 \times 5.9 \pm 1.7$ (range, 8.9 to 20.8×4.1 to 9.2; N = 25). Both sexes have a shape index (length: breadth ratio) of 2.14.

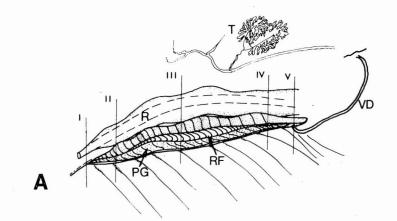
Male Reproductive System

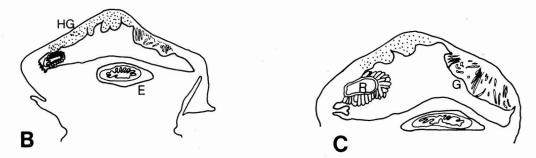
Figure 1.

The testes are a yellow color. The collecting duct runs adjacent to the columella, parallel to the esophagus. On reaching the pallial cavity, the duct expands into a chamber that opens to form the pallial gonoduct, i.e., a groove created ventrally by the floor of the pallial cavity and dorsally by a ciliated fold hanging down from the pallial wall and slightly reflected ventrally in the middle of the pallial cavity (Figure 1D). The gonoduct, the lining of which is ciliated but not noticeably glandular, runs parallel to the intestine and opens near the mantle skirt.

¹ Contribution from the Heron Island Research Station. This work was completed while the author held a Queen's Fellowship in Marine Science. Manuscript accepted 1 October 1974.

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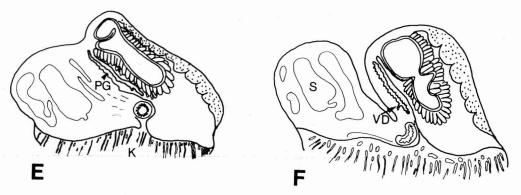
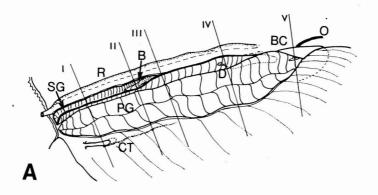
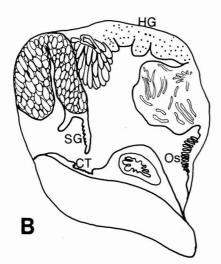
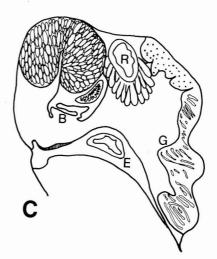


FIGURE 1. The male reproductive system of *Cerithium moniliferum* Kiener. A, whole system as seen by dissection; B-F, sections of pallial cavity looking posteriorly through points corresponding to I (anterior) to V (posterior) and illustrating the nature of the pallial gonoduct.

ABBREVIATIONS: E, esophagus; G, gill; HG, hypobronchial gland; K, kidney; PG, pallial gonoduct; R, rectum; RF, reflexed fold; S, stomach; T, testes; VD, vas deferens.







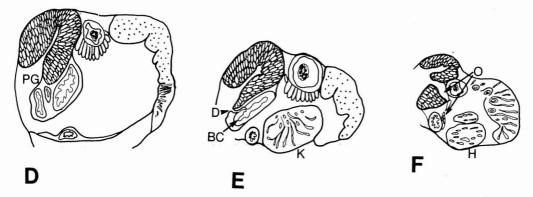


FIGURE 2. The female reproductive system of *Cerithium moniliferum* Klener. A, whole system as seen by dissection; B-F, sections of the pallial cavity looking posteriorly through points corresponding to I (anterior) to V (posterior) and illustrating the nature of the pallial gonoduct.

ABBREVIATIONS: B, baffle; BC, bursa copulatrix; CT, ciliated tract; D, duct; E, esophagus; G, gill; H, heart; HG, hypobronchial gland; K, kidney; O, oviduct; Os, osphradium; PG, pallial gonoduct; R, rectum; SG, sperm gutter.

Ciliary currents transport particles (and thus presumably sperms) down the gonoduct and out onto the right side of the head to where small, ciliated folds of the floor of the pallial cavity converge.

The eupyrene sperm have a short, bulletshaped head, a long middle shank, and a short tail, and are about 70 to 80 μ long.

Female Reproductive System

Figure 2.

The ovary is a cream color. The oviduct also runs adjacent to the columella, parallel to the esophagus, until it enters the pallial cavity and opens through a wide, lateral slit just anterior to the blind end of the pallial oviduct. The oviduct is open, formed by a creamy white glandular thickening of the pallial wall (sometimes yellow posteriorly), which dorsally meets a glandular fold running parallel to the intestine and hanging down into the pallial cavity. The staining qualities of the posterior glandular region (albumen gland) differ from those of the anterior region (capsule gland). The oviduct is ciliated, ends adjacent to the anus, and carries particles slowly to the opening of the mantle cavity on the right side.

An open, ciliated sperm gutter runs along the ventral edge of the anterior one-third of the oviducal fold (Figure 2B). Passing posteriorly, the gutter becomes enclosed as a tube, not by the fusion of the outer edges of the gutter but by a fold of tissue that extends across the open gutter from the wall adjacent to the oviducal groove to meet the opposite wall, thus leaving the outer edges of the gutter free (Figure 2C). At this point a second fold from the same wall of the gutter extends across the still-open gutter to meet the opposite wall several hundred microns farther back. This fold hangs down diagonally across the gutter making a baffle dividing the gutter into anterior and posterior regions. Posteriorly the free edges of the anterior gutter (one wall of which is the baffle) fuse before the baffle and gutter wall fuse completely. A short blind tube is thus created. Similarly, the posterior gutter behind the baffle closes off to form another short blind tube. In cross section, therefore, three tubes appear (Figure 2D), but the outer two do not extend far posteriorly.

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The deeper sperm duct has folded, ciliated walls in which the ciliary movements are very strong, and even large particles are quickly drawn into the duct and pushed to the slightly muscular expanded posterior region. Here a small duct connects this chamber (seen packed with sperms) and the pallial cavity at the edge of the glandular region of the hanging fold of the pallial oviduct (Figure 2E). No glandular region was observed about this duct.

On the floor of the mantle cavity, opposite to the opening of the pallial oviduct, is a ciliated tract with slightly raised edges forming a shallow gutter anteriorly near the distal end of the oviduct (Figure 2B).

Copulation

What appeared to be copulation was observed only one time, this being in the field at high tide on 28 September 1972. The female was clinging upside down underneath a slab of beachrock. The male was attached to the female's shell with his anterior curved so that his right mantle aperture was pressed to the right mantle aperture of the female. The female had a partially formed egg mass.

Spawn

The duration of egg laying has not been observed, but the female usually attaches eggs to the underside of rocks. While laying eggs she applies the right mantle aperture to the substratum. Eggs that pass singly to join the egg mass are embedded into a flattened cluster, formed by a broad ribbon four to six eggs across being wound back and forth on itself several times. Clusters contain 1500 to 2000 eggs and measure about 10 mm in greatest diameter though they are rarely circular (Figure 3). It is not known if females spawn repeatedly.

Spawn has been found in the field at all times of the year but is most common in September and October. In the laboratory, spawning has been observed only in October, though snails collected in January, April, and July were treated similarly. Spawn was deposited on the undersides of rocks placed in aquaria or, if rocks were not available, on the corners of the aquaria where the substratum was black. Water

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FIGURE 3. Part of egg mass of *Cerithium moniliferum* Kiener. Scale is 5 mm.

temperatures fluctuated from 22° to 26° C during the spawning period.

Egg capsules measured $\overline{x} \pm s = 286 \pm 6 \mu$ (N = 10) in diameter, and embryos, 150 to 180 μ in diameter. Capsules consisted of an outer layer 4 to 5 μ thick, all embedded in jelly.

Development

Development was relatively slow. After 2 days embryos showed some invagination. After 4 days they were spherical, but with little differentiation. By 7 to 8 days, however, some had developed a shell, velar lobes, and eyespots and were seen feebly moving within the capsule. At this stage the shell was finely reticulate, but showed no signs of darkening. Within 12 to 14 days some embryos appeared fully mature; the heart beat was clearly evident, and eyespots, small velar lobes, statocysts, and an operculum were seen. Darkening of the shell was observed from the 10th to the 14th day. Embryos on the outer layers of the egg mass developed before those deeper within the coil.

Hatching

Hatching was first observed after 16 days and continued for 8 days. In the laboratory young snails fell from the capsule and remained relatively inactive for 24 hours, moving slowly in a circular motion with their cilia while on the bottom. They did not swim. The velar lobes were not extended. After 24 hours the velar lobes were no longer apparent and the young began to crawl. Mortality was quite high during this period. Young snails measured $\overline{x} \pm s =$ 225 ± 9 in the greatest diameter (range, 186 to 240μ ; N = 10).

Snails measuring from 300 to 500 μ and identical with these young *Cerithium* have been found in mid-December in the fine, silty sand on the landward side of the beachrock at Heron Island.

Hatching, as with development, began with the outer layers of the egg mass, which became ragged, and collected debris and a fauna of ciliates and copepods. Those capsules closest to rock and farthest from the surface of the egg mass hatched last.

Growth

Limited success was achieved with growing these snails in the laboratory. After 2 months, 25 young snails were recovered from the fine, silty, algal-rich sand in which they had been placed. These measured $\overline{x} \pm s = 431 \pm 95 \ \mu$ in greatest diameter (range, 266 to 692 μ). This growth would seem to agree with that seen in the field, i.e., maximum spawning in October and snails 300 to 500 μ in diameter recovered in mid-December.

DISCUSSION

The pallial gonoducts of *C. moniliferum* are very similar to those of *C. nodulosum* described by Houbrick (1971). In the male *C. moniliferum* the principal differences are (1) an even lesser degree of glandular proliferation in the proximal region of the duct which is considered to function as a prostate (Houbrick 1971, Marcus and Marcus 1964), and (2) a reflexed edge to the free fold of the pallial gonoduct. The male pallial genital ducts of *Cerithium* show little variation among species, however, and *C. obeliscus* and *C. gemmulatus* described by Risbec (1943), *C. atratum* described by Marcus and Marcus (1964), and *C. vulgatum* described by Johannson (1953) all appear to be similar.

Greater variation has been reported in the female ducts. A thick-walled, glandular, pallial oviduct is common to all species for which the ducts have been described. Details of the sperm gutter vary with the species and *C. moniliferum* differs from all others with regard to the complex baffle in the sperm gutter.

Besides the closed sperm gutter similar to that described in C. vulgatum by Johannson (1953) and C. nodulosum by Houbrick (1971), which in both cases closes off about one-third of the way back from the anterior, there are two additional blind tubes. In C. atratum, according to Marcus and Marcus (1964), a seminal receptacle lies as a tube with a narrow opening in the wall of the bursa canal, opening into the pallial oviduct. Risbec (1943) gave no details of these structures in the species he discussed. In both C. moniliferum and C. nodulosum a small duct does run from the bursa copulatrix to the oviduct, its bursa end surrounded by glandular epithelium in C. nodulosum but not in C. moniliferum. This small structure in no way resembles the large sperm-containing organ described and illustrated by Marcus and Marcus (1964) for C. atratum. The function of this duct is not known, but perhaps it serves for the passage of sperm from the bursa to the upper end of the pallial oviduct, as was intimated by Houbrick (1971). In C. moniliferum this seems at least probable, as no large sperm-storing pocket, other than the bursa copulatrix, is present to act as a seminal receptacle. In C. vulgatum a large pocket (seminal receptacle) opens in the floor of the mantle cavity opposite the closure of the open sperm gutter (Johannson 1953). Houbrick (1971) described a similar seminal receptacle in the same place in C. nodulosum. This structure apparently is elaborated greatly in C. gemmulatus, according to Risbec (1943). In C. moniliferum only a ciliated tract is seen in this position. The cilia beat weakly and definitely toward the exterior in both this tract and the pallial oviduct but beat very strongly into the bursal canal. It seems inconceivable that sperm, once drawn into the bursal canal, could find their way back to the oviduct for fertilization in any way but along the fine duct discussed above. The muscular walls of the bursa at the level of the duct would suggest that sperm could be forced into the oviduct. The functions of the baffle and the blind tubes in the sperm gutter remain a mystery.

D'Asaro (1970) observed C. literatum pairing

during spawning, as was seen in this study in C. moniliferum; presumably this pairing is copulation. Development of the spawn of Cerithium species is of two kinds: (1) thin strings of spawn containing many eggs which develop rapidly and emerge as free-swimming, planktotrophic veligers-found in stenohaline species, and (2) fewer larger eggs which develop slowly with fully metamorphosed snails emerging from the capsules-found in euryhaline species (Houbrick 1970). Most earlier workers with Cerithium reported the first developmental pattern. Raeihle (1968) reported the slow development of C. variabile, and Houbrick (1970) observed the similar slow development of C. muscarum. Cerithium moniliferum clearly exhibits this second slow developmental pattern.

Spawning of other *Cerithium* species has been seen from January to August in Northern Hemisphere studies, with spring and summer most often quoted. At Heron Island egg masses were most abundant in spring although they were seen throughout the year. In the laboratory spawning was only observed in October, i.e., spring. Hatching appears to be similar in *C. moniliferum* to that described for *C. algicola* by Davis (1967) and for *C. variabile* by Raeihle (1968), i.e., mechanical damage preceded by enzymic digestion.

Young snails presumably accumulate by physical forces in the fine, silty sand between the beach and the beachrock at Heron Island. This is where a high organic content in the sand appears to exist. The passivity of the snails for the first 24 hours after hatching would allow concentration in this region. It seems possible that *C. moniliferum* exhibits a life cycle pattern intermediate between those cerithiids with a long planktonic life and those with no planktonic stage at all. As compared with snails that have a planktonic stage, those snails without such a stage in their life cycle would be limited in their ability to disperse.

SUMMARY

Details of the male and female reproductive systems of *Cerithium moniliferum* Kiener from Heron Island, Great Barrier Reef, have been given, along with notes on the spawn and development. The anatomy of the gonoducts is similar to that of *C. nodulosum*, but the spawn and development are similar to the other euryhaline intertidal species *C. variabile* and *C. muscarum* which lack planktonic larvae.

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