Observations on the biology of the common egg shell *Ovula ovum* in Majuro, Marshall Islands

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The common egg shell, *Ovula ovum*, is found in shallow reefs (down to 20 m) throughout the Indo-Pacific. It belongs to the family Ovulidae and is closely related to the true cowries of the family Cypraeidae (Abbott and Dance 2000). *O. ovum* are very common in the Marshall Islands especially around Majuro atoll where the local people collect them extensively. The shiny white shells are sold alone or as decorative elements in handicraft items.

The current literature on *O. ovum* remains scarce. Most of the existing knowledge has been gathered from anecdotal mentions, often generalised for all ovulids. A number of authors have mentioned that *O. ovum* is commonly found in association with large fleshy soft coral (Wilson and Gillett 1979). Furthermore, Johnson (1991) and Griffith (1995) indicated that egg shells feed on soft coral, while other sources state that they prey specifically on *Sarcophyton* and *Sinularia* and on some toxic species. Rudman (2003) recently reported that the genus *Ovula* feeds on polyps of soft and stony coral, like other ovulids. The reproduction of *O. ovum* is known to follow the typical pattern of ovulids, with egg capsules being deposited on soft coral, although specific accounts are lacking.

This report presents novel information on the daily activity, feeding, reproduction and development of *O. ovum*. These data will contribute to a better understanding of ovulids, which are under increasing threat from human activities in many island countries of the Indo-Pacific.

Collection and maintenance

Egg shells, *Ovula ovum*, were collected by local people at a depth of 3 to 5 m on the outer fringing reef of Majuro atoll in the Marshall Islands in July 2001. The habitat was characterized by dead and live hermatypic corals, coral pebbles and abundant crevices with only rare occurrences of soft corals and sponges. The egg shells were abundant (ca 1.7 individuals m^{-2}) and distributed in patches of ca 14 individuals within the area explored (400 x 10 m). A total of 237 adults were collected in ca 3 h of snorkelling, and most of them were returned to their natural habitat immediately after data collection. The lengths of individual shells varied between 5.9 and 8.3 cm. No juveniles were found.

Following collection, a few individuals were transferred to 10-ton tanks filled with a substrate of coral sand and pebbles (ca 15 cm thick), and a few concrete blocks. The specimens were kept at a density of 0.8 individuals m^{-2}, and seawater flow-through was adjusted at ca 3000 L h^{-1} to maintain water quality. The tanks were exposed to the natural light regime. The salinity fluctuated between 29 and 33‰ and the temperature between 24 and 29.5°C.

Daily activity

Laboratory observations revealed that *O. ovum* remained immobile, usually hidden in crevices, from 05:30 to 18:15 h. In 87% of cases, they always used the same crevice or area as diurnal shelter and started moving in search of food or a mate when the sun went down. After 5 months in captivity, all individuals (marked on the shell) retained the same homing behaviour. The egg shells seemed to move (ca 2.2. cm min^{-1}) and feed simultaneously (observation of the radula through a glass aquarium), thus ingesting food continuously. Analysis of intestinal contents (see below) indeed revealed the continuous presence of food in the first section of the digestive tract between sunset and sunrise. Furthermore, the addition of artificial light delayed and even prevented the nocturnal feeding behaviour.

Observations showed that the mantle of *O. ovum* is continuously stretched out, day and night, only

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occasionally revealing a tiny section of the white shell underneath. The only exception noted was for specimens in poor physical condition which eventually stopped feeding and sometimes died. The mantle of healthy individuals also remained fully extended during copulation.

Diet

Some of the freshly collected *O. ovum* were preserved by injection of 70% ethanol. Investigation of the digestive tract revealed the presence of large quantities of benthic algae, although most of the content was made up of unrecognizable structures. No trace of sponge elements, spicules or other, were found. Under laboratory conditions, the egg shells fed on deposited organic matter and grazed on the benthic algae growing on the various surfaces available in the tanks. Several species of sponges, hermatypic corals and soft corals (described as the main diet of *O. ovum* in the field) were introduced alternatively in the tanks for several weeks. They did not seem to significantly attract starved individuals or well-fed ones, and no sign of predation was noted.

Copulation

Formation of pairs became evident as the breeding period approached, often several days before copulation (usually between 2 and 6 days under laboratory conditions). In 27 cases, the female was observed to carry the generally smaller male on its back without any signs of copulation for 3 to 4 days. In those instances, the same male was found on the back of the same female every day, yet they moved separately during the night even if they remained close to each other.

Copulation was typically observed 2 to 3 days before the full moon, every month from July to November. No multi-copulation involving different individuals was ever recorded. Most copulations occurred in the morning between 04:00 and 10:00 h, although a few were recorded at various times of the day. Breeding behaviour accounted for the rare instances where *O. ovum* were observed to be active during daytime. In preparing for copulation, individuals positioned themselves head to tail, the male being located alongside the female or sometimes directly mounted on its shell. Copulation typically lasted between 34 and 72 min, both male and female generally remaining immobile throughout the process. After copulation, the female usually moved away first, thus stretching the male's reproductive organ. The male started moving, generally in the opposite direction, and finally detached ca 20 sec later. Nonetheless, male and female remained close together (less than 5 cm apart) for ca 5–10 h before dispersing definitively. Females were found to store spermatozoa for 1 to 7 days before spawning.

Capsule-laying (spawning)

O. ovum laid egg capsules every month from July to November on hard substrata (e.g. on the sides of the tanks or inside crevices in the concrete blocks). Spawning either coincided with the full moon or occurred a few days afterward. The laying of egg capsules by a single female could take as long as 74 h, although the average was between 32 and 48 h. Sometimes the process was uninterrupted, even during the daytime. It took between 5 and 15 min to release a single capsule, but the interval between each laying varied greatly. Some females released their capsules in a rapid sequence

Figure 1. Female *Ovula ovum* with capsule mass.

(a maximum of ca 20 capsules per hour was observed), especially during the night, whereas the process was commonly slower during daytime (as slow as 1 to 3 capsules in 4 hours). An average of 86 egg capsules were deposited by a single female, with a maximum recorded of 102 capsules.

During spawning, the female covered portions of the capsule mass, or the entire mass, with its foot. No interaction with conspecifics was noted throughout the capsule-laying process, the other specimens remaining at a distance, usually more than 20 cm away. The females laid their capsules in a pattern of almost equally distanced rows (Fig. 1). Each whitish capsule was firmly attached to the substratum. The final shape of the capsule mass was usually rounded and the female moved away from it as soon as it was deposited. The capsules were translucent in the beginning, becoming yellowish and more opaque during the development of the embryos. Each capsule measured ca 4 mm wide and 5 mm high (Fig. 1) and contained between 150 and 212 embryos in an intracapsular fluid.

Development inside the capsule

Embryonic development began as soon as the capsules were laid. The survival rate varied throughout the various stages and was not uniform among the capsules. Most of the first egg capsules that were spawned contained several non-viable embryos. For example, the first third of the capsules showed up to 79% of non-viable embryos and larvae, and ca 25 ± 8% of the capsules spawned by each female eventually decayed without producing any pelagic larvae. The high percentage of abnormal development (irregular cellular divisions) among the first deposited capsules seemed to be associated with polyspermic fertilization, as revealed by microscopic examination. Moreover, between 20 to 31% of all oocytes in each of the last two-thirds of the capsules never developed. These oocytes showed no sign of fertilization or further cleavage.

Table 1 and Figures 2 and 3 illustrate the development of those eggs/embryos that developed normally. For detailed observation of the developing embryos, some egg capsules were collected at regular intervals from different spawns (n = 9) with a stainless steel scalpel. The first cleavage was completed ca 70 min after spawning and produced two rounded blastomeres of equal size (Fig. 2b). The 4-cell stage occurred 25 minutes later (Fig. 2c). The first micromeres appeared soon afterward, ca 160 min after spawning (Fig. 2d). Subsequent cleavage of the micromeres resulted in the formation of a cap of micromeres at the animal pole (Fig. 2e). The blastula stage was reached after ca 8 h and the early gastrula after 10 h (Fig. 2f). At that stage, the larvae developed their

Table 1: **Development of *Ovula ovum* under naturally fluctuating temperature (24 to 29.5°C), salinity and photoperiod. A new stage was usually considered attained when ca 50% of the individuals reached it.**

Stage	Time from egg capsule laying
Capsule laying	0
2-cell	70 min
4-cell	95 min
Cleavage stage	160 min
Blastula	485 min
Early gastrula	605 min
Gastrula	28 h
Hatching from fertilization envelope	63h
Late gastrula	72 h
Early trochophore	5 d
Trochophore elongation	6 d
Early veliger	8 d
Veliger	10–12 d
Late veliger	15–18 d
Free-swimming veliger (swimming at the surface)	20–22 d
Free-swimming veliger (swimming near the bottom)	22–25 d

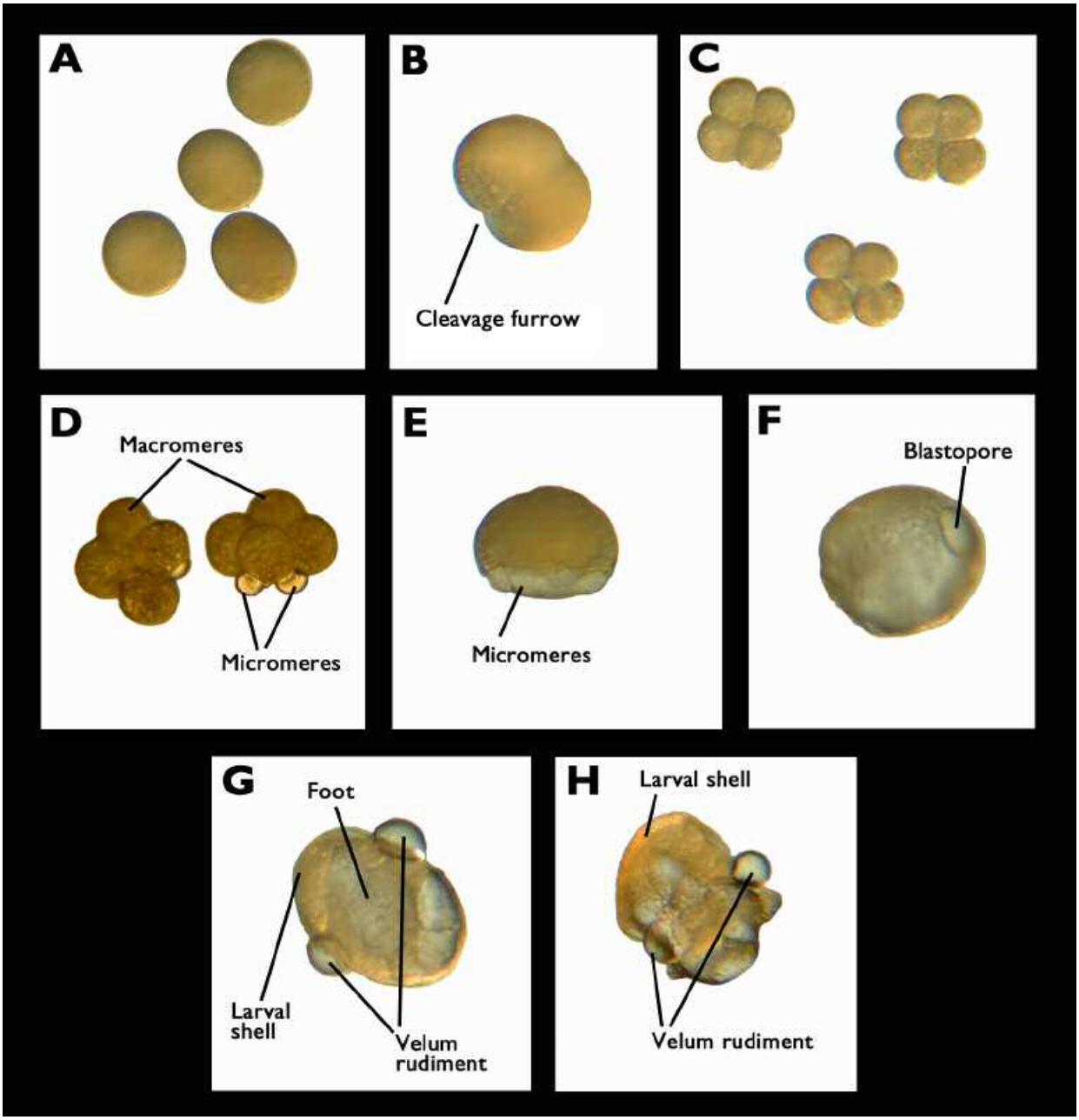

Figure 2. **Development of *Ovula ovum*.**

(A) Newly encapsulated eggs;
(B) 2-cell stage;
(C) 4-cell stage;
(D) and (E) cleavage stages showing the micromeres and macromeres;
(F) gastrula stage showing the blastopore;
(G) and (H) trochophore showing the larval shell, foot and velum rudiment.

first cilia. The gastrula hatched from the fertilization envelope after ca 63 h and started moving freely in the egg capsule. After harbouring an elongated shape for ca 72 h, the embryos slowly entered the early trochophore stage and were fully developed after 5 days. At that stage, the larvae started developing a foot and a larval shell, and the rudiment of a velum (Fig. 2g, h).

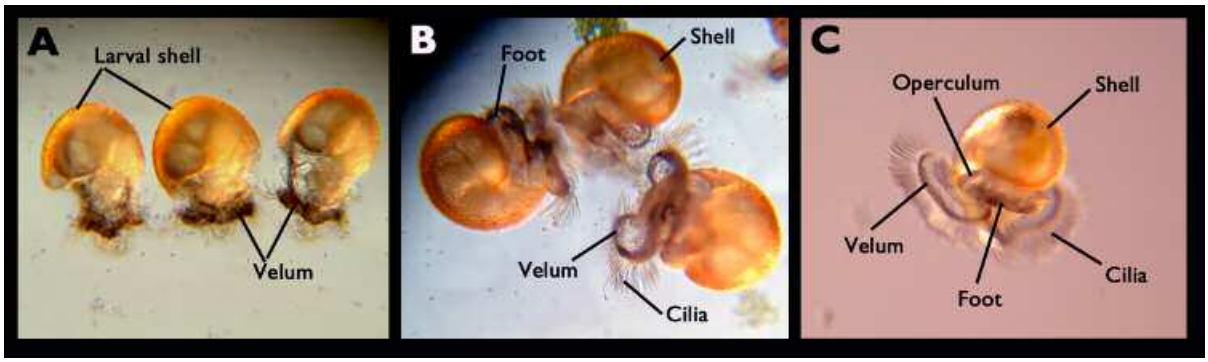

Figure 3. **Development of *Ovula ovum*.**
(A) Veliger larvae after ca 20 days of development just before hatching;
(B) and (C) free-swimming veligers after ca 25 days of development.
The larval shell, foot, velum, operculum and cilia are shown.

After 8 days, the larvae reached the veliger stage (Fig. 3). They started accumulating bluish-black pigments that were especially visible in the velum, whereas the foot possessed an operculum, and the cilia crowns were well developed. Furthermore, the shell became clearly visible and the heart was apparent through the transparent body (Fig. 3). On the outside, the stretched capsules seemed larger, measuring ca 5 x 5 mm.

Pelagic development

As the free-swimming veligers were about to emerge (Fig. 3a), several capsules were collected from different spawns and transferred to 50-L aquaria under similar environmental conditions. The veligers were left to hatch naturally (Fig. 3b, c). Densities were then adjusted to ca 1 larva per 50 mL of water. Due to unavailability of live microalgae at the time, various powdered preparations, such as *Spirulina* and Algamac, as well as ground green macrophytes were used to feed the larvae.

The free-swimming veliger larvae emerged after 20 to 22 days of development (Table 1). About 4 days later, all the larvae died on the verge of metamorphosis after spending some time swimming close to the bottom of the tank. Mortality was due to either the lack of appropriate food or settlement substrate. The investigation was thus terminated abruptly after 26 days of culture.

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