Spawning and Early Life History of *Murex pomum* Gmelin, 1791

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(2 Plates; 2 Text figures)

INTRODUCTION

The literature on reproduction and larval development of tropical marine prosobranchs has recently been greatly expanded. Of this group, the genus *Murex* has been investigated by Knudsen (1950), Natarajan (1957), Cernohorsky (1965), Fioroni (1966), Gohar & Eisawy (1967), D'Asaro (1970), Spight, Birkeland & Lyons (1974), and Bandel (1976). Observations on the spawning behavior and egg capsules of *M. pomum* have been made by D'Asaro (*op. cit.*) and Bandel (*op. cit.*), but as these formed parts of general surveys of many prosobranchs from the South Florida-Bahamas region and the South Caribbean Sea respectively, detailed accounts, especially of the development of the hatchlings, were not given. This study, inasmuch as it was possible to monitor closely the early development of *M. pomum* from egg masses deposited by adults in the laboratory, will extend existing information on the species. Specifically, the use of two separate sample groups of *M. pomum* differing in size and geographical origin (St. Kitts and St. Vincent, West Indies) served to establish what is the norm for this species, and also helped to provide comparative information on spawning as well as quantitative and qualitative data on the capsules, eggs and young hatchlings.

ACKNOWLEDGMENTS

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DESCRIPTION, DISTRIBUTION AND HABITAT

Murex pomum is among the larger of the Muricidae. Humphrey (1975) gave measurements of adults of 2 to 4.5 inches (ca. 5 - 11.5 cm), but our largest specimen was just over 12.5 cm long. The shell is heavy and strong with a rough surface, but shell quality varies impressively from one adult to the next and with the age of the newest varix. The colour of the shells is usually a combination of cream, tan, and dark brown, and occasionally tints of purple. The interior aperture is polished, and most often is coloured yellow to ivory, but may be light pink, and least often has all these shades inter-mixed with purple tints. There is usually one dark spot on the upper end of the parietal wall and 2 or 3 on the outer lip.

According to Abbott (1958) and Humphrey (1975), it has a distribution ranging from South Carolina in the southeastern United States to Trinidad in the West Indies. It has been collected from Biscayne Bay in Florida (D'Asaro, 1970), and reported as quite common in Cuba and Puerto Rico (Abbott, *op. cit.*), as common in the Bahamas (Zeiller, 1974) and off the coast of Colombia (Bandel, 1976), and as the most common *Murex* snail in Jamaica (Humphrey, *op. cit.*). It has been found by the junior author to be quite abundant in St. Kitts and St. Vincent and off the coast of Venezuela, but for some reason it is very scarce around Barbados. Only a single

specimen was taken from numerous dives over years of shell collecting in Barbados.

For this study *Murex pomum* was obtained from Frigate Bay, St. Kitts, at a depth of approximately 4.5 to 6m. The animals inhabited an area of mixed rubble and sand, in which *Thallassia testudinum* grass flourished, and were invariably seen in groups of 2 - 4 in shallow depressions. In St. Vincent, *M. pomum*, which was generally larger than the average St. Kitts specimens, was collected off Young's Island in 4.5 - 6m of water, also in an area of rubble and sand. However, unlike the St. Kitts specimens, these were always seen buried in the sand with little or no part of the shell protruding above the substratum. Curiously, although HUMPHREY (1975) has described *M. pomum* as located in every imaginable environment, this species was obtained at only one site in St. Vincent and not in numerous other bays of comparable bottom.

The species has been described both as a carnivore (BANDEL, 1976; and others) and a browser (ZEILLER, 1974). The specimens under study exhibited both feeding patterns. They were routinely fed on the flesh of *Strombus pugilis*, alternated with that of the sea urchins, *Tripneustes esculentus* and *Diadema antillarum*.

MATERIALS AND METHODS

Eighteen adult specimens of *Murex pomum*, captured at St. Vincent on the 29th of February, 1976, were transferred to the Bellairs Research Institute, Barbados, where they were kept in a concrete aquarium of 228L[1] capacity with running sea water. Ambient temperatures averaged 27.1° C.

Within 4 weeks of arrival a large mass of egg capsules and a few smaller clusters were deposited by some of the animals. Since the major part of this event occurred over a week-end, when they were not under close observation, there was no certainty which of the animals were involved in the process. Just over a week later a specimen was observed to have deposited a few capsules. It was immediately marked with a numbered tag attached by nylon fibre and kept under close watch from 8:00p. m. to 10:00p. m. each day. It was the only specimen seen associated with the increasing egg mass and was not observed to leave the mass until 6:30p. m. on the 3rd day. Thus, not only was the identity of the egg layer certain, but also the time taken for deposition was determined to within minutes. Figure 1 is a photograph of the egg-depositing female and the egg-capsule mass. The latter is hereinafter referred to as sample A.

The egg-capsule mass was removed from the concrete wall of the tank and after careful blotting, was weighed and partitioned. The largest portion was put into a nylon basket of mesh size 0.239mm, which was then suspended in the water table and kept under observation. The second portion was frozen for later biochemical and histological studies, and the third was used for estimation of the total number of egg-capsules, number of eggs per capsule, and for dry weight determinations.

In May, another batch of 20 *Murex pomum* was captured in waters off St. Kitts, labelled, and housed in the same water table. No egg-capsules had been deposited up to 10:00p. m. on June 17th, but by the following morning there was a mass of oothecae on the upright wall of the tank. Five specimens were observed associated with this egg-mass, but 4 of these moved off at various times during that day and only one continued to be associated with the growing mass until 5:00p. m. on the 21st. Thus in both cases a single female was responsible for depositing at least the majority of the egg-capsules. This second capsule mass, now designated sample B, was treated like the first.

Daily samples of 5- 6 capsules were removed from the egg-mass and preserved for later study of development. Almost daily observations were made on the development of the hatchlings. From the 21st day onward, samples of the larvae were transferred to nursery baskets, sometimes still in the capsules and in other instances without capsules. In this way it was possible to determine at what stage they were most likely to survive removal from the egg capsules. The surrounding fluid in the nursery basket was regularly sampled for veligers.

The sizes of egg capsules, larvae and adults were determined and a size factor for the latter was calculated from length and width (L × W).

RESULTS

Adult Sizes

The adult animals from St. Kitts and St. Vincent clearly constituted two distinct size populations. Average length and width for the St. Kitts snails were 6.6cm (5.3 - 7.9cm) and 4.5cm (3.6 - 5.4cm) respectively, while the same measurements for the St. Vincent specimens were 10.4cm (8.5 - 12.5cm) and 6.5cm (5.8 - 7.9 cm). The single female (from St. Vincent) observed in the deposition of sample A egg mass measured 12.3cm in length and 6.95cm in width and weighed 191.50g

[1] "The Veliger" has adopted the SI metric prefixes and abbreviations exclusively, according to which L stands for liter.

after egg deposition. Of the 5 specimens from St. Kitts associated with capsule mass B, average measurements were: length, 7.1 cm; width, 4.8 cm; and weight, 62.70 g. The female that deposited for the longest time was 7.7 cm in length, 5.4 cm in width, and weighed 76.86 g.

Egg Deposition

All the egg-capsule clusters were deposited just on the waterline in the aquarium. Areas free of fouling seemed to have been preferred, but the animals themselves also seemed to do some clearing away of tubiculous worms. The capsules were very firmly cemented to the upright surface of the tank and to each previous layer by their basal points. The time taken for deposition by the first single female was 54 hours. It is not known whether this female had contributed to any of the other clusters deposited earlier or whether it had spawned earlier in the year but did not do so again up to October of that year. The same observations hold for the second set of depositors. In this instance, one female was spawning continuously over a period of approximately 87 hours. The total wet weight of sample A capsule mass was 129.90 g and that of sample B, 53.49 g. The number of capsules estimated from counting an approximate $\frac{1}{8}$ subsample was 1 862 for sample A and 1 662 for sample B. Capsules from sample A contained 45 - 110 eggs and those from B, 25 - 45. The capsules were filled with additional albuminous fluid and lined by a thin albumen membrane.

Description of Egg Cases

The egg cases of *Murex pomum* are roughly tongue-shaped with the convex side uppermost. This side is patterned with striations of variable thickness. The striations are mostly in the vertical plane but those towards the shoulders branch and anastomose to make a network. The pattern is variable. The concave side has striations of much thinner fibres. An exit-window of much more even consistency is located in the apical half of this side (Figure 2). The egg capsules of sample A averaged 7.8 ± 0.5 mm at the base and 7.5 ± 0.5 mm in height. For sample B, width and height measurements averaged 5.3 ± 0.4 and 5.4 ± 0.5 mm respectively. There was little difference in thickness, capsules in sample A averaging 2.0 ± 0.2 mm and in sample B, 1.8 ± 0.1 mm. The oothecae are leathery in texture and strength and of a creamy off-white colour when deposited, but develop a more yellow colour with age. They retain this colour long after the eggs have hatched. Several times during the late pre- and early-hatching stages, the oo-tests became infested and covered with black fungus. For treatment of this infection, 2 mg of streptomycin and 2 mg of sulphadiazine were dissolved in 1 L of millipore-filtered sea water, and the capsules were immersed therein for 8 hours. But, curiously, after hatching was completed, the portions of egg capsules kept in sea water did not develop any fungal growth or discolorations.

Pre-Hatching Development

Development was not synchronized throughout the egg-mass, nor within the same capsule. This was evidenced by the fact that, although deposition of egg capsules was accomplished within 54 and 87 hours for samples A and B respectively, hatching continued over a 12 day period in both instances. Furthermore, individual capsules removed from the mass during any of the hatching days contained

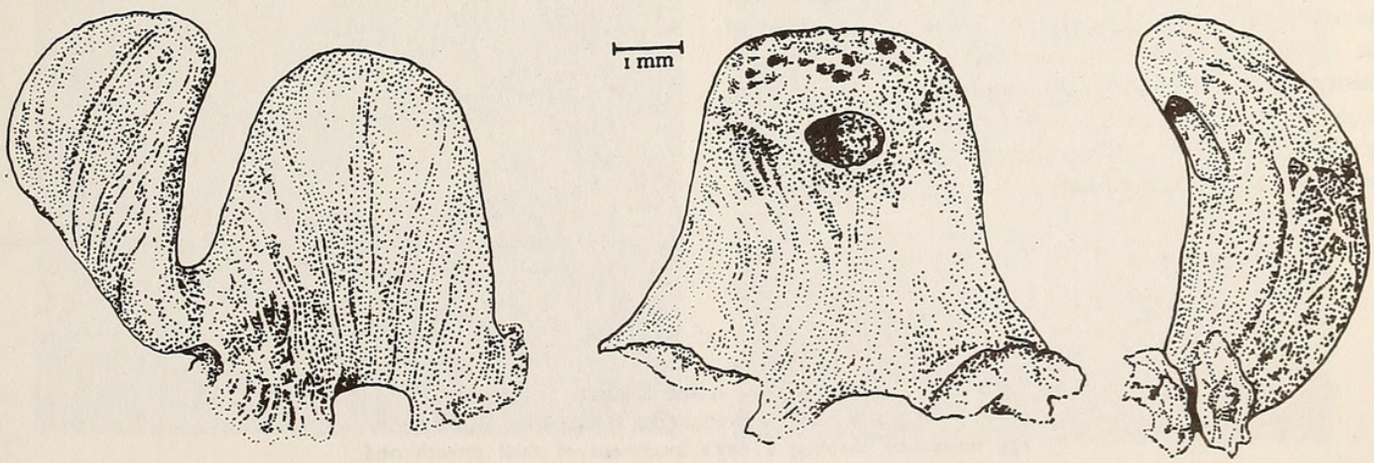

Figure 2

Murex pomum egg capsules taken from an original drawing by the late Dr. Gunnar Thorson, by courtesy of Dr. Jørgen Knudsen

young of different sizes and showing different increments of growth. Nevertheless, it was possible to follow the developmental sequence quite easily. The qualitative data on larval stages, hatching times, and later development showed 100% comparability.

In the most advanced larvae, the foot was apparent by the 18th day after spawning had ended. The velum was formed and so was the pulsatile larval heart. The frequency of the heart beat seemed to be related to velar activity, ceasing for several seconds when the velum was withdrawn. Eye-spots were barely visible. The gut was observed extending from the stomodeum, with the gut diverticulum, seen as a coarsely granular mass, jutting towards the posterior end of the larva, which was by then encased in a membrane-like shell. Between the 19th and 21st day torsion took place. New shell material was deposited and the larva then assumed definitive shape. The eyes had been formed, and the gut diverticulum had increased in size.

By the 22nd day the shell had 2½ whorls, was gritty on the outside and quite brittle with a smooth outline on the outer lip. In the St. Kitts specimens, however, the last ½ whorl was marked by a prominent mid-whorl shoulder. At the anterior end of the larva the 4-lobed velum, foot and operculum showed further growth. Orange and brown pigmentation had begun in the foot and operculum. There was also brown pigment in the eyes which were by then supported on short stalks. Tentacles were also formed. The pulsating larval heart could be seen through the still transparent shell just below the outward curvature for the siphon which was not well formed. The gills, however, were present and could be seen coiling backwards from the stomodeum. The mid-gut gland extended into the apical whorl but did not fill it. At this stage the larval velum was very active, and the larvae moved about within the capsules. Some exit-windows of the capsules opened but most of the veligers remained inside. When flushed from the capsules, they swam quite strongly up and down the water column. The foot was by then quite well developed and pigmented, and the larva used it to a limited extent. Larvae, that were transferred to nursery baskets at this stage, did not survive. The causes of death were not known, but were not related to shell damage inflicted during handling as most shells remained intact.

By the 23rd day the shell began to develop colour, and a layer of new material was laid down on the outer lip (Figure 3). In the St. Vincent specimens the tubercle marking the beginning of the mid-whorl shoulder was then apparent. The eyestalks had grown to extend beyond the shell. The velum had increased in size – when fully extended each lobe on a sample A specimen measured 1.25 mm long. Between the 24th and 26th day the foot became more active and was preferred as a means of locomotion. Pigmentation intensified, particularly in the shell, and so internal structures were less discernible, except for the mid-gut gland which then occupied more of the 2nd whorl. Shell growth continued at the rate of one layer per day, the layers averaging 32 μm in width. Larvae from any capsule showed from 2 - 6 layers on the outer lip. As a result of this variation, their lengths varied in the same way as the lengths of the hatchlings given in Table 1 and shown in Figure 4. At this stage the highest mortality in nurslings from all causes of death (discussed later in this text) was among the lesser developed specimens.

Table 1

Size variations (in mm) in twenty hatchlings from three connecting egg capsules taken from sample B. L and W denote length and width respectively.

L	W	L	W
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.4	1.2	1.6	1.2
1.5	1.1	1.6	1.2
1.5	1.2	1.6	1.3
1.5	1.2	1.6	1.3
1.5	1.2	1.7	1.2
1.5	1.2	1.8	1.3
1.5	1.2	1.9	1.4

Explanation of Figures 1, 3, 4

Figure 1: Egg capsule mass A and depositor

Figure 3: *Murex pomum* pre-hatching larvae about 24 days after egg deposition showing a day's increment of shell growth and developing foot

Figure 4: Difference in size of *Murex pomum* hatchlings taken from the same egg-capsule

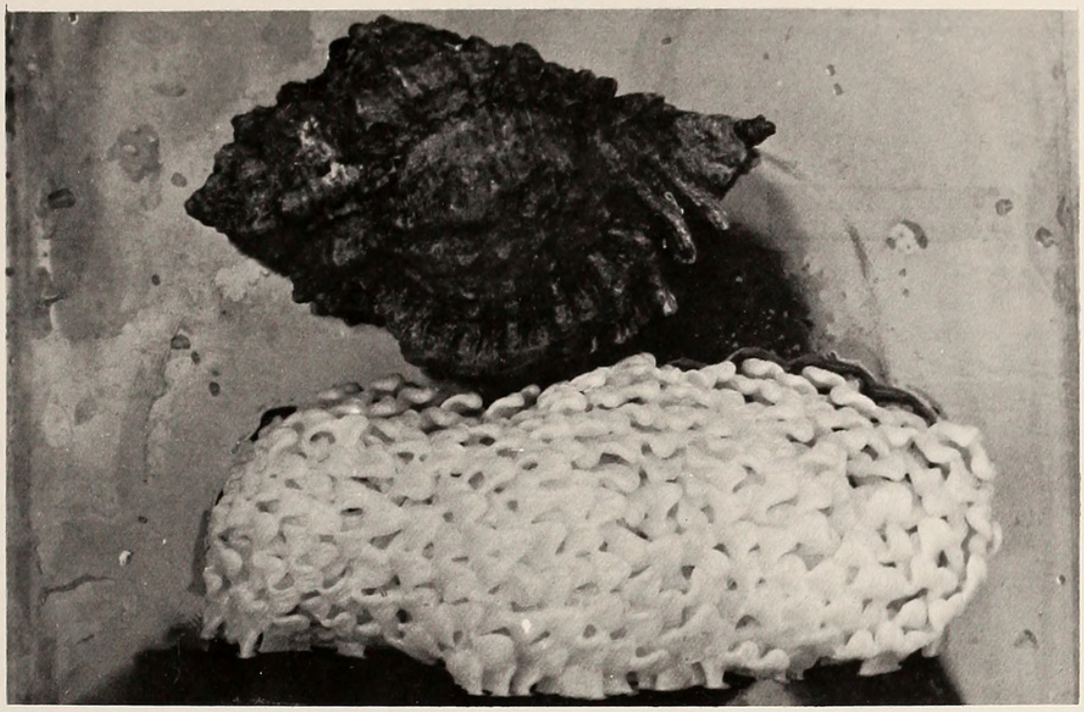

Figure 1

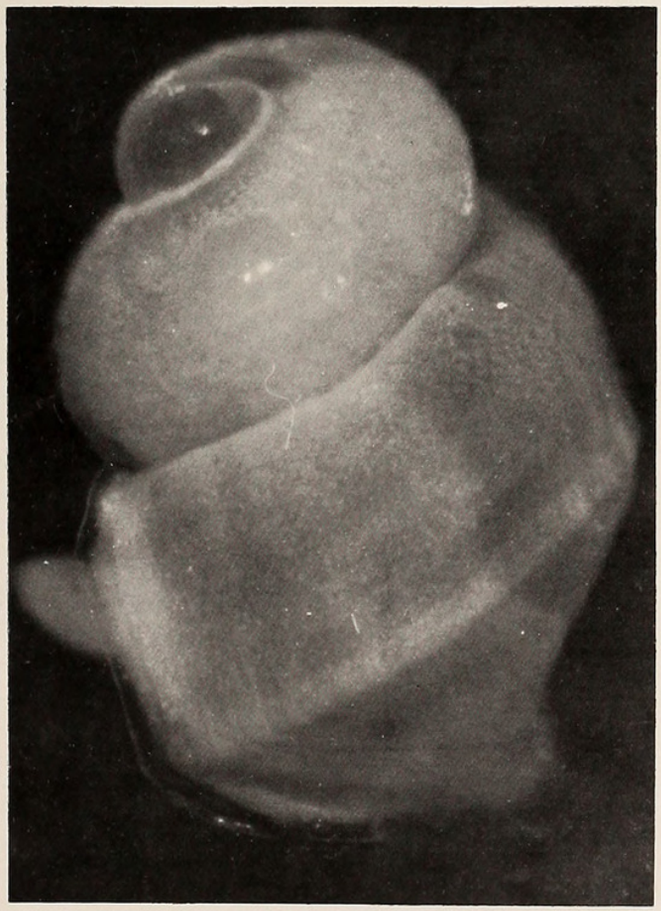

Figure 3

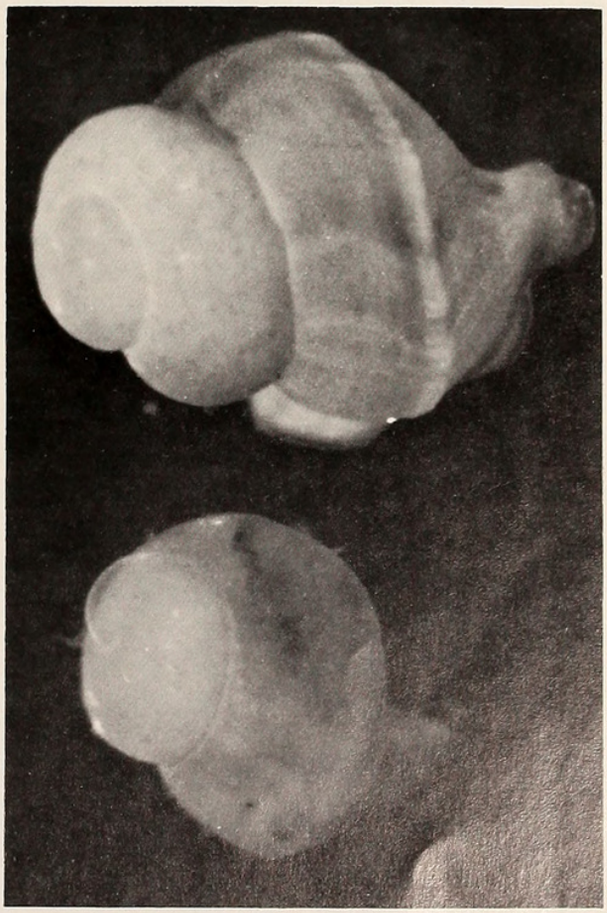

Figure 4

There seemed to be a gradual recession in use of the velum, and by the 28th day there was no outward sign of it. When turned over, the protoconchs all righted themselves by extending the foot until contact was made with the surface – none extended the velum although it had not yet degenerated and could still be seen when the shell was broken.

Hatching

From observations on the transfers to nursery baskets and daily sampling of the water from the main hatchery basket, it was determined that successful hatching occurred from the 26th day onwards. None of the transfers made before that day survived, nor did any of the veligers that emerged into the main basket, even though this could be considered a well-protected environment. By then the larvae had 4- 6 extra layers on the outer lip, the apical whorl was almost filled by the hepatopancreas, and the shell was heavily pigmented. Hatchlings varied in size as shown in Table 1 and Figure 4. Hatching continued up to the 38th day, the visually-determined peak being between the 32nd and 33rd days. By the 40th day all veligers remaining in capsules, although well developed, showed no sign of life. This happened mainly in the cases where the windows remained closed, but also in instances where the windows were opened. Necrotic larvae were quickly devoured by saprozoic protozoa, leaving only shells.

Most hatching protoconchs crawled out on foot, but many, particularly the early hatchlings, did so when both foot and velum were equally active. Some of them travelled relatively great distances in the first few hours after hatching; many of them crawled up above the water line and perished as a result. Presumably this was an instinctive dispersal response and in their natural environment the problem of desiccation would be of a lesser degree.

Table 2 gives a summary of relevant pre-hatching and hatching data for the 2 samples studied.

Post-Hatching Development

Since hatching continued up to the 38th or 39th day, some later hatchlings undoubtedly were more developed than the earlier ones and so passed some of the so-called post-hatching stages inside the capsule. Early in this period there was marked extension of the eye-stalks and the proboscis became quite prominent. The foot elongated and presumably development and differentiation of internal organs continued – the most obvious of which was the hepatopancreas which continued to extend towards the apical whorl. Colour intensified, further occluding internal structures. Visible growth was by the daily increment of shell material at the outer lip of the aperture (Figure 5).

When 7 - 8 layers had been laid down (*i. e.*, 3 - 5 days after hatching), crenellation of the outer lip began (Figure 6). At the 9 - 10 layer stage, multiple layers were put down at the same time and same level, somewhat like a set of flounces. This formed the first varix as shown in Figure 7. The lip was continued from the innermost of these at the same rate of one layer per day. The day's increment could always be seen as the thinnest translucent layer at the edge, since older layers were progressively thickened by new material added from the inside.

The second varix was formed similarly to the first at the 12th layer of the new extension, *i. e.*, roughly 18 days after hatching. The third extension involved 14 layers. This possibly marked the real end of the larval stage, since in the 4th growth stage shell deposition was more complicated. The shell material was much thicker and the surface was rougher and corrugated both vertically and transversely, markedly different from the earlier nuclear whorls. Fluting at the lip edge was more pronounced so the number of corrugations at the edge increased gradually (*cf.* Figures 6 and 7). This occurred 30 - 32 days after hatching. Because of the intensity of colour and the difficulty in handling the by then very active protoconchs, it was not certain whether growth continued by the same daily increments, but growth measurements done at wider

Table 2

Summarized data on the respective spawn from the St. Vincent and St. Kitts animals. H, W and T denote height, width and thickness respectively.

Collection site of samples	Average size measurements of capsules in mm (N = 20) H	W	T	Calculated average net weights of capsules in g.	Average number of eggs per capsule (N = 20)	Average number of eggs hatching per capsule (N = 40)	Percentage of eggs hatching	Average number of nurse eggs per embryo
St. Vincent	7.5	7.8	2.0	0.070	78.7	18.3	23.3	3.3
St. Kitts	5.4	5.3	1.8	0.032	34.4	7.9	23.0	3.3

time intervals on a single individual showed that the 32 μm per day input was closely approximated (Table 3).

Table 3

Growth measurements in mm for a single hatchling from sample B.

Date	Length	Width
20/7/76	1.45	1.20
26/7/76	1.55	1.20
4/8/76	1.80	1.30
10/8/76	1.95	1.35
27/8/76	2.40	1.46
10/9/76	2.90	1.87
14/10/76	3.30	1.90
28/10/76	3.30	1.90
15/11/76	3.30	1.90

By the end of the 10th post-hatching week the snails had each completed one new whorl and were then 3½ whorls big. By far the greater portion of the last whorl was of the thicker corrugated shell type. The 3 last measurements in Table 3 show that no growth took place for a month after this stage had been reached. Presumably the protoconchs had by then adopted the growth pattern of the adults; this involves massive shell growth over a relatively short period of time with increasingly large "resting" intervals. BANDEL (1976) has described how older well-fed animals will bury themselves in the sand, and put on a new chamber in about a week. Our experience confirms this and shows further that, if interrupted in the process, the murex will carry around the half-completed chamber for weeks until it finds conditions suitable to resume shell building. This seems to involve some factor other than the availability of sand or mud.

Survival of Young

There was a very high mortality in the hatchlings. Of an estimated 16268 veligers in Sample A, 99% either failed to emerge or died before reaching the age of 3 months, and that in a protected environment. It has already been pointed out that all naturally and artificially hatched veligers died, some from shell damage; many of the veligers and later stages died because their shells were perforated and viscera eaten out by boring worms. Many of the young snails died apparently from dehydration upon crawling above the water level, but others died from no readily discernible cause. The same results were obtained with sample B.

The best rearing results were obtained from those cultures that contained portions of the egg-capsule mass and turtle grass, *Thallasia testudinum*. Coincidentally, relatively large populations of cyclopoid copepods also developed in the same cultures, and the protoconchs, as they crawled over grass and egg capsules, no doubt fed on the crawling nauplius stages as well as nematode worms and bryozoan larvae found on the turtle grass. Later-stage juveniles were fed on the same diet as the adults.

DISCUSSION

High mortality is usually concomitant with high fecundity in animals. Despite the results obtained from rearing in a medium with turtle grass and egg capsules, it is most unlikely that lack of food played an important part in mortality among the young. SPIGHT (1976) has pointed out that few hatchlings starve to death (citing his experience of keeping many young *Thais lamellosa* alive without food for a month or more). Physical stresses and predation are more of a threat to the newly hatched snail than is starvation. Shell damage, dehydration and shell boring by worms naturally qualify as stress factors along with others that would occur in the natural environment. SPIGHT (1975) has calculated that a newly hatched *T. lamellosa* has a 1 - 2% chance to survive its first 3 months. A snail reaching 3 months has a 35% chance to reach age 1, and older snails have a 40 - 60% chance to survive through subsequent years. With this rapid increase in survival rates a 2mm snail should have much better prospects than a newly hatched 1mm snail. Our 1% survival of young tallies with Spight's 1 - 2% for *T. lamellosa*.

Explanation of Figures 5 to 7

Figure 5: A *Murex pomum* protoconch showing several daily increments of growth and also the mid-whorl ridge

Figure 6: *Murex pomum* protoconch showing crenellation of lip as well as pigmented foot, gills and portions of the gut

Figure 7: *Murex pomum* shell of 14 week old protoconch showing nuclear whorls and subsequent increments of growth

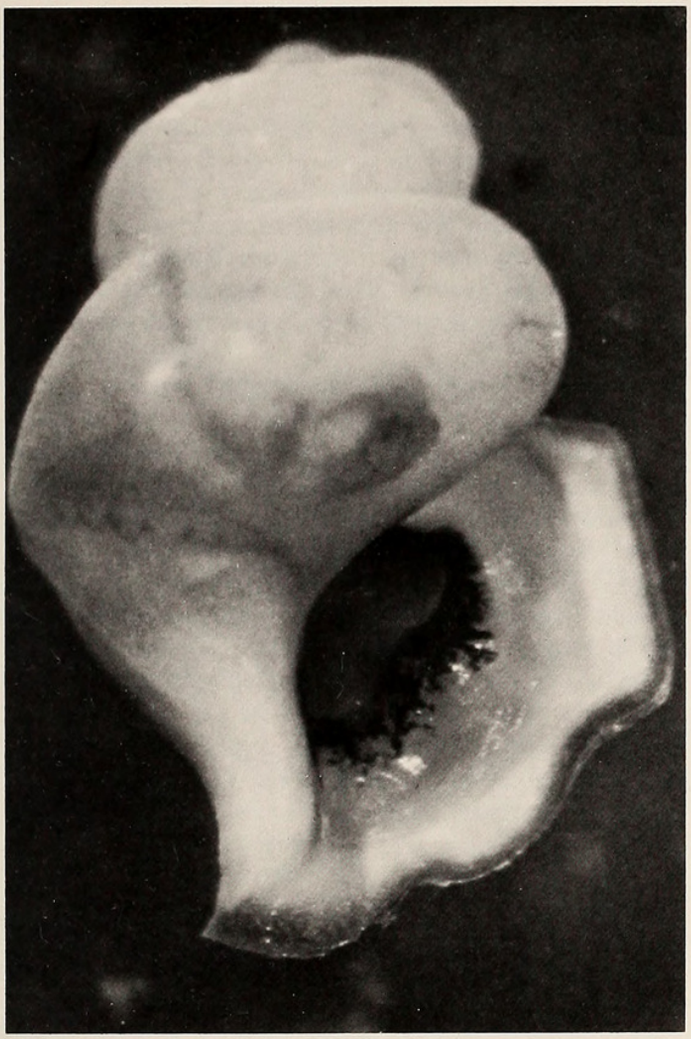

Figure 6

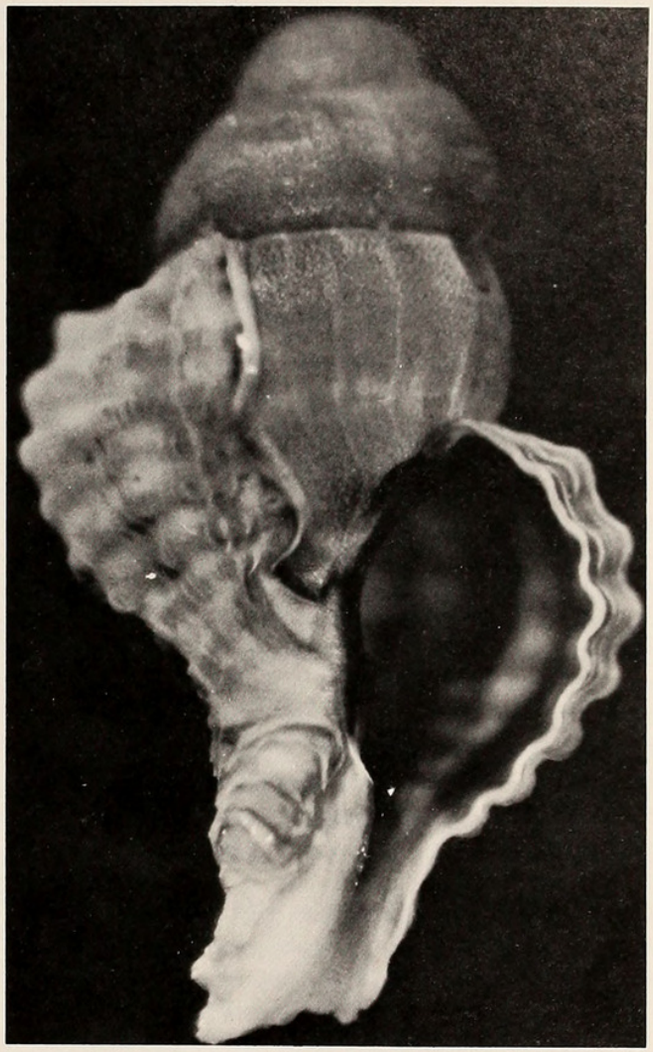

Figure 7

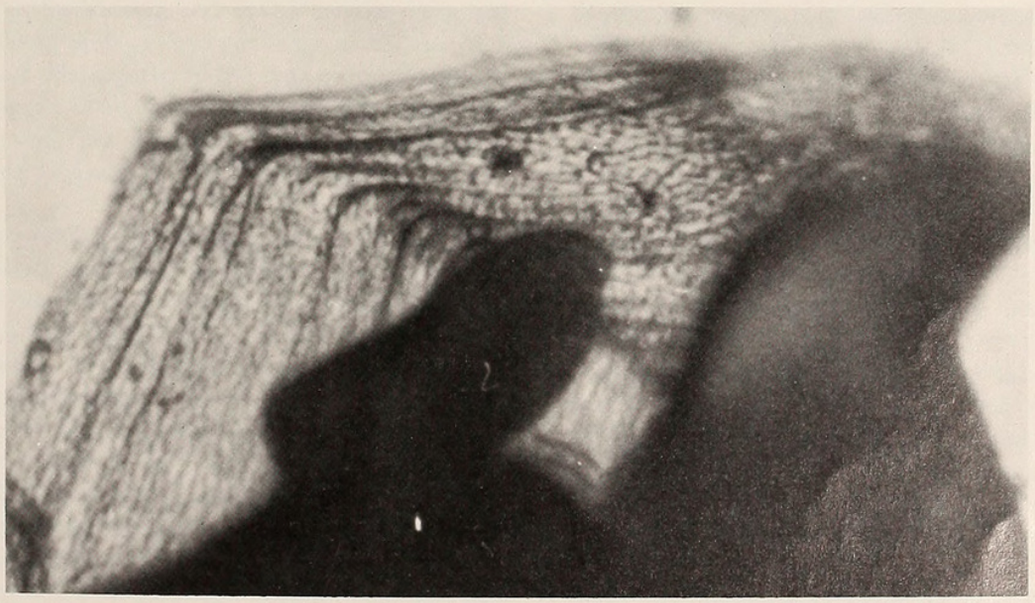

Figure 5