Development and Growth of Larvae of the Dog Conch, *Strombus canarium* (Mollusca: Gastropoda), in the Laboratory

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Zaidi Che Cob, Aziz Arshad, Mazlan Abd. Ghaffar, Japar Sidik Bujang, and Wan Lotfi Wan Muda (2009) Development and growth of larvae of the dog conch, *Strombus canarium* (Mollusca: Gastropoda), in the laboratory. *Zoological Studies* **48**(1): 1-11. *Strombus canarium* egg masses used in this study were collected while still underneath spawning females, and embryonic and post-hatching larval development was observed in the laboratory. *Strombus canarium* larvae were reared at 200 larvae/L in 2-L containers with 0.22 μm filtered seawater medium at a salinity of 30 ± 1 PSU, and fed a single algal species, *Isochrysis galbana*, at 1000 cells/ml. Fecundity was estimated at 48,745 ± 877 to 93,643 ± 1685 (*n* = 10) eggs/egg mass. The incubation time was between 110.4 and 134.4 h (mean 122.43 ± 3.07 h, *n* = 7) at 29 ± 1°C, with a high hatching rate (mean 93.34% ± 1.68% hatched, *n* = 3). The larvae have 2 velar lobes and 1.5 shell whorls at the time of hatching, with an average shell length of 216.77 ± 5.72 μm (*n* = 10). Based on prominent larval characters and visible morphological features, *S. canarium* larvae can be assigned to 4 different development stages, i.e. stages I, II, III, and IV, which are described in this paper. The larvae reached metamorphic competence at 17-23 d post-hatching, and only metamorphosed when settlement cues (sediments from its natural habitat and 15 mM KCl) were introduced. They showed a short period of metamorphic competence, and no spontaneous metamorphosis was observed. Morphological changes and larval behaviors at the onset and during metamorphosis are also described. http://zoolstud.sinica.edu.tw/Journals/48.1/1.pdf

Key words: Veliger, Development, Metamorphosis, Malaysia.

The dog conch, *Strombus canarium* Linnaeus, 1758, is an important gastropod mollusk native to the Indo-Pacific region. The species is widely distributed from southern India to Melanesia, northward to Japan and south to Australia (Abbott 1960, Poutiers 1998). The species is highly associated with sandy mud bottoms and seagrass beds and is normally found in large colonies (Abbott 1960, Cob et al. 2005 2008).

In Malaysian waters, they are present in many seagrass bed areas along coasts and sheltered islands, particularly at the southern tip of Peninsular Malaysia where locals have traditionally harvested them (Chuang 1961, Purchon and Purchon 1981, Cob et al. 2005 2008). The conch is a favorite seafood item in the Southeast Asian region, and is highly prized as a local delicacy (Amini 1986, Erlambang and Siregar 1995, Cob et al. 2008). The species is also among the most dominant herbivorous mollusks within the study site and possibly contributes to the well-being and maintenance of the seagrass bed ecosystem (Cob et al. 2005). However, recent developments in the vicinity of these areas such as coastal reclamation, over-harvesting, and lack of regulations have wiped out some conch populations within the

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Johor Straits (Bujang et al. 2007). In addition, no attempts have been made to propagate conch species by aquaculture in Malaysia. Therefore, the present study elucidates and hopefully will entice the development of larviculture and larval production of conch seeds in an effort to restore depleted natural populations of this species.

Elsewhere, the family Strombidae has generally been widely studied, particularly the economically important Caribbean species of *S. gigas*, *S. costatus*, and *S. pugilis* (Davis et al. 1993, Aldana-Aranda and Patino-Suarez 1998, Aldana Aranda et al. 2001). Many aspects of their life history have been documented, and advances have been made in the mariculture potential of these species (Heyman et al. 1989, Rodriguez 1996). In contrast, information on *S. canarium* is very limited. In the present work, embryonic and larval development stages of *S. canarium* are documented, which to our knowledge, has never been thoroughly investigated before.

MATERIALS AND METHODS

Strombus canarium egg masses were collected from Merambong Shoal in the Johor Straits, Malaysia (01°19'N, 103°35'E). Only freshly laid egg masses beneath spawning females were sampled for the culture experiment in order to ascertain their identity and to better estimate the incubation time in the laboratory. Spawning behavior was also observed and described. An egg mass was kept in a container filled with filtered seawater (0.22 μm) with moderate aeration during transportation. In the laboratory, the egg masses were cleaned of sand and debris, and kept in separate containers filled with 0.22 μm filtered seawater at 30 ± 1 PSU and 29 ± 1°C. The culture medium was changed every other day with freshly filtered (0.22 μm) seawater. Embryonic development and its evolution in time were periodically observed and described.

In order to assess the fecundity, egg masses were cleaned, blotted damp-dry, and weighed to the nearest 0.01 g using an analytical balance. Fragments of different lengths were taken from the mass, and numbers of eggs per unit length and unit weight were established. From these values, the total number of eggs contained within each egg mass and the egg mass total length were then interpolated.

Immediately after hatching, the swimming veligers were filtered-off using a 63 μm mesh filter, and were then transferred into 2-L round-bottomed glass containers at concentrations of 200 larvae/L. Natural 0.22 μm filtered seawater was used as the culture medium, with only very mild aeration. The salinity of the larval culture medium was maintained at 30 ± 1 PSU, a temperature of 29 ± 1°C, and a photoperiod of 12:12 h light dark conditions. The culture medium was totally exchanged every 2 d with freshly filtered (0.22 μm) natural seawater. *Strombus canarium* veliger larvae were fed the alga, *Isochrysis galbana*, at 1000 cells/ml throughout the culture period.

Veliger larvae were examined under both dissecting and compound microscopes, and were analyzed using an image analysis system (Motic™, Vancouver, Canada). Veliger shell length, from the tip of the spire to the end of the siphonal canal, was measured to the nearest 0.01 μm. Stages of *S. canarium* veligers along the continuum of larval development were described and illustrated on the basis of various morphological features such as the number of lobes, number of shell whorls, tentacles, eye stalks, presence of an adult heart, presence of a proboscis, radula, and pigmentation.

Larval behaviors were also observed by monitoring their activities for several seconds up to a minute. Locations of the larvae within the culture vessels (i.e., top, middle, and bottom) and swimming patterns (i.e., twirling, bouncing, remaining stationary, and swimming-crawling behavior) were recorded. Definitions of swimming patterns followed an earlier description by Davis (1994a): twirling was defined as a larva rotating in place; bouncing was defined as an up-and-down motion of a larva at the water surface; and remaining stationary was defined when the larval lobes were extended with only ciliary motion observed. Larval behaviors during metamorphosis were also observed and described. In this study, metamorphosis was induced using natural substrate taken from the nursery site (sediments) as well as the addition of potassium chloride (KCl: 15 mM) as suggested by Davis et al. (1990).

RESULTS

Egg mass description and pre-hatching larval development

Strombus canarium produced a long gelatinous tube of an egg strand that coiled and intertwined to form an egg mass. The egg mass gradually formed from one end to the other by

dorsoventral looping movements of the propodium, which was molded by the shape of the outer lip margin, resulting in a roughly crescentic shape. The coil was rather compact, with only a few internal spaces lying parallel to each other at right angles to the long axis.

The egg strand was covered by a protective translucent, membranous outer layer and a smooth, transparent inner layer (Fig. 1). There were indistinct linear plications and occasional annulations at irregular intervals on the outer layer that were probably caused by pulsative movements during oviposition. Egg masses were found securely attached to seagrasses, mostly *Halophila* spp., a few on *Thalasia hemprichii*, and rarely on *Enhalus acoroides* blades. These egg masses were also covered or camouflaged with fragments of drifting algae, *Ulva* spp., and lightly covered with sand particles.

The egg strand was packed with only a single row of spherical and transparent egg capsules, each containing a single embryo. These egg capsules were densely packed with no spaces between them. The diameter of the egg strand ranged 388.68-438.3 (mean, 412.82 ± 9.72) μm (*n* = 5), and the average capsule diameter (at spawning) was 244.54 ± 1.83 μm (*n* = 9). The egg masses weighed 4.23-6.13 (mean, 5.28 ± 0.38) g wet-weight (*n* = 5), with an estimated number of eggs (fecundity) in a single mass ranging from 48,745 ± 877 to 70,594 ± 1270 (*n* = 10). The estimated total length of the egg masses ranged between 22.01 ± 0.68 and 31.87 ± 1.33 (*n* = 10) m. The cleaned egg masses were beige or creamy-white.

Fertilization occurred internally before the egg was spawned followed by embryonic development inside the capsule. A chronology of early embryological development events is summarized in table 1. Cleavage and embryonic development stages lasted about 48 h, followed by development of the early larval stages. The gastrula was oval, with an average length of 218.66 ± 0.91 μm (*n* = 9) and width of 197.4 ± 0.63 μm (*n* = 9). After
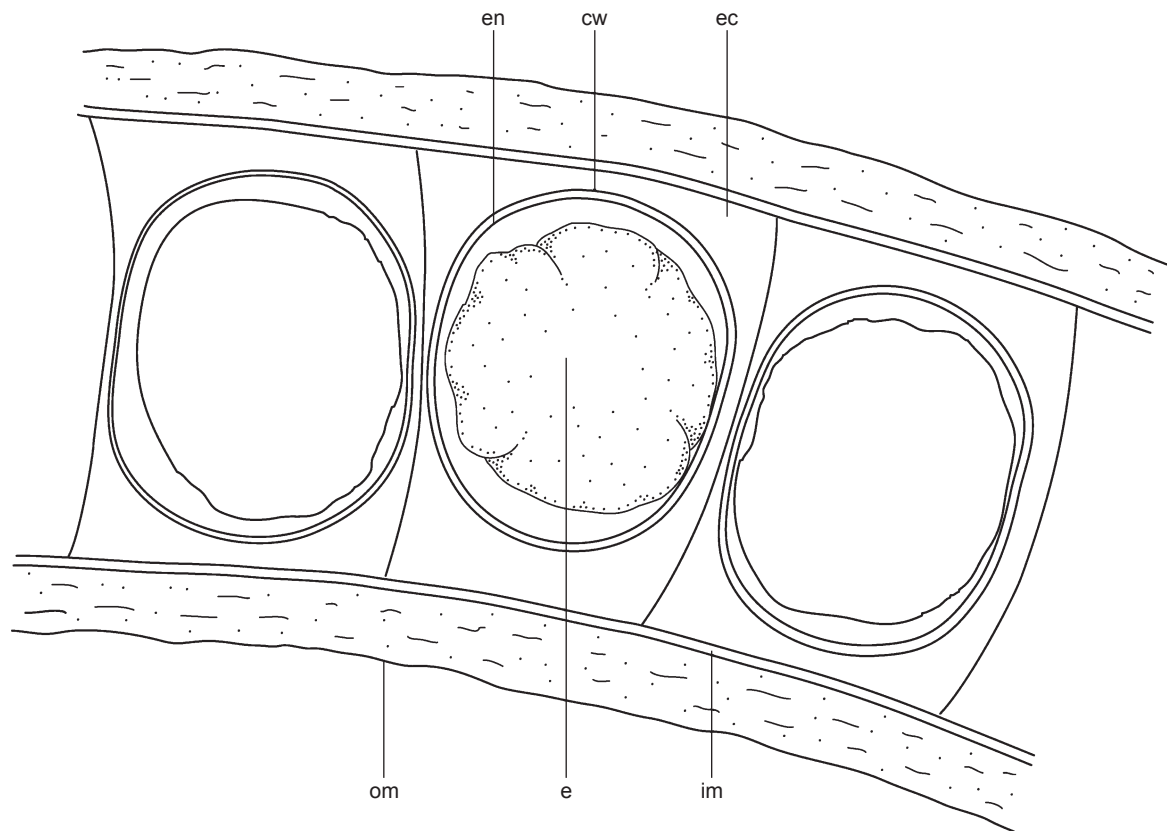
Fig. 1. Longitudinal section of a fragment of a *Strombus canarium* egg mass. cw, capsule wall; e, developing egg; ec, egg capsule; en, envelope; im, inner layer of protective membrane; om, outer layer of protective membrane. Scale bar = 100 μm.

2-3 d, trochophore larvae developed, which were elongated, with a flat velar field and a small pedal rudiment. Trochophore eyes were visible by day 3, and at this stage, the embryo began to revolve within the capsule.

Veligers first appeared by day 3 (71-88 h), and had a small, thick, bilobed velar with 1 row of short cilia. At this early veliger stage, the shell was cup-shaped, very thin, without a shell beak, and highly transparent. The shell was still relatively small and only covered the visceral mass, while the velar lobes and foot remained totally exposed. At this stage, the velum remained expanded and had brownish-red pigment along the rounded margin, with its cilia already in motion. The sub-velar ridge and sub-velar cilia appeared by 3.5 d. Eyes and statocysts (with a single statolith) were also visible. The posterior foot (metapodium) developed with turf of cilia at its terminus, but it lacked an operculum. At this stage, the internal organs began to develop.

By day 4, the shell had grown to cover the visceropallial mass, and had 1+ whorls with a prominent shell beak. At this stage, the velum was well developed and was clearly visible through the transparent shell. It was slightly curled, with more-prominent brownish-red pigmentation along the velar margin. Velar and sub-velar cilia wells developed and were capable of metachronic beating and reversals. Larval retractor muscles had also developed, but allowed for only incomplete retraction of larvae, leaving the velar lobes and foot partially exposed. The internal organs, although still yolky, were better defined, and the digestive glands were becoming more

distinct.

The veligers hatched after 110.4-134.4 h (mean 122.43 ± 3.07 h, $n = 7$) of incubation at 29 ± 1°C. Most of the larvae were still within the capsules when they emerged from the egg strand via an escape hatch. Shortly afterwards, the egg capsule burst, and the veligers immediately swam up the water column and began feeding on phytoplankton. Hatching rates were high, ranging 90%-95% (mean, 93.34% ± 1.68%, $n = 3$), and the entire hatching process, from the time when the 1st veliger emerged to completion, ranged 11-15 h (mean 13 ± 1.15 h, $n = 7$). The average size of a veliger at hatching was 216.77 ± 5.72 μm ($n = 10$).

Post-hatching larval development

Based on prominent characters and visible morphological features of the larvae, *S. canarium* veligers can be assigned to 4 different development stages throughout their short planktonic life cycle. Davis et al. (1993) used a similar development scheme for 3 species of *Strombus* larvae, i.e., *S. gigas*, *S. costatus*, and *S. pugilis*. Recent work by Harding (2006) found that the scheme was also applicable to other gastropod species. Line drawings representative of each stage are presented in figures 2A-D.

Stage I veligers (days 0 to 3; Fig. 2A) had a small bilobed smoothly rounded velum, with 2 rows of cilia (velar and sub-velar cilia), and reddish-brown pigment along the margin. The velum was faintly 4-lobed at day 2, which indicated the beginning of the first velar division. The shell had 1.5 whorls at hatching, with a smoothly

Table 1. Summary of the major events in the embryonic development of *Strombus canarium* at 29 ± 1°C. The egg masses ($n = 7$) were kept in 0.22 μm filtered seawater with a salinity of 30 ± 1 PSU

Time	Description
0 h	Single cell stage. Egg mass taken from beneath a spawning female. Size 181.3 ± 3.87 μm.
3-4 h	Single-cell stage. First and 2nd polar bodies observed.
24-39 h	Multiple-cell stage. Morula stage developed after ~24 h. Size 198.15 ± 0.49 μm in length, 134.51 ± 2.73 μm in width.
40-48 h	Gastrula stage. Gastrula oval and slightly elongated, with a characteristic blastophore. Size 218.66 ± 0.49 μm in length, 197.4 ± 0.63 μm in width.
47-66 h	Trochophore stage. Trochophore eyes visible. Velar rudimentary with very short cilia, posterior foot rudiment observed, embryo beginning to revolve in the capsule.
71-88 h	Early veliger stage. Shell incomplete, eyes and statocysts visible, posterior foot with turf of cilia, internal organs beginning to develop.
86-98 h	Veliger stage. Shell with 1 complete whorl and shell-beak beginning to develop. Velum developed, velar and sub-velar cilia visible, internal organs developed.
106-122 h	Late veliger stage. Shell with 1.5 whorls and prominent shell-beak. Hatching process requiring 12-15 h to complete.

rounded spire and a very pronounced beak on the shell's outer lip. The shell was colorless or lightly brownish, transparent, and sculptureless, apart from a few growth lines near the aperture of older larvae. The shell was around 200-300 µm in length. The columella was well developed at hatching, but the larval operculum was very thin, transparent, and barely visible. The foot was translucent and relatively small in comparison to the larval size. The pedal turf (i.e., a prominent cluster of elongated cilia on the tip of the foot) was present throughout larval development. The eyes were clearly visible at the base of the antennae but without a peduncle. At this stage, only the right antenna was present (ciliated), while the left antennae only began to develop on day 3. The
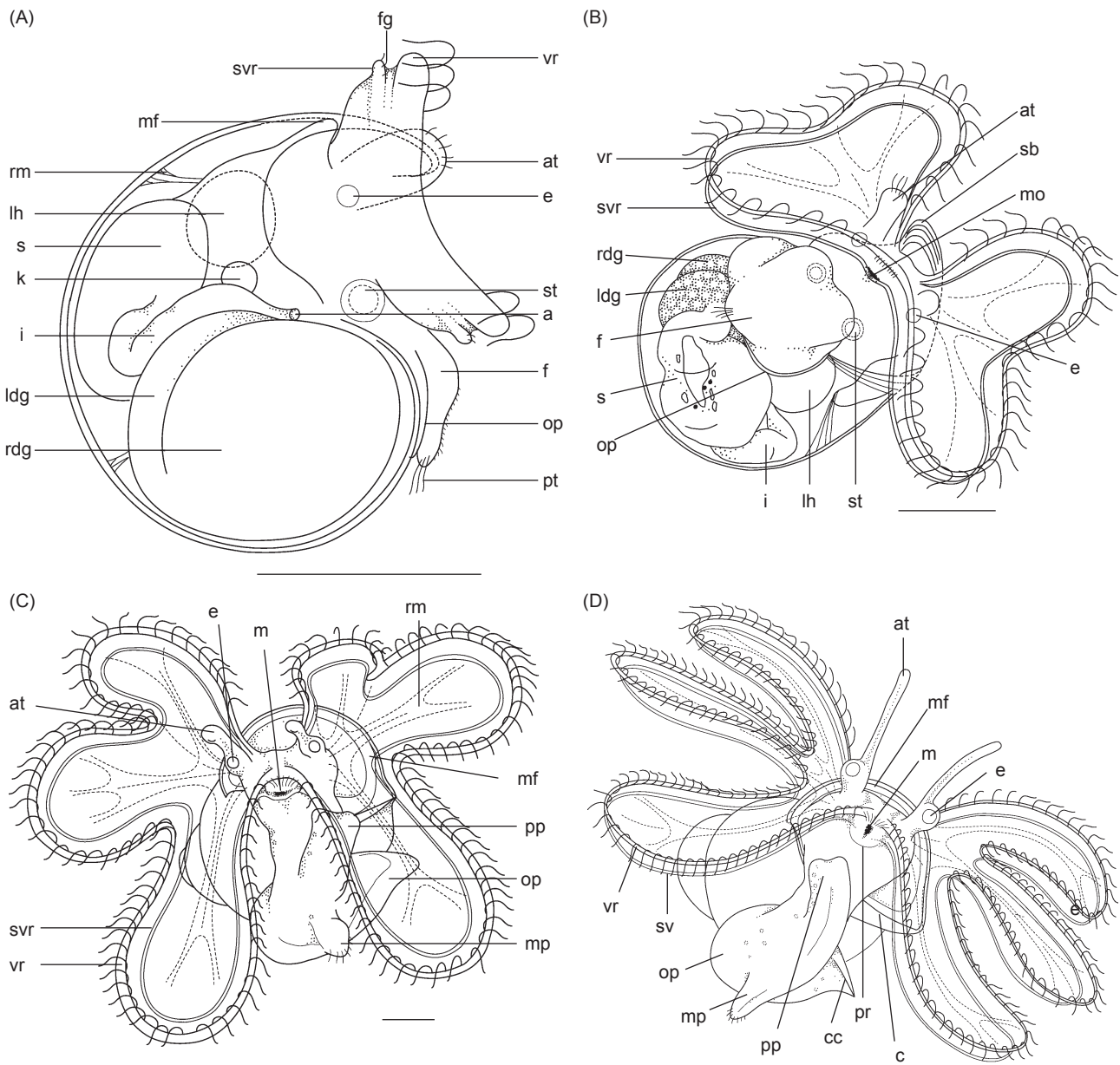
Fig. 2. Larval development of *Strombus canarium*. (A) Veliger stage I, lateral view; (B) stage II, latero-anterior view; (C) stage III, anterior view; (D) stage IV, anterior view. a, anus; at, antennae; c, columella; cc, conchiolin claw; e, eye; f, larval foot; fg, food groove; i, intestine; k, kidney; ldg, left digestive gland; lh, larval heart; mf, mantle fold; mo, mouth; mp, metapodium/posterior foot; op, operculum; pp, propodium/anterior foot; pr, proboscis; pt, pedal turf; rdg, right digestive gland; rm, retractor muscle; s, stomach; sb, shell beak; st, statocysts; svr, sub-velar ridge; vr, velar ridge. Scale bar = 100 µm.

mouth was positioned between the velar cilia (i.e., the pre-oral cilia or prototroch) and the sub-velar ridge (i.e., the post-oral cilia or metatroch). Larvae were highly phototactic, immediately moving towards a light source after hatching. At this stage, the beating heart, intestinal tract, stomach with a hyaline rod, and digestive gland were clearly visible through the transparent shell.

Stage II veligers (days 4 to 8; Fig. 2B) had a 4-lobed velum that was proportionate in size. By day 8, the anterior lobes had begun to expand and divide again. The shell was smooth at the spire, translucent, and light brown. At this stage, the larvae had 2-2.5 shell whorls, with an elongated and very prominent shell beak. The siphonal canal had begun to develop, and the shell was around 300-600 μm in length. The larval operculum was clearly visible and translucent white. The foot was opaque, with its posterior end beginning to acquire a spade shape. At this stage, the foot could be divided into a propodium (anterior foot) and metapodium (posterior foot). The left antenna had developed but was less than 1/2 the length of the right one, and by day 8, it had grown to 3/4 of the length of the right one. At this stage, larvae were actively swimming and intensely feeding with the aid of the extended velar lobes, and most of them congregated in the upper parts of the culture vessel.

Stage III veligers (days 9 to 16; Fig. 2C) had a 6-lobed velum, which was not proportionate in size. The anterior lobes appeared more rounded while the posterior lobes were more elongated. The velum had more-prominent reddish-brown pigmentation, and the food groove was clearly visible along the velar margin. At this stage, the shell had 2.5 whorls, with 2 prominent shell shoulders. The 3rd whorl and 3rd shell-shoulder began to develop by days 14-15. The shell at this stage appeared brownish and translucent, and measured around 600-800 μm in length. The shell beak was relatively less elongated compared to the earlier stage. A few beige-white spots were present on the body whorl. The columella and siphonal canal were well developed, and the operculum neatly fit in the columella opening. The foot was whitish and fairly muscular. At this stage, the foot and mantle had numerous beige-white blotches, which changed to the reddish-brown pigment at a later stage. The propodium and metapodium were clearly distinguishable, with the latter developing a prominent spade-shaped character. At this stage, the eyes were bigger, prominently bulging at the base of both antennae.

Throughout the larval development period, an outward migration of the eyes occurred, which began on day 13. At this period, the left and right antennae were roughly the same length and were lightly pigmented with some white spots. By days 10-11, the adult heart appeared. The proboscis began to develop on day 16 and was only observed being used for grazing 2 d later. At this juncture, the larvae were more dispersed within the water column, some in the upper parts and some in the middle, while others hovered at the bottom of the culture vessels.

Stage IV veligers (day 17 to settlement; Fig. 2D) had a 6-lobed velum that was much more elongated and was finger-like in appearance. The shell had 3 whorls and 3 prominent shell shoulders, and a much-elevated spire. Faint axial sculpturing was visible on the last whorl. During metamorphic competence, the velum decreased in size and was finally shed during metamorphosis. At this stage, the veliger had 4 whorls, with a prominent siphonal canal. Numerous dark green blotches also appeared on the body whorl. The shell beak was no longer visible but had been replaced by the outer columella margin. The columella was well developed with reddish-brown pigment on the inner lip margin. The adult operculum began to develop where the 1st conchiolin claw appeared. Veligers reached metamorphic competence as early as day 17, with a measured size at settlement ranging 978.87-1125.5 μm (mean, 1033.55 ± 30.48) in shell length. The propodium was well developed and highly mobile and had prominent reddish-brown pigment in the earlier stage followed by dark green pigment at the later stage. Similar changes in pigmentation were also observed on the proboscis and mantle margin area. At this stage, the eyestalks were visible with eyes well-developed at the termini and pigmented with white spots. The antennae were long and slender and still attached to the eyestalks, and were also pigmented with white spots. The proboscis was well-developed and pigmented with dark green pigment at the later stage. At this stage, the whitish radula was visible through the translucent proboscis.

Metamorphosis in *S. canarium* was recognized when the velar lobes were lost (shed), and juvenile conchs began to crawl with their propodium, as was observed in other *Strombus* species (Brownell 1977, Davis et al. 1990, Davis 1994a). It took about 17-23 d for the veligers to become competent and then to metamorphose. Sediment taken from the species' natural habitat successfully induced metamorphosis in

S. canarium, although the precise nature of the cue has yet to be determined. There was no spontaneous metamorphosis observed during this study. After the post-competent period (day 23 onwards), only a few larvae were able to further metamorphose, while the others weakened and finally died of exhaustion.

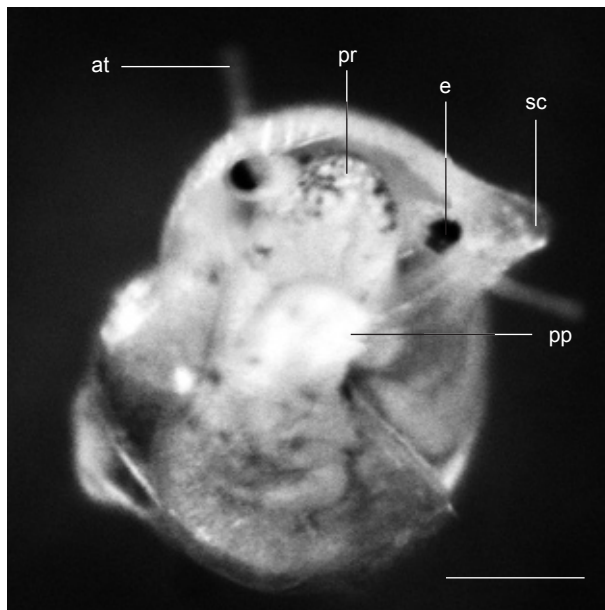**Description of newly metamorphosed juveniles**

Newly metamorphosed juveniles (Fig. 3) had 4 (or 4+) complete whorls, and were light brown. The spire was smooth, translucent, and sculptureless. The body whorl was translucent with clearly visible growth lines. Numerous blotches of dark green pigment were visible on the body whorl, particularly on the ventral side. The opercular opening was large, with reddish-brown pigment on its margin, particularly on the inner collumella lip. The operculum had white pigment on the peripheral but greenish pigment on the inner section. The 1st conchiolin claw of the adult operculum was visible, with reddish-brown or rarely orange pigmentation. The animal's body mass was translucent, but heavily pigmented with dark green and white blotches. The proboscis was heavily pigmented with dark green blotches in the basal area, with numerous white spots around the snout/mouth area. The tentacles were

relatively long and slender but were still joined to the eyestalk, with numerous white spots along the length. There was no dark green pigmentation on the tentacles, and both left and right ones were about the same length. The eyestalks were well developed, with big and bulging eyes at the termini, and both had numerous white and dark green blotches, mainly in the basal areas. The buccal mass and radula were visible. The propodium and metapodium were pigmented with dark green pigment and a few white blotches.

Behavioral observations

Larval behavior, particularly the swimming pattern, changed with age. Larvae were highly phototactic (or negatively geotactic) at hatching, as they immediately swam toward the surface. They moved around with the aid of ciliary movements, which also created water currents that brought food (via the food groove) to the mouth. Younger larvae (veliger stages I, II, and III) spent more time in the upper column and actively swam (and fed) throughout the period. Older larvae (veliger stage IV) showed more bouncing and swimming-crawling behavior, and occasionally just hovered at the sides of the container, or just below the surface. Some larvae were seen twirling at or near the bottom of the container. Upon reaching metamorphic competence, the swimming-crawling behavior became more pronounced, accompanied by active probing of the bottom area and sides of the container using the proboscis.

A sequence of behavioral patterns related to metamorphosis was observed when competent larvae were transferred to containers filled with bottom sediments taken from their natural nursery habitat. After a short period of swimming-crawling and active probing behavior, the larvae seized up (stopped swimming) and immediately sank to the bottom. They then anchored themselves to the bottom (using the foot and mucus thread), and began twirling and spinning, and sometimes vigorously kicking, with simultaneous secretion of mucus substances, followed by a stationary period with the velar lobes remaining extended. This behavior was repeated several times before actual metamorphosis took place. As a result, the shell surface was covered with sand and particles from the sediment even before they metamorphosed. We recognized this behavior as the initiation of metamorphosis, which to our knowledge has never been reported before. After 24 h, when the metamorphic process was completed (having lost


Fig. 3. Newly metamorphosed juvenile *Strombus canarium* (day-0 juvenile), still facing upwards. at, antennae; e, eye; pp, propodium (anterior foot); pr, proboscis; sc, siphonal canal. Scale bar = 100 μm.

the velar lobes, facing down, crawling, and feeding with the proboscis), the newly metamorphosed juveniles were completely camouflaged and physically blended into the surrounding sediments (Fig. 4). The same behavioral patterns were also observed when the larvae were induced to metamorphose (using 15 mM KCl), even in containers completely void of sediments.

The newly metamorphosed juveniles showed the characteristic conch-hopping movement immediately after they metamorphosed. They were very active, constantly in motion, and repeatedly probed the sediment surface with the proboscis in search of food. They grazed on the algal film that coated the tank walls and bottom. In the treatment tank filled with bottom sediments, the juveniles were observed to be very selective during feeding. They selectively ingested particulate matter, probably feeding on the microalgae and bacterial film coating it, and quickly expelled unpalatable items.

DISCUSSION

Strombus canarium produces a long, coiled, intertwined gelatinous egg strand, the gross
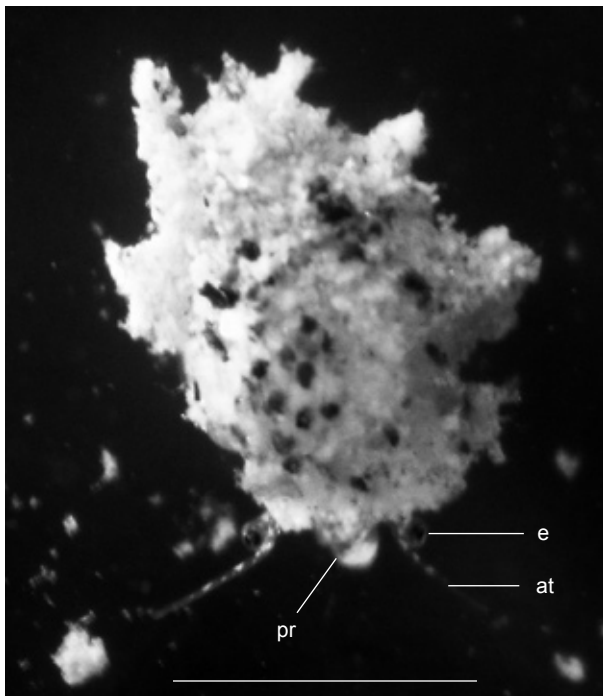
Fig. 4. Juvenile day 7 *Strombus canarium*, completely camouflaged with sediment particles, sand, and debris. at, antennae; e, eye; pr, proboscis. Scale bar = 1000 μm.

anatomy of which is quite similar to those of *Strombus* spp. from other regions (Robertson 1959, D'Asaro 1970 1986). Within the jelly-like tube of the egg strand, there is only a single row of eggs (capsule), each of which has one only 1 ovum. This observation is in agreement with a previous description by Risbec (1936). The fecundity is, however, far inferior compared to other Strombaceae. D'Asaro (1986) reported that the *S. alatus* egg mass contained approximately 87,000-97,000 eggs. Robertson (1959) reported that *S. costatus* produced 185,000-210,000 eggs, while *S. raninus* had 400,000-460,000 eggs in a single egg mass. Robertson (1959), D'Asaro (1965), and Randall (1964) on the other hand reported that *S. gigas* produced more than 400,000 eggs in a single mass. All these species however have different arrangements of eggs within the egg masses where the tube has multiple rows of eggs, and furthermore, each egg contains more than 1 embryo. Nevertheless, incubation periods were quite similar to that of *S. canarium*. *Strombus gigas* veligers emerged after approximately 112 h (Robertson 1959, D'Asaro 1965, Brownell 1977), *S. raninus* veligers emerged after 80 h (Robertson 1959), and those of *S. costatus* emerged after 100-150 h of incubation (Robertson 1959, Brownell 1977).

Newly hatched *S. canarium* larvae showed similar numbers of shell-whorls and velar lobes as was reported for other *Strombus* spp., e.g., *S. gigas*, *S. costatus*, and *S. pugilis* (Brownell 1977, Davis et al. 1993, Brito-Manzano and Aldana-Aranda 2004). This characteristic appears to be common for *Strombus* species. Veliger size at hatching recorded for *S. canarium* in this study was however quite inferior compared to other *Strombus* larvae. Grana-Rafucci and Appeldorn (1997) in their study of *S. gigas* reported an initial larval length of 300 ± 6.17 μm, while Brito-Manzano and Aldana Aranda (2004) reported an initial larval size of 325 ± 35.36 μm for the same species. Grana-Rafucci and Appeldorn (1997) also reported a mean initial larval length of 345 ± 32.6 μm for *S. costatus*.

Strombus canarium veligers can be assigned to one of the 4 development stages similar to those described by Davis et al. (1993) for 3 species of *Strombus* larvae, i.e. *S. gigas*, *S. costatus* and *S. pugilis*. Recent work by Harding (2006) found that the scheme was also applicable to other gastropod species. Each stage differed morphologically and physiologically. Its application might therefore contribute to better management and better

hatchery practices for these species e.g., for better food and feeding management, and better administration of metamorphic cues which are normally quite expensive (Harding 2006).

The onset of competence in *Strombus* larvae can be recognized through various developments in both physical and behavioral characteristics (Davis 1994a b, Brito-Manzano and Aldana-Aranda 2004). According to Davis (1994a), the onset of competence in *S. gigas* was first recognized as an ontogenetic change in locomotory behavior, which was also true for the currently studied species. Larvae shifted from swimming to a swimming and crawling mode, using the propodium and adult opercular claw to glide or leap across the substrate surface, and at times using the velar lobes to swim. Berg (1972) described similar behaviors in competent larvae of *S. maculatus*, noting this is a general characteristic among the Strombacea. This swimming-crawling behavior may be important for conch larvae to test the substrate for metamorphosis and resume swimming if an inappropriate habitat is detected (Davis 1994a). In *S. canarium*, the presence of the proboscis is an important feature to note in order to recognize competency, which in this study was observed as early as day 16, and it began to function within 2 d. Brownell (1977) reported that the proboscis of *S. gigas* and *S. costatus* appeared as early as the 25th d, and began to function for grazing within 2 d. Brito-Manzano and Aldana Aranda (2004) however reported that the proboscis of *S. gigas* appeared on day 17th and began to function after 3 d.

Development of larval stages up to metamorphosis in *Strombus* larvae has been reported for only a few species, particularly within the Caribbean region, with some variations within and among species. The settlement period for *S. gigas* widely varied, ranging 18-25 d (Brownell 1977, Davis and Hesse 1983, Aldana-Aranda and Torrentera 1987, Davis 1994a, Brito-Manzano and Aldana-Aranda 2004). The onset of settlement for *S. costatus* was reported to occur between 29 and 32 d (Aldana-Aranda et al. 1989, Davis et al. 1993), while for *S. pugilis*, it ranged 27-31 d (Bradshaw-Hawkins 1982, Brito-Manzano and Aldana-Aranda 1998, Brito-Manzano et al. 2000). The onset of settlement for the currently studied species was however shorter than those of the species mentioned above. Prior to the competent period (pre-competent period, days 0-17), *S. canarium* larvae were unable to metamorphose even though they were chemically induced, and beyond day 23 (the post-competent period), only

a few larvae metamorphosed, but they produced relatively weaker, poorer-quality juveniles. The studied species showed a short period of metamorphic competence, similar to other *Strombus* larvae (Davis 1994a).

The mean shell length of *S. canarium* larvae at metamorphosis is in agreement with other reported data on *Strombus* where maximal veliger sizes are about 1200 μm for *S. gigas* (Brownell 1977, Davis et al. 1993, García-Santaella and Aldana-Aranda 1994, Brito-Manzano and Aldana-Aranda 2004), about 1270 μm for *S. costatus* (Aldana Aranda et al. 1989, Davis et al. 1993), and about 1150 μm for *S. pugilis* (Brito-Manzano and Aldana-Aranda 1998, Brito-Manzano et al. 2000). Growth of *Strombus* larvae in general is quite similar, but some variations might be evident due to culture conditions and food, and also according to the authors' criteria (Brito-Manzano and Aldana-Aranda 2004). Although larval shell lengths at competence are also quite similar within the genus, this character can only be used as a relative indicator for competency, as Davis (1994a) found no significant difference in size between pre-competent larvae and newly metamorphosed juveniles.

Specific behavioral characteristic were observed for *S. canarium* larvae at the onset and during metamorphosis, which ultimately produced well-camouflaged juveniles. Since the larval shell is very thin and fragile, sand particles and debris adhering to it might provide extra protection for newly metamorphosed juveniles, which spend their early life as epifauna. At this stage, juveniles were still unable to burrow into the sediments, but this ability developed at a later stage as the posterior foot and operculum become more mature. In addition, they also had very limited locomotive ability to escape predation. Sediment particles were strongly glued to the shell, and it was quite difficult to remove them even with a dissecting needle and brush.

In summary, the current study showed that *Strombus canarium* larval development is generally quite similar to those of other *Strombus* species. With increasing demand and good market value, there are definitely high prospects for the aquaculture of this species. However, further work on a larger scale is needed to determine the costs and techniques for nursery grow-out and the degree of success of reseeding as a means of increasing the adult conch populations in the area.

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