Australian Journal of Basic and Applied Sciences

2022 December; 16(12): pages 17-24
https://doi.org/10.22587/ajbas.2022.16.12.3

ORIGINAL ARTICLE AENSI Publications

A note on the Intra-Capsular Development of *Neritina turrita Gmelin* 1791

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Received date: 19 August 2022, Accepted date: 28 November 2022

Citation: K. K. Hristov., 2022. A note on the intra-capsular development of *Neritina turrita Gmelin* 1791. Australian Journal of Basic and Applied Sciences, 16(12): 17-24. DOI: 10.22587/ajbas.2022.16.12.3.

ABSTRACT: Background: *Neritina turrita Gmelin 1791* is an amphidromous gastropod mollusk found in the tropical coastal swamps. They are popular in the ornamental fish trade, and not successfully bred in captivity. Objective: The work aims to optimise a monitoring protocol for the early stages of *N. turrita* development in artificial habitat. Method: Long-term observations of *N. turrita* egg capsules in 5 g/L saline-water at 25°C. Results: 6 observable steps were identified, namely: i) deposition; ii) sinking of the developing embryos after 5 days; iii) movement of the developing trochophores after 9-17 days; iv) growth - packing the limited space of the capsule (18-24 days); v) darkening after the 25th day; and vi) hatching. Viable veligers are produced after day 33, however signs of cachexia due to undernourishment are noticeable between days 84-107. Subsequently, no live veligers were present. The approximate veliger size (length ~ 165-176 um and diameter of ~ 110-122 um), volume (~ 0.0010-0.0014 mm³) and relative density (> 1.3471 g/cm³) were determined, suggesting a possible buoyant depth of ~300 m. Conclusions: 1) *N. turrita* can be maintained and reproduce in artificial conditions. 2) The monitoring steps of the observable egg capsule changes determined, and related to the morphology of the developing embryo. 3) During their migratory journeys in the ocean they travel on the edge of the photic zone (200 m) or bellow, in the dysphotic zone, where photosynthesis is very limited or not possible, restricting *N. turrita* veligers' diet to bacterias, fungi and decaying organic matter.

Keywords: *Neritina turrita Gmelin 1791*, gastropod mollusk, amphidromous, artificial habitat..

INTRODUCTION

The *Neritina turrita Gmelin 1791* is an amphidromous gastropod mollusk (Fig. 1) found throughout the Indo-Pacific region (Madagascar, Japan, western Pacific Ocean Islands and Indonesia), but not in India and Australia (Kerr, 2013). *Neritina*, and the related genera *Clithon* and *Septaria* settle on the tropical coasts after a marine planktonic veliger stage, lasting from weeks to months (Abdou et al., 2015). Veliger transforms in the tidal, brackish waters near the mouths of rivers and streams. However, in the mangrove swamps, the benthic young are exposed to the influence of fresh water. The imaginings are herbivores observed during upstream migrations (Bandel, 2001). *Neritina turrita* is a popular animal in the ornamental aquarium trade. However, they are not successfully bred in captivity. The available animals are wild-caught and present a potential biohazard and consuming natural populations. My laboratory study (Hristov, 2020) aims to optimise a breeding protocol for *Neritina turrita* for the ornamental aquarium trade and biomedical research.

MATERIALS AND METHODS

Neritina turrita adult snails were maintained long-term in 30 L glass vessels in 5 g/L saline water: 5 g 'Salinity for reefs' (Aquavitro, SeaChem Laboratories Inc., Madison, USA) in 1 L local tap water (pH 7.42; GH 0.89 meq/L; conductivity 115.4

uS/cm, and Cl 0.11 mg/L; Sofiyska voda Ltd., Sofia, Bulgaria) at 25ºC and 12/12 hr light/dark cycle (947 lm, colour 7700 K light lux illumination; EHEIM Classic LED lights, EHEIM GmbH & Co. KG, Germany). The animals were sustained on leaves of spring and autumn oak (Quercus robur). Light microscope images were acquired with the help of Prof. N. E. Lazarov and Ms D. Brazicova with a Nikon research microscope equipped with a DXM1200c digital camera in the Department of Anatomy, Histology and Embryology, Medical University - Sofia, Sofia, Bulgaria. The density gradient centrifugations were performed in 15 ml tubes. *Neritina turrita* veligers were stained with malachite green (a generous gift from Prof. H. Najdenski, Department of Infectious Microbiology, the Stephan Angeloff Institute of Microbiology, Bulgarian Academy of Sciences, Sofia, Bulgaria) and laid over either 20 and 26% sodium chloride (S9888, Sigma-Aldrich Chemie GmbH, Germany), or 5, 10, 20, 25, 30, 35, 40, 50, and 70% sucrose (S0389, Sigma-Aldrich Chemie GmbH, Germany), and centrifuged at 400 g for 30 min at 20ºC on NEYA 16R bench top centrifuge with the help of Prof. S. Hayrabedyan, and Dr. M. Mourdjeva, Department Molecular Immunology, Institute of Biology and Immunology of Reproduction, Bulgarian Academy of Sciences, Sofia, Bulgaria.

Figure 1: Neritina turrita Gmelin 1791, an amphidromous gastropod mollusk, is maintained in 5 g/L saline water, at 25oC, on oak (Quercus robur) leaves

RESULTS

To accomplish a monitoring protocol for the early intra-capsular developmental steps of *Neritina turrita Gmelin 1791*, long-term observations were carried out. The snails were maintained in 5 g/L saline water at 25ºC. Egg capsules (convex, oval 1 x 1.5 mm, glossy and white initially) are laid regularly throughout the year. Monitoring of the visible changes before hatching of the egg capsules identified 6 steps, namely: deposition, sinking, movement, growth, darkening and hatching (Fig. 2). This was controlled with similar observations on egg capsules from *Clithon corona Linnaeus 1758*. At the deposition time, the egg capsules are white without clearly distinguishable eggs or embryos. However, five days after deposition, a sinking of the developing embryos is clearly visible. In *C. corona* egg capsules, the sinking of the embryos is observable between 4th and 7th day. Later movement within the egg capsule of the developing trochophores is easily identifiable (9 - 17 days for *N. turrita* and 5-10 days for *C. corona*). Between the 18th and 24th day for *N. turrita* (7-13 day for *C. corona*), the growing trochophores fill the limited space of the capsule, and 25 days after deposition embryos darken (15-18 days for *C. corona*). While hatching of *C. corona* egg capsules occurs 18-23 days after deposition when maintained in fresh-water, *N. turrita* egg capsules hatch much later: 84-107 days after deposition when maintained in 5 g/L saline water.

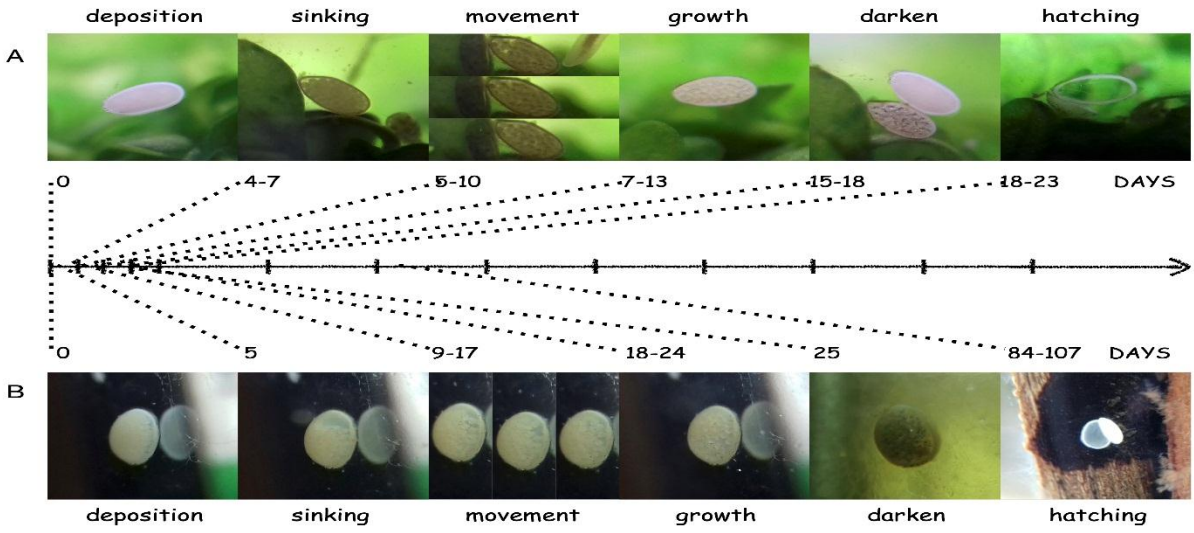


Figure 2: Monitoring protocol of *Neritina turrita Gmelin 1791* intra-capsular development (B): visible changes of the egg capsules identified 6 steps, namely: deposition (1 day), sinking (5 days), movement (9 - 17 days), growth (18-24 days), darken (25 days) and hatching (33-107 days) when maintained in 5 g/L saline water at 25ºC. This was controlled with similar observations on egg capsules from *Clithon corona Linnaeus 1758* (A), maintained in fresh water at 25ºC.

The morphology of *N. turrita* embryo development was related to the changes in the appearance of the egg capsules (Fig. 3). A much slower growth was noted: 30-50 embryos per capsule are usually present (rarely 5-10 eggs in a dense mucous). During the 1st day after deposition, the initial divisions of *N. turrita* embryos are easily observable (Fig. 3 and 5C). The early embryo covered by quiescent ectodermal micromeres (spread by epiboly) (Fig. 3, 4 and 5D) is clearly visible after day 5, coinciding with the sinking step described above. The movement of the developing *N. turrita* trochophores (Fig. 3, 4 and 5E) is observable through the transparent egg capsule after day 9. Shell gland appears, and the shell synthesis is noticeable at the late trochophore stage. The developed N. turrita veligers with eyes, ciliated velum, and shell cause the darkening of the capsular contents after day 25 (Figs. 3, 4, and 5F). The shell matures as the veliger grows, losing its elasticity and becoming more rigid, as seen by the presence of shell debris after the 94th day (Fig. 3). Although spontaneous hatching of *N. turrita* egg capsules at 5 g/L is possible, veligers were released from the capsules either mechanically (detachment from the substrate), or osmotically (placing the substrate in fresh-water). `Viable veligers were obtained between days 33 and 107, although, as seen in Fig. 6, signs of cachexia due to undernourishment are present after day 84.

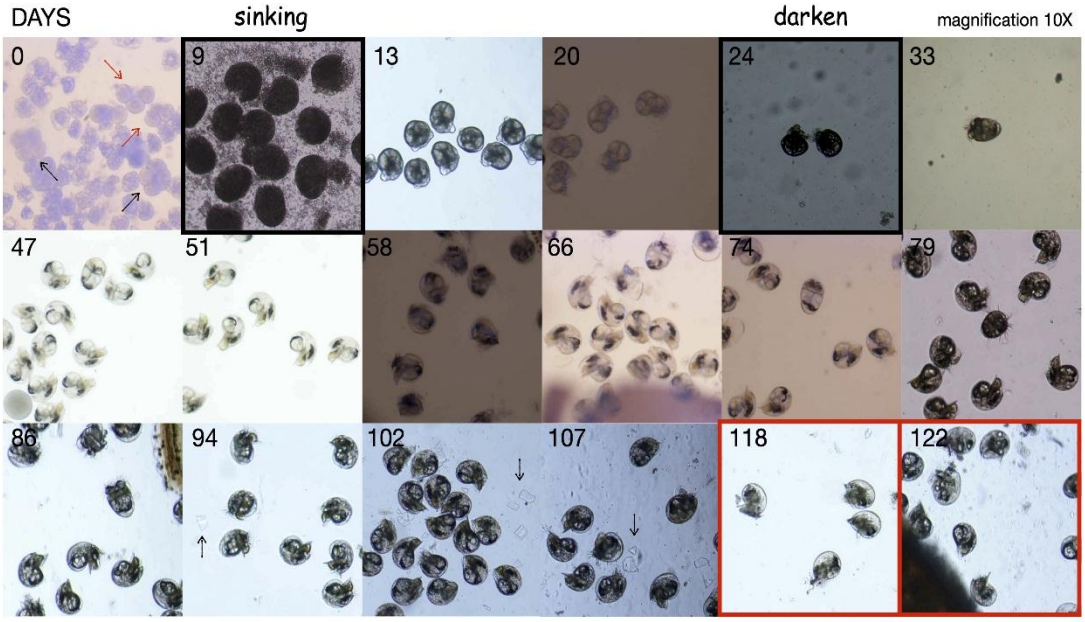


Figure 3: Morphology of *Neritina turrita Gmelin 1791* embryos: Light microscopy at 4X magnification. See text for details. Day 0: The black arrows indicate the intact 4 macromere embryos seen from the vegetal pole, and the red arrows - damaged 3 and 2 macromere embryos among scattered micromeres-only embryos. Day 94, 102, and 107: the black arrows indicate the shell debris. Late veligers have more rigid shells, some of which break during the mechanical opening of the capsule—day 118 and 122: death veligers.

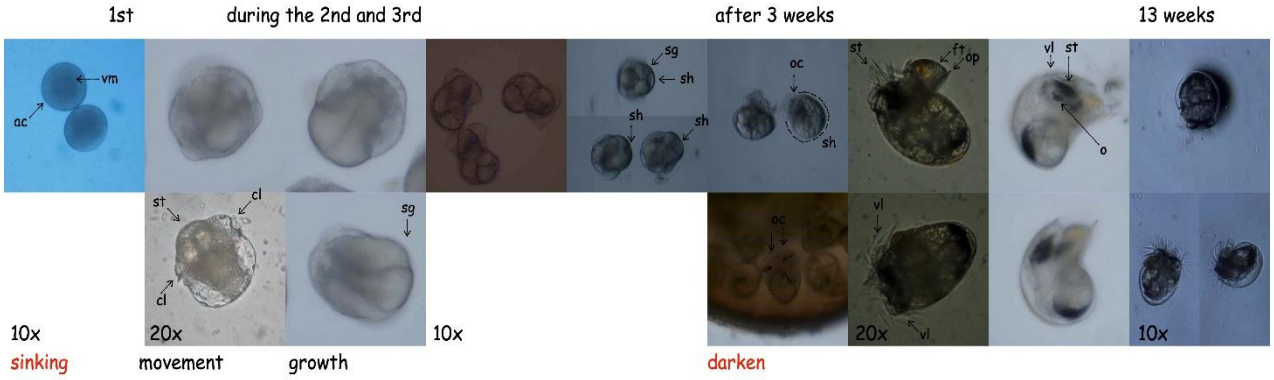


Figure 4: Morphology of *Neritina turrita Gmelin 1791* embryos: Light microscopy of early embryos - after day 5 following completion of the epiboly (ac, apical cells - the ectoblast covering the macromeres during the epiboly; vm, vegetal macromeres), early and late trochophores (st, stomodeum; cl, cilia; sg, shell gland; sh, shell), early and late veligers (oc/o, ocelli; vl, velar lobe; sh, shell; st, stomodeum; ft, foot; op, operculum).

The mature veliger has a length ~ 165-176 um and a diameter of ~ 110-122 um (Fig. 5B). The size of the developing embryos before and after epiboly, late trochophores and early veligers was compared with the size of mature veligers (Fig. 5). The veliger's volume was approximated to the volume of an ellipsoid, and calculated to ~ 0.0010-0.0014 mm^3 (0.0010448-0.0013709 mm^3).

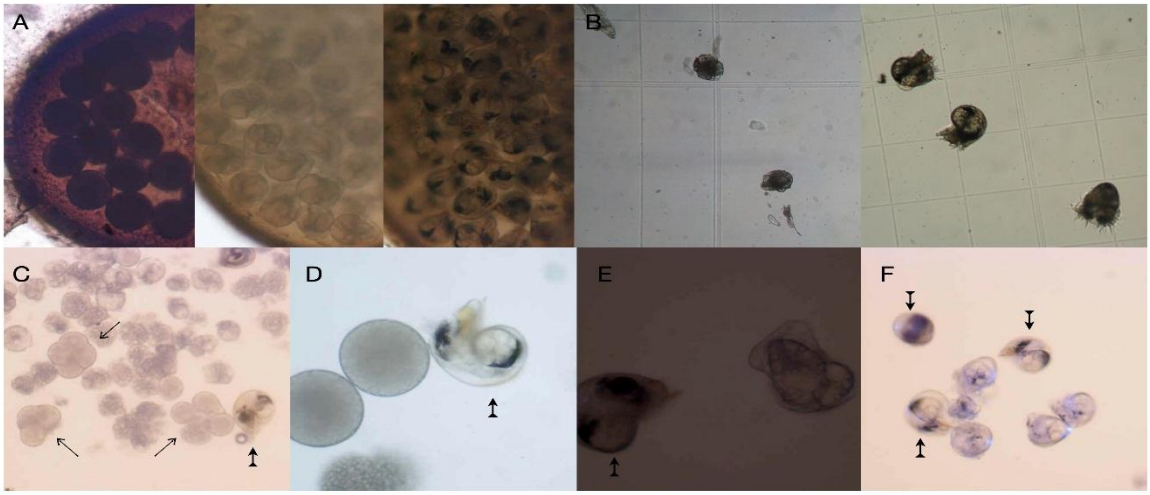


Figure 5: *Neritina turrita Gmelin 1791* embryos size: A) The size of the early embryos (after sinking), trochophores (after movement), and veligers (after darkenning) looks similar. B) Fuchs-Rosenthal counting chamber was used (250 um is the length of the small square's side) to determine the size of the trochophores (length ~110.8 um) and the veligers (length ~165-176 um and diameter of ~110-122 um). C) Mature veligers were mixed with early embryos - the spiralian apical micromeres and the underlying macromeres are visible. D) Mature veligers were mixed with early embryos - after completing the epiboly. E) Mature veligers were mixed with late trochophores - there are no distinct eyes and shell. F) Mature veligers were mixed with early veligers - visible eyes and shell.

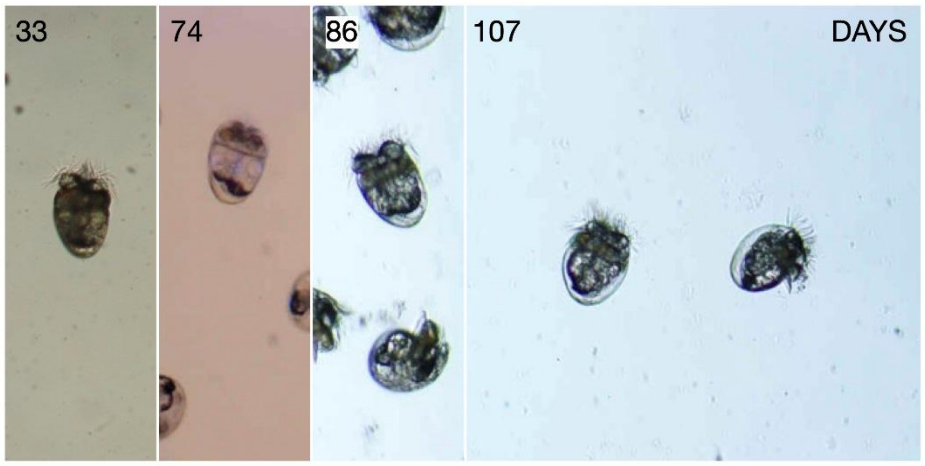
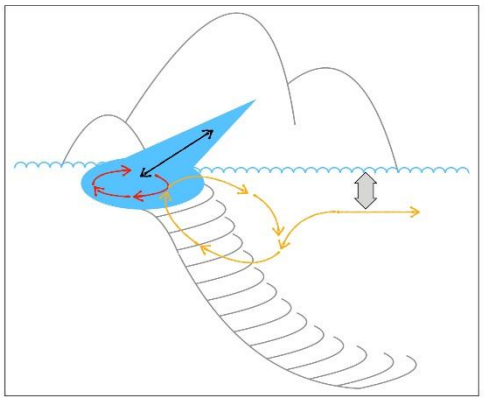


Figure 6: Viable *Neritina turrita Gmelin 1791* veligers were obtained between days 33 and 107 but after day 86 signs of cachexia due to undernourishment are present.



buoyant water depth (m)								
	ro ~1.077 g/ml				ro ~1.5 g/ml			
salinity (ppt)	30°C	25°C	20°C	15°C	30°C	25°C	20°C	15°C
0	22	22	21	20	255	310	480	-
5	21	21	20	19	260	310	460	-
17	19	18	17	17	275	313	415	1405
20	18	17	17	16	280	315	410	1055
30	16	15	15	14	300	320	385	645
34	15	14	14	13	305	320	375	570
40	14	13	13	12	320	325	360	495

Figure 7: The proposed model for *Neritina turrita Gmelin 1791* veliger development: A) Growth and maturation in the estuarine environment (red arrows), and the dispersal in the ocean (yellow arrows). The black arrow depicts the adult habitat. B) The approximate buoyant water depth in meters at which the veligers float, with density approximated to the density of blood lymphocytes (~1.077 g/ml), and the hydrated cellulose (~1.5 g/ml) (http://www.csgnetwork.com/water_density_calculator.html; Millero et al., 1980).

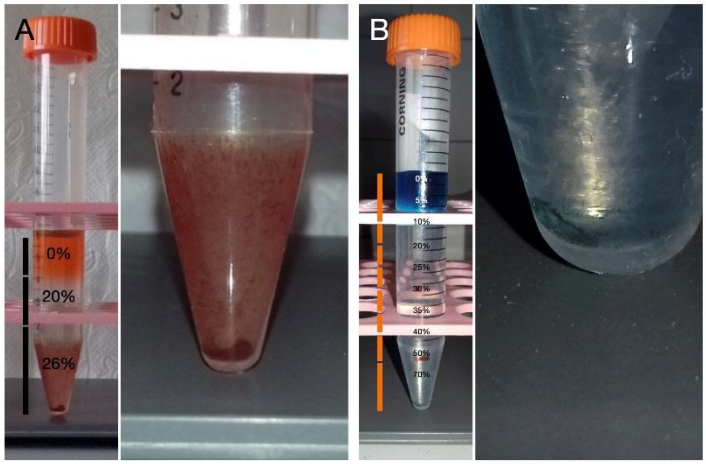


Figure 8: Density gradient centrifugation: A) Murine blood (erythrocytes) and pieces of tissue paper, stained with eosin were laid over a 20/26% sodium chloride density gradient, and centrifuged at 400 g for 30 min at 20°C. 20% and 26% NaCl have densities of 1.1453 and 1.1944 g/cm^3, respectively. B) *N. turrita* veligers were stained with malachite green and laid over a 5 - 70% sucrose density gradient, and centrifuged at 400 g for 30 min at 20°C. 20% and 70% sucrose have densities of 1.0809 and 1.3471 g/cm^3, respectively. Reference densities: lymphocytes - 1.077 g/ml; erythrocytes - 1.110 g/ml; hydrated starch - 1.3 g/cm^3; hydrated cellulose - 1.5 g/cm^3.

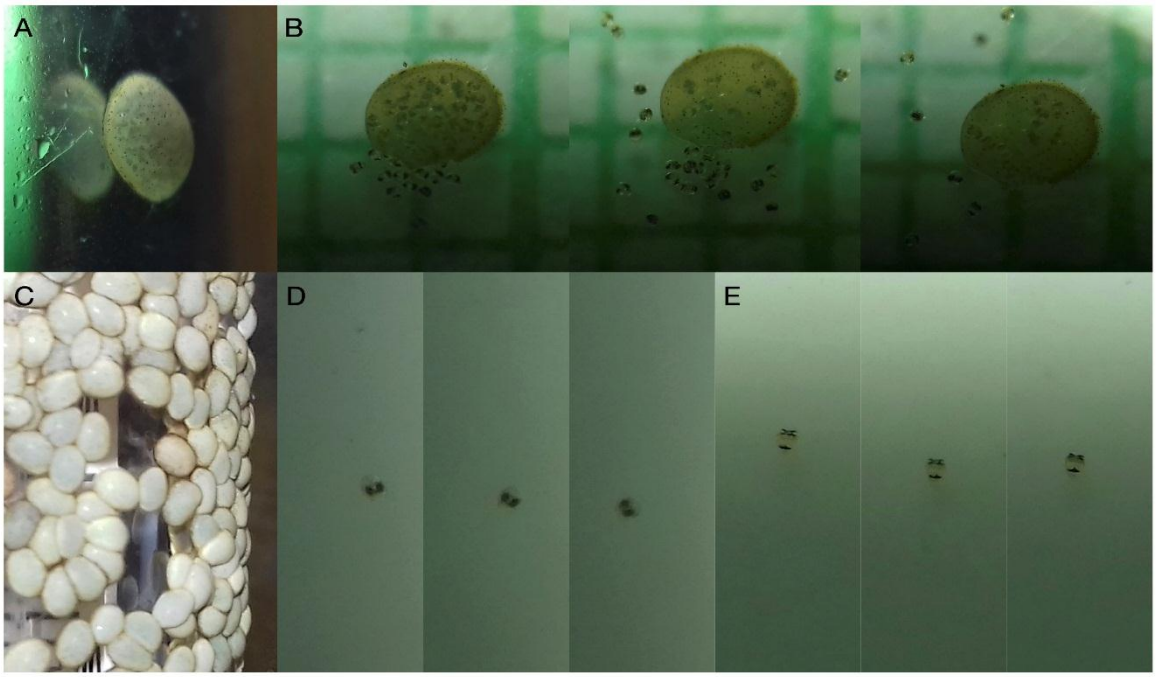


Figure 9: *Neritina turrita Gmelin 1791* egg capsule (A) and veligers (B) actively leaving the egg capsule 85 days after deposition. C) Egg capsules were kept in 5 g/L saline water at 25°C. *N. turrita* veliger hovering in 5 g/L saline water (D, above; E, side view).

If the density of the veligers was comparable to this of the lymphocytes (1.077 g/cm^3), the buoyant depth should have been ~15 m. Sucrose and sodium chloride density gradient measurements (Fig. 8) suggest much higher density values - probably in the range of these of glycogen, starch and cellulose (1.3 - 1.5 g/cm^3). The veligers pelleted after 30 min, 400 g, 20°C in 70% sucrose (1.3471 g/cm^3) (Anton Paar, 2022) and 26% sodium chloride (1.1944 g/cm^3) (Simion et al., 2015). Thus, suggesting a much deeper buoyancy of ~300 m (see Fig. 7). The density gradient procedure was controlled with erythrocytes (murine blood) and cellulose (tissue paper). Although the density of murine erythrocytes is suggested as 1.110 g/cm^3 they go through the 26% sodium chloride layer (1.1944 g/cm^3), suggesting a higher density number of ~1.3471 g/cm^3 (70% sucrose).

DISCUSSION

Usually, planktotrophic veliger larvae develop from small eggs (120-256 um), while larger eggs (240-540 um) produce either craw-away juveniles or short-lived non-feeding pediveliger larvae. Generally, the species with planktotrophic larvae hatch at a shell length of 220-500 um, and direct developers hatch at a shell length of 700-3000 um (Henry et al., 2010). *N. turrita*

veligers hatch at about 170 um following a month-long intracapsular development. During the 1st week of development, the overall size decreases, and growth is observable after the early trochophore stage. Spiral cleavage (obvious from the 3rd through 5th cell division) is a form of early embryonic development that occurs widely within the lophotrochozoan superphylum. Initial differential cell divisions in a radially symmetric pattern result in forming the quiescent macromeres (forming the vegetal pole) and the faster dividing micromeres, forming the animal pole. Later, the micromeres stop to divide and spread over the macromeres, converging at the vegetal pole. A process termed epiboly. Subsequently, the animal-vegetal axis bends, forming the definitive dorsal and ventral ectoderm. The birth of 4d mesentoblast marks the 28-cell stage, marking the definitive median plane that gives rise to a bilateral (left and right) pair of mesodermal and endodermal stem cell lineages. (Goulding, 2009; Henry et al., 2010). The mediolateral blastopore closure forms the protostomes (mouth and anus) and the differentiation of the ciliary band into prototroch (and adoral ciliary zone, Metatron and telotroch) (Nielsen, 2012). Later the trochophore transforms into a veliger with a through the gut. Some of the first neurons are detected in a structure known as ASO, the apical sensory organ, linking it to veliger's velum and foot, providing the sensory input necessary for settlement and metamorphosis (Croll, 2009; Nielsen, 2012).

The veliger's shells are moulds of polysaccharides (chitin), calcite, aragonite and proteins, making them heavier, suggesting that during their migratory journeys, they probably travel on or below the edge of the photic zone (200 m). The dysphotic zone in the ocean, where photosynthesis is very limited or not possible, will restrict their diet to bacteria, fungi, and decaying organic matter. Prokaryotes make up 59% of the ocean microbiome. The cell concentrations in ocean waters vary between 10^4, and 10^5 - 10^6 cells/mL when in bloom (Cui et al. 2019). Temperature, dissolved oxygen and light have stronger effects than nutrients or salinity. Vertical stratification is present. There is a reduction of dissolved oxygen from 6.87 mg/ml at 30 m to 4.3 mg/ml at 150 m, and temperature - from 28.4^{o}C at 30 m to 20^{o}C at 150 m. While there is an increase in both taxonomic and functional richness with depth, the cell abundance differs between different studies (Cui et al., 2019; Sunagawa et al., 2015; Sripan et al., 2021). *Poteobacteria* dominate the oceans (68%), mostly *Piscirickettsiaceae* (12.3%), followed by *Bacteroidetes* (11.3%). Planktonic microbes are classified into free-living (like *SAR11* and *SAR86*) and particle-associated bacteria (like *Bacteroidetes*, *Planktomycetes*, *Verrucomicrobia*). *Alphaproteobacteria* (*SAR11*, *SAR116*), *Deltaproteobacteria* (*Helieaceae*) in the soluble fraction and *Cyanobacteria* and *Planctomycetaceae* in the particulate fractions are found in the surface layer. In contrast, *Oceanospirillales*, *SAR406*, and *Salinisphaeraceae* in the soluble fraction and *Xanthomonadalaes*, *Desulfobulbaceae*, and *Desulfobacteraceae* in particulate fractions are more enriched in the bottom layer. *Bdellovibrionaceae*, obligate predators, and *Desulfobulbaceae* and *Desulfobacteraceae*, anaerobic sulfate-reducing bacteria, are enriched on the marine particles (Cui et al., 2019; Sripan et al., 2021). Photosynthetic cyanobacteria (*Prochlorococcus* and *Synechococcus*) are found in the sinking particles in the mesopelagic zone (1%) (Sunagawa et al., 2015).

Food concentration is critical for the successful maintenance of suspension feeders. For example, food concentrations above 15 x 10^4 cells/ml lead to decreased feeding rates due to the rejection of *Crepidula fornicata Linnaeus 1758* and *Crepipatella fecunda Gallardo 1979* larvae (Henry et al., 2010). Further, the growth and development of the miniature shrimp *Caridina multidentata Stimpson 1860* zoea might be able to help find the right conditions: live *Tetraselmis suecica* (3.5 - 25 um algae) and *Brachionus plicatilis* 210 - 235 um rotifers (fed on *Nannochloropsis* spp. 2 - 8 um algae) are the chosen nourishment (Hamasaki et al., 2020; Kondo et al., 2021). The marine gastropod *Tritia reticulata Linnaeus 1758* veligers have been successfully reared using *Nannochloropsis* spp. and artificial dry food containing *Spirullina* powder (*Arthrospira* spp.) and 5 - 10 um single-celled fungus *Saccharomyces cerevisiae* (Zupo and Patti, 2009). *Crepidula fornicata* larvae that are food-limited metamorphose at smaller sizes. Further, in the absence of appropriate cues for settlement, *C. fornicata* larvae will continue to grow (pre-competent for up to 11 days) and delay the metamorphosis for up to 16 days. The larvae will eventually metamorphose spontaneously. Delayed metamorphosis does not affect the juveniles' growth or survival. Further, competent larvae can be induced to metamorphose by excess K+ and dibromomethane. Depletion of L-DOPA, chlorpromazine, R(+)-Sch-23309, spiperone and nitric oxide can alter metamorphosis (Henry et al., 2010). *Neritina turrita* veligers (following induced hatching) are maintained in 17 g/L pH 8.2 saline water (Fig. 9). Veligers do not entrap on the water surface, ruling out the need for hexadecanol as an agent to prevent entrapment. Both temperature and salinity have been shown to affect larval feeding, survival and development. Along the different foods, the effect of differential salinities and temperatures on larval survival is being studied at the moment.

CONCLUSIONS

Neritina turrita Gmelin 1791 can be maintained and reproduced successfully in artificial conditions. More extended embryonal development (compared with *Clithon corona Linnaeus 1758*) was observed, the monitoring steps of the observable egg capsule changes determined, and related to the morphological stages of the developing embryos. Intra-capsular survival of the late veliger ranges from 33 to 107 days. Veliger's density suggests a buoyant depth of ~300 m, indicating that during their migratory journeys, they travel on or below the edge of the photic zone (200 m). The dysphotic zone in the ocean will restrict their diet to bacteria, fungi, and decaying organic matter. Therefore, the essence and concentrations of veliger's diet and the appropriate temperature and salinity are critical for their maturation to metamorphosis, survival and growth in artificial conditions.

Acknowledgements

The author would like to express his gratitude to Prof. N. E. Lazarov and Ms D. Brazicova for their help during the acquisition of the results in the Department of Anatomy, Histology and Embryology, Medical University - Sofia, Sofia, Bulgaria, and to Prof. S.

Hayrabedyan and Dr. M. Mourdjeva (Institute of Biology and Immunology of Reproduction, Bulgarian Academy of Sciences, Sofia, Bulgaria) for the assistance during the density gradient centrifugation, and Prof. G. Branch (Department of Biological Sciences, University of Cape Town, South Africa) for the valuable suggestions.

Author's contributions

The author is the only contributor to the work presented in this manuscript and the manuscript itself.

Conflict of Interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Funding information

The work presented here has been privately funded.

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