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LARVAL AND EARLY JUVENILE DEVELOPMENT OF *Tegula eiseni* (JORDAN, 1936) (GASTROPODA: TROCHIDAE)

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ABSTRACT. Larval and early juvenile development was studied in *Tegula eiseni* (Jordan, 1936) for 63 days under laboratory conditions at temperatures of 20 ± 2°C in order to have a photographic sequence of the stages that help identify wild early juvenile specimens. Larvae were obtained by induced spawning. Postlarvae and juveniles were fed *Nannochloropsis oculata* and *Phaeodactylum tricornutum*. Elapsed time from fertilization to veliger was 2 days. All larvae settled by day 4. Development of the teleoconch began on day 12. Juveniles (570 ± 60 µm long) had a teleoconch with 11 longitudinal ribs on day 51. On days 58 through 63, the umbilicus and shell spiral provided juveniles with adult-like morphological characteristics (610 ± 60 µm long). We conclude that the identification of early juveniles of this and other associated gastropods coming from wild populations should be performed by selecting those specimens that show a teleoconch in advanced stages to assure a correct identification.

Keywords: Development, early juvenile, larvae, *Tegula eiseni*

Desarrollo larvario y primeros estadios juveniles de *Tegula eiseni* (Jordan, 1936) (Gastropoda: Trochidae)

RESUMEN.Se estudió el desarrollo larvario y primeros estadios juveniles de *Tegula eiseni* (Jordan, 1936) durante 63 días en condiciones de laboratorio, a temperaturas de 20±2 °C, para obtener una secuencia fotográfica que ayude a identificar los primeros estadios juveniles de especímenes silvestres. Las larvas fueron obtenidas por desove inducido. Las postlarvas y juveniles fueron alimentados con *Nannochloropsis oculata* y *Phaeodactylum tricornutum*. El tiempo transcurrido desde la fertilización hasta la etapa veliger fue de 2 días. Las larvas se asentaron al día 4. El desarrollo de la teleoconcha inició en el día 12. Los juveniles (570±60 µm de talla) presentaron una teleoconcha con once costillas longitudinales en el día 51. Entre los días 58 a 63, el ombligo y la espiral de la concha provee a los juveniles de las características morfológicas de adulto (610±60 µm de longitud). Concluimos que la identificación de juveniles tempranos de este y otros gasterópodos asociados que provienen de poblaciones silvestres, debe de realizarse seleccionando aquellos especímenes que muestren una teleoconcha en estados avanzados de desarrollo, a fin de asegurar una correcta identificación.

Palabras clave: Desarrollo, juvenil inicial, larva, *Tegula eiseni.*

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INTRODUCTION

The banded snail *Tegula eiseni* (Jordan, 1936) is a trochid gastropod inhabiting rocky shorelines of the central, eastern Pacific, from the lowest ebb tide to 18 m deep in the subtidal kelp forest from Monterey, California U.S.A. to Bahía Magdalena, Baja California Sur, México (Morris *et al*., 1980; Keen, 1971). Along the coastline of Baja California, *T. eiseni* is a common species of the rocky community reefs associated with abalone (*Haliotis* spp.) and a variety of other gastropod species like *Megastraea* (= *Astraea*) *undosa* (Wood, 1828), *Megathura crenulata* (Sowerby, 1825), *Fissurella volcano* (Reeve, 1849), and species of *Tegula funebralis* (Adams, 1855) and *T. aureotincta* (Forbes, 1852) (Guzmán del Próo *et al*., 1991). In the central part of the Baja California peninsula *T. eiseni* is one of the dominant species (Guzmán del Próo, unpublished data).

Studies carried out in Baja California on the microhabitat of rocky reef gastropods that focused on the settlement and juvenile recruitment of more conspicuous species (Carreón-Palau *et al*., 2003) have required to identify early life stages of *T. eiseni* from field samples. However, identification of these stages on this and other gastropods has proved to be difficult because of the few available descriptions on reproduction and early development of the members of the family Trochidae. Studies on the genus *Tegula* refer to descriptions of five species: *T. excavata, T. brunnea, T. angiostoma, T. funebralis,* and *T. rustica* (Morán, 1997; Kulikova & Omel'yaneko, 2000). From these, the most complete descriptions available are for *T. funebralis* from the west Pacific coast (Morán, 1997; Guzmán del Próo *et al*., 2006) and *T. rustica* from the Sea of Japan (Kulikova & Omel'yaneko, 2000).

In order to contribute to the identification of the early development stages of gastropods in-

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habiting the rocky reefs of Baja California, the authors conducted culture experiments in the laboratory to induce spawning and larval development of the most common gastropods of the rocky community like *Megastraea undosa* (Guzmán del Próo *et al*., 2003), T*egula funebralis* (Guzmán del Próo *et al*., 2006), *Fissurella volcano* (Reynoso-Granados *et al*., 2007), and *Megathura crenulata* (in preparation). This paper describes morphological changes in laboratory-cultured larvae and early juveniles of *Tegula eiseni*, one of the most common species of *Tegula* that inhabit the western coast of Baja California.

MATERIALS AND METHODS

Collection and maintenance of specimens

Two hundred adults of *T. eiseni* (shell height 14.5 ± 0.5 mm, basal diameter 19.3 ± 0.9 mm) were collected in the rocky subtidal bottom at Los Morros, Bahía Tortugas, B.C.S., México (27.7°N and 114.9°W). The snails were wrapped in several layers of the giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh 1820 and transported to the laboratory in a cooler to maintain adequate moisture. Interior temperature was 10 °C. In the laboratory, specimens were divided into five groups of 40 snails; each group was placed in a 40 L plastic aquarium with 1 µm filtered seawater and kept at 20 ± 2 °C under constant aeration and salinity of 37–39 psu. The snails were fed rehydrated kelp leaves. Water and food were replaced every two days.

Gonad conditioning and induced spawning

Of the total capture, 15 snails were sacrificed to determine gonad maturation. All were immature. To obtain optimum gonad development, snails were fed *ad libitum* with rehydrated kelp leaves and kept at 20 ± 2 °C for 60 days. During this period, the gonadal condition was monitored every 15 days by sacrificing 10 snails. The specimens were dissected and gender was determined by the color of the gonad (cream-colored males and moss green-colored females). Gamete ripeness was determined by the shape of oocytes and sperm motility when examined under a compound microscope. Mature oocytes had a spherical form and mature sperm had active motility.

When specimens were mature, different techniques were tested to induce spawning, including thermal shock (Loosanoff & Davies, 1963; ASTM, 1980), electric shock (Iwata, 1951), and air exposure (Galtsoff, 1964). Because these techniques failed to achieve spawning, we tested a combined method that included freshwater shock, exposure to air, and rising temperature. In this method, 15 snails were placed in a 40 × 70 × 30 cm plastic container with freshwater. Immediately after exposure, freshwater was discarded and the snails were exposed to air for 3 h. The container was filled with seawater at 20 ± 2 °C and the temperature was gradually raised to 26 °C over a period of 3 h, which was maintained until spawning and fertilization took place after 12–14 h. In some trials, females spawned first; in others, males did. This technique was successful to obtain new gametes when needed. Polyspermy was avoided using less than seven spermatozoids per oocyte (Monsalvo-Spencer *et al*., 1997).

Sieving of Embryos and Larvae

Embryos up to the benthic stage were kept in 32 × 47 × 29 cm fiberglass containers filled with seawater. Embryos were sieved at the gastrula stage using 150, 100, and 70 µm pore Nytex mesh, while larvae were sieved every 48 h during the experiment, using 500, 330, 236, and 160 µm pore mesh. Postlarval and juvenile snails were fed the microalgae *Phaeodactylum tricornutum* (Bohlin, 1897) and *Nannochloropsis oculata* (Droop & Hibberd, 1977) in a 1:1 ratio. Both species were grown in f/2 medium (Guillard & Ryther, 1962).

Seawater temperature in the aquaria was maintained at 20 ± 2 °C with salinity of 37–39 psu during the development of larvae and early juveniles. The temperature was closer to 20-23 °C, which occurs during the spawning season of *T. eiseni* in wild conditions (Velez-Arellano *et al*., 2009). Morphological changes were monitored and recorded with a video camera attached to a microscope. Size (major axis of the shell) was calculated as the mean and SD from five observations. The assay finished at day 63 when the juveniles showed adult-like morphological characteristics.

RESULTS

Once spawning and fertilization occurred, the embryonic, larval, and postlarval stages were continuously monitored. The following description identifies the prominent features during early development. All the length measurements are referred to maximum shell length.

Embryonic development

Day 1. Diameter of unfertilized oocytes was 129 ± 2.5 µm. Oocytes were covered in a membrane extending their diameter to 165 ± 5 µm. The space between an oocyte and the membrane was 15 µm. The fertilized egg was bright green and retained this color through the larval stage. The first polar body developed at 30–35 min (Fig. 1A); the second polar body formed at 40–45 min (Fig. 1B).

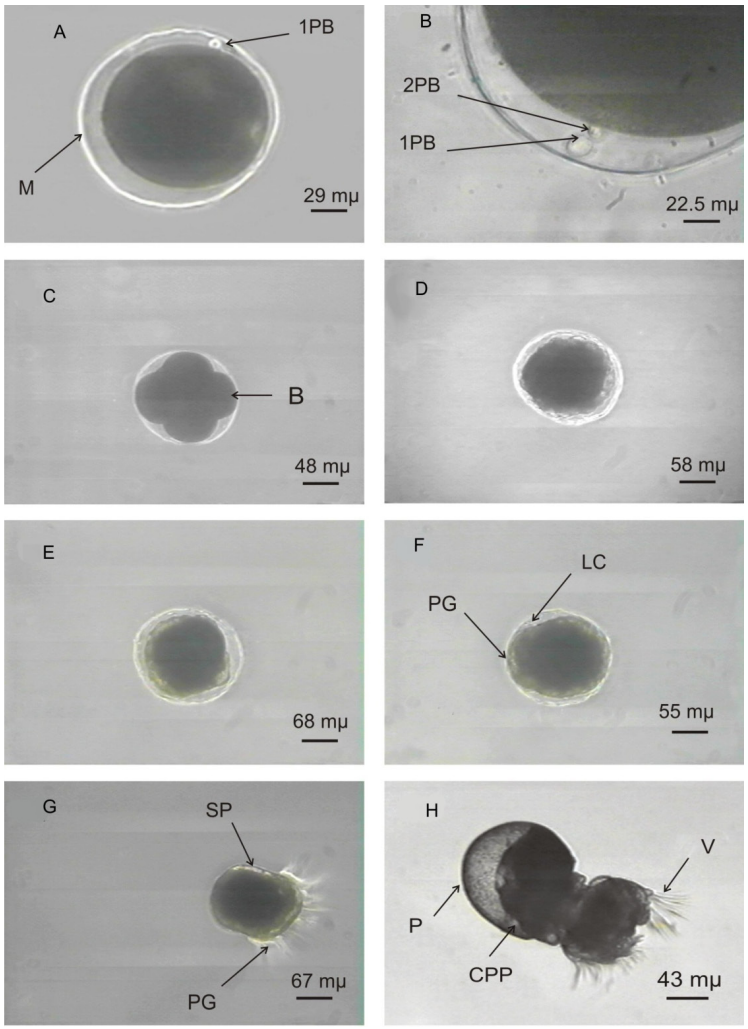

Figure 1. Development stages in *Tegula eiseni*. A and B, Egg; C, Second cleavage; D, Blastula; E, Ciliate gastrula; F, Encapsuled trochophore; G, Free-swimming trochophore; H, Membrane-free early veliger. Key: 1PB= first polar body, M= membrane, 2PB=second polar body, B= blastomere, PG= prototrochal girdle, LC= tuft of lateral cilia, SP=secretion of protoconch, PG= prototrochal girdle, P= protoconch, CPP= cephalo-pedal primordium, V= velum.

First cleavage occurred at 50–56 min after fertilization, forming two blastomeres of equal size. Second cleavage took place at 1:15–1:30 h, giving rise to four blastomeres (Fig. 1C). The morula formed at 3–3:47 h having a diameter of 145 ± 5 μm. Blastula formed at 4:40–4:45 h; embryo size was unchanged (Fig. 1D). Ciliated gastrula with a diameter of 150 ± 10 μm was first observed at 6:30–7:00 h (Fig. 1E). Embryonic trochophore developed at 8:30–9 h and was 155 ± 15 μm long; most of it remained enclosed by the embryonic membrane. As the embryo elongated, the prototrochal girdle began to develop at one end, and two tufts of lateral cilia formed at its base (Fig. 1F). During this stage, at 12–13 h, some larvae were able to break through the membrane with spinning movements and ciliary activity and remained suspended in the water column. Length was 160 ± 10 μm. The protoconch formed around the larva, except in the area of the prototrochal girdle (Fig. 1G).

Early veliger occurred at 15–16 h and was 165 ± 5 μm long. Velum and cephalo-pedal mass primordium was observed. Most larvae were still enclosed by the membrane at this stage. The protoconch covered the entire body except the velum which had not withdrawn into the shell. Membrane-free early veligers were observed at 21 h, length 190 ± 5 μm (Fig. 1H).

Day 2. The veliger stage occurred between 34–36 h, and the torsion process began. Veligers were 195 ± 5 μm long. Cephalo-pedal mass showed retractile movements, with the operculum already formed. The velum was retractile and split into two lobes (Fig. 2A).

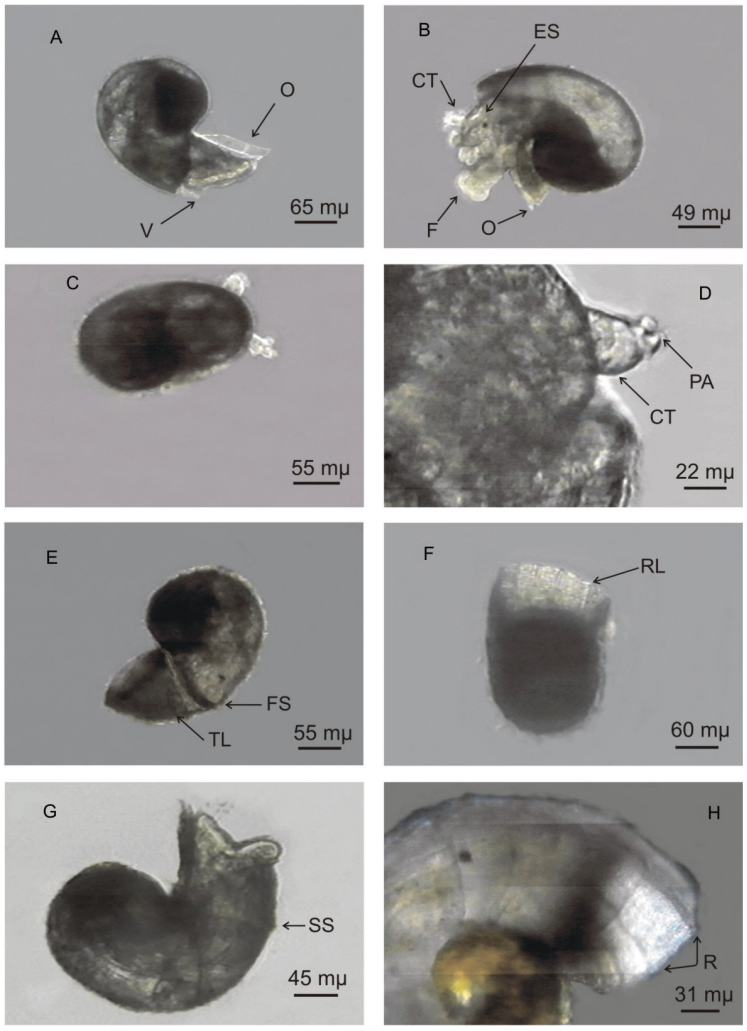

Figure 2. Development stages in *Tegula eiseni*. A, Veliger; B, Late veliger; C- G, benthonic post-larva; H, Early juvenile. Key: CT= cephalic tentacles, ES= eyespot, F= foot, FS= first suture, O= operculum, PA= papillae, R= ribs, RL= new rib lines, SS= Second suture, TL= teleoconch, V= velum.

The veliger stage occurred at 44–48 h; veligers were 195 ± 5 μm long. Eye spots were present. Velum cilia began to detach, starting metamorphosis. Larvae exhibited exploratory movements in search of attachment substrates, at times crawling and then returning to the water column.

Day 3. Late veliger stage. Protoconch size unchanged; cephalic tentacle primordia became evident. Foot and operculum were prominent. Remnant tufts of velum cilia were still present but had slight motility (Fig. 2B).

Benthic phase

Day 4. Postlarvae were 197 ± 8 μm long. All larvae had settled and began to feed (fig. 2C).

Day 5. Postlarvae size unchanged. Cephalic tentacles with papillae (Fig. 2D) were present.

Day 12. Postlarvae were 225 ± 25 μm long. Development of teleoconch began; a suture remained between the teleoconch and the protoconch (Fig. 2E).

Day 15. Postlarvae were 250 ± 30 μm long. Six ribs began to form as thin longitudinal lines on the anterior margin of the teleoconch (Fig. 2F).

Day 16. Postlarvae were 250 ± 30 μm long. The teleoconch continued to grow and a second suture was present (Fig. 2G).

Juveniles

Day 19. Early juveniles were 285 ± 15 μm long. Longitudinal ribs were more conspicuous and new ribs started developing as delicate

lines on the lateral edges of the teleoconch. First whorl was formed with an oval-shaped aperture (Fig. 2H). Metamorphosis was completed.

Days 35–37. Early juveniles were 430 ± 50 µm long. Second whorl formed, rising in a dextrogyrate direction; its growth bordered the exterior rim of the first whorl. The organism as a whole took on a conical shape; a hollow occurred at the center of the whorls, which gave rise to the umbilicus of the shell (Fig. 3A).

Day 42. Early juveniles were 505 ± 25 µm long. Cephalic tentacles had 12–15 papillae on each one (Fig. 3B). Four transverse sutures were conspicuous on the teleoconch (Fig. 3C).

Day 51. Juveniles were 570 ± 60 µm long. Teleoconch had 11 longitudinal ribs. Two fully whorls were formed; open umbilicus was now conspicuous with a diameter of 40-60 µm (Fig. 3D).

Days 58–63. Juveniles were 610 ± 60 µm long. Third whorl developed. Diameter of umbilicus was 60–80 µm, and shell spiral provided juveniles an adult-like morphology (Fig. 3E).

Table 1 and Figures 1 to 3 summarize the various developmental stages and structures described above. The average growth rate was 7.7 µm·day^{-1} (Fig. 4).

DISCUSSION

During gonad conditioning and testing of the different techniques to induce spawning, the snails showed the typical clustering that is displayed by many trochids just before spawning (Hickman, 1992; Kulikova & Omel'yanenko, 2000), except when they were stimulated with

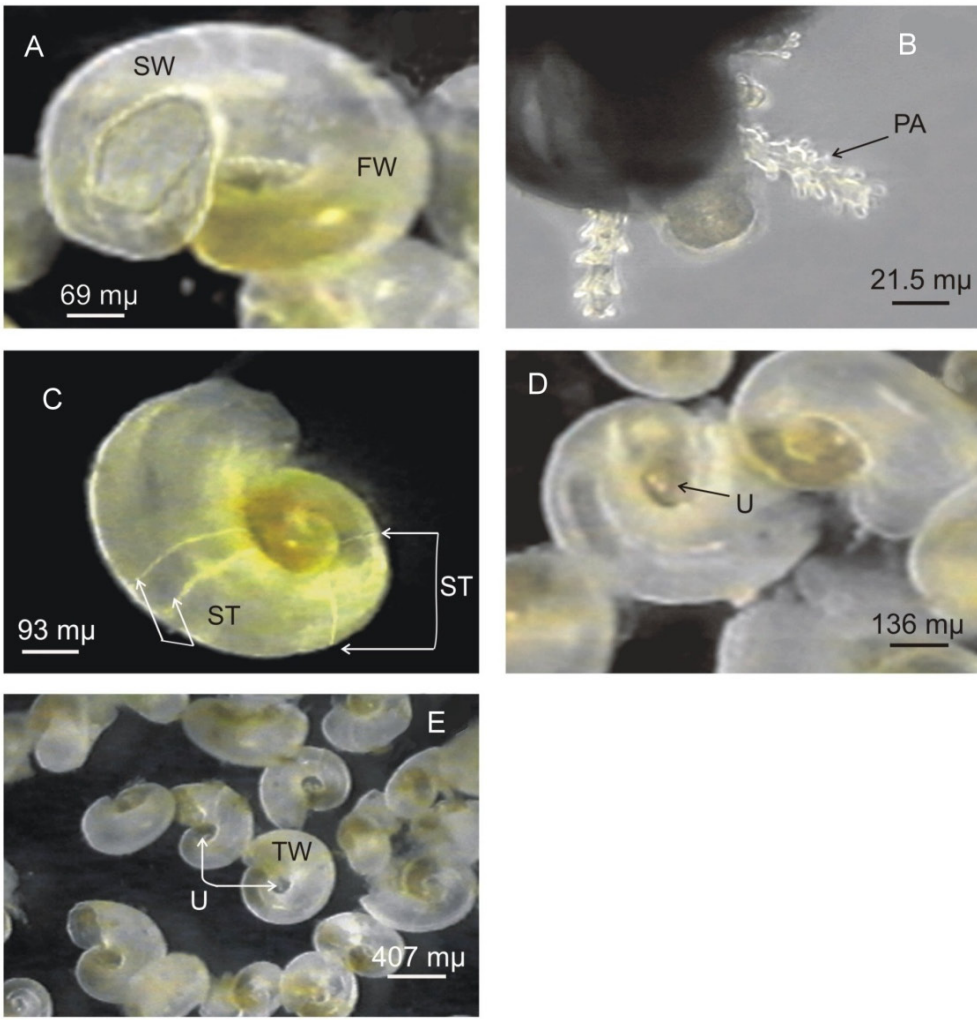

Figure 3. Development stages in *Tegula eiseni*. A-E, juveniles. Key: FW= first whorl, PA= papillae, ST= teleoconch sutures, SW= second whorl, TW= third whorl, U= umbilicus.

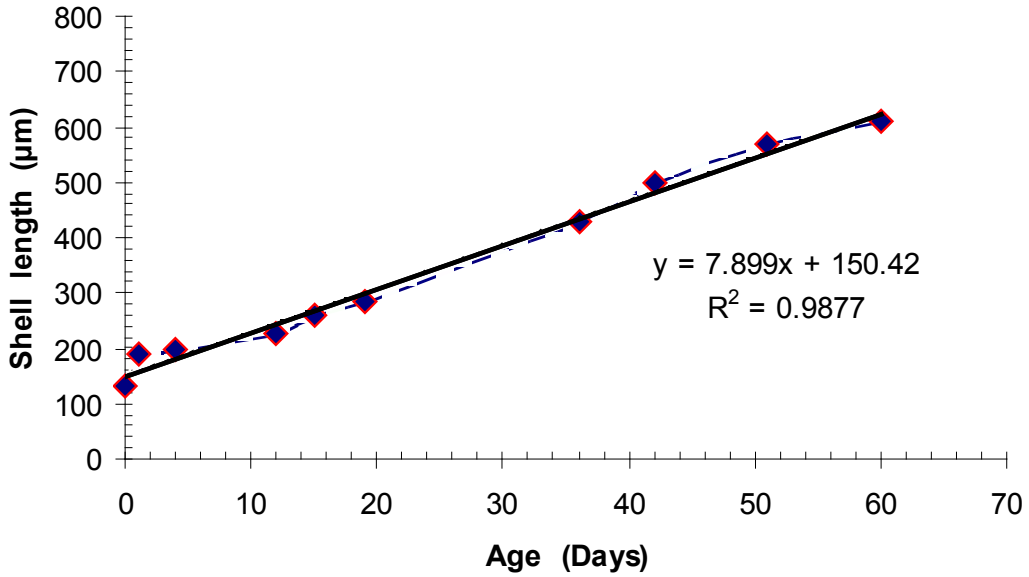

Figure 4. Larval and juvenile growth of *Tegula eiseni*. Day 0 corresponds to the fertilized oocyte. ♦ = mean (± SD) of 5 measurements.

freshwater. In the latter case, specimens exhibited slow travel movements at the beginning of the stimulus, remained motionless after this, and did not form clusters. It is difficult to ascribe this change in behavior to a single factor, but it was most likely a response to the freshwater procedure to induce spawning since the specimens remained separated after all inductions using this technique. However, this behavior should be confirmed in future trials.

The family Trochidae contains species that deposit benthic egg masses and species that broadcast spawn their gametes (Hickman, 1992). In this study we found that *T. eiseni* broadcast spawn their gametes as *T. funebralis* does (Morán, 1997; Guzmán del Próo *et al*., 2006). But female gametes of *T. funebralis* have very fragile membranes that break when manipulated (Guzmán del Próo *et al*., 2006), while the gamete membrane in *T. eiseni* is more resistant to handling. The membrane is lost at different times in related species: in *T. rustica*, it disappears just after fertilization (Kulikova & Omel'yanenko, 2000) and during the trochophore stage in *T. funebralis* (Morán, 1997; Guzmán del Próo *et a*l., 2006). In our experiment, the membrane in *T. eiseni* disappeared at the veliger stage.

Embryonic development up to the veliger stage took 3 days in *T. eiseni* and 4–7 days in *T. funebralis* (Guzmán del Próo *et al*., 2006; Morán, 1997). *T. eiseni* reached the settlement stage within 4 days. For example, *T. funebralis*, *T. rustica*, and *Cantharidus callichroa callichroa* did not begin settlement before 6–8 days (Ho Sun & Yun Hong, 1994; Morán, 1997; Kulikova & Omel'yanenko, 2000; Guzmán del Próo *et al*., 2006). These differences in development rate may account for the temperature of each experiment, since development time is dependent on temperature (Leighton, 1974; Strathman, 1987; Kulikova & Omel'yanenko, 2000). Embryonic and larval development of *T. eiseni* is morphologically similar to the development of the species that we have studied, *Megastraea undosa*, *Fissurella volcano*, and *T. funebralis* (Guzmán del Próo *et al*., 2003, 2006; Reynoso-Granados *et al*., 2007). Thus, differences between these species can be observed until secretion of the teleoconch occurs.

The fine details of the teleoconch of gastropods, which include form and surface striations on the shell in addition to growth lines and ornamentations, are important in the identification of larvae and pre-juveniles of gastropods (Fretter & Pilkington,1971). For instance, in *T. eiseni* the teleoconch is tubiform, spiral-shaped, and extends toward the anterior part of the shell, as it occurs in *T. funebralis* and *M. undosa*, while in *F. volcano* the teleoconch is fan-shaped and extends toward the posterior region. In early juveniles of *T. eiseni* and *T. funebralis* very fine longitudinal striations are formed on the anterior edge of the teleoconch, which become longitudinal ribs in juveniles. In *T. eiseni* 11 ribs were observed, while in *T. funebralis* the number of ribs was 7 to 8 (Guzmán del Próo *et al*., 2006).

Table 1. Development time in the banded snail, *Tegula eiseni* from embryo to juvenile under laboratory conditions at 20 ± 2 °C

STAGE	TIME
Oocyte	0
Egg with first polar body	30–35 min
Egg with second polar body	40–45 min
First cleavage (2 blastomeres)	50–56 min
Three cells (two blastomeres and one polar lobe)	1–1:10 h
Second cleavage (4 blastomeres)	1:15–1:30 h
Morula	3–3:47 h
Blastula	4:20–4:45 h
Ciliate gastrula	6:30–7 h
Encapsuled trochophore, prototrochal girdle, tufts of lateral cilia	8:30–9 h
Free-swimming trochophore	12–13 h
Early veliger (with membrane)	15–16 h
Membrane-free early veliger	21 h
Veliger (operculum, velum split into two lobes)	2 days
Late veliger, eyespots, velum cilia are detaching	2 days
Late veliger, tentacle primordium	3 days
Benthic stage.	4 days
Postlarva, tentacles with papillae	5 days
First teleoconch suture	12 days
Onset of 6 longitudinal ribs	15 days
Second teleoconch suture	16 days
Early juvenile, first whorl fully formed; aperture is oval-shaped; formation of new ribs	19 days
Second whorl (dextrogyrous), umbilicus begins to form	35–37 days
Juvenile, tentacles with 12–15 papillae; 4 transverse sutures on teleoconch	42 days
Two full whorls, 11 ribs, and open umbilicus 40–60 µm diameter	51 days
Development of third whorl. Open umbilicus 60-80 µm in diameter.	58–63days
Adult-like appearance	

In adults, the umbilicus is open in both species at early stages, but it is closed in *T. funebralis* after juveniles reach 3 mm in size (Morán, 1997), while in *T. eiseni* it remains open during its life.

However, in spite of all the characteristics here described, the identification of *T. eiseni* at early stages remains difficult to separate from *T. funebralis*, except when early juveniles have completed their development; for example, the number of striations in the teleoconch is evident and the presence of an open or closed umbilicus becomes a conspicuous and definitive character. Therefore, we conclude that for microhabitat studies or experiments with artificial collectors for settlement studies (Ventura-López, 2007), the identification of early juveniles of *Tegula* species and other associated gastropods should be done further of early stages, and preferably with specimens that show a teleoconch in advanced stages to assure a correct identification.

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