Duration of Intracapsular Development of *Zidona dufresnei* (Gastropoda: Volutidae) at its Southern Distributional Limit

Author(s): Andrea Roche , Matías Maggioni , Alejandra Rumi and Maite Narvarte
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RESEARCH NOTE

Duration of intracapsular development of *Zidona dufresnei* (Gastropoda: Volutidae) at its southern distributional limit

Andrea Roche[1], Matías Maggioni[1], Alejandra Rumi[2,3] and Maite Narvarte[1,3]

[1]Instituto de Biología Marina y Pesquera Almirante Storni, Universidad Nacional del Comahue. San Antonio Oeste, Río Negro, Argentina.

[2]División Zoología Invertebrados, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires, Argentina.

[3]Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

Correspondence, Andrea Roche: andrearoche@ibmpas.org

Abstract. *Zidona dufresnei* Donovan, 1823 is an endemic snail of the southwestern Atlantic Ocean. In San Antonio Bay, Río Negro Province, it is commonly found in the intertidal zone all year round and from October to April the females deposit planoconvex egg capsules attached to hard substrates. The population of *Z. dufresnei* studied is an exception because it is unique in that inhabits shallow waters. The main goal of this study was to determine the duration of the direct intracapsular development of *Z. dufresnei* in the field. Results show that the intracapsular development takes 34.5 ± 3.8 days. In late developmental stages, a mean of three embryos per capsule was observed. Developmental duration under natural conditions was shorter than in lab conditions previously studied. The shorter developmental period than that reported for other temperate neogastropods may be related to the high summer water temperatures and high salinity at the location studied. Shorter embryonic duration would be important for this population of *Z. dufresnei* which inhabits an environment of high predation pressure on egg capsules.

Key words: endemic snail, shallow waters, direct development, egg capsules, field observations.

Many marine gastropods enclose their embryos inside elaborated egg capsules mostly without parental care. Egg capsules of this group show broad morphological variations (Gallardo 1979, Leiva *et al*. 1998, Penchaszadeh *et al*. 1999, Nasution 2003, Naegel and Gomez del Prado Rosas 2004, Bigatti 2005, among others), and, jointly with their respective embryonic stages, were described for several South American neogastropods (Penchaszadeh 1971a, b, 1988, Penchaszadeh and de Mahieu 1976, Penchaszadeh and Rincon 1996, Penchaszadeh and Miloslavich 2001, Bigatti 2005).

The volutid *Zidona dufresnei* Donovan, 1823 occurs from Rio de Janeiro (Brazil, 22°S) to San Matías Gulf (Argentina, 42°S), occupying sandy or silty-sandy substrates from 5 to 110 meters depth (Giménez and Penchaszadeh 2003, Carranza *et al*. 2008). Particularly, in San Antonio Bay, the southern distributional limit of this species (Fig. 1), adults (with individual shell size up to 120 mm while at other sites they may reach over 200 mm) are found in a quite small channel, in shallow waters with maximum depths of 4 m during low tide, on bottoms mainly comprised of sandy substrates with boulders and sponges (Roche *et al*. 2011). At this site every summer, *Z. dufresnei* has been supporting an artisanal fishery for more than 30 years (Narvarte *et al.* 2007).

Individuals of *Zidona dufresnei* spend most of their time buried, and the females have to dig themselves up to deposit the egg capsules on the substrate. Like other neogastropods (Rawlings 1999, Uyan and Aral 2003), after leaving the oviduct the egg capsule is transferred to the foot for attachment. The capsule is fixed to a benthic substrate such as mollusc shells or pebbles (Penchaszadeh and de Mahieu 1976, Pereyra *et al*. 2009), after which the soft egg capsule acquires a lenticular convex shape and solidifies (hemi-elliptic-shaped, whitish and 21 mm maximum diameter). The reproductive period extends from October to April. Our preliminary observations and those from Pereyra *et al*. (2009) indicate that (1) no more than six embryos develop within each capsule, (2) the capsule walls become transparent as embryos feed on the capsular fluid which allow the visual observation of the embryos/juveniles inside at late developmental stages, and (3) at the size of about 1 cm length, the shell is well developed and embryos hatch. Roche *et al*. (2011) identified predators of egg capsules which can contribute to high rates of capsule loss in the field.

With the exception of the studies conducted by Penchaszadeh and de Mahieu (1976) to describe some morphological characteristics of the egg capsules and Pereyra *et al*. (2009) in San Antonio Bay (41°S) to describe egg capsule maturation

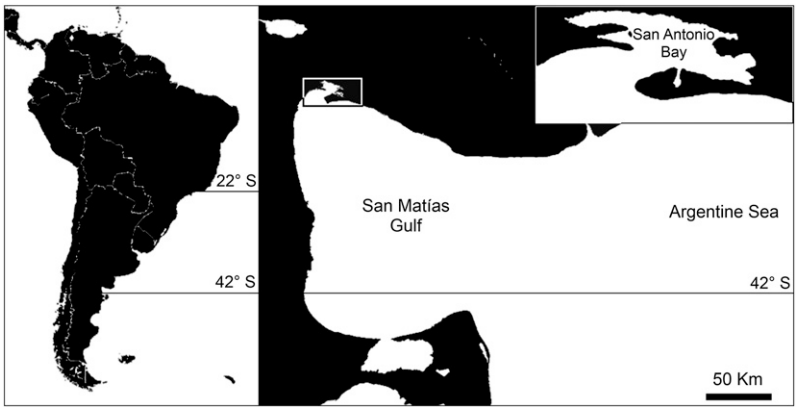

Figure 1. Location of the study site in San Antonio Bay, within San Matías Gulf, Argentina.

stages, the embryonic development of this species has been scarcely studied. Development time in the field is not reported for most species and it is almost always based on lab-based estimates. In this study, our central aim was to determine the duration of intracapsular development in the field and discuss our results with studies mostly carried out under lab conditions.

This study was carried out in an internal channel of San Antonio Bay (40°43.6′S, 64°55.1′W) (Fig. 1), commonly visited by fishermen and tourists. The tides are semidiurnal, with maximum amplitude of 9 m (Schnack *et al.* 1996). Salinity in this bay is highly variable, commonly higher than 37 pps in the summer (Bas *et al.* 2005). The surveys were carried out at sites where density of *Zidona dufresnei* was relatively high (0.91 ± 0.51 ind/m^2) (Roche *et al.* 2011). Besides *Z. dufresnei*, the dominant macroinvertebrate fauna includes crabs (*Neohelice granulata* Dana, 1851 and *Cyrtograpsus angulatus* Dana, 1851), octopuses (*Octopus tehuelchus* d'Orbigny, 1834), gastropods (*Tegula patagonica* d'Orbigny, 1840; *Buccinanops globulosus* Kiener, 1834 and *Crepidula* spp.), bivalves (*Brachidontes rodriguezii* d'Orbigny, 1842; *Glycimeris longior* Sowerby, 1833 and *Pitar rostratus* Koch, 1844), chitons (*Chaetopleura isabellei* d'Orbigny, 1841) and a variety of polychaetes.

During the summer of 2008 and 2009, 42 and 19 egg capsules were collected, respectively, at the same time, between 0.5 and 3.0 m depth by snorkeling during low tide. Egg capsules were classified according to their developmental stages (Table 1) following Pereira *et al.* (2009). In 2008 both E0 and E1 capsules were obtained, but in 2009 only E0 capsules (with females still associated with them), were collected. The capsules with their substrates (pebbles) were fixed (using two-component adhesive putty) to a concrete plate (30x30 cm^2) and placed on the sandy bottom at low tide (Fig. 2). In 2008, two plates were installed containing 25 and 16 egg capsules, respectively, separated by 2 m from each other. In 2009, 19 capsules were placed on the same plate. Daily or every other day, each plate was observed to check the developmental stages of the embryos, and to record the number of embryos/juveniles per capsule. The duration of each developmental stage was then estimated.

In the field, a sampling of egg capsules was simultaneously performed with the concrete experimental study. Intact and broken capsules were recorded along a transect 100 m long. Broken capsules were examined to determine whether they had been attacked by predators or developed embryos had hatched naturally. If capsules were empty but had been breached all the way into the capsule chamber, they were considered as opened by predators. Such capsules were identified by distinctive bite marks left on the capsule walls (Roche *et al.* 2011). Sea water temperatures were registered along the study period using an underwater probe.

During 2008, among the 42 egg capsules monitored only 5 (14.3% of a total of 16 juveniles) reached the hatching stage after a mean of 33.8 days (*SD* = 3.9). A high percentage (69.1%) was consumed (Fig. 2b); from the consumed capsules (*N* = 29), 18 (62.1%) corresponded to stage E1, 6 (20.7%) to E2 and 5 (17.2%) to E3. Some egg capsules (16.7%) were entirely lost from the pebbles attached to the concrete plate (Fig. 2c). The number of embryos/juveniles per capsule varied from 1 to 5 (mean = 2.9; *SD* = 0.9).

During 2009, from the 19 egg capsules studied, only 3 reached the hatching stage (15.8% of a total of 8 juveniles) after a mean of 35.3 days (*SD* = 3.5). Losses of egg capsules constituted 36.8%. In this season, 47.4 % of the egg capsules were consumed, 55.5% of them corresponding to advanced stages (E3) and 44.5% to early ones (E1). The number of embryos/juveniles per capsule varied between 2 and 3 (mean = 2.64; *SD* = 0.5).

The early developmental stages were brief taking from 13 to 16 days to reach the coil veliger and 3 more days to reach

Table 1. Description of the egg capsule developmental stages (adapted from Pereyra *et al.* 2009)

STAGE	DESCRIPTION
E0– E1	whitish and capsule wall still soft, with or without the female still there, respectively
E2	capsule wall tough and fluid with large clear areas
E3	transparent fluid, embryos clearly visible
E4	capsule with a hole or slit-like hatching opening, with or without embryos

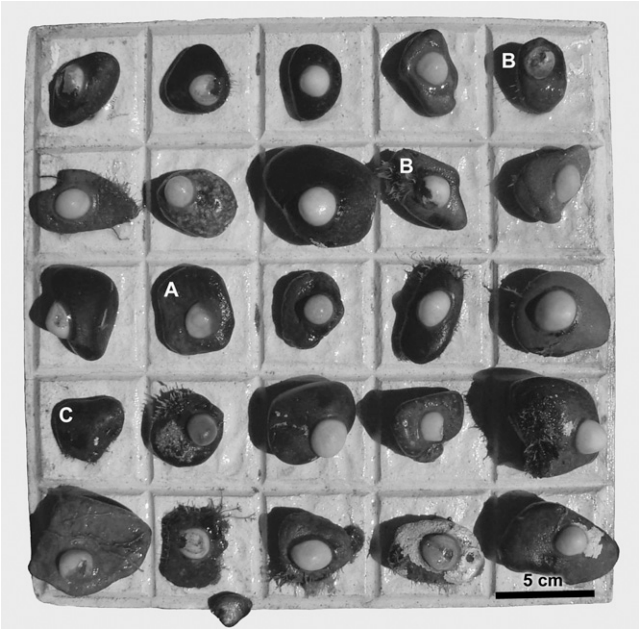

Figure 2. Photograph of the concrete plate showing: **A**, veliger stage, **B**, consumed, and **C**, lost capsules (one individual of *Tegula patagonica* d'Orbigny, 1840 can be observed at the bottom of the concrete plate).

the juvenile stage (with the typical form and shell coloured as adults). The mean number of days since the evident slit-like hatching window was 4.6 days (range = 2–9 days; *SD* = 2.37; *N* = 6 egg capsules; Table 2). The embryonic development within each egg capsule was synchronous, however differences in size of the veligers were observed visually through the transparent capsule wall but not measured quantitatively. There were no statistical differences in the overall hatching time between years, although there were statistical differences in the time from E2 to E3 stages (t-test: $t_7 = 2.82$, $P < 0.05$), and to arrive at coil veliger stage (t-test: $t_{13} = 4.84$, $P < 0.001$) (Table 2).

Mean water temperatures varied from 20.05 °C (January) to 21.0 °C (March) in 2008 and from 23.3 °C (January) to 20.1 °C (March) in 2009. The highest recorded temperature was 26.5 °C in January 2009.

A high predation rate was evident, by the presence of capsules particularly injured, throughout the breeding season. Percentages of consumed capsules on the developmental peak (December to February), calculated from wild observations, were less than a half of those calculated for the experimental concrete plate (Fig. 3).

This is the first study on the duration of developmental stages of *Zidona dufresnei* in the field. Under natural environment conditions juveniles *of Z. dufresnei* emerged after approximately 35 days from the egg capsules. Hatching time

Table 2. Mean (± *SD*) duration in days of the capsular stages observed throughout development of *Z. dufresnei* on the concrete plate placed in the internal channel of San Antonio Bay during the summers of 2008 and 2009.

STAGES	2008	2009
E0–E2	14.00 ± 5.66 (*N* = 2)	12.20 ± 1.64 (*N* = 5)
E2–E3	2.57 ± 0.53 (*N* = 7)	2.00 ± 0.0 (*N* = 6)
E3–E4	23.16 ± 3.82 (*N* = 4)	23.33 ± 3.51 (*N* = 3)
E0–E4	nd	35.33 ± 3.51 (*N* = 3)
To CV	12.62 ± 1.76 (*N* = 13)	16.00 ± 1.41(*N* = 8)
From CV to J	3.00 ± 1.76 (*N* = 7)	3.67 ± 0.82 (*N* = 6)

CV: coil veliger stage; J: juvenile ready to hatch; *N*: number of egg capsules observed; nd: no data.

was similar between study years, although there were some negligible differences in the time from E2 to E3, and to arrive at the coil veliger stage. This shorter developmental period than that reported for other neogastropods (Gallardo 1979, Leiva *et al*. 1998, Nasution 2003, Bigatti 2005) may be related to the high summer water temperatures (usually higher than 20 °C), as was also found for other species (Gallardo and González 1994, Naegel and Gomez del Prado-Rosas 2004) and to high salinity levels. Low salinities retard intracapsular development of *Stramonita haemastoma canaliculata* (Gray, 1839) (Roller and Stickle 1989) and *Concholepas concholepas* Bruguière, 1789 (Gallardo and González 1994, Naegel and Gomez del Prado-Rosas 2004). As salinity in San Antonio Bay during summer exceeds 36 pps, we suggest that high salinities may reduce the development of *Z. dufresnei* at this location. Depth, in relation or not with water temperature regime, may also play a role as was observed by Gallardo (1979) for muricacean gastropods.

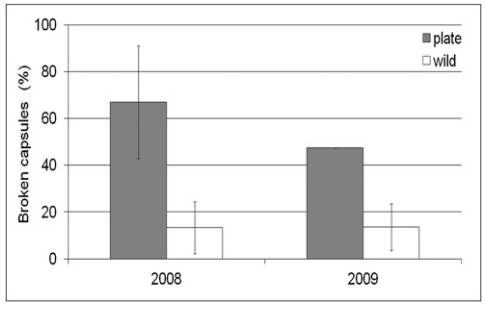

Figure 3. Comparison of broken (consumed) egg capsules (percentages) between the experimental concrete plate and observations in natural conditions (Error bars represent *SD*). Total numbers of capsules were: 64 and 78 for 2008 and 2009, respectively, in natural conditions; and 42 and 19, respectively, for the experimental concrete plate.

Pereyra *et al*. (2009) reported a mean developmental duration of 74 days for *Zidona dufresnei* under laboratory conditions (*i.e.*, constant aeration, regular change of water, salinity around 35–36 pps and temperatures between 16 and 22 °C; Pereyra, pers. comm). No information exists on the developmental duration of this species under field conditions in other locations of its distributional range to allow for intraspecific comparisons. The population of *Z. dufresnei* here studied is unique because it inhabits shallow waters, different from the other populations which live in deeper waters (Giménez and Penchaszadeh 2003, Carranza *et al.* 2008).

We observed 1 to 5 larvae/juveniles inside each egg capsule, similar to Penchaszadeh and De Mahieu (1976) who reported 2 to 6 in a northern population (38°20′S, 57°37′W), and Pereira *et al.* (2009), who observed 2 to 4 in the same area of the present study. Although this oviposition rate (as a proxy of fecundity) seems to be low, we do not know how many egg capsules are laid per female per season, or whether fecundity increases with age or size. The absence of parental care may be a determinant factor in the distribution of reproductive energy investment, with more energy investment in protective structures such as capsules walls and less energy devoted to the production of gametes (Perron 1981, Chaparro and Flores 2002).

In this study there were high numbers of lost and consumed egg capsules. Capsule predators, identified by Roche *et al.* (2011), were observed in direct contact with the egg capsules. Likely, the predation by chitons may explain the complete disappearance of the capsules, as was demonstrated under lab conditions (Roche *et al*. 2011). However, the effect of the concrete plate increasing concentration of predators should be considered in future studies focusing on predation patterns on egg capsules, since a higher predation rate was obtained for the plate (Fig. 3). Since predation appears to be an important source of embryo mortality during the encapsulated life of *Zidona dufresnei*, a shorter developmental duration as a defence against predators may be naturally selected. Performing field studies to estimate developmental duration seems to be important, considering the wide variations found between studies performed at lab and field, since in lab conditions not all parameters would be similar to those in nature.

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