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Research Article

Encapsulated development, spawning and early veliger of the ranellid snail *Fusitriton magellanicus* (Röding, 1798) in the cold waters of the Magellan Strait, Chile

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ABSTRACT. Field and laboratory study of egg masses, encapsulated development stages and early-hatched veliger larvae of the sub-Antarctic observations *Fusitriton magellanicus* (Röding, 1798) are described from samples collected in the Magellan Strait (Santa Ana Point: 53º38'15"S, 70º54'38"W), Chile, between 2005 and 2006. We aimed to determined if: i) if these gastropod shows a reproductive pattern development similar to low-latitude ranellids, and with respect to other sub-Antarctic locations within the Gondwanian distributional range (Australia, New Zealand, South America); ii) if *F. magellanicus* exhibit similar patterns as other Chilean ranellids; and iii) if *F. magellanicus* exhibit developmental attributes that define as long-distance broadcasters from cold water. *F. magellanicus* laid around 125 capsules/egg mass. Each contained an average of 2,789 ± 481 embryos, grouped in one circular arrangement. Mean eggs size was 180 µm. Encapsulated period lasted between 55 and 67 days at 10°C, and hatched larvae of 245 to 349 µm in shell length. Spawning occur during spring (October to November; 8°C) associated to an increment of freshwater discharge of San Juan River. A comparison of eggs/embryos/larvae abundance between temperate and tropical Ranellidae allow us to predict that *Fusitriton magellanicus* shows developmental attributes that indicate higher fecundity in relation to Chilean ranellids and that define it as a long-distance broadcaster.

Keywords: mollusc, gastropod, sub Antarctic benthos, seasonal reproduction, Ranellidae, Magellan Strait.

Desarrollo intracapsular, oviposturas y velígeras tempranas del caracol ranélido *Fusitriton magellanicus* (Röding, 1798) en aguas frías del estrecho de Magallanes, Chile

RESUMEN. Antecedentes de terreno y laboratorio fueron utilizados para describir las oviposturas, los estadios del desarrollo intracapsular y las larvas velígeras recién eclosionadas del gasterópodo subantártico *Fusitriton magellanicus* (Röding, 1798), recolectado en el estrecho de Magallanes, sector Punta Santa Ana (53º38'15"S, 70º54'38"W), Chile, entre el 2005 y 2006 para determinar: i) si este gasterópodo ranélido muestra un patrón reproductivo similar a aquellos ranélidos de bajas latitudes como en aquellas especies distribuidas dentro del círculo subantártico, dentro del rango distribucional Gondwánico (Australia, Nueva Zelanda, Sudamérica), ii) si *F. magellanicus* exhibe características del desarrollo similares a otros ranélidos de la costa de Chile, y iii) si *F. magellanicus* presenta atributos del desarrollo que lo puedan definir como una especie de aguas frías de alto potencial de dispersión. *F. magellanicus* deposita aproximadamente 125 cápsulas/ovipostura agrupadas en un círculo, cada una de las cuales contiene, en promedio, 789 ± 481 embriones. El tamaño promedio de los huevos fue de 180 µm. El desarrollo intracapsular duró entre 55 y 67 días (10ºC), eclosionando larvas cuya longitud de concha varió entre 245 y 349 µm. La producción de oviposturas ocurrió durante primavera (octubre a noviembre; 8°C) y se relacionó con un incremento en la descarga del río San Juan. El análisis comparativo de la abundancia de huevos/embriones/larvas entre especies de ranélidos de zonas tropicales y templadas, ha permitido postular que *Fusitriton magellanicus* presenta atributos del desarrollo intracapsular que indican una alta fecundidad y lo definen como una especie con gran potencial de dispersión larval.

Palabras clave: moluscos, gasterópodos, bentos subantártico, reproducción estacional, Ranellidae, estrecho de Magallanes.

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INTRODUCTION

Since the middle of the last century, the so-called Thorson's Rule (Mileikovsky, 1971) was consolidated as a generally accepted paradigm that predicts a latitudinal gradient for marine invertebrates from tropical to polar waters for modes of development. In essence, it describes the tendency of an egg to increase in size associated with a higher frequency of species with direct development *(i.e.*, lecithotrophic) as latitude and/or depth increase in the marine environment. Hence, both gradients involve a gradual decrease in temperature. Ecologically, the latitudinal change in the development type was attributed to a greater restriction on the availability of food for the planktotrophic larval type in colder waters. At the same time, low temperatures at high latitudes would be inappropriate for the development of pelagic larvae in the water column.

However, in recent decades, several studies have critically reviewed this paradigm, indicating that the predicted relationship between latitude and development has many exceptions and is more complex than expected (Pearse *et al.*, 1991; Arntz & Gili, 2001; Gallardo & Penchaszadeh, 2001; Poulin *et al.*, 2002; Pearse & Lockhart, 2004; Laptikhovsky, 2006; Bowden *et al.*, 2009). As this was reviewed in other invertebrate taxa, the original formulation of the rule (based mostly on gastropods from the northern hemisphere) was later replaced by one that instead predicted changes in the proportions of species with planktotrophic larvae to species with lecithotrophic larvae along these environmental gradients (Vance, 1973a, 1973b; Levin & Bridges, 2001 *fide* Laptikhovsky, 2006). In many Antarctic invertebrates, the development of pelagic larvae (many of lecithotrophic type) is more frequent than predicted by the model. Pearse *et al.* (1991) state that this frequent pelagic lecithotrophy in cold waters may be an adaptation to a combination of poor food conditions most of the year and slow rates of development. These authors also noted that, contrary to what is expected, some of the most abundant and widespread Antarctic marine invertebrates have pelagic planktotrophic larvae, which take a long time to complete their development.

These studies have also shown that whether the trend predicted by Thorson's Rule is confirmed also depends on the types of dominant taxa in certain latitudes and their particular evolutionary histories (or phyletic constraints) with respect to reproduction and development strategy. For example, in echinoids and bivalves, latitudinal gradients in development occur because predominantly incubating taxa dominate the southern ocean (Levin & Bridges, 2001). This trend is absent at the North Pole; therefore, direct development by incubation is not a phenomenon associated with polar conditions. Consequently, latitudinal gradients in patterns of larval development would not be an adaptation to low temperatures and low larval food supply, as supposed by Thorson's Rule. The abundance of brooders probably shows enhanced speciation under unique conditions in the Antarctic that did not occur in the Arctic (Pearse & Lockhart, 2004; Laptikhovsky, 2006). In the case of Antarctic invertebrates, Poulin *et al.* (2002) proposed distinguishing reproductive strategies that have developed on an evolutionary time-scale from those that could be explained by processes operating on an ecological time-scale. Thus, the high proportion of brooding species in Antarctic waters would correspond to species-level selection occurring over geological and evolutionary times, derived from climatic changes (glacial-interglacial episodes) experienced by the austral region since the Miocene, with negative consequences for broadcaster species, most of which would have become extinct. In contrast, the ecological dominance of some broadcasters occurring today would be the result of ecological processes associated with the advantage of having pelagic larvae under highly disturbed or with spatial heterogeneity conditions, facilitating interpopulation connectivity (Cowen *et al.*, 2007).

Similarly, when we considered gastropods from the Atlantic coast of South America (Gallardo & Penchaszadeh, 2001), the latitudinal gradient in development modes predicted by Thorson's Rule was not observed. The dominant taxa had evolutionarily lost their free-living larvae at the ancestral level; thus, the direct development type predominates. This may reflect a response to conditions on the South American Atlantic coast (*e.g.*, the predominant sandy bottom type, where families like Volutidae and Olividae and several Nassaridae of the genus *Buccinanops* have found suitable conditions for expansion).

As summarised by Bowden *et al.* (2009), the longest-standing paradigm of larval ecology has been that pelagic larvae are negatively selected at high latitudes, due to an apparent incompatibility of intensely seasonal primary production with extended larval development times at low temperatures. Now, however, the antecedents on which this prediction was based are being reviewed and show a complex relationship between larval strategy and cost of dispersion (Bonte *et al*., 2012).

Subantarctic waters of the Magellan Strait are particularly interesting for examining the reproductive strategies of marine invertebrates in high-latitude seas of the southern hemisphere, focusing on species that typically possess planktotrophic larvae. This is particularly the case for gastropods, which are an exception to the predictions of Thorson's paradigm. One of these cases in the subantarctic waters of the Magellan Strait is the ranellid snail, *Fusitriton magellanicus* (Röding, 1798). This species has a wide geographical distribution in the southern hemisphere; it lives on both coasts of South America, from Brazil to Chile's southern coast, where it reaches a northern limit of 36°S in the southeastern Pacific (Reid & Osorio, 2000; Osorio *et al.*, 2002). It has also been reported in New Zealand, East Southern Australia and off of New South Wales (Beu, 1998). This species inhabits subtidal waters to depths of 90 to 850 m (Olivier & Scarabino, 1972). It has pelagic larvae, presumably planktotrophic (Penchaszadeh & De Mahieu, 1975), which could drift a relatively large period in the plankton, if we consider that this is a typical feature of several species in this family, showing teleplanic larvae (Scheltema, 1971; Pechenik *et al.*, 1984; Laursen, 1981 *fide* Govan, 1995; Paulay & Meyer, 2006; Strathmann & Strathmann, 2007).

What adaptations does this gastropod have to keep planktotrophic pelagic larvae in latitudes where primary productivity is limited and highly seasonal, and where the water column tends to be homogeneous and dynamic and has supposedly unfavourable temperatures for its development (Antezana, 1999). A first approach is to examine key features of the reproductive strategy of this snail in the Magellan Strait area, where water masses originating in the Pacific, Atlantic and Antarctic oceans converge, and where local variations caused by the presences of rivers, glaciers and fjords that determine estuarine conditions exist (Dávila *et al*., 2002; Valdenegro & Silva, 2003; Silva & Palma, 2008). The present study examined the reproductive activity of *F. magellanicus* in an area of Magellan Strait, particularly its oviposition activity over two annual cycles of field observations. In the laboratory, we examined the intracapsular development (*i.e.*, the speed and duration of the process, the hatching stage that defines the mode of development for the species and the parameters of fertility achieved through this strategy). With this background, we established the reproductive timing that the species show in these latitudes and determined how the level of larvae production and their release into the environment could adjusts to the phytoplankton seasonality in the Magellan Strait, the temperature regime and other locally prevailing abiotic conditions.

MATERIALS AND METHODS

Study area

Santa Ana Point is located on the northeastern side of San Juan Bay in the Magellan Strait, Chile (Fig. 1), which is a very shallow embayment with a sandy bottom (<5 m depth, and covering a large section of the bay). In this embayment, freshwater discharge from the San Juan River flows with an average rate of 18.02 m^3 s^{-1}, decreasing the salinity to the river/sea junction (Fig. 2). Seasonally, the freshwater flow to the bay is reduced during the summer (6.3 to 9.4 m^3 s^{-1}); it is frozen in winter and achieves maximum values from September to October (spring in the southern hemisphere) of 29.0 to 32.7 m^3 s^{-1} (Cañete *et al*., 2008). The northern side of Santa Ana Point is characterized by the presence of steep rock walls and large boulders (Newcombe & Cárdenas, 2011).

Oceanography

During each sampling, temperature, salinity, density and transparency of water column were recorded. The first three variables were determined using an oceanographic probe or CTD (Sea-Bird Model 19), and the transparency was measured with a 30-cm diameter Secchi disk.

Spawning and brooding season

To determine the egg mass production period and a possible minimum size for reproductive (mature) animals, a census of ovigerous capsules per unit area (m^2) was conducted by scuba diving in different seasons (Spring: October 2005 and 2006, December 2005; Autumn: April; Winter: July and Spring: November 2006). Ovigerous capsules were counted, and the abundance and sizes of females were determinate. In the Ranellidae family, females tend to stay over the oviposition to protect them from predation) (Beesley *et al.*, 1998; Romero *et al*., 2003, personal observation). Additionally, the develop-

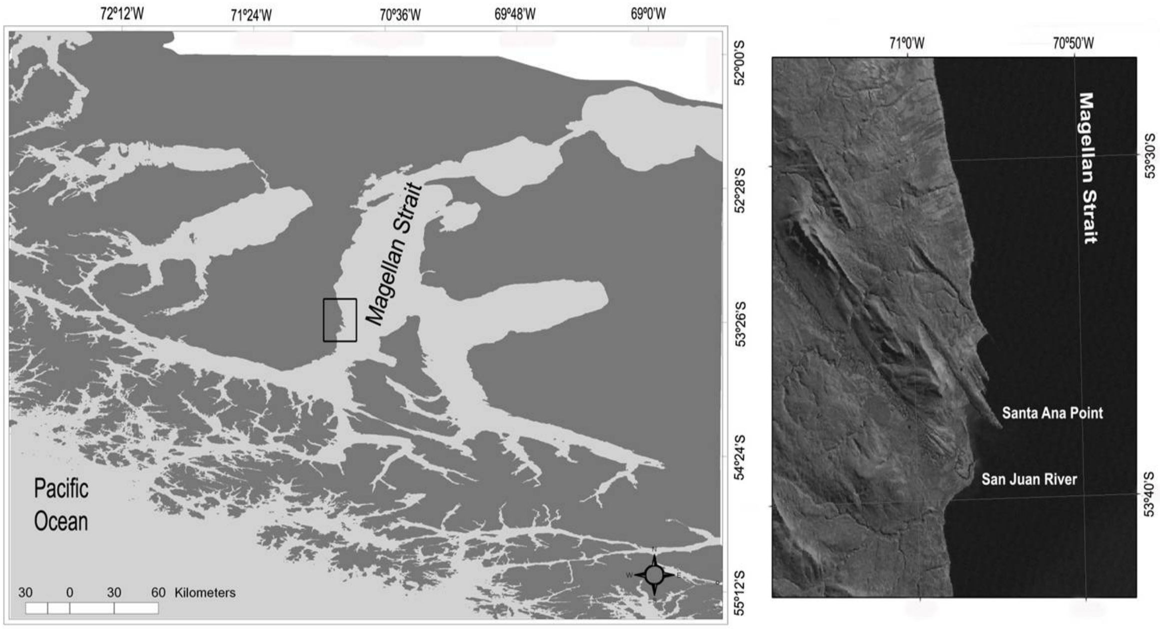

Figure 1. Location of Santa Ana Point, Magellan Strait, Chile, where adults and ovipositions of *Fusitriton magellanicus* was collected and zone where the mouth of San Juan is River located.

Figura 1. Localización de Punta Santa Ana, Estrecho de Magallanes, Chile desde donde se recolectaron individuos adultos y ovipusturas de *Fusitriton magellanicus* y zona donde se ubica la desembocadura del río San Juan.

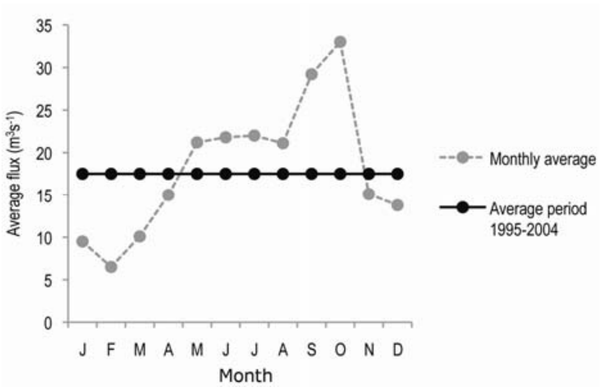

Figure 2. Monthly average flux of San Juan River (2005-2006). The river mouth is located 1.5 km off Santa Ana Point, Magellan Strait (1995-2004 data provided by Dirección de Aguas, Punta Arenas, Chile).

Figura 2. Caudal medio mensual del río San Juan (205-2006). La boca del río se localiza a 1,5 km de Punta Santa Ana (los datos del caudal del río San Juan 1995-2004, fueron provistos por la Dirección de Aguas, Punta Arenas, Chile).

mental stages of the ovipositions were determined to examine their degree of synchronisation or the simultaneity of production within the study population. The following criteria were used to determine the stage of development; a) yellow colour indicated early embryos, b) yellow/brown colour indicated mid-stage embryos, c) dark brown egg capsules indicated embryos near hatching, and d) empty egg capsules indicated recently hatched snails.

Egg masses: collection, laboratory rearing and study of encapsulated development

F. magellanicus egg capsules with embryos at different stages of development were carefully collected by Scuba diving from depths ranging from 5 to 25 m between November 2005 and October 2006 on the subtidal rocky bottom on the northern side off Santa Ana Point. The egg capsules were transported to the Mineduc Lab, Universidad de Magallanes, Punta Arenas, within plastic bags filled with seawater. In the laboratory, the egg capsules were classified according to developmental stage, and adult individuals were sexed and kept in small tanks (10 L) with filtered circulating sea water in a closed circuit within a conditioned hatchery (10°C) similar to the one used to keep breeding adults.

To determine the morphological changes experienced during development, 3-5 ovigerous capsules per oviposition were obtained daily in the first three days and weekly thereafter. The stages were photographed and identified by comparison with embryo-larval morphology criteria applied to other Ranellidae species, such as *Priene scabrum* (Romero *et al.*, 2003) and *Argobuccinum pustulosum* Gallardo *et al.*, in press); particularly the terms pre-trocophore and pre-veliger Gallardo *et al.*, 2012, were applied as used by these latter authors. Measurements of embryos and larvae (diameter, height or shell-length) were made using ProSeries Capture KIT MV™ (version 1.0 for Windows, produced by Cybernetic) coupled to a stereoscopic microscope. Over 100 embryos/larvae were measured per egg capsule. Mortality was minimal, and mortality-related changes in colour, such as the typical violet tone in muricid egg capsules, were not observed.

Once the larvae hatched from the capsules, the extent of the planktonic larval life under laboratory conditions was recorded. A total of six larvae samples were kept in 50 mL Erlenmeyer flasks and were fed with *Chlorella* sp. microalgae. In each flask, all hatched larvae per oviposition were included. Larvae naturally hatched from *F. magellanicus* egg capsules were collected with a 100 µm sieve and transferred to six aquaria (20 L capacity each) where they were maintained with 1 µm filtered seawater at 30 psu and at approximately 10°C. Larvae were fed daily *ad libitum* with *Chlorella* sp. Every two days, the water was replaced and a sample of larvae was collected to measure shell length. Rearing experiment of post-hatched bilobed larvae was extended by at least seven days.

Collection and maintenance of adult snails

A group of adult individuals were also collected by Scuba diving. These adults were transported to the laboratory, measured, weighed, sexed, separated in pairs and placed in aquaria with a closed circuit flow with weekly water replacement. They were kept in a cold room at a constant temperature (7°C in autumn-winter and 10°C in spring-summer), with photoperiods of 16:8 h darkness: day light in autumn-winter and 8:16 h in spring-summer. The animals were kept for almost a year and were fed weekly with pieces of the clam *Venus antiqua*. This adult snail took approximately 11 months after the collection to start laying ovigerous masses under laboratory condition.

RESULTS

Oceanographic conditions

The presence of oviposition of *F. magellanicus* in the study area coincided with the presence of estuarine, marine and diluted waters (Valdenegro & Silva, 2003), vertically homogeneous in terms of temperature, salinity and density. In periods without the presence of oviposition, the temperature and salinity fluctuated between 6 and 8°C, and 30.5 and 31.2 psu, respectively. Density was close to 24.5 Sigma-t (σ_t). During the snow melt, in the early spring, there was a significant increase in the average flow of the San Juan River (> 25 $m^3 s^{-1}$), that reduced the salinity to 29 psu and increased the water temperature between 9 and 10°C. The density varied slightly but did not exceed 25 σ_t. In contrast, during the summer, the river flow was significantly reduced.

In winter, the transparency of the water column enabled us to view the Secchi disk down to a depth of 7 m, while in spring it was only possible to detect the disk at a depth of no more than 3 to 4 m, which indicates a potential increase in primary production and/or an increase in the turbidity of the water column by sediments transported by the San Juan River (Fig. 2).

Reproductive cycle

Although the study did not provide a monthly analysis over both years at the study site, underwater observations allowed the identification of oviposition, and the months in which *F. magellanicus* began its reproductive activity. In both years, oviposition spawn occurred between October and November. During the egg-laying season, each female produced one egg mass, with an abundance that varied between 3 and 10 m^2 (Fig. 3). In December, all egg masses were empty, and many egg capsules remained attached to the rock with their apertures open. In autumn and winter, no egg masses were observed on the rocky bottom.

The females maintained under laboratory conditions, between September 2005 and November 2006, produced egg capsules after 11 months, which was in agreement with field observations made in October 2006 (Fig. 4).

Egg capsules

The lateral views of early and late *F. magellanicus* egg capsules are shown in Figure 5. The early stages are white-yellow, and the late stages are yellow-brown. The change in colour occurs during larval development, with the presence of trocophore larvae. The egg capsules were attached to the rocky substrate with a slope of >45° and were separated by almost 20 cm in instances where they were located together. The edges of the capsules were smooth, transparent and with no special architectural arrangements. In the field, brooding female sizes ranged between 75 and 87 mm in shell length (n = 11). A positive linear fit was found between the female size (LH) and the capsule height (AC (mm) = -0.6070 + 0.118 LH (mm) (r = 0.89, $P < 0.05$), and between LH and the number of ovigerous capsules (NC) (NC = -0.11 + 13.36 LH; r = 0.83, $P < 0.05$).

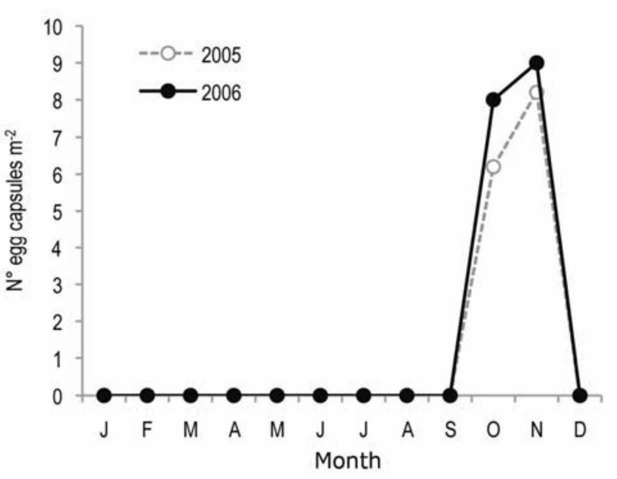

Figure 3. Seasonal production of ovipositions by the ranellid gastropod *Fusitriton magellanicus* in the rocky subtidal of Santa Ana Point, Magellan Strait, Chile.

Figura 3. Producción estacional de oviposturas por el gasterópodo ranélido *Fusitriton magellanicus* en un sector rocoso submareal de Punta Santa Ana, estrecho de Magallanes, Chile.

Larval production

Table 1 shows some quantitative aspects of the *F. magellanicus* reproduction and the encapsulated development to establish comparison with other Chilean ranellid snail. In *F. magellanicus* the maximum number of larvae was nearly 600,000 per egg mass. There was a positive linear relationship between LH (mm) and the total abundance of embryos per oviposition (NEM) (NEM = -0.21 + 4,500 LH, n = 11, r = 0.87, $P < 0.011$). Thus, the total production of capsules per oviposition ranged between 123 and 259, and the number of embryos per oviposition ranged between 291,510 and 593,887.

The difference between reproductive variables between both Chilean ranellids seems to be related to the shell size. *Fusitriton* is largest than *Priene*, having superior values of larval production, number and size of egg greater capsules. Egg size and hatchling size are relatively similar in both species.

Encapsulated development: embryo development

All eggs deposited in a capsule developed into embryos. No uncleaved eggs or nurse eggs were observed. The initial cleavage is spiral, and a spherical blastula is formed, with the yolky macromere-derived cell at the vegetal pole. Gastrulation is by epiboly and results in a rounded gastrula. The sizes of the embryo stages and the number of measures are shown in Table 2. Embryonic and larval stages of *F. magellanicus* are shown in Figure 5. The total encapsulated development lasted between 55 and 67 days, in which 17% of the total time involved the embryonic stages.

Encapsulated development: larval development

The different encapsulated larval stages observed during the study are shown in Figure 5. Larval development lasted nearly 38 days and finished with the hatching of all larvae, with approximately similar sizes and bilobed velum.

Pelagic larvae

After hatching, the larvae swam and fed in the water column for about seven days without attaining the size for metamorphosis into benthic juveniles. The larvae begin their pelagic life with an average shell length of 283 µm (sd = 22, n = 252), growing during this experiment to a length of 302 µm. The changes in larval size over the duration of this experiment under laboratory conditions are shown in Table 2. The shells are extremely thin, smooth, transparent and gently spiralled. During this experiment, no evidence of teleplanic larvae was observed. All larvae died simultaneously. An evident feature is the long cilia of larval lobes (Fig. 5).

DISCUSSION

Our findings contrasted with that reported for other Ranellidae, as discussed below. *F. magellanicus* is a snail with planktotrophic pelagic larvae. This is consistent with Penchaszadeh & De Mahieu (1975) suggestions for populations of the Atlantic coast of Argentina. According to predictions from Thorson's Rule, such a developmental mode is contrary to what is normally expected for marine gastropods inhabiting such high latitudes as the Magellan Strait. How could this apparent discrepancy be explained?

Thorson (1936, 1946, 1950), whose finding was later confirmed by Mileikovsky (1971), described a trend of increasing egg size and a non-planktonic, non-feeding development type with increasing latitude and water depth; both gradients involving a decrease in water temperature. Ecological explanations for this trend included restricted food availability for planktotrophic larvae in colder waters at high latitudes. Thus, pelagic larvae would be selected against, at these geographic locations, given an apparent incompatibility of intensely seasonal planktonic food availability with extended larval development times at low temperatures (reviewed by Pearse, 1994; Young, 1994; Pearse & Lockhart, 2004; Bowden *et al*., 2009). Without denying the validity of this trend in the

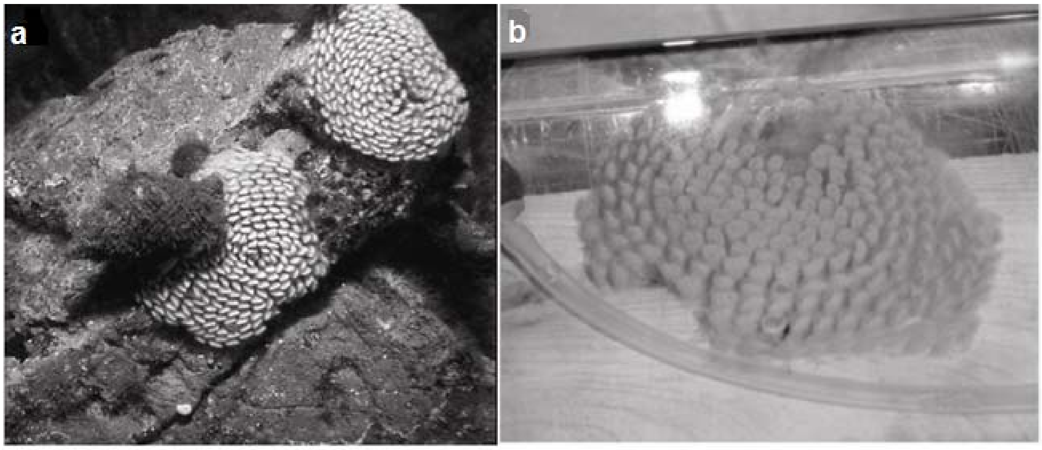

Figure 4. *Fusitriton magellanicus*. a) Female and oviposition photographed *in situ*, b) oviposition obtained under laboratory condition. Fig. 4a shows an 25 x 25 cm^2 area photographed on subtidal rocky reefs in from subtidal rocky shore of Santa Ana Point, Magellan Strait, Chile (Source: César Cárdenas).

Figura 4. *Fusitriton magellanicus*. a) Hembra y ovipostura fotografiada *in situ*, b) ovipostura obtenida bajo condiciones de laboratorio. La Fig. 4a muestra un área de 25 x 25 cm^2 de la zona rocosa submareal de Punta Santa Ana, estrecho de Magallanes, Chile (Fuente: César Cárdenas).

Table 1. Comparative encapsulated development of two ranellid gastropods from the Chilean coast: *Fusitriton magellanicus* and *Priene scabrum*. These data were used to estimate the larval production and potential fecundity in each species.

Tabla 1. Análisis comparativo del desarrollo intracapsular de dos especies de gasterópodos ranélidos de la costa de Chile: *Fusitriton magellanicus* y *Priene scabrum*. Estos datos fueron utilizados para estimar la producción de larvas y la fecundidad potencial en cada especie.

Parameters	*F. magellanicus*	*P. scabrum*
Mean shell size (mm)	90 ± 7	45
Egg diameter (um)	180 ± 20	170 ± 19
Number of egg capsules	179 ± 50	129 ± 46
Size of egg-capsules (mm)	5.1 ± 0.9	3.6
Egg capsule wide	5.1 ± 0.9	3.5 ± 0.4
Egg capsule height	9.6 ± 1.0	6.0 ± 0.7
Embryos per egg capsule	2,439	1,466
Duration of encapsulated development (days)	55 (8-9ºC)	38 (13ºC)
Hatching size (um)	296.2 ± 24.7	263 ± 13.7
Larvae per egg mass, average	436,664	189,114
Reference	This study	Romero *et al*. (2003)

development type in general (validated in some particular taxa of benthic invertebrates), this does not exclude the notion that some species with pelagic larvae (even planktotrophic larvae) are highly successful in these high-latitude cold waters (Pearse *et al*. 1991; Hain & Arnaud, 1992; Pearse & Lockhart, 2004; Peck *et al*., 2006; Bowden *et al*., 2009).

Such species seems to adopt reproductive strategies that suit them to such conditions or that, in some manner, allow them to bypass the limiting effects of the potential constraints mentioned above. In this sense, as is revealed in this study, *F. magellanicus* shows a marked seasonality in reproduction, restricting their reproductive events for the months that are more favourable in the Southern Ocean. The egg-masses laying that begins in October continues as embryonic development until November, just the period of the year when encapsulated

Table 2. Chronology of encapsulated development of *Fusitriton magellanicus* under laboratory conditions. Females collected in the Magellan Strait, Chile (September 2006).

Tabla 2. Cronología del desarrollo intracapsular de *Fusitriton magellanicus* bajo condiciones de laboratorio. Las hembras se recolectaron en el estrecho de Magallanes, Chile (septiembre 2006).

Stage	Size range (μm)	Average size and standard deviation of stage (μm)	Number of measurements	Time since egg mass laying (days)	Duration of each stage (days)
Egg	141-218	180 ± 19	192	0	2
Four cells	154-198	179 ± 12	150	3	1
Eight cells	156-195	180 ± 7	150	4	2
Blastulae	143-230	178 ± 23	150	6	4-6
Gastrulae	160-231	197 ± 23	157	11.71 ± 0.75	5-10
Pre-trocophore	146-205	173 ± 13	107	19.71 ± 1.79	5-8
Trocophore	197-258	207 ± 19	150	25.85 ± 2.54	1-5
Pre-veliger	210-280	257 ± 16	194	29.71 ± 4.15	5-6
Veliger	211-342	279 ± 23	743	35.0 ± 4.39	21-24
Veliger at hatching	245-349	283 ± 20	252	57.28 ± 5.02	5-7
Hatching veliger, free larvae	236-356	296 ± 25	618	63.85 ± 4.91	-

development elapses. Under laboratory conditions, this period, lasted around 55 days. It was remarkable that the spawning season in the field was exactly replicated by animals maintained in aquaria, suggesting the existence of a type of biological clock capable of synchronizing *F. magellanicus* oviposition at the exact period of the year in this southern latitude. Some authors have experimentally shown that seasonally changing photoperiods are important factors for regulating the timing of reproduction in some marine invertebrates (Pearse 1998; Pearse & Bosch 2002). Additionally, it has been demonstrated that the extreme seasonality of primary production in polar waters (Clarke, 1988), among other factors drives the intensity, if not the timing of reproduction (Meidling *et al*., 1998; Chiantore *et al*., 2002; Tyler *et al*., 2003).

According to this study, hatching of *F. magellanicus* larvae in the waters of the Magellan Strait occurs in December. Thus, the development of larvae would occur mostly in the summer season, with maximum surface temperatures that vary from 9.2 to 10.1°C (recorded from 2005 to 2009), and when one significant phytoplankton productivity occurs at this time of year (Magazzu *et al*., 1996; Iriarte *et al*., 2001). This synchronisation with the narrow temporal window in the Southern Ocean confirms the trend that has also been observed in other species with planktotrophic larvae, documented in many cases for benthic invertebrates in Antarctic waters (Stanwell-Smith *et al*., 1999; Bowden *et al*., 2009). There is also evidence that, when compared to the Antarctic, the presence of benthic invertebrate larvae is more common in the Magellan Strait and in the Beagle Channel (Thatje & Fuentes, 2003). Moreover, many of these larvae are planktotrophic, with either full or abbreviated development. For example, in November 1994, meroplankton was dominated by decapod larvae, followed by polychaetes, echinoderms, barnacles and molluscs (Arntz *et al*., 2005).

Seasonal oviposition of *F. magellanicus* in October-November (austral spring) in the Magellan Strait was repeated in both years of observations, suggesting a marked regularity over successive years. Another ranellid off the coast of Chile (*Priene scabrum*) also shows interannual regularity for this process, but clearly shifted to the winter months (June-July), in the temperate waters of La Herradura Bay (Coquimbo, Chile). This study was supported by seven years of continuous records, which indicate that spawning occurs during the minimum winter temperature (near 13°C) in these temperate waters (Romero *et al*., 2003) (Table 1). Another interesting aspect of *F. magellanicus* seems to be a close synchronisation in the timing of larval hatching. Direct inspection by diving in December, revealed that practically all the ovipositions had empty capsules (*i.e.*, they had hatched). This could be synchronised as well with lunar spring tides, thus ensuring an effective long distance transport of larvae by the action of such currents. A connection of this type for ranellid species with a similar development mode has also been

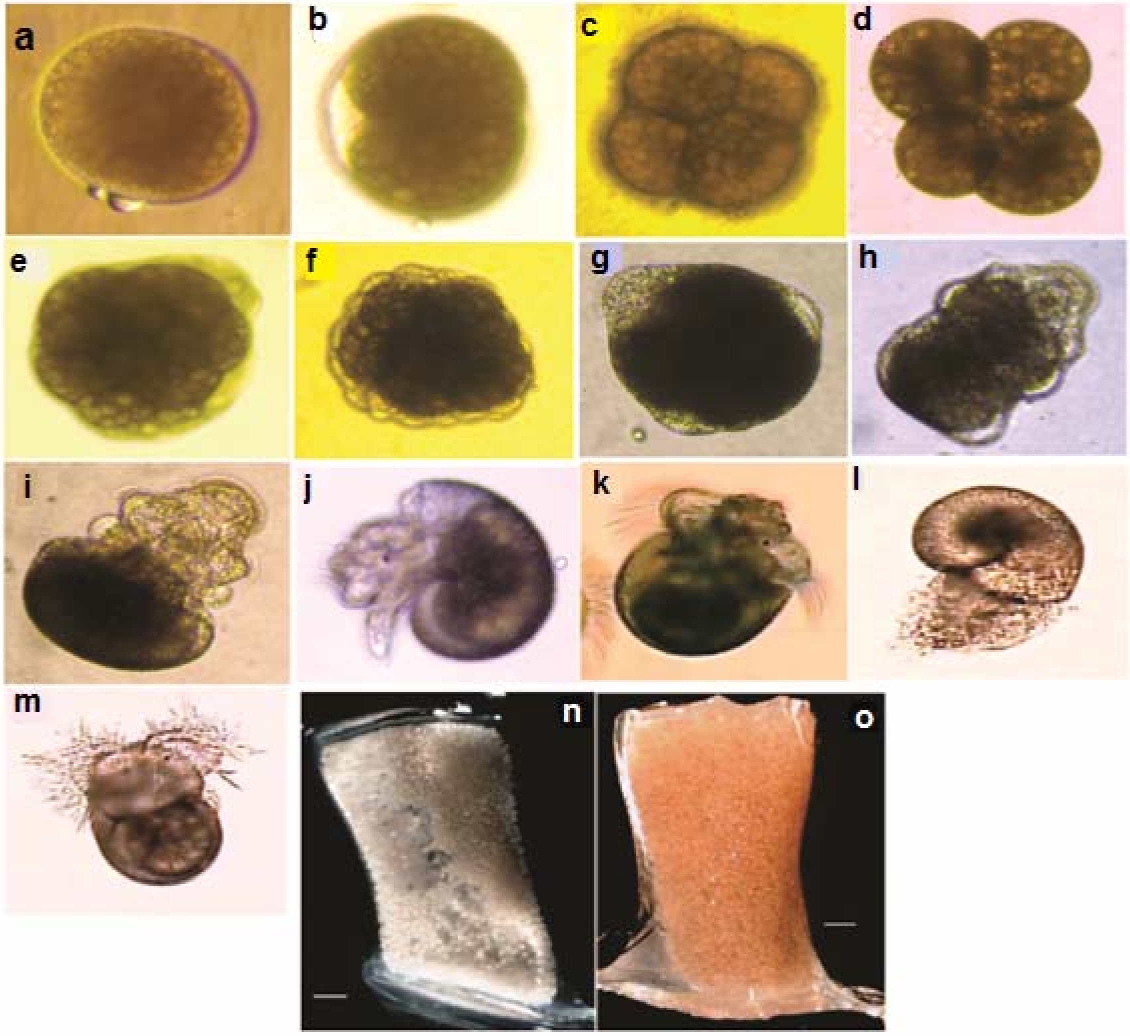

Figure 5. Intracapsular developmental stages of *Fusitriton magellanicus,* Magellan Strait, Chile. a) ovocyte, b) 2-blastomere stages, c-d) 4-blastomeres stages, e-f) blastulae-gastrulae, g-h) pre-trocophore larvae, i) pre-veliger, j-k) recently hatched veligers, l-m) late veliger, n) egg-capsule with early embryos, o) ovigerous capsule with late larvae. Scale Fig. 5n and 5o = 0.5 mm.

Figura 5. Estadios de desarrollo intracapsular de *Fusitriton magellanicus*, estrecho de Magallanes, Chile. a) ovocito, b) estadío 2 blastómeros, c-d) estadío 4 blastómeros, e-f) blástula y gástrula, g-h) larvas pre-trocófora, i) pre-velígera, j-k) velígeras recién eclosionadas, l-m) velígeras tardías, n) cápsula ovígera con embriones tempranos, o) cápsula ovígera con larvas tardías. Escala Fig. 5n y 5o = 0,5 mm.

suggested by Govan (1995), when analyzing strategies of reproduction in four species of the genus *Cymatium*. He also observed that the hatching of veligers from egg capsules took place almost simultaneously, suggesting that, in some cases, this action could be induced by the parent.

Another synchronisation factor of the oviposition onset of *F. magellanicus* in the study area could be the variation in surface salinity in the Magellan Strait, which tends to fluctuate between 30 and 31 psu, but in early spring tends to decrease to 29.5 psu. According to Figure 2, the flow of the San Juan River, about 1 km away from Santa Ana Point, also increases significantly in early spring and decreases in early summer. This could be a strategy to avoid predation by sea stars, which are very abundant and diverse in the study area (Cañete *et al*., 2008) being the largest and are the larger predators because of their inability to regulate their internal and because osmotic pressure (Brusca & Brusca, 2005). Larvae will hatch when salinity conditions become more suitable for pelagic development, which are re-established in December. According to Valdenegro & Silva (2003), the middle of the Magellan Strait is characterised by brackish middle section estuarine conditions, with a homogeneous water column in terms of temperature, salinity and density which could favour larval development by providing a predictable habitat with similar oceanographic features.

Indirectly, our results could demonstrate a clear coordination between the pelagic-benthic coupling in the areas of Paso Ancho and the Magellan Strait, as proposed by Cattaneo-Vietti *et al.* (1999), based on previous results of Fontolan & Panella (1991). This author proposed that this is the most productive area of the Strait, with high chlorophyll content (Chl-*a* > 1 μg L^{-1}), a C:N ratio of 6:1 and a particulate organic carbon (POC) count of 124 μg L^{-1}, with its main feature being autotrophy dominance compared to other watersheds in which detritus is predominant (*i.e.*, the eastern shallower strait area), or a mixture of heterotrophy/detritus, such as on the western side (*i.e.*, the deeper strait area). This background allows us to postulate that it is possible that other molluscs living in other basins of the Strait could couple their larval and reproductive processes differently than the gastropods from the middle of the strait, as exemplified here by *F. magellanicus*.

The attributes of intracapsular development in *F. magellanicus*, compared to other species of the family, suggest that it is a ranellid whose planktotrophic larvae have a relatively large planktonic drift, thereby achieving a wide spatial dispersion during its planktonic stage in the Southern Ocean. This feature is common in the Ranellidae species for which there is information (Scheltema, 1966; Bandel *et al*., 1994; Govan, 1995; Beu, 1998; Strathmann & Strathmann, 2007). In general, ranellids are characterised by having eggs of approx. 150-200 µm (Laxton, 1969), with a total female fertility that can reach several hundreds of thousands (*e.g.*, 200,000-250,000 eggs in *Charonia lampas* (Cazaux, 1972 *fide* Govan, 1995), 602,000 in *C. pileare* (Muthiah & Sampath, 2000), 660,000 larvae in *C. nicobaricum* (Purtymun, 1974 cited by Govan, 1995), 1,000,000 eggs in *Argobuccinum tumidum* (Graham, 1942) and up to 1,500,000 eggs in *Fusitriton oregonensis* (Strathmann & Strathmann, 2007). Species recognized as having long planktonic lives include *F. oregonensis, F. laudandus, Cymatium parthenopeum, C. nicobaricum, C. pileare, Cymatoma kampala* and *Charonia lampas,* according to Lebour (1945), Scheltema (1966), Pilkington (1974), Pechenik *et al.* (1984) and Strathmann & Strathmann (2007). In *Cymatium* species studied by Govan (1995), when hatching, the larvae measures 230-250 µm and have approximately one turn, a bilobed veil, a small triangular foot and a visible operculum, slightly larger in *F. laudandus* and *A. tumidum* (330 and 400 µm) (Pilkington, 1974). Later in larval development, the veil is tetralobular, as is characteristic in teleplanic gastropod larvae, particularly in ranellid larvae (Scheltema, 1966; Pilkington, 1976; Bandel *et al*., 1994, Strathmann & Strathmann, 2007). The veliger of a cymatid, illustrated by Pilkington (1976), begins to form four lobules at approximately 1.5 whorls (510 µm shell length), clearly distinguishable at 2.5 whorls (1.05 mm).

Teleplanic larvae of ranellids are usually associated with major ocean current systems, through which they can achieve transoceanic dispersal (Scheltema, 1966, 1968, 1971, 1988; Pechenik *et al*., 1984), particularly *C. parthenopeum, C. nicobaricum* and *Charonia variegata*. As a result, many ranellids achieve a wide geographic distribution (Beu, 1998), often with amphi-oceanic populations (*i.e.*, populations on both sides of a given ocean). The species for which the longest duration of a pre-metamorphic free larval stage has been reported is a ranellid, congeneric with the species in this study (Strathmann & Strathmann, 2007), that corresponds to *Fusitriton oregonensis*. In the laboratory, the larvae lived over four years, which is an extreme case for invertebrates in general. In the laboratory, females generate about 2,200-2,700 larvae per capsule while in nature, this figure may reach about 4,500-5,500. The number of larvae per oviposition (around 300 capsules) varies from around 700,000-800,000 in the laboratory to about 1.5 million in the wild.

The encapsulated development and geographical distribution of *F. magellanicus* exhibit features consistent with these aforementioned ranellids, supporting the proposition of a long planktonic life for its larvae, as is the norm in this family. Their eggs are about 180 µm, and they release an average of about 436,000 larvae per oviposition, with a peak of about 630,000 larvae in the largest oviposition observed in this study (*ca.* 260 capsules). Penchaszadeh & De Mahieu (1975) found a maximum of 4,200 eggs per capsule and ovipositions with up to 290 capsules on the coast of Argentina, allowing the authors to estimate a maximum possible count that could easily exceed one million larvae per oviposition. To this, we must add that females may spawn more than one oviposition per season, as it has been observed in other species (Govan, 1995; Muthiah & Sampath, 2000), a situation that must be recognized before estimating the fecundity of a female for that period.

The comparison of numbers of eggs/embryos/larvae in egg masses between temperate and tropical species of the family Ranellidae allow us to predict that the sub-Antarctic *Fusitriton magellanicus* show developmental attributes that define them as long-distance broadcasters.

The wide geographical distribution of *F. magellanicus* covers the coast of Chile (32°S to Tierra del Fuego, including the Juan Fernandez Archipelago; Osorio 2002), to Rio Grande do Sul as the northern boundary and including the Falkland/Malvinas Islands, South Georgia and Marion in the Atlantic of South America (Powell, 1951; Cárdenas *et al*., 2008), South Africa, New Zealand and New South Wales in southern Australia (Beu, 1998). Such wide distribution of the kind, observed for *F. magellanicus*, allow us to postulate that the effective connectivity and gene flow between these distant populations is possibly due to transoceanic dispersal of their larvae, mediated through large inflows as the vehicle for such transportation. This approach is consistent with an earlier proposal by Beu (1978), which was stated when discussing the ancestral geographic origin and radiation of the *Fusitriton* genus, particularly in the Southern Hemisphere. It spread from western North America to Japan by the Miocene and to South America by the Pliocene. He hypothesized that during the Pleistocene, perhaps because of the lengthening of larval life resulting from the slowing of metabolism (caused by the cooling of the seas), it has spread, by transport of planktonic larvae in the west-wind drift, to South Africa and then to Australia and New Zealand.

More recently, in other taxa, several authors have stressed the importance of the ocean current system in the high latitudes of the southern hemisphere (West Wind Drift and Antarctic Circumpolar Current), for the long distance transport of propagules in the southern open ocean. Undoubtedly, the existence of these great ocean currents connecting the world's major landmasses in the southern hemisphere have allowed the evolution of remote dispersal strategies in various marine invertebrate taxa and are important mechanisms explaining the evolution and phylogeography of various benthonic groups (Beu *et al*., 1997; Gordillo, 2006; Waters *et al*., 2007; Waters, 2008). For marine gastropods, including some Ranellidae, remote transoceanic larval dispersal has been documented in the northern hemisphere, focusing on amphi-Atlantic species, whose larvae scattered across the Gulf Stream and became the pioneers and classic studies on this type of phenomenon (Scheltema, 1966, 1968, 1988; Pechenik *et al*., 1984). To our knowledge, equivalent studies in waters of the southern currents are almost non-existent. Records of this sort could highlight the equivalent role that such circulation plays to explain the amphi-Atlantic and amphi-Pacific distribution of several marine invertebrates in the Southern Seas, including some gastropods. Besides ranellids, in Chile, there are other gastropods that seem to possess extensive larval dispersal patterns, such as the muricids *C. concholepas* and *Thais chocolata*. Like ranellids, *C. concholepas* has also been found on the South African coast and, in the past, it was a genus of greater diversity and wide geographic distribution (Beu, 1970). Kensley (1985) described their Late Pleistocene occurrence in South Africa; in his opinion, such a fossil record would represent a short-lived pioneer population, established by larvae drifting through the currents from South America.

Thus, wide dispersal by planktotrophic larvae appears to be a characteristic feature of Ranellidae. In fact, the only species with direct development belongs to the *Sassia* genus (Beu, 1998). In this sense, Ranellidae makes a close parallel, but in the opposite direction, with Volutidae. Species of the latter taxon also share a unique offspring development type (direct type in this case), as a general feature of the family. Families like these, whose diversity of development modes appears to be restricted by an evolutionary event committing the entire taxon, can be distributed over a wide latitudinal range; therefore, their development mode does not conform to the predictions of Thorson's Rule, a fact made evident by the Volutidae on the Atlantic coast of South America (Gallardo & Penchaszadeh, 2001). Phyletic constraints of this type are added to other considerations that must be taken into account to explain the cases that, in this regard, are the exceptions to the above mentioned rule.

According to Table 1, preliminary antecedents suggest that the Chilean warm temperate ranellid (*Priene scabrum;* 12-13ºC) could have a shorter encapsulated time than subantarctic *Fusitriton magellanicus* (55-67 days; 8-9ºC). Gallardo *et al.* (2012) indicates that in other subantarctic ranellid, *Argobuccinum pustulosum,* the encapsulated development lasts around 54-56 days (11-12ºC). Thus, the duration of encapsulated development in ranellids could be closely associated to the temperature of sea water showing a latitudinal pattern.

Evidences of large variation in size within each embryo and larval stages, shown in Table 2, could be due to different females size used in the lab experience as well as in the field. Similar results found Gallardo *et al.* (2012) for *A. pustulosum* populations from southern Chile.

On the Chilean coast, it is interesting to note those dispersers with long-lived planktotrophic larvae, which are distributed in a wide latitudinal range (sometimes from subtropical to subpolar waters) have an invariable and evolutionarily persistent developmental pattern, breaking the latitudinal trend predicted by this rule. Most notable in this regard is the muricid *Concholepas concholepas*, with long-lived planktotrophic larvae (Gallardo, 1979; DiSalvo, 1988); according to a paleontological review of the genus (Beu, 1970), it was the only species of the group that has remained until today and it is restricted to the western coast of South America from southern Peru and the Chilean coast to Cape Horn. Beu (1970) attributed this to the possibility that this species had a pelagic larva with long-lived planktonic characteristics and adapted to cold waters under the influence of coastal upwelling processes. Incredibly, both predictions were fully confirmed when, years later, the developmental mode of this muricid became well known. Early on, palaeontologists Valentine & Jablonski (1986) postulated the association between developmental mode and adaptation to survive marine extinction events that occurred in the past. Undoubtedly, a better understanding of Ranellidae larval biology in the southern hemisphere will also allow us to use this family to explore the evolutionary history of the group to better understand its biology, population connectivity potential and current geographical distribution.

Finally, it is noteworthy that, although ranellids are species with high potentials for dispersal and colonisation at a distance, they (including *F. magellanicus*) are almost absent in the geological and current records of gastropods that have colonised the Antarctic coast. The only Antarctic ranellid seem to be *Obscuranella papyrodes* (Kantor & Harasewych, 2000). It appears as this species has populated the Antarctic for a long time, and it now lives in the deep abyssal zone (A.G. Beu, *pers. comm.*). We do not know how much the Antarctic Circumpolar Current (ACC) or the Antarctic Polar Front have formed an effective barrier that has prevented the dispersal of *F. magellanicus* larvae to successfully colonise the coast of the Antarctic Peninsula (González-Wevar *et al.*, 2010, 2011). An alternative explanation argued by some authors is that *Fusitriton,* and ranellids in general, are just not cold-adapted enough to inhabit Antarctica, rather than being kept away by the ACC. They are tropical and temperate taxa. The distribution of these taxa could perhaps be explained in the evolutionary context that would have followed the Antarctic benthic communities, as proposed by Aronson *et al.* (2007). These authors proposed that the barriers to biological invasions into the Southern Ocean are primarily physiological rather than geographic; cold temperatures would impose limits to performance that have excluded modern predators, and the Ranellidae snails are considered to be among these.

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