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Development of the gastropod *Trochita pileus* (Calyptraeidae) in the sub-Antarctic Southwestern Atlantic

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Abstract

The family Calyptraeidae is widely distributed around the world and shows several types of development all with physical care. Adults and broods of *Trochita pileus* from sub-Antarctic waters were collected during two cruises off Tierra del Fuego and Burdwood Bank at depths between 39 and 298 m. A total of 43 brooding females and 314 egg capsules of *T. pileus* were collected. Shell diameter of brooding females ranged from 12.6 to 28.8 mm. The egg capsules were flattened triangular sacs with rounded vertices and lateral margins longer than the distal margin. The number of egg capsules per brood increased significantly with increasing shell diameter of brooding females from 1 to 15 and a mean number of 7.9 ± 2.8. *T. pileus* has direct development from embryos which start consuming nurse eggs (oophagy) and then continue eating developing embryos (adelphophagy). The 80.7% of the initial eggs of *T. pileus* did not initiate development. From about 1000 initial uncleaved eggs per egg capsule (diameter around 250 μm), only 8 complete their development hatching as crawling juveniles. The observation of the post-gastrula stage of *T. pileus* swallowing all nurse eggs and latter also other embryos in the same stage of development is the first case of oophagy and adelphophagy in the genus *Trochita*. No late intracapsular cannibalism has been observed. To our knowledge, there are no records of Antarctic Calyptraeidae and this would be the development of one of the southernmost species described.

Keywords Development · Calyptraeidae · Brooding · Nurse eggs · Adelphophagy · MPA Namuncurá/Burdwood Bank

Introduction

Species in the family Calyptraeidae all provide maternal care to their clusters of egg capsules which are laid above the substrate and below the neck and propodium of the female (Hoagland 1986; Collin 2000, 2003a, b). Planktotrophic and direct development are the two common types of development in this family. In species with direct development, all embryonic development occurs within the capsule and offspring hatch as crawling juveniles, e.g., some species of *Crepidula*, *Calyptraea*, *Trochita*, *Sigapatella* and *Crucibulum* (Collin 2003a, b; Chaparro et al. 2005). The embryos can develop from large eggs, or they can feed on nurse eggs, nurse embryos or intracapsular nutritional resources

(Gallardo 1977a, b, 1979; Hoagland 1986; Collin 2000, 2005; Chaparro et al. 2002, 2005; Lesoway et al. 2014).

Spawn and development in the genus *Trochita* has been studied only in the giant (shell diameter up to about 11 cm) *Trochita trochiformis* (Born, 1778) in Coquimbo, Chile (as *Calyptraea (Trochita) trochiformis* in Cañete and Ambler 1992). This species has direct development from large eggs, an uncleaved egg mean diameter of 460 ± 14 μm and 17–132 embryos per capsule without nurse eggs. In addition, this species displays planktonic drifting during its early juvenile life that is uncommon particularly among gastropods with holobenthic life cycles (Cañete et al. 2007).

Trochita pileus (Lamarck, 1822) lives subtidal on hard substrates from Buenos Aires Province ($\sim 36°$S $54°$W) to Burdwood Bank in the Southwestern Atlantic ($\sim 55°$S $66°$W) and from Isla Dawson to Puerto Harris in the Southeastern Pacific (Pastorino and Urteaga 2012). It occurs from shallow water to 253 m depth (Powell 1951). The apex is central, with a prominent protoconch with 1.5 whorls. The first whorl is smooth, but later there are multiple weak spiral threads that cross growth lines which vanish on the teleoconch

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(Pastorino and Urteaga 2012). In a preliminary study, Torroglosa and Giménez (2012) found that *T. pileus* laid 7–8 egg capsules per brooding female and 5–14 embryos per egg capsule (from 4 brooding females studied from a population of Buenos Aires Province 37°33′S 55°57′W at depths of 82–120 m). The type of development was not reported. In this study, the spawn of *Trochita pileus* from sub-Antarctic waters is described, including the characterization of egg capsules and embryonic development.

Materials and methods

Adults and egg capsules of *T. pileus* were collected by the Argentine R/V "Puerto Deseado" from 4 stations during one cruise off Tierra del Fuego in April 2014 at depth ranges of 39–52 m and from 6 stations during one cruise nearby Burdwood Bank in April–May 2017 at depth ranges of 41–298 m (Table 1, Fig. 1). A total of 43 brooding females and 314 egg capsules of *Trochita pileus* were collected. All material was collected using a bottom net trawl and a modified Agassiz dredge (Table 1). The egg capsules were preserved in a 4% formalin–seawater solution, which is most suitable for histology and preservation of eggs and embryos. The shell maximum diameter and capsules height and width were measured with a 0.1-mm precision caliper, and the embryos were measured using a 0.01-mm precision ocular micrometer. The shell maximum diameter or length was measured according to Ming-Hui and Keryea (2000).

The specimens and egg capsules were preserved in the invertebrate collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In 41753–41762). All shells and capsules were photographed using a Nikon D100 camera with a 60-mm Micro Nikkor lens and a Leica IC 80 HD camera for those items smaller
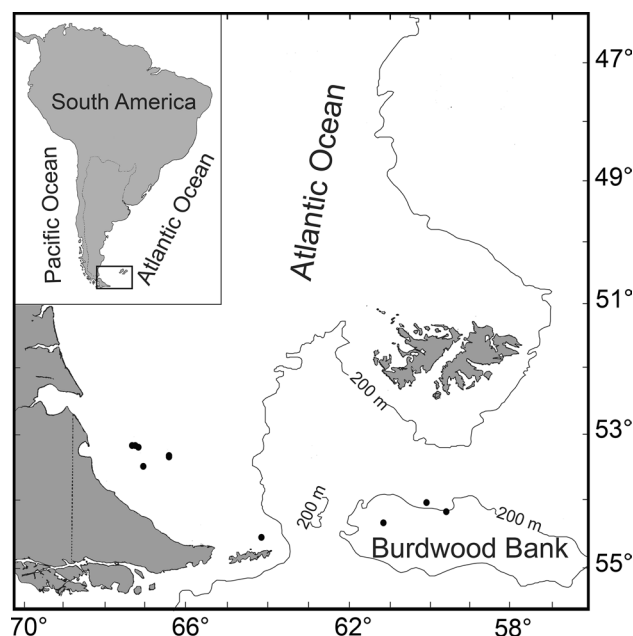

Fig. 1 Map showing the location of collected samples

than 5 mm. Photographs were digitally processed with Adobe suite software.

Embryos were critical point dried, mounted and coated with gold and observed using a Philips XL 30 scanning electron microscope (SEM) at MACN. Other embryos were dehydrated using an ascending series of ethanol concentrations and then embedded in resin (Leica Historesin®). Sections were cut at 5 μm with an electronic microtome (Leica® RM 2155) and stained with hematoxylin and eosin. All sections were examined histologically under a Zeiss Axio Imager Z1 microscope and photographed with a SV Micro-Sound-Vision digital camera.

Statistical analysis

To corroborate whether there are any relationships between (1) the maximum shell diameters of the brooding females and the number of egg capsules; (2) the maximum shell diameter of brooding females and the mean capsules size; and (3) the mean diameter and number of post-gastrula stage embryos linear regression analyses were evaluated with STATISTICA 7.0.

Results

The shell diameter of brooding females ranged from 12.6 to 28.8 mm ($n = 43$) (mean ± SD 19.9 ± 3.4 mm). The number of egg capsules increased significantly with increasing shell diameter of the brooding females (linear regression,

Table 1 Summary of station sampled with latitude, longitude and depths

Latitude S	Longitude W	Depth (m)	Date	Adults	Egg capsules
53°26.261′	67°48.691′	41	4/25/2017	1	15
53°26.632′	67°46.805′	39	4/01/2014	1	8
53°27.900′	67°36.016′	52	4/01/2014	1	6
53°35.008′	66°35.016′	51	4/01/2014	5	48
53°36.289′	66°36.916′	51	4/01/2014	2	19
53°58.664′	67°0.317′	50	4/25/2017	6	37
54°5.501′	60°41.978′	122	5/09/2017	1	8
54°19.994′	59°59.225′	96	5/01/2017	3	28
54°36.234′	61°30.088′	298	4/28/2017	1	1
54°52.915′	64°19.992′	153	4/24/2017	22	144

Total number of adult and egg capsules of *Trochita pileus*

$r^2 = 0.17$, $n = 38$, $p = 0.006$) (Fig. 2). The number of capsules observed in brooding females ranged from 1 to 15 ($n = 314$; mean 7.9 ± 2.8). The egg capsules were flattened triangular sacs with rounded vertices, with their lateral margins longer than the distal one (wall thickness between 10 and 25 μm). A laminar peduncle (2.8 ± 0.7 mm) extends from the proximal vertex of each capsule and anchors it to hard substrate as shells of scallops and oysters. The size of the egg capsules (height and width) increased significantly with increasing shell diameter of the brooding females (linear regression, $r^2 = 0.49$, $n = 36$, $p < 0.0001$ and $r^2 = 0.48$, $p < 0.0001$, respectively). The average size was 3.9 ± 0.8 mm in height and 4.4 ± 0.7 mm in width.

Embryos of each brooding female began to develop synchronously. Recently laid egg capsules showed a mean number of uncleaved eggs of 1004.1 ± 282.2 ($n°$ of egg capsules = 16) (Table 2) with a mean diameter of 247.4 ± 24 μm (range 100–380 μm) ($n°$ of eggs = 340). Eggs were spherical and creamy white in color. The first cleavage occurred in 19.3% of the eggs ($n = 5$), but only 1.8% of the uncleaved eggs in each capsule showed the second cleavage and 1.1% showed the post-gastrula stage, while the rest remained as nurse eggs (Table 2). Cleavage was spiral and holoblastic. First cleavage with the formation of polar bodies was observed, a second cleavage with a 4-cell stage occurred

Fig. 2 Relationship between shell diameter of brooding females of *Trochita pileus* and number of egg capsules

and measured 330.2 ± 7.9 μm in diameter (number of egg capsules = 5 of different brooding females) (Fig. 3a–c).

The phase between cleavage and gastrulation was not clearly observed except in one case, a gastrula with a central invagination forming the stomodeum and blastopore (Fig. 3d) (as observed by Chaparro et al. (2002) in *Crepipatella dilatata* (Lamarck, 1822) and by Lyons et al. (2015) in *Crepidula fornicata* (Linnaeus, 1758)). After the gastrulation, the ventral and dorsal lips of the embryos were developed and they started swallowing nurse eggs (Fig. 4a). This post-gastrula stage developed a cephalic vesicle, a stomodeum surrounded by densely packed microvilli and cilia. These embryos continued swallowing nurse eggs (oophagy) and later also other embryos at the same stage of development (adelphophagy) (Figs. 3e–g, 4b). The number of post-gastrula embryos decreased significantly (from 48 to a minimum of 3) with an increase in their mean diameter (from 487.1 ± 196.2 μm to 1244 μm) (linear regression, $r^2 = 0.45$, $n = 69$, $p < 0.0001$) (Fig. 5). During this stage of development, the shell field developed from the dorsal part of the posterior region as a circular suture (Figs. 3e–g, 4a). In histological sections of the post-gastrula stage, the embryos were still nearly spherical and symmetrical. At this stage, the stomodeum contained columnar cells and developed short cilia and the ventral and dorsal lips were ciliated (Fig. 6a, b). The nurse eggs ingested intact by the post-gastrula embryos were observed through the wall and clearly seen by stereoscopic microscope and in histological sections (Figs. 4a, b, 6a, b). The total number of embryos decreased significantly with their increasing size (linear regression, $r^2 = 0.41$, $n = 107$, $p < 0.0001$) (Fig. 7).

As intracapsular development progressed, pre-torsional intracapsular embryos with increased growth of the cephalopodial structures, velum and shell were observed (Fig. 4c), and later, coiled embryos showing a gradual reduction in the velum and a growth of the foot, food groove, eyes, tentacles and shell (Figs. 3h, 4d, e) could also be seen. No operculum was ever observed. The number of veliger stages seen within egg capsules ranged from 2 to 19 with a mean number of 8.1 ± 4.2 and a mean shell diameter of 1.3 ± 0.16 mm (range 1.1–1.9 mm) (Table 2).

The protoconch of females was similar to that described by Pastorino and Urteaga (2012) with a central apex and a
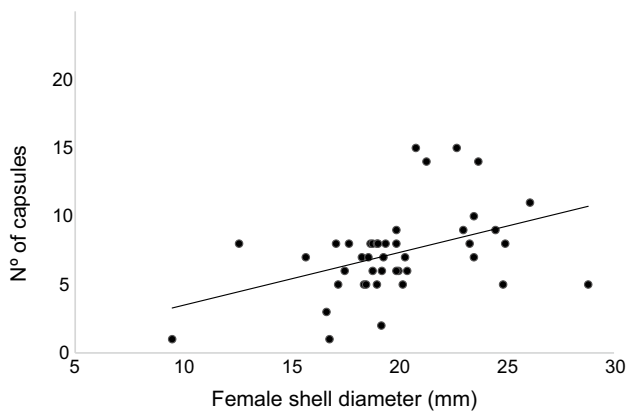
Table 2 Mean and SD of number of different stages of embryo development/capsule

Stage of development	Mean number and range	Mean diameter
Unsegmented eggs/capsule and range ($n = 16$)	1004.1 ± 282.2 (413–1757)	247.4 ± 24 μm (100–380)
4-cell stage/capsule and range ($n = 5$)	18 ± 7.2 (7–26)	330.2 ± 7.9 μm (276–370)
Post-gastrula stage/capsule and range ($n = 71$)	11.2 ± 9.0 (3–48)	853.9 ± 189.8 μm (487–1244)
Veliger stage/capsule and range ($n = 48$)	8.1 ± 4.2 (2–19)	1.3 ± 0.16 mm (1.0–1.9)

n number of egg capsules of *Trochita pileus* analyzed
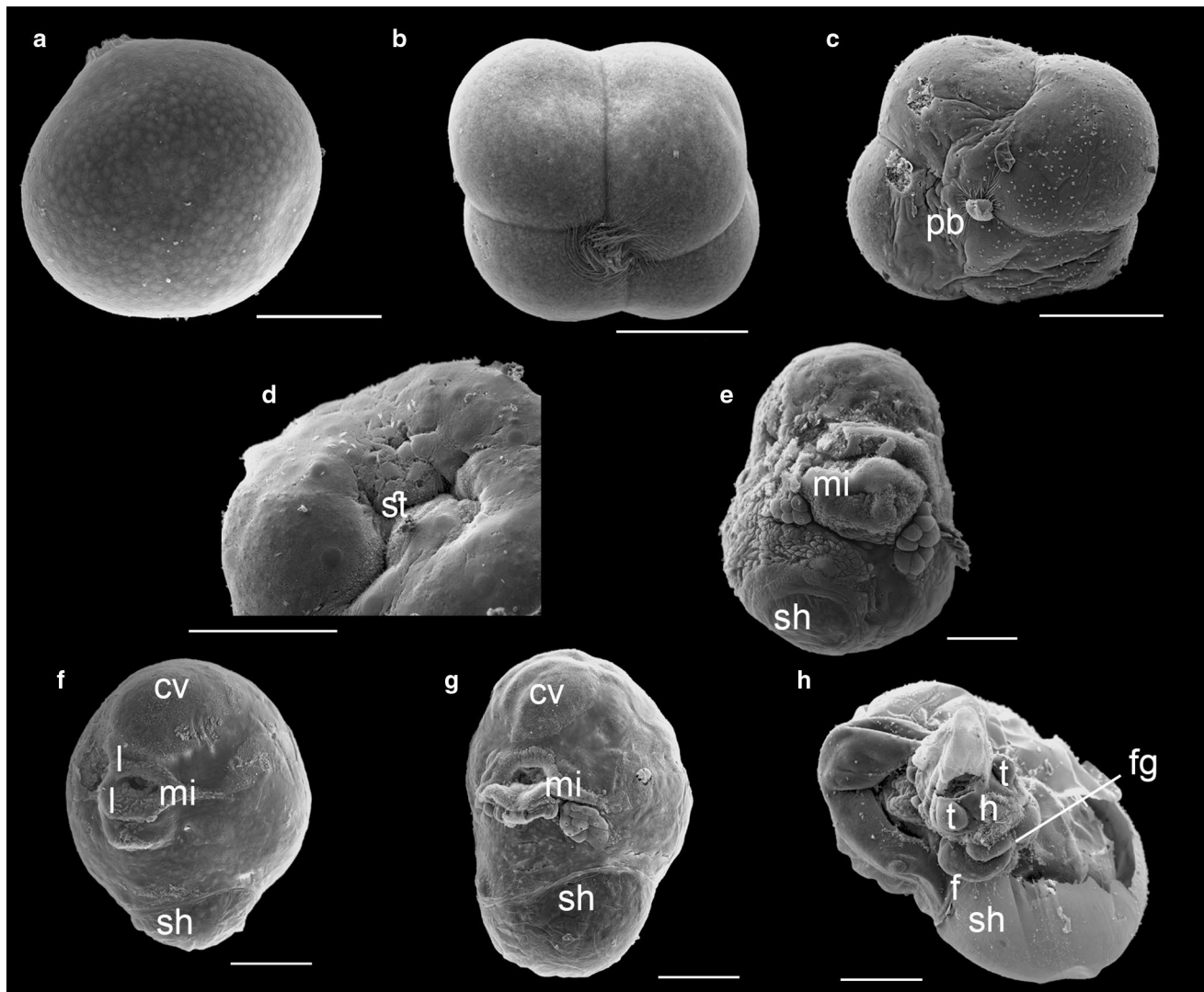
Fig. 3 SEM images of *Trochita pileus* developmental stages: **a** fertilized egg before first cleavage with the beginning of the formation of the polar body; **b**, **c** vegetal and animal view of the second cleavage with polar bodies (pb), respectively; **d** gastrula with the central part invaginated to form the stomodeum (st); **e–g** post-gastrula stages with a developed a cephalic vesicle (cv), lips (l) well developed, microvilli (mi) and formation of the shell (sh); **h** coiled veliger embryo with tentacles (t), head (h), shell (sh), foot (f) and food groove (fg). Scale bars: **a** 50 μm, **b**, **e** 100 μm, **f**, **h** 200 μm

mean shell diameter of 1.3 ± 0.2 mm (range 1.1–1.6 mm) and 1.5 whorls. The first whorl is smooth, followed by multiple weak spiral threads that cross growth lines that vanish on the teleoconch (Fig. 8).

Discussion

Trochita pileus has direct development; embryos start consuming nurse eggs (unsegmented eggs) and continue eating developing embryos at the post-gastrula stage to finally hatch as crawling juveniles. The strategy where large numbers of eggs are deposited in each egg capsule and only a subset develops to hatching is common in marine gastropods (Thorson 1950; Fioroni 1988) and particularly within the family Calyptraeidae. In our case, from an initial number of 1004.1 ± 282.2 eggs per egg capsule of about 250 μm in diameter only 8.1 ± 4.2 complete their development. Collin (2003a, b) reported this type of development in several species of calyptraeids as the Southwestern Atlantic *Bostrycapulus odites* Collin, 2005 and *Crepipatella dilatata* (Penchaszadeh et al. 2002; Collin 2003b). The same pattern was observed in *Crucibulum auricula* (Gmelin, 1791) from Venezuela (Miloslavich and Penchaszadeh 2001) that also showed cannibalism. Torroglosa and Giménez (2012) found 4 brooding females of *T. pileus* from a population of Buenos Aires Province. All embryos in the egg capsules were at a pediveliger stage,
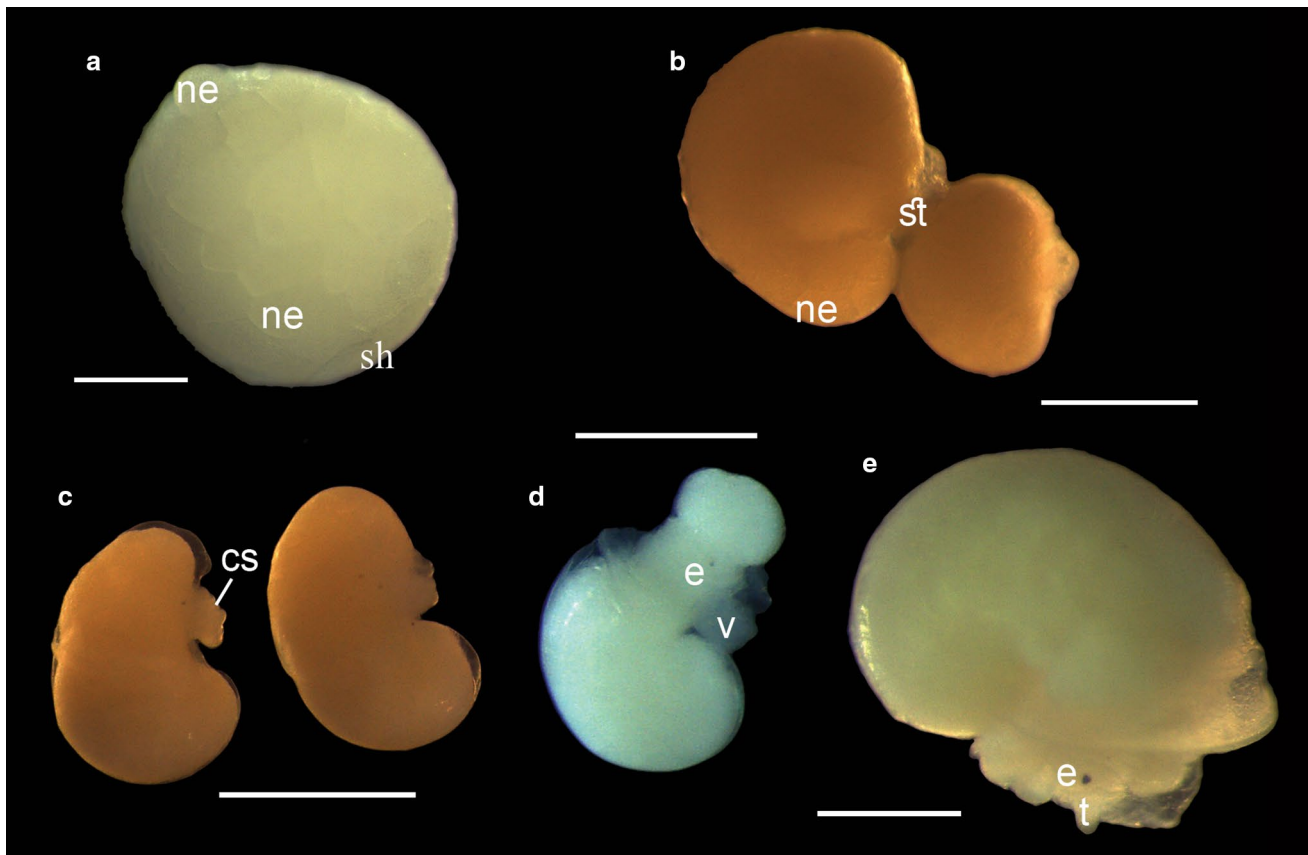
Fig. 4 Images of *Trochita pileus*'s developmental stages: **a** post-gastrula stage swallowing nurse eggs (ne) and formation of the shell (sh), **b** post-gastrula stage swallowing other embryo with the stomodeum (st), **c** pre-torsional intracapsular embryos with cephalopodial structures (cs), **d, e** coiled veliger embryos with tentacles (t), eyes (e) and velum (v). Scale bars: **a** 200 µm, **b, e** 500 µm, **c, d** 1 mm
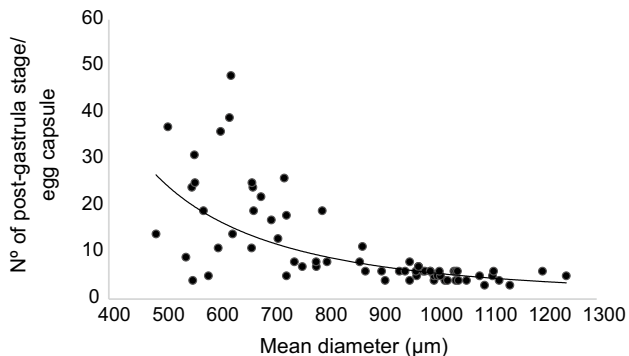

Fig. 5 Relationship between the mean diameter of post-gastrula stage and the number of post-gastrula specimens of *Trochita pileus* per egg capsule

and some "uncleaved eggs" according to the scale of Fig. 4 of Torroglosa and Giménez (2012) would have a diameter of 820 µm which represents a volume 35 times larger than the initial eggs measured in this study. This large size suggests that the photograph of the "uncleaved egg" more likely belongs to an abortive post-gastrula stage.

Nurse eggs are sterile eggs or eggs that in some way are programmed to stop developing at an early stage, which varies among species (Fioroni and Schmekel 1976; West 1983). In several species of calyptraeids, the nurse eggs initiate development but become arrested at some point prior to the development of the definitive juvenile body plan (Thomsen et al. 2014; Lesoway et al. 2014). In others as *B. odites* and *Calyptraea lichen* Broderip, 1834, the nurse eggs could not be distinguished from the embryos after gastrulation (Collin 2005; McDonald et al. 2014). The 80.7% of the initial eggs of *T. pileus* did not initiate development. In *C. auricula,* all eggs develop to the first four cleavages; however, 93% of them arrested development at this stage and were ingested by the remained developing embryos (Miloslavich and Penchaszadeh 2001). Lesoway et al. (2014) reported three types of embryos within the egg capsules of the direct developer *Crepidula navicella* (Lesson, 1831), i.e., viable embryos, gastrula-like embryos which arrested development after gastrulation and post-gastrula-like embryos that were more variable in morphology. On the other hand, in *C. dilatata* (as *Crepidula dilatata* in Gallardo (1977a) and Gallardo and Garrido (1987)), *Crepidula philipiana* Gallardo, 1977b and
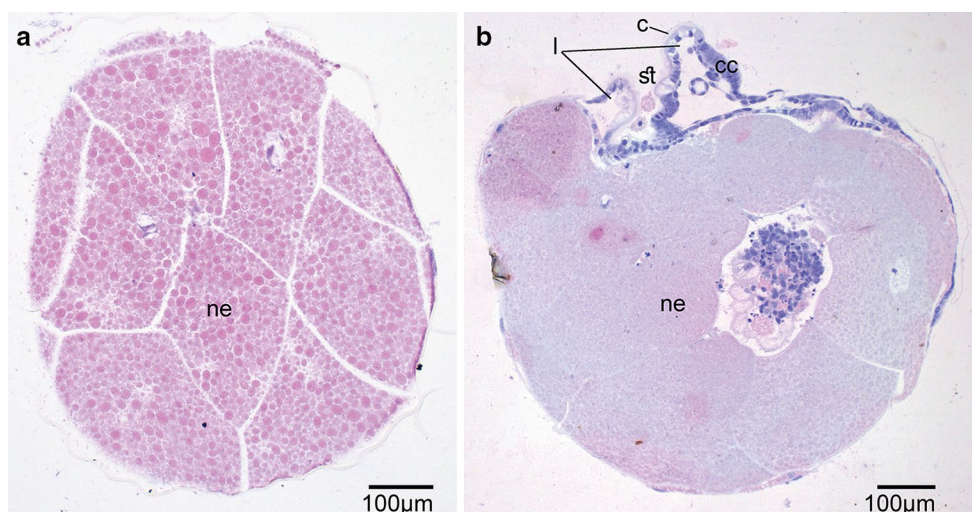
Fig. 6 Histological sections of post-gastrula specimens of *Trochita pileus*. **a** The nurse eggs (ne) are visible within the post-gastrula specimen; **b** post-gastrula specimen with a stomodeum (st) contained columnar cells (cc) surrounded by densely cilia (c), nurse eggs and lips (l). Scale bars: 100 μm
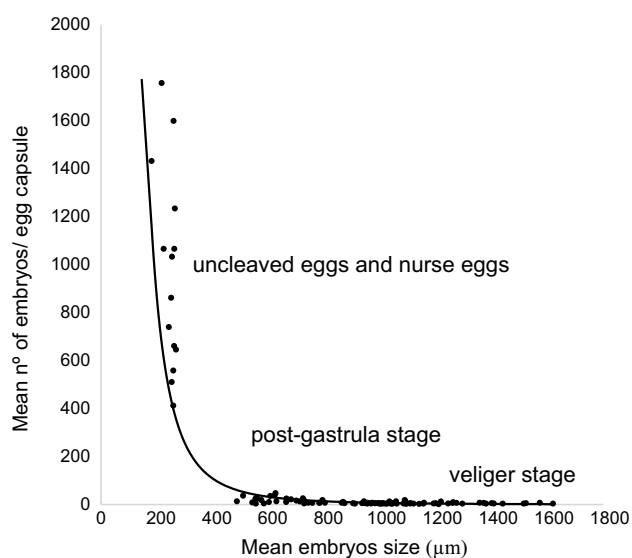

Fig. 7 Relationship between mean embryo size and mean number of embryos of *Trochita pileus* in the different stages of development per egg capsule

Maoricrypta monoxyla (Lesson, 1831) (as *Crepidula monoxyla* in Collin 2003b) the nurse eggs did not appear to be fertilized and did not initiate development (Gallardo 1977a, b; Gallardo and Garrido 1987; Collin 2003b).

The morphology of the post-gastrula stage of *T. pileus* was similar to that found by Miloslavich and Penchaszadeh (2001) as "stage 2" in *C. auricula*; by Collin (2005) as "early post-gastrula stage" of *Bostrycapulus urraca*; by Collin (2000) as "early embryonic stage" of *Crepipatella lingulata* (Gould, 1846) (as *Crepidula lingulata*). The post-gastrula

stage started swallowing all the available nurse eggs within the egg capsule and later, also eating other embryos at the same stage of development (post-gastrula stage). As a result, approximately 0.8% of the uncleaved initial eggs of *T. pileus* complete development giving a ratio of 124 nurse eggs per embryo. In *C. dilatata* that has the same type of development as *T. pileus* with small uncleaved eggs (195–263 μm), about 8% of the eggs develop into embryos, with the remaining 92% serving as nurse eggs. But on the contrary of *T. pileus*, the embryos of *C. dilatata* began to consume nurse eggs later in their development (Gallardo 1977a, 1979). In addition, only 7% of the eggs of *C. navicella* complete development (Lesoway et al. 2014). Oophagy, adelphophagy and later cannibalism have been reported in several species of different genera of the family Calyptraeidae (Hoagland 1986; Miloslavich and Penchaszadeh 2001; Collin 2003b; Miloslavich et al. 2003; Brante et al. 2013; McDonald et al. 2014). Oophagy and adelphophagy in the genus *Trochita* are reported here for the first time. In addition, there is no late intracapsular cannibalism.

The protoconch of *T. pileus* was similar to those reported by Collin (2005) in juvenile shells of *Bostrycapulus* species from Brazil and Argentina, large with slightly more than a single whorl, and irregular growth lines typical of direct development with nurse eggs.

The mean shell diameter (19.9 ± 3.4 mm) and the mean number of capsules per female (7.9 ± 2.8) found in brooding females of *T. pileus* in this study were similar to those found in the females from the population of Buenos Aires Province (19.4 ± 1.9 mm; 7–8, respectively) (Torroglosa and Giménez 2012). Gallardo (1977a) reported 15–75 capsules per female and a mean shell diameter of 32.5 mm in
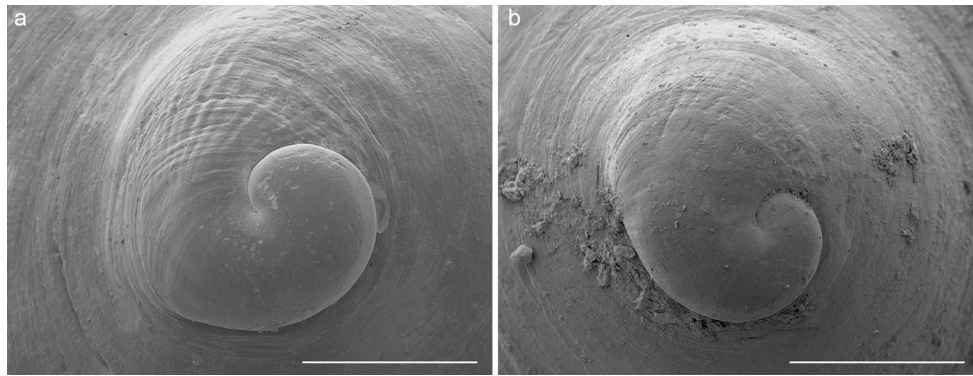
Fig. 8 SEM images of the protoconch of two specimens of brooding female adults of *Trochita pileus*. **a** MACN-In 25072, **b** MACN-In 41758. Scale bar (**a**, **b**) 1 mm

C. dilatata. A significant relationship was found between the shell diameter of brooding females of *T. pileus* and the number of egg capsules per brood. Comparable results were found in populations of *T. trochiformis*, *C. dilatata*, *Crepidula argentina* Simone, Pastorino and Penchaszadeh, 2000 and *B. odites* (Gallardo 1977a; Cañete and Ambler 1992; Cledón and Penchaszadeh 2001; Cledón et al. 2016). The positive relationship between the size of the capsule and that of the brooding female parent found for *T. pileus* has also been reported for *C. auricula* by Miloslavich and Penchaszadeh (2001), for *C. dilatata* by Gallardo (1976) and Chaparro et al. (1999) and for *C. argentina* by Cledón and Penchaszadeh (2001).

The fact that all embryos in the egg capsules of each brooding females of *T. pileus* were simultaneously at the same stage of development was also reported in several oophagic and adelphophagic species of Calyptraeidae, such as *C. dilatata, Crepidula aplysioides* Reeve, 1859, *C. navicula, C. auricula* and *B. odites*, among others (Gallardo 1979; Chaparro et al. 1999; Miloslavich and Penchaszadeh 2001; Miloslavich et al. 2003; Collin 2003a, b, 2005).

The different stages of development found in *T. pileus* were similar to those reported for other calyptraeids with direct development and other families, i.e., Vermetidae, Muricidae, Buccinidae (West 1983; Stöckmann-Bosbach 1988; Cañete and Ambler 1992; Calvo et al. 1998; Chaparro et al. 2002; Calvo and Templado 2004; Collin 2005; Lyons et al. 2015). The formation of the polar bodies and a preveliger III stage (here referred as post-gastrula stage) were similar to the development found in *T. trochiformis* (Cañete and Amber 1992). However, the latter species has a different type of development with large viable eggs (mean diameter of 460 ± 14 µm) and without nurse eggs. Collin (2005) reported three types of development in the genus *Bostrycapulus*: (1) planktotrophic larvae; (2) direct development with large eggs; and (3) direct development from small eggs with nurse eggs. According to that in the genus *Trochita,* there are at least two different types

with *T. pileus* belonging to the type (3) and *T. trochiformis* to the type (2).

According to the recent works on Antarctic malacofauna, there are no records of Calyptraeidae farthest south of South America (i.e., Powell 1951; Dell 1990; Arnaud et al. 2001; Griffiths et al. 2003; Linse et al. 2006, among others). In this scenario, this is the southernmost material studied in this family. *Trochita pileus* has direct development with nurse eggs in sub-Antarctic waters. This reinforces the pattern observed already by Collin (2003b). She recorded that Calyptraeids from Southern Hemisphere mostly have direct development and nurse embryos while these are rarely found in the Northern Hemisphere, where predominates direct development from large eggs.

Compliance with ethical standards

Conflict of interest No potential conflict of interest was reported by the two authors of the manuscript.

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