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Reproductive biology in the South Western Atlantic genus *Buccinanops* (Nassariidae): the case of *Buccinanops paytensis*

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ABSTRACT

The reproductive biology of the nassariid *Buccinanops paytensis* is considered and compared with the other species in the genus. In *B. paytensis* an average of 42 egg capsules were attached to the shell of each female. A mean of 2738 eggs (246 µm in diameter) occurred per capsule and generally only one embryo developed inside, measuring c. 5 mm in shell length when hatching; eggs at pre-hatching stage are still abundant. Four percent of the egg capsules contained two pre-hatching embryos of unequal size, in which nurse eggs were totally consumed. ‘Larval kidneys’ were recorded at advanced developmental stages (‘pediveliger’). Adaptations to reproduction in soft substrates involve a great amount of energy being invested by the females (nurse eggs and maternal care of the capsules), which enhance the survival of juveniles. *Buccinanops paytensis* had the highest number of nurse eggs per embryo (c. 2600), but *B. cochlidium* had more eggs and embryos per female (c. 3100 and c. 800, respectively). Hatching of crawling juveniles occurred in about 4 months in all species. When multiple embryos occur in an egg capsule, food becomes limiting, hatching size is reduced and unequal. Evidence of sibling cannibalism was observed in *B. monilifer*. Major differences are related to the spawn size, and the amount of nurse eggs and feeding modality of each species, which impact on the reproductive output (number and size of the juveniles) per female. The South African nassariid genus *Bullia* differs in egg capsule morphology and attachment, but is similar in having nurse eggs and direct development.

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Adelphophagy; *Bullia*; egg capsules; intracapsular development; nurse eggs; parental care

Introduction

Among caenogastropods, the eggs are usually packaged into capsules (Voltzow 1994) which protect the embryos throughout development. The hatching stage may be achieved as swimming larvae (e.g. ‘veliger’), either lecithotrophic or planktotrophic, or as a crawling juvenile known as direct development (Strathmann 1985; McEdward 1997). In species with direct development, extravitelline nutritive resources occur inside the egg capsule together with embryos; these include proteins in the intracapsular fluid, nurse eggs and even sibling cannibalism (Fretter and Graham 1994; Miloslavich 1996; Penchaszadeh and Miloslavich 2001; Collin and Spangler 2012). The advantages of intracapsular development also include the reduction of vulnerability to sources of mortality such as predation, salinity stress, desiccation, bacterial attack and ultraviolet light (reviewed by Rawlings 1994).

In Argentina’s temperate waters most marine caenogastropods species spawn egg capsules, in general with direct development (Gallardo and Penchaszadeh 2001). Typical examples are the volutids with large egg capsules containing a few direct developing embryos and large amounts of soluble proteins in the intracapsular fluid (Penchaszadeh *et al.* 1999;

Penchaszadeh and Segade 2009; Bigatti *et al.* 2014), the calyptraeids that spawn and brood their egg capsules which contain nurse eggs inside (hatching as planktonic larvae or crawling juveniles) (Cledón and Penchaszadeh 2001; Penchaszadeh *et al.* 2002), the olivids that spawn egg capsules with extremely large (> 1 mm diameter) viable eggs (Borzzone 1995), direct developer muricids such as *Trophon* sp. with nurse eggs inside the capsules (Penchaszadeh 1976; Pastorino and Penchaszadeh 2009; Cumplido *et al.* 2011) and nassariids, mainly represented by species of *Buccinanops* d’Orbigny, 1841.

Species of the genus *Buccinanops* are endemic along the coastal waters of the South Western Atlantic ocean, typically inhabiting soft bottoms (Penchaszadeh 1971a; Pastorino 1993). In previously studied *Buccinanops* species, the sex ratio did not differ from 1:1 in populations not affected by imposex (Penchaszadeh *et al.* 2001; Averbuj *et al.* 2010; Averbuj and Penchaszadeh 2010b). These snails are gonochoric with internal fertilisation. Adult individuals attach several flattened and flexible egg capsules to the callus region of the shell by means of peduncles (Penchaszadeh 1971a). Embryos in this genus complete their development within the egg capsule by the ingestion of nurse eggs, and then hatch as

crawling juveniles through a distal opening (Penchaszadeh 1971a, 1971b).

The number of egg capsules, eggs and embryos varies among *Buccinanops*. Usually a unique embryo develops within each capsule (Penchaszadeh 1971a). Cannibalism might occur in some species of this genus, as in *B. monilifer* (Kiener, 1834) (Averbuj and Penchaszadeh 2010a). Concurrently, competition among embryos within each egg capsule was reflected in a heterogeneous hatching size (Averbuj and Penchaszadeh 2010b). A comparative description of *Buccinanops* species reproductive features (developmental time and modality, number and size of eggs, number and size embryos per capsule, etc.) will be insightful.

Buccinanops species are distributed from Brazil (19 S) to southern Argentina (48 S). In Argentina all valid species are present, including: *B. cochlidium* (Dillwyn, 1817), *B. duartei* Klappenbach, 1961, *B. globulosus* (Kiener, 1834), *B. monilifer*, *B. uruguayensis* (Pilsbry, 1897) and *B. paytensis* (Kiener, 1834). Most of them have been studied regarding their oviposition and embryonic development (Table 1). The reproductive biology of *B. paytensis* and *B. uruguayensis* has not previously been studied.

In this article we describe the spawn and developmental biology of the southernmost species, *B. paytensis*, for the first time. We also review the available knowledge dealing with reproductive biology aspects of *Buccinanops* species in Argentina including unpublished data on *B. uruguayensis*.

Materials and methods

Sampling

Samples of adult *B. paytensis* were hand gathered in the intertidal zone in November 2011, January 2012 and February 2013 at La Mina beach (49°15'S, 67°0'W), 27 km north of Puerto San Julian, Santa Cruz province, Argentina. The collection site has fine sandy bottoms. Total shell lengths (TSL) of each individual carrying egg capsules were measured with a 0.1 mm precision Vernier calliper.

The individuals carrying egg capsules were fixed in 5% formalin and transferred to the laboratory for reproductive and developmental studies.

Data from four *B. uruguayensis* carrying egg capsules collected in Mar del Plata (38°00'S, 57°33' W) during the summer months (January and February) in 2001 were included, which represent the only knowledge on its reproductive biology. This species is probably the most uncommon of the genus and spawn are rarely seen.

Reproductive features

All individuals carrying intact spawn were studied. Egg capsules were counted in each spawn mass. Four egg

capsules were randomly chosen from each snail, detached from the shells, measured (for total length, maximum width and total peduncle length) and dissected.

The number of nurse eggs per capsule was counted under a light microscope. Individual fecundity was estimated as the mean number of eggs/embryos per female. The intracapsular egg diameter was measured before cellular division; for this purpose 50 eggs were randomly chosen from each egg capsule.

Field observations were focused on mating, oviposition and presence of egg capsules during the sampling period. Oviposition timing (presence of spawning females or egg masses in early stages of development) and developmental time (time elapsed from spawning to hatching) were also considered whenever possible.

Embryonic development

Embryos within the egg capsules were classified according to developmental stages used in previous studies of *Buccinanops* species (Averbuj and Penchaszadeh 2010b; Averbuj *et al.* 2014), according to morphological features: uncleaved egg; cell cleavages; 'veliger'; 'pediveliger'; pre-hatching.

Total length of the embryos was measured at each of the developmental stages. At the latest stage the number of juveniles per capsule was counted and measured in all intact capsules. All measurements were made with stereoscopic microscope with a 0.1 mm precision ocular micrometre.

Results were compared with previous publications on *Buccinanops* species spawning and developmental biology.

Statistical analysis

The relation between the TSL of the snail carrying egg capsules and the number of egg capsules was evaluated by linear regression analysis. The relationship of the number of embryos per egg capsule and the TSL was also considered (by a linear regression analysis). All tests and descriptive statistical analysis were done with the Statistica 7.0 statistical package.

Results

Reproductive features

A total of 29 individuals (13 in November, eight in January and eight in February) of *B. paytensis* carrying egg capsules were studied. All of them were females that measured between 37.4–48.7 mm in shell length. The spawn contained on average 42.41 ± 9.77 (mean \pm SD) egg capsules (Table 1). These were similar to other *Buccinanops* species in aspect, generally varying in size according to the female's size.

Table 1. Comparison of reproductive aspects of *Buccinanops* species.

Species	Spawn seasonality	Female size	No. of EC	No. of eggs/EC	Egg size (μm)	No. of embryos/EC	Hatching size (mm)*	No. of eggs/embryos in EC
<i>B. monilifer</i> ^{b,e}	October–February	45.1 \pm 4.3 (38.5–53.9); <i>n</i> = 20	22.6 \pm 9.0 (746–2317); <i>n</i> = 18	1120.3 \pm 252.6 (1200–1600); <i>n</i> = 18	291.2 \pm 36.8 (220–400); <i>n</i> = 185	1	5.75 \pm 0.7 (4.8–7.5); <i>n</i> = 6	1120.3
<i>B. cochlidium</i> ^{a,c,d}	July–February	90.8 \pm 4.8 (80.0–102.0); <i>n</i> = 50	142.2 \pm 30.0 (80–238); <i>n</i> = 50	3101.5 \pm 494.3 (2005–3898); <i>n</i> = 50	227.5 \pm 13.5 (160–320); <i>n</i> = 2500	5.4 \pm 2.5 (1–20); <i>n</i> = 172	4.0 \pm 0.6 (2.4–7.0); <i>n</i> = 626	574.3
<i>B. duartei</i> ^a	**	–	10–14	–	265–291	1	4	–
<i>B. globulosus</i> ^{a,f}	October–March	26.3 \pm 4.3 (20.7–41.2); <i>n</i> = 75	31.06 \pm 8.3 (15–49); <i>n</i> = 75	1422.1 \pm 264.0 (762–2500); <i>n</i> = 100	204.0 \pm 3.0 (190–212); <i>n</i> = 3600	1.02 \pm 0.02 (1–4); <i>n</i> = 58	3.4 \pm 0.4 (2.3–6.3); <i>n</i> = 68	1394.2
<i>B. paytensis</i> (p.s.)	November–March	43.7 \pm 2.6 (37.4–48.7); <i>n</i> = 29	42.4 \pm 9.8 (21–65); <i>n</i> = 29	2738.1 \pm 545.7 (1871–3729); <i>n</i> = 116	246.1 \pm 50.7 (184.5– 341.0); <i>n</i> = 4200	1.03 \pm 0.17 (1–2); <i>n</i> = 32	4.9 \pm 0.6 (3.3–6.1); <i>n</i> = 31	2658.3
<i>B. uruguayensis</i> ^a (p.s.)	**	30.9 \pm 2.04 (27.9–31.9); <i>n</i> = 4	(13–55); <i>n</i> = 4	(14–54); <i>n</i> = 2	(307.5–328); <i>n</i> = 100	1	–	–

Note: Values represent mean size \pm SD and range (brackets). Abbreviations: EC—egg capsules; p.s.—present study.

**Buccinanops paytensis* the late pre-hatching was latest developmental stage measured.

**Samples were obtained during summer (January–February).

Sources: ^aPenchaszadeh (1971a); ^bPenchaszadeh (1971b); ^cPenchaszadeh (1973); ^dAverbuj and Penchaszadeh (2010a); ^eAverbuj and Penchaszadeh (2010b); ^fAverbuj et al. (2014).

Table 2. Features of egg capsules of species of *Buccinanops*.

Species	Width (mm)	Length (mm)	Peduncle (mm)
<i>B. monilifer</i>	c. 7	c. 6	–
<i>B. cochlidium</i>	8.55 ± 0.68 (5.85–10.15); n = 97	14.03 ± 1.22 (11.69–17.69); n = 97	1.38 ± 0.53 (0–2.92); n = 97
<i>B. duartei</i>	c. 3.4	c. 4.5	–
<i>B. globulosus</i>	4.5 ± 0.65 (2.86–6.86); n = 300	4.14 ± 0.73 (3.13–6.16); n = 300	0.87 ± 0.22 (0.53–1.76); n = 300
<i>B. paytensis</i>	6.35 ± 0.57 (5.23–9.27); n = 88	7.54 ± 0.61 (6.46–8.84); n = 88	1.41 ± 0.51 (0.48–3.33); n = 88
<i>B. uruguayensis</i>	2.86 ± 0.24 (2.39–3.52); n = 13	4.29 ± 0.38 (3.8–4.94); n = 13	0.73 ± 0.19 (0.42–0.95); n = 13

Values represent mean size ± SD and range (brackets).

Each egg capsule contained a mean of 2738.13 ± 545.74 eggs ($n = 4200$). Uncleaved eggs measured on average $246.09 \pm 50.72 \mu\text{m}$ ($n = 4200$) in diameter (Table 1). Adult female fecundity in *B. paytensis* represents a mean of c. 116,000 eggs and 43 embryos per female, and the mean number of eggs per embryo is 2658.3 (Table 1).

No significant linear relationship was found between TSL and the number of egg capsules attached to the shell ($F = 2.59$; $P = 0.119$; $df = 27$; $n = 29$). The linear regression analysis between TSL and the number of nurse eggs per capsules did not detect a significant relationship ($F = 0.011$; $P = 0.916$; $df = 29$; $n = 31$).

During sampled months no copulation was observed in *B. paytensis* and no spawning event was seen *in situ*. Reproductive seasonality is shown in

Table 1. In November all females carrying egg capsules were in early (eggs or cleavage) stages of development ($n = 13$). In late February all egg capsules contained embryos in pre-hatching stages of development ($n = 8$).

The egg capsule measurements for all species, including total length, maximum width and peduncle length are included in Table 2.

Embryonic development

Egg capsules of *B. paytensis* collected in November (spring) were all in early stages of development (Figure 1A), mostly uncleaved eggs or at the two to four cell cleavage stage (Figure 2A and 2A inset a). The capsules were filled with up to 3729 rounded whitish eggs, most of which will serve as nurse eggs,

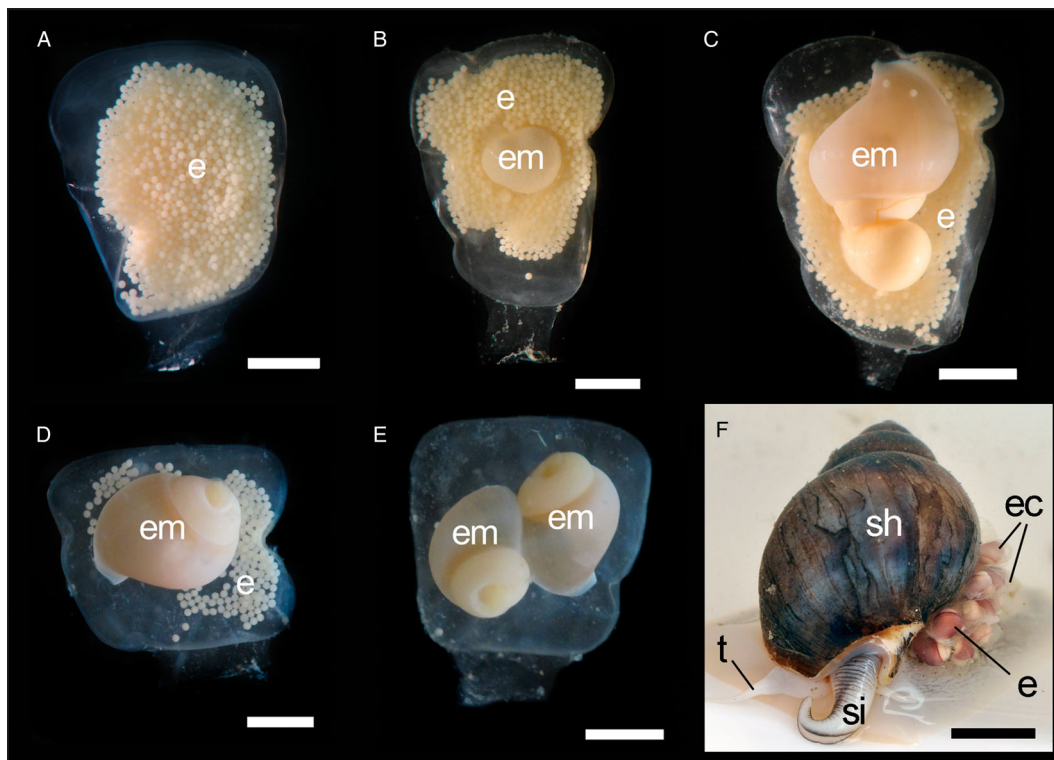


Figure 1. Intracapsular embryonic development of *Buccinanops paytensis*. Note the reduction in the amount of nurse eggs through development. **A**, Uncleaved eggs; **B**, 'veliger' embryo; **C**, early and late pre-hatching; **D**, late pre-hatching embryos; **E**, pre-hatching, note that the two embryos consumed all nurse eggs; **F**, female carrying egg capsules with hatching juveniles. Abbreviations: e—eggs; ec—egg capsule; em—embryos; sh—shell; si—siphon; t—tentacle. Scale bars: A–F = 2 mm.

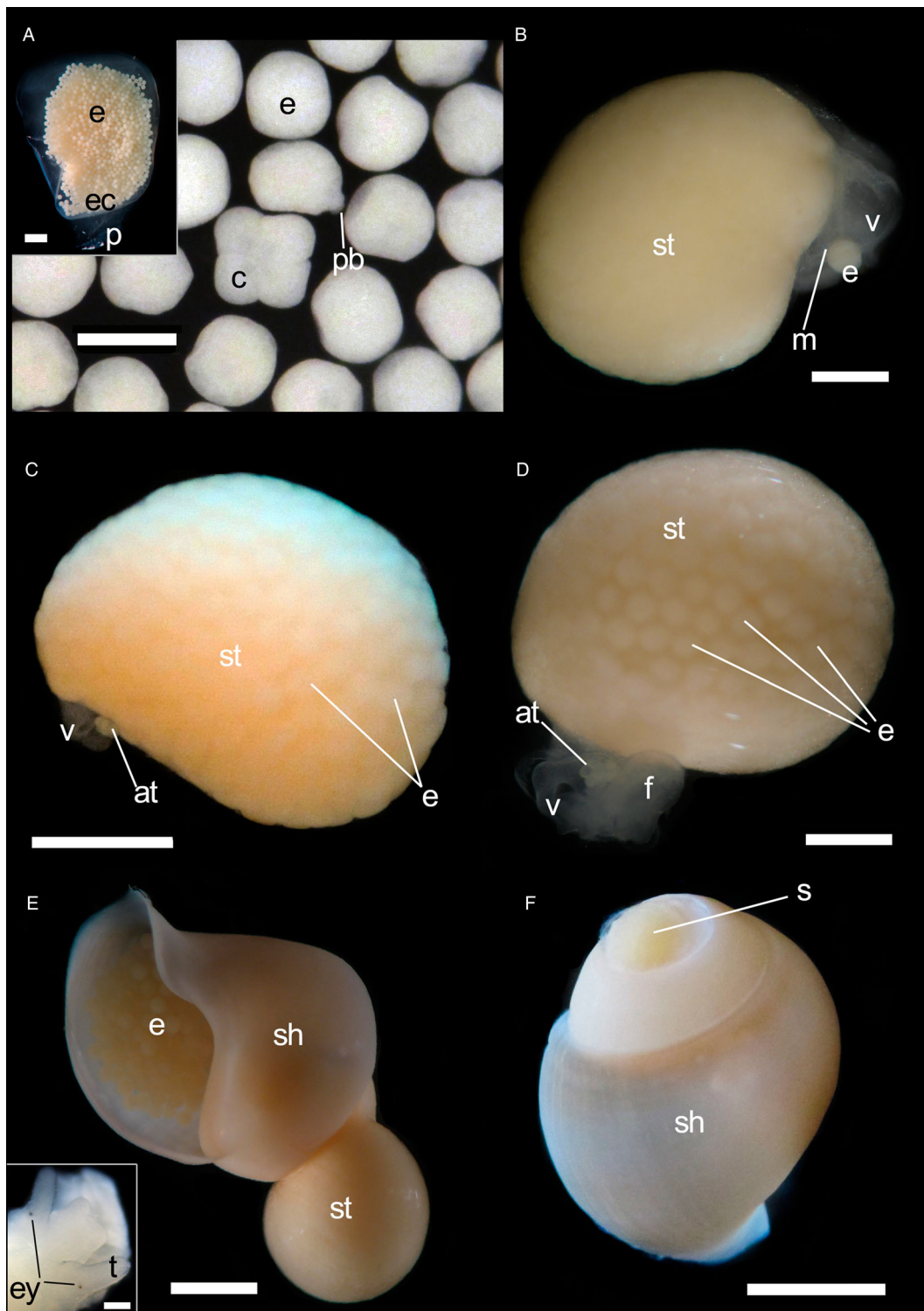


Figure 2. Embryonic development of *Buccinanops paytensis*. **A**, Eggs and cleavage cells (inset: egg capsule with nurse eggs); **B**, 'veliger' consuming an entire egg; **C**, large 'veliger' embryo filled with entire nurse eggs, 'larval kidney' is present; **D**, 'pediveliger' with velum, foot and 'larval kidney' or athrocyte cells at the cephalic region, filled with numerous entire nurse eggs; **E**, early pre-hatching with developing white and thin shell, the stomach is exposed (inset: cephalic region of the embryo showing the eyes at the base of each tentacle); **F**, pre-hatching embryo. Abbreviations: at—athrocyte cells; c—cleavage cells; e—eggs, ec—egg capsule; ey—eye; f—foot; m—mouth; p—peduncle; pb—polar body; sh—shell; st—stomach; t—tentacle; v—velum. Scale bars: A = 250 μm (inset = 1000 μm); B = 500 μm , C–D = 1000 μm ; E = 1000 μm (inset = 500 μm); F = 2000 μm .

while usually one is a viable embryo (Figure 2B). They are indistinguishable from one another before cleavage (Figure 1A) and rarely more than one or two eggs underwent cleavage. Cleaved cells (two to four cells) measured $261.47 \pm 19.07 \mu\text{m}$ ($n = 110$).

In January embryos were mostly in 'pediveliger' stage (Figure 2D) and in a few cases in late 'veliger' (Figure 2B–C); the former measured $2.52 \pm 0.19 \text{ mm}$ ($n = 19$), while the latter measured $2.41 \pm 0.36 \text{ mm}$ ($n = 5$). In the late 'veliger' the velum was completely

developed, associated to egg ingestion, and the stomach progressively increased in size with the ingestion of entire nurse eggs (Figure 2B–C). At the end of this stage the ‘larval kidneys’ were observed in two individuals ($n=5$) (Figure 2C). In the ‘pediveliger’ the velum was present and functional. During this stage the foot developed gradually and the stomach was still filled in with entire nurse eggs (Figure 2D). In both stages there are abundant nurse eggs available within the egg capsule, although apparently decreasing in the later stage (Figure 1B–C). Another remarkable characteristic is the presence of conspicuous ‘larval kidneys’ or athrocyte cells in all individuals at ‘pediveliger’ stage (Figure 2D). Eyes were observed at the base of the cephalic tentacles at the end of ‘pediveliger’ and early pre-hatching stages, but they were not found at advanced pre-hatching stage (Figure 2E and 2E inset b).

In February embryos at pre-hatching stage of development were observed. At this stage the velum was not present (resorbed) (Figure 2E–F). The embryonic shell was present, firstly white and thin (partially protecting the body); the stomach was outside the shell, although as the development and digestion advanced it became difficult to distinguish the eggs inside the stomach (Figure 2E). Later in development the shell became coiled, thicker and coloured. The apex zone was not calcified (Figure 2F). A mean of 574.56 ± 343.16 nurse eggs ($n=31$ egg capsules) accompanied the pre-hatching embryo, which is usually one per capsule (Figure 1D); however, in some cases two embryos in advanced stages of development were observed per capsule (3.6% of the capsules; $n=56$); in those egg capsules no nurse eggs were observed (at pre-hatching stage) (Figure 1D–E). The late pre-hatching embryos (almost indistinguishable from hatched ones) measured on average 4.94 ± 0.65 mm in shell length ($n=31$) and can reach more than 6 mm (Figure 1D–E and 2F); however, when twin sibling embryos occurred their sizes were unequal and reduced on average (Table 1). Other *Buccinanops* species hatching sizes are included in Table 1.

It is remarkable that at each sampling event all spawn were practically at the same stage of development. Moreover, all the egg capsules in each spawn showed a high synchronicity in developmental stages. This explains the difficulties in finding some developmental stages (as early ‘veliger’) in the samples.

***Buccinanops uruguayensis* reproductive features**

Buccinanops uruguayensis spawns were attached to females that measured between 27.9 and 32.4 mm in shell length and carried between 13 and 55 (mean \pm SD = 33.25 ± 18.5 ; $n=4$) egg capsules. Some egg capsules were broken or detached, probably underestimating the total number of capsules per female. A

maximum of 55 eggs was counted inside the intact capsules, which measured 219.81 ± 19.50 μm ($n=400$) in diameter, previous to segmentation (Table 1). Individuals of *B. uruguayensis* were collected by bottom trawling, thus copulation and spawning events were not observed.

Discussion

Buccinanops paytensis egg capsules resemble those in other *Buccinanops* species in shape and attachment mode. As in other nassariids, individuals adapted to infaunal life need to secure egg capsules to hard substrata or brood them (D’Asaro 1993). In all *Buccinanops* species the capsules are attached to the shells of the females, thus avoiding the problem of finding spawning substrate (Averbuj and Penchaszadeh 2010b). This is probably the most remarkable feature of the reproductive adaptations of the genus to life on soft bottoms. Spawn attached to hard objects in mobile substrate avoid being buried by storms or stranded on the beach. Other gastropod species spawn on other living individuals’ shells (including those of other species and of the same species, although not on the shell of the individual that is spawning), as for example, *Prunum prunum* (Gmelin, 1791), *Mazatlaniana fulgurata* (Philippi, 1846) or species of the genus *Olivancillaria* d’Orbigny, 1840 (Penchaszadeh *et al.* 1983; Borzone, 1995; Penchaszadeh and Rincon 1996), among others. In this sense, the differences between *Buccinanops* and *Bullia* (Gray cited in Petit and Coan 2008) species are remarkable with females of the latter fastening their egg capsules to the sole of their foot. This mode of spawning is convergent with another African group, the volutid genus *Cymbium* spp. (Marche-Marchad 1980). As a consequence of these contrasting adaptations, egg capsule morphology differs markedly between *Bullia* and *Buccinanops*, but is conserved within each genus (Penchaszadeh 1971a; Brown 1982).

Spawning seasonality of all *Buccinanops* species studied in Argentine waters coincided, disregarding latitudinal differences (between 38°S and 49°S). Recently laid egg capsules are observed mainly from mid spring (October–November) and hatch in late summer (February–March), although some females may spawn earlier from July (winter) (Averbuj and Penchaszadeh 2010a, 2010b; Averbuj *et al.* 2014). Spawning seasonality in *Bullia* species that inhabit an equivalent latitudinal range is similar, with spawn observed in spring–summer months (Brown 1982). Species of this genus are also direct developers using nurse eggs as a nutritive resource. Another notable characteristic of *Buccinanops* species is the enormous number of eggs laid in each capsule, usually serving a single embryo. Adult female fecundity in *B. paytensis* represents a mean of c. 116,000 eggs and

43 embryos per female, greater than all other species in the genus (of similar adult sizes), with the exception of the largest species *B. cochlidium* that produces more than 400,000 eggs and almost 800 embryos per female (up to 4000 eggs in each egg capsule, with one to 20 embryos; Table 1). The number of nurse eggs available to each embryo (no. of eggs/no. of embryos) in *B. paytensis* is, however, the highest of the genus, which has an observable effect on the hatching size. In contrast, *B. cochlidium* has multiple embryos per capsule and competition for food resources, and hatchlings are smaller than in other species of smaller adult size (Averbuj and Penchaszadeh 2010b). Miloslavich (1996) studied the biochemical content in the nurse eggs of species of *Buccinum* Linnaeus, 1758 (Buccinidae) which was enough to account for the hatchlings content (i.e. no extra nutritive resource is needed). This does not exclude intracapsular competition for food that would affect offspring size and chances of survival. Nonetheless, it is clear that such a great amount of energy invested by the female (in the form of nurse eggs and maternal care), has an impact, increasing the survival chances of the crawling juveniles. These are extraordinary adaptations to reproduction in soft bottoms, even at high latitudes, where extracapsular larval development would be predicted by 'Thorson's rule' (Gallardo and Penchaszadeh 2001).

The egg capsules in *B. paytensis* contain thousands of nutritious eggs (oophagy), which are not distinguishable from viable eggs; a single embryo usually develops per capsule. The only exceptions are *B. cochlidium* females which lay a mean of five (up to 20) viable embryos in each capsule that reach hatching stages, and *B. monilifer* females which may lay several embryos in each capsule but only one hatches after consuming all nurse eggs and smaller embryos (adelphophagy). However, recent studies reported *B. globulosus* females carrying egg capsules with more than one embryo per capsule, together with other capsules with only one embryo; the occurrence of this varies in frequency in different populations (Averbuj *et al.* 2014; Primost *et al.* in press). Occasionally, some nurse eggs begin cleavage and then stop. This highlights the limited knowledge available regarding the mechanisms that determine the viability of eggs (Averbuj and Penchaszadeh 2010b). *Bullia* species differ in that a single embryo per capsule is an exception (*B. tenuis*), while other species may include up to 200 viable embryos per capsule. This discussion would benefit from further comparative studies of the reproductive biology of *Bullia* and *Buccinanops*, in particular focusing on availability of food and synchrony in development.

'Larval kidneys' are present in the embryos of many gastropod species, even when they are sometimes not easily observed. The role of this organ and the large

refracting cells that form it, called athrocytes, is linked to absorption of nutrients prior to ingestion (Rivest 1992; Bigatti *et al.* 2014). Thus, they would be expected to be present at early stages of development, in particular, in species with direct development such as *B. cochlidium* or *B. globulosus*, before the ingestion of nurse eggs (Averbuj and Penchaszadeh 2010b; Averbuj *et al.* 2014). In *B. paytensis* these organs apparently developed later, being found in some late 'veliger' embryos and present in all 'pediveliger' embryos, when nurse egg ingestion was already occurring. All observed pre-hatching individuals lacked these structures.

The egg ingestion modality in *B. paytensis* is like that of *B. cochlidium* which also ingests entire eggs. In *B. cochlidium*, multiple embryos occur per capsule that ingest many entire eggs as fast as possible, thus reaching different hatching sizes, suggesting competition for the feeding resource (Averbuj and Penchaszadeh 2010b). This modality requires developmental asynchrony and fast ingestion of food as described in *Buccinum undatum* Linnaeus, 1785 (Smith and Thatje 2013). In *B. globulosus*, in contrast, individuals feed progressively on egg particles and at the hatching stage there are remnant nurse eggs (Averbuj *et al.* 2014). *Buccinanops paytensis* embryos adopt an intermediate feeding strategy as food is not limited for the only embryo that usually develops and ingestion occurs throughout the entire development. The high synchronicity in developmental stages (within and between spawn) also explains this lack of competition for food. It is pertinent to mention the case of *B. monilifer*, also a particle egg feeder, but with cannibalism of sibling embryos (Averbuj and Penchaszadeh 2010a) which modifies the importance of food limitation and the food intake speed.

Embryos hatch as crawling juveniles in all *Buccinanops* species. Intracapsular developmental time (i.e. time between spawning and hatching peak) is approximately the same in all studied species (3 to 4 months). Species progeny dispersal is thus restricted (no free larval stages), and juveniles may obtain some advantages by staying close to adults of their population. For example, in *B. cochlidium*, hatchlings were observed to feed on carrion generated by adult predatory behaviour (Averbuj *et al.* 2012).

This review on the spawn and developmental biology of *Buccinanops* species clearly expresses a conserved modality of reproduction of the genus. Major differences include the spawn size, the number of nurse eggs and the feeding modality of each species, all of which impact on the reproductive output (number and size of the juveniles) per female.

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References

- Averbuj, A., Bigatti, G. & Penchaszadeh, P.E. (2010) Gametogenic cycle and size at first maturity of the edible snail *Buccinanops cochlidium* (Dillwyn, 1817) from Golfo San José (Patagonia, Argentina). *Marine Biology* 157(10), 2229–2240.
- Averbuj, A., Palomo, G., Brogger, M.I. & Penchaszadeh, P.E. (2012) Diet and feeding of the nassariid *Buccinanops cochlidium* from northern Patagonia, Argentina. *Aquatic Biology* 17, 261–268.
- Averbuj, A. & Penchaszadeh, P.E. (2010a) On the reproductive biology and impact of imposex in a population of *Buccinanops monilifer* from Mar del Plata, Argentina. *Journal of the Marine Biological Association of the United Kingdom* 90, 729–734.
- Averbuj, A. & Penchaszadeh, P.E. (2010b) Reproductive seasonality, oviposition and development of the nassariid whelk *Buccinanops cochlidium* (Dillwyn, 1817) in Patagonia, Argentina. *Journal of Molluscan Studies* 76, 25–32.
- Averbuj, A., Rocha, M. & Zabala, M.S. (2014) Embryonic development and reproductive seasonality of *Buccinanops globulosus* (Nassariidae) (Kiener, 1834) in Patagonia, Argentina. *Invertebrate Reproduction & Development* 58, 138–147.
- Bigatti, G., Giraud-Billoud, M., Vega, I.A., Penchaszadeh, P.E. & Castro-Vazquez, A. (2014) Embryonic development in the Patagonian red snail *Odontocymbiola magellanica* (Neogastropoda: Volutidae): morphology and biochemistry. *Zoologischer Anzeiger-A Journal of Comparative Zoology* 253, 372–381.
- Borzone, C.A. (1995) Ovicápsulas de prosobranquios (Mollusca: Gastropoda) de una playa arenosa expuesta del sur de Brasil. *Iheringia* 79, 47–58.
- Brown, A.C. (1982) The biology of sandy beach whelks of the genus *Bullia* (Nassariidae). *Oceanographic Marine Biology Annual Review* 20, 309–361.
- Cledón, M. & Penchaszadeh, P.E. (2001) Reproduction and brooding of *Crepidula argentina*, Simone, Pastorino and Penchaszadeh, 2000 (Gastropoda: Calyptraeidae). *The Nautilus* 115, 15–21.
- Collin, R. & Spangler, A. (2012) Impacts of adelphophagic development on variation in offspring size, duration of development, and temperature-mediated plasticity. *The Biological Bulletin* 223, 268–277.
- Cumplido, M., Pappalardo, P., Fernandez, M., Averbuj, A. & Bigatti, G. (2011) Embryonic development, feeding and intracapsular oxygen availability in *Trophon geversianus* (Gastropoda: Muricidae). *Journal of Molluscan Studies* 77, 429–436.
- D'asaro, C.N. (1993) Gunnar Thorson's world-wide collection of prosobranch egg capsules: Nassariidae. *Ophelia* 38, 149–215.
- Fretter, V. & Graham, A. (1994) *British Prosobranch Molluscs: their functional anatomy and ecology*. The Ray Society of London, London, UK. 589 pp.
- Gallardo, C.S. & Penchaszadeh, P.E. (2001) Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the southern hemisphere. *Marine Biology* 138, 547–552.
- Marche-Marchad, I. (1980) Sur la stratégie de la reproduction chez le genre *Cymbium* Röding, 1798 (Gastropoda, Volutidae). *Haliotis* 10, 94.
- McEdward, L.R. (1997) Reproductive strategies of marine benthic invertebrates revisited: facultative feeding by planktotrophic larvae. *The American Naturalist* 150, 48–72.
- Miloslavich, P. (1996) Nurse-egg feeding prosobranchs: a comparative biochemical and electrophoretic analysis of eggs and hatchlings. *American Malacological Bulletin* 13, 37–46.
- Pastorino, G. (1993) The taxonomic status of *Buccinanops* d'Orbigny, 1841 (Gastropoda: Nassariidae). *The Veliger* 36, 160–165.
- Pastorino, G. & Penchaszadeh, P.E. (2009) Egg capsules, eggs and embryos of *Trophon acanthodes* (Gastropoda: Muricidae) and its new generic position. *Journal of Molluscan Studies* 75, 337–341.
- Penchaszadeh, P.E. (1971a) Aspectos de la embriogénesis de algunos gasterópodos del género *Buccinanops* d'Orbigny, 1841 (Gastropoda, Prosobranchiata, Buccinidae). *Physis* 30, 475–482.
- Penchaszadeh, P.E. (1971b) Observaciones sobre la reproducción y ecología de *Dorsanum moniliferum* (Valenciennes, 1834) (Gastropoda: Buccinidae) en la región de Mar del Plata. *Neotropica* 17, 49–54.
- Penchaszadeh, P.E. (1973) Nuevas observaciones sobre la reproducción de *Buccinanops gradatum* (Deshayes, 1844) (Gastropoda: Prosobranchiata, Dorsaninae). *Physis Seccion A* 32, 15–18.
- Penchaszadeh, P.E. (1976) Reproducción de Gasterópodos prosobranquios del Atlántico suroccidental. El género *Trophon*. *Physis* 35, 69–76.
- Penchaszadeh, P.E., Averbuj, A. & Cledón, M. (2001) Imposex in gastropods from Argentina (South-Western Atlantic). *Marine Pollution Bulletin* 42, 790–791.
- Penchaszadeh, P. E., de Mahieu, G., Farache, V. & Lera, M. E. (1983) Ecology of the sandy beach gastropod *Mazatlantia aciculata* in Quizandal (Carabobo, Venezuela). *Developments In Hydrobiology* 19, 655–660.
- Penchaszadeh, P.E. & Miloslavich, P. (2001) Embryonic stages and feeding substances of the South American volutid *Voluta musica* (Caenogastropoda) during intracapsular development. *American Malacological Bulletin* 16, 21–31.
- Penchaszadeh, P.E., Miloslavich, P., Lasta, M. & Costa, P.M.S. (1999) Egg capsules in the genus *Adelomelon* (Caenogastropoda: Volutidae) from the Atlantic coast of South America. *The Nautilus* 113, 56–63.
- Penchaszadeh, P.E., Pastorino, G. & Cledón, M. (2002) *Crepidula dilatata* Lamarck, 1822 truly living in the South Western Atlantic. *The Veliger* 45, 172–174.
- Penchaszadeh, P. E. & Rincón A. (1996) Egg capsules and development of *Prunum prunum* (Gmelin, 1791) (Prosobranchia: Marginellidae) from the Venezuelan Caribbean. *The Veliger* 39, 83–86.
- Penchaszadeh, P.E. & Segade, M.E. (2009) Spawn characteristics in *Adelomelon ferussacii* (Donovan, 1824)

- (Gastropoda: Volutidae) from southern Patagonia, Argentina. *The Nautilus* 123, 172–176.
- Petit, R. E. & Coan E. V. (2008). "The molluscan taxa made available in the Griffith & Pidgeon (1833–1834) edition of Cuvier, with notes on the editions of Cuvier and on Wood's Index Testaceologicus." *Malacologia* 50, 219–264.
- Primost, M., Averbuj, A. & Bigatti, G. (in press) Imposex affects spawning in the marine gastropod *Buccinanops globulosus*. *Revista del Museo Argentino de Ciencias Naturales n.s.* 17(2).
- Rawlings, T.A. (1994) Encapsulation of eggs by marine gastropods: effects of variation in capsules from on the vulnerability of embryos to predation. *Evolution* 48, 1301–1313.
- Rivest, B.R. (1992) Studies on the structure and function of the larval kidney complex of prosobranch gastropods. *Biological Bulletin* 182, 305–323.
- Smith, K.E. & Thatje, S. (2013) Nurse egg consumption and intracapsular development in the common whelk *Buccinum undatum* (Linnaeus 1758). *Helgoland Marine Research* 67, 109–120.
- Strathmann, R. (1985) Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* 16, 339–361.
- Voltzow, J. (1994) Gastropoda: Prosobranchia. In: Harrison, F. W. & Kohn, A.J. (Eds), *Microscopic Anatomy of Invertebrates*. Wiley-Liss, Inc., New York. pp. 111–252.