Embryonic development and reproductive seasonality of *Buccinanops globulosus* (Nassariidae) (Kiener, 1834) in Patagonia, Argentina

Andrés Averbuj[a]*, Miriam N. Rocha[b] and S. Zabala[a]

[a]*Centro Nacional Patagónico – CONICET, Bvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina;* [b]*Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Bvd. Brown S/N; 9120 Puerto Madryn, Chubut, Argentina*

Buccinanops globulosus mated all year round, with higher frequency from May to September, prior to spawning months. Gravid females were found between October and March. Oviposition peaked during rising temperatures and longest day-length while hatching peaked with high water temperature and declining daylength. Gravid females measured between 20 and 41 mm in shell length. The spawn consisted on average of 31 egg capsules, each containing 1266 eggs. Embryos usually completed development within each egg capsule by ingesting small fragments of the uncleaved nurse eggs, which were not a limiting resource. Egg capsules with more than one embryo were not common; in those cases, the embryos had different sizes probably related to intracapsular competition for nutrients and were on average smaller than solitary embryos in the other capsules. Embryos hatched as crawling juveniles with a mean hatchling shell length of ~3.4 mm. In a few cases, malformed embryos were found, but it was not a common phenomenon. The information recorded in this study, as the minimum reproductive size and spawning season, is valuable for fisheries management.

Keywords: Gastropoda; nurse eggs; intracapsular development; fishery resource

Introduction

Among species of the Nassariidae Iredale, 1916, spawning and development have been described for species of *Nassarius* (Northern hemisphere), *Bullia,* and *Buccinanops* (Southern hemisphere) (Penchaszadeh 1971; Brown 1982; D'Asaro 1993). In the Nassariidae, both free larval (after short intracapsular period) and direct development may occur within a genus, as for example in *Bullia* spp. (Brown 1982), *Nassarius* spp., and *Dorsanum* spp. (Pechenik 1975; D'Asaro 1993). Nurse eggs may be present in species of this family with direct development. All species of *Buccinanops* including *Buccinanops globulosus* have direct development and ingest nurse eggs (Penchaszadeh 1971; D'Asaro 1993). This may imply a variable number of offspring whose size (=survival chances) become an advantage in uncertain environmental conditions (Collin and Spangler 2012; Smith and Thatje 2013). In *Buccinanops*, the number of embryos per capsule is commonly one, with a variable number of nurse eggs available among species. The exception to this is *Buccinanops cochlidium*, which has a mean of five embryos per capsule and no remnant nurse eggs at the end of development (Averbuj and Penchaszadeh 2010a). The reproductive biology (including reproductive seasonality) of *Buccinanops* species needs to be re-examined in the context of fisheries management (Leiva and Castilla 2002; Averbuj and Penchaszadeh 2010a).

Buccinanops d'Orbigny, 1841, is distributed along the coast of the southwestern Atlantic Ocean. Species of this genus are gonochoric with internal fertilization; adults spawn a variable number of elongated and flexible egg capsules that are attached to the females' own shells (Penchaszadeh 1971; Averbuj and Penchaszadeh 2010a). Embryonic development in this genus is completed within the egg capsule by the ingestion of nurse eggs, and juveniles hatch through a distal opening (Penchaszadeh 1971). Cannibalism may occur in some of these species as observed in *Buccinanops monilifer* (Averbuj and Penchaszadeh 2010b). The number of egg capsules, eggs, and embryos varies among *Buccinanops* species. Cannibalism and competition for food (nurse eggs) are also related to the reproductive output of the females (Averbuj and Penchaszadeh 2010a, 2010b; Smith and Thatje 2013). A description of the developmental biology (developmental time and modality, number and size of eggs, number and size of hatchlings, etc.) of *B. globulosus* will clarify differences among species of the genus.

B. globulosus is distributed from Uruguay (34° S) to Santa Cruz province (48° S) (Rios 2009), in Argentina. In Patagonia, *B. globulosus* lives in temperate coastal waters on soft bottoms of the lower intertidal and upper subtidal zones, usually at depths < 5 m (at low tide). As previously described for this genus, sexual dimorphism

*Corresponding author. Email: averbuj@cenpat.edu.ar
Authors contributed equally to this work

2   *A. Averbuj* et al.

is subtle, with the maximum size in males being smaller than in females (Narvarte 2006; Averbuj et al. 2010). *B. globulosus* is fished for local markets (Ciocco 1999; Narvarte 2006), and exported on a small scale to China (Averbuj Pers. Com.), underlining the importance of increasing knowledge of its reproductive biology. Parameters such as the minimum reproductive size, fecundity (in terms of egg capsules/eggs/embryos per female), spawning season, and its relationship with environmental parameters are also relevant to plan sustainable exploitation (Leiva and Castilla 2002; Averbuj et al. 2010). Although there are several recent studies on this species (Avaca, Narvarte, and Martín 2013; Avaca, Narvarte, Martín, et al. 2013), including some related to reproductive parameters (Narvarte et al. 2008; Avaca et al. 2012), reproductive biology data were not analyzed in the context of fisheries management for *B. globulosus*.

Penchaszadeh's early studies on *B. globulosus* were carried out based on a few individuals collected in the field, and museum specimens, from which he described the egg capsules and aspects of some stages of embryonic development (Penchaszadeh 1971). Our study is based on two years' worth of monthly samples of abundant live material. Environmental conditions were also different 40 years ago, considering the absence of the imposex phenomenon recorded for the first time in Argentina by Penchaszadeh et al. (2001). The study site is affected by marine traffic that has been associated with the imposex phenomenon in Argentina (Penchaszadeh et al. 2001; Bigatti et al. 2009). This caused low fecundity in *B. monilifer* from Mar del Plata (Averbuj and Penchaszadeh 2010b) and embryonic malformation (Cumplido et al. 2011).

In this paper, we describe embryonic development in the context of reproductive seasonality of *B. globulosus* from Bahia Nueva, Argentina.

Materials and methods

Samples and observations were obtained monthly from October 2010 to February 2012, in Bahia Nueva, Golfo Nuevo, Argentina (42°8′S, 65°5′W; Figure 1).

During the sampling period, each month a baited (decomposed lamb meat) trap (see McQuinn and Gendron 1988) was set underwater at the upper level of low tide (<2 m depth), for about 2 h. The samples obtained represented all adult sizes of *B. globulosus*, as the net mesh was <1 cm. At the same time, gravid individuals of *B. globulosus* (Figure 2) were collected manually from the subtidal and lower intertidal zones during extreme low tides. The collection site has fine sand/muddy bottoms. The collected specimens were dissected immediately, sexed by the presence or absence of a vagina and accessory glands, and the total shell length (TSL) measured with a 0.1 mm precision digital caliper.
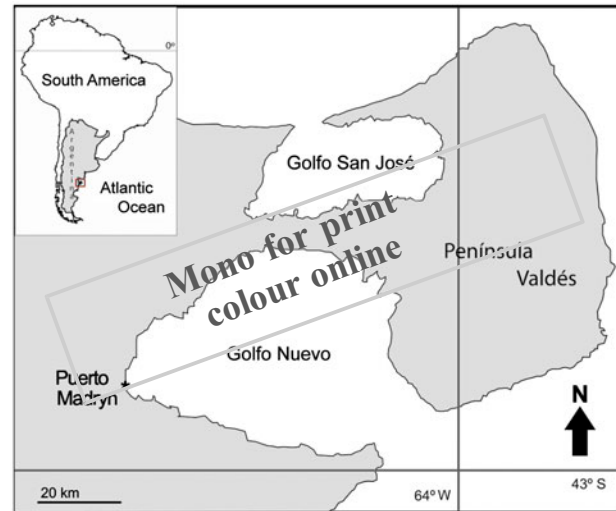

Figure 1. Location of Puerto Madryn in Golfo Nuevo, Argentina.

The egg capsule masses were studied fresh, when this was not possible they were fixed in 5% formalin. To study intracapsular development, all individuals carrying egg capsule masses were used, to represent the complete range of adult shell sizes, and excluding the incomplete or damaged egg capsule masses. Egg capsules were counted in each spawn mass. Four egg capsules were randomly chosen from each snail, detached from the shells, measured to the nearest 0.1 mm (for total length, maximum width, and total stalk length), and dissected.

Development

The number of nurse eggs per capsule was counted under a light microscope. The intracapsular egg diameter was measured before cellular division; for this purpose, 50 eggs were randomly chosen from each egg capsule.

Embryos within the egg capsules were classified into one of eight developmental stages: 0: egg; 1: cell cleavages; 2: early "Veliger" stage; 3: mid "Veliger" stage; 4: late "Veliger" stage; 5: "Pediveliger" stage; 6: pre-hatching; 7: hatchling (Table 1).

Total length of the embryos was measured at each of the developmental stages. At the hatching stage the number of juveniles per capsule was counted and measured in all intact egg capsules. The mean hatching shell length was calculated. All measurements were made with a stereoscopic microscope with a 0.1 mm precision ocular micrometer. To detect the first appearance of the radula, embryos in all developmental stages were dissected.

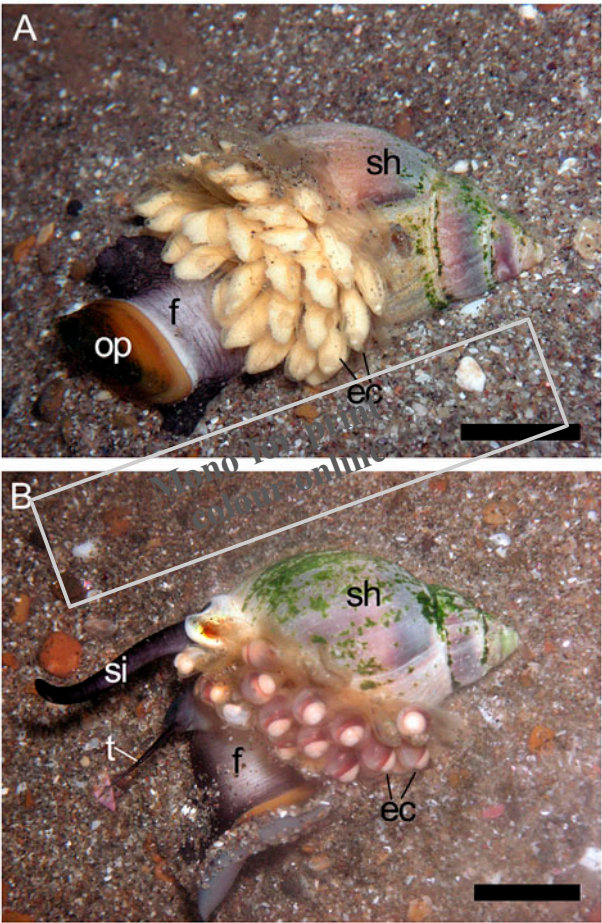All statistical analysis was done with the *Statistica 7.0* statistical package.

Figure 2. Spawn. Gravid *B. globulosus*. (A) Female with a complete spawn (early stage); the white appearance is due to thousands of eggs inside. (B) Female with a complete spawn (hatching stage), with colored shell embryos. Abbreviations: ec, egg capsule; em, embryos; f: foot; t: tentacles; sh: shell; si: siphon. Scale bars: (A)–(B) = 1 cm.

Reproductive seasonality

Monthly water and air temperature (WT and AT) were obtained from the weather service database (CENPAT) and used together with photoperiod (daylength) to compare with reproductive seasonality for the complete period of study.

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. The presence of mating individuals (male individual coupled over a larger female, with male penis introduced under the female's shell and into the gonopore) was recorded, sexes were confirmed by the presence or absence of a penis and pedal gland, and individual TSL was measured to assess the minimum reproductive size.

Table 1. Embryonic intracapsular development.

Stage	Description	Mean embryos size (mm)
0 (Egg)	Round and whitish, before cellular cleavage	0.204 ± 0.003 (0.200–0.212) $n = 3600$
1 (Cell cleavages)	Embryo with 2–8 macromeres and micromeres	0.27 ± 0.05 (0.204–0.344) $n = 23$
2 (Early "Veliger")	Translucent oval shaped embryo with incipient ciliated velum, "larval" kidneys, mouth and empty stomach	0.28 ± 0.04 (0.241–0.365) $n = 23$
3 (Mid "Veliger")	More conspicuous velum, mouth and oesophagus, increasing quantities of nurse eggs inside the stomach	0.55 ± 0.07 (0.410–0.650) $n = 20$
4 (Late "Veliger")	Large embryo, stomach full of eggs. Completely developed velum with cilia. First calcified translucent shell. Incipient tentacles with eyes	0.77 ± 0.102 (0.480–0.890) $n = 16$
5 ("Pediveliger")	Developed foot and white thin shell. Conspicuous tentacles with eyes. Stomach reduced and the velum disappears.	1.13 ± 0.13 (0.920–1.320) $n = 20$
6 (Pre hatching)	Crawling stage, shell grows coiled. Juvenile with calcified white shell or brown-purple colored. Apex is not calcified and the stomach (almost empty) is visible through it	2.65 ± 0.30 (2.100–2.980) $n = 22$
7 (Hatchling)	Crawling juvenile miniature of the adult	3.37 ± 0.44 (2.720–3.950) $n = 68$

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

Results

All of the 75 adults carrying egg capsules that we examined were females with a shell length of 20.7–41.2 mm. There were no significant differences between the sizes of mating and spawning females (df = 74, t = 0.491, p = 0.624).

Egg masses consisted of 31.1 ± 4.3 egg capsules (mean $\pm$ SD) (range = 15–49; n = 75) attached to the female's shell by means of short stalks. The stalks measured 0.87 ± 0.22 mm (range = 0.53–1.76, n = 300). Egg capsules were rectangular in shape and flattened, measuring 4.14 ± 0.73 mm (range = 3.16–6.16, n = 300) in length and 4.5 ± 0.65 mm (range = 2.86–6.86, n = 300) in maximum width. Table 2 summarizes reproductive aspects.

Development

The mean egg diameter prior to segmentation was 204.0 ± 3.0 µm (mean $\pm$ SD) (n = 3600). Each egg capsule contained 1266.5 ± 302.7 eggs (range = 762–1729; n = 75) (Table 1, Figure 3(A)). Commonly, only one egg (mean = 1.015, range = 1–3) developed completely and hatched as a miniature snail. The remaining eggs were ingested, uncleaved, by the developing snail; these nurse eggs were available in the egg capsules at all stages until the pre-hatching stage (and in some cases after hatching).

The cleavage pattern was characterized by the appearance of a conspicuous polar body before the first cellular division and subsequent spiral holoblastic cleavage (Figure 3(B)). The morulae and gastrulae stages, as well as a "trochophore" stage, were not observed in this study. The early "Veliger" stage showed a rudimentary mouth and esophagus, a ciliated line surrounding the mouth (undeveloped velum), and a pair of conspicuous "larval" kidneys (Figure 3(C) and (D)) with four visible large cells at each side of the cephalic region that rapidly

Table 2.   Mating and oviposition in the field during the period of study.

| Months | Mating | Egg capsules | | |
		Stage 0–1	Stage 2–7	Empty
Jan	+	++	++	+
Feb	+	+	+++	++
Mar	+	−	++	+++
Apr	+	−	−	−
May	+++	−	−	+
Jun	+++	−	−	−
Jul	+++	−	−	−
Aug	+++	−	−	+
Sep	+++	−	−	−
Oct	++	+	+	−
Nov	++	++	−	−
Dec	+	+++	−	−

Note: +++ = High, ++ = medium, + = low frequency, − = not observed.

disappeared at the time the embryo began to feed on the nurse eggs. At the end of the early "Veliger" stage, the velum was more developed (Figure 3(E)) and the embryos began ingesting the nurse egg particles with the velar lobes and through the mouth. Ingestion of entire eggs was not observed in this study, corroborated by dissection of embryo stomachs at every stage that showed no entire egg inside. Eggs were attracted to the mouth by ciliated velar currents and then egg fragments entered the mouth. The eggs particles were found in the stomach from early "Veliger" to pre-hatching stages (Figures 3(E)–(I) and 4(A)–(F)). The ingestion of nurse eggs was rapidly reflected in a size increment. The number of eggs within the egg capsule decreased as the embryonic size increased. This is evidenced from early "Veliger" to "Pediveliger", and more intensively at the pre-hatching and hatching stages (Figure 5). The digestion of the eggs and embryonic growth occurred simultaneously with the ingestion throughout the development.

Throughout the mid "Veliger" stage, velum development was complete and the total embryonic size rose with increasing stomach content (Figure 3(F) and (G)); at the end of this stage, a pair of tentacles appeared between the upper area of the velar lobes (more easily observed at beginning of late "Veliger" stage, Figure 3(H)). During the late "Veliger" stage, the tentacles grew and a dark eye appeared at its base. The "Pediveliger" embryo was characterized by the development of a foot (Figures 3(I) and 4(A)), which became functional by the end of this stage, and a thin translucent shell (Figure 4(B) and (C)). Another organ developed in this stage was the radula (observed as a refrigent toothed structure).

The growth and the posterior coiling of a whitish shell occurred as the foot developed (Figure 4(B)–(F)) and the velum disappeared (Figure 4(D)). This coiled growth of the shell occurred towards the anterior direction, but before hatching calcification took place also in the opposite direction (towards the posterior of the shell) enclosing the apex region (Figure 4(F) and (G)). At the end of the process, the embryo became a crawling juvenile, but remained inside the egg capsule until the shell apex (a zone occupied by the residual of a sac which was formerly the stomach filled with eggs) was completely closed (Figure 4(H)). The shell was colored purple to brown, and the epidermis that was previously white became dark colored, typical of adults of this genus in the area (Figure 4(G) and (H)). Occasionally, at the hatching stage, a few nurse eggs were still observed within the capsule.

An embryo hatched from each egg capsule (1.015 ± 0.023; n = 58), with the exceptions of five females that had one egg capsule each, in which two to four embryos occurred simultaneously. The mean hatched embryonic shell length in egg capsules with one embryo was 3.37 ± 0.44 mm (2.31–4.04; n = 68), whereas the mean shell

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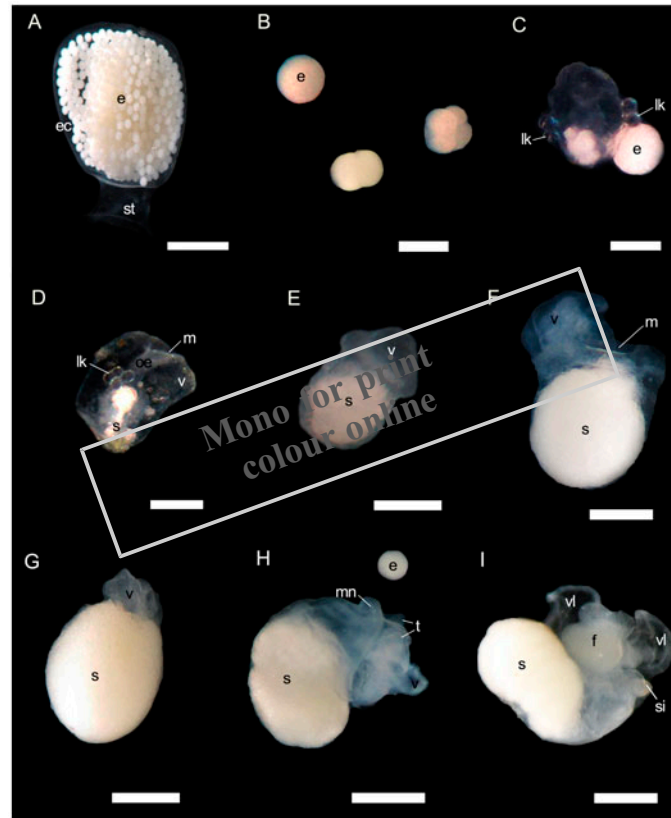
Invertebrate Reproduction & Development   5

Figure 3. Embryological development. (A) Egg capsule full of eggs (stage 0). (B) Egg and cellular cleavage stages (2 and 8 macromeres and micromeres). (C) Early "Veliger" with "larval" kidneys at both sides of the embryo close to a nurse egg, egg particles can be observed through the digestive tract. (D) Early "Veliger"; note the "larval" kidneys (4-cells). (E) Early "Veliger" stage embryo with developing velum and increasing stomach content (egg particles inside). (F) Mid "Veliger" stage embryo; note increasing size and stomach content and more developed velum. (G) Mid "Veliger" stage embryo full of egg particles; note size enlargement. (H) Late "Veliger" stage embryo with totally developed, expanded velum (ciliated), short tentacles. (I) "Pediveliger" stage embryo, velum with two expanded velar lobes, and developing foot; evident coiling growth. Abbreviations: e: egg; ec: egg capsule; f: foot; m: mouth; mn: mantle; lk: "larval" kidneys; oe: esophagus; t: tentacles; s: stomach; si: siphon; st: stalk; v: velum; vl: velar lobes. Scale bars: (A): 2 mm; (B)–(F): 200 μm, (E): 150 μm, (G): 250 μm, (H)–(I): 300 μm.

length of embryos sharing an egg capsule (space and nutritional resources) was 2.49 ± 0.73 mm ($n = 14$). There were also different hatching sizes between embryos of different egg capsules (Figure 4(G) and (H)). The juveniles crawled from the egg capsule through a distal opening, which is an apical ridge opposite the stalk (Figure 4(H)).

Abnormal embryos were recorded sporadically ($n = 3$ from different spawn) in this study. They had an altered general shape, and organs such as the velum, mouth esophagus were not easily identified (Figure 6), but in all cases embryos were mobile and alive.

Reproductive seasonality

Water temperature (WT) varied seasonally between 10 °C in September, at the end of the Winter, and 18 °C in March (late Summer). Mean AT varied between 7 °C in July–August and 22 °C in January. The seasonality of both parameters and photoperiod (daylength) together with oviposition is shown in Figure 7. Mating was observed in the field all year round, increasing in frequency from May (with short daylength and decreasing WT and AT) to September (low WT and increasing daylength and AT), prior to the beginning of oviposition (October). Copulation occurred between a couple (one male and one female) or aggregations of snails (up to six males and two females). Mating males and females measured 15.6–26.8 ($n = 173$) and 17.3–38.4 ($n = 98$) in shell length, respectively. All seasonality of reproduction is summarized in Table 3.

The females carrying egg capsules in stages 0–1 (recently laid, Figure 3(A)) occurred from October after the mating peak to February (with a peak in December); however, occasionally premature spawn occurred and was reflected in advanced stages in October and empty
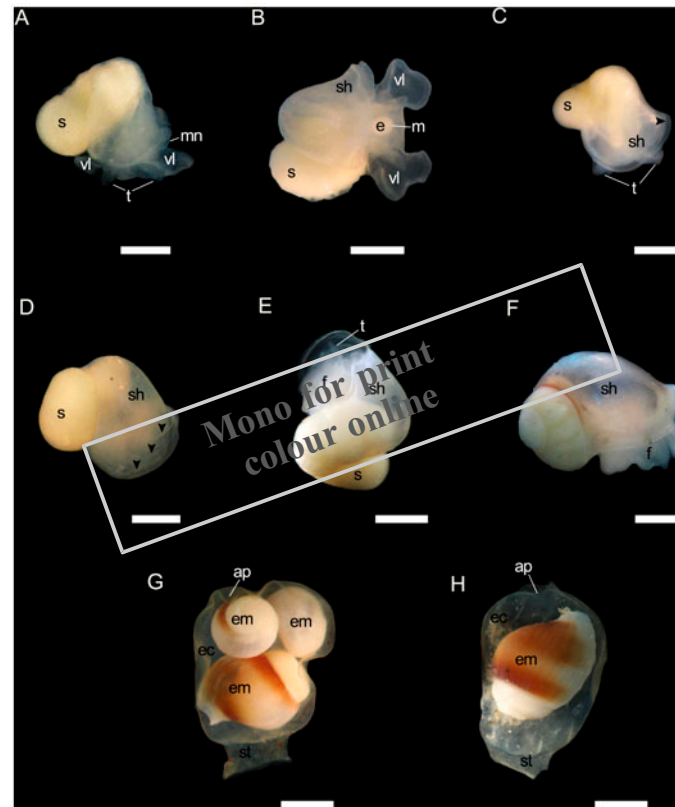
6   *A. Averbuj* et al.

Figure 4.   Embryological development. (A) "Pediveliger" stage embryo; note coiled body, stomach content and velum (2 velar lobes). (B) "Pediveliger" stage embryo with thin translucent shell, developed tentacles, and expanded velar lobes with a nurse egg close to the mouth. (C) "Pediveliger" stage embryo with growing coiled shell; note growth line (arrow) at the shell ridge. (D) Pre-hatching stage with 1-whorl translucent shell and stomach still visible and full of egg particles; note growth lines (arrows). (E) Pre-hatching stage embryo; the velum is absent and a developed foot is present. (F) Pre-hatching stage embryo with colored shell almost completely calcified in the apex, and functional foot. (G) Embryos sharing an egg capsule; note the difference in size and color of their shells. (H) Hatching stage embryo, ready to emerge through the apical ridge. Abbreviations: e: egg; ec: egg capsule; f: foot; m: mouth; mn: mantle; ap: apical ridge; t: tentacles; s: stomach; sh: shell; st: stalk; vl: velar lobes. Scale bars: (A): 300 µm; (B): 400 µm; (C)–(D): 600 µm; (E): 700 µm; (F): 900 µm; (G)–(H): 1500 µm.
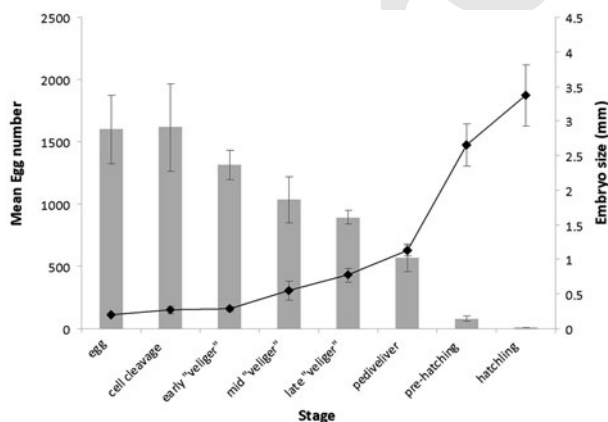

Figure 5.   Variation of egg per capsule and embryo size (mm) vs. stages of development. Gray bars and black dotted line express Mean ± SD of mean egg number and mean embryo size, respectively.

egg capsules in May and August. Stages 2–7 (developing embryos, Figure 3(B)) were observed from January to March. In March (high WT and dropping AT and daylength), most females were free of egg masses or possessed only residual empty capsules; recently, hatched juveniles were observed in the field at that time. Developmental time, estimated from the spawn peak to the hatching peak, was about 3 months.

Discussion

Development

As previously studied in other *Buccinanops* species, all individuals carrying egg capsules were females (Averbuj and Penchaszadeh 2010a, 2010b), which is probably a generic condition of females attaching the egg capsules to their own shells, as it was recorded *in situ* for *B. cochlidium* (Averbuj and Penchaszadeh 2010a).
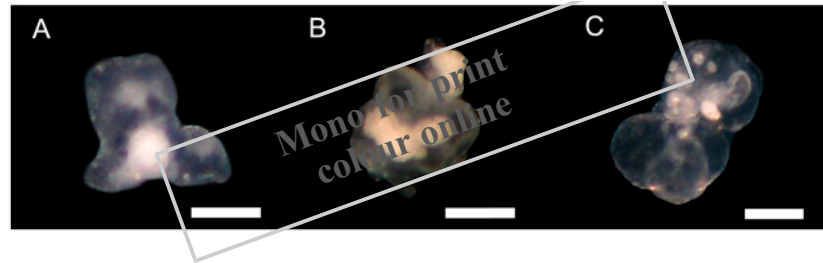
Figure 6.   Embryonic malformation. Early stages of development with abnormal developmental morphology. Scale bars: (A)–(C): 100 µm.
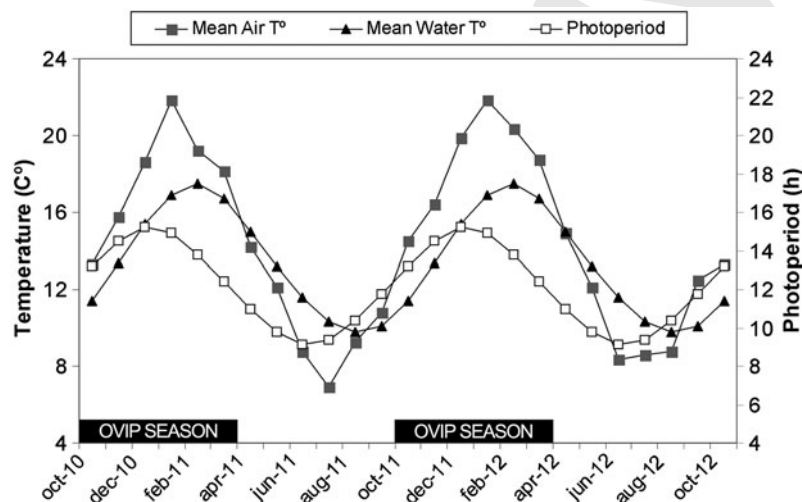

Figure 7.   WT and AT, photoperiod, and spawning period (October 2010–February 2012).

AQ12   Table 3.   Reproductive parameters of *B. globulosus*.

Spawning females shell length	Egg capsules per female	Eggs per capsule	Egg diameter (µm)	Hatchlings per capsule	Hatchlings length (mm)
26.34 ± 4.31 (20.7–41.2) $n = 75$	31.06 ± 8.3 (15–49) $n = 75$	1266.55 ± 302.7 (762–1927) $n = 100$	0.204 ± 0.03 (200–212) $n = 3600$	1.015 ± 0.023 (1–4) $n = 58$	3.37 ± 0.44 (2.72–3.95) $n = 68$

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

B. globulosus has complete intracapsular development with embryos that hatch as crawling juveniles, as in many other neogastropods (Pechenik 1986; Fretter and Graham 1994). The nutritional resources required for embryos to achieve the hatching stage are provided by oophagy as in all other studied *Buccinanops* (Penchaszadeh 1971) or the genus *Trophon* (Penchaszadeh 1976). The addition of nutrients into the small quantities of intracapsular fluids may also occur as in *Buccinum* spp. (Miloslavich 1996), but this was not determined in this study. The presence of "larval" kidneys in early stages of development in this study, that were associated with intracapsular nutritional absorption (Rivest 1992; Brante et al. 2009), might be related to the presence of nutritional fluids in the capsule that complement nurse egg feeding, which begins later in more advanced stages of development. Cannibalism was not observed in *B. globulosus* in contrast with observations of *B. monilifer* (Averbuj and Penchaszadeh 2010b) or *Nassarius festivus* (Chiu et al. 2010).

The egg capsules always had some remnant nurse eggs at the hatching stage, suggesting that it was not a limiting factor for the embryo growing inside (size). This is in contrast to *B. cochlidium* with a mean of five embryos per capsule that compete for nurse egg resources and deplete them at the "Veliger" stage (Averbuj and

8   *A. Averbuj* et al.

Penchaszadeh 2010a). The lack of competence of the single embryo developing in *B. globulosus* egg capsules was reflected in the nurse egg ingestion rate (eggs/embryo), modality, and speed. "Veliger" embryos and later stages of development attract the nurse eggs with the help of velar movements (intracapsular currents) and ingest the uncleaved nurse eggs as small particles (throughout the complete developmental time). Opposite modalities were reported for *B. cochlidium* and *Buccinum undatum* with several embryos per capsule, which engulf entire eggs in a short period of time, resulting in remarkable hatching size differences of siblings within an egg capsule (Averbuj and Penchaszadeh 2010a; Smith and Thatje 2013).

B. globulosus mean per female fecundity may be expressed as a spawn of ~40,000 eggs (mean diameter = 204 μm) and 36 hatchlings measuring 3.37 mm in shell length. These numbers are remarkably lower than the 450,000 eggs and 800 embryos, with a shell length of 4 mm of *B. cochlidium* (Averbuj and Penchaszadeh 2010a), and even lower than the 490,000 eggs laid by *Buccinum isaotakii* from Japanese cold waters, while the number of total hatching embryos is 8000, with a shell length of 2.5 mm (Ilano et al. 2004). By contrast, the average number of eggs available to each embryo is larger: 576 in *B. cochlidium* and 61 in *B. isaotakii* to 1247 in *B. globulosus*. The hatching size: Adult size ratio was approximately 3% (*B. cochlidium* adult size about 120 mm), 2% (*B. isaotakii* adult size about 100 mm), and 8.5% (*B. globulosus* adult size about 40 mm), respectively. These differences may be explained by different competitiveness for the nurse egg resources within the capsules between species, regardless of (and probably related to) environmental divergences. Observations on other *B. globulosus* populations indicate that the number of embryos per capsule, and the available nurse eggs to each individual, varies among populations from different sites in the north patagonic gulf regions (unpublished data). Further studied should focus on this aspect. A similar pattern was recorded for *Concholepas concholepas* in Chile (Fernández et al. 2007).

The time elapsed between the peak of oviposition (December) and the peak of hatching (March) suggests that the total developmental time of *B. globulosus* is about 3 months. This is similar to other neogastropods from this region, e.g. *B. cochlidium* (4 months; Averbuj and Penchaszadeh 2010a), *Trophon geversianus* (3–4 months; Cumplido et al. 2011), *Odontocymbiola magellanica* (2–3 months; Bigatti 2005), and *Adelomelon ancilla* (5–6 months; Zabala 2013).

Malformed embryos observed during this study coincided with other records from the same site for *T. geversianus* (Cumplido et al. 2011) and also observed in the volutid *A. ancilla* (Zabala 2013) collected near Puerto Madryn harbor (<5 km). In all cases, the morphology of the embryos was abnormal, their aspect and shapes modified (e.g. the shell curls but not following the collumelar axis), probably related to environmental pollution (TBT among other compounds associated to marine traffic) recorded in the area (Bigatti et al. 2009).

Reproductive seasonality

The reproduction of intertidal marine invertebrates may be influenced by photoperiod (daylength) and temperature (water and air: WT and AT), as well as food availability (Sternberg et al. 2010). Moreover, gastropods are sensitive to changes in the local environment. Consequently, their activities exhibit seasonal and circadian variations (Chase 2002) and are also able to anticipate changing conditions using internal timing mechanisms (Chase 2002; Sternberg et al. 2010).

The reproductive activities of the studied population of *B. globulosus* include mating that occurs all year round (peak previous to spawning), oviposition that begins in October and continues until January (peak in December), and intracapsular development that continues until March when hatchlings emerge (peak). Greater mating activity is related to low (declining and rising) parameters, and the cue to begin peaking may be the low daylength that might be related to gametogenic cycle control (Sternberg et al. 2010). Oviposition begins with low WT (rising AT and daylength) and stops when both WT and AT are high (maximum daylength). Development occurs with increasing WT and AT, while hatching seems to be related to maximum WT (other parameters declining).

According to Sternberg et al. (2010), daylength appears to be the predominant environmental signal that regulates reproductive tract recrudescence. Secondary cues include temperature and nutrition, which control the timing of breeding and egg laying. *B. globulosus* is a low intertidal and very shallow subtidal (<2 m in this study) species; extreme amplitude of AT may occur seasonally and even daily. It is possible that a complex combination of daylength, AT, and WT is associated with reproductive seasonality (Sternberg et al. 2010).

Minimum reproductive size is usually considered a management parameter in fisheries biology (Leiva and Castilla 2002). A minimum mating female shell length of 17.3 mm and minimum gravid female size of 20.1 mm represent values of sexual maturity. Although there were no significant differences between these parameters, the former was shorter than the later suggesting that *B. globulosus* females may begin copulation before being ready to spawn. In any case, both parameters should be considered in proper fisheries management policies to prevent resource depletion if

large scale exploitation is established for this species (Leiva and Castilla 2002; Averbuj et al. 2010). Similar suggestions based on reproductive information were made for *B. cochlidium* (Averbuj and Penchaszadeh 2010a; Averbuj et al. 2010), and other neogastropods from the same region such as the muricid *T. geversianus* (Cumplido et al. 2010, 2011) or the volutid *A. ancilla* (Penchaszadeh et al. 2009). In this sense, it is relevant that in other *B. globulosus* populations, within the north Patagonic gulf, individuals attain larger sizes (Narvarte et al. 2008; Avaca, Narvarte, Martín, et al. 2013). Females carrying egg capsules should not be collected.

The values recorded herein may be a good estimation for other *B. globulosus* in Golfo Nuevo; on the other hand, it is known that species may differ in individual sizes, and consequently in reproductive maturity size from different localities as proposed by Narvarte et al. (2008) for Golfo San Matías populations. This phenomenon was also recorded for the buccinid *B. undatum*, from the Northern hemisphere, in which maturity size may vary from 5 to 8 cm depending on the sampling site (Martel, Larrivée, and Himmelman 1986; Martel, Larrivée, Klein, et al. 1986, 1986b; Kideys et al. 1993).

Marine gastropod fisheries are relevant in the region, with Chile as the most developed country (Leiva and Castilla 2002). However, Argentina is growing rapidly as a consequence of resource deployment and international markets (Leiva and Castilla 2002). *B. globulosus* is a fishery resource with growing interest for local markets (Narvarte 2006) and incipiently exported to China (Averbuj Pers. Com.). Recent suggestions for *B. globulosus* fishery management have mainly focused on population dynamics studies (Narvarte 2006; Narvarte et al. 2008; Avaca, Narvarte, and Martín 2013; Avaca, Narvarte, Martín, et al. 2013). A proper management of this species as a fishery resource should also consider excluding snails carrying egg capsules and capturing only snails over the minimum mating/oviposition size. The extended developmental period and absence of free larval (dispersive) stages that may reduce stock renewal emphasizes the need of establishing regulative policies for sustainable exploitation of *B. globulosus*.

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