1 ORIGINAL ARTICLE

Nurse egg consumption and intracapsular development in the common whelk *Buccinum undatum* (Linnaeus 1758)

4 **Kathryn E. Smith · Sven Thatje**

7 **Abstract** Intracapsular development is common in marine
8 gastropods. In many species, embryos develop alongside
9 nurse eggs, which provide nutrition during ontogeny. The
10 common whelk *Buccinum undatum* is a commercially
11 important North Atlantic shallow-water gastropod. Devel-
12 opment is intracapsular in this species, with individuals
13 hatching as crawling juveniles. While its reproductive cycle
14 has been well documented, further work is necessary to
15 provide a complete description of encapsulated develop-
16 ment. Here, using laboratory reared *B. undatum* egg masses
17 from the south coast of England intracapsular development
18 at 6 °C is described. Number of eggs, veligers and juveniles
19 per capsule are compared, and nurse egg partitioning, timing
20 of nurse egg consumption and intracapsular size differences
21 through development are discussed. Total development took
22 between 133 and 140 days, over which 7 ontogenetic stages
23 were identified. The number of both eggs and veligers were
24 significantly related to capsule volume, with approximately
25 1 % of eggs developing per capsule. Each early veliger
26 consumed nurse eggs rapidly over just 3–7 days. Within
27 each capsule, initial development was asynchronous, but it
28 became synchronous during the veliger stage. No evidence
29 for cannibalism was found during development, but large
30 size differences between embryos developing within each
31 capsule were observed, and occasionally 'empty' veligers
32 were seen, which had not successfully consumed any nurse
33 eggs. These results indicate a high level of competition for
34 nurse eggs within each capsule during development in the
35 common whelk. The initial differences observed in nurse
36 egg uptake may affect individual predisposition in later life.

Keywords Intracapsular development · *Buccinum*
undatum · Nurse egg partitioning · Competition ·
Reproduction

Introduction

Many marine gastropods undergo intracapsular development inside egg capsules (Thorson 1950; Natarajan 1957; D'Asaro 1970; Fretter and Graham 1985). Embryos develop within the protective walls of a capsule that safeguards against factors such as physical stress, predation, infection and salinity changes (Thorson 1950; Pechenik 1983, 1999; Strathmann 1985; Rawlings 1995, 1999). Periods of encapsulation vary; some species are released as veligers and undergo a plank-tonic stage before reaching adult life (mixed development), while others display direct development, hatching from capsules as crawling juveniles (Natarajan 1957; D'Asaro 1970; Pechenik 1979). When direct development occurs, embryos are often accompanied in a capsule by nurse eggs, non-developing food eggs, which provide nutrition during development (Thorson 1950; Spight 1976b; Rivest 1983; Lahbib et al. 2010). These are usually indistinguishable from embryos in the very early stage of ontogeny and are consumed during development, potentially increasing size of juveniles at hatching (Thorson 1950). In some species, nutrition may also be provided by intracapsular fluid or protein from capsule walls (Bayne 1968; Stöckmann-Bosbach 1988; Moran 1999; Ojeda and Chaparro 2004).

Generally speaking, nurse egg consumption occurs over a period of several weeks or months. It commences some

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weeks into development as embryos form and nurse eggs are then slowly consumed throughout much of development (Chaparro and Paschke 1990; Ilano et al. 2004; Lahbib et al. 2010). The number of nurse eggs consumed during this period varies across species. Ratios range from 1.7 nurse eggs per embryo in the Pacific shallow-water muricid *Acanthinucella spirata* (Spight 1976a), to between 50,000 and 100,000 nurse eggs per embryo in the North Atlantic deep-sea buccinid *Volutopsius norwegicus* (Thorson 1950). Often, within a species, the nurse egg to embryo ratio varies from capsule to capsule within one clutch (Thorson 1950; Spight 1976a). For example, Rivest (1983) found this ratio in the buccinid *Lirabuccinum dirum* to vary from 11 to 46 across capsules. Similar differences have been reported for other gastropods (Natarajan 1957; Spight 1976a). Within a capsule however, there is usually little variation in the number of nurse eggs ingested by each embryo, with all embryos generally being equal in their ability to consume. Any differences observed are minimal, and juveniles hatching from each capsule are normally of a very similar size (Natarajan 1957; Spight 1976a; Rivest 1983; Chaparro and Paschke 1990; Chaparro et al. 1999; Lloyd and Gosselin 2007). Large size differences amongst capsulemates are unusual, but have been reported in some species of muricid gastropod (Gallardo 1979; González and Gallardo 1999; Cumplido et al. 2011). In gastropods, the number of eggs inside a capsule is usually positively related to capsule size. Within a species, larger capsules hold more eggs and more developing embryos (Gallardo 1979; Pechenik et al. 1984; Miloslavich and Dufresne 1994). The relationship between capsule size and number of eggs (including nurse eggs) has, however, previously been shown to be stronger than the relationship between capsule size and number of developing embryos (Spight 1976b). In some cases, the number of developing embryos within a capsule has been found to be independent of capsule volume. This suggests that embryos are distributed at random, while nurse eggs are regularly placed amongst capsules (Rivest 1983; Chaparro et al. 1999).

Intracapsular development and nurse egg and embryo partitioning have been investigated in several species of marine gastropod (Natarajan 1957; D'Asaro 1970; Spight 1976a; Rivest 1983; Cumplido et al. 2011). While some attempts have been made to examine encapsulated development in the common whelk *Buccinum undatum* (Portmann 1925; Fretter and Graham 1985; Nasution 2003), it has not yet been fully described. Nasution (2003) gives the most in-depth account of development to date, but his descriptions are incomplete and his reports of nurse egg consumption do not match our observations. Descriptions from Portmann (1925) better fit our observations but lack detail. There are also gaps in the current literature, and very limited knowledge exists on nurse egg partitioning and intracapsular embryo size ranges through development. The common whelk is a scavenger found widespread in coastal areas in the North Atlantic. It is generally found from the shallow subtidal down to a few hundred metres of water depth (Valentinsson et al. 1999; Valentinsson 2002; Rosenberg 2009), with a latitudinal range from 38°N to 79°N spanning the North Atlantic and Arctic Oceans (OBIS http://iobis.org/mapper/?taxon=Buccinumundatum). *Buccinum undatum* is an important commercial species, providing locally valuable fisheries in several areas around the North Atlantic including the UK, the USA and Canada (Hancock 1967; Morel and Bossy 2004). It has been suggested as a good candidate for aquaculture (Nasution and Roberts 2004) and globally, demand for it is continuously increasing (Department of Marine Resources www.maine.gov/dmr/rm/whelks.html). Its reproductive cycle has been well documented across its range (Hancock 1967; Martel et al. 1986a, b; Kideys et al. 1993; Valentinsson 2002). Females group to deposit small creamy coloured spherical egg capsules (Martel et al. 1986a). Each lays approximately 80–150, which collectively can create large egg masses of 100–1,000 of capsules (Fretter and Graham 1985; Valentinsson 2002). The time of year for spawning varies in this species across its distribution. In coastal waters of the UK, egg capsules are laid during the autumn and winter months (predominantly late November–January) as annual water temperatures drop below 9 °C (Hancock 1967; Kideys et al. 1993). In the northwest Atlantic, egg laying instead takes place in spring (late May to mid July) as water temperatures warm (approximately 2–39 °C) (Martel et al. 1986a). Intracapsular development takes between 2.5 and 9 months across the species range (Fretter and Graham 1985; Martel et al. 1986a; Kideys et al. 1993; Nasution 2003). Given the widespread distribution of *B. undatum*, its current commercial importance and its potential as a future candidate for aquaculture, it is important to understand fully the development in this species.

Here, we examine intracapsular development in *B. undatum* using a population from the south coast of England, at the southern end of the species distribution. Number of eggs and number of developing veligers and juveniles are examined through development. Ontogenetic stages are described in detail including nurse egg partitioning, nurse egg consumption and intracapsular ranges in embryo sizes.

Materials and methods

Embryonic development

In order to study the intracapsular development in *B. undatum,* 150 adults were collected from Viviers UK in late November 2009 (www.fishmarketportsmouth.co.uk).

168 Adults were originally gathered from the Solent, UK (50°39′
169 N, 001°37′ W) from approximately 15 m water depth by
170 Viviers using whelk traps. They were taken to the aquarium
171 at the National Oceanography Centre, Southampton, and
172 placed in a large outdoor tank with continuous seawater flow
173 through. Whelks were fed scrap fish ad libitum 3 times a
174 week, and the tank was checked daily for laying activity. Egg
175 laying occurred between early December 2009 and early
176 February 2010, predominantly when water temperatures fell
177 below 8 °C. All egg masses were laid on aquarium walls
178 within a few centimetres of the water line.

179 Three egg masses laid in early January were removed for
180 examination through development. Each was left undis-
181 turbed for 24 h after egg laying had ceased before being
182 removed from the aquarium walls and maintained in 1 μm
183 filtered seawater at 6 °C. This was close to local water
184 temperatures, which ranged 4.0–8.3 °C between January
185 and March 2010 (local temperature data obtained brambl-
186 emet (www.bramblemet.co.uk/) and CEFAS (www.cefas.
187 defra.gov.uk/our-science/observing-and-modelling/monitor
188 ing-programmes/sea-temperature-and-salinity-trends/presen
189 tation-of-results/station-22-fawley-ps.aspx) databases). Each
190 week 3 capsules were randomly selected and dissected from
191 each egg mass. For each mass, the outer layer of egg capsules
192 was removed prior to any examination as these are often
193 empty or hold a very small number of eggs. The contents of
194 each capsule were examined, ontogenetic stage was descri-
195 bed and eggs or embryos were measured along their longest
196 axis using an eyepiece graticule. When a capsule contained
197 loose eggs, approximately 20 were measured per capsule.
198 When embryos were present of any age, all were measured
199 (on average 9–11). From the trochophore stage and for the
200 duration of nurse egg feeding, 3 capsules per egg mass were
201 examined daily to determine the duration of short ontoge-
202 netic stages and the time taken to consume nurse eggs. Each
203 egg mass was also examined non-invasively each week.
204 Transparency of the capsule wall approximate
205 ontogenetic stage to be determined, and the percentage of the
206 mass at each developmental stage was estimated (Fig. 1a, b).
207 From this, embryonic development was described, including
208 ontogenetic stages, developmental timing, change in embryo
209 size, nurse egg partitioning and intracapsular size differ-
210 ences during development. Ontogenetic stages were defined
211 as egg, trochophore, early veliger, veliger, pediveliger, pre-
212 hatching juvenile and hatching juvenile (see below for
213 descriptions).

214 Intracapsular contents through development

215 In order to investigate the intracapsular contents, *B. und-*
216 *atum* egg masses were collected from Southampton Water

217 (Southampton, UK, 50°50′ N, 001°19′ W) from approxi-
218 mately 10 m water depth between January and March,
219 2009 and 2010. Seawater temperatures ranged from 4 to
220 10 °C during these periods. Collection took place using
221 beam trawls deployed by the University of Southampton
222 research vessel *RV Callista*. In total, 35 egg masses were
223 collected, all of which were fixed in 4 % formalin for later
224 investigation.

225 Capsules were selected at random from all 35 egg
226 masses. As above, the outer layer of each egg mass was
227 removed prior to this. *Buccinum undatum* egg capsules are
228 relatively ellipsoid in shape, with a convex/concave face.
229 Each capsule was measured in three dimensions (length,
230 width, depth; ±0.01 mm) using digital calipers (Absolute
231 digimatic caliper, Mitutoyo (UK) Ltd, Andover, UK). From
232 these measurements, the volume of each egg capsule was
233 estimated using an adaptation of equations used by Pech-
234 enik (1983), Rawlings (1990). The following equation was
235 used.

$$V = (\pi ab) \times c$$

237 where a = length/2, b = width/2 and c = depth.

238 Each capsule was then dissected, number of embryos
239 was counted (using a bogorov counting chamber) and
240 ontogenetic stage determined under a compound-micro-
241 scope. To investigate the relationship between capsule
242 volume and number of eggs or veligers within a capsule,
243 approximately 160 capsules at egg stage (i.e. prior to any
244 development occurring; 15 egg masses; 10–11 capsules
245 from each) and 160 capsules at veliger stage were exam-
246 ined (18 egg masses, 8–9 capsules from each). Capsules
247 ranging from 5.15 to 10.49 mm length (39.0–287.5 mm³
248 volume) were compared. Regression analyses were carried
249 out to examine the relationship between capsule volume
250 and number of eggs, and capsule volume and number of
251 veligers (Fig. 1a).

252 Change in number of embryos per capsule during
253 development was investigated by examining 100 capsules
254 at veliger stage (12 egg masses, 8–9 capsules from each)
255 and 100 capsules at pre-hatching juvenile stage (9 egg
256 masses, 11–12 capsules from each). Since the number of
257 eggs and embryos per capsule is related to capsule size,
258 for this comparison, capsules of a narrower size range
259 (length 6–8 mm, volume 52.4–146.2 mm³) were used.
260 This eliminated the possibility of any change in number
261 of embryos per capsule to be influenced by capsule size.
262 Only veligers containing nurse eggs were counted; it was
263 presumed veligers with no nurse eggs would not develop
264 successfully. An unpaired t test was carried out to
265 compare number of veligers per capsule to number of
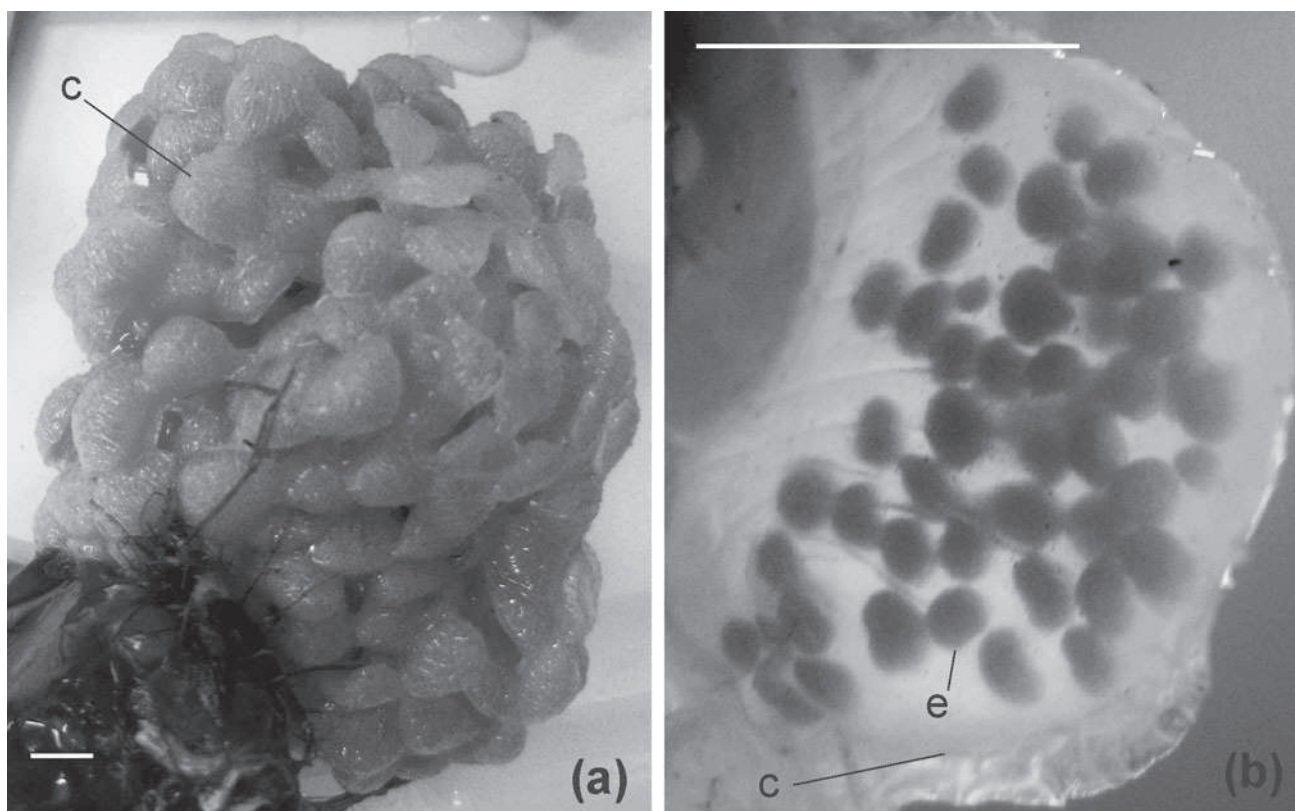266 pre-hatching juveniles per capsule.

Fig. 1 **a** Egg mass of *B. undatum* showing individual capsules. **b** A large individual egg capsule showing many developed embryos inside, post nurse egg consumption. *Scale bars* represent 5 mm. *c* Capsule, *e* embryo

Results

Ontogenetic stages

Seven ontogenetic stages were identified. These are described below.

Egg

Each capsule contains 475–2,639 (mean 1,094) small spherical eggs with no definition. Eggs are cream or yellow in colour and have an average diameter of 234 μm. Within a capsule, egg diameter varies on average by 36 μm. Approximately 1 % of these eggs are developing embryos. The remaining are nurse eggs. At this stage, both developing and nurse eggs are identical (Fig. 2a; Table 1). Egg capsules remain at this stage on average for 49 days.

Trochophore

After 42–70 days developing embryos become globular shaped with a non-circular translucent membrane around the darker embryo. A cilia band (prototroch) is present around approximately one-third to half of the outer circumference of the membrane (Fig. 2b). Each trochophore is a little larger than an egg, with an average length of 321 μm. Each embryo remains at the trochophore stage for just 2–3 days (Table 1).

Early veliger

As the early veliger stage is reached, the prototroch extends laterally to form paired velar lobes with marginal cilia around a central simple mouth. Velar lobes are used for collection of eggs and locomotory movement. Each early veliger is mobile but lacks obvious intentional direction. Behind each lobe and just in front of the main body of the early veliger, paired larval kidneys develop, slightly opaque in colour. Whole (generally nurse) eggs are manipulated into the mouth section using the cilia. These are engulfed and stored in the midgut (Portmann 1925), which forms a circular ball directly behind the mouth section, surrounded by a thin outer membrane. There is some asynchrony in the early development of the embryos from individual capsules. In total, between 2 and 35 veligers develop per capsule (average 11). Each embryo consumes nurse eggs for 3–7 days (at 6 °C). Total consumption by all embryos within a capsule occurs during the early veliger stage, over 4–10 days. Eggs are not damaged during consumption but are stored in the midgut, conserved for later nutritional use.

Fig. 2 Intracapsular developmental stages of *B. undatum.* (**a**) Egg, (**b**) trochophore, (**c**) early veliger, (**d**) veliger, (**e**) pediveliger and (**f**) pre-hatching juvenile. *n* Nurse egg or undeveloped embryo, *om* outer membrane, *c* cilia, *vl* velar lobe, *m* mouth, *mg* midgut, *me* mantle edge, *mc* mantle cavity, *vm* visceral mass, *lh* larval heart, *lk* larval kidney, *s* shell, *si,* siphon, *sg* siphonal groove, *t* tentacle, *e* eye, *f* foot, *o* operculum, *sa* shell apex, *sr* spiral ribs, *ar* axial ribs
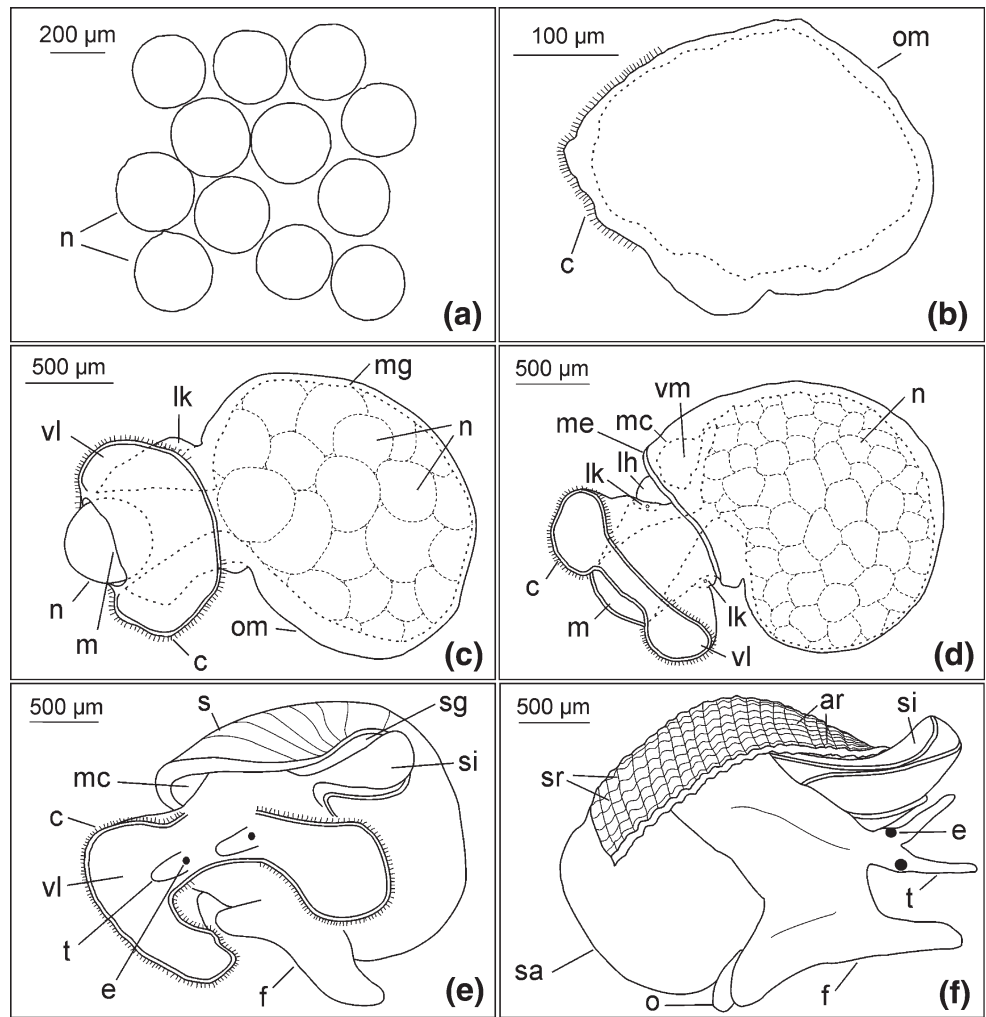

Table 1 Developmental periods for intracapsular development in *B. undatum* from the south coast of England at 6 °C

Ontogenetic stage	Mean time in days spent at each stage (individual)	Time at developmental stage in days (whole egg mass)	Mean size (mm ± SD)	Mean size variation within one capsule (mm)[a]	*n*	*n* (capsules)
Egg	49	0–56	0.23 (±0.01)	0.04	3,235	142
Trochophore	2	42–56	0.32 (±0.02)	0.01	19	12
Early veliger	5	42–56	1.46 (±0.15)	0.33	121	15
Veliger	18	42–77	1.65 (±0.17)	0.27	97	17
Pediveliger	18	70–98	1.91 (±0.32)	0.42	144	20
Pre-hatching juvenile	44	91–140	2.15 (±0.29)	0.38	74	14
Hatching juvenile	n/a	133–140	2.43 (±0.39)	n/a	102	n/a

Mean size at each ontogenetic stage is displayed (mm). Means are determined as an average of *n* measurements; *n* dictates total number of individuals measured. *n* (capsules) dictates number of capsules individuals were measured from and that were examined at each stage. Where n/a is stated, value was inapplicable or not determined

[a] Only capsules with 2 or more individuals included

Whole, undamaged nurse eggs can be seen inside the each early veliger. Early veligers average 1.46 mm across their longest axis. Within one capsule, embryo size may vary by as much as 0.85 mm. These size differences continue to be observed throughout development. Once all nurse eggs are consumed, early veligers, veligers and even pediveligers are

occasionally found in a capsule, which have consumed no nurse eggs at all (Figs. 1b, 2c, 3a, b; Table 1).

Veliger

In the veliger, the mantle edge thickens and a thin larval shell becomes visible around the midgut, creating a transparent layer. The midgut appears important in dictating the dimensions of this shell. The velar lobes become more separated, and distinct and the larval kidneys continue to be seen, often with a central yellow spot. The central mouth section becomes more opaque, early foot development begins and no further nurse egg consumption is possible.

The mantle edge and the visceral mass (white in colour) beneath it become obvious. A transparent pulsating membrane located dorsolaterally in front of the mantle edge becomes evident; this is often named the larval heart (Hughes 1990; Khanna and Yadav 2004). Nurse eggs stored beneath the mantle are still clearly individually discernible at this stage and even going into the pediveliger stage (Figs. 2d, 3b, c; Table 1). It is possible to break the mantle or shell on the back of the veliger or pediveliger and find nurse eggs still inside, which are not degraded and have not yet been digested. Embryos remain at the veliger stage for approximately 14–21 days. During this period, development within a capsule becomes synchronised.
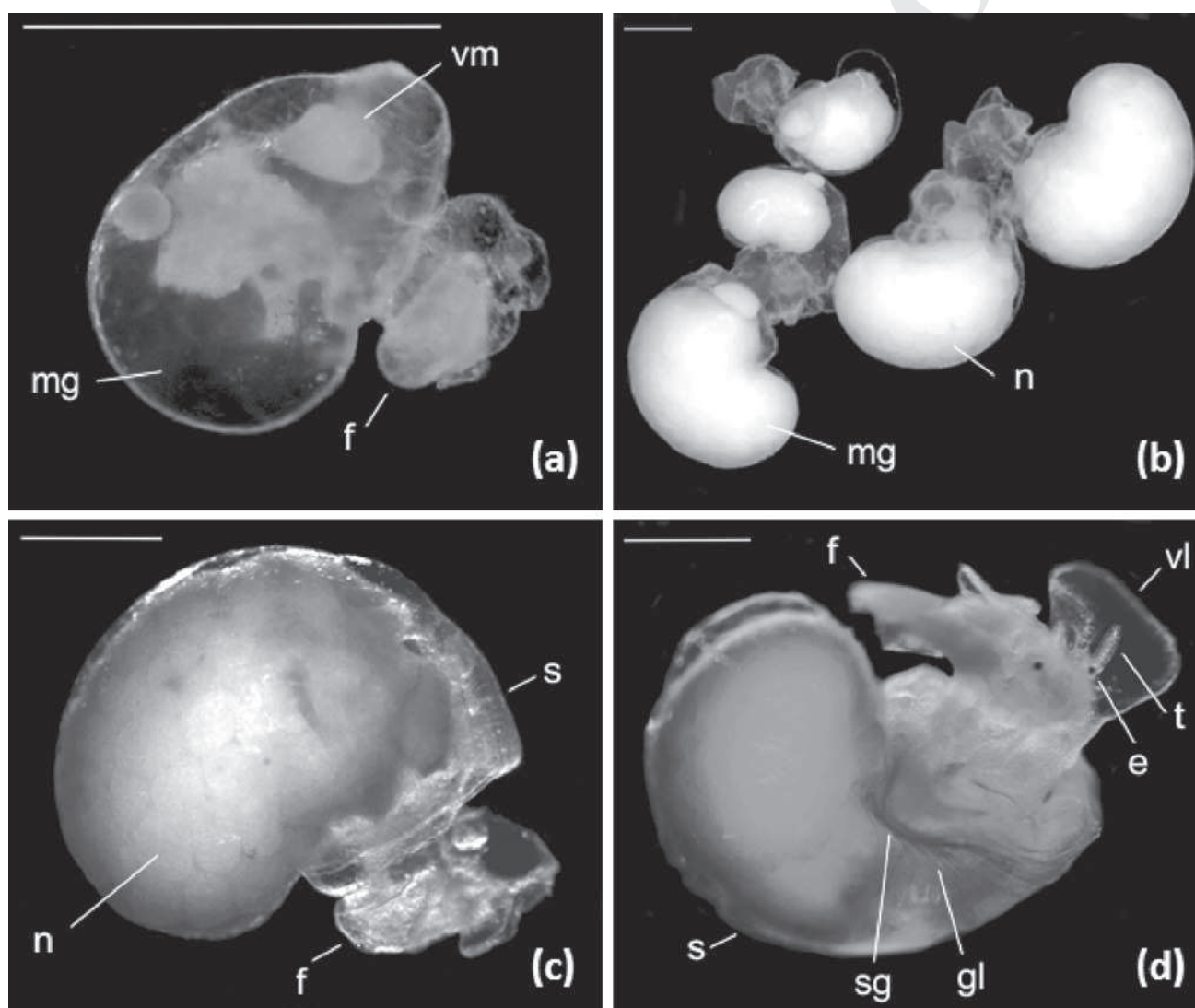

Fig. 3 Early development in *B. undatum*. (**a**) Early pediveliger stage with empty midgut indicating few or no nurse eggs were consumed. (**b**) Veligers of varying sizes developing alongside each other; within one capsule and following nurse egg consumption. (**c**) Early pediveliger stage with individual nurse eggs still clearly discernible under the shell. (**d**) Well-developed mid pediveliger stage with velar lobes still present. Growth lines can be observed on shell. *n* Nurse egg, *vl* velar lobe, *mg* midgut, *vm* visceral mass, *s* shell, *sg* siphonal groove, *t* tentacle, *e* eye, *f* foot, *gl* growth lines. *Scale bars* represent 500 μm

Pediveliger

At the pediveliger stage, the shell thickens and becomes increasingly apparent. The mantle cavity is initially visible beneath the mantle edge and the siphonal groove begins to form. The foot, eyes, tentacles and siphon appear. The velum and cilia, which are large at the beginning of this stage, begin to shrink back. They disappear by the end of the pediveliger stage. The larval kidneys and larval heart also disappear. Embryos remain at this stage for approximately 14–21 days (Figs. 2e, 3c, d; Table 1).

Pre-hatching juvenile

Shell growth continues and spiral and axial ribs begin to develop in the shell as the pre-hatching juvenile stage is reached. The shell thickens and colours brown (becomes pigmented). The first whorl becomes obvious and the shell shape elongates. Head, foot, tentacle and siphon features become more prominent and the operculum appears. The feeding proboscis also develops internally during this time. Pre-hatching juveniles complete development over a further 35–49 days before hatching commences. Pre-hatching juvenile size ranges from 1.57 to 3.06 mm. (Fig. 2f; Table 1).

Hatching juvenile

The features described for pre-hatching juveniles become more prominent. The juvenile emerges from the egg capsule through an opening created through radular scraping. They remain on the egg mass for a few days before moving off to feed. Overall hatching size ranged from 1.70 to 3.45 mm (Table 1).

Embryonic development

Each egg mass took between 9 and 11 days to be laid, with complete intracapsular development taking 133–140 days (19–20 weeks) at 6 °C. Within each egg mass, development was asynchronous by up to 14 days throughout the developmental period. Within each capsule, development was initially asynchronous; both trochophore and early veliger stages, and early veliger and veliger stages were observed together in capsules. By late veliger stage development within a capsule was synchronous. Following an initial increase in embryo size as nurse egg consumption occurred, individual size (measured as change in length) increased at a steady rate throughout the remainder of the encapsulated period (Figs. 4, 5; Table 1). Within each capsule, large size differences were observed between embryos at all stages of development. Whole, undamaged nurse eggs were visible inside embryos throughout the veliger and pediveliger stages. Occasional early veligers, veligers and pediveligers were
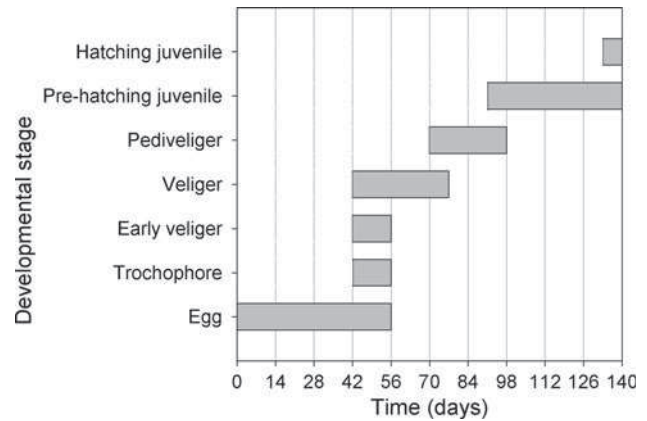

Fig. 4 Developmental time (days) for *B. undatum* from Southampton Water (UK) at 6 °C. *Times* shown represent development across whole egg masses
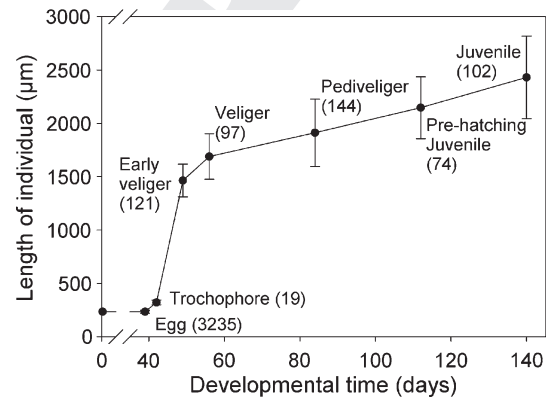

Fig. 5 Change in size of individuals (measured as length along longest axis) during intracapsular development. Size displayed is average length of individual at each stage in μm. Nurse egg consumption occurs between trochophore and early veliger stages. The average size displayed for early veliger is taken post nurse egg consumption. *Error bars* indicate ±1 SD

found, which had not consumed any nurse eggs. Apart from the absence of nurse eggs, these embryos were completely normal in their development (Fig. 3a–c; Table 1).

Intracapsular contents through development

Relationship between capsule volume and number of embryos per capsule

Egg capsule volume ranged from 39.0 to 287.5 mm^3 (capsule length 5.15–10.49 mm). Overall, number of eggs per capsule averaged 1,094 and number of veligers per capsule averaged 11. Regression analysis showed there to be a significant relationship between capsule volume and number of eggs ($r^2 = 0.7646$; $p < 0.001$), and capsule volume and number of veligers ($r^2 = 0.5615$; $p < 0.001$). As a percentage of total eggs, on average 1 %, develop into veligers (Fig. 6a, b).
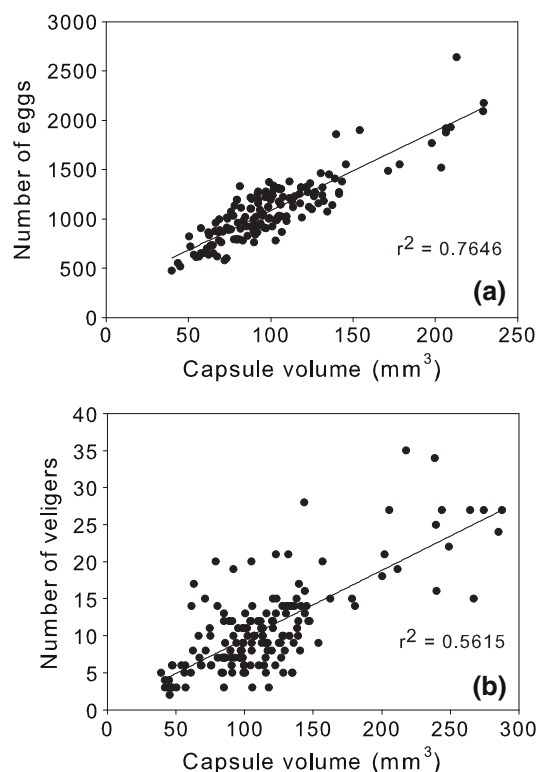
Fig. 6 Relationship between capsule volume and (**a**) number of eggs, (**b**) number of veligers in egg masses of *B. undatum*. Both relationships are significant to $p < 0.001$. The r^2 values are displayed

Change in number of embryos per capsule through development

When examining capsules ranging from 6 to 8 mm in length (volume 52.4–146.2 mm^3), number of developing veligers per capsule ranged from 3 to 21 (average 9) and number of pre-hatching juveniles per capsule ranged from 2 to 20 (average 9). An unpaired *t* test showed there to be no difference between the two groups ($p = 0.772$).

Discussion

Embryonic development and intracapsular contents data

The distribution of *B. undatum* extends from the southern coast of the UK, northwards up into the North Atlantic and Arctic oceans, across a temperature range of −1.5 to 22 °C (Bramblemet; CEFAS; Martel et al. 1986a). For the population used in the present study, annual temperatures vary seasonally from approximately 4–22 °C, and egg laying and development normally occur in rises water temperatures ranging 4–10 °C. With temperatures maintained at 6 °C, the duration of intracapsular development (4.5–5 months) was similar to previous estimates of *B. undatum* development in British waters (Kideys et al. 1993; Valentinsson 2002). Longer and shorter periods have been reported across the species distribution (e.g. Martel et al. 1986a; Nasution 2003). The observed differences in duration of development can be attributed to the known effects of temperature on metabolic rates in ectotherms.

In the present study, the number of eggs per capsule averaged 1,094 and the number of developing veligers averaged 11. While egg numbers were similar to those indicated in previous studies, veliger numbers were similar to figures reported by Hancock (1967), but lower than other estimates (Portmann 1925; Martel et al. 1986a). Since number of veligers is often significantly related to capsule volume (Gallardo 1979; Pechenik et al. 1984; Valentinsson 2002), it is likely that larger capsules were examined in the latter studies. Results indicate approximately 1 % of eggs developed, giving a ratio of 109 nurse eggs per embryo, almost identical to the 110 eggs per embryo reported by Portmann (1925). The percentage of eggs developing was also comparative to other previous estimates for *B. undatum* (Martel et al. 1986a; Valentinsson 2002; Nasution 2003). Similar results have been reported for other buccinids including 1.1–2 % for *Buccinum isaotakki* (Ilano et al. 2004), 0.2–1.8 % for *Buccinum cyaneum* (Miloslavich and Dufresne 1994) and 1 % for *Colus stimpsoni* (West 1979).

Past studies provide conflicting views on the occurrence of intracapsular cannibalism in *B. undatum* (Table 2). Portmann (1925) indicated a reduction in number of individuals per capsule during development (from early veligers to veligers and pre-hatching juveniles), which was suggested to be due to cannibalism (Fretter and Graham 1985). Contrary to this, other studies have shown the number of developing embryos per capsule to remain constant during development, indicating no cannibalism (Hancock 1967; Martel et al. 1986a). Our results were in agreement with these latter studies. Similarly, no cannibalism during development was reported in the buccinids *B. cyaneum* (Miloslavich and Dufresne 1994) and *B. isaotakki* (Ilano et al. 2004), and only very rarely was it observed in the buccinid *L. dirum* Rivest (1983). It has, however, been reported in some other gastropods including *Crucibulum quiriquinae* (Véliz et al. 2001), *Crepidula coquimbensis* (Véliz et al. 2003; Brante et al. 2009) *Trophon geversianus* (Cumplido et al. 2011) and a vermetid gastropod (Strathmann and Strathmann 2006).

Capsule size or volume has previously been shown to be a good indicator of number of eggs and veligers within a capsule. In the current study, these figures were both significantly related to capsule volume. Number of eggs was more closely related to volume than number of veligers, suggesting eggs are more regularly distributed amongst

Table 2 Reproductive biology of *B. undatum* from present and previous studies

Study	Location	Development temperature (°C)	Time to hatching (months)	Capsule size (length mm)	No. of eggs per capsule	Egg diameter (μm)	% of eggs that develop	No. of veligers per capsule	No. hatching juveniles per capsule	Length of shell at hatching (mm)
Portmann (1925)	Roscoff, France	5–9	n/a	n/a	50–>2,000	n/a	n/a	av. 30	av. 10	n/a
Hancock (1967)	Burnham on Crouch, UK	n/a	3–4	n/a	≤3,000	n/a	n/a	13–14	n/a	n/a
Fretter and Graham (1985)	n/a	n/a	3–9	6–12	500–3,000	200–300	n/a	av. 30	3–10	1–1.4
Martel et al. (1986a)	Gulf of St Lawrence, Canada	2–3	5–8	n/a	2,700	n/a	1.10	av. 30	av. 30	3
Kideys et al. (1993)	Douglas, Isle of Man	n/a	3–5	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Valentinsson (2002)	Skagerrak, Sweden	4–8	3–4	7–9.5	700–2,300	245–285	0.20–1.20	n/a	2–16	1.9–2.8
Nasution (2003)	Irish Sea, Northern Ireland	8–11	2.5–3	n/a	av. 2,360[a]	340	0.47–1.65	n/a	n/a	Nearly 2[b]
Nasution et al. (2010)	Irish Sea, Northern Ireland	10	3	n/a	558–4,196	n/a	0.47–1.65	n/a	n/a	2.1–3.1
Present study	Southampton Water, UK	6	4.5–5	5–10.5	475–2,639	200–260	1.01	av. 9–11	av. 9	1.70–3.45
Author, personal observations	Breidafjordur, Iceland	Approx. 3	n/a	7–10	804–1,441	n/a	1.48	av. 17	n/a	n/a

n/a not available in study, *av.* average, *no.* number

[a] Range stated in journal was not possible

[b] No accurate value was stated in publication

capsules than are developing embryos. This pattern has been reported before for both *B. undatum* (Valentinsson 2002; Nasution et al. 2010) and other gastropods, including *B. cyaneum* (Miloslavich and Dufresne 1994), *B. isaotakki* (Ilano et al. 2004), *Hexaplex (Trunculariopsis) trunculus* (Lahbib et al. 2010), *Acanthina monodon* (Gallardo 1979), *Nucella lapillus* (Pechenik et al. 1984) and *Nucella lamellosa* (Spight 1976b). Contrary to this, number of eggs has been found to be related to, but number of veligers to be independent of capsule size in *L. dirum,* the calyptraeid *Crepipatella dilatata* (Chaparro et al. 1999) and the muricid *Nucella ostrina* (Lloyd and Gosselin 2007).

An initial rapid increase in embryo size was observed at the early veliger stage in the present investigation. This was followed by a relatively linear increase in size for the remainder of intracapsular development. Similar changes in size during development have been reported for *B. cyaneum* (Miloslavich and Dufresne 1994) and *B. isaotakki* (Ilano et al. 2004). For both, however, the initial increase was slower than was observed in this investigation. In *B. isaotakki*, it is likely that this is reflective of the slower nurse egg consumption rate previously observed in this species (Ilano et al. 2004). Probably, nurse eggs are also taken up at a slower rate in *B. cyaneum*.

Previous hatching sizes for *B. undatum* have been reported ranging from 1.0 to 3.1 mm (e.g. Fretter and Graham 1985; Nasution et al. 2010). These are similar to hatching sizes observed in the present investigation, which averaged just below 2.5 mm in length.

Nurse egg partitioning

Life history theories suggest parental fitness is maximised by investing equally into all offspring (Smith and Fretwell 1974). Traditionally, resource partitioning (in the form of nurse eggs) during intracapsular development follows this trend. Embryos compete for nurse eggs, but within a capsule competitiveness is normally equal. As a result, nurse eggs are consumed quite evenly by all embryos. This does not mean hatchlings are always of a similar size; within one species, or even one clutch, the ratio of nurse eggs to developing embryo may vary greatly between capsules, resulting in large differences in offspring size. This is usually believed to be due to irregular distribution of embryos amongst capsules (Thorson 1950; Rivest 1983; Spight 1976a; Miloslavich and Dufresne 1994). Within a capsule however, generally only small differences in offspring size are reported. For example, Spight (1976a) examined 2 species of muricid gastropod (*Nucella emarginata* and *A. spirata*) and found that although embryo size varied considerably between capsules, within a capsule large differences were rare. Previous studies

Table 3 Periods of development and nurse egg consumption times for different species of gastropods

Species	Temperature (°C)	Duration of intracapsular development (days)*	Duration of nurse egg consumption (days)*	Percentage of development over which nurse eggs are consumed (%)	Authors
B. isaotakii	2.5–10.2	200	40	20	Ilano et al. (2004)
B. undatum	8–11	70	28	40	Nasution (2003)
B. undatum	6	133–140	3–7	2–5	Present study
C. dilatata	17	18–26	Up to 26	100	Chaparro and Paschke (1990)
Hexaplex (Trunculariopsis) trunculus	22–24	49	35	71	Lahbib et al. (2010)
L. dirum	12	84–98	7–21	8–20	Rivest (1983)
T. geversianus	12–14	112	38	34	Cumplido et al. (2011)

All species included are direct developers

* Some timings have been converted from weeks stated in original study

examining development in *B. undatum* have indicated similar results, and comparable observations have also been reported for the gastropods *L. dirum* (Rivest 1983) and *C. dilatata* (Chaparro and Paschke 1990; Chaparro et al. 1999). In contrast, the present study found nurse egg partitioning to be quite different to that previously described for *B. undatum* or other buccinids. Large size differences were continually observed between embryos from any one capsule, and regularly individuals were found alongside a capsulemate four times their size (Fig. 3b). Although to our knowledge, variations in nurse egg consumption have not previously been reported in other buccinids, such intracapsular differences have been described for a small number of gastropods, predominantly from the muricidae family. These include *A. monodon* (Gallardo 1979), *Chorus giganteus* (González and Gallardo 1999) and *T. geversianus* (Cumplido et al. 2011). In *A. monodon* and *C. giganteus*, intracapsular size differences continue to be evident at hatching, presumed to be related to earlier nurse egg consumption (Gallardo 1979; González and Gallardo 1999). In *T. geversianus*, sibling cannibalism (which can also affect offspring size) occurs during later developmental stages, and it is not clear whether hatching sizes vary (Cumplido et al. 2011).

It is widely assumed that offspring quality increases with size (e.g. Thorson 1950; Spight 1976a; Rivest 1983; Gosselin and Rehak 2007; Lloyd and Gosselin 2007; Przeslawski 2011). Larger hatchlings are less likely to be affected by factors such as physical stress, predation and starvation. While intracapsular size differences are generally believed to be due to competition (Gallardo 1979; González and Gallardo 1999), in the present investigation, they are probably enhanced by a combination of asynchrony in development and short nurse egg consumption periods. We found nurse egg feeding to be very rapid, with each early veliger consuming eggs for just 3–7 days. This relates to 2–5 % of the developmental period. In comparison, in most gastropods, nurse egg consumption occurs over a large proportion of intracapsular development (Table 3). Even the shortest uptake periods previously reported (8–20 % of the developmental period) (Rivest 1983) are still more than double the length of the consumption period observed by us. Within a capsule, the potential to take up nurse eggs is limited by the amount already consumed by earlier developers. Thus, while intracapsular asynchrony in early development is not uncommon (e.g. Vasconcelos et al. 2004; Fernández et al. 2006; Lahbib et al. 2010), when it is combined with the short nurse egg consumption period seen in *B. undatum,* it follows that even a 24-h lag in initial embryonic development will put individuals at a distinct disadvantage. Rapid nurse egg consumption in *B. undatum* is consistent with findings by Portmann (1925), but contradictory to those of Nasution (2003). Additionally, 6 °C is towards the lower end of the temperature range that southern populations of *B. undatum* naturally develop in. Nurse egg consumption is even faster at warmer temperatures (Authors, unpublished data). This may lead to larger intracapsular size differences during development, and with predicted sea temperature elevations, intracapsular size ranges may increase.

Normal veligers and pediveligers that had not successfully consumed any nurse eggs were occasionally found within a capsule in the present investigation (Fig. 3a). It is likely that these individuals reached the feeding stage after all resources had been consumed. Since no further feeding occurs between nurse egg consumption and hatching, these embryos had no nutrition available to them for development and we assumed they did not survive. This in itself is very unusual and even in the few reported cases of large intracapsular size differences between embryos (Gallardo

1979; González and Gallardo 1999; Cumplido et al. 2011), to our knowledge completely 'empty' embryos have not been observed.

In the current study, it was noted that for several weeks following consumption, individual nurse eggs could still be observed through the thin veliger mantle and early shell (Fig. 3c). Throughout this period, if the mantle or shell was broken, whole eggs would spill out. This indicated that although eggs were rapidly consumed, they were not immediately utilised but instead were stored for later nutritional use. This phenomenon was also noted by Portmann (1925), who recognised that nurse eggs stayed intact inside *B. undatum* veligers for long periods of time. In comparison, he found they disintegrated directly after consumption in *N. lapillus*. Nurse eggs have also been shown to be visible internally throughout the feeding period in *A. monodon* (Gallardo 1979), *L. dirum* (Rivest 1983) and *C. dilatata* (Chaparro and Paschke 1990). In each case however, the literature suggests nurse eggs begin to be assimilated shortly following consumption. In other species such as *T. geversianus,* nurse eggs break down prior to consumption by embryos (Cumplido et al. 2011).

The range in size of embryos within a capsule and the occurrence of 'empty' embryos observed in this investigation indicates that a higher level of competition is occurring in *B. undatum* than is normally observed during intracapsular development in gastropods. While large intracapsular size differences have been observed in some muricid gastropods, to our knowledge, competition for nurse eggs to the degree that some embryos are left with no nutrition for development has never previously been reported.

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