REPRODUCTION OF THE VERMETID GASTROPOD *DENDROPOMA MAXIMUM* (SOWERBY, 1825) IN MOOREA, FRENCH POLYNESIA

NICOLE E. PHILLIPS AND JEFFREY S. SHIMA

Victoria University Coastal Ecology Laboratory (VUCEL) and School of Biological Sciences, PO Box 600, Victoria University of Wellington, Wellington 6140, New Zealand

ABSTRACT

Vermetidae are sessile molluscs with tubular shells cemented to the substrate. Although they are common inhabitants of coral reefs and rocky shores, little is known about the basic biology of most species. *Dendropoma maximum* is the largest vermetid species and is common across its Indo-Pacific range. Here we report on a study of reproductive and morphological traits in *D. maximum* from the lagoon around Moorea, French Polynesia. Both body length and diameter of shell aperture (generally the only visible part of the animal in the field) were good predictors of body weight and this relationship did not differ between males and females. Shell apertural diameter is therefore a good index of body size in *D. maximum*. The sex ratio became increasingly dominated by females with increasing body size, which is suggestive of protandric hermaphroditism. Probability of brooding, the number and size of brooded egg capsules, and the number of embryos per capsule were all positively related to female size. Females released veliger larvae that lived without additional food for up to 10 days, but were observed to feed when offered cultured phytoplankton on the final day. This is the first direct observation of feeding by larvae in this genus, and a planktotrophic larval stage has implications for potential dispersal in *D. maximum*.

INTRODUCTION

Vermetid gastropods are conspicuous and common on coral reefs (Hughes & Lewis, 1974; Zuschin, Hohenegger & Steininger, 2001) and rocky shores (Hughes, 1979; Hadfield, 1989; Calvo, Templado & Penchaszadeh, 1998), but nevertheless have been surprisingly little studied. Vermetids are sessile and their shells are tube-like and affixed to, or embedded within, coral or other hard substrata. *Dendropoma maximum* (Sowerby, 1825) is the largest vermetid species and is common across its extensive Indo-Pacific range. It can attain substantial densities on reef rock, and on both dead and live coral (Hughes & Lewis, 1974; Smalley, 1984; J.S.S. & C.W. Osenberg, unpubl.), but its ecology and reproductive biology remain poorly known. Demographic studies are hindered by the typical growth form of *D. maximum*, which generally leaves only the shell aperture visible and accessible. Studies on this species have focused on its mechanism of feeding with a mucus net (Hughes & Lewis, 1974; Smalley, 1984; Kappner, Al-Moghrabi & Richter, 2000), and information on reproduction is limited to a description based upon a single brooding female (Hughes & Lewis, 1974). That study found that larvae are brooded in capsules attached to the inner wall of the tube and the authors suggested that crawl-away juveniles rather than planktonic larvae emerge from the capsules (Hughes & Lewis, 1974), as is common for other species in the genus *Dendropoma* (Hadfield *et al.*, 1972; Hughes, 1979; Miloslavich & Penchaszadeh, 1992; Calvo *et al.*, 1998). However, emergence and a description of live larvae or hatchlings have not been reported in this species.

Improved understanding of its biology is necessary because *D. maximum* is often abundant on a variety of species of live coral and may have detrimental effects on coral growth and survival (Smalley, 1984; Colgan, 1985; Zvuloni, Armoza-Zvuloni & Loya, 2008; J.S.S. & C.W. Osenberg, unpubl.). Further, this species (like other vermetids, e.g. Barry *et al.*, 1995) appears to be increasing at sites throughout its range (J.S.S. & C.W. Osenberg, unpubl.). Given the potential deleterious effects on coral reef communities, there is a need to understand more about the demographics of *D. maximum*, particularly with respect to its life history, dispersal potential, growth rate and mortality. Studies of population dynamics of *D. maximum* in the field require reliable and repeatable measurements of a suitable proxy for body size, to obviate the need for destructive sampling.

Here we report a study of *D. maximum* in Moorea, French Polynesia, where it is common and abundant (Augustin, Richard & Salvat 1999; J.S.S. & C.W. Osenberg, unpubl.). Our aims are (1) to derive relationships among morphological traits (length, weight and shell aperture diameter); (2) to investigate brooding and fecundity (numbers of egg capsules and embryos per capsule); and (3) to determine if females release planktonic larvae or crawl-away juveniles.

MATERIAL AND METHODS

Individual *Dendropoma maximum* were haphazardly collected from seven sites within the lagoon on the northeast shore of Moorea, French Polynesia (149°50′W, 17°30′S). Several vermetid species, including *D. maximum*, are common within this lagoon (N.E.P., J.S.S. & C.W. Osenberg, unpubl.). Surveyed sites ranged from *c*. 1.5 to 2.5 m in depth. Sampling occurred in April and September 2008 ($n = 6–28$ individuals per site in April, $n = 27–49$ in September). *Dendropoma maximum* were collected from different patch reefs across each site, and sampling targeted a representative range of sizes within each site. However, the largest individuals at a site were rarely collected because they were often embedded deep within the middle of a head of the large coral *Porites* sp. or were otherwise inaccessible.

Collections were made by carefully chiselling individual *D. maximum* (intact in their tubes) from the coral matrix.

Correspondence: N.E. Phillips; e-mail: nicole.phillips@vuw.ac.nz

Most specimens were removed from dead coral substrates, to minimize damage to living coral colonies. To facilitate collection, the specimens were generally individuals from the more accessible periphery of small patch reefs, where substrates could be easily broken off and returned to the lab. Live *D. maximum* were placed in coolers, covered in seawater and transported back to the University of California Berkeley Gump Research Station. At the station's sea water facility, each individual *D. maximum* was carefully removed from its tube. For samples collected in April only, the diameter of the tube aperture was measured with callipers to the nearest 0.1 mm prior to removing animals. Once removed, sex, length and blotted wet weight were recorded. We distinguished sex primarily by the presence/absence of a mantle slit (present in females) and also appearance of the gonads. For females, incidence of brooding was recorded and, if females were brooding, capsule numbers were counted. In April, we also counted and measured lengths (to the nearest 0.01 mm) of capsules.

We examined how sex and log body length influenced the dependent variable log body weight of *D. maximum* using ANCOVA. Because we were most interested in overall morphological relationships and how these varied among sexes, we pooled data across sites and sample dates for these analyses. We conducted a similar ANCOVA using log shell aperture diameter as the covariate and sex as a fixed factor; these data were only collected in April so we pooled across sites.

Using a generalized linear model, we conducted a logistic regression with binomial errors, and a logit link function to examine the frequency of brooding as a function of female weight, a continuous variable. We examined the fit of the logistic curve to the data using graphical tests (Crawley, 2007), and found this model to be a good fit to the data.

We used regression analyses to examine the relationship between female body weight and number of capsules per female, number of embryos per capsule and capsule size, as well as between capsule size and number of embryos per capsule.

We removed capsules with late-stage veligers from females and maintained these in beakers of filtered sea water (FSW, mesh size $= 0.5$–1.0 μm) in the lab to evaluate hatching success. Embryos in capsules remained alive for >1 week (based on visible movement inside the capsule), but never hatched and eventually died. We then altered our strategy and collected and maintained females (intact in their tubes) in the lab. We ascertained the brooding status of female *D. maximum* by gently poking them until they slowly retreated into their tubes. If late-stage capsules were observed attached to the inside of the tube, we placed those females inside mesh-sided cages (mesh $= 150$ μm), firmly secured the mesh around the female's tube with cable ties, and placed them in a sea table with flowing seawater. We collected hatchlings and recorded the larval length of 15–20 larvae per female. Hatchlings were maintained in beakers of FSW for 10 days, after which time the study was terminated. We changed the water every 2–3 days. Just prior to ending the study, we added a small aliquot of cultured phytoplankton (putatively *Dunaliella tertiolecta*) to some larvae in a Petri dish under a dissecting microscope, to examine whether larvae would feed.

RESULTS

There was a strong linear relationship between log length and log body weight of *Dendropoma maximum* ($y = 2.3698x - 3.6506$, $R^2 = 0.89$, $P < 0.0001$; Fig. 1A). There was no difference between males and females (effect of sex: $F_{(1,333)} = 0.0195$, $P = 0.889$) and the relationship with length did not vary with sex (interaction between sex and log length: $F_{(1,333)} = 0.008$, $P = 0.930$). Log shell aperture diameter predicted 75% of variation
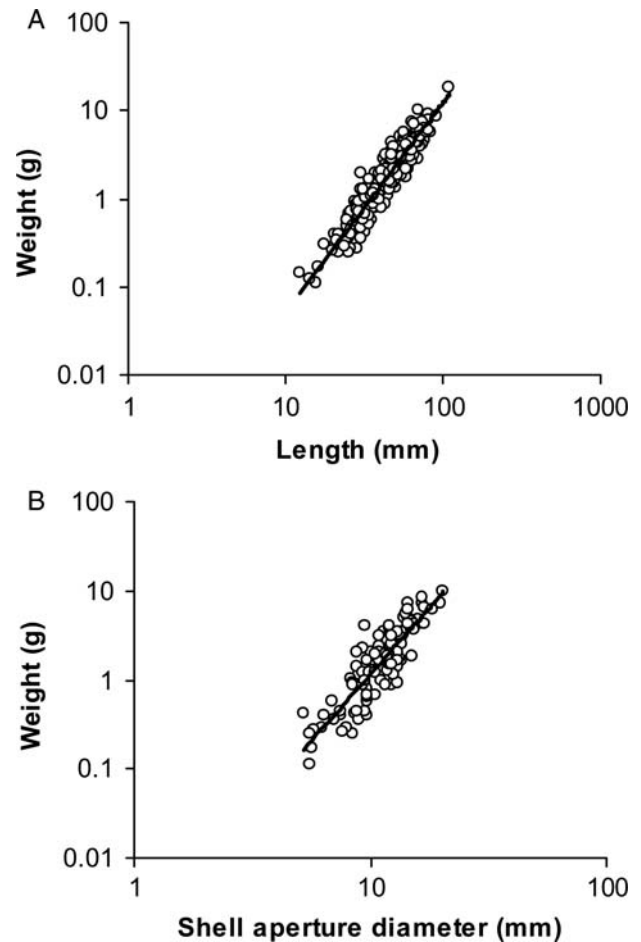
Figure 1. Strong relationships between (**A**) body length and (**B**) shell aperture diameter and body weight of *Dendropoma maximum*. Note the log scales of the axes. Data were pooled across sexes and sites and, for **A** only, months. Data in **B** were only collected in April. For **A** $n = 337$, for **B** $n = 110$.

in log body weight ($y = 2.9802x - 2.9199$, $P < 0.0001$; Fig. 1B). This relationship was not dependent on sex (effect of sex: $F_{(1,106)} = 0.001$, $P = 0.973$; interaction of between sex and log shell diameter: $F_{(1,106)} = 0.285$, $P = 0.594$).

The sex ratio became increasingly dominated by females with increasing body size. Only 34% of small animals (<2 g body weight) were female, but 63% of medium-sized animals (2–4 g) were female, and 75% of the large animals sampled (>4 g). In addition, no males were found over 7.1 g in body weight, but we sampled 11 females with body weights 7.1–17.9 g.

Brooding frequency was dependent on female body weight ($P = 0.0004$). The minimum size for brooding was *c*. 1 g. Approximately 40% of small females (1–2 g) were likely to be brooding, whereas 60–80% of medium to large females (>2 g) were likely to be brooding (Fig. 2).

The number of capsules per female ranged from 1 to 58. Female body weight was the only significant factor in a model examining number of capsules per female ($F_{(1,77)} = 10.43$, $P = 0.002$). Neither month nor the interaction in the model was significant ($P > 0.29$ in both cases). Although bigger females tended to have more egg capsules, the relationship was relatively weak ($y = 1.4092x + 10.345$, $R^2 = 0.10$, $P = 0.004$; Fig. 3A).

Similar to those described by Hughes & Lewis (1974), capsules were ovoid and attached to the inner wall of the tube by a short stalk (mean stalk length $= 0.486$ mm, SD $= 0.154$ mm,

$n = 10$) in multiple rows. It was common for females to brood egg capsules at different stages of development simultaneously, and capsule size varied with stage of development ($F_{(2,324)} = 34.798$, $P < 0.0001$, $n = 327$). Capsules with embryos at earliest stages of development (mean length = 3.05 mm, SD = 0.60 mm, $n = 244$) were smaller than those with mid- (mean length = 3.93 mm, SD = 1.40 mm, $n = 40$) to late-stage larvae
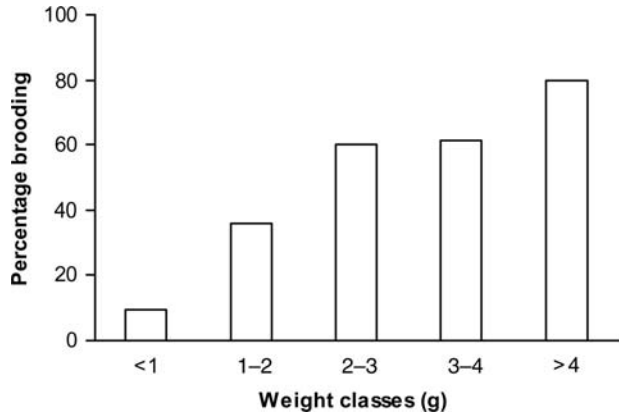

Figure 2. Percentage of females of *Dendropoma maximum* in each size class that contained egg capsules. Data were pooled over sites and months ($n = 18–48$ in each size class).

(mean length = 4.08 mm, SD = 1.57 mm, $n = 43$) (Tukey HSD, $P < 0.0001$). Capsules appeared to swell over time and take up fluid. For capsules with mid- to late-stage veligers, there were significant, positive, linear relationships between female size and capsule size ($y = 0.4854x + 2.5113$, $R^2 = 0.47$, $P < 0.0001$; Fig. 3B) and number of embryos per capsule ($y = 36.819x + 115.06$, $R^2 = 0.49$, $P < 0.0001$; Fig. 3C). Additionally, larger capsules housed larger numbers of embryos ($y = 59.275x - 9.1007$, $R^2 = 0.69$; Fig. 3D). Overall, the number of embryos per capsule ranged from 73 to 571.

When females brooding late-stage capsules were placed in mesh-sided cages, swimming larvae were released by seven females over the following 1–3 days. Mean size of veligers at hatching was 491.3 μm in length (SD = 39.3, $n = 125$, range = 400–550 μm). Veligers had a large, bi-lobed velum, with two dark purple bands of pigmentation around the edge, and a well-developed foot (Fig. 4A). The protoconch had 1.5–2 whorls, with strong axial ribs on the second whorl (Fig. 4B). Yellow material, possibly yolk, was visible through the shell of the first whorl (Fig. 4B), and appeared to diminish over time. We maintained larvae in beakers of FSW for up to 10 days after hatching; many individuals remained alive and swimming (although we did not quantify mortality), but did not grow. When cultured phytoplankton was added to a dish of larvae 10 days after hatching, we observed larvae feeding. Larvae readily captured phytoplankton cells with the velar cilia, and cells were transported along the velar lobe to the mouth and consumed. Within minutes a green bolus could be seen in the stomach.
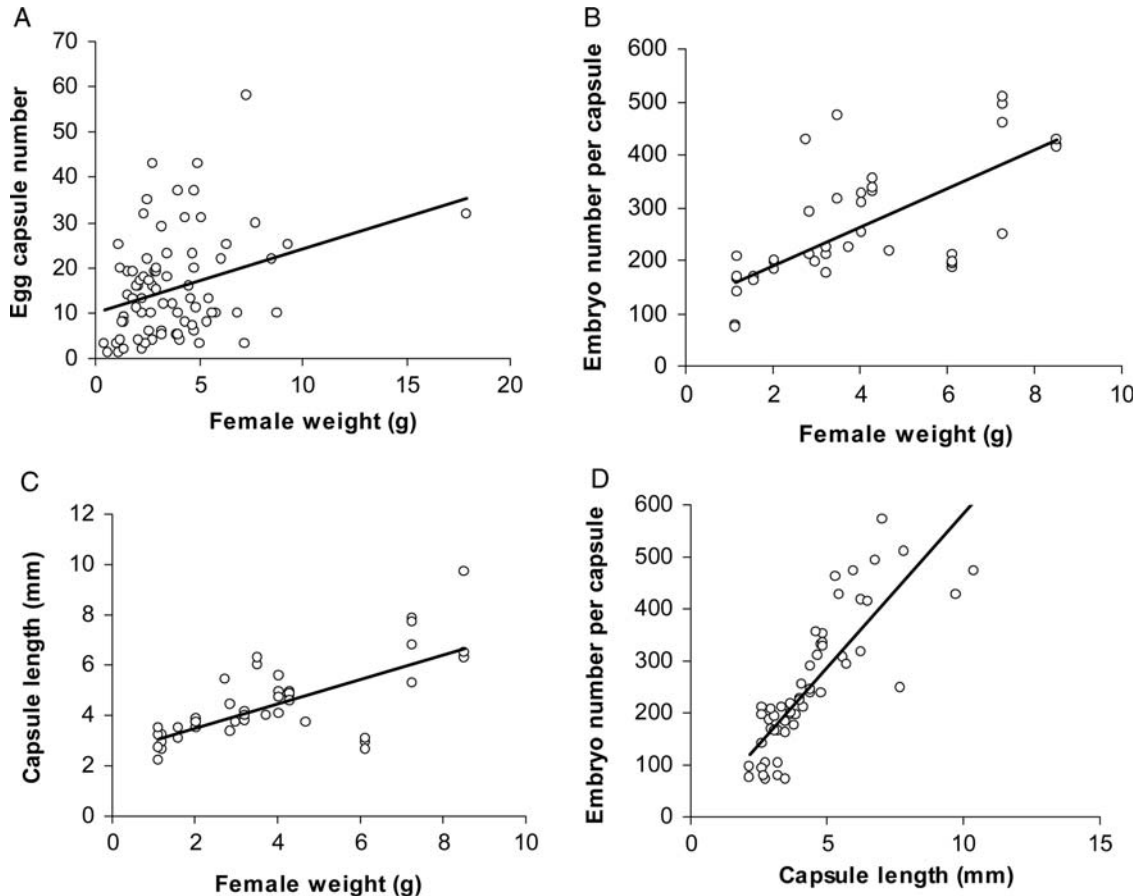

Figure 3. A positive linear relationship between body weight of female *Dendropoma maximum* and the number of egg capsules she was brooding ($n = 84$) (**A**), capsule size for mid- to late-stage embryos ($n = 35$) (**B**) and number of embryos per capsule ($n = 44$) (**C**); whereas capsule size had a positive relationship with number of embryos per capsule ($n = 41$) (**D**).
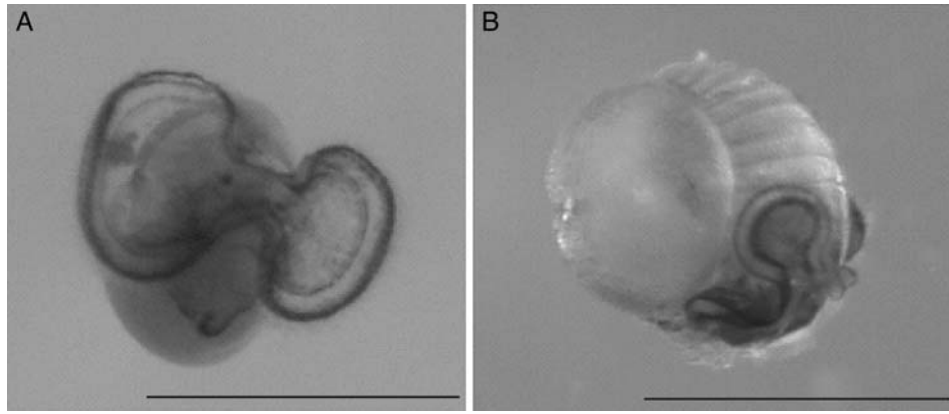
Figure 4. *Dendropoma maximum* larva with velar lobes extended (**A**) and showing the protoconch with what may be yolk stores visible (**B**). Scale bars = 0.5 mm.

DISCUSSION

We found that different indices of body size in *Dendropoma maximum* (i.e. body length, body weight and shell aperture diameter) were strongly correlated, and that these relationships were invariant with regard to sex of the animal. These relationships should facilitate future field-based demographic studies, because shell aperture diameter is easily measured. Consistent relationships in both sexes are also useful, because the sex of individuals cannot be determined without removing animals from their tubes (unless females are brooding).

Our data show that the sex ratio of *D. maximum* changed with body size, from being male dominated at small sizes to female dominated at large sizes, suggesting that this species may exhibit protandric hermaphroditism. Because we were unable to sample many of the largest individuals, and did not examine gonads histologically, further study is required to confirm this reproductive strategy. Few data are available on sex ratios of vermetids. Although Calvo *et al.* (1998) reported a female-biased sex ratio of 71% in *Dendropoma petraeum*, they did not take account of body size. It is thought that most vermetid species are gonochoristic, although sequential hermaphroditism has been found in *Serpulorbis squamigerous* (Hadfield, 1966), *Serpulorbis arenarias* (Calvo & Templado, 2005) and suggested for an unidentified vermetid in Hawaii (tentatively *Thyladedus rugulosus*: Strathmann & Strathmann, 2006).

Protandric hermaphroditism is postulated to be an advantageous reproductive strategy if female reproductive output increases with size and male reproductive success is independent of size (Ghiselin, 1969). Several reproductive traits were associated with female body size in *D. maximum*. Larger females were more likely (1) to be brooding, (2) to brood more and larger capsules, and (3) to brood more embryos within capsules. It is therefore plausible that large females contribute disproportionately to the larval pool. Although positive relationships between female size and fecundity or reproductive output are known for other invertebrates (reviewed by Ramirez Llodra, 2002), including gastropods (e.g. Spight, Birkeland & Lyons, 1974; Spight & Emlen, 1976; Miloslavich & Defresne, 1994; Chaparro *et al.*, 1999; Valentinsson, 2002), there is little published information on the topic for vermetids. No relationship between female size and number of capsules was reported for *D. corrodens* (Miloslavich & Penchaszadeh, 1992) the only other species in the genus *Dendropoma* for which we could locate comparable data. However in *Serpulorbis arenaria*, which exhibits sequential hermaphroditism, there are positive relationships between both the number of eggs per capsule and total number of eggs per brood, and female body size (Calvo & Templado, 2005).

A maximum of 58 capsules was found in a single *D. maximum* female. This is a much greater number than for other species in this genus, in which a maximum of 15 capsules per female has been reported (Miloslavich & Penchaszadeh, 1992: table 3). The exception is *D. petraeum* from Spain, where females brooded a large number of capsules (up to 86, with a mean of 25), but in that case each capsule only contained a single embryo (Calvo *et al.*, 1998). In the Red Sea Hughes & Lewis (1974) were able to extract a single female *D. maximum* (opercular diameter 15.5 mm) with 11 egg capsules. These capsules were on average 6 mm long (sample size of 3) and contained roughly 335 embryos per capsule. These values for capsule size, number and numbers of embryos per capsule are consistent with our results for similar sized, relatively large, females (equivalent weight of *c.* 7 g).

In general, *D. maximum* appears capable of brooding larger numbers of capsules, and embryos per capsule, than other species in the genus reported from other localities, e.g. *D. corallinaceum* from South Africa (Hughes, 1979), *D. corrodens* from Venezuela (Miloslavich & Penchaszadeh, 1992), *D.* cf. *meroclista* from Sinai (Safriel & Hadfield, 1988), *D. petraeum* from Spain (Calvo *et al.*, 1998), or *D. meroclista*, *D. platypus*, *D. psarocephala* and *D. rhyssoconcha* all from Hawaii (Hadfield *et al.*, 1972). As in several other studies, females brooded capsules at different stages of development simultaneously. This has been interpreted as evidence for continuous reproduction (Hadfield, 1989; Miloslavich & Penchaszadeh, 1992). Swelling of the capsule during development has also been reported in *D. corrodens* and in *Vermetus* species (Miloslavich & Penchaszadeh, 1992; Calvo & Templado, 2004), and has been attributed to increased permeability to water (Miloslavich & Penchaszadeh, 1992).

Encapsulated *D. maximum* veligers measured by Hughes & Lewis (1974) were smaller (311–434 μm) than hatching veligers in this study (469–533 μm). Hughes & Lewis (1974) also stated the veligers 'were not equipped for planktonic life', though they did not specify traits that were lacking. In contrast to this earlier report, and our expectations, female *D. maximum* in this study released swimming larvae. Interestingly, the protoconch was very similar in appearance to that described in Hadfield *et al.* (1972) for *D. rhyssoconcha*, which hatches crawling larvae with regressing velar lobes. Further, swimming larvae were only released when capsules remained *in situ* in the females' tubes, and not when removed and placed in FSW, suggesting there may be a release cue, or that females may facilitate hatching. Larvae were relatively large at hatching, with a well-developed velum and protoconch. Larvae were able to stay alive and active for at least 10 days without

feeding but, when offered food at the end of this period, they ingested it. The likelihood of yolk storage in the veligers at hatching may indicate that *D. maximum* larvae are facultative planktotrophs rather than obligate planktotrophs, although confirmation requires further study.

It has been suggested that some species of *Dendropoma* may have mixed developmental strategies, releasing either crawl-away juveniles or short-lived planktonic larvae (Hadfield *et al.*, 1972; Taylor, 1975), and this may be the case for *D. maximum*, although we only ever observed the release of swimming larvae. However, the only other report of planktotrophic veligers in this genus is for *D.* cf. *meroclista* from Sinai and Madagascar, and this developmental strategy was inferred from differences in protoconch size at hatching *vs* settlement (Safriel & Hadfield, 1988). This study is the first report of direct observations of swimming larvae and larval feeding in this genus, and has revealed the potential for a planktonic larval phase in *D. maximum* of at least several days, which has implications for potential dispersal capability of this species.

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