

**Body size variation in the sexually dimorphic scaphopod *Rhabdus rectius* (Carpenter, 1864) (Dentaliida: Rhabdidae)**

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**ABSTRACT**

Male-biased sexual size dimorphism typically evolves via sexual selection for larger males that are favoured by choosy females or are more successful in mate competition with other males. Among marine invertebrates that broadcast their gametes into the ocean for fertilisation, this form of sexual size dimorphism is rare because such species lack direct interactions among males or between the sexes. However, the broadcast-spawning tusk shell *Rhabdus rectius* was recently reported to show strong male-biased sexual size dimorphism. That pattern might imply interesting and undiscovered sexual selection in this species. We found instead that the distribution of body size variation (weight, shell length) was similar between males and females of *R. rectius*, and mean sizes were not different between the sexes. However, we noted a male-biased sex ratio (~1:1.3) in our large sample of individuals. Many live scaphopods (and several dead shells) showed partial or complete boreholes drilled by predatory gastropods. Boreholes were observed on males and females in similar proportions. We collected scaphopods along with multiple individuals of one likely scaphopod predator, the small moon snail *Euspira pallida*, and in the lab we observed successful attacks by moon snails on tusk shells.

Keywords: sexual conflict, SSD, sex ratio, sperm competition, Naticidae

Running head: Sexual dimorphism in scaphopods

**Introduction**

Differences in the strength or direction of sexual selection on female and male reproductive success are common features of animal reproduction that frequently lead to the evolution of secondary sex differences (sexual dimorphisms) and skewed sex ratios (Andersson 1994; Parker et al. 2018). Both are predicted to arise through interactions among members of the same sex or

between mates of opposite sexes (Ghiselin 1974; Lande 1980; Arak 1988; Reeve and Fairbairn 2001; Arnqvist and Rowe 2002; Seger and Stubblefield 2002).

Male-biased sexual size dimorphism (SSD) is common among vertebrates, and is associated with several modes of sexual selection in species in which larger males compete more successfully for access to females (e.g., elephant seals) or females choose among males or sperm in part on the basis of large male size (e.g., great bustards) (Fairbairn 2013), or in species with protogynous sex change in which individuals switch from female to male at a large body size (e.g., many coral reef fish; Choat and Robertson 2002). By contrast, female-biased SSD is associated with sexual selection mainly in atypical species with so-called sex role reversal in which females compete for males, males choose among females, and males make relatively large investments in offspring care and protection (e.g., some pipefishes that have polygamous mating, female competition for mates, and extended male brood care; Vincent et al. 1992). Female-biased operational sex ratios are common among parthenogenetic species (e.g., rotifers), polygynous species (e.g., gorillas), and protogynous sex-changers (e.g., wrasses; Benvenuto et al. 2017). Male-biased operational sex ratios are well known from polyandrous species (e.g., pipefishes; Vincent et al. 1992) and protandrous sex-changers (e.g., Nile perch; Benvenuto et al. 2017). Skewed sex ratios can also arise from sex-specific mortality rates outside the context of sexual selection (Parker et al. 2018).

Theories and observations of SSD and sex ratios are primarily derived from vertebrates and arthropods that exhibit courtship or copulation behaviour. By contrast, most marine invertebrates broadcast their gametes into the plankton for fertilisation and therefore lack direct interactions between spawning adults (Strathmann 1990). Sexual size dimorphism is therefore uncommon in these groups. As Fairbairn (2013) noted, ‘The sexes tend to be most similar in species that release their eggs and sperm directly into the environment with no courtship or sexual contact between the spawning individuals.’ Sexual selection may still be strong in these species (Franke et al. 2002), but competition among males or interactions between mates may be mediated by the evolution of sex differences in other types of behaviour (such as spawning time; Levitan 2005) or in gamete traits (such as binding proteins; Evans and Sherman 2013) rather than by the evolution of SSDs. Where SSDs do arise in broadcast-spawning marine invertebrates, they appear to be female-biased and caused by natural selection (rather than sexual selection) on females for large body size and high fecundity (Fairbairn 1997, 2013). Primary sex ratios in broadcast spawners, as in all animals, would be predicted to be approximately 1:1 (Seger and Stubblefield 2002). In a review of operational sex-ratio estimates in broadcast spawners, Parker et

al. (2018) found that most ratios were indistinguishable from equal; of the skewed sex ratios that were statistically significant, male bias was approximately twice as common as female bias.

Scaphopods are broadcast-spawning marine molluscs with separate sexes and a well-established primary sexual dimorphism in gonad colour (McFadieu-Carter 1979; Lamprell and Healy 1998). Little is known about scaphopod SSD or sex ratios, but several interesting reports based on unpublished data warrant further exploration. Lamprell and Healy (1998) reported both female- and male-biased dimorphism in radular dimensions of four Australian scaphopod species, and commented on female-biased SSD in body size in ‘a number’ of species. Sigwart et al. (2017) reported male-biased SSD in body weight for the northeastern Pacific scaphopod *Rhabdus rectius* (Carpenter, 1864). Shimek (1989) commented that the adult sex ratio was 1:1 in *Gadila aberrans* (Whiteaves, 1887), and hermaphroditism was reported for one species of *Dentalium* Linnaeus, 1758 (Reverberi 1971; Shimek and Steiner 1997). In each of these cases, further quantitative data on body size or sex ratios were not provided, and these topics have not otherwise been discussed in reviews of scaphopod biology (Shimek and Steiner 1997; Lamprell and Healy 1998; Reynolds 2002).

These previous reports suggest that there could be many undiscovered features of reproductive biology among organisms like scaphopods, about which little has been studied and less has been published (see McFadieu-Carter 1979; Buckland-Nicks et al. 2002; Sigwart et al. 2017). In particular, the report of male-biased SSD in *R. rectius* might indicate that other sexually selected traits (such as the potential for sperm competition or complex male-female interactions during spawning) warrant further study in this species and perhaps in other scaphopods. Here we used new data to explore that possibility in one previously well-studied population of *R. rectius*. We did not find size differences between the sexes, and we conclude that male-biased SSD (and its associated sexually-selected traits) is unlikely to occur in this species. In the course of that study, we also observed a male-biased sex ratio, and the frequent occurrence of boreholes on scaphopod shells. We made incidental laboratory observations of predation on live scaphopods by small predatory naticid gastropods [*Euspira pallida* (Broderip & G. B. Sowerby I, 1829)] that were collected along with scaphopods in our field samples. We propose that individuals of *E. pallida* may be an important source of mortality in this study population of scaphopods. We offer some interpretations of those results (size, sex ratio, predation), including a hypothesised sex difference in mortality as a possible cause of the male-biased sex ratio.

## **Materials and methods**

### ***Study location and collections***

We collected scaphopods (*Rhabdus rectius*) and associated animals (predominantly polychaetes, clams, snails, brittle stars, and burrowing sea urchins) by using a small towed dredge (opening approximately 80 by 50 cm) to collect mud from a depth of about 82 m in Imperial Eagle Channel, Barkley Sound, off the southwestern coast of Vancouver Island, British Columbia. This same population was studied by Shimek (1990), Reynolds (1992), and Sigwart et al. (2017). The full dredge was hoisted into a sorting table onboard the R/V *Alta*, and the mud was released into the table. Scaphopods were picked from the table by hand, and by sieving a mixture of mud and seawater through a series of stacked screens (smallest mesh size ~3 mm) as the mixture drained from the sorting table. We transferred scaphopods and mud to small plastic containers, and took them directly to the Bamfield Marine Sciences Centre where the animals were held with mud under gently flowing seawater at ambient temperature (approximately 9–10° C) in a flow-through seawater table.

We collected three samples of scaphopods. The first sample consisted of 36 live scaphopods selected arbitrarily from among a larger number of individuals collected in two mud dredges, one northwest of Diana Island (coordinates approximately 48.86°N, -125.21°W) and one northwest of Sanford Island (approximately 48.88°N, -125.18°W), on 7 May 2018. The second sample consisted of all 311 live scaphopods found in two mud dredges in the same area northwest of Diana Island, on 25 May 2018. The third sample consisted of all 103 live scaphopods found in two mud dredges in the same area northwest of Diana Island, on 15 September 2018 (approximately 48.87°N, -125.20°W).

We measured the length of the shell of all individual scaphopods from all three samples (N=450). We calculated sex ratio and observed the frequency of boreholes on all individuals from the second and third samples only (N=414) because these were complete samples, not arbitrary selections. We measured both shell length and dry weight for all individuals in the first sample plus 40 individuals from the second sample (N=76 total; 38 females, 38 males) (see below).

After observing evidence in the first sample of boreholes with the distinctive beveled edge characteristic of predation by drilling naticid gastropods, we examined all 414 individuals in the second and third samples for evidence of drilling on the shell, and we collected all naticid snails [*Euspira pallida*, N=16 live animals and 16 empty shells] from the second and third samples. We photographed the shells of live and dead snails against a millimetre ruler to estimate their length. To document predation, we housed live individuals of *E. pallida* with several dozen arbitrarily selected scaphopods of both sexes in several small plastic containers filled with mud

approximately 5 cm deep, in the flow-through seawater table, and checked them periodically over 3 days for boreholes and evidence of predation.

### ***Scoring secondary sexual dimorphism***

We examined each individual scaphopod under a dissecting microscope and noted the gonad colour. We confirmed the sexes by crushing the shell of several individuals of each colour and transferring some of the gonad material to a glass slide with a raised glass coverslip. We photographed gametes in brightfield illumination on a compound microscope by using a cellphone camera (iPhone SE) and microscope adapter lens (LabCam Pro) fitted to the ocular tube of the microscope. We estimated gamete sizes by using an ocular micrometer that was calibrated against a stage micrometer. We did not include a micrometer in the micrographic images, so our characterizations of gamete sizes are approximate estimates (from measurements on the live specimens using the ocular micrometer) rather than precise measurements.

We measured shell length to the nearest 0.5 mm under a dissecting microscope against a millimetre ruler (Figure 1). The shell of *Rhabdus rectius* is a slightly curved cone in which the larger aperture of the cone is ventral, the smaller tapered aperture is dorsal, and the concave edge of the cone corresponds to the anterior side of the animal (see Shimek 1989 and Sigwart et al. 2017; note that the concave edge has often been designated dorsal in other biological and paleontological literature, e.g., Reynolds 1992). We measured shell length as the straight-line distance along the concave side, from the anterior edge of the large ventral shell aperture to the anterior edge of the smaller dorsal aperture (Figure 1). The shell was always oriented with the concave side next to the ruler. This is the same measure of shell length used by Shimek (1989) and Reynolds (1992).

To estimate the length:weight relationship, we measured shell length and dry weight for 76 individuals, including all animals in the first sample plus a subset of the second sample. We measured dry weight by briefly (3–5 seconds) dipping the live scaphopod in tap water to remove excess seawater. Most individuals responded to this rinse by withdrawing the head and foot deeper into the ventral aperture, which had the benefit of displacing seawater from the mantle cavity. We then blotted excess water from the shell, and put the scaphopod into a small preweighed aluminum pan. Scaphopods were then dried to a constant weight at 40° C. We weighed each individual to the nearest 0.1 mg on an Ohaus AV264 balance; each scaphopod was weighed at intervals of 6–18 hours until sequential weights differed by 0.3 mg or less (typically after 36–48 hours), and the minimum of those two weights was taken as the final weight.

## Results

### *Sexual colour dimorphism*

Females and males of *R. rectius* could be readily distinguished by gonad colour: females of this species develop a vivid yellow ovary that occupies a large proportion of the body and can be easily observed through the translucent dorsal portion of the shell (Kozloff 1996, Sigwart et al. 2017; Figure 1A); males develop a pale white testis that is also readily visible through the shell (Figure 1B). Each gonad consisted of a series of tubules that could be seen under the dissecting microscope as fine transverse lines (Figure 1C). In some individuals, the number and extent of those tubules was limited, but ovaries were consistently distinguishable from testes by their yellow colour even when the ovary was relatively small. Only in our third sample did we observe individuals with no distinct gonad: in addition to the 103 scaphopods included in our size and sex-ratio observations, we found 4 individuals without an identifiable gonad and thus could not be sexed (so were not included in our analyses).

Individuals with yellow gonads contained yellow oocytes that could be released by dissection. Oocytes were prolate spheroids or discs  $\sim 240 \mu\text{m}$  long and  $\sim 210 \mu\text{m}$  wide, with an extracellular coat approximately  $5\text{--}8 \mu\text{m}$  thick, and a large internal germinal vesicle (Figure 2A). Individuals with white gonads released large numbers of actively swimming sperm with heads  $\sim 5\text{--}6 \mu\text{m}$  long (Figure 2B). The sizes and shapes of gametes were similar to previous reports for other scaphopod species (e.g., oocytes  $\sim 240 \mu\text{m}$ , Rokop 1977; oocytes  $220\text{--}240 \mu\text{m}$ , Moreau et al. 1989; oocytes  $200 \times 10 \mu\text{m}$ , Dufresne-Dube et al. 1983; oocytes in the shape of a ‘yellow or red pigmented disc’, Reverberi 1971; ‘biscuit-shaped’ oocytes, McFadien-Carter 1979; Dufresne-Dube et al. 1983; an ‘imposing barrier of jelly which surrounds the egg’, Reverberi 1971; sperm heads  $\sim 5 \mu\text{m}$  in length, Moreau et al. 1989; Dufresne-Dube et al. 1983).

### *No sexual size dimorphism*

Mean scaphopod shell lengths ( $\pm 1$  S.D.) were indistinguishable between female ( $29.0 \pm 4.9$  mm,  $N=182$ ) and male ( $29.5 \pm 6.4$  mm,  $N=232$ ) *R. rectius* ( $t=0.87$ ,  $P=0.38$ ) (Figure 3). For this comparison we used only individuals from the second and third samples ( $N=414$ ) for which we obtained unbiased population samples of males and females, and we left out the first sample ( $N=36$ ) which represented an arbitrary selection of individuals. The difference in mean shell

length was similar to the precision of the individual shell length measurements (0.5 mm). The overall estimated mean shell length was  $29.3 \pm 5.8$  mm (N=414). The distributions of shell lengths for females and males were similar and broadly overlapping (Figure 3).

Mean scaphopod dry weights were indistinguishable between females ( $32.2 \pm 10.1$  mg, N=38) and males ( $32.8 \pm 12.9$  mg, N=38) ( $t=0.21$ ,  $P=0.83$ ). Scaphopod dry weight was strongly correlated with shell length ( $r=0.79$ ; Figure 4), and the relationships between dry weight and shell length were not different between the sexes by an analysis of covariance ( $F_{1,72}=0.65$ ,  $P=0.42$ ), so shell length is a good proxy for overall body size. Only at the tails of the distributions were there any apparent differences between the sexes: the few shortest and longest shells (<16 mm and >42 mm respectively) were males, but the heaviest individual we sampled was female (almost 70 mg; Figure 4).

### ***Sex ratio***

The female:male sex ratio (1:1.3, N=414) was biased toward males, which was significantly different from a 1:1 sex ratio (binomial exact test,  $P=0.016$ ). Males are not expected to be significantly more common than females in *R. rectius*. One possible source of the biased sex ratio is errors in sex identification. The sexes may be more difficult to distinguish among small individuals with small or indistinct gonads, but we observed many individuals of both sexes among those with the shortest shells (Figure 3). Those results suggest that this population has a male-biased sex ratio with the very longest and very shortest 1% of shells found only among males. All other evidence indicated that male-biased sexual size dimorphism is weak or absent in this population: the heaviest individual was female (Figure 3), the distributions of shell length were similar between the sexes (Figure 3), but both mean dry weight and mean shell length were similar between the sexes (Figure 4).

### ***Association between scaphopods and boring predators***

We found 30 out of 414 individuals with evidence of attack by a drilling snail, including two (both males) with complete boreholes (Figure 5A), giving a minimum drilling frequency of <1%, and 28 others (12 females, 16 males) with one or more incomplete boreholes (Figure 5B). The proportion of females with boreholes in that sample (14 out of 182) was not significantly different from the proportion of males with boreholes (16 out of 232) (Fisher's exact test  $P=0.85$ ). The complete boreholes were approximately circular and ~1 mm in diameter, with a sharp inner edge

and a beveled margin. Incomplete boreholes were typically found near the dorsal end of the shell (overlying the dorsal region of the mantle and mantle cavity). By contrast, the two complete boreholes occurred on a relatively wider region of the shell closer to the ventral end (in the region overlying the visceral mass). Those boreholes were similar to boreholes in several dead tusk shells that we collected alongside live scaphopods, and similar to boreholes typically made by naticid snails.

The second mud sample contained 11 live *Euspira pallida* (Figure 5C), giving a naticid:scaphopod ratio of ~1:30; the third sample contained 5 live *E. pallida*, for a ratio of ~1:20. The live snail shell lengths ranged 6–20 mm. When housed in the lab, the scaphopods burrowed into the mud in their characteristic posture with the dorsal aperture sticking out above the surface. The naticids actively burrowed into the mud. One was observed with its extended foot wrapped around a scaphopod. After three days, we found five boreholes among 45 scaphopods housed with six snails (Figure 5D).

## Discussion

We found a male-biased sex ratio in *Rhabdus rectius* (1:1.3), but no evidence of sexual size dimorphism in the mean length, mean dry weight, or length or weight frequency distributions, except that the longest and shortest individuals (~1% of the sample in each case) were male. These results suggest that females and males are part of the same single size distribution in this population of *R. rectius*. The overall estimated mean shell length ( $29.3 \pm 5.8$  mm,  $N=414$ ) was similar to that estimated by Shimek (1989) for the same population of '*Dentalium*' *rectius* ( $27.6 \pm 8.8$  mm,  $N=483$  adults of unreported sex). We were not able to corroborate the previous report of male-biased SSD in *R. rectius* (Sigwart et al. 2017).

Other published reports of SSD in scaphopods had mixed results. Lamprell and Healy (1998) noted that females tended to be larger than males among some Australian scaphopod species, but did not report shell lengths or other measures of overall body size. They did note that shell length tended to covary with the size of the radula, and reported SSD in radular tooth sizes for four of 28 species. The direction of SSD was not always the same for all teeth (central, lateral, marginal) within a species, but based on total radular widths one species showed male-biased SSD (radula 23% wider in males), and two species showed a small female-biased SSD (radula 2% and 4% wider in females). A fourth species showed likely male-biased SSD, but comparative data for marginal teeth were unavailable. Since these species were examined from multiple collections of relatively few individuals each, and sample sizes and variation were not reported



for the tooth dimensions, it is unclear whether these size differences are representative (for each species) or biologically meaningful (in general).

Our observation of a male-biased sex ratio, in a study population in which other researchers have not previously reported data on sex ratios (Shimek 1989, 1990; Reynolds 2002; Sigwart et al. 2017), suggests that interesting and important aspects of the mating system of *Rhabdus rectius* are yet to be discovered. Unfortunately, there are few previous studies of mating systems and sexual selection in scaphopods for comparison. As noted by Collin (2013), ‘[T]he scaphopods... are under-studied and seldom reared in the laboratory, [so] the apparent absence of diversity in sexual systems may simply be due to a lack of information about all but a handful of species.’

Our observations of sex ratio and predation were made incidentally to our planned study of sexual size dimorphism. Although our data on size differences between the sexes do not seem to indicate future directions for research on sexual selection in scaphopods, our incidental observations on sex ratio and predation may suggest other interesting lines of future research. Below we suggest several complementary interpretations of the sex ratio and predation results, and hope that our speculation about the causes and significance of those patterns might lead to additional discoveries in this study population and in other scaphopod species.

### ***Size and sex in scaphopods***

One plausible cause of the biased sex ratio in *R. rectius* is sex change. Collin (2013) noted that sequential hermaphroditism is common among molluscs, and that a combination of biased sex ratio plus SSD can be used to predict the occurrence of sex change at the population level. Mollusc species with well-characterised systems of sex change often have broadly overlapping distributions of male and female size (Collin 2006), in which sex differences are apparent only among very large or very small individuals (Collin 2013). Species with protandrous sex change that switch from male (when small) to female (when large) typically have male-biased (or unbiased) sex ratios (Allsop and West 2004) and female-biased SSD (Collin 2013). In *R. rectius* we found a male-biased sex ratio, but no pronounced sexual size dimorphism (even at the extremes of the size distribution) that would be consistent with either protandrous or protogynous sex change. Although D’Anna (1974) reported hermaphrodites in one species [*Antalis entails* (Linnaeus, 1758)], scaphopods are consistently described as gonochoric (e.g., Lamprell and Healy 1998, Reynolds 2002), and sex change of either form has not been previously reported. Although

sex change might occur, the broadly overlapping distribution of female and male sizes seems to argue against it.

### ***Death in the mud***

A second plausible cause of the male-biased sex ratio is a higher mortality rate for females (Collin 2013). Pathogens, parasites (including haplosporidians, trematodes, and copepods; Desportes and Nashed 1983; Koie et al. 2010; Boxshall and O'Reilly 2015), and predators (including fish, crabs, and gastropods; Shimek 1989, Abello 1995, Eilertsen and Malaquias 2013, Mallick et al. 2017) are all possible causes of mortality.

One possible mechanism leading to higher female mortality is sexual selection for greater female investment in reproduction. Parker et al. (2018) developed a game theoretic model of tradeoffs between investment in gonads versus investment in somatic maintenance or future growth for broadcast-spawning marine invertebrates, and showed that the model could account for some observed patterns of variation in relative ovary and testis sizes in some taxa. In particular, the model can potentially account for the evolution of biased sex ratios in species where one sex invests more heavily in gonads and gametes at the expense of somatic maintenance, leading to a sex bias in mortality rates (higher in the sex with lower investment in maintenance) and a biased adult sex ratio. Unfortunately, Parker et al. (2018) noted that the few available data for molluscs do not seem to conform to the predictions of this model: they reviewed data for 13 species of broadcast-spawning gastropods and bivalves that had male-biased sex ratios (range 1:1.2–1:2.3), but found no strong tendency for females to invest more heavily in ovaries and eggs (relative to male investment in testes and sperm) among those 13 species. Such comparative data from other molluscs do not strongly suggest that the costs of greater female investment in reproduction are likely to explain the biased sex ratio we observed in *R. rectius*, but data on the relative weights of gonads are needed to specifically test that prediction in this species.

A second possible mechanism leading to higher female mortality is sexual dimorphism in spawning behaviour (Levitan 2005). Steiner (1993) reported that, in one gadilid scaphopod species, males spawned through the small dorsal aperture that protrudes above the surface of the sediment, whereas females spawned through the larger ventral aperture; Reynolds (2002) speculated that this behaviour would require females to move to the sediment surface. Such a behavioural difference could expose spawning females to higher risk of predation, particularly by visual predators. The spawning behaviour of *R. rectius* is unknown, but in two other dentaliid

species both sexes spawn through the smaller dorsal aperture (Steiner 1993), so this hypothesis seems unlikely to account for the male-biased sex ratio.

Boring by naticid gastropods may be an important source of mortality for some scaphopod populations (Reynolds 2002), and associations between naticid predators and scaphopod prey are widespread in the fossil record (recently reviewed by Mallick et al. 2017). Our observations of a common predatory naticid (*Euspira pallida*) in collections of *R. rectius*, including dead tusk shells with naticid boreholes collected in the field, and our observations of live scaphopods successfully attacked by these moon snails in the lab, are therefore not surprising. The common occurrence of incomplete boreholes (unsuccessful predation attempts) on the dorsal end of the shell of live individuals, and the relative rarity of complete holes (successful predation attempts), is also consistent with the hypothesis that predation pressure is higher on scaphopod individuals at least partially exposed on the sediment surface.

If *E. pallida*, or other predators, preyed on females more often than on males, their selection could contribute to the male-biased sex ratio we observed. Like so many other features of the natural history of *R. rectius* and other scaphopods, knowledge of predator–prey interactions among live individuals in nature is scarce, and testing that hypothesis seems to require observation of interactions between predators and prey in the field.

### ***Conclusion***

We analysed the distribution of body size (dry weight, shell length) among female and male individuals of the scaphopod *Rhabdus rectius*. We found no significant size differences between the sexes, but we observed a significant male bias in sex ratio. We made some incidental observations on the occurrence of predators and evidence of predation on scaphopod shells that may help to account for a biased sex ratio. Specifically, differences in predation rates on females and males seem like one plausible explanation of the observed sex ratio. We found a well-known predatory snail in our collections of scaphopods, including scaphopod shells that showed evidence of predation attempts, and we observed successful attacks by snails on scaphopods in the lab. We propose that this predatory interaction might account for the discovery of a biased sex ratio without sexual size dimorphism, but direct observations of reproduction and predation are needed to test that proposal.

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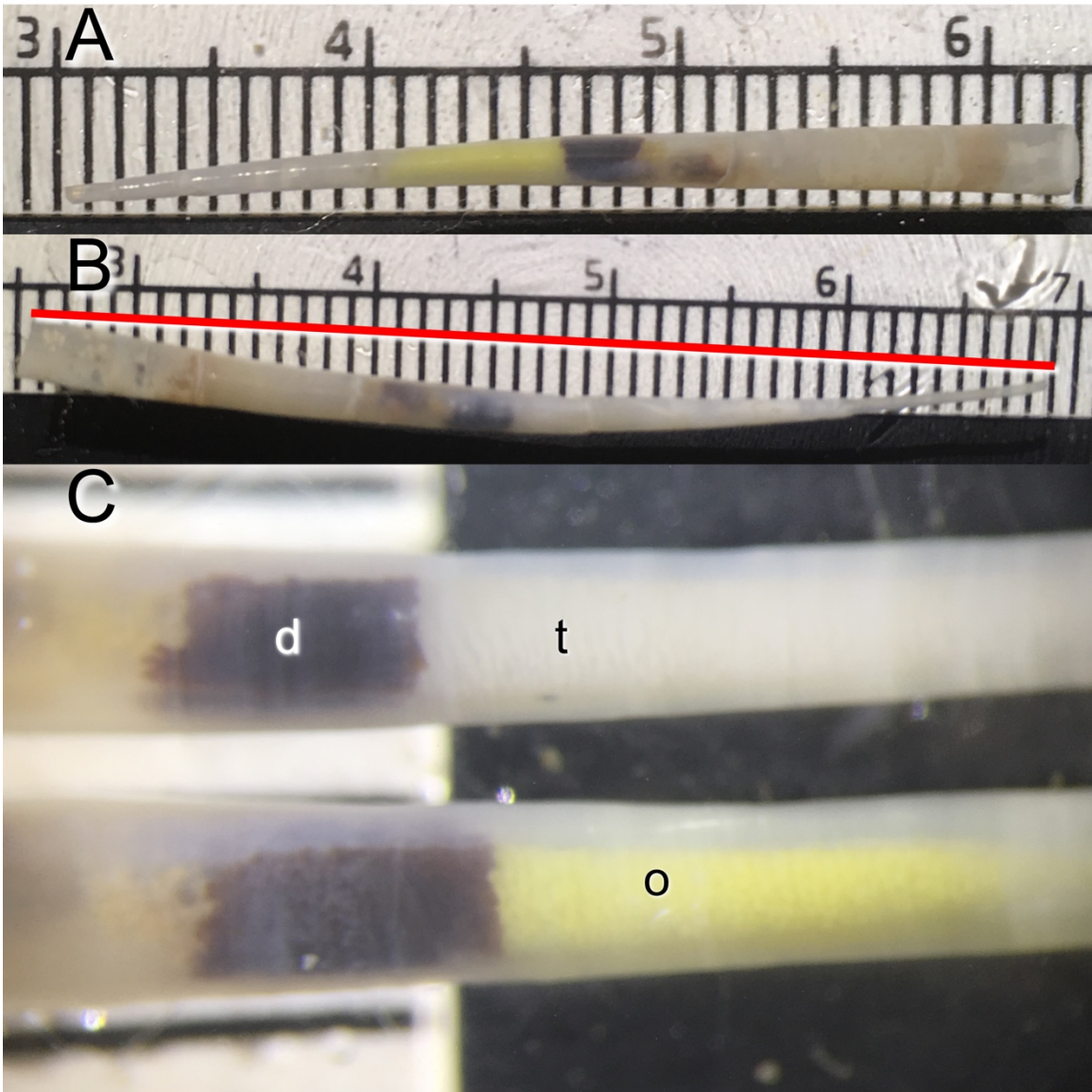
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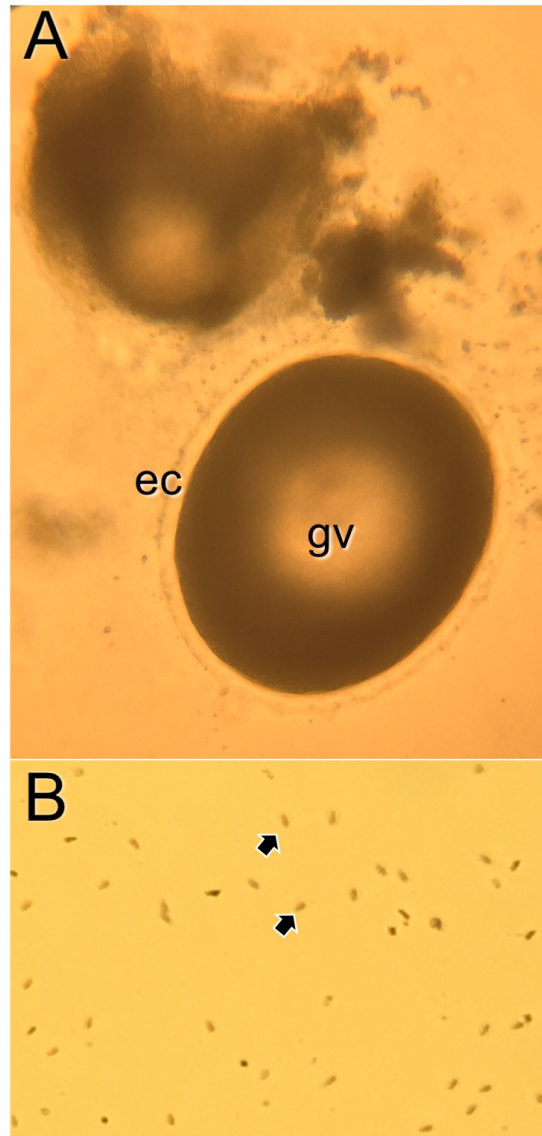
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**Figures and figure legends**

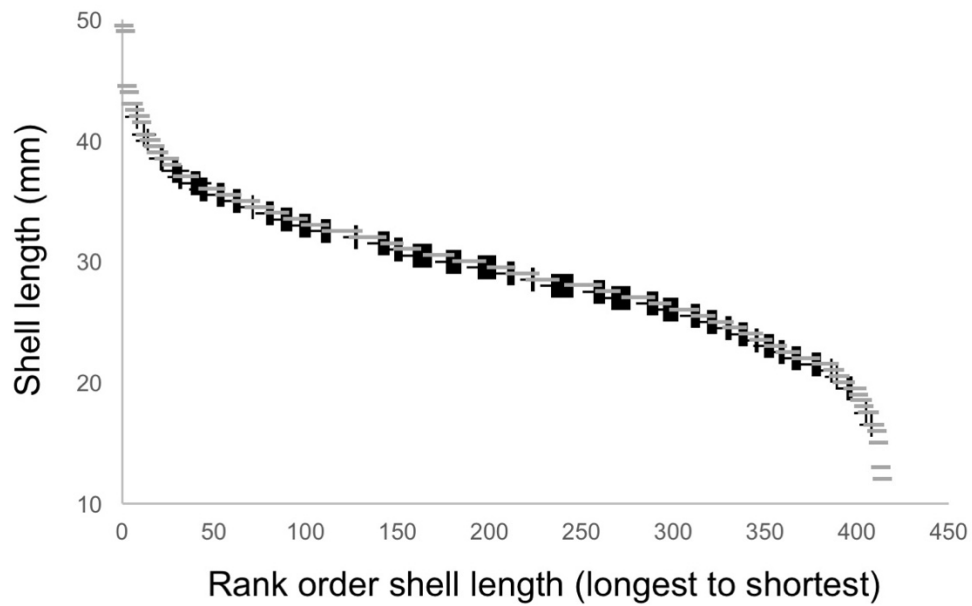


**Figure 1.** Primary sex differences in scaphopods *Rhabdus rectius*. **A**, female individual with the larger ventral shell aperture to the right and the smaller dorsal aperture to the left; **B**, male individual with the ventral aperture to the left; the red line shows the straight-line measurement of shell length along the ventral edge of the shell (43 mm, measured against a millimetre ruler); **C**, close-up view of a male and female in the same orientation as in B; the shell of each individual in C is ~1 mm wide (shown against a millimetre ruler in the background); d–digestive gland; o–ovary; t–testis.

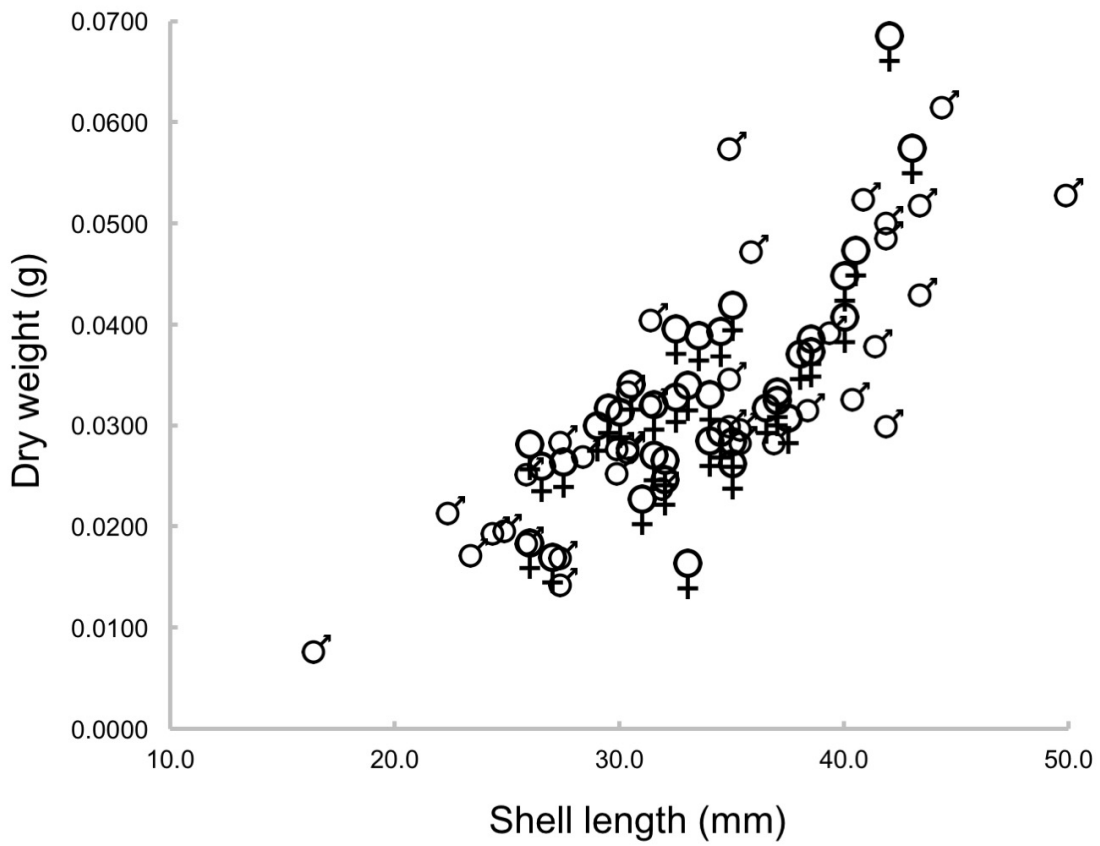




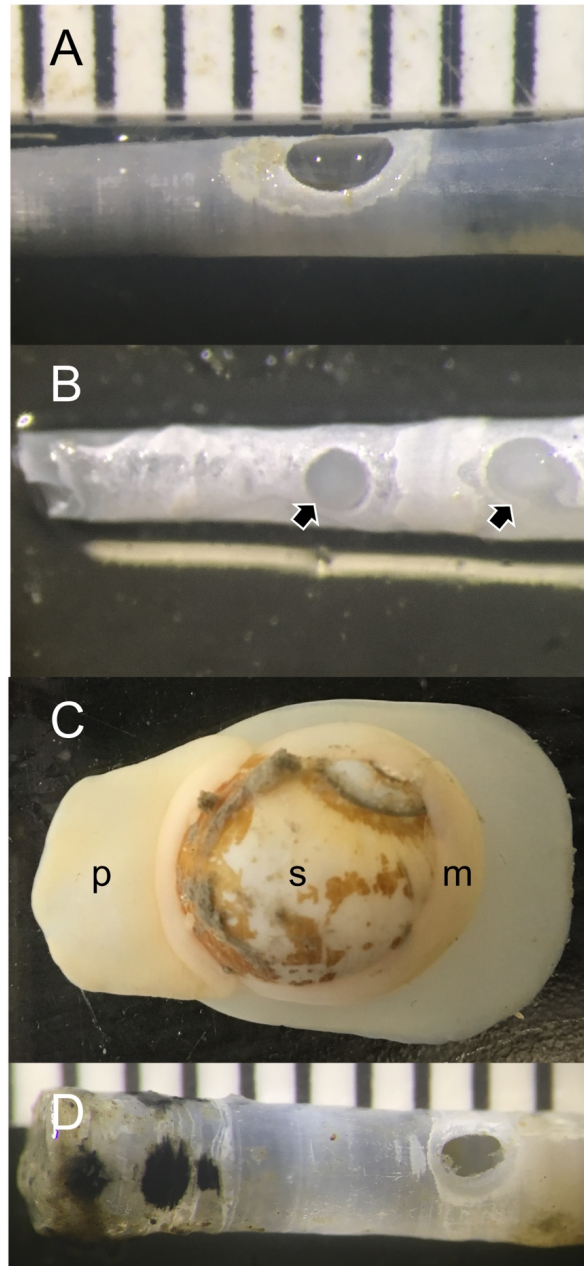
**Figure 2.** Gametes of scaphopods *Rhabdus rectius*. **A**, an oocyte in its egg coat, and part of a second damaged oocyte, dissected from a female with a yellow gonad; ec–egg coat; gv–germinal vesicle; **B**, sperm dissected from a male with a white gonad; arrows indicate individual sperm heads. The dimensions of the oocyte are approximately 240  $\mu\text{m}$  long and 210  $\mu\text{m}$  wide; the sperm heads are approximately 5  $\mu\text{m}$  long; the two images are taken at approximately the same magnification.



**Figure 3.** Distribution of shell length in 232 males (grey bars) and 182 females (black crosses) of scaphopods *Rhabdus rectius*; shell lengths are shown ordered from longest (left) to shortest (right).



**Figure 4.** Shell length and dry weight in 38 females and 38 males of scaphopods *Rhabdus rectius*.



**Figure 5.** Scaphopods and their possible predators. **A**, a dead scaphopod (*Rhabdus rectius*) with a complete hole probably drilled by a naticid gastropod; **B**, a live scaphopod with two incomplete boreholes (arrows); images in A and B are taken at the same magnification (relative to the millimetre ruler in A); **C**, the predatory naticid snail *Euspira pallida* (shell length ~15 mm); m–mantle; p–propodus; s–shell; **D**, a complete borehole drilled through the shell of a scaphopod by a moon snail in the lab. The boreholes in A and D are similar in size relative to the millimetre ruler in each image, but the orientations are different (the wide ventral aperture is out of the field of view to the right in A and B; the ventral aperture is shown on the left side of the panel in D).