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Parental care in *Sphaerium striatinum* Lamarck: evidence for retention of competent offspring

Mark A. Beekey, Ronald H. Karlson, and Alyse R. Greenberg

Abstract: The timing of offspring release is a fundamental turning point in the life history of any organism. It represents the end to many of the most costly forms of parental care (e.g., provisioning of nutrients for developing eggs and zygotes) and the beginning of an independent life for the offspring. Generally temporal variation in this event is attributed to a variety of physiological and evolutionary trade-offs. Here we examine the retention of offspring in the freshwater clam *Sphaerium striatinum* Lamarck. Brooded offspring are typically not released into the environment until they are 4.0 mm shell length (SL). We provide evidence that offspring as small as 2.0 mm SL are competent to process particles and produce both fecal and pseudofecal material. Furthermore, such small clams are shown to experience higher mortality than larger individuals once they are removed from brood pouches. Hence, the retention of competent offspring within brood pouches represents a form of extended parental care.

Résumé : Le moment de la libération des rejetons est un point tournant dans le cycle de n'importe quel organisme. Ce moment représente la fin de plusieurs des formes les plus coûteuses de soins parentaux (e.g., mise en réserve de nutriments pour les oeufs et les zygotes en développement) et le début de l'autonomie chez les rejetons. De façon générale, la variation temporelle de cet événement est attribuée à un ensemble de compromis physiologiques et évolutifs. Nous examinons ici le phénomène de la rétention des rejetons chez la Sphaerie striée, *Sphaerium striatinum* Lamarck. Les rejetons du couvain ne sont ordinairement pas relâchés dans l'environnement avant d'atteindre 4,0 mm de longueur. Nous apportons ici la preuve que des rejetons qui ne mesurent pas plus de 2,0 mm de longueur sont capables de manipuler les particules et de produire des matières fécales et pseudofécales. De plus, il est démontré que ces petites sphaeries subissent une mortalité plus importante que les gros individus une fois qu'ils ont quitté le couvain. Ici, la rétention de rejetons potentiellement autonomes dans le couvain représente une forme de prolongation des soins parentaux.

[Traduit par la Rédaction]

Introduction

The timing of offspring release is a fundamental turning point in the life history of any organism. This release marks the end of many forms of parental care and the beginning of an independent existence. Natural selection might be expected to maximize the amount of time that developing offspring spend in the safest stages of development and to minimize the time spent where the risks of mortality are high (Shine 1978, 1989). For instance, when egg mortality is low relative to juvenile mortality, selection should favor prolonged development of the egg and a concomitant increase in egg size. Conversely, when egg mortality is high relative to juvenile mortality, selection should favor prolonged development in the juvenile stage. Thus, the timing of life-history transitions are predicted to vary with these relative mortality rates.

The retention of offspring (a form of extended parental care) is often associated with harsh or unpredictable environments (Hinton 1981; Zeh and Smith 1985; Tallamy and Wood 1986). Offspring retention ensures a minimal reproductive success in small species with relatively short life-spans (Strathmann and Strathmann 1982; Clutton-Brock 1991). Since parental care is generally costly to the parent in terms of reduced survival and subsequent reproductive performance, we might expect to find extended parental care where there are even higher costs to offspring. During this time, parents may protect offspring from competitors, predators, or environmental factors. The retention of offspring may also buffer extreme effects of environmental fluctuations in both physical and biological factors (Hogarth 1976).

Sphaerium striatinum Lamarck is a small, ovoviviparous, freshwater clam, which broods its offspring and releases fully developed juveniles. *Sphaerium striatinum* produces oocytes that are simultaneously fertilized within the gonadal tract (Heard 1977) and released into the mantle cavity. Oocytes (100 μm diameter) are enclosed by evaginations of gill filaments (marsupial sacs) between the lamellae of the inner demibranch (brood pouch), where they undergo direct development (intra-marsupial) (see Fig. 1). The eggs contain insufficient yolk to supply the nutrients necessary to complete development (Raven 1958; Mackie 1978). Marsupial sacs are thought to provide nourishment to developing offspring (Okada 1935). Over the course of development intra-marsupial offspring break free of the marsupial sacs (≈3.0 mm shell length (SL)) and are retained within the brood pouch (extra-marsupial) (Fig. 1). Extra-marsupial offspring are normally released into the environment around 4.0 mm SL.

According to life-history theory, the retention of extra-marsupial offspring in *S. striatinum* should promote growth and enhance juvenile survivorship in the external environment (Stearns 1992). However, previous research on this

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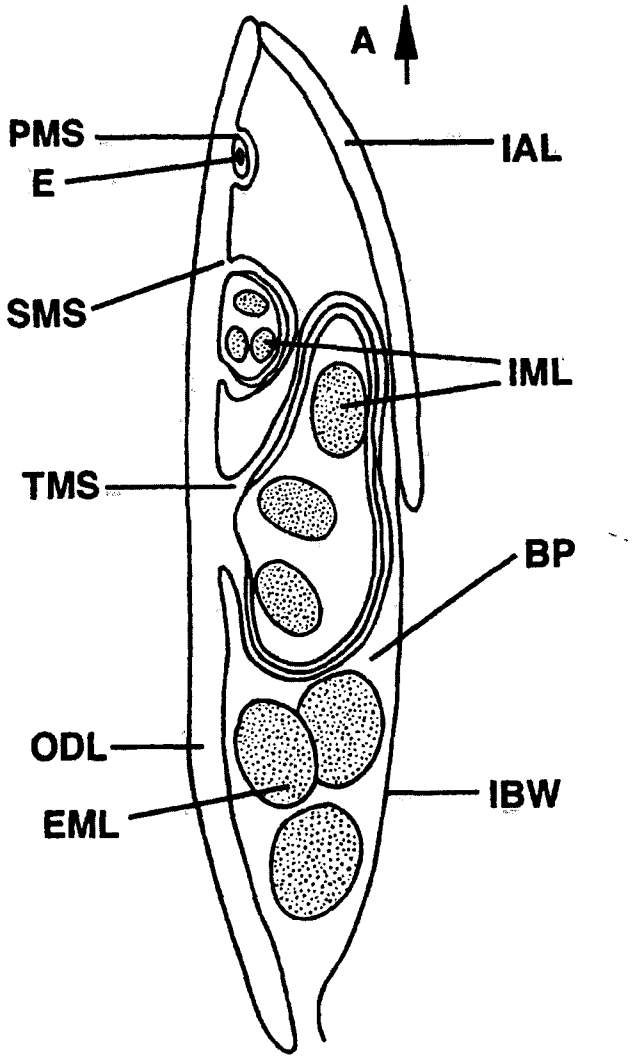
Fig. 1. Frontal view of a left anterior (i.e., inner) demibranch of *Sphaerium striatinum*. A, anterior; E, embryo; EML, extra-marsupial larvae; IML, intra-marsupial larvae; IAL, inner ascending lamellae; IBW, inner wall of the brood pouch; BP, brood pouch; ODL, outer descending lamellae; PMS, primary marsupial sac; SMS, secondary marsupial sac; TMS, tertiary marsupial sac. Redrawn from Heard (1977).



species has failed to clarify whether or not retained offspring are competent and experience enhanced survivorship. In this paper, competence is defined in terms of the ability to ingest food, process particulate matter, and survive outside of the adult. Our results indicate that brooded offspring as small as 2.0 mm SL are competent. However, offspring <4.0 mm SL experience extremely high size-dependent mortality, once removed from the brood pouch. Thus, the retention of offspring <4.0 mm SL reduces size-dependent mortality by promoting juvenile growth within the adult.

Materials and methods

Sphaerium striatinum is known to feed on a wide size range of suspended and deposited particulates in stream environments (<1.5–10 mm, McMahon 1991). Preliminary observations indicated that adult *S. striatinum* would ingest and defecate Carmine Red (<5 mm particle size). Using this as an indicator, we investigated the ability of brooded offspring to ingest particulate matter by presenting Carmine Red in solution (300 mg/L distilled H_2O) to adults and excised offspring. We then observed the uptake of these particles by the examination of the digestive tract and plotted the ability to feed versus SL.

Particle feeding

Retained offspring

To examine the ability of retained offspring to ingest particles, we placed 40 adults (10.6 ± 0.2 mm SL, mean ± SE) into eight 100-mL beakers with 60 mL of distilled H_2O. Ten millilitres of Carmine Red were added to six beakers and 10 mL of distilled H_2O were added to the remaining two beakers. After 2, 4, and 6 days, one adult from each beaker was removed and dissected. The digestive tract of the adult and all brooded offspring were examined for the presence of Carmine Red. The location and length of offspring within all adults (intra- versus extra-marsupial) were also recorded.

Excised offspring

To demonstrate that intra-marsupial offspring are competent, 100 excised offspring (2.5 ± 0.1 mm SL) were individually placed into 25-mL tubes filled with 20 mL of filtered stream water. We excised the offspring from the brood pouches of freshly collected adults. By carefully excising brooded offspring we managed to collect a wide range of different-sized offspring. We carefully examined each excised offspring for damage from the dissection process. Second, we observed excised offspring for pedal movement and siphon extensions. Any offspring that exhibited signs of shell damage and did not extend their foot or siphons were not used in this experiment. Two millilitres of Carmine Red were added to 70 tubes, while the remaining tubes received 2 mL of distilled H_2O. After 3 days, the excised offspring were examined under a dissecting microscope for the presence of Carmine Red in their digestive tract.

Survivorship

Excised offspring

To demonstrate that offspring size directly affects survivorship outside of the adult, 90 excised offspring (2.30 ± 0.1 mm SL) were divided into six 500-cm^3 plastic boxes containing a 2-mm layer of sifted stream sediment (particle size = <1.0 mm). Five millimetre diameter holes were cut into each side of the plastic boxes and covered by 1-mm wire mesh to allow for water flow. The boxes were placed in an outdoor 906-L recirculating freshwater tank. After 2 weeks, the offspring were removed, measured, separated by length, and scored for survivorship.

Results

Particulate feeding

Brooded offspring

The ability of retained offspring to ingest particles depends on their size and the location of the offspring within the brood pouch. SL was significantly related to the ability to ingest food (G = 177.8, df = 4, $p < 0.001$). Offspring <2.0 mm SL had no Carmine Red in their digestive tract (Fig. 2). Among offspring larger than 2.0 mm SL, particles were only present in extra-marsupial offspring. All adults contained particulate matter within their digestive tract. The

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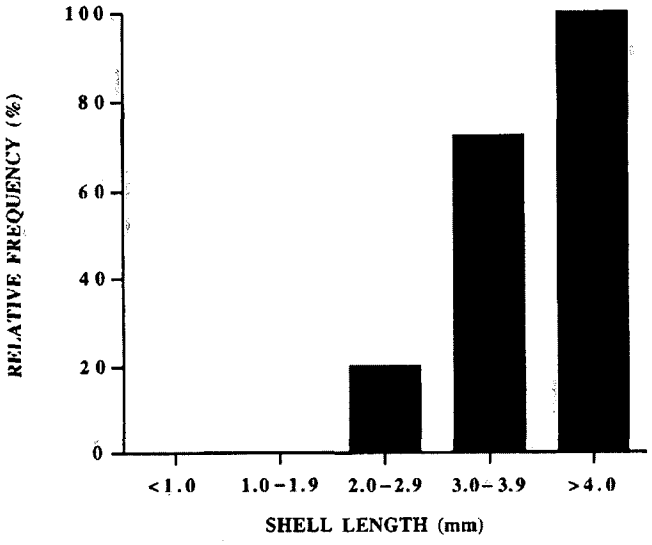
Fig. 2. Relative frequency of adults and brooded offspring with Carmine Red in the digestive tract. N = 172 (<1.0 mm shell length (SL)), 94 (1.0–1.9 mm SL), 41 (2.0–2.9 mm SL), 32 (3.0–3.9 mm SL), and 64 (4.0 mm SL) clams. Adults are grouped with brooded offspring in the 4.0-mm size class.



addition of Carmine Red had no effect on adult survivorship (χ^2 = 0.12, df = 1, p > 0.05). The mean number of offspring per adult was 4.5 ± 0.3 SE. The number of extra-marsupial offspring ranged from 0–3 per adult (0.6 ± 0.1, mean ± 1 SE). The mean size of intra-marsupial offspring was 0.8 ± 0.1 mm SL compared with 3.1 ± 0.1 mm SL for extra-marsupial offspring.

Particulate feeding

Excised offspring

The ability of offspring to ingest particulate matter independently of the adult is significantly related to SL (G = 149.26, df = 4, p < 0.001). All offspring larger than 1.4 mm SL contained Carmine Red in the digestive tract (Fig. 3). Excised offspring smaller than 1.0 mm SL contained no particulate material in their digestive tract. Similarly, the formation of pseudofeces also varied in this same manner with the size of the excised offspring (Fig. 3).

Survivorship

Excised offspring

Survivorship among excised offspring increased proportionately with SL (Fig. 4). Maximum survivorship occurred among offspring larger than 4.0 mm SL (72%) and no individuals smaller than 2.0 mm SL survived. SL was a significant factor determining offspring mortality (G = 177.8, df = 4, p < 0.001).

Discussion

These results clearly demonstrate that offspring (2–4 mm SL) retained in the brood pouches of *S. striatinum* are competent (Fig. 3). Since these offspring are also shown to experience extremely high size-dependent mortality when they

Fig. 3. Relative frequency of excised offspring with Carmine Red in pseudofeces, stomach, and rectum. N = 16 (<1.0 mm shell length (SL)), 26 (1.0–1.4 mm SL), 21 (1.5–1.9 mm SL), and 37 (2.0 mm SL) clams.

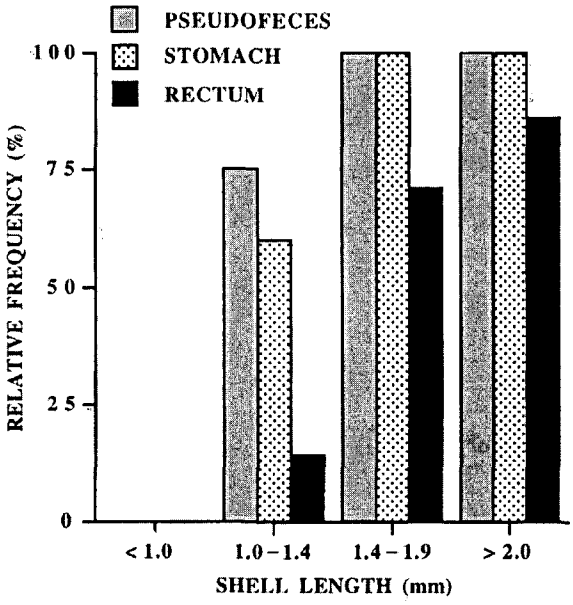
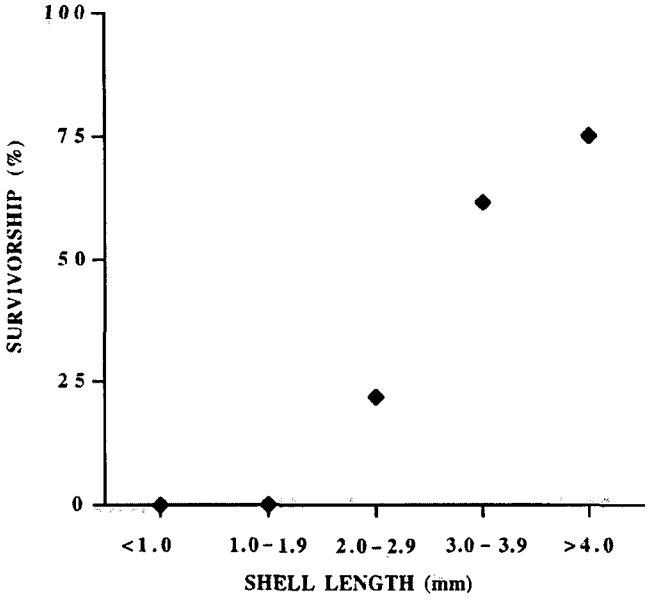


Fig. 4. Survivorship of excised offspring after 2 weeks in an outdoor tank. N = 16 (<1.0 mm shell length (SL)), 21 (1.0–1.9 mm SL), 16 (2.0–2.9 mm SL), 14 (3.0–3.9 mm SL), and 23 (4.0 mm SL) clams.



are removed from the brood pouch (Fig. 4), the retention of competent offspring represents an important form of extended parental care. The retention of offspring in *S. striatinum* is predicted to reduce size-dependent mortality after release by promoting growth. Our results agree with this prediction.

The ability of retained offspring as small as 2.0 mm SL to feed and survive externally of the adult clearly satisfies the

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definition of competency. In the first experiment only, extra-marsupial offspring ingested particles presented to adults in the water column. Intra-marsupial offspring ingested no particles. Thus, marsupial sacs act as a barrier to particles in the water column. Therefore, the development of intra-marsupial offspring is fueled solely by yolk and dissolved organics in the adult hemolymph. Evidence for the translocation of nutrients from adults to brooded offspring has been documented in freshwater mussels (Schwartz and Dimock 1998). Our results support the notion that nutrients are provided to brooded offspring by the adult in *S. striatinum* (Okada 1935). However, if offspring are removed from marsupial sacs, individuals as small as 1.0 mm SL are able to process particles (Fig. 3). Thus, offspring are competent to feed long before they break free from the marsupial sacs and are retained in the brood pouch.

Retained offspring as small as 2.0 mm SL are able to survive outside of the adult (Fig. 4). Juvenile survivorship increases with SL. Offspring size is important in regulating size-dependent mortality in many small freshwater bivalves (Fuller 1974; Dreier 1977; Thompson and Sparks 1977, 1978; Covich et al. 1981; Dyduch-Falniowska 1982; Smith et al. 1986). Previous research on sphaeriids has documented that increased shell size affects survival in coarse-grained sand environments, prevents damage from shifting sands, allows for effective locomotion, buffers changes in water chemistry (Servos and Mackie 1986), and increases the ability to avoid dessication (Mackie 1979; McKee and Mackie 1980). Since retained offspring increase in length within the adult (Avolizi 1976), the delayed release of smaller offspring into the environment reduces such size-dependent mortality. Thus, the brood pouch provides a stabilized environment for developing offspring until they reach a size with relatively high survivorship (Shine 1978, 1989).

Clearly, offspring as small as 2.0 mm SL are competent and can survive outside of the adult. Offspring retention in *S. striatinum* promotes growth and reduces size-dependent mortality. It is not known how the retention of offspring physically affects the adult, but the retention of glochidia larvae in a freshwater mussel had no affect on filter-feeding in adults (Tankersley and Dimock 1993). However, the large size of brooded offspring in *S. striatinum* (up to 4.5 mm SL in this study) highlights the potential for severe limitation on brood size. Evidence supporting such a size limitation in *S. striatinum* is the observation that up to 90% of the brood die before offspring are released (Hornbach et al. 1982). Brood reduction in this species is most likely related to the retention of competent offspring and the physical limitations on the adult. However, experimental data supporting this notion are lacking. Future studies should focus on these limitations and how the retention of competent offspring affects brood reduction in this species.

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