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Apparent sibling rivalry in the freshwater fingernail clam *Sphaerium striatinum*

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Abstract In *Sphaerium striatinum*, a freshwater brooding bivalve, up to 97.5% of offspring that adults initially produce fail to reach independence. Marsupial sacs, specialized extensions of gill filaments that act as nurseries, initially contain multiple offspring in various sizes and stages of development. However, by the time offspring reach later stages of development, marsupial sacs typically contain only one offspring. Brood mortality is hypothesized to be the result of competition among embryos for nutrients and/or space. Sphaeriid eggs do not contain enough yolk for offspring to complete development. Adults supply additional nutrients required to reach independence. Brood capacity is limited by adult size. Adults cannot physically brood all offspring they produce. Here, we examine the validity of the competition hypothesis for brood mortality. We reared offspring, in vitro, through metamorphosis under varying nutrient levels and embryo densities. While hatching success and time to hatching were not influenced by nutrients or density, both factors had significant effects on the percentage of embryos completing metamorphosis and timing of metamorphosis. A higher percentage of offspring completed metamorphosis in higher nutrient levels and lower densities. Offspring reared with higher nutrient levels and lower densities also completed metamorphosis more rapidly. We discuss these results in relation to hypotheses for the overproduction of offspring, sibling ri-

valries, as well as factors that might explain brood mortality in this species.

Keywords Bivalves · Brooding · Brood mortality · Sibling rivalry

Introduction

Size-limited brood capacity is common among invertebrates that brood offspring inside the adult body (Strathmann and Strathmann 1982; Shine 1988). Invertebrates with hard exoskeletons such as cladocerans (Perrin 1987) and amphipods (Glazier 2000) or with shells such as bivalves (Bayne et al. 1983; Calow 1983; Sebens 1987; Nakaoka 1998) and gastropods (Chaparro et al. 1999) are particularly susceptible to size-related constraints on brood capacity. In these species, the physical space available for brooding determines the critical upper limit of brood size (Olsson and Shine 1997). While spatial constraints need not limit initial numbers of offspring, they may become increasingly severe over the course of offspring development (Strathmann and Strathmann 1982). Consequently, species with size-limited brood capacity often produce more offspring than they can physically rear to independence.

The continued production of supernumerary offspring has been categorized theoretically in a number of ways (see Mock and Parker 1997). The resource-tracking hypothesis states that the production of supernumerary offspring allows parents to capitalize on unpredictable favorable ecological conditions (Kozlowski and Stearns 1989). Parents may create optimistic brood sizes to take advantage of years when food is abundant and offspring can be fully supported. Alternatively, the insurance hypothesis states that the creation of a core brood (number of offspring that can normally be supported) plus a number of marginal offspring (offspring that are expendable) ensures that parents won't have to settle for an undersized brood if some core brood members fail to develop properly (Forbes 1990). Finally, the progeny-

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choice hypothesis posits that the production of supernumerary offspring enhances the potential for quality control (Mock and Forbes 1995). Parents benefit by producing a wide array of offspring and “choosing” which offspring to support, or by allowing sibling rivalry to select for the best-fit offspring through competitive interactions.

While sibling rivalries have been the subject of intense theoretical and empirical research (see Mock and Parker 1997), most empirical research has been restricted to vertebrates, especially birds. Among invertebrates, sibling rivalries have been documented primarily in beetles, bees, and molluscs (see Elgar and Crespi 1992). In general, internal fertilization, prolonged retention, brooding or guarding of offspring, and dependence upon nutritive resources prior to independence in molluscs favor sibling rivalries (Mock and Parker 1997). Perhaps the most common context for sibling rivalries in molluscs is the deposition of eggs inside a nursery where food is a discrete resource shared by multiple offspring (Spight 1976). Certain kinds of molluscan “nurseries” feature physical barriers where there are no options available for offspring to alleviate the constraints imposed by limited resources. In these nurseries, siblings may compete for limited resources via scramble or contest competition. Sibling rivalries in gastropods have received much attention with respect to sibling cannibalism, sibling competition for limited resources, effects of sibling density on sibling competition, and asynchronous hatching (Desbuquois et al. 2000).

Asynchronous hatching and/or differential development may also intensify sibling rivalries. Early-hatched offspring generally have faster growth rates and higher survivorship than later-hatched offspring (Mock and Forbes 1995; Forbes and Glassey 2000). Because offspring typically gain weight from the time they hatch, early-hatched offspring will grow more rapidly than later-hatching individuals. Larger offspring intrinsically command a disproportionate share of available resources (such as food or space) at the expense of their smaller siblings (Mock and Parker 1997). The disproportionate amount of resources remaining for later-hatched offspring ultimately results in brood mortality arising as a consequence of differential resource allocations among offspring and age/size hierarchies (Mock and Parker 1997).

Sphaerium striatinum (Bivalvia: Sphaeriidae) is a small (<14.0 mm in length) freshwater bivalve that broods offspring internally (McMahon 1991). Oocytes (~100 µm diameter) are fertilized within the gonadal tract and released into the mantle cavity where they are encapsulated by marsupial sacs located between the lamellae of the inner demibranchs (gills). Offspring undergo direct development and are eventually released into the environment as fully developed juveniles (3–4 mm in length). *S. striatinum* is a sequential brooder. Adults repeatedly produce small cohorts of offspring throughout the year and simultaneously brood them. Reproduction in this manner is analogous to an assembly line. At any one time, adults contain an array of marsupial sacs each with a

discrete size class of embryos. At the earliest stages of embryonic development (<1.0 mm), marsupial sacs typically contain multiple offspring (between 5 and 12 embryos; M.A. Beekey and R.H. Karlson, personal observation). By the time offspring reach later stages of development (>1.0 mm in length), only one offspring per marsupial sac is typical (Beekey 2001). In fact, up to 97.5% of offspring produced fail to reach independence (Avolizi 1976; Hornbach et al. 1982; Beekey 2001). This degree of brood mortality is indicative of serious constraints on brood size. The challenge has been to identify the mechanism(s) responsible for brood mortality and explain the continued production of supernumerary offspring in a theoretical context.

The proposal that brood mortality is related to competition among embryos for nutrients and/or space has merit (Groenewegen 1926; Meier-Brook 1970, 1977; Heard 1977). First, sphaeriid eggs do not contain enough yolk for offspring to complete development (Raven 1958; Mackie 1978). Adults provide offspring with additional nourishment by bathing them in nutrient-rich hemolymph inside the marsupial sac (Okada 1935; Heard 1977). Second, nutrition and the physical space available for brooding are limited (Beekey and Karlson 2003; Beekey and Hornbach 2004). Finally, differential development within marsupial sacs has repeatedly been observed among multiple populations (Groenewegen 1926; Avolizi 1976; Meier-Brook 1970, 1977; Heard 1977; Hornbach et al. 1982; Beekey 2001). Size differences observed within marsupial sacs are not due to the presence of multiple cohorts because each marsupial sac represents a single reproductive event (Mackie et al. 1978). Thus these differences likely emerge as a consequence of differential development and/or hatching asynchrony. Offspring provisioning, limited nutrition and space, and the presence of size hierarchies are all factors that enhance the prospects for sibling rivalry in *S. striatinum*. The difficulty has been observing and manipulating siblings within adults.

Since in vivo manipulations are not feasible, we conducted a laboratory experiment in which we removed embryos from field-collected adults and reared them in vitro, varying nutrient concentrations and embryo densities. Embryo density may mediate competition by serving as a density dependent feedback mechanism (Stearns 1987, 1992). An increase in embryo density under limited resources would increase competition due to a proportional decline in the amount of resources available per offspring. Alternatively, once embryo density declines to levels where resources are no longer limiting, all remaining offspring may complete development. Under the competition hypothesis, one would predict that proportionately more embryos would complete development in higher serum and lower embryo density treatments.

Methods

We reared offspring in vitro using a modification of basic culture techniques for rearing unioniid embryos developed by Isom and

Hudson (1982) and later refined by Keller and Zam (1990). We collected 56 adult *S. striatinum* from Big Elk Creek in Fair Hill Natural Resources Management Area, Maryland, in late April. All adults were measured to the nearest 0.1 mm (greatest anterior to posterior shell length, SL) and dissected under a microscope. If present, embryos were removed from the mantle cavity and placed into 500 ml of sterile phosphate buffered solution (PBS). All 56 adults [11.5 mm SL \pm 1.04 (mean \pm 1 SD), range 9.8–13.4 mm] contained offspring in marsupial sacs. However, only 26 adults contained embryos lying freely within the mantle cavity. A total of 714 embryos were removed from 26 adults. The mean number of embryos per adult (\pm 1 SD) was 27.5 \pm 42.9 (range: 1–212).

All embryos were washed 3 times in PBS and collectively stored in a petri dish containing 30 ml of Dulbecco's Modified Eagle's Media (DMEM, 4.5 g/L D-Glucose, L-Glutamine and 110 mg/L sodium pyruvate, Gibco BRL). Individual embryos were randomly assigned to five densities (1, 2, 3, 4, and 5 embryos per well) in five, 96-well culture plates. Embryos were not grouped according to maternal source. Each well contained 500 μ m of DME and antibiotics. Antibiotics including carbenicillin (50 μ g/ml), gentamicin (50 μ g/ml), amphotericin (2.5 μ g/ml), and rifampicin (50 μ g/ml) were added to stock DME in order to reduce bacterial and fungal contamination. Horse serum (Gibco BRL) concentrations (5%, 2.5%, 1.0%, and 0% by volume), hereafter referred to as nutrient levels or nutrient availability, were randomly assigned to each well so that each plate had equal numbers of all combinations. A total of 600 embryos was used in this experiment. There were ten replicates for each density and nutrient level combination. The embryos were reared in an incubator at 18 $^{\circ}$ C \pm 2 $^{\circ}$ C. Each day, we removed 300 μ l of media from each well and replaced it with 300 μ l of corresponding fresh sterile media (containing respective amounts of horse serum/nutrients). Media was replaced each day to avoid a build-up of metabolic wastes that might kill or inhibit embryonic development.

Every 2 days, embryos were removed from the incubator and examined with a Nikon phase contrast microscope (60 \times) for evidence of embryonic development (hatching, metamorphosis, and/or embryonic mortality). We define hatching as the rupture of the oocyte wall and metamorphosis as the transition to adult like feature (presence of a muscular foot, demibranchs, and shell formation). These observations allowed us to record time to hatching (from the beginning of the experiment to hatching), percent hatching success, time to metamorphosis (from hatching to metamorphosis), and percent metamorphosis. The experiment was terminated after 61 days. At this time, all embryos had either metamorphosed or started to disintegrate.

The effects of nutrient availability and embryo density on time to hatching and proportion of embryos hatching were evaluated using two-way ANOVA (Statview 5.0.1). Because no embryos completed metamorphosis in the absence of serum, we analyzed time to metamorphosis and the proportion of embryos completing metamorphosis using non-parametric statistics (Kruskal-Wallis ANOVA by ranks). After determining significance, we then used two-way ANOVA to analyze the effects of these treatments on only those embryos receiving serum. We used the mean values for each well as the dependent variable in analyses of time to hatching and time to complete metamorphosis.

Results

Out of 600 embryos, 388 (65%) hatched 12–28 days after the initiation of the experiment. The mean time to hatching per well was 18.7 \pm 3.0 (\pm SD) days. Hatching success (the proportion of embryos hatching per well) was not influenced by nutrient availability or embryo density (ANOVA, $df=3, 4, F=0.4, P>0.05$). Likewise, there was no significant effect on the mean time to hatching per well

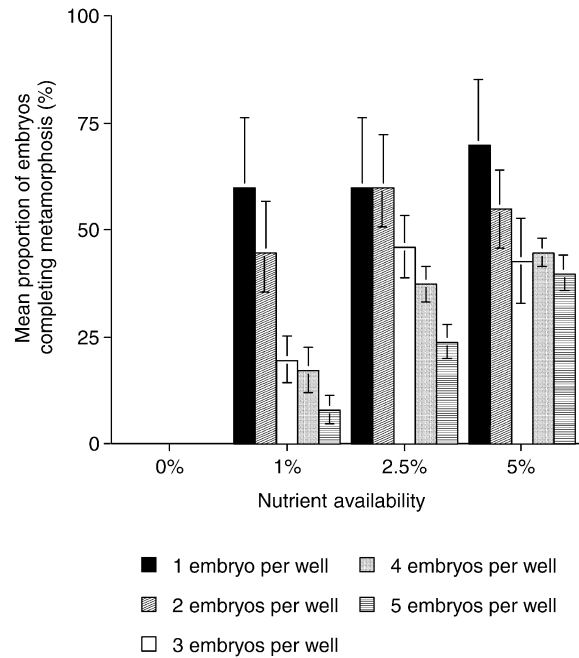


Fig. 1 Averaged proportion of embryos of *Sphaerium striatinum* per well completing metamorphosis (\pm SE) plotted as a function of nutrient availability (0, 1, 2.5, or 5% serum concentration in culture media) and embryo density (1, 2, 3, 4, or 5 initial embryos per culture well). No embryos completed metamorphosis in the absence of nutrients (0% serum). $n=10$ for all treatment combinations

with respect to nutrient availability or embryo density (ANOVA, $df=3, 4, F=0.9, P>0.05$).

In sharp contrast, the proportion of embryos completing metamorphosis was strongly influenced by nutrient availability and embryo density (Fig. 1). In the absence of nutrients (serum), no embryos completed metamorphosis. In the presence of nutrients, 26% of the original 600 embryos and 40% of the 388 embryos that hatched completed metamorphosis. The proportion of embryos completing metamorphosis was significantly higher among embryos receiving more nutrients (Kruskal-Wallis ANOVA by ranks, $H=73.9, df=3, P<0.0001$), but the effect of variation in embryo density was not significant using all the data (Kruskal-Wallis ANOVA by ranks, $H=6.4, df=4, P=0.169$). When the treatment lacking nutrients (0% serum) was removed from the analysis, the decreasing trend in the proportion of embryos completing metamorphosis with higher embryo densities was highly significant (Kruskal-Wallis ANOVA by ranks, $H=16.7, df=4, P=0.0022$). Two-way ANOVA on the proportion of embryos completing metamorphosis corroborates this highly significant effect of nutrient level and embryo density on treatments containing serum (Table 1).

Time to metamorphosis was shorter with greater nutrient availability and lower embryo densities (Fig. 2). The mean time (\pm SD) to metamorphosis at the highest nutrient level and lowest density was 19.0 \pm 2.6 days, but it was 36.4 \pm 1.7 days at the lowest level of nutrient availability and highest density. Since no embryos completed

Table 1 Analysis of variance of the effect of nutrient availability (1, 2.5, or 5% serum concentration in culture media) and *Sphaerium striatinum* embryo density (1, 2, 3, 4, or 5 initial embryos per

culture well) on proportion of offspring completing metamorphosis. The dependent variable was the percentage of embryos that completed metamorphosis

Source	df	Sum of squares	Mean square	F	P
Nutrient availability	2	9,864.4	4,932.2	5.1	0.0074
Embryo density	4	26,466.2	6,616.5	6.8	<0.0001
Nutrient × density	8	4,602.2	575.3	0.6	0.7819
Residual	135	1.3×10^5	969.3		
Total	149	1.7×10^5			

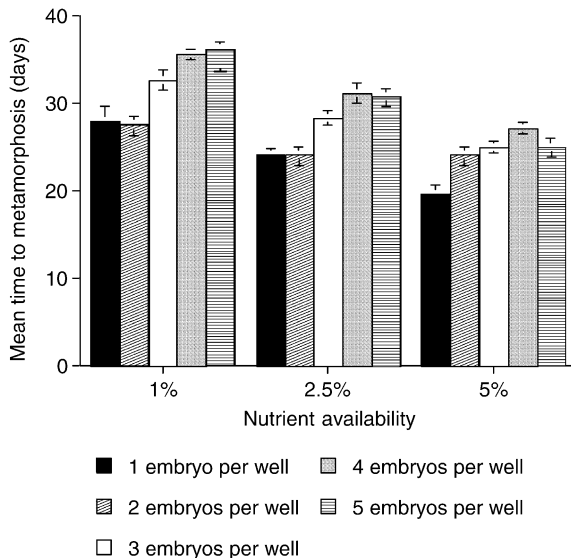


Fig. 2 Averaged mean time to metamorphosis of embryos per well (\pm SE) plotted as a function of nutrient availability (1, 2.5, or 5% serum concentration in culture media) and embryo density (1, 2, 3, 4, or 5 initial embryos per culture well). *n* as follows: 1% (5, 7, 6, 6, 5), 2.5% (6, 8, 9, 10, 9), and 5% (5, 9, 7, 10, 10) for 1, 2, 3, 4, and 5 embryos per well, respectively

metamorphosis in treatments lacking serum, we only analyzed time to metamorphosis using treatments containing serum (1%, 2.5%, 5%). Time to metamorphosis was strongly influenced by nutrient availability and embryo density (Kruskal-Wallis ANOVA by ranks, $H=30.4$, $df=2$, $P<0.0001$ and $H=33.5$, $df=4$, $P<0.0001$, respectively). Further analysis on time to metamorphosis using only treatments with serum and two-way ANOVA reveals highly significant main effects due to both treatments (Table 2).

Table 2 Analysis of variance of the effect of nutrient availability (1, 2.5, or 5% serum concentration in culture media) and embryo density (1, 2, 3, 4, or 5 initial embryos per well) on time to metamorphosis. The dependent variable was the average time

Discussion

Our results demonstrate that in vitro development of *S. striatinum* is strongly influenced by variation in nutrient availability and embryo density. The proportion of offspring completing metamorphosis increased with corresponding increases in nutrient concentration and decreases in embryo density (Fig. 1). Likewise, developmental rates increased with more nutrients and lower densities (Fig. 2). These manipulations directly influenced per capita resource availability and resulted in significant resource limitation at lower nutrient concentrations and higher embryo densities. We interpret the delayed development rates and lower proportions of embryos completing metamorphosis as evidence for significant competition among embryos. This in vitro evidence supports earlier speculation about competition for nutrients based on observations of differential development within marsupial sacs. The fact that no embryos completed metamorphosis in the absence of nutrients further emphasizes the importance of these resources during embryonic development.

Competition for limited resources can involve exploitative or interference mechanisms. The former invokes differential utilization of a limited resource as each embryo interacts with the resource. The latter invokes various types of interactions (e.g., physical, chemical, behavioral) in which embryos interfere with one another's access to or utilization of a resource. Sphaeriid embryos are extremely mobile within marsupial sacs even in early stages of development (Beekey 2001). It is plausible that physical interactions between larger and smaller embryos could impede the intake of nutrients by smaller embryos. Alternatively, Meier-Brook (1977) suggested brood mortality was a consequence of chemical inhibition from developing embryos. Such inhibitors

(days) to metamorphosis for all embryos in a single well. Data from the 0% nutrient treatment were removed prior to analysis. $n=113$ (number of wells containing embryos that completed metamorphosis)

Source	df	Sum of squares	Mean square	F	P
Nutrient availability	2	948.2	474.1	71.4	<0.0001
Embryo density	4	921.2	230.3	34.7	<0.0001
Nutrient × density	8	13.1	13.1	1.9	0.0572
Residual	98	650.7	6.6		
Total	112	2,533.2			

have been documented in tadpoles (Richards 1958; Rose 1960; Akin 1966), but not bivalves. Regardless of the specific form of competition, there is an obvious advantage to early hatching and rapid development.

Numerous examples of age/size hierarchies have been documented across a wide array of taxa: plants (Mock and Forbes 1995), birds (Lack 1954), mammals (Clutton-Brock 1991), fish (Ahnesjö 1996), sharks (Springer 1948), and invertebrates (Desbuquois et al. 2000). Hatching asynchrony and age/size hierarchies do not directly facilitate brood reduction; rather they lead to differential resource allocation, deficient levels of provisioning for some offspring, and offspring mortality (Forbes and Glassey 2000). In this experiment, embryos in various stages of development were present over all treatments with multiple embryos. Hatching occurred over a period of 16 days. While this might be a consequence of mixing eggs at different stages of development from multiple adults, a similar pattern can be found in nature. Previous studies on *S. striatinum* have documented variation in developmental stages among embryos within a single marsupial sac (Okada 1935; Avolizi 1976; Heard 1977; Hornbach et al. 1982; Beekey 2001). Since marsupial sacs are closed after the initial encapsulation of zygotes (Mackie 1978), variation in embryonic development in nature must be the result of differential development.

Egg viability has been previously mentioned as a potential contributor to brood mortality in the Sphaeriidae. For example, Mackie et al. (1978) demonstrated that increased brood size in *Musculium seures* was achieved by an increase in the viability of embryos rather than an increase in the number of embryos produced. In this experiment, only 65% of the initial 600 eggs we used hatched while 12% of the embryos exhibited no signs of development, though whether or not they had been fertilized is unknown. An additional 23% of the embryos exhibited some evidence of development, but failed to hatch. One might argue that our experiment was not truly representative of embryonic development under natural conditions because so many of the eggs failed to hatch. This loss may be attributable to problems related to our culture techniques. Embryo viability and development might have been affected by the production of metabolic wastes within the culture wells. In vivo these wastes would be removed by the highly vascularized marsupium. Our attempt to counteract the production of metabolic wastes was to remove and replace media throughout the course of the experiment. Whether or not media replacement had an effect on the removal of metabolic wastes is unknown. Future experiments might resolve this problem by rearing embryos in a flow-through system. However, flow-through systems might also disrupt potential chemical interactions among embryos as mentioned previously. If we assume that our results are indicative of natural development, then it appears that egg viability plays a significant role in determining brood size in *Sphaerium* as has been documented in the closely related genus *Musculium*.

With respect to theoretical explanations for the continued production of supernumerary offspring, we conclude that both the insurance and “progeny choice” hypotheses are applicable to *S. striatinum*. The degree of developmental failure observed in this experiment certainly favors the insurance hypothesis. The production of supernumerary offspring in *S. striatinum* ensures that brood size will not fall below the size imposed by physical constraints. Competition among offspring within marsupial sacs would select for the survival of the best-fit offspring increasing both offspring survivorship in the external environment and overall reproductive success of the adult. While resource availability clearly has an impact on offspring development and survivorship, the resource-tracking hypothesis lacks merit in this case. In species with highly predictable brood capacity (a function of adult size), the production of supernumerary offspring in response to unpredictable favorable ecological conditions seems unlikely.

In conclusion, we have clearly demonstrated that nutrient availability and embryo density affect in vitro offspring development in *S. striatinum*. Increased nutrient availability and decreased embryo density resulted in faster development times and a higher proportion of offspring completing metamorphosis. Based on observations from previous studies and our own data, we conclude that size hierarchies within marsupial sacs are the result of differential development and perhaps hatching asynchrony. The continued production of supernumerary offspring in *S. striatinum* ensures adults ultimately rear broods that do not fall below the limits set by size-limited brood capacity. Marsupial sacs are likely to act as competitive arenas where early hatching provides a competitive advantage and ensures the survival of the fittest offspring (Stearns 1987). Finally, brood mortality in *S. striatinum* is likely consequence of sibling rivalries over limited resources and developmental failure.

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