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Effect of food availability on reproduction and brood size in a freshwater brooding bivalve

Mark A. Beekey and Ronald H. Karlson

Abstract: Brood size is often constrained by the amount of energy available to produce offspring. Yet, energetic constraints may not be as important if the physical capacity to brood offspring is limited. Investigating the relative importance of energetic and physical constraints on brood size is necessary to understand how reproductive strategies are molded by natural selection. We investigated how food availability affects brood size in *Sphaerium striatinum*, a freshwater bivalve. We reared juveniles to adulthood under three food levels in a common garden experiment. The number of reproductive attempts, brood size, and stage of offspring development were measured. Clams reared with the most food reproduced more often, produced more offspring per reproductive attempt, and contained larger broods than clams reared with less food. These data support the notion that food availability is an important factor in the production of offspring and overall brood size. However, the number of offspring surviving to later stages of development was not different among treatments. In fact, clams reared with the most food lost proportionately more offspring than clams reared with less food. We conclude that physical constraints are more important in determining overall brood size than energetic constraints in *S. striatinum*.

Résumé : La taille d'une portée est souvent limitée par la quantité d'énergie disponible pour produire des rejetons. Néanmoins, les contraintes énergétiques peuvent ne pas être si importantes si la capacité physique d'élever des petites est restreinte. Pour comprendre comment les stratégies reproductives sont façonnées par la sélection naturelle, il est nécessaire de déterminer l'importance relative des contraintes énergétiques et des contraintes physiques sur la taille de la portée. Nous avons étudié comment la disponibilité de la nourriture affecte la taille de la portée chez *Sphaerium striatinum*, un bivalve d'eau douce. Nous avons élevé des jeunes jusqu'au stade adulte dans trois concentrations de nourriture dans une « expérience de jardin commun » et nous avons déterminé le nombre de tentatives de reproduction, la taille des portées et les stades de développement des petits. Les bivalves gardés dans les meilleures conditions de nourriture se reproduisent plus souvent, ils produisent plus de petits à chaque tentative de reproduction et ils contiennent des portées plus grandes que les bivalves élevés dans des conditions moindres de nourriture. Ces données s'accordent avec l'idée que la disponibilité de la nourriture est un facteur important dans la production de rejetons et la taille globale des portées. Cependant, le nombre de petits qui survivent jusqu'aux stades plus avancés de leur développement ne varie pas d'un traitement à l'autre. En fait, les bivalves gardés dans les meilleures conditions alimentaires perdent en proportion plus de petits que les bivalves élevés dans des conditions moins bonnes. Nous concluons que les contraintes physiques sont plus importantes dans la détermination de la taille de la portée chez *S. striatinum* que les contraintes énergétiques.

[Traduit par la Rédaction]

Introduction

A central issue in life-history theory is how organisms optimize brood size under variable environmental factors such as resource availability (Roff 1992; Stearns 1992). Resource availability may limit the ability of adults to produce and rear offspring through independence (Morris 1987). In fact, numerous studies have demonstrated that brood size is regulated by food availability across a wide range of taxa. In reptiles, the production of eggs is limited by food availability (Olssen and Shine 1997). Avian brood size is strongly limited by the ability of parents to feed offspring (Lack 1954). In mammals, the ability of parents to produce milk limits brood size (Clutton-Brock 1991). Among marine invertebrates, food availability has been documented as one of the most important factors affecting brood size (Helm et al. 1973; Checkley 1980; Bayne et al. 1983; MacDonald and Thompson 1985; Levin and Creed 1986; Zajac 1986; Barber et al. 1988; Qian and Chia 1991). However, food availability may not be as important in regulating reproductive output if the capacity to brood offspring is limited by physical constraints.

Physical constraints on brood size, such as the space available to brood offspring, are common among species that brood offspring inside or on the adult body (Strathmann and Strathmann 1982; Shine 1988). In invertebrates, constraints on brood size are often seen in species with hard exoskeletons

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such as cladocerans (Perrin 1987) and amphipods (Glazier 2000) or species with shells such as bivalves (Bayne et al. 1983; Calow 1983; Sebens 1987; Nakaoka 1998) and gastropods (Chapparo et al. 2001). In such species, the capacity for egg production increases faster than the capacity to brood offspring (Heath 1977; Strathmann and Strathmann 1982). Furthermore, as offspring increase in size, the space available per offspring becomes proportionately smaller. Although physical constraints represent a fixed upper limit to brood size, energetic constraints may explain variation in brood size both among and within populations (Olssen and Shine 1997).

Investigating the relative importance of physical and energetic constraints on reproduction is necessary to understand how reproductive strategies are molded by natural selection. Freshwater brooding bivalves are an interesting group with which to conduct these types of investigations. Offspring are brooded either beneath or within the adult lamellibranchs. Consequently, the space available to brood offspring might limit brood size. Freshwater bivalves occupy habitats that experience both seasonal and stochastic variation in food availability. As a result, brood size may be limited by the adult's ability to acquire energetic resources required for reproduction.

Sphaerium striatinum is a small (12–14 mm long) ovoviviparous bivalve found in streams, rivers, ponds, and lakes (McMahon 1991). Adults repeatedly produce small cohorts of oocytes (100 μm in diameter) throughout the year that are fertilized within the gonadal tract and released into the mantle cavity. The oocytes are enclosed in marsupial sacs located between the lamellae of each inner demibranch (intra-marsupial offspring) (Mackie et al. 1974). Intra-marsupial offspring undergo direct development and eventually break free from the marsupial sacs around 3.0 mm in shell length (extra-marsupial offspring). Although extra-marsupial offspring are competent (Beekey et al. 2000), they are retained within the adult. The retention of extra-marsupial offspring promotes growth within a safe environment. Extra-marsupial offspring become independent, that is, they are released into the environment, at around 4.0 mm long (Hornbach et al. 1982; Beekey 2001).

Up to 97.5% of the offspring that the parents initially produce fail to reach independence (Hornbach et al. 1982). During the early stages of offspring development, marsupial sacs typically contain multiple intra-marsupial offspring. However, by the time intra-marsupial offspring reach the extra-marsupial stage, only one (rarely two) offspring remains within each marsupial sac. Brood mortality is indicative of substantial constraints on brood size. The loss of offspring over the course of offspring development has been attributed to food availability (Avolizi 1976; Heard 1977; Hornbach et al. 1982). Sphaeriid oocytes contain insufficient yolk for offspring to complete development (Raven 1958; Mackie 1978). Adults provide the additional nourishment required for development by bathing offspring in hemolymph within the marsupial sacs (Okada 1935; Heard 1977; Schwartz and Dimock 1998). However, the retention of large offspring inside the adult body highlights the potential for severe limitation on brood size due to physical constraints. Variation in brood size among sphaeriid populations has been correlated with differences in adult shell morphology and volume (Kilgour and Mackie 1990).

We conducted an experiment in which juveniles were reared to adulthood under three food levels to explicitly examine if food availability limits brood size in *S. striatinum*. If the upper limit to brood size were set by food availability, then one would predict that brood size should increase in proportion to food availability regardless of adult size. However, if the upper limit for brood size were set by physical constraints, then one would predict that brood size would remain constant regardless of food availability. Our results clearly support the notion that food availability regulates the production of offspring, number of reproductive attempts, and brood size in *S. striatinum*. The results also support the notion that physical constraints represent a fixed upper limit to brood size.

Materials and methods

To circumvent geographic variability and adult nutritional condition, we used juveniles from a single locality and reared them to reproductive maturity under tightly controlled conditions. Juveniles (5.8 ± 0.1 mm, mean ± 1 SE) were collected from Big Elk Creek in Fair Hill Natural Resources Management Area, Elkton, Md. One randomly selected juvenile was placed into each of 120 plastic cups (230 mL each) with 20 cm^3 of autoclaved stream sediment (<0.5 mm grain size) to provide a suitable substrate for growth and 200 mL of filtered (15-μm pore) stream water. All of the sediment used in the experiment was collected from a 1-m^2 area within Big Elk Creek. The sediment was autoclaved to prevent excessive algal growth within the cups throughout the experiment. Sphaeriids are deposit feeders (Hornbach et al. 1984). Therefore, the use of stream sediment could influence the amount of food initially available to individuals in the experiment. To help control for differences in organic content of the sediment between cups, we thoroughly mixed the sediment prior to the addition to cups. Water was exchanged every 2–3 days with fresh filtered (15-μm pore) stream water adjusted to the experimental temperature. The cups and sediment were changed once per month. The cups were immersed in a large water bath held constant at 22 ± 1°C by an external water chiller and lightly aerated.

Food treatments were randomly assigned to each cup. Research has shown that freshwater clams fed on ground flake fish food can readily grow and reproduce in the laboratory (Hornbach and Cox 1987). Therefore, every 4 days, 0.05, 0.50, and 5.00 mg of ground Tetramin™ Flake Fish Food was added to each container for low, medium, and high treatment groups, respectively. Based on physiological studies of metabolism in fingernail clams (Hornbach et al. 1984), we felt that the amount of food added would bracket conditions in Big Elk Creek, although we did not determine this quantitatively. The experiment ran for 143 days from April to September 1999. Upon termination of the experiment, shell length was measured for each individual to the nearest 0.1 mm. Each individual was dissected to determine the number of marsupial sacs and the number, size, and location of offspring.

Table 1. Multivariate analysis of covariance of food level treatments on growth and reproduction in *Sphaerium striatinum*: effects of covariate.

(A) Overall effect of covariate.			
Source	Wilks' λ	p	
Initial mass	0.32793	<0.001	
(B) Effect of covariate on dependent variables.			
Variable	β	$F_{[1,57]}$	p
Shell length	−0.067	46.94	<0.001
Tissue mass	−0.731	65.66	<0.001
Marsupial sacs	0.445	14.05	<0.001
Brood size	0.534	22.76	<0.001

Note: The dependent variables are the change in shell length (mm), change in wet tissue mass (mg), number of marsupial sacs, and brood size (no. of offspring/adult). The covariate is initial wet mass (mg).

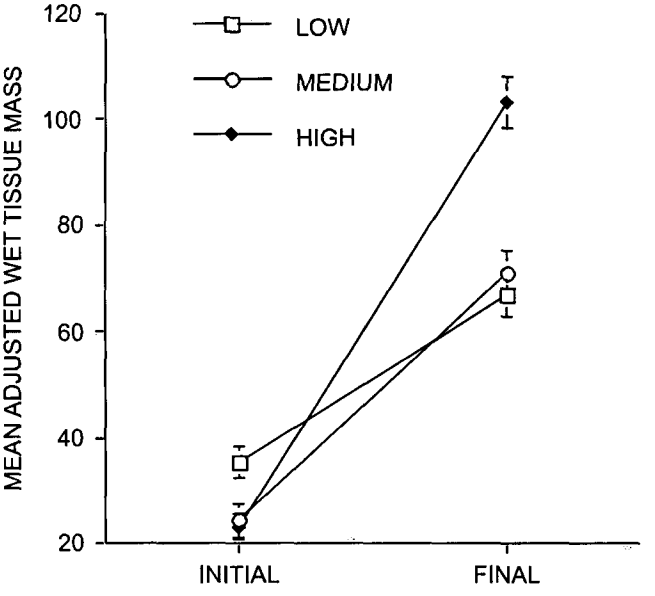
Since uncontrolled differences in initial mass might be correlated with reproductive effort, the data were analyzed using ANCOVA with initial wet tissue mass as the covariate. However, since we could not directly weigh wet tissue mass without killing individuals used in this experiment, we estimated initial wet tissue mass instead. To estimate wet tissue mass, we subtract shell mass from the total wet mass of individuals. Shell mass (SM) was estimated by linear regression of shell length (SL) on shell mass ($\ln(SM) = 2.838(\ln(SL)) - 1.821$; $R^2 = 0.93$, $F = 1232.2$, $p < 0.0001$, $N = 88$) from additional individuals collected from same locality in Big Elk Creek as experimental individuals. To assess changes in tissue mass over the experiment, we subtracted estimated soft tissue mass from final soft tissue mass (measured to the nearest 0.1 mg) for each adult. We excluded the mass of brooded offspring from these measurements.

Finally, one might argue that this laboratory experiment is not indicative of natural conditions. To relate the experimental data to natural conditions, we collected clams from Big Elk Creek at the conclusion of the experiment. Seventeen individuals (10.0 ± 0.5 mm) similar in length to our experimental animals were dissected. Shell length, wet tissue mass (minus brooded offspring), number of marsupial sacs, and brood size were recorded. These data were compared with our experimental results to give an indication of how our food levels relate to field conditions.

Results

In nutritional experiments, it is important to control for initial differences in the physiological status of individuals when comparing measures of reproduction. We found that initial tissue mass had a significant effect on each of four dependent variables (Table 1). Individuals that initially weighed more exhibited, on average, smaller changes in shell length and final tissue masses, yet contained more marsupial sacs and larger broods. Regardless, analyses of the adjusted dependent variables indicate that food availability significantly influenced final tissue mass, the number of marsupial sacs, and brood size (Table 2). Clams reared with the most food gained nearly three times more tissue mass than did clams reared with the least food (Fig. 1). Clams reared with medium food levels attained a final tissue mass that was only slightly higher than clams reared with the least food.

Fig. 1. Mean (± 1 SE) adjusted initial and final tissue masses (mg) are plotted for *Sphaerium striatinum* individuals reared in three food levels for 143 days. Initial and final tissue masses are plotted. Sample sizes are 17, 21, and 23 for low, medium, and high food levels, respectively.



Both the number of marsupial sacs and brood size were greater in higher food levels than lower food levels (Figs. 2 and 3). Clams reared with the highest food levels contained six times more marsupial sacs than did clams reared with the least food (Fig. 2). Only 67 and 35% of the clams reared with medium or low food treatments, respectively, contained marsupial sacs. Interestingly, three adults reared with the least food contained empty marsupial sacs. Clams reared with the most food contained 10 times more offspring than clams reared with the least food (Fig. 2).

Brood composition also differed in response to food level. Individuals reared with the most food contained significantly more intra-marsupial offspring and were the only individuals to release offspring (Fig. 3). Overall, adults reared with the most food contained larger offspring than adults reared in either medium or low food treatments (Fig. 4). Clams reared with the least food contained only offspring less than 0.8 mm in length. Only individuals reared with the highest food contained offspring greater than 3.0 mm in length. Finally, clams reared with the most food contained more offspring per marsupial sac in the smallest stages of development (average offspring length <0.6 mm) (Fig. 4) than clams reared at medium or low food levels. Clams reared with the least food never contained more than one offspring per marsupial sac regardless of offspring size.

Mean brood size and number of marsupial sacs of field-collected individuals fall within the interval bracketed by the medium and high food treatments (Figs. 2 and 3). Mean brood size was significantly greater in individuals reared with the most food than in individuals collected from the field ($t = 3.54$, df = 38, $p < 0.001$) (Fig. 2). The mean number of marsupial sacs was not significantly different ($t = 0.88$, df = 38, $p > 0.05$) (Fig. 2). Likewise, mean tissue mass of individuals reared with the most food was not signifi-

Table 2. Multivariate analysis of covariance of food level treatments on growth and reproduction in *S. striatinum*: effects of food level.

(A) Overall effect of food level.				
Source	df	Wilks' λ	F	p
Food level	2	0.128	24.17	<0.001
Error	57			
(B) Effect of food on dependent variables.				
Source	df	MS effect	MS error	$F_{[2,57]}$	p
Shell length	2	0.23	0.20	1.18	0.313
Tissue mass	2	13510.45	448.89	30.10	<0.001
Marsupial sacs	2	125.19	1.51	83.06	<0.001
Brood size	2	745.09	4.82	154.55	<0.001

Note: The dependent variables are the change in shell length (mm), change in tissue mass (mg), number of marsupial sacs, and brood size (no. of offspring/adult).

Fig. 2. Mean (± 1 SE) number of *S. striatinum* marsupial sacs and brood size (no. of offspring/adult) versus food level and stream individuals. Sample sizes are 17, 21, 23, and 17 for low, medium, high, and stream, respectively.

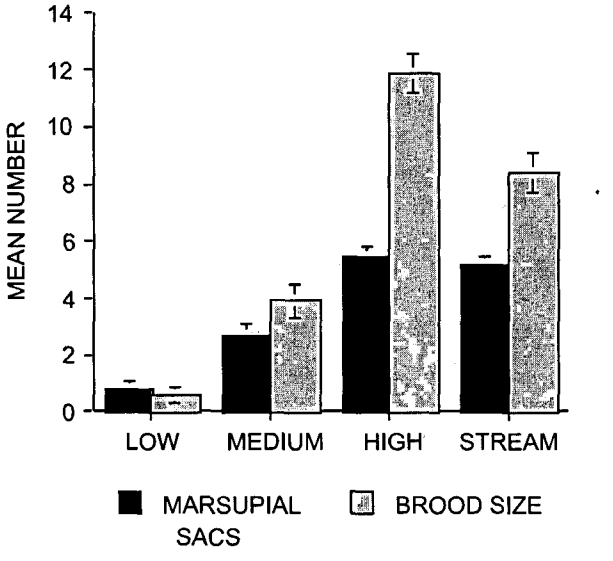
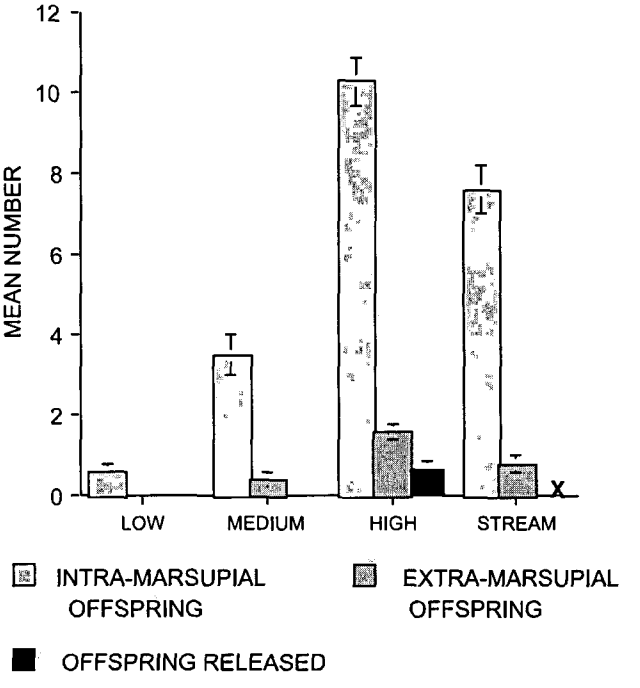


Fig. 3. Mean (± 1 SE) number of *S. striatinum* intra-marsupial, extra-marsupial, and released offspring per adult versus food level. Sample sizes are 17, 21, 23, and 17 for low, medium, high, and stream, respectively. The number of offspring released in the stream individuals (X) is unknown.



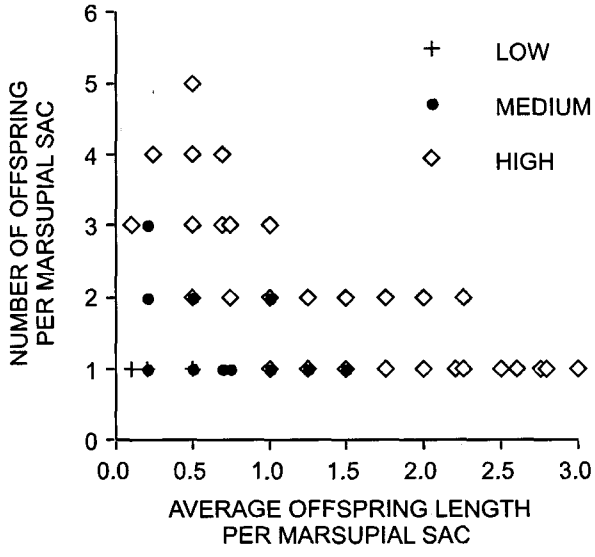
cantly different from the mean tissue mass of field-collected individuals (t = 1.33, df = 38, p > 0.05). No data were collected on the number of offspring released in the stream (Fig. 3).

Discussion

The results of this experiment clearly show that food availability has a significant effect on brood size in *S. striatinum*. Although final adult length was not significantly different among treatments, final adult tissue mass increased significantly with food level. Clams reared with the most food contained significantly more marsupial sacs and offspring than clams reared with the least food. Furthermore, clams reared with the most food also contained larger offspring and were the only ones to release offspring by the termination of this experiment. These data support the notion that variability in brood size among similarly sized individuals within and among sphaeriid populations can be attributed to differences in food availability. Below, we discuss these results in relation to the effect of food availability on brood size and possible interactions between both energetic and physical constraints.

Food availability is an important factor in determining the level of reproductive investment in *S. striatinum*. These results agree with previous studies investigating the effect of food availability on reproduction in aquatic invertebrates (Bayne et al. 1983; Zajac 1986; Barber et al. 1988; Qian and Chia 1991). The number of marsupial sacs increased significantly with food level (Fig. 2). The number of marsupial sacs per adult is a clear indication of the number of reproductive attempts (Mackie et al. 1974). Adults typically form two marsupial sacs (one per demibranch) each time offspring are produced. Thus, a simple way to find the number

Fig. 4. Number of *S. striatinum* offspring per marsupial sac versus the length (mm) of the largest offspring within each sac for each food level. The data represent only those adults containing offspring in each treatment. Sample sizes are 6, 16, and 23 adults for low, medium, and high, respectively.



of reproductive attempts in sphaeriids is to divide the total number of marsupial sacs in half. Given this, clams reared with the most food produced offspring three times more often than clams reared with the least food (Fig. 2). Not only did food availability have an effect on reproductive effort but elevated food levels also resulted in larger brood sizes.

Brood size increased significantly with food availability (Fig. 2). One might argue that this result is purely a function of the number of marsupial sacs. However, if one examines the number of offspring per marsupial sac in the earliest stages of offspring development (<0.6 mm) (Fig. 4), clams reared with the most food clearly contained more offspring per marsupial sac than clams reared in either other food level. Based on these data, we argue that the number of offspring produced per reproductive attempt, or initial fecundity, increased with food availability. However, if food availability was the primary determinant of brood size in *S. striatinum*, then one would have predicted that individuals reared with the most food would contain more offspring than individuals reared with the least food over all stages of offspring development. The number of offspring per marsupial sac converges towards one as offspring increase in size regardless of food availability (Fig. 4). In fact, the proportion of offspring lost over the course of development increases with increasing food availability (Fig. 4).

Life-history studies and analyses of shell morphometry suggest that adult size limits brood size in sphaeriids (Holopainen and Kuiper 1982; Holopainen and Hanski 1986; Mackie 1986). Kilgour and Mackie (1990) substantiated this notion by analyzing shell morphometry in *Pisidium casertanum*. Adults with wider shells tended to contain more offspring than clams with narrower shells but of similar lengths. If the physical capacity to brood offspring was the primary determinant of brood size, then one would have expected to see a pattern where brood size is limited even under excess levels of food availability. Although we cannot exclusively rule out other factors that may limit brood size, we strongly believe that our data support this prediction (Fig. 4). Clearly, this aspect of reproduction deserves further consideration.

In conclusion, we have demonstrated that food availability significantly affects the number of reproductive attempts, initial fecundity, and overall brood size in *S. striatinum*. Adults reared with the most food reproduced more often, produced more offspring per reproductive attempt, and brooded more offspring than clams reared in either medium or low food treatments. However, the number of offspring per marsupial sacs converges towards one as offspring increase in size regardless of food availability. These data support the notion that physical constraints are the primary limitation on brood size in *S. striatinum*.

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