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The Effect of Size-limited Brood Capacity on Brood Size in a Freshwater Bivalve

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ABSTRACT.—Size limited brood capacity is common among species with hard exoskeletons or shells. In these species, brood size is limited by the physical capacity to hold offspring. Here we present evidence that brood size is limited by physical constraints in *Sphaerium striatinum*, a small brooding bivalve. *Sphaerium striatinum* is a sequential brooder and produces offspring throughout the year. Offspring are brooded in marsupial sacs located on the inner demibranch. In an unconstrained brooder one would predict that brood size would increase as a function of adult length cubed, a volumetric relationship. In *S. striatinum*, brood size increases as less than a function of adult length squared. We demonstrate that brood size is limited by two general constraints: marsupial sacs and the retention of extra-marsupial offspring. The number of marsupial sacs increases as less than a function of adult length squared. This relationship may be a result of physiological process such as feeding and respiration. Offspring size at independence is a crucial factor in determining offspring survivorship. The retention of extra-marsupial offspring promotes growth inside a safe environment and increases survivorship upon independence. However, the exponent relating brood size to adult length is significantly less for adults that contain extra-marsupial offspring than compared to adults that do not contain extra-marsupial offspring. Although the evolution of brooding in *S. striatinum* has resulted in severe constraints on brood size, the benefits of brooding outweigh the cost of limited brood capacity. We discuss our results in relation to brooding strategies and size limited brood capacity in other brooding bivalves.

INTRODUCTION

Brooding is associated with small body size in many invertebrates (Strathmann and Strathmann, 1982). The explanation for this association is that larger adults produce more offspring than they can physically brood (Strathmann *et al.,* 1984). Following allometric principles of morphological design, the ability to produce and brood offspring is directly related to adult size (Huxley, 1932; Thompson, 1942). For example, fecundity is directly proportional to gonad volume and scales to the cube of adult length (Peters, 1983). The surface area of a body increases as an exponential function of adult length squared. For organisms that brood offspring along the surface of a body wall, the capacity to brood offspring will increase at a slower rate (proportional to length) than the ability to produce offspring. Therefore, the number of offspring larger adults can produce increases more quickly with increasing body size than the capacity to brood offspring.

Size-limited brood capacity is regulated by the arrangement of offspring inside adults, duration of incubation and size of offspring at independence (Strathmann, 1995). Fixing

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adult size, organisms that arrange offspring in a three-dimensional mass can retain proportionately more offspring than adults that arrange offspring along a two dimensional plane (Strathmann and Strathmann, 1982). If offspring size increases during incubation, then the amount of space available per offspring becomes proportionately smaller as offspring increase in size (Clutton-Brock, 1991). While physical constraints need not limit the initial production of offspring, they may become increasingly severe over the course of offspring development.

Size-limited brood capacity is common among species with hard exoskeletons such as crustaceans (Perrin, 1987; Glazier, 2000) and molluscs (Bayne *et al.*, 1983; Calow, 1983; Sebens, 1987). Numerous species of bivalves brood offspring in both marine and freshwater environments. While all brooding bivalves retain offspring within the mantle cavity beneath or within the demibranchs, the mode of brooding varies widely across species. Variation in brooding is apparent in the physical arrangement of offspring and is influenced by adult size and size and number of offspring. In the marine Veneridae, offspring are brooded in a three-dimensional mass between the descending lamellae of the inner demibranch and the visceral mass. Offspring are not attached to the gills, individually or collectively. Adults (<10 mm in valve length) typically brood between 50 and 250 offspring (Kabat, 1985). Offspring size at independence is around 500 μm. In the freshwater Pisidiidae, offspring are also brooded in a three-dimensional mass. However, offspring are encapsulated within a brood sac attached to the outer descending filaments of the inner demibranch. Adults (<6 mm valve length) typically brood between 6 and 40 offspring (Kilgour and Mackie, 1989). Offspring size at independence is around 1.0 mm in length (Hornbach and Cox, 1987). In the freshwater Sphaeriidae, offspring are brooded in multiple brood sacs arranged along the surface of the inner demibranch. Adults (8.0–14.0 mm in length) typically brood between 3 and 24 offspring (McMahon, 1991). Offspring size at independence is around 4.0 mm in length. Brooding in the Sphaeriidae differs from Veneridae and Pisidiidae in that adults are larger brood size is smaller, offspring size at independence is larger and offspring are arranged in a two dimensional plane along the surface of the demibranchs.

Kabat (1985) demonstrated that brood size was not constrained by adult size in *Transenella tantilla*. Brood size increased as a function of adult length cubed (slope of 3.02), a volume relationship. In contrast to *T. tantilla*, brood size was constrained by adult size in *Pisidium casertanum* (Kilgour and Mackie, 1989). Adults that were lower, wider and had a more rounded anterior brooded more offspring than clams that were higher, narrower and had an elongated antero-ventral margin. Based on previously established allometric relationships between brood size and adult size in *P. casertanum* (Kilgour and Mackie, 1989), we predicted that brood size in the Sphaeriidae was also limited by adult size. Although variation in brood size has been related to adult size in sphaeriids by numerous researchers (Thiel, 1926; Holopainen and Kuiper, 1982; Holopainen and Hanski, 1986; Mackie, 1986), this is the first study to examine the relationship in detail.

Study organism.—*Sphaerium striatinum* (Lamarck) is a small ovoviviparous fingernail clam commonly found in streams, rivers, ponds and lakes (Mackie, 1978; McMahon, 1991). Adults are sequential brooders, meaning that they repeatedly produce small cohorts of embryos throughout the year (Heard, 1977). In general, each adult contains a graded sequence of developing offspring from just fertilized to pre-hatching stages throughout the year. Each cohort is encapsulated by a marsupial sac located on the surface of each inner demibranch (Okada, 1935). Marsupial sacs are formed by the evagination of gill filaments and remain attached to the filaments from which they arise (Mackie *et al.,* 1974). As demibranchs increase in length, more filaments are available for the formation of marsupial

sacs. Therefore, the potential number of marsupial sacs present is directly related to gill length. Adults (>8.0 mm in length) may contain up to as many as 12 marsupial sacs divided equally between both inner demibranchs (Beekey, 2001). Each cohort of offspring produced by the adult is divided between two marsupial sacs, one on each demibranch. Initially, offspring size is around 100 μm in diameter (Beekey, 2001). Around 3.0 mm in length offspring break free from the marsupial sac (extra-marsupial offspring), but are retained inside the adult. Offspring are released into the external environment around 4.0 mm in length.

In *Sphaerium striatinum*, up to 97.5% of the offspring adults initially produce fail to reach independence (Hornbach *et al.*, 1982). The loss of offspring over the course of offspring development has been documented in a number of streams (Heard, 1977; Hornbach *et al.*, 1982; Beekey, 2001) and lakes (Avolizi, 1976). In the early stages of offspring development, each marsupial sac may contain up to as many as 12 embryos (~100 μm diam) per marsupial sac. However, when offspring reach 3.0 mm in length, only one offspring (rarely two) remains inside the marsupial sac. The loss of offspring over the course of development in *S. striatinum* is indicative of severe constraints on brood size.

MATERIALS AND METHODS

We examined individuals collected from two geographically distinct populations; Little Four Mile Creek (LFMC) near College Corner, Ohio (39°43.8′N, 84°48.2′W) and Big Elk Creek (BEC) near Elkton, Maryland (39°42.4′N, 75°50.1′W). Little Four Mile Creek has a maximum width of approximately 10 m and a maximum non-flooding depth of approximately 0.7 m. It is bordered throughout most of its length by deciduous trees and receives runoff from agricultural lands. Big Elk Creek has a maximum width of 12 m and an average depth of 0.5 m. The surrounding land is mainly used for agriculture and generates a large amount of nutrient runoff. Additional information concerning the habitats and demography for these two populations can be found in Hornbach *et al.* (1982) and Beekey (2001).

Adults were collected from Little Four Mile Creek each month throughout 1977 and 1978 and from Big Elk Creek each month throughout 1996–1998. Adults were returned to the lab and preserved in 70% ethanol or processed immediately. All adults were measured to the nearest 0.1 mm SL (SL, greatest anterior-posterior dimension) with Vernier calipers or a stage micrometer under a dissecting scope. A total of 205 individuals ranging in size from 5.0 to 13.4 mm SL were collected from Big Elk Creek and 202 individuals ranging in size from 5.4–14.0 mm SL were collected from Little Four Mile Creek. Each individual was dissected under a dissecting microscope in order to determine the number of marsupial sacs, number and size (measured with a stage micrometer to the nearest 0.1 mm) and location (intra- or extra-marsupial) of offspring. Parasitized adults or adults containing no offspring were excluded from the analyses.

Volume was calculated for each adult and their respective brood by using the equation to calculate the volume of an ellipsoid. The length, width and height of 136 individuals from Big Elk Creek ranging in size from 0.1 to 13.0 mm SL and 836 individuals from Little Four Mile Creek ranging in size from 4.0 to 14.6 mm SL were measured with Vernier calipers. These data were then used to calculate volumes for each individual. Although there was no significant difference between populations with respect to volume (ANCOVA, $F = 1.37$, $P > 0.05$), there were slight differences with respect to shell morphology (relationship between length, width and height) between populations, so we performed separate regressions on each population to reduce variance in later analyses. Volume (mm^3) was regressed with length (mm) to generate an equation for volume by measuring length alone. The following

equations were used for Big Elk Creek and Little Four Mile Creek: $\ln(\text{volume}) = 3.18$ $(\ln(\text{length})) - 1.86$, ($R^2 = 0.99$, $P < 0.001$, $N = 136$); $\ln(\text{volume}) = 3.12(\ln(\text{length})) - 1.71$, ($R^2 = 0.99$, $P < 0.001$, $N = 836$), respectively. Brood volume was calculated by summing the calculated volumes of all offspring within each adult.

We tested for differences with respect to both intra- and inter-population variability before proceeding with regression analyses. Sphaeriidae are sequential brooders and produce offspring throughout the year. Therefore, it is important to account for intra-population differences in reproductive measures (*e.g.,* the number of marsupial sacs and broods size) due to seasonal variability. We performed ANCOVAs on each population with month as the independent variable, length or volume as the covariate and the number of marsupial sacs, brood size and brood volume as dependent variables. Prior to all analyses, the data were natural log transformed to satisfy the assumptions of homogeneity of variance. We then examined the data for differences between populations with respect to the number of marsupial sacs, brood size and brood volume using ANCOVA (Statview, version 5.0.1) with population as the independent variable and adult length or volume as the covariate for all dependent variables. If there were no significant differences either within or between populations, the data were combined and analyzed using linear regression analyses for evidence of size-limited brood capacity.

We used the equation $y = a(x)^b$ where b is the exponent relating the two variables and a is the coefficient to examine relationships between x (adult length or adult volume) and y (number of marsupial sacs, brood size or brood volume) (Huxley, 1932; Roff, 2002). As previously stated, the data were natural log transformed prior to regression analyses. To test for significant differences between exponents from our regression equations and $b = 2$ (surface area relationship), and $b = 3$ (volume relationship), we used a two-tailed *t*-test of significance (Sokal and Rohlf, 1969; Strathmann *et al.,* 1984). To test for significant differences between exponents relating different stages of offspring development, we used a one tailed *t*-test in which $t = (b_1 - b_2)/\sqrt{s^2{}_{b_1} + s^2{}_{b_2}}$ with s_b the being the standard error of the exponent (Strathmann *et al.,* 1984).

We examined the data for four general indications of size-limited brood capacity. First, we examined the relationship between the number of marsupial sacs and adult length. Second, we determined the relationship between brood size and adult length. Next, we examined how the stage of offspring development affects the relationship between brood size and adult length. In particular, we investigated whether the relationship between brood size and adult length changes for adults containing only intra-marsupial offspring and adults containing both extra- and intra-marsupial offspring. Finally, we determined the relationship between brood volume and adult volume.

<center>RESULTS</center>

Marsupial sacs and adult length.—The exponent relating the number of marsupial sacs to adult length was less than $b = 2$ for both LFMC and BE adults (Fig. 1). While the number of marsupial sacs per adult varied widely in both populations throughout the year, there was no significant difference with respect to month in LFMC (ANCOVA, $F = 0.37$, $P > 0.05$, $DF = 1$, 202) or in BEC adults (ANCOVA, $F = 1.43$, $P > 0.05$, $DF = 1$, 205). Larger LFMC adults typically contained more marsupial sacs than similarly sized adults from BEC. However, the number of marsupial sacs per adult was not significantly different with respect to source population (ANCOVA, $F = 3.82$, $P > 0.05$, $DF = 1$, 405). When data from both populations were combined, the regression of marsupial sacs on adult shell length yielded the equation $\ln(\text{marsupial sacs}) = 1.61*\ln(\text{adult shell length}) - 2.078$ ($R^2 = 0.39$, $P < 0.001$, $N = 405$). The value of the exponent, $b = 1.61$, was significantly less than $b = 2.0$ (Table 1).
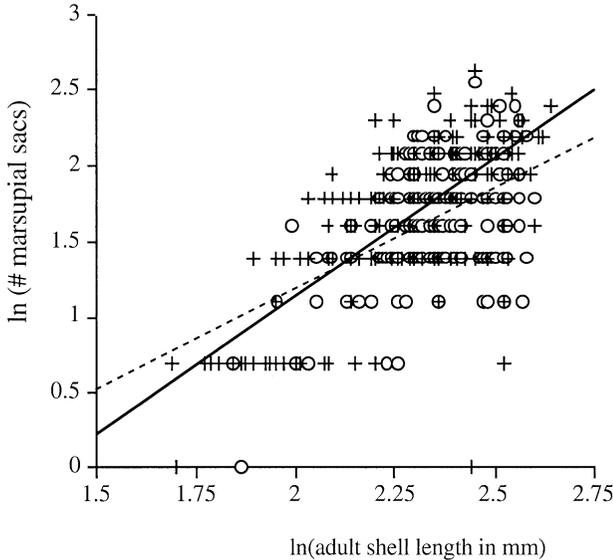
$+$ LFMC $\ln(\text{SACS}) = 1.82*\ln(\text{ASL}) - 2.51$, $R^2 = 0.22$, $P < 0.0001$, DF $= 202$

$\circ$ BEC $\ln(\text{SACS}) = 1.35*\ln(\text{ASL}) - 1.51$, $R^2 = 0.52$, $P < 0.0001$, DF $= 205$

FIG. 1.—The number of marsupial sacs vs. adult shell length. The number of marsupial sacs per adult are plotted for adults from Little Four Mile Creek ($+$) (N $= 202$) and Big Elk Creek ($\circ$) (N $= 205$). Regression lines and their equations are shown for Little Four Mile Creek (solid) and Big Elk Creek (dashed)

Brood size and adult length.—The exponent relating brood size and adult length was less than $b = 2$ for both LFMC and BE adults (Fig. 2). Like the number of marsupial sacs, brood size also varied widely within both populations throughout the year. However, there were no significant differences with respect to month in either LFMC (ANCOVA, F $= 0.82$, P > 0.05, DF $= 1$, 202) or BEC adults (ANCOVA, F $= 1.71$, P > 0.05, DF $= 1$, 205). There was also no significant difference between populations with respect to brood size (ANCOVA, F $= 2.10^{-5}$, P > 0.05, DF $= 1$, 405). The regression of brood size on adult length using data from both populations yielded the equation $\ln(\text{brood size}) = 1.51*\ln(\text{adult shell length}) - 1.45$ ($R^2 = 0.27$, P < 0.0001, N $= 405$). The exponent relating brood size to adult shell length ($b = 1.51$) was significantly less than $b = 2$ (Table 1). Brood size increased as less than a function of adult length squared.

Effect of offspring development on brood size and adult length.—To examine if the stage of offspring development had an effect on brood size, we compared the relationship between brood size and adult length for individuals containing only intra-marsupial offspring and individuals containing both intra- and extra-marsupial offspring. We combined data from both populations since there were no significant differences between LFMC and BEC adults with respect to the number of intra- or extra-marsupial offspring (MANCOVA, F $= 1.68$, P > 0.05, DF $= 1$, 405).

The exponent relating brood size to adult length was dependent upon the stage of

TABLE 1.—Brood size and number of marsupial sacs as a function of adult size for *Sphaerium striatinum*. Equations are for data combined from both populations since ANCOVAs indicated not significant difference between populations for any dependent variable (*see* results). Regression of fecundity measures on adult size using the equation: $\ln Y = a + b(\ln \text{size})$, where b is the exponent. Exponents are presented relating the number of marsupial sacs and brood size to adult length for all adults, for adults containing only intra-marsupial offspring and for adults containing both extra- and intra-marsupial offspring. Standard error (s_b) and 99% confidence intervals are presented for each exponent as well as P-values for a two tailed test of significance for the difference between the exponent and $b \neq 3.0$ and $b \neq 2.0$

	b	a	R^2	s_b	99% CI	$b \neq 3$	$b \neq 2$	N
Overall								
Marsupial sacs	1.61	−2.08	0.39	0.10	1.36–1.86	P < 0.05	P < 0.05	407
Brood size	1.51	−1.45	0.26	0.13	1.19–1.94	P < 0.05	P < 0.05	407
Intra-marsupial only								
Marsupial sacs	1.94	−2.77	0.55	0.11	1.72–2.16	P < 0.05	P > 0.05	246
Brood size	1.53	−1.52	0.26	0.17	1.09–1.95	P < 0.05	P < 0.05	246
Extra- and intra-marsupial								
Marsupial sacs	0.71	0.01	0.43	0.27	0.01–1.42	P < 0.05	P < 0.05	161
Brood size	0.86	0.16	0.56	0.28	0.13–1.58	P < 0.05	P < 0.05	161

offspring development. The slope of the line relating brood size and adult length for adults containing only intra-marsupial offspring was greater than the slope of the line for adults containing both extra- and intra-marsupial offspring (Fig. 3). The regression of brood size on adult length for adults containing only intra-marsupial offspring yielded the following equation: $\ln(\text{brood size}) = 1.53*\ln(\text{adult shell length}) - 1.52$ ($R^2 = 0.26$, P < 0.001, N = 245). The exponent relating brood size and adult length for adults containing only intra-marsupial offspring was significantly less than $b = 2$ (Table 1). For adults containing both extra- and intra-marsupial offspring, the regression of brood size and adult length yielded the equation: $\ln(\text{brood size}) = 0.86*\ln(\text{adult shell length}) + 0.16$ ($R^2 = 0.06$, P < 0.05, N = 160). Like the exponent relating the length of adults containing only intra-marsupial offspring and brood size, the exponent relating the length of adults containing both offspring types and brood size was also significantly less than $b = 2$ (Table 1). However, the exponent relating brood size and adult length was significantly higher for adults containing only intra-marsupial offspring than for adults containing both extra- and intra-marsupial offspring ($t = 2.04$, P < 0.05, DF = 1).

The stage of offspring development also affected the relationship between the number of marsupial sacs and adult length. The exponent relating the number of marsupial sacs and adult length was less for adults containing both extra- and intra-marsupial offspring than for adults containing only intra-marsupial offspring (Table 1). For adults containing only intra-marsupial offspring the exponent relating marsupial sacs and adult length increased as a function of adult length squared (Table 1), whereas the exponent relating the marsupial sacs and adult length for adults containing extra- and intra-marsupial offspring increased as less than a function of adult length squared.

Brood volume and adult volume.—In general, brood volume was higher in BE than LFMC adults (Fig. 4). Brood volume varied in both populations over the course of the year. In BE, brood volume increased in April and May as well as in September and October. In LFMC,
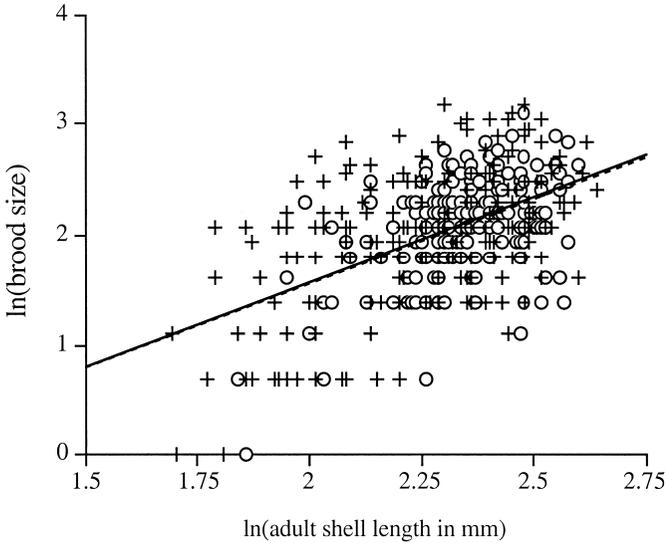
+   LFMC ln(BS) = 1.54*ln(ASL) - 1.49, R^2 = 0.28, P < 0.0001, DF = 202

○   BEC ln(BS) = 1.52*ln(ASL) - 1.49, R^2 = 0.22, P < 0.01, DF = 205

FIG. 2.—Brood size vs. adult shell length. The number of offspring per adult are plotted for adults from Little Four Mile Creek (+) (N = 202) and Big Elk Creek (○) (N = 205). Regression lines and their equations are shown for Little Four Mile Creek (solid) and Big Elk Creek (dashed)

brood volume also increased in the early spring and late fall. However, the effect of month on brood volume was only significant in BE adults (ANCOVA, F = 1.97, P < 0.05, DF = 1, 205), not in LFMC adults (ANCOVA, F = 1.35, P > 0.05, DF = 1, 202). There was no significant difference between populations with respect to the relationship between overall brood volume and adult volume (ANCOVA, F = 0.40, P > 0.05, DF = 1, 407). The combined regression of brood volume on adult volume yielded the equation ln(brood volume) = 1.4*ln(adult volume) − 5.76 (R^2 = 0.47, P < 0.0001, N = 406). The value of the exponent was not significantly different from b = 1 (t = 0.421, P > 0.05, DF = 1).

DISCUSSION

Brood size is clearly constrained by the physical arrangement of offspring and the retention of extra-marsupial offspring in *Sphaerium striatinum*. In an unconstrained brooder, one would expect to see brood size increase as a function of adult length cubed (*i.e.*, a volumetric relationship). For *S. striatinum*, the regression of brood size on adult length indicates that brood size increases as less than the square of adult length (a surface area relationship) (Table 1). Based on our analyses, two general constraints are responsible for the limitation of brood size in this species. The first constraint is the encapsulation of offspring inside marsupial sacs along both inner demibranchs. The number of marsupial sacs also increases as less than a function of adult length squared, a surface-area relationship (Table 1). The second constraint on brood size is the retention of extra-marsupial offspring. The exponent relating brood size to adult length is significantly less for adults containing extra-marsupial offspring than for adults containing only intra-marsupial offspring (Table
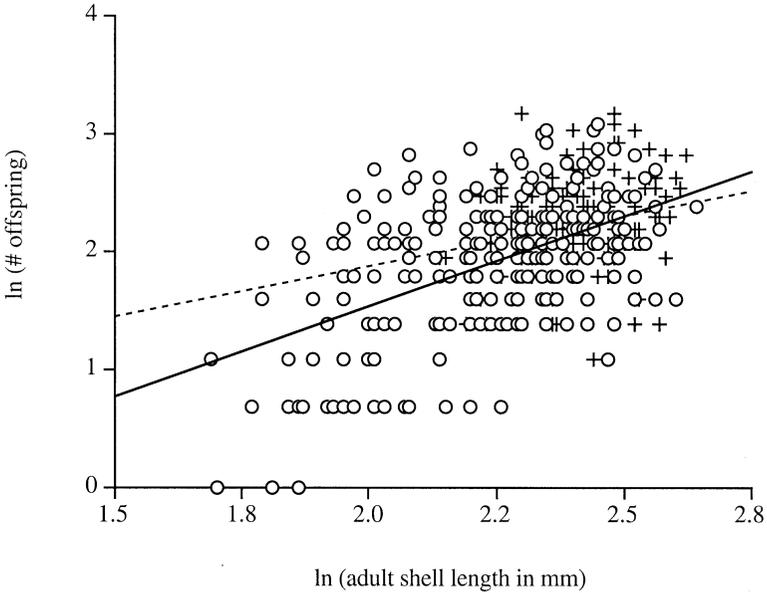
FIG. 3.—Brood size as a function of stage of offspring development. Brood size is plotted for adults containing only intra-marsupial offspring (+) (N = 246) and adults which contain both intra- and extra-marsupial offspring (○) (N = 161). Regression lines are shown with their equations adults with only intra-marsupial offspring (solid line) and adults containing both intra- and extra-marsupial offspring (dashed line)

1). Below we discuss these findings in relation to the mode of brooding in *S. striatinum* and other species of brooding bivalves.

The physical arrangement of offspring inside adults has a significant effect on brood size. In the marine bivalve *Transenella tantilla*, brood size increases as a function of adult length cubed, a volumetric relationship (Kabat, 1985). In the marine bivalve *Mysella bidentata* (Leptonacea), brood size increases as more than a function of adult length cubed with an exponent of 4.7 (Ockelmann and Muus, 1978). Reproductive output increases at a faster rate than adult weight or volume. Interestingly, *M. bidentata* is a short-term brooder whose embryos are released as veliger larvae. Clearly, the three-dimensional arrangement of offspring in *T. tantilla* and *M. bidentata* does not constrain brood size. In contrast, one would predict that the exponent relating brood size to adult length would increase as a function of adult length squared with an exponent of $b = 2$ for species that brood offspring along the surface of a body wall (Strathmann and Strathmann, 1982). In *Sphaerium striatinum*, offspring are brooded along the surface of the inner demibranchs. Yet, the exponent (*b*)
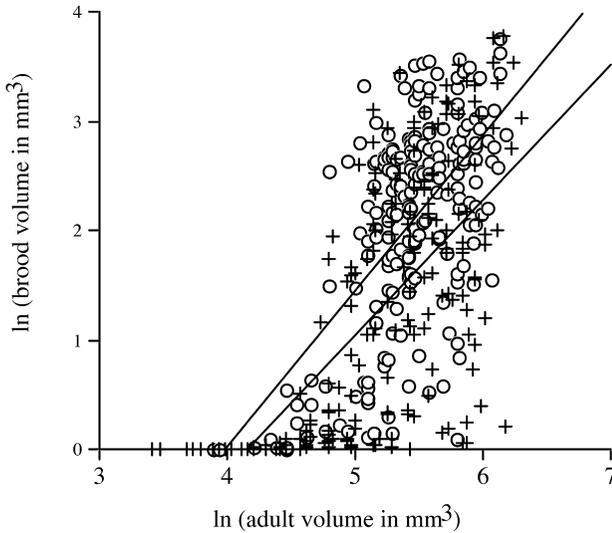
FIG. 4.—Brood volume (BV) as a function of adult volume (ADV). The total volume of offspring per adult are plotted for adults from Little Four Mile Creek (+) (N = 202) and Big Elk Creek (○) (N = 205). Regression lines are solid and dashed for Little Four Mile Creek and Big Elk Creek, respectively

relating brood size to adult length in *S. striatinum* is significantly less than $b = 2$ (a surface area relationship) (Table 1).

Filling the entire demibranch with marsupial sacs and developing offspring may pose significant problems for physiological process such as filter feeding and respiration. For example, an 11 mm long adult would have a volume of 369 mm³. Adults may contain up to as many as 12 offspring per marsupial sac in the earliest stages of offspring development (0.6 mm in length, 0.006 mm³). Total brood volume would be 0.33 mm³ accounting for 0.1% of the adult's volume. If all of these offspring completed development and reached the size where offspring are released (3.5 mm in length, 9.54 mm³), total brood volume would be 236 mm³ accounting for 64% of adult volume. The retention of many large offspring would likely interfere with physiological processes of adults. In fact, research on other brooding bivalve species has established that offspring interfere with both the adult's ability to feed (Burky *et al.*, 1985; Schwartz and Dimock, 2001) and respire (Tankersley and Dimock, 1993). Interestingly, the relationship between brood volume and adult volume appears to saturate around 35 mm³ (Fig. 4). At this point, brood volume may reach an optimal point where adults can function without excessive interference from developing offspring. A second explanation for why the exponent relating brood size to adult length is significantly less than $b = 2$ is offspring size.

Offspring development may pose significant constraints on brood capacity (Hess, 1993). Given constant adult volume and brood size, the amount of space available per offspring will become proportionally smaller over the course of development. If space becomes limiting as offspring increase in size, adults would have to alter brood volume or brood size in order

to accommodate growing offspring size. There is no evidence for changes in brood volume in *Sphaerium striatinum*. In fact, brood volume increases isolinearly with adult volume (Fig. 4). However, as offspring increase in size, the exponent relating brood size to adult length decreases. The exponent relating brood size to adult length is significantly less for adults that contain both extra- and intra-marsupial offspring than for adults containing only intra-marsupial offspring (Table 1).

In *Sphaerium striatinum*, offspring size at independence has limited how many offspring parents' brood and release compared to other bivalves that broadcast gametes or bivalves that brood and release thousands of small offspring. For example, freshwater unionaceans brood and release between 10^3–10^6 offspring (<200 μm in length at independence) per adult per reproductive season (McMahon, 1991). In contrast, sphaeriids brood and release between 3 to 24 offspring (3 mm in length at independence) in any given reproductive season (McMahon, 1991). The vast difference in fecundity between unionids and sphaeriids is primarily due to offspring size at independence. For example, a unionid 50 mm in length with a brood of 200,000 offspring 200 μm in length would have a brood volume of 1600 mm^3 with an adult volume of 125,000 mm^3. Offspring would constitute 1.3% of the adult volume. A 12 mm long sphaeriid with a typical brood of 24 offspring ranging in size from 0.1–4.0 mm would have a brood volume of approximately 51 mm^3 with an adult volume of 345 mm^3. Sphaeriid offspring would constitute 14.8% of adult volume. Unionids have less than one tenth the brood volume but nearly 8000 fold more offspring. If unionid offspring were to grow as large as sphaeriid offspring then unionids would undoubtedly experience severe limitations on brood capacity.

The lack of significant differences between populations from Little Four Mile Creek in Ohio and Big Elk Creek in Maryland reinforce the conclusion that physical constraints such as adult size limit brood size in *Sphaerium striatinum*. One might be concerned that the low R^2 values associated with regressions of dependent variable versus adult shell length reflect variability in sphaeriid reproduction. However, the distribution of marsupial sacs and brood size in relation to adult shell length (Figs. 1, 2) is typical for this species (Hornbach *et al.*, 1982). In general, Sphaeriidae exhibit wide variation in brood size (Holopainen and Hanski, 1986; Kilgour and Mackie, 1989). A second reason for the high degree of variability was the incorporation of data for each population over two years. Previous research has documented that habitat characteristics such as water chemistry, disturbance, as well as food availability all play an important role in regulating brood size in sphaeriids (Way *et al.*, 1980; Mackie and Flippance, 1982; Hornbach and Childers, 1986; Hornbach and Cox, 1987; Beekey, 2001). While these characteristics may influence the timing of reproduction, number of reproductive bouts, initial fecundity, offspring size at independence, it is clear that the upper limit to brood size is regulated by physical constraints.

One might argue that our data are indicative of factors other than size limited brood capacity regulating reproductive output in sphaeriids. Previous studies have suggested that reproductive output is energetically limited (Avolizi, 1976; Heard, 1977; Hornbach *et al.*, 1982). Simply stated, adults cannot provide all offspring with the nutrients required to complete development. Recent research contradicts this hypothesis (Beekey and Karlson, 2003). Juveniles were reared through adulthood under different food levels. Clams reared with the most food produced more embryos than clams reared with the least amount of food. Thus, initial fecundity increased with a corresponding increase in food availability. However, adults that initially produced more embryos in high food treatments lost proportionately more embryos over the course of development than adults reared with the least amount of food. Beekey and Karlson (2003) clearly demonstrated that energetic costs constrain the timing of reproduction, number of reproductive bouts and number of

offspring produced per reproductive attempt. The authors' data substantiate the hypothesis that brood size regulated by physical constraints on brood capacity.

The results of our analyses indicate conflicting evidence for scaling constraints in brooding bivalves is likely due to differences in the arrangement of offspring and size of offspring at independence. Few studies have explicitly compared brood volume in unionids and sphaeriids. Although unionids brood far more numbers of offspring than sphaeriids, it appears that unionids brood proportionately "fewer" offspring than sphaeriids based on their proportion in offspring volume. This observation would support the size-limited brood capacity hypothesis (Strathmann and Strathmann, 1982). The variety of brood strategies among freshwater bivalves provides a suitable set of organisms for further testing the hypothesis for the association of brooding and small adult size. Scaling constraints are important determinants of brood size in freshwater bivalves when one takes into account the mode of brooding.

In *Sphaerium striatinum*, adult size, the arrangement of offspring in marsupial sacs along the surface of the inner demibranchs and the retention of extra-marsupial offspring limit brood size. At first it would seem that constraints on brood size due to limitations associated with adult size and mode of brooding would be disadvantageous. However, development of offspring inside marsupial sacs ensures offspring receive a constant supply of nutrients (Heard, 1977; Schwartz and Dimock, 2001). The retention of extra-marsupial offspring promotes growth and ultimately enhances offspring survivorship upon release into the external environment (Beekey *et al.,* 2001). Therefore, brooding remains advantageous even in the face of scaling constraints as the benefits of enhanced offspring survival outweigh the costs of limited brood capacity.

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