Why do larger mothers produce larger offspring? A test of classic theory

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Abstract. Across a wide range of taxa, larger mothers produce larger offspring. Theory assumes that larger, more fecund mothers create higher local densities of siblings, and so larger mothers produce larger offspring to offset sibling competition. This assumption has been debated for over 30 yr, but direct empirical tests are surprisingly rare. Here, we test two key assumptions of classic theories that predict sibling competition drives maternal-size–offspring-size (MSOS) correlations: (1) independent effects of offspring size and sibling density on offspring performance or (2) as a product of an interaction between these two factors. To simultaneously test these alternative assumptions, we manipulate offspring size and sibling density in the marine invertebrate, *Bugula neritina,* and monitor offspring performance in the field. We found that depending on the fitness metric being considered, offspring size and sibling density can either independently or interactively affect offspring performance. Yet sibling density did not affect offspring performance in the ways that classic theories assume. Given our results, it is unlikely that sibling competition drives the positive MSOS correlation observed in this species. Empirical support for these classic theories remains lacking, suggesting alternative explanations are necessary.

Key words: density dependence; fecundity; life-history theory; maternal body size; maternal effects; offspring performance; offspring size; sibling competition.

INTRODUCTION

Within species, larger mothers tend to produce larger offspring than smaller mothers. Maternal-size–offspring-size (MSOS) correlations are common within a range of taxa, from invertebrates to vertebrates (reviewed in Lim et al. 2014). Despite the ubiquity of MSOS correlations, their underlying drivers remain unresolved (Rollinson and Rowe 2015). Classic life-history theory predicts that all mothers should produce offspring of a single optimal size that maximizes maternal fitness within a given environment (Smith and Fretwell 1974). As such, the fact that larger mothers often produce larger offspring challenges Smith and Fretwell's (1974) classic theory, but subsequent theories have explicitly considered adaptive explanations (e.g., Parker and Begon 1986, Venable 1992, Hendry and Day 2003, Kindsvater et al. 2010, Jørgensen et al. 2011).

Parker and Begon (1986) were among the first to explore why offspring size increases with maternal size by introducing two main innovations to the Smith-Fretwell model. First, females are allowed to vary in resource status, such that larger females have more reproductive resources, and thus higher fecundities, than smaller females. Second, for species with limited dispersal, larger, more fecund mothers create higher local densities of siblings that compete with each other. In their model, offspring performance not only increases with offspring size (as per Smith-Fretwell), but also declines with fecundity via density-dependent effects (Fig. 1a). Under these assumptions, Parker and Begon (1986) predict that selection should favor larger mothers that produce larger offspring to offset the negative density effects associated with the higher fecundities of larger mothers.

Building on Parker and Begon's model, whereby positive MSOS correlations are driven by independent effects of offspring size and sibling density on performance, Venable (1992) explored MSOS correlations as the product of interactions between offspring size and sibling density. Specifically, a positive MSOS correlation can arise when the performance benefits of larger offspring sizes are stronger at higher densities of siblings, but weaker at lower densities (Fig. 1b). This assumption seems reasonable given that previous studies find that conspecific density typically alters the offspring size-performance relationship in this direction (Marshall et al. 2006, Allen et al. 2008), though these studies did not examine competition among siblings. Thus, theory predicts that positive relationships between maternal size and fecundity can drive adaptive MSOS correlations in two ways: (1) by generating sibling densities that negatively affect offspring performance, independently of offspring size (Parker and Begon 1986), or (2) by generating sibling densities that alter the offspring size–performance function (Venable 1992; Fig. 1).
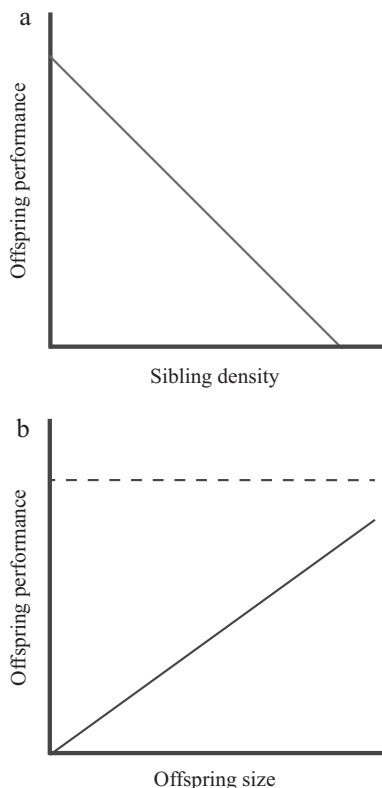
Fig. 1.   Schematic showing the two assumptions underlying classic offspring-size models that predict larger, more fecund mothers produce larger offspring to offset sibling competition: (a) increasing sibling densities negatively affect offspring performance, and does so independently of offspring size (Parker and Begon 1986) and (b) sibling density alters the offspring size–performance relationship (Venable 1992) such that larger offspring perform better at high sibling densities (solid line), but all offspring perform equally well at low densities (broken line).

In a recent review, Rollinson and Rowe (2015) argued that theories that invoke sibling competition as drivers of MSOS correlations are unlikely to be generally applicable to a broad range of taxa. They conclude that the few indirect tests of these ideas provide little support for sibling competition effects, and that alternative theories are more likely to successfully explain MSOS correlations. However, Rollinson and Rowe (2015) also noted that few studies have explicitly tested the assumptions of sibling competition models, and field tests are rare (but see Rollinson and Hutchings 2010). To our knowledge, there have been no formal tests examining the prediction that MSOS correlations arise as a product of interactions between offspring size and sibling density (Venable 1992). Given that sibling competition has been widely invoked to explain MSOS correlations, it is surprising that there are few direct tests of these influential theories.

Identifying the mechanism underlying MSOS correlations is not only of fundamental interest to life-history theory, but also has important ecological implications. Anthropogenic activities have reduced the average body size of individuals in many systems (Gardner et al. 2011, Hixon et al. 2014). For example, commercial fishing truncates size distributions in favor of younger, smaller spawners (reviewed in Hixon et al. 2014). Many studies also show that larger offspring out-perform smaller offspring within a given environment (Einum and Fleming 2000, Marshall et al. 2003, Berkeley et al. 2004). Therefore, the likelihood that larger mothers produce offspring that are intrinsically fitter than those of smaller mothers is one argument for why larger females should be preserved in exploited populations (Hixon et al. 2014). However, if females provision offspring to compensate for sibling competition associated with maternal fecundity, then theory predicts that the offspring of different-sized mothers will have the same per capita fitness (Parker and Begon 1986, Marshall et al. 2010). Determining the drivers of MSOS correlations, therefore, has important implications for the management of natural populations.

Here, we simultaneously test the two key assumptions of classic theories that predict sibling competition will drive MSOS correlations: (1) that sibling density reduces offspring performance, and does so independently of offspring size (Parker and Begon 1986), or (2) that sibling density alters the offspring size-performance relationship such that larger offspring perform better at high sibling densities, but all offspring perform equally well at low densities (Venable 1992, Fig. 1). To test these assumptions, we manipulate offspring size and sibling density using the marine invertebrate, *Bugula neritina,* and monitor the consequences for offspring performance in the field.

Materials and Methods

Study species

Bugula neritina is an arborescent bryozoan common to sessile marine communities world-wide. *Bugula neritina* is a clonal organism that grows by asexual budding of individual modules (zooids) of a relatively fixed size (Thompson et al. 2015). Growth is therefore indeterminate in this species, such that colony size (number of individual zooids) is the key index of maternal size. Indeed, MSOS correlations occur at the scale of colonies in this species; a twofold increase in colony size is shown to correspond to a 72% increase in larval volume (Marshall and Keough 2003, Marshall et al. 2003). *Bugula neritina* displays many traits that make it ideal for testing the assumptions of models that invoke sibling competition as a driver of MSOS correlations (e.g., Parker and Begon 1986, Venable 1992). For instance, offspring size positively affects the survival, growth, and reproduction of *B. neritina*, particularly at high conspecific densities (Marshall et al. 2003, Allen et al. 2008). Furthermore, larval durations are typically very short,

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which limits the potential for long-distance dispersal in the field, and there is evidence for sibling aggregation and interactions at settlement (Keough 1984, Burgess and Marshall 2011, Aguirre et al. 2013). Maternal fecundity also positively correlates with colony size, with a doubling in colony size corresponding to an approximate doubling in fecundity (Marshall et al. 2003). Thus larger mothers likely create higher local densities of siblings relative to smaller mothers (D. Marshall, *unpublished data*), and post-settlement interactions between siblings are likely to be negative (Allen et al. 2008, Aguirre and Marshall 2012).

Experimental methods

To determine whether sibling interactions influence offspring performance according to the assumptions of Parker and Begon (1986) and Venable (1992), we experimentally manipulated sibling density and offspring size. We manipulated sibling density to simulate the assumption that local settlement densities of siblings would be higher for larger, more fecund mothers. We manipulated offspring size by allocating a single individual of known larval size (focal individual) into each density treatment, and monitored several fitness metrics of these focal individuals in the field.

To obtain larvae for our experiment, we collected reproductive *B. neritina* colonies from Altona Pier (Port Phillip Bay, Victoria, Australia) from December 2014 to February 2015. These colonies were returned to the laboratory in insulated aquaria containing seawater. We used standard techniques to induce individual colonies to spawn (Marshall et al. 2003). Briefly, colonies were held in separate, dark, insulated aquaria at 19°C for 2 d before being exposed to bright light to stimulate larval release. Seven colonies were spawned in separate beakers to ensure our manipulations were applied to sibling larvae. As we collected colonies that had been fertilised in the field and were already brooding their larvae, only maternal identity was known. Given that multiple paternity is common for other sperm-casting marine invertebrates (Johnson and Yund 2007), multiple paternity is also likely in *B. neritina*, although this has not been confirmed for any Bryozoan. All offspring from a single colony in our experiment were therefore at least half siblings, although some were likely full siblings.

Focal larvae, positioned with the cilial groove facing directly upwards, were digitally photographed on a glass slide at 100× magnification. We then measured larval length along the axis of the cilial groove using image analysis software (Image J, V. 1.48, Bethesda, Maryland, USA). We targeted larvae in the upper and lower size classes for measurement to ensure the relationship between offspring size and performance was estimated for the full range of larval sizes available. For each parental colony, we measured between 80 and 110 focal larvae. Focal larvae were then settled on pre-roughened,

biofilmed acetate sheets. Non-focal larvae used to create sibling competitive environments were haphazardly allocated to density treatments and settled (without measurement) onto pre-roughened, biofilmed PVC plates (5 × 5 × 0.6 cm). All experimental larvae (focal individuals and competitors) were settled within 3 h of spawning to minimize effects of delayed settlement on larval quality (Wendt 1998). After this time, any unsettled larvae were rinsed from settlement surfaces with filtered seawater. Settlers were then left overnight in trays of filtered (0.22 μm) seawater at 19°C to complete metamorphosis.

On the following day, we cut successful focal settlers from acetate sheets and glued them to the PVC plates bearing sibling competitors. A single focal settler was systematically assigned to each sibling density treatment, ensuring that larval sizes were equally distributed among densities. Our manipulation of sibling density (per 25 cm^2) had four levels: no competition (0 competitors + 1 focal settler), low competition (3 competitors + 1 focal settler), intermediate competition (6 competitors + 1 focal settler), and high competition (12 competitors + 1 focal settler). Sibling densities used in our experiments were based on pilot studies showing that a four-fold difference in maternal colony size yields a four-fold change in sibling densities (D. Marshall, *unpublished data*). We circled all experimental settlers with a pencil prior to deployment to distinguish them from field-settled recruits.

Experiments were deployed in the field at the Royal Brighton Yacht Club (Victoria, Australia). Settlement plates were attached to PVC backing panels (55 × 55 × 0.8 cm) and hung 1 m below the water surface with plates facing downwards to avoid smothering by sediment. Each backing panel had 64 plates, such that each of the four levels of sibling density were replicated 16 times per panel (N = 112 for each level of sibling density across the experiment). Intraspecific competition among *B. neritina* typically occurs at the scale used in our study (5 × 5 cm plates), but density-dependent effects beyond this scale are small or non-existent (Hart and Marshall 2009, Hart et al. 2012). Thus, plates within a backing panel were unlikely to interact with one another. The experiment was replicated across seven panels, with each panel representing a single family unit (i.e., all individuals within a panel were maternal siblings). We processed a single family per day in the laboratory, therefore, the deployment of panels in the field was staggered, such that panels combine family-level phenotypic variation, as well as spatial and temporal variation.

We measured the performance of focal individuals (N = 448) by monitoring their survival and growth after 4 weeks in the field. Survival was determined by the presence of the focal individual (scored as 1), while absent focal individuals were assumed to be dead (scored as 0). Growth was measured as the number of times the colony had bifurcated along the longest branch, which is a good indication of colony biomass in this species (see Keough and Chernoff [1987] for details). We randomized the position of plates on PVC backing panels

weekly. We removed any new settlers of any species from our plates weekly with a scalpel to eliminate spurious competition.

Statistical analysis

The effects of larval size and sibling density on offspring performance after four weeks in the field were analysed using generalized linear mixed models (GLMM). Post-settlement survival was modelled as a binomial distribution with a logit link, while colony size (bifurcations) was modelled using a Poisson distribution with a log link and an estimated scale parameter (i.e., quasi-Poisson GLMM). For both analyses, larval size and sibling density were continuous fixed effects, and backing panel was a random effect. For our survival analysis, we modelled sibling density as the initial number of settlers on a plate. For the analysis of colony size, we modelled sibling density as the average number of initial settlers within our four density levels for several reasons. First, mortality mostly occurred early in the experiment (though it did continue throughout) and varied among plates, such that initial settlement was not always reflective of densities throughout the experiment. Given most mortality occurred early, we regarded initial density as the most relevant environmental predictor of a focal colony's survival. In contrast, colony growth is affected slightly by initial settlement densities, but affected much more strongly by later densities. Given we had no a priori expectation of when density affects would be strongest, our averaging approach best captures the broad differences in densities experienced during colony growth. Second, a model for colony growth that used average settlement densities was an equivalent (or slightly better) fit than a model that used initial sibling densities (ΔAIC = 0.6).

We reduced both models by removing non-significant interactions if their inclusion did not improve model fit (Quinn and Keough 2002). Variance components were estimated using restricted maximum likelihood, and model fit and significance was assessed via likelihood ratio tests (at $P = 0.05$). Fixed effects were estimated using maximum likelihood, with model fit assessed by AIC values and significance interpreted from χ^2 tests provided in the final model output. Neither GLMM showed signs of over-dispersion, although the quasi-Poisson regression was slightly under-dispersed (Pearson $\chi^2 = 0.41$). All models were fitted using PROC GLIMMIX in SAS, version 9.4 (SAS Institute, Cary, North Carolina, USA) using pseudo-likelihood estimation (Bolker et al. 2009).

RESULTS

After four weeks in the field, we found that post-settlement survival of *B. neritina* was not affected by an interaction between offspring size and sibling density (Table 1). We also found no effect of sibling density on offspring survival. Offspring size did,

TABLE 1. Generalized mixed-model (binomial) for the relationship between larval length (μm) and sibling density (initial no. settlers/25 cm^2) on post-settlement survival in *Bugula neritina* after four weeks in the field.

Source	Parameter (95% CI)	χ^2	P
Fixed effects			
Larval length	**0.012 (0.00009, 0.024)**	**3.91**	**0.048***
Density	**0.009 (−0.042, 0.061)**	**0.12**	**0.732**
Larval length × density	0.0002 (−0.0023, 0.0028)	0.03	0.873
Random effects			
Panel	**0.344 (0.120, 3.180)**	**28.66**	**<0.0001***
Panel × density	0.003 (0.0006, 3.677)	1.95	0.163
Residual	**0.993 (0.870, 1.145)**		

Notes: Terms included in final model are shown in boldface type; other terms are reported for completeness but were removed from the final model because they did not improve model fit (see *Materials and methods*). All df = 1.

* $P < 0.05$.

however, slightly increase the probability of post-settlement survival, with a unit increase in larval size increasing the odds of survival by 1.15% (Table 1, Fig. 2).

We found an interaction between sibling density and offspring size on colony size after four weeks in the field (Table 2). In the absence of siblings and at low sibling densities, offspring size had a strong effect on post-settlement growth, with larger offspring growing into larger colonies than those that originated as smaller larvae (Fig. 3). In comparison, the effect of offspring size
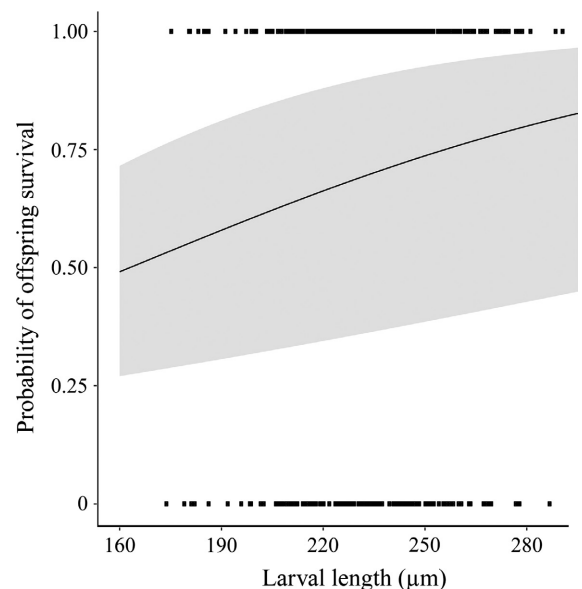

FIG. 2. Estimated relationship between larval size and the probability of survival (± SE [gray zone]) of *Bugula neritina* colonies after four weeks in the field. Data points (binary at 1.0 and 0) show the raw data for survival at this time point ($N = 448$).

TABLE 2. Generalized mixed-model (quasi-Poisson) for the relationship between larval length (µm) and sibling density (average no. initial settlers/25 cm^2) on post-settlement colony size (bifurcations) of *Bugula neritina* colonies after four weeks in the field.

Source	Parameter (95% CI)	χ^2	P
Fixed effects			
Larval size	**0.004 (0.0013, 0.0075)**	**8.17**	**0.004***
Density	**0.13 (0.012, 0.25)**	**5.41**	**0.02***
Larval size × density	**−0.0006 (−0.001, −0.00006)**	**5.62**	**0.018***
Random effects			
Panel	**0.084 (0.059, 0.130)**	**8.97**	**0.003***
Panel × density	0.0009 (0, 0)	1.23	0.267
Residual	**0.370 (0.337, 0.472)**		

Notes: Terms included in final model are shown in boldface type; other terms are reported for completeness but were removed from the final model because they did not improve model fit (see *Materials and methods*). All df = 1.

*$P < 0.05$.

on post-settlement growth became less pronounced at higher sibling densities. The direction of the offspring size effect on growth was also inverted at higher sibling densities relative to lower densities: smaller larvae formed colonies that were larger than colonies formed by larger larvae at the highest densities investigated (Fig. 3).

DISCUSSION

Theory has sought to explain the widespread tendency for larger, more fecund mothers to produce larger offspring. Here, we test two assumptions underlying classic theories that invoke sibling competition as a driver of MSOS correlations: (1) independent effects of offspring size and sibling density on performance (Parker and Begon 1986) and (2) effects on performance that arise as a product of an interaction between offspring size and density (Venable 1992, Fig. 1). While many aspects of *Bugula neritina*'s life history suggest that the assumptions of these models should apply, sibling density did not affect offspring performance in either of the ways assumed by these theories. Our results, therefore, suggest that sibling competition is unlikely to drive the positive MSOS correlation in this species.

The theory of Parker and Begon (1986) assumes that offspring performance increases with offspring size, but that performance declines with sibling density. In accordance with Parker and Begon (1986) and most offspring-size models (e.g., Smith and Fretwell 1974, McGinley et al. 1987), we found that larger *B. neritina* larvae had higher post-settlement survival relative to smaller larvae. In contrast to Parker and Begon (1986), however, we found offspring survival was not affected by sibling density. Instead, in our study, mortality appeared to be density independent (average survival was 69%). Other studies find mixed effects of sibling density on offspring performance (Einum and Fleming 1999, Takahashi et al. 2005, Rollinson and Hutchings 2010, Eberhart and Tielbörger 2012). Surprisingly, *B. neritina* siblings have been shown to compete more intensely relative to non-related conspecifics (Aguirre and Marshall 2012), but in our study at least, the consequences of sibling competition are not density dependent.
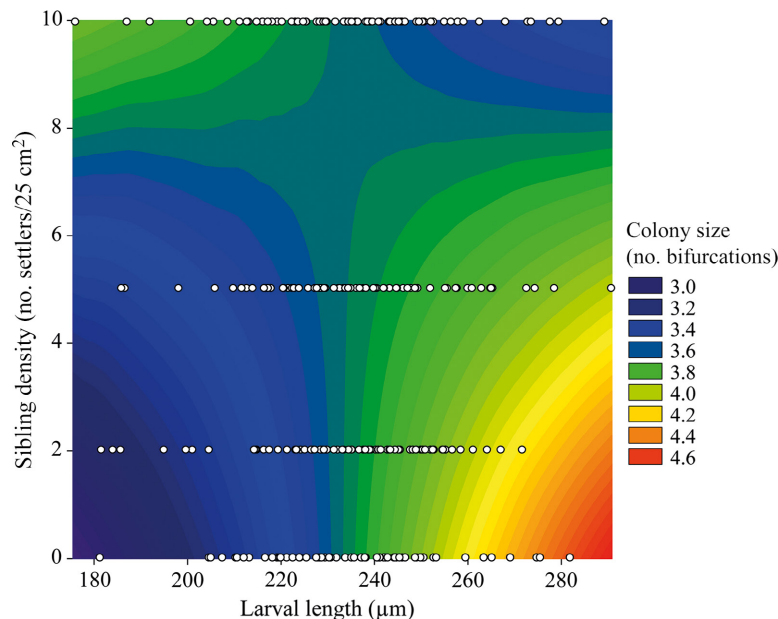

FIG. 3. Estimated relationship between larval size and sibling density on colony size (number of bifurcations; side bar) for *Bugula neritina* settlers after four weeks in the field. Data points (white circles) show the distribution of offspring sizes surviving at this time point ($N = 292$).

We found an interaction between sibling density and offspring size on post-settlement growth, again contradicting the assumptions of Parker and Begon (1986). The presence of an interaction between offspring size and sibling density was anticipated by Venable (1992). He predicted that the MSOS correlation will be positive when larger offspring have superior performance at high sibling densities, but all offspring perform equally well at low densities (Fig. 1b). Instead, we found the reverse: at low sibling densities larger offspring grew better than smaller offspring, but at higher densities, smaller offspring grew as large (or even slightly larger) than large offspring. In other words, we found that smaller *B. neritina* offspring were positively affected by increasing sibling densities, while larger offspring were negatively affected by increasing densities. This contrasts previous studies (including studies in our system) that find smaller offspring typically experience the negative effects of high conspecific densities more strongly than larger offspring (Beckerman et al. 2006, Allen et al. 2008). Previous studies on *B. neritina* that did not measure offspring size have found colony growth to decrease with increasing densities, particularly when individuals were closely related (Aguirre and Marshall 2012, Svensson and Marshall 2015). Phenotype-specific responses to density-dependence in our study, however, suggest that density affects may not be as straightforward in this system as previously thought. Indeed, the fitness consequences of aggregating with genetically similar individuals is phenotype specific in other systems (although in these studies these phenotypes were not offspring size; Sinervo and Clobert 2003).

In our study, phenotype-specific density-dependence may occur if the relative strength of facilitation and competition depends on offspring size at higher sibling densities. Smaller *Bugula* larvae become juveniles with smaller, less efficient, feeding structures relative to juveniles formed by larger larvae (Kosman and Pernet 2011). At high densities, however, neighboring colonies may generate feeding currents and reduce flow, conditions known to increase feeding efficiencies in bryozoans, and feeding efficiencies of smaller colonies are especially enhanced (Best and Thorpe 1986; Okamura 1984). Aggregating with siblings may therefore facilitate food intake for colonies from smaller larvae, enhancing their growth at higher densities. For larger larvae, however, the benefits of facilitation may be outweighed by the negative effects of resource depletion at higher densities. Such a scenario may arise if smaller larvae have lower resource requirements than colonies from larger larvae (which seems likely given colonies from larger larvae have larger feeding structures and greater biomass; Pettersen et al. 2015). While our proposed mechanism is speculative, this could explain why larger larvae grew less at higher densities relative to when they were isolated from siblings. Regardless of the mechanism underlying offspring-size-specific density effects, the direction of this interaction in our study contradicts the assumptions of the major MSOS theories, suggesting that sibling competition is unlikely to explain the MSOS correlation in *B. neritina*.

While we found no support for the assumptions of Parker and Begon (1986) or Venable (1992), the positive correlation between maternal size and offspring size may still have an adaptive explanation in *B. neritina*. For example, larger mothers may produce larger larvae to facilitate their dispersal to habitats where they perform best (i.e., in isolation from siblings), whereas smaller mothers may produce smaller, less-dispersive offspring that perform best among siblings. This idea is supported by previous studies showing that relatively larger *B. neritina* larvae typically swim for longer before settlement, and are more likely to access habitats away from siblings (Marshall and Keough 2003, Burgess and Marshall 2011). Phenotype-specific dispersal has been considered in the context of optimal provisioning strategies, and is predicted to maximize maternal fitness under some conditions (e.g., McGinley et al. 1987). However such models are yet to consider whether phenotype-specific dispersal may provide an adaptive explanation for MSOS correlations.

Non-adaptive arguments have also been invoked to explain MSOS correlations. It has been argued that allometric relationships between maternal size and the size of the brood space or reproductive tract may determine offspring size (Congdon and Gibbons 1987). Such an explanation seems unlikely in a colonial organism such as *B. neritina*. Allometric relationships between colony size and ovicell (brood chamber) size are yet to be investigated, but individual module size (lophophore volume) does not appear to be correlated with colony size (Thompson et al. 2015). We argue, therefore, that brood space is unlikely to impose a constraint on offspring size in this species. Instead, we suspect that resource state at the level of the entire colony determines MSOS correlations for *B. neritina*. For example, Sakai and Harada (2001) find that if larger mothers can provision their offspring more efficiently, they should also produce larger offspring. Their model assumes that because larger mothers have larger resource stocks, they can deploy resources more quickly and waste less energy while provisioning offspring. While Sakai and Harada (2001) considered plants specifically, similar arguments could be applied to our system, since offspring provisioning appears to be determined by total colony size and resource state (Marshall and Keough 2004).

In a recent review of competing MSOS models, Rollinson and Rowe (2015) argued that theories that invoke sibling interactions lack empirical support. Our experimental results support this argument, since sibling density did not affect offspring performance in the ways that classic theories assume. Here, we have suggested that the positive MSOS correlation may be driven by selection for phenotype-specific dispersal in *B. neritina*.

Alternatively, theories that invoke differential offspring provisioning efficiencies of different sized mothers (Sakai and Harada 2001) or over-head metabolic costs associated with brooding different sized offspring (Filin 2015, Pettersen et al. 2015) are more general, and could provide a unifying explanation for why larger mothers produce larger offspring (Rollinson and Rowe 2015). Empirical tests of these theories remain a challenging next step in increasing our understanding of why offspring size positively covaries with maternal size across a wide range of taxa.

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