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Offspring Size Plasticity in Response to Intraspecific Competition: An Adaptive Maternal Effect across Life-History Stages

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abstract: When provisioning offspring, mothers balance the benefits of producing a few large, fitter offspring with the costs of decreased fecundity. The optimal balance between offspring size and fecundity depends on the environment. Theory predicts that larger offspring have advantages in adverse conditions, but in favorable conditions size is less important. Thus, if environmental quality varies, selection should favor mothers that adaptively allocate resources in response to local conditions to maximize maternal fitness. In the bryozoan *Bugula neritina*, we show that the intensity of intraspecific competition dramatically changes the offspring size/performance relationship in the field. In benign or extremely competitive environments, offspring size is less important, but at intermediate levels of competition, colonies from larger larvae have higher performance than colonies from smaller larvae. We predicted mothers should produce larger offspring when intermediate competition is likely and tested these expectations in the field by manipulating the density of brood colonies. Our findings matched expectations: mothers produced larger larvae at high densities and smaller larvae at low densities. In addition, mothers from high-density environments produced larvae that have higher dispersal potential, which may enable offspring to escape crowded environments. It appears mothers can

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adaptively adjust offspring size to maximize maternal fitness, altering the offspring phenotype across multiple life-history stages.

Keywords: maternal effects, adaptive phenotypic plasticity, offspring size, dispersal, competition, transgeneration.

The amount of resources a mother provisions her offspring can have dramatic fitness consequences for those offspring throughout their life histories (Bernardo 1996*b*). For organisms that provide no parental care, maternal investment is restricted to prenatal provisioning and can be estimated by offspring size (Clutton-Brock 1991). Across many taxa, larger offspring are fitter than their smaller conspecifics (e.g., in plants [Stanton 1984; Roach and Wulff 1987; Houssard and Escarre 1991], marine invertebrates [Moran and Emlet 2001; Marshall et al. 2003*a*, 2003*b*, 2006], arthropods [Fox and Czesak 2000], reptiles [Sinervo 1990], and fish [Bagenal 1969*a*; 1969*b*; Einum 2003]). Because resources available for reproduction are finite, there is selection for balance between producing a few larger (fitter) offspring and more numerous, smaller (less fit) offspring (Lack 1947; Smith and Fretwell 1974; Lloyd 1987). The optimal balance between offspring size and number depends on the relationship between offspring size and fitness (Smith and Fretwell 1974). Typically, the offspring size/fitness relationship is positive, where larger offspring are fitter, but the slope of the relationship depends on the environment. For example, adverse conditions such as highly competitive environments are predicted to have a steeper offspring size/fitness relationship than more favorable (less competitive) conditions, so a larger offspring size is more beneficial in adverse conditions, and offspring size is less important in favorable environments (Brockelman 1975; Parker and Begon 1986; Lloyd 1987; Sibly et al. 1988; Braby 1994; Tamate and Maekawa 2000; Hendrickx et al. 2003; Marshall et al. 2006). Consequently, mothers should gain fitness benefits by producing a few large offspring in harsh environments and more numerous smaller offspring in relatively benign

environments (Brockelman 1975; Parker and Begon 1986; Fox and Mousseau 1996; Fox et al. 1997; Marshall et al. 2006). Thus, theory predicts that different environments will select for offspring of different sizes and selection should favor mothers that provision offspring according to the environment they are likely to encounter (McGinley et al. 1987; Mousseau and Fox 1998; Marshall et al. 2006). In other words, offspring size is expected to be an adaptive maternal effect.

Maternal effects are expressions of offspring phenotype that arise through an interaction between the maternal genotype and the environment, and their ecological and evolutionary importance is increasingly being recognized (Bernardo 1996*a*; Mousseau and Fox 1998; Agrawal et al. 1999). While it has long been established that environmental change can affect offspring provisioning (Bernardo 1996*b*), there are only a few examples that show this type of maternal effect is adaptive. For example, a few studies have shown that in unfavorable environments where larger offspring carry a fitness advantage, larger offspring are produced (Jonsson et al. 1996; Fox et al. 1997; Hendrickx et al. 2003; Bashey 2006). However, in order to have confidence that a change in offspring size does indeed represent an adaptive response to environmental change, the offspring size fitness function must be estimated in each environment the offspring is likely to encounter. Such estimates are understandably rare, and so our confidence that offspring size plasticity is an adaptive maternal effect remains somewhat limited. In addition, studies examining offspring size and maternal effects under field conditions are also rare despite clear evidence that such tests are crucial for reliable estimations of fitness (Fox 2000).

Like other traits, there are constraints on the evolution of adaptive plasticity and, therefore, constraints on the ability of mothers to produce offspring of optimal size for local conditions (DeWitt et al. 1998; van Kleunen and Fischer 2005). The costs and limitations of phenotypic plasticity have received much attention over the past 3 decades, and there are a number of comprehensive reviews that discuss this topic in depth (Gotthard and Nylin 1995; DeWitt et al. 1998; van Kleunen and Fischer 2005). This study does not attempt to explore all the possible sources of constraints on adaptive phenotypic plasticity but focuses on one that is relevant to organisms with complex life cycles: the adaptive value of a single trait (offspring size) across multiple life-history stages that encounter different environments (Via and Lande 1985). Offspring size can have pervasive effects on fitness, and a size that increases fitness in one life-history stage may reduce fitness in another (Marshall et al. 2002). Thus, if we hope to estimate the relationship between offspring size and fitness for determining the optimal size mothers "should" produce,

then we must estimate offspring size effects across the entire life history.

Sessile marine invertebrates with biphasic life cycles (a planktonic larval stage and a sessile adult stage) provide an excellent opportunity to study offspring size plasticity as an adaptive maternal effect under field conditions. Both stages encounter two very different environments (Vance 1973), and offspring size can affect fitness in both (Marshall and Keough 2003*b*; Marshall et al. 2003*b*, 2006). In the larval phase, offspring size affects dispersal potential: larger larvae swim for longer in the plankton and are more likely to reject poor-quality habitats for settlement (Marshall and Keough 2003*b*; Gribben et al. 2006). Offspring size is correlated with condition, and organisms in better condition are more likely to reject poor habitats (Stamps 2006). After settlement, offspring size affects survival, growth, resistance to competition, and reproduction (Marshall and Keough 2003*a*, 2006; Marshall et al. 2003*b*, 2006). These pervasive effects of offspring size greatly complicate selection acting on offspring size and raise some important questions: do mothers optimally provision their young when maternal provisioning can have effects across multiple life-history stages, and if so, what changes in the environment elicit changes in maternal provisioning?

One of the most common and important environmental parameters that can change across small spatial scales in the marine environment is the density of conspecific juveniles/adults (Underwood and Keough 2001). High conspecific densities directly reduce the availability of food and space (Creighton 2005), greatly reducing postsettlement success (e.g., Marshall and Keough 2003*a*). Importantly, previous studies show that the benefits of increased offspring size can depend on the density of conspecifics: larger offspring tend to have an advantage when intraspecific competition is present (Marshall and Keough 2003*a*; Marshall et al. 2006). Thus, if the maternal environment is a good predictor of offspring postsettlement environment, then we would expect mothers under high levels of competition to produce larger offspring that are better able to escape the harsh competitive conditions and/or better able to cope with high levels of competition. This form of transgenerational plasticity has rarely been explored in a marine organism (but see Jonsson et al. 1996). Here we first examine the relationship between offspring size and performance across multiple environments in the field and then determine whether mothers adaptively adjust the size of their offspring according to their own environment. Using the marine bryozoan *Bugula neritina*, our objectives were to (1) investigate the relationship between larval size and fitness at different levels of intraspecific competition, measuring postmetamorphic survival and subsequent colony size under field conditions as estimates of fitness; (2) determine whether mothers expe-

riencing different levels of competition differentially allocate resources to their offspring; and (3) investigate whether larval dispersal potential changes when mothers experience different levels of competition.

Material and Methods

General Methods

Study Species. *Bugula neritina* is an arborescent bryozoan found in sessile marine communities worldwide and is an invasive species in Australia (Hewitt et al. 2004). Colonies grow by asexual budding of zooids to form branches, and each branch bifurcates at regular intervals. The number of bifurcations in a colony is proportional to the number of zooids per colony and is thus a good estimate of colony size (Keough and Chernoff 1987).

Reproductively active colonies retain the zygote throughout embryogenesis inside modified zooids called ovicells. Here, the embryo receives nutrients via a placenta-like system that results in a 500-fold increase in size from egg to larvae (Woollacott and Zimmer 1975). Embryogenesis takes approximately 1 week, and thus mothers can increase or reduce the amount of resources embryos receive. Importantly, previous studies show that offspring size is a plastic trait in *B. neritina* (Marshall and Keough 2004). The released larvae are capable of immediate settlement and when provided with a suitable substratum typically settle within 2 h, most within 15 min (Keough 1989*a*; Marshall and Keough 2003*b*). Therefore, Australian *B. neritina* larvae exhibit a limited ability to disperse, and the natal environment is likely to reflect the maternal environment (although this depends on the scale of environmental variation).

Like all bryozoans, adult *B. neritina* are suspension feeders that actively filter microplankton from the water column. In other *Bugula* species, increasing the density of conspecifics directly reduces the amount of available food in the water column and therefore reduces colony feeding success (Okamura 1984).

Study Site. All collections and experiments were conducted at the privately owned floating docks of the East Coast Marina, Manly (153°10′59″S, 27°28′01″E), Queensland, from April to October 2006. A breakwater and additional floating docks protect the marina from weather extremes and wave action from Moreton Bay. The sessile marine community is typical of that inhabited by *B. neritina*, and densities of *B. neritina* recruits range from <1 colony/m^2 to approximately 150 colonies/m^2 (R. M. Allen, unpublished data).

Larval Collection, Spawning, and Settling. Adult colonies of *B. neritina* were taken from the floating docks approximately 1 m below the water surface. They were transported to the laboratory in thermally insulated tanks and then placed into dark tanks with fresh seawater and held there for 24 h. To collect larvae, we used standard light shocking techniques (e.g., Marshall et al. 2003*b*): in short, colonies were removed from dark tanks, placed in a glass beaker, and exposed to bright light. In each spawning event, approximately 50 colonies were spawned, releasing >2,000 competent larvae. Larvae were released from ovicells within 15 min of light exposure and were extracted with a pipette. Larvae were allocated to their experimental treatments within an hour of being spawned. As appropriate to different experiments, some larvae were measured at this point (see experiment 1), while others were allowed to settle immediately. Larvae were settled on roughened petri dishes (90 mm in diameter) that also had a biofilm to encourage settlement (Marshall and Keough 2003*b*). Larvae were placed into dishes with 20 mL of seawater and allowed to settle in darkness at a constant temperature (20°C) for 24 h, unless otherwise stated. Settlement success was approximately 95%, and any unsettled larvae were discarded. Once settled, larvae were individually marked and identified by circling and labeling them with a graphite pencil. This distinguished our focal settlers from unmeasured settlers and natural settlement in the field.

Measuring Larvae. Larvae were measured using standard techniques developed for *B. neritina* (Marshall et al. 2003*b*). Larvae were placed in a drop of seawater and digitally photographed with the cilial groove facing the camera (PixeLINK Capture SE, ver. 1.0) and parallel to the horizon. Larval cross-sectional area, a good predictor of larval volume (Marshall et al. 2003*b*), was then estimated with Image Pro Express, version 5.1, to the nearest square micrometer.

Field Protocols. To deploy our experimental units (petri dishes with settled larvae attached) into the field, we drilled a 5-mm hole in the center of each dish and then bolted the dishes to 500 × 500 × 8-mm gray PVC backing plates. Each backing plate contained four petri dishes, and treatments were randomly assigned to backing plates.

For a number of our experiments, we manipulated the density of *B. neritina* colonies (see experiments 1 and 2), and because we were unsure of the relevant scale at which density would have effects, we varied density at two scales simultaneously: at the scale of settlers within petri dishes and at the scale of petri dishes within backing plates. We varied density within petri dishes by simply manipulating the number of larvae that we settled in each dish. For backing plates, we altered the arrangement of dishes on backing plates. For plates that were assigned as high density (see

experiments 1 and 2), dishes were concentrated in the middle of the plates, and low-density dishes were located in each corner of the plates to provide maximum distance from each other. Plates were hung 1 m below the surface, facing down to reduce the effects of sedimentation. Throughout our experiments we scraped away newly settled fouling organisms with a scalpel blade every week. While organisms did settle between scrapings, their growth was not sufficient in a week that they represented a major source of competition.

Experiment 1: Relationship between Offspring Size and Performance under Different Levels of Competition

We examined the relationship between offspring size and subsequent performance in a number of different competitive environments. In the first phase of this experiment, we examined the relationship between offspring size and performance in two environments: in the absence of competition and in the presence of competition from newly settled recruits. In the second phase, we examined the relationship between offspring size and performance in two other environments: in the presence of a single adult conspecific competitor and in the presence of many adult conspecifics. These two phases represent the range of conspecific competition that *B. neritina* is likely to encounter, both from contemporary settlers and from established adults.

Postmetamorphic survival and adult colony size were the two measures of performance used in our study. Together, they are a good predictor of fitness in *B. neritina* (Marshall et al. 2003*b*; Marshall and Keough 2006). Survival was determined by the presence or absence of the marked individual. If an individual was absent it was assumed to be dead because detached colonies are unlikely to survive in soft benthic substrate. This procedure is frequently used to estimate mortality (e.g., Keough 1986, 1989*a*). Adult colony size was measured as the number of times a focal colony bifurcated, along the longest branch. This measure is a good indicator of overall colony size, and colony size is strongly related to reproductive output (Keough 1986, 1989*b*; Marshall et al. 2003*b*).

Experiment 1a: Effect of Offspring Size on Postmetamorphic Performance in the Presence and Absence of Contemporary Recruits. The goal of this experiment was to estimate the relationship between larval size and postmetamorphic performance in environments of no competition and high intraspecific competition. Thirty-two larvae were measured, settled, and marked in individual dishes as described above. To manipulate density of settlers in the petri dishes, approximately 20 larvae were added to the high-density treatment, and no extra larvae were added to the no-competition treatment. The 32 dishes were bolted to eight backing plates and deployed into the field. After the first week, the number of colonies per dish in the high-density treatment was reduced to 10 (one focal colony and nine competitors). This procedure allowed us to maintain constant density across replicates and represents typical density of this species found in the local habitat (R. M. Allen, personal observation). The survival and size of the focal colonies were then recorded after 6 weeks in the field. The experiment was repeated, beginning 1 week after the initiation of the first. Thus, the experimental design had two runs, with 64 larvae total (32 larvae per run).

Experiment 1b: Effect of Offspring Size on Postmetamorphic Performance in High and Low Levels of Competition from Adults. We examined the relationship between larval size and postmetamorphic performance in the presence of high and low densities of *B. neritina* adults. Adult colonies were grown in the field from laboratory-settled larvae as described above, and after 3 weeks in the field, their densities were reduced to one and nine adults per petri dish for the low- and high-density treatments, respectively. To keep size constant both within and between treatments, only colonies that had bifurcated five or six times were retained. Focal larvae were then measured, settled, and marked in these dishes as described above. We deployed 32 dishes on eight backing plates into the field as described above. The survival and size of the focal colonies were recorded after 6 weeks in the field.

Experiment 2: Influence of Maternal Environment on Offspring Phenotype

We examined how the competitive environment that mothers experience in the field affects the provisioning of their offspring. We created two treatments in the field, high-competition and low-competition environments, and then spawned the colonies from these treatments in the laboratory to examine the phenotype (size and dispersal potential) of larvae that were produced. Our earlier experiments showed that the relationship between offspring size and performance was strongly affected by the intensity of intraspecific competition (see "Results"), and so the two environments were chosen to elicit phenotypic extremes. To create the environments, approximately 40 and 10 larvae were placed in petri dishes in the laboratory to create the high- and low-density treatments, respectively. Initial numbers of settlers per dish were high to account for attrition once the dishes were deployed into the field. We then left the plates in the field to grow for 5 weeks. After the first week, the number of individuals per dish was reduced to the desired experimental levels of 10 (nine

competitors and one focal colony) for high density and one focal colony with no competitors for low density. Initially there were 48 high-density dishes and 32 low-density dishes.

Colony size can affect larval size in *B. neritina* (Marshall et al. 2003*b*; Marshall and Keough 2004). Our density treatment was predicted to affect colony size, potentially confounding our treatment of interest, so we needed to control for potential colony size effects on larval provisioning. Embryogenesis in *B. neritina* takes place in approximately 1 week (Marshall and Keough 2004), and so a week before returning the focal colonies to the laboratory, we switched treatments for half of the high- and half of the low-density treatments. By switching half of each treatment 1 week before spawning, we could manipulate maternal environment independent of colony size. Therefore, the experiment had four treatments (fig. 1): high → high, low → low, high → low, and low → high, where the former word indicates the density that the colony started in and the latter word indicates the treatment the colony was in for the final week of the experiment (for brevity, the treatments that were not switched will be referred to as the high and low treatments). The low → high treatment was achieved by cutting a small section of petri dish that a low-density colony was attached to and gluing this piece to a small cleared section on a high-density donor dish. A nonfocal colony was also removed from this treatment to keep all high-density treatments at a constant 10 colonies per dish (one transplanted focal colony and nine competitors). The shift from a low density to a high density of adults is probably an unlikely event under natural conditions, but this was required for a control. The high → low treatment was achieved by removing all but one colony from 16 high-density dishes. This drop is probably more common under natural conditions whereby some colonies experience mortality, leaving only a few behind. Each treatment had four backing plates with four dishes on each. The colonies were left in the field for 1 week after the controls had been created.

Experiment 2a: Effect of Maternal Density on Larval Size. A week after the creation of controls (which was 5 weeks after the experiment had begun), we returned the colonies to the laboratory and spawned the focal colonies from each dish in individually marked cups. A maximum of 10 larvae from each colony were fixed in 5-mL vials containing seawater and two drops of formalin (12%; fixing in formalin has no effect on *B. neritina* larval size; Marshall et al. 2003*b*), the larvae were measured, and the mean larval size for each colony was used for analysis. Two runs of this experiment were completed. Initially, the number of focal colonies was 64 in each run, but as a result of some loss of colonies, this number was reduced.

Experiment 2b: Effect of Maternal Density on Larval Dispersal Potential. To test the effect of maternal density on dispersal potential, the above manipulation of the maternal environment was repeated, but for this experiment, mean larval swimming duration was measured instead of size. The time a larva takes to settle is a proposed proxy for the dispersal of lecithotrophic larvae (Grantham et al. 2003; Marshall and Keough 2003*b*; Shanks et al. 2003).
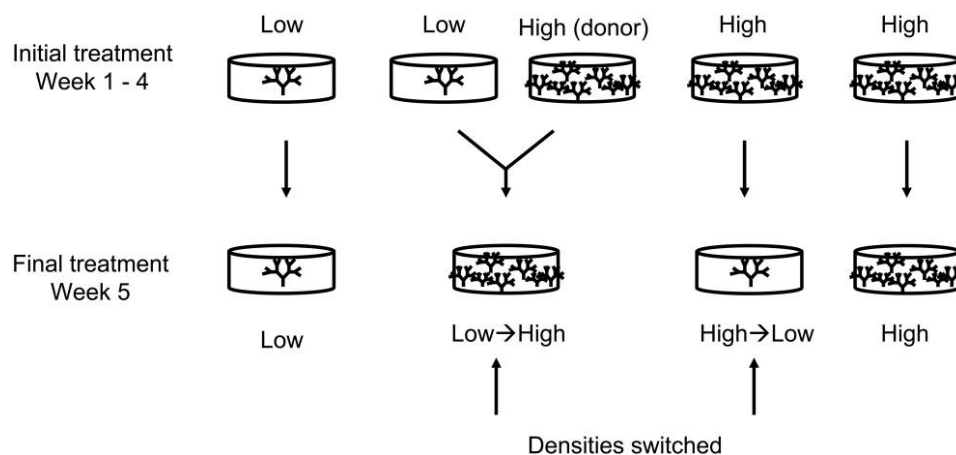

Figure 1: Experimental design for the effect of maternal density on larval size in *Bugula neritina*. For the first 4 weeks of the experiment there were 32 low- and 48 high-density petri dishes. For the final week of the experiment, 16 low-density colonies were transplanted into 16 high-density dishes (donor dishes), becoming the low → high treatment. Also at this time, 16 high-density dishes were reduced from 10 colonies/dish to one colony/dish, becoming the high → low treatment. The densities in the remaining 16 high- and 16 low-density dishes were kept constant for the duration of the experiment.

After colonies were spawned, approximately 10 larvae from each maternal colony were placed in roughened petri dishes (dish was the unit of replication). We checked the settlement of larvae every hour for 3 h after release. A larva was deemed settled if it was attached to the dish surface and could not be removed by a gentle jet of water from a pipette.

Data Analysis

Data were analyzed using SYSTAT (ver. 11). In all of our analyses, we used density as a fixed factor and experimental run and backing plate as random factors. All data were checked and met the assumptions for the appropriate statistical analysis, with transformation where necessary, unless otherwise stated. In experiment 1, larval size was treated as a continuous factor, and in experiment 2, colony size was treated as a continuous factor.

The effect of larval size and conspecific density on survival was examined using logistic ANCOVA (alternatively termed a generalized linear mixed model). For this analysis, we treated larval size as the covariate and density as a categorical factor. Experimental run and backing plate(run) were treated as random factors. There was no effect of backing plate in either experiment, and it was removed from the final model (table A1 in the online edition of the *American Naturalist*). Other nonsignificant terms in experiment 1a were also omitted from the final model (table A1; for a description of model reduction procedures for nonbiological units of experimental convenience, see Quinn and Keough 2002).

The effect of larval size and conspecific density on subsequent colony size was examined with ANCOVA, where larval size was a covariate, conspecific density was a categorical factor, and experimental run and backing plate(run) were random factors. There was no effect of backing plate in either experiment (table A1), so it was omitted from the model. There was also no effect of or any interactions between the treatments of interest and run (table A1), so they were also omitted from the final model.

The effect of maternal colony density on larval size was examined with ANCOVA. Backing plate was nested within each of the four treatments and treated as a random factor. Backing plate had no effect on larval size and was omitted from the final model, and there were no interactions between run and the treatments of interest, so these were also removed (table A1). We used a Tukey pairwise-comparisons post hoc analysis to determine differences among treatments.

To examine the effect of maternal colony density on larval dispersal potential, we first tested whether maternal colony size had any effects, using ANCOVA, where colony size was a covariate. However, this was not significant, nor, more important, was there any interaction with density (table A1), and so maternal colony size was omitted from the final model. Thus, we examined the effect of maternal colony density on larval dispersal potential with a nested ANOVA where backing plate was nested within treatment. We arcsine–square root transformed the response variable because it was proportion data. Our earlier experiments on the effects of maternal colony density on offspring size suggested that the "switch" treatments were an unnecessary precaution. The switch treatments had been conducted to guard against any systematic differences in colony size between the different density treatments, but our experiments on larval size showed that there were no differences in colony size among treatments (see "Results"). Thus, for simplicity, we pooled the treatment groups into low and high density, depending on what treatment they had experienced for the final week in the field. This was a conservative step because it added more variation to the within-group estimates, making it less likely to detect any weak effects.

Results

Experiment 1: Relationship between Offspring Size and Performance in Different Competition Environments

Experiment 1a: Effect of Offspring Size on Postmetamorphic Performance in the Presence and Absence of Contemporary Recruits. After 6 weeks in the field, our focal settlers had slightly higher survivorship in the absence of competition from other recruits than settlers in the presence of competition from other recruits (82% vs. 73%), but this difference was not significant ($\chi^2 = 2.247$, $P = .134$). Furthermore, there was no effect of offspring size on subsequent survival ($\chi^2 = 0.005$, $P = .943$), nor was there an interaction between competition and offspring size on survival ($\chi^2 = 2.149$, $P = .143$). There was, however, an interaction between run and offspring size; in the first run, survival in the field was correlated with offspring size, but in the second run (where there was a narrower range of offspring sizes), there appeared too little to no effect (table A2 in the online edition of the *American Naturalist*).

After 6 weeks in the field, the different levels of intraspecific competition strongly affected the relationship between offspring size and colony size (table 1). In the absence of competition, offspring size had only a weak effect on subsequent colony size, with all colonies reaching at least seven bifurcations (offspring size–colony size relationship: $R^2 = 0.039$; fig. 2; table 1, "Experiment with no competition versus high recruit competition"; table A3 in the online edition of the *American Naturalist*). In contrast,

there was a much stronger relationship between offspring size and colony size when settlers faced higher levels of competition from contemporary recruits (offspring size–colony size relationship: $R^2 = 0.363$; fig. 2; table 1, "Experiment with no competition versus high recruit competition"). Under high competition, colony sizes were smaller overall (relative to competition-free colonies; table A3), and doubling larval size from 40,000 to 80,000 μm^2 yielded an increase in final colony size from four to seven bifurcations, which results in approximately eight times more zooids (calculated from the relationship between the number of zooids and bifurcations; see Keough and Chernoff 1987).

Experiment 1b: Effect of Offspring Size on Postmetamorphic Performance in High and Low Levels of Competition from Adults. In our experiment examining the effect of adult density, survival to 6 weeks in the field again appeared to differ between the density treatments, with 82% of colonies surviving in the low-density treatment and 69% of colonies surviving in the high-density treatment, but this difference was not statistically significant ($\chi^2 = 0.738$, $P = .391$). However, in this experiment, colonies from larger larvae were more likely to survive for 6 weeks than colonies from smaller larvae ($\chi^2 = 4.277$, $P = .039$). This positive effect of offspring size on colony survival was independent of adult densities, as indicated by a nonsignificant interaction between offspring size and density treatment ($\chi^2 = 0.398$, $P = .528$).

High densities of conspecific adults had a strong negative effect on subsequent colony size (fig. 3; table A3); at high adult densities no focal colonies exceeded three bifurcations, but at low adult densities most colonies had more than six bifurcations (a difference in zooids of more than eight times). There was a strong interaction between
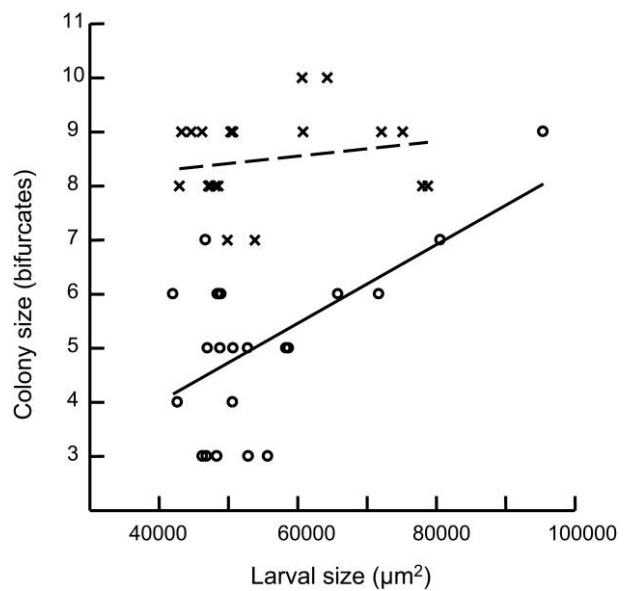

Figure 2: Effect of larval size and conspecific, contemporary recruit density on colony size after 6 weeks in the field for *Bugula neritina*. Crosses and dashed line represent no competition ($R^2 = 0.039$); circles and solid line represent focal individual competing with nine recruits of the same age. The solid line is the line of best fit ($R^2 = 0.363$) for the competition treatment. Each point represents one colony. Larval size is the cross-sectional area. Colony size was measured as the number of bifurcations along the longest branch.

offspring size and the density of adult competitors, but the nature of this interaction differed from that of the previous experiment (table 1, "Experiment with high versus low adult density"). Adult density had a converse effect (relative to that of the previous experiment) on the relationship between offspring size and subsequent colony size

Table 1: ANCOVA testing the effect of larval size and level of competition on colony size for *Bugula neritina* after 6 weeks in the field

Source	df	MS	F	P
Experiment with no competition versus high recruit competition:				
Larval size	1	22.301	19.793	<.001
Density	1	11.834	10.502	.002
Density × larval size	1	5.558	4.933	.032
Error	41	1.127		
Experiment with high versus low adult density:				
Larval size	1	2.565	1.95	.178
Density	1	.006	.005	.947
Density × larval size	1	11.587	8.808	.008
Error	20	1.316		

Note: Model was reduced after no significant effect of backing plate, run, or run interactions was found; see "Material and Methods."
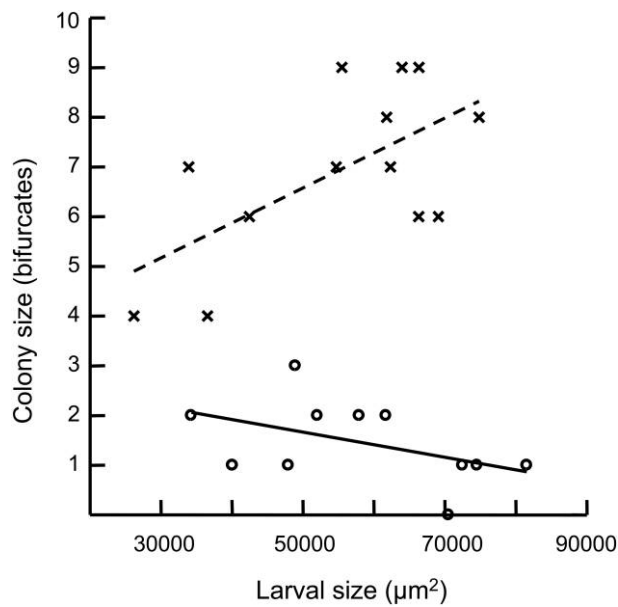
Figure 3: Effect of larval size and conspecific density on colony size after 6 weeks in the field for *Bugula neritina*. Crosses and dashed line represent focal individual competing with one adult colony, and dashed line is the line of best fit ($R^2 = 0.397$). Circles and solid line represent focal individual competing with nine adult colonies ($R^2 = 0.22$). Each point represents one colony. Larval size is the cross-sectional area. Colony size was measured as the number of bifurcations along the longest branch.

after 6 weeks in the field. While the presence of contemporary competitors increased the effect of offspring size on colony size in the previous experiment, the presence of adult competitors obscured any relationship between offspring size and colony size in this experiment. At low adult densities, there was a strong, positive relationship between offspring size and final colony size ($R^2 = 0.397$, $P < .05$; fig. 3), but there appeared to be no relationship between offspring size and colony size at high adult densities ($R^2 = 0.220$, $P > .05$; fig. 3). Across the range of offspring sizes in this experiment, at low adult densities, increasing larval size from 30,000 to 75,000 μm^2 yielded approximately eight times more zooids (from five to eight bifurcations) after 6 weeks (calculated from the relationship between the number of zooids and bifurcations; see Keough and Chernoff 1987).

Experiment 2: Influence of Maternal Environment on Offspring Phenotype

Experiment 2a: Effect of Maternal Density on Larval Size. Our concerns regarding the effects of density on maternal colony size appeared to be largely unfounded—the sizes of colonies in the various treatments were rela-

tively similar (table A4 in the online edition of the *American Naturalist*) and suggested that our various "switching" treatments were unnecessary precautions. The competitive environment experienced by mothers strongly affected the size of the offspring they produced. Mothers that experienced low density for the entire 5 weeks in the field produced larvae that were, on average, 10,641 μm^2 (13.75%) smaller than larvae from mothers that were in high density for the same period (fig. 4; table 2). The switch treatments where mothers experienced high density for at least 1 week resulted in mothers producing offspring that were significantly larger than those in the low-density treatment but were not significantly different from those in the high-density treatment (fig. 4; table 2; table A5 in the online edition of the *American Naturalist*).

Experiment 2b: Effect of Maternal Density on Larval Dispersal Potential. For the first hour after release, most of the larvae were swimming regardless of the experimental treatment their mothers had experienced. After 2 h, there was a strong effect of the environment that mothers experienced on the dispersal potential of their offspring. Larvae from mothers that had experienced high densities were more likely to be swimming than larvae from mothers that had experienced low densities (table 3, "After 2 h"; fig. 5*a*). However, after 3 h, the effect of maternal experience on larval dispersal potential had diminished, and while
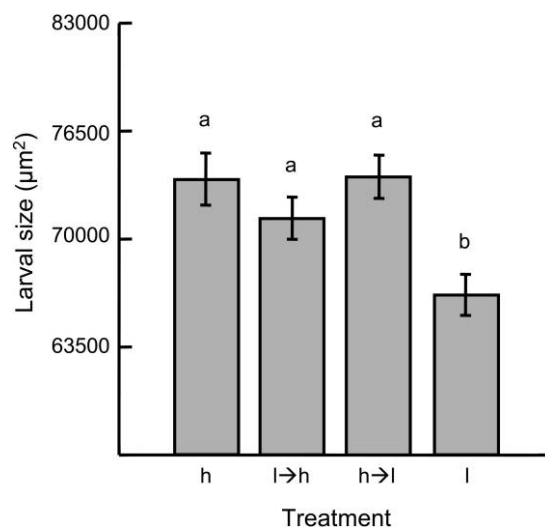

Figure 4: Mean larval size produced by maternal colonies of *Bugula neritina* at high (*h*) and low (*l*) density and colonies that were switched from low to high ($l \rightarrow h$) and high to low ($h \rightarrow l$) density during the final week of the experiment. Bars with the same letter above indicate results that are not significantly different. Error bars are $\pm$ SE. Larval size is the cross-sectional area.

Table 2: ANCOVA testing the effect of maternal density, maternal colony size, and experimental run on larval size for *Bugula neritina*

Source	df	MS	*F*	*P*
Density	3	199.428	6.03	<.001
Maternal colony size	1	16.273	2.067	.246
Run	1	420.687	12.538	.001
Error	74	33.552		

Note: Model was reduced after no significant effect of backing plate, density × run, treatment × run × maternal colony size, run × maternal colony size, or treatment × maternal colony size was found; see "Material and Methods." Maternal density was high, low, or switched from low to high or high to low. Maternal colony size was measured in bifurcations.

there was a trend similar to that at 2 h, it was marginally nonsignificant (table 3, "After 3 h"; fig. 5*b*).

Discussion

Offspring size appears to be a remarkably adaptive plastic trait in *Bugula neritina*. We found that the relationship between offspring size and performance strongly depends on the intensity of intraspecific competition that offspring experience, and mothers differentially provision their offspring according to the likely environment their offspring will encounter.

Effect of Larval Size on Postmetamorphic Performance in Four Different Competition Environments

The relationship between offspring size and postmetamorphic growth depended strongly on the local competitive environment. In the absence of competition, we could not detect a relationship between offspring size and postmetamorphic performance, with colonies growing well regardless of their size as larvae. In contrast, when our focal colonies were in competition with many recruits or a single adult, there was a strong relationship between offspring size and postmetamorphic colony size. These results agree with previous empirical and theoretical studies showing that the benefits of larger offspring are increased in harsher conditions (Brockelman 1975; Parker and Begon 1986; Lloyd 1987; Sibly et al. 1988; Braby 1994; Tamate and Maekawa 2000; Hendrickx et al. 2003; Marshall et al. 2006). What was unexpected in our study was that at high adult densities (the environment in which growth was poorest overall) there was no (or at least very little) relationship between offspring size and postmetamorphic colony size; all colonies grew relatively poorly regardless of their original size as larvae. Clearly the hypothesis that larger offspring are fitter under competitive conditions is more complex than previous studies suggest. In very be-

nign environments (i.e., no competition), offspring size has no effect on offspring performance, and maternal fitness is increased by producing the maximum number of (very small) offspring. In intermediate environments (in our case, competition from recruits or a single adult), offspring size has a strong effect on offspring performance, and thus maternal fitness is maximized by producing larger offspring. However, when conditions are very harsh, offspring size no longer confers a strong advantage (although larger offspring still had a survival advantage in our experiments), and maternal fitness is maximized by producing offspring that are smaller than those that are optimal at intermediate levels of competition. Thus, the relationship between the predicted size of offspring that will maximize maternal fitness and environmental quality is not linear as previously thought but is more likely to be hyperbolic, with smaller offspring sizes being favored at the two extremes of environmental quality (fig. 6). Such a concept was briefly mentioned by Brockelman (1975) in his theoretical considerations of offspring size and again by Sibly and Calow (1989). If true, this may explain why mothers respond to some stresses by reducing offspring size (Bayne et al. 1979; Marshall and Keough 2004) but increase offspring size in response to other stresses (Krug 1998; Hendrickx et al. 2003; Marshall and Keough 2006). Previously, this variability has been attributed to the type of stress that mothers experience, but equally, it could be due to the intensity of the stress (Marshall and Keough 2007).

Influence of Maternal Environment on Larval Phenotype

In *B. neritina*, the benefits of producing offspring of a certain size appear to be highly context dependent. When conditions are good, mothers should produce smaller off-

Table 3: ANCOVA testing the effect of maternal density on the number of *Bugula neritina* larvae swimming after 2 and 3 h

Source	df	MS	*F*	*P*
After 2 h:				
Treatment	1	1.605	4.653	.049
Backing plate(treatment)	14	.345	2.586	.007
Error	48	.133		
After 3 h:				
Treatment	1	1.069	4.453	.053
Backing plate(treatment)	14	.24	2.16	.026
Error	45	.111		

Note: Model was reduced after no significant of maternal colony size or treatment × maternal colony size was found at either time; see "Material and Methods." Maternal density was pooled into high or low based on the density experienced during the final week. Maternal colony size was measured as the number of bifurcations.
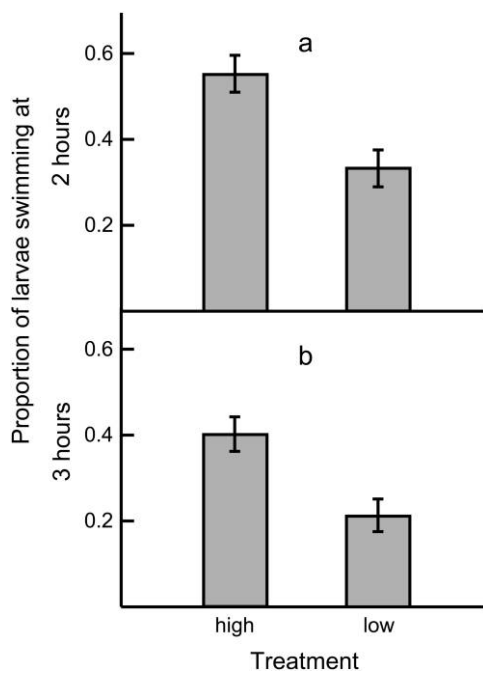
Figure 5: Effect of manipulating high and low maternal colony density in the field on the dispersal potential for *Bugula neritina* larvae under laboratory conditions. The graphs indicate the proportion of larvae that were swimming after (*a*) 2 h and (*b*) 3 h.

Switched colonies (high → low and low → high treatments) produced large larvae that did not differ in size from larvae from colonies that experienced high densities throughout the experimental period. The increase in larval size for low → high colonies suggests that maternal experience during the week preceding the release of offspring is an important factor in determining the provisioning of offspring. However, brood colonies that experienced a high → low switch did not reduce the size of their offspring as would be expected, and the reason for this lack of an effect is unclear. *Bugula neritina* colonies can reduce the provisioning of their offspring in response to other environmental cues (Marshall and Keough 2004), and so there is no physiological explanation for the absence of a size change. The switch in environments may constitute a signal to the mothers that the environment is unpredictably variable. Under such conditions, some theoretical studies suggest that producing better-provisioned offspring is a strategy for buffering offspring from environmental change (Einum and Fleming 2004). While the differential effects of the switch treatments were interesting, our overall finding was that the maternal competitive environment strongly affects offspring size. Importantly, the effect of maternal environment on offspring size was in the same direction as one would expect if mothers were adaptively provisioning their offspring in order to better deal with increased competition themselves. However, while it is tempting to view the increase in offspring size as an adaptive response to likely postmetamorphic environment, the pervasive nature of offspring size effects in marine invertebrates mean that we cannot rule out other explanations for the change in offspring size.

In a wide variety of taxa, when conditions degrade, mothers produce more dispersive offspring that are more likely to escape the poor-quality conditions (Dixon 1998; Mandak and Pysek 1999, 2005; Krug 2001). Throughout our study, competition generally reduced postmetamorphic performance; therefore, if the maternal environment is a good predictor of the offspring environment, mothers may be favored by producing larvae that are more likely to disperse out of that poor environment, and, indeed, this is what we found. In *B. neritina*, larger larvae swim for longer than smaller larvae and are more likely to reject low-quality settlement sites (Marshall and Keough 2003*b*), and in this study, larvae from mothers that had experienced high competition were larger and remained planktonic for longer in the laboratory. Planktonic duration is strongly correlated with dispersal potential in marine invertebrates (Grantham et al. 2003; Shanks et al. 2003), and thus larvae from mothers that experienced competition had greater dispersal potentials than larvae from mothers that experienced little competition. Stamps
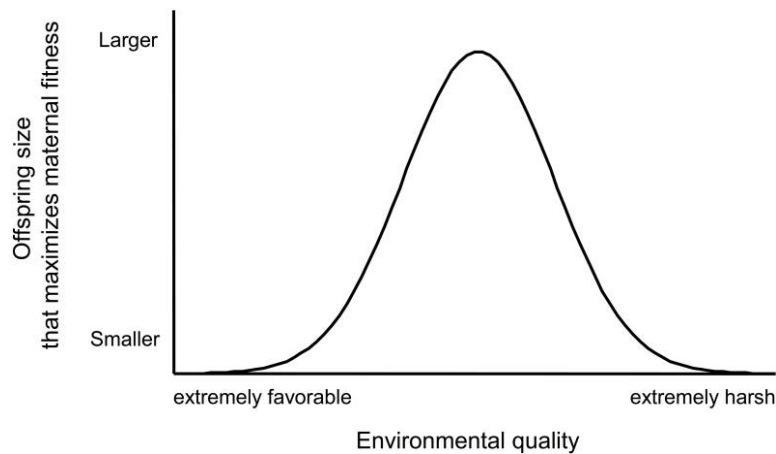
spring; when conditions are moderately bad, mothers should produce larger offspring; when conditions are very poor, mothers should again produce smaller offspring. Thus, if the maternal experience regarding the competitive environment is a good predictor of the likely offspring environment, we would expect mothers to increase the size of their offspring under conditions of higher competition (i.e., exhibit adaptive transgenerational plasticity). We did observe such an increase in the size of offspring: when mothers experienced competition, they produced larger offspring, strongly suggesting that offspring size is an adaptive maternal effect in *B. neritina*. Such effects have been observed in terrestrial studies (Fox et al. 1997), but this is one of the first that has conclusively demonstrated an adaptive effect in a marine system (but see Jonsson et al. 1996; McCormick 2006).

Our manipulation of the maternal environment included two controls where mothers were switched from their environment in the final week before offspring were released. This was a conservative strategy that proved unnecessary because the brood colonies experiencing different levels of competition did not differ significantly in size (table A4). However, this experiment revealed some interesting aspects regarding the nature of transgenerational plasticity in offspring size in *B. neritina*.

Figure 6: Relationship between the predicted offspring size that will maximize maternal fitness and environmental quality. At the extremes of environmental quality, offspring size has little effect. In extremely favorable environments, all offspring perform well regardless of size. In extremely harsh environments, all offspring perform poorly regardless of size. In both situations, mothers should produce smaller offspring in favor of fecundity. In intermediate levels of environmental quality, size is positively correlated to performance. Here, mothers should increase offspring size to increase offspring performance, thus increasing maternal fitness. We use a normal probability distribution for ease and clarity to illustrate the point.

(2006) outlined the "silver-spoon effect," where dispersing organisms in better condition are more likely to settle in favorable conditions. It would be interesting to see whether *B. neritina* exhibits silver-spoon behavior with regard to conspecific competition.

It is difficult to disentangle what selection factors are driving the observed increased in offspring size. If mothers are producing larger offspring so that they are more likely to escape poor-quality environments, then the increased competitive ability of offspring from high-density mothers is simply a side effect of the increase in size. Alternatively, the increased dispersal potential may be a side effect of increasing the competitive ability of offspring. Or, finally, the benefits of increased dispersal potential and competitive ability could both be driving the increase in size. For this last hypothesis, we suggest that the presence of such strong offspring size plasticity in *B. neritina* is due to selection pressures in two very important life stages on a single trait. These pressures may vary in strength, but at the very least, selection for a given offspring size in one life stage is not countered in the other. Ultimately, distinguishing among these explanations requires more knowledge regarding the scale of larval dispersal and the scale of clumping of competition in *B. neritina*. Increasing the dispersal potential of offspring is likely to carry a benefit only if the increase exceeds the scale at which high-competition clumps occur. Interestingly, extending the swimming period of *B. neritina* larvae decreases the advantages of increased offspring size, potentially nullifying any competition advantage (Marshall and Keough 2006). Thus, we suspect that the observed increase in offspring

size under higher densities is principally an escape response rather than a competition response.

Regardless of whether there is an underlying adaptive explanation for the increase in offspring dispersal potential, this maternal effect can lead to changes in the ecological function of populations. Fowler (2005) produced a theoretical model for dispersing organisms that showed that maternal effects on offspring dispersal can have complex outcomes on population dynamics. In the absence of maternal effects, Fowler (2005) predicted populations to fluctuate chaotically; however, increasing the strength of maternal effects produced a simplified cyclic population dynamic. In *B. neritina*, low-density populations would seem more likely to be self-recruiting in that larvae would be smaller and have poorer dispersal potentials, but as the population density increases, the breeding colonies would become more likely to produce offspring that dispersed out of the population. As offspring were dispersing from a high-density population, the local population would return to low density, and the cycle would repeat.

The significance of adaptive maternal effects as both an ecological and evolutionary driving force is becoming increasingly clear (Roach and Wulff 1987; Gliwicz and Guisande 1992; Fox et al. 1997; Mousseau and Fox 1998; Agrawal et al. 1999; Hendrickx et al. 2003; Bashey 2006). Here, *B. neritina* mothers change the phenotype of their offspring in two life-history stages. This study highlights the complex nature of maternal effects in organisms with complex life cycles and the pervasive nature of offspring size effects. Because offspring size affects both life-history

stages, by manipulating this single trait, mothers can produce offspring that are not only more likely to escape poor conditions but also better able to perform in those poor conditions. Offspring size is a surprisingly dynamic and adaptive trait in marine invertebrates, and we look forward to further studies examining how other environmental factors affect provisioning in this group.

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