Complex life cycles and offspring provisioning in marine invertebrates

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Synopsis Offspring size can have pervasive effects throughout an organism's life history. Mothers can make either a few large or many small offspring, and the balance between these extremes is determined by the relationship between offspring size and performance. This relationship in turn is thought to be determined by the offspring's environment. Recently, it has become clear that events in one life-history stage can strongly affect performance in another. Given these strong carryover effects, we asked whether events in the larval phase can change the relationship between offspring size and performance in the adult phase. We manipulated the length of the larval period in the bryozoan *Bugula neritina* and then examined the relationship between offspring size and various parameters of adult performance under field conditions. We found that despite the adult stage being outplanted into identical conditions, different offspring sizes were predicted to be optimal, depending on the experience of those adults as larvae. This work highlights the fact that the strong phenotypic links between life-history stages may result in optimal offspring size being highly unpredictable for organisms with complex life cycles.

Introduction

The level of maternal investment an organism receives can have dramatic consequences throughout its life history (Bernado 1996). In marine organisms, maternal investment is largely restricted to provisioning the gamete or embryo and as such offspring size is viewed as approximating maternal investment. In a growing list of species, offspring size can have strong, pervasive effects on subsequent performance across a range of marine taxa and appears to be a major source of carryover effects (Hart 1995; Moran and Emlet 2001; McCormick 2003; Marshall and Keough 2005) in marine organisms. Generally, larger offspring perform better than smaller conspecific larvae during at least one life-history stage (Levitan 1996a; Gimenez and Anger 2001; Marshall and others 2003; Marshall and Keough 2003c). The benefits of producing larger, fitter offspring, however, are not without costs—larger offspring are thought to be more energetically expensive to produce (Vance 1973) and at the very least require more brood space than do smaller offspring. Thus mothers must balance the benefits of producing larger, fitter offspring with the fecundity costs of producing fewer offspring (Smith and Fretwell 1974).

For more than 30 years, life-history biologists have used optimality models to visualize the trade-off between offspring size and number and thus predict an "optimal" offspring size (Vance 1973; Smith and Fretwell 1974; Levitan 1993; Podolsky and Strathmann 1996; Marshall and others 2006). Critical to these models is the relationship between offspring size and performance, with steeper relationships (that is small changes in offspring size cause large changes in performance) generally resulting in a larger optimal size (Marshall and others 2006). This relationship between offspring size and performance is in turn strongly affected by local environmental conditions such that there can be a range of optimal sizes corresponding to different conditions (Bernado 1996). For example, in the colonial ascidian *Botrylloides violaceus*, if offspring settle in high densities and competition is high, then a larger offspring size is optimal than if the larvae settle at lower densities (Marshall and others 2006). Thus, if mothers are to maximize their fitness, theory predicts that they will adjust the size of their offspring according to the range of local environmental conditions that their offspring will experience (McGinley and others 1987; Mousseau and Fox 1998; Hendry and others 2001). There are examples of such adaptive adjustment of offspring size in a number of organisms including a marine invertebrate (Fox, Thakar, and others 1997; Fox,

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Waddell, and others 1997; Krug 1998; Hendrickx and others 2003).

For organisms with direct development or a sedentary larval stage, the environment their offspring will experience is likely to be somewhat predictable. For organisms with complex life cycles and dispersive young, however, mothers face significant challenges with regard to predicting the likely relationship between offspring size and performance and thus optimally provisioning their young. First, and most obviously, dispersive young will probably leave the maternal habitat and disperse to habitat that differs greatly from it. If the relationship between offspring size and performance varies over small spatial scales, then mothers could provision their offspring in a way that is optimal for their own environment but not for that of their offspring.

Second, for organisms with complex life cycles, there are actually 2 (or more) environments that can affect the relationship between offspring size and performance, 1 in the larval environment and 1 in the adult (the adult stage is defined here as anything post-metamorphosis, despite the fact that this may include the pre-reproduction, juvenile stage) environment. The relationship between offspring size and (larval) performance can be highly sensitive to the larval environment (Kaplan 1992). Similarly, the juvenile/adult environment can strongly affect the offspring size/performance relationship (Moran and Emlet 2001; Marshall and others 2006). If the relationship between offspring size and performance in the 2 life-history stages are very different then there may be 2 different optima, and species with complex life cycles face the significant challenge of optimally provisioning their offspring for 2 environments simultaneously. For example, smaller eggs have an advantage at fertilization when the density of adult *Ciona intestinalis* is high because local sperm concentrations will be high and under such conditions larger eggs are more likely to suffer polyspermy (Marshall and Keough 2003b). However, these same high population densities are likely to result in an increased risk of intraspecific competition for newly settled juveniles. Increased levels of intraspecific competition selects for larger *C. intestinalis* settlers because larger settlers cope with competition better than smaller offspring (Marshall and Keough 2003a). Thus, smaller offspring are "better" for one stage but larger offspring are "better" for the subsequent stage.

The third challenge facing mothers with complex life cycles is more subtle and has received little attention. It is clear that the larval environment can affect the relationship between offspring size and performance in the *larval stage* (that is everything up to metamorphosis) but the larval environment could also affect the relationship between offspring size and performance in the *adult stage*. Numerous studies now show that events in the larval stage or the larval environment can strongly affect subsequent adult performance (Pechenik and others 1998; Wendt 1998; Pechenik and Rice 2001). Despite this strong phenotypic link between adult performance and larval environment, we are unaware of any study that examines whether the larval environment affects the relationship between offspring size and adult performance.

Here we examine how events during the larval phase affect the relationship between offspring size and performance in the adult stage of the marine bryozoan *Bugula neritina*. During the larval phase we manipulated the length of time larvae spent swimming before being allowed to metamorphose—a likely source of environmental variation in the larval phase under natural conditions (Marshall and Keough 2003c). To estimate performance in the adult phase, we measured survival, growth, fecundity, and the quality (size) of offspring produced in the next generation, all under field conditions. Larval swimming changed the relationship between offspring size and performance as an adult, so to examine the consequences of this change we used our data to produce a simple optimality model to determine whether predicted optimal offspring size was affected by larval swimming.

Methods

B. neritina is a cosmopolitan shallow-water bryozoan of temperate and subtropical waters. *Bugula* colonies produce non-feeding larvae that are brooded in specialized chambers (ovicells) attached to individual zooids of the colony, and the roughly spherical, ciliated larvae are released at a size of 250–350 μm. We examined the effect of larval environment on the size–performance relationship using 2 field experiments at a site in temperate southeastern Australia. In each experiment, we manipulated the larval environment in the laboratory, allowed larvae to settle and metamorphose, and then transplanted them to the field and measured their performance.

All collections of reproductively mature colonies and experiments were performed at Breakwater Pier in Williamstown, Victoria, near the end (January–March) of the southern hemisphere summer in 2000 and 2001. The water temperature for the experimental period was 18–21°C in both years. Reproductively mature colonies were collected from artificial settlement plates that had been placed in the field 2 months earlier. To collect larvae, the colonies were held in

aquaria (as part of a recirculating system) in constant darkness for 2 days before being exposed to bright light. The larvae were immediately measured as described by Marshall and colleagues (2003) and were then either allowed to settle immediately or had their settlement delayed. We haphazardly allocated approximately half of the spawned larvae into a "Delay" group. Larvae in the delayed group were each placed in their own clear tissue culture well with 5 ml of filtered (0.45 μm) seawater. The tissue culture wells were then illuminated with bright light from above and below for 4 h to prevent settlement and no larvae were observed to settle during the delay period. This delay period approximates inferred delayed periods in the field for *Bugula* at Breakwater Pier (Marshall and Keough 2003c). After the delay period, the larvae were transferred to their own settlement plates and allowed to settle.

Each larva was placed onto a settlement plate (roughened black Perspex: 2.5 cm × 5 cm × 1 cm) in a small drop of seawater and allowed to settle. Any larva that failed to settle within 30 min was discarded. We then marked the place of each settled larva by placing a small dot next to it using a pencil. The settlement plates were then placed into recirculating aquaria at 15°C for 12 h. Approximately 16 h after settlement, the settlement plates were transported to the field site (∼20 min away) in insulated aquaria. The settlement plates were attached to PVC backing plates (40 cm × 40 cm × 0.8 cm) using stainless steel bolts. The settlement plates were placed on the backing plate so in haphazard locations. The backing plates were then hung horizontally with the settlement plates facing down (to minimize the effects of light and sedimentation) at a depth of ∼2 m below mean low tide.

Experimental design and sampling

The first experiment, with 25 settled individuals, we deployed on January 29, 2000. After 3 weeks in the field, we hauled the backing plate up and placed it into a shallow bath of seawater. We then assessed the survival of colonies, the entire survey taking ∼60 min, after which the colonies were placed back under the pier. After 6 weeks in the field, we again collected all the settlement plates and brought them back to the laboratory. Once at the laboratory, we assessed colony survival, growth, and fecundity. We assessed colony growth by counting the number of bifurcations on each colony, following the method of Keough and Chernoff (1987), which makes use of the regular branching patterns of a colony. For an undamaged colony, the number of bifurcations is equivalent to the log of the number of zooids. We assessed colony fecundity by counting the number of ovicells present on each colony under a dissecting microscope (×10 magnification). We placed the colonies in lightproof boxes with recirculating seawater. After 2 days in complete darkness, the colonies were removed and each was placed in small 2 l plastic containers filled with seawater. We then placed the containers under bright fluorescent light. The colonies began spawning larvae almost immediately, and 30 min after the initiation of spawning, we collected a small ($n = 20$) sample of larvae from each colony. The larvae were then killed with a few drops of formalin and measured as in Marshall and colleagues (2003). It should be noted that we measured the cross-sectional area of the parental larvae whereas we only measured the length of the second-generation larvae. Both are good predictors of subsequent adult performance (Marshall and others 2003).

The second experiment ($n = 16$ settlers) was deployed on March 13, 2000 and we assessed colony survival after 3 weeks in the field. No further data collection was possible after 3 weeks because the backing plate was lost in a storm.

Data analysis

To test the effects of larval size and delayed metamorphosis on colony survival after 3 weeks in the field, we used logistic ANCOVA where larval size was a covariate and delay and experimental Run were categorical factors. For all the logistic ANCOVAs, Wald tests were used to test the significance of particular effects. We first tested for an interaction between the covariate and the categorical factors, and as there was no interaction, we ran a reduced model with the interaction terms removed (Quinn and Keough 2002). Run also explained little variation and was of no interest, so it was omitted from the final model.

To test the effects of initial larval size and delayed metamorphosis on subsequent colony size, fecundity, and size of offspring after 6 weeks in the field, we used ANCOVA. First we tested for an interaction between larval size and delay (test for homogeneity of slopes) for both growth and fecundity. There was no interaction (growth: $F_{1,9} = 1.62$, $P = 0.235$; fecundity: $F_{1,9} = 0.81$, $P = 0.393$), so we ran a reduced model with the interaction term removed.

We were interested in the relative effect on growth after 1 week of settler size and of delayed metamorphosis. To compare effect sizes, we compared the size of colonies that came from the largest and smallest larvae (as a measure of the effect of larval size) with the difference in adjusted mean sizes for colonies that

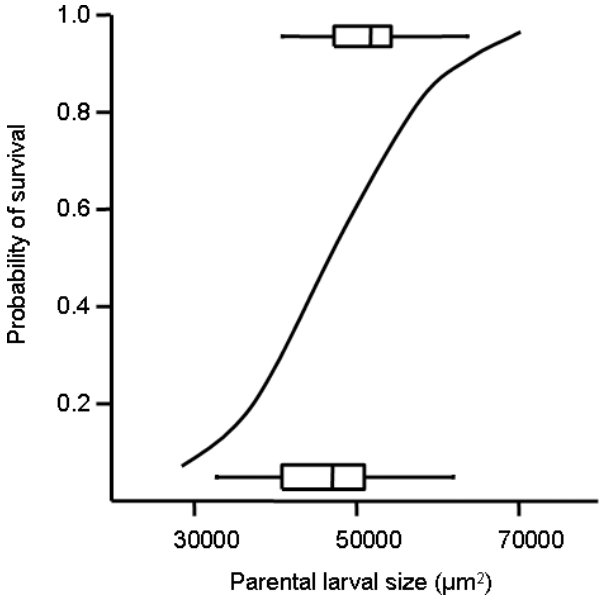

Fig. 1 Relationship between larval size and survival for *Bugula neritina* colonies after 3 weeks in the field. Line indicates predicted survival from logistic regression equation. Upper box-plot represents size distribution of larvae that survived as colonies and lower box-plot indicates the size distribution of larvae that died as colonies.

came from delayed and undelayed larvae (as a measure of the effect of delayed metamorphosis).

Results

Mortality after 3 weeks in the field was ~50% in both experimental runs, and in Run 1 no further mortality occurred after that time. There was no effect of a 4 h metamorphic delay on the chances of colonies surviving past 3 weeks (Metamorphic delay: $\chi^2 = 0.017$, d.f. = 1, $P = 0.89$; survival of colonies in delay treatment: 54%; survival of colonies in control treatment: 63%) but colonies that came from larger larvae were much more likely to survive than were colonies that came from smaller larvae (Larval size: $\chi^2 = 5.6$, d.f. = 1, $P = 0.018$; Fig. 1).

After 6 weeks in the field, colony size was affected by the initial size of larvae and whether or not those larvae had been delayed, with these effects being independent of each other (Table 1, Fig. 2). The number of ovicells on each colony after 6 weeks in the field was unaffected by initial larval size but was strongly affected by whether or not colonies had their metamorphosis delayed as larvae (Table 1, Fig. 3). The effects of delay on growth after 6 weeks in the field were approximately equal to the effects of parental larval size. The adjusted least-squares mean size of colonies that had been delayed as larvae was 6.6 (±0.3) and for those that were not delayed was 8.1 (±0.3), which is comparable to the size range of colonies from the smallest and the largest larvae (6 and 8 bifurcations, respectively).

Table 1 ANCOVA for effect of initial larval size and metamorphic delay on colony size and colony fecundity for *Bugula neritina* after 6 weeks in the field. Note that each model is reduced after testing for homogeneity of slopes

Source	d.f.	MS	*F*	*P*
Colony size				
Larval size	1	3.706	7.245	0.021
Metamorphic delay	1	7.065	13.810	0.003
Residual	11	0.512		
Colony fecundity				
Larval size	1	1808	1.703	0.219
Metamorphic delay	1	60 174	56.676	<0.0001
Residual	11	1061		

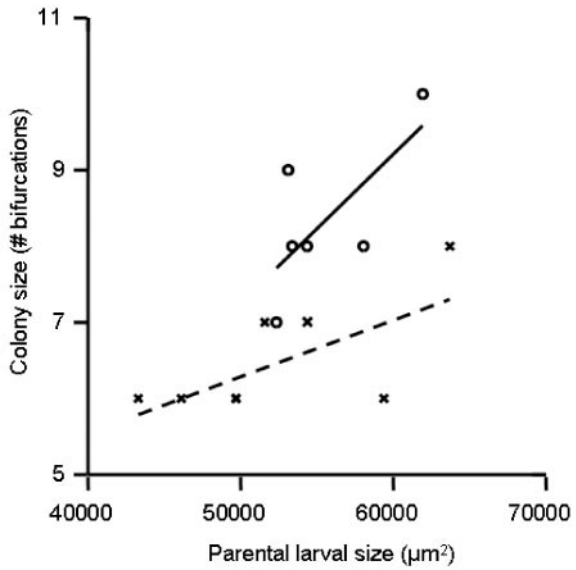

Fig. 2 Relationship between larval size and colony size after 6 weeks in the field for *B. neritina*. Circles and solid line represent colonies that did not experience a delay of metamorphosis as larvae and crosses and broken line represent colonies that did experience a delay as larvae. Each point represents a single colony.

There was a strong interaction between the effects of larval size and delays in metamorphosis on the size of offspring produced by colonies after 6 weeks in the field (ANCOVA: Larval size × Delay: $F_{1,10} = 6.52$, $P = 0.029$; Fig. 4). In those colonies that had not had their metamorphosis delayed as larvae, there was a positive relationship between parental larval size and offspring larval size ($R^2 = 0.61$). In those colonies that had their metamorphosis delayed, however, there appeared to be no relationship

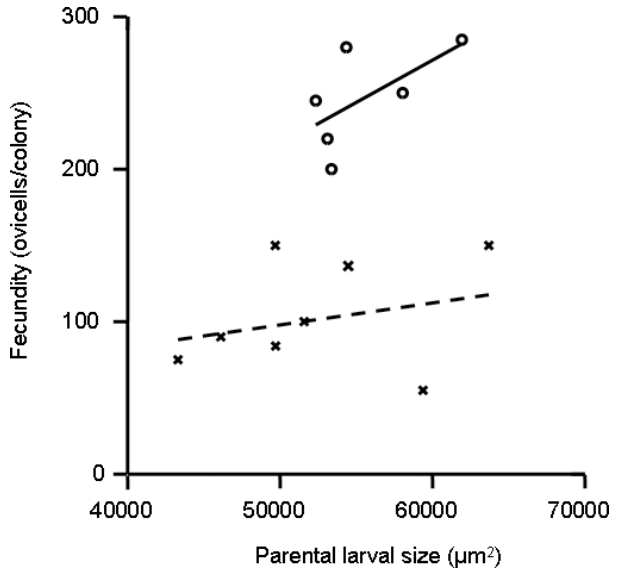

Fig. 3 Relationship between larval size and colony fecundity after 6 weeks in the field for *B. neritina*. Circles and solid line represent colonies that did not experience a delay of metamorphosis as larvae and crosses and broken line represent colonies that did experience a delay as larvae. Each point represents a single colony.

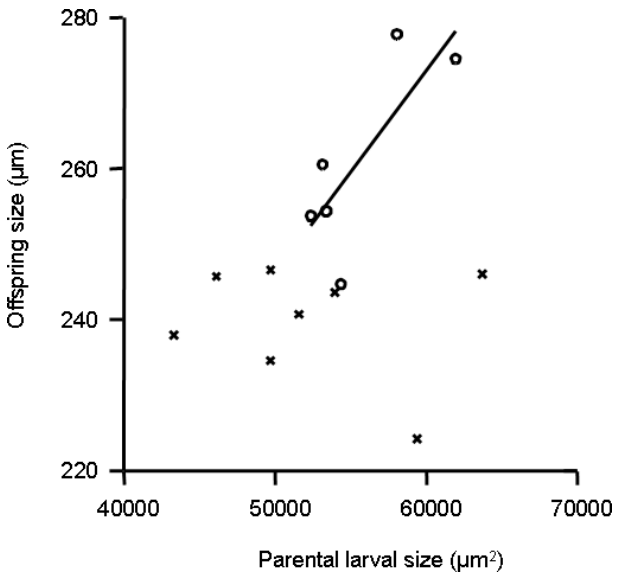

Fig. 4 Relationship between larval size and the size of larvae produced in the second generation for *B. neritina*. Circles and solid line represent colonies that did not experience a delay of metamorphosis as larvae and crosses represent colonies that did experience a delay as larvae. Each point represents the mean size of larvae from each colony.

between parental larval size and offspring larval size ($R^2 = 0.03$).

Model

From our field data, we created an optimality model to examine whether predicted optimal offspring size would be altered by the observed effect of delayed metamorphosis. We focused solely on post-metamorphic fitness although it should be noted that offspring size also affects the planktonic period in this species (see Discussion). The model used estimates of the effect of offspring size on survival and reproduction (both fecundity and second-generation offspring size), from the results of our experiments, and we varied offspring size across the range of values observed in the study. We used larval cross-sectional area (see Marshall and others 2003) as our measure of offspring size, so to calculate offspring volume, and therefore investment, we raised our size measure to the power of 1.5. As in previous models (for example Smith and Fretwell 1974; Levitan 1996b) the number of offspring produced by mothers is inversely proportional to per-offspring investment,

$$N = \frac{M}{s^{1.5}}, \tag{1}$$

where $N =$ number of settling larvae that are produced, M is the amount of resources available for reproduction (an arbitrary value kept constant throughout), and s is offspring size (measured as larval cross-sectional area). To predict the probability that a settling larva of a given size will survive through 6 weeks of benthic life (B), we used the overall logistic regression equation from the 2 experiments, with $\alpha = 1.808$ and $\beta = -6.45$. We found no relationship between offspring size and fecundity (F), so we used our field results of $F = 110$ larvae per colony for colonies that had been delayed as larvae and $F = 230$ larvae per colony for colonies that had not been delayed. Finally, we also included second-generation offspring quality (size) with the equation

$$Q = 0.0026s + 106. \tag{2}$$

This equation was used for colonies that came from undelayed larvae; for colonies that came from delayed larvae we used a constant ($Q = 228$) because our field results showed that there was no relationship between larval size and second-generation offspring size.

We then used the cumulative reproductive output of each offspring colony (which is a product of individual colony fecundity and the size of offspring that were produced) as a surrogate for maternal fitness. Maternal fitness, Ψ, then is given by putting Equations 1 and 2 together with size-specific survivorship (B) to produce the equation

$$\Psi = NBQF. \tag{3}$$

We then plotted maternal fitness versus larval size under 2 different conditions: when first-generation larvae experienced a delay and when they did not.

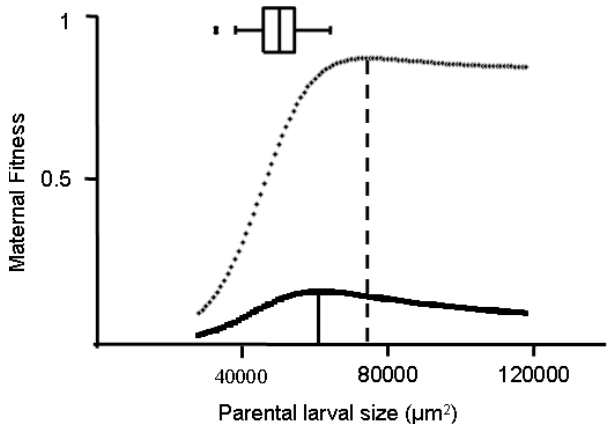

Fig. 5 Output from optimality model under 2 different conditions for *B. neritina*. The broken gray line indicates the size of offspring that mothers should produce in order to maximize their fitness (optimal offspring) if their larvae do not experience a metamorphic delay. The solid line indicates the size of offspring that mothers should produce in order to maximize their fitness if their larvae do experience a metamorphic delay. The box-plot shows the size distribution of larvae that were collected from wild colonies at Williamstown, Australia.

Model results

The model predicts that when larvae experience a metamorphic delay, maternal fitness is maximized by mothers reducing the size of their offspring (Fig. 5). This decrease in predicted optimal offspring size is due solely to the fact that when colonies experience a delay as larvae, the relationship between first-generation larval size and second-generation larval size is removed. Thus, the benefits of increased offspring size past a minimum threshold are lessened such that there is a fitness cost to producing offspring larger than this threshold. It should be noted that this "threshold" only applies to the minimum size of larvae that will survive in the study (as predicted by the logistic regression), at other locations or times, larvae smaller than this threshold may still survive.

Discussion

Delaying the metamorphosis of *B. neritina* larvae affected their performance as adult colonies as did the initial size of those larvae. Presumably both larval size and metamorphic delay affect the amount of energy reserves that are available for post-metamorphic performance (Wendt 2000; Moran and Emlet 2001). Surprisingly, these 2 factors affected different aspects of adult life, acting in isolation on most post-metamorphic traits but interacting in another trait. Larval size strongly affected post-metamorphic survival but delaying metamorphosis did not. Interestingly, there was no interaction between larval size and delaying metamorphosis on survival, with small larvae just as likely to survive regardless of their experience as larvae. This is remarkable given that larval swimming depletes energy reserves in *Bugula* (Wendt 2000) and it has been assumed that colonies from smaller larvae have higher mortality because of energy constraints (Marshall and others 2003). There are a number of alternative explanations for this lack of an interaction. It may be that smaller larvae are not near the minimum energy reserves required for post-metamorphic survival, but if this is the case, then why do smaller larvae have higher mortality overall? Alternatively, smaller larvae may use relatively less energy during swimming and thus do not use sufficient resources to affect energy reserves but this seems unlikely because colonies from larger and smaller larvae had their post-metamorphic growth reduced by similar levels. Furthermore, smaller larvae will actually have a greater surface area:volume ratio and thus have relatively more cilia than larger larvae, suggesting that if anything, smaller larvae will be less efficient. Another potential explanation is that larval swimming for the short period used here (c.f. Wendt 1996) does not strongly impinge the level of resources available for post-metamorphic survival. Regardless, post-metamorphic survival was affected by larval size only but colony growth was affected by both larval size and larval experience. Finally Hunter and colleagues (1999) showed that the larval period does not utilize proteins but metamorphosis does. It could be that adequate protein is the most important requirement for metamorphosis/survival and so the short swimming periods do not decrease survival but do affect growth. This explanation requires either that larval size affects survival due to the physical effects of size (Connell 1961) or that larger larvae have more protein than smaller larvae. Clearly, more work on the relative composition of large and small larvae is necessary.

The combined effect of larval size and larval experience on colony growth can be explained if both components essentially affect larval energy reserves. Colonies that came from larger larvae had higher growth than did colonies from smaller larvae and colonies that came from undelayed larvae had higher growth than did colonies that came from larvae that were delayed. The effects of larval size and experience were less predictable with regard to reproduction. Larval experience affected fecundity but larval size did not, which contrasts with some previous studies ([Marshall and others 2003] but see [Marshall 2005]), and seems odd given that larval size affected colony size. This lack of an effect of larval size should be treated with caution because the power to detect

such effects was low and there was a slight trend in both groups (delayed and not delayed) for colonies from larger larvae to have higher fecundity. The most interesting effect of larval size and experience was their interactive effect on second-generation offspring size—for colonies that did not experience a delay as larvae, there was a strong relationship between initial larval size and second-generation offspring size but for colonies that did experience a delay as larvae, this relationship was obliterated.

The de-coupling of the relationship between first-generation and second-generation offspring size has a number of interesting implications. First, this de-coupling means that the benefits of producing larger offspring are significantly reduced; apart from survival benefits, larger larvae that experience a metamorphic delay will have similar fecundity and offspring quality as smaller larvae. This reduction in the benefits of increased offspring size resulted in a significant reduction in predicted optimal offspring size. This is surprising given that the favored prevailing view is that harsher environments should result in larger offspring (Einum and Fleming 1999; Fox 2000), but see (Moran and Emlet 2001). *A priori*, we would have expected that a metamorphic delay would have increased the benefits of offspring size because we would have predicted an increase in the minimum size of larvae that could survive. We await studies on other species (ideally, species with smaller offspring) to determine the generality of our finding. Given that feeding larvae are less affected by delayed metamorphosis, we would predict that there are smaller effects of delaying metamorphosis on predicted optimal offspring size in planktotrophs. However, we would be interested in determining how decreases in food availability (the equivalent to delaying metamorphosis in non-feeding larvae) during the planktonic stage affect optimal offspring size in planktotrophs.

Overall, our results show that the offspring size–performance relationship is highly variable and sensitive to events in multiple life-history stages. Previous studies show that the *adult* environment can strongly affect the relationship between offspring size and performance and thus optimal offspring size (Marshall and others 2006). Here we show, however, that the *larval* environment can also affect the relationship between offspring size and adult performance. Given that the larval environment can strongly affect adult performance in other species (Relyea 2003), interactions between the larval environment and offspring size may be relatively common. For species with complex life cycles, it appears that mothers must produce offspring that are an optimal size for both the larval and adult environments. The fact that the larval and adult environments can both influence optimal offspring size (potentially in differing directions) may make the optimal offspring size for an organism with a complex life cycle impossible to anticipate (from the perspective of the provisioning mother). Nevertheless, there are some intriguing indications that mothers may still exhibit adaptive plasticity with regard to offspring size in response to a changing environment in marine invertebrates.

Our model predicted that optimal offspring size is decreased when larvae are likely to experience a metamorphic delay. Our field results also found that when larvae experienced a delay, the size of offspring produced by the subsequent colonies was lower and essentially "flat" with regard to colony size. This could represent a form of transgenerational adaptive plasticity (*sensu* Mousseau and Fox 1998). Mothers that experienced a long metamorphic delay as larvae may be using this information to adjust the size of their offspring. Given that a long delay represents a long time in the plankton, in nature, mothers that experience long metamorphic delays will probably finish up in isolated patches of a suitable habitat (if good habitats were abundant, they should have been able to settle immediately). Thus, mothers may produce smaller offspring themselves because their offspring are likely to experience a long delay, thereby changing optimal size. This would have an additional benefit because smaller larvae tend to settle sooner in *Bugula* and this may increase the chances of retaining the larvae in a habitat of good quality, but isolated. This line of thought is highly speculative but it is interesting that colonies that were delayed as larvae produced smaller larvae regardless of their own colony size. Interestingly, predicted optimal offspring size when larvae are kept swimming is much closer to the observed distribution of larval sizes in the field than is the predicted optimum when larvae can settle immediately (this assumes that laboratory spawned colonies collected from the field produce offspring similar in size to those that are released in the field). Given that data on lengths of metamorphic delays in the field are rare (Pechenik 1990), this is at least some further indirect evidence (see Marshall and Keough 2003c) that at least some *Bugula* larvae delay metamorphosis for intervals that are likely to impinge on post-metamorphic performance.

Regardless of the proximal causes, larval size is clearly a plastic trait in *Bugula* and can change in response not only to events occurring during the adult stage (Marshall and Keough 2004) but also to those taking place during the larval stage. The optimal size of offspring that mothers should produce can be very different depending on whether those offspring will spend a long or short time swimming, despite

the adults living in identical habitats. This highlights the strongly linked nature of marine life histories; events in one stage can manifest themselves in unpredictable ways at other stages, emphasizing the need for examining an organism's life history as a whole rather than as a series of disconnected modules.

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References

Bernado J. 1996. The particular maternal effect of propagule size, especially egg size: patterns models, quality of evidence and interpretations. Am Zool 36:216–36.

Connell JH. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol Monogr 31:61–104.

Einum S, Fleming IA. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proc R Soc Lond B 266:2095–100.

Fox CW. 2000. Natural selection on seed-beetle egg size in nature and the laboratory: Variation among environments. Ecology 81:3029–35.

Fox CW, Thakar MS, Mosseau TA. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. Am Nat 149:149–63.

Fox CW, Waddell KJ, DesLauriers J, Mousseau TA. 1997. Seed beetle survivorship, growth and egg size plasticity in a paloverde hybrid zone. Ecol Entom 22:416–24.

Gimenez L, Anger K. 2001. Relationships among salinity, egg size, embryonic development and larval biomass in the estuarine crab *Chasmagnathus granulata*, Dana 1851. J Exp Mar Biol Ecol 260:241–57.

Hart MW. 1995. What are the costs of small egg size for marine invertebrate with feeding planktonic larvae. Am Nat 146:415–26.

Hendrickx F, Maelfait JP, Speelmans M, Van Straalen NM. 2003. Adaptive reproductive variation along a pollution gradient in a wolf spider. Oecologia 134:189–94.

Hendry AP, Day T, Cooper AB. 2001. Optimal size and number of propagules: Allowance for discrete stages and effects of maternal size on reproductive output and offspring fitness. Am Nat 157:387–407.

Hunter E, Shimizu K, Fusetani N. 1999. Role of protein in larval swimming and metamorphosis of *Bugula neritina* (Bryozoa: Cheilostomatida). Mar Biol 133:701–7.

Kaplan RH. 1992. Greater maternal investment can decrease offspring surivival in the frog *Bombina orientalis*. Ecology 73:280–8.

Keough MJ, Chernoff H. 1987. Dispersal and population variation in the bryozoan *Bugula neritina*. Ecology 68:199–210.

Krug PJ. 1998. Poecilogony in an estuarine opisthobranch: planktotrophy, lecithotrophy, and mixed clutches in a population of the ascoglossan *Alderia modesta*. Mar Biol 132:483–94.

Levitan DR. 1993. The importance of sperm limitation to the evolution of egg size in marine invertebrates. Am Nat 141:517–36.

Levitan DR. 1996a. Effects of gamete traits on fertilisation in the sea and the evolution of sexual dimorphism. Nature 382: 153–5.

Levitan DR. 1996b. Predicting optimal and unique egg size in free spawning marine invertebrates. Am Nat 148:174–88.

Marshall DJ. 2005. Geographical variation in offspring size effects across generations. Oikos 108:602–8.

Marshall DJ, Bolton TF, Keough MJ. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. Ecology 84:3131–7.

Marshall DJ, Cook CN, Emlet RB. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. Ecology 87:214–25.

Marshall DJ, Keough MJ. 2003a. Effects of settler size and density on early post-settlement survival of *Ciona intestinalis* in the field. Mar Ecol Prog Ser 259:139–44.

Marshall DJ, Keough MJ. 2003b. Sources of variation in larval quality for free-spawning marine invertebrates: Egg size and the local sperm environment. Inv Repro Dev 44:63–70.

Marshall DJ, Keough MJ. 2003c. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. Mar Ecol Prog Ser 255:145–53.

Marshall DJ, Keough MJ. 2004. When the going gets rough: Effect of maternal size manipulation on offspring quality. Mar Ecol Prog Ser 272:301–5.

Marshall DJ, Keough MJ. 2005. Offspring size effects in the marine environment: a field test for a colonial invertebrate. Aust Ecol 30:275–80.

McCormick MI. 2003. Consumption of coral propagules after mass spawning enhances larval quality of damselfish through maternal effects. Oecologia 136:37–45.

McGinley MA, Temme DH, Geber MA. 1987. Parental investment in offspring in variable environments: theoretical and empirical considerations. Am Nat 130:370–98.

Moran AL, Emlet RB. 2001. Offspring size and *performance* in variable environments: field studies on a marine snail. Ecology 82:1597–612.

Mousseau TA, Fox CW. 1998. The adaptive significance of maternal effects. Trends Ecol Evol 13:403–7.

Pechenik JA. 1990. Delayed metamorphosis by larvae of benthic marine-invertebrates—does it occur—is there a price to pay. Ophelia 32:63–94.

Pechenik JA, Rice ME. 2001. Influence of delayed metamorphosis on postsettlement survival and growth in the sipunculan *Apionsoma misakianum*. Inv Biol 120:50–7.

Pechenik JA, Wendt DE, Jarrett JN. 1998. Metamorphosis is not a new beginning. Bioscience 48:901–10.

Podolsky RD, Strathmann RR. 1996. Evolution of egg size in free spawners: consequences of the fertilisation-fecundity trade-off. Am Nat 148:160–73.

Quinn GP, Keough MJ. 2002. Experimental design and data analysis for biologists. Cambridge, UK: Cambridge University Press.

Relyea RA. 2003. Predators come and predators go: the reversibility of predator-induced traits. Ecology 84:1840–8.

Smith CC, Fretwell SD. 1974. The optimal balance between size and number of offspring. Am Nat 108:499–506.

Vance RR. 1973. On reproductive strategies in marine benthic invertebrates. Am Nat 107:339–52.

Wendt DE. 1996. Effect of larval swimming duration on success of metamorphosis and size of the ancestrular lophophore in *Bugula neritina* (Bryozoa). Biol Bull 191:224–33.

Wendt DE. 1998. Effect of larval swimming duration on growth and reproduction of *Bugula neritina* (Bryozoa) under field conditions. Biol Bull 195:126–35.

Wendt DE. 2000. Energetics of larval swimming and metamorphosis in four species of *Bugula* (Bryozoa). Biol Bull 198:346–56.