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Effects of Egg Size on the Development Time of Non-feeding Larvae

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*The evolution of egg size in marine invertebrates remains a topic of central importance for life-history biologists, and the pioneering work of Vance has strongly influenced our current views. Vance's model and most models developed since have assumed that increases in egg size result in an increase in the prefeeding period of marine invertebrate larvae. For lecithotrophic species, this means that the entire development period should be correlated with egg size. Despite the importance of this assumption, it has not been tested at the appropriate scale-within species. We investigated the effects of egg size on development time for three lecithotrophic species from two phyla: the ascidians *Phallusia obesa* and *Ciona intestinalis*, and the echinoid *Heliodidaris erythrogramma*. We found that within individual broods of eggs, larger eggs took longer than smaller eggs to develop or become metamorphically competent larvae. It has long been recognized that producing larger eggs decreases fecundity, but our results show that increasing egg size also carries the extra cost of an extended planktonic period during which mortality can occur. The substantial variation in egg sizes observed within broods may represent a bet-hedging strategy by which offspring with variable dispersal potentials are produced.*

The study of offspring size is central to life-history theory and has long fascinated evolutionary ecologists (1). Marine invertebrates exhibit variation in offspring sizes among species and accordingly have also been the focus of research for many years (2). This variation among species resulted in an effort to explain or identify interspecific patterns of offspring size variation. Arguably, the most influential attempts at understanding interspecific variation in offspring

size are Vance's (3, 4) mathematical models that examine the influence of offspring size, development time, and planktonic periods in marine invertebrates with planktonic larvae. Vance assumed that the length of the prefeeding period increased with offspring size, and that the length of the feeding period decreased with offspring size. Vance's models predicted that mothers should produce either very small or very large offspring, and vigorous debate has continued over whether these patterns are observed in nature (5). Since Vance's models were published, several modified or appended models have been created that incorporate the effects of offspring size on fertilization kinetics and use more realistic relationships between offspring size and the length of the feeding period (6–9).

The two most recent and widely cited models of offspring size provisioning in marine invertebrates both contain explicit assumptions regarding the effects of egg size on development time. McEdward's model (10) is identical to Vance's model with regard to lecithotrophs, and Levitan's model (7) explicitly assumes that egg size has no effect on prefeeding development. Given that some models assume a strong effect of egg size on development time and some assume no effect at all, what empirical evidence is available?

The suggestion that larger lecithotrophic eggs take longer to develop (or hatch) comes largely from older work using interspecific comparisons with ascidians and crustaceans (2, 11), and more recently, asteroids (12). However, despite initial controversy (11, 13) the notion that larger eggs take longer to develop than smaller eggs within species of marine invertebrates has become almost axiomatic in the absence of much evidence. We believe that this conclusion about the relationship between egg size and development time is premature for several reasons.

First, while some interspecific comparisons have found a relationship between offspring size and development time in species with non-feeding larvae (*e.g.*, ascidians [2, 12]), others have found no significant relationship in urochordates or echinoderms (14) (although the number of replicates was low in both groups). Second, interspecific comparisons that do not account for phylogenetic relationships and that treat individual species as independent replicates can produce misleading results (15). Finally, the use of interspecific comparisons to infer functional or evolutionary relationships between offspring size and other life-history characteristics is generally problematic (16, 17). Thus if we are to understand the evolution and ecological implications of variation in offspring size in marine invertebrates, we should examine the effects of that variation at the within-species level. Here we examine the effects of egg size variation on the development time of nonfeeding larvae for three species of marine invertebrate from two phyla. We examined how egg size affected time until metamorphic competence in the ascidians *Ciona intestinalis* and *Phallusia obesa* (within broods) and the sea urchin *Heliocidaris erythrogramma* (both within and among broods).

Larval hatching was asynchronous in both ascidian species. Larvae of *Ciona intestinalis* began hatching 18 h post-fertilization, and hatching continued for a further 6 h. Larger *C. intestinalis* larvae took longer to hatch than smaller *C. intestinalis* larvae: on average, larvae hatching 22 h post-fertilization were about 4% larger than those hatching after 22 h (Fig. 1a, Table 2). Larvae of *Phallusia obesa* began hatching at 14 h post-fertilization, but hatching continued through 20 h post-fertilization. Development time was similarly dependent on offspring size in *P. obesa*: larvae that hatched after 15 h were on average about 22% smaller than larvae that hatched after 20 h (Fig. 1b). For both ascidian species, there was no effect of parental identity on development time and no interaction between larval size and parental identity on development time (Table 1). In *C. intestinalis*, larval size was strongly correlated with egg size ($R^2 = 0.82$, $n = 25$, $P < 0.001$) and did not change after hatching (paired Student's *t* test: 1.4, $P = 0.174$, $df = 24$).

High levels of variation in egg size were apparent within and among broods of eggs of *Heliocidaris erythrogramma*. The average coefficient of variation in egg size within broods was 23% (data from three broods), and the coefficient of variation among broods was 11% (data from 20 broods). Within single broods of eggs, smaller larvae were more likely to settle in response to a settlement cue 4 days post-fertilization than larger larvae, irrespective of the maternal source of the eggs (Table 2). Among broods of eggs, the time until metamorphic competence was also strongly dependent on original egg size. Four days after fertilization, in the presence of a settlement cue, larvae from smaller eggs metamorphosed at a higher rate than larvae from larger eggs

(Fig. 2, Table 2). Eight days after fertilization, all of the larvae from large and small eggs metamorphosed in response to the settlement cue.

In each of the species studied here, increased egg size resulted in larvae taking longer to become competent to metamorphose. For the ascidian species, larger larvae took 14%–25% longer to hatch than smaller larvae within the same batch. However, for *Phallusia*, we did not measure whether larger eggs indeed became larger larvae, so use of the indirect measure of larval size should be treated with caution. Nevertheless, in all three species, offspring size apparently strongly affected the time until larvae could settle. In *Heliocidaris erythrogramma*, larvae that came from larger eggs showed much lower settlement rates 4 days post-fertilization than larvae that came from smaller eggs both among and within different broods of eggs. These data for these species at least support the long-held assumption that in non-feeding larvae, planktonic period increases with egg size. The mechanism behind larger eggs taking longer to develop than smaller eggs remains unclear. Staver and Strathmann (14) found that among species, larvae developing from larger eggs take longer to begin swimming than larvae developing from smaller eggs and, among ascidians, species with larger eggs have a slower cell cycle. They suggest that larger eggs take longer to develop in ciliated species because in larger embryos more cilia are required for locomotion. This may explain our findings in *H. erythrogramma*, but it is unclear why we saw an effect of egg size on development in the both solitary ascidian species. Alternatively, increased metabolic demands for oxygen, coupled with a decrease in the capacity to acquire oxygen by diffusion, may explain the longer embryonic development times of larger offspring observed here (18).

Regardless of the mechanism responsible for the effect of egg size on developmental times, such an effect has some interesting implications given that within species, and even within clutches of eggs, egg size varies remarkably. For the species in this study, egg size is strongly correlated with the *minimum* planktonic period of the embryo and larva, and planktonic period is thought to be strongly correlated with dispersal potential (19). Thus, if mothers produce eggs of variable size, then they will be producing offspring with variable dispersal potentials—offspring from larger eggs are more likely to disperse farther than offspring from smaller eggs. Given the high levels of variation in egg size observed within broods in this study and others (*e.g.*, 20, 21), the minimum dispersal potential of offspring is likely to be highly polymorphic within a brood. Raimondi and Keough (22) argue that variation in larval behavior may be adaptive for mothers, ensuring that offspring are spread throughout a range of habitats and mitigating intraspecific competition. In an analogous argument for birds, Laaksonen (23) argues that hatching asynchrony is an adaptive strategy that maximizes parental fitness by reducing variation in the

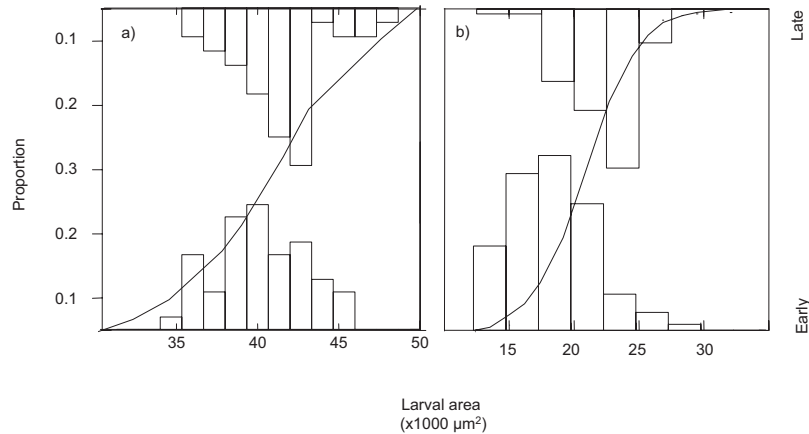


Figure 1. Effect of offspring size on the timing of hatching of larvae of *Phallusia obesa* (panel a) and *Ciona intestinalis* (panel b). For each species, the size distribution of larvae hatching early is shown on the bottom histogram, and the size distribution of larvae hatching late is shown on the top histogram. The line in each panel represents the logistic regression line of best fit. For *P. obesa*, “early” and “late” hatching were respectively classed as all larvae hatching prior to 15 and 20 h post-fertilization. For *C. intestinalis*, “early” and “late” hatching were respectively classed as all larvae hatching prior to 19 h and 24 h post-fertilization.

The ascidians were collected from pier pilings in Port Lincoln, South Australia. Gametes were strip-spawned from adults within one day of collection (see 26 for method). Larvae of *P. obesa* were cultured using sperm and eggs from eight individuals for a total of four sperm egg/combinations. Each brood of eggs was exposed to a dilute solution of sperm from a different individual; after 30 min of exposure, the eggs were gently rinsed in filtered seawater on a 100- μm plankton mesh. Developing embryos were transferred into small culture vessels filled with 80 ml of filtered seawater, and the containers were immersed in a flow-through seawater system to maintain a constant temperature. Embryos were kept at a density of 2 embryo \cdot ml $^{-1}$. Hatching began about 14 h after fertilization. We collected *P. obesa* larvae 15 h ($n = 15\text{--}32$ per brood) after fertilization by placing a lamp above the culture vessels and collecting the larvae that swam toward the light (the larvae were strongly positively phototactic). These larvae were transferred to plastic vials and immediately fixed with a few drops of formalin solution (12% v/v formalin in fresh water). The same techniques were used to collect larvae that had hatched 20 h after fertilization ($n = 15\text{--}32$ per brood). Larvae of *C. intestinalis* were cultured from sperm and eggs from 10 individuals for a total of 5 sperm/egg combinations. Eggs were exposed to sperm ($\sim 10^5$ sperm \cdot ml $^{-1}$) for 15 min and then rinsed repeatedly in sperm-free seawater. Fertilized eggs were placed in a 70-ml polyethylene jar with 50 ml of sperm-free seawater, and the base of the jar was immersed into a flow-through aquarium (ambient seawater temperature 19°C). The zygotes were left to develop overnight at a density of 4 embryos \cdot ml $^{-1}$, and each jar was checked for signs of hatching every 30 min on the following day. We removed all the larvae that had hatched 19 h after fertilization and immediately measured a subsample of these larvae ($n = \sim 20$ larvae per female). Twenty-four hours after fertilization, we again collected larvae that had hatched in the intervening period ($n = \sim 20$ larvae per female).

Larvae of both species were digitally imaged against a micrometer scale under a dissecting microscope (40 \times magnification). The sizes of images were calibrated against the micrometer scale, and the planar area of each larva was determined by digitizing its outer edges with image analysis software (Olympus, Olysia ver. 3.2, and ImagePro ver. 9.0). We assumed that larval planar area was a good predictor of larval volume. There was no evidence that larvae differed in any systematic way between treatments in the relationship between area and volume, but we did not test this explicitly. Because we used larval size as an indirect measure of egg size, we also tested whether (a) larval size did reflect egg size and (b) larval size did not change over time after hatching in *Ciona* only. To examine both questions, we measured 25 eggs (5 eggs from five different individuals), fertilized them, and then measured the resultant larvae 15 and 20 h post-fertilization..

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success of their offspring (*i.e.*, bet-hedging). It is unclear whether variation in egg size within broods in marine invertebrates is an adaptive or bet-hedging trait (24) or merely an inevitable consequence of egg production (see 25).

Egg size variation among mothers also affected the minimum dispersal potential of larvae for at least one species here. In *H. erythrogramma*, larvae from mothers producing larger eggs showed lower settlement rates 4 days after fertilization than larvae from mothers produc-

ing smaller eggs. Thus, larvae from larger eggs appear to have an obligately longer dispersal period than larvae from smaller eggs. For a large number of marine invertebrates, offspring size varies greatly among populations (*e.g.*, 26, 27) and among mothers within populations (*e.g.*, 26, 28) depending on the quality of the habitat, maternal nutrition levels, or maternal size. Offspring size is also often correlated with maternal size, with larger mothers producing larger eggs than smaller mothers do (20, 29).

Table 1

Logistic ANCOVA for the effect of maternal identity and egg size variation within broods on hatching time in *Ciona intestinalis*, *Phallusia obesa*, and *Heliocidaris erythrogramma*

Parameter	χ^2	<i>P</i>
<i>Ciona</i>		
Larval size	4.195	0.041
Maternal identity	0.135	0.713
McFaddens ρ^2		0.037
<i>Phallusia</i>		
Larval size	42.7	<0.001
Maternal identity	2.037	0.153
McFaddens ρ^2		0.342
<i>Heliocidaris</i>		
Egg size	3.969	0.046
Maternal identity	1.131	0.252
McFaddens ρ^2		0.367

Offspring size (larval size for the ascidians, egg size for the urchin) was a covariate and maternal source was a categorical, random factor in the model. Models are reduced after testing for homogeneity of slopes (*Ciona*: maternal identity \times size: $\chi^2 = 0.085$, *df* = 1, *P* = 0.771; *Phallusia*: $\chi^2 = 0.084$, *df* = 1, *P* = 0.772; *Heliocidaris*: maternal identity \times size: $\chi^2 = 0.3760$, *df* = 1, *P* = 0.383). Significant *P* values are shown in **bold**.

Our results suggest that larger mothers will not only produce offspring that are of better quality than smaller offspring (*e.g.*, 30), they will produce offspring that have greater dispersal potentials. Previously, one of us has shown that in brooding species, larval size affects the settlement behavior of larvae, with larger larvae tending to remain “choosier” than smaller larvae about settlement surfaces (31). Although this also results in larger offspring that have a greater dispersal potential than smaller offspring, there is an important difference between the two findings. For the colonial invertebrate species examined in Marshall and Keough (31), the increased dispersal potential of larger offspring was facultative: settlement could occur immediately in larger offspring but was

Table 2

Two-way ANOVA was used to examine the effect of egg size on time to metamorphic competence among clutches of eggs in *Heliocidaris erythrogramma*

Source	<i>df</i>	<i>MS</i>	<i>P</i>
Egg size	1	0.162	0.025
Experimental run	1	5.326	< 0.001
Residual	39	0.030	

Individual clutches of eggs were replicates; egg size class was a fixed, categorical factor; and experimental run was a random, categorical factor. Model is reduced after testing for run \times egg size interaction ($F_{1, 38} = 0.119$, *P* = 0.732).

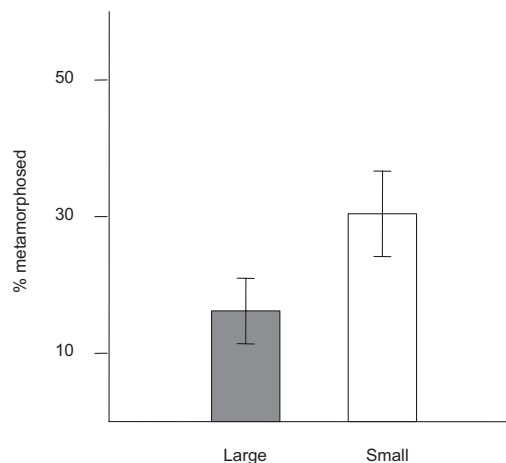


Figure 2. Effect of among-brood variation in egg size on time until metamorphic competency in the sea urchin *Heliocidaris erythrogramma*. Bars show mean proportion (\pm SE) of larvae from large (shaded bar) and small (open bar) eggs that initiated metamorphosis in response to a positive settlement cue 4 days after fertilization. See below for definition of large and small egg sizes.

The sea urchins were collected from Bare Island, Botany Bay, New South Wales, during January and February 2004. Gametes were obtained and larvae cultured using established methods (26). Larvae of *H. erythrogramma* were cultured for two experimental runs, and each run involved the eggs of 20 females. For each run, we allocated the eggs of each female into either the “large egg” or “small egg” size class so that we did not have to follow individual developing eggs. Eggs were measured (see 26 for method), and the eggs of each female were allocated to large or small size classes according to whether the mean diameter of eggs for each brood was greater or less than 380 μm (the median size of the population). The number of females whose eggs were allocated to the large-egg category was 12 in the first run and 8 in the second run. For each run, a mixture of sperm from 6 males was used to fertilize the eggs of each female, so on average the resultant larvae within each run were likely to be half-sibs. The eggs were exposed to the sperm solution of 2×10^3 sperm ml^{-1} for 15 min, after which the eggs were rinsed thoroughly in filtered seawater. The zygotes from each female were maintained in 200-ml polyethylene jars (1 embryo \cdot ml^{-1}) in a constant-temperature room (21°C). Seawater was replaced daily with freshly collected, filtered seawater. Four days after fertilization, we exposed 50 larvae from each female to a settlement inducer by placing a small (<6 cm length) piece of coralline algae, *Amphiroa anceps*, into a culture jar containing the larvae. This alga is the strongest known settlement inducer of *H. erythrogramma* larvae (M. J. Watson, University of New South Wales, Australia, unpubl. data). Twenty-four hours after exposing the larvae to the settlement inducer, we measured the proportion of larvae that had completed metamorphosis. Larvae were classed as “metamorphosed” if they had several tube feet visible and had begun to form spines. We repeated the exposure of larvae to the settlement inducer 8 days after fertilization and again determined the proportion of larvae that settled. Among different batches of eggs, we found strong effects of egg size on the competence of *H. erythrogramma* larvae to metamorphose (see Table 2), and we were therefore interested in whether similar effects occurred within individual broods of eggs. We collected eggs from two females and fertilized and cultured them as described above. We then separated individual developing embryos into their own culture vials with 10 ml of filtered seawater (*n* = 7–12 larvae from each female). Two days after fertilization, we measured the length of each larva (as described in 26). Four days after fertilization, we exposed each larva to the settlement inducer (as described above); the following day we determined whether each larva had metamorphosed.

dependent on the availability of cues. In contrast, the increased dispersal potential of larger offspring in this study is obligate: larger offspring cannot settle sooner than smaller offspring. Thus the only means by which mothers with external fertilization can reduce the planktonic period of their offspring is by reducing the size of the offspring that they produce.

Given that planktonic mortality can be high in lecithotrophs (see 32), we would predict that larger larvae would suffer higher planktonic mortality overall than smaller larvae because of their increased time in the plankton. For species with lecithotrophic larvae, mothers are viewed as provisioning their larvae with more resources than they need to complete metamorphosis, and these extra resources are thought to increase post-metamorphic performance (33, 34). Traditionally, the cost associated with increased egg size has been a reduction in fecundity (3), but our results show that it can also result in a dramatic increase in the vulnerable planktonic period. Thus in addition to being more costly to produce, larger eggs are likely to be more risky because any increase in maternal provisioning to enhance post-settlement survival comes with a concurrent increase in the risk of larvae suffering higher mortality in the plankton. This represents a relatively unrecognized cost of producing larger offspring.

The magnitude of the effects of egg size on development time in our studies was surprising and has some interesting implications for the way in which egg size evolution is modeled. Vance's model (3) and several subsequent ones assumed that the effects of egg size variation on the feeding period were much larger than its effects on the prefeeding period (in terms of the model, $p \gg l$; pg. 342), so that any increase in egg size would result in a large decrease in the feeding period and only a small increase in the prefeeding period. Later models even remove the effects of egg size on the prefeeding period, regarding it as constant (*e.g.*, ref. 7, pg. 178). Given that our results show that small increases in egg size can dramatically increase development time (*e.g.*, for *Ciona* a ~4% increase in offspring size resulted in a 15% increase in development time), it appears that the effect of egg size on the prefeeding period should not be assumed to be substantially less than its effect on the feeding period. Interestingly, several studies comparing planktonic periods of planktotrophic species have found no overall relationship between egg size and planktonic period (35, 36). It may be that egg size has much stronger effects on the prefeeding period than has previously been assumed. Thus the effects of egg size on the prefeeding period may partially balance the effects of egg size on the feeding period, thereby obscuring any relationship; but this requires further testing on planktotrophic species.

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