CHAPTER 3

Evolutionary Ecology of Parental Investment and Larval Diversity

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3.1 Introduction

Marine larvae vary enormously in the amount of care—be it in the form of energy or other costly caregiving that increases offspring fitness—they receive from their parents. At one end of the spectrum of parental investment, the offspring of some species receive very little from their parents: they are released as tiny eggs (< 40 μm diameter), and must complete every element of their development independently, from fertilization all the way through to metamorphosis. At the other extreme, some species are released as fully formed juveniles ~2000 μm in length, with their entire development complete. Between these two extremes lie every possible level of parental investment, and most species lie somewhere along this continuum. In contrast to terrestrial taxa, parental investment is less coupled to phylogeny in marine taxa, such that closely related species may have wildly different parental investment strategies (Marshall et al., 2012). For example, the congeneric sea urchins *Heliocidaris erythrogramma* and *H. tuberculata* live in the same habitat but produce offspring that differ in volume by 35-fold (Marshall et al., 2012). Such diversity demands explanation, and marine biologists have been fascinated by variation in parental investment for over 100 years. In this chapter, we will review patterns in parental investment in space, review the theory of parental investment in life history theory, explore the key assumptions of life history theory as it pertains to parental investment, and then examine the evolutionary causes and ecological consequences of variation in parental investment for marine organisms. Finally, we will provide some suggestions as to future work in this field.

Before we consider parental investment in detail, it is first important to define it. General life history theoreticians, such as Clutton-Brock and Stearns, have provided elegant descriptions and justifications of parental investment, and we use a similar definition here: the best measure of parental investment is the proportion of surplus power devoted to reproduction for each offspring (Clutton-Brock, 1991; Stearns, 1992). Whether that surplus power is direct energy investments into offspring in the form of provisioning eggs, embryos, or juveniles; the construction of protective capsules or egg masses; or the energy expended ventilating a clutch of eggs—all these acts involve the use of energy specifically for reproduction. One key element of parental investment we will focus on in this chapter is offspring size. We have that focus for several reasons: first, offspring is an axis of parental investment that shows enormous variation among species; second, it maps to major differences in life history; third, it is likely that this axis captures much (but certainly not all; see following) of the variation in parental investment in marine organisms; and, finally, offspring size is a component of parental investment for which we have the most data both in terms of its variation and in terms of its consequences for the ecology marine organisms.

As we begin the chapter, we would first like to acknowledge and recommend the work of the giants in this field, including but not limited to the early works of Mortensen, Thorson, Strathmann, Emlet, and McEdward (e.g., Mortensen, 1922; Thorson, 1950;

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Strathmann, 1985; Emlet et al., 1987; McEdward and Miner; 2001). Furthermore, this chapter hopefully builds on work by Will Jaeckle and Jon Havenhand (see Havenhand, 1995; Jaeckle, 1995), and we strongly recommend these as an excellent starting point.

3.2 The Biogeography of Parental Investment in the Sea

Biologists have noticed patterns in parental investment in marine systems for at least 100 years. The great larval biologist Gunnar Thorson reviewed the literature in the early 1900s and concluded that there were latitudinal gradients both in larval development types and offspring size in marine invertebrates (Thorson, 1936). Specifically, he suggested that species that lacked a larval stage were more common in high latitudes and that offspring sizes were generally larger at the poles relative to the tropics (Thorson, 1950). Though Thorson was always troubled by the fact that some species with small eggs and extended larval phases still thrived in the poles, he came to believe that the poles "suppressed" such species and favored species that lacked a larval phase and produced larger offspring (Thorson, 1950). Thorson believed that the colder temperatures of the poles and the lack of planktonic food were the drivers of the life history patterns he observed. These ideas remained highly influential for the next 30 years, with extensions of the pattern beyond marine invertebrates to marine fishes. This eventually came to be known as "Thorson's rule" (Laptikhovsky, 2006).

In the 1990s, marine biologists started to challenge the orthodoxy of Thorson's rule for several reasons (Pearse, 1994). Thorson's ideas were not without problems; his understanding was limited by the data at the time. He thought that species with nonfeeding larvae were rare and did not occur at the poles. As studies accumulated, it became clear that many species have nonfeeding larvae and these were particularly common at the poles (Pearse, 1994). Thorson assumed that the poles were foodless deserts, but later studies showed that phytoplankton blooms, while brief, were significant in both the Arctic and Antarctic (Marshall et al., 2012). By the end of the 1990s there was a growing consensus that Thorson's ideas were outdated and that latitudinal patterns in marine organisms were less clear than once thought (Pearse and Lockhart, 2004).

Over the next decade, life history data continued to accumulate and explorations of biogeographical patterns in marine life histories became more sophisticated (Fernandez et al., 2009). More recent studies have taken advantage of technological achievements that were unavailable in Thorson's day. These include, for example, more formal statistical analyses of the association between life history and latitude, an exploration of the biophysical drivers underlying latitudinal gradients, and the introduction of phylogenetic techniques to control for common ancestry in constraining biogeographical patterns (Marshall et al., 2012). Today, a modified version of Thorson's rule has been revived (Marshall et al., 2012). Generally, higher latitudes are associated with larger offspring sizes, regardless of clade or hemisphere. This pattern appears most associated with latitudinal gradients in mean temperature. The tropics tend to have a higher proportion of species with feeding larvae while the poles are dominated by species with larvae that do not feed. Higher latitudes in the southern hemisphere tend to have much higher proportions of species that lack a larval phase, but this pattern does not occur in the northern hemisphere. While the poles and tropics are extremes and most different with respect to marine life history patterns, it is worth noting that they don't drive these patterns exclusively—the gradients exist within just the temperate latitudes as well (Marshall et al., 2012).

Interestingly, some life history patterns were not correlated with differences in mean environmental conditions. For example, the proportion of species with planktonic-feeding larvae and the size of offspring in this group are both unrelated to the mean abundance of planktonic food. This finding is surprising given that feeding larvae depend on planktonic food to complete their development. Instead, it seems that the predictability and seasonality of planktonic food at any one latitude is more important than the simple mean abundance for determining the prevalence and offspring size of species with feeding larvae (Marshall and Burgess, 2015). Accordingly, future studies should move beyond using simple means as a descriptor of environmental conditions and formally incorporate variability and predictability, as these clearly also act to shape marine life histories (Marshall and Burgess, 2015).

Given the strong biogeographical relationship we observe between temperature and developmental mode, it seems reasonable to predict that future global change will alter the global distribution of developmental modes. Specifically, we would predict a poleward extension of species with feeding larvae associated with global temperature increases. Initial evidence supports this prediction, with some species with feeding larvae greatly extending their range to higher latitudes (Marshall et al., 2012). There is some support for this prediction already (Ling et al., 2009). Whether species with nonfeeding or aplanktonic development are made more rare by global climate change remains unclear but is certainly a concerning possibility.

3.3 Theory of Parental Investment in Marine Organisms

One of the starkest dichotomies in marine invertebrate life histories is the grouping of species with feeding vs. nonfeeding larvae (Strathmann, 1985). There are a very few species, known as facultative planktotrophs, which can feed but can also complete development without feeding (Herrera et al., 1996), but the overwhelming majority of marine invertebrate larvae either do not feed at all or must feed to complete development. Offspring size covaries with developmental mode strongly (Figure 3.1): eggs smaller than around 120 µm in diameter tend to produce feeding larvae, while eggs larger 300 µm tend to only produce nonfeeding larvae (with the notable exception of *Conus*, in which feeding larvae can be up to 400 µm in diameter; Kohn and Perron, 1994). For a detailed consideration of the differences between planktotrophy, lecithotrophy, and feeding and nonfeeding larvae, see Strathmann (1985). The covariance between egg size and developmental mode has long fascinated biologists, and there have been repeated theoretical attempts to explain the evolution of egg size and development starting almost 50 years ago.

Richard Vance developed a theoretical model for predicting offspring size in 1973, and he developed it specifically for marine invertebrates (Vance, 1973). Smith and Fretwell published a more general model the following year (Smith and Fretwell, 1974), and this has received more attention from a broader audience, but it is worth noting that the first optimality model of offspring size was Vance's—a fact not often appreciated among life history theoreticians more generally. Vance's model has two key components, an offspring size-number trade-off and

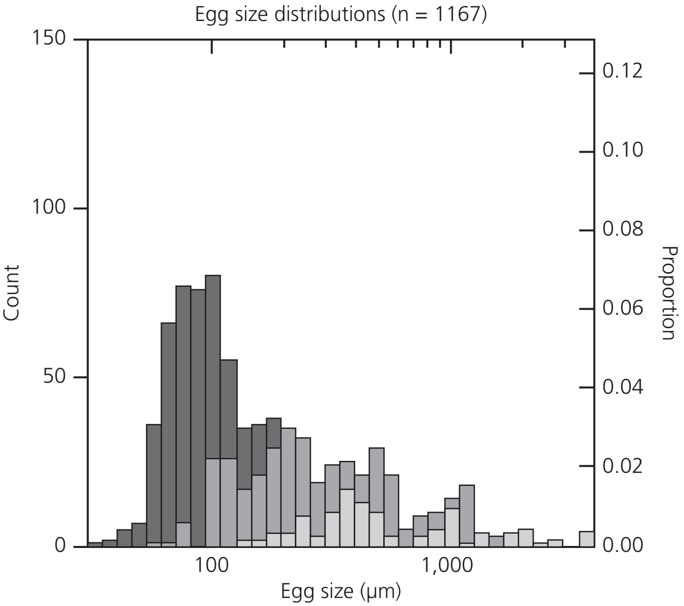

Figure 3.1 Distribution of offspring sizes (data taken from Marshall et al., 2012) across three developmental modes. The darkest bars are for species with feeding larvae, the intermediate shade for species with nonfeeding larvae, and the lightest bars are for species that lack a planktonic larval phase (see Plate 6).

an offspring size-fitness function (Vance, 1973). As far as we are aware, these two basic components have been retained in all models of offspring size since then. In this section we will consider the basic model of Vance, and outline some modifications that have been added in order to better reflect our understanding of how offspring size affects marine invertebrate life histories. We will later deal with empirical evidence for each component (the size-number trade-off and the offspring size-fitness function) separately. We will now briefly consider Vance's model (for a more detailed review see Marshall and Keough, 2008a).

In six relatively simple equations, Vance laid out his assumptions about how egg size affected fitness in marine invertebrates (Vance, 1973). He assumed that larger eggs took longer to develop through the embryonic stage before becoming larvae that could either feed or not feed. Thus, in species with nonfeeding larvae, the length of the larval phase was positively correlated with egg size. This was a particularly prescient assumption given there was little supporting data in 1973, but since then several studies have confirmed this relationship (Marshall and Keough, 2008a). Vance further assumed that in species with feeding larvae, larger eggs developed into larvae that spent less time in the plankton before accumulating sufficient resources to metamorphose—relative to the pre-feeding phase, Vance assumed that the length of the feeding period was much greater. Vance made no assumptions about size-specific mortality rates, though later models did (Christiansen and Fenchel, 1979). Vance also assumed that larvae would only ever be large enough to complete metamorphosis, a size he called s—there was no fitness advantage to producing eggs that are larger than s. Later studies by Herrera et al. (1996) and McEdward and Miner (2006) further discussed and quantified s in relation to maternal investment and nutritional mode of larvae. Vance also assumed that mortality rates were constant in the plankton, such that any extension of the larval period incurred more mortality. Finally, Vance assumed a direct energy trade-off between the size and number of offspring that mothers could produce: any increase in size yields a concomitant reduction in the number of offspring that mothers could make due to energy constraints.

Vance's model predicted that mothers should either produce the smallest possible offspring or the largest possible offspring (to a maximum size $s = 1$), and that local conditions would alter the balance between these extremes (Vance, 1973). The model predicted that food availability should affect the relative advantages of producing feeding vs. nonfeeding larvae: higher food abundances should favor the production of feeding larvae. However, as we saw in the previous section, this intuition is not supported in a straightforward way. Vance's model had the problem of "lost souls": infinitely (and therefore infinitely numerous) small offspring still had some fitness because the model always predicts fitness is maximized by producing infinitely small eggs—Vance assumed an arbitrary minimum viable offspring size to work around this problem.

The theoretical framework that Vance provided was an invaluable contribution to the field, and the paper should still be considered required reading by today's marine evolutionary ecologists. Nevertheless, the model contains assumptions that today have less support, and is limited to only one section of the life history, whereas it now appears that egg size has pervasive consequences across the entire life cycle. In what follows, we consider the key components of Vance's model and revise these in light of our current understanding.

3.4 Parental Investment, Egg Size, and the Size-Number Trade-Off

Vance's original suggestion that mothers must balance the size and number offspring that they can produce due to energy constraints has reverberated through the literature ever since. Upon initial consideration, such a constraint has intuitive appeal—mothers have a limited amount of energy they can devote to reproduction and so increases in the energy contained in each offspring must come at a cost to the number of offspring that can be produced. Thus, it could be argued that the natural unit of parental investment is the energy content of offspring rather than the size of offspring, and so studies should seek to measure energy content wherever possible. Such an approach raises the practical difficulty of measuring energy content of very small individuals, often in destructive ways. If offspring size is well correlated with energy content, then offspring size would be a convenient proxy for energy content, with the additional advantage of being a nondestructive measure. Offspring size also has the convenient property of capturing other potential trade-offs and can directly affect performance (more about this later). Thus, the crucial question remains: how well are offspring size and energy content correlated?

3.4.1 Does Offspring Size Reflect Energy Content?

Interspecific studies show strong relationships between egg size and energy content, but these are largely irrelevant to our considerations here given selection acts within species (Jaeckle, 1995). Likewise, while Vance's model has often been invoked to explain differences among species, the processes that operate to increase fitness of one phenotype over another operate within species. Indeed, Vance's model is explicitly intraspecific in its approach, though it is used to make inferences about interspecific patterns. Thus, while macroevolutionary patterns among species may provide clues as to the microevolutionary processes that produced them, the key relationships to be considered are the covariances between offspring size, energy content, and offspring performance within species.

Two problems with estimating the relationship between offspring size and energy content within species are that we're often working with relatively small amounts of variation in offspring size, such that the "signal" of covariation is likely to be small, and relatively imprecise methods for estimating content—though technological advances are improving methods all the time—such that the "noise" is likely to be substantial. This low signal-to-noise ratio makes tests of the relationship between offspring size and content highly susceptible to Type II statistical errors (false negatives). One might erroneously conclude that there is no relationship between offspring size and content simply because the range of sizes tested is too small and the imprecision of the measurement of content is too great. A good illustration of this problem is provided by *Solaster stimpsoni*, where an influential study using only a small number of replicates found no relationship between egg size and content (McEdward and Coulter, 1987), but a better replicated study later found that such a relationship did exist (McEdward and Chia, 1991), suggesting the earlier analysis had suffered a Type II error. There are a few different ways of dealing with this issue that we recommend. One approach would be to simply use a different α for concluding that a relationship is significantly different from zero (for a detailed consideration of adjusting α, see Quinn and Keough, 2002). We would argue, however, that even this approach is probably not the most informative.

Imagine that we find a significant relationship between offspring size and content. Under a standard frequentist approach, this tells us that the relationship is significantly different from zero, but it tells us nothing about how a single unit increase in size results in a corresponding increase in content. Yet for the strict energy-based trade-off that is often modeled to apply, there needs to be a one-to-one relationship between offspring size and content. We recommend that future studies focus on this one-to-one relationship; specifically, a more appropriate statistical approach would be to test whether the relationship between offspring size (volume) and content scale significantly differently from 1.

There are several ways of doing this. The simplest might be to determine whether the confidence intervals on the coefficient linking size and content overlap 1. Alternatively, a Wald test—where the difference between the coefficient and 1 is divided by the standard error of the coefficient and then compared against a t distribution (as in a standard Wald test for whether a slope is sufficiently different from 0, but here 0 is replaced by 1)—could be used to determine whether the relationship is significantly different from 1. The equivalent approach under a Bayesian framework would also work well. Regardless of the specific approach, we suggest that simply testing whether the relationship between offspring content and size is different from 0 is relatively uninformative, and future studies should instead formally test whether offspring size (volume) and content scale differently to a one-to-one ratio (Moran et al., 2013). As always, a power analysis should also be considered to determine whether such an effect can even be detected. This approach also reduces the likelihood of committing a Type II error.

3.4.2 Does Energy Content or Size Reflect Total Per-Offspring Investment?

Vance's original focus on the energy content of offspring means that subsequent studies have typically estimated the energy content of offspring once they are released from the parent, or have completed development. For example, there have been several subsequent reviews that cover the differences in composition of eggs from species with various developmental modes (Moran and McAlister, 2009). An issue with such an approach is that it only captures a proportion of the energy that the parent expended on each offspring. Similarly, offspring size only estimates the physical dimensions of an offspring upon release, and may not estimate all of the investment made to produce that offspring.

Ideally, any measure of parental investment should include the total costs of producing each offspring; this would include the costs of creating the reproductive structure that produced the egg, the reproductive tract for either receiving the sperm or spawning the egg, any accessory costs associated with the egg (e.g., follicle cells, egg coats, mucilage, and thickeners), and costs of moving to a spawning site. Gametes stored in the gonad are unlikely to be completely metabolically inert, and will consume some resources until release. In species that brood developing offspring, some require costly ventilation (e.g., crustacean egg broods) and others draw resources from the mother while developing (e.g., bryozoans, echinoderms; McClary and Mladenov, 1990). For mothers that release offspring into egg masses or capsules, the costs of the protective structures, as well as nutritive eggs or yolk material, must also be factored into the energy costs of producing the offspring. These costs matter because they will influence the per capita energy costs of producing offspring and alter the optimal balance between the size and number of offspring that mothers should produce. For example, Sakai and Harada (2001) predict that, because brooded offspring (in their case seeds, but the theory equally applies to brooded offspring) consume resources while increasing in size, the rate at which offspring consume resources relative to their supply while being brooded alters the predicted optimal offspring size that mothers should produce in order to maximize fitness. While a few studies have estimated the costs of brooding, and ventilation in marine invertebrates (McClary and Mladenov, 1990), the energy content of accessory structures (Bolton et al., 2000), and the provisioning of nurse egg structures (Collin and Moran, this volume), there are too few to generalize, and existing theory is yet to incorporate these overhead costs into offspring size-number models.

3.4.3 Does Energy Content Reflect the Proximal Constraints on Maternal Investment?

One problem with assuming that mothers are limited by energy in determining how they should balance the size and number of offspring that they produce is that it assumes that energy is the proximal limiting factor. Instead, in any one reproductive bout, the reproductive capacity of a female may simply be limited by size. For species that broadcast spawn, total investment in reproduction may be limited by maximum gonad size, and for species that brood, total investment might be limited by the maximum size of a brood that can be maintained or oxygenated (Strathmann and Strathmann, 1982). From this perspective, offspring size may represent a more natural currency to consider as a direct trade-off for number. However, too few studies have examined how space limited brood or gonad capacity is in marine invertebrates (though Strathmann and others have argued that it does represent an important limit).

3.5 Offspring Size-Fitness Functions

Regardless of what costs (space, energy) are associated with increasing offspring size, it seems reasonable to assume that if offspring size does not affect subsequent offspring fitness, then mothers should produce the smallest, cheapest (in terms of energy) offspring possible because this will maximize maternal fitness. If, on the other hand, offspring size does positively affect fitness, then mothers must balance the costs of producing larger, more expensive offspring with the benefits of each offspring having higher fitness. Ever since Vance's assumption that offspring size affects planktonic duration alone, we now have a wealth of data that suggests that offspring size affects every aspect of offspring fitness, from initial fertilization through metamorphosis, and can affect adult reproduction and even lifespan. Throughout the following, we will consider only the effects of offspring size on subsequent performance within species, as this is an appropriate scale for considering the eco-evolutionary dynamics of parental investment. For an exploration of among-species covariation between offspring size and performance, see Marshall and Keough (2008a).

3.5.1 Offspring Size and Fertilization Success

By recent estimates, around 50% of all marine invertebrates have external fertilization, where eggs and sperm must meet in water (Monro and Marshall, 2015). External fertilization is fraught, with the probability of being fertilized strongly dependent on sperm concentration and thus the density of spawning males. When sperm concentrations (and male densities) are too low, the probability of an egg being contacted by a sperm is low and so fertilization success is sperm-limited. When sperm concentration (and male densities) are too high, then the probability of eggs being contacted by multiple sperm simultaneously is high, and if multiple sperm enter the egg before the egg has a chance to create a block, then the egg suffers a condition known as polyspermy and usually dies. While there has been debate regarding the prevalence of both sperm limitation and polyspermy in natural populations, it is reasonable to assume that both happen and their likelihood depends mostly on the density of spawning males and local hydrodynamic conditions. It now seems that egg size also affects fertilization with consequences for selection on offspring size.

Vogel et al. (1982) predicted and Levitan (1996) showed that egg size affects the kinetics of fertilization: larger eggs are more likely to be contacted by sperm simply because they present a larger target for sperm to hit. Levitan showed that under sperm-limiting conditions, larger eggs were favored; Levitan incorporated the influence of egg size on fertilization into a modified version of the Vance model (Levitan, 2000). Later, Marshall et al. (2002) showed that not only were larger eggs more likely to be fertilized under sperm-limiting conditions, but they are also more likely to suffer polyspermy under sperm-saturating conditions. Thus, all else being equal, high densities of sperm/males should favor smaller eggs and low densities should favor larger eggs, a prediction that has some empirical support (e.g., Crean and Marshall, 2008).

3.5.2 Offspring Size and the Planktonic Period

Looking across species and developmental modes, species with small eggs and feeding larvae tend to have longer planktonic periods than species with larger eggs and nonfeeding larvae. A study of echinoderm life histories found that planktonic duration did not correlate well with developmental mode (Mercier et al., 2013); in only two classes out of four (echinoids and ophiuroids) did species with feeding larvae have longer durations than species with nonfeeding larvae. The failure to find an effect of developmental mode for holothuroids and asteroids is surprising, and we decided to reanalyze those data. Importantly, we included the effect of rearing temperature in the analysis for which data were available because planktotrophic species are more likely to occur in warmer waters and nonfeeding species are more likely to occur in cooler waters; in other words, temperature could confound the effect of developmental mode. Given that temperature is likely to drive developmental times strongly and that the key comparison of interest is the effect of developmental mode on developmental period for a given temperature, we therefore statistically controlled for temperature by including it as a covariate. Using an ANCOVA approach, we found a strong effect of developmental mode in both holothuroids ($F_{1,24} = 15.15$, $P < 0.001$) and asteroids ($F_{1,50} = 22.59$, $P < 0.001$). For asteroids, we find that for a given temperature, feeding larvae have a developmental period that is twice as long as nonfeeding larvae, and for holothuroids, feeding larval periods are almost eight times longer than nonfeeding larval periods. Thus, we would agree with Mercier et al. (2013) that larval developmental mode alone is a poor predictor of developmental period across wide temperature ranges. Nevertheless, once the confounding influence of temperature is taken into account, we would instead conclude that larval mode is an excellent predictor of developmental period across all echinoderm classes. Thus, Vance's intuition that planktotrophs are cheaper to make but spend longer in the plankton and therefore accumulate more mortality holds true for Echinodermata in any one thermal environment. We will now examine patterns within each developmental mode and within species.

Vance's predictions about how offspring size affects planktonic period were remarkably prescient. In species with nonfeeding larvae, larger eggs generally take longer to develop and hatch than smaller eggs (though there are exceptions). Larger nonfeeding larvae also tend to be more selective with respect to settlement, taking longer to reach competence to metamorphose, but are also more likely to reject low quality settlement sites for longer (Marshall and Steinberg, 2014).

In species that are released as competent nonfeeding larvae (e.g., colonial ascidians, bryozoans, and sponges), larger larvae tend to have longer planktonic periods than smaller larvae. Though larger larvae are capable of ending the larval period as soon as smaller larvae, it is thought that larger larvae are more likely to delay settlement in the absence of cues for high quality habitat. A recent study (Pettersen et al., 2015) suggests that larger larvae not only begin life with more energy, but because of the allometric relationship between offspring size and offspring metabolism, larger larvae also utilize a lower proportion of their energy reserves, such that delaying metamorphosis is less costly in larger larvae relative to smaller larvae. Regardless of the mechanism, it seems that larger larvae have a higher chance of settling into higher quality.

In species with feeding larvae, limited evidence suggests that larger eggs take longer to hatch into feeding larvae than smaller eggs. A series of elegant manipulations of egg size by Sinervo and McEdward (1988) as well as Hart (1995) showed that egg size also affects the duration of the larval feeding period in sea urchins in the manner predicted by Vance. Later studies also show that generally, larger eggs require less time as feeding larvae in order to complete development.

While the effects of egg size on the overall planktonic period are increasingly well understood, more detailed explorations of the mechanisms by which offspring size affects fitness in species with feeding larvae are lacking. For example, it is easy to imagine how offspring size may affect the ability of larvae to feed, exploit different food resources, or resist starvation. Furthermore, offspring size has long been predicted to affect susceptibility to predation (Christiansen and Fenchel, 1979), a prediction that has some initial support (Allen 2008).

3.5.3 Offspring Size Effects on Post-metamorphic Performance

Offspring size affects the survival, growth, reproduction, and longevity of marine invertebrates (Table 3.1). Within a range of species and developmental modes, larger offspring tend to survive better than smaller offspring. The mechanisms by which larger offspring have a survival advantage are unclear. Larger offspring can be better buffered against starvation, more resistant to predation, and more competitive than their smaller conspecifics (Marshall and Keough, 2008a).

Larger offspring also tend to show higher rates of post-metamorphic growth than smaller offspring (Table 3.1). In contrast, one study (Jacobs and Sherrard, 2010) on seven ascidians failed to find a relationship between initial offspring size and subsequent size though this study had limited replication (an average of nine replicates per species). In some colonial marine invertebrates, offspring size affects initial asexual budding rates with larger offspring producing more daughter zooids than smaller offspring. In other species, the mechanism by which offspring size affects growth remains unclear, though viable explanations include size-based differences in feeding structures or foraging behavior such that larger offspring can gain resources more efficiently (Kosman and Pernet, 2011). A recent study (Pettersen et al., 2015) also shows that metamorphosis is relatively less costly for larger offspring than smaller offspring. Pettersen et al. (2015) show that, because metabolism scales allometrically with size, smaller offspring burn ~47% of their energy reserves in order to complete metamorphosis while larger offspring will burn ~22%. Thus, as well as possibly beginning life with a higher research of energy, larger offspring are also more efficient in passing through the costly

Table 3.1 Studies Examining Effect of Offspring Size on Post-Metamorphic Performance in Marine Invertebrates.

Study	Location	Species	Survival	Growth	Reproduction
Emlet and Sadro, 2006	Field	*Balanus glandula*	✗	✓	
Kosman and Pernet, 2011	Lab	*Bugula californica*		✓	
Burgess et al., 2013	Field	*Bugula neritina*	✓	✓	✓
Monro et al., 2010	Field	*Bugula neritina*	Mixed	✗	
Monro et al., 2010	Lab	*Bugula neritina*	✗	✓	
Kosman and Pernet, 2011	Lab	*Bugula neritina*		✓	
Dias and Marshall, 2010	Field	*Celleporaria* sp.		✓	✓
Kosman and Pernet, 2011	Lab	*Cryptosula pallasiana*		✓	
Allen and Marshall, 2014	Field	*Hydroides diramphus*	✗	✓	
Allen and Marshall, 2013	Field	*Hydroides diramphus*	✓	✓	
Kesselring et al., 2012	Field	*Janua pagenstecheri*	✓(negative effect)	✓	✓
Gehman and Bingham, 2009	Lab	*Leptasterias aequalis*	✓	✓	
Rius et al., 2010	Field	*Microcosmus squamiger*	✓	✓	
Sun et al., 2015	Lab	*Urticina felina*	✗		
Davis and Marshall, 2014	Field	*Watersipora subtorquata*		✓	
Marshall and Monro, 2012	Field	*Watersipora subtorquata*		✓	✓
Marshall and Keough, 2008	Field	*Watersipora subtorquata*	✓	✓	
Lange and Marshall, 2016	Field	*Watersipora subtorquata*		✓	
Crean et al., 2011	Field	*Styela plicata*	✓	✓	
Jacobs and Sherrard, 2010	Field	*Boltenia villosa*	✗		
Jacobs and Sherrard, 2010	Field	*Styela gibbsii*	✗		
Jacobs and Sherrard, 2010	Field	*Corella inflate*	✗		
Jacobs and Sherrard, 2010	Field	*Diplosoma macdonaldi*	✗		
Jacobs and Sherrard, 2010	Field	*Distaplia occidentalis*	✗		
Jacobs and Sherrard, 2010	Field	*Botrylloides violaceus*	✗		
Jacobs and Sherrard, 2010	Lab	*Boltenia villosa*		✗	
Jacobs and Sherrard, 2010	Lab	*Styela gibbsii*		✗	
Jacobs and Sherrard, 2010	Lab	*Corella inflate*		✗	
Jacobs and Sherrard, 2010	Lab	*Ciona savigni*		✗	
Jacobs and Sherrard, 2010	Lab	*Diplosoma macdonaldi*		✗	
Jacobs and Sherrard, 2010	Lab	*Distaplia occidentalis*		✗	
Jacobs and Sherrard, 2010	Lab	*Botrylloides violaceus*		✗	
Carrasco et al., 2012	Lab	*Cominella virgata*	✗	✓	
Carrasco et al., 2012	Lab	*Cominella maculosa*	Mixed	✓	
Pernet et al., 2012	Lab	*Capitella teleta*	✓	✓	

Note. Unless otherwise stated, crosses indicate no significant effect, and check marks indicate a significant, positive effect of offspring size on performance. Where mixed effects were recorded, the effects of offspring size were inconsistent among different experiments.

metamorphic stage. Though there are fewer studies, offspring size effects on post-metamorphic performance also occur in species with feeding larvae (Allen and Marshall, 2010). It seems that even small differences in initial investment can still manifest in the adult stage despite an extended larval feeding stage. This persistent difference may be due to the differences in efficiency between smaller and larger offspring discussed above, but tests of metabolic scaling in species with feeding larvae suggest otherwise (Moran and Allen, 2007).

Experimental studies within species that differ in relative investment suggest that offspring size may have complex relationships with reproduction. For example, both Marshall et al. (2003) and Dias and Marshall (2010) find that larger offspring tend produce more offspring themselves relative to smaller offspring. These effects are not always straightforward, however: Kesselring et al. (2012) showed that while larger offspring tended to reproduce more in any one reproductive bout, they also died sooner than smaller offspring such that they took part in fewer reproductive events. These experimental results are essential in order to provide empirical tests for hypotheses developed in the context of models or comparative datasets. Given that reproductive output is one of the best estimates of true fitness, we would argue that more studies that follow the entire life history, including life span and total reproductive output, are needed.

3.6 Eco-evolutionary Dynamics of Parental Investment

3.6.1 Ecological Importance of Offspring Size

Given the effects of offspring size on subsequent performance, it seems reasonable to assume that variation in offspring size is likely to be an important driver of ecological dynamics. While marine ecologists have long focused on the role of variation in the quantity of larvae entering the population as a driver of population dynamics, offspring size effects suggest that we should also consider the quality of larvae entering the population. Indeed, larval quality effects more generally can overwhelm the effects of larval quantity effects in marine populations (Burgess and Marshall, 2011a). Examination of the ecological importance of offspring size for populations are exceedingly rare but the one study that has explored this formally found that offspring size plays only a limited role: offspring size only accounted for between 0.1% and 15% of total variation in post-metamorphic performance in the bryozoan *Watersipora subtorquata* (Lange and Marshall, 2016). Importantly, offspring size may not only affect the dynamics of the focal species in which offspring size varies, rather it can also affect the assembly of the surrounding community. Davis and Marshall (2014) found that offspring size in a resident species can be more important in driving community assembly in the field than the density of the resident species. Paradoxically, when the resident species originated from larger offspring (and therefore grow faster), the community that subsequently assembled was denser than when the resident species originated from smaller offspring (and therefore grew slower). These results suggest that offspring size affects not only the performance of the focal species but also affects its niche usage and the capacity for other species to coexist. Whether offspring size has community-level effects in other systems or species remains completely unexplored, but as Davis and Marshall (2014) argue, such effects are likely to be widespread.

3.6.2 Drivers of Among-Environment Variation in Offspring Size

Previous reviews (e.g., Marshall et al., 2008a; 2012) have identified the drivers of broadscale temporal (e.g., seasonal) and spatial (e.g., latitudinal) patterns in offspring size, and so here we focus on local-scale source of variation in offspring size. Similarly, the role of maternal phenotypes such as size in altering the offspring size relationship has also been dealt with in a separate review.

Life history theory predicts that changes in the offspring size-performance relationship should alter the offspring size that mothers should produce (Parker and Begon, 1986; Kindsvater and Otto, 2014). Formal theory predicts that optimal offspring size is dependent on the steepness of the relationship between offspring size and performance. Generally, if the relationship is steep, then mothers will be better off producing larger offspring because the per capita fitness return of high performing, larger offspring exceeds the per capita cost of producing larger offspring. Conversely, when the relationship is shallow, mothers should produce smaller offspring because they get much of a less fitness return for a given increase in per capita investment and are better off maximizing the number of offspring that they can produce. Thus, any changes in the environment that alter the offspring size-performance relationship should alter the fitness returns of a given offspring size.

If the maternal environment changes, and it is a good predictor of the offspring environment, then selection should favor mothers that alter the size of their offspring accordingly (Burgess and Marshall, 2014). There is increasing evidence that such transgenerational plasticity is widespread in marine invertebrates both among and within populations. The environmental cues to which mothers modify the investment in eggs include diverse factors: biotic and abiotic, as well as natural and anthropogenic. In the bryozoan *Bugula neritina*, colonies reared in high-competition environments produce larger offspring that are better competitors and more likely to disperse away from local competitive conditions (Allen et al., 2008). Similarly, colonies exposed to a heavy metal stress will also produce larger, more resistant offspring that are more likely to disperse away, potentially to avoid the physiological stressor in the next generation (Marshall, 2008). Mothers exposed to higher temperature tend to produce smaller offspring that perform better in higher temperatures themselves (Burgess and Marshall, 2011b). Mothers can also alter the phenotype of their offspring in relatively subtle ways. For example, in the ascidian *Styela clava*, individuals reared at high densities produce smaller eggs than individuals reared at low densities (Crean and Marshall, 2008). The change in overall egg size comes from a decrease in the size of egg accessory structures (follicle cells) such that the overall target of the egg is smaller and less susceptible to polyspermy. Even though the overall egg size is smaller, the ovicell, the portion of the egg that provides nutrition for the offspring, actually increases in size in individuals reared at high densities—presumably to increase the dispersal potential and competitive ability of those individuals (Crean and Marshall, 2008).

Such size-based changes in offspring size are not universal. For example, in tubeworms, mothers exposed to lower salinities or higher temperatures do not change the size of their offspring, even though the performance of their offspring changes dramatically, suggesting that mothers can manipulate the phenotype of their offspring in numerous ways (Jensen et al., 2014; Guillaume et al., 2015), which may differ between populations (Collin and Salazar, 2010).

3.6.3 Environmental Dependent Variation in Offspring Quality Other than Size

Mothers may be able to manipulate the phenotype of the eggs and offspring in ways that are unrelated to size. Maternal effects beyond offspring size are common in diverse organisms (e.g., oviparous vertebrates, insects, vascular plants; Rossiter, 1996) and are surely present in marine invertebrates as well. Thus, while much of the theoretical and empirical work on ecologically and evolutionary related variation in marine invertebrate offspring has focused on size as a proxy for investment, additional elements of the egg phenotype affect offspring fitness.

Vitellogenesis broadly refers to the period of oocyte development in the ovary where protein, lipids, and carbohydrates are synthesized or assimilated into the maturing egg. These biochemical components can either be synthesized in a non-ovarian tissue (liver in mammals, fat body in insects) or in the ovary and transported into the oocyte via endocytosis (termed, heterosynthetic), or they can be synthesized by the egg itself after small molecule uptake (termed, autosynthetic). Research by Eckelbarger (2005) suggests that species with heterosynthetic mechanisms of yolk synthesis can produce mature eggs rapidly because large molecules like vitellogenin are delivered and endocytosed in mature form. Furthermore, Eckelbarger (2005) hypothesized these mechanisms and the ovary may exert significant effects on egg investment, among other factors, important for larval development. Thus, these vitellogenic mechanisms could promote different forms of plasticity in egg composition. For species with heterosynthetic yolk production, the quantity of yolk deposited into each egg could be altered by environment-dependent shifts in vitellogenin and other large molecules available during oocyte maturation or the modification of lipoproteins and vitellogenin-specific cell receptors on the oocyte membrane. For autosynthetic species, the environment may shift the proportion of amino acids, monosaccharides, and fatty acids circulating in the female during egg maturation and thus the small molecules available from which larger nutritive molecules are synthesized. In both cases, the mature egg may more closely match the maternal nutritive profile and thus may better match the current environment. Mature oocytes provide the initial nutrition to the embryo in the form of yolk protein. In many oviparous organisms, vitellogenin serves as the precursor yolk protein that is enzymatically cleaved into lipoproteins and phosphoproteins. Biochemical measurements of mature oocytes have determined the quantity of lipids, proteins, and carbohydrates and, in some cases have treated these as species' characteristics that represent maternal investment. However, females may shift not only the total caloric investment but potentially the representation of each category of molecule in functionally important ways, particularly in response to environmental variation (Moran and McAlister, 2009; Marshall and Keough, 2008b). For example, females experiencing lower food environments at time of reproduction may produce eggs with higher relative protein in place of lipid for their size than conspecifics in more food rich environments. Thus, while the size and total caloric content may remain the same, the molecules may shift.

Furthermore, mature eggs are incredibly complex cells with subcellular localization of proteins to the membrane and other regions of the cell, diverse RNA types, and organelles. For example, proteomic approaches applied to oocytes have shown that mature eggs are composed of hundreds to thousands of proteins that are not explicit sources of energy but instead involved in the development of the embryo (Lotan et al., 2014). These proteins have diverse roles including cell cycle regulation, RNA silencing, membrane signaling, and metabolism. Thus, females may provision their eggs with proteins to better suit their offspring to the current environment. For example, the aforementioned tubeworms exposed to low salinity may have increased relative amounts of mRNA or proteins into their eggs favoring performance in these more stressful environments. Potential candidates could include general chaperon proteins like heat-shock proteins or process-specific proteins like aquaporins.

We should also recognize that the evolution of environmental manipulations to eggs is limited by the costs and limits common to any plasticity response. The environment may not represent reliable cues to mothers such that there is no selection for mothers to alter their offspring size—formal estimates of environmental predictability are necessary if tests of transgenerational plasticity are to be reliable (Burgess and Marshall, 2014).

3.6.4 Within-Brood Variation

Offspring size varies not only among broods and mothers, but it also varies within broods. Whether this variation is adaptive is hard to determine. It has been suggested that within-brood variation represents a form of bet-hedging, mothers may make a range of offspring sizes when their future environment is unpredictable (Crean and Marshall, 2009). Among species patterns in within-brood variation suggest that species with more dispersive larvae (and less predictable experience) tend to have higher within-brood variation in offspring but any number of factors could drive these effects (Marshall et al., 2008b). Within species tests of this idea are rare and inconclusive (Crean and Marshall, 2009). Empirically distinguishing between adaptive bet-hedging strategies and simple developmental instability may prove difficult in most systems and so for now, the adaptive significance of within-brood variation in offspring size remains unclear.

3.7 Future Directions

Marshall et al. (2012) reviewed the biogeography of marine invertebrate life histories, and their Figure 1 provides a striking visual indication that there are still vast swaths of the global marine environment that remain unexplored (or at the least, undocumented). With respect to marine invertebrate life histories, the possibility exists that some of these unexplored areas have in fact been studied and that difficulties in obtaining published work in languages utilizing a non-Latin alphabet may bias our understanding. However, the majority of global locations are represented by only one to two published studies, and in only three areas (the Puget Sound region of North America, the English Channel, and Eastern Australia) do the number of studies fall into the article's highest category (55–104 published studies). These results suggest that well-studied areas are outliers to the overwhelming paucity of data on marine invertebrate life histories, globally.

Further study of this image reveals broader-scale patterns of our lack of information. There is a bias toward more information from northern than southern hemisphere locations, toward temperate over tropical regions, and data from polar locations is largely absent, aside from two moderately well studied locations in Antarctica adjacent to polar research stations. Other largely unexplored coastal areas include the majority of the coasts of Africa, South America, and Antarctica, the Middle East and India, Indonesia, northern Russia and the Kamchatka Peninsula, northern Canada, Alaska and the Aleutian Islands, as well as many isolated island archipelagos worldwide. The life histories of marine invertebrates inhabiting the vast majority of the deep-sea benthos (the largest habitat on Earth) are also unknown to science.

Going forward, how may exploration into these biogeographically understudied areas be important for refining a general theory of offspring investment? Temperature and food availability are recognized as the dominant variables contributing to latitudinal patterns in offspring size and maternal investment (Thorson, 1950; Vance, 1973; Laptikhovsky, 2006; O'Connor, 2007). Additional latitudinal and longitudinal sampling will allow us to ascertain if these variables function in similar ways at similar geographical positions, or if other organism or ecosystem specific variables play significant roles. For example, marine habitats off the western coasts of North and South America, and Northwestern and Southwestern Africa all experience wind-driven coastal upwelling. Comparing patterns of offspring size and maternal investment within and among taxa from these four areas would provide a strong test of whether patterns of offspring size and maternal investment hold across species found in similar marine ecosystems at similar latitudes or if they differ longitudinally or across taxa. Increasing depth may also yield patterns of offspring size and maternal investment that are similar to those found by latitude. Although the available data to test this hypothesis are limited and results appear to vary by taxa and location, there is a trend toward the production of larger eggs with increasing depth (Gage and Tyler, 1991; Auel, 2004). Refinement of this hypothesis would require additional deep-sea research efforts to specifically examine reproductive biology. If these types of studies are conducted within a comparative framework, taking advantage of unique replicated environments, they may provide for powerful tests of the biogeographical ideas presented here. Lastly, modern technological advances in computing and social connectivity make it feasible to establish online databases that compile offspring size data that is collected and uploaded directly by local researchers. Large-scale projects of empirical data collection based on a crowd-source model may be possible and may yield unique insights into how reproductive patterns are changing globally in our rapidly warming world.

3.8 Summary

1. Parental investment varies dramatically in marine invertebrates and is largely unrelated to phylogeny. Instead, strong biogeographical patterns in parental investment exist with the largest offspring being produced at the poles and the smallest in the tropics.
2. Offspring size is a convenient proxy for parental investment but uncertainty remains regarding how completely offspring size captures total parental investment.
3. Some of the first life history models of offspring size were developed for marine invertebrates, and for over 40 years marine biologists have sought to parameterize these models but key gaps our understanding regarding the offspring size-number trade-off remain.
4. Offspring size not only affects the larval period, as was initially thought, but instead affects the entire life history, from fertilization through to post-metamorphic performance.
5. There is increasing evidence that mothers manipulate the size and phenotype of their offspring in response to local environmental variation in order to maximize offspring fitness.
6. Despite decades of study, much of the world's life history variation remains unknown; instead,

we know a lot about only a few places. We also have little understanding of the mechanisms by which mothers manipulate the phenotype of offspring in order to maximize fitness.

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