THE EVOLUTIONARY ECOLOGY OF OFFSPRING SIZE IN MARINE INVERTEBRATES

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Contents

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Abstract

Intraspecific variation in offspring size is of fundamental ecological and evolutionary importance. The level of provisioning an organism receives from its mother can have far reaching consequences for subsequent survival and performance. In marine systems, the traditional focus was on the remarkable variation in offspring size among species but there is increasing focus on variation in offspring size within species. Here we review the incidence and consequences of intraspecific offspring-size variation for marine invertebrates.

Offspring size is remarkably variable within and among marine invertebrate populations. We examined patterns of variation in offspring size within populations using a meta-analysis of the available data for 102 species across 7 phyla. The average coefficient of variation in offspring size within populations is 9%, while some groups (e.g., direct developers) showed much more variation (15%), reflecting a fourfold difference between the largest and smallest offspring in any population.

Offspring-size variation can have for reaching consequences. Offspring size affects every stage of a marine invertebrate's life history, even in species in which maternal provisioning accounts for only a small proportion of larval nutrition (i.e., planktotrophs). In species with external fertilization, larger eggs are larger targets for sperm and as such, the sperm environment may select for different egg sizes although debate continues over the evolutionary importance of such effects. Offspring size affects the planktonic period in many species with planktotrophic and lecithotrophic development, but we found that this effect is not universal. Indeed, much of the evidence for the effects of offspring size on the planktonic period is limited to the echinoids and in this group and other taxa there is variable evidence, suggesting further work is necessary. Post-metamorphic effects of offspring size were strong in species with non-feeding larvae and direct development: bigger offspring generally have higher post-metamorphic survival, higher growth rates and sometimes greater fecundity. Although there is limited evidence for the mechanisms underlying these effects, the size of post-metamorphic feeding structures and resistance to low-food availability appear to be good candidates. There was limited evidence to assess the effects of offspring size on post-metamorphic performance in planktotrophs but surprisingly, initial indications suggest that such effects do exist and in the same direction as for species with other developmental modes. Overall, we suggest that for direct developers and species with non-feeding larvae, the post-metamorphic effects of offspring size will be greatest source of selection.

Offspring-size variation can arise through a variety of sources, both within and among populations. Stress, maternal size and nutrition, and habitat quality all appear to be major factors affecting the size of offspring, but more work on sources of variation is necessary. While theoretical considerations of offspring size can now account for variation in offspring size among mothers, they struggle to account for within-brood variation. We suggest alternative approaches such as game theoretic models that may be useful for reconciling within-clutch variation. While some of the first theoretical considerations of offspring size were based on marine invertebrates, many of the assumptions of these models have not been tested, and we highlight some of the important gaps in understanding offspring-size effects. We also discuss the advantages of using offspring size as a proxy for maternal investment and review the evidence used to justify this step.

Overall, offspring size is likely to be an important source of variation in the recruitment of marine invertebrates. The quality of offspring entering a population could be as important as the quantity and further work on the ecological role of offspring size is necessary. From an evolutionary standpoint, theoretical models that consider every life-history stage, together with the collection of more data on the relationship between offspring size and performance at each stage, should bring us closer to understanding the evolution of such a wide array of offspring sizes and developmental modes among species.

1. INTRODUCTION

Offspring size is a trait of fundamental interest to evolutionary biologists and ecologists. Offspring size, for our purposes, will be defined as the volume of a propagule once it has become independent of maternal nutritional investment. According to this definition, the size of freely spawned egg is the appropriate measure of offspring size but the size of a direct developing snail egg before the embryo has ingested nurse eggs is not. The enormous range of offspring sizes observed among species, even closely related ones (Fig. 1.1), has long fascinated biologists as to the selection pressures that led to such divergent sizes (Lack, 1947). Offspring size is of particular interest because while it has fitness consequences for both the offspring and mother, selection acts to maximize maternal fitness only (Bernardo, 1996). Thus, mother and individual offspring may be in conflict with regards to the strategy that maximizes fitness (Einum and Fleming, 2000). Similarly ecologists have long been interested in the role of maternal investment in population dynamics (Bagenal, 1969) and for most organisms, offspring size is the sole source of maternal investment. If we hope to understand the evolutionary pressures acting on offspring size, then we must first determine the ecological consequences of this variation within species. In his excellent review of propagule size effects, Bernardo (1996, pp. 219–220) points out 'The ecological and evolutionary implications of variation in propagule size are evaluated by selection and modelled by theoreticians as a within-population variance component. . . . It is at the within- to among-population (intraspecific) level that we should seek evidence of the ecological role and evolutionary dynamics of propagule size and their relationship to parental phenotypes . . .'. The goals of evolutionary

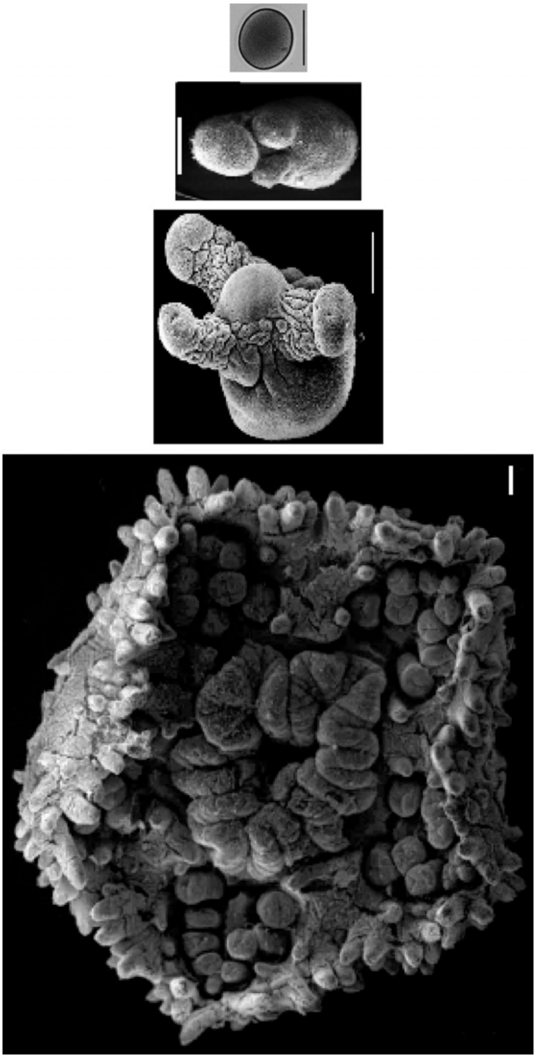


Figure 1.1 Micrographs of the offspring from four species of closely related Australian sea stars within the Asterinidae, left to right is the brooded *Parvulustra parvivipara*, the benthic lecithotroph *Parvulustra exigua*, the lecithotrophic broadcast spawner *Meridiastra calcar* and the planktotrophic broadcast spawner *Patiriella regularis*. Scale bar is 100 μm and note that for *P. parvivipara*, the scale bar is half the size of the others. Micrographs courtesy of Maria Byrne.

biology and ecology can be achieved by the same means then—the examination of the effects of offspring size within individual species.

Marine invertebrates have one of the most diverse and striking range of offspring sizes exhibited among species. For example, latitudinal patterns in offspring size were noted more than 50 years ago by Thorson (1950). Consequently, one of the first attempts at modelling offspring size was done with marine invertebrates in mind (Vance, 1973a). In their excellent review of *Conus* life-history strategies, Kohn and Perron (1994) concluded that, '... egg size is the single most important attribute of understanding (1) reproductive energetics; (2) the temporal patterns of embryonic development and larval biology; (3) dispersal potential, which is tightly linked to (1) and (2) but is an evolutionary "byproduct"...'. However, despite a long fascination with offspring-size evolution, intraspecific variation in offspring size and its effects have only recently been examined in detail. One of the first studies on intraspecific offspring-size variation in marine invertebrates was done in the late 1970s (Turner and Lawrence, 1977), but for the most part earlier work tended to focus on the effects of interspecific variation (e.g., Berrill, 1935; Dickie *et al.*, 1989; Emlet *et al.*, 1987; Hoegh-Guldberg and Pearse, 1995; Staver and Strathmann, 2002; Steele, 1977 but see Kohn and Perron, 1994). Indeed, it has been our personal experience that people are surprised when we present remarkably high levels of variation in offspring size within species. However, in both the terrestrial and marine literature, offspring-size studies have increasingly focused on within-species variation. We believe that this is appropriate: as pointed out by Bernardo (1996), it is inappropriate to use interspecific studies to infer ecological effects or evolutionary transitions without controlling for species relationships (for detailed discussion, see Harvey and Pagel, 1991). More importantly, intraspecific variation in offspring size has the potential to dramatically change our view of the dynamics of marine invertebrate populations. Settling larvae are traditionally viewed (and modelled) as being homogenous in their chances of recruiting and their post-settlement performance (Eckman, 1996; Vance, 1973). However, it has become clear that settling larvae vary greatly in their potential to survive and grow to reproduction. Exposure to pollutants, increased swimming durations or larval activity levels and larval nutrition can strongly affect post-metamorphic performance in a range of taxa (Highsmith and Emlet, 1986; Marshall *et al.*, 2003b; Ng and Keough, 2003; Pechenik *et al.*, 1998, 2001; Phillips and Gaines, 2002; Wendt, 1998). Many of these 'carry-over' effects are thought to be mediated by variation in larval energetic reserves (Bennett and Marshall, 2005; Wendt, 2000) such that if larger offspring have more energetic reserves than smaller offspring, then similar effects would be expected. Thus, offspring size could be an important source of variation in larval quality and, consequently, variation in recruitment. Traditionally, we have viewed marine invertebrate populations as being strongly affected by the *quantity* of larvae entering a population; intraspecific variation in offspring could also mean that the *quality* of larvae could have equally important effects.

In light of the evolutionary and ecological importance of intraspecific variation in offspring size, we have several aims for this review:

1. Document and quantify the amount of variation in offspring size within marine invertebrate species.
2. Review the known effects of offspring size across the various life-history stages of marine invertebrates.
3. Identify the common sources of intraspecific variation in offspring size within and among marine invertebrate populations.
4. Summarize the findings of the theoretical literature on offspring-size effects in marine invertebrates.
5. Identify the key knowledge gaps that currently limit our understanding of the ecological and evolutionary consequences of offspring-size variation.

Our first aim represents an attempt to highlight the fact that offspring sizes are extremely variable within and among marine invertebrate populations. Our second aim is a first attempt at integrating the various findings for different life-history stages, and we hope to demonstrate that selection is likely to act on offspring size across multiple, if not all, life-history stages. We will demonstrate that offspring-size variation can have pervasive and important effects on performance at each life-history stage, so the next obvious step is to identify some of the sources of this variation. We will then examine whether current theoretical considerations of the issue match our empirical findings and the problems associated with various approaches. We will then attempt to identify the appropriate next steps in understanding the evolutionary and ecological consequences of offspring-size variation within species.

2. HOW VARIABLE IS OFFSPRING SIZE WITHIN SPECIES?

2.1. Meta-analysis of the literature

In this section, we summarize the degree of variation in offspring sizes from species, from a range of taxa and from 7 phyla (including 35 orders, 58 families and 102 species) and compare the relative variation from each of the three major developmental modes (planktotrophic, lecithotrophic and direct development). Here, lecithotrophic is used as a general term for non-feeding larvae; however, it is recognized that not all non-feeding larvae are necessarily ‘yolk feeding’. Facultative planktotrophs (species that can feed but do not necessarily need to in order to become competent to metamorphose McEdward, 1997) are considered to be lecithotrophic for the purposes of this chapter. For the purposes of our analysis and our review more generally, we define 'direct development' here as any development whereby the offspring are fully formed juveniles independent of maternal nutrition sources (although not necessarily maternal nutrition: these juveniles may still be utilizing maternal yolk reserves). The two groups with planktonic development were further partitioned into internal and external fertilizers. We compiled data on variation in offspring size from the available literature and from our own unpublished data (see Appendix). The most commonly reported measure of offspring size was length of embryos/newly hatched larvae or egg diameter. For a number of species (especially the gastropods), the sizes of a range of different developmental stages were available. Because we were interested in variation in total maternal investment per offspring, the measure that best reflected this investment was utilized. For example, for gastropods that fed on nurse eggs prior to hatching, we utilized measures of size and variation in size for newly hatched juveniles rather than those parameters for newly laid eggs (cf. Kohn and Perron, 1994). We used data for species only where the eggs of two or more individuals were measured. Often the source of the variation (among broods or within broods) was not reported and so for the majority of cases we cannot determine the principal source of the variation. Data on offspring size were compiled from studies that collected females from the same population and in most cases the same time, although in some cases data were compiled from a single reproductive season. Many other studies were excluded because no details were provided of the numbers of individuals on which the summary of offspring size was based. Egg volume was also a commonly reported measure, although we did not include data using this parameter in most of the analyses because variance [and more importantly, coefficients of variation (CVs)] in diameter and volume are not equivalent and, more importantly, do not scale linearly. Thus, we would discourage the approach used by Einum and Fleming (2002) whereby CVs in egg volume and diameter are pooled because this could introduce biases to the analysis.

To overcome the problems associated with traditional comparative analyses (i.e., treating individual species as replicates), we used the method of higher node contrasts (Harvey and Pagel, 1991). We tested the effects of developmental type and reproductive mode at the species, family and order level. The effects of developmental type (direct, lecithotrophic and planktotrophic as different levels) on CVs of offspring size within populations were tested with ANOVA. For the planktotrophs and lecithotrophs, we also compared the CV of offspring size within developmental types for two reproductive modes: internal and external fertilization.

The level of within-population variability in offspring size differed considerably between species, with CVs ranging from 0.7% to 51% (Fig. 1.2). The average CV across the entire set of species was approximately 9% and is

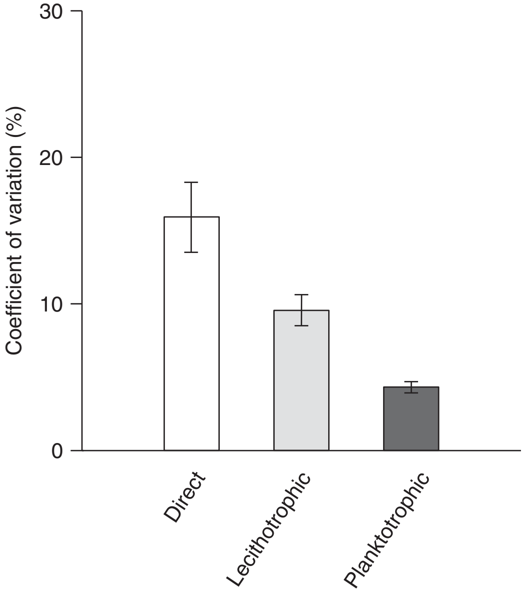


Figure 1.2 Mean (±SE) CV for offspring size within populations of marine invertebrates. Data are compiled from the literature for three developmental types: direct developers, lecithotrophic and planktotrophic.

similar to previous averages reported for *Conus* species (Kohn and Perron, 1994). This level of variation in diameter means that within any group of eggs, about a third of all the offspring will be 25% larger or smaller in volume than the average size and about 5% will be 50% larger or smaller in volume than the average size. Note that our calculations assume a normal distribution of egg sizes, and the data appear to reflect this distribution. Intra-population variation in offspring size varied strongly with developmental mode, and this pattern was consistent at all taxonomic levels that were tested (analysis using species, $F_{2,99} = 27.13$; families, $F_{2,64} = 24.6$; orders, $F_{2,40} = 22.51$; all $P < 0.001$; and all pairwise comparisons $P < 0.001$). Variation was greatest in the direct developers, least in planktotrophs and intermediate in lecithotrophs (Fig. 1.2).

For the direct developers only, a CV of 14% means that about a third of all the offspring will be 48% larger or smaller in volume than the average size and 5% of offspring will be more than twice the average size. Put in another way, this means a fourfold difference between the smallest 5% and largest 5% of individuals within any one population. These figs. show that there is an impressive range of offspring sizes being produced within any one population of marine invertebrate. Given that the size of direct developers was, on average, greater than indirect developers, we were concerned that the effects of developmental type were confounded with offspring size. Generally, however, CV was not correlated with offspring size within all three reproductive modes (direct developers: $R^2 = 0.104$, $n = 20$, $P = 0.165$; planktotrophs: $R^2 = 0.03$, $n = 39$, $P = 0.3$; lecithotrophs: $R^2 = 0.02$, $n = 43$, $P = 0.8$).

Within the lecithotrophs, internal fertilizers had higher levels of within-population variation in offspring size than external fertilizers ($F_{1,37} = 10.85$, $P = 0.002$, Fig. 1.3). For planktotrophs, there was no effect of fertilization mode on the level of within-population variation in offspring size ($F_{1,40} < 0.01$, $P = 0.99$, Fig. 1.3) despite the fact that the power to detect an effect similar to that seen for non-feeding larvae was high at 0.9.

Given the strong effects of relatively small differences in offspring size discussed later in this chapter, it seems that among all the developmental modes, the quality and performance of offspring will be highly variable within any single population. Our results suggest that the relative importance of larval quality and quantity for subsequent population dynamics will depend on developmental type. Overall, variation in offspring size in direct developers was very high—thus, larval quality may be particularly important for explaining variation in recruitment in this group because different individuals can vary markedly in quality.

It is difficult to speculate as to the cause of the pronounced differences in offspring-size variation between developmental and fertilization modes as a

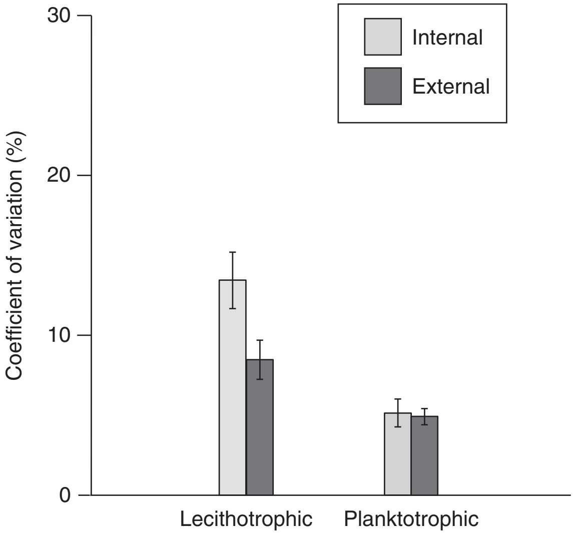


Figure 1.3 Mean (±SE) CV for offspring size within populations for marine invertebrates with planktotrophic or lecithotrophic development. The shaded bars represent species with external fertilization and open bars represent species with internal fertilization.

number of factors could be driving this effect. However, it is worth noting that there appears to be a strong, negative relationship between the dispersal potential of offspring and variation in offspring size, the most variation in the non-dispersing direct developers through to internally fertilized lecithotrophs and the least variation in the highly dispersive externally fertilized planktotrophs. Further work distinguishing between the two sources of intrapopulation variation (within brood and among individuals; e.g., Kohn and Perron, 1994) may shed light on the causes behind the systematic differences between the various developmental groups.

3. EFFECTS OF OFFSPRING SIZE

From our analysis of within-population offspring-size variation, it is clear that offspring sizes can be highly variable within species and populations. In this section, we review the effects of offspring-size variation on each of the major life-history stages across the various developmental modes. We do not consider the differential benefits to mothers of brooding smaller versus larger offspring but note that in some other groups this can be a major factor (Sakai and Harada, 2001). Unfortunately, there are far too few data on this important issue in marine invertebrates and so we focus on each of the life-history stages following the release of gametes/offspring.

3.1. Fertilization

In Thorson's consideration of free-spawning invertebrates, he concluded that '. . . . failure of insemination, cannot explain the enormous waste [of eggs] found in most marine invertebrates during development. The heavy waste takes place after fertilisation, during the free swimming pelagic life' (Thorson, 1950). Since then it has become clear that fertilization is not assured in free-spawners, and the production of zygotes can be a potentially limiting factor in the population dynamics of some species (Levitan, 1991, 1995; Levitan and Petersen, 1995; Levitan *et al.*, 1992; Pennington, 1985; Yund, 2000). Here we define 'free-spawning' as the release of both sperm and eggs into the water column. While free-spawning has alternatively been termed 'broadcast spawning' (Byrne *et al.*, 2003; Oliver and Babcock, 1992), we prefer the term free-spawning, partly because in many species, eggs are not 'broadcasted' into the water column but remain in a viscous matrix near the spawning female (Marshall, 2002; Thomas, 1994; Williams *et al.*, 1997). However, we should note that we separate free-spawning/broadcast spawning from species where only sperm are shed into the water column while eggs are retained (sometimes termed 'spermcast spawning'; Pemberton *et al.*, 2003). The principal factor determining the fertilization rate of spawned eggs is the collision rate between eggs and sperm (Vogel *et al.*, 1982). The collision rate between eggs and sperm is affected by a range of factors, but most important is the concentration of sperm present (Marshall *et al.*, 2000; Styan, 1998). Thus, any factors that change the amount of sperm present in the water column will affect female fertilization success and, accordingly, the density of spawning males and local hydrodynamic conditions will strongly affect fertilization rates in the natural environment (Denny and Shibata, 1989; Denny *et al.*, 1992; Franke *et al.*, 2002; Lasker *et al.*, 1996; Levitan, 1991; Levitan *et al.*, 1992; Marshall, 2002; Marshall *et al.*, 2004b; Mead and Denny, 1995; Yund, 1990). Given that sperm can quickly dilute to ineffective concentrations in the field (Babcock *et al.*, 1994; Denny and Shibata, 1989), a number of adaptations exist that enhance fertilization success in free-spawners and most relevant to the discussion here is the effect of egg size.

Larger eggs present a larger 'target' for sperm and are therefore more likely to be contacted within a given period of time than smaller sperm (Levitan, 1996a; Marshall *et al.*, 2002; Styan, 1998; Vogel *et al.*, 1982). Both in the laboratory and the field, when sperm are scarce, larger eggs are more likely to be fertilized than smaller eggs (Levitan, 1996a,b; Marshall and Keough, 2003; Marshall *et al.*, 2002). However, when sperm are abundant, larger eggs are more likely to suffer polyspermy than smaller eggs either because they are more likely to be contacted by multiple sperm before they have formed a block to polyspermy or because such blocks are slower (Marshall and Keough, 2003; Marshall *et al.*, 2002; Millar and Anderson, 2003; Styan, 1998). Therefore, under sperm-limiting conditions, larger eggs are more likely to be successfully fertilized, while under polyspermy conditions, smaller eggs are more likely to be fertilized. Debate continues about the prevalence of sperm limitation and polyspermy under natural conditions, but it is clear that both can occur simultaneously in the same spawning population (Brawley, 1992; Franke *et al.*, 2002; Marshall, 2002).

The effects of egg size on fertilization rate have led to speculation about the evolution of egg sizes of free-spawning marine invertebrates and the evolution of anisogamy (Levitan, 1993, 1996a; Podolsky, 2001; Podolsky and Strathmann, 1996). It has been suggested that in habitats that are conducive to sperm-limiting conditions, larger eggs have evolved relative to species in habitats where sperm limitation is unlikely (Levitan, 1998, 2002). More broadly, Levitan argues that the evolution of egg size in marine invertebrates will be strongly influenced by the pre-zygotic selection associated with fertilization. In contrast, Podolsky and Strathmann (1996) argue that the benefits of increased egg size for fertilization will be outweighed by the reduction in fecundity associated with this increase. Furthermore, they argue that post-zygotic selection (i.e., the effects of offspring size on developmental and post-metamorphic performance) will also shape offspring size and overall pre-zygotic selection (i.e., effects on fertilization alone) will be less important (Podolsky and Strathmann, 1996). This debate has been broadened by the discussion of the effects of egg accessory structures. Many invertebrates produce eggs that have large accessory structures such as jelly coats or follicle cells surrounding the eggs (reviewed in Podolsky, 2001). It has been argued that, as accessory structures are energetically inexpensive relative to egg material (Bolton and Thomas, 2000), any selection to increase egg target size will result in an increase in these structures rather than the egg cell itself (Podolsky, 2001, 2002; Podolsky and Strathmann, 1996). Farley and Levitan (2001) propose that despite the effects of accessory structures on fertilization, there will still be substantial selection on egg size due to fertilization effects. Podolsky (2001) raises the interesting possibility that egg accessory structures may mediate sperm–egg interactions in ways other than just size (e.g., increase the variance in sperm arrival times, thereby reducing polyspermy); it will be interesting to determine if this is indeed the case. Overall, this debate remains unresolved. Nevertheless it seems unlikely that pre-zygotic selection on egg size will be the sole force in the evolution of egg size in free-spawners, especially given the post-zygotic effects of egg size outlined later in this chapter.

An important consequence of the size-dependent fertilization of eggs is that under different sperm concentrations, the same brood of unfertilized eggs will produce zygotes of different sizes. At low sperm concentrations larger zygotes will be produced, but if that same brood is exposed to a high sperm concentration then (because of polyspermy effects) smaller, viable zygotes will be produced (Levitan, 1996a,b; Marshall and Keough, 2003; Marshall *et al.*, 2002). Therefore, free-spawning marine invertebrates appear to be unusual in that the size distribution of zygotes is a product not only of maternal investment but also of the local 'sperm environment'. This raises the interesting possibility that free-spawning males and females may be in conflict at fertilization whereby male fitness is maximized by a strategy that may reduce female fitness (Franke *et al.*, 2002). Finally, size-dependent fertilization means that producing offspring of optimal size is further complicated in free-spawning species because an additional 'layer' of size-dependent selection occurs at fertilization. For example, because free-spawning mothers may be competing for limiting sperm (Marshall and Evans, 2005), selection at this stage could act to increase optimal egg size (and thus competitive ability) but selection at another stage could act to decrease optimal egg size (i.e., size-independent mortality at settlement). Clearly, the effects of egg size at fertilization in free-spawners have the potential to influence egg size evolution; further research on the effects of offspring size across the entire life history of an organism will determine the relative strength of selection on egg size at each stage.

3.2. Development

Our view of the effects of offspring size on developmental time (time to a functional stage such as feeding or metamorphic competence) has been shaped largely by the early models of Vance (1973a,b). In both of Vance's original papers, it is assumed that the length of the pre-feeding period (or λ) increased with offspring size, and that the length of feeding period (ρ) decreased with offspring size. For non-feeding larvae with planktonic development, this means that the total planktonic period should be *positively* correlated with egg size because ρ is zero (although Vance restricted his considerations for $S \leq 1$). For feeding larvae, Vance (1973a, p. 342) made another assumption that the influence of egg size on λ was much smaller than its influence on ρ (in terms of the model $P \gg 1$) and so concluded that for planktotrophic species, egg size should be *negatively* correlated with planktonic period. Vance's models predicted that only very small or very large offspring should be selected and since then various modifications of the model have been made that better approximate the distribution of egg sizes observed in nature (Levitan, 1993, 2000; Podolsky and Strathmann, 1996; Styan, 1998). Since Vance's work, the assumptions that increases in egg size result in decreases in the planktonic period for feeding larvae and increases in the planktonic period of non-feeding larvae have become accepted in theoretical considerations of the topic and some conceptual works (Levitan, 2000; Ramirez-Llodra, 2002 but see Strathmann, 1977). For direct developers, there has been little speculation on the effects of offspring size on subsequent development but some general offspring-size models do assume a relationship between offspring size and developmental time (Sargent *et al.*, 1987). In this section, we review the available evidence for each of these assumptions.

3.2.1. Planktotrophs

3.2.1.1. Pre-feeding period There are very few studies examining the effects of egg size on the pre-feeding period alone in marine invertebrates. In one of the few studies to examine the effects of intraspecific variation in egg size on pre-feeding developmental time, McLaren (1965, 1966) showed that larger eggs took longer time to hatch than smaller eggs for the copepod *Pseudocalanus minutus*. Similarly in another copepod, Lonsdale and Levinton (1985) found across four populations that female *Scottolana cnadensis* from the population that produced the largest eggs also produced eggs that took the longest time to hatch into nauplii. In contrast, Jones *et al.* (1996) found no correlation between egg size and embryonic developmental period among populations in the nudibranch *Adalaria proxima*. Among species, the effect of egg size on the length of pre-feeding period is also unclear. Dickie *et al.* (1989) compared the length of pre-feeding periods among strongylocentrotid sea urchin species and found no influence of egg size, although only one clutch from each species was used in this study. In a study across 20 different species with feeding larvae from a number of phyla, Staver and Strathmann (2002) found that the time until first swimming was positively correlated with egg size, but within individual groups (Urochordates, Echinoderms and Spiralia), the effects of egg size were less clear and were limited by small sample sizes. Some of the best evidence comes from Kohn and Perron's study showing a positive relationship between the pre-feeding (pre-hatching) period and egg size among species of *Conus* (Kohn and Perron, 1994).

3.2.1.2. Entire planktonic period: Interspecific comparisons Emlet (1995) considered the relationship between overall length of the developmental period (from the fertilization of eggs to metamorphic competence) of 28 echinoids with feeding larvae and 5 echinoids with non-feeding larvae. He found that the larval period decreased with increased egg size across both developmental modes (Emlet, 1995). Extending Emlet's work, Levitan (2000) examined the relationship between egg size and planktonic duration for 37 echinoid species, all with feeding larvae. Again, it was found that those species with larger eggs had a shorter planktonic period than those with smaller eggs. It should be noted that for both studies, developmental periods were first adjusted with Q_{10} values so that comparisons could be made across species that occurred at different water temperatures. Before adjusting for temperature, Emlet (1995) found no relationship between egg size and larval developmental period. Importantly, Levitan (2000) found that the relationship between egg size and planktonic period was not linear (as assumed by Vance, 1973a,b), rather, it was curvilinear with initial increases in egg size resulting in a large decrease in the planktonic period; however, with increased egg size the concomitant reduction in planktonic period was less.

Analysing the available data for Asteroidea (Echinodermata), across the planktotrophs and lecithotrophs, there is the expected relationship between egg size and planktonic period (Emlet *et al.*, 1987). However, the effects of egg size on developmental rate within feeding larvae alone are less clear. Using Q_{10} values of 2, there is a significant negative correlation between egg size and planktonic period but using values of 3–3.6 (typical values for echinoderm larvae, see Emlet, 1995), there is no significant correlation between egg size and planktonic period. Similar results were reported by Hoegh-Guldberg and Pearse (1995).

There have been far fewer studies examining the effects of egg size on the planktonic period of feeding larvae that are not focused on echinoderms. Kohn and Perron (1994) showed a strong negative relationship between the minimum planktonic period and egg diameter in *Conus* (Fig. 1.5). Havenhand (1993) compared the developmental time (again standardizing for differences in temperature) of opisthobranch molluscs with a range of different egg sizes. He found that across developmental modes (planktotrophic and lecithotrophic) there was a strong negative relationship between egg size and developmental time, with lecithotrophs having a shorter developmental period (Havenhand, 1993). However, when lecithotrophs and planktotrophs are considered separately, there is no relationship between egg size and developmental time for either group (planktotrophs: $R^2 = 0.01$, $n = 18$, $P > 0.5$; lecithotrophs: $R^2 = 0.269$, $n = 13$, $P = 0.069$). This suggests that apart from the broad differences between planktotrophs and lecithotrophs, there is no effect of egg size on developmental time in this group despite the comparisons being made across a broad range of egg sizes within each group (e.g., for planktotrophs between 65 and 149 μm; Fig. 1.4). Further studies on other, non-echinoid groups are necessary to determine if the relationship between egg size and the planktonic period for feeding larvae is applicable to other groups of organisms.

We compiled the data from the review by Kupriyanova *et al.* (2001) on serpulimorph polychaetes, to examine the relationship between egg size and developmental time and to be conservative, we compared our results across two values of Q_{10}: 2 and 3.6 (the results were qualitatively independent of the Q_{10} that was used). Once again, the polychaete data do not resemble the data on echinoids. Across feeding and non-feeding larvae, developmental

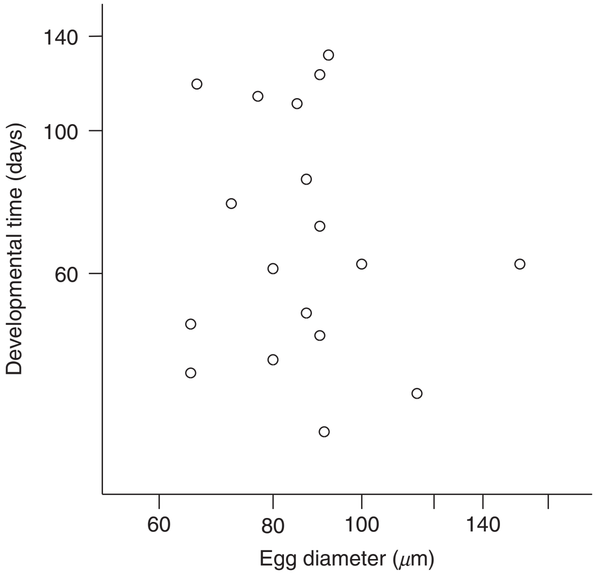


Figure 1.4 Relationship between egg size and developmental time (adjusted to development at 10 °C using Q_{10} values) for opisthobranch molluscs with planktotrophic larvae, each point represents a single species. Data taken from Havenhand (1993), note the log scale. Developmental time is defined here as the time from egg release/fertilization through to metamorphic competence.

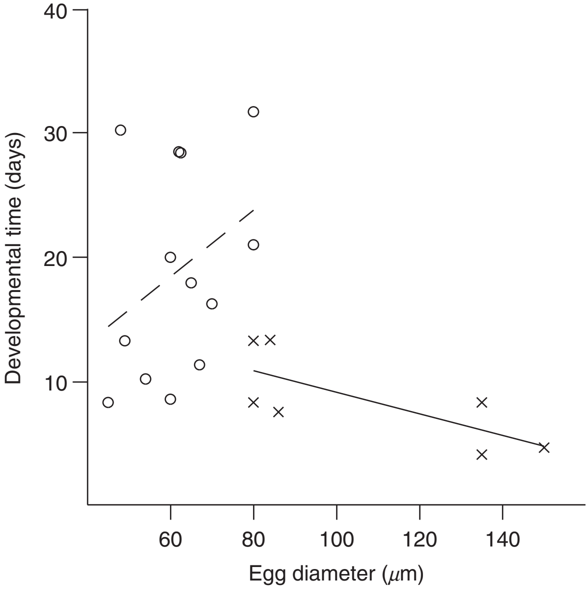


Figure 1.5 Relationship between egg size and developmental time (adjusted to development at 20 °C using Q_{10} values) for serpulimorph polychaetes with planktotrophic (as indicated by circles and the dashed line) or lecithotrophic (as indicated by the crosses and solid line). Data taken from Kupriyanova *et al.* (2001), and developmental time was defined as time taken to reach metamorphic competence.

time does decrease with increasing egg size ($Q_{10} = 2$, $R^2 = 0.199$, $n = 20$, $P = 0.048$; $Q_{10} = 3.6$, $R^2 = 0.212$, $n = 20$, $P = 0.041$). However, there is no statistically significant relationship between egg size and developmental time ($Q_{10} = 2$, $R^2 = 0.299$, $n = 13$, $P = 0.053$; $Q_{10} = 3.6$, $R^2 = 0.154$, $n = 13$, $P = 0.184$) when planktotrophs are examined on their own (Fig. 1.5). In fact, there is almost a positive relationship between egg size and developmental time in planktotrophic polychaetes (Fig. 1.6). Our discussion of interspecific patterns that have been adjusted using Q_{10} values should be tempered with the fact that such measures that assume Q_{10} values remain constant across temperature ranges, a condition that is unlikely in some instances (Hoegh-Guldberg and Pearse, 1995). This further emphasizes the advantages of examining offspring-size effects within rather than among species.

For holoplanktonic species, the pattern appears to be similar. Guisande and Harris (1995) found that hatching success and naupliar survival under conditions of starvation were positively correlated with egg size in the copepod *Calanus helgolandicus*. Similarly, Lonsdale and Levinton (1985) found, among populations, that egg size was positively correlated with naupliar survival under low-food conditions but not high-food conditions.

In summary, it appears that for planktotrophic larvae, the echinoids and *Conus* gastropods are the only groups where egg size consistently affects the

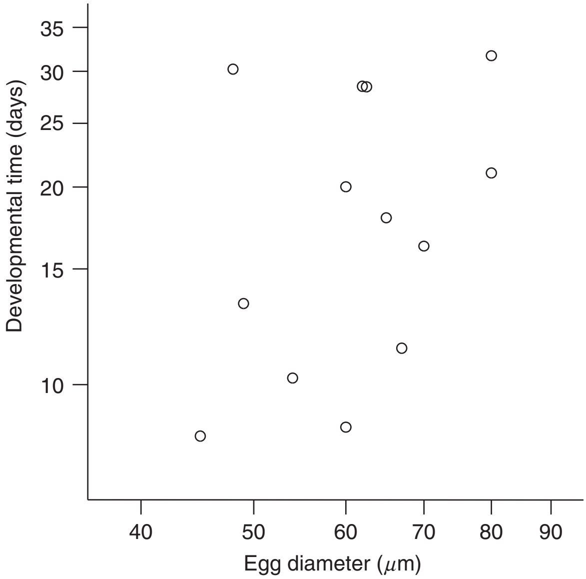


Figure 1.6 Relationship between egg size and developmental time (adjusted to development at 20 °C using Q_{10} values) for serpulimorph polychaetes with planktotrophic larvae. Data taken from Kupriyanova *et al.* (2001), note the log scale. Developmental time is defined here as the time from egg release/fertilization through to metamorphic competence.

planktonic period, whereas for other groups there appears to be little support for the idea that larvae from smaller eggs require longer time to develop. This may be because the influence of egg size on the pre-feeding period is actually much larger than has previously been assumed, potentially balancing out (or perhaps even overcoming in the case of polychaetes) the effects of egg size on the length of the feeding period.

3.2.1.3. Entire planktonic period: Intraspecific comparisons The number of studies on feeding larvae that examine the effect of egg size on developmental time *within* species is severely limited. Bertram and Strathmann (1998) found a small effect of maternal source habitat (and thus egg size) on the developmental rate of larvae of the urchin *Strongylocentrotus droebachiensis* fed in the laboratory. However, Meidel *et al.* (1999) found that increased egg size in *S. droebachiensis* resulted in an increase in the rate of metamorphosis for larvae fed high but not low food rations. George *et al.* (1990) found that larvae from larger eggs were competent to settle sooner than larvae from smaller eggs in the echinoids *Arbacia lixula* and *Paracentrotus lividus*, although these comparisons are based on mothers from different sites.

While examinations of the effect of natural variation in egg size are rare, several studies have examined the effects of manipulating egg size.

Hart (1995) halved the size of developing eggs in the echinoid *S. droebachiensis* with no effect on time to metamorphose and only a small effect on juvenile size. Surprisingly, he found no effect of egg size on the time taken to progress through the larval stage despite strong effects on larval feeding rates, with larvae coming from halved eggs having lower clearance rates than those from unmanipulated eggs. Sinervo and McEdward (1988) manipulated the size of *S. droebachiensis* eggs and found that egg size strongly affected developmental rate with larvae coming from smaller eggs taking longer time to reach metamorphosis than larvae from larger eggs.

3.2.2. Non-feeding larvae

3.2.2.1. Interspecific comparisons Berrill's (1935) examination of the effect of egg size on developmental time (measured as time to swimming) in ascidians is perhaps the best-known example of the effects of offspring size on developmental rate in non-feeding larvae. Species with larger eggs took longer to develop than species with smaller eggs at the same temperature. Interestingly, there are very few other examinations of the effects of offspring size on developmental time in this group. Staver and Strathmann (2002) found that egg size and time to swimming appeared to positively (although statistically non-significantly) correlated among three species of Urochordate. In contrast, Emlet *et al.* (1987) found a strong, positive correlation between egg size and planktonic period across 36 species of non-feeding asteroid larvae.

3.2.2.2. Intraspecific comparisons There are very few examinations of the intraspecific effects of offspring size on developmental time or planktonic period in species with non-feeding larvae. Isomura and Nishimura (2001) found that larger larvae had longer lifetimes (measured as the time from the free-swimming stage to when the larvae died and therefore probably exceeds the time taken to become metamorphically competent) than smaller larvae within three species of pocilloporid corals. More recently, Marshall and Bolton (2007) showed that egg size strongly affected time until hatching in two species of ascidian (*Ciona intestinalis* and *Phallusia obesa*) and the sea urchin *Heliocidaris erythrogramma*. The magnitude of the effects of egg size on developmental time in this study was surprising, with small increases in egg size dramatically increasing developmental time (e.g., for *Ciona* an approximately 4% increase in offspring size resulted in a 15% increase in developmental time). This has some interesting implications for the way in which egg size evolution is modelled. As discussed above, Vance's (1973a) model assumed that the effects of egg size variation on the feeding period were much larger than its effects on the pre-feeding period, so any increase in egg size would result in a large decrease in the feeding period and only a small increase in the pre-feeding period. Later models even removed the effects of egg size on the pre-feeding period, regarding it as constant (e.g., Levitan, 2000, p. 178). The effect of egg size on the pre-feeding period should not be assumed to be substantially less than its effect on the feeding period. Given the lack of an effect of egg size on total developmental time discussed above, we suggest that the effects of egg size on the pre-feeding period may partially balance the effects of egg size on the feeding period, thereby obscuring any relationship between egg size and time to metamorphic competence. Alternatively, differences in the size at metamorphosis among species may also be obscuring any egg size–feeding period relationship in planktotrophs (Strathmann, 1977).

Offspring size can also affect larval behaviour. Our own work on brooding species has shown that larger larvae actually spend longer in the plankton than smaller larvae, at least for species with brooded larvae (Marshall and Keough, 2003). However, this is not due to differences in the developmental time of larvae, indeed the larvae of each of the species in our study were capable of settlement immediately (Marshall and Keough, 2003). The differences appear to be due to the fact that larger larvae are more 'choosy' with respect to settlement surfaces. Hence for any given larva, the larval period is a product of the availability of suitable substrates and the size of the larva.

The effect of larval size on the developmental time/settlement behaviour of non-feeding larvae has some interesting implications for variation in the dispersal potential of this group. All else being equal, larger larvae will have greater dispersal than smaller larvae. Thus, if a mother produces offspring of variable size, then she will also produce offspring that are likely to disperse to varying amounts. It is unclear whether this production of larvae with variable dispersal potentials represents a 'bet-hedging' strategy (Laaksonen, 2004; Raimondi and Keough, 1990) or is merely a physiological artefact (Eckelbarger, 1986). Nonetheless, it appears marine invertebrates that produce non-feeding larvae have the previously unanticipated potential to control the dispersal of their offspring (Marshall and Keough, 2003c). Interestingly, McGinley *et al.* (1987) state that for a strategy of producing offspring of variable size to be adaptive, mothers must be able to control the dispersal of their offspring into different habitats and this criterion may apply for this group of organisms. Further work is necessary to determine the prevalence of the larval size–swimming time relationship, but we believe a relationship is likely given the demonstrated post-metamorphic cost of extended larval swimming in marine invertebrates with non-feeding larvae (Maldonado and Young, 1999; Marshall *et al.*, 2003b; Wendt, 1998, 2000). If larger larvae have greater nutritional resources, they may be better able to 'afford' to delay their metamorphosis until a suitable settlement surface is found. Alternatively, for the ciliated bryozoan larvae at least, larger larvae will have a lower ciliated surface area to volume ratio and thus may expend proportionately less energy than smaller larvae while in the plankton (Wendt, 2000).

3.2.3. Direct developers

As far as we are aware, there is very little information on how offspring size affects developmental time in direct developers. Kohn and Perron (1994) provide an excellent compilation of the literature on *Conus* that show that egg size is strongly related to the length of the pre-hatching period, pooling across indirect and direct developers and this strongly suggests that among these species, larger offspring take longer time to develop. In another example for direct developers, Steer *et al.* (2004) found that manipulating maternal nutrition affected offspring size in the squid *Euprymna tasmanica* and that hatching success was positively correlated with offspring size.

3.2.4. Summary

Table 1.1 summarizes our findings regarding offspring-size effects on the developmental/planktonic period. In general, the apparent lack of a clear effect of egg size on pre-feeding developmental time or the overall planktonic period of planktotrophs was surprising given the number of modelling studies including this as an explicit assumption. Based on the above information, it would appear premature to conclude that increasing egg size results in a decrease in the planktonic period of species with feeding larvae, and further work is needed to establish the relative effects of egg size on the

Table 1.1 Summary of the effects of offspring size on developmental time in planktotrophs and non-feeding larvae

Group	Interspecific	Intraspecific
Planktotrophs: pre-feeding period		
Gastropods (*Conus*)	✓ (+ve)	
Copepods		✓ (+ve)
Echinoids	×	
Opisthobranchs	No data	×
Planktotrophs: planktonic period		
Gastropods (*Conus*)	✓ (−ve)	
Echinoids	✓ (−ve)	Variable
Asteroids	×	No data
Opisthobranchs	×	No data
Polychaetes	×	No data
Lecithotrophs		
Opisthobranchs	No data	×
Ascidians	✓ (+ve)[a]	✓ (+ve)
Anthozoa	No data	✓ (+ve)
Bryozoa	No data	✓ (+ve)

[a] Developmental time only.

Ticks indicate an effect of offspring size and crosses indicate that no effect was detected.

pre-feeding and feeding periods. In particular, more information on groups other than the echinoids and more intraspecific comparisons are necessary if we hope to understand the crucial relationship between egg size and planktonic period in planktotrophs.

The effects of offspring size on developmental/planktonic period in species with non-feeding larvae appear to be more consistent, but in this group there were also some surprises regarding the settlement behaviour of larvae. Offspring size may not only affect developmental time as previously thought but it also appears to affect larval settlement behaviour (and thus overall planktonic period) in at least two phyla. Together, these data suggest that marine invertebrate mothers may have more ‘control’ over the dispersal potential of their offspring than previously thought.

3.3. Post-metamorphosis

3.3.1. Planktotrophs

There have been few studies examining the post-metamorphic effects of egg size in planktotrophs. Given that most planktotrophic larvae greatly increase in size from fertilization through to metamorphosis and take in a large amount of exogenous resources through feeding, it is perhaps unsurprising that there has been little interest in post-metamorphic egg size effects in this group. Intuitively, one would expect there to be a weaker link between maternal provisioning and post-metamorphic performance in this group than in other groups where the newly metamorphosed individuals rely entirely on maternal provisioning. However, the lack of studies reduces our confidence in any predictions about the strength of post-metamorphic effects of size in this group. Because no study has examined the effects of offspring size on post-metamorphic performance directly for planktotrophs, here we examine whether egg size affects post-metamorphic/juvenile size. Juvenile size in lecithotrophs and direct developers has strong effects on post-metamorphic performance (see Section 3.3.3) and settler size variation due to larval feeding can have strong effects on the post-metamorphic performance of planktotrophs (Phillips, 2002). Thus, we use post-metamorphic size as a proxy for performance to examine if egg size can affect this parameter in planktotrophs.

Interspecific comparisons of egg size and juvenile size in planktotrophs show variable results. Levitan (2000) found no relationship between egg size and size at metamorphosis among 25 species of echinoids after adjusting for phylogenetic effects. He concluded that it was reasonable to assume that size at metamorphosis was independent of egg size in this group. Similarly, Hadfield and Miller (1987) found no relationship between egg size and settler size among species of opisthobranchs, and Kohn and Perron (1994) found no relationship among species of *Conus*. In contrast, for calyptraeid gastropods there is a positive relationship between egg size and settler size.

Collin (2003) found no relationship overall between egg size and settler size, but we found a significant positive relationship ($R^2 = 0.413$, $n = 10$, $P = 0.045$) in our analysis of Collin's data for just the planktotrophs.

Intraspecific comparisons of egg size effects on post-metamorphic size come exclusively from the echinoids and have also yielded variable results. For the echinoid *A. lixula*, George *et al.* (1990) found strong effects of initial egg size and population source on the size of metamorphosed post-larvae. Post-larvae from large eggs from adults from a favourable site were (mean ± SE) 346 μm (±26.3) in diameter, whereas post-larvae from small egg from adults from a less favourable site were 290 μm (±28.9). However, studies that utilize natural variation in egg size in planktotrophs without the confounding effect of coming from different sites appear to be rare. Most of the remaining comparisons are based on the fairly extreme reduction in offspring size by halving (or quartering) egg size experimentally during development. We have reservations regarding the relevance of this technique for examining the ecological role of natural variation in egg size in planktotrophs, but it does serve to parameterize the potential effects of egg size. Hart (1995) found that experimentally halving the eggs of *S. droebachiensis* resulted in juveniles that were significantly smaller than juveniles from unmanipulated eggs. Although he concluded that the effects were small, the differences in test diameters that he observed resulted in an approximately 15% difference in volume between the two groups and explained the bulk of the variation in juvenile size (Hart, 1995). In contrast, similar experiments on the same species conducted by Sinervo and McEdward (1988) found no effect of egg size manipulation on subsequent juvenile size. Interestingly, Sinervo and McEdward (1988) found an effect of initial egg size on developmental time (halved eggs took longer to develop) whereas Hart (1995) did not. It may be that initial egg size can affect either length of planktonic period or juvenile size even in the same species. Allen *et al.* (2006) demonstrated that manipulating egg size had strong effects on post-settlement size in *Clypeaster rosaceus* and generally, halving egg size had a larger effect than manipulating larval food. It is possible that egg size has more of an effect in planktotrophs with large eggs (*C. rosaceus* is facultatively planktotrophic) than species with small eggs. Alternatively, the different larval food levels could also explain variation in the results of different studies. Regardless, it appears that in some species at least, significant differences in initial egg size can persist through to metamorphosis despite a period of larval feeding and therefore, egg size has the potential to affect post-metamorphic performance in planktotrophs.

3.3.2. Non-feeding larvae

Most of the evidence of post-metamorphic effects of offspring size on post-metamorphic performance comes from species with a non-feeding larval stage. This is probably due to the fact that a number of these studies focus on colonial invertebrates where post-metamorphic survival and growth are easily quantified. The majority of studies examining offspring-size effects for this group involve field studies where larvae are measured in the laboratory, settled onto artificial substrata and then transplanted into the field. However, the effects of larval size on post-metamorphic growth are not restricted to colonial organisms. Emlet and Hoegh-Guldberg's working on the sea urchin *H. erythrogramma* was one of the first studies to show that, in lecithotrophic species, the majority of maternal investment (in their case lipid reserves) was unnecessary for larval development and was probably for post-metamorphic performance (Emlet and Hoegh-Guldberg, 1997). Accordingly, they found that larval lipid reductions did not affect larval performance but had a strong effect on post-metamorphic survival and growth in this species. Ito (1997) also showed that time until starvation in newly metamorphosed 'benthic larvae' of the opisthobranch *Haloa japonica* was positively correlated with initial egg size.

For the bryozoan *Bugula neritina*, larval size affects early post-settlement mortality, early growth, reproduction and the quality of offspring produced in the subsequent generation (Marshall *et al.*, 2003a). The effects of larval size differed between populations for this species: an effect of larval size on survival was detected throughout the life of *B. neritina* colonies in southern Australia, but these effects were more transient in Florida, United States. We suggested that the differential effects of larval size on survival were due to different intensities and sources of mortality between the two sites. At Florida, the principal source of mortality appeared to be detachment during severe storms. While survival was size-dependent initially in Florida, the size-independent mortality associated with storms removed any relationship between larval size and adult survival. In contrast, the only mortality that Australian *B. neritina* experienced was early mortality after settlement, and thus overall mortality was strongly dependent on larval size. This early, size-dependent mortality of sessile invertebrates appears to be relatively common and one of the few generalizations that can be made about the post-metamorphic effects of offspring size. Settlers coming from larger larvae have higher initial survivorship than those from smaller larvae in at least four different taxa (Table 1.2). For non-feeding larvae, the first time an individual is able to feed is once metamorphosis is complete and feeding structures are fully functioning. This is clearly an energetically expensive process and values of 10–60% of total energetic reserves being expended during metamorphosis have been reported (reviewed in Bennett and Marshall, 2005). Given the high energetic cost of metamorphosis, it may be that settlers from smaller larvae are closer to their energetic minimum and if conditions are not ideal (i.e., abundant food available immediately after settlement), then these larvae are more likely to starve to death. Alternatively, settlers from smaller larvae may be unable to exploit food resources as efficiently because they can have smaller feeding structures (Marshall and Keough, 2003a, 2005).

Table 1.2 Summary of studies of post-metamorphic effects of offspring size in marine invertebrates

Study	Location	Species	Size range	Survival	Growth	Reproduction
Marshall *et al.*, 2006	Field	*Botrylloides violaceus*	3-fold	✓ (0–100%)	✓	N/A
Marshall *et al.*, 2003	Field	*Bugula neritina* (Australia)	2-fold	✓ (0–90%)	✓	✓
Marshall *et al.*, 2003	Field	*Bugula neritina* (Florida)		× (early effects only)	✓	N/A
Marshall and Keough, 2003	Field	*Ciona intestinalis*	∼1.2-fold	✓ (22–65%)	N/A	N/A
Marshall and Keough, 2004a	Field	*Watersipora subtorquata* (settlement plates)	2.5-fold	✓ (47–98%)	×	N/A
Marshall and Keough, 2004	Field	*Watersipora subtorquata* (pier pilings)		×	✓	N/A
Marshall and Keough, 2005	Field	*Diplosoma listerianum*		× (early effects only)	× (early effects only)	N/A
Moran and Emlet, 2001	Field	*Nucella ostrina*	∼1.5-fold	✓ (43–62%)[a]	✓	N/A
Rivest, 1983	Lab	*Searlesia dira*		✓	✓	N/A
Emlet and Hoegh-Guldberg, 1997	Lab	*Heliocidaris erythrogramma*		✓	✓	N/A
Ito, 1997	Lab	*Haloa japonica*		✓ (time until starvation)		

[a] Calculated from Figure 4, p. 1604.

Ticks indicate a positive effect of offspring size and crosses indicate that no effect was detected.

Regardless, the effect of larval size on post-metamorphic survival for species with non-feeding larvae (at least for filter feeders) appears to be mediated by nutrition. This is supported by the fact that the effects of larval size on survival in the ascidian *C. intestinalis* are exacerbated at higher settler densities when competition for food is more likely to occur (Marshall and Keough, 2003a). Thus, we predict that when food is more abundant, the effects of larval size on post-metamorphic survival are likely to be reduced.

Initial studies suggest that disturbance as a source of post-settlement mortality acts in a size-independent manner. As described above, colony survival was unrelated to initial larval size in Florida due to storms causing high mortality of *B. neritina* colonies throughout the adult stage. In a study on the encrusting bryozoan *Watersipora subtorquata*, we found that colony survival was dependent on initial larval size for colonies on settlement plates but was independent of larval size for colonies on pier pilings among natural communities (Marshall and Keough, 2004a). Mortality was much higher for colonies on pier pilings, and we suggested that increased mortality through trampling or predation for settlers in this habitat was likely to act in a size-independent way. Overall, we propose that larval size will mediate the nutritional aspects of post-settlement survival but will have little effect on survival if there are high levels of (both biotic and abiotic) disturbance (Brockelman, 1975). Generally, more work is necessary to examine explicitly how biotic factors like predation and competition affect the relationship between larval size and post-settlement survival.

The effects of larval size appear to persist throughout so as to affect subsequent growth in some marine invertebrates with non-feeding larvae. For *B. neritina*, colonies from larger larvae have higher growth rates than colonies from smaller larvae, and these effects can be detected for up to six weeks post-settlement (Marshall *et al.*, 2003). Other sources of variation in larval quality affect *B. neritina* in a similar manner (Wendt, 1998), and it may be that larval quality effects are particularly persistent in this species. For two other species of colonial invertebrate, *Diplosoma listerianum* and *W. subtorquata*, we found initial effects of larval size on colony growth, although these effects were generally less persistent in both species (Marshall and Keough, 2004a, 2005). We speculate that in ‘weedy’ species, such as *D. listerianum* and *W. subtorquata*, larval-size effects on growth can be quickly obscured due to factors such as the availability of free space and colony fragmentation affecting colony growth. This suggestion is partially supported by the finding that larval-size effects on colony size are far more persistent in the superior competitor *Botrylloides violaceus* (Marshall *et al.*, 2006). The mechanism underlying the effect of larval size on post-metamorphic growth appears to vary between species. For example, in the colonial ascidians *D. listerianum* and *B. violaceus*, larval size positively affects the size of feeding structures (Marshall and Keough, 2005; Marshall *et al.*, 2006). However, larval size can also affect the budding rate of new settlers with settlers from larger larvae budding at higher rates than settlers from smaller larvae (Marshall and Keough, 2004a; Marshall *et al.*, 2006). Given the strong effects of offspring size on growth in colonial invertebrates, it is perhaps unsurprising that offspring size also strongly affects intraspecific competitive interactions. For the colonial ascidian *B. violaceus*, not only were larger larvae more likely to survive and grow faster as colonies than smaller larvae but also they were better competitors (Marshall *et al.*, 2006). When established colonies were present, new recruits from larger larvae were more likely to survive than recruits from smaller larvae, and at higher settler densities the advantages of increased offspring size were exacerbated. Finally, when settlers were placed within proximity to one another, settlers from smaller larvae were more likely to lose territory (without being overgrown) to settlers derived from larger larvae.

The effect of larval size on subsequent reproduction is the most important life-history variable to measure as this parameter gives the most relevant measure of offspring fitness (Stearns, 1992). However, we are aware of only one species for which the effect of larval size on subsequent reproduction has been determined: we found that colonies from larger larvae generally have greater reproduction than colonies from smaller larvae in *B. neritina* (Marshall, 2005; Marshall *et al.*, 2003a). However, these effects vary among different populations, apparently according to local selection pressures. For example, for *B. neritina* colonies that come from populations that are highly seasonal with mortality at the end of the summer, larval size affects the time until reproduction with colonies from larger larvae reproducing before colonies from smaller larvae (Marshall, 2005). In contrast, for colonies where there are high rates of predation but colonies as a whole persist year round, larval size affects growth rates and fecundity much more strongly (Marshall, 2005). Although direct evidence is limited, the strong effects of larval size on post-metamorphic growth suggest that larval size will also affect reproduction in a range of taxa (especially colonial organisms) but more tests are needed.

3.3.3. Direct developers

The direct developers as a group have received less attention with regard to the effects of offspring size on post-metamorphic performance, perhaps because they are mobile as juveniles and therefore harder to track than sessile invertebrates. Despite the challenges involved, Moran and Emlet (2001) examined the effects of offspring size on post-metamorphic performance in the field for an intertidal, direct developing gastropod. After one month in the field, they found that larger hatchlings were more likely to be recovered from the field (the authors inferred greater survivorship from recovery rates) than smaller hatchlings during the winter but during the summer, when survival was lower overall, they found no effect of offspring size on recovery rates. They suggested that desiccation or thermal stress was the main source of mortality (this was supported by the fact that more snails died on the sun-exposed experimental patch than the shaded patch), and that this source of mortality was likely to be independent of offspring size (Moran and Emlet, 2001). Moran and Emlet (2001) also showed that larger hatchlings had higher post-metamorphic growth in the field in all experimental runs. This may be due to the fact that larger hatchlings are more likely to be successful when attacking larger prey items (barnacles; Palmer, 1990). Rivest (1983) found that hatchling size affected post-metamorphic growth rates in the snail *Searlesia dira* with larger hatchlings growing faster. Interestingly, he also found that larger hatchlings were less likely to be successfully preyed upon by the crab *Pagurus hirsutiuculus*, which showed strong preferences for smaller hatchlings. This appears to be the only study to have addressed the effect of offspring size on predation rates in marine invertebrates.

3.3.4. Summary

Offspring size has the potential to affect post-metamorphic survival, growth and even reproduction although evidence is limited by the paucity of studies. Table 1.2 compares the average survivorship of individuals across the size ranges observed for each field study. The effects of size are variable among species with some small differences in size resulting in large differences in survivorship (e.g., *Nucella*) and vice versa (e.g., *Watersipora*). Thus, even small differences in maternal provisioning can result in differential survivorship, and this raises an interesting possibility concerning planktotrophs. Given the range of offspring sizes over which survival differences are observed in lecithotrophs and direct developers, we believe that the degree of variation in settler sizes was induced by egg size in planktotrophs, means that post-metamorphic effects of egg size in the group should not be ruled out.

We propose a number of predictions with regard to offspring-size effects on post-metamorphic performance, all of which should be relatively straightforward to test. First, for species with non-feeding larvae that produce offspring that are at the smaller end of the size spectrum (e.g., most solitary ascidians), we predict that offspring size will affect post-metamorphic survival much more strongly than for those species with extremely large/yolky eggs or larvae that are brooded (e.g., colonial ascidian larvae). In other words, we predict that the *within*-species effects of offspring size will vary *among* species with different mean offspring sizes. Species with smaller eggs are probably closer to their energetic minimum requirements, and less well-provisioned offspring within this group probably require high-food conditions immediately after settlement to survive. In contrast, in species with much larger offspring, larvae are probably further from their energetic minimum requirements and therefore variation in offspring size is likely to affect subsequent growth rates rather than survival. At the very least, we expect that the relationship between offspring size and survival to be more sensitive to variation in food availability in species with relatively smaller eggs as opposed to those with larger eggs.

Second, we predict that different sources of mortality will be more or less likely to act in an offspring size-dependent manner. For example, physical disturbance and stress (e.g., salinity or heat stress) are likely to cause mortality irrespective of offspring size whereas competition and food availability are likely to be size-dependent. The effects of predation on the relationship between offspring size and performance seem less clear: in some instances offspring size will strongly affect predation rates (Palmer, 1990), but other predators, or biological sources of mortality (e.g., bulldosing by limpets of newly settled barnacles), seem less likely to act in a offspring size-dependent manner. Regardless, we strongly believe that a simple division between 'good' and 'bad' environments (Einum and Fleming, 1999; McGinley *et al.*, 1987; Sargent *et al.*, 1987; Stearns, 1992) is uninformative, and generalizations such as larger offspring being better in a bad environments (while useful in some taxa, e.g., Fox, 2000; Fox and Mousseau, 1996) are unlikely to apply to marine invertebrates. Rather than focusing on merely the intensity of the mortality, the source of mortality should also be considered.

Finally, we predict that offspring size will have very different effects on different post-metamorphic traits among different populations (such as those in Marshall, 2005). Traditionally, the effects of offspring size are viewed as being constant among different environments but a genetic component of offspring-size effects clearly exists (Reznick, 1981). Therefore, it is reasonable to expect that offspring size will affect different traits among different populations.

4. SOURCES OF VARIATION IN OFFSPRING SIZE

Offspring size varies within broods (e.g., Marshall *et al.*, 2000), among broods from the same mother (Chester, 1996; Jones *et al.*, 1996), among mothers and among populations (e.g., George, 1994a; George *et al.*, 1990). Here, we review the sources of variation in offspring size at the within- and among-population levels. A huge literature is devoted to various parameters that cause variation in offspring size and to cover them all here would be tedious and uninformative, so we have attempted to highlight some common and major sources of variation.

4.1. Within populations

4.1.1. Stress

A variety of stresses can affect the size of offspring. One of the earliest studies by Bayne *et al.* (1978) showed that salinity, temperature and food availability can all strongly affect the size (mass) of eggs produced by *Mytilus edulis*. More generally, maternal nutrition can have a strong effect on offspring size in a variety of species (Chester, 1996; George, 1995; Meidel *et al*., 1999; Qian, 1994; Qian and Chia, 1991; Steer *et al*., 2004), but not in others (Lewis and Choat, 1993). Our own studies have shown that when the bryozoan *B. neritina* suffers a simulated predation event, colonies reduce the size of their offspring (and therefore offspring fitness) dramatically (Marshall and Keough, 2004b). This may be to increase the colony's ability to recover (Marshall and Keough, 2004b). Generally, offspring size is often positively correlated with maternal resource state, but the effects are variable and more work is needed.

Other stresses can also affect offspring size but have received less attention. Gimenez and Anger (2001) found that salinity stress resulted in an increase in egg size for the crab *Chasmagnathus granulate*. Cox and Ward (2002) found strong effects of pollution on the size of larvae produced by *Montipora capitata* with a remarkable 17% decrease in larval volume (assuming spherical larvae) due to exposure to increased ammonium. Studies in terrestrial organisms suggest that pollution could act as a strong selection pressure on offspring size (Hendrickx *et al*., 2003a,b). It will be interesting to determine the effect that pollution will have on offspring size in other species as this may represent a previously unrecognized mechanism by which pollution can negatively affect marine populations.

4.1.2. Maternal size

Within species across a wide variety of taxa, offspring size is correlated with maternal size (Sakai and Harada, 2001; Stearns, 1992). This correlation can be negative, for example in *Conus marmoreus*, egg size is negatively correlated with maternal size (Kohn and Perron, 1994) and in *B. neritina*, larval size can be positively or negatively correlated with colony size (Marshall, 2005). However, generally, if there is a correlation between offspring and maternal size, it is positive (Table 1.3).Table 1.3 is probably not an accurate representation of reality given that in many cases the absence of a relationship between maternal size and offspring size is unlikely to be reported. Therefore, the percentage of species where no relationship is present is probably dramatically underestimated. Nevertheless, it is clear that within a range of species, larger mothers produce larger offspring. Interestingly, comparisons among species show the opposite pattern, smaller species tend to produce larger offspring than larger species (Emlet *et al*., 1987). In non-marine species, maternal–offspring size relationships are common and a variety of adaptive explanations have been proposed for the observed correlations. For example, Sakai and Harada (2001) propose that if larger mothers can provision their offspring more efficiently than smaller mothers, then this will result in a correlation between maternal and offspring size. Alternatively, Parker and Begon (1986) predict that if competition between siblings is likely, then larger, more fecund mothers should produce larger offspring to compensate for increased levels of competition. This may apply

Table 1.3 Summary of studies reporting a relationship between maternal size and offspring size in marine invertebrates

Study	Species	Development	Relationship
Dugan *et al.*, 1991	*Emerita analoga*	P	+ve in 8/22 sites
Damiani, 2003	*Pagurus longicarpus*	P	–
Gimenez and Anger, 2001	*Chasmagnathus granulata*	P	+ve
Clarke, 1992	*Ceratoserolis trilobitoides*	B	+ve
Clarke, 1992	*Serolis polita*	B	–
Willows, 1987	*Ligia oceanica*	?	+ve
Oullet and Plante, 2004	*Homarus americanus*	P	+ve
Kim and Hong, 2004	*Palaemon gravieri*	P	–
Dunn and McCabe, 1995	*Gammarus duebeni*	D	+ve
Chaparro *et al.*, 1999	*Crepidula dilatata*	D	+ve
Valentinsson, 2002	*Buccinum undatum*	D	–
Ito, 1997	*Haloa japonica*	L	+ve
Kohn and Perron, 1994	*Conus* spp. (13 sp.)	P	No relationship in 11/12 species but −ve in *C. armoreus*
Steer *et al.*, 2004	*Euprymna tasmanica*	D	–
McCarthy *et al.*, 2003	*Phragmatpoma lapidosa*	P	–
Bridges and Heppell, 1996	*Streblospio benedicti*	L	+ve
Marshall, 2005; Marshall *et al.*, 2003	*Bugula stolonifera*	L	+ve in 2/3 sites, −ve in 1/3
Marshall *et al.*, 2000	*Pyura stolonifera*	L	+ve

Table 1.3 (*continued*)

Study	Species	Development	Relationship
Marshall and Keough, 2003	*Ciona intestinalis*	L	+ve
Marshall and Keough, 2003	*Uniophora granifera*	L	+ve

P, B, L and D indicate planktotrophic, brooding, lecithotrophic and direct development, respectively. '+ve' indicates a positive correlation between maternal size and offspring size and '–' indicates no relationship.

to direct developers, but competition among sibling larvae in planktotrophic species seems unlikely. Hendry *et al.* (2001) suggest that if the maternal phenotype influences the quality of natal environment (e.g., larger mothers having access to the best spawning sites), then a correlation between offspring size and maternal size should be expected. These are all intriguing possibilities, but we currently have insufficient data to determine if any of these models apply to marine invertebrates. Alternatively, the maternal size–offspring size relationship may be non-adaptive and simply be a product of anatomical scaling constraints (Fox and Czesak, 2000). Regardless, it appears in some species, larger mothers produce larger offspring and so not only are larger mothers contributing *more* offspring to the next generation but also they are contributing offspring of the highest quality. This has interesting implications for fisheries and population demographic models because, generally, populations with larger individuals are more likely to supply recruits in populations that contain mostly small individuals (Birkeland and Dayton, 2005).

4.2. Among populations

4.2.1. Habitat quality

Given the effects of maternal nutrition and stress on offspring size, it is perhaps unsurprising that habitat quality also has a strong effect on the size of offspring. However, as with maternal nutrition, the direction of the effects of habitat quality on offspring size is highly variable (George, 1994, 1995; George *et al.*, 1990). Habitat quality can vary due to an almost endless variety of factors but some commonly reported factors include tidal height, water depth (Bertram and Strathmann, 1998) and wave exposure (Etter, 1989). Generally, in poorer quality/more stressful habitats, offspring size is smaller (references above in Section 4.1.1); however, this is not always the case. It is unclear whether these responses are adaptive: the lack of information emphasizes the fact that very few studies have examined the consequences of offspring-size variation in multiple habitats.

4.2.2. Latitudinal clines

Thorson (1935) first suggested that egg size increases from lower to higher latitudes and initial evidence in *Balanus balanoides* supported this idea (Barnes and Barnes, 1965), but it was noted that the trend was inconsistent and appeared to be more related to winter temperatures than latitude per se. Interest in the effects of latitude on offspring size (in crustaceans in particular) has resumed more recently, and for some species, there is a strong latitudinal cline in offspring size (Hadfield, 1989; Hagstrom and Lonning, 1967; Kokita, 2003; Lardies and Castilla, 2001; Lardies and Wehrtmann, 2001; Wagele, 1987; Wehrtmann and Kattner, 1998). Clearly, selection pressures that act on offspring size are likely to predictably change along latitudinal clines, but we are unaware of any study that specifically addresses the relationship between offspring size and performance and how this changes along latitudes. We believe that such studies are warranted given the surprising results from similar studies on seed size (Moles *et al.*, 2004).

5. OFFSPRING-SIZE MODELS

In this section, we review the various models examining offspring size in marine invertebrates, some of the fundamental knowledge gaps that are currently slowing progress and some problems with the traditional approach to modelling offspring size.

Given the astonishing range of offspring sizes exhibited in marine invertebrates, it comes as no surprise that one of the first attempts using models to understand the selection pressures operating on mothers was done with reference to benthic marine invertebrates (Vance, 1973). Vance's classic work used arbitrary units to determine what size offspring maximized maternal fitness (the number of settling larvae) with respect to a number of parameters. While Vance's work was the earliest work on the issue, Smith and Fretwell's (1974) work was probably more influential among the broader community of ecologists. The two models share two basic features: a trade-off between the size and number of offspring and offspring size-fitness function, with these parameters forming the basis of most of the subsequent life-history models of offspring size. We will now examine these basic components of offspring-size models before examining some of the variations on the theme.

5.1. Offspring size-number trade-off

This is the simplest and most conserved feature of offspring-size optimality models, which typically assume that the number of offspring a mother can produce is inversely proportional to the size of their offspring:

$$N = \frac{C}{s}$$

where N is the number of offspring produced, C is the total resources available for reproduction and s the size of offspring.

Typically, this trade-off is presented as an energetic argument: mothers have a limited amount of energy available for reproduction, so any increase in offspring size will result in a concomitant decrease in fecundity. Note that this argument pertains specifically to the *energetic costs* to the mother rather than the *energetic content* of the offspring, a subtle but important difference. Since the early models of Vance and Smith and Fretwell, there has been a significant effort devoted to determining the relative energetic content of large and small offspring among and within species. Across species, there now appears to be reasonable evidence for a relationship between egg size and energetic content in annelids and echinoderms at least (Jaeckle, 1995; McEdward and Miner, 2001; Pernet and Jaeckle, 2004; Wendt, 2000). Within species, the relationship between egg size and energy content is viewed as being more variable. Table 1.4 summarizes those studies that have examined the relationship between egg size and energetic content within marine invertebrate species. McEdward and colleagues have repeatedly suggested that egg size is not a reliable indicator of maternal investment because some regression equations required large differences in egg size to predict a difference in energetic content (McEdward and Carson, 1987; McEdward and Chia, 1991; McEdward and Coulter, 1987; McEdward and Miner, 2001). We would argue that offspring size is probably a reasonable reflection of offspring energetic content for a number of reasons. First, the most common method by which the energetic content of eggs was estimated in many of the studies that found no relationship between offspring size and energy content was the dichromate oxidation technique as modified by McEdward and Coulter (1987). This technique is now viewed as producing unreliable results for a number of reasons (Gosselin and Qian, 1999; Pernet and Jaeckle, 2004), and so the lack of a relationship may be due to methodological problems. Second, the lack of a significant relationship within some species is almost certainly due to a Type II error as a result of a lack of statistical power. The latter seems likely in some studies where only a small number of eggs were examined per species [e.g., McEdward and Chia (1991) used three values for two of the species in their study]. Thus, we believe it is likely that larger offspring have a higher energetic content than

Table 1.4 Summary of studies examining the relationship between offspring size and energetic content

Study	Species	Method	Correlation	*n* of eggs/ female	Notes
McEdward and Chia, 1991	*Henricia* sp.	PD	No, $R = 0.37$	18/2	One point highly influential
McEdward and Chia, 1991	*Solaster endeca*	PD	Yes, $R = 0.84$	20/2	Calculated from graph
McEdward and Chia, 1991	*Solaster dawsoni*	PD	Yes, $R = 0.84$	20/2	
McEdward and Chia, 1991	*Mediaster aequalis*	PD	Yes, $R = 0.616$, P value from 1 tailed test significant	10/1	Calculated from graph
McEdward and Chia, 1991	*Pteraster tesselatus*	PD	Yes, $R = 0.9$	20/2	Calculated from graph
McEdward and Coulter, 1987	*Pteraster tesselatus*	PD	No, $R = 0.25$	44/1	
Clarke, 1992	*Chorismus antarticus*	Elemental carbon	Yes, $R = 0.34$	?/111	Square root from % variance explained
Clarke, 1992	*Notocrangon antarticus*	Elemental carbon	Yes, $R = 0.51$	?/29	Square root from % variance explained
Clarke, 1992	*Eulus gaimadrii*	Elemental carbon	Yes, $R = 0.506$	?/99	Square root from % variance explained

PD = Potassium dichromate micro-oxidation technique.

smaller offspring. However, this does not necessarily mean that offspring size perfectly represents energetic content or, more importantly, that larger offspring cost more to produce.

Although we believe that offspring size may be a reasonable indicator of energetic content in marine invertebrates, we suggest that this line of research is somewhat irrelevant to the central issue of whether mothers face a trade-off between the size and number of their offspring. The crucial component of the offspring size-number trade-off is that larger offspring 'cost' more to produce than small offspring. Remarkably, there have been no tests, to our knowledge, that have examined this or that find a trade-off between the size and number of offspring that are produced. As a first step, comparative analyses across species could be useful (e.g., Elgar, 1990) and Kohn and Perron's (1994) comparisons among *Conus* species certainly suggest a trade-off. However, Stearns (1992) highlights the dangers associated with inferring trade-offs from interspecific studies, and empirical measures of the size and number of offspring produced among different individuals of the same species may be more informative. The lack of tests is surprising given that there are some indications that the relative cost of producing large and small offspring could be non-intuitive. For example, the costs of embryo packaging are likely to be non-trivial (for direct developers especially) and may not scale linearly with offspring size (volume). For example, *Conus* species with larger eggs also produce more expensive protective capsules than species with smaller eggs (Kohn and Perron, 1994). Thus, the relative costs of packaging larger offspring will be different than packaging smaller offspring (assuming that one offspring is included per package), resulting in differences in provisioning efficiency between large and small offspring. Finally, Sakai and Harada (2001) have suggested that if offspring are metabolizing resources as they are provisioned (e.g., in brooding species) and the rate at which mothers can provision their offspring is limited, then larger offspring will tend to take longer time to be provisioned and therefore are less efficient to produce.

Overall the energetic costs of producing offspring may not scale with size and caution should be exercised regarding this assumption. It could be argued that the use of size-number trade-offs may still be appropriate because although offspring size and number may not trade off because of energetic constraints, they almost certainly will trade off because of simple space constraints. The brood capacity of mothers to hold eggs or developing offspring is finite if a mother produces more offspring; she may have to produce offspring of smaller size so that they still fit within her reproductive structures. Furthermore, while offspring size may not perfectly represent energetic investment, it does capture some effects of offspring size that would not be represented by energetic content alone. As shown earlier, some offspring-size effects are essentially energetic effects; larger offspring perform better because they have more resources (e.g., resistance to starvation).

However, other effects of offspring size are simply a product of the physical effect of increased size (e.g., increased target size for fertilization, developmental time), and still others are probably composites of the two (larger ciliated larvae may swim for longer because they have more reserves *and* a lower surface area to volume ratio). Therefore, offspring size captures two aspects of subsequent performance that energetic content alone may not, and given the relative ease of measuring offspring size we suggest that it remains a useful proxy. Nevertheless, more work on the energetic costs of producing large and small offspring is clearly necessary to further resolve this issue.

5.2. Offspring size-fitness function

This part of the offspring-size optimality models has received the most attention while it has been revised repeatedly, a common thread remains at its fundamentals (Table 5). Initial attempts at modelling offspring size focused solely on planktonic survival with decreases in offspring size resulting in a longer planktonic period and thus higher overall mortality (Christiansen and Fenchel, 1979; Vance, 1973a,b). However, later attempts also incorporated the effects of offspring size on fertilization rates (Levitan, 1993; Podolsky and Strathmann, 1996), facultative feeding (McEdward, 1997), generation time (Havenhand, 1993) and post-metamorphic effects of offspring size (Marshall *et al.*, 2006). As shown in Table 1.5, most of the models contain a planktonic mortality function and a function linking offspring size to time spent in the plankton with the majority of modifications of Vance's original model occurring at one or both of these functions.

There are some fundamental knowledge gaps that could drastically change the predictions of each of the models and some reproductive modes that are common in marine invertebrates that are completely ignored. For example, although Christiansen and Fenchel (1979) included the effects of size-dependent planktonic mortality in their model, there have been no empirical studies examining whether larger or smaller larvae (of the same species and age) have a greater probability of survival [note that Levitan (2000) includes a similar component in his model]. We have shown that larger larvae are more likely to reject poor settlement surfaces than are smaller larvae, and so are more likely to settle in higher quality habitats (Marshall and Keough, 2003c). Thus, the benefits of increasing offspring size could be much higher than current models would predict. One group that has been mostly ignored in theoretical models is direct developers. Most marine invertebrate models do not explicitly include any phases that are relevant to this major group. More general models have considered how offspring size might be optimally balanced in a group with high levels of maternal protection (packaging).

Table 1.5 Summary of offspring-size optimality models that are most relevant to marine invertebrates

Study	Provisioning	Fertilization	Planktonic period	Post-metamorphic period
Vance, 1973a	×	×	$\Psi = e^{-MT}$	×
Christiansen and Fenchel, 1979	×	×	$\Psi = e^{-M^{\star}T}$	×
Sargent *et al.*, 1987	×	×	×	$\Psi = EL(S)$
McEdward, 1997	×	×	$\Psi = e^{-MT^{\star}}$	×
Levitan, 1993	×	$\Psi = 1 - e^{-\alpha S}$	$\Psi = e^{-MT}$	×
Levitan, 2000	×	$\Psi = 1 - e^{-\alpha S}$	$\Psi = e^{-MT^{\star\star}}$	×
Marshall *et al.*, 2006	×	×	×	$\Psi = L(S)$

Note that the models have been greatly simplified so that their essential structures can be compared. In all of the models, M denotes planktonic mortality rate, T denotes time spent in the plankton and S denotes offspring size. A cross indicates that the model does not include this life-history stage.
Ψ represents offspring fitness. E represents pre-hatching survival: e^{-mS}, where m = mortality rate while in the egg; $L(S)$ represents post-metamorphic performance and is a function of S; $T = \lambda + \rho$ where $\lambda = S\beta$ and $\rho = \alpha(1 - S)$, where β and α are constants; $M^{\star} = P + FS$ where P is mortality common to all sizes and F is a larval size-specific mortality rate; $T^{\star} = DS + D(1 - S)/F$ where D = time taken to develop at the maximum rate and F = food availability; $T^{\star\star} = S_{fp}/(S - 1) + T_{fp}$ where S_{fp} = minimum size where planktonic feeding is unnecessary and T_{fp} = a minimum time in the plankton when feeding does not occur. Note: this assumes that there is no effect of egg size on the pre-feeding period.

The model of Sargent *et al.* (1987) is relevant to encapsulated direct developers: this model assumes that maternal care (packaging) increases offspring survival, larger juveniles have greater performance and larger offspring have longer periods until hatching. Overall, this model predicts that for species with greater levels of maternal care, larger offspring sizes should be favoured (Sargent *et al.*, 1987). For marine direct developers, there is good evidence for each of these assumptions (Kohn and Perron, 1994; Moran and Emlet, 2001; Strathmann, 1995; Strathmann and Chaffee, 1984; Strathmann *et al.*, 2002). We suggest that this model could be applied to direct developers successfully as a way of modelling offspring-size evolution in this group. However, this assumes that the costs of egg packaging can reliably be estimated.

5.3. Reconciling within-clutch variation

All offspring-size optimality models predict at least two stable optima, a 'large offspring-size optimum' where fitness benefits exceed fecundity costs and a 'small offspring-size optimum' where producing infinitely small offspring yields an infinite fecundity (Vance, 1973a,b). The latter optimum is clearly non-sensical and is simply a product of the functions that are used rather than an accurate reflection of biology. Thus, if we ignore optima based on unfeasibly small offspring, in a constant environment, we should expect a single optimum size. Models incorporating the effects of maternal phenotype on the natal environment have become more common (Hendry *et al.*, 2001; Parker and Begon, 1986; Sakai and Harada, 2001). For example, Sakai and Harada (2001) predict that if larger mothers can provision their offspring more efficiently than smaller mothers, then maternal size and offspring size should be correlated. Further, in species of fish where the maternal phenotype has the potential to affect the offspring size–fitness relationship, offspring-size variation within populations is higher (Einum and Fleming, 2004a). These models predict the observed variation in offspring sizes among different mothers and initial empirical evidence is supportive (see Section 4.1.2). While a substantial theory base can now account for variation in offspring size among mothers, explaining the variation in offspring sizes from the same mother has been more problematic. While there are numerous verbal arguments for producing a brood of offspring that vary in size (e.g., Capinera, 1979; Crump, 1981; Dziminski and Roberts, 2005; Lips, 2001), the few theoretical considerations of intra-brood offspring-size variation struggle to find an adaptive basis for this variation (e.g., Einum and Fleming, 2004b; McGinley *et al.*, 1987). In most instances, producing offspring of identical size has the greatest advantage or if producing variable offspring is advantageous, it is only under restrictive and unlikely assumptions. For example, McGinley *et al.* (1987) found that producing offspring of variable size was advantageous only when mothers could strictly control the dispersal of their offspring into the appropriate habitat. Rather than having an adaptive basis, intra-brood variation is increasingly viewed as a product of physiological or genetic constraints that prevent mothers from producing offspring of identical size (Einum and Fleming, 2004b; Fox and Czesak, 2000). In their review of offspring-size effects on insects, Fox and Czesak (2000; p. 358) concluded that '. . . some authors have suggested that at least some of the variation within families is an adaptive response to living in a variable environment. At this time however, there are few experimental studies and too little theoretical work to generalize'. Therefore, despite the intuitive appeal of intra-clutch variation in offspring size as a mechanism for coping with environmental heterogeneity, theoretical evidence for the concept remains elusive. We suggest that the ubiquitous variation in offspring size seen within clutches does not solely occur due to constraints on producing offspring of uniform size and may yet have an adaptive explanation. We believe that the lack of theoretical evidence for adaptive within-clutch variation reflects the modelling approaches that have traditionally been used; optimality models, by definition, predict a single offspring size to maximize fitness (ignoring the nonsensical, minimum optimum). Alternative approaches such as game theoretic models (Geritz, 1995; Geritz *et al.*, 1999) may provide better tools for exploring adaptive variation in offspring size within clutches whereas more traditional, optimality models may still be useful for exploring variation among mothers, populations and species.

5.4. Summary of offspring-size models

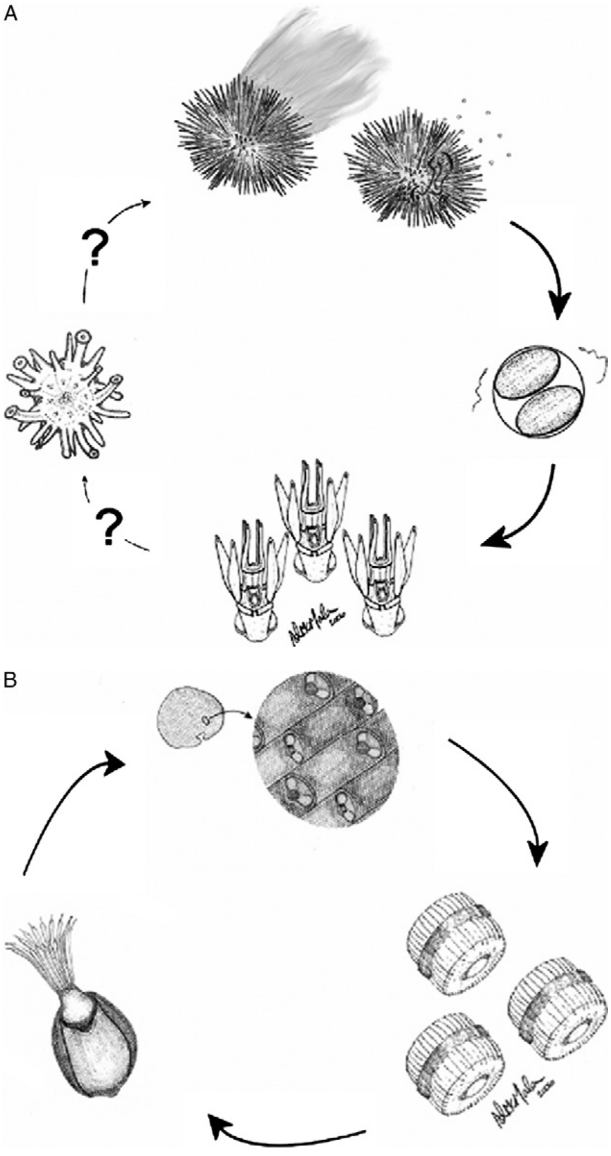
One point this chapter has hopefully made clear is that variation in offspring size can have effects on performance in every life-history stage. Accordingly, theoretical models need to reflect the pervasive nature of offspring-size effects across life-history stages. Ideally, a realistic optimality model should contain the influence of maternal nutritional state, and the relationships between offspring size and fertilization success, planktonic survival, settlement choice and post-metamorphic performance. Once this model has been constructed, then perturbations of the environment in each of these conditions and the relative importance of each life-history stage can be assessed. We suggest that this is where the real value of optimality modelling lies, that is, as tools for examining the relative contribution of each life-history stage to the selective pressures acting on offspring size and for making predictions about how the variation in environmental conditions will influence optimal offspring size. In contrast, these models have been used inappropriately to explain interspecific patterns in offspring-size distributions (e.g., Sewell and Young, 1997; Vance, 1973a,b), and a great deal of effort has been expended to try and match optimality model predictions with the observed distribution of offspring sizes among species (McEdward and Miner, 2006). Such comparisons are inappropriate given that, depending on the relationship between offspring and performance (which of course will vary greatly among species), a very different optimal offspring size will be predicted for each individual species.

6. SUMMARY

Figure 1.7A–C summarize our view of the effects of maternal nutrition on each of the life-history stages for the three broad developmental modes, highlighting the major unknowns for each group and stage. Size of arrow represents our view of the relative strength of offspring-size effects between each stage. The relative strengths also vary with developmental mode.

6.1. Planktotrophs

Despite maternal nutrition constituting a lesser proportion of total larval nutrition in planktotrophs than in other developmental modes, there are strong effects of offspring size on multiple life-history stages of



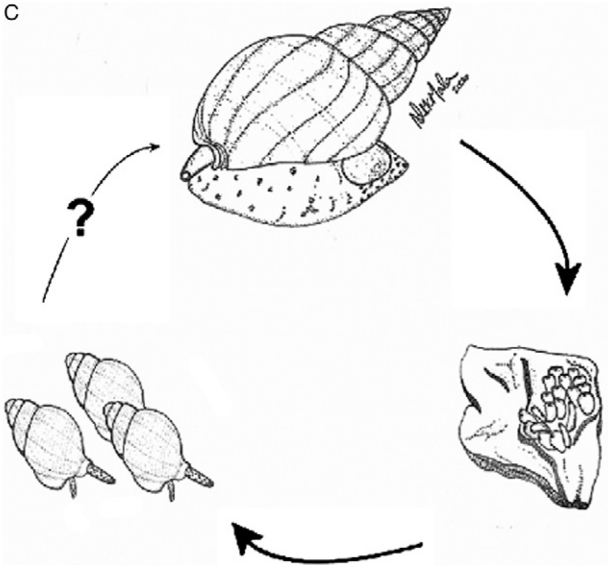


Figure 1.7 Summaries of the effects of offspring size on the various life-history stages of (A) a 'typical' planktotrophic species with external fertilization, (B) a 'typical' lecithotrophic species with internal fertilization and (C) a 'typical' species with direct development. Arrows indicate that we believe there is strong effect of offspring size on that particular life-history stage and question marks indicate that the effects at this stage have not been examined.

planktotrophs. Egg size has strong effects on fertilization in free-spawning species; larger eggs are more likely to be contacted by sperm than smaller eggs (although this may be mitigated by egg accessory features). In many taxa, larvae from larger eggs also spend less time in the plankton than smaller eggs because they appear to require fewer resources before reaching metamorphic competence, although this finding is not universal and more tests are necessary, particularly at the intraspecific level and on 'non-echinoids'. There may be synergistic effects between larvae from larger eggs having greater feeding capacities and more initial resources. The most likely mechanism is increased feeding capacity in larger larvae, leading to higher growth rates. However, there are currently so few data on intraspecific effects of egg size that it is difficult to generalize. Similarly, there are too few data to make definitive conclusions about post-metamorphic effects in planktotrophs but we suggest that post-metamorphic effects cannot be ruled out, because several inter- and intraspecific studies indicate that larger eggs do become larger settlers. Thus, despite its intuitive appeal, the notion that exogenous, larval nutrition overrides any effect of maternal provisioning may be incorrect for planktotrophs.

6.2. Non-feeding

Perhaps unsurprisingly, this group shows the strongest effects of offspring size. Egg size affects fertilization success, developmental time before metamorphic competency in some groups, larval settlement behaviour, maximum larval life span and all elements of post-metamorphic performance, including reproduction and offspring provisioning in the subsequent generation. However, most of the examples come from our own work on colonial invertebrates, and more work on unitary species is necessary to determine the generality of the patterns of offspring-size effects in this group. Non-feeding taxa as a whole are of particular interest because, presumably, larval size affects post-metamorphic performance because of differing levels of larval energetic reserves at metamorphosis. Because larvae do not feed in this group and extended swimming has post-metamorphic consequences (Marshall *et al.*, 2003b; Pechenik *et al.*, 1998), an interesting trade-off exists with regard to whether larger larvae should 'use' their extra resources for swimming and maximize their chances of encountering an optimal habitat, or for settling immediately and utilizing these extra resources for enhanced juvenile/adult performance. It would be interesting to determine the relative impact of larval swimming and larval size on post-metamorphic performance and how these two larval nutrition factors interact.

6.3. Direct developers

We suspect that offspring size–performance relationships in the field are likely to be strongest and most consistent in direct developers because there is no larval stage that can affect (through either extended swimming or larval feeding) the relationship between juvenile energy reserves and original maternal provisioning. This is also the group where the highest level of within-population variation in offspring size was observed across species. Interestingly, numerous different pathways for increasing per offspring maternal investment have evolved in species with this developmental mode, including intragonadal sibling cannibalism (Byrne, 2006), nurse eggs (Spight, 1976) and even partial predation on maternal body parts (Emlet, personal communication). Some reproductive strategies will result in mothers having more 'control' over the provisioning of offspring than others, for example nurse eggs versus cannibalism. We would expect mothers with more control of the provisioning of their individual offspring to be more likely to be able to adaptively adjust the size of their offspring according to local conditions. Given that direct developers tend to disperse less than other groups and the post-metamorphic effects of offspring size can be so strong in this group, we suggest that local population dynamics are particularly susceptible to variation in offspring quality in this group but this requires testing.

6.4. Ecological implications

What are the consequences of offspring-size variation for recruitment and subsequent population dynamics? Consider a broadcast spawning marine invertebrate with short-lived, lecithotrophic larvae. Clearly, offspring size will affect the number of eggs that are produced, the percentage of eggs that are fertilized, the time that the larvae spend in the plankton, the microhabitats in which the larvae settle and the number of those settled larvae that will survive to reproduction. Hence, offspring-size variation can be viewed to act as a ‘filter’ on the number of individuals that pass through each stage. If offspring sizes are relatively large, then (all else being equal) more of the eggs will become successful recruits than if offspring sizes are relatively smaller. In other words, the strength of the link between adult reproductive output and subsequent recruitment will be strongly mediated by offspring size. Furthermore, the strength of links among populations will be strongly affected by offspring-size variation through two mechanisms: first, by affecting the dispersal potential of offspring and second, by affecting the chances of those offspring surviving in the new habitat. Offspring-size effects also change the way in which we view source and sink populations; a population that produces very few, large (high quality) offspring may actually contribute more to the recruitment pool than a population that produces many, low quality offspring. It is particularly interesting that maternal phenotype or habitat quality can strongly affect the size of offspring that are produced, suggesting recruitment is coupled not only to offspring quality and quantity but also to broodstock quality.

6.5. Evolutionary implications

In this chapter, we have found strong evidence for offspring size affecting multiple life-history stages. For species with planktonic larvae, this comprises at least three life-history stages (gamete, larvae and juvenile) and three different habitats (maternal habitat, plankton and juvenile habitat) that can be widely separated in space and time. Consequently, it presents a remarkable challenge to marine invertebrate mothers to optimally provision their offspring, especially since there could be conflicting selection pressures on offspring size at each life-history stage. For example, an adult *C. intestinalis* could be at very high densities and so during spawning, its eggs could be more likely to suffer polyspermy, thereby selecting for smaller eggs. However, smaller eggs are less likely to disperse from this high-competition environment, and less likely to perform well under a higher competitive regime than larger eggs (Marshall and Keough, 2003a,b). The way in which marine invertebrate mothers balance these selection pressures and which life-history stage gets 'priority' as a selection pressure remains an intriguing unknown. In other organisms, offspring size is regarded as a highly plastic, adaptive maternal effect (Fox and Czesak, 2000; Fox *et al*., 1997). Given the complex 'web of selection' acting on marine invertebrate mothers, it will be interesting to determine whether mothers can adaptively adjust the size of their offspring according to local environmental conditions. Our review indicates that direct developers as the most appropriate group for the first examination of this issue as the offspring are less dispersive, and there are few life-history stages in which offspring size can affect performance.

The strong offspring-size effects on fertilization and subsequent performance also have some interesting implications for sexual selection in broadcast spawners. First, it seems that in this group, males will determine the ultimate size of offspring while females determine the range of sizes that can be fertilized. This is because males can control the sperm environment in which eggs are fertilized and ultimately zygote size due to size-dependent fertilization effects (Marshall *et al*., 2002). Thus, there is the potential for sexual conflict, with females getting the greatest fitness benefits from all of their eggs being fertilized whereas males may get greater benefits if they only release small amounts of sperm, 'prudently' fertilizing only the largest eggs that will have the greatest performance (for discussion of 'prudent' males with regards to sperm release see Wedell *et al*., 2002). Egg size-dependent fertilization and performance also has some consequences for males: if a male accesses eggs after they have been exposed to another male, then he can only fertilize the 'left over' eggs, which may be eggs that were smaller and less likely to be fertilized by the first male. Therefore, by accessing eggs second, a male suffers two fitness costs: fertilization of fewer eggs (because the remaining eggs are smaller and harder to 'hit') and siring offspring that will have lower performance (Marshall *et al*., 2004a). Consequently, males will be under strong sexual selection pressure to access a female's brood before any other males.

6.6. Future research directions

The study of post-metamorphic effects of offspring size in marine invertebrates has only just begun and so more work generally is needed. However, we feel there are some priority areas that require addressing. The most commonly cited mechanism for the advantage of increased offspring size is nutritional: larger larvae are more resistant to starvation as settlers than settlers from smaller larvae. There is currently little direct evidence to support this hypothesis. Simple experiments examining the relative importance of offspring size under high- and low-food regimes could address this important gap in our knowledge. Apart from preliminary laboratory studies, there are few studies examining how offspring size affects predation rates. Plant ecologists have been addressing the analogous problem in plants for many years and have used caging studies to examine the interaction between herbivory and optimal seed size (Stanton, 1984, 1985). These experiments could be easily transferred to sessile invertebrates. The final priority area that we feel requires urgent attention is examination of offspring-size effects in more diverse habitats. Thus far, post-metamorphic offspring-size effects in marine invertebrates have focused entirely upon temperate, hard substrate environments (benthic subtidal and rocky intertidal), whereas soft sediment environments (intertidal and subtidal) and coral reefs have received no attention whatsoever. Clearly, this important gap in our understanding of offspring-size effects requires addressing and especially given that offspring sizes show similarly high levels of variation for organisms in these environments when compared to those that have been better studied.

Throughout the discussion of post-metamorphic offspring-size effects, we have emphasized that among different environments or conditions, the effects of offspring size are highly variable. This is a crucial point because ultimately, for any particular species the goal is to determine the relative importance of offspring size. Focusing on any single set of conditions will have limited applicability. Given that the effects of offspring size are so sensitive to local conditions, we believe any study examining offspring-size effects should (1) examine offspring-size effects under as realistic conditions as possible and (2) examine how these effects vary across a range of ecologically relevant stresses. While laboratory studies are essential for the initial establishment of any offspring-size effects (particularly for mobile species), the importance of these effects cannot be estimated until they have been examined in a field context. Numerous studies have shown that laboratory examinations of offspring size will produce misleading conclusions about the strengths of these effects (e.g., Einum and Fleming, 1999; Fox, 2000). We also suggest that further studies on offspring size be conducted at multiple sites with offspring from several populations. By doing so, two issues can be addressed simultaneously. First, the generality of the offspring-size effects can be determined and second, by using several populations, one avoids the potentially erroneous assumption that there is no population-level variation in the relationship between offspring size and performance (Marshall, 2005). Finally, the effects of offspring size should be examined over as much of an organism's life history as possible so as to gather more accurate measures of fitness. Obviously the above suggestions greatly increase the workload of anyone wishing to examine offspring-size effects and, as an example, thus far our own studies have neglected to include all of the above components. However, we believe strongly that the sensitivity of offspring-size effects and their apparent variability among populations lead a risk of highly over- or underestimating the effects of offspring size.

To date, offspring-size effect studies have largely been limited to one or two populations but, given the effects of offspring size on post-metamorphic survival, and the levels of among-population variation in offspring size, it would be interesting to determine whether offspring-size effects 'scale up' to the level of populations. For example, do 'source' populations produce offspring of increased size relative to 'sink' populations. Of particular interest is the examination of how maternal stresses at the level of populations (such as anthropogenic factors like pollution and nutrient enrichment) affect maternal provisioning. In terrestrial systems, it is becoming clear that like many other traits, offspring size is under novel selection pressure from human influences (Hendrickx *et al*., 2003a,b). Given the likely consequences of offspring-size variation for recruitment in marine invertebrates and the initial strong effects of pollutants on maternal provisioning (Cox and Ward, 2002), there may be strong underlying impacts of pollutants that are going undetected.

With regard to the next steps in theoretical studies, we suggest the need for more integrative models that take the effects of offspring size on every life-history stage into account, from the production of gametes through to reproductive maturity of the offspring. Models that examine the influence of recruit quality and its consequences for population connectivity would also greatly enhance our ability to determine the relative importance of larval quality and quantity.

APPENDIX

Variation in offspring size in marine invertebrates with direct (D), lecithotrophic (L) and planktotrophic (P) development and internal (I) or external (E) fertilization. Offspring sizes are given as diameters and CVs are calculated as total variation.

Phylum, Class	Order	Family	Species	Study	Development	Fertilization	Eggs/ mother	Number of mothers	Offspring size	CV
Cnidaria, Anthozoa	Scleractinia	Acroporidae	*Acropora spathulata*	Baird *et al.*, 2001	L	E	32	6–8	557	9.33
	Scleractinia	Acroporidae	*Acropora hyacinthus*	Baird *et al.*, 2001	L	E	18	6–8	553	4.70
	Scleractinia	Acroporidae	*Acropora millepora*	Baird *et al.*, 2001	L	E	32	6–8	541	5.91
	Scleractinia	Acroporidae	*Astreopora myriophthalma*	Baird *et al.*, 2001	L	E	49	6–8	538	3.38
	Scleractinia	Faviidae	*Favites halicora*	Baird *et al.*, 2001	L	E	20	6–8	401	8.72
	Scleractinia	Faviidae	*Goniastrea retiformis*	Baird *et al.*, 2001	L	E	38	6–8	371	5.66
	Scleractinia	Agariciidae	*Pachyseris speciosa*	Baird *et al.*, 2001	L	E	30	6–8	368	5.16
	Scleractinia	Acroporidae	*Montipora digitata*	Baird *et al.*, 2001	L	E	39	6–8	337	12.16
	Scleractinia	Pocillporidae	*Pocillopora damicornis*	Harii *et al.*, 2002	L	I	20	5	1000	20
	Helioporacea	Helioporidae	*Heliopora coerulea*	Harii *et al.*, 2002	L	I	25	10	3700	10.81
Cnidaria, Hydrozoa	Hydroida	Tubulariidae	*Tubularia mesenbryanthemum*	Yamashita *et al.*, 2003	L	I	30	10	305	10.88
Platyhelminthes, Turbellaria	Polycladida	Stylochidae	*Stylochus ellipticus*	Chintala and Kennedy, 1993	P	I	50	?	68.5	4.52
Annellida, Polycheata	Sabellida	Serpulidae	*Hydroides dianthus*	Toonen and Pawlik, 2001	P	E	?	15	60.7	8.23
	Sabellida	Spirorbidae	*Bushiella abnormis*	Hess, 1993	L	I	?	9	185	21.62
	Sabellida	Spirorbidae	*Circeis armoricana*	Hess, 1993	L	I	?	11	167	10.17
	Sabellida	Spirorbidae	*Paradexiospira vitrea*	Hess, 1993	L	I	?	11	196	9.18
	Sabellida	Spirorbidae	*Pileolaria berkelyana*	Hess, 1993	L	I	?	5	169	7.69
	Sabellida	Spirorbidae	*Protolaeospira exima*	Hess, 1993	L	I	?	7	199	10.55
	Terebellida	Sabellariidae	*Phragmatopoma lapidosa*	McCarthy *et al.*, 2003	P	E	?	20	90.4	4.09
Mollusca, Bivalvia	Pteroida	Pectinidae	*Chlamys bifrons*	Styan and Butler, 2000	P	E	10	8	116.5	2.66
	Pteroida	Pectinidae	*Chlamys asperrima*	Styan and Butler, 2000	P	E	10	6	71.2	5.67
	Mytiloida	Mytilidae	*Brachidontes virgiliae*	Bernard *et al.*, 1988	L	I	300	?	383	13.31
	Veneroida	Tellinidae	*Macoma mitchelli*	Kennedy and Lutz, 1989	P	E	25	?	59	3.89
	Ostreina	Ostreidae	*Ostrea edulis*	Jonsson *et al.*, 1999	P	I	40	120	202	5.94
	Veneroida	Tridacnidae	*Tridacna squamosa*	Fitt and Trench, 1981	P	E	10	?	158	4.43
Mollusca, Gastropoda	Archaeogastropoda	Trochidae	*Cantharidus callichroa*	Ho Sun and Hong, 1994	L	I	30	?	446	10.76
	Neogastropoda	Buccinidae	*Engoniophos unicinctus*	Miloslavich and Penchazadeh, 1994	D		?	49	1007.5	25.60
	Neogastropoda	Columbellidae	*Strombina francesae*	Cipriani and Penchazadeh, 1993	D		20	1	571	6.12
	Neogastropoda	Columbellidae	*Strombina pumilio*	Cipriani and Penchazadeh, 1993	D		11	?	947	10.24
	Mesogastropoda	Cypraeidae	*Cypraea caputdraconis*	Osorio *et al.*, 1992	P	I	125	11	112	5.1
	Mesogastropoda	Strombidae	*Strombus gigas*	Davis *et al.*, 1993	P	I	20	3	225	7.56
	Mesogastropoda	Strombidae	*Strombus costatus*	Davis *et al.*, 1993	P	I	30	3	262	2.29
	Mesogastropoda	Strombidae	*Strombus raninus*	Davis *et al.*, 1993	P	I	20	9	140	2.85
	Neogastropoda	Muricidae	*Drupella cornus*	Turner, 1992	P	I	200	7	170	1.47
	Mesogastropoda	Vermetidae	*Vermetus* sp.	Miloslavich and Penchazadeh, 1992	L	I	33	49	240	5.83

(*continued*)

Appendix (*continued*)

Phylum, Class	Order	Family	Species	Study	Development	Fertilization	Eggs/ mother	Number of mothers	Offspring size	CV
	Mesogastropoda	Vermetidae	*Dendropoma corrodens*	Miloslavich and Penchazadeh, 1992	D		134	27	512	11.52
	Mesogastropoda	Cassidae	*Cypraecassis testiculus*	Hughes and Hughes, 1987	P	I	28	2	149	10.06
	Mesogastropoda	Vermetidae	*Petaloconchus montereyensis*	Hadfield, 1989	D		74	16	1450	5.51
	Neogastropoda	Buccinidae	*Babylonia areolata*	Chaitanawisuti and Kritsanapuntu, 1997	P	I	?	35	425.7	5.40
	Neogastropoda	Buccinidae	*Searlesia dira*	Rivest, 1983	D		?	?	1490	18.12
	Neogastropoda	Muricidae	*Nucella crassilabrum*	Gallardo, 1979	D		?	?	1131	8.71
	Neogastropoda	Muricidae	*Thais emarginata*	Spight, 1976	D		?	?	1330	13.23
	Neogastropoda	Muricidae	*Acanthina spirata*	Spight, 1976	D		?	?	671	8.64
	Mesogastropoda	Vermetidae	*Dendropoma petraeum*	Calvo *et al.*, 1998	D		40	?	756	10.73
	Mesogastropoda	Naticidae	*Polinices lewisii*	Pedersen and Page, 2000	P	I	5	?	235.4	2.33
	Mesogastropoda	Calyptraeidae	*Crepidula adunca*	Collin, 2000	D		?	?	2200	25.71
	Neogastropoda	Muricidae	*Nucella lapillus*	Etter, 1989	D		40	5	1270	14.40
	Stylommatophora	Odostomiidae	*Odostomia columbiana*	Collin and Wise, 1997	P	I	??	23?	74	2.17
	Mesogastropoda	Calyptraeidae	*Crucibulum quirqinae*	Veliz *et al.*, 2001	P	I	309	14	325.8	6.59
	Mesogastropoda	Calyptraeidae	*Crucibulum quirqinae*	Veliz *et al.*, 2001	D		69	18	720	17.12
	Neogastropoda	Buccinidae	*Buccinum cyaneum*	Miloslavich and Dufresne, 1994	D		204	33?	1520	19.078
	Mesogastropoda	Calyptraeidae	*Crepidula dilatata*	Gallardo, 1977	P	I	?	?	218	3.66
	Mesogastropoda	Calyptraeidae	*Crepidula dilatata*	Gallardo, 1977	D		?	?	234	7.86
	Archaeogastropoda	Trochidae	*Calliostoma zizyphinum*	Holmes, 1997	L	E	100	9	300	3.12
	Mesogastropoda	Cymatiidae	*Cymatium cutaceum*	Ramon, 1991	P	I	15	1	151	5.03
	Mesogastropoda	Cymatiidae	*Cymatium corrugatum*	Ramon, 1991	P	I	15	1	216	3.425
Mollusca, Opisthobranchia	Cephalaspidea	Atyidae	*Haminoea vesicula*	Gibson and Chia, 1989	P	I	15	30	90	3.33
	Nudibranchia	Doridae	*Aldaria proxima*	Jones *et al.*, 1996	P	I	12	18	168	4.57
	Cephalaspidea	Bullidae	*Bulla gouldiana*	Farfan and Ramirez, 1988	P	I	?	15–30	84.5	4.52
Mollusca, Celphalopoda	Teuthida	Loliginidae	*Sepioteuthis australis*	Steer *et al.*, 2003	D	?	?	5	4800	13.12
Crustacea, Malacostraca	Decapoda	Geryonidae	*Geryon (Chaceon) fenneri*	Hines, 1988	P	I	?	12	567	2.64
	Decapoda	Geryonidae	*Geryon (Chaceon) quinquedens*	Hines, 1988	P	I	?	17	731	3.83
	Decapoda	Paguridae	*Pagurus longicarpus*	Damiani, 2003	P	I	?	49	410	6.09
Crustacea, Copepoda	Harpacticoida	Harpacticidae	*Euterpina acutifrons*	Guisande *et al.*, 1996	P	I	290–497	20	62.4	0.70
Crustacea, Maxillopoda	Thoracia	Balanidae	*Balanus balanoides*	Barnes and Barnes, 1965	P	I	?	?	283	4.94
	Thoracia	Verrucidae	*Verruca stroemia*	Barnes, 1953	P	I	?	?	565	5.3
	Thoracia	Chamalidae	*Chthamalus dentatus*	Achituv and Wortzlavski, 1983	P	I	?	16	190.9	4.6

	Thoracia	Chthamalidae	*Octomeris angulosa*	Achituv and Wortzlavski, 1983	P	I	?	10	211.7	3.77
Bryozoa, Gymnolaemata	Cheilostomata	Bugulidae	*Bugula stolonifera*	Wendt, 2000	L	I	?	?	160	7.90
	Cheilostomata	Bugulidae	*Bugula simplex*	Wendt, 2000	L	I	?	?	207	19.43
	Cheilostomata	Bugulidae	*Bugula turrita*	Wendt, 2000	L	I	?	?	202	6.64
	Cheilostomata	Bugulidae	*Bugula neritina*	Marshall *et al.*, 2003	L	I	?	?	271	6.90
	Cheilostomata	Watersiporidae	*Watersipora subtorquata*	Marshall and Keough, 2004	L	I	?	?	323.18	11
Echinodermata, Echinoida	Clypeasteroida	Dendrasteridae	*Dendraster excentricus*	Podolsky, 2002	P	E	10	6	129	3.5
	Arbacioida	Arbaciidae	*Arbacia lixula*	George *et al.*, 1990	P	E	100	10	76.6	4.30
	Cidaroida	Cidaridae	*Phyllacanthus imperialis*	Olson *et al.*, 1993	L	E	10	20	507	6.29
	Clypeasteroida	Clypeasteridae	*Clypeaster rosaceus*	Emlet, 1986	FP	E	25	?	280.3	2.74
	Clypeasteroida	Clypeasteridae	*Clypeaster subdepressus*	Emlet, 1986	P	E	25	?	152.6	2.29
Echinodermata, Asteroida	Platyasterida	Luidiidae	*Luidia maculata*	Komatsu *et al.*, 1994	P	E	?	?	173	3.46
	Platyasterida	Luidiidae	*Luidia foliolata*	George, 1994	P	E	20	1	144.3	4.78
	Spinulosida	Echinoasteridae	*Echinaster* morph 1	Scheibling and Lawrence, 1982	L	E	9	10 × 12 × 3	840	4.76
	Spinulosida	Echinoasteridae	*Echinaster* morph 2	Scheibling and Lawrence, 1982	D	E	12	10 × 12 × 3	960	5.2
	Platyasterida	Luidiidae	*Luidia quinaria*	Komatsu *et al.*, 1982	P	E	60	?	124	4.91
	Paxillosida	Astropectentidae	*Astropecten gisselbrechti*	Komatsu and Nojima, 1985	L	E	17	?	353	5.09
	Forcipulata	Asteriidae	*Pisaster brevispinus*	Fraser *et al.*, 1981	P	E	?	?	165	3.33
	Forcipulata	Asteriidae	*Pisaster ochraceus*	Fraser *et al.*, 1981	P	E	30	5	163	3.68
	Spinulosida	Poraniidae	*Porania antarctica*	Bosch, 1989	P	E	30	4	548	9.23
	Spinulosida	Poraniidae	*Porania* sp.	Bosch, 1989	L	E	35	7	554	17.08
	Spinulosida	Pterasteridae	*Pteraster militaris*	McClary and Mladenov, 1990	D		?	75	2171	25.10
	Forcipulata	Asteriidae	*Diplasterias brucei*	Bosch and Pearse, 1990	D		105	1	3000	20
	Spinulosida	Asterinidae	*Patiriella regularis*	Byrne, 1991	P	E	10	~10	197	1.92
	Spinulosida	Asterinidae	*Asterina minor*	Komatsu *et al.*, 1979	L	E	37	?	437	6.86
Echinodermata, Ophiuroida	Phrynophiurida	Asteroschematidae	*Astrobrachion constrictum*	Stewart and Mladenov, 1994	L	E	400	16	415	13.49
Echinordermata, Holothuroida	Dendrochirotida	Psolidae	*Psolus chitonoides*	McEuen and Chia, 1991	L	E	10	5	627	5.58
	Dendrochirotida	Psolidae	*Psolidium bullatum*	McEuen and Chia, 1991	L	E	10	2	330	5.15
	Aspidochirotida	Holothuriidae	*Holothuria scabra*	Ramfafia *et al.*, 2000	P	E	?	?	157	2.27
	Apodida	Synaptidae	*Leptosynapta clarki*	Sewell, 1994	D		100	6	2000	52
Chordata, Ascidia	Stolidobranchia	Pyuridae	*Pyura stolonifera*		L	E	100	34	269	9.18
	Aplousobranchia	Didemnidae	*Diplosoma listerianum*		L	I	10	12	976	9.32
	Phlebobranchia	Cionidae	*Ciona intestinalis*		L	E	100	20	145	5.17
	Stolidobranchia	Pyuridae	*Pyura fissa*		L	E	50	10	175.7832	5.21
	Stolidobranchia	Styelidae	*Styela plicata*		L	E	50	10	163	7.9

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