

## The relationship between maternal phenotype and offspring quality: Do older mothers really produce the best offspring?

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**Abstract.** Maternal effects are increasingly recognized as important drivers of population dynamics and determinants of evolutionary trajectories. Recently, there has been a proliferation of studies finding or citing a positive relationship between maternal size/age and offspring size or offspring quality. The relationship between maternal phenotype and offspring size is intriguing in that it is unclear why young mothers should produce offspring of inferior quality or fitness. Here we evaluate the underlying evolutionary pressures that may lead to a maternal size/age–offspring size correlation and consider the likelihood that such a correlation results in a positive relationship between the age or size of mothers and the fitness of their offspring. We find that, while there are a number of reasons why selection may favor the production of larger offspring by larger mothers, this change in size is more likely due to associated changes in the maternal phenotype that affect the offspring size–performance relationship. We did not find evidence that the offspring of older females should have intrinsically higher fitness. When we explored this issue theoretically, the only instance in which smaller mothers produce suboptimal offspring sizes is when a (largely unsupported) constraint on maximum offspring size is introduced into the model. It is clear that larger offspring fare better than smaller offspring when reared in the same environment, but this misses a critical point: *different* environments elicit selection for different optimal sizes of young. We suggest that caution should be exercised when interpreting the outcome of offspring-size experiments when offspring from different mothers are reared in a common environment, because this approach may remove the source of selection (e.g., reproducing in different context) that induced a shift in offspring size in the first place. It has been suggested that fish stocks should be managed to preserve these older age classes because larger mothers produce offspring with a greater chance of survival and subsequent recruitment. Overall, we suggest that, while there are clear and compelling reasons for preserving older females in exploited populations, there is little theoretical justification or evidence that older mothers produce offspring with higher per capita fitness than do younger mothers.

*Key words:* egg size; fisheries management; life-history theory; marine protected areas; maternal effects; optimal offspring size.

### INTRODUCTION

Do older, larger females produce offspring with relatively higher fitness? In animals and plants with indeterminate growth, there is no question that larger females tend to have higher fecundity, and life-history theory provides an adaptive framework for such a

relationship (Roff 1992). But when that reproductive effort is finely partitioned (that is, when investment per young is low relative to total investment), is there reason to expect that older females should invest more in each offspring than their younger counterparts? Decades ago, Smith and Fretwell (1974) suggested that all females of a population should be constrained by the same size–number trade-off, and the optimal investment per young should be determined by the environment that the young will face. Thus, females releasing offspring in the same place and time should invest the same amount per

Manuscript received 30 January 2009; revised 17 February 2010; accepted 18 February 2010. Corresponding Editor: A. S. Flecker.

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young, regardless of the total amount of resources they have available. On first inspection, this argument makes evolutionary sense. However, there are many reports in the literature of cases where larger, older females appear to be producing higher-quality young, and this is often posed as an expected trait of larger females (see the following section). Here we address the question of age- or size-related maternal effects, injecting a note of caution about the assumption that the offspring of larger/older mothers are intrinsically more fit.

The notion that older, larger females produce higher-quality young has recently become one of the arguments for preserving such females in marine populations, thereby increasing population productivity and resilience (Berkeley et al. 2004*b*, Birkeland and Dayton 2005). Many fishes and marine invertebrates have high fecundity and indeterminate growth, and an increase in adult mortality through fishing reduces the proportion of older, larger fish in a population, even when large fish are not directly targeted (Birkeland and Dayton 2005). Establishing no-take areas allows a return to a less truncated size distribution within the reserve, with a concomitant increase in local production (Birkeland and Dayton 2005). Protection of large females through refugia would undoubtedly increase per capita reproductive output (e.g., Kaiser et al. 2007), and provide an added bonus to population productivity if larger females produced offspring of higher fitness, because the recruitment rates of these offspring should be correspondingly high. Given the increasing popularity of spatial management of marine resources, it is critical to evaluate the ubiquity of the female age/size and offspring quality relationship, so the potential for increased productivity can be verified.

*Prevalence of a relationship between maternal age/size and offspring size*

Across the literature, there are numerous examples of larger and/or older mothers producing offspring of different size than smaller/younger conspecifics. Several reviews of maternal effects have shown that a relationship between maternal age/size and offspring size is relatively common, although by no means universal (Chambers 1997, Heath and Blouw 1998, Fox and Czesak 2000, Sakai and Harada 2001, Marshall et al. 2008*a*). The relationship between offspring size and maternal phenotype is complex for two reasons: (1) both maternal age and maternal size are predicted to influence selection on maternal investment strategies (Pianka and Parker 1975, Parker and Begon 1986); and (2) maternal age and maternal size are often inextricably related, and disentangling the effects of each can be problematic. In some systems, there are indications that maternal age has a strong effect on the offspring phenotype (Berkeley et al. 2004*a*, Benton et al. 2008) but in others, maternal size alone seems to be a stronger influence (Sakai and Harada 2001, Marshall et al. 2003). Throughout this review, we assume that these relation-

ships represent an adaptive shift in the provisioning of offspring among mothers with different phenotypes regardless of whether maternal age or size are driving this pattern—an assumption that appears to be supported by both empirical (Sakai and Harada 2001, Benton et al. 2008) and theoretical (Pianka and Parker 1975, Parker and Begon 1986) studies. We do acknowledge, however, that maternal age and maternal size could act as different, potentially conflicting, selection pressures on maternal provisioning strategies and that much more work is needed in order to disentangle the competing influences on optimal offspring size. Overall, the maternal phenotype–offspring size relationship raises two important questions: (1) Why might optimal offspring size differ for mothers of different sizes/ages? and (2) Do differences in the size of offspring produced by mothers of different sizes/ages necessarily translate into differences in offspring quality?

A BRIEF REVIEW OF OFFSPRING SIZE EFFECTS

Offspring size effects are ubiquitous and pervasive. Across plants, invertebrates, and vertebrates, larger offspring tend to perform better than smaller offspring when confronted with the same environment. Within individual taxa, offspring size effects manifest across every life-history stage from fertilization through to reproduction (Marshall and Keough 2008*a*). Several authors have pointed out that offspring size alone is not necessarily the best measure of maternal investment and that offspring performance can differ due to differential provisioning independently of size (Bernardo 1996). We agree and recognize the complexities associated with this issue, but throughout this review we will use the term “offspring size” for several reasons. First, most studies that have directly measured energy content find that the majority of variation in energy content is explained by offspring size (Marshall and Keough 2008*a*). Second, offspring size affects offspring fitness across a wide range of taxa, suggesting that offspring size alone explains a significant proportion of the variation in offspring performance (Williams 1994, Marshall and Keough 2008*a*). Third, while offspring size may not be a perfect reflection of energy provisioning, larger offspring take up more space, and mothers face a trade-off between the size and number of offspring that they can produce regardless of the energy costs of producing offspring of increased size (assuming that maternal brood capacity is finite). Finally, because the term “offspring size” is familiar to most readers, this represents a convenient shorthand for the more accurate term “per offspring maternal investment.”

A comprehensive review of offspring size effects across taxa is beyond the scope of this paper, but it is worth noting that offspring size represents one of the major determinants of early performance in most taxa that have been studied (Wade 1998). In particular, organisms with minimal parental care exhibit strong offspring size effects relative to taxa with substantial

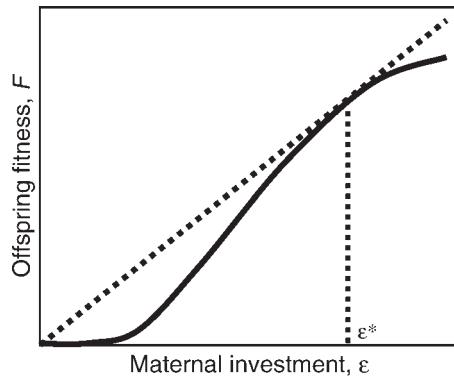


FIG. 1. Graphical determination of optimal investment. The horizontal axis is investment per offspring. The expected offspring fitness function is indicated by the solid black line. Optimal investment ( $\epsilon^*$ ) is determined by the point at which a line through the origin is tangent to the line.

parental care, probably because differential provisioning of offspring post-release can obscure pre-release provisioning effects (Russell et al. 2007). Most studies have focused on the effects of offspring size on early life-history stages and while some find strong, positive effects (Chambers 1997, Fox and Czesak 2000), others find that these effects diminish over time (Heath et al. 1999, Lindholm et al. 2006). Furthermore, some studies find that increases in offspring size can actually reduce offspring performance under some conditions (Kaplan 1992, Marshall et al. 2002, Dibattista et al. 2007). Nevertheless, positive offspring size effects can be remarkably persistent and, in some cases, pervade multiple generations (Benton et al. 2008, Marshall and Keough 2008a, Dias and Marshall 2010, Rius et al. 2010). Interestingly, some studies have shown that offspring size effects are stronger and more persistent when estimated in the field relative to the laboratory (Einum and Fleming 1999, Fox 2000, Monro et al. 2010). We speculate that some studies find transitory or weak offspring size effects because they are conducted in the relatively benign conditions of the laboratory but we eagerly await tests of this prediction. Given that larger offspring typically have a survival advantage over smaller offspring in common environments, why don't mothers produce the largest possible offspring?

Offspring size is an intriguing trait in that it affects the fitness of offspring and mothers simultaneously, but selection is thought to act largely to maximize maternal fitness only (Smith and Fretwell 1974, Trivers 1974, Bernardo 1996). The best illustration of this fact is that most species produce more than one large, maximally provisioned offspring per reproductive bout. Because the amount of resources available to mothers for reproduction is finite, mothers can either make many small offspring or fewer, larger offspring. Thus the fitness of mothers and offspring may be partially decoupled and, indeed, mothers and offspring may be in conflict with regards to the provisioning strategy that

maximizes their respective fitness (Trivers 1974). Overall, mothers must balance the costs of producing larger, well-provisioned offspring (that will perform well) with the fecundity benefits of producing many small offspring. This balance between producing a few, large or many, small offspring has been the focus of optimality models for over 30 years. Critically, the relationship between offspring size and performance determines the optimal size of offspring that mothers "should" produce in order to maximize their own fitness. As such, the selection pressures acting on mothers are highly context dependent—in some environments mothers will be favored if they produce larger offspring, but in others they will be favored if they produce smaller offspring—and ecologists have long used size–number trade-off models to understand selection on offspring provisioning in mothers.

#### Classic egg size–egg number trade-off models

The classic model is that of Smith and Fretwell (1974), which assumes that a mother has some fixed quantity of resources,  $E$ , and that the expected fitness of offspring,  $\phi$ , is a function of the energy invested per offspring,  $x$ . Assuming that  $n$  offspring are each given the same amount of energy, the total resource constraint requires that  $nx = E$ . The mother's fitness is then given by

$$W = n\phi(x) = \frac{E}{x}\phi(x).$$

Fitness is maximized over the choice of  $x$ , leading to the following condition for optimality:

$$\phi(x^*) - \phi'(x^*)x^* = 0$$

with the important conclusion that the optimal strategy depends only on the energy per offspring. That is, in any given environment, all mothers should make offspring of identical quality, but mothers with greater resources should make more of them. The solution may be found graphically by recognizing that  $F = \phi'(x^*)x$  specifies a line through the origin with slope  $\phi'(x^*)$ , so that the condition for optimality is the point where the tangent to the curve passes through the origin (Fig. 1). The graphical representation makes clear several properties that  $\phi$  must have: (1) either there is a minimal value of  $x$  below which  $\phi$  is zero or  $\phi''(0) > 0$ , and (2)  $\phi''(x) < 0$  for some  $x > 0$ .

There has been some debate as to the meaning of the "offspring fitness" term ( $\phi$ ) and whether it really means fitness over the lifetime of offspring, offspring survival, or something in-between (Hunt et al. 2004). Because  $\phi(x)$  is the expected fitness of an offspring of size  $x$ , it represents average fitness of offspring up to the age where their survival and reproduction are independent of  $x$ . This age may be relatively short or long depending on the amount and type of provisioning and the amount of environmentally driven variation in fitness.

All else being equal, the slope of the relationship between offspring size and offspring performance

determines optimal offspring size. When the relationship between offspring size and performance is steep, maternal fitness is maximized by producing relatively larger offspring because mothers receive a large per offspring fitness return for small increases in offspring size (Smith and Fretwell 1974). On the other hand, when the relationship between offspring size and performance is shallow, maternal fitness is maximized by producing relatively smaller offspring because increasing offspring size decreases fecundity but yields only a small per offspring fitness return. This raises an important point: mothers that produce smaller offspring may not have lower fitness than mothers of the same species that produce larger offspring; ultimately, the fitness returns of different reproductive strategies will depend on the offspring size–performance relationship.

The principal factor determining the relationship between offspring size and performance is the environment that offspring experience (Marshall and Keough 2008*b*). Thus, any element of the environment that changes the relationship between performance of offspring and offspring size should affect optimal offspring size. There are a variety of environmental factors that have been demonstrated to affect optimal offspring size, including intra- and interspecific competition, abiotic stress, predation, and food availability (Marshall and Keough 2008*a*). While there are exceptions (Moran and Emler 2001, Allen et al. 2008), generally selection favors the production of smaller offspring in more benign environments (i.e., when all offspring have a good chance of surviving, mothers can gain fecundity benefits by producing smaller offspring) and the production of larger offspring in harsher environments (i.e., when only larger offspring will survive, selection will favor the production of a few, larger offspring). Importantly, it appears that mothers react to changes in the local environment of their offspring and provision them accordingly (Fox et al. 1997).

Mothers in a range of taxa appear to adjust the size of the offspring they produce adaptively in accordance with the environment the offspring are likely to experience. The classic example of this “adaptive” maternal effect is that of seed beetles, where mothers produce larger offspring when they lay their eggs on better-defended seeds and smaller offspring when they lay their eggs on poorly defended seeds (Fox et al. 1997). Mothers also increase offspring size in response to intraspecific competition: larger offspring are often better competitors, and so mothers reared at higher densities produce larger offspring in marine invertebrates, fish, and plants (Bashey 2006, McCormick 2006, Galloway and Etterson 2007, Allen et al. 2008, Bashey 2008). Implicit in these findings is that, when competition is weak, offspring size will have little effect on offspring fitness and therefore mothers will gain fecundity (and therefore, fitness) benefits by producing smaller offspring. While competition and food are the best studied, a range of other environmental factors such

as temperature, predation, and pollution can also induce adaptive plasticity in offspring size (Kaplan 1992, Fox and Czesak 2000, Marshall 2008, Marshall and Keough 2008*a*). Crucially, for such plasticity in offspring size to carry adaptive benefits, mothers must be able to anticipate the environment their offspring will experience (Marshall and Uller 2007). For example, if a mother produces larger offspring when the environment is relatively benign, she will suffer reduced fitness relative to a mother that produces smaller (and therefore, more numerous) offspring. Similarly, if conditions worsen, mothers that fail to increase the size of offspring that they produce will have lower fitness because very few of her offspring are likely to survive. This raises an important question: Can mothers anticipate the environment their offspring will experience?

The environment that offspring will face is not always predictable. Offspring can disperse to new environments that cannot be assessed by the mothers (spatially generated stochasticity in the offspring environment) or, if offspring do not disperse far from their mothers, the maternal environment could vary unpredictably (temporally generated stochasticity in the offspring environment). Environmental stochasticity represents an important selection pressure on life-history traits generally (Benton et al. 1995) and offspring size specifically (Einum and Fleming 2004, Marshall et al. 2008*b*). Thus, throughout our discussions of selection pressures on offspring size, it is worth noting that in the real world there will rarely be a single, easily defined, optimal offspring size that exists over large spatial and temporal scales. Rather, mothers are more likely to produce offspring of a size that broadly matches the mean conditions at any one time, but may also make adjustments to offspring size in response to small-scale changes in local environmental conditions. However, these adjustments in offspring will only be favored if mothers can predict the local offspring environment with some certainty.

Predictability of the offspring environment can come via two mechanisms: (1) cues from the maternal environment or phenotype must be a reliable indicator of the offspring environment; or, alternatively, (2) the maternal phenotype must be a strong determinant of the offspring environment (Marshall and Uller 2007). Both these mechanisms represent a correlation between the maternal phenotype and the offspring environment, but the first is correlative (i.e., one does not necessarily cause the other, they simply co-vary) whereas the second mechanism is asymmetrically causative. Thus, changes in the maternal phenotype can strongly affect optimal offspring size through two mechanisms, and shifts in the maternal phenotype could cause mothers to produce offspring of different sizes. One of the best-studied maternal phenotype–offspring size correlates is maternal size/age.

*Why would optimal offspring size differ  
for mothers of different sizes/ages?*

In many organisms, maternal size/age can determine the environment offspring experience and thus the optimal offspring size mothers should produce. For example, in phytophagous insects, older mothers can be more “desperate” to lay their eggs and therefore are more likely to lay on lower-quality plant hosts (Singer et al. 1992, Sadeghi and Gilbert 2000). In contrast, in some species of fish, older, larger mothers may be better competitors and therefore secure access to better-quality oviposition sites (van den Berghe and Gross 1989). One of the most common ways in which maternal size can affect the offspring environment is via maternal fecundity effects (Parker and Begon 1986). In most organisms, the relationship between maternal size and reproductive output is allometric: larger mothers typically produce many more offspring than smaller mothers (Calder 1984). If offspring do not disperse immediately following release from mothers (both from the mother and from each other), then differences in fecundity can result in differences in the environment offspring experience (Einum and Fleming 2002). For example, differences in maternal fecundity can affect the offspring’s oxygen availability and risk of predation—both of which are likely to affect the optimal size of offspring (Strathmann and Chaffee 1984, Strathmann 1995, Hendry et al. 2001, Hendry and Day 2003, Kudo 2006). Most importantly, when offspring are not immediately highly dispersive, differences in maternal fecundity are likely to result in differences in the level of intraspecific (sibling) competition, and this may have strong effects on optimal offspring size (Parker and Begon 1986).

Intraspecific competition has been demonstrated to affect optimal offspring size across a wide variety of organisms. Increased levels of intraspecific competition typically select for larger offspring because larger offspring are better competitors (Marshall et al. 2006). Thus, larger or older mothers that are more fecund could produce larger offspring in order to offset the change in the offspring size–performance relationship caused by sibling competition (Parker and Begon 1986). Crucially, a shift in optimal offspring size due to increased fecundity depends on whether increased densities of offspring at release correspond to increased levels of competition for some limiting resource (Parker and Begon 1986).

In each of the examples above, maternal phenotype affects the offspring environment by influencing the type of *place* offspring are released. The maternal phenotype can also affect the offspring environment by changing the *time* that offspring are released. Maternal age/size can affect timing of reproduction such that older/larger mothers reproduce at very different times than younger mothers (Shultz et al. 1991, Wright and Gibb 2005). Given that offspring size–performance relationships can change significantly over time, we expect mothers to

adjust the size of their offspring accordingly (Marshall and Keough 2008b). There are many examples of mothers of different ages/sizes reproducing at different times of year. Most notably, some Eastern Pacific rockfishes (*Sebastes* spp.) appear to show this pattern (Bobko and Berkeley 2004), and it is these fish that are cited as examples where older/larger mothers produce “higher quality” offspring.

The above examples demonstrate situations where the maternal phenotype can be a good predictor of the offspring environment because the maternal phenotype determines the offspring environment (in terms of time or space) directly. However, the maternal phenotype can also be a good predictor of the offspring environment because the maternal phenotype is correlated with the likely offspring environment. For organisms that colonize ephemeral habitats, time since colonization (and thus maternal age in organisms with a dispersal stage) can be a good indicator of the offspring environment. For example, Plaistow et al. (2007) found that older soil mite mothers produce larger offspring than younger mothers, and that age was a good indicator of the intensity of competition that offspring will face. Similarly, for organisms that live for only one year but have multiple bouts of reproduction, maternal age can be a good predictor of the offspring environment because maternal age will be correlated with seasonal factors (Landa 1992, Rijnsdorp and Vingerhoed 1994). In all of the examples discussed above, maternal size/age can indirectly affect optimal offspring size by altering or predicting the offspring environment rather than through any direct effect of maternal size constraints on offspring size.

*Physiological factors affecting the maternal  
age–offspring size relationship*

While we suspect that correlations between maternal age/size and the offspring environment (and thus the offspring size–performance relationship) drive the majority of the observed relationships between maternal age/size and offspring size, there are alternative mechanisms that may result in older/larger mothers making larger offspring. Physiological constraints are the most obvious alternative drivers of a relationship between maternal age/size and offspring size, but these constraints may determine selection on offspring size in ways that are perhaps more subtle than initially considered (Mousseau and Fox 1998). It was first suggested for turtles that allometric relationships between the size of reproductive tracts and offspring size placed some limit on maximum offspring size (Congdon and Gibbons 1987). This may have led to the idea that small mothers simply cannot produce larger offspring and, therefore, if larger offspring perform better than smaller offspring, smaller mothers are forced to produce poorly performing offspring. We disagree with this suggestion for several reasons. First, it is unclear that smaller mothers cannot make larger offspring in most

species. In fact, looking across species, some groups show the converse trend: in some marine invertebrates, body size is *negatively* correlated with offspring size (Strathmann and Strathmann 1982). Second, the idea that smaller mothers are constrained from making larger offspring so they resort to making smaller, poorly performing offspring does not make sense from an evolutionary perspective. If offspring have low fitness because they are constrained to be small, mothers may profit more by allocating resources to their own growth in order to overcome the constraint. We next consider a simple model where we determine what conditions will result in mothers producing offspring that are not of optimal size.

*Is there ever a time when smaller mothers should make suboptimal offspring?*

Here we consider the question of when, if ever, a mother should choose to produce offspring of a size less than the Smith-Fretwell optimum as a consequence of a constraint on the maximum size of offspring produced.

To begin, assume that the energy available for reproduction and growth,  $E$ , is an allometric function of body size,  $y$ , specifically,  $E = \beta y^\gamma$ . A fraction  $u$  of energy is allocated to the mother's growth, such that  $dy/dt = uE$ . The remaining energy is allocated to reproduction, such that  $nx = (1 - u)E$ , where  $n$  is the number of offspring produced per unit time and  $x$  is the energy per offspring. Offspring energy is constrained by maternal size, such that  $x \leq cy$  where  $c < 1$ . Offspring survival to independence is a function of offspring energy, i.e.,  $\phi(x)$ . We denote the mortality rate for the mother by  $\mu$ .

The allocation strategy that maximizes fitness is most easily found using dynamic programming (see, e.g., Mangel and Clark 1988). Ignoring for the present the effects of seasonality and stochasticity, the dynamic programming equation is given by

$$\max \left\{ -F(y)\mu + \frac{dF}{dy} \frac{dy}{dt} + n\phi(x) \right\} = 0.$$

With the specific models for growth rate and reproduction described above, the dynamic programming equation becomes

$$\max_{\substack{0 \leq u \leq 1, \\ 0 \leq x \leq cy}} \left\{ -F(y)\mu + \frac{dF}{dy} u\beta y^\gamma + \frac{\phi(x)}{x} (1 - u)\beta y^\gamma \right\} = 0.$$

From here, we can see that a mother will allocate energy to reproduction only if

$$dF/dy < \max\{\phi(x)/x\}.$$

That is, a mother should allocate to reproduction whenever the maximum attainable survival per unit energy is greater than the increment in fitness to be gained by growing. There is, therefore, some size  $y_r$  at which a mother begins reproduction, which is given by the point at which  $dF/dy = \max\{\phi(x)/x\}$ . Further, the maximum

attainable survival per unit energy occurs at either the Smith-Fretwell optimum,  $x^*$ , which satisfies  $x \, d\phi/dx = \phi(x)$  or the constraint energy,  $cy$ , whichever is smaller.

A complete analysis of this model is beyond the scope of this review and we focus on determining the conditions under which a mother should produce offspring which are smaller than  $x^*$ . Note that this only occurs if  $x^* > cy_r$ . Conversely, the constraint never occurs if  $x^* \leq cy_r$ . We can determine the conditions under which this occurs as follows. Assuming that a mother is reproducing (i.e.,  $u = 0$ ), the dynamic programming equation can be re-arranged as

$$F(y) = \mu^{-1} \beta y^\gamma \max \left\{ \frac{\phi(x)}{x} \right\}.$$

Assuming that the constraint is not active,  $dF/dy$  is

$$\frac{dF}{dy} = \mu^{-1} \beta \gamma y^{\gamma-1} \max \left\{ \frac{\phi(x)}{x} \right\}.$$

Since the onset of reproduction occurs when  $dF/dy = \max\{\phi(x)/x\}$ , we have

$$y_r = \left( \frac{\beta \gamma}{\mu} \right)^{\frac{1}{1-\gamma}}$$

provided that the constraint was not active. Since the constraint is only active if  $x^* < cy_r$ , we find that a mother will never produce offspring at a size below  $x^*$  provided that

$$x^* \leq c \left( \frac{\beta \gamma}{\mu} \right)^{\frac{1}{1-\gamma}}.$$

Thus we find that there is only small region of parameter space where smaller mothers gain a net fitness benefit from producing suboptimal offspring, particularly when growth rates are very low and mortality rates are very high. Perhaps most importantly, all of these findings only apply if there is a strong constraint on the maximum size of offspring small mothers can produce—an assumption that has very little support. In our model, we introduced a size constraint that forces mothers to reproduce below a level at which producing an optimal size is accessible. Such a constraint could also occur if mothers achieve additional fitness benefits by reproducing at a suboptimal size (e.g., if habitats are ephemeral or there are advantages to preempting other females). Thus, we suggest that simple size constraints alone are unlikely to ever result in mothers producing offspring of suboptimal size; but we do note that if other temporal or density-dependent factors result in benefits to reproducing at a smaller size, then such an effect remains possible.

Importantly, physiological constraints are *only* likely to result in a maternal size–offspring size relationship if the optimal offspring size for a particular environment exceeds that which smaller mothers can produce. This is particularly unlikely when young are small relative to

the mother. For the situation to occur at all, there should be persistent, directional (rather than stabilizing) selection for increased offspring size. There is little evidence to suggest that selection on offspring size is strongly directional; rather, most studies suggest that offspring size is under stabilizing selection (Marshall et al. 2008b). It is possible that the view that mothers “should” produce as large offspring as possible stems from an inappropriate focus on offspring rather than maternal fitness.

Nevertheless, there may be some situations where offspring size and maternal size/age should be correlated despite a constant relationship between offspring size and performance. Sakai and Harada (2001) suggest an intriguing mechanism whereby larger mothers are able to provision their offspring more efficiently than are smaller mothers. Assuming that offspring consume resources during the provisioning process, an increase in provisioning efficiency results in a shift in optimal offspring size without any change in the offspring size–performance relationship. Fox et al. (2003) suggest another reason why older mothers might produce different-size offspring to younger mothers: they may represent a different genetic subset of a polymorphic population. The suggestion is that if mortality is genotype specific, then the average genotype of young mothers could be different from the average genotype of older mothers. Different genetic subsets of a population might have different optimal offspring sizes (e.g., due to correlations with differences in other traits) and produce different offspring sizes accordingly. Thus we do not rule out the possibility that some evolutionary process could select for a correlation between maternal size and offspring size in the absence of a change in the offspring size–performance relationship; however, does such a correlation necessarily result in larger mothers producing better quality offspring?

*Does a relationship between offspring size and maternal size result in differences in realized offspring quality?*

If larger mothers do indeed produce larger offspring than smaller mothers, and if larger offspring typically perform better than smaller offspring under experimental conditions, two basic questions can be asked. (1) Does it really matter why larger mothers produce larger offspring? (2) Does it follow that larger mothers produce *higher quality* offspring than smaller mothers, in terms of realized fitness? We would argue that the answers to these two questions are “yes” and “no,” respectively.

In most instances, a relationship between maternal size/age and offspring size will be driven by differences in the environment that offspring will experience. At the very least, it seems likely that in most instances mothers of different sizes/ages produce offspring of different sizes because optimal offspring size differs for mothers with different phenotypes. This has crucial implications for whether larger mothers do in fact produce offspring of

higher fitness, because fitness is context dependent (Plaistow et al. 2006).

Larger mothers often have more resources available for reproduction and so typically have higher fecundity. Offspring that come from more fecund mothers may therefore experience higher levels of sibling competition post-release than offspring from less fecund mothers, and this difference in offspring environment may generate differences in optimal offspring size and even outweigh any effects of offspring size (Beckerman et al. 2006). Parker and Begon (1986) were among the first to examine this problem theoretically by incorporating a sibling-competition effect into the basic model proposed by Smith and Fretwell (1974), whereby offspring performance is determined not only by offspring size, but also maternal fecundity:

$$S(n) = 1 - kn$$

where  $S(n)$  is the decrease in offspring performance due to sibling competition,  $n$  is the number offspring produced by a mother and  $k$  is a positive constant specifying the rate of decline in  $S$  with  $n$ . Parker and Begon (1986) then solved for optimal offspring size in the absence and presence of a sibling competition effect for mothers with a wide range of maternal resources, and found that as maternal resource availability increased, so too did optimal offspring size. Fig. 2 shows the effect of increasing maternal resources on optimal offspring size for one set of parameters from Parker and Begon (1986), but is broadly representative of most of the parameter space considered. Note that as maternal resources increase, maternal fitness ( $W$ ) increases, but this figure does not give any indication of how maternal fecundity-driven shifts in optimal offspring size affects offspring performance. To examine how shifts in optimal offspring size due to maternal fecundity affects offspring fitness, we substitute the optimal offspring-size value for a particular level of maternal resources into the offspring size–fitness function:

$$W(s) = \{1 - \exp[-(x - x_{\min})]\}S(n)$$

where  $x$  is offspring size, and  $x_{\min}$  is the minimum size offspring must be to survive. Fig. 2 shows that while optimal offspring size increases substantially over the range of maternal resources, the actual performance of offspring stays relatively constant across that range and, if anything, decreases slightly. This prediction matches an empirical study that also found that sibling competition had a strong, negative effect that overwhelmed the benefits of increased offspring size (Beckerman et al. 2006). Thus, one of the few models that shows how the relationship between maternal resources and offspring size is adaptive also shows that offspring fitness does not increase with maternal resource state. Importantly, this model also assumes that offspring of a single mother remain in close

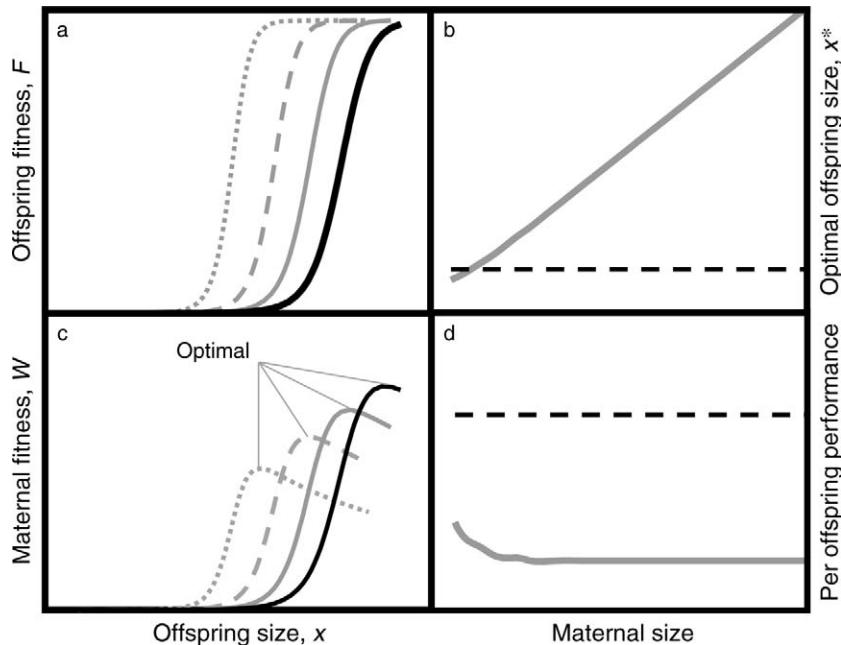


FIG. 2. Left-hand panels show the predicted relationship between offspring size,  $x$ , and (a) offspring performance (fitness) and (c) maternal fitness based on the Parker and Begon (1986) model where maternal size (and therefore resources available for reproduction) varies ( $R = 100, 500, 1000$ , and  $1500$  represented by the gray dotted, gray dashed, gray solid, and black solid lines, respectively; note the rate of decline of offspring performance with brood size was  $k = 0.01$ ). With increases in maternal size, both maternal fitness and the optimal size of young [represented by the shoulder of the offspring-performance curve in panel (a)] increase. Right-hand panels show the predicted relationship between maternal size and (b) optimal offspring size and (d) optimal offspring performance (in order to maximize maternal fitness) based on the models of Smith and Fretwell (1974), where fecundity has no effect (dashed line), and Parker and Begon (1986), where maternal fecundity decreases offspring performance because of sibling competition (solid gray line; note that  $k = 0.01$ ). While optimal offspring size increases with maternal size level in the latter model, offspring performance (i.e., offspring fitness) does not.

proximity for a long enough time that sibling competition affects survival. It is unclear whether this assumption holds for marine organisms with dispersive larval stages, but it is worth noting that, in some species, siblings can settle in proximity to each other despite lengthy larval periods (Selkoe et al. 2006, Veliz et al. 2006).

In the above model, we find that, despite mothers with more resources producing larger offspring, the mean performance of offspring is similar for all mothers—but that does not mean that all mothers contribute equally to recruitment. We explored the effect of incorporating the effects of resource-based changes in optimal offspring size on the relative contribution of females of different age classes using a third model (see Appendix). This model specifically included both shifts in optimal offspring size such that older mothers produced larger offspring (as in our preceding model) and resource-based differences in maternal fecundity. As in the preceding model, larger offspring from older mothers performed similarly to smaller offspring from younger mothers because of the context-dependent nature of offspring fitness (see Appendix for a full description of the model). We find that, because older females are far more fecund, they contribute disproportionately more to recruitment, but offspring size differences do not affect

the relative contribution of each age class (Fig. 3). Thus, this third model predicts that older mothers do not produce offspring of intrinsically higher quality, but older mothers are still the principal contributors to population growth.

The theoretical predictions described above highlight a major point: when larger mothers are reacting to differences in the offspring environment, offspring survival should be largely equivalent to that of young of smaller mothers. While our model (and Fig. 2) focuses on sibling competition as the mechanism that drives the difference in offspring environments and thus optimal offspring size, similar predictions would be generated if there were shifts in optimal offspring size due to any change in environmental quality. Such a compensatory interaction between offspring size and offspring environment has been demonstrated empirically by Russell et al. (2007), who also noted that compensatory interactions between the offspring environment and maternal investment strategies can mask the underlying selection pressures. In addition to the compensatory effects that the maternal phenotype has on the offspring environment, the maternal phenotype can also affect the offspring phenotype independently of offspring size. Recent studies on terrestrial organisms show that the maternal phenotype (specifically, age) changes the

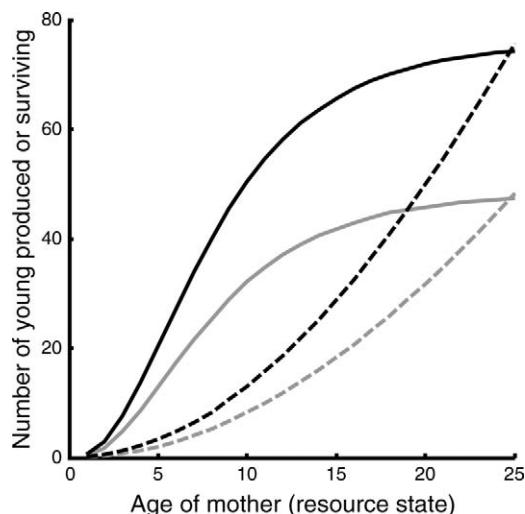


FIG. 3. Model predictions of the relative contribution of mothers of different age classes (unitless) to production and to recruitment. The black lines give the number of offspring produced at each age, and the gray lines give the number of surviving offspring at that age (i.e., the effects of quality and density dependence). Solid lines correspond to the case where energy available for reproduction is saturating, and the dashed lines correspond to the case where the amount of energy available for reproduction increases continuously with age (these represent the two alternative assumptions of our model; see Appendix for details). Across all of the parameter space explored, larger/older mothers contribute more surviving offspring than younger/smaller mothers, but this difference is primarily due to a fecundity effect, rather than differences in offspring quality.

relationship between offspring size and offspring performance (Benton et al. 2008). Several studies have demonstrated that offspring longevity declines with maternal age (the Lansing effect; Marshall and Uller 2007, Benton et al. 2008) and examining the effects of offspring size on early life-history stages only may overestimate the benefits associated with increased offspring size (Dias and Marshall 2010). Thus, confounding environmental and physiological factors associated with maternal phenotype may result in larger offspring from older/larger mothers having the equivalent per capita fitness of smaller offspring from younger/smaller mothers.

The fact that there can be compensatory effects that change the relationship between offspring size and performance raises an important point regarding the investigation of offspring size–performance relationships among clutches of offspring from different mothers. Many studies examine the relationship between offspring size and performance in a common environment or “garden” (e.g., Kaplan 1992, Marshall et al. 2003, Berkeley et al. 2004a). Unfortunately, by conducting offspring size–effect studies in a common environment, the offspring are inevitably isolated from some of the elements of the environment that determined their particular offspring size–fitness relationship (Plastow et

al. 2006, 2007). Thus it is perhaps unsurprising that common-garden experiments find that larger offspring have greater performance than smaller offspring. By homogenizing the experience of offspring from different mothers, common-garden experiments effectively remove the selection that induced these mothers to make different per offspring investments in the first place. We do not wish to criticize common-garden studies as a tool for understanding selection on offspring size generally (indeed, in other studies, we have used such approaches ourselves), but simply point out that when offspring are taken out of the context for which they were provisioned, inappropriate conclusions about their relative performance may be drawn. As an alternative, we suggest that experiments comparing the performance of offspring from mothers of varying fecundities be done at a range of offspring densities so that density-dependent effects (and perhaps more importantly, the interaction between offspring size and density) can be estimated. In the absence of such studies, we maintain that there is little unequivocal evidence that larger mothers that produce larger offspring do indeed produce offspring that have higher per capita fitness.

#### MANAGEMENT IMPLICATIONS FOR FISHERIES

Most of the current models used for population assessment and management use adult spawner biomass and density-dependent relationships between spawning adult biomass and subsequent juvenile recruitment as indicators of population status and resilience to exploitation (Hilborn and Walters 1992). Fishing mortality inevitably truncates age distributions by reducing the proportion of fish that reach older age classes; this will lead to a larger proportion of breeders that are “young” or “naïve,” particularly when coupled with potential increases in growth or survival of juveniles due to density-dependent compensation (Beamish et al. 2006, Berkeley 2006). Recently it has been shown that fishing mortality can also induce evolutionary responses in exploited populations such that multiple traits can undergo rapid change: fished populations evolve to be smaller and less fecund, and produce smaller, more timid offspring (Walsh et al. 2006). If fecundity is the primary indicator of likely reproductive success, models based on spawner biomass should be adequate, because fecundity is a function of body mass. But if maternal effects on offspring quality or fitness make older females more successful spawners, population dynamics may depend even more heavily on age structure. Tantalizing evidence from analyses of fished populations suggests that recruitment variability increases with exploitation rate and may be attributable to changes in the intrinsic productivity of “younger” spawning stocks (Anderson et al. 2008), but the role of offspring quality in this relationship is not yet clear.

In the commercially important rockfishes (genus *Sebastes*) of the North Pacific, females release small

(2–3 mm total length) larvae that then disperse pelagically. Larger females appear to invest more per young (in the form of a larger oil droplet) than do smaller females (Berkeley et al. 2004a, Sogard et al. 2008), but they also give birth over a longer time period, starting considerably earlier in the season (Bobko and Berkeley 2004). In an influential series of papers, Berkeley and colleagues demonstrated that larvae of larger females grew more quickly, were more resistant to starvation, and survived better than larvae from small females when raised under common-garden conditions (Berkeley et al. 2004b). This observation was interpreted as a demonstration that larger females produced higher-quality (and, by implication, higher-fitness) young, and inspired a series of commentaries on the fishery value of preserving large females (for example, in marine reserves) because of their greater per capita productivity and the higher quality of their young (Berkeley et al. 2004b, Palumbi 2004, Birkeland and Dayton 2005). The notion that larger females may produce young with higher per capita survival is now being incorporated into predictive fisheries modeling (e.g., Lucero 2008, 2009, Venturelli et al. 2009). While we agree (and our third model explicitly shows) that large females are worth preserving because of their higher fecundity or greater variation in the timing and location of spawning, we urge caution in assuming that large females produce young that have higher fitness than the young of smaller females. Common-garden experiments or simple physical/physiological comparisons cannot be used to demonstrate fitness differences if the classes of young being compared face different expected environments. In the case of rockfishes, given that mothers of different sizes reproduce at different times of the year, it is very likely that young from different mothers will face different environments. Thus, the shift in offspring size could reflect the fact that different optimal offspring sizes exist for these different times of year, and, as we have shown, such shifts do not necessarily result in a shift in mean offspring fitness.

Given that investment per young can change over the life of a female, there is ample reason (and some evidence) to believe that this trait can be a phenotypically plastic character (Fox et al. 1997, Plaistow et al. 2006, Allen et al. 2008). If offspring size is plastic, we would expect that the factors strongly affecting investment per young would be those that are good indicators of the environment that the young are likely to face (Warner 1997). The biological environment in marine reserves will be expected to be different from unprotected areas (Halpern 2003), and it may well be true that females in reserves will be induced to change the investment that they make in each young they produce.

While we have presented a number of evolutionary arguments regarding the relationship between maternal phenotype, offspring environment, optimal offspring size, and offspring quality, many of these arguments are

yet to be evaluated empirically. We propose that a number of crucial elements of the maternal phenotype–offspring size relationship can be directly tested. Estimates of the relationship between offspring size and performance for offspring under high and low sibling competition are an important first step; for species with highly dispersive offspring such tests are difficult, but for other species this test should be relatively straightforward. In species such as rockfish, where offspring disperse after release, sibling competition seems less likely to occur but, remarkably, recent studies show some level of kin aggregation at settlement in both kelp bass and barnacles, species with lengthy (several weeks) planktonic periods (Selkoe et al. 2006, Veliz et al. 2006). For species where mothers of different sizes reproduce at different times of the year, an examination of the relationship between offspring size and performance (and thus optimal offspring size) at these different times seems like an appropriate direct test of whether differential provisioning is being driven by selection for different optimal offspring sizes (e.g., Landa 1992, Marshall and Keough 2008b).

#### CONCLUSIONS

There is clear evidence that larger mothers produce larger offspring in a range of taxa, including commercially exploited fishes. It is also clear that larger offspring tend to have higher fitness than smaller offspring when reared in the same environment. However, we argue that it is unclear whether these two elements necessarily imply that larger/older mothers produce higher-fitness offspring than do smaller mothers if they place their offspring into different environments. Our argument does not challenge the notion that larger/older fish should be protected from harvesting in some places due to their greater contribution to recruitment—clearly larger/older mothers contribute far more to recruitment than smaller mothers via fecundity effects alone. We simply point out that there are few evolutionary arguments for a maternal size–offspring quality relationship, and that the necessary experiments for assessing this proposed relationship remain to be done.

#### ACKNOWLEDGMENTS

The authors thank Susan Sogard, Tim Benton, and two reviewers who provided extremely valuable comments. D. J. Marshall was supported by the Australian Research Council during the preparation of this manuscript. S. S. Heppell was supported in part by a grant from the North Pacific Research Board (Project number 629). Support was also provided by the Partnership for the Interdisciplinary Study of Coastal Oceans (PISCO), funded by the Packard Foundation and the Moore Foundation. This is PISCO contribution 368.

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## APPENDIX

Details of a model that explores the fitness benefits of mothers of various sizes producing suboptimal-sized offspring (*Ecological Archives* E091-203-A1).