

Does interspecific competition affect offspring provisioning?

DUSTIN J. MARSHALL^{1,3} AND MICHAEL J. KEOUGH²

¹*School of Integrative Biology, The University of Queensland, Brisbane, Queensland, 4072 Australia*

²*Department of Zoology, The University of Melbourne, Melbourne, Victoria, 3010 Australia*

Abstract. Offspring size is one of the most well-studied life-history traits, yet it is remarkable that few field studies have examined the manner in which the relationship between offspring size and performance (and thus, optimal offspring size) is affected by the local environment. Furthermore, while offspring size appears to be plastic in a range of organisms, few studies have linked changes in offspring size to changes in the relationship between offspring size and performance in the field. Interspecific competition is a major ecological force in both terrestrial and marine environments, but we have little understanding of its role in shaping selection on offspring size. Here we examine the effect of interspecific competition on the relationship between offspring size and performance in the field for the marine bryozoan *Watersipora subtorquata* along the south coast of Australia. Both interspecific competition and offspring size had strong effects on the post-metamorphic performance of offspring in the field, but importantly, they acted independently. While interspecific competition did not affect the offspring size–performance relationship, mothers experiencing competition still produced larger offspring than mothers that did not experience competition. Because larger offspring are more dispersive in this species, increasing offspring size may represent a maternal strategy whereby mothers produce more dispersive offspring when they experience high competition themselves. This study shows that, while offspring size is plastic in this species, post-metamorphic factors alone may not determine the size of offspring that mothers produce.

Key words: egg size; marine bryozoan; offspring size; phenotypic plasticity; *Watersipora subtorquata*.

INTRODUCTION

Offspring size is one of the critical life-history traits common to all multicellular organisms (Bernardo 1996). The relative size of an offspring when it is released will have dramatic consequences for its chances of survival, its growth rate, and even its reproductive success (Williams 1994, Moles et al. 2005, Marshall and Keough 2008a). Offspring size varies at all levels, from the striking variation among species to variation within individual broods (Fox and Czesak 2000, Einum and Fleming 2002, Marshall and Keough 2008b), and understanding the causes of offspring size variation remains a major challenge to life-history biologists. Offspring size is particularly interesting in that it affects the fitness of both the offspring and the mother, but selection acts largely to maximize maternal fitness only (Bernardo 1996, Mousseau and Fox 1998). Bigger offspring tend to have higher fitness than smaller offspring but are more expensive to produce. Smith and Fretwell's (1974) now-classic model predicts that the relationship between offspring size and offspring performance is the principal determinant of the optimal offspring size that mothers should produce in order to maximize their own fitness. When there is a steep relationship between offspring size and performance, the

fitness gains derived from producing high-performing offspring outweigh the costs of reduced fecundity (Smith and Fretwell 1974). In contrast, when there is a shallow relationship between offspring size and performance, increasing offspring size results in only a small increase in per offspring fitness that fails to outweigh the costs of reduced fecundity. Thus, any change in the relationship between offspring size and performance should result in a change in the optimal size of offspring that mothers should produce. Overall then, in attempting to understand offspring size variation, two fundamental questions are raised. (1) What factors affect the relationship between offspring size and performance and thus optimal offspring size? (2) Do mothers actually differentially provision their offspring in response to changes in optimal offspring size? It is remarkable that there have been few studies that directly address these questions, particularly under field conditions. In birds, mothers adjust the size of their offspring in response to a range of factors (in this field, known as “differential allocation”; Williams 1994, Cunningham and Russell 2000), and recent evidence suggests that the nutritional environment of the hatchling (and thus optimal offspring size) can be an important determinant of offspring size (Russell et al. 2007). These studies suggest that mothers are adaptively adjusting the size of their offspring in response to different environmental conditions, but in the absence of field estimates of offspring

Manuscript received 16 February 2008; revised 5 June 2008; accepted 16 June 2008. Corresponding Editor: S. G. Morgan.

³ E-mail: d.marshall1@uq.edu.au

size–performance relationships, these findings are inconclusive.

Because offspring are typically dispersive, measuring the relationship between offspring size and performance in the field is difficult. As such, there are few studies that (1) estimate optimal offspring size empirically and (2) determine how environmental change affects optimal offspring size. Most commonly, offspring size–performance relationships are estimated under laboratory conditions (Brody and Lawlor 1984, Azevedo et al. 1997, Santo et al. 2001, Berkeley et al. 2004, Bashey 2006, Lindholm et al. 2006). While laboratory studies are very useful for identifying potentially important factors that may affect optimal offspring size, the few field studies that have been conducted suggest that the effects of offspring size are unlikely to be consistent between the laboratory and the field (Einum and Fleming 1999, Fox 2000). Thus, while many laboratory studies predict that a range of factors may affect optimal offspring size, only a handful of field studies have tested these predictions.

While field examples are rare, initial indications suggest that mothers do adjust the size of their offspring in response to environmentally induced changes in optimal offspring size. One of the best examples of maternal adjustment of offspring size in response to a shift in optimal offspring size under field conditions comes from Fox and colleagues (Fox et al. 1997). In a series of experiments, they demonstrated that seed beetle mothers increased the size of their offspring when they laid their eggs on better-defended seeds. More recently, Allen et al. (2008) demonstrated that intraspecific competition increased the predicted optimal offspring size of a marine invertebrate and that mothers indeed increased the size of their offspring when they experienced competition themselves. However, while laboratory studies suggest that many other factors are likely to affect optimal offspring size, we lack field tests.

One of the most important factors that could potentially affect optimal offspring size is interspecific competition, which has long been recognized as one of the most powerful ecological interactions determining population dynamics (Connell 1961). Furthermore, interspecific competition has repeatedly been implicated in observed differences in offspring size among populations (e.g., Brockelman 1975, Olsen and Vollestad 2003). However, we are aware of no study that has directly examined the manner in which interspecific competition affects the offspring size–performance relationship in the field. Furthermore, no study has yet examined whether increased interspecific competition results in mothers changing the size of their offspring. Here we estimate the relationship between offspring size and offspring performance in the presence and absence of interspecific competition in the field for the marine bryozoan *Watersipora subtorquata*. We then examine whether mothers adjust the size of their offspring in response to interspecific competition in the field.

Watersipora subtorquata is an excellent species for examining the relationship between offspring size and performance in the field. Previous studies have shown that offspring size affects performance in the larval and adult phases (Marshall and Keough 2003b, 2004) and offspring size can be reliably measured in field-settled juveniles (Marshall and Keough 2008b). Interestingly, most of the variation in offspring size in *W. subtorquata* occurs within populations, suggesting that offspring size plasticity is likely (Marshall and Keough 2008b). Finally, colonial marine invertebrates are interesting candidates to examine with regard to offspring size effects because the outcomes of interspecific competition in these organisms are thought to be dependent on colony size (Russ 1982).

MATERIALS AND METHODS

Study species and sites

Watersipora subtorquata is an encrusting bryozoan and an abundant member of the “fouling community” on man-made structures along the south coast of Australia. It broods its larvae for approximately two weeks, whereupon the non-feeding larvae are released and spend only minutes to hours in the plankton before settling and metamorphosing (Marshall and Keough 2003b). A review of the available evidence shows that offspring size (rather than energy content) is a good measure of maternal investment in marine invertebrates (Marshall and Keough 2008a). Settler size is correlated with larval size in *W. subtorquata*, and the correlation is independent of the length of the larval period (Marshall and Keough 2003b), so that offspring size can be reliably inferred from measurements of newly settled juveniles.

We did experiments at two field sites: St Kilda Yacht Marina (37°51'48.52" S, 144°57'55.61" E, hereafter referred to as “St Kilda”) and Williamstown Workshops Pier (37°51'39.54" S, 144°54'28.70" E, hereafter “Williamstown”). Both sites are relatively sheltered from the prevailing weather conditions, either by a man-made breakwater or natural headlands. The fauna in both sites is very similar and include bryozoans (such as *W. subtorquata* and several species of *Bugula*), ascidians (including didemnids and botryllids and several solitary species), serpulid polychaetes, and barnacles (for a detailed description, see Keough and Raimondi 1995). However, there are differences in the size distribution of settling *W. subtorquata* between the two sites (Marshall and Keough 2008b).

General methods

We used naturally settled *W. subtorquata* settlers as our experimental subjects and measured the size of settlers ~24 h after settlement, using the methods described in Marshall and Keough (2008b). To collect settlers in the field, we used black Plexiglas settlement plates (100 × 100 × 6 mm) that had been roughened with sandpaper to encourage settlement. We affixed the settlement plates to PVC backing panels (440 × 440 ×

8 mm) with stainless steel bolts (16 plates per backing panel). At each site, the plates were suspended at a depth of ~1.5 m below the mean low water mark. Plates were deployed on the morning of 23 January 2006 ("day 1"); settlement of *W. subtorquata* (and other species) then occurred over that day and through to the following morning. On the next day ("day 2"), the plates were retrieved and returned to the laboratory, where the *W. subtorquata* settlers from day 1 were measured using a digital camera attached to a microscope (40× magnification). Any that had settled on day 2 had only recently commenced metamorphosis and were easy to recognize and disregard. To individually identify each settler, we used a 10 × 10 grid system on each settlement plate and recorded the settlement plate and the grid reference for each settler. In the rare event that two settlers were in the same grid reference on the same settlement plate, one was randomly selected and removed. At the end of day 2, the settlers were returned to the field and reattached to the backing plates. The travel time between the laboratory and the field was typically <40 min, and the plates were transported in insulated aquaria filled with 20 L of field-collected seawater.

We allocated settlers randomly into two treatments: "competition" and "no competition." In the no-competition treatment, we physically removed any newly settled organisms on the plate surrounding the focal colonies with a stainless-steel scraper every two weeks for the duration of the experiment. Because two focal colonies would occasionally begin to interact as colonies grew, we culled one focal colony at random in the no-competition treatment ($n = 7$). In the competition treatment, we allowed organisms to settle and grow on the plates naturally, although importantly, most of competitive interactions we observed were heterospecific.

Estimating performance

To estimate the performance of colonies in the field, we photographed colonies in the field with a digital camera kept at a constant distance from the plate. We later used calibrated image analysis software to measure colony size. In this species, there is little variation in the size of individual zooids, so colony size is a reasonable measure of zooid number. For our estimates of survival, colonies were classed as "alive" if they were present and clearly had some living zooids or "dead" if they were absent or all the zooids were blackened and showed no signs of feeding. We estimated the performance of the colonies every two weeks for the first six weeks and again after a total of 15 weeks in the field. Because we were also interested in the size of larvae that colonies produced in the presence and absence of competition, we brought all the plates back into the laboratory after nine weeks in the field. The colonies were held in complete darkness for 24 hours in recirculating aquaria at 20°C. We then exposed the colonies to bright light so that any reproductive colonies released the larvae that they were brooding. We collected the spawned larvae from

individual colonies, fixed them with a few drops of formalin, and then measured them as in Marshall and Keough (2003b).

Data analysis

Over the course of our study, it became quickly apparent that *W. subtorquata* settlement, colony survival, growth rates, and the intensity of competition differed greatly between the uncleared treatments of the two study sites. We therefore analyzed the data from the two sites separately, but our approach overall was mirrored for each site.

To examine the effects of offspring size and the presence/absence of competition on subsequent colony survival, we used logistic ANCOVA with offspring size as a continuous predictor and competition treatment as a categorical, fixed factor. The large settlement panels were a logistical convenience, but we checked that they had no effect on our results by initially including panel as a categorical, random factor. For most of our analyses, we found no simple or complex effects of panel, so we omitted this term from the final model (Quinn and Keough 2002; see also Appendix: Table A1). We did not include settlement plate in our analyses because it was also an experimental convenience that explained very little variation in any of our response variables (D. J. Marshall and M. J. M. Keough, *unpublished data*). This finding is consistent with another study on *W. subtorquata* at these sites that had much higher levels of replication, which found that settlement plate did not have a significant effect on any of the parameters of interest and explained <2% of the observed variation (Marshall and Keough 2008b).

To examine the effect of offspring size and the presence/absence of competition on subsequent colony size, we used repeated-measures ANCOVA, as described in Marshall et al. (2003), and we used the same factors as those described for survival. As for the analysis of survival, we first tested for an effect of panel (and more importantly, the interactions between panel and the treatments of interest). Because none of the interactions were significant and the panels themselves were of no biological interest nor explained much of the variation, we omitted them from the final model (Appendix: Table A2). There was a significant main effect of panel for the Williamstown data (see Table 2), so in this case we retained it as a random, blocking factor. We next tested for an interaction between the covariate (offspring size) and the categorical factor (competition). There was none ($F_{1,21} = 0.04$, $P = 0.846$), so, despite this being the main focus of our investigation into the relationship between offspring size and performance in different environments, this interaction was also omitted from the final model. For the St Kilda data, we repeated the approach outlined for Williamstown, except that panel was omitted as a factor because it was not significant (Appendix: Table A3). We applied a similar approach to our analyses of fecundity and subsequent offspring

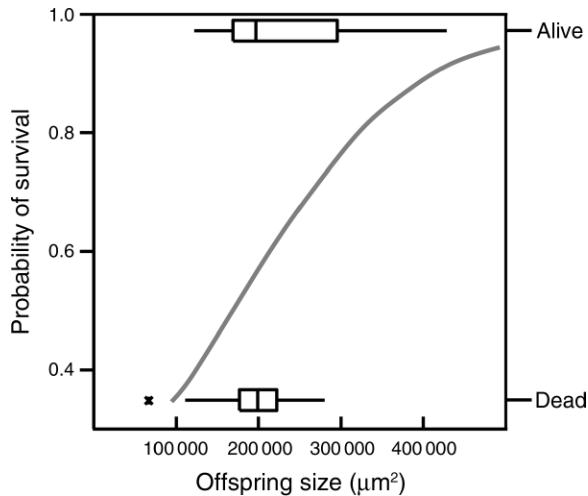


FIG. 1. Effect of offspring size on the probability of survival of *Watersipora subtorquata* marine bryozoan colonies after six weeks in the field at St Kilda, Australia. The bottom box plot represents initial offspring size distribution of colonies that died, and the top box plot represents initial offspring size distribution of colonies that lived. The line represents the logistic regression line of best fit. In the boxplots, the center line represents the mean, the bar outlines represent the interquartile range, and the whiskers represent those data within 1 SD of the mean.

size measures, and omitted nonsignificant panel terms from each of these analyses (Appendix: Tables A4, A5, and A6).

RESULTS

St Kilda

At St Kilda, offspring size affected the survival of *W. subtorquata* colonies after six weeks in the field, but there was no effect of competition nor was there an interaction between offspring size and competition (offspring size, $\chi^2 = 3.96$, $P = 0.046$; treatment, $\chi^2 = 2.12$, $P = 0.145$; treatment \times offspring size, $\chi^2 = 0.108$, $P = 0.742$; Fig. 1). After 15 weeks in the field, there was no longer an effect of offspring size on survival, nor was there an interaction between offspring size and competition (Appendix: Table A7). However, there was an effect of the competition treatment on overall survival after 15 weeks, with colonies under competition suffering nearly twice the mortality of colonies under no competition ($\chi^2 = 4.46$, $df = 1$, $P = 0.035$; Fig. 2).

Interspecific competitors had little effect on initial colony size, but resulted in smaller *W. subtorquata* colonies by the end of the study (Table 1, Fig. 2), and offspring size had no effect on colony size throughout the study at this site (Table 1, Fig. 3). After nine weeks in the field, colonies that experienced competition

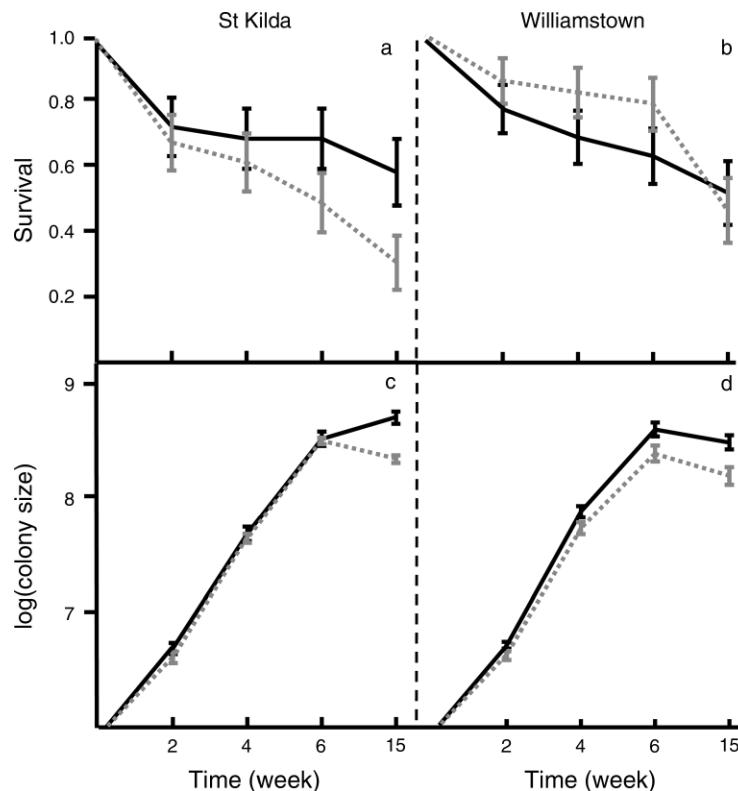


FIG. 2. Performance (mean \pm SE) of *Watersipora subtorquata* colonies in the presence (gray dotted lines) and absence (black solid lines) of interspecific competition over 15 weeks in the field: survival of colonies at (a) St Kilda and (b) Williamstown; size of colonies at (c) St Kilda and (d) Williamstown. Log-transformed colony size was originally measured in square millimeters.

TABLE 1. Repeated-measures ANCOVA examining effects of offspring size and interspecific competition on subsequent *Watersipora subtorquata* colony size across 15 weeks at St Kilda, Australia.

Source	df	MS	F	P
Between subjects				
Competition	1	81.04	16.144	0.001
Offspring size	1	6.86	1.367	0.255
Error	22	5.02		
Within subjects				
Time	2	33.68	20.049	< 0.001
Time × competition	2	46.61	27.742	< 0.001
Time × offspring size	2	1.98	1.181	0.316
Error	44	1.68		

Note: The model has been reduced. The within-subjects P values are Huynh-Feldt adjusted as HF $\epsilon = 1.00$. Significant P values are shown in boldface.

produced dramatically fewer larvae than colonies that did not experience competition (0.3 larvae/colony vs. 13.1 larvae/colony, respectively; $F_{1,31} = 9.19$, $P = 0.005$). Not only were colonies that experienced competition less fecund, they were also less fecund for their size: the number of larvae produced per unit of colony area in colonies that experienced competition was 1/20th of that for colonies that did not experience competition ($F_{1,31} = 9.96$, $P = 0.004$).

Colonies that experienced competition produced larger offspring than colonies free of competition ($F_{1,15} = 5.56$, $P = 0.032$; Fig. 4). Competition not only affected the mean size of offspring that mothers produced, it also affected within-brood variation: colonies that experienced competition produced less variably sized offspring than colonies that did not experience competition ($F_{1,6} = 19.8$, $P = 0.004$; competition, $SD = 0.785$, no competition, $SD = 14.92$; Fig. 4).

Williamstown

There was no effect of offspring size, the competition treatment, or their interaction on the survival of *W. subtorquata* colonies after six weeks in the field in Williamstown (offspring size, $\chi^2 = 0.09$, $P = 0.765$; treatment, $\chi^2 = 0.145$, $P = 0.703$; treatment × offspring size, $\chi^2 = 0.01$, $P = 0.99$). Similarly, after 15 weeks in the field, there was no effect of offspring size or competition on survival (Fig. 3; Appendix: Table A7).

Offspring size and interspecific competitors did have strong effects on the size of *W. subtorquata* colonies at this site (Table 2, Fig. 3). There was a positive relationship between offspring size and colony size that persisted for 15 weeks in the field (Fig. 3). While Fig. 3 suggests that offspring size had only a weak effect on colony size after 15 weeks in the field, analyses focused on colony size at week 15 only confirm that larger

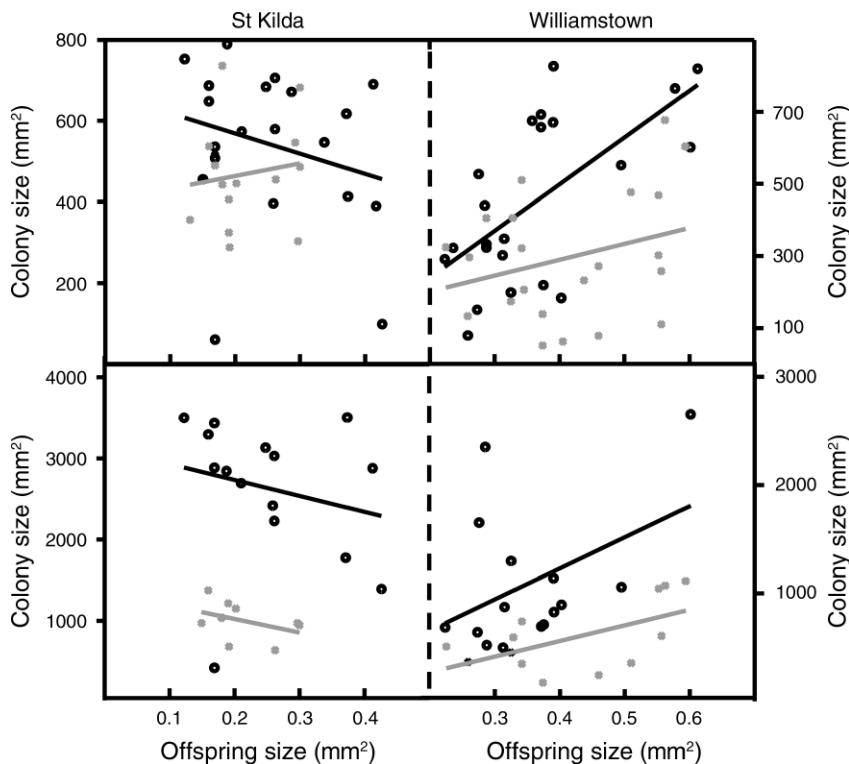


FIG. 3. Effect of offspring size and interspecific competition on the size of *Watersipora subtorquata* colonies after 6 weeks (top panels) and 15 weeks (bottom panels) in the field at St Kilda (left panels) and Williamstown (right panels). The solid black line and circles represent colonies that did not experience interspecific competition; the dotted gray line and gray symbols represent individual colonies that did experience interspecific competition. Each point represents an individual colony.

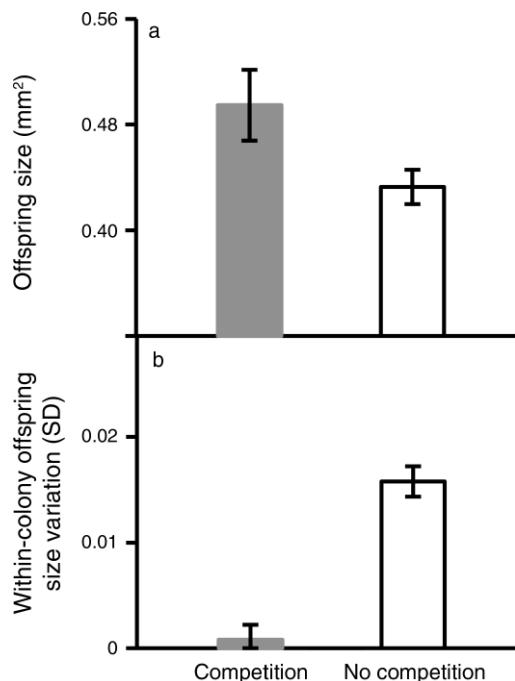


FIG. 4. Effect of maternal experience of interspecific competition on the size of offspring produced by *Watersipora subtorquata* colonies after 9 weeks in the field at St Kilda: (a) offspring size (mean \pm SE) produced by colonies that did or did not experience interspecific competition; (b) variation in offspring size (mean \pm SE, measured as SD in offspring sizes within each colony) produced by colonies that did or did not experience interspecific competition.

offspring became larger colonies ($F_{1,25} = 5.67$, $P = 0.025$). After 15 weeks, colonies that grew in the presence of interspecific competitors were, on average, about half the size of colonies that grew in the absence of competitors. There was no interaction between offspring size and the competition treatment (Table 2, Fig. 3).

There was no effect of interspecific competition on the size of offspring produced by colonies after nine weeks in the field ($F_{1,10} = 0.085$, $P = 0.777$), nor was there an effect on fecundity ($F_{1,13} = 0.826$, $P = 0.38$) or on the number of larvae produced per unit of colony area ($F_{1,13} = 0.255$, $P = 0.622$). There was also no effect of interspecific competition on variation in offspring size produced by individual colonies ($F_{1,6} = 0.03$, $P = 0.862$; competition, $SD = 14.92$; no competition, $SD = 13.79$).

DISCUSSION

Interspecific competition decreased the performance of *Watersipora subtorquata* colonies at both study sites. In contrast, offspring size had persistent effects on colony performance in the field at one site (Williamstown) but not the other (St Kilda). Interestingly, the two factors of interest, offspring size and competition, did not interact: larger offspring tended to perform better as colonies than smaller offspring (though this effect varied in type and persistence between sites), regardless of

whether they faced interspecific competition, and competition reduced survival and growth regardless of offspring size effects. Interspecific competition also affected the provisioning of offspring by focal colonies at St Kilda; that is, mothers under competition here made larger offspring of more uniform size than did mothers facing no competition. This increase in per offspring provisioning in response to competition may be an adaptive response, in that larger larvae tend to disperse for longer in the field in this species and may therefore be more likely to escape a competitive environment (Marshall and Keough 2003b).

There appeared to be differences in the intensity of competition between our two study sites, which may explain why we observed effects of competition on offspring provisioning at St Kilda only. Survival in the absence of competition was similar at both study sites, but the survival of colonies in the presence of competition was far lower at St Kilda than at Williamstown. We did not formally estimate the intensity of competition experienced by colonies at each site, but we did observe that the densities of serpulid polychaetes, arborescent bryozoans, and solitary ascidians were far higher at St Kilda than at Williamstown. Interestingly, this reduction in the growth of colonies in the competition treatment appeared to be mediated by noncontact competition: for the first six weeks of the experiment, colonies were largely free of direct contact from competitors, and it was only after several months in the field that colony growth became physically restricted by competitors. There is a growing list of examples of noncontact competition in fouling community sessile marine invertebrates (Dalby 1995, Marshall and Keough 2003a, Marshall et al. 2006, Allen et al. 2008), and we suggest that in the low-flow conditions of man-made marinas (which are likely to result in relatively thick boundary layers), increased densities of filter feeders can deplete local food availability.

TABLE 2. Repeated-measures ANCOVA examining effects of offspring size and interspecific competition on subsequent *Watersipora subtorquata* colony size over 15 weeks at Williamstown, Australia.

Source	df	MS	F	P
Between subjects				
Offspring size	1	57.70	9.163	0.006
Competition	1	97.07	15.415	0.001
Panel	3	74.38	11.812	<0.001
Error	22	6.29		
Within subjects				
Time	2	10.03	2.833	0.104
Time \times offspring size	2	35.46	10.019	0.004
Time \times competition	2	68.44	19.336	<0.001
Time \times panel	6	61.39	17.345	<0.001
Error	44	3.53		

Note: The model has been reduced. The within-subjects P values are Greenhouse-Geisser adjusted as $GG \epsilon = 0.52$. Significant P values are shown in boldface.

The effects of offspring size also varied among sites. In St Kilda, there was an initial effect of offspring size on survival that diminished over time; however, in Williamstown, the effects of offspring size on colony growth persisted for 16 weeks. Comparing the survival of our focal colonies at the two sites in this study and considering previously published work on this species (Marshall and Keough 2008b), we would suggest that St Kilda is the harsher of the two environments. Interestingly in St Kilda, offspring size (initially) affected post-metamorphic survival, whereas in the more benign Williamstown, offspring size affected post-metamorphic growth. We have previously suggested that the type of offspring size effects that are observed (e.g., effects on survival vs. growth) will depend on the harshness of the local environment (Marshall and Keough 2008b). Our results are consistent with this suggestion, although the strength of this support is tempered by the fact that we only had two study sites. More generally, several authors have suggested that offspring size effects are more likely to occur in harsh environments rather than benign ones (Einum and Fleming 1999, Fox and Czesak 2000, Marshall et al. 2006). Our results do not support this suggestion: both between sites and between treatments, offspring size effects were the same or stronger in the benign environment. Looking more generally, there is mixed support for the suggestion that offspring size effects are stronger in harsher environments (Moran and Emler 2001, Marshall and Keough 2008a), and we believe that the interaction between local environment and offspring size effects is more complex than previously thought.

In both study sites, the presence/absence of interspecific competition had no effect on the relationship between offspring size and post-metamorphic performance. In contrast, previous studies suggest the benefits of producing larger offspring are increased in the presence of intraspecific competition (Einum and Fleming 1999, Allen et al. 2008, Bashey 2008). The fact that interspecific competition did not have similar effects is surprising to us. Competitive interactions in colonial organisms are traditionally viewed as being size-dependent (Russ 1982, Buss 1990). Hence, given that offspring size affects colony size in *W. subtorquata*, we expected larger offspring to become better competitors than smaller offspring. It may be that we simply lacked sufficient power to detect a difference in the relationship between offspring size and colony performance between our treatments, but we think this unlikely. Levels of replication in our study were at least as high as others that have examined the effects of intraspecific competition (Marshall et al. 2006). If interspecific competition does affect the relationship between offspring size and performance, this effect must therefore be subtler than those observed in intraspecific studies. We cannot account for why intraspecific competition affects the relationship between offspring size and performance while interspecific competition does not. It is clear that

interspecific competition does affect colony performance overall, given a sharp decrease in performance at both sites in the presence of competition. It could be that *Watersipora* is simply different from *Botrylloides violaceus* studied in Marshall et al. (2006). We have not examined the effects of intraspecific competition on the offspring size–performance relationship in *Watersipora* and it may be that no form of competition affects the relationship between size and performance in this species. Alternatively, competition from conspecifics may cause higher levels of nutritional stress than competition from other species. Both theory and empirical studies certainly suggest that competition should be more intense among conspecifics and congenetics than among distantly related species (Barnes 2003; but see Woodin and Jackson [1979] for the opposite view), and this may be why we observed no change in the relationship between offspring size and performance in our study. Regardless, our study suggests that the slope of the relationship between offspring size and performance is relatively similar in the presence and absence of interspecific competition, which has interesting implications for observed and predicted offspring sizes in this species.

Theory predicts that the relationship between offspring size and performance determines the optimal offspring size for maternal fitness (Smith and Fretwell 1974). Our analyses revealed no difference in the slope of the offspring size–performance relationship, suggesting that the offspring size that maximizes maternal fitness is unaltered by interspecific competition. In St Kilda, however, we found that mothers experiencing competition produced larger, less variably sized offspring than mothers that did not experience competition. This raises the interesting question: why did mothers under competition produce larger, higher-quality offspring than mothers not under competition? It seems certain that St Kilda mothers were under nutritional stress from competition, as evidenced by lower relative fecundity (i.e., reproduction per unit area), total reproductive output (fecundity \times offspring size), and lower post-reproduction growth rates in the competition treatment. The answer may lie in the fact that in *Watersipora subtorquata*, larger larvae swim for longer in the field (Marshall and Keough 2003b). By producing larger, more dispersive larvae, mothers experiencing competition might increase the chance that their offspring will disperse to a habitat with lower levels of competition. Such an effect is analogous to classic studies on aphids, showing that mothers produce more dispersive offspring in response to food limitation (Sutherland 1969) and also mirrors work on reptiles (Shine and Downes 1999) and plants (Parciak 2002). Our supposition that mothers manipulate the dispersal of their offspring to avoid competition depends critically on the ratio of the scale of offspring dispersal to scale of local environmental heterogeneity. In the absence of data it is difficult to speculate: both the scale of larval dispersal and the grain

size of heterogeneity with regards to competition are poorly understood in this system. However, it is interesting that mothers experiencing competition produced offspring of relatively uniform size, whereas mothers that did not experience competition produced offspring that were far more variable in size. Thus, whichever factor induced a change in the size of offspring produced by mothers in the competition treatment also induced a change in the variation in offspring size. If there is an upper limit for larval size beyond which offspring fitness suffers, it may be that any increase in offspring size beyond a certain point must necessarily result in a decrease in size variation (see Marshall et al. 2008 for details).

This study joins a growing list of studies on marine organisms showing that the degradation of conditions in the maternal habitat (through intraspecific competition, reduced food availability, or pollution) causes mothers to produce more-dispersive offspring that are more likely to escape the local environment (Krug and Zimmer 2000, Krug 2001, Allen et al. 2008, Marshall 2008). In these previous studies, it was difficult to disentangle pre- and postmetamorphic selection pressures on larval size. For example, mothers experiencing higher intraspecific competition in the bryozoan *Bugula neritina* may benefit from producing larger offspring because of their increased dispersal potential or because larger offspring are better competitors after metamorphosis (Allen et al. 2008). In this study, we could find no evidence that larger offspring are better able to deal with interspecific competition, and thus, we believe it is likely that mothers are producing more dispersive offspring in response to local competition.

ACKNOWLEDGMENTS

We thank Rebecca Loughman for crucial assistance in the field. This study benefited from helpful discussions with Richard Emler and the comments of an anonymous reviewer, Keyne Monro, and Patrick Krug. This research was supported by the Australian Research Council with grants to D. J. Marshall and M. J. Keough.

LITERATURE CITED

- Allen, R. M., Y. M. Buckley, and D. J. Marshall. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *American Naturalist* 171:225–237.
- Azevedo, R. B. R., V. French, and L. Partridge. 1997. Life-history consequences of egg size in *Drosophila melanogaster*. *American Naturalist* 150:250–282.
- Barnes, D. K. A. 2003. Competition asymmetry with taxon divergence. *Proceedings of the Royal Society B* 270:557–562.
- Bashey, F. 2006. Cross-generational environmental effects and the evolution of offspring size in the Trinidadian guppy *Poecilia reticulata*. *Evolution* 60:348–361.
- Bashey, F. 2008. Competition as a selective mechanism for larger offspring size in guppies. *Oikos* 117:104–113.
- Berkeley, S. A., C. Chapman, and S. M. Sogard. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* 85:1258–1264.
- Bernardo, J. 1996. The particular maternal effect of propagule size, especially egg size: patterns models, quality of evidence and interpretations. *American Zoologist* 36:216–236.
- Brockelman, W. Y. 1975. Competition, fitness of offspring, and optimal clutch size. *American Naturalist* 109:677–699.
- Brody, M. S., and L. R. Lawlor. 1984. Adaptive variation in offspring size in the terrestrial isopod, *Armadillidium vulgare*. *Oecologia* 61:55–59.
- Buss, L. W. 1990. Competition within and between encrusting clonal invertebrates. *Trends in Ecology and Evolution* 5:352–356.
- Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecological Monographs* 31:61–104.
- Cunningham, E. J. A., and A. F. Russell. 2000. Egg investment is influenced by male attractiveness in the mallard. *Nature* 404:74–77.
- Dalby, J. E. 1995. Consequences of aggregated living in the ascidian *Pyura stolonifera*: evidence for non-contact intra-specific competition. *Marine and Freshwater Research* 46:1195–1199.
- Einum, S., and I. A. Fleming. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proceedings of the Royal Society B* 266:2095–2100.
- Einum, S., and I. A. Fleming. 2002. Does within-population variation in fish egg size reflect maternal influences on optimal values? *American Naturalist* 160:756–765.
- Fox, C. W. 2000. Natural selection on seed-beetle egg size in nature and the laboratory: variation among environments. *Ecology* 81:3029–3035.
- Fox, C. W., and M. E. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology* 45:341–369.
- Fox, C. W., M. S. Thakar, and T. A. Mosseau. 1997. Egg size plasticity in a seed beetle: an adaptive maternal effect. *American Naturalist* 149:149–163.
- Keough, M. J., and P. T. Raimondi. 1995. Responses of settling invertebrate larvae to bioorganic films: effects of different types of films. *Journal of Experimental Marine Biology and Ecology* 185:235–253.
- Krug, P. J. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Marine Ecology Progress Series* 213:177–192.
- Krug, P. J., and R. K. Zimmer. 2000. Developmental dimorphism and expression of chemosensory-mediated behavior: habitat selection by a specialist marine herbivore. *Journal of Experimental Biology* 203:234–244.
- Lindholm, A. K., J. Hunt, and R. Brooks. 2006. Where do all the maternal effects go? Variation in offspring body size through ontogeny in the live-bearing fish *Poecilia parae*. *Biology Letters* 2:586–589.
- Marshall, D. J. 2008. Transgenerational plasticity in the sea: a context-dependent maternal effect across life-history stages. *Ecology* 89:418–427.
- Marshall, D. J., T. F. Bolton, and M. J. Keough. 2003. Offspring size affects the post-metamorphic performance of a colonial marine invertebrate. *Ecology* 84:3131–3137.
- Marshall, D. J., R. Bonduriansky, and L. F. Bussiere. 2008. Offspring size variation within broods as a bet-hedging strategy in unpredictable environments. *Ecology* 89:2506–2517.
- Marshall, D. J., C. N. Cook, and R. B. Emler. 2006. Offspring size effects mediate competitive interactions in a colonial marine invertebrate. *Ecology* 87:214–225.
- Marshall, D. J., and M. J. Keough. 2003a. Effects of settler size and density on early post-settlement survival of *Ciona intestinalis* in the field. *Marine Ecology Progress Series* 259:139–144.
- Marshall, D. J., and M. J. Keough. 2003b. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Marine Ecology Progress Series* 255:145–153.

- Marshall, D. J., and M. J. Keough. 2004. Variable effects of larval size on post-metamorphic performance in the field. *Marine Ecology Progress Series* 279:73–80.
- Marshall, D. J., and M. J. Keough. 2008a. The evolutionary ecology of offspring size in marine invertebrates. *Advances in Marine Biology* 53:1–60.
- Marshall, D. J., and M. J. Keough. 2008b. The relationship between offspring size and performance in the sea. *American Naturalist* 171:214–224.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. *Science* 307:576–580.
- Moran, A. L., and R. B. Emlen. 2001. Offspring size and performance in variable environments: field studies on a marine snail. *Ecology* 82:1597–1612.
- Mousseau, T. A., and C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology and Evolution* 13:403–407.
- Olsen, E. M., and L. A. Vollestad. 2003. Microgeographical variation in brown trout reproductive traits: possible effects of biotic interactions. *Oikos* 100:483–492.
- Parciak, W. 2002. Environmental variation in seed number, size and dispersal of a fleshy-fruited plant. *Ecology* 83:780–793.
- Quinn, G. P., and M. J. Keough. 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.
- Russ, G. R. 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. *Oecologia* 53:12–19.
- Russell, A. F., N. E. Langmore, A. Cockburn, L. B. Astheimer, and R. M. Kilner. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science* 317:941–944.
- Santo, N., M. Caprioli, S. Orsenigo, and C. Ricci. 2001. Egg size and offspring fitness in a bdelloid rotifer. *Hydrobiologia* 446/447:71–74.
- Shine, R., and S. J. Downes. 1999. Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia* 119:1–8.
- Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. *American Naturalist* 108:499–506.
- Sutherland, O. R. W. 1969. Role of crowding in production of winged forms by 2 strains of pea aphid, *Acyrtosiphon pisum*. *Journal of Insect Physiology* 15:1385–1410.
- Williams, M. D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68:38–59.
- Woodin, S. A., and J. B. C. Jackson. 1979. Inphyletic competition among marine benthos. *American Zoologist* 19:1029–1043.

APPENDIX

Tables with nonsignificant terms that were omitted from the final analyses examining the effects of competition on offspring provisioning in the bryozoan *Watersipora subtorquata* (*Ecological Archives* E090-034-A1).