

Variable effects of larval size on post-metamorphic performance in the field

Dustin J. Marshall^{1,2,*}, Michael J. Keough¹

¹Department of Zoology, The University of Melbourne, Victoria 3010, Australia

²Present address: School of Biological, Environmental & Earth Sciences, University of New South Wales, New South Wales 2052, Australia

ABSTRACT: Larval quality may be capable of explaining much of the variation in the recruitment and subsequent population dynamics of benthic marine invertebrates. Whilst the effects of larval nutritional condition on adult performance have received the most attention, recent work has shown that larval size may also be an important and ubiquitous source of variation in larval quality. We examined the effects of variation in larval size on the post-metamorphic survival and growth of *Watersipora subtorquata* in 2 very different habitats—experimental substrata and pier pilings. We found strong effects of larval size on colony performance, although these varied among experiments. For colonies on experimental substrata, larval size positively affected adult survival and, initially, growth. However, after 3 wk in the field, there was no relationship between larval size and colony size, possibly because colonies were completely surrounded by newly settled organisms. Larval size also positively affected post-metamorphic growth of colonies on pier pilings, but, surprisingly, colonies that came from larger larvae had lower survival than colonies from smaller larvae. Overall, variation in larval size will strongly affect the recruitment and subsequent performance of adults in this species, although this may vary among different habitats. This study highlights the importance of examining the effects of larval quality on adult performance in as realistic conditions as possible, because of the strong interaction between larval size effects and the environment.

KEY WORDS: Bryozoan · Carry-over effects · Egg size

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INTRODUCTION

One of the principal factors determining the distribution and abundance of benthic marine invertebrates is the recruitment of new individuals into populations (Underwood & Fairweather 1989, Underwood & Keough 2001). The recruitment of marine invertebrates can be remarkably variable and, for many years, marine ecologists have attempted to identify and understand the sources of this variability (Hunt & Scheibling 1997). Much of the work to date has focused on how variation in the quantity of larvae reaching adult populations affects recruitment and subsequent population dynamics, but there is a growing recognition that the quality of larvae may also be important (Hunt

& Scheibling 1997). There appear to be strong links between the quality of settling larvae and their probability of recruiting into the adult population. Variation in physiological condition of larvae has been shown to affect important determinants of fitness, including survival, growth and reproduction of adults (Pechenik et al. 1998, Pechenik 1999). These 'carry-over' effects have been documented in a wide variety of phyla, spanning most larval developmental modes and in both solitary and colonial organisms.

Whilst the link between larval quality and adult performance is clear, this link is only ecologically relevant if there is significant, natural variation in the quality of settling larvae (Phillips & Gaines 2002). The most commonly cited source of variation in larval quality is

*Email: d.marshall@unsw.edu.au

nutritional condition (Hunt & Scheibling 1997, Pechenik et al. 1998, Pechenik 1999). The quality of larvae settling in nature can vary significantly within and among cohorts according to their nutritional history or length of metamorphic delay (Barnes 1953, Connell 1961, Pechenik 1990, Jarrett & Pechenik 1997, Phillips & Gaines 2002), and the consequences of this variation for adult growth have been studied for a range of organisms (Jarrett & Pechenik 1997, Pechenik et al. 1998, Wendt 1998, Vaitilingon et al. 2001, Phillips 2002, Jarrett 2003, Marshall et al. 2003a). Another potential source of variation in larval quality is size, although the effects of larval size on adult performance have received relatively less attention (Moran & Emler 2001, Marshall & Keough 2003a, Marshall et al. 2003b). This lack of attention is remarkable given the wide intraspecific variation in offspring size for a wide range of marine invertebrate taxa (George 1994, Jones et al. 1996, Marshall & Keough 2003b,c). Because variation in larval size is so common, it has the potential to explain much of the currently unaccounted for variation in the recruitment success and subsequent performance of marine invertebrates (Hunt & Scheibling 1997); however, more field tests are needed.

Offspring size has long been assumed to be positively correlated with offspring fitness and is central to life-history theory (e.g. Smith & Fretwell 1974, Stearns 1992, Hendry et al. 2001), but field tests in the marine environment are rare (Moran & Emler 2001). There is some indirect evidence for increased offspring investment resulting in higher fitness in marine invertebrates. In the colonial ascidian *Botryllus schlosseri*, related settlers fuse, thereby becoming larger colonies which are known to have higher fitness (Grosberg & Quinn 1986). Viewed from the perspective of the maternal colonies, the fusion of sibling settlers represents a form of increased per capita investment. This is an extreme example of the advantages of increasing maternal investment (i.e. doubling) but it does suggest that offspring size effects may be common in marine invertebrates. The effects of offspring size on offspring fitness appear to vary strongly under different environmental conditions, and so field tests should include as wide a range of conditions as possible in order to assess whether offspring size effects are widely relevant (Einum & Fleming 1999, Moran & Emler 2001). Here, we examine the effects of variation in larval size on subsequent adult survival and growth in the field for the encrusting bryozoan *Watersipora subtorquata*. In one set of experiments, we transplanted metamorphosing colonies into the field on artificial settlement plates. Later, we repeated our experiments at the same site under more realistic conditions—on the pier pilings where *W. subtorquata* is commonly found.

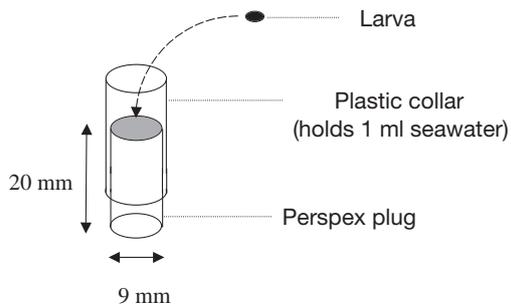
MATERIALS AND METHODS

Field site and collection of larvae. All experiments and the collection of reproductively mature colonies were done at Breakwater Pier in Williamstown, Victoria, Australia, during March 2001 (settlement plate experiments) and July 2001 and March 2002 (pier piling experiments). The site is sheltered from the prevailing weather by a large rocky breakwater, and the sessile invertebrate community has been described by Keough & Raimondi (1995). The water temperature for the experimental period was 18 to 21°C in March in both years and 12°C in July 2001. Reproductively mature colonies were collected from artificial settlement plates that had been placed in the field 2 mo earlier. To collect larvae, colonies were held in recirculating aquaria in constant darkness for 2 d before being exposed to bright light. *Watersipora subtorquata* colonies began spawning after about 30 min of exposure to light. The larvae were collected quickly with a pipette and each was offered a settlement surface within 20 min of release from the parent colony. We collected larvae from 10 colonies, taking care to select a range of larval sizes from each colony. The size range of larvae used in our experiments was 2.5-fold and pilot studies indicated that the size range of *W. subtorquata* settlers obtained from the laboratory was well within that of natural settlers at Williamstown (Marshall & Keough 2003c).

Measurement of larvae and field deployment. Settlement plates: Ideally, to assess the effects of offspring size on post-metamorphic performance, we would have measured larval size directly. However, measuring larvae is time-consuming and we were concerned that delaying the metamorphosis of the larvae could affect post-metamorphic performance (e.g. Wendt 1998, Marshall et al. 2003a). Consequently, we allowed larvae to settle immediately after collection and measured the size of the subsequent settlers 12 h after settlement. Settler size is a good ($R^2 = 0.78$) estimate of larval size in *Watersipora subtorquata* (Marshall & Keough 2003c). We placed larvae on their own individual settlement plate in a small drop of seawater (see Marshall et al. 2003a). The settlement plates (10 × 10 × 1 cm) were made of grey PVC and had been roughened with sand paper to encourage settlement. Any larvae that failed to settle within 30 min were discarded. We then marked the place of each settled larva by placing a small dot next to the metamorphosing individual with a pencil. The settlement plates were then placed into recirculating aquaria at 15°C for 12 h. Approximately 12 h after settlement, we briefly videotaped each settler, digitised the footage and measured each settler using SigmaScan (Jandel Scientific Ver. 3; see Marshall et

al. 2003b). The measurements were then calibrated against footage of a haemocytometer grid that had been videotaped with the same equipment. Once the settlers had been measured, the settlement plates were immersed in seawater and transported to the field site (approximately 20 min away) in insulated aquaria. The settlement plates were attached to large (90 × 90 cm) Perspex backing plates with stainless steel bolts. Settlement plates were arranged so that their position on the backing plate was haphazard. The backing plates were then hung horizontally with the experimental plates facing down (to minimise the effects of light and sedimentation) at a depth of ~2 m below mean low tide.

Pier pilings: For our experiments on pier pilings, we settled the larvae onto the ends of small Perspex plugs rather than settlement plates (see Fig. 1). One end of each plug was roughened to encourage settlement. A tight-fitting, clear plastic collar was placed around the roughened end so that it could hold ~1 ml of seawater.



Laboratory

Field

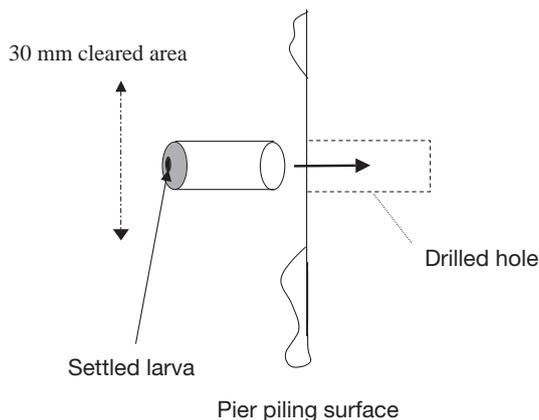


Fig. 1. Schematic of apparatus to deploy *Watersipora subtorquata* settlers onto pier pilings in the field at Williamstown, Australia

We allowed settlement to occur as described above and then sorted larvae into large (>0.23 mm²) and small (<0.23 mm²) size classes with an ocular micrometer. Approximately 12 h after settlement, the Perspex plugs (with settlers and plastic collars attached) were transported to the field immersed in seawater in insulated plastic aquaria. The plastic collars protected the settlers during transportation and no settlers were damaged or killed in the process of deploying them into the field.

One wk prior to placing the settled larvae into the field, small (~1 cm diameter) holes had been hand-drilled into the pier pilings at a depth of 2 m below the low water mark. At this depth *Watersipora subtorquata* is a common component of the fouling community in Williamstown (authors' pers. obs.). A small (3 cm diameter) area around each hole was cleared of encrusting organisms. Once the settlers had been brought to the field, we used SCUBA to deploy the Perspex plugs. Underwater, we removed the plastic collars and carefully placed the Perspex plugs into the drilled holes so that the end of the plug (with settler attached) was flush with the pier piling surface (Fig. 1). Large and small settlers were distributed haphazardly across 8 pier pilings, with 6 to 12 settlers (approximately equal number of both size classes) placed on each. The Perspex plugs were a snug fit in the drilled holes and no adhesive was necessary to hold them in place.

Sampling. For *Watersipora subtorquata* on settlement plates, Run 1 (n = 30) was deployed on March 3, 2001, and Run 2 (n = 21) on March 18, 2001. Run 1 was in the field for 2 wk and Run 2 for 3 wk. For both Runs, we assessed colony survival and growth after 2 wk in the field, and for Run 2, again after 3 wk in the field. To measure colony survival and growth, we hauled the backing plates onto the pier and placed them face up in a shallow bath of seawater. We then determined the presence/absence of colonies and, for those colonies that were still present, we counted the number of zooids that had developed orifices. Each census took approximately 30 min, after which the backing plates were immediately redeployed.

For *Watersipora subtorquata* on pier pilings, Run 1 was deployed into the field on July 31, 2001 (n = 29). Run 2 was deployed (n = 100) on March 21, 2002; during this time 12 Perspex plugs fell out of the pilings and were disregarded from further analysis. We assessed colony survival and size after 3 wk in the field by examining each settlement plug underwater with a magnifying glass and a torch whilst on SCUBA. Colony size was assessed as above.

Larval size and budding rate. We found that larger settlers had higher post-metamorphic growth than

smaller settlers (see 'Results'). We hypothesised that this higher growth rate was due to a higher initial budding of new daughter zooids in larger settlers. To test this hypothesis, we collected reproductively mature colonies and spawned them in the laboratory as described above. We allowed the larvae to settle on Petri dishes and measured the settlers as described above and then measured the number of new zooids formed 5 d after settlement.

Data analysis. In all analyses, we first checked that the data satisfied the assumptions of each analysis. For the *Watersipora subtorquata* on settlement plates, we used logistic analysis of covariance (ANCOVA) to assess survival after 2 wk in the field, where experimental run was a categorical, random factor and settler size was a covariate. We first tested for an interaction between run and settler size and, as this interaction was not significant ($p = 0.294$), we ran a reduced model with the interaction term removed. We then used the equation produced from the logistic ANCOVA to generate survival probabilities for the size range of larvae in our study. To assess survival at the other time period (3 wk), we used logistic regression, where settler size was a continuous predictor variable. To examine the effect of settler size on subsequent colony size after 2 wk in the field, we used ANCOVA, where settler size was a covariate and run was a categorical factor. We first tested for an interaction between settler size and run, and because this interaction was not significant ($F_{1,40} = 0.03$, $p = 0.864$), we ran a reduced model with the interaction term removed. For Run 2, we examined whether settler size affected colony size after 3 wk using linear regression.

To assess the survival of *Watersipora subtorquata* on pier pilings we used a paired *t*-test, where the proportionate survival of large and small settlers on each pier piling was the response variable, pooling across runs. We first tested whether there was any interaction between larval size and run, and as there was no significant interaction ($p = 0.489$) and run was of no biological interest and explained little of the variation, it was omitted from further analysis (Quinn & Keough 2002). To test the effects of settler size on subsequent *W. subtorquata* colony size on pier pilings, we again removed the non-significant run factor from the model and used ANOVA, where settler size was a fixed factor and pier piling was a random, blocking factor.

To assess the effect of larval size on initial ancestrulae (the first feeding zooid in the colony) budding rate, we used logistic regression, where settler size was a continuous predictor variable and budding (new daughter zooid formed or not) was a categorical response variable.

RESULTS

Settlement plates

For *Watersipora subtorquata* on settlement plates, the majority of mortality occurred in the first week after deployment in the field. Pooling across runs for *W. subtorquata* on settlement plates, ~16% of all the juvenile colonies died in the first 2 wk. The mortality of juvenile colonies after 2 wk in the field was size dependent for both runs (Table 1). Across the range of settler sizes (~2.5-fold difference), the predicted survivorship ranged from 47% for the smallest settler and 98% for the largest (values back-calculated from logistic regression equation). Mortality remained size dependent for Run 2 after 3 wk in the field (Table 1).

Colony growth varied between experimental runs on settlement plates, but colony size after 2 wk remained strongly influenced by settler size in both runs (Table 2, Fig. 2). However, after 3 wk in the field, no effect of settler size on colony size could be detected in Run 2 ($R^2 = 0.001$, $p = 0.904$, $n = 14$), but, interestingly, colony size after 3 wk was still correlated with colony size after 2 wk ($R^2 = 0.69$, $n = 14$). After 3 wk in the field, the growing edges of the colonies were almost completely surrounded by newly settled barnacle species and various serpulid worms.

Pier pilings

For *Watersipora subtorquata* on pier pilings, mortality was much higher than on settlement plates, with 56 to 45% (Runs 1 and 2, respectively) mortality in the first 3 wk after settlement. Mortality was size dependent for *W. subtorquata* on pier pilings ($t = 2.341$, $df = 10$, $p = 0.041$; Fig. 3). Colonies that came from smaller larvae were more likely to survive than colonies that

Table 1. *Watersipora subtorquata*. Logistic ANCOVA (at 2 wk) and regression (3 wk) of the effects of initial settler size on subsequent mortality of colonies on settlement plates after 2 and 3 wk in the field at Williamstown, Australia. Wald tests were used to test the significance of particular effects with degrees of freedom of 1 for both settler size and run effects. p values <0.05 shown in **bold**. For Run 1, $n = 30$, for Run 2, $n = 21$

Field duration	Parameter	Odds ratio	χ^2	p
2 wk (Runs 1 and 2)	Size	1.000	3.902	0.048
	Run		0.064	0.8
	McFadden's ρ^2			0.183
3 wk (Run 2)	Size	1.000	4.702	0.030
	McFadden's ρ^2			0.250

Table 2. *Watersipora subtorquata*. ANCOVA of effects of settler size on the growth of colonies on settlement plates after 2 wk in the field at Williamstown, Australia. Note the model is reduced after testing for heterogeneity of slopes

Source of variation	df	MS	F	p
Settler size	1	57.6	7.5	0.009
Run	1	226.9	29.4	<0.001
Residual	41	7.7		

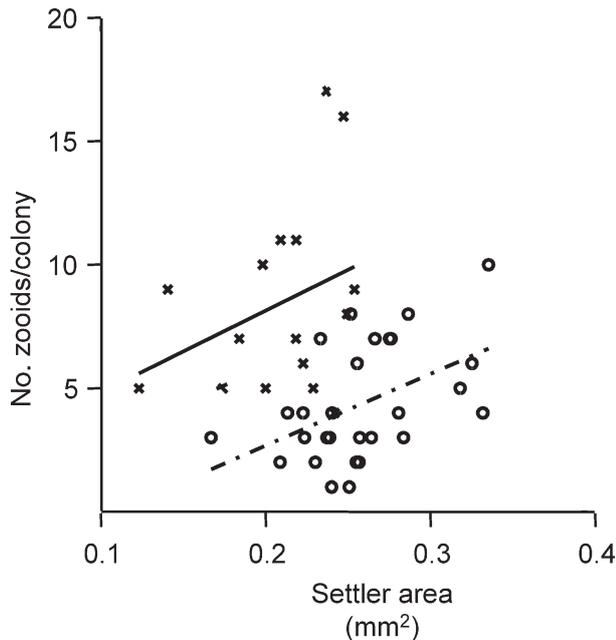


Fig. 2. *Watersipora subtorquata*. Effect of settler size on colony size after 2 wk in the field at Williamstown Australia. Individual colonies from Run 1 (○) and Run 2 (×) are shown

came from larger larvae. For *W. subtorquata* on pier pilings, colony growth was much slower than on settlement plates. Nevertheless, colony size 3 wk after settlement was still strongly affected by initial settler size in both runs (Table 3, Fig. 4). The settlement of solitary organisms onto the cleared area surrounding the experimental colonies appeared to be very low when compared to the amount of settlement typically found on settlement plates during the same period.

Settler size and budding rate

Larger settlers formed a new zooid more quickly than smaller settlers in the laboratory. Five days after settlement, larger settlers were more likely to have a second zooid than smaller settlers (Wald test: $\chi^2 = 4.286$, $p = 0.038$, $n = 29$).

DISCUSSION

Overall, larval size strongly affected post-metamorphic performance in *Watersipora subtorquata*, but these effects differed in both direction and type between the 2 sets of experiments. For our experiments on settlement plates, colonies that came from larger larvae survived better than colonies that came from smaller larvae. Larval size may affect early survival because larger settlers become larger colonies and may be more resistant to predation and other sources of mortality (Sebens 1982, 1987, Davis 1988). Alternatively, the period immediately after settlement may be an energetically critical stage and if larger larvae have greater energy resources, this may explain their higher survival rates. In a previous study, we found that initial settler size affected the early post-settlement survival of the solitary ascidian *Ciona intestinalis* (Marshall & Keough 2003a). An interesting test of whether the effects of larval size on early post-settlement survival are driven by nutritional constraints would be to determine if supplemental food given to new settlers removes the effects of larval size.

After 2 wk in the field, colonies on settlement plates that came from larger larvae were larger than those that came from smaller larvae. This species joins a growing list of species for which initial growth rates

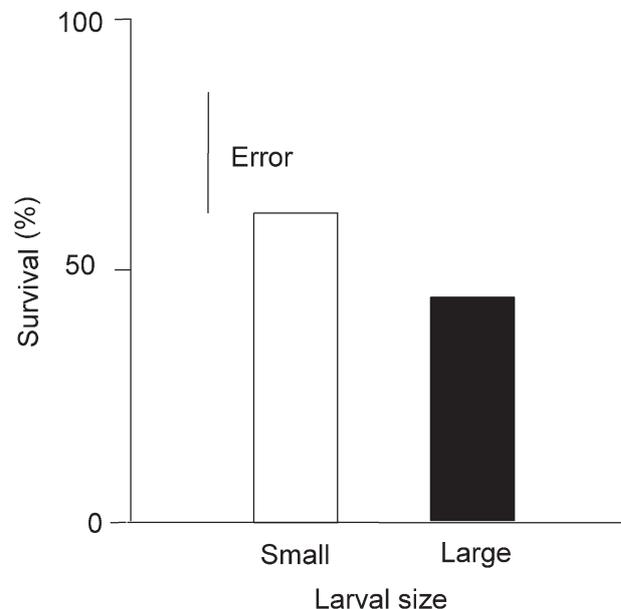


Fig. 3. *Watersipora subtorquata*. Effect of settler size on the percentage survival of large and small settlers on pier pilings at Williamstown, Australia. Open bar indicates small settlers, solid bar indicates large (see 'Materials and methods' for definition of sizes). The length of the error bar shown represents the standard deviation of the difference in survival of colonies within pier pilings

Table 3. *Watersipora subtorquata*. ANOVA of the effect of settler size on the growth of colonies after 3 wk in the field on pier pilings at Williamstown, Australia. p values <0.05 shown in **bold**. Model is reduced after removing the non-significant effect of run

Source of variation	df	MS	F	p
Size	1	49.72	16.211	0.005
Piling	7	13.523	4.532	0.001
Piling × Size	7	3.067	1.028	0.424
Error	48	2.984		

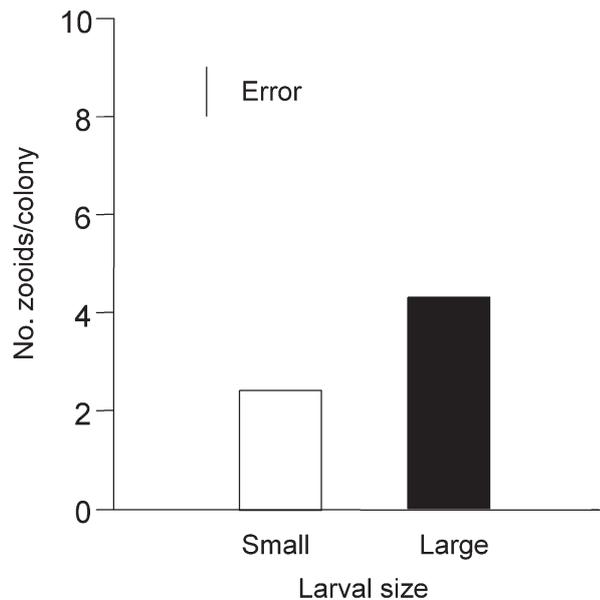


Fig. 4. *Watersipora subtorquata*. Effect of settler size on the size of colonies on pier pilings (Run 1) after 3 wk in the field at Williamstown, Australia. Open bar indicates small settlers, solid bar indicates large (see 'Materials and methods' for definition of sizes). The length of the error bar represents the square root of the mean square for the interaction between piling and settler size, used to test the effect of size

are affected by larval size (Moran & Emlet 2001, Phillips 2002, Marshall et al. 2003b). Larger *Watersipora subtorquata* settlers bud into new daughter zooids sooner than smaller settlers, and this is probably because larger settlers have greater nutritional reserves. The daughter zooids begin to form before the ancestrulae have fully developed their lophophores (feeding structures) and begun to feed. Consequently, the initial development of the daughter zooids may be entirely due to endogenous reserves (i.e. larval size). This initial difference in budding rate may explain why larval size affects initial colony growth rates and size after 2 wk. Wendt (1996) and Marshall et al. (2003a)

found that colonies from larvae that had their nutritional reserves depleted by extended swimming produced smaller feeding structures. It appears that there is a range of mechanisms by which larval quality can affect the initial growth of colonial marine invertebrates.

After 3 wk in the field, the experimental colonies on settlement plates were completely surrounded by other settled organisms (mainly serpulid polychaetes and barnacles) and we could no longer detect an effect of larval size on colony size. *Watersipora subtorquata* is a poor competitor (Barnby 1999) and it seemed that the growth of colonies was extremely limited by the settlement of other organisms, thereby obscuring any effect of larval size. Previously, we found that the effects of larval quality on colony growth were not persistent in another poor competitor, the colonial ascidian *Diplosoma listerianum* (Marshall et al. 2003a). Larval size affected initial growth in *D. listerianum*, but after 3 wk in the field, colonies had begun to fragment and we could no longer detect an effect of larval size (Marshall et al. 2003a). In contrast, experiments on the arborescent bryozoan *Bugula neritina* showed persistent effects of larval size on colony growth for up to 6 wk in the field (Marshall et al. 2003b). The effects of larval size may have been more persistent in *B. neritina* because of its growth form; *B. neritina* colonies can continue to grow upwards away from the substratum whilst in the presence of high densities of other competitors (Marshall et al. 2003b). Interestingly, for *W. subtorquata* on pier pilings (where the settlement of other organisms was very low), the effects of larval size on colony size persisted for 3 wk. It may be that the effects of larval size on growth may be more persistent when growth is not constrained by competition for space and, therefore, these effects may be more persistent in solitary, mobile organisms (e.g. Moran & Emlet 2001).

The effects of larval size on the growth rates of colonies on pier pilings were similar in some respects to our results for those on settlement plates—colonies that came from larger larvae had higher growth rates than those that came from smaller larvae. However, colony growth rates on pier pilings were generally lower than those on settlement plates and, surprisingly, those from larger larvae had lower survival than those from smaller larvae. This contrasts with a number of other studies for marine organisms, where juveniles and adults that come from larger larvae generally have higher survivorship than those from smaller larvae (Moran & Emlet 2001, Marshall & Keough 2003a, Marshall et al. 2003b). The negative effects of increased larval size for colonies on pier pilings could be due to a range of factors. For example, larger settlers may be more attractive prey items to micropreda-

tors (e.g. Osman & Whitlatch 1995). If so, then previous studies on offspring size effects on settlement plates (that do not have the full range of predators) may have overestimated the positive benefits of larval size for adult performance (e.g. Marshall & Keough 2003a, Marshall et al. 2003b). Alternatively, the different experimental period or substrates could also be responsible for the differential effects of larval size between the 2 sets of experiments. Regardless of the mechanism behind the negative correlation between larval size and colony survival, it is clear that offspring size and fitness are not always positively related in *Watersipora subtorquata*. This is a surprising result; few theoretical or empirical studies have demonstrated that larger offspring have lower fitness (but see Kaplan 1992, Hendry et al. 2001 for exceptions).

There is a growing body of literature on the effects of variation in larval quality on post-metamorphic performance (reviewed in Pechenik et al. 1998, Marshall et al. 2003a). This study highlights the importance of examining such carry-over effects in as realistic an environment as possible because, clearly, these effects are strongly dependent on local environmental conditions. Consequently, it may be inappropriate to use laboratory studies (e.g. Pechenik et al. 1996, Gebauer et al. 1999, Vaitilingon et al. 2001), where organisms are insulated from a range of mortality sources and pressures, to infer the importance of larval quality effects in the field. The use of small plugs to transplant newly metamorphosed individuals into the field appears to be an effective technique for exposing individuals to the widest possible range of environmental pressures.

It is important to note that throughout this study we have assumed that larval size is equivalent to larval energy content, an assumption that does not always hold in marine invertebrates (McEdward & Coulter 1987). The positive effects of larval size on initial survival and growth in the absence of competitors (our experiments on settlement plates) suggest that larger larvae do have more energy reserves, but there are instances where this may not be the case. For example, delaying the metamorphosis of larger larvae may deplete their energy reserves so that they are energetically the same 'size' as smaller larvae (Wendt 2000). More tests are needed to examine how increased duration of larval swimming and larval size interact to affect post-metamorphic performance and compare their relative effects. Previously, we have shown that larger *Watersipora subtorquata* larvae are choosier with respect to settlement surfaces, and they swim for longer than smaller larvae (Marshall & Keough 2003c). Smaller larvae have fewer energy resources to spare and have higher energy costs relative to their size (Wendt 2000). Therefore, we predict that the negative

effects of increased larval swimming would be more detrimental for smaller larvae than larger larvae, but this remains to be tested.

Larval size affected the subsequent survival of *Watersipora subtorquata* colonies in both habitats in this study, although the direction of effects varied. We suggest that larval size will strongly affect the relationship between the abundance of settlers and the abundance of recruits: when larval size is more variable, the relationship between settlers and recruits will be weak and vice versa. Thus larval size will have a strong influence on the relative applicability of supply-side ecology in this species (Hunt & Scheibling 1997, Underwood & Keough 2001).

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Editorial responsibility: Charles Peterson (Contributing Editor), Morehead City, North Carolina, USA

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