Offspring size effects in the marine environment: A field test for a colonial invertebrate

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Abstract   A central tenet of life-history theory is the presence of a trade-off between the size and number of offspring that a female can produce for a given clutch. A crucial assumption of this trade-off is that larger offspring perform better than smaller offspring. Despite the importance of this assumption empirical, field-based tests are rare, especially for marine organisms. We tested this assumption for the marine invertebrate, *Diplosoma listerianum*, a colonial ascidian that commonly occurs in temperate marine communities. Colonies that came from larger larvae had larger feeding structures than colonies that came from smaller larvae. Colonies that came from larger larvae also had higher survival and growth after 2 weeks in the field than colonies that came from smaller larvae. However, after 3 weeks in the field the colonies began to fragment and we could not detect an effect of larval size. We suggest that offspring size can have strong effects on the initial recruitment of *D. listerianum* but because of the tendency of this species to fragment, offspring size effects are less persistent in this species than in others.

Key words: carry-over effects, egg size, maternal effect.

INTRODUCTION

The evolution of offspring size and the wide variation of offspring sizes observed in nature have long fascinated evolutionary ecologists (Lack 1947). The theoretical literature discussing the evolution of offspring size is rich (Vance 1973; Smith & Fretwell 1974; McGinley *et al.* 1987; Stearns 1992; Hendry *et al.* 2001; Sakai & Harada 2001). Most discussion is based on models that describe an optimal trade-off between producing a few, large propagules or many, smaller ones (reviewed in Stearns 1992). Implicit in these models is the assumption that larger offspring perform better than smaller offspring (reviewed in Moran & Emlet 2001) yet surprisingly, tests of this assumption under field conditions are generally rare (but see Sinervo 1990; Sinervo & Doughty 1996; Einum & Fleming 1999). Offspring size effects are likely to be prevalent in marine organisms because (i) a clear link between larval quality and adult performance has been demonstrated; and (ii) the wide variation in offspring sizes within marine invertebrate species. Accordingly, for marine organisms, strong effects of offspring size have been noted for some species but more tests are needed (Moran & Emlet 2001; Marshall & Keough 2003a; Marshall *et al.* 2003a).

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For marine invertebrates with complex life-cycles, variation in the physiological condition of larvae affects important determinants of adult fitness, including survival, growth and reproduction of adults (Pechenik *et al.* 1996; Pechenik *et al.* 1998; Wendt 1998; Moran & Emlet 2001; Phillips 2002; Marshall & Keough 2003a; Marshall *et al.* 2003b). 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 (see References above). Despite the substantial morphological changes and tissue reorganization that accompany the metamorphosis of most species, there are examples of these carry over effects being remarkably pervasive (Wendt 1998; Marshall *et al.* 2003a). For the most part, carry-over effects appear to be driven by variation in larval nutritional condition (Pechenik *et al.* 1996; Phillips 2002; Shima & Findlay 2002; but see Ng & Keough 2003). Assuming that larger larvae have greater nutritional reserves it seems likely that offspring size will affect post-metamorphic performance in a similar way to carry-over effects.

The wide variation in egg sizes observed among marine invertebrates has long been a source of interest for marine biologists and has prompted the development of models that describe optimal egg size in marine invertebrates (Thorson 1950; Vance 1973; Havenhand 1993; Hendry *et al.* 2001). Similar to optimality models in terrestrial systems, these models assume a trade-off between the size and number of larvae that are produced. These models typically predict a single 'optimal' offspring size for a given set of environmental conditions (Levitan 1993; Podolsky &

Strathmann 1996). In reality, offspring sizes are highly variable within species, populations and even individual broods (George 1994; Marshall *et al*. 2000; Ramirez-Llodra 2002). This variation in offspring size is generally viewed as a response to environmental unpredictability – different environments select for different offspring sizes and so mothers hedge their bets by producing a range of offspring sizes (Einum & Fleming 2002). For marine invertebrates, we still lack models that appropriately reflect the complexity of the relationship between offspring size and environmental variability. Furthermore most models about the effects of offspring size in marine invertebrates are restricted entirely to pre-metamorphic traits (Vance 1973; Levitan 1993, 2000; but see Havenhand 1993 for an exception). If we are to gain a better understanding of the evolution of offspring size in marine invertebrates, then more empirical data are needed on the effects of offspring size on each life-history stage. Furthermore, these tests must be conducted under the most realistic conditions possible, otherwise the effects of offspring size can be dramatically over- or underestimated (Einum & Fleming 1999).

Here we examine the effects of offspring size on post-metamorphic survival and growth in the field for the colonial ascidian, *Diplosoma listerianum*. *Diplosoma listerianum* is a common member of marine benthic assemblages in temperate waters and is extremely cosmopolitan. Like all colonial ascidians, the larvae of this species do not feed, but attach to the substrate and metamorphose after approximately 2 h (Marshall & Keough 2003b). After metamorphosis, the colony grows by asexual budding, spreading out across surfaces. Previously, we have shown that offspring size strongly affects the larval stage and there are strong carry-over effects for this species (Marshall & Keough 2003a; Marshall *et al*. 2003b). We now determine if offspring size has equally strong effects on the juvenile/adult stage.

METHODS

Study site and study species

Diplosoma listerianum is a 'weedy' species that is abundant on sheltered, subtidal surfaces. Colonies grow quickly and reproduce at a relatively small size and young age. Two week old colonies can release larvae but the relationship between size and reproduction is highly variable in this species (D. J. Marshall unpubl. data, 2001). *Diplosoma listerianum* is a poorly competing species and readily fragments, often in response to nearby competitors (Marshall *et al*. 2003b). When free space becomes available in subtidal assemblages this species can quickly invade and occupy the space, but

it does not persist for very long and is soon (within 3–4 weeks) displaced by other more competitive species.

All experiments and collections of reproductively mature colonies were conducted at Breakwater Pier in Williamstown, Victoria, during March and April 2001. The site is sheltered from the prevailing weather by a large rocky breakwater. The encrusting invertebrate community was described by Keough and Raimondi (1995). The water temperature for the experimental period was 18–21°C.

Collection and measurement of larvae

Reproductively mature colonies were collected from artificial settlement plates that had been placed in the field 2 months earlier. To collect larvae, the colonies were held in aquaria (as part of a recirculating system) in constant darkness for two days, then exposed to bright light. *Diplosoma listerianum* colonies began spawning about 1 h later. The larvae were collected and each larva was offered a settlement surface within 20 min of release from the parent colony. We collected larvae from 4 colonies for the first experimental run and larvae from 10 colonies for the second experimental run (see '*Experimental design*' below). Pilot studies indicated that the size of *D. listerianum* settlers obtained in the laboratory was within the range of sizes observed from natural settlement in the field at Williamstown pier.

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 (Marshall *et al*. 2003b). Furthermore, our estimates of the size of larvae in the field were based on settled rather than free-swimming larvae. Consequently, we allowed larvae to settle immediately after collection and measured the size of the subsequent settlers 12 h after settlement. Pilot studies showed that settler size was a good predictor of larval size for *D. listerianum* ($R^2 = 0.682$, $n = 7$, $P = 0.022$). In a previous study, we found that extending the larval period of *D. listerianum* reduced the size of the feeding structures (branchial baskets) of the juvenile colonies and this resulted in reduced post-metamorphic growth (Marshall *et al*. 2003b). Consequently, in this study we also measured the size of the branchial baskets of the newly metamorphosed colonies (see Marshall *et al*. 2003b for method).

Experimental design

We placed larvae on their own individual settlement plate in a small drop of seawater (see Marshall *et al*.

2003b for method). The settlement plates (10 cm × 10 cm × 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 marked the position of each settled larva with a small pencil dot next to the metamorphosing individual. The settlement plates were then placed into recirculating aquaria at 15°C for 12 h. Then we briefly videotaped each settler, digitized the footage and measured each settler using SigmaScan (Jandel Scientific Ver. 3, San Rafael, CA, USA). After this, the settlement plates were transported to the field site (approximately 20 min away) in insulated aquaria and were attached to large (90 cm × 90 cm) perspex backing plates using stainless steel bolts. The settlement plates were arranged in haphazard positions on the backing plate. The backing plates were then hung horizontally from the pier, with the experimental plates facing down (to reflect larval settlement preferences and minimize the effects of light and sedimentation) at a depth of ~2 m below mean low tide.

We deployed two batches of settlers (hereafter referred to as 'runs'), each from a different set of parent colonies (pooling the larvae from four colonies per run) with variation in settler size. Each run was deployed on a separate backing plate and we deployed two separate runs. Run 1 was deployed ($n = 19$ settlers) on 18 March 2001 and Run 2 was deployed ($n = 32$ settlers) on 23 March 2001. For both runs, we assessed survival and growth after 2 weeks in the field, and for Run 1, we measured colony survival and growth again after a further week in the field.

Sampling and analysis

To measure colony survival and growth, the backing plates were placed face up in shallow seawater. We then determined whether colonies were still present and in each persisting colony, we counted the number zooids using a magnifying glass. After 3 weeks in the field, many of the colonies had begun to fragment and it was difficult to identify individual colonies reliably. Consequently, we only recorded survival and growth data for whole colonies we could confidently identify.

To assess survival after 2 weeks in the field, we used logistic ANCOVA, where experimental run was a categorical factor and settler size was a covariate. We first tested for an interaction between run and settler size. This interaction was not significant (Wald test: $\chi^2 = 0.108$, $P = 0.742$) and we then ran a reduced model with the interaction term removed. For Run 1, to assess survival after 3 weeks in field we used logistic regression where settler size was a continuous predictor variable.

We tested the effects of settler size on subsequent colony size 2 weeks after settlement with 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 as this interaction was non-significant ($F_{1,27} = 0.037$, $P = 0.848$), we then ran a reduced model with the interaction term removed.

RESULTS

Twelve hours after settlement, larger settlers (and hence larger larvae) had wider branchial baskets than smaller larvae ($R^2 = 0.392$, $P = 0.016$, $n = 14$).

In the field, most mortality occurred in the first 2 weeks after deployment in the field. Pooling across runs, about 33% of all the juvenile colonies died in the first 2 weeks and ~11% of the initial number of colonies (in Run 1) died in the following period. Pooling across runs, the mortality of juvenile colonies was size dependent after 2 weeks in the field (Table 1). We used the equation produced from the logistic ANCOVA (equation after logit transformation: Survival% = (0.009 × larval size) – 7.9) to generate survival probabilities for the size range of larvae in our study. Across the range (>1.5-fold difference) of settler sizes, the predicted probability of survival ranged from a 14% chance of survival for the smallest settler to 93% for the largest settler. In the longer run, mortality after 3 weeks in the field was not size dependent (Table 1).

In both runs, the size of colonies after 2 weeks in the field increased with larger settler size (Table 2, Fig. 1). However, after 3 weeks in the field, the *Diplosoma* colonies had begun to fragment and no effect of settler size was apparent in Run 1 ($R^2 = 0.111$, $P = 0.466$, $n = 7$). Interestingly, there was no relationship between the size of colonies after 2 weeks in the field and after 3 weeks in the field ($R^2 = 0.368$, $n = 7$, $P = 0.148$).

Table 1. Logistic regression and ANCOVA of the effects of initial settler size on subsequent mortality of *Diplosoma listerianum* colonies after 2 weeks and 3 weeks in the field at Williamstown, Victoria, Australia

Time after settlement	Parameter	Odds ratio	χ^2	P
2 weeks	Size	1.009	5.35	**0.021**
(Runs 1 and 2)	Run	NA	0.332	0.564
	Size × Run	NA	0.207	0.656
	McFadden's ρ^2	NA	NA	0.096
3 weeks	Size	1.007	1.719	0.190
(Run 1)	McFadden's ρ^2	NA	NA	0.069

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 are shown in bold.

NA, not applicable.

Table 2.   ANCOVA of effects of settler size on the growth of *Diplosoma listerianum* colonies after 2 weeks in the field at Williamstown, Victoria, Australia

Parameter	d.f.	MS	F	P
Settler size	1	89.8	4.6	**0.04**
Run	1	21.6	1.1	0.30
Residual	28	19	ND	ND

Note the model is reduced after testing for heterogeneity of slopes. *P*-values < 0.05 are shown in bold.
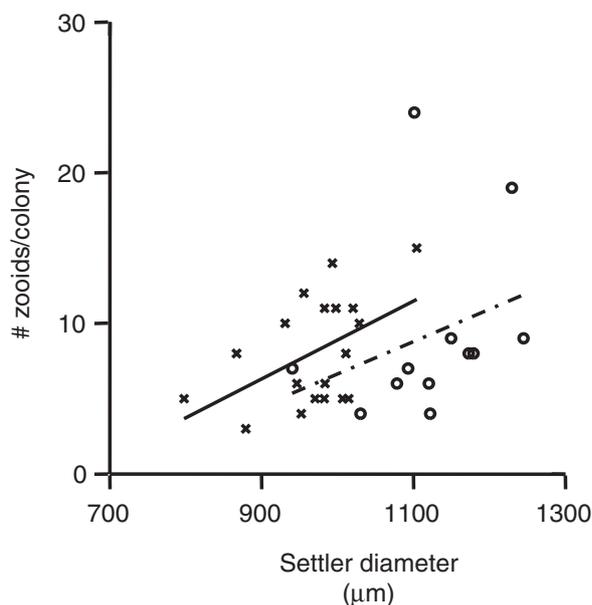
ND, no data.

Fig. 1.   Effect of settler size on *Diplosoma listerianum* colony size after 2 weeks in the field at Williamstown, Victoria, Australia. Circles represent individual colonies from Run 1, crosses represent individual colonies from Run 2.

DISCUSSION

Settler size (and thus larval size) had strong effects on the initial post-settlement survival and growth of *D. listerianum* colonies in the field. Larger settlers survived better and grew into larger colonies than smaller settlers after 2 weeks in the field. This species joins the growing list of marine invertebrates for which it has been demonstrated that there are effects of offspring size on post-metamorphic performance (Moran & Emlet 2001; Phillips 2002; Marshall & Keough 2003a; Marshall *et al.* 2003a). In a previous study, we showed that settlers that had their metamorphosis delayed (and thus consumed more energetic reserves) as larvae had smaller feeding structures (Marshall *et al.* 2003b). Here, we observed a similar effect of larval size on feeding structures with larger settlers having larger branchial baskets than smaller settlers. Larger settlers

with larger feeding structures can probably feed at a higher rate and therefore can accumulate more nutritional resources (Wendt 1996). Presumably, this effect of larval size on feeding ability was responsible for the effects we observed on post-metamorphic survival and growth. It would be interesting to determine how food availability mitigates the effects of offspring size in this species.

For a wide variety of marine invertebrates, there is a strong relationship between the abundance of settlers and the abundance of recruits (reviewed in Hunt & Scheibling 1997). This relationship can be obscured by early post-settlement mortality and consequently, can be highly variable (reviewed in Delany *et al.* 2003). The relationship between settler abundance and recruit abundance for any species provides an estimate of the relative importance of 'supply side' ecology to the population dynamics of that species (Hunt & Scheibling 1997). For *D. listerianum*, the strength of the relationship between settler abundance and recruit abundance will be influenced greatly by the size of larvae that settle. For example, if larval size is relatively uniform, then there will be a strong relationship between settler abundance and recruit abundance, but if larval size is variable, the relationship between settlers and recruits may be weaker. Thus the importance of larval supply to the population dynamics of this species will in part be determined by the size or quality of larvae settling into the population. Larval size can be extremely variable within species (George 1994; Marshall *et al.* 2000, 2002; Phillips & Gaines 2002) and this may explain much of well-documented variation in the relationship between settler and recruit abundance (Underwood & Keough 2001).

Despite the strong effects of settler size on colony survival and growth in the first 2 weeks, we could not detect an effect of settler size on colonies that remained in the field for an additional week. Settler size may be unimportant to the survival of colonies in the longer term. It has been suggested that as an organism ages, maternal effects (such as offspring size) become less important and other effects (e.g. environmental) become more important (Einum & Fleming 1999). In a previous study on *Bugula neritina*, we observed more persistent effects of larval size on colony survival, growth and reproduction. Interestingly, the effects of larval size on survival persisted in *B. neritina* when adult mortality was restricted to the first 2 weeks after settlement (Marshall *et al.* 2003a). However, when mortality was recurrent throughout the adult phase (resulting from storms), the effects of larval size on survival did not persist (Marshall *et al.* 2003a). It may be that when initial mortality is resulting from endogenous factors (e.g. colony nutrition), larval size is more important but when mortality is resulting from environmental factors, larval size effects are less important.

A second explanation is that *D. listerianum* colonies of all sizes had begun to fragment substantially after 3 weeks in the field and this may have obscured any effect of offspring size. For example, colonies may have fragmented into a number of different ramets (fragments). An effect of larval size may have persisted in each (or the whole genet) but because we did not follow ramets after fragmentation, no effect was observed. Alternatively, once colony fragmentation occurred, the original effects of larval size may simply disappear. For modular organisms, colony size is a predominant factor that affects a range of life-history variables (Hughes & Connell 1987). Larger colonies are better able to survive partial predation and physical disturbance. Because larger colonies have more zooids, it is more likely that some of these zooids will remain after a disturbance or predation event and will be able to regenerate (Karlson 1986; Davis 1988). Accordingly, in *B. neritina*, there is a strong relationship between past and present colony size (Marshall *et al.* 2003a) but in *D. listerianum* no such relationship exists. It may be that the tendency of *D. listerianum* to fragment obscures any relationship between initial settler size and long-term colony survival and growth.

Putting together the results of this study and previous work on this species, it appears that there are strong links between the ecology of both the larval and adult stages of *D. listerianum*. Previously we have shown that delaying the metamorphosis of this species strongly affects post-metamorphic performance (i.e. colony growth; Marshall *et al.* 2003b). We have also shown that larval size strongly affects larval swimming duration with larger larvae swimming for longer than smaller larvae (Marshall & Keough 2003b). It appears that smaller *D. listerianum* larvae are at their energetic minimum for post-metamorphic survival and as prolonged swimming reduces post-metamorphic success, they cannot 'afford' any further reduction in their nutritional reserves. Thus, smaller larvae settle quickly whereas larger larvae may be able to swim longer.

Previous models examining the evolution of offspring size in marine invertebrates have focused on the effects of offspring size on pre-metamorphic events such as fertilization or planktonic period (Vance 1973; Levitan 1993; Styan 1998; Podolsky 2001). The results presented here and elsewhere, suggest offspring size can also influence post-metamorphic performance and future models should take this into account.

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