Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2014, **83,** 322–331 doi: 10.1111/1365-2656.12136

Offspring size in a resident species affects community assembly

Kurt Davis[1] **and Dustin J. Marshall**[1,2]*

[1]*School of Biological Sciences, The University of Queensland, Brisbane, Qld 4072, Australia; and* [2]*School of Biological Sciences, Monash University, Melbourne, Vic. 3800, Australia*

Summary

1. Offspring size is a trait of fundamental importance that affects the ecology and evolution of a range of organisms. Despite the pervasive impact of offspring size for those offspring, the influence of offspring size on other species in the broader community remains unexplored. Such community-wide effects of offspring size are likely, but they have not been anticipated by theory or explored empirically.

2. For a marine invertebrate community, we manipulated the size and density of offspring of a resident species (*Watersipora subtorquata*) in the field and examined subsequent community assembly around that resident species.

3. Communities that assembled around larger offspring were denser and less diverse than communities that assembled around smaller offspring. Differences in niche usage by colonies from smaller and larger offspring may be driving these community-level effects.

4. Our results suggest that offspring size is an important but unexplored source of ecological variation and that life-history theory must accommodate the effects of offspring size on community assembly. Life-history theory often assumes that environmental variation drives intraspecific variation in offspring size, and our results show that the converse can also occur.

Key-words: egg size, life-history theory, maternal effect, phenotypic plasticity, seed size

Introduction

Offspring size is an important life-history trait from both an ecological and evolutionary perspective. Ecologically, offspring size influences offspring performance and population dynamics across generations (Wade 1998; Benton *et al.* 2005). Evolutionarily, the selective pressures that affect offspring size have been studied for over 60 years (Thorson 1936; Fox & Czesak 2000; Krist 2011). Because offspring size affects the fitness of both mothers and offspring, offspring size is thought to be a balance between the interests of mothers (for whom selection favours producing the maximum number of high performing offspring) and the interests of offspring (for whom selection favours a higher investment in individual offspring; Wolf & Wade 2001). Attempts to understand variation in offspring size have centred on estimating the relationship between offspring size and performance because this relationship determines the fitness return of a particular level of maternal investment. Over the past 60 years, we have accumulated many estimates of the offspring size–performance relationship from a wide variety of taxa (Fox & Czesak 2000; Moles *et al.* 2005; Marshall & Keough 2008a; Krist 2011) with many (though not all) studies showing that larger offspring tend to have higher performance than smaller offspring.

While the consequences of offspring size variation for those offspring are well-established, the consequences of offspring size variation for other species in the broader community are much less clear. There are, however, good reasons for expecting offspring size variation to have consequences that extend beyond the focal species alone. Differences in offspring size can generate differences in the performance, behaviour, competitive ability, susceptibility to predators, foraging ability and feeding preferences of those offspring (Palmer 1990; Fox 2000; Marshall & Keough 2008a; Pfennig & Martin 2009; Segers & Taborsky 2011; McGhee *et al.* 2012). Intraspecific variation in each of these traits (generated by variation in offspring size) is likely to affect the distribution and abundance of other species. For example, increasing seed size often results in greater plant growth rates (Stanton 1984; Gomez 2004) – we would therefore expect that individuals derived from larger seeds would generate more shade than individuals from smaller seeds, altering the light conditions for

---

*Correspondence author. E-mail: dustin.marshall@monash.edu

understorey plants and subsequent community dynamics. Despite the intuitive appeal of such effects, the effects of seed size on other plant species have not been explored. In animals, smaller offspring are sometimes more susceptible to predators (Rivest 1983; Gomez 2004), such that shifts in offspring size should generate changes in the abundance of predators, although again, such effects have not been examined. It is therefore reasonable to expect that variation in offspring size has effects that extend beyond the performance of the focal species alone and pervade the broader community. If such community-wide effects of offspring size do exist, then they may represent a heretofore neglected phenotypic source (c.f. exclusively genetic effects Whitham *et al.* 2003) of ecological variation in communities. Furthermore, essential elements of offspring size theory would need to be revisited as current theory does not include effects of offspring size beyond the focal species alone (Smith & Fretwell 1974; McGinley, Temme & Geber 1987; Charnov & Downhower 1995; Sakai & Harada 2001; Marshall *et al.* 2010; Jorgensen, Auer & Reznick 2011).

We manipulated offspring size and density of a resident species and examine the subsequent assembly of a community around that species in the field. We focused on a marine bryozoan, *Watersipora subtorquata*, a species in which offspring size effects on performance are strong and persistent. Specifically, colonies from larger offspring tend to survive better, grow more and have higher fecundity than colonies from smaller offspring in this species (Marshall & Keough 2008b; Marshall & Monro 2013). *Watersipora* has also been shown to affect the assembly of some elements of epibenthic communities (Sellheim, Stachowicz & Coates 2010). We hypothesized that larger offspring would grow faster than smaller offspring and occupy greater proportions of space on experimental substrata. As patch size can strongly affect community assembly in marine invertebrate communities (Keough 1984), we expected that offspring size would indirectly affect community assembly by affecting the availability of free space. To test these hypotheses, we deployed two size classes of offspring into the field at two densities on to artificial substrata in experimental arrays and monitored the community of sessile marine invertebrates that assembled on these arrays over time. The offspring size manipulation was to directly test the hypothesis of interest, and the density manipulation was to test for the effect of differences in the availability of free space independently of offspring size. We found effects of offspring size on community assembly, but surprisingly, these effects were not driven by differences in free space.

Materials and methods

STUDY SPECIES & SITE

Watersipora subtorquata (hereafter to referred to by its genus name) is an encrusting, cheilostome bryozoan, commonly found in fouling communities world-wide (Sellheim, Stachowicz & Coates 2010; Marshall & Monro 2013). *Watersipora* forms large colonies of unspecialized modular units called zooids; zooids fuse to form a colonial encrusting sheet that spreads over available hard surfaces. In Californian populations, *Watersipora* forms complex 3-dimensional structures (Sellheim, Stachowicz & Coates 2010), but in Australia, colonies tend to be simpler and flatter (D. J. Marshall, pers. obs.). After reaching maturity, individual zooids generally brood a single offspring for *c.* 2 weeks, after which the non-feeding larvae are released into the water column (Marshall & Keough 2003). Larvae are immediately competent to settle and metamorphose, but can remain in the water column for up to six hours (Marshall & Keough 2003). Once metamorphosis is complete, the first zooid formed is called the 'ancestrula' or 'settler'. Size of the ancestrula is strongly correlated with larval size when they are released from the mother (Marshall & Keough 2003). Previous studies have shown that offspring size can strongly affect the post-metamorphic survival, growth and reproduction in this species (Marshall & Monro 2013; Marshall & Keough 2008b). At our field site, colonies live for around 2 months.

We conducted the experiments at Manly marina (27°27′10″ S, 153°11′22″ E, Brisbane, Queensland, Australia) over 2010 and 2011. Manly marina is a low flow embayment, sheltered from prevailing currents and surge by a man-made breakwater. The floating pontoons and pilings of the marina provide suitable habitat for a diverse community of benthic marine invertebrates, including several bryozoans (e.g. *Watersipora* and *Bugula stolonifera*), colonial and solitary ascidians (such as botryllids and *Styela plicata*), spirorbid and serpulid polychaetes, and barnacles. *Watersipora* is one of the earliest and most consistent colonizers of new settlement plates at our field site (D. J. Marshall, pers. obs.).

GENERAL METHODS

We directly manipulated initial offspring size and the density of *Watersipora* settlers to examine their effects on community assembly. Offspring size was manipulated by collecting field settled *Watersipora,* measuring within 24 hours of settlement (when settler size is still a good predictor of original larval size; Marshall & Keough 2003) and splitting offspring sizes into two size classes (see below for details). These field collected individuals of known size were then placed onto new settlement plates in the laboratory and deployed into the field. Density was manipulated by placing either three or six individual ancestrula onto our community assembly plates, and these densities are typical of those occurring naturally at this site. We haphazardly arranged *Watersipora* ancestrulae in each of the four treatment combinations (two offspring sizes classes × two densities) on 100 × 100 × 3 mm grey PVC settlement plates, placed these plates into the field and monitored the development of communities on each plate in the field. Across all of our experiments, these settlement plates were our unit of replication.

To test for the temporal consistency of any effects that we observed, we repeated the experiment three times across 2010 and 2011. Each 'run' had a different number of replicates due to variability in the availability of *Watersipora* settlers. We deployed 98 replicates of the large and small treatments across three experimental runs ($N_{run\ 1} = 40$, $N_{run\ 2} = 35$, $N_{run\ 3} = 23$).

EFFECT OF OFFSPRING SIZE AND DENSITY ON COMMUNITY ASSEMBLY

For each experimental run, to collect *Watersipora* of known offspring size, we used standard methods following Marshall &

Monro (2013). Briefly, we placed roughened acetate collector sheets into the field for 24 hours. One hundred and twenty acetate collector sheets were attached facing downwards to 420 × 420 × 8 mm PVC backing panels (Backing Panel was a random factor nested within run in our analyses) that were attached to the pontoons of the marina *c.* 1 m below the surface. We retrieved the acetate sheets, returned them to the laboratory and measured the size of *Watersipora* ancestrulae with a digital camera attached to a stereomicroscope (40×). Once all of the settlers were measured, we allocated the smallest 30% of settlers in that run to the 'small' size class and the largest 30% of settlers to the 'large' size class (mean small: $1{\cdot}7 \times 10^{-4}$ mm^2; mean large: $2{\cdot}3 \times 10^{-3}$ mm^2; specific size classes used in each run are summarized in Appendix S1, Supporting information). We haphazardly allocated individuals within each size class to different density treatments and settlement plates, taking care to use a mix of individuals from different collector sheets for each settlement plate. To create our treatments, we manually removed each individual from the acetate sheets by cutting around the attached ancestrula with a scalpel and then gluing the acetate to a clean, unfouled settlement plate. We attached six or three randomly selected ancestrulae in single size class to each settlement plate to create the high or low density treatments respectively. To control for differences in the number of acetate sheet pieces glued to plates between high and low density treatments, we attached three equally sized, but unoccupied, pieces of acetate sheet to the settlement plates in low density treatments. At this point, our settlers occupied <1% of the total surface area of our settlement plates.

We also deployed settlement plates with no *Watersipora* present at all (with acetate pieces included as a control) – this control treatment was to determine how communities assembled with and without the focal species.

We then attached these settlement plates to backing panels in the field (as described above), taking care to intersperse equal numbers of replicates of all four treatment combinations on each backing panel. All settlement plates within a run were deployed at the same time, and all were deployed within 72 hours of settlement.

After 2 weeks and 6 weeks in the field, we retrieved settlement plates from the field for processing in the laboratory. These plates resemble natural local communities in most ways although settlement plates remain imperfect representations of the broader community (Keough 1984), and the effects of offspring size differ between settlement plates and natural communities (Marshall & Keough 2004). Settlement plates were returned to the laboratory in insulated aquaria and returned to the field within 24 hours of collection. In the laboratory, we photographed each settlement plate and quantified the abundance of different species present in communities. We also estimated the size (estimated as both colony area and zooid number) and number of experimental *Watersipora* individuals remaining on each plate. Both spirorbid and serpulid polychaetes were extremely abundant (3000 per m^2 in week two and 109 800 per m^2 in week six) and appeared to be evenly distributed within settlement plates, so we subsampled a randomly selected quarter of each plate for these species. We discontinued our experimental runs after 6 weeks in the field because after this time, this species tends to switch from asexual reproduction (i.e. growth) to sexual reproduction and the colony begins to senesce rapidly (D. J. Marshall, pers. obs.).

Watersipora colonies can be an important source of habitat for other epibenthic species in Californian communities (Sellheim, Stachowicz & Coates 2010), and in Australia, very large colonies can senesce in the centre of the colony with some colonization by other species in the central senesced region. In our study, however, our focal colonies were not heavily colonized. As such, while we counted any species that were attached to our focal colonies, <1% of individuals in our communities grew on the focal colonies and no species grew exclusively on our focal colonies.

EFFECT OF OFFSPRING SIZE ON COLONY MORPHOMETRICS

We found that *Watersipora* offspring size affected subsequent community assembly (see Results), and were interested in whether larger offspring produced colonies with traits that differed to colonies that came from smaller offspring. Specifically, we were interested in whether colonies from different offspring sizes had traits that may affect the use of the available planktonic food. We therefore repeated the above methods to generate colonies that originated from different offspring sizes and measured the relationship between offspring size and size (and therefore spacing) of zooids, as well as the relationship between offspring size and the subsequent size of feeding structures (lophophores). We would expect the spacing between feeding zooids and the size of feeding structures to affect the amount and type of food that is captured (Okamura 1984). After 2 weeks in the field, we returned colonies to the laboratory and photographed them with a digital camera connected to a microscope. We measured the distance between feeding structures within colonies by estimating the density of feeding structures per unit area. To measure the size of the feeding structures, two lophophores from each colony were randomly selected, and we took care to ensure that all photographs showed all lophophores in same orientation. We measured the total size of feeding structure (crown area), the size and spacing of feeding tentacles, as well as the diameter of the lophophore 'mouth' (for a detailed description of lophophore morphometrics, see Burgess & Marshall 2011b).

DATA ANALYSIS

To examine the effects of offspring size and density on the size of individual *Watersipora* colonies and on the total amount of area occupied by these colonies on each plate, we used repeated measures ANOVA. To examine differences in communities among the four treatment combinations, we first compared standard community summary metrics (total abundance, evenness, species richness and Shannon's diversity index), with repeated measures ANOVA. For all of the metrics, we detected various complex interactions between our factor of interest (offspring size), random effects and time, indicating that the effects of offspring size were not consistent across the two census dates. We therefore analysed the 2 and 6 week census periods separately. We were interested in the amount of variance that our factor of interest explained relative to temporal variation (here, estimated by the factor run) and spatial variation (here estimated by the factor backing panel [run]), so we used a variance partitioning approach as advocated by Quinn & Keough (2002; see page 249 for a discussion of this approach). We also examined the abundance of individual species with MANOVA.

In all of our analyses, *Watersipora* offspring size and density were fixed factors, Experimental run was a random factor, and backing panel (run) was a random factor. Including space unoccupied by our focal *Watersipora* as a covariate had no qualitative effect on our analyses (Appendix S4, Supporting information). Following Quinn & Keough (2002), we removed non-significant interactions between fixed and random factors. We did not formally include our control plates in our analyses as the treatment is not orthogonal to our other treatments of interest (density and offspring size). As such, we present the data for only one run including the control to provide an indication of how our experimental communities compare to control communities where *Watersipora* was absent. We also did planned comparisons in MANOVA to formally compare differences between control communities and small and large treatment communities (pooling across both densities in each offspring size treatment). All analyses were performed in Systat Ver 13 (Chicago, IL 60606, USA).

Results

PERFORMANCE OF THE FOCAL SPECIES

The average size of colonies that originated from larger offspring was *c*. 30% larger than colonies that originated from smaller offspring (Fig. 1). Density had no effect on colony size, but there was an indication of an interaction between offspring size and density (Table 1a). This interaction appeared to be driven by the lower density treatment reducing the performance of smaller offspring but increasing the performance of larger offspring (Fig. 1). The total area occupied by colonies was strongly affected by both density and offspring size, with greater areas being occupied at high densities and larger offspring sizes (Table 1b). While both effects were significant, generally, density had stronger, larger effects on total area occupied than did offspring size (average difference in total area between size treatments: 36%; average difference in total area between density treatments: 70%). The effects of offspring size and density on total area occupied by colonies were, of course, mirrored in their effect on the amount of *Watersipora*-free space available on plates. After 6 weeks in the field, the total space taken up by the focal species varied between 1% and 5%.

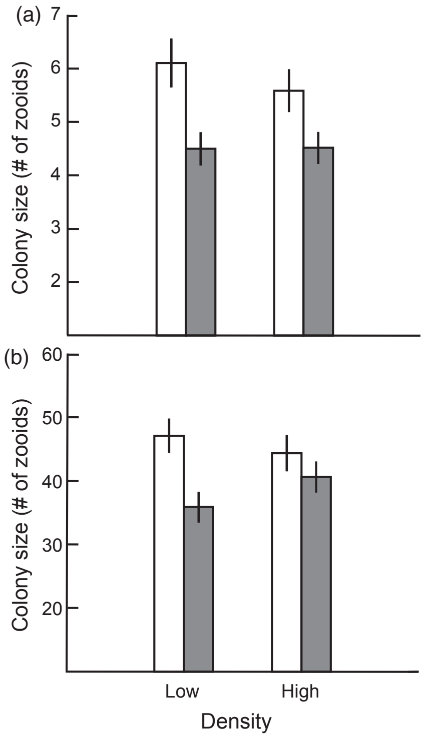

Fig. 1. Effect of offspring size and offspring density on the size of *Watersipora subtorquata* colonies after (a) 2 and (b) 6 weeks in the field. Bars show mean (±SE) size of colonies for large and small offspring size in open and shaded bars, respectively.

EFFECT OF OFFSPRING SIZE ON COLONY MORPHOMETRICS

Colonies that came from larger offspring had feeding structures that were on average *c*. 10% further apart from each other than feeding structures on colonies that came from smaller offspring ($F_{1,52} = 5{\cdot}59$, $P = 0{\cdot}022$). Original offspring size had few effects on the size and shape of

Table 1. (a) Effects of offspring size on *Watersipora subtorquata* colonies after 2 and 6 weeks in the field. (b) total area occupied by *Watersipora subtorquata* colonies after 2 and 6 weeks in the field

Source	d.f.	MS	F	*P*
(a)				
Between subjects				
Run	2	936	4·877	**0·010**
Offspring size	1	1898	9·886	**0·002**
Density	1	140	0·731	0·395
Offspring size*Density	1	714	3·718	0·057
BP (Run)	6	28	0·151	0·988
Error	86	192		
Within subjects				
Time	1	76 453	39·092	**0·025**
Time*Run	2	1955	10·681	**< 0·001**
Time*Offspring size	1	1150	6·283	**0·014**
Time*Density	1	108	0·591	0·444
Time*Offspring size* Density	1	601	3·286	0·073
Error	86	183·096		
(b)				
Between subjects				
Run	2	5660	3·371	**0·039**
Offspring size	1	21 501	12·805	**0·001**
Density	1	64 356	38·327	**< 0·001**
Offspring size*Density	1	46	0·028	0·868
BP (Run)	6	960	0·572	0·752
Error	86	1679		
Within subjects				
Time	1	763 766	73·375	**0·013**
Time*Run	2	10 409	6·691	**0·002**
Time*Offspring size	1	16 532	10·627	**0·002**
Time*Density	1	47 680	30·649	**< 0·001**
Time*Offspring size* Density	1	81	0·053	0·819
Error	86	555		

Note that models are reduced after removing non-significant fixed × random interactions. Significant *P*-values shown in bold.

feeding structures in the colony, but the average distance between feeding tentacles within feeding structures was significantly smaller in colonies from smaller offspring relative to colonies from larger offspring (Appendix S2, Supporting information).

OFFSPRING SIZE EFFECTS ON COMMUNITY ASSEMBLY

After 2 weeks in the field, the effects of offspring size on community assembly were weak and inconsistent. Community assembly varied due to density, offspring size and as well as varying significantly in space and time (across panels and experimental runs): analysis of Shannon diversity and MANOVA both detected a significant three-way interaction (Shannon: $F_{2,80}$ = 4·75, P = 0·011; MANOVA: Pillai trace = 0·325, $F_{10,154}$ = 2·99, P = 0·002; Appendix S3, Supporting information; Table 1). No other community metric (richness, evenness or total abundance) showed any response to our factors of interest (Appendix S3, Supporting information; Table 1). When we explored the effects of density and size in each run separately for Shannon diversity, we found that diversity was generally greater on plates with larger offspring at higher densities or smaller offspring at lower densities in runs 1 and 2, but in run 3, there was higher diversity on plates with larger offspring and lower densities.

After 6 weeks in the field, the effects of offspring size on community assembly were stronger and more consistent. Larger offspring sizes increased total abundance, but decreased the diversity and evenness of the communities on the plates (Table 2; Fig. 2). The effects of offspring size on richness were more variable in space and time – larger offspring sizes resulted in higher richness across most runs and backing panels, but not all (Fig. 2). Overall, offspring size explained remarkably high amounts of variation in the total abundance of individuals in the community relative to both spatial and temporal variation (Table 3). The level of variance in total abundance in the community due to offspring size was much greater than variation among communities that were separated by tens of metres on different experimental panels and was comparable to the level of variation generated when communities assembled months apart (Table 3). For the other community metrics, variation due to offspring size was much less than variation in time or space.

Visual comparisons of treatment plates to control plates suggest that communities in the 'large' treatment were more similar to control plates, while communities in the 'small' treatment differed from both controls and the large treatment (Fig. 3). Planned comparisons with MANOVA confirmed this pattern, there was a significant difference between small treatment and control communities (Pillai trace = 0·460, $F_{10,46}$ = 3·96, P = 0·001), but no significant difference between large treatment and control communities (Pillai trace = 0·199, $F_{10,54}$ = 1·42, P = 0·233).

Table 2. Effects of offspring size, density and experimental run on community summary metrics after 6 weeks in the field

Source	d.f.	MS	F	*P*
Abundance				
Run	2	95 582	10·04	**< 0·001**
Offspring size	1	132 678	13·94	**< 0·001**
Density	1	826	0·087	0·769
Offspring size*Density	1	3931	0·413	0·522
BP (Run)	6	19 786	2·08	0·064
Error	86	9518		
Evenness				
Run	2	0·064	31·368	**< 0·001**
Offspring size	1	0·010	4·836	**0·031**
Density	1	<0·001	0·013	0·920
Offspring size*Density	1	0·001	0·726	0·396
Density*Run	2	0·006	3·043	0·053
BP (Run)	6	0·008	3·771	**0·002**
Error	84	0·002		
Shannon				
Run	2	1·681	27·908	**< 0·001**
Offspring size	1	0·240	3·983	**0·049**
Density	1	0·010	0·167	0·684
Density*Offspring size	1	0·011	0·190	0·664
BP (Run)	6	0·580	9·624	**< 0·001**
Error	86	0·060		
Richness				
Run	2	19·299	15·082	**< 0·001**
Offspring size	1	0·923	0·721	0·399
Density	1	0·602	0·471	0·495
Density*Offspring size	1	2·997	2·342	0·130
Density*Run	2	2·690	2·102	0·130
BP (Run)	6	0·374	0·292	0·939
Density*BP (Run)	6	1·979	1·546	0·176
Offspring size*BP (Run)	6	2·949	2·305	**0·043**
Error	72	1·280		

Note model has been reduced after testing for non-significant random factors. Significant *P*-values shown in bold.

MANOVA showed effects of offspring size on individual species abundances but no effect of density, nor density × offspring size (offspring size: Pillai trace = 0·221, $F_{7,80}$ = 3·25, P = 0·004; density: Pillai trace = 0·084, $F_{7,80}$ = 1·64, P = 0·134; offspring size × density: Pillai trace = 0·084, $F_{7,80}$= 1·06, P = 0·400). Further exploration suggested that larger offspring sizes resulted in greater abundances of polychaete worms (both serpulids and spirorbids), but had mixed effects on other species (Fig. 4). Polychaete worms were also the most abundant organisms on the plates (Fig. 4). Offspring size explained more variation in the abundance of serpulid polychaetes than did time or space (time: 14·5%; space: 0·8%, offspring size: 15%). Spirorbid polychaetes also showed notable variation in both space and time (space: 20%; time: 18%), but offspring size still explained levels of variation similar the level it explained in serpulids (offspring size: 13%).

Discussion

We found that the initial offspring size of a resident species (*Watersipora subtorquata*) affected the subsequent

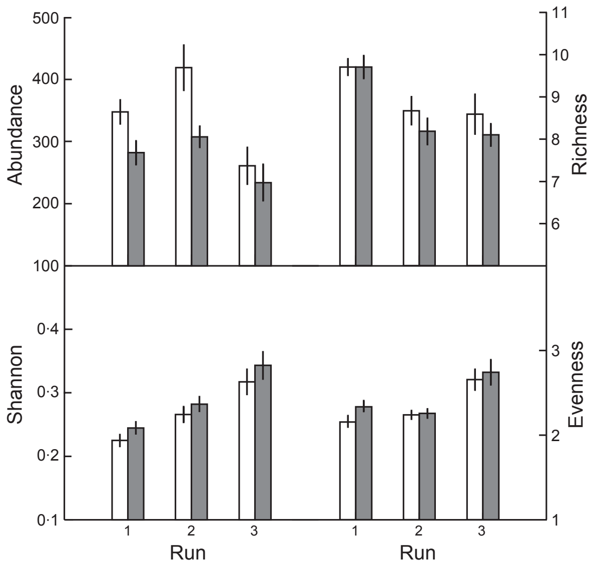

Fig. 2. Effect of offspring size and experimental run on community summary metrics after 6 weeks in the field. Note that despite apparently variable effects of offspring size across runs, for none of the community metric was the offspring size × run interaction significant ($P > 0{\cdot}25$). For each community metric, bars show mean (±SE) value for large and small offspring size in open and shaded bars, respectively.

assembly of the broader community in the field. After 6 weeks of community assembly, these effects were consistent across replicate field trials. Generally, communities that assembled around individuals that came from larger offspring sizes were denser but less even and less diverse. Some species (e.g. spirorbids, serpulids, *Bugula stolonifera*) were less common on plates bearing *Watersipora* originating from smaller offspring sizes while other species (e.g. *Celloporaria*) were unaffected. Previous studies have shown that variation in offspring size can affect intraspecific interactions – larger offspring can grow into better exploitative (Allen, Buckley & Marshall 2008; Bashey 2008) and interference (Marshall & Keough 2008a) competitors. The current study illustrates that the consequences of differential maternal investment extend beyond the focal species alone to affect the broader community. The strongest effect of offspring size was on the most abundant members of the community (polychaete tube worms); surprisingly, these species were actually more common on plates bearing colonies that originated from larger offspring. While the precise mechanism underlying the effects we observed remains unclear, the existence of these effects alone has a number of interesting ecological and evolutionary consequences.

WHY DOES OFFSPRING SIZE AFFECT COMMUNITY ASSEMBLY?

Our *a priori* hypothesis was that offspring size would affect colony growth rates, affecting the availability of free space on our settlement plates which could generate differences in community assembly. This hypothesis was based on earlier studies showing larger offspring grow faster in this species (Marshall & Monro 2013; Marshall & Keough 2008a,b) and that marine invertebrates differentially recruit to areas of free space that vary in size (Keough 1984). Our results provided very little support for this hypothesis – the effects of offspring size on community assembly were not driven by differences in the total area occupied by the focal species (the inverse of *Watersipora*-free space) among treatments. The density rather than the original offspring size of *Watersipora* drove most of the variation in the availability of free space, but density had little effect on community assembly and no effect on the two groups that drove most of the effects – serpulids and spirorbids. Moreover, the focal species occupied only a small proportion of the available space (generally <5%), suggesting that the effects of offspring size on community assembly were not mediated by a direct effect of colony size.

A number of alternative mechanisms may explain why offspring size in the resident species affects community assembly. Interestingly, the effects of offspring size on community assembly strengthened and became more consistent over time in all three runs. This increase suggests that whatever mechanism drove the effect of offspring size became stronger as our focal colonies grew. We hypothesize that offspring size may covary with functional traits of the colonies that affect the broader community. We found that *Watersipora* colonies from larger offspring had more widely spaced lophophores (feeding structures). Furthermore, the spacing between feeding tentacles within lophophores was greater in colonies from larger offspring. Both these traits could result in colonies from larger offspring being less efficient at capturing smaller particles. In other systems, smaller individuals have occasionally also been shown to better exploit scant food resources (Marshall & Keough 1994) although usually it is larger

Table 3. Variance components (%) for community metrics after 6 weeks in the field as influenced by offspring size and density relative to spatial and temporal variation

Metric	Space	Time	Offspring size	Density	Size × Density	Unexplained
Abundance	6·3	16·8	16·1	0	0	60·6
Evenness	11·0	39·6	3·3	0	0	45·7
Shannon	34·6	23·3	2·7	0	0	39·3
Richness	0	27·3	0*	0	0·08	70·1

*1·6% variance explained by Size × BP(Run) interaction.

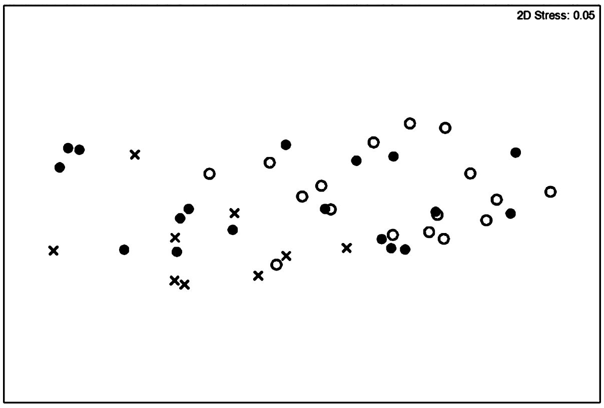

Fig. 3. NMDS based on Bray-Curtis matrix of dissimilarities of communities on control plates (containing no *Watersipora*; indicated by crosses), plates containing *Watersipora* colonies from large offspring (indicated by closed circles) and plates containing *Watersipora* colonies from small offspring (indicated by open circles).

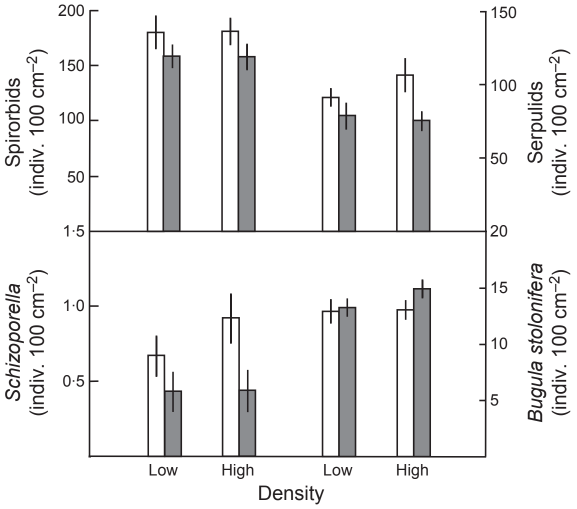

Fig. 4. Effect of offspring size and density on the abundance of different community members after 6 weeks in the field. For each community metric, bars show mean (±SE) value for large and small offspring size in open and shaded bars, respectively.

individuals who are the more effective competitors, particularly in colonial species (Buss 1990). If lophophore size or spacing affects the size of food particles that colonies capture, then colonies originating from offspring of different size may have different food niches and subsequent community assembly could be influenced by this effect on the size spectrum of available food adjacent to our focal colonies. When we compared our experimental communities to control plates that did not contain any *Watersipora,* large or small to begin with – our large offspring size treatment most resembled the control plates. This suggests that colonies from smaller offspring distorted the community trajectory more strongly than did colonies from larger offspring. The groups most affected by offspring size effects were serpulids and spirorbids, with the densities of these groups being much lower on small offspring size plates than larger offspring size plates (or controls). Thus, it would be interesting to determine whether serpulids and spirorbids feed on similar size classes of plankton as *Watersipora* colonies that originate from smaller offspring.

Alternatively, although less likely, hypotheses could also explain our results. *Watersipora* originating from different size offspring could differentially feed on settling larvae, generating differences in the subsequent community. Intraspecific variation in prey usage of a resident species has been demonstrated to affect subsequent community structure in other systems (Post *et al.* 2008). In our system, however, direct consumptive effects of our resident species on settling larvae are highly unlikely as bryozoans typically feed on prey that are much smaller than the typical size of marine invertebrate colonizers (Gosselin & Qian 2000). Furthermore, the colonies from larger offspring had larger lophophores suggesting that, if anything, these colonies should be able to consume more larvae, but it was on these plates where we found higher overall abundances in the community. Alternatively, allelopathy could affect community assembly, but such an explanation would require that colonies originating from larvae of different sizes have different allelopathic effects – a possibility we consider unlikely. Furthermore, we did not notice any spatial effects of our focal colonies – the differences in communities appeared to be fairly uniform across our settlement plates, rather than being restricted around our focal colonies alone.

ECOLOGICAL CONSEQUENCES OF OFFSPRING SIZE EFFECTS ON COMMUNITY ASSEMBLY

Our results suggest that offspring size variation may be non-negligible but unexplored source of variation in communities. Variation in resident species identity is a well-recognized source of variation in community assembly (Sutherland 1974; Tilman 2004); more recently, it has become apparent that intraspecific variation in individual phenotype can also affect communities (Whitham *et al.* 2003). The principal source of intraspecific variation in individual phenotype studied thus far has been genotypic variation, and the effects of this variation can be strong and pervasive (Whitham *et al.* 2003; Post *et al.* 2008; Johnson, Vellend & Stinchcombe 2009; Bassar *et al.* 2010; Crutsinger, Strauss & Rudgers 2010). In many systems, however, offspring size effects are likely to generate variation in the phenotype of focal species that is greater than that of genotypic variation (Wolf & Wade 2001). Assuming that the magnitude of the effect of intraspecific variation on community assembly is proportional to phenotypic variation in the focal species, offspring size variation in resident species may have even greater effects on community assembly than do community genetics effects.

To our knowledge, this is the first study to show that offspring size affects community assembly, but we predict that such effects are much more widespread. In many systems, offspring size can affect an offspring's consumption of species at lower trophic levels (Fox 2000; Pfennig & Martin 2009) and can affect their susceptibility or attractiveness to predators (Rivest 1983; Stanton 1984; Gomez 2004; Bassar *et al*. 2010; McGhee *et al*. 2012), as well as behavioural interactions within and among species (Leblanc *et al*. 2011; Segers & Taborsky 2011), such that offspring size variation should generate variation in the dynamics of other species. We predict that offspring size variation in one species could therefore have manifold consequences for other species across trophic levels. For example, spadefoot toad tadpoles from larger eggs are more likely to be carnivorous than tadpoles from smaller eggs (Martin & Pfennig 2010). In this example, predation pressure on local prey communities could covary with the local distribution of offspring sizes. More generally, offspring size can vary systematically among populations (Johnston & Leggett 2002; Marshall & Keough 2008b); all else being equal, this population-level variation in offspring size may generate variation in the surrounding community. Offspring size variation is increasingly recognized as an important source of variation for the population dynamics of the focal species (Benton, St Clair & Plaistow 2008; Burgess & Marshall 2011a); we suggest that the focus on the ecological consequences of offspring size variation be expanded to consider the broader community and environment.

CONSEQUENCES FOR LIFE-HISTORY THEORY

If our results apply more generally, important elements of life-history theory must change to accommodate new assumptions about how offspring size variation and the local environment interact to affect selection on maternal provisioning. It has long been recognized that mothers can influence their offspring's environment by selectively releasing them in different areas (Mousseau & Dingle 1991). Our results suggest that because offspring size can influence community assembly, mothers may also be able to influence their offspring's environment in more subtle ways than simple release site effects. Traditionally, mothers have been thought to respond to environmental variation by manipulating the size of their offspring (Smith & Fretwell 1974). For example, some environments (e.g. more competitive environments; Bashey 2008) select for larger offspring sizes, others (e.g. warmer environments; Kaplan 1992) select for smaller offspring sizes. Different communities can also impose different selection on offspring size. For example, communities early in succession can favour smaller offspring sizes while later successional communities favour larger offspring sizes (Marshall & Monro 2013). In a range of species, mothers are thought to respond to this environmentally mediated variation in selection by altering offspring size accordingly (so called 'adaptive' or 'anticipatory' maternal effects; Marshall & Uller 2007). Under this view, mothers and offspring are largely 'passive' players: variation in the environment drives selection on (and variation in) offspring size. If on the other hand, offspring size has broader effects on the community assembly, as seen in this study, then the relationship between offspring size and some forms of environmental variation may be more reciprocal than previously recognized. Variation in offspring size could generate variation in the local community such that mothers could manipulate offspring size so as to modify their offspring's environment, as opposed to the environment 'dictating' the size of offspring mothers produce. This may also render the environment that offspring face more predictable from the perspective of mothers – by altering the offspring size and therefore the local community, they may reduce some of the uncertainty.

Our results have interesting implications for the rich theoretical literature on offspring size. For example, in their classic model, McGinley, Temme & Geber (1987) found that if mothers could control the dispersal of their offspring into different environments, mothers should provision their offspring differently relative to species where mothers cannot control offspring dispersal. They extended their reasoning to predict that adaptive plasticity in offspring size should be more common in animals than plants because dispersal is less directed in seeds relative to animal propagules (McGinley, Temme & Geber 1987). Our results challenge this idea – even in species such as ours where mothers cannot control the dispersal of their offspring directly, they may still be able affect the environment their offspring experience by manipulating offspring size. Theoretical considerations of offspring size evolution have considered the role that the maternal phenotype and the density of siblings play in shaping selection on offspring size (Parker & Begon 1986; Sakai & Harada 2001) – our results suggest that new theory that includes the potential for covariance between offspring size and the offspring environment is needed. For example, colonies from larger offspring are generally better competitors in this species (Marshall & Monro 2013), yet our results here suggest that they may also experience more intense competition, as communities will tend to be more abundant around colonies from larger offspring. We eagerly await further studies to determine whether the effect of offspring size on community assembly is widespread among other taxa.

Acknowledgements

Thanks to Tracey Price and the MEEG members for help with the data collection in this study. DJM was supported by grants from the ARC. We thank Martin Thiel and anonymous reviewers for providing very helpful comments on earlier versions of this manuscript. The authors declare no conflict of interest.

References

Allen, R.M., Buckley, Y.M. & Marshall, D.J. (2008) Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *The American Naturalist*, **171**, 225–237.

Bashey, F. (2008) Competition as a selective mechanism for larger offspring size in guppies. *Oikos*, **117**, 104–113.

Bassar, R.D., Marshall, M.C., Lopez-Sepulcre, A., Zandona, E., Auer, S.K., Travis, J., *et al.* (2010) Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 3616–3621.

Benton, T.G., St Clair, J.J.H. & Plaistow, S.J. (2008) Maternal effects mediated by maternal age: from life histories to population dynamics. *Journal of Animal Ecology*, **77**, 1038–1046.

Benton, T.G., Plaistow, S.J., Beckerman, A.P., Lapsley, C.T. & Littlejohns, S. (2005) Changes in maternal investment in eggs can affect population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1351–1356.

Burgess, S.C. & Marshall, D.J. (2011a) Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics. *Journal of Animal Ecology*, **80**, 681–687.

Burgess, S.C. & Marshall, D.J. (2011b) Field estimates of planktonic larval duration in a marine invertebrate. *Marine Ecology Progress Series*, **440**, 151–161.

Buss, L.W. (1990) Competition within and between encrusting clonal invertebrates. *Trends in Ecology & Evolution*, **5**, 352–356.

Charnov, E.L. & Downhower, J.F. (1995) A trade-off-invariant life-history rule for optimal offspring size. *Nature*, **376**, 418–419.

Crutsinger, G.M., Strauss, S.Y. & Rudgers, J.A. (2010) Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. *Ecology*, **91**, 1237–1243.

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. & Czesak, M.E. (2000) Evolutionary ecology of progeny size in arthropods. *Annual Review of Entomology*, **45**, 341–369.

Gomez, J.M. (2004) Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, **58**, 71–80.

Gosselin, L.A. & Qian, P. (2000) Can bacterivory sustain survival and growth in early juveniles of the bryozoan *Bugula neritina*, the polychaete *Hydroides elegans* and the barnacle *Balanus amphitrite*? *Marine Ecology Progress Series*, **192**, 163–172.

Johnson, M.T.J., Vellend, M. & Stinchcombe, J.R. (2009) Evolution in plant populations as a driver of ecological changes in arthropod communities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **364**, 1593–1605.

Johnston, T.A. & Leggett, W.C. (2002) Maternal and environmental gradients in the egg size of an iteroparous fish. *Ecology*, **83**, 1777–1791.

Jorgensen, C., Auer, S.K. & Reznick, D.N. (2011) A model for optimal offspring size in fish, including live-bearing and parental effects. *The American Naturalist*, **177**, E119–E135.

Kaplan, R.H. (1992) Greater maternal investment can decrease offspring surivival in the frog *Bombina orientalis*. *Ecology*, **73**, 280–288.

Keough, M.J. (1984) Effects of patch size on the abundance of sessile marine invertebrates. *Ecology*, **65**, 423–437.

Krist, M. (2011) Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews*, **86**, 692–716.

Leblanc, C.A.L., Benhaim, D., Hansen, B.R., Kristjansson, B.K. & Skulason, S. (2011) The importance of egg size and social effects for behaviour of arctic charr juveniles. *Ethology*, **117**, 664–674.

Marshall, P.A. & Keough, M.J. (1994) Asymmetry in intraspecific competition i the limpet *Cellana tramocerica* (Sowerby). *Journal of Experimental Marine Biology and Ecology*, **177**, 121–138.

Marshall, D.J. & Keough, M.J. (2003) 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. & Keough, M.J. (2004) Variable effects of larval size on post-metamorphic performance in the field. *Marine Ecology Progress Series*, **279**, 73–80.

Marshall, D.J. & Keough, M.J. (2008a) The evolutionary ecology of offspring size in marine invertebrates. *Advances in Marine Biology*, **53**, 1–60.

Marshall, D.J. & Keough, M.J. (2008b) The relationship between offspring size and performance in the sea. *The American Naturalist*, **171**, 214–224.

Marshall, D.J. & Monro, K. (2013) Interspecific competition alters nonlinear selection on offspring size in the field. *Evolution*, **67–2**, 328–337.

Marshall, D.J. & Uller, T. (2007) When is a maternal effect adaptive? *Oikos*, **116**, 1957–1963.

Marshall, D.J., Heppell, S., Munch, S.B. & Warner, R.R. (2010) The relationship between maternal phenotype and offspring quality: do older mothers really produce the best offspring? *Ecology*, **91**, 2862–2873.

Martin, R.A. & Pfennig, D.W. (2010) Maternal investment influences expression of resource polymorphism in amphibians: implications for the evolution of novel resource-use phenotypes. *PLoS ONE*, **5**, e9117.

McGhee, K.E., Pintor, L.M., Suhr, E.L. & Bell, A.M. (2012) Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined stickleback. *Functional Ecology*, **26**, 932–940.

McGinley, M.A., Temme, D.H. & Geber, M.A. (1987) Parental investment in offspring in variable environments: theoretical and empirical considerations. *The American Naturalist*, **130**, 370–398.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. (2005) A brief history of seed size. *Science*, **307**, 576–580.

Mousseau, T.A. & Dingle, H. (1991) Maternal effects in insect life histories. *Annual Review of Entomology*, **36**, 511–534.

Okamura, B. (1984) The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryzoa. I. *Bugula stolonifera* Ryland, an aborescent species. *Journal of Experimental Marine Biology and Ecology*, **83**, 179–193.

Palmer, A.R. (1990) Predator size, prey size and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology*, **71**, 759–775.

Parker, G.A. & Begon, M. (1986) Optimal egg size and clutch size - effects of environment and maternal phenotype. *The American Naturalist*, **128**, 573–592.

Pfennig, D.W. & Martin, R.A. (2009) A maternal effect mediates rapid population divergence and character displacement in spadefoot toads. *Evolution*, **63**, 898–909.

Post, D.M., Palkovacs, E.P., Schielke, E.G. & Dodson, S.I. (2008) Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology*, **89**, 2019–2032.

Quinn, G.P. & Keough, M.J. (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK.

Rivest, B.R. (1983) Development and the influence of nurse egg allotment on hatching size in *Searlesia dira* (Reeve, 1846) (Prosobranchia: Buccinidae). *Journal of Experimental Marine Biology and Ecology*, **69**, 217–241.

Sakai, S. & Harada, Y. (2001) Why do large mothers produce large offspring? Theory and a test. *The American Naturalist*, **157**, 348–359.

Segers, F. & Taborsky, B. (2011) Egg size and food abundance interactively affect juvenile growth and behaviour. *Functional Ecology*, **25**, 166–176.

Sellheim, K., Stachowicz, J.J. & Coates, R.C. (2010) Effects of a nonnative habitat-forming species in mobile and sessile epifaunal communities. *Marine Ecology Progress Series*, **398**, 69–80.

Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of offspring. *The American Naturalist*, **108**, 499–506.

Stanton, M.L. (1984) Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology*, **65**, 1105–1112.

Sutherland, J.P. (1974) Multiple stable points in natural communities. *The American Naturalist*, **108**, 859–873.

Thorson, G. (1936) The larval development, growth and metabolism of arctic marine bottom invertebrates compared with those of other seas. *Meddelelser om Grønland*, **100**, 1–155.

Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 10854–10861.

Wade, M.J. (1998) The evolutionary genetics of maternal effects. *Maternal Effects as Adaptations*, (eds T.A. Mousseau & C.W. Fox), pp. 5–21. Oxford University Press, Oxford.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M., *et al.* (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 559–573.

Wolf, J.B. & Wade, M.J. (2001) On the assignment of fitness to parents and offspring: whose fitness is it and when does it matter? *Journal of Evolutionary Biology*, **14**, 347–356.

Received 14 April 2013; accepted 9 August 2013
Handling Editor: Jean Clobert

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Summary of the mean size of offspring (mm^2) for each size class of *Watersipora subtorquata* offspring used for each experimental run.

Appendix S2. Effects of offspring size on colony morphometrics in *Watersipora subtorquata*.

Appendix S3. ANOVA models of effects of offspring size, density and experimental run on community summary metrics after 2 weeks in the field.

Appendix S4. Summary table of interactions and main effects of the covariate free space on key response variables.