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# Dispersal duration mediates selection on offspring size

**Karin Svanfeldt, Keyne Monro and Dustin J. Marshall**

*K. Svanfeldt (karin.svanfeldt@monash.edu), K. Monro and D. J. Marshall, Centre of Geometric Biology/School of Biological Sciences, Monash University, Victoria 3800, Australia.*

Offspring size varies at all levels of organisation, among species, mothers and clutches. This variation is thought to be the result of a tradeoff between offspring quality and quantity, where larger offspring perform better but are more costly to produce. Local environmental conditions alter the benefits of increased offspring size and thereby mediate selection on this trait. For sessile organisms, dispersal is a crucial part of the offspring phase, and in animals, bigger offspring tend to better endure longer dispersal distances than smaller offspring because they have more energy. Theory predicts that increasing distances between suitable habitats strengthens selection for larger offspring. We manipulated the dispersal duration of offspring of different sizes in the bryozoan *Watersipora subtorquata* and then examined the relationship between offspring size and post-metamorphic performance in the field. We found that selection on offspring size is altered by larval experience. Larger offspring had higher post-settlement performance if the larval period was short but, contrary to current theory, performed worse when the larval period was extended. The reversal of the relationship between offspring size and performance by extending the larval phase in *Watersipora* may be due to the way in which offspring size affects growth in this species. Regardless of the mechanism, it appears that experiences in one life-history stage alter selection on offspring size in another stage, even when they occupy identical habitats as adults.

Offspring size is a highly variable trait that has pervasive consequences across the life history (Thorson 1950, Bagenal 1969, Stearns 1992). Variation in offspring size occurs at all levels of organisation: among species, but also within species, mothers and clutches (Williams 1994, Marshall and Keough 2008). The size of individual propagules is often linked to fitness – generally, larger offspring perform better than smaller offspring (Smith and Fretwell 1974, McGinley et al. 1987). However, it can be more costly to produce larger offspring, therefore mothers must trade off the size and number of offspring that they produce, from few larger offspring to many smaller offspring (Vance 1973a, b, Smith and Fretwell 1974, Marshall and Uller 2007).

While many studies support the assumption that larger offspring perform better, an increasing number of studies have shown that the relationship between offspring size and performance is highly context-dependent. Environmental variation has the potential to alter both the strength and direction of the offspring size–fitness relationship Kaplan 1992, Benton et al. 2005, (Bashey 2006, Marshall et al. 2006, Sams et al. 2015). If large, costly offspring and small, less-costly offspring have similar levels of fitness in a given environment, selection should favour mothers producing many small offspring. Conversely, if smaller offspring perform poorly relative to larger offspring in a given environment, mothers benefit from producing fewer, larger offspring (Geritz 1995, Geritz, et al. 1999). A generally-held hypothesis is therefore that the offspring size–fitness relationship is determined by local environmental conditions (Fox 1997, Allen et al. 2008). Even slight changes in these conditions could alter the offspring size–fitness relationship (Bashey 2006, Gagliano et al. 2007, Marshall and Keough 2008), and studies have shown that mothers can alter offspring size in response to changes in the environment (Fox 1997, Bertram and Strathmann 1998, Marshall et al. 2000, Allen et al. 2008). While the role of environmental variation in altering the offspring size–performance function is well recognised, the potential for other factors to alter this key relationship remains unexplored. Most importantly, the role of dispersal in altering the offspring size–performance relationship is largely unresolved.

For sessile species, a crucial function of the offspring phase is dispersal (Massot et al. 2002, Stamps et al. 2005, Bonte et al. 2012). Dispersal for most plant species is a passive process where offspring are dispersed by the wind. In general, smaller seeds have greater dispersal potential, due to increased aerodynamics (Howe and Smallwood 1982, Levin and Muller-Landau 2000). Furthermore, producing smaller seeds presumably allows mothers to produce more seeds, and through sheer weight of numbers, disperse further and to more sites (Geritz 1995). In contrast to terrestrial plants, dispersal for most sessile marine invertebrates can be particularly costly (Woollacott et al. 1989, Marshall et al. 2003a, b). For species that have a nonfeeding larval phase, as is the case for more than 50% of coastal marine invertebrates (Marshall et al. 2012), the larval phase incurs energetic costs as well as an elevated risk of mortality. Nonfeeding larvae are dependent on maternally invested energy reserves until they complete metamorphosis, and across a wide range of phyla, nonfeeding individuals that experience an extended larval period have poorer performance after metamorphosis, likely caused by depletions in their energy stores (Pechenik et al. 1998, Marshall and Keough 2003, Bennett and Marshall 2005, Pechenik 2006, Elkin and Marshall 2007). Generally, larger larvae disperse for longer and are thought to be better able to cope with extensions of the larval period (Marshall and Keough 2003, Dias and Marshall 2010, Burgess et al. 2013, Marshall and Steinberg 2015, Pettersen et al. 2015). Thus, it is clear that offspring size can affect dispersal in marine invertebrates (Marshall and Keough 2003). What is less clear is whether dispersal can affect selection on offspring size.

We have good reasons to suspect that dispersal will alter selection on offspring size. For instance, if larger offspring are better able to disperse, then greater distances between suitable habitats should favour the production of larger offspring (Burgess et al. 2013). Furthermore, recent physiological studies suggest that larger offspring are better able to withstand the energetic stress of a prolonged dispersal phase because they have lower mass-specific energy requirements than smaller offspring (Pettersen et al. 2015). Though scarce, studies of offspring size, dispersal and performance suggest that dispersal can alter selection on offspring size. In a relatively recent study, Burgess et al. (2013) predicted that mothers producing many small offspring should be favoured if the distances between suitable habitats were short, but increasing habitat spacing causes changes in selection to favour larger offspring. In the same study, this theory was empirically tested and supporting evidence was found on the bryozoan *Bugula neritina*, where the post settlement survival of smaller offspring decreased compared to bigger offspring if the dispersal period was extended. Whereas Burgess et al. (2013) conclude that offspring size provisioning impact the potential for dispersal, they also acknowledge that for a more general understanding of the offspring size and habitat spacing relationship, further investigations in additional species are needed. Here, we experimentally prolonged the length of the dispersal phase of offspring of known size in the encrusting bryozoan *Watersipora subtorquata*, and then monitored the performance of these individuals in the field, from settling to late life adult stages. We monitored performance as post-metamorphic survival, area and senescence of each individual for three months in the field.

# Methods

## Study species

*Watersipora subtorquata* is an encrusting, bright red bryozoan found in shallow waters of temperate and subtropical regions, and is an invasive, but now common member of the sessile marine communities of the south coast of Australia (Marshall and Keough 2009). Like all bryozoans, *Watersipora* forms colonies by asexual budding. Dispersal and new settlement is initialized by sexual reproduction where nonfeeding, free-swimming larvae are released into the water column. After dispersal, permanent attachment to suitable surfaces usually takes place within a few hours after release provided suitable settlement surfaces are available, but the larval period can extend for as long as 15 h (Marshall and Keough 2003, 2004). During dispersal, there are two typical larvae behaviours: passive surface exploring and active swimming (Burgess et al. 2009). Whilst actively swimming, it is likely that the energy expenditure of larvae is excessively higher than in the more passive behaviour, exploring, as shown empirically for other marine invertebrate larvae (Bennett and Marshall 2005). Once settled, the individual metamorphoses (an energetically expensive process; Pettersen et al. 2015), and the first zooid, the ancestrula, begins to feed. Colony growth occurs via asexual budding of daughter zooids. The initial budding rate is offspring size-dependent, where bigger settlers faster produce more buds (Marshall and Keough 2004). With time, older zooids at the centre of the colony lose their red hue, senesce and die, while growth and reproduction continue in younger zooids at the colony margin (Hart and Keough 2009, Marshall and Monro 2013).

## Species collection and spawning

The study was conducted from autumn to spring 2013 at Royal Brighton Yacht Club, Port Phillip Bay, Australia (37°54′29.9″S, 144°58′52.4″E).We collected *Watersipora* colonies from St Kilda Pier (37°51′50.3″S, 144°57′56.7″E), which is situated within Port Phillip Bay, and is located about 4.5 km from our field site at the Royal Brighton Yacht Club. We brought the colonies to the laboratory within insulated aquaria, and kept them in constant darkness for two days before exposing them to light to induce them to spawn brooded larvae (Marshall and Keough 2004). We collected and pooled spawned larvae from all collected colonies, and either allowed the larvae to settle immediately following release (undelayed treatment), or delayed their settlement while keeping the larvae actively swimming for 2 h (delayed treatment) representing a moderate dispersal stress. For the delayed treatment, larvae were placed in sample jars with filtered seawater under constant light exposure and placed on a mechanical roller, which gently rolled the jars and forced larvae to continue swimming. Throughout the spawning period (~30 min), we took care to allocate larvae to both treatments continuously. The delay method resulted in ~20% mortality. After the appropriate larval duration (0 and 2 h for undelayed and delayed treatments, respectively), we settled the larvae in seawater droplets on pre-roughened PVC plates (10 × 10 cm). All larvae were allowed approximately 3 h in darkness to settle within seawater drops before unsettled larvae were discarded. Whereas settlement success for delayed larvae was nearly 90%, non-delayed larvae settled with a success of 60%. This pattern matches expectations regarding the 'desperate larvae' hypothesis for non-feeding larvae – younger larvae tend to reject low quality settlement sites while older larvae settle more indiscriminately (Marshall and Keough 2003). Post-settlement, our experimental setup consisted of in total 90 undelayed settlers and 86 settlers that had experienced an extended larval phase. Offspring size was estimated from measurements of the first zooids (ancestrulae), where the average of offspring size in this study measured 0.22 mm$^2$ (SD = 0.06). In comparison, *Watersipora* offspring in a study by Marshall and Keoug (2003) measured on average 0.17 mm$^2$.

### Deployment and monitoring

We deployed the experiments by haphazardly allocating the PVC plates to PVC backing panels and submerging panels at ~1.5 m depth at our field site, Royal Brighton Yacht Club. In total, the experiment consisted of four panels, each holding 16 plates, with one *Watersipora* settler per plate. Though the final numbers of each treatment varied slightly across each run (due to the varying pre-settlement survival and settlement success), we took care to allocate settlers from both treatments as evenly as possible on each backing panel. We photographed all plates weekly in the field, and from the photos, survival, colony area and area of senescence were measured in ImageJ software (available at <http://imagej.net>). Survival was measured as presence or absence of vivid (red) zooids, colony area, and senescence as proportional area of grey zooids that had lost their species characteristic red colour (Marshall and Monro 2013). To keep our field conditions realistic, we let sessile communities from natural colonisation form on the plates around the *Watersipora* colonies during the course of the experiment. Nevertheless, we could track our focal colonies, initially from pen circles around them and later on from their positions on the plates. We replicated the experiment three times, which we refer to here as runs. The difference in initiation time between each run was one week, and in total, 176 individuals with known size and known larval experience were deployed, whereof 91 experienced no delay in metamorphosis and 85 experienced a delay of 2 h before metamorphosis could initiate.

### Data analysis

Throughout the three replicate runs of our experiment, we appeared to have a higher representation of larger larvae in the delayed treatment compared to the undelayed treatment. There are both biological and statistical implications of having a different covariate range represented. From a statistical perspective, it may be inappropriate to compare slopes across the entire covariate range when one treatment is not represented across that range. We believe that the most conservative approach in our case is to truncate the data so that the ranges overlap. We did so excluding all offspring smaller than 0.136 mm$^2$, and re-ran all of our analysis. Truncating the data did not affect the directions or significance of our results, and therefore we present the un-manipulated data set including all offspring sizes. All our analyses were run in SAS ver. 9.4 software and individual settlers were the units of replication.

To examine the effect of delayed settlement on survival, we used repeated logistic binary regression. Offspring size, delay-treatment and time were modelled as fixed effects and panel was modelled as random. When running our model through repeated measures, all of our time points in the same data set would not converge. Instead, we ran the data from early stage colonies and late stage colonies separately. Therefore, the model was repeated through time for early stage colonies (week 2, 3, 4 and 5 in the field) and late stage colonies (week 10, 11, 12 and 13 in the field). To reduce the full model to the simplest model that best fit our data, we performed log-likelihood ratio tests. However, we had difficulties in fitting time and the interactions with time which led to abnormalities in our reduction of singled-out main effects. To include all main effects, we therefore instead present the F-test of our analysis on survival.

To examine the effect of offspring size and delay treatment on colony area, we used repeated linear mixed-effect model (fitted using ML). For the mixed model, offspring size, delay-treatment and time were modelled as fixed effects (continuous, categorical and categorical respectively). Panel was modelled as random effect. As with our survival analysis, our model would not converge when fitted through all time points. Instead, early (week 2, 3, 4 and 5) and late (week 10, 11, 12 and 13) stage colonies were analysed separately. As the random effect was simply an experimental convenience, we reduced the models according to Quinn and Keough (2002), using likelihood ratio tests and then tested each parameter separately in the finalised model by reducing them one by one and then adding them back to the model.

The effects of offspring size, delay treatment and time on percentage of colony senescence were analysed on late stage colonies (week 10, 11, 12 and 13 in the field) using linear mixed model (fitted through ML). Offspring size, delay treatment and time were modelled as fixed effects and panel was modelled as random. Once again, the random effect was simply experimental conveniences and the model was reduced according to Quinn and Keough (2002) using likelihood ratio tests. The effects of each parameter in the final model was then tested separately by reducing them on by one and then adding them back to the mode.

### Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.71121> (Svanfeldt et al. 2016).

## Results

As mentioned in our methods section, we observed a difference in settlement success between our two delay treatments, where delayed larvae settled at a higher rate (about 90%) than undelayed larvae (about 60%). Our delay treatment also resulted in some mortality (about 20%). Whereas it is very unlikely that sizes between the larvae assigned to each treatment would have varied (since they were collected simultaneously from the same cohorts), we did have offspring size differences between our treatments after settlement, with a higher representation of smaller larvae in our non-delayed treatment.

We found that in the treatment where larvae were not delayed, survival in the early stage weeks (week 2 to week 5 in the field) was higher for larger than for smaller larvae. In the treatment where metamorphosis was delayed, there was no apparent relationship between offspring size and early stage colony survival (Table 1, Fig. 1). However, in the delayed treatment, there was also a lack in representation of smaller offspring, possibly due to the loss of larvae prior to settling. For later stage colonies (week 10–13 in the field), we

Table 1. Effects of offspring size, delay treatment and time on the survival of early-stage colonies from week 2 to week 5 in the field. Significant effects are presented in bold.

| Colony survival, test of fixed effects, early stage colonies | | | | | |
|---|---|---|---|---|---|
| Effect | DF | $\chi$ | F | Pr > $\chi^2$ | Pr > F |
| offspring size | 1 | 1.9 | 1.9 | 0.17 | 0.17 |
| delay | 1 | 2.6 | 2.6 | 0.10 | 0.10 |
| time | 3 | 15.6 | 5.2 | **0.00** | **0.00** |
| offspring size × delay | 1 | 4.3 | 4.3 | **0.04** | **0.04** |

Table 2. Effects of offspring size, delay treatment and time on the survival of late-stage colones from week 10 to week 13 in the field. No effects were significant.

| Colony survival, test of fixed effects, late stage colonies | | | | | |
|---|---|---|---|---|---|
| Effect | DF | $\chi$ | F | Pr > $\chi^2$ | Pr > F |
| offspring size | 1 | 3.4 | 3.4 | 0.07 | 0.07 |
| delay | 1 | 0.3 | 0.3 | 0.62 | 0.62 |
| time | 3 | 6.9 | 2.3 | 0.07 | 0.07 |
| offspring size × delay | 1 | 0.4 | 0.4 | 0.53 | 0.53 |

found no effects of delay treatment, offspring size or time on survival (Table 2).

Colony area in our early stage colonies (week 2–5 in the field) increased with offspring size if metamorphosis had not been delayed. If metamorphosis had been delayed, there was initially, at week 2 and 3, no difference in colony area depending on offspring size. At week 4 and 5 for colonies from delayed offspring, colony area decreased with offspring size (Table 3, Fig. 2). For early stage colonies, we also found a significant blocking effect by panel. At late stages of colony development (week 10, 11, 12 and 13 in the field), the effect of offspring size and delay treatment on colony area had faded and we found no significant effect of these effects at this stage. Throughout the late life development though, colonies that were delayed as offspring were larger as adults than colonies that were not delayed as offspring (Table 4, Fig. 3).

Neither offspring size nor delay treatment had any effect on colony senescence at our late stage colonies (week 10 to 13 in the field). What we found was merely that the percentage of senesced zooids within colonies increased slightly over time and had a significant blocking effect by panel (Table 5).

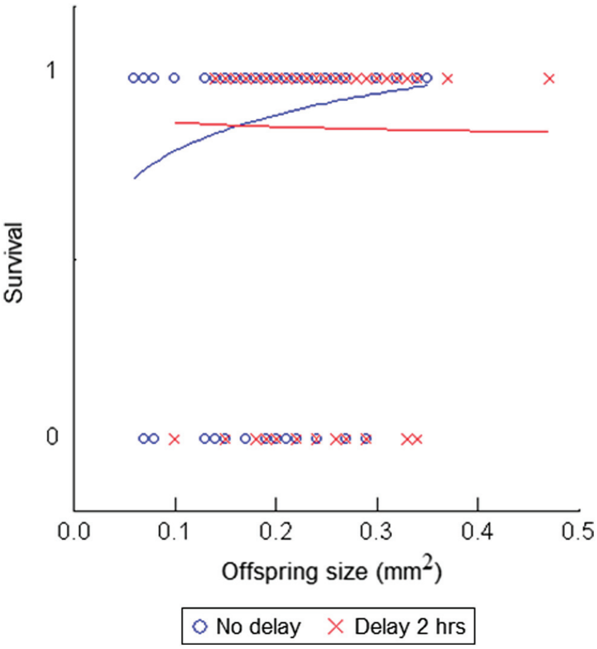

Figure 1. Effects of offspring size and delay treatment on survival for early stage colonies, week 2 to 5 in the field, where 1 represents colonies alive and 0 represents dead colonies. Each dot represents a single colony, where non-delayed colonies are shown in blue and delayed colonies are shown in red. Whereas colony survival for early stage colonies increases with offspring size uin the non delayed treatment, there is no apparent difference in survivala of early stage colonies in the delayed treadment.

## Discussion

While it has long been recognised that selection on offspring size is context-dependent (Kaplan 1992, Benton et al. 2005, Bashey 2006, Marshall et al. 2006, Sams et al. 2015), few studies have shown that events in one life-history stage alter selection in another stage (Crean et al. 2011, Burgess et al. 2013). We show that the length of the dispersal period prior to metamorphosis alters selection on offspring size, even if individuals experience identical conditions as adults. Our results suggest that not only does the habitat in which individuals find themselves affect selection on offspring size, but also the experience of offspring prior to habitat selection. This serves to be an emerging pattern in marine systems, where there is a link between the length and nature of the dispersal period, and subsequent dynamics of the adult phase (Shima and Swearer 2010, Marshall and Morgan 2011).

We found that the relationship between offspring size and fitness depends on offspring experience. Whereas survival and colony area for early stage adults increased with offspring size if the dispersal phase was short, colonies that had experienced a longer dispersal phase showed no relationship between offspring size and survival. More surprisingly, we found that for colonies that had experienced a longer dispersal phase, their size early in adult stage actually decreased with increased offspring size. Also, at later life stages, colonies that experienced delayed metamorphosis as offspring had larger areas than colonies that had experienced no delay. It is worth nothing, though, that our dispersal duration of two hours only shows the impacts of mild dispersal stress in *Watersipora*, and that both shorter and longer dispersal durations may have affected the offspring differently.

Table 3. Effects of offspring size, delay treatment, time and panel on the area of early-stage colonies from week 2 to week 5 in the field. Significant effects are presented in bold.

| Colony area early weeks | | | |
|---|---|---|---|
| Term tested | $\chi$ | DF | p |
| panel | 6.4 | 1 | **0.01** |
| offspring size × delay | 8.3 | 1 | **0.00** |
| delay × time | 3.9 | 3 | 0.27 |
| offspring size | 18.8 | 1 | **0.00** |
| delay | 4.8 | 1 | **0.03** |
| time | 138 | 3 | **0.00** |

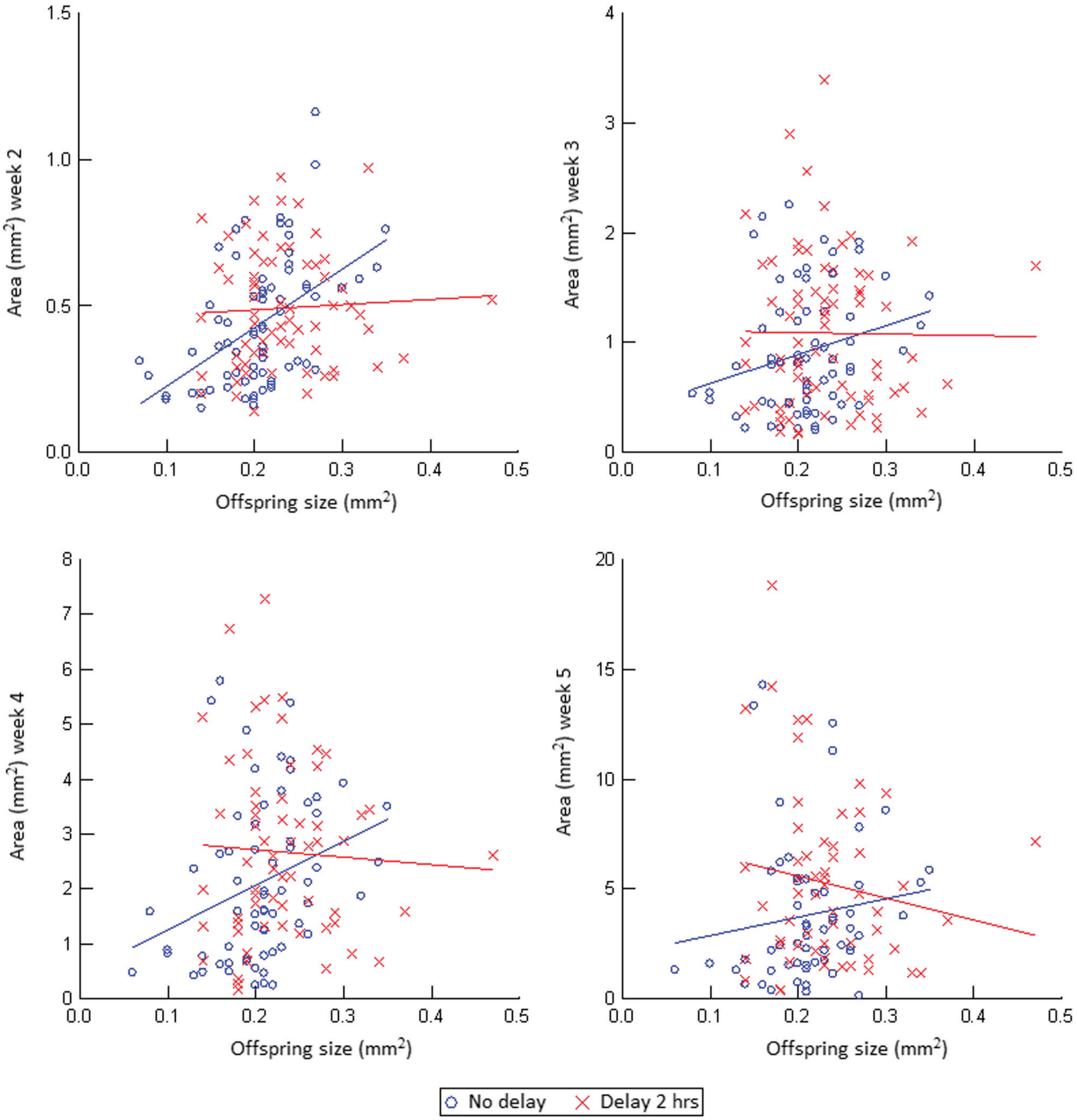

Figure 2. Effects of offspring size and delay treatment on area for early stage colonies at week 2, 3, 4 and 5 in the field. Each dot represents a single colony, where non-delayed colonies are shown in blue and delayed colonies are shown in red. Whereas colony area increased with offspring size at all weeks in the non-delayed treatment, colony area at week 2 and week 3 showed no difference due to initial offspring size in the delay treatment. At week 4 and week 5 in the delay treatment, colony area decreased with offspring size.

Burgess et al. (2013) found that when the dispersal period of a bryozoan with a similar life history, *Bugula neritina*, is extended, there is selection for larger offspring size. Burgess's findings have intuitive appeal for three reasons: dispersal is costly for nonfeeding offspring (Strathmann 1985, Bennett and Marshall 2005), larger offspring are released with more energy, and larger offspring use proportionally less energy during dispersal than smaller offspring (Pettersen et al. 2015). These three criteria also apply to our study species, *Watersipora*, but we found the reverse pattern to Burgess: colonies that were larger as offspring perform initially worse when they experience an extended dispersal period.

We were also slightly surprised that neither offspring size nor delay treatment had any effect on colony senescence. In other senescing species, such as plants, senescence acts as an energetic budgeting system, where the organism

Table 4. Effects of offspring size, delay treatment and time on the area of late-stage colonies from week 10 to week 13 in the field. Significant effects are presented in bold.

| Colony area late weeks | | | |
|---|---|---|---|
| Term tested | χ | DF | p |
| delay × time | 7.8 | 3 | **0.05** |
| offspring size | 0.3 | 1 | 0.58 |
| delay | 7.6 | 1 | **0.01** |
| time | 90 | 1 | **0.00** |

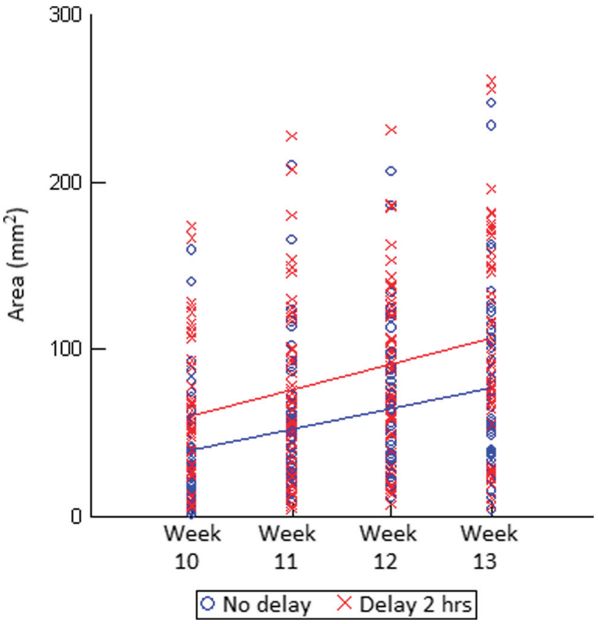

Figure 3. Effects of delay treatment over time on area for late stage colonies at week 10, 11, 12 and 13 in the field. Each dot represents a single colony, where non-delayed colonies are shown in blue and delayed colonies are shown in red. For all weeks, colony area was greater for colonies in the delay treatment than colonies in the non-delay treatment.

by reabsorption have the ability to redistribute energy and nutrients from ineffective modules in order to enhance performance in vivid and more useful units (Vitousek 1982, Aerts 1996, Eckstein et al. 1999).We suspected that if the initial energy and/or energy expenditure would affect the adult colony area, it would also show as differences in colony senescence as faster growing colonies, according to studies on plants (Ryser 1996), would have higher turnover rates and thus more senescence. Little is still known about why and how marine invertebrates senesce. That we found no evidence for a link between experience in the larval phase and senescence, even though larval experience affected colony area, may not necessarily mean that senescence is acting very differently in marine invertebrates than in plants. After all, our results showed effects on early stage adult area of colonies, but these effects seemed to have faded over time and disappeared in later stage colonies. Since senescence does not occur until later life stages, potential effects of our treatments that could have affected senescence may therefore no longer be noticeable for our *Watersipora* colonies. More interesting though, were the effects of offspring size and dispersal duration on colony survival and area – that a prolonged dispersal phase should favour smaller offspring sizes. There could be a few reasons for our unexpected findings, and we will discuss them each separately.

Table 5. Effects of offspring size, delay treatment, time and panel on the senescence of early-stage colonies from week 2 to week 5 in the field. Significant effects are presented in bold.

| Colony senescence %, late weeks | | | | |
|---|---|---|---|---|
| Term removed | –2LL | χ | DF | p |
| panel | 2183.0 | 23.0 | 3 | **0.00** |
| offspring size × delay × time | 2161.9 | 2.0 | 3 | 0.57 |
| offspring size × delay | 2162.2 | 0.3 | 1 | 0.58 |
| offspring size × time | 2164.9 | 2.7 | 1 | 0.10 |
| delay × time | 2166.2 | 1.3 | 3 | 0.73 |
| offspring size | 2167.1 | 0.9 | 1 | 0.34 |
| delay | 2167.1 | 0.0 | 1 | 1.00 |
| time | 2176.0 | 8.9 | 3 | **0.03** |

First, in our two delay treatments, we had differences both in settlement success and in the distribution of offspring sizes. Since the larvae assigned to each treatment were pooled cohorts from the same mothers, it is very unlikely that the offspring size differed by chance alone. Rather, we suspect that we differentially 'lost' smaller larvae in the delay treatment both during the treatment and at settlement. Previous studies show that smaller *Watersipora* larvae tend to settle indiscriminately sooner than larger larvae (Marshall and Keough 2003). In addition, larger larvae in our treatment that were not delayed may have rejected the settlement substrate, since larger *Watersipora* larvae tend to remain choosier longer before settlement (Marshall and Keough 2003). Regardless, whether the size difference between our two treatments depended on selection for large delayed larvae or small non-delayed larvae, similar processes will operate under field conditions. From a biological perspective, our results also imply that the smaller larvae that did persist through the delay process are a non-random subset – perhaps of higher quality in dimensions other than offspring size. In contrast, the larger larvae did not appear to go through this selection for other quality axis. That stressful conditions during the dispersal phase can lead to selection for higher performing offspring has also been shown in previous studies (Hamilton et al. 2008), and may explain some of the counter-intuitive findings in our delay treatment where smaller offspring appeared to better cope with stress, and also that colonies that were delayed as offspring performed better later in life than colonies that had not been delayed.

The poor growth of larger offspring in our delay treatment may also be the result of early growth patterns of *Watersipora.* Previous studies show that the initial growth strategy of *Watersipora* depends on offspring size (Marshall and Keough 2004). Following metamorphosis into the first feeding zooid (the ancestrula), *Watersipora* grows by asexual budding of new daughter zooids. These daughter zooids take days to begin feeding, and as such, they are initially dependent on resources supplied by the ancestrula. Ancestrulae originating from larger offspring tend to bud sooner after metamorphosis and produce more buds than ancestrulae from smaller offspring (Marshall and Keough 2004). This has also been observed in other marine invertebrate species (Marshall et al. 2003a, b). Thus, young colonies that come from larger offspring have a lower feeding-zooid: developing-zooid ratio and therefore higher energy demands than young colonies from smaller larvae. Initial differences in budding rate of different sized offspring can have persistent effects on colony size throughout the life-history (Marshall and Keough 2008), which potentially explains the faster growth of *Watersipora* colonies from larger offspring relative to smaller offspring. Presumably, ancestrulae from larger offspring can sustain a higher initial budding rate because they have more resources than smaller offspring. However, if the larval period is extended and larval resources are depleted, then the low ratio of feeding zooids versus developing zooids that is typical of colonies from larger offspring may not be sustainable, such that performance is greatly reduced. Studies show that larval swimming does not change the relationship between offspring size and budding rate; larger offspring invariably produce ancestrulae with higher budding rates than smaller offspring (Marshall and Keough 2004, 2006). In other words, larger offspring create early colonies that depend heavily on initial resources to supply a larger number of developing zooids. However, if larval resources are depleted by extending the larval period (i.e. swimming time), then a higher budding rate may become unsustainable, resulting in lower colony performance overall.

Another explanation for why extending the dispersal period changes the relationship between offspring size and post-metamorphic performance is that offspring size also affects larval energy budgets in *Watersipora*. Larger larvae tend to engage in active swimming more than smaller larvae, whereas smaller larvae spend 500% more time exploring settlement surfaces than swimming in the water column (Burgess et al. 2009). Furthermore, as larval duration increases, larger larvae tend to maintain active swimming for longer than smaller larvae (Burgess et al. 2009). Given that *Watersipora* larvae are negatively buoyant and must actively avoid sinking, larger larvae that engage in active swimming for longer than smaller larvae are likely to consume more energy. Unfortunately, metabolic rates in *Watersipora* larvae have only been estimated for very young larvae (Pettersen et al. 2015). We currently have no estimates for how delayed settlements may alter the metabolic rate of larvae, but this is an important next step to completely understand the connection between the pre- and post-metamorphic life stages for *Watersipora*.

Regardless of the mechanism driving the change in relationship between offspring size and performance, the fact that dispersal duration alters the offspring size–performance relationship has implications for selection on offspring size in this system. As noted earlier, selection on offspring size is driven by the relative benefits of producing larger offspring that perform better, or producing smaller, more numerous offspring (Vance 1973a, b, Smith and Fretwell 1974). If different offspring sizes perform equally well, selection favours mothers that produce smaller offspring, since they then can produce more of them (Geritz 1995, Geritz et al. 1999). We found that post-settlement, larger offspring perform initially worse than smaller offspring when the dispersal period is extended. Therefore, this presents a double cost in producing larger offspring if they must disperse for extended periods, since they are more expensive to make and have lower post-metamorphic fitness. Increasing distances between suitable habitat patches, which requires increased dispersal from the natal environment, should therefore select for the production of smaller offspring in *Watersipora*. However, we also found that smaller offspring have higher early life mortality, and that very small offspring sizes may not last during dispersal. With these findings, we have shown that the length of the dispersal period prior to metamorphosis alters the phenotypic selection on offspring size, even if individuals experience the same environment as adults. While it has long been recognised that selection on offspring size is context-dependent, it is rarely shown that events in one life-history stage alter selection in another stage of the life-history.

Dispersal for sessile species is ubiquitous but costly (Bélichon et al. 1996, Baguette and Van Dyck 2007, Bonte et al. 2012). That dispersal processes impose strong selection on life histories is clear – though it is less clear whether dispersal per se is the target of selection or the product of selection on other traits. In this study, we show that dispersal has manifold consequences for selection on the key trait of offspring size. Factors that extend or reduce the dispersal phase will alter selection on offspring size with cascading and pervasive consequences for fitness throughout the life history. Our findings contradict previous studies that showed extending the dispersal period creates stronger selection for larger offspring – instead we find ambivalent effects. If we are to make broader generalisations about how dispersal mediates selection on offspring size, then further tests of how dispersal affects the relationship between offspring size and fitness are necessary.

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