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Costs of dispersal alter optimal offspring size in patchy habitats: combining theory and data for a marine invertebrate

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Summary

1. Much of the theory on offspring size focuses on the effects of habitat quality on the relationship between offspring size and fitness. Habitat spacing may be another important factor that affects selection on offspring size when offspring disperse prior to colonization and accrue deferred costs that are mediated by offspring size.

2. We developed a theoretical model, based on a well-known optimality model, of how selection on offspring size changes with dispersal distance. The model assumes that offspring fitness depends on both offspring size and dispersal duration and that dispersal time and distance are positively related. Such assumptions are based on thousands of marine invertebrate species with non-feeding larvae, but our model also applies more generally to any organism where offspring size modifies the energetic costs of dispersal, and there is a positive relationship between dispersal duration and distance.

3. Our model predicts that, even when habitat quality does not vary, more isolated habitats may favour the production of fewer, larger offspring if smaller offspring incur greater deferred costs of dispersal. We then empirically demonstrate that offspring size and dispersal duration have interactive effects on post-settlement survival in a marine invertebrate (*Bugula neritina*), and such size-dependent deferred costs of dispersal are of a magnitude sufficient enough to potentially favour larger offspring in isolated habitats.

4. Together, our results indicate that the spatial pattern of suitable habitat could impose very different selective regimes on offspring size compared with the effects of habitat quality. Furthermore, our predictions contrast to those predicted for seed size and dispersal in plants, where the production of smaller, more numerous seeds is often a more efficient way for mothers to access distant, suitable habitat.

Key-words: dispersal, habitat fragmentation, offspring size, reproductive strategies, size–number trade-off, spatial dynamics

Introduction

Offspring size is one of the most important and well-studied life-history traits (Stearns 1992; Bernardo 1996). Increasing investment in individual offspring generally increases offspring fitness, but does not always increase maternal fitness (Wolf & Wade 2001). Because maternal resources available for reproduction are limited, investing more resources per offspring can reduce maternal fecundity. Thus, mothers are thought to produce fewer, larger offspring or more numerous, smaller offspring. The optimal balance between the size and number of offspring is determined by the shape of the relationship between offspring size and fitness (Vance 1973; Smith & Fretwell 1974). It follows then that in environments where large and small offspring have similar fitness, mothers benefit from producing many (and hence smaller) offspring. While there are many models examining offspring size (e.g. Vance 1973; Smith & Fretwell 1974; Cohen & Motro 1989; Geritz, Meijden & Metz 1999; Levin & Muller-Landau 2000), all share the same basic features: a trade-off

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between the size and number of offspring and some relationship between offspring size and fitness.

The crucial relationship between offspring size and fitness is thought to depend primarily on the quality of the habitat that offspring experiences (e.g. McGinley, Temme & Geber 1987; Fox, Thakar & Mousseau 1997; Allen, Buckley & Marshall 2008; Fischer, Taborsky & Kokko 2010). A variety of habitat conditions affect the relationship between offspring size and fitness including food availability (Bashey 2006), intraspecific competition (Allen, Buckley & Marshall 2008), herbivory (Agrawal 2001), predation (Allen 2008), temperature (Fischer *et al.* 2003a) and pollution (Hendrickx *et al.* 2003). For example, larger offspring of the seed beetle, Stator limbatus, have higher fitness than smaller offspring on seeds that are more resistant to boring (Fox, Thakar & Mousseau 1997). Selection should therefore favour mothers that provision their offspring according the habitat their offspring are likely to encounter (Parker & Begon 1986; McGinley, Temme & Geber 1987; Garcia-Dorado 1990; Geritz 1995; Fox, Thakar & Mousseau 1997; Einum & Fleming 2004; Marshall & Keough 2008a; Fischer, Taborsky & Kokko 2010), and indeed, an increasing number of studies have shown that mothers change the size of their offspring in response to changes in habitat type (Fox, Thakar & Mousseau 1997; Fischer, Brakefield & Zwaan 2003b; Allen, Buckley & Marshall 2008).

While the habitat dependence of the offspring size–fitness relationship is increasingly well recognized, the spatial pattern of habitat itself could impose very different selective regimes on offspring size compared with the effects of habitat quality. In many species, offspring disperse away from their parents as seeds, eggs, larvae or juveniles, and mothers can influence the dispersal potential of their offspring in a number of ways (Massot *et al.* 2002; Stamps 2006; Bonte, Van Belle & Maelfait 2007; Rubio de Casas, Willis & Donohue 2012). In plants, for example, competition or predation on seedlings near parents can cause selection for mothers to produce seeds that disperse further away (Augspurger 1986; Ganeshaiah & Shaanker 1991; Greene & Johnson 1993; Westoby, Leishman & Lord 1996; Geritz, Meijden & Metz 1999; Levin & Muller-Landau 2000; Parciak 2002a,b). Smaller seeds often travel further in wind (Ganeshaiah & Shaanker 1991; Greene & Johnson 1993) or via animals (Parciak 2002a,b), generating a negative relationship between offspring size and dispersal distance. Furthermore, because of the increased fecundity of producing small seeds, decreasing seed size may also allow offspring to reach a greater number of sites (Augspurger 1986; Greene & Johnson 1993). Smaller seeds, however, can also have relatively lower establishment success than larger seeds, so optimal offspring size depends on the relative importance of dispersal limitation and establishment limitation (Ganeshaiah & Shaanker 1991; Geritz, Meijden & Metz 1999; Levin & Muller-Landau 2000; Parciak 2002a,b).

The interaction between dispersal and offspring size in animals is thought to differ from that in plants. Offspring dispersal in animals, especially benthic marine invertebrates with non-feeding larvae, often entails energetic or physiological costs (Hunter *et al.* 1998; Wendt 1998; Marshall & Keough 2003, 2006, 2008b; Stamps, Krishnan & Reid 2005; Pechenik 2006; Bonte *et al.* 2012). Longer dispersal durations can increase the risk of mortality during dispersal (Vance 1973), but also increase mortality after settlement when dispersal experiences 'carry over' to influence survival in adult habitat (Highsmith & Emlet 1986; Wendt 1998; Stamps, Krishnan & Reid 2005; Marshall & Keough 2006; Pechenik 2006; Bonte *et al.* 2012). For example, starvation (Highsmith & Emlet 1986) or the consumption of finite resources when delaying metamorphosis in the absence of settlement cues (Hunter *et al.* 1998; Wendt 1998; Pechenik 2006) can result in fitness declines in juveniles and adults. Under this scenario, smaller offspring with fewer resources are hypothesized to incur greater energetic costs of dispersal, and hence lower fitness, with increasing dispersal duration compared with larger offspring (Marshall & Keough 2006). Given that average dispersal time generally scales positively with average dispersal distance (Shanks 2009), selection could favour mothers that produce fewer, well-provisioned (larger) offspring in isolated habitats, as these offspring can better cope with the energetic demands of colonizing distant habitats. Finally, size-dependent dispersal costs are an essential ingredient in models of the evolution of condition-dependent dispersal, where parental provisioning strategies can influence the co-evolution of offspring size and dispersal independently of the spatial and temporal patterns in habitat quality (Kisdi, Utz & Gyllenberg 2012).

Here, we developed a theoretical model of how optimal offspring size would be expected to change with habitat spacing when offspring fitness depends on both offspring size and dispersal duration. Our model is based on an influential size–number optimality model (Smith & Fretwell 1974) and is expected to be particularly relevant to benthic marine invertebrates with brooded, non-feeding (lecithotrophic) larvae. This group contains many species from diverse phyla, and many species are often dominant members of marine communities (Marshall *et al.* 2012). Our model also applies more generally to any organism where offspring size modifies the energetic costs of dispersal, and there is a positive relationship between dispersal duration and distance. We then empirically estimated the relationship between offspring size and survival under different dispersal durations in a marine bryozoan (*Bugula neritina*) in the field. We then used the empirical data to parameterize the offspring size–fitness function in the theoretical model. Together, our results show that, in isolated habitats, expected maternal fitness is maximized by producing fewer, larger offspring. When habitats are close and accessible, expected maternal fitness is greatest when many, small offspring are produced. Importantly, these results occur when the conditions in the habitat that offspring colonize do not vary, so represent a case of distance-dependent establishment limitation due to deferred dispersal costs, rather than habitat quality.

Materials and methods

THEORY

To generate a predicted optimal offspring size for a given patch distance, we combined a size–number trade-off model (Smith & Fretwell 1974; Marshall & Keough 2008a) with a dispersal model in a one-dimensional domain. The resulting model provides a mechanistic relationship between dispersal time and distance. Maternal fitness across a given interpatch distance d, $w(d,t,s)$, was determined by the total amount of resources a mother invests in reproduction (R, held constant), divided by the amount of resources invested per offspring (s, estimated as offspring size), multiplied by the time-dependent number of offspring that arrive at a patch at a given distance, $p(d,t)$, and subsequent offspring survival $g(s,t)$:

$$w(d,t,s) = p(d,t)g(s,t)\frac{R}{s} \qquad \text{eqn 1}$$

Maternal resource constraints therefore create a trade-off between the number of offspring, N, and their size s (Smith & Fretwell 1974): $N(s) = R/s$. The expected relationship between and offspring size s and maternal fitness w depends on the dispersal kernel and the distance to the nearest patch d:

$$w(d,s) = \frac{R}{s}\int_{t_{\min}}^{t_{\max}} p(d,t)g(s,t)\,\mathrm{d}t \qquad \text{eqn 2}$$

Note that the interpatch distance d has a similar interpretation to the spatial scale at which the space surrounding the parent is occupied by other organisms.

We model dispersal as the result of a random-walk process (Largier 2003; Siegel *et al.* 2003), and dispersal duration varies between larvae (i.e. at a given patch distance, there is a distribution of dispersal durations). Equation 2 is therefore integrated across all possible dispersal durations (bounded by biologically relevant dispersal durations $t_{\min}$ and $t_{\max}$). Figure 1 shows the relationship between offspring size and maternal fitness at several patch distances (equation 2). If we assume that the expected density of offspring at a given time after release t and for a given patch distance d depends on diffusion K and the rate of mortality during dispersal λ, then offspring are distributed according to the Gaussian kernel:

$$f(d,t) = \frac{1}{\sqrt{4\pi Kt}}\exp\left[-\frac{d^2}{4Kt} - \lambda t\right] \qquad \text{eqn 3}$$

The spatial spread of this kernel increases with time as $(Kt)^{0\cdot5}$ (Largier 2003). If offspring settle on suitable habitat the first time it is encountered, the expected dispersal duration of settling offspring at a given patch distance is distributed according to an inverse Gaussian distribution:

$$p(d,t) = \frac{d}{\sqrt{4\pi Kt^3}}\exp\left[-\frac{d^2}{4Kt} - \lambda t\right] \qquad \text{eqn 4}$$

The survival of offspring after settlement was assumed to follow an exponential form, where an offspring has an instantaneous probability of survival (β) that is constant with dispersal time, but proportional to the inverse of its size:

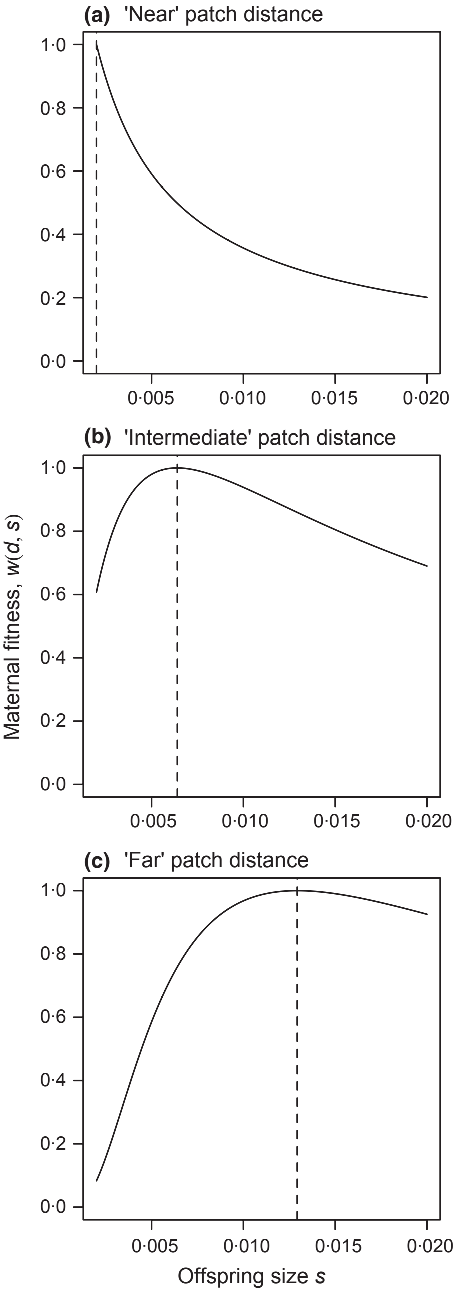

Fig. 1. Evaluation of equation 2 (β = 0·0008) at (a) near, (b) intermediate and (c) far patch distances showing the relationship between offspring size and maternal fitness at each distance. The dashed vertical line indicates the optimal offspring size for that interpatch distance.

$$g(s,t) = e^{-\beta t/s} \qquad \text{eqn 5}$$

In essence, larger offspring have a higher per-unit-time probability of survival after settlement because they begin with more resources. When we applied the model to data, we used a different form of $g(s,t)$, equation 6, which had more parameters and better fit the data. Results between the two versions of $g(s,t)$ were qualitatively similar (Figs 2 and 4).

Model analysis

We could not analyse this model analytically because we could not obtain a closed-form version of $p(d,t)$. We therefore evaluated the equations numerically using discrete approximations of the continuous distributions $p(d,t)$ and $g(s,t)$ and the Simpson's rule for numerical integration. At each interpatch distance, the optimal offspring size was found by finding the (discretized) value of s associated with the highest maternal fitness (Fig. 1). We chose values of offspring size s ranging from 0·002 to 0·02 mm^3, reflecting the typical ranges of egg volumes in marine invertebrates (Marshall & Keough 2008b). Time t has units of hours. As the value of the diffusion coefficient K is dependent on the spatial and temporal scales of interest (Largier 2003), we express interpatch distance d as a proportion of the diffusive length scale $L_{\text{diff}} = (Kt)^{0·5}$: d/L_{diff} (Largier 2003). L_{diff} has a similar interpretation to the mean displacement distance for a one-dimensional Gaussian dispersal kernel, which is calculated as $\sigma\sqrt{2/\pi}$, where σ is the standard deviation of the kernel or the spread (Lockwood, Hastings & Botsford 2002). Our choice of dispersal model, while an obvious simplification in the absence of real data, reflects the general pattern that mean planktonic duration is positively correlated with mean dispersal distance in marine invertebrates and fishes (Grantham, Eckert & Shanks 2003; Shanks 2009). The shape of the relationship between dispersal duration and distance can vary for a variety of reasons, including how K scales with t, physical retention zones, coastal boundary layers or larval behaviours, but what matters qualitatively for our analysis is that the relationship is positive.

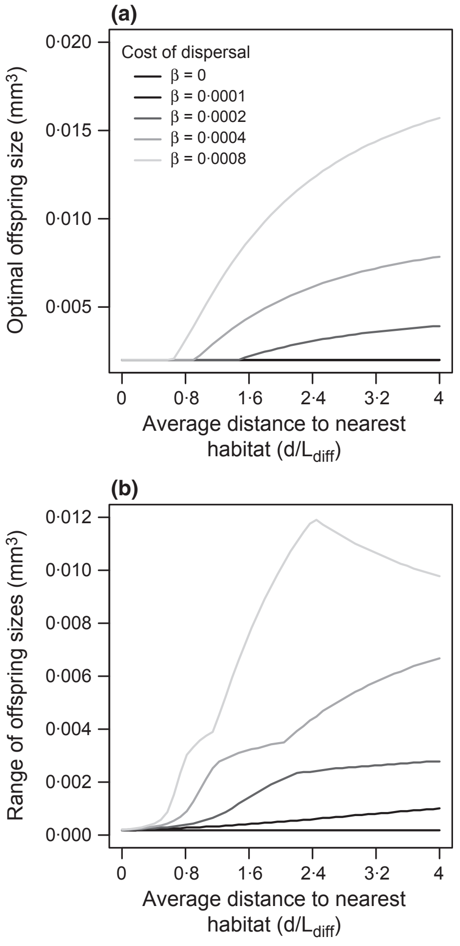

Fig. 2. The relationship between average distance to the nearest habitat (d relative to the diffusive length scale L_{diff}) and (a) optimal offspring size and (b) range of offspring sizes in the top 10% of the parental fitness curve (an indication of the width of the fitness curve) for increasing costs of dispersal (lighter lines).

DATA

Study organism

Bugula neritina (Bryozoa: Cheilostomata, Linnaeus, 1758) has a cosmopolitan distribution and lives on patches of habitat, such as boat hulls, pilings, pontoons, rock walls or seagrass patches. *Bugula neritina*, like many benthic invertebrates (representing many phyla) occupying hard substrates (e.g. Grantham, Eckert & Shanks 2003), release non-feeding larvae that are competent to settle upon release. When offered an appropriate settlement cue in the laboratory (e.g. rigid, roughened and biofilmed surfaces), most larvae settle within about 15 min to 4 h. In laboratory studies, the absence of habitat suitable for settlement forces competent larvae to delay metamorphosis and continue searching (Wendt 1998; Pechenik 2006), and larvae can remain metamorphically competent for at least 36 h. In the field, on average, 19% of settlers experience metamorphic delays greater than approx. 6 h, despite being competent to settle upon release from the parent colony (Burgess & Marshall 2011).

Experimental methods

We manipulated the dispersal duration, and hence the energetic costs of dispersal, of *B. neritina* larvae in the laboratory, measured their size and allowed them to settle onto settlement plates and then outplanted the settlement plates to the field and measured survival and growth of individuals up to an age where colonies become reproductive. To obtain larvae for the experiment, reproductively mature colonies of *B. neritina* were collected from the sides of floating docks at the Moreton Bay Boat Club at Redcliffe, Brisbane, Australia, in February 2008. Colonies were spawned and larval size measured with standard techniques (Marshall & Keough 2003). Briefly, colonies were held in dark, aerated aquaria at 23–25 °C for at least 24 h before being exposed to bright light to stimulate larval release. Larval size was estimated by measuring cross-sectional area (a good predictor of larval volume; Marshall & Keough 2003) with image analysis software (Image-Pro Express 5.1, Media Cybernetics, Bethesda, MD, USA) from photographs obtained from a camera (PixelLINK Capture SE, v1.0; Ottawa, ON, Canada) fitted to a dissecting microscope. Colonies were spawned separately and then larvae from all colonies were pooled and randomly allocated to each 'dispersal duration' treatment of 0, 4, 8, 12 or 24 h. As larvae are competent to settle upon release, dispersal duration was manipulated by placing larvae in 0·45-μm-filtered seawater in a 500-mL glass bottle on a roller, which slowly rolls the bottle (at 40 revolutions per minute) so that larvae are prevented from settling and forced to continue swimming. After each of the prescribed dispersal durations, ca. 30 larvae were removed from the bottles, and the size of each larva was measured. Immediately after measuring their size, each larva was then allowed to settle on experimental settlement plates (1 larva per 9 cm^2 diameter petri dish). Individual settlers were marked by drawing a circle around them in pencil. Settlement plates were kept in sea water for several days prior to settlement to allow the development of a biofilm to encourage settlement. Most larvae settled within 30 min. Settlement was uniformly high across all offspring size and dispersal duration combinations, and averaged 94% (89–97, 95% CI).

Settlement plates were transported to the field (back to the Moreton Bay Boat Club) in insulated aquaria and attached to backing plates tethered to the sides of the floating pontoon and hung 1 m below the water surface facing downwards. Survival of the marked settlers was measured in the field at 7, 21 and 42 days after settlement (colonies begin reproducing at about 14–21 days at our field site). Growth was estimated as the probability that individual colonies had bifurcated at 7 days after settlement, the number of zooids per colony at 21 days after settlement and the wet mass of colonies at 42 days after settlement.

STATISTICAL ANALYSES

The effects of offspring size and dispersal duration were analysed with generalized linear mixed-effects models (GLMM). Post-settlement survival was modelled as a binomial GLMM:

$$g(s,t) = \frac{1}{1 + e^{-(\beta_0+\beta_1 s+\beta_2 t+\beta_3 st)}} \qquad \text{eqn 6}$$

We replaced equation 5 with this version of $g(s,t)$ when applying the above model to derive the expected optimal offspring size for *B. neritina,* given the empirically derived relationship between offspring size, dispersal duration and post-settlement survival.

The number of zooids per colony (square-root-transformed) and the wet mass of colonies were analysed using Gaussian GLMM's. Offspring size and dispersal duration were (continuous) fixed effects, and backing panels were random effects. We tested for the presence of curvature by fitting polynomials; however, these did not improve the fit of models. There was no correlation among the fixed effects of size and duration. To compare the relative strengths of offspring size and dispersal duration, each factor was standardized as $(x - \text{mean}(x))/\text{sd}(x)$ prior to analyses. The appropriate standardized solution was used for the interaction term $[(x_1x_2 - \text{mean}(x_1x_2)/\text{sd}(x_1x_2)]$. Standardization equalizes the numerical ranges among the different scales of measurement and allows the direct comparison of the parameter estimates. The parameters (the β values) for the variables offspring size and dispersal duration estimate the change in the response variable for a standardized unit change in one variable, at the mean value of the other variable. The interaction term estimates the degree to which a unit change in dispersal duration modifies the relationship between offspring size and post-settlement performance. Likelihood ratio tests (LRT) were also performed to assess whether offspring size, dispersal duration or their interaction had significant effects on post-settlement survival. All analyses (theory and data) were performed in R (R Core Development Team 2012).

Results

THEORY RESULTS

Optimal offspring size increased with increasing distance to the nearest habitat when there were dispersal costs (Fig. 2). Mothers benefited from producing the smallest observed offspring size when the patch was relatively close (less than ~1 diffusive length scale; Fig. 2). Greater distances to the nearest habitat favoured larger offspring sizes, especially if energetic costs of dispersal were high (Fig. 2).

EXPERIMENTAL RESULTS

Survival – After 7, 21 and 42 days in the field, there were interactive effects of offspring size and dispersal duration on survival (Table 1, Fig. 3), although the significance of the interaction was marginal at 7 days ($\chi^2 = 2{\cdot}96$, $P = 0{\cdot}086$). Smaller offspring experienced a greater rate of decline in post-settlement survival with increasing dispersal durations (Fig. 3). Offspring size and dispersal duration had no influence on the probability of colonies budding at 7 days, the number of zooids per colony at 21 days or the wet mass of colonies after 42 days (Table 1).

EXPECTED OPTIMAL OFFSPRING SIZE IN BUGULA NERITINA

Given the statistical relationship between offspring size, dispersal duration and post-settlement survival estimated in *Bugula neritina* (Fig. 3), greater modelled distances between patches also favoured larger offspring (Fig. 4). While the two versions of $g(s,t)$ produced qualitatively similar patterns, the statistical version (equation 6) produced a more abrupt transition from smaller to larger offspring than the more simpler version (equation 5). The transition from small to large offspring in *B. neritina* occurred when the interpatch difference was approximately twice as much as the diffusive length scale (Fig. 4).

Discussion

Much of the theory on offspring size is focused on how habitat conditions influence the relationship between offspring size and fitness (Capinera 1979; Parker & Begon 1986; McGinley, Temme & Geber 1987; Garcia-Dorado 1990; Geritz 1995; Einum & Fleming 2004; Marshall & Keough 2008a; Fischer, Taborsky & Kokko 2010). For a given habitat quality, most models suggest that producing a single, optimal offspring size maximizes maternal fitness (Smith & Fretwell 1974; Parker & Begon 1986; McGinley, Temme & Geber 1987). Our study indicates that, even when habitat quality does not vary, more isolated habitats may favour the production of larger offspring in species where smaller offspring incur greater costs of dispersal and where dispersal duration and distance are positively related. By combining theory and empirical measurements, we demonstrated that deferred costs of dispersal are incurred by *Bugula neritina* at a magnitude that could potentially favour larger offspring in more isolate habitats. Our results represent a departure from traditional considerations of offspring size theory because selection on offspring size will be determined not only by the conditions of the habitat where offspring settle, but also by the spatial structure of landscape.

The effects of habitat spacing on offspring provisioning in benthic marine invertebrates is in the opposite direction to that predicted for plants, where producing smaller,

Table 1. Estimates of the relative importance of offspring size, dispersal duration and their interaction are given here by the partial β's estimated from (generalized) linear mixed-effects models. Offspring size and dispersal duration were standardized prior to analysis, so each parameter (β) indicates the amount of change in the response variable for a standardized unit change in one explanatory variable, at the mean of the other explanatory variable (see Materials and methods for more details). Comparisons of the parameters within (not among) a particular response variable quantify the relative importance of offspring size, dispersal duration and their interactive effects. 95% confidence intervals of parameters are given in brackets. Numbers in bold indicate parameter values significantly different to zero (at $P = 0{\cdot}05$ from Likelihood ratio tests) and indicate when offspring size, dispersal duration or their interaction had significant effects

	Parameters			
Response variable	Intercept	β_1: Offspring size	β_2: Dispersal duration	β_3: Interaction
Survival 7 days	1·09 (0·64, 1·54)	−0·34 (−1·03, 0·35)	**−2·83 (−5·58, −0·08)**	2·25 (−0·42, 4·91)
Survival 21 days	0·77 (0·28, 1·26)	−0·56 (−1·22, 0·09)	−4·11 (−7·09, −1·13)	**3·65 (0·76, 6·55)**
Survival 42 days	0·61 (0·17, 1·04)	−0·61 (−1·24, 0·03)	−3·92 (−6·81, −1·03)	**3·47 (0·68, 6·26)**
Probability of bifurcation 7 days	1·38 (0·86, 1·90)	0·50 (−0·46, 1·46)	−0·35 (−4·40, 3·70)	−0·07 (−4·00, 3·86)
No. of zooids 21 days	29·31 (26·53, 32·09)	1·15 (−4·34, 6·64)	−4·22 (−29·40, 20·96)	0·45 (−23·31, 24·20)
Mass (g) 42 days	0·76 (0·62, 0·90)	−0·01 (−0·20, 0·18)	−0·40 (−1·28, 0·48)	0·30 (−0·55, 1·15)

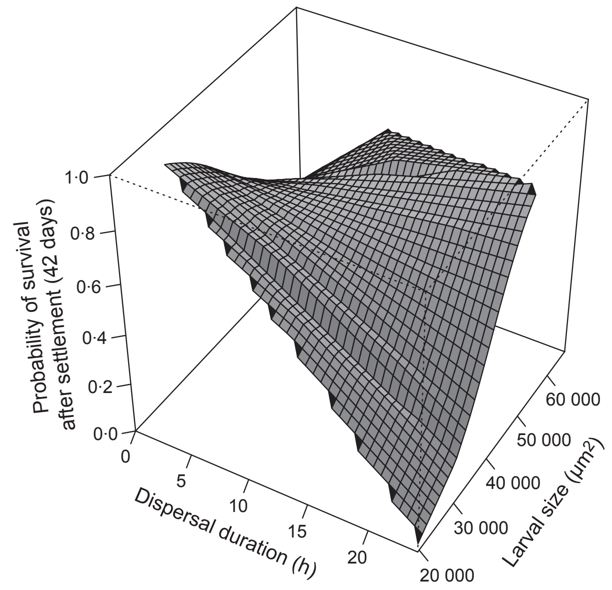

Fig. 3. Experimental results for *Bugula neritina* estimating the relationship between offspring dispersal duration and offspring (larval) size on the probability of survival to 42 days after settlement in the field. See also Table 1. $\sigma_{\mathrm{backing.panel}} = 0{\cdot}41$.

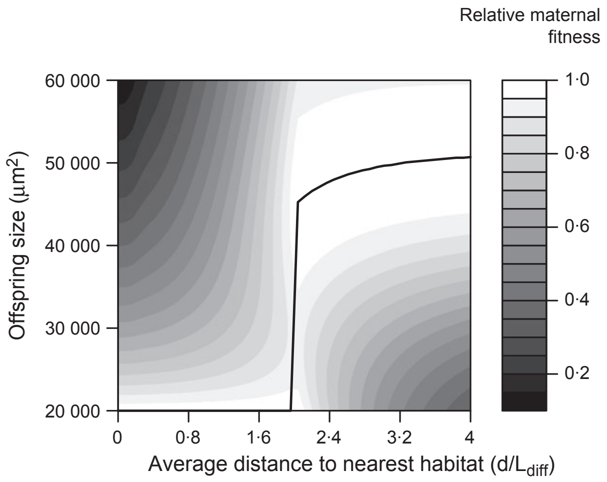

Fig. 4. *Bugula neritina.* How the expected maternal fitness (relative within each distance; side bar) varies according to offspring size and distance to nearest patch, based on the theoretical model combined with the empirical relationship between dispersal duration and larval size with post-settlement survival is shown (Fig. 3, equation 6). The solid black line indicates the optimal offspring size.

more numerous, seeds is favoured in isolated habitats (Westoby, Leishman & Lord 1996; Geritz, Meijden & Metz 1999; Levin & Muller-Landau 2000; Parciak 2002a, b). The difference is generated by the greater movement capabilities of smaller seeds vs. a greater capacity to withstand energetic costs in larger larvae. Clearly, covariation between offspring size and dispersal distance is complex and can be generated in more ways than indicated by the differences between plants and lecithotrophic marine invertebrates. For example, development time in marine invertebrate and fish larvae is expected to depend on egg size (Vance 1973; Levitan 2000). For non-feeding invertebrate larvae with planktonic development, larger eggs are expected to have longer development times, so mothers producing larger offspring could be favoured in isolated habitats, independent of any dispersal costs. In contrast, smaller eggs in species with feeding larvae are expected to have longer development times if settlement is only possible at some minimum size (Vance 1973; Levitan 2000), but whether mothers producing smaller offspring are favoured in isolated habitats remains to be tested (Krug 2009). As applies to plants, releasing more, and hence smaller, offspring is likely to increase the average distances moved because it increases the number of offspring that reach distant habitat (Levin & Muller-Landau 2000; Siegel *et al.* 2003). In situations where dispersal is optional and kin competition is prevalent, theoretical models of dispersal evolution often predict that isolated habitats select against dispersal (e.g. Bonte, Hovestadt & Poethke 2010), which can result in most offspring settling close to the parent. Mothers producing fewer, and hence larger, offspring may therefore be favoured to avoid the negative effects of kin competition in addition to reducing the fraction of offspring that disperse (Bonte, Hovestadt & Poethke 2010; Kisdi, Utz & Gyllenberg 2012). An important consideration in understanding the effects of habitat spacing on offspring provisioning is the shape of the dispersal kernel, in which the strength of any covariation between offspring size and dispersal distance should be assessed. Furthermore, parents can influence the dispersal of their offspring in spatially complex environments in other ways not directly related to offspring size (Massot *et al.* 2002; Stamps 2006; Bonte, Van Belle & Maelfait 2007).

Ultimately, the importance of habitat spacing and dispersal limitation relative to the more well-studied effects of habitat quality and establishment limitation will depend on the scale at which habitat conditions vary relative to the scale of offspring dispersal. If habitat conditions vary (i.e. if selection on offspring size varies across space) at a much smaller scale than the distance that offspring move (i.e. fine-grained environment; Levins 1968), then environmental conditions within habitats are expected to interact with the effects of patch spacing in determining overall selection on offspring size. Therefore, we do not necessarily expect a pattern in nature where mothers in isolated habitats produce larger offspring than mothers in accessible habitats. Patches that are far apart may more consistently favour larger offspring as a result of dispersal costs, but patches that are close may favour smaller or larger offspring depending on the quality of the habitat. Furthermore, observed offspring size in isolated patches will likely be due to some combination of selection on parents in that patch or selection on parents in other patches where larger offspring that survived and eventually reproduced there themselves produced larger offspring. Dispersal and establishment limitation may not necessarily have opposing effects on optimal offspring size in marine invertebrates as in plants (Parciak 2002a,b).

While our study modelled the effects of habitat spacing, it is unlikely to incorporate the full effects of spatial structure in organisms with complex life cycles. In particular, it has long been known that the larval environment, the juvenile or adult environment, and the offspring phenotype all likely determine offspring fitness (Hjort 1914). For example, dispersal costs may be mediated by the quality of the water mass that offspring disperse through (Sponaugle & Grorud-Covert 2006; Shima & Swearer 2009). Differences in larval environments would affect our model by requiring offspring fitness, $g(s,t)$, to be dependent on the spatial or temporal variability in environmental conditions between patches. Differences in larval environments or uncorrelated temporal variability in patch spacing or suitability could potentially give rise to an optimal range of offspring sizes (e.g. McPeek & Holt 1992; Toonen & Pawlik 2001; Einum & Fleming 2004; Krug 2009; though see McGinley, Temme & Geber 1987), rather than the single optimal offspring size predicted by the Smith & Fretwell's (1974) model.

Our empirical results showed that the relationship between offspring size and performance in a marine bryozoan (*Bugula neritina*) with non-feeding larvae depends on dispersal duration. Presumably, both offspring size and dispersal duration influence the amount of resources available to an individual after dispersal (Hunter *et al.* 1998; Marshall & Keough 2006). A steeper relationship between offspring size and survival at increasing dispersal durations probably occurred because smaller larvae simply began with fewer resources (Marshall & Keough 2008b). If this were the case, the energy used to prolong the larval stage in smaller offspring might come at the expense of that used for growth and development after colonization (Wendt 1998). Energy reserves are also likely to affect swimming and settlement behaviour in species with non-feeding larvae (Marshall & Keough 2003; Burgess, Hart & Marshall 2009). We did not include such behaviour in our model, but in *B. neritina* at least, larger offspring could have even greater dispersal potential through size-dependent larval behaviour and habitat selection (Marshall & Keough 2003; Stamps, Krishnan & Reid 2005; Burgess, Hart & Marshall 2009).

Our expectation that isolated habitats favour the production of larger offspring could also apply to situations where conditions near the parent degrade (Allen, Buckley & Marshall 2008; Krug 2009). A previous study on *B. neritina* showed that mothers produce larger offspring in higher competitive environments compared with lower competitive environments (Allen, Buckley & Marshall 2008). Given our results, an associated consequence of an increase in offspring size in response to competition is that offspring are more likely to be able to minimize any energetic costs associated with dispersing outside the competitive environment, provided that the spatial scale of high-competition environments is within the scale of dispersal. Such a role of offspring size in degrading environments could occur in addition to the effect of offspring size on overall dispersal duration and competitive ability (Allen, Buckley & Marshall 2008).

In summary, our results show that when offspring require larger dispersal distances to colonize suitable habitat, selection is expected to favour mothers that produce fewer, larger offspring when there are size- and duration-dependent costs of dispersal. Importantly, these results occur even when there is no heterogeneity in the conditions of the habitat that offspring colonize. In general, the benefits of larger offspring size at larger patch distances, if patches far away are the only option, could outweigh the costs of far fewer offspring travelling to the tails of the dispersal kernel. Given that individuals from many marine invertebrate species can release millions of offspring throughout their lifetime (Ramirez Llodra 2002), it is easily possible for at least some offspring to colonize patches at the tails of the dispersal kernel. In nature, habitat quality often varies in space and time and will likely impose selective pressures on how mothers provision their offspring in addition to habitat spacing. What we have done here is to isolate and characterize a previously overlooked component of the overall selective pressures likely to act on offspring size and number in nature.

Future studies of offspring provisioning strategies in other taxa that consider the covariation between offspring size, dispersal distance and offspring performance will reveal the relative importance of habitat spacing to offspring provisioning strategies more generally.

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