

# Are numbers enough? Colonizer phenotype and abundance interact to affect population dynamics

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## Summary

1. Ecologists have long recognized that the number of colonizers entering a population can be a major driver of population dynamics, but still struggle to explain why the importance of colonizer supply varies so dramatically. While there are indications that differences in the phenotype among dispersing individuals could also be important to populations, the role of phenotypic variation relative to the number of individuals, and the extent to which they interact, remains unknown.

2. We simultaneously manipulated the phenotype (dispersal duration) and abundance of settlers of a marine bryozoan and measured subsequent population structure in the field.

3. Increases in the number of colonizing individuals increased the subsequent recruitment and biomass of populations, regardless of colonizer phenotype. However, the relationship between colonizer abundance and the subsequent reproductive yield of the population was strongly reduced in populations containing individuals that had long dispersal durations.

4. The interactive effects of colonizer phenotype and abundance on the reproductive yield of populations occurred because longer dispersal durations decreased the proportion of individuals that reproduced. In fact, populations established from a few individuals with short dispersal durations had similar reproductive yield to populations *c.* 30 times larger established from individuals with long dispersal durations.

5. Interactions between colonizer phenotype and abundance have important implications for predicting population dynamics beyond those previously provided by numerical abundance or recruit phenotype alone.

**Key-words:** density-dependent fecundity, dispersal costs, larval condition, larval quality, propagule pressure, realized connectivity, stock-recruitment

## Introduction

Variation in the number of colonizers that enter a population is a key driver of population dynamics (Caley *et al.* 1996; Nathan & Muller-Landau 2000). The abundance of colonizers sets the scene for the complexity of interactions that follow. Increasing abundance of colonizers can result in a greater number of adults (where larvae, seeds or juveniles colonize habitat; Gaines & Roughgarden 1985; Lockwood, Cassey & Blackburn 2005) or influence the environment that offspring develop in (where adults colonize habitat; Clutton-Brock, Albon & Guinness 1987; Plaistow & Benton 2009). The abundance of colonizers also influences the strength of density-dependent interactions (Harper 1977; Caley *et al.* 1996; Poulsen *et al.* 2007), the biomass and the reproductive yield of populations (Harper 1977; Clutton-Brock, Albon &

Guinness 1987; Myers & Barrowman 1996; Hughes *et al.* 2000), as well as the roles of competition and predation in shaping communities (Tilman 1997; Connolly, Menge & Roughgarden 2001).

Although colonizer abundance can be important, predictions of population dynamics based solely on the numbers of individuals are still very imprecise (Myers & Barrowman 1996; Nathan & Muller-Landau 2000), indicating the need for research to focus on the causes and consequences of recruitment variability beyond numbers alone (Benton *et al.* 2005). In the past, most empirical studies focused on how density-dependent and environmental factors modified the importance of recruitment (Connell 1961; Harper 1977; Nathan & Muller-Landau 2000), and much ecological theory was developed under the notion that individuals equally contributed to population dynamics (e.g. Levin 1974; Roughgarden, Iwasa & Baxter 1985; but see DeAngelis & Gross 1992). More recently, an increasing number of studies

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find that the phenotype of individuals prior to colonization is closely linked to survival, growth and reproduction after colonization (e.g. Baker & Rao 2004; Pechenik 2006; Hamilton, Regetz & Warner 2008; Revilla & Wiegand 2008) and that differences in the phenotype among individuals are likely to affect population dynamics and community processes (Sinervo, Svensson & Comendant 2000; Hairston *et al.* 2005; Saccheri & Hanski 2006; Fussmann, Loreau & Abrams 2007; Kokko & Lopez-Sepulcre 2007; Pelletier *et al.* 2007). Population persistence requires that enough individuals not only survive, but also reproduce, yet there are still few studies that estimate how phenotypic variation mediates the effects of abundance on population dynamics (Sinervo, Svensson & Comendant 2000; Benton *et al.* 2005; Hairston *et al.* 2005; Coulson *et al.* 2006; Pelletier *et al.* 2007).

The phenotype of individuals determines their potential to survive and reproduce and can vary across space and time in a variety of ways. For example, dispersal can be costly and prolonged search times, starvation and environmental conditions prior to colonization can reduce the size, growth rate, survival or fecundity of individuals after colonization (e.g. Wendt 1998; Jarrett 2003; Baker & Rao 2004; Phillips 2004; Stamps, Krishnan & Reid 2005; Hamilton, Regetz & Warner 2008; Shima & Swearer 2009a). Selective mortality during dispersal can change the distribution of phenotypes that determine colonizer performance (Hamilton, Regetz & Warner 2008; Shima & Swearer 2009a). Environmental conditions in natal habitats (George 1994), the sizes of individuals (Birkeland & Dayton 2005) and the provisioning of offspring by mothers (Benton *et al.* 2005; McCormick 2006; Marshall, Allen & Crean 2008) will also influence the phenotype and performance of colonizers. Furthermore, because populations experience different environmental conditions, divergent selection and local adaptation can alter the potential for individuals to colonize new sites relative to natal sites (Nosil, Vines & Funk 2005; Marshall *et al.* 2010).

While there are good indications that the phenotype of colonizers may affect recruitment (above references), the influence of phenotypic variation is rarely assessed in relation to the, often large, variation in colonizer abundance (Johnson 2008; Plaistow & Benton 2009). Recent work suggests that the phenotypes of recruits (and their potential to survive and reproduce) can vary dramatically among and within populations (Johnston & Leggett 2002; Benton *et al.* 2005; Hamilton, Regetz & Warner 2008; Marshall & Keough 2008), but it is unclear whether such variation matches or exceeds the influence of the ubiquitous spatial and temporal variation in colonizer abundance. Thus, while at the individual level it is well recognized that colonizer phenotypes vary, few studies consider the importance of phenotypic variation at the population level (though see for e.g. Sinervo, Svensson & Comendant 2000; Benton *et al.* 2005; Hairston *et al.* 2005; Coulson *et al.* 2006; Pelletier *et al.* 2007). Studies that manipulate individual phenotype and abundance simultaneously are needed if their relative importance is to be determined, but such studies are rare (Johnson 2008; Stopher *et al.* 2008; Plaistow & Benton 2009).

Importantly, the effects of colonizer phenotype and abundance may not be additive. For example, populations of individuals with a less favoured phenotype (i.e. a phenotype that selection acts against) may experience stronger density-dependent effects than populations of individuals with a favoured phenotype. Such a situation could arise if the ability of individuals to compete for resources, or change the allocation of acquired resources between growth and reproduction, with increasing density depends on the phenotype (or 'condition') of the individual (Rubenstein 1981; Stopher *et al.* 2008). Alternatively, the effects of colonizer phenotype might only manifest at low densities (Clutton-Brock, Albon & Guinness 1987). Such interactions between colonizer phenotype and abundance could hinder our ability to predict population dynamics using estimates of numbers alone.

Here, we experimentally manipulate the phenotype and abundance of colonizers simultaneously to examine their relative strength and the degree to which they interact to affect subsequent population structure (recruitment, biomass, size of the breeding population, reproductive yield). We manipulated the dispersal duration and density of over 1000 settlers of a marine bryozoan, *Bugula neritina*, in the laboratory and then measured subsequent performance in the field. As a result, all individuals were subject to natural sources of density-independent effects (such as environmental variability or disturbances) on survival, growth and fecundity. We show here that the phenotype of colonizers modifies the importance of colonizer abundance for subsequent population dynamics.

## Materials and methods

### STUDY SPECIES

*Bugula neritina* (Bryozoa: Cheilostomata, Linnaeus, 1758) is an arborescent bryozoan with a global distribution and often occurs on man-made structures (e.g. pontoons, pilings, and jetties) in protected harbours around the coast of Australia. Recruitment of *B. neritina*, like most sessile plants and animals, is notoriously variable in space and time (Keough & Chernoff 1987). *Bugula neritina* larvae, like those of the majority of benthic invertebrates occupying hard substrates in inter-tidal and sub-tidal habitats (e.g. Grantham, Eckert & Shanks 2003), are lecithotrophic (non-feeding). In laboratory studies, the absence of habitat suitable for settlement forces competent larvae to delay metamorphosis and continue searching, although prolonged larval durations can reduce post-settlement survival, growth and fecundity (Wendt 1998; Pechenik 2006), presumably driven by declines in energy that would otherwise be used after settlement. Therefore, a natural and major source of phenotypic variation among settlers in patchy habitat arises from variation in larval durations. The majority of colonies are reproductively mature within 2–3 weeks after settlement (Wendt 1998), and most colonies live only several months (Keough & Chernoff 1987). Colonies grow by asexual budding of zooids to form branches, and each branch bifurcates at regular intervals. Together, these characteristics allowed us to estimate the consequences of colonizer phenotype and abundance to population dynamics (biomass, recruitment into the breeding population, and reproductive yield), and not just survival to census.

## GENERAL METHODS

Reproductively mature colonies of *B. neritina* were collected from the floating docks at the East Coast Marina (Brisbane, Queensland, Australia) on 1 February 2010. In the laboratory, colonies were kept in dark, aerated aquaria at 23–25 °C for 2 days. Colonies were then placed in separate containers and spawned by exposing them to bright light. The larvae used in the experiment were randomly selected from all containers. As larvae are competent to settle upon release and are non-feeding, we manipulated their phenotype by delaying the settlement of larvae (i.e. dispersal duration) to reflect larval behaviour in the absence of settlement cues. Larvae were placed in 4 × 500-mL glass bottles containing 200 mL of 0.45 µm filtered seawater, which were then placed on a mechanical roller mixer (Model 205-RM; Hwashin Technology Co., Seoul, Korea) that slowly rolled the bottle (at 40 revolutions per minute) so larvae were prevented from settling and forced to continue swimming. After 0, 4, 8 and 12 h, larvae were randomly taken from each of the four bottles and placed in 24 (96 in total) roughened, biofilmed plastic petri dishes (63.62 cm<sup>2</sup>) to settle. Once settled, individuals were marked by drawing a circle around them. The final densities of settlers varied from 1 to c. 29 individuals per dish (1198 individuals were used in total). These densities reflect the range of natural settlement densities recorded in the field, which averaged 5.7 per 64 cm<sup>2</sup> and ranged from 0 to 26 per 64 cm<sup>2</sup>. Effort was made to ensure an even distribution of densities across all dispersal durations. About one-quarter (50 mL) of the water in each bottle was also exchanged at each time. Dishes were transported to the field (East Coast Marina) the following day in insulated aquaria and attached to six PVC backing panels (550 × 550 × 6 mm). Each backing panel was attached to the floating pontoon and hung c. 1 m below the water surface. Dishes were allocated to backing panels such that every dispersal duration and the full range of densities were present on every backing panel.

After 20 days in the field, dishes were bought back into the laboratory and several estimates of performance were recorded with the aid of a dissecting microscope:

- 1 Recruitment (the number of marked colonies still alive in each dish),
- 2 Biomass (the total number of zooids on each colony, summed per dish; number of zooids,  $z$ , was estimated from counts of the total number bifurcations on each colony,  $b$ , as  $z = 16b + 8$ , because there are four zooid pairs between each bifurcation, and colonies have a regular branching pattern; Keough & Chernoff 1987),
- 3 Size of the breeding population (for each dish, the number of colonies with ovicells present. Ovicells are brood chambers on each zooid within which larvae develop), and
- 4 Reproductive yield of the population (the total number of ovicells on each colony, summed per dish).

Because of the time taken to count bifurcations and ovicells, and in an effort to minimize handling stress, biomass and reproductive yield were estimated on half (three) of the backing panels (a total of 44 experimental populations). Population size and the size of the breeding population were recorded from all six backing panels (a total of 93 experimental populations). All dishes were returned to the field within 2 days. After 32 days in the field, dishes were bought back into the laboratory again with the intention to estimate performance once more, but all of the colonies either had died or had high levels of partial mortality, effectively ending the experiment. This pattern of mortality is common in our system and occurred in *B. neritina* across the whole field site (possibly because of low salinity stress from

several days of rainfall prior to collection) and was not restricted to our experimental colonies. Thus, our measure of reproductive yield came close to estimating lifetime reproductive output for most of our experimental populations.

## ANALYSES

The effects of dispersal duration ('colonizer phenotype') and the abundance of colonizers ('colonizer abundance') on subsequent population size, biomass, size of the breeding population and reproductive yield were analysed using linear mixed-effects models. To compare the relative strengths of phenotype and abundance, dispersal duration and the abundance of colonizers were standardized ( $(x_i - \mu_x) / \sigma_x$ ) prior to analyses. The appropriate standardized solution was used for the interaction term (Aiken & West 1991). Standardization equalizes the numerical ranges among the different scales of measurement and allows the direct comparison of the parameter estimates. The parameters ( $\beta$ 's) for the variables dispersal duration and the number of colonizers estimate the change in the response variable for a standardized unit change in one variable, at the mean value of the other variable (Aiken & West 1991). The interaction term estimates the degree to which a unit change in the phenotype of colonizers modifies the relationship between the abundance of colonizers and the response variable. Marginal  $F$ -tests of parameters were also carried out to assess whether density, phenotype or their interaction had significant effects on population structure. Recruitment, size of the breeding population and reproductive yield were square root transformed prior to analysis. Plots of the data revealed no evidence of curvature, and including second-order polynomials in the models did not explain any additional variance. We did not estimate an intercept for the model estimating recruitment because recruitment was constrained by settlement density (essentially we fitted a linear version of the Beverton-Holt function with no density-dependent mortality, where  $P_0 = 1$  and  $R_{\max} \rightarrow \infty$ , see Poulsen *et al.* 2007 for more details). Random intercepts were fitted for each backing panel ( $\sigma_{\text{backing-panel}}$  and  $\sigma_{\text{residual}}$  estimate the standard deviation among and within backing panels, respectively). In all models, there were no interactions associated with backing panels. All analyses were carried out in R 2.10.1 (R Development Core Team 2009), and the 'lme' function was used for linear mixed-effects modelling.

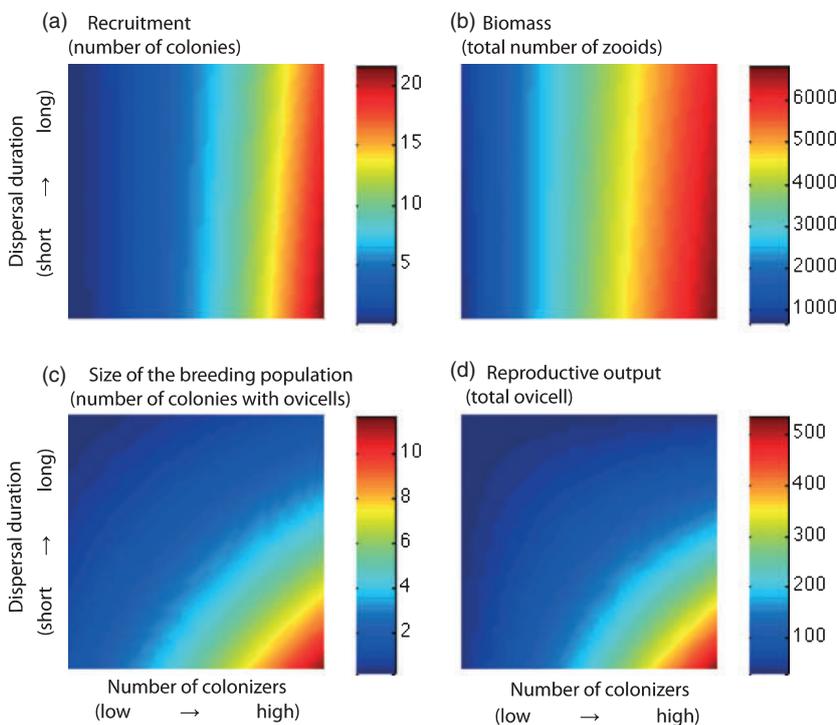
## Results

## RECRUITMENT

The number of individuals established at settlement was a good predictor of recruitment (the subsequent number of colonies alive at 20 days; Fig. 1a; Table 1,  $\beta_1$ : abundance of colonizers). The phenotype of colonizers (dispersal duration) had very little influence on recruitment ( $\beta_2$ : dispersal duration, Table 1) or on the relationship between the number of colonizers at settlement and subsequent recruitment (Fig. 1a; Table 1,  $\beta_3$ : interaction). The survival of colonies was uniformly high at 80% (95% CI = 77–82%).

## POPULATION BIOMASS

The number of individuals established at settlement was a good predictor of the biomass (the number of zooids) of each



**Fig. 1.** Fits from linear mixed-effects models showing the relative strengths of colonizer phenotype (dispersal duration, 0–12 h; vertical axis) and colonizer abundance (number of settlers, 0–30 per dish; horizontal axis) after 20 days in the field on (a) recruitment (the number of colonies alive), (b) population biomass (the total number of zooids), (c) size of the breeding population (the total number of colonies with ovicells) and (d) total reproductive yield (the total number of ovicells). The response variable in (a, c and d) was square root transformed for the analyses, but was converted to the original scale of measurement for plotting. Quantitative estimates of relative importance of parameters and fits of the models are given in Table 1.

**Table 1.** Estimates of the relative importance of colonizer abundance, phenotype (dispersal duration), and their interaction, are given here by the partial  $\beta$ 's estimated from linear mixed-effects models (plotted in Figure 1)

Response variable	Constant	$\beta_1$ : abundance of colonizers	$\beta_2$ : dispersal duration	$\beta_3$ : Interaction
Recruitment <sup>a,b</sup>	0	<b>1.28 (1.13, 1.43)</b> <i>1.15–1.42<sup>d</sup></i>	0.03 (–0.11, 0.17) <i>–0.19–0.17<sup>e</sup></i>	–0.10 (–0.30, 0.10)
Population biomass <sup>c</sup>	3638.32 (3212.52, 4064.11)	<b>1862.17 (1232.05, 2492.28)</b> <i>1621.91–2104.16<sup>d</sup></i>	–62.62 (–586.06, 710.61) <i>–324.96–302.91<sup>e</sup></i>	–179.92 (–1051.10, 691.27)
Size of the breeding population <sup>a,f</sup>	1.55 (1.38, 1.71)	0.69 (0.43, 0.95) <i>0.18–1.20<sup>d</sup></i>	–0.20 (–0.44, 0.05) <i>–1.02–0.31<sup>e</sup></i>	<b>–0.38 (–0.72, –0.04)</b>
Reproductive yield <sup>a,g</sup>	10.02 (7.15, 12.90)	5.38 (3.26, 7.50) <i>–0.22–11.02<sup>d</sup></i>	–0.11 (–2.05, 2.26) <i>–8.91–5.71<sup>e</sup></i>	<b>–4.19 (–7.10, –1.28)</b>

Each parameter ( $\beta$ ) indicates the amount of change in the response variable for a standardized unit change in one explanatory variable, at the mean and range (italicized) 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 abundance, phenotype, and their interactive effects. Ninety-five percent confidence intervals of parameters are given in brackets. Numbers in bold indicate parameter values significantly different to zero (at  $P = 0.05$  from marginal F-tests) and indicate when abundance, phenotype, or their interaction, had significant effects on population structure. Abundance and dispersal duration were standardized prior to analysis.

<sup>a</sup>Square-root transformed for analyses; <sup>b</sup> $\sigma_{\text{backing panel}} = 2.93$ ,  $\sigma_{\text{residual}} = 0.39$ ; <sup>c</sup> $\sigma_{\text{backing panel}} = 178.17$ ,  $\sigma_{\text{residual}} = 1182.78$ ; <sup>d</sup> $\beta_1 + \beta_3$  dispersal duration<sub>min,max</sub>; <sup>e</sup> $\beta_2 + \beta_3$  density<sub>min,max</sub>; <sup>f</sup> $\sigma_{\text{backing panel}} = 0.11$ ,  $\sigma_{\text{residual}} = 0.66$ ; <sup>g</sup> $\sigma_{\text{backing panel}} = 2.22$ ;  $\sigma_{\text{residual}} = 3.92$ .

population (Fig. 1b, Table 1). For every additional individual, population biomass increased by 187 zooids (for populations with the longest dispersal durations) to 210 zooids (for populations with the shortest dispersal durations). There was very little influence of colonizer phenotype on population biomass.

#### SIZE OF THE BREEDING POPULATION

Not all of the colonies within the experimental populations reproduced. Both the phenotype and abundance of colonizers strongly interacted to affect which individuals reproduced

and therefore the subsequent size of the breeding population (number of colonies with ovicells; Fig. 1c; Table 1,  $\beta_3$ ; interaction). The largest breeding populations were founded by a high abundance of colonizers with short dispersal durations (Fig. 1c). When colonizers had long dispersal durations, there was little effect of increasing initial abundance on the size of the breeding population. The square root size of breeding population increased with the number of colonizers 6.7 times as much (which translates to  $c. 74$  times as much on the original scale of the data) when colonizers had short dispersal durations, than it did when colonizers had long dispersal durations (Table 1).

## REPRODUCTIVE YIELD

The reproductive yield of populations (estimated as the total number of ovicells) reflected the patterns in the size of the breeding populations (Fig. 1d). The reproductive yield of the populations could not be predicted based on the phenotype or abundance of colonizers alone because these two factors interacted – reproductive yield only increased with abundance when colonizers had short dispersal durations. The total reproductive yield was highest (631 ovicells, 95% CI = 431–869) when there was a higher abundance of colonizers with short dispersal durations. Populations founded by a higher number of colonizers with long dispersal durations produced on average 68 (95% CI = 15–159) ovicells, which was indistinguishable from the number of ovicells produced by populations with a lower number of colonizers with short dispersal durations, which was 40 (95% CI = 4–114) ovicells.

## Discussion

The process of colonization is a fundamental element in most fields of biology, including invasion ecology (Lockwood, Cassey & Blackburn 2005; Simberloff 2009), metapopulation ecology (Figueira & Crowder 2006), population persistence (Caley *et al.* 1996), evolution of life histories (Kokko & Lopez-Sepulcre 2007) and the maintenance of genetic diversity (Willi, Van Buskirk & Hoffmann 2006) and species diversity (Connolly, Menge & Roughgarden 2001). All of these fields emphasize the importance of the number of individuals arriving at a site. Variability among individuals, if considered at all, is often assumed to be small in relation to the spatial and temporal variability in simple numerical abundance (cf. Kokko & Lopez-Sepulcre 2007). By manipulating both the phenotype and abundance of colonizers, we show that, while the abundance of colonizers was a good predictor of recruitment and biomass of populations in the field, colonizer abundance was a poor predictor of the size of the breeding population and total reproductive output. This decoupling occurred because increases in the dispersal duration of colonizers obscured the relationship between the initial abundance of colonizers and the subsequent size of the breeding population and total reproductive output. In fact, we found that populations founded by a few individuals with short dispersal durations actually had a similar reproductive output to populations founded by many individuals with long dispersal durations. While the idea that individuals can differ in their performance is by no means new, we show here that such differences are large enough to manifest at the population level and interact with, and even override, the importance of colonizer numbers for subsequent population structure.

Traditionally, recruitment has been viewed as a good predictor of reproductive yield, which at some spatial scale must then relate back to recruitment in the next generation (Myers & Barrowman 1996; Hughes *et al.* 2000; Chambers & Aarssen 2009). A decoupling of the relationship between recruitment and subsequent reproductive output has far reaching

consequences. Simply estimating the survival of colonizers may not predict establishment success (Lockwood, Cassey & Blackburn 2005; Simberloff 2009), population growth rates (Benton *et al.* 2005) or patch dynamics within metapopulations (Gotelli 1991; Figueira & Crowder 2006). The intrinsic ‘quality’ of colonizers could be as important to the reproductive output of populations and the creation of sink habitats as extrinsic factors (such as habitat quality, resource availability, or mate accessibility) that have traditionally received far more attention (Figueira & Crowder 2006). Our results suggest that future studies should focus as much attention on factors that influence colonizer phenotype as has previously been devoted to factors influencing numerical abundance as phenotypic effects are neither trivial nor simple.

There are many factors that can influence the phenotype and performance of colonizers and importantly, colonizer phenotype and abundance are likely to covary in a range of systems. For example, the nutritional state of colonizers (Baker & Rao 2004; Pechenik 2006), the magnitude of phenotype-environment mismatches (Nosil, Vines & Funk 2005; Marshall *et al.* 2010), and the density of colonizers (Moilanen & Nieminen 2002) are likely to vary with the distances travelled prior to colonization. Furthermore, the abundance and average phenotypes of colonizing cohorts are both likely to vary over time such that periods of high recruitment coincide with an increase or decrease in colonizer performance (Connell 1961; Phillips & Gaines 2002; Jarrett 2003; Baker & Rao 2004; McCormick 2006; Hamilton, Regetz & Warner 2008; Shima & Swearer 2009b). If colonizer phenotype and abundance do covary in space or time, such covariance will dramatically change the relationship between recruitment and subsequent population dynamics, especially when individuals in poor condition dominate large recruitment events (Shima & Swearer 2009b).

Given that our measure of colonizer phenotype was dispersal duration and longer dispersal durations are required to reach distant habitats, our results would suggest that isolated habitats, or those with low natal recruitment, would receive colonizers in poorer condition and have low reproductive yield – regardless of the numbers of larvae that disperse there. Therefore, patterns of dispersal estimated by how many larvae move a particular distance would be a poor predictor of the scales and magnitudes of dispersal required for population persistence at larger scales (Revilla & Wiegand 2008).

The phenotype of colonizers can modify the relationship between abundance and reproductive performance of the population through two, non-mutually exclusive, ways. First, individuals with less favoured phenotypes (i.e. poor ‘quality’; Wilson & Nussey 2010) may be disproportionately influenced by density compared to individuals with favoured phenotypes (good ‘quality’). Under this scenario, the mean fecundity and proportion of individuals that reach reproductive maturity in poor quality populations decline with density more rapidly than that for good quality populations. When summed, this results in a lower total reproductive output of the population because an increase in numerical abundance

does not compensate for the increasingly poor reproductive capacity of poor quality individuals. For example, with increasing population densities, poorer quality individuals could have reduced ability to acquire (either through contest or through interference mechanisms of competition) and convert resources into offspring. Poorer quality individuals may also change the allocation of resources, acquired previously, away from current reproduction to maximize future reproduction (Goulden & Hornig 1980). Second, increases in density often increase the hierarchy (or inequality) in a population (Harper 1977) and phenotypes with lower performance may remove this hierarchy. A hierarchical population is one where a few individuals contribute a disproportionate amount towards the total reproductive output of the population and can influence the summed reproductive output independent of the 'average' fecundity of the population (Harper 1977; Rubenstein 1981; Chambers & Aarssen 2009). Our results suggest the latter scenario applies in our study because greater reproductive yield occurred because more individuals reproduced, rather than from changes in mean fecundity.

Because we tracked over 1000 individuals from birth (and most until they began reproducing or died), logistics prevented us from doing our experiment at multiple sites. As a result, it is unclear how the relative importance of colonizer phenotype and abundance to the structure of populations changes at other sites. As an example, temperature determines rates of energy use, and if depleting energy reserves cause the decline in performance with increasing dispersal duration, then we would predict that dispersal duration would contribute less to heterogeneity in individual performance at sites with cooler water temperatures. The deleterious effects of density on individual performance may also change under different levels of resource availability (which includes space, food, and oxygen for our study species). More generally, the environment influences the nature of selection on phenotypes and is likely to change which phenotypes contribute to the axis of phenotypic variation that best explains differences in fitness (i.e. individual quality, Wilson & Nussey 2010), as well as the overall magnitude of fitness differences.

It is clear that the abundance of colonizers influences population-level processes and the phenotype of colonizers influences individual-level processes, but rarely have these two lines of inquiry informed each other. For many species, large variability in recruitment is a dominant feature of their population dynamics, and there are also numerous potential sources of spatial and temporal variability in the phenotype and performance of colonizers. Our results highlight the importance of studying how processes influencing individuals scale up to the population level and influence the predictability of population dynamics (DeAngelis & Gross 1992; Benton *et al.* 2005; Pelletier *et al.* 2007). In an applied sense, a focus on the number of individuals, without considering the phenotype of individuals, reduces the accuracy of predictions of invasion success, fisheries yield, or rates at which new sites are colonized (Myers & Barrowman 1996; Verling *et al.* 2005). Understanding spatial and temporal phenotypic variability among individuals should provide a better

mechanistic understanding and predictive capabilities beyond that provided by the numbers of colonizers alone.

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