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Propagule size and dispersal costs mediate establishment success of an invasive species

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Abstract. Bio-invasions depend on the number and frequency of invaders arriving in new habitats. Yet, as is often the case, it is not only quantity that counts, but also quality. The process of dispersal can change disperser quality and establishment success. Invasions are a form of extra-range dispersal, so that invaders often experience changes in quality through dispersal. To study effects of dispersal on invader quality, and its interactions with quantity on invasion success, we manipulated both in a field experiment using an invasive marine invertebrate. Establishment success increased with the number of individuals arriving in a new habitat. Prolonged larval durations – our manipulation of prolonged dispersal – decreased individual quality and establishment success. Groups of invaders with prolonged larval durations contributed only a third of the offspring relative to invaders that settled immediately. We also found an interaction between the quality and quantity of invaders on individual growth: only within high-quality cohorts did individuals experience density-dependent effects on growth. Our findings highlight that dispersal not only affects the quantity of invaders arriving in a new habitat but also their quality, and both mediate establishment success.

Key words: bio-invasion; Bugula*; connectivity; deferred costs; population dynamics.*

Introduction

Successful invasions require a species not only to arrive at a new area but also to establish and spread while avoiding exclusion by the local community (Williamson 1996, Facon et al. 2006). Invasion success is a multi-step process where establishment and spread are determined by the interaction of colonizers and receiving communities at each step (Lodge 1993, Holle and Simberloff 2005, Drake 2006). While high species diversity and low disturbance can reduce the invasibility of communities (Stachowicz et al. 1999, Colautti et al. 2006, Clark and Johnston 2009), these effects can be overridden by high propagule pressure (Holle and Simberloff 2005, Colautti et al. 2006).

As defined by invasion biology, propagules are groups of individuals of a species arriving in a new habitat, and propagule pressure is a product of propagule size (individuals per propagule) and the frequency of arriving propagules. Both factors can predict invasion success (Wittmann et al. 2014). While hard to disentangle, recent evidence suggests that propagule size is a good predictor of invasion success through both demographic effects and increasing genetic diversity of the founding population (Hufbauer et al. 2013). Less well understood is the role of the quality of invading individuals in mediating invasion (for a definition of phenotypic quality see Wilson and Nussey 2010).

Phenotypic quality of propagules is relevant because invaders not only need to arrive but also survive, reproduce, and ultimately create a self-sustaining population in a new habitat (Marshall et al. 2010, Bonte et al. 2012). Individuals of a high-quality phenotype are better able to survive, compete, and reproduce (Pechenik 2006, Hamilton et al. 2008, van Allen et al. 2010, Saino et al. 2012), with lasting impacts on community dynamics (Hairston et al. 2005, Pelletier et al. 2007, Davis and Marshall 2014). Sources of variation in phenotypic quality are diverse and range from maternal effects (Mousseau and Fox 1998) to (context-dependent) adaptive differentiation (Kawecki and Ebert 2004) to dispersal (Bonte et al. 2012). The influence of dispersal on phenotypic quality is particularly important to

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invasion success because invasive species by definition have to disperse from their natal habitat to outside of their range, known as extra-range expansion (Wilson et al. 2009).

While dispersal can potentially unlock new habitats and aid in-range expansions, dispersal entails energy, risk, and time costs which can decrease the chances of settlement or post-settlement performance (reviewed in Bonte et al. 2012). Prolonged dispersal decreases pre- and post-settlement survival (Vance 1973, Maldonado and Young 1999, Baker and Rao 2004), post-metamorphic performance (Wendt 1998), and alters habitat selection behavior (Jaenike 1990, Stamps et al. 2005, Elkin and Marshall 2007). In other words, compared to locally retained individuals, dispersers often arrive in poorer condition.

The costs of dispersal are non-trivial. In some cases, the quality of individuals arriving in a new habitat can outweigh the effects of propagule pressure (Sinervo et al. 2000, Allen et al. 2008, Burgess and Marshall 2011*a*). Burgess and Marshall (2011*a*) demonstrated that individuals that dispersed less had higher-quality phenotypes with reproductive yields about 30 times larger than individuals that had dispersed more. Clearly then, the effects of propagule quality and dispersal durations may influence whether propagules successfully invade.

The link between dispersal duration and phenotypic quality is considered particularly strong in organisms in which the dispersive stage does not feed: the energetic costs of dispersal are considered to be aggravated (Wendt 1998, Pechenik 2006, Burgess and Marshall 2011*a*). Non-feeding larvae are found in about half of all coastal marine invertebrates (including globally invasive species such as *Watersipora subtorquata*, *Ciona intestinalis* or *Bugula nertitina,* cf. Marshall et al. 2012). These species use energy reserves during dispersal and typically have larval durations that are much shorter than in species with feeding larvae (Thorson 1950, Wendt 1998, Pineda et al. 2007). To test for the effects of prolonged dispersal and propagule size on invasion success, we experimentally invaded existing communities with a common marine invasive species with non-feeding pelagic larvae, *Bugula neritina*. We specifically tested for the chances of establishment and spread by experimentally controlling the number of recruits, which is a direct product of propagule size (cf. Clark and Johnston 2005, 2009). Establishment and spread are critical phases during invasion. Short-term increases in fitness during these phases can prevent extinction and aid invasion, known as the "catapult effect" (Drake 2006).

While the link between dispersal costs and phenotypic quality is relatively well-established in general studies of population connectivity (Bonte et al. 2012, Burgess et al. 2012), there are no studies on how this link affects invasion success. Specifically, previous experiments on this species on the effects of phenotypic quality had been tested in the absence of interspecific competition (Burgess and Marshall 2011*a*, Burgess et al. 2012). Effects of phenotypic quality are highly context-dependent and can have different effects under varying levels of competition (Marshall and Monro 2013). Because invasion success depends on the interaction of invaders and receiving communities, including interspecific competition is necessary to experimentally mimic the invasion process.

Material and Methods

Study species and collection

Bugula neritina is an invasive, cheilostome bryozoan commonly found in marinas in temperate water regions. Its distribution is cosmopolitan and it is often found in marinas as part of the fouling community. Within a few weeks of settlement, colonies gain reproductive maturity and each zooid can potentially brood one egg at a time in an externally visible brood chamber (Wendt 1998).

We chose this species because its qualities can be considered typical for an invasive species. While the exact properties of what makes some species invasive remain unknown, *Bugula neritina* shares many of the traits that appear typical of marine invasive species (non-feeding larvae, filter feeding adult, high reproductive outputs). Its native range is unknown, but it is thought to originally have been widespread throughout the tropics and subtropics (Mackie et al. 2006).

Experimental design

Mature *Bugula neritina* colonies were collected from boat hulls located at Blairgowrie Yacht Squadron, Blairgowrie, Australia (38°21′20.16″ S, 144°46′22.82″ E) in December 2014 and January 2015. Colonies were then transported to Monash University, Clayton and kept in a 26 L plastic container filled with seawater. Colonies were kept at 17°C under compete darkness for 4 d.

We induced spawning using standard techniques and haphazardly allocated larvae to two different dispersal treatments. We experimentally manipulated prolonged dispersal by hindering *Bugula* larvae from settling, which prolongs larval duration (Burgess and Marshall 2011*a*). Our larval duration treatments were the following: instantaneous opportunity for settlement, or 2 h delay of opportunity. Our manipulation of larval duration was set to capture the majority of dispersal durations in the field (Burgess and Marshall 2011*b*), thus being ecologically relevant to the species. We delayed larval settlement using standard methods (see Burgess and Marshall 2011*a*). Larvae of both treatments were then settled larvae on to pre-roughened, biofilmed acetate sheets. We counted the number of larvae before and after washing off to estimate settlement success (proportion of settled larvae). The settlers were left overnight to metamorphose in filtered seawater. On the next day, larvae were cut out of the sheet in 0.5 cm^2 rectangles, to be attached to acrylic plates (11 cm × 11 cm) that had preexisting fouling communities growing on them. These communities were created by submerging these plates in Blairgowrie 7 weeks prior to the experiment and retrieving them on the same day as we added our treatment groups. To mimic the arrival of the invasive *Bugula neritina* into a community and ensure the community was naïve to this species, we manually removed any *B. neritina* from the community plates at weekly intervals.

Our settlers were attached in four different propagule size treatment configurations: 1, 4, 8, and 16 settlers per plate. Our larval duration treatments were equally spread over the propagule size treatments. Settlers were haphazardly allocated into each treatment combination, evenly spaced and glued into the community using a small drop of superglue.

Plates were attached facing down to 60 cm × 60 cm acrylic panels submerged under water and attached to a floating pontoon with a stainless steel cable. Each panel was allocated with eight plates and each treatment combination (four propagule pressure and two larval duration treatments) was represented once per panel. We had two trials of this experiment, the first one had eight panels with 484 individuals, and the second run had seven panels with 406 individuals. In trial one two plates detached, and we lost 24 individuals.

Two weeks after deployment, we photographed each plate using a Canon EOS 600D camera at 35 mm focal length. Since we had previously marked the location of each settler, these photographs could be used to score post-settlement recruitment (scored as presence or absence). It was often unclear from the photographs whether settlers were overgrown but present or completely absent, which we scored as missing data ($N = 27$). Missing data were not biased by treatments. Seven weeks after deployment, we retrieved all plates from the field and scored biomass and reproductive yield. Unfortunately, a particularly aggressive competitor (another encrusting bryozoan) emerged during the second trial and overgrew more than 90 % of our plates. We therefore could only score biomass and reproductive yield of the surviving settlers from the first run ($N = 185$). Biomass was scored by counting the number of bifurcations on this arborescent bryozoan, which reliably correlates with total mass (Keough and Chernoff 1987). Reproductive yield was scored counting the total number of brood chambers on a colony using a stereomicroscope and later on assigning to fecundity categories (0: 0 eggs, 1: 1–50 eggs, 2: 51–100 eggs, etc.). This assignment had better distributional qualities than the original data.

Statistical analysis

We first analyzed the influence of larval duration on settlement success (proportion of settled larvae) by using a censored regression model to reflect the right-censoring in our dependent variable (the distribution of settlement success was cut off at 1).

We analyzed our response variables recruitment, biomass, and reproductive yield separately as individual-level effects and as population-level effects. This was done because the effect of increased propagule size may be positive on the experimental population seen as a whole, but density-dependent effects may lead to reduced fitness per individual with increasing propagule size, and we were interested in exploring such effects.

Our deployment design grouped individuals on plates, plates on panels, and panels in runs, which generates spatial and temporal dependencies. To address these dependencies, we included nested random factors to our analyzes. Our random factors were plates nested within panel nested within run (run only in the analysis of survival). All statistical analyzes were performed in R (R Core Team 2013). We analyzed settlement success using the VGAM package (Yee 2010). Individual- and population-level recruitment, propagule biomass, and propagule reproductive yield were analyzed in in a generalized linear mixed-model framework with a Poisson error distribution using the lme4 package (Bates et al. 2013); individual reproductive output was analyzeanalyzed in a generalized linear mixed-model framework with a poisson error distribution and zero-inflation using the glmmADMB package (Fournier et al. 2012, Skaug et al. 2013); individual colony biomass using a linear mixed-model with Gaussian error distribution and the lme4 package (Bates et al. 2013).

Our full models contained one dependent fitness variable, the fixed factors propagule size and larval duration, the fixed factor interaction, and the random nested factors. We then performed a stepwise model reduction to test if our models could be simplified and non-significant interaction terms were dropped (Zuur et al. 2009). Finally, we assessed homogeneity and normality of error variances using graphical tools (Zuur et al. 2009). Because two outliers strongly influenced our analysis on propagule reproductive yield, we present its analysis with and without the inclusion of those outliers.

RESULTS

Settlement success

Larval duration had a small, but significant effect on settlement success: larvae that could settle immediately after spawning had higher settlement success (mean ± SD: 77% ± 14%) than larvae that were kept from settling for 2 h (68% ± 20%) (censored regression, $n = 66$, $z = -2.02$, $P = 0.046$).

Post-settlement success

Large propagule size and short larval durations increased the success of experimental populations establishing within naïve communities (Table 1, Fig. 1). Experimentally increasing propagule size strongly increased post-settlement recruitment, cumulative

Table 1. Population- and individual-level factor effects taken from generalized linear mixed model (all response variables except per individual colony biomass) and linear mixed model (individual colony biomass). Sample sizes are noted in Material and Methods section. Statistical significance is noted by bold lettering.

	Estimate	SE	*t*- or *z*-value	*P*
Population				
Post settlement recruitment				
Dispersal duration	−0.11	0.04	−2.63	**<0.01**
Propagule pressure	0.13	0.01	16.91	**<0.001**
Colony biomass				
Dispersal duration	−0.08	0.01	−8.79	**<0.001**
Propagule pressure	0.12	0.01	15.35	**<0.001**
Reproductive yield				
Incl. 2 outliers				
Dispersal duration	−0.71	0.14	−4.96	**<0.001**
Propagule pressure	0.04	0.01	3.16	**<0.01**
Dispersal * propagule pressure	0.03	0.01	2.70	**<0.01**
Excl. 2 outliers				
Dispersal duration	−0.17	0.08	−2.16	**0.03**
Propagule pressure	0.10	0.01	7.37	**<0.001**
Individual				
Post settlement recruitment				
Dispersal duration	−0.30	0.11	−2.70	**0.01**
Propagule pressure	0.00	0.02	0.03	0.98
Colony biomass				
Dispersal duration	−0.64	0.33	−1.95	**0.05**
Propagule pressure	−0.09	0.04	−2.46	**0.01**
Duration * propagule pressure	0.06	0.03	2.35	**0.02**
Reproductive yield				
Dispersal duration	−0.32	0.14	−2.35	**0.01**
Propagule pressure	−0.03	0.03	−0.97	0.33

biomass, and reproductive yield; prolonging larval duration for 2 h had the opposite effects. There was an interaction between larval duration and propagule size on the reproductive yield of populations, which was driven by two outliers.

Regarding effects on individuals, the effects of larval duration were more pervasive than the effects of propagule size (Table 1). Individuals with longer larval durations recruited more poorly, grew to smaller size, and had a lower reproductive yield than individuals that could settle immediately. When taking the cumulative effects of settlement success, post-settlement survival, growth and fecundity into account, the overall reproductive output of populations that experienced no extended larval duration was more than three times higher than that of populations that experienced an extended larval duration (see Fig. 2). Propagule size had no effects on individual post-settlement recruitment and reproductive yield, but interacted with larval duration on colony biomass (Fig. 2). When individuals immediately settled, overall propagule size had a negative effect on colony biomass, but when settlement was delayed this effect disappeared.

Discussion

By experimentally manipulating the larval durations of invaders and testing their success at establishing within a naïve community, we showed that reductions in individual quality decreased the chance and extent of establishment. Propagules that experienced longer larval periods had less chance of survival once settled, grew to smaller size, and were less fecund. These effects were cumulative: propagules that dispersed for 2 h longer produced only a third of the offspring that propagules who settled immediately produced. Propagule size also mediated establishment success: bigger propagules (higher densities of settlers) recruited more, and

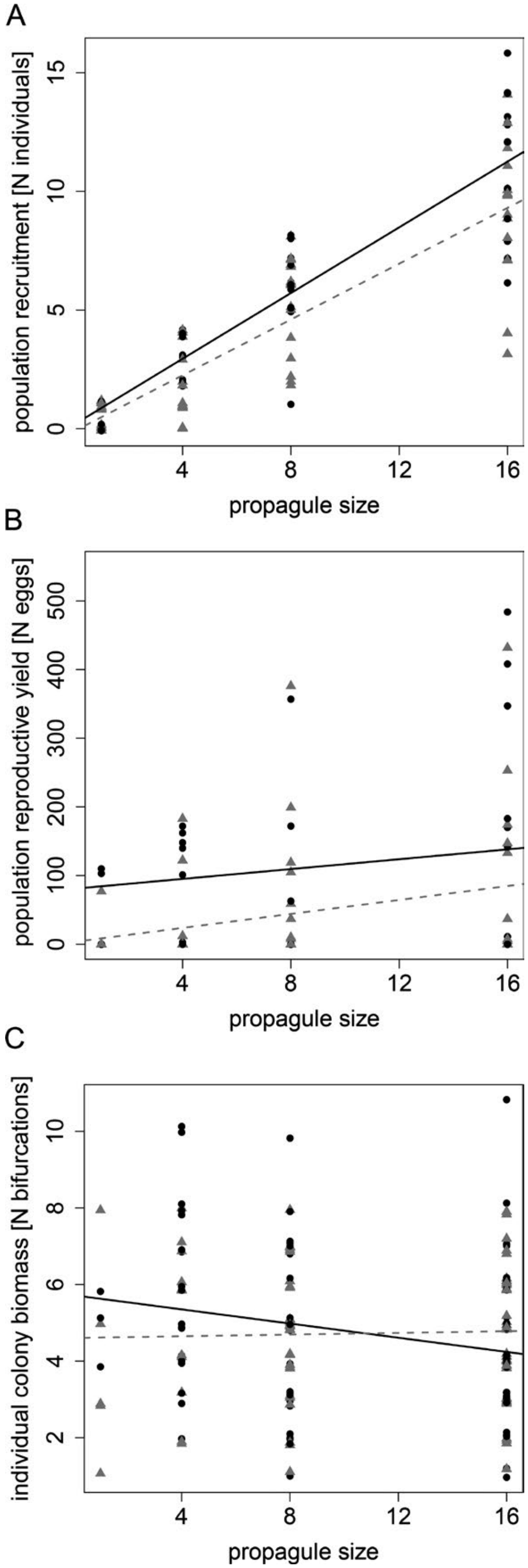

FIG. 1. Effects of propagule pressure and dispersal duration on invasion success. A: Effects on population recruitment, measured as the number of surviving individuals per propagule. B: Effects on population reproductive yield, measured as the total number of eggs produced by all surviving individuals. C: Effects on individual colony biomass, measured as the number of bifurcations per colony. Black, solid lines and black circles: 0 h dispersal duration; grey, dashed lines and grey triangles: 2 h dispersal duration.

had a higher biomass and reproductive yield. Yet, regarding individual performance, propagule size did not affect recruitment or reproductive yield, its only influence was in an interaction with larval duration to affect colony biomass. Only when propagules settled immediately did high propagule size decrease colony biomass.

Density-dependent effects therefore only manifested in cohorts of higher quality (i.e., those that experienced short larval durations). While density-dependent decreases in individual performance are common in invasive species (Burgess and Marshall 2011*a*, Hedge et al. 2012), it is the direction of the interaction that is surprising. Poorer-quality individuals often experience negative-density dependent effects more strongly than higher-quality individuals (Rubenstein 1981, Clutton-Brock et al. 1987, Stopher et al. 2008). These studies were, however, studied in populations with heterogeneous individual quality: individuals of poorer quality had to compete with individuals of higher quality, such that density-dependent effects were exacerbated. In our study, poor-quality individuals did not interact with higher-quality individuals. We speculate that poor-quality individuals were unable to grow as quickly, achieved smaller sizes and so did not reach the carrying capacity per unit area, whereas higher-quality, faster-growing individuals did. These complex interactions between individual quality, density and invasion should be studied further as standard theory fails to predict such interactions.

Propagule quality was decreased by prolonged larval duration in our study, and this decrease was likely caused by a decrease in nutritional reserves (Pechenik et al. 1998, Wendt 1998). Similar effects of dispersal or prolonged larval durations on propagule quality should apply to other invasive species, given that many costs of dispersal are ubiquitous across terrestrial and marine systems (Bonte et al. 2012). Dispersal-costs may also induce non-random or context-dependent dispersal patters (Bonte et al. 2012). For instance, Marshall and Keough (2003) found that in the absence of settlement cues, larger bryozoan larvae delayed settlement for longer and were choosier towards settlement surfaces. Therefore, large larvae, or high-quality phenotypes, may have higher dispersal potential and perhaps compensate for dispersal costs relative to small larvae that settle close to their natal habitat. This scenario is predicated on the assumption that realized dispersal is a sole product of dispersers' size. More likely is a scenario where larval size affects larval

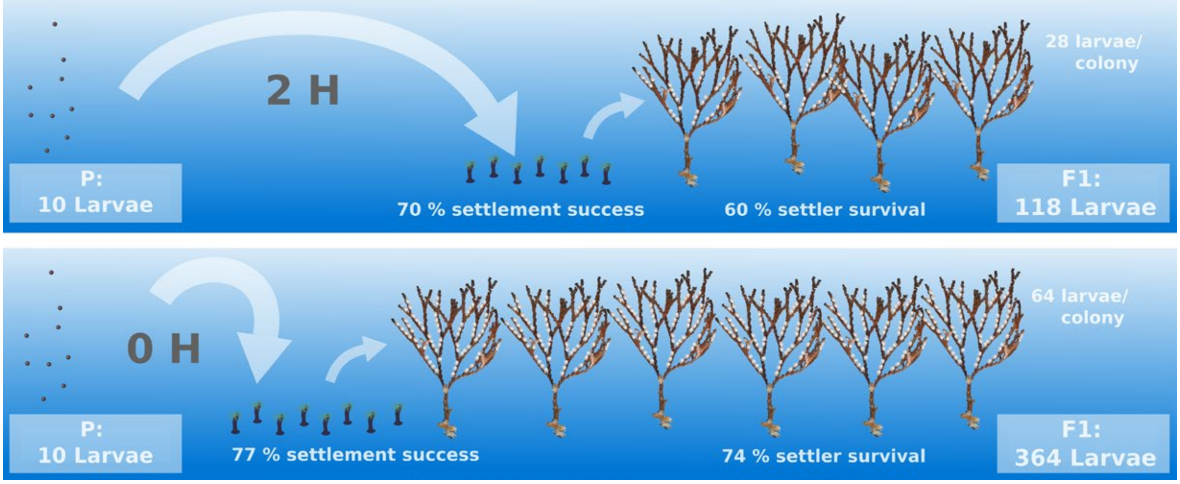

FIG. 2. Cumulative effect of prolonged dispersal duration on the reproductive output of propagules, values are taken from experimental trait means. A batch of invaders arriving in a new habitat will produce three times more larvae if settling immediately, compared to delaying dispersal for 2 h.

behaviour (see also Burgess et al. 2012), such that both small and large larvae will settle into proximate and suitable habitats.

Covariance between propagule size, dispersal duration, and propagule quality may be common: more isolated patches are likely to receive smaller propagule size and poorer-quality propagules. Yet this covariance and its links to invasibility need to be more firmly established. In our study, we tested effects of propagule size and quality on establishment, and we experimentally controlled recruitment. Therefore, the results of our study can be used only to draw conclusions on the effects of propagule size and quality during those steps of the invasion process. We did not test for quality and quantity effects on recruitment success, but other studies suggest that recruitment success depends on propagule size (Clark and Johnston 2009) and propagule frequency (Wittmann et al. 2014 and references therein). Recruitment of *Bugula* larvae into established communities in the field is often low (only 2–10% of all larvae recruit) (Clark and Johnston 2005), and being of low quality decreases the chances of finding a suitable habitat (Burgess et al. 2012). Overall our results suggest that the effective distance by which this species may successfully invade new habitats will then be shorter than estimated by the effects of dispersal duration or propagule pressure alone.

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