

# How do dispersal costs and habitat selection influence realized population connectivity?

SCOTT C. BURGESS,<sup>1,2,3</sup> ERIC A. TREML,<sup>1</sup> AND DUSTIN J. MARSHALL<sup>1</sup>

<sup>1</sup>*School of Biological Sciences, University of Queensland, Brisbane QLD 4072 Australia*

<sup>2</sup>*Climate Adaptation Flagship, CSIRO Marine and Atmospheric Research, Cleveland QLD 4163 Australia*

**Abstract.** Despite the importance of dispersal for population connectivity, dispersal is often costly to the individual. A major impediment to understanding connectivity has been a lack of data combining the movement of individuals and their survival to reproduction in the new habitat (realized connectivity). Although mortality often occurs during dispersal (an immediate cost), in many organisms costs are paid after dispersal (deferred costs). It is unclear how such deferred costs influence the mismatch between dispersal and realized connectivity. Through a series of experiments in the field and laboratory, we estimated both direct and indirect deferred costs in a marine bryozoan (*Bugula neritina*). We then used the empirical data to parameterize a theoretical model in order to formalize predictions about how dispersal costs influence realized connectivity. Individuals were more likely to colonize poor-quality habitat after prolonged dispersal durations. Individuals that colonized poor-quality habitat performed poorly after colonization because of some property of the habitat (an indirect deferred cost) rather than from prolonged dispersal per se (a direct deferred cost). Our theoretical model predicted that indirect deferred costs could result in nonlinear mismatches between spatial patterns of potential and realized connectivity. The deferred costs of dispersal are likely to be crucial for determining how well patterns of dispersal reflect realized connectivity. Ignoring these deferred costs could lead to inaccurate predictions of spatial population dynamics.

**Key words:** *Brisbane, Australia; Bugula neritina; deferred costs; dispersal condition; dispersal phenotype; landscape structure; larval quality; marine bryozoans; metapopulations; population connectivity.*

## INTRODUCTION

Population connectivity is the outcome of the dispersal of individuals between habitats and their subsequent establishment within habitats (Bowler and Benton 2005, Revilla and Wiegand 2008, Clobert et al. 2009). Connectivity affects the dynamics of spatially structured populations and the persistence of species, as well as influences genetic diversity within populations and species diversity within communities (Lenormand 2002, Hastings and Botsford 2006). Many frameworks exist for estimating connectivity: most are based on the spatial structure of the landscape and the movement of individuals between habitats (Taylor et al. 1993, Tischendorf and Fahrig 2000, Moilanen and Nieminen 2002, Dingle and Drake 2007, Hedgecock et al. 2007, Treml et al. 2008). Dispersal, however, is often costly to the individual. Costs may be paid during or after movement, and interact with both the structure and quality of the habitat, thereby potentially influencing the scales and strength of population connectivity (Bowler

and Benton 2005, Kokko and Lopez-Sepulcre 2006, Revilla and Wiegand 2008, Clobert et al. 2009, Shima et al. 2010). Although many studies consider dispersal costs with regard to the evolution of dispersal (Rousset and Gandon 2002, Ronce 2007), few examine the ecological role of dispersal costs. Several recent reviews have highlighted a major gap in current theory: the lack of empirical tests of how dispersal costs influence the strength of connectivity relevant to populations (Bowler and Benton 2005, Dingle and Drake 2007, Pineda et al. 2007, Ronce 2007, Nathan et al. 2008, Clobert et al. 2009). Failing to account for the ecological role of dispersal costs will at best result in the overestimation of connectivity, and at worst, preclude explanations for complex, distance-independent patterns of connectivity (Marshall et al. 2010, Shima et al. 2010).

Some costs of dispersal are obvious whereas others are subtler. Obvious costs of moving between habitats occur during movement itself, such as mortality from predation, physiological stress, or failing to find a suitable habitat (“immediate costs”; Rousset and Gandon 2002, Yoder et al. 2004). Less obvious are those costs that accrue during movement but are experienced after colonization (“deferred costs”; Stamps et al. 2005). Deferred costs are a particularly relevant, although overlooked, aspect of population connectivity because, for realized connectivity to occur, individuals must not only arrive, but also survive. Even when

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<sup>3</sup> Present address: Department of Environmental Science and Policy, University of California, One Shields Ave., Davis, California 95616 USA.  
E-mail: scburgess@ucdavis.edu

deferred costs do not affect survival, sublethal effects (such as reduced growth rate or fecundity) can influence the consequences of connectivity for population dynamics and persistence, so they must not be neglected (Burgess and Marshall 2001a, Hastings and Botsford 2006). Importantly, deferred costs of dispersal can occur through direct and indirect sources. *Direct* deferred costs can occur when experiences during transit reduce body condition, which then reduces fitness after settlement (Roff 1977, Phillips 2002, Baker and Rao 2004, Pechenik 2006, Hamilton et al. 2008, Shima et al. 2010, Marshall and Morgan 2011). For example, the probability that desert isopods survive after settlement declines with increasing dispersal distance because of dehydration while dispersing (Baker and Rao 2004). Planktotrophic larvae of two species of sand dollar that had experienced metamorphic delays of 4–7 weeks suffered reduced survival as juveniles compared to larvae that metamorphosed soon after becoming competent (Highsmith and Emler 1986). Deferred costs can also occur *indirectly* when individuals immigrate to habitat to which they are less suited (Nosil et al. 2005). For example, seeds and aquatic larvae that are transported by wind or currents incur the risk of landing in poor-quality habitat from which they cannot escape (Ronce 2007). This is especially relevant in “fine-grained” environments, where environments vary within the spatial scale of dispersal. Even organisms that can actively choose habitats can settle in poor-quality habitats and incur indirect deferred costs; individuals with time or energy constraints often become more likely to select lower quality habitat over the duration of dispersal (Ward 1987, Jaenike 1990, Stamps et al. 2005, Elkin and Marshall 2007). Therefore, in organisms that can actively choose habitat, indirect costs also include changes in habitat selection behavior.

Understanding the causes of post-settlement mortality, i.e., after the dispersal phase, is crucial for predicting how well dispersal (potential connectivity) reflects realized connectivity. This mortality will not be independent of the dispersal processes itself, but instead will depend on the relative importance of direct and indirect deferred costs. Direct costs derive from events “carrying over” from the dispersal phase and these costs can increase with dispersal distance, especially when they begin accruing early during movement and accumulate with time (Roff 1977, Verhulst et al. 1997, Baker and Rao 2004, Lin and Batzli 2004). How indirect deferred costs increase with dispersal distance will depend not only on the spatial pattern of habitat qualities, but also on how habitat selection behavior changes during movement. If individuals are more likely to accept poor-quality habitat with increasing dispersal duration, then more individuals could potentially colonize distant poor-quality patches, compared to nearby poor-quality patches. Even if colonization does not increase with distance (which will depend on encounter rates with habitats), time-dependent habitat selection could have

different effects on realized connectivity relative to the case if all individuals had the same likelihood of colonizing poor-quality habitat once encountering it (as might occur in seeds, for example). Importantly, direct and indirect deferred costs may also interact, resulting in potentially nonintuitive patterns that cannot be explained without considering both simultaneously (Moilanen and Hanski 1998, Bonte et al. 2003, Matter et al. 2009). Different types of dispersal costs could therefore mediate the mismatch between potential connectivity and realized connectivity, thereby altering inferences on which local populations are sustained by immigrants or by local retention as well as the role of gene flow in local adaptation (Lenormand 2002).

Here, our aim was to empirically estimate the relative importance of direct and indirect sources of dispersal costs, and then explore how they interact to influence realized population connectivity. We conducted a series of experiments on a marine bryozoan (*Bugula neritina*), and used those data to parameterize a theoretical model of connectivity. We manipulated the direct deferred dispersal costs by varying the length of time that non-feeding larvae spent swimming prior to settlement (and presumably larval energy reserves; Wendt 1998). We manipulated indirect deferred cost by simulating stressful and benign post-settlement environments (surfaces with different orientations) because we found that larvae that experienced a metamorphic delay were more likely to settle in a stressful environment. By combining experimental results in the field and laboratory with a parameterized theoretical model, we show that the costs of dispersal can decouple the relationship between potential and realized population connectivity, which has a number of implications for our understanding and management of spatially structured populations.

## MATERIALS AND METHODS

### *Study species*

We used a marine, arborescent bryozoan, *Bugula neritina* (Bryozoa: Cheilostomata, Linnaeus, 1758) to explore the role of direct and indirect sources of deferred costs. *Bugula neritina* has a cosmopolitan distribution and often occurs on patches of habitat, such as boat hulls, pilings, pontoons, rock walls, or seagrass patches, with a range of orientations. The majority of colonies are reproductively mature within 2–3 weeks after settlement (Wendt 1998), and most colonies live only several months (Keough and Chernoff 1987; S. C. Burgess, *personal observation*). Colonies grow by asexual budding of zooids to form branches, and each branch bifurcates at regular intervals.

*Bugula neritina* release brooded, 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 minutes to 4 hours, although a lower proportion will remain metamorphically competent for at least 1 day in the absence of suitable habitat

(*personal observation*). In laboratory studies, the absence of habitat suitable for settlement forces competent larvae to delay metamorphosis and continue searching, although prolonged larval durations can sometimes reduce post-settlement survival, growth, and fecundity (Wendt 1998, Pechenik 2006). The lowered post-settlement performance associated with extended larval periods presumably occurs because prolonging the larval stage expends maternally derived resources that are otherwise used for metamorphosis and the development of structures to acquire and compete for food and space (Wendt 1998, Pechenik 2006). Therefore, a realistic source of a direct deferred cost of dispersal in *B. neritina* is extending the larval period. In organisms such as *B. neritina*, indirect costs of dispersal occur because individuals often become “desperate” to settle after prolonged larval durations and accept a wider range of settlement cues (Marshall and Keough 2003), which is thought to be a way to offset direct deferred costs (Elkin and Marshall 2007). We used habitat orientation (settlement surfaces facing up or down) as a measure of habitat quality because, in the field, sessile marine invertebrates occur on surfaces with different orientations, which are likely to experience different degrees of water flow, sedimentation, light, and grazing. Because these factors can be a major source of mortality and affect performance, especially in newly settled benthic invertebrates, fitness was expected to be lower on surfaces facing up, compared to surfaces facing down.

#### *General methods*

Larvae were obtained from reproductively mature colonies of *B. neritina* collected from the sides of floating docks at Moreton Bay Boat Club (Brisbane, Queensland, Australia) from May 2008 to June 2009. Colonies were spawned in the laboratory and larvae were measured using standard techniques (Marshall and Keough 2003). Briefly, colonies were held in dark, aerated aquaria at 20–21°C for 48 h before being exposed to bright light to stimulate larval release. Larvae were photographed with a camera (PixeLINK Capture SE, v1.0; PixeLINK, Ottawa, Ontario, Canada) mounted on a dissecting microscope and larval size was estimated by measuring cross-sectional area with image analysis software (Image-Pro Express 5.1; Media Cybernetics, Bethesda, Maryland, USA). Colonies were spawned separately, and then larvae from all colonies were randomly allocated to different dispersal duration treatments. Because larvae are competent to settle upon release, dispersal duration was manipulated by placing larvae in 200 mL of 0.45- $\mu$ m filtered seawater in a 500-mL glass bottle on a mechanical roller (Model 205-RM, Hwashin Technology, Seoul, Korea), which slowly rolled the bottle (40 revolutions per minute) so that larvae were prevented from settling and forced to continue swimming. We manipulated dispersal duration and settlement density over ranges observed in the field (Burgess and Marshall 2011b). All laboratory and field

experiments were repeated multiple times and we refer to each repeat as a “run.” Each run in the laboratory experiments consisted of different batches of adult colonies to obtain larvae and each run was done on a different day.

#### *Experiment 1: Habitat selection in the field*

To investigate which habitat larvae prefer to settle on in the field, the density of settlers was estimated on settlement plates facing either up or down. These experiments were repeated twice in June 2009 at Moreton Bay Boat Club in Brisbane, Australia. We predicted that the density of settlers would be higher on settlement plates facing down, compared to settlement plates facing up. Settlement plates were pre-roughened 21  $\times$  21  $\times$  0.5 mm acetate sheets that were attached with clips to plastic backing panels (600  $\times$  600  $\times$  10 mm). Two replicate settlement plates were attached to the bottom (facing down), and two were attached to the top (facing up), of each of the 8 backing plates (16 settlement plates per habitat treatment). The backing panels were attached to floating pontoons and hung horizontally 1 m below the water surface. Settlement plates were placed in the field at 15:00 hours, retrieved 24 hours later, and transported back to the laboratory in insulated aquaria. Some mortality could have occurred between settlement and subsequent measurement, but, in our experience, mortality is minimal during the first day after settlement in this species and pilot studies indicated minimal mortality during transport (<1%; S. C. Burgess, *unpublished data*). Importantly, later experiments revealed that survival did not differ between individuals on downward-facing surfaces and individuals on upward-facing surfaces (see *Results*). Settlement plates were transported and stored in 250- $\mu$ m filtered seawater so that no additional settlement could occur. The number of *B. neritina* settlers on each settlement plate was counted under a dissecting microscope. Data on settlement density were analyzed using Poisson generalized linear mixed models. Backing panels within each run (16 in total) were modeled as random slopes and intercepts.

#### *Experiment 2: Habitat selection in the laboratory*

To estimate the relationship between dispersal duration and the probability of settling on a good surface, settlement of larvae after various dispersal durations was recorded in settlement choice arenas immersed in seawater. Settlement choice arenas consisted of a surface facing down and up. Arenas were constructed by attaching together the top and bottom of 90 mm diameter plastic petri dishes. The distance between the top and bottom surfaces was 10 mm, so that larvae could potentially encounter and explore both surfaces. Both surfaces of the dishes were pre-roughened with sandpaper and placed in seawater for 3 days to allow a biofilm to develop to encourage settlement. A small hole was drilled in the top of each arena, through which

larvae were gently introduced with a pipette at one larva per arena. The hole was then covered with a reusable adhesive (Blu-tack; Bostik, Fort Wayne, Indiana, USA). The arenas were placed in the dark to eliminate phototactic settlement responses, because light can affect settlement behavior of larvae of this species, as in other species of benthic marine invertebrates. Larval size was measured prior to larvae being introduced into the arenas. Within 30 minutes of measurement, larvae were randomly allocated to arenas. One hour after larvae were allocated to arenas, the top and bottom of the arena were separated and the surface that larvae settled on was recorded (1 for upward, 0 for downward). Larvae were considered to have settled if they were firmly attached and could not be removed using a gentle jet of water from a pipette.

In each of three runs, larvae were allocated to several dispersal duration treatments ranging from 0 to 8 hours. In each dispersal duration treatment, 31 (run 1), 20 (run 2), or 32 (run 3) replicate arenas were used. The probability that larvae settled (on any surface) and the probability that larvae settled on good- or poor-quality surfaces were modeled using a binomial generalized linear mixed model. Run was modeled as a random effect. Larval size was measured in run 1 and was assessed by analyzing this run only. In addition, for each dispersal duration in each run, the proportion of larvae that settled on a downward-facing surface was analyzed using a Pearson's chi-squared test.

#### *Experiment 3: Sinking rates*

We found that larvae preferred to settle on surfaces facing down rather than up in the field, but were more likely to settle on surfaces facing up compared to down with increasing dispersal time in the lab (see *Results*). Thus, we investigated whether this was due to older larvae having greater densities (which could occur if larvae consume buoyant lipids as they age), and therefore being unable to swim upward. Larvae were split into 2–4 dispersal duration treatments (ranging from 0 to 24 hours), depending on the run. After the prescribed dispersal duration, larvae were sacrificed by placing them in 20% formalin (80% seawater) for 1 hour. Larvae were then washed three times in a series of seawater baths and photographed under dissecting microscope to estimate size. Sinking rates were measured in a total of 66 larvae (30 and 36 in each run). Sinking rate was measured by introducing larvae at the top of a 1-L measuring cylinder (length 43.4 cm, diameter 6 cm) filled with 0.45- $\mu$ m filtered seawater and measuring the time taken for larvae to sink a distance of 10.3 cm (from the 1000-mL to the 700-mL mark). Larvae were allowed to sink for 9.3 cm (the distance from the water level to the 1000-mL mark) prior to measurements commencing. Measurements stopped 23.8 cm from the base of the cylinder. Larvae were gently introduced into the water using a pipette and great care was taken to minimize the addition of water

from the pipette. The order in which sinking rate measurements were made was randomized with respect to their dispersal duration treatment. Sinking rates were not influenced by the order in which larvae were measured. Seawater in the cylinder was allowed to stand for at least 24 hours in a temperature-controlled room (at 21°C) before measurements were taken. Data were analyzed using ANOVA, where dispersal duration and larval size were continuous, fixed factors, and run was a random factor.

#### *Experiment 4: Post-settlement performance in different habitat qualities in the field*

To examine how dispersal duration and habitat quality affected post-settlement performance in the field, we used an orthogonal experimental design that measured post-settlement survival, growth, and fecundity of laboratory-settled individuals in the field. Larvae were randomly allocated to either short (0 hours) or long (10 hours in run 1, 8 hours in run 2) dispersal duration treatments. After the prescribed dispersal duration, several larvae were placed into each settlement plate (9 mm diameter, roughened, plastic petri dish), resulting in  $4.54 \pm 1.8$  settlers per dish (mean SE) in both runs. The density of individuals in each dish did not vary among the treatments. Dish was the unit of replication and the number of replicate dishes used in each habitat for each dispersal duration was 7–8 in run 1 and 14–16 in run 2. Settled individuals were marked with a pencil after 1 hour and any larvae that did not settle were discarded. Settlement plates were then transported to the field in insulated aquaria and allocated to either the top (“poor” habitat) or bottom (“good” habitat) of 2 (run 1) or 4 (run 2) backing panels, with all treatments replicated on each backing panel.

Survival, growth, and fecundity were measured after 5 weeks in the field. Survival was estimated as the number of circled individuals that were alive or dead at census and growth was estimated as the number of zooids per colony. The number of zooids,  $z$ , was estimated from counts of the total number of bifurcations on each colony,  $b$ , as  $z = 16b + 8$ , as there are four zooid pairs between each bifurcation and colonies have a regular branching pattern (Keough and Chernoff 1987). Fecundity was estimated as the number of ovicells per colony. An ovicell is a brood chamber, located on a zooid, within which a larva develops and is a good predictor of fecundity.

Survival and the probability of reproducing (presence or absence of ovicells) were modeled using binomial generalized linear mixed models. Growth was modeled using linear mixed models. The data on fecundity contained many zeros (whole-treatment combinations) and were highly skewed (to the right) so could not be analyzed quantitatively. In all models, petri dishes (nested within backing panels, which were nested within runs) were modeled as random intercepts. Dispersal duration and habitat type were treated as continuous

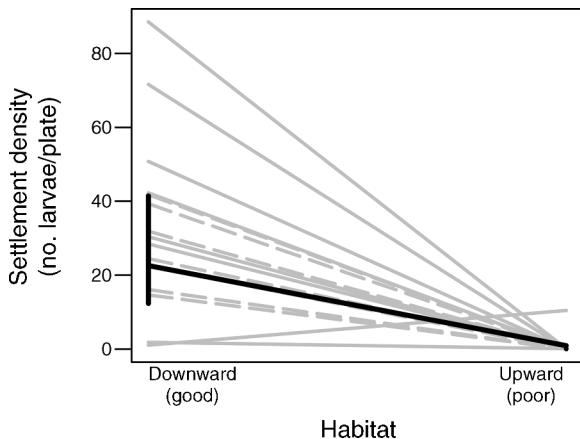


FIG. 1. Density of larvae of the marine bryozoan *Bugula neritina* settling in the field (Moreton Bay Boat Club, Brisbane, Australia), recorded on settlement plates (21 × 21 cm) facing downward (good habitat) and upward (poor habitat) within a 24-h period (Experiment 1). The black line represents the average densities across all backing panels (estimated from a Poisson generalized linear mixed model; endpoint error bars are 95% confidence intervals; the error bar for the upward habitat is shown but is very small). The gray lines represent the conditional means on each backing panel. Solid gray lines are run 1, and dashed gray lines are run 2. Lines are joined to the link backing panels, which contained both upward- and downward-facing surfaces.

and categorical fixed effects, respectively. In all analyses using mixed models, the significance of the fixed parameters was assessed using a likelihood ratio test. Parameter estimates and 95% confidence intervals are also presented. All analyses were performed in R 2.10.1 (R Development Core Team 2009) using the functions “glm” and “lmer.”

*Connectivity model*

In order to understand the sensitivity of population connectivity to direct and indirect deferred costs, we developed a model of connectivity in one dimension (1-D) that incorporated dispersal, habitat selection behavior, and post-settlement performance. The latter two were parameterized using our empirical data. We present the effects of dispersal costs and habitat selection as a distance-dependent ratio between potential connectivity  $p(d,t)$  and realized connectivity  $p(d,t)s(h,t)f(h)$ , in which the latter includes habitat selection  $s(h,t)$  and post-settlement performance  $f(h)$ . We call this ratio a mismatch  $m(d)$  between potential and realized connectivity and define it as

$$m(d) = 1 - \left[ \frac{\int_0^{t_c} p(d,t)s(h,t)f(h)dt}{\int_0^{t_c} p(d,t)dt} \right] \quad (1)$$

where  $p(d,t)$  is the probability distribution for the first time an individual arrives at a given patch distance  $d$  from an origin after time  $t$ :

$$p(d,t) = \frac{1}{2\sqrt{\pi Kt}} e \left[ -\frac{(d-ut)^2}{4Kt} - \lambda t \right] \quad (2)$$

and where  $K$  is a diffusive coefficient, which influences kernel width;  $u$  is an advection coefficient, which influences kernel displacement; and  $\lambda$  is the immediate cost of dispersal (planktonic mortality). We also explored the effects of a delay in the time that costs begin to accrue (as would occur in marine invertebrates with a pre-competent period for example) and the results are presented in the Appendix. The probability of accepting good or poor habitat  $h$  (estimated from Experiment 2, see *Results*;  $\alpha = 1.31$  and  $\beta = -0.27$ ) was

$$s(h,t) = \begin{cases} 0.95 & \text{if habitat } h \text{ is good} \\ \frac{1}{1 + e^{\alpha + \beta t}} & \text{if habitat } h \text{ is poor.} \end{cases} \quad (3)$$

The performance of individuals after settlement was not influenced by direct deferred costs (see *Results*), but differed between good and poor habitat  $h$ . To reflect the 1.7-fold increase in performance in the good habitat compared to the poor habitat (see results from Experiment 4), post-settlement performance was included as

$$f(h) = \begin{cases} 1 & \text{if habitat } h \text{ is good} \\ 0.59 & \text{if habitat } h \text{ is poor.} \end{cases} \quad (4)$$

Our exploration of realized connectivity therefore extends to connectivity where individuals not only survive to reproduction, but also successfully reproduce.

RESULTS

*Experiment 1: Habitat selection in the field*

In the field, settlement onto plates facing down (“good” habitat) was 25 (95% CI = 8.49–73.35) times higher than settlement onto plates facing up (“poor” habitat;  $\chi^2 = 106.61$ ,  $P < 0.001$ ; Fig. 1). Although settlement, on average, was higher into good habitat, proportional differences varied among backing plates ( $\chi^2 = 125.35$ ,  $df = 2$ ,  $P < 0.001$ ).

*Experiment 2: Habitat selection in the laboratory*

*Probability of settlement.*—The probability that larvae settled at all was unrelated to dispersal duration (slope parameter = 0.11 [95% CI = -0.02 to +0.23],  $\chi^2 = 2.92$ ,  $P = 0.09$ ). The average proportion of larvae that settled in each run ranged from 80% in run 3 to 91% in run 1. There was no interaction between dispersal duration and run (deviance = -0.62,  $df = 2$ ,  $P = 0.73$ ). In run 1, the probability that larvae settled was unrelated to larval size (deviance = -0.29,  $df = 1$ ,  $P = 0.59$ ,  $n = 93$  larvae).

*Probability of settling in good or poor habitats.*—The probability that larvae settled on poor surfaces was positively related to dispersal duration: older larvae were more likely to settle on poor habitats than younger larvae (slope parameter = 0.27 [95% CI = 0.16 to 0.38],  $\chi^2 = 25.91$ ,  $P < 0.001$ ; Fig. 2). There was no interaction

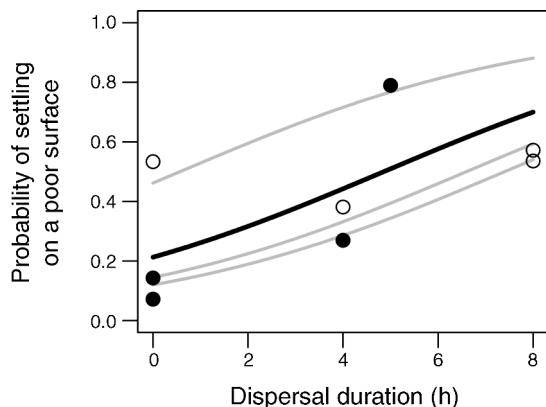


FIG. 2. The probability that *B. neritina* larvae settled on an upward-facing (poor-quality) surface increased with dispersal duration in the laboratory (Experiment 2). The black line represents the average probability across all three runs, estimated from a binomial generalized linear mixed model (raw data are 1's and 0's). Gray lines indicate the conditional mean probability in each run. Circles are proportions calculated from the raw data and are included as a visual guide for the fit of the model. Solid circles indicate where more larvae settled on a particular surface than by chance, which was determined by a Pearson's chi-square test. In each dispersal duration treatment, 31 (run 1), 20 (run 2), or 32 (run 3) replicate arenas were used.

between dispersal duration and run (deviance =  $-0.99$ ,  $df = 2$ ,  $P = 0.61$ ). In run 1 (when larval size was measured), the probability that larvae settled on good or poor surfaces was unrelated to larval size (deviance =  $-2.02$ ,  $df = 1$ ,  $P = 0.155$ ,  $n = 82$  larvae).

The differential settlement of older and younger larvae on different surfaces was driven by different processes among runs. In two of the runs, individuals with short dispersal durations were more likely than by chance to settle on surfaces facing down, whereas individuals with longer dispersal durations showed no such preference for habitat type (solid circles in Fig. 2). In the third run, individuals with short dispersal durations were equally likely to settle on any surface, whereas individuals with longer dispersal durations were more likely to settle on upward-facing surfaces than by chance.

#### Experiment 3: Sinking rates of larvae

Sinking rates of larvae were not influenced by dispersal duration ( $F_{1,63} = 1.81$ ,  $P = 0.183$ ), but differed between runs ( $F_{1,64} = 86.63$ ,  $P < 0.0001$ ). There was no interaction between dispersal duration and run ( $F_{1,1} = 0.009$ ,  $P = 0.98$ ). In run 2, when larval size was measured, there was an interaction between dispersal duration and larval size ( $F_{1,32} = 4.61$ ,  $P = 0.039$ ): for every  $10\,000\text{-}\mu\text{m}^2$  increase in larval size, sinking time increased by 19.13 (95% CI = 1.96–36.3) seconds in larvae with short dispersal durations (0 hours). Sinking time changed very little ( $-3.56$  [95% CI =  $-8.0$ – $15.1$ ]

seconds) with larval size for larvae with long dispersal durations (22 hours).

#### Experiment 4: Post-settlement performance in different habitat qualities in the field

**Survival.**—Settlers survived equally well in both habitats regardless of their dispersal duration. Survival across the six backing plates (from all runs) averaged 79.2% (95% CI = 48.07–84.90).

**Growth.**—Colonies in the good habitat had on average 41.56 (95% CI = 33.74 to 49.73) more zooids than colonies in the poor habitat (Fig. 3). Dispersal duration had neither additive ( $\chi^2 < 0.001$ ,  $P > 0.99$ ) nor interactive effects ( $\chi^2 < 0.001$ ,  $P > 0.99$ ) on the average growth of colonies.

**Fecundity.**—Habitat quality strongly influenced fecundity. After 34 days in the field, ovicells were present on only four (3%) out of the 132 individual colonies alive in the poor habitat. Of those four individuals, three had experienced long dispersal durations (10 hours) and one had experienced a short dispersal duration. These four individuals were all from the same run (run 1). Ovicells were present on 59 (49%) out of the 139 individual colonies alive in the good habitat. The probability of reproducing in the good habitat was not related to dispersal duration ( $\chi^2 = 0.28$ ,  $P = 0.59$ ). Similarly, of those colonies that reproduced, the number of ovicells per colony in the good habitat was also unrelated to dispersal duration ( $\chi^2 < 0.001$ ,  $P > 0.99$ ).

#### Connectivity model

Given that increases in dispersal duration increased the probability that *B. neritina* larvae accepted poor-

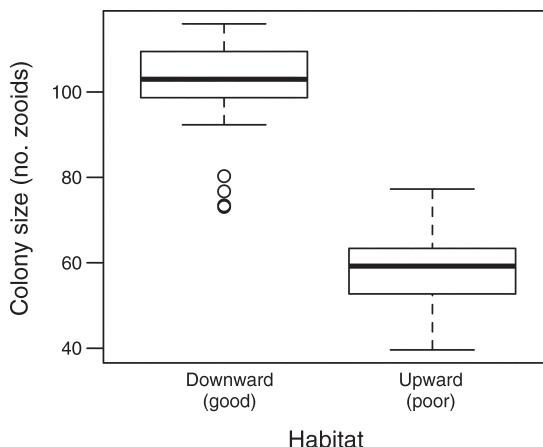


FIG. 3. Boxplot of the size of *B. neritina* colonies (estimated as the number of zooids) in each habitat type after 34 days in the field (Experiment 4). Plotted are the fitted values for each colony from the linear mixed model with dish (nested within backing panel, which was nested within run) as a random effect. The box represents the middle 50% of the data (interquartile range), the line inside the box represents the median, whiskers extend to 1.5 times the interquartile range, and points are outliers.

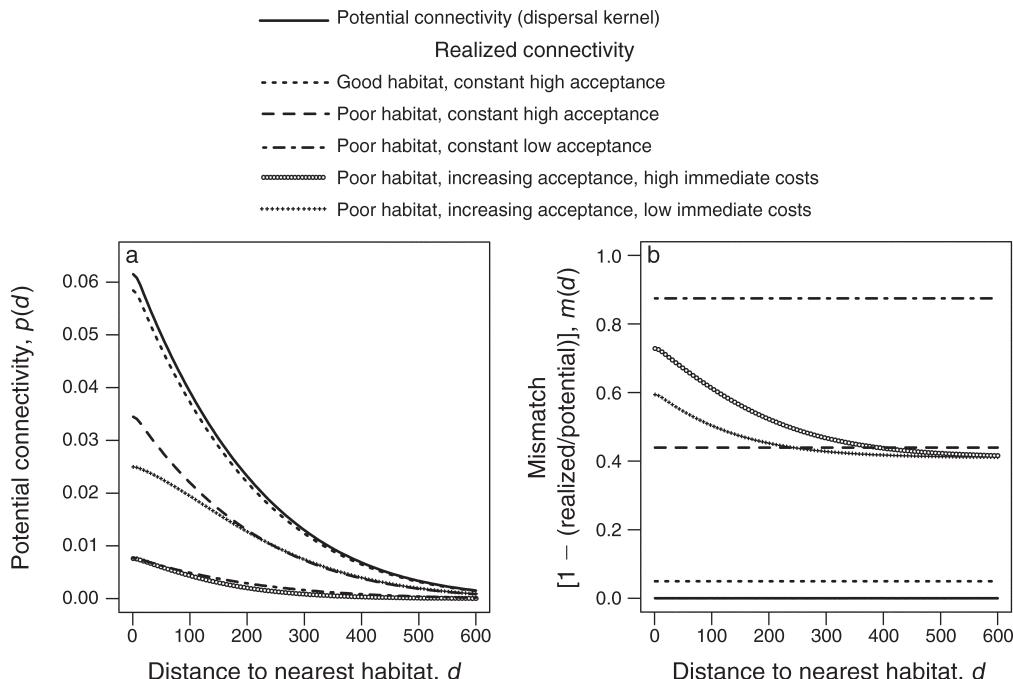


FIG. 4. Plot of model output showing (a) potential and realized connectivity and (b) the mismatch in connectivity (as defined by Eq. 1) for different habitat qualities  $f(h)$  and habitat selection behavior  $s(h,t)$  (“acceptance” once encountering habitat). There is no advection included in these outputs. Including advection, or changing the diffusion coefficient changes panel (a), but changes panel (b) very little. Our empirical results are predicted to result in proportional changes in the mismatches between spatial patterns of dispersal and realized connectivity (solid lines). For low immediate costs,  $\lambda = 0.01$ ; for high immediate costs,  $\lambda = 0.1$ . Also shown is the mismatch when holding acceptance of poor habitat constant at either that for good habitat (0.95), or when  $\beta = 0$  in  $s(h,t)$ . The bottom and middle horizontal lines in panel (b) compare the effect of habitat quality only. The middle and the top horizontal lines in panel (b) compare the effect of accepting poor-quality habitat at different constant rates.

quality habitat (Fig. 2), the relationship between potential and realized connectivity may not be straightforward. We defined a mismatch as 1 minus realized connectivity divided by potential connectivity (Eq. 1). A high mismatch therefore occurs when realized connectivity is a low proportion of potential connectivity. Our theoretical model showed that time-dependent habitat selection behaviors (Fig. 2) resulted in nonlinear mismatches between spatial patterns of potential and realized connectivity (Fig. 4); that is, the proportional differences between realized and potential connectivity changed with distance to the nearest habitat. At shorter distances, the mismatch in poor-quality habitat was as high as  $\sim 70\%$  (i.e., realized connectivity to poor-quality habitats was only  $\sim 30\%$  of potential connectivity). With increasing distances, the mismatch between realized and potential connectivity to poor-quality habitats decreased. The importance of habitat selection behaviors in affecting connectivity decreased as distance increased, such that at greater distances, realized connectivity was similar to a scenario in which only habitat quality influenced realized connectivity. Importantly, nonlinear mismatches were only revealed when considering habitat quality and habitat selection behavior simultaneously (Fig. 4). That is, the habitat selection behavior observed in Fig. 2 had effects on realized connectivity that were

different to the effects of habitat quality or constant habitat selection behavior (straight lines in Fig. 4b).

Our model predicts that mortality during movement (immediate cost) increases the effects of indirect deferred costs (Fig. 4), but has no influence on the mismatch when acceptance of habitat is constant over time. Furthermore, although the width and displacement of the dispersal kernel affected the distance-dependent strength of realized connectivity, they had minor influence on the mismatch between potential and realized connectivity when there were indirect deferred costs of dispersal. Width and displacement of the dispersal kernel had no influence on the mismatch when habitat selection was constant. Nonlinear mismatches still occurred when a pre-competency period was included (Appendix: Fig. A1), although to a lesser extent. Delaying the time at which costs begin accumulating still changed the overall mismatch relative to the effects of habitat quality or constant habitat acceptance behaviors (Appendix).

DISCUSSION

Many previous frameworks for estimating connectivity have focused only on dispersal and assumed that post-dispersal success is unrelated to experiences during dispersal. Useful measures of connectivity require an

understanding of who is surviving and why. Although the need to move beyond numerical responses and focus on phenotypic linkages among life-history stages is widely recognized (Bowler and Benton 2005, Pineda et al. 2007, Revilla and Wiegand 2008, Shima et al. 2010, Marshall and Morgan 2011), a major impediment has been a lack of data combining dispersal experiences and post-dispersal survival (Ronce 2007). We found that older larvae that settled in poor-quality habitat had lower post-settlement performance because of indirect costs mediated through habitat effects rather than a direct effect of prolonged larval durations. When we combined our empirical results with a theoretical model of connectivity, we found that indirect costs that included time-dependent habitat selection behaviors resulted in nonlinear mismatches between spatial patterns of dispersal and realized connectivity. That is, not only did dispersal patterns overestimate realized connectivity when there were deferred dispersal costs, but also the proportional overestimation changed with distance. Our study supports a growing number of recent studies that have been able to explicitly consider how the behavior and traits of individuals, the costs of dispersal, and the demographic condition of subpopulations influences population connectivity (Bowler and Benton 2005, Clobert et al. 2009, Shima et al. 2010).

Our results have implications for understanding how landscape structure influences spatial population dynamics and the effectiveness of networks of protected areas. The spatial pattern of a network of protected areas is often designed to maintain connectivity, with the underlying assumption that increasing the distance between protected or non-protected areas reduces their connectivity because fewer individuals move greater distances (Botsford et al. 2001, Moilanen and Nieminen 2002, Bowler and Benton 2009). Successful connectivity only occurs when individuals survive and reproduce after dispersing between habitats. Previous studies have included the interaction between habitat spacing and quality in estimates of connectivity (Moilanen and Hanski 1998, Bonte et al. 2003, Figueira and Crowder 2006, Matter et al. 2009). For example, habitat quality (density of nectar flower) strongly interacted with the distance between habitat patches to influence immigration rates in a high-altitude butterfly (Matter et al. 2009). The point of departure from previous work showing the interactive effects of habitat spacing and quality is that time-dependent habitat selection behavior can result in nonlinear mismatches between the spacing of poorer quality habitat and realized connectivity to those habitats. For populations of *B. neritina* (an invasive species in many areas) at least, factors that influence larval settlement choices in less than optimal habitat are likely to be important in determining connectivity. Although it is difficult to obtain individual-based estimates of dispersal costs for many species, using unrealistic assumptions of connectivity may yield

inaccurate, and possibly deleterious, predictions of the effectiveness of networks of protected areas.

Previous theoretical considerations of the evolution of habitat selection in time-limited dispersers would predict little benefit to *B. neritina* larvae in decreasing habitat selectivity because indirect costs were greater than direct costs (Ward 1987, Stamps et al. 2005, Elkin and Marshall 2007). As a result, selection should favor larvae that continue to search for downward-facing (good-quality) settlement surfaces, at the expense of direct deferred costs (Elkin and Marshall 2007). In contrast, we found that larvae increasingly settled on poor-quality habitat as they aged (Experiment 2), and this was not due to potential passive effects associated with any changes in larval mass (Experiment 3). As previous theoretical studies also highlight, the benefits of continued searching, however, will reduce as the strength of immediate costs increase or the chance of locating habitat decreases (Ward 1987, Baker and Rao 2004, Stamps et al. 2005). Our findings are consistent with the prediction from previous models that high mortality during dispersal, or low habitat availability, selects for decreased habitat selectivity (Stamps et al. 2005, Elkin and Marshall 2007). The key parameters, however (mortality during dispersal and encounter rates with habitats), are notoriously difficult to measure, especially in marine environments, so it remains unknown exactly why larvae increasingly settled on poor-quality habitat as they aged, despite stronger indirect than direct deferred costs. One reason why larvae increasingly settled on poor-quality habitat as they aged could be that larvae with lower energy reserves were weaker swimmers and had a reduced ability to swim upward to access good habitat, but this remains untested.

That settlement density in the field was higher on downward than upward surfaces raises the potential for an additional cost to dispersal—settling in good habitats may not be favored if good-quality habitat is crowded (Fretwell 1972, Kokko and Lopez-Sepulcre 2007, Johnson 2008). If settlement densities are consistently higher in good habitats (Fig. 1) and there is strong negative density dependence (Johnson 2008, Burgess and Marshall 2011a), then the costs of settling on poor surfaces may be offset by being at relatively lower densities. Individuals in poor habitats may not experience greater deferred costs if the higher density in good habitats is enough to equalize any fitness differential between habitats. Previous results on *B. neritina* indicate that density has little influence on survival on downward surfaces but strongly influences the size and number of offspring (Allen et al. 2008), especially after longer dispersal durations (Burgess and Marshall 2011a). Potential connectivity is increased when more individuals are released. Releasing more individuals does not necessarily guarantee greater realized connectivity (Watson et al. 2010), but could influence the how costs of dispersal manifest if there is density-dependent post-

settlement survival. An important next step, therefore, would be to estimate the three-way interaction between habitat quality, dispersal duration, and settlement density.

Our results are likely to be relevant to a range of organisms where multiple deferred costs of dispersal probably manifest in a similar way to that shown here (Roff 1977, Phillips 2002, Baker and Rao 2004, Stamps et al. 2005). Our results are less likely to apply to organisms that can avoid incurring deferred costs during dispersal (e.g., individuals that can feed under conditions of abundant food). Still, our work here moves us closer to understanding the ecological role of dispersal costs in population dynamics more generally and represents a link between often conflicting estimates of connectivity derived from tracking individuals vs. population genetic structure (Hedgcock et al. 2007). More empirical studies on the species- or taxa-specific sources of deferred costs are required if we are to better link predictions from theoretical models to the species for which they are intended.

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#### SUPPLEMENTAL MATERIAL

##### Appendix

The effects of dispersal costs and habitat selection on realized connectivity in marine invertebrates with non-feeding larvae and a pre-competent larval stage (*Ecological Archives* E093-121-A1).