



Natal habitat conditions have carryover effects on dispersal capacity and behavior

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Abstract. Local habitat quality affects regional dynamics, including metapopulation persistence and speciation, by altering dispersal. However, most previous studies have not been able to determine whether dispersal is more strongly affected by habitat quality experienced at the dispersal stage, or carryover effects of habitat quality from previous life stages. Strong carryover effects will cause dispersal to be temporally disconnected from its drivers, altering the impact of dispersal on metapopulation dynamics, and potentially complicating empirical estimates of context-dependent dispersal. Here, we used a fully factorial mesocosm experiment to assess how both habitat quality experienced during development and at adulthood affected emigration in adult backswimmers (*Notonecta undulata*). We found strong carryover effects of natal habitat quality on dispersal; individuals from high-quality natal environments had higher emigration rates than individuals from low-quality natal environments. However, emigration did not depend on adult habitat quality. This suggests that conditions experienced during development can outweigh the effects of habitat quality at later life stages, resulting in time lags between environmental triggers and the onset of dispersal behavior. If there are critical life stages at which dispersal rates are determined, habitat quality at those stages may have outsized impacts on biological dynamics in spatiotemporally variable landscapes.

Key words: carryover effects; context-dependent dispersal; dispersal; habitat quality; *Notonecta undulata*.

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INTRODUCTION

Understanding the causes of dispersal behavior and how dispersal varies among patches in the landscape is vital because dispersal shapes multiple aspects of the ecology and evolution of species. Dispersal among habitat patches influences metapopulation persistence (Kuno 1981), local adaptation (Holt and Gomulkiewicz 1997, Rasanen and Hendry 2008), and interspecific interactions including the coexistence of species with competitors, predators, and parasites (Sabelis and Diekmann 1988, Comins and Hassell 1996). The habitat conditions organisms experience influence

the costs and benefits associated with dispersal, and thus affect the number and phenotypes of emigrants and settlers (Bowler and Benton 2005, Clobert et al. 2012). One way in which habitat conditions can influence dispersal is via carryover effects, whereby conditions experienced during development affect the capacity and motivation for dispersal in a subsequent life stage (Benard and McCauley 2008, O'Connor et al. 2014). For example, when the potato tuberworm (*Phthorimaea operculella*) is reared on a low-quality host plant, they are more likely to disperse as adults, and dispersers are more likely to have traits that reduce the cost of flight including low wing

loading and high lipid content (Coll and Yuval 2004). This apparent increased investment in dispersal-related traits may facilitate escape from low-quality habitats.

The effects of natal habitat conditions on dispersal will depend on ecological context and therefore may differ among systems (Benard and McCauley 2008). Individuals should be motivated to disperse away from low-quality habitats. This may promote investment into dispersal capacity (e.g., wings, lipid reserves) and result in higher emigration from low-quality habitats (Harada et al. 1997, Coll and Yuval 2004, Dmitriew et al. 2009). However, low-quality habitats may also constrain investment into dispersal capacity, resulting in low dispersal rates even if motivation to disperse is high (Anholt 1990, Lens and Dhondt 1994, Harada and Spence 2000, Chelgren et al. 2006, O'Sullivan et al. 2014). These opposing effects may occur at different points along a continuum of natal habitat quality; empirical evidence suggests that organisms may increase investment in dispersal capacity as natal habitat quality decreases (Johnson 1965, Harada et al. 1997, Dmitriew et al. 2009), but very low-quality habitats may produce individuals that do not have sufficient resources to develop dispersal traits. For example, Muraji et al. (1989) showed that when the wing dimorphic, semi-aquatic insect, *Microvelia douglasi*, is reared at high densities, they are more likely to develop into winged adults. However, when they are food limited during development, very few individuals produce wings and the effect of density on wing development disappears. Negative correlations between dispersal motivation and dispersal capacity along a continuum of natal habitat quality may often result in non-linear relationships between habitat quality and dispersal (Benard and McCauley 2008, Gyllenberg et al. 2008).

Heterogeneous habitat quality leading to asymmetry in the number or phenotypes of emigrants and immigrants among patches has wide-reaching effects on ecological dynamics. For example, Vuilleumier and Possingham (2006) found that when habitat patches have asymmetrical colonization rates, the risk of metapopulation extinction increases. Moreover, a larger number of connected patches are required for the metapopulation to be viable when dispersal rates

are asymmetric. Habitat quality effects on the phenotype of dispersers can also influence ecological dynamics. For example, Van Allen and Rudolf (2013) found that mealworm beetles (*Tribolium castaneum*) that had developed in high-quality habitats had higher population growth rates in their colonized patches than beetles that had developed in low-quality habitats. Further, patches established with beetles from high-quality habitats had higher carrying capacities, and this effect lasted for multiple generations after the initial colonization event. Hence, understanding the effect of habitat quality on dispersal is an important question in ecology, and understanding these effects will provide novel insights into how dispersal affects population dynamics and stability.

One aspect of this question that has historically been overlooked is the timing of the dispersal response to changes in habitat quality. If conditions experienced at one life stage often have carryover effects on dispersal in subsequent life stages, then the factors shaping dispersal may be temporally disconnected from the dispersal period itself. This has important implications for theoretical dispersal models; time lags between changes in habitat quality and the resulting dispersal behavior could fundamentally change the predicted consequences of dispersal for ecological processes including metapopulation persistence and synchrony (Benard and McCauley 2008). Temporal disconnects can also cause difficulty for studies attempting to empirically estimate the effects of environmental factors on dispersal and may result in the overestimation of the variance in effect sizes across studies. Yet, very few studies have considered carryover effects on dispersal (Benard and McCauley 2008) and, to our knowledge, only one study has attempted to disentangle the carryover effects of past natal habitat from the effects of the habitat experienced at the dispersal stage. Van Allen and Bhavsar (2014) found that both natal and current habitat conditions influenced emigration rates, as well as the strength of density dependence in the dispersal response. This single study suggests that carryover effects of habitat quality at early life stages influence dispersal in combination with current habitat quality. We therefore require additional studies that measure the dispersal response to habitat conditions experienced at

multiple life stages and determine whether carry-over effects are a common phenomenon influencing dispersal across taxonomic groups.

Carryover effects may produce time lags between the trigger of dispersal and the dispersal behavior itself, but we also expect that habitat quality experienced at different life stages may have different types of effects on dispersal capacity and motivation (De Meester and Bonte 2010). For example, natal conditions determine structural body size (Anholt 1990, Chelgren et al. 2006), which is often an important factor influencing dispersal capacity in intra- and interspecific comparisons (Beck and Congdon 2000, O'Sullivan et al. 2014, Stevens et al. 2014). In taxa in which structural body size and morphology (e.g., wing presence or size) is fixed at adulthood, conditions experienced after maturity cannot influence dispersal through effects on morphology. Habitat quality experienced during adulthood likely influences more labile aspects of dispersal capacity (e.g., lipid reserves; Baines et al. 2015), but its impacts on dispersal motivation are probably more important than effects on capacity at this life stage. Finally, changes in habitat quality through time or across life stages may influence dispersal propensity. For example, experience in the natal habitat may influence the perception of habitat quality later in life (Stamps et al. 2009) and therefore influence dispersal motivation. Understanding how individual phenotypic variation related to natal habitat conditions (e.g., variation in body size) interacts with habitat conditions experienced at the dispersal stage is important for understanding dispersal in spatiotemporally variable environments.

In this study, we tested whether natal habitat conditions interacted with adult habitat quality to determine emigration rates in adults using a full factorial experiment on the backswimmer (*Notonecta undulata*). Furthermore, we measured the effect of natal habitat quality on dispersal capacity (body size, lipid content, protein content, and wing morphology), to test whether individual variation in these traits could explain variation in dispersal behavior. We predicted that emigration rates would increase with decreasing adult habitat quality, but that the expression of this dispersal behavior would depend on natal habitat quality. Specifically, we predicted that emigration out of high-quality adult patches

should be low overall, and not dependent on natal patch quality, whereas motivation to disperse out of low-quality adult patches should be high, and dispersal probability should increase with increasing dispersal capacity, which we predicted would be a positive function of natal habitat quality. Therefore, we expected mean emigration rates in the treatment groups to rank in the following order (in order from highest to lowest emigration rate): (1) high natal/low adult habitat quality, (2) low natal/low adult habitat quality, (3) high natal/high adult habitat quality, and (4) low natal/high adult habitat quality. In addition, we predicted that within a given treatment, large individuals should have higher emigration probabilities because they have higher dispersal capacity than small individuals, and so will be more likely to attempt dispersal.

MATERIALS AND METHODS

Study system

Notonecta spp. are semi-aquatic heteropterans that live in lakes, streams, and ponds. They swim under the water but breathe air at the surface. *Notonecta* are carnivores which eat a variety of aquatic prey (including zooplankton and mosquito larvae), but also scavenge for dead animals on the water surface. *Notonecta* undergo five juvenile instars which are wingless and restricted to the body of water in which they were oviposited. Adult notonectids have wings and can disperse between water bodies by flight. *Notonecta undulata* lives in ponds across North America. They are facultative dispersers and increase dispersal rates when conditions are poor (Baines et al. 2014). All individuals in the populations studied here appear to be fully developed wings and wing muscles for their entire adult lives (C. Baines, unpublished data).

Manipulating natal habitat quality

We collected third- and fourth-instar *N. undulata* from two fishless ponds at the University of Toronto's Koffler Scientific Reserve (KSR) in Ontario, Canada, from 11 to 17 July 2017. On the day they were collected, they were placed individually in plastic cups (diameter, 11 cm; height, 9 cm) filled with ~250 mL of dechlorinated well water. The cups were placed on shelves in the laboratory at KSR (mean water temperature, 19°C).

We randomly assigned notonectids to one of two diet treatments: high natal quality (306 juveniles) or low natal quality (432 juveniles). Juveniles in the high-quality treatment were fed a mixture of zooplankton and mosquito larvae every day (approximately 7 mosquito larvae and 52 zooplankton daily). This amount of food corresponds to approximately the maximum amount they can eat in a single day. Juveniles in the low-quality treatment were fed the same food mixture two of every three days but were starved the third day. Similar types of diet regimes have been used previously to manipulate food availability in heteropterans (Muraji et al. 1989). This protocol ensured that individuals in the low-quality treatment were receiving less food and experiencing periods in which they perceived food availability to be low. This feeding regime may also be similar to conditions notonectids experience in natural ponds: long periods with no or low food availability, followed by a large meal.

We monitored all cups daily and recorded the date of death of any individuals that died, and the date that each individual molted to the adult stage. Once most (>95%) of the individuals had matured, we ended the diet manipulation. On 31 August and 1 September 2017, we recorded the sex of each adult and measured fresh adult body mass to the nearest milligram (VWR 403B scale (VWR International, Radnor, Pennsylvania, USA)). We randomly selected 27 individuals from the high-quality natal treatment and 16 individuals from the low-quality natal treatment, and preserved them in 70% ethanol, in order to measure the effects of the juvenile diet treatment on dispersal traits (body condition, body size, wing morphology).

Dispersal experiment

We measured emigration probability using a mesocosm experiment in the field at KSR. We marked each notonectid by writing a unique four-digit number on their hemelytra using a Sharpie permanent marker, in order to track individual dispersal behavior. On 1 September 2017, we placed 10 notonectids from the high-quality natal treatment or 10 from the low-quality natal treatment in each of 18 tanks (19 L) filled with dechlorinated well water. Notonectids from the high and low-quality natal treatments were separated into different tanks to minimize cannibalism. Notonectids exhibit size-structured intraguild predation

(Sih 1982; I. M. Ferzoco, *personal communication*), and individuals from the low-quality natal treatment were smaller than individuals from the high-quality natal treatment.

Notonectids were randomly chosen from the natal habitat treatments and assigned to adult tanks. Each tank had structures made out of fiberglass mesh and plastic ribbon to provide refuge. We randomly assigned each tank to one of three adult habitat quality treatments (low, medium, or high food availability). Low, medium, and high adult treatments received food (zooplankton) at a ratio of 1:3:9 units, respectively, per day (1 food unit was approximately 700 zooplankton). Therefore, the density of prey (no. of prey per unit volume of water) in the low-quality adult treatment was lower than prey density in the juvenile diet, and the density of prey in the high-quality adult treatment was greater than that in the juvenile diet. We covered the tanks for two days to allow notonectids to acclimate to their new environments. On 3 September 2017, we randomly selected one notonectid from each tank and preserved it in 70% ethanol in order to estimate the effects of the adult habitat quality treatments on body condition. We took this sample before any dispersal occurred so that we could estimate the effects of adult habitat quality treatment on a random sample of notonectids, without the potentially confounding effects of mass-dependent dispersal.

On 3 September 2017, we removed the covers from the mesocosm tanks and allowed notonectids to disperse. Every three days from 6 September to 15 September 2017, we recorded the ID numbers of each individual remaining in the tanks, as well as the ID numbers of dead individuals. Notonectids that were missing from the tanks were assumed to have dispersed by flight (we did not attempt to recapture dispersers, and no notonectids flew from one mesocosm into another). Dispersers can be distinguished from cannibalized individuals because notonectids are piercing, sucking predators that leave the exoskeletons of their prey whole, so we were able to read the ID numbers of cannibalized individuals. At the end of the experiment, all remaining notonectids were preserved in 70% ethanol.

Measurement of dispersal capacity

To estimate the effects of the natal treatment on dispersal capacity, we measured several traits

in individuals that were preserved immediately after the juvenile diet manipulation was terminated: body size, dry body mass, dry lipid mass, dry protein mass, and wing area. We took digital photographs of each individual and measured pronotum width as a proxy for body size (C. Baines, *unpublished data*) using ImageJ (Schneider et al. 2012). We also photographed the right wing of each notonectid, after removing it from the rest of the body. We measured the area of each wing using ImageJ. We then measured dry body mass, dry lipid mass, and dry protein mass using the same methods as Baines et al. (2015). In brief, we dehydrated the notonectids to a constant mass in a drying oven and weighed them to the nearest 0.01 mg using a Mettler AE240 scale (Mettler Toledo, Columbus, Ohio, USA). We used chloroform *redux* to dissolve triglyceride fat, and then dried and weighed the notonectids again. Finally, we submerged the notonectids in 0.2 mol/L potassium hydroxide to dissolve protein, and then dried and weighed them a final time. Dry lipid mass was calculated as the difference between dry body mass and dry fatless mass, and dry protein mass was calculated as the difference between dry fatless mass and dry fatless, proteinless mass. The same person took all of the measurements of mass, body size, and wing area and was blind to the sex and treatment of the notonectids.

We estimated the effect of the adult habitat quality treatment on body condition by measuring the dry body mass, dry lipid mass, and dry protein mass of individuals preserved on 3 September 2017 (after the acclimation period in the adult tanks but before the dispersal period) and a random subset of those remaining on 15 September 2017 (after the dispersal period). These traits were measured as described above.

Statistical analysis

To test whether natal habitat quality influenced structural body size, we used an ANOVA on the pre (individuals preserved immediately after the juvenile diet manipulation) samples. We used body width as the response, and natal habitat quality, sex, and their interaction as predictors.

To test whether natal habitat quality influenced body mass, we used an ANOVA on the pre samples. We used dry body mass as the response and natal habitat quality, sex, and their

interaction as predictors. Using fresh mass as the response variable gave similar results (data not shown).

We tested whether body mass changed, while notonectids were in the adult tanks using an ANOVA with dry body mass as the response variable, and natal habitat quality, sex, date of preservation, and the two-way interactions between natal habitat quality and date of preservation, and sex and date of preservation as predictors. There was a significant interaction between natal habitat quality and the date of preservation on dry body mass, so we performed post hoc tests to examine whether the high and low natal quality treatments both increased in body mass while in the adult tanks. We used a Bonferroni corrected $\alpha = 0.025$ to account for multiple comparisons.

We tested whether the quality of the adult habitat influenced dry body mass by conducting a linear mixed model (LMM) on the post samples (individuals who were used in the dispersal experiment, but did not disperse, and were preserved at the end of the experiment). We used dry body mass as the response variable, and adult habitat quality, natal habitat quality, sex, and all two-way interactions as fixed predictors. Mesocosm tank was used as a random effect. The LMM was built using the *lme4* package in R (Bates et al. 2015).

To test whether wing area depended on natal habitat quality, we conducted an ANCOVA on the pre samples. We used wing area as the response, and natal habitat quality, fresh body mass, and their interaction as predictors. We used fresh mass as a covariate when analyzing wing area rather than dry mass because fresh mass is more relevant to their actual flight ability.

To test the effects of natal and adult habitat quality on dispersal probability, we built a generalized linear mixed model with a binomial error structure and a logit link using the *lme4* package in R (Bates et al. 2015). We used dispersal status at the end of the experiment (dispersed or did not disperse) as the response variable. We included fresh body mass, sex, natal habitat quality, adult habitat quality, and the interaction between natal and adult habitat quality as fixed predictors. We did not perform a full interaction model because sample sizes were insufficient to handle a large number of predictors. We included the identity of

the adult (dispersal) tank and adult age (days since adult emergence) as random effects. Age was included in the model because insects may be unable to fly for several days after emergence (Johnson 1969), and so time since emergence may explain some variation in dispersal probability. Individuals that died during the dispersal experiment (37 in total) were excluded from the analysis. Therefore, our analysis included 125 individuals, 20 of which were dispersers. In addition, we calculated the odds ratio for dispersal in the high vs. low natal habitat treatments using a standard formula; odds ratio = (number of HN dispersers \times number of LN non-dispersers) / (number of HN non-dispersers \times number of LN dispersers), where HN = high natal habitat quality treatment, and LN = low natal habitat quality treatment.

The significance of all terms was evaluated using type II sum of squares. Nonsignificant interaction terms ($P > 0.05$) were removed before evaluating the significance of main effects. All analyses were conducted in R v 3.3.3 (R Core Team 2017).

RESULTS

Effects of habitat quality on survival, development rate, body size, and body composition

The natal habitat quality treatment had large effects on notonectid survival and development. Individuals from the high-quality natal treatment had higher survival ($\chi^2_1 = 165.2$, $P < 0.0001$; Appendix S1: Fig. S1) and developed faster ($\chi^2_1 = 162.2$, $P < 0.0001$; Appendix S1: Fig. S2) than individuals from the low-quality natal treatment.

Immediately after the juvenile diet manipulation, notonectids reared in the high-quality natal environment were larger ($F_{1,37} = 9.96$, $P = 0.003$; Fig. 1), and heavier ($F_{1,37} = 47.16$, $P < 0.0001$; Fig. 2A) than individuals in the low-quality natal treatment. Total wing area increased with fresh body mass ($F_{1,18} = 44.00$, $P < 0.0001$; Fig. 3), but after controlling for body mass, natal habitat quality had no effect on wing area ($F_{1,18} = 1.30$, $P = 0.27$; Fig. 3).

There was an interaction between timing of preservation and natal treatment on body mass ($F_{2, 111} = 5.42$, $P = 0.0057$; Fig. 2A, C). Post hoc tests revealed that notonectids from the low-quality natal treatment gained weight during the

dispersal experiment, but notonectids from the high-quality natal treatment did not (low natal: $F_{2,52} = 11.43$, $P = 0.0001$; high natal: $F_{2,60} = 0.39$, $P = 0.68$; Fig. 2A, C). As a result, by the end of the experiment, the difference in body mass between the high and low natal habitat treatments was no longer significant ($\chi^2_1 = 2.64$, $P = 0.10$; Fig. 2C). Body mass was a positive function of adult habitat quality ($\chi^2_2 = 9.23$, $P = 0.0099$; Fig. 2C).

Lipid mass and protein mass were both positively related to total body mass (Appendix S1). After controlling for differences in total body mass, the effects of natal and adult habitat quality on lipid and protein mass were minimal. Further details on the statistical analysis and results for body composition can be found in Appendix S1.

Dispersal

Notonectids from the high-quality natal habitat were more likely to disperse than those from the low-quality natal habitat ($\chi^2_1 = 6.89$, $P = 0.008$; Figs. 4, 5). The odds ratio for dispersal for individuals in the high natal habitat quality treatment compared to individuals in the low natal treatment was 5.78. Overall, the probability of dispersal increased with body mass (fresh body mass: $\chi^2_1 = 3.91$, $P = 0.048$; Fig. 4). There was no main effect of adult habitat quality on dispersal ($\chi^2_2 = 0.0051$, $P = 0.997$; Fig. 5), and no interaction between natal habitat quality and adult habitat quality ($\chi^2_2 = 1.69$, $P = 0.43$; Fig. 5). Males and females did not significantly differ in

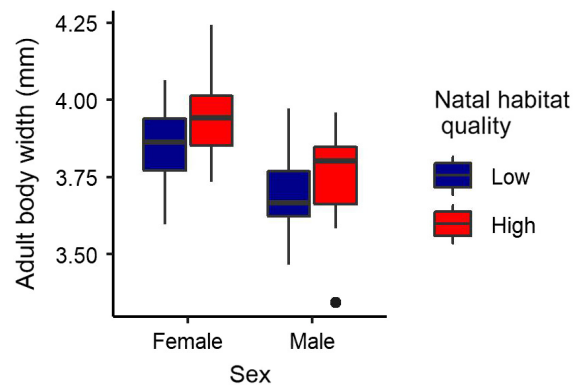


Fig. 1. Body width (mm) of female and male notonectids in both natal habitat quality treatments. Results shown are from the pre samples (animals that were preserved immediately after the juvenile diet manipulation).

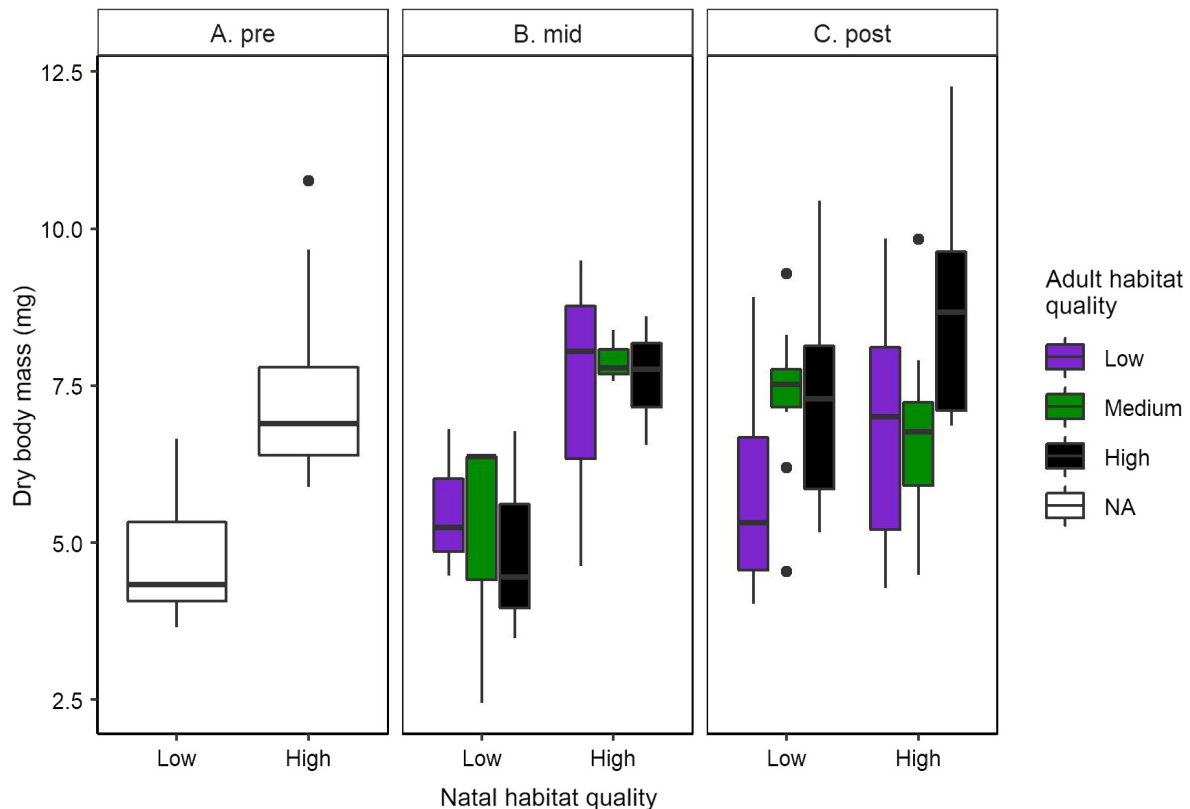


Fig. 2. Dry body mass (mg) as a function of natal habitat quality, adult habitat quality, and the time at which the notonectids were preserved. (A) pre indicates animals that were preserved immediately after the juvenile diet manipulation. (B) mid indicates animals that were preserved after the acclimation period in the adult tanks, but before the dispersal experiment. (C) post indicates animals that were preserved after the dispersal experiment.

dispersal probability ($\chi^2_1 = 3.22$, $P = 0.073$; Appendix S1: Fig. S7).

DISCUSSION

Natal habitat quality had strong effects on dispersal capacity and dispersal probability; notonectids in the high-quality natal treatment were larger, heavier, and more likely to disperse (the odds of dispersal were more than five times higher for individuals from the high natal habitat quality treatment than for those from the low natal habitat quality treatment). This suggests that low-quality natal habitat constrains investment in dispersal capacity and thereby reduces dispersal rates. Our results are congruent with previous studies that have found that small body size resulting from low food availability during development can decrease dispersal probability

(Anholt 1990, Chelgren et al. 2006, Van Allen and Bhavsar 2014), or lead to delayed dispersal (Nunes and Holekamp 1996). Reduced or delayed dispersal can negatively affect fitness. For example, Spear et al. (1998) found that philopatric western gulls (*Larus occidentalis*) experienced higher fitness costs (lower survival in males and lower reproductive success in females) than dispersive gulls, and Lens and Dhondt (1994) found that late dispersers were less likely to settle in high-quality habitats than early dispersers.

Our study suggests that the developmental environment is an important determinant of dispersal rates in notonectids. We found that low-quality habitat patches produce fewer dispersers, and therefore likely contribute less to demographic and genetic connectivity than high-quality habitat patches. This may have important consequences for ecological and evolutionary

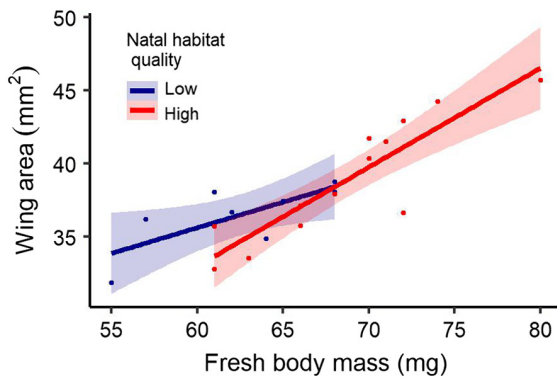


Fig. 3. Wing area (mm²) as a function of fresh body mass (mg) and natal habitat quality. All data shown are from pre samples (animals that were preserved immediately after the juvenile diet manipulation). Lines and bands represent mean wing area \pm 95% confidence intervals as a function of fresh body mass and natal habitat quality.

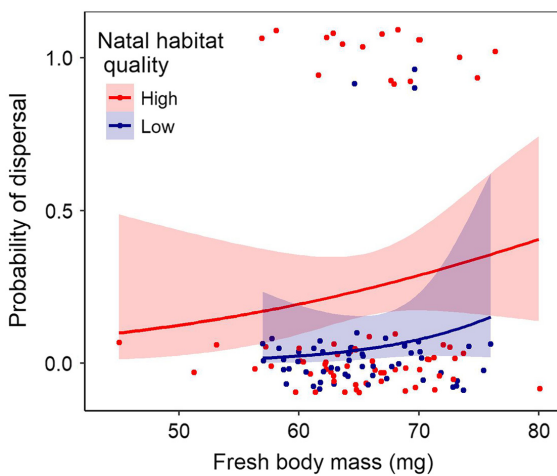


Fig. 4. Dispersal status at the end of the experiment for each individual notonectid, as a function of fresh body mass, and natal habitat quality. Each point represents an individual. Note that individuals either dispersed ($y = 1$) or did not disperse ($y = 0$), but points are jittered with respect to the y -axis to improve visibility. Lines and bands represent the probability of dispersal \pm 95% confidence intervals as a function of fresh body mass and natal habitat quality. Regression lines were generated using a generalized linear model with a binomial error structure.

dynamics. For example, asymmetries in the number of dispersers each patch contributes may increase the probability of metapopulation extinction (Vuilleumier and Possingham 2006). If

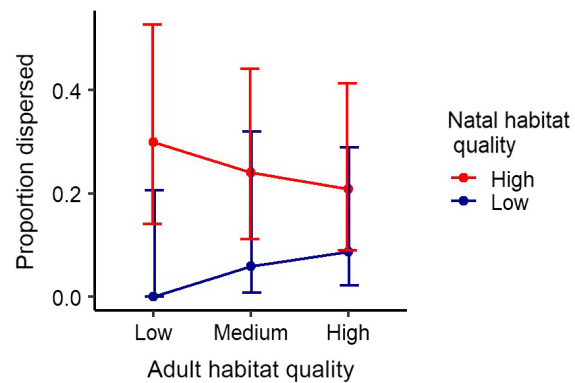


Fig. 5. Proportion of notonectids dispersed \pm 95% confidence intervals for each natal habitat quality \times adult habitat quality treatment.

individuals in low-quality patches are unable to disperse because of their low dispersal capacity, this may also lead to increased extinction of lineages as the result of being trapped in low-quality patches subject to stochastic extinction. Asymmetries in dispersal rates may also influence local adaptation. For example, in spatially heterogeneous landscapes, large numbers of dispersers from high-quality habitat types may impede the rate of adaptation to low-quality habitat types (Rasanen and Hendry 2008).

Contrary to our prediction, adult habitat treatment did not influence dispersal probability, and there was no interaction between natal and adult habitat treatments. This is surprising given that previous studies have observed that habitat quality at the dispersal stage influences dispersal probability (Baines et al. 2014, Van Allen and Bhavsar 2014), and that the adult habitat treatment in our study had a strong enough influence on body mass that effects were measurable after only two weeks (the duration of the time notonectids were in the adult tanks). There are several potential explanations for the lack of an effect of adult habitat quality on dispersal. It is possible that notonectids perceived the adult mesocosms to be poor quality regardless of adult habitat treatment because the mesocosms were smaller and had lower prey diversity than typical notonectid habitats. In this case, they may all have been motivated to disperse, but some (mostly from the low-quality natal habitats) were prevented from dispersing by insufficient dispersal capacity. Since the notonectids from the low-

quality natal treatment gained weight (and lipid mass; Appendix S1) during the dispersal experiment, but still had low dispersal rates, the constraint on dispersal capacity could be due to small structural body sizes, or improperly developed flight musculature. Another possible explanation is that two weeks of low food availability may not trigger dispersal in notonectids. Notonectids scavenge for dead arthropods on the surface of the water and may go long periods with low food availability, followed by a large scavenged meal. Therefore, dispersal in notonectids may not be triggered unless prey densities are low for a longer period of time than the duration of this experiment. Finally, food availability may influence dispersal probability, but not within the range of prey densities tested in this experiment.

If natal habitat quality tends to have large effects on dispersal, then temporally variable landscapes may exhibit only weak relationships between dispersal rates and concurrent habitat quality. This may help to explain some observations in the empirical literature. For example, dispersal generally exhibits positive density dependence (Johnson 1965, De Meester and Bonte 2010, Nowicki and Vrabec 2011, Baines et al. 2014), but several studies have reported no relationship between dispersal and density (Arcese 1989, Keppie and Towers 1992, Gaillard et al. 2008). These null relationships could be due to time lags in dispersal responses to natal population density. The effects of spatiotemporal variability on dispersal evolution have been well studied (Roff 1975, McPeck and Holt 1992, Mathias et al. 2001, Leturque and Rousset 2002, Kun and Scheuring 2006), but the carryover effects of natal habitat conditions on dispersal in subsequent life stages have received less attention (Benard and McCauley 2008). Modeling carryover effects in spatiotemporally variable landscapes would be a useful line of future research that may provide new insights into dispersal behavior and explain dispersal patterns that currently remain poorly understood.

In our study, dispersal probability was a positive function of body mass. This was evident from the fact that notonectids from the high-quality natal treatment were heavier and had higher dispersal rates. Additional evidence of a positive body mass–dispersal association comes from the observation that after controlling for natal and

adult habitat treatments, individuals with high body mass were more likely to disperse than small individuals. This positive body mass-dependent dispersal is consistent with previous studies (Holekamp 1986, Wahlström and Liberg 1995, Debeffe et al. 2012, Selonen et al. 2012). These results indicate that in notonectids, dispersers are expected to be disproportionately sampled from high-quality patches and are expected to have higher body mass than the metapopulation average. Since body size is positively correlated with reproductive success in insects (Honěk 1993, Wiklund and Kaitala 1995), positive mass-dependent dispersal may have consequences for metapopulation dynamics. For example, heavy dispersers may contribute more to rescue effects (Brown and Kodric-Brown 1977) and gene flow than would be expected if we assumed that dispersers were a random sample of the metapopulation. This effect may be amplified if large dispersers have higher immigration success (Bonte et al. 2011, Remy et al. 2011, O'Sullivan et al. 2014).

Spatial variation in habitat quality that results in asymmetries in dispersal rates between habitat patches can influence ecological and evolutionary processes including metapopulation persistence and local adaptation. Here, we show that carryover effects of habitat quality experienced during juvenile development influenced dispersal capacity and probability at the adult stage. However, although conditions experienced at the adult stage may have influenced dispersal capacity through effects on body mass, adult habitat quality did not influence dispersal probability. Moreover, we found that dispersal probability was a positive function of body mass. These results indicate that high-quality natal patches contribute more to demographic and genetic connectivity than low-quality natal patches. Variation among patches in resource availability during juvenile development and its effects on traits such as body size is likely to be an important determinant of dispersal rates and therefore influence ecological and evolutionary dynamics in metapopulations.

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