Consequences of variable larval dispersal pathways and resulting phenotypic mixtures to the dynamics of marine metapopulations

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Larval dispersal can connect distant subpopulations, with important implications for marine population dynamics and persistence, biodiversity conservation and fisheries management. However, different dispersal pathways may affect the final phenotypes, and thus the performance and fitness of individuals that settle into subpopulations. Using otolith microchemical signatures that are indicative of ‘dispersive’ larvae (oceanic signatures) and ‘non-dispersive’ larvae (coastal signatures), we explore the population-level consequences of dispersal-induced variability in phenotypic mixtures for the common triplefin (a small reef fish). We evaluate lipid concentration and otolith microstructure and find that ‘non-dispersive’ larvae (i) have greater and less variable lipid reserves at settlement (and this variability attenuates at a slower rate), (ii) grow faster after settlement, and (iii) experience similar carry-over benefits of lipid reserves on post-settlement growth relative to ‘dispersive’ larvae. We then explore the consequences of phenotypic mixtures in a metapopulation model with two identical subpopulations replenished by variable contributions of ‘dispersive’ and ‘non-dispersive’ larvae and find that the resulting phenotypic mixtures can have profound effects on the size of the metapopulation. We show that, depending upon the patterns of connectivity, phenotypic mixtures can lead to larger metapopulations, suggesting dispersal-induced demographic heterogeneity may facilitate metapopulation persistence.

1. Introduction

Dispersal enables organisms to move from one place to another and replenish distant populations [1,2]. In coastal marine ecosystems, the relative importance of dispersal versus local retention of propagules (eggs or larval stages that develop in offshore waters) has been the subject of much recent attention, with potentially important consequences for metapopulation dynamics, biodiversity conservation and fisheries management [3–5].

Most marine reef animals disperse as larvae, and individuals may travel via different routes, experiencing different environmental conditions as they move from one location to another. These different dispersal pathways taken by larvae may create variation in the phenotypes of colonizers, with potentially important demographic consequences after settlement [6–9].

Here, we integrate empirical observations and a metapopulation model to evaluate the potential population-level consequences of different dispersal pathways via their effects on energetic reserves and growth potential of offspring, for the common triplefin, Forstericyon lapillum. The common triplefin is a small reef fish, native to shallow rocky reefs of New Zealand. Adults are site attached but spawn pelagic larvae that develop for approximately 52 days before replenishing...
adult subpopulations [7]. Our previous work suggests the existence of two distinct (coastal versus oceanic) dispersal pathways in a sampled population that are unrelated to natal origin [7], and that have consequences for the colonizers’ future survival in the adult subpopulations [8]. Our aims in this paper are to (i) evaluate potential sources of phenotypic variation that may contribute to the observed differences in survivorship and (ii) explore the potential consequences of the resulting demographic heterogeneity in a metapopulation context.

2. Material and methods

(a) Effects of dispersal pathways

We sampled recently settled common tripletail (F. lapillum) from the Wellington region and used otolith microstructure and microchemistry to characterize variation in larval growth rate and larval dispersal pathways (methods detailed in references [7,8]; see also the electronic supplementary material, appendix A). Briefly, we used LA-ICP MS (laser ablation inductively coupled plasma mass spectrometry) to quantify trace element concentrations in the larval portions of otoliths, followed by clustering approaches to define and characterize two discrete dispersal pathways [7]. Our previous work demonstrated that individuals with otolith signatures indicative of development in coastal/near-shore waters (‘non-dispersive’ larvae) differed in their phenotype [7] and had increased probabilities of survival to reproductive age [8] relative to individuals with signatures indicative of development in offshore waters (‘dispersive’ larvae).

We estimated pre-settlement (larval) growth rate and post-settlement (juvenile) growth rate, respectively, as the mean daily growth rate of the daily otolith growth increments immediately preceding or following a conspicuous settlement check [10] on sagittal otoliths [7]. We estimated post-settlement age (days) as the number of daily otolith increments between the settlement check and the edge of the otolith. Post-settlement growth rate could be estimated for individuals only with post-settlement age ≥5 days. We estimated total lipid concentration (a measure of energetic reserves) from a spectrophotometric analysis of 127 homogenized, freeze-dried fish for which we had also characterized growth histories and dispersal pathways. We extracted total lipids using a dichromate oxidation assay assessed against a tripalmitin standard [11] and estimated lipid concentration for each fish as total lipids divided by sample dry mass. Finally, we estimated the strength of a carry-over effect (i.e. ability of an individual to continue pre-settlement growth rate into the post-settlement stage) as log(post-settlement growth rate/pre-settlement growth rate).

We compared energetic reserves and post-settlement growth rate between the two observed dispersal pathways (i.e. ‘dispersive’ and ‘non-dispersive’ larvae). We hypothesized that carry-over effects might depend upon energetic reserves at settlement. Because lipid concentrations declined linearly with post-settlement age (see Results), we estimated lipid concentration at settlement for each individual as the sum of the residual lipids from a linear regression (PROC GLM, model: lipid concentration = post-settlement age, SAS v. 9.3) and the intercept of this regression (i.e. a global estimate of lipid concentration at settlement). Our previous work [8] indicated fish from different dispersal pathways varied in their post-settlement mortality rates, and here we hypothesized that selective mortality might favour individuals (or dispersal pathways) with higher energetic reserves at settlement. If true, we expect among-individual variation in estimated lipid concentration at settlement to decline with post-settlement age. We explored this separately for each dispersal pathway by (i) pooling individuals based on their post-settlement age (bins = 0–4, 5–9, 10–14 or 15–19 days; determined a priori), (ii) calculating the coefficient of variation (CV) of ‘estimated lipid concentration at settlement’ for each bin and (iii) using analysis of covariance (ANCOVA) to evaluate variation in the relationship between CV and post-settlement age (bin median), with steep negative slopes consistent with strong selective mortality.

(b) Consequences of dispersal-induced variation

We explored the potential population-level consequences of dispersal-induced variation among individuals in a simple metapopulation model with two identical subpopulations connected by dispersal of larvae (see electronic supplementary material, appendix A). The fraction p of offspring from each subpopulation is locally retained, and the remaining fraction 1 − p disperses to the other subpopulation. We assume survival from hatching to settlement is lower (by a factor of s) for dispersers than for non-dispersers. Dispersal also reduces post-settlement growth rate (see Results). We assume that maturation occurs at a fixed size; hence, disperser phenotypes require more time to reach reproductive maturity and suffer greater mortality than non-disperser phenotypes prior to spawning as adults. Finally, we assume survival from settlement to maturation decreases with adult density (see electronic supplementary material, appendix A for rationale of assumptions). At equilibrium, the rate at which disperser and non-disperser phenotypes enter adult subpopulations is equal to the adult death rate:

\[ p f N_s^d e^{-\delta t} + (1-p)f N_s^d e^{-\delta t} = \delta N_a^d. \]  

where f is the number of larvae produced by each adult that potentially survives to settlement, \(N_a^d\) is the equilibrium adult density, \(\delta\) is the background juvenile death rate, \(\alpha\) is the rate at which settler mortality increases with adult density, \(\tau_s\) is the adult death rate, and \(\tau_d\) are maturation delays (time from settlement to initial reproduction) for non-disperser and disperser phenotypes, respectively.

We calculated the equilibrium density for the model with demographic heterogeneity and for the case in which dispersal does not affect post-settlement maturation delay. In the latter case, we set the maturation delay for all settlers equal to the mean of the values for disperser and non-disperser phenotypes; the equilibrium solution is otherwise identical to equation (2.1) (see electronic supplementary material, appendix A). We examined the effects of the direct cost of dispersal (reduced pre-settlement survival, s) and proportion of locally retained larvae on the ratio of adult equilibrium density with and without demographic heterogeneity.

3. Results

(a) Effects of dispersal pathways

Larvae with ‘non-dispersive’ otolith signatures settled with and maintained higher energetic reserves for at least two weeks after settlement. Fish assigned to this dispersal pathway had an additional 6.6 μg lipids·mg dry tissue⁻¹ relative to larvae with ‘dispersive’ otolith signatures (ANCOVA with post-settlement age as covariate: \(F_{1,124} = 5.50, p = 0.02\); reduced model after removing a non-significant interaction term). Lipid concentration for both dispersal pathways declined at a rate of 2.76 μg lipids·mg dry tissue⁻¹ per day (\(F_{1,124} = 46.31, p < 0.0001\); figure 1a). ‘Non-dispersive’ larvae also grew faster than ‘dispersive’ larvae after settlement (post-settlement otolith growth was approximately 15% faster for the first 5 days after settlement; ANOVA: \(F_{1,77} = 17.69, p = 0.002\), figure 1b). Most individuals exhibited accelerated otolith growth rates across the settlement transition (approx. 80% carry-over effects > 0). The strength of carry-over effects also increased with estimated
energetic reserves at settlement (ANCOVA, effect of covariate: $F_{1,75} = 5.12, p = 0.027$) but did not otherwise vary with dispersal pathway (main effect: $F_{1,75} = 0.01, p = 0.91$; interaction term: $F_{1,75} = 0.02, p = 0.90$, figure 1c). The CV for estimated lipid concentration at settlement declined with cohort age for both dispersal pathways, but CVs reduced more quickly for ‘non-dispersive’ relative to ‘dispersive’ larvae (ANCOVA with age as covariate; interaction term: $F_{1,4} = 9.06, p = 0.04$, figure 1d).

(b) Consequences of dispersal-induced variation
The model suggests that demographic heterogeneity can increase or decrease the equilibrium population density relative to the prediction for homogeneous settlers (figure 2). If a large proportion of larvae recruit to their natal subpopulation (high $p$), the settlers are predominantly the non-disperser phenotype in the heterogeneous case. Because survival from settlement to maturation for non-dispersers is greater than average, high $p$ increases the equilibrium adult density relative to the prediction for homogeneous settlers. This occurs, regardless of the relative survival ($s$) of larvae that disperse between subpopulations. However, if only a small proportion of larvae are non-dispersers, the predicted equilibrium in the heterogeneous case is lower than for the homogeneous case, unless the relative survival of dispersers is low. When dispersal is extremely costly ($low s$), producing a few individuals with a non-disperser phenotype more than makes up for the loss of comparatively low-quality disperser phenotypes.

4. Discussion
Coastal marine environments comprise a heterogeneous landscape [12] with substantial scope to shape the dispersal process via environmentally induced costs that may be immediate (e.g. mortality during dispersal) or deferred [9]. The direct costs of dispersal contribute to spatio-temporal variability in recruitment and the importance of this is well recognized by ecologists and fisheries scientists. Several recent studies [9,13] provide clear examples of how deferred costs can shape population-level outcomes of marine organisms. We extend this framework to show how environmentally induced demographic heterogeneity in successful colonizers can increase the equilibrium density (i.e. quantity of fish) of a metapopulation. Our simple model does not include asymmetric competitive effects between the two phenotypes, or the possibility that local phenotypic structure could modify predation rates through, e.g. apparent competition, although such interactions...
are certainly plausible. We speculate that the de facto production of variable phenotypes (mediated by dispersal pathways) could represent an adaptive strategy in systems where dispersal rates are variable or high. Our results have similarities with evolutionary bet-hedging strategies that can maintain phenotypic diversity under environmental uncertainty [14,15].

The notion of ‘survival of the fittest’ is a cornerstone of biology that conveys the idea that demographic heterogeneity and the supremacy of higher quality individuals are the drivers of evolution and population dynamics [16]. Perhaps counter-intuitively, we show how the presence of lower-quality individuals may enhance populations in certain conditions.

Figure 2. Ratio of adult equilibrium density predicted by the metapopulation model with dispersal-induced demographic heterogeneity relative to the predicted density when all settlers have the mean growth rate. Shaded area indicates combinations of parameter values that result in ratios greater than 1 (i.e. demographic heterogeneity produces larger population densities).

References