

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

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Summary

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.

Introduction:

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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 colonisers, 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, *Forsterygion 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 ~52d before replenishing adult subpopulations (7). Our previous work suggests the existence of two distinct (coastal vs oceanic) dispersal pathways in a sampled population that are unrelated to natal origin (7), and that have consequences for the colonisers' 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.

Material and Methods

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A. Effects of dispersal pathways

We sampled recently settled common triplefin (*Forsterygion lapillum*) from the Wellington region and used otolith microstructure and microchemistry to characterise variation in larval growth rate and larval dispersal pathways (methods detailed in 7-8; see also Appendix A). Briefly, we used LA-ICPMS to quantify trace element concentrations in the larval portions of otoliths, followed by clustering approaches to define and characterise two discrete dispersal pathways (7). Our previous work demonstrated that individuals with otolith signatures indicative of development in coastal/nearshore 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 width of the five consecutive daily otolith growth increments immediately preceding or following a conspicuous settlement check (10) on sagittal otoliths (7). We estimated post-settlement age (d) as the number of daily otolith increments between the settlement check and the edge of the otolith. Post-settlement growth rate could only be estimated for individuals with post-settlement age $\geq 5d$. 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 characterised 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

94 (i.e., ability of an individual to continue pre-settlement growth rate into the post-settlement
95 stage) as $\log(\text{post-settlement growth rate}/\text{pre-settlement growth rate})$.

96 We compared energetic reserves and post-settlement growth rate between the two
97 observed dispersal pathways (i.e., ‘dispersive’ and ‘non-dispersive’ larvae). We hypothesised
98 that carry-over effects might depend upon energetic reserves at settlement. Because lipid
99 concentrations declined linearly with post-settlement age (see Results), we estimated lipid
100 concentration at settlement for each individual as the sum of the residual lipids from a linear
101 regression (PROC GLM, model: lipid concentration = post-settlement age, SAS v9.3) and the
102 intercept of this regression (i.e., a global estimate of lipid concentration at settlement). Our
103 previous work (8) indicated fish from different dispersal pathways varied in their post-
104 settlement mortality rates, and here we hypothesised that selective mortality might favour
105 individuals (or dispersal pathways) with higher energetic reserves at settlement. If true, we
106 expect among-individual variation in estimated lipid concentration at settlement to decline
107 with post-settlement age. We explored this separately for each dispersal pathway by: (i)
108 pooling individuals based upon their post-settlement age (bins = 0-4d, 5-9d, 10-14d, or 15-
109 19d; determined *a priori*), (ii) calculating the coefficient of variation (CV) of ‘estimated lipid
110 concentration at settlement’ for each bin, and (iii) using ANCOVA to evaluate variation in
111 the relationship between CV and post-settlement age (bin median), with steep negative slopes
112 consistent with strong selective mortality.

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114 ***B. Consequences of dispersal-induced variation***

115 We explored the potential population-level consequences of dispersal-induced
116 variation among individuals in a simple metapopulation model with two identical
117 subpopulations connected by dispersal of larvae (see Appendix A). The fraction p of
118 offspring from each subpopulation is locally retained, and the remaining fraction $1-p$ disperse

119 to the other subpopulation. We assume survival from hatching to settlement is lower (by a
 120 factor of s) for dispersers than for non-dispersers. Dispersal also reduces post-settlement
 121 growth rate (see Results). We assume that maturation occurs at a fixed size; hence, disperser
 122 phenotypes require more time to reach reproductive maturity and suffer greater mortality than
 123 non-disperser phenotypes prior to spawning as adults. Finally, we assume survival from
 124 settlement to maturation decreases with adult density (see Appendix A for rationale of
 125 assumptions). At equilibrium, the rate at which disperser and non-disperser phenotypes enter
 126 adult subpopulations is equal to the adult death rate:

$$127 \quad pfN_a^* e^{-(\delta_j + \alpha N_a^*)\tau_n} + (1 - p)fsN_a^* e^{-(\delta_j + \alpha N_a^*)\tau_d} = \delta_a N_a^* \quad (1)$$

128 where f is the number of larvae produced by each adult that potentially survives to settlement,
 129 N_a^* is the equilibrium adult density, δ_j is the background juvenile death rate, α is the rate at
 130 which settler mortality increases with adult density, δ_a is the adult death rate, and τ_n and τ_d
 131 are maturation delays (time from settlement to initial reproduction) for non-disperser and
 132 disperser phenotypes, respectively.

133 We calculated the equilibrium density for the model with demographic heterogeneity
 134 and for the case in which dispersal does not affect post settlement maturation delay. In the
 135 latter case, we set the maturation delay for all settlers equal to the mean of the values for
 136 disperser and non-disperser phenotypes; the equilibrium solution is otherwise identical to Eq.
 137 1 (see Appendix A). We examined the effects of the direct cost of dispersal (reduced pre-
 138 settlement survival, s) and proportion of locally retained larvae on the ratio of adult
 139 equilibrium density with and without demographic heterogeneity.

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Results

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A. Effects of dispersal pathways

143 Larvae with ‘non-dispersive’ otolith signatures settled with and maintained higher
144 energetic reserves for at least 2 weeks after settlement. Fish assigned to this dispersal
145 pathway had an additional $6.6 \mu\text{g lipids} \cdot \text{mg dry tissue}^{-1}$ relative to larvae with ‘dispersive’
146 otolith signatures (ANCOVA with post-settlement age as covariate: $F_{1,124}=5.50$, $p=0.02$;
147 reduced model after removing a non-significant interaction term). Lipid concentration for
148 both dispersal pathways declined at a rate of $2.76 \mu\text{g lipids} \cdot \text{mg dry tissue}^{-1}$ per day
149 ($F_{1,124}=46.31$, $p<0.0001$; Fig 1a). ‘Non-dispersive’ larvae also grew faster than ‘dispersive’
150 larvae after settlement (post-settlement otolith growth was ~15% faster for the first 5d after
151 settlement; ANOVA: $F_{1,77}=17.69$, $p=0.02$, Fig 1b). Most individuals exhibited accelerated
152 otolith growth rates across the settlement transition (~80% carry-over effects >0). The
153 strength of carry-over effects also increased with estimated energetic reserves at settlement
154 (ANCOVA, effect of covariate: $F_{1,75}=5.12$, $p=0.027$) but did not otherwise vary with
155 dispersal pathway (main effect: $F_{1,75}=0.01$, $p=0.91$; interaction term: $F_{1,75}=0.02$, $p=0.90$, Fig
156 1c). The CV for estimated lipid concentration at settlement declined with cohort age for both
157 dispersal pathways, but CVs reduced more quickly for ‘non-dispersive’ relative to
158 ‘dispersive’ larvae (ANCOVA with age as covariate; interaction term: $F_{1,4}=9.06$, $p=0.04$, Fig
159 1d).

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161 ***B. Consequences of dispersal-induced variation***

162 The model suggests that demographic heterogeneity can increase or decrease the
163 equilibrium population density relative to the prediction for homogeneous settlers (Fig. 2). If
164 a large proportion of larvae recruit to their natal subpopulation (high p), the settlers are
165 predominantly the non-disperser phenotype in the heterogeneous case. Because survival from
166 settlement to maturation for non-dispersers is greater than average, high p increases the
167 equilibrium adult density relative to the prediction for homogeneous settlers. This occurs

168 regardless of the relative survival (s) of larvae that disperse between subpopulations.
169 However, if only a small proportion of larvae are non-dispersers, the predicted equilibrium in
170 the heterogeneous case is lower than for the homogeneous case, unless the relative survival of
171 dispersers is low. When dispersal is extremely costly (low s), producing a few individuals
172 with a non-disperser phenotype more than makes up for the loss of comparatively low quality
173 disperser phenotypes.

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Discussion

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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 recognised by ecologists and fisheries scientists. Several recent studies (e.g., 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 colonisers 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).

192 The notion of “survival of the fittest” is a cornerstone of biology that conveys the idea
193 that demographic heterogeneity and the supremacy of higher quality individuals are the
194 drivers of evolution and population dynamics (16). Perhaps counterintuitively, we show how
195 the presence of lower quality individuals may enhance populations in certain conditions.

196

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201

202 **Author contributions:** JS and SS collected the empirical data. EN developed the theoretical
203 model in consultation with JS and SS. All authors contributed the analysis and writing of this
204 paper.

205

206 **Ethics:** All appropriate ethical approvals were obtained. Research was conducted in
207 accordance with an animal ethics permit from Victoria University of Wellington (AEC
208 Permit#2002R4), and a scientific collecting permit from the New Zealand Ministry of
209 Primary Industries.

210

211 **Data accessibility:** Raw data is available as electronic supplementary material, in Appendix
212 B (Table B1).

213

214 **Competing interests:** We have no competing interests.

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219 evolution. Oxford, UK: Oxford University Press.
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256 **Figure legends**

257

258 **Figure 1.** Effects of dispersal pathways on individual performance at a life-history transition.

259 Fish with coastal signatures in otoliths (putative non-dispersers) are indicated with orange

260 symbols and fitted lines. Fish with oceanic signatures in otoliths (putative dispersers) are

261 indicated with blue symbols and fitted lines. **(a)** Energetic reserves of recently settled fish. **(b)**

262 Growth rates after settlement (mean \pm 1SE). **(c)** Carry-over effects depend upon estimated

263 energetic reserves at settlement but do not vary with dispersal pathway (solid line = fitted;

264 dashed line = neutral carry-over effect). **(d)** Variation in estimated energetic reserves at

265 settlement declines more quickly with post-settlement age for ‘dispersers’ and for ‘non-

266 dispersers’ (consistent with stronger selective mortality).

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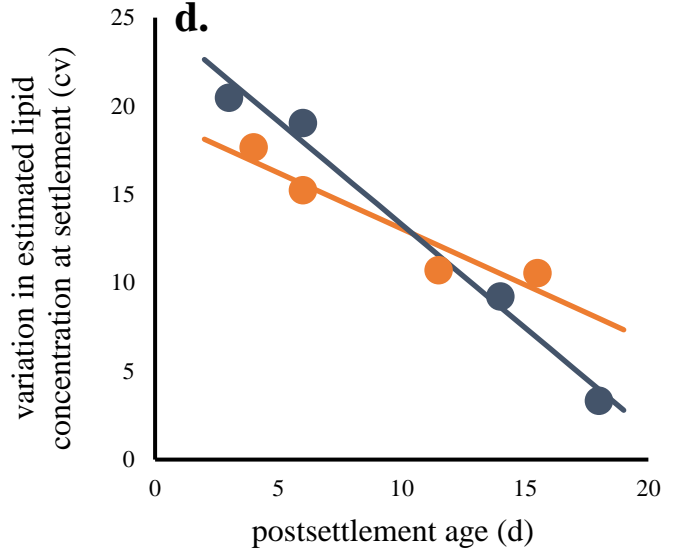
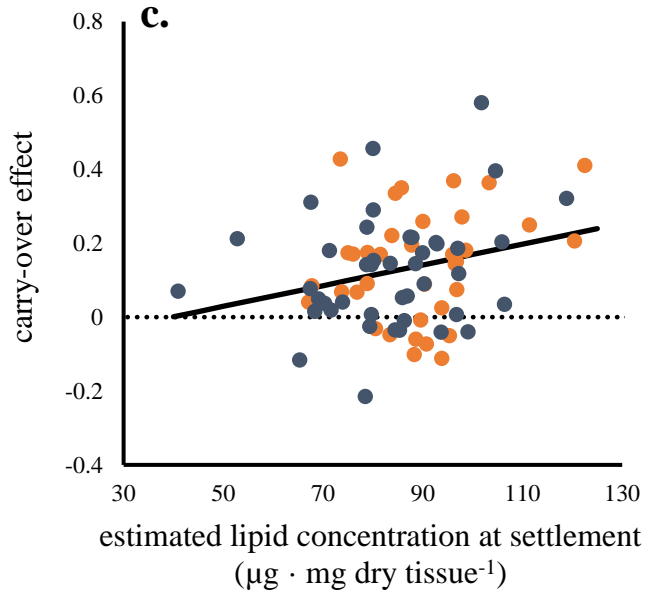
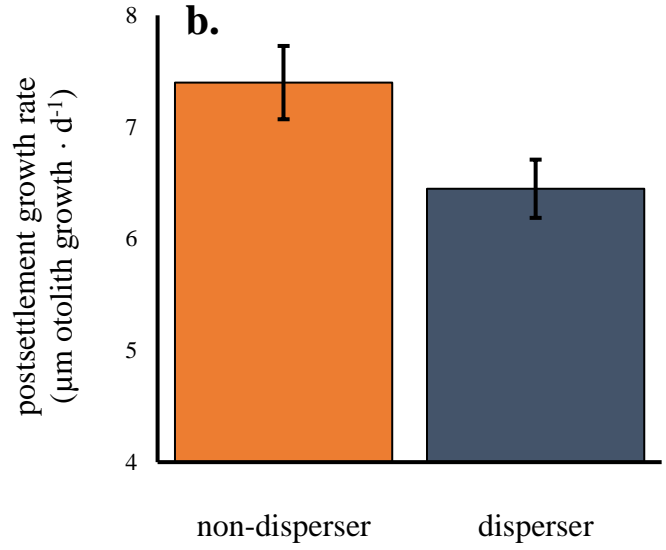
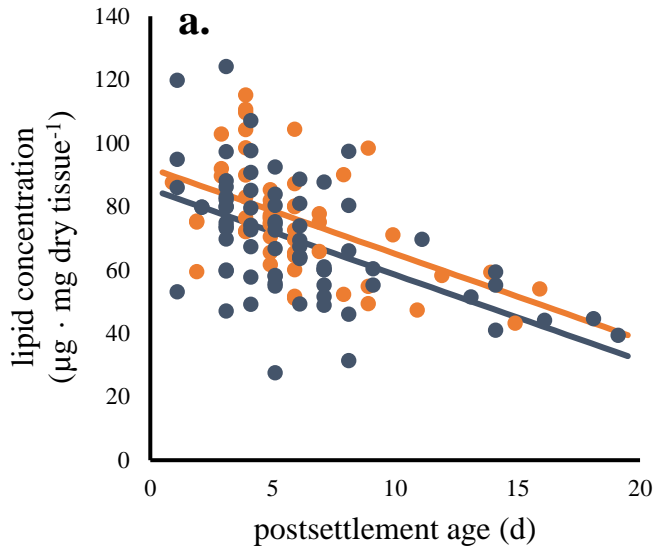
268 **Figure 2.** Ratio of adult equilibrium density predicted by the metapopulation model with

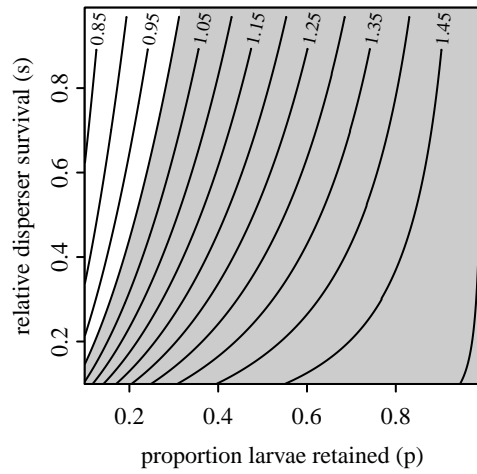
269 dispersal-induced demographic heterogeneity relative to the predicted density when all

270 settlers have the mean growth rate. Shaded area indicates combinations of parameter values

271 that result in ratios greater than 1 (i.e., demographic heterogeneity produces larger population

272 densities).







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