
Mean Time to Fixation versus Fitness Variance

![Figure A1: Mean time to fixation versus fitness variance for m = 0.05. For a given value of s1 offspring size (s_o = 0.001, the optimal size), mean time to fixation increases with longer spawning durations/decreased fitness variance. Note the log scale on the Y-axis. For each value of offspring size s_o, the mean time to fixation is calculated for a series of spawning duration values using equation (8), and fitness variance is estimated via simulation. Spawning duration of type 1 ranges from 9 to 180 days, and the spawning duration type 2 is 100 days. The fully provisioned larval size s_o is 0.0103 mm^3, and the corresponding pelagic larval duration t_o is 14 days, taken from the echinoderm model of Levitan (2000). The eddy timescale is 15 days, taken from Siegel et al. (2008). The size of the spatial domain is 10 times the size of eddies (e.g., 400 km of coastline/40 km of eddies = 10), the probability of reaching viable adult habitat is 50% (h = 0.5), the number of attachment sites N is 100, and the probability of adult death (d) is 0.8.](image-url)
Figure A2: Mean time to fixation versus fitness variance for $m = 0.5$. For a given value of $s_1$, offspring size ($s_2 = 0.005$, the optimal size), mean time to fixation increases with decreased fitness variance (or longer spawning durations). Note the log scale on the Y-axis. For each value of offspring size $s_1$, the mean time to fixation is calculated for a series of spawning duration values using equation (8), and fitness variance is estimated via simulation. All other parameters are as in figure A1.

Diffusion Approximation for Qualitative Insights into How Variance in Fitness and the Correlated Nature of Larval Dispersal Affect Selection and Genetic Drift

A diffusion approximation takes the form

\[
\frac{\partial \phi(q,t)}{\partial t} = - \frac{\partial}{\partial q} (S(q)\phi(q,t)) + \frac{1}{2} \frac{\partial^2}{\partial q^2} (D(q)\phi(q,t)),
\]

where \(\phi(q,t)\) is the probability that type 1 will be at frequency \(q\) at time \(t\), selection \(S(q)\) is the expected change in frequency of type 1 over an infinitesimal interval of time, and drift \(D(q)\) is the expected squared change in frequency of type 1. Snyder (2017) shows that for our model,

\[
S(q) = \delta q(1 - q)\left(\beta_1 - \beta_2 - [qv_1 - (1 - q)v_2]\right)
\]

\[
- \frac{1}{N}(w_1 - w_2) + (2q - 1)R,
\]

\[
D(q) = \delta q^2(1 - q)^2 \left[v_1 - v_2 - 2R \right]
+ \frac{1}{N} \left(1 - \frac{1}{q}w_1 + \frac{1}{1 - q}w_2\right),
\]

(note that \(S(q)\) and \(D(q)\) were called \(M(q)\) and \(V(q)\), respectively, in Snyder 2017). Here

\[
\beta_i = \frac{b(s_i)}{\bar{b}} - 1,
\]

\[
v_i = \frac{\rho_i}{(hb)^2} \text{var}(\alpha_i),
\]

\[
w_i = \frac{1 - \rho_i}{(hb)^2} \text{var}(\alpha_i),
\]

where \(\bar{b} = (b_1 + b_2)/2\) is the effective fecundity averaged across types, \(\text{var}(\alpha_i)\) is the variance in the number of offspring produced by an individual of type \(i\), \(\rho_i\) is the correlation in the number of offspring between two randomly chosen individuals of type \(i\), and \(R\) is the covariance in the number of offspring of an individual of type 1 and an individual of type 2, divided by \((hb)^2\). The covariance \(R\) depends on the degree to which larvae of types 1 and 2 share the same packets.

For our model, \(\text{var}(\alpha_i)\) is the squared number of larvae per packet times the variance in the number of successful packets, \((b_i/M)^2 M, h(1 - h)\), while \(\rho_i\) is the probability that two larvae end up in the same packet, \(1/M_i\), where we have written \(b_i\) for \(b(s_i)\) and \(M_i\) for \(M(T_i)\). Thus,

\[
v_i = \left(\frac{b_i}{\bar{b}}\right)^2 \frac{1}{M^2} \frac{1 - h}{h},
\]

\[
w_i = \frac{M - 1}{M^2} \left(\frac{b_i}{\bar{b}}\right)^2 \frac{1 - h}{h}.
\]
Looking at equation (2), we see that type 1 is selected for to the degree that it has higher expected fitness than type 2 ($\beta_1 > \beta_2$) and lower fitness variance, weighted by frequency ($q v_1 < (1 - q) v_2$ and $w_1 < w_2$). If the two types share larval packets so that fitnesses of the two types are positively correlated ($R > 0$), then the more frequent type benefits from this correlation ($2q - 1$ is positive if $q > 0.5$). This makes sense because the relative frequencies of the larval types are the same for each packet, so that the more frequent type benefits more from a successful packet than the less frequent type. Finally, we see from equation (5) that as the number of larval packets $M$ increases, the variance in fitness decreases ($v_i$ and $w_i$ decrease with $M_i$), and expected fitness has a greater relative contribution to selection.

If there are no larval packets and each larva disperses independently, then $\rho_i = 1/b_i$ and $\text{var}(c_i) = b_i h (1 - h)$, so that

$$v_i = \frac{1}{b^2} \frac{1 - h}{h},$$
$$w_i = \frac{b_i - 1}{b^2} \frac{1 - h}{h}.$$  \( \text{(B6)} \)

These variances are much smaller than those in equation (5). This means that if larvae disperse independently, the variance in fitness plays a much smaller role in selection. Dynamics are closer to deterministic, and there will be no trade-off between maximizing expected fitness and reducing variance.