Salmon straying description

Introduction

Model Description

Here we consider two populations N_1 and N_2 that are separated in space, each with trait values x_1 and x_2 determining recruitment rates. We assume that there is an optimum trait value θ_1 and θ_2 associated with each habitat, where recruitment is maximized if the trait value of the local population $x = \theta$. Moreover, we assume that $x_{1,2}$ are normally distributed with means μ_1 and μ_2 and have a shared standard deviation σ. As such, the recruitment rate for both populations is determined by the mean trait value of the local population, such that $r_1 = R_1[\mu_1(t)|\theta_1]$. Trait means for each population are subject to selection, the strength of which depends on the difference between the population mean and the local trait optimum at a given point in time.

The two populations are assumed to reproduce in spatially separate sites that are close enough such that a proportion of the population m can stray into the wrong site, and where mortality occurs before individuals return to spawn. If there is no straying between these populations (such that they are independent), then the mean trait evolves towards the optimal value such that $x_1 \to \theta_1$, and the recruitment rate for that population will be maximized. If there is straying between populations at rate m, then the traits in each respective location will be pulled away from the optimum, and recruitment rates will be lowered. As $m \to 0.5$, the populations are perfectly mixed, acting as a single population.

We use the discrete Ricker population dynamic framework described by Shelton and Mangel [] as the basis for our two-site model, with the added effect of the local population N_i mixing with a set proportion m of a remote population N_j that is straying into it. We first assume that the proportion e^{-Z} of both populations survive, and that the aggregated mix of the populations (local individuals in addition to the straying individuals) are subject to the same compensatory effects, determined by the parameter β. For a local site $i \in (1,2)$ that collects straying individuals from a remote site $j \in (1,2)$, if N_i is the local site and N_j is the remote site, the difference equation that determine changes in population size is

$$
\begin{aligned}
N_i(t+1) = {}& \left((1-m)N_i(t) + mN_j(t)\right) e^{-Z} \\
& + \Big((R_i[\mu_i(t)|\theta_i] + \tilde{P})(1-m)N_i(t) + (R_i[\mu_j(t)|\theta_i] + \tilde{P})mN_j(t) \Big) e^{-\beta((1-m)N_i(t)+mN_j(t))},
\end{aligned}
\tag{1}
$$

where we include demographic process error with $\tilde{P} \sim \mathcal{N}(0,s)$, where s is assumed to be small, and where the difference equation for N_j mirrors that for N_i.

The combined recruitment of local individuals $(1-m)N_i(t)$ and incoming strays $mN_j(t)$, as a function of their mean trait value at time t and given the local trait optimum θ_i, is then

$$
\begin{aligned}
R_i[\mu_i(t)|\theta_i] &= \int_{-\infty}^{\infty} r_{\max} \exp\left\{ \frac{(x_i(t) - \theta_i)^2}{2\tau^2} \right\} \mathrm{pr}(x_i(t)|\mu_i, \sigma^2) \mathrm{d}x_i(t) \\
&= \frac{r_{\max}\tau}{\sqrt{\sigma^2 + \tau^2}} \exp\left\{ -\frac{(\theta_i - \mu_i(t))^2}{2(\sigma^2 + \tau^2)} \right\}.
\end{aligned}
\tag{2}
$$

As stated previously, it is the mismatch between the local trait mean $\mu_i(t)$ and the local optimum θ_i that determines the recruitment rate for the population. The parameter τ controls the sensitivity of recruitment to changes in the mean trait value away from the optimum, which we set as $\tau = 1$ here and throughout.

Because individuals from the local population are mixed with individuals from the remote population via staying, the resulting trait distribution is a mixed normal with weights corresponding to the proportion of the mixed population that are local individuals, w_i, and for the straying individuals, $1 - w_i$, where $w_i = (1-m)N_i(t)/((1-m)N_i(t)+mN_j(t))$. We make two simplifying assumptions. First, we assume that the distribution resulting from the mix of remote and local individuals, following reproduction, is also normal with a mean value being that of the mixed-normal. Second, we assume that changes in trait variance through time are minimal, such that σ is assumed to be constant.

An increasing flow of incoming strays is thus expected to pull the mean trait value of the local population away from its optimum, which will decrease its rate of recruitment. The mean trait value thus changes through time according to the difference equation

$$\mu_i(t+1) = w_i\mu_i(t) + (1-w_i)\mu_j(t) + \frac{\partial}{\partial\mu_i} \ln\left(w_i R_i[\mu_i(t)|\theta_i] + (1-w_i)R_i[\mu_j(t)|\theta_i]\right), \tag{3}$$

where the first two factors determine the mixed normal average of the now-mixed local and remote populations. This mixed normal is weighted by the proportion of the population that is local and remote, respectively, which depends on the stray rate m. The partial derivative in the Eq. 3 determines how the mean trait changes through time due to natural selection (REF), which is proportional to the change in mean fitness with respect to μ_i.

We have so far assumed that the proportion of strays leaving and entering a population is constant, however there is good evidence that at least in some species the stray rate is density dependent. Specifically, the rate at which individuals stray has been linked directly to a collective decision-making phenomenon, where greater numbers of individuals tends to decrease the rate at which individuals stray, thus reducing the overall proportion of a population that strays. According to REF, given the probability that an individual strays m_0, the proportion of the local population $N_i(t)$ that strays is

$$m(t) = m_0 - m_0\left(\frac{N_i(t)}{C + N_i(t)}\right) \tag{4}$$

where C is the half-saturation value of N_i where the density-dependent stray rate decreases sharply. We note that at the limit $C \to \infty$, the density dependent stray rate becomes constant such that $m(t) \to m_0$, and this corresponds to the original model formulation where $m = m_0$. A similar observation shows that when the population density is very high, $m(t) \to 0$, and when it is close to extinction, $m(t) \to m_0$. Thus, for realistic population densities, $m(t) < m_0$.

Results

Initial results – subject to to change: As the proportion of strays increases, the average traits of both populations veer farther from their optimal values, and this results in the decline of the population steady state (because the recruitment rate is now sub-optimal for both populations). This is the nice, expected result.

The unexpected result are the alternative stable states that arise for lower values of m. Just where these alternative stable states arise depends on the variance as well as the difference in optimal trait values between sites $(\theta_i - \theta_j)$, but you can see that this has big impacts on the portfolio effect. Which trajectory goes to the higher or lower alternative stable state is random - an effect of the process noise injected into the system. The change in the PE appears to be caused by large spikes in the variance of individual population trajectories where the alternative stable states begin (at the fold bifurcation). This is a well-known phenomenon that forms the basis for early warning signals of phase transitions.

The differences in optimal trait values between sites $(\theta_i - \theta_j)$ influence at what straying rate the alternative stable states appear. Large differences in θ_i and θ_j can be interpreted as high environmental heterogeneity. A cursory analysis shows that increasing environmental heterogeneity tends to lower the stray rate value m^* at which the maximum PE is expected to occur. Moreover, if the trait variance is much larger than the difference in optimal trait values between sites (such that selection is weaker), the alternative stable state phenomenon disappears, as does the spike in the portfolio effect.
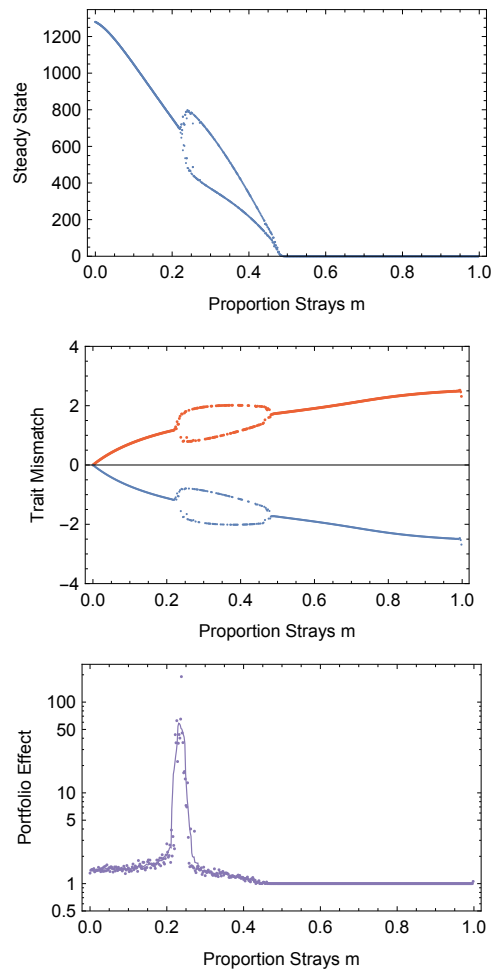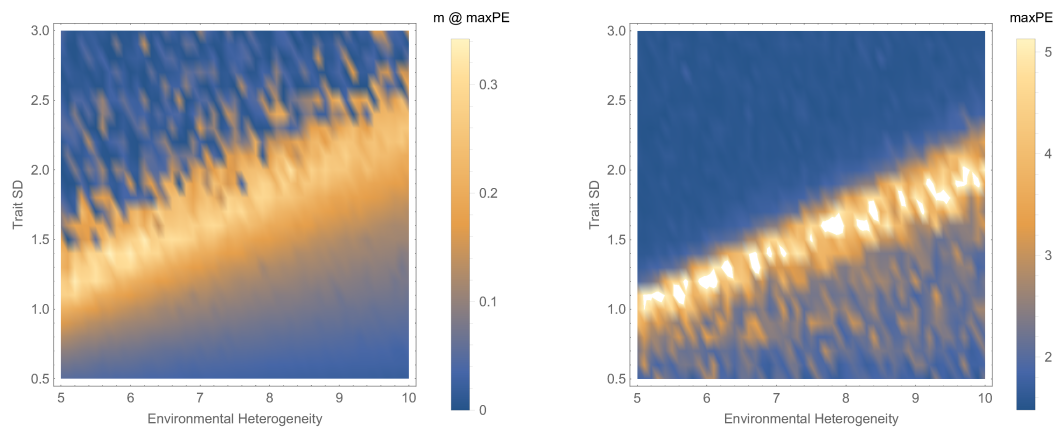
Discussion

Figure 1:

Figure 2: