Eco-evolutionary model of salmon straying in a metapopulation (but with a cool title)

Introduction

Salmony salmons

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

$$N_i(t+1) = \tag{1}$$
$$((1-m)N_i(t) + mN_j(t))\,\mathrm{e}^{-Z}$$
$$+ (R_i[\mu_i(t)|\theta_i](1-m)N_i(t) + R_i[\mu_j(t)|\theta_i]mN_j(t))$$
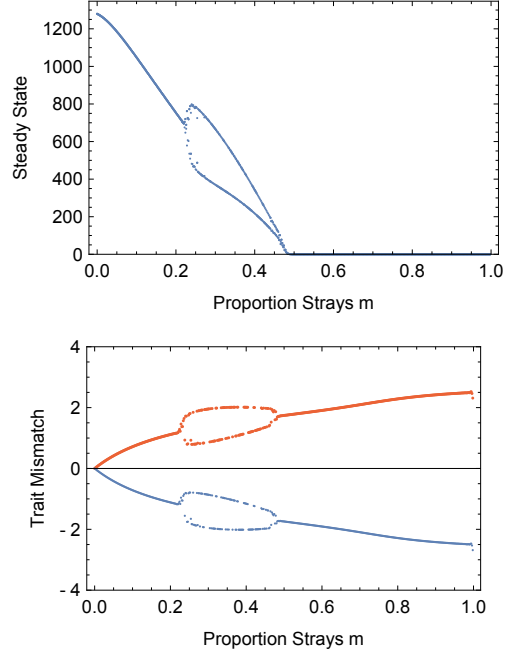$$\times \mathrm{e}^{-\beta((1-m)N_i(t)+mN_j(t))},$$

Figure 1: A) The steady state densities of N_1 and N_2 as a function of a constant stray rate m. B) The steady state trait values measured as $theta_i - x_i$, as a function of a constant stray rate m.

where a small amount of demographic process error is added to the reproductive rate, 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

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

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
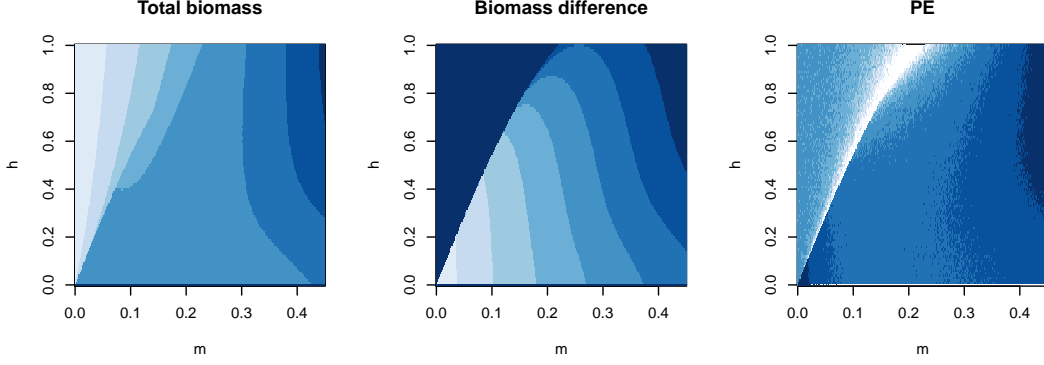
Figure 2: Total means N_t, difference in means ΔN, and the portfolio effect PE as a function of heritability h^2 and a constant stray rate m. Light colors = high values.

mixed population that are local individuals, w_i, and for the straying individuals, $1 - w_i$, where

$$w_i = \frac{(1-m)N_i(t)}{(1-m)N_i(t) + mN_j(t)}. \tag{3}$$

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

$$\mu_i(t+1) = w_i\mu_i(t) + (1-w_i)\mu_j(t) \tag{4}$$
$$+ \frac{\partial}{\partial\mu_i} \ln\left(w_i R_i[\mu_i(t)|\theta_i] + (1-w_i)R_i[\mu_j(t)|\theta_i]\right),$$

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. ?? 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

$$m(t) = m_0 \left(1 - \frac{N_i(t)}{C + N_i(t)}\right), \tag{5}$$

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 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, $m(t) < m_0$.

Stray rate is intrinsically linked to the distance between the local and straying population. The greater the distance between two populations, the lower the expected rate of straying (REF). We can account for this interdependence in our model by assuming that m (if the stray rate is constant) or m_0 (if the stray rate is density dependent) is a function of $theta_i - theta_j$, which can be assumed to be large if the remote site j is a great distance away from the local site i. If sites i and j are very close, the stray rate is assumed to maximized at $m, m_0 = 0.5$. Thus, we can integrate these two variables by setting $m, m_0 = (2 + \epsilon(\theta_i - \theta_j))^{-1}$, where ϵ sets the sensitivity of a declining m to increasing distance (greater values of $\theta_i - \theta_j$).

Results

Nonlinear effects of straying on the Portfolio Effect Straying generally lowers steady state densities for both local and remote populations. The decline in steady state densities is not gradual: as straying increases, the system crosses a fold bifurcation whereby the single steady state among both sites becomes two alternative steady states: one at high biomass density, and
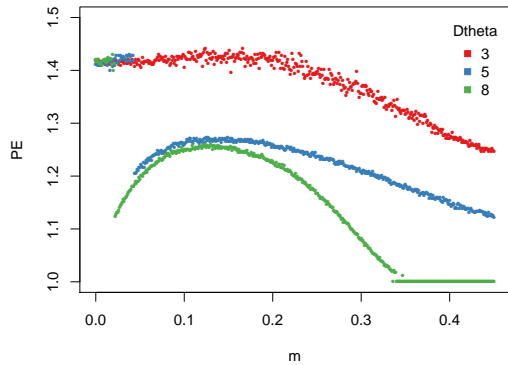
Figure 3: Median portfolio effect as a function of stray rate m for lower trait heritability ($h^2 < 0.5$)

one at low biomass density (Fig. 1A,B). This bifurcation occurs at lower values of the stray rate m for low trait heritability h^2 (Fig 2A), indicating that greater coupling between ecological and evolutionary dynamics in addition to greater rates of straying results in alternative stable states among the two sites.

Trait heritability also has a large impact on the sensitivity of both the total steady state density ($N_T^* = N_1^* + N_2^*$) as well as the difference between steady state densities ($\Delta N = \sqrt{(N_1^* - N_2^*)^2}$). Greater trait heritability results in a larger decline in N_T^* for increasing stray rates m, though results in only moderate changes to ΔN (Figs. 2A,B). Conversely, if the trait is less heritable, an increase in the stray rate has little impact on the total biomass density and contrastingly large effects on the difference in population densities between sites (Fig. 2A,B).

Together these changes in steady state population densities in terms of N_T and ΔN as a function of trait heritability and the rate of straying between populations give rise to highly nonlinear portfolio effects, quantified here as

$$\text{PE} = \frac{\overline{\text{CV}}_{i,j}}{\text{CV}_T}. \qquad (6)$$

We define $\overline{\text{CV}}_{i,j}$ as the average coefficient of variation across the local population i and the remote population j at steady state densities, and CV_T as the coefficient of variation of the total or aggregated population at steady state densities. The minimum portfolio effect is by definition $\text{PE}_{\text{m}}\text{in} = 1$, whereas portfolio effects greater than unity corresponds to a greater potential for ecological rescue among populations, thus buffering the system as a whole against extinction.

In the region where there is a single steady state among both populations, we find a correspondingly high portfolio effect, primarily due to the elevated mean values of N_T. As the fold bifurcation is approached with greater

rates of straying, the portfolio effect spikes due to a large increase in the standard deviation of both populations. This explosion in variance is a well-known phenomenon that occurs near a fold bifurcation and lies at the heart of early warning signal theory (REFS). For larger values of m (to the right of the fold bifurcation in Fig 2C), where there is a high and low steady state density among the sites, if heritability is low the portfolio effect becomes minimized, is elevated and then declines as $m \to 0.5$. If heritability is high, the portfolio effect declines steadily after the explosion in variance associated with the development of alternative stable states.

The role of habitat heterogeneity Increased differences in optimal trait values between sites ($\Delta\theta = |\theta_i - \theta_j|$) corresponds to greater between-site differences in conditions that favor different physiologies, which we interpret here as increased habitat heterogeneity. If both populations were isolated, natural selection would direct the mean trait values for both populations towards the respective optima. However, when straying is allowed, increasingly different trait optima generally lowers N_T and exaggerates ΔN, such that one population has the majority of the biomass. The impact of habitat heterogeneity on the portfolio effect is more complex, serving to emphasize the nonlinear relationship between the stray rate and the PE, regardless of heritability. We find that the nonlinear nature of the PE depends very much on $\Delta\theta$, particularly when trait heritability is low, such that $h^2 < 0.5$. As habitat heterogeneity increases, the PE spike generally occurs for lower values of stray rates, meaning that a smaller amount of straying can give rise to alternative stable states (Fig. 3). In the region where alternative stable states are encountered (Fig. 3), additional straying increases the portfolio effect to a local maximum before its negative effects serve to lower PE with $m \to 0.5$, and this effect is exaggerated with increasing habitat heterogeneity.

If we assume that the rate of straying is density dependent, the probability of straying at the individual level m_0 determines the rate of straying within the group, such that $m(t)$ becomes lower as $N(t)$ increases. At steady state values, $m(t)$ also becomes constant, though by definition is always less than m_0, such that $0 < m(t) < m_0$. We find that this dynamic has negligible impact on the qualitative results on our system (Fig. 2). Quantitatively, density dependent straying serves to lessen the effect of straying on N_T, ΔN and PE, given that the effective stray rate is effectively lessened by collective navigation.

Linking stray rate and habitat heterogeneity We have so far treated $\Delta\theta$ and m as independent parameters, however we may also assume that if environmental heterogeneity increases with distance – in particular North-South difference if trait optimality is largely temperature-dependent – the rate of straying may be expected to decline with distance. If we assume this interdependence of m and $\Delta\theta$, low values of straying would correspond to mixing dissimilar (distant) populations, and high values
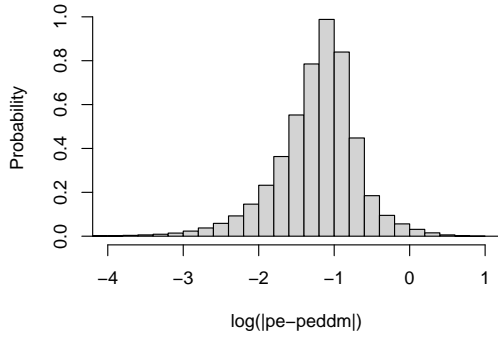
Figure 4: Log_{10} absolute differences in PE when stray rates are constant m vs. when stray rates are density dependent m_0.

of straying would correspond to mixing similar (nearby) populations.

In this case we find that alternative stable states now appear for low stray rates and low trait heritability, whereas increasing stray rates result in a single stable state with relatively high N_T. As before, there is a spike in the PE along the fold bifurcation separating the alternative stable state regime from the single stable state regime, but a sharp decline in the PE as stray rates become very low. This is in accordance with intuition as increasing stray rates mean that two very similar populations are mixing, resulting in little negative effect of trait dissimilarity.

However, that alternative stable states appear and that PE becomes severely depressed for very low values of PE is surprising: this means that even a small amount of straying of individuals from distant or dissimilar populations can qualitatively alter the dynamics of the metapopulation. (for the discussion: an example of this situation may be the salmon populations during the last glacial maximum, where any mixing would be from geographically distant populations)
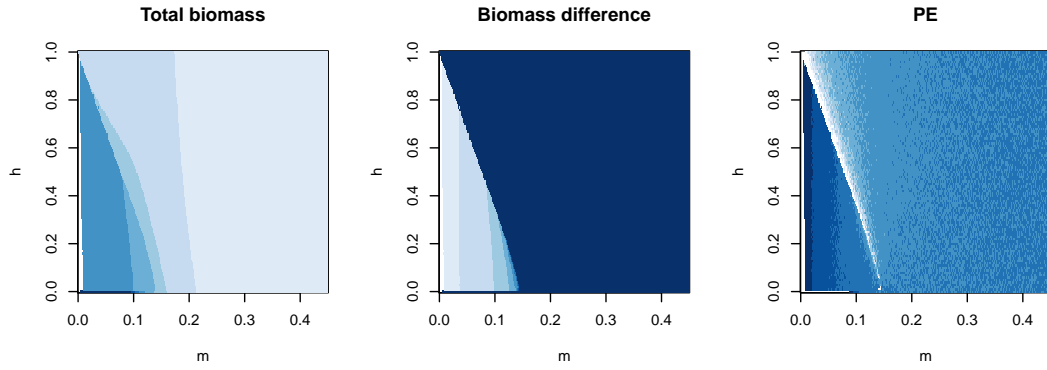
Discussion

Figure 5: Assuming that the rate of straying is linked directly to habitat heterogeneity. A low stray rate corresponds to very different (or distant) habitats (high $\Delta\theta$), whereas a higher rate of straying corresponds to very similar (or nearby) habitats (low $\Delta\theta$). Light colors = high values.
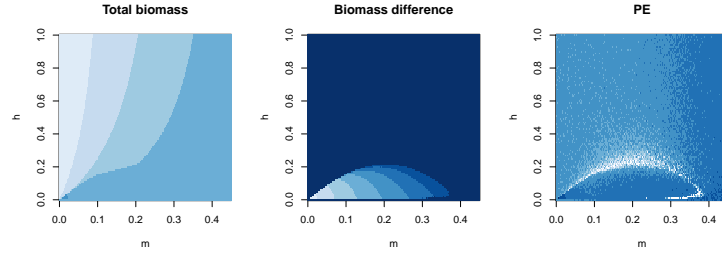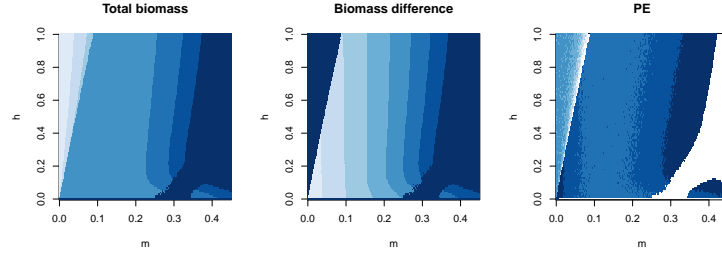
Appendix

(a) Low habitat heterogeneity ($\Delta\theta = 3$)

(b) High habitat heterogeneity ($\Delta\theta = 8$)

Figure 1: Total means N_t, difference in means ΔN, and the portfolio effect PE for different habitat heterogeneities $\Delta\theta$. Light colors = high values.
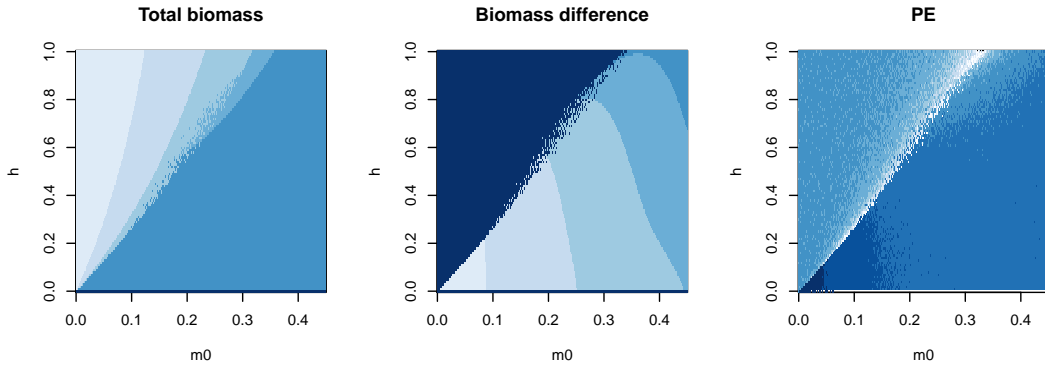

Figure 2: The same simulations as presented in Figure 2, except with density dependent straying, where $m(t) = m_0 \left(1 - N(t)/(C + N(t))\right)$. Light colors = high values.