Drivers of spatial synchrony in giant kelp populations

Max Castorani

1   The Model

We used the lottery model, previously studied, for instance, by REFS. Model equations are

$$N_i(t+1) = (1-\delta)N(t) + \delta N \frac{B_i(t)N_i(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)} \tag{1}$$

for species $i = 1, 2$. Here, $N_i(t)$ is the population density of species i at time t, and $N = N_1(t) + N_2(t)$ is fixed through time. The parameter, δ is a mortality rate, and $B_i(t)$ is the fecundiity of specise i at time t. The model postulates that individuals die at rate δ at each time step, and are replaced by juveniles in population to the reproductive output of the two species that year. We take, for each i, $B_i(t)$ to be *iid* through time. We let $B_i = exp(b_i)$, where (b_1, b_2) is some distribution such that $b_i \sim N(\mu_i, \sigma^2)$ and such that $cov(b_1, b_2) = \rho$, a fixed quantity we will specify later. However, (b_1, b_2) is not necessarily a bivariate normal distribution. We will consider various distributions of (b_1, b_2) with these properties, corresponding to our symmetric and asymmetric tail associations cases defined in the main text and elaborated below. We assume without loss of generality that $\mu_1 \leq \mu_2$, so that species 1 is the weaker competitor.

2   Noise

We created three cases for (b_1, b_2), the case of symmetric tail association and the cases of asymmetrical left- and right-tail association. To generate M points $(b_1^{(i)}, b_2^{(i)})$, $i = 1, .., M$, for the left tail association case, we first generated M points $(a_1^{(i)}, a_2^{(i)})$, $i = 1, ..., M$, from a bivariate normal distribution $N(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \Sigma)$, where here $\Sigma = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$. Then, for each index i, we randomly, with 50% probability, either (A) let $\tilde{b}_1^{(i)} = -|a_1^{(i)}|$ and $\tilde{b}_2^{(i)} = -a|_1^{(i)}|$, or (B) let $\tilde{b}_1^{(i)} = |a_1^{(i)}|$ and $\tilde{b}_2^{(i)} = |a_2^{(i)}|$. We then let $b_1^{(i)} = \sigma \tilde{b}_1^{(i)} + \mu_1$ and $b_2^{(i)} = \sigma \tilde{b}_2^{(i)} + \mu_2$. Perfect association in the left tails of the resulting distribution (b_1, b_2) results from the fact that, in case (A) above, both $\tilde{b}_1^{(i)}$ and $\tilde{b}_2^{(i)}$ were assigned to the same value. For speed of computation, when samples $(\tilde{b}_1^{(i)}, \tilde{b}_2^{(i)})$, $i = 1, ..., M$ were needed for every distinct set of values of the parameters μ_1, μ_2, and σ^2, we used the same $(\tilde{b}_1^{(i)}, \tilde{b}_2^{(i)})$, $i = 1, ..., M$, simply transforming these values differently (using the different valus of μ_1, μ_2, σ) for each set of parameter values. Right-tail associated noise was generated in an analogous way.

Noise with symmetric tail association was generated by taking a very large sample (1000?) of left-tail associated noise, as described above, and then calculating the Pearson correaltion coefficient, rho. The value obtained was ... . The symmetric noise was then generated once from $N(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \Sigma)$ where $\Sigma = \begin{pmatrix} 1 & \rho \\ \rho & 1 \end{pmatrix}$, denoting the points so generated by $(\tilde{b}_1^{(i)}, \tilde{b}_2^{(i)})$ for $i = 1, ..., M$. We then set $b_1^{(i)} = \sigma \tilde{b}_1^{(i)} + \mu_1$ and $b_2^{(i)} = \sigma \tilde{b}_2^{(i)} + \mu_2$.

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Thus, overall, our model was completely specified by specifying δ, μ_1, μ_2, σ and whether noise was generated from the left-tailed association, right-tailed association or symmetric tail association cases specified above.

3   Invasion growth rate of species 1, and storage effects

We consider the invasion growth rate of species 1, $\bar{r}_1 = \mathrm{E}(\ln(\frac{N_1(t+1)}{N_1(t)}))$, when N_1 is close to 0 and N_2 is close to N. Hence $\mathrm{E}(\cdot)$ represents expected value. We have

$$\frac{N_1(t+1)}{N_1(t)} = (1 - \delta) + \delta N \frac{B_1(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)}, \tag{2}$$

but setting $N_1 = 0$ and $N_2 = N$ here gives the result that

$$\bar{r}_1 = \mathrm{E}(\ln[(1 - \delta) + \delta exp(b_1 - b_2)]). \tag{3}$$

We considered the various cases for the joint distribution (b_1, b_2), specified in the main text and in the previous section.

To study storage effect for the model, we also consider the contribution of EC covariance to the difference between the invader's and the resident's mean growth rates, to be denoted ΔI. Following REF, we define

$$\bar{r}_1^{\#} = \mathrm{E}(\ln[(1 - \delta) + \delta exp(b_1^{\#} - b_2)]), \tag{4}$$

where $b_1^{\#}$ is distributed in the same way as b_1, but is independent of it and b_2. Then $\bar{r}_1 - \bar{r}_1^{\#}$ is the contribution of EC covariance to the mean growth rate species 1, the invader. We know, a priori, that the mean growth rate of the resident, species 2, must be 0, $\bar{r}_2 = 0$, but equation (1) also implies that

$$\frac{N_2(t+1)}{N_2(t)} = (1 - \delta) + \delta N \frac{B_2(t)}{B_1(t)N_1(t) + B_2(t)N_2(t)}. \tag{5}$$

Setting $N_2 = N$ and $N_1 = 0$ then gives

$$\frac{N_2(t+1)}{N_2(t)} = (1 - \delta) + \delta = 1 \tag{6}$$

so

$$r_2 = (\ln(\frac{N_2(t+1)}{N_2(t)})) = 0, \tag{7}$$

as expected. Again, following REF, we also define

$$\bar{r}_2^{\#} = \mathrm{E}(\ln[(1 - \delta) + \delta exp(b_2^{\#} - b_2)]), \tag{8}$$

where $b_2^{\#}$ is distributed in the same way as b_2, but is independent of it and of b_1. Thus $\bar{r}_2 - \bar{r}_2^{\#} = -\bar{r}_2^{\#}$ is the contribution of EC covariance to the mean growth rate of species 2, the resident. And so

$$\Delta I = (\bar{r}_1 - \bar{r}_1^{\#}) - (\bar{r}_2 - \bar{r}_2^{\#}) = \bar{r}_1 - \bar{r}_1^{\#} + \bar{r}_2^{\#} \tag{9}$$

has been defined in terms of expected values of elementary expressions of the random variables (b_1, b_2), $(b_1^{\#}, b_2)$, and $(b_2^{\#}, b_2)$.

Having already specified that b_1 (and therefore also $b_1^{\#}$) is distributed as $N(\mu_1, \sigma^2)$, and that b_2 (and therefore also $b_2^{\#}$) is distributed as $N(\mu_2, \sigma^2)$, we know, using Σ as notation for a covariance matrix that

$$(b_1^\#, b_2) \sim N(\begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix}, \Sigma) \tag{10}$$

and

$$(b_2^\#, b_2) \sim N(\begin{pmatrix} \mu_2 \\ \mu_2 \end{pmatrix}, \Sigma) \tag{11}$$

where

$$\Sigma = \begin{pmatrix} \sigma^2 & 0 \\ 0 & \sigma^2 \end{pmatrix}. \tag{12}$$

Thus the difference $b_1^\# - b_2$ that occurs in the expression for $\bar{r}_1^\#$ (4) is a normally distributed random variable with mean $\mu_1 - \mu_2$ and variance $2\sigma^2$. Thus

$$\bar{r}_1^\# = \mathrm{E}(\ln[(1 - \delta) + \delta exp(u)]), \tag{13}$$

where $u \sim N(\mu_1 - \mu_2, 2\sigma^2)$. Likewise, the difference $b_2^\# - b_2$ in (8) is a normally distributed random variable with mean $\mu_2 - \mu_2 = 0$ and variance $2\sigma^2$, so

$$\bar{r}_2^\# = \mathrm{E}(\ln[(1 - \delta) + \delta exp(u)]), \tag{14}$$

where now $u \sim N(0, 2\sigma^2)$. The expression (3) for $\bar{r}_1$ can also be further simplified, in a similar way, when we are in the symmetric tail association case considered in section 2. In that case,

$$(b_1, b_2) \sim N(\begin{pmatrix} \mu_2 \\ \mu_2 \end{pmatrix}, \Sigma) \tag{15}$$

where now

$$\Sigma = \begin{pmatrix} \sigma^2 & \rho \\ \rho & \sigma^2 \end{pmatrix}. \tag{16}$$

and $rho = putinvalue$ was determined as in section 2. Therefore, the expression $b_1 - b_2$ that occurred in 3, in the symmetric tail association case, is a normally distributed random variable with mean $\mu_1 - \mu_2$ and variance

$$\mathrm{var}(b_1 - b_2) = \mathrm{cov}(b_1 - b_2, b_1 - b_2) \tag{17}$$
$$= \mathrm{cov}(b_1, b_1) + \mathrm{cov}(b_2, b_2) - \mathrm{cov}(b_1, b_2) - \mathrm{cov}(b_2, b_1) \tag{18}$$
$$= 2\sigma^2 - 2\rho. \tag{19}$$

Thus, again only in the symmetric tail association case,

$$\bar{r}_1 = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), \tag{20}$$

where here $u \sim N(\mu_1 - \mu_2, 2\sigma^2 - 2\rho)$. As for all we know there is no simplicifaction of the expression 3 for $\bar{r}_1$ in the left and right-tail association cases.

Thus for in summary,

$$\bar{r}_1 = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(\mu_1 - \mu_2, 2\sigma^2 - 2\rho), \tag{21}$$

for the symmetric case, and

3

$$\bar{r}_1^{\#} = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(\mu_1 - \mu_2, 2\sigma^2), \tag{22}$$

$$\bar{r}_2^{\#} = \mathrm{E}(\ln[1 - \delta + \delta \exp(u)]), u \sim N(0, 2\sigma^2). \tag{23}$$

We next use the expressions to develop methods to estimate $\bar{r}_1$ and ΔI for any given paramters $\delta, \mu_1, \mu_2, \sigma$.

4 Estimating $\bar{r}_1$ and ΔI

First, for a large ?artigen? M, carry out the following steps once:

1. Generate left-tail assocated noise $(\tilde{b}_{l1}^{(i)}, \tilde{b}_{l2}^{(i)})$, $i = 1, ..., M$, as described in the section 2. Hence $\tilde{b}_{l1}^{i)}$ and $\tilde{b}_{l2}^{(i)}$ are distributed as $N(0, 1)$.

2. Generate right-tail associated noise $(\tilde{b}_{r1}^{(i)}, \tilde{b}_{r2}^{(i)})$, $i = 1, ..., M$, via the analogous procedure. Again, $\tilde{b}_{r1}^{i)}$ and $\tilde{b}_{r2}^{(i)}$ are distributed as $N(0, 1)$.

3. Generate M points $\tilde{u}_i$, $i = 1, ..., M$ from a standard normal distribution.

Next, given values of parameters δ, μ_1, μ_2, and σ, proceed as follows to get estimates of $\bar{r}_1, \bar{r}_1^{\#}, \bar{r}_2^{\#}$, and ΔI.

1. Estimate $\bar{r}_1$ for the left-tail associated case as $\hat{\bar{r}}_1 = \mathrm{mean}_i(\ln[1 - \delta + \delta \exp(b_{l1}^{(i)} - b_{l2}^{(i)})])$ where $b_{l1}^{(i)} = \sigma \tilde{b}_{l1}^{(i)} + \mu_1$ and $b_{l2}^{(i)} = \sigma \tilde{b}_{l2}^{(i)} + \mu_2$. The standard error of this estimate is $\mathrm{se}(\hat{r}_1) = \frac{\mathrm{sd}_i(\ln[1 - \delta + \delta \exp(b_{l1}^{(i)} - b_{l2}^{(i)})])}{\sqrt{M}}$, where $\mathrm{sd}_i(\cdot)$ is standard deviation.

2. Estiate $\bar{r}_1$ for the left-tail associated case as $\hat{\bar{r}}_1 = \mathrm{mean}_i(\ln[1 - \delta + \delta \exp(b_{r1}^{(i)} - b_{r2}^{(i)})])$ where $b_{r1}^{(i)} = \sigma \tilde{b}_{r1}^{(i)} + \mu_1$ and $b_{r2}^{(i)} = \sigma \tilde{b}_{r2}^{(i)} + \mu_2$. The standard error of this estimate is $\mathrm{se}(\hat{r}_1) = \frac{\mathrm{sd}_i(\ln[1 - \delta + \delta \exp(b_{r1}^{(i)} - b_{r2}^{(i)})])}{\sqrt{M}}$.

3. Estimate $\bar{r}_1$ in the symmetric tail association case as $\hat{\bar{r}}_1 = \mathrm{mean}_i(\ln[1 - \delta + \delta \exp(u_i)])$, where $u_i = \sqrt{(2\sigma^2 - 2\rho)}\tilde{u}_i + \mu_1 - \mu_2$. The standard error of this estimation is $\mathrm{se}(\hat{r}_1) = \frac{\mathrm{sd}_i(\ln[1 - \delta + \delta \exp(u_i)])}{\sqrt{M}}$.

4. Estimate $\bar{r}_1^{\#}$ (for all three tail-assocaition cases) as $\hat{\bar{r}}_1^{\#} = \mathrm{mean}_i(\ln[1 - \delta + \delta \exp(u_i)])$, where $u_i = \sqrt{2\sigma^2}\tilde{u}_i + \mu_1 - \mu_2$. The standard error is $\mathrm{se}(\hat{r}_1^{\#}) = \mathrm{sd}_i \frac{ln[1 - \delta + \delta \exp(u_i)]}{\sqrt{M}}$.

5. Estimate $\bar{r}_2^{\#}$ (for all three tail-assocaition cases) as $\hat{\bar{r}}_2^{\#} = \mathrm{mean}_i(\ln[1 - \delta + \delta \exp(u_i)])$, where $u_i = \sqrt{2\sigma^2}\tilde{u}_i$. The standard error is $\mathrm{se}(\hat{r}_2^{\#}) = \mathrm{sd}_i \frac{ln[1 - \delta + \delta \exp(u_i)]}{\sqrt{M}}$.

6. $\hat{\Delta I} = \hat{\bar{r}}_1 - \hat{\bar{r}}_1^{\#} + \hat{\bar{r}}_2^{\#}$, estimated ?syparatilly? for the left-tail associated, right-tail associated and symmetric noise cases. We obtained conservative standard error estimates by adding the standard error of the estimates of $\hat{\bar{r}}_1, \hat{\bar{r}}_1^{\#}$, and $\hat{\bar{r}}_2^{\#}$.

For large enough M, standard error should be very small. Since random variables are generated once only, computation of these quantities for a large number of parameter sets should be fast.

5 Additional quantities influencing invasion success

Not only does the expected value $\bar{r}_1$ influence the capacity for species 1 to invade where rare, but so do other aspectf of the distribution of

$$r_1 = \ln[1 - \delta + \delta \exp(b_1 - b_2)]. \tag{24}$$

We here elaborate how some other aspects of the distribution of r_1 were quantified, for our three tail association cases and for any of our parameters $\delta, \mu_1, \mu_2, \sigma$.

First, we considered $\mathrm{sd}(r_1)$, the standard deviation. If this is large enough, then r_1 can occasionally be positive even if $\bar{r}_1$ is strongly negative, and this invasion can occur under the right environmental circumstances.

We also considered the probability $\mathrm{P}[r_1 > 0]$, which is, explicitly, the probability that environmental variables that permit invasion. We have

$$\mathrm{P}[r_1 > 0] = \mathrm{P}[1 - \delta + \delta \exp(b_1 - b_2)] > 1] \tag{25}$$
$$= \mathrm{P}[\exp(b_1 - b_2) > 1] \tag{26}$$
$$= \mathrm{P}[b_1 > b_2], \tag{27}$$

?? should the above have ln? so this was computed for each considered parameter set of $\delta, \mu_1, \mu_2, \sigma$, and for each of our three tail association cases.

We also consider the mean value of the possible part of the distribution of r_1, $\mathrm{E}(r_1 | r_1 > 0)$. This characterizes how quickly invasion may happen, when it happens, with larger values corresponding to faster invasion. If it takes several time steps for the population of the invader to rise from negligible level at which species 1 is a noticeable presence in the community, then environmental conditions must be suitable for invasion for several sequential time steps. Thus large values of $\mathrm{E}(r_1 | r_1 > 0)$ should also correspond to a greater probability of invasion because they should correspond to faster invasions and therefore to reduced need for sequential periods of suitable environmental conditions.

Finally, for a ?low? of species of? parameters $\delta, \mu_1, \mu_2, \sigma$, we displayed the whole distribution of r_1, values for each of our tail association cases, to make visual comparisons.

6 Symmetries and parameter reduction

The quantities we consider to address invasion prospects for the weaker competitor, species 1 (see sections 3 and 5) depend only on $\mu_1 - \mu_2$ and not, independtly, on μ_1 and μ_2, and also are the same for our left- and right-tailed association cases. We prove these statements in this section.

Equations 21 - 23 obviously depend only on $\mu_1 - \mu_2$, and not independently on μ_1 and μ_2, ?some? only $\mu_1 - \mu_2$ appears in these expressions if μ_1 or μ_2 appear at all. Equation 21 is $\bar{r}_1$ in the asymmetric? tail association cases. But letting $\beta_1 = b_1 + \eta$ and $\beta_2 = b_2 + \eta$ and substituting into 21, we get

$$\bar{r}_1 = \mathrm{E}(\ln[1 - \delta + \delta \exp(\beta_1 - \eta - (\beta_2 - \eta))]) \tag{28}$$
$$= \mathrm{E}(\ln[1 - \delta + \delta \exp(\beta_1 - \beta_2)]). \tag{29}$$

And so altering the mean of both b_1 and b_2 distributions by the same amount has no affect of $\bar{r}_1$, and thus $\bar{r}_1$ in the asymmetric tail associations also depends only on $\mu_1 - \mu_2$ and not independtly on μ_1 or μ_2.

In section 5, we introduce several other metrics. These are all based on the distribution

$$r_1 = \ln[1 - \delta + \delta \exp(b_1 - b_2)] \tag{30}$$

But, again making the substitutions $\beta_1 = b_1 + \eta$ and $\beta_2 = b_2 + \eta$, we can see via the same resoning as above that the whole distribution r_1 depends only on $\mu_1 - \mu_2$, and not on μ_1 and μ_2 independently, for all three of our tail association cases.

To see that our various metrics are the same for out left- and right-tail associated noise ?parameters?, let (b_1, b_2) denote our left-tail associated random variable with parameters μ_1, μ_2, σ. Then define $\beta_1 = -b_2 + \mu_1 + \mu_2$, $\beta_2 = -b_1 + \mu_1 + \mu_2$. It is easy to see that $\mathrm{E}(\beta_1) = \mu_1$, $\mathrm{E}(\beta_2) = \mu_2$, $\mathrm{sd}(\beta_1) = \mathrm{sd}(\beta_2) = \sigma$, so β_1 and β_2 are normally distributed. From there it is easy to see that β_1 and $beta_2$ are distributed in the same wat as our right-tail associated noise with parameter μ_1, μ_2, and σ. Making the substitutions $b_2 = -\beta_1 + \mu_1 + \mu_2$ and $b_1 = -\beta_2 + \mu_1 + \mu_2$ in refr1distribution, we get

$$r_1 = \ln[1 - \delta + \delta \exp(-\beta_2 + \mu_1 + \mu_2 - (\beta_1 + \mu_1 + \mu_2))] \tag{31}$$
$$= \ln[1 - \delta + \delta \exp(\beta_1 - \beta_2)]. \tag{32}$$

And since (β_1, β_2) is distributed in the same way as our right-tail associated noise, this proves all metrics based on the distribution of r_1 30 are the same for left- and right-tail associated noise.