A   Appendix

In Appendix A.1, we provide the details for assessing the persistence of a population with an integrodifference model and we discuss the effect of the harvesting function on population persistence. In Appendix A.2, we provide the details for assessing population persistence with separable dispersal kernels. In Appendix A.3 and A.4, we derive expressions for the critical harvesting rate and rate of environmental shift for Gaussian and sinuosoidal dispersal kernels. In Appendix A.5, we derive approximate expressions for these critical rates. In Appendix A.6 we provide details on differences between small and large MPA simulations.

A.1   Determining stability Let $n_t(x)$ be the number of adults at position x at time t, let $k(x)$ be a dispersal kernel describingt the probability of a larva traveling a distance x, let $f(n)$ be the recruitment function describing the number of offspring produced by a population of size n, and let $g(n)$ be the harvesting function describing the number of adults harvested from a population of size n. In the absence of harvesting, the integrodifference model describing the population over time is given by

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y))dy \tag{1}$$

as described in Zhou and Kot [2011]. With the addition of harvesting, the model becomes

$$n_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y)-g(n_t(y)))dy. \tag{2}$$

In evaluating persistence, we apply the methods of Zhou and Kot [2011] to the new model, Equation 2. A traveling pulse is a solution such that population size relative to location within the patch (rather than absolute position) is constant over time, i.e.

$$n^*(\overline{x}_t) \equiv n^*(x-ct) = n_t(x),$$

where $\overline{x}_t \equiv x - ct$ gives position relative to the patch.

The integrodifference equation (2) gives us an expression for n^*:

$$\begin{aligned}
n^*(\overline{x}_{t+1}) &= n_{t+1}(x) \\
&= \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y)-g(n_t(y)))dy \\
&= \int_{-L/2+ct}^{L/2+ct} k(x-\overline{y}_t-ct)f(n^*(\overline{y}_t)-g(n^*(\overline{y}_t)))dy \\
&= \int_{-L/2+ct}^{L/2+ct} k(\overline{x}_t-\overline{y}_t)f(n^*(\overline{y}_t)-g(n^*(\overline{y}_t)))dy \\
\Rightarrow n^*(\overline{x}_t - c) &= \int_{-L/2+ct}^{L/2+ct} k(\overline{x}_t-\overline{y}_t)f(n^*(\overline{y}_t)-g(n^*(\overline{y}_t)))dy \\
\Rightarrow n^*(\overline{x}_t) &= \int_{-L/2}^{L/2} k(\overline{x}_t+c-\overline{y}_t)f(n^*(\overline{y}_t)-g(n^*(\overline{y}_t)))d\overline{y}_t \tag{3}
\end{aligned}$$

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As long as $f(0) = 0$, there is a trivial solution to this problem where $n^*(\overline{x}) \equiv 0$ for all $\overline{x}$, i.e., there is a trivial traveling pulse with no fish in it. If the trivial traveling pulse is unstable, even very small populations will persist or grow and avoid crashing back to the trivial pulse. To evaluate the stability of a traveling pulse, we introduce a small perturbation to the traveling pulse $n^*(\overline{x})$ and see if this perturbation grows or shrinks over time:

$$n_t(x) = n^*(\overline{x}_t) + \xi_t(x)$$

$$\Rightarrow \xi_{t+1}(x) = n_{t+1}(x) - n^*(\overline{x}_{t+1})$$

$$= n_{t+1}(x) - n^*(\overline{x}_t - c)$$

$$= \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y) - g(n_t(y)))dy - \int_{-L/2}^{L/2} k(\overline{x}_t - \overline{y}_t)f(n^*(\overline{y}_t) - g(n^*(\overline{y}_t)))d\overline{y}_t \text{ using (3)}$$

$$= \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y) - g(n_t(y)))dy - \int_{-L/2}^{L/2} k(\overline{x}_t - \overline{y}_t)f(n^*(\overline{y}_t) - g(n^*(\overline{y}_t)))d\overline{y}_t$$

$$= \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y) - g(n_t(y)))dy - \int_{-L/2+ct}^{L/2+ct} k(x - ct - (y - ct))f(n^*(\overline{y}_t) - g(n^*(\overline{y}_t)))d\overline{y}_t$$

$$= \int_{-L/2+ct}^{L/2+ct} k(x-y)f(n_t(y) - g(n_t(y)))dy - \int_{-L/2+ct}^{L/2+ct} k(x - y)f(n^*(\overline{y}_t) - g(n^*(\overline{y}_t)))d\overline{y}_t$$

$$= \int_{-L/2+ct}^{L/2+ct} k(x-y)\Big(f(n_t(y) - g(n_t(y))) - f(n^*(\overline{y}_t) - g(n^*(\overline{y}_t)))\Big)dy$$

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)(1 - g'(n^*(\overline{y})))f'(n^*(\overline{y}) - g(n^*(\overline{y}))\xi_t(y)dy$$

by linearizing around the traveling pulse

$$\Rightarrow \xi_{t+1}(x) = \int_{-L/2+ct}^{L/2+ct} k(x-y)(1 - g'(0))f'(0)\xi_t(y)dy \text{ if } n^*(\overline{x}) = 0 \tag{4}$$

If we assume $\xi_t(x) = \lambda^t u(x - ct)$ for some $\lambda \in \mathbb{R}$ and $u : [-L/2, L/2] \to \mathbb{R}$, then the perturbation grows in time if and only if $\lambda > 1$. Using Equation (4), we can rewrite $\xi_{t+1}(x)$,

$$\lambda u(x - ct - c) = (1 - g'(0))f'(0) \int_{-L/2+ct}^{L/2+ct} k(x-y)u(y - ct)dy$$

$$\Rightarrow \lambda u(\overline{x}) = (1 - g'(0))f'(0) \int_{-L/2}^{L/2} k(\overline{x} + c - \overline{y})u(\overline{y})d\overline{y}$$

Define the integral operator

$$\psi_f(u)(x) = (1 - g'(0))f'(0) \int_{-L/2}^{L/2} k(x + c - y)u(y)dy.$$

Then the perturbation to the traveling pulse will satisfy

$$\psi_f(u)(x) = \lambda u(x) \tag{5}$$

λ and u are thus an eigenvalue and eigenfunction of the functional operator ψ_f. The trivial traveling pulse is unstable when the dominant eigenvalue of ψ_f is greater than 1.

The biomass in the equilibrium traveling wave depends on the specific functional form of the harvesting function $g(n)$. However, the persistence of the population only depends on $g'(0)$ so in this paper, we only considered a proportional harvesting function, i.e. the amount of fish harvested obeyed $g(n) = hn$. For this function, $g'(0) = h$.

A.2 Separable dispersal kernels It is not immediately obvious that the operator ψ will have any eigenfunctions. However, Jentzsch's theorem guarantees that there is an eigenfunction u, provided that the kernel k satisfies some properties [Zhou and Kot, 2011]. Finding the eigenfunctions and eigenvalues is in general a hard problem to solve. It becomes easier if the kernel k is separable, i.e., there are functions a_n, b_n such that $k(x - y) = \sum_{n=1}^{\infty} a_n(x)b_n(y)$. In that case, (5) becomes

$$\lambda u(x) = f'(0) \sum_{n=1}^{\infty} \left(a_n(x) \int_{-L/2}^{L/2} b_n(y - c)u(y)dy \right)$$

$$\Rightarrow \lambda \int_{-L/2}^{L/2} b_k(x - c)u(x)dx = f'(0) \sum_{n=1}^{\infty} \left(\int_{-L/2}^{L/2} b_n(x - c)u(x)dx \right) \left(\int_{-L/2}^{L/2} a_n(y)b_k(y - c)dy \right) \text{ for any } k$$

$$\Rightarrow \lambda d_k = f'(0) \sum_{n=1}^{\infty} A_{nk}d_n \tag{6}$$

where

$$A_{nk} = \int_{-L/2}^{L/2} a_n(x)b_k(x - c)dx \text{ and } d_k = \int_{-L/2}^{L/2} b_k(x - c)u(x)dx$$

Finding the eigenvalues of (5) then reduces to finding the eigenvalues of the matrix $(A_{nk})_{n,k=1}^{\infty}$.

A.3 Gaussian dispersal kernel The Gaussian dispersal kernel is given by

$$k(x - y) = \frac{1}{2\sqrt{D\pi}}e^{\frac{-(x-y)^2}{4D}},$$

where $D = \frac{\pi}{4}\langle d \rangle$ and $\langle d \rangle$ is the expected distance a larva disperses. This is a separable kernel with $a_n(x) = b_n(x) = \frac{1}{\sqrt{2n!\sqrt{D\pi}}}e^{-x^2/4D}\left(\frac{x}{\sqrt{2D}}\right)^n$ [Latore et al., 1998].

As a first approximation to k we ignore all but the 0th terms for a_n and b_n so that Equation (6) becomes

$$\lambda d_0(c) = (1 - h)f'(0)A_{00}(c)d_0(c)$$
$$\Rightarrow \lambda = (1 - h)R_0 A_{00}(c)$$
$$\text{where } A_{00}(c) = 2\sqrt{2}\exp\left(\frac{-c^2}{8D}\right)\left[\text{erf}\left(\frac{L - c}{2\sqrt{2D}}\right) - \text{erf}\left(\frac{-L - c}{2\sqrt{2D}}\right)\right]$$

where erf is the error function. The critical rate of environmental shift c^* and the critical harvesting rate h^* are those values of c and h, respectively, that make $\lambda = 1$.

A.4 Sinusoidal dispersal kernel The sinusoidal dispersal kernel is given by

$$k(x-y) = \begin{cases} \frac{w}{2}\cos(w(x-y)) & , \quad |x-y| \le \frac{\pi}{2w} \\ 0 & , \quad |x-y| > \frac{\pi}{2w} \end{cases}$$

where L is the length of the patch and we assume $\frac{\pi}{2w} > L, c < \frac{\pi}{2w} - L$.

In this case, $k(x-y) = \frac{w}{2}\cos(wx)\cos(w(y-c)) + \frac{w}{2}\sin(wx)\sin(w(y-c))$ so that A_{ij} and d_i can be found for $i,j = 1,2$ and (6) reduces to

$$\lambda^2 - \left(\frac{R_0(1-h)wL}{2}\cos(wc)\right)\lambda + \frac{R_0^2(1-h)^2}{16}\left(w^2L^2 - \sin^2(wL)\right) = 0.$$

If we solve for λ, we find

$$\lambda = (1-h)R_0\left[\frac{wL\cos(wc)}{4} + \frac{1}{4}\sqrt{\sin^2(wL) - w^2L^2\sin^2(wc)}\right].$$

Zhou and Kot [2011] solve for the critical speed, c^*, at which the population will be driven extinct:

$$c^* = c^*(R_0) = \frac{1}{w}\cos^{-1}\left[\frac{16 + R_0^2(1-h)^2(w^2L^2 - \sin^2(wL))}{8R_0(1-h)wL}\right].$$

In our model, we can additionally solve for the critical harvesting rate, h^*, at which the population will be driven extinct:

$$h^* = 1 - \frac{1}{R_0}\cdot\frac{4wL}{w^2L^2 - \sin^2(wL)}\left[\cos(wc) - \sqrt{\cos^2(wc) - 1 + \frac{\sin^2(wL)}{w^2L^2}}\right]$$

A.5 Approximate critical harvesting proportions

We will use the following Taylor series to make approximations of the critical harvesting proportions under the two dispersal kernels:

$$\cos(x) = 1 - \frac{x^2}{2}$$
$$\cos^2(x) = 1 - x^2$$
$$\sin^2(x) = x^2 - \frac{x^4}{3}$$
$$erf(x) = \frac{2}{\sqrt{\pi}}(x - \frac{x^3}{3})$$
$$\exp(x) = 1 + x + \frac{x^2}{2}$$

For the Gaussian kernel we found

$$h^* = 1 - \frac{2\sqrt{2}\exp\left(\frac{c^2}{8D}\right)}{R_0\left[erf\left(\frac{L-c}{2\sqrt{2D}}\right) - erf\left(\frac{-L-c}{2\sqrt{2D}}\right)\right]} \tag{7}$$

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Using the Taylor series and the fact that $D = \frac{\sigma^2}{2}$ where σ^2 is the variance of the exponential kernel,

$$h^* \sim 1 - \frac{\sqrt{2\pi}(1 + \frac{c^2}{8D} + \frac{c^4}{128D^2})}{R_0\sqrt{\pi}\left[\frac{L-c}{2\sqrt{2D}} - \frac{(L-c)^3}{3(2\sqrt{2D})^3} - \frac{-L-c}{2\sqrt{2D}} + \frac{(-L-c)^3}{3(2\sqrt{2D})^3)}\right]}$$

$$= 1 - \frac{1}{R_0} \cdot \frac{3\sqrt{2\pi}}{8L} \frac{(32\sigma^4 + 8c^2\sigma^2 + c^4)}{\sigma\left(12\sigma^2 - (L^2 + 3c^2)\right)}$$

For the sinusoidal kernel we found

$$h^* = 1 - \frac{1}{R_0} \cdot \frac{4wL}{w^2L^2 - \sin^2(wL)}\left[\cos(wc) - \sqrt{\cos^2(wc) - 1 + \frac{\sin^2(wL)}{w^2L^2}}\right] \tag{8}$$

Using the Taylor series and the fact that $w = \frac{\sqrt{\frac{\pi^2}{4} - 2}}{\sigma}$ where σ^2 is the variance of the sinusoidal kernel,

$$h^* \sim 1 - \frac{1}{R_0} \cdot \frac{12wL}{w^4L^4}\left[1 - \frac{w^2c^2}{2} - \sqrt{1 - w^2c^2 - \frac{w^2L^2}{3}}\right]$$

$$= 1 - \frac{1}{R_0} \cdot \frac{4\sqrt{3}}{L^3(\pi^2 - 8)^{3/2}} \cdot \sigma\left[8\sqrt{3}\sigma^2 - (\pi^2 - 8)\sqrt{3}c^2 - 4\sigma\sqrt{12\sigma^2 - (\pi^2 - 8)(3c^2 + L^2)}\right]$$

In the case of both kernels, the critical harvesting proportion can be approximated by a function that looks like

$$h^* \sim 1 - \frac{1}{R_0} \cdot g(L)q(\sigma^2, c^2, L^2 + 3c^2) \tag{9}$$

where $g(L)$ is a decreasing function of the length of the viable patch L.

A.6 MPA fluctuations

After the simulations come to equilibrium, the fluctuations in total biomass per generation fluctuate more in MPAs that are larger and spaced farther apart than simulations in which the MPAs that are smaller and more closely spaced. The large MPAs have a slightly larger average population, however large MPAs here can induce fluctuations of biomass even in deterministic simulations. Thus we expect if reproduction was stochastic, large MPAs spaced far apart would be more likely to result in extinction of the population than more closely spaced, smaller MPAs.
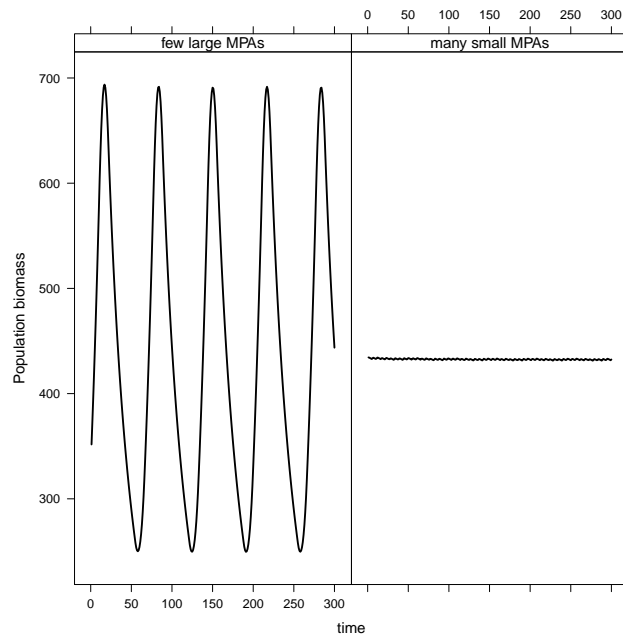

Figure 1: Total population biomass is on the y axis, and generation is on the x axis. These simulations were run with climate velocity = 0.1, and a proportional harvest rate = 0.08.

References

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