Critical domain size problems for stage-structured integrodifference equations

Mark A. Lewis

University of Alberta

Outline

Persistence dynamics

- There is a history of mathematical ecologists asking "is this piece of habitat sufficient for local persistence of a given species?"
- Early work goes back to Kierstead, Slobodkin and Skellam (KISS) and the critical domain size problem is a key component in mathematical ecology textbooks (eg., Kot 2001)
- The classical model includes a scalar reaction diffusion equation (logistic growth and diffusion) with hostile boundary conditions.
- For this case it is shown that the species persists if and only if the domain size L satisfies $L > L^* = \pi\sqrt{D/r}$, where D is the diffusion coefficient and r the intrinsic growth rate.
- I will discuss the critical domain size problem for systems of integrodifference equations, focusing on an applied example: persistence of invasive zebra mussels in rivers.

Spread of zebra mussels in streams

threelakecouncil.org

- Zebra mussels were introduced to North America from the Ponto-Caspian region, likely via ballast water exchange in the Great Lakes ecosystem.
- They have established in eastern North America, but have not yet made it to all the western provinces and states.
- They grow in great numbers, cover beaches, clog cooling systems (including those for nuclear plants) and threaten other species.
- They do fine in lakes, but have been unable to colonize certain stretches of rivers, particularly when flow rates are high.
- We are going to model this system and try to understand why.

Outline

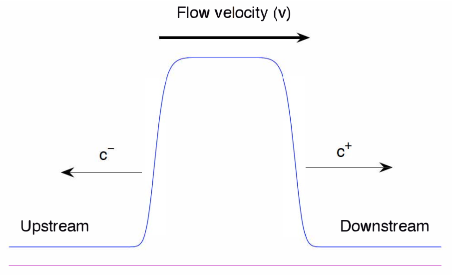
Including advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = D\frac{\partial^2 u}{\partial x^2} + g(u)u$$

$$\begin{aligned} v &= \text{Advection velocity} \\ D &= \text{Diffusion coefficient} \\ g(u) &= r(1-u) \quad \text{per capita growth rate } (g(0) = r) \end{aligned}$$

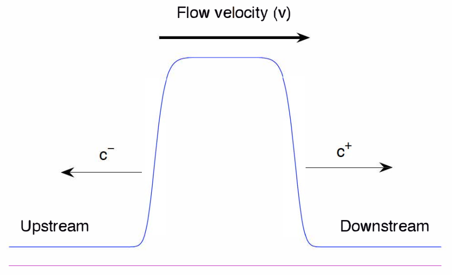
Including advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = D\frac{\partial^2 u}{\partial x^2} + g(u)u$$



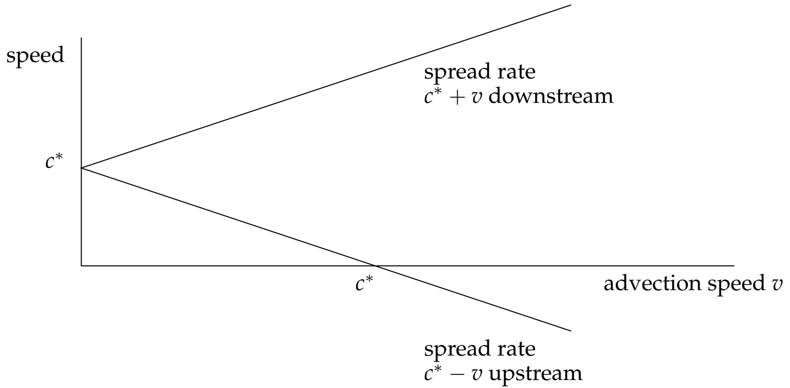
Including advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = D\frac{\partial^2 u}{\partial x^2} + g(u)u$$



$$\begin{aligned} c^- &= 2\sqrt{rD} - a = c^* - v \\ c^+ &= 2\sqrt{rD} + a = c^* + v \end{aligned}$$

Advection can cause spread to stall



Critical patch size with advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = f(x,u) + D\frac{\partial^2 u}{\partial x^2}$$

Critical patch size with advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = f(x,u) + D\frac{\partial^2 u}{\partial x^2}$$

where

$$\begin{aligned} f(x,u) &= u\,g(x,u) \text{ for all } x \in \mathbb{R} \\ g(x,u) &= \begin{cases} -d, & x \notin (0,L) \\ r\big(1-u\big), & x \in (0,L) \end{cases} \end{aligned}$$

Critical patch size with advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = f(x,u) + D\frac{\partial^2 u}{\partial x^2}$$

where

$$\begin{aligned} f(x,u) &= u\,g(x,u) \text{ for all } x \in \mathbb{R} \\ g(x,u) &= \begin{cases} -d, & x \notin (0,L) \\ r\big(1-u\big), & x \in (0,L) \end{cases} \end{aligned}$$

v: speed of advection;
L: length of the good patch;
d: death rate in the unsuitable regions;
r: per capita growth rate in the good habitat;
D: diffusion coefficient.

Critical patch size with advection

$$\frac{\partial u}{\partial t} + v\frac{\partial u}{\partial x} = f(x,u) + D\frac{\partial^2 u}{\partial x^2}$$

where

$$\begin{aligned} f(x,u) &= u\,g(x,u) \text{ for all } x \in \mathbb{R} \\ g(x,u) &= \begin{cases} -d, & x \notin (0,L) \\ r\big(1-u\big), & x \in (0,L) \end{cases} \end{aligned}$$

v: speed of advection;
L: length of the good patch;
d: death rate in the unsuitable regions;
r: per capita growth rate in the good habitat;
D: diffusion coefficient.

How large a good patch (L^*) is needed for population persistence?

Existence of a steady state solution

$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0,L)$$

Existence of a steady state solution

$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0, L)$$

with boundary conditions

$$\begin{aligned} 0 &= \kappa^{+}U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^{-}U(L) - \frac{dU}{dx}(L) \end{aligned}$$

where

$$\kappa^{\pm} = \frac{a \pm \sqrt{v^2 + 4Dd}}{2D}$$

Existence of a steady state solution

$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0,L)$$

with boundary conditions

$$\begin{aligned} 0 &= \kappa^+ U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^- U(L) - \frac{dU}{dx}(L) \end{aligned}$$

where

$$\kappa^\pm = \frac{a \pm \sqrt{v^2 + 4Dd}}{2D}$$

v: speed of advection;
L: length of the good patch;
d: death rate in the unsuitable regions;
r: per capita growth rate in the good habitat;
D: diffusion coefficient.

Existence of a steady state solution

$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0, L)$$

with boundary conditions

$$\begin{aligned} 0 &= \kappa^+ U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^- U(L) - \frac{dU}{dx}(L) \end{aligned}$$

where

$$\kappa^{\pm} = \frac{a \pm \sqrt{v^2 + 4Dd}}{2D}$$

v: speed of advection;
L: length of the good patch;
d: death rate in the unsuitable regions;
r: per capita growth rate in the good habitat;
D: diffusion coefficient.

How large a good patch (L^*) is needed for nontrivial solution?

Existence of a steady state solution

$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0, L)$$

with boundary conditions

$$\begin{aligned} 0 &= \kappa^+ U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^- U(L) - \frac{dU}{dx}(L) \end{aligned}$$

where

$$\kappa^{\pm} = \frac{a \pm \sqrt{v^2 + 4Dd}}{2D}$$

Linearization about $U = 0$ yields critical patch size

We solve the boundary value problem

$$D\frac{d^2U}{dx^2} - v\frac{dU}{dx} + rU = 0 \qquad \text{for } x \in (0, L)$$

$$\begin{aligned} 0 &= \kappa^+ U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^- U(L) - \frac{dU}{dx}(L) \end{aligned}$$

where

$$\kappa^\pm = \frac{a \pm \sqrt{v^2 + 4Dd}}{2D}$$

and observe that a nontrivial solution emerges when L is larger than the critical patch size

$$L^*(c^*, a) := \frac{\frac{c^*}{r}}{\sqrt{1 - \left(\frac{a}{c^*}\right)^2}} \arctan\left(\frac{\sqrt{\frac{d}{r} + \left(\frac{a}{c^*}\right)^2}}{\sqrt{1 - \left(\frac{a}{c^*}\right)^2}}\right)$$

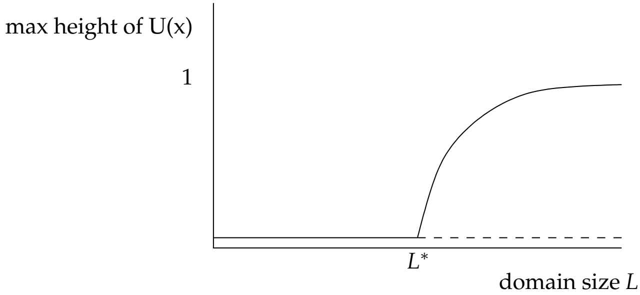
where $c^* = 2\sqrt{rD}$.

Existence of a steady state solution

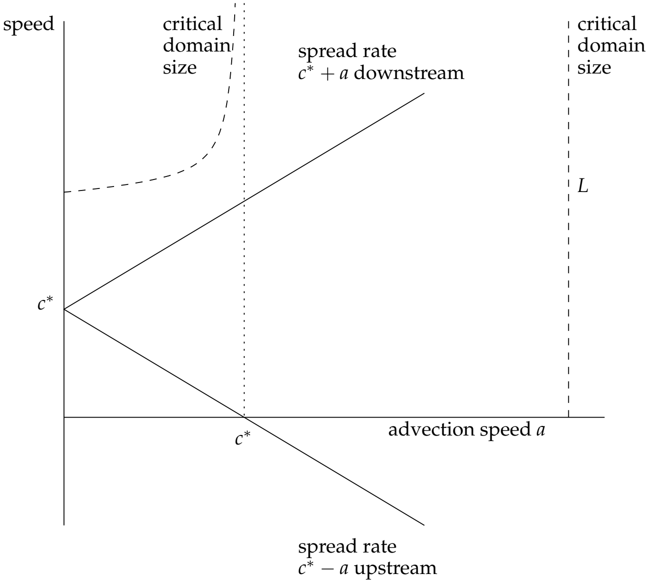
$$v\frac{dU}{dx} = rU(1-U) + D\frac{d^2U}{dx^2} \qquad \text{for } x \in (0, L)$$

with boundary conditions

$$\begin{aligned} 0 &= \kappa^+ U(0) - \frac{dU}{dx}(0) \\ 0 &= \kappa^- U(L) - \frac{dU}{dx}(L) \end{aligned}$$



Patch size becomes infinite when spread stalls



Patch size becomes infinite when spread stalls

The connection between infinite patch size and the advection speed at which spread stalls can be extended to account for

- Different boundary conditions (McKenzie et al., 2012)
- Long-distance dispersal via integro-difference or integrodifferential equations (Lutscher et al., 2005)
- Spatial heterogeneity (Lutscher et al., 2006)
- Seasonality in growth and dispersal (Jin and Lewis, 2011)
- Impulsive reaction-diffusion models (Fazly et al., 2020)

A summary of some of these idea is found in Lutscher et al. (2010)

Critical domain size for zebra mussels

- How large a length of river do the zebra mussels need to survive?
- When the length of good river habitat is too short then the mortality from the hostile surrounding regions may dominate.
- However, when the river is longer, boundary mortality should be less important.
- How do other factors such as temperature and water velocity play a role?
- Critical domain size problems have been well studied for reaction diffusion models, but also can be calculated for systems of integrodifference equations.
- There are two key elements to be discussed
  - What are the general theoretical results?
  - How can we calculate the critical domain size for the zebra mussel problem?
- We will also look for new biological and theoretical insight.

Critical domain size analysis

Consider the stage-structured model

$$\mathbf{N}(x, n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{B}(\mathbf{N})]\mathbf{N}(y,n)dy. \tag{1}$$

There is a trivial solution $\mathbf{N}^* = \mathbf{0}$. We are interested in conditions on the domain size L that guarantee existence of a stable nontrivial solution $\mathbf{N}^*(x)$.

We would like to examine the stability of the model linearized about $\mathbf{N}^* = \mathbf{0}$

$$\mathbf{N}(x, n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{2}$$

where $\mathbf{A} = \mathbf{B}(\mathbf{0})$, and show that, as L increases through L^*, $\mathbf{N}^* = \mathbf{0}$ becomes unstable and a stable nontrivial solution $\mathbf{N}^*(x)$ emerges.

Conditions for emergence of stable nontrivial solution

Roughly speaking, the following conditions are sufficient (Lutscher and Lewis, 2004):

- Conditions on the dynamics
  - The matrix $\mathbf{B}(\mathbf{N})$ is primitive for all $\mathbf{N} \geq 0$.
  - There is no "Allee effect", and the growth function $\mathbf{B}(\mathbf{N})\mathbf{N}$ is monotonic and saturating.
  - The highest per capita growth rate $\mathbf{B}$ for each component is at $\mathbf{N}^* = \mathbf{0}$.
- Conditions on the dispersal
  - There is a constraint on the structure of the nonzero entries of the dispersal matrix to ensure sufficient dispersal.
  - With sufficient iterations, each dispersal kernel will allow dispersal from every point in the domain to every other point.
- Conditions on the effects of increasing the domain size
  - Increasing the domain size does not result in a decrease in the per capita growth rate $\mathbf{B}(\mathbf{N})$.
  - Increasing the domain size does not result in a decrease in dispersal success from y to x.

Under these conditions, the dominant eigenvalue of the linearized system will increase through 1 and the trivial solution will lose its stability as L increases through the *critical domain size* L^*. A stable nontrivial solution will emerge.

Outline

Integrodifference model for zebra mussels in streams

Population dynamics plus dispersal

$$J(x,n+1) = \varphi(J(x,n),A(x,n),T)\; s_l(T)\; r \int_\Omega A(y,n)K(x,y)dy,$$
$$A(x,n+1) = \varphi(J(x,n),A(x,n),T)\; [s_j(T)J(x,n) + s_a(T)A(x,n)], \qquad (3)$$

Symbols	Definitions	Estimates
r	Reproduction rate of adults	4218/year
φ	Temperature-dependent competition function	
s_l, s_j, s_a	Temperature-dependent survival functions	
m	Mortality rate of dispersing larvae	1.44/day
σ	Settling rate of dispersing larvae	0.00144/day

Huang and Lewis (2017)

Integrodifference model for zebra mussels in streams

Population dynamics plus dispersal

$$J(x, n+1) = \varphi(J(x,n), A(x,n), T)\ s_l(T)\ r \int_\Omega A(y,n) K(x,y) dy,$$
$$A(x, n+1) = \varphi(J(x,n), A(x,n), T)\ [s_j(T) J(x,n) + s_a(T) A(x,n)],$$

Competition

$$\varphi(J, A, T) = \frac{1}{1 + \beta[\ell_j(T) J + \ell_a(T) A]}, \tag{4}$$

Survival

$$s_l(T) = s_j(T) = s_a(T) = \frac{\exp(b_0 + b_1 T + b_2 T^2)}{1 + \exp(b_0 + b_1 T + b_2 T^2)},$$

Initial conditions for juveniles and adults

$$J(x, 0) = J^0(x), \quad A(x, 0) = A^0(x), \quad x \in \Omega.$$

Outline

Mechanistic dispersal kernels: Gaussian

- Consider a propagule moving randomly in one dimension, released from the point $x = 0$ at time $t = 0$.
- The probability density function $w(x, t)$ for the propagule's location at time t satisfies the diffusion equation

$$\frac{\partial w}{\partial t} = D\frac{\partial^2 w}{\partial x^2} \tag{5}$$

with initial condition $w(x, 0) = \delta(x)$.

Mechanistic dispersal kernels: Gaussian

- Consider a propagule moving randomly in one dimension, released from the point $x = 0$ at time $t = 0$.
- The probability density function $w(x, t)$ for the propagule's location at time t satisfies the diffusion equation

$$\frac{\partial w}{\partial t} = D\frac{\partial^2 w}{\partial x^2} \tag{5}$$

  with initial condition $w(x, 0) = \delta(x)$.
- The solution to the problem is

$$w(x,t) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(\frac{-x^2}{4Dt}\right). \tag{6}$$

- Thus, for individuals released from the point $y = 0$, moving randomly and settling at time t, the dispersal kernel becomes

$$K(x) = \frac{1}{\sqrt{4\pi Dt}} \exp\left(\frac{-x^2}{4Dt}\right). \tag{7}$$

Dispersal kernels: Laplace Kernel

- Laplace kernel comes from random motion plus settling:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \sigma u, \tag{8}$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \tag{9}$$

- Consider a point release $u(x,0) = \delta(x)$ and $u_s(x,0) = 0$.
- Define the dispersal kernel to be long term settling density $K = u_s(x,\infty)$.

Dispersal kernels: Laplace Kernel

- Laplace kernel comes from random motion plus settling:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \sigma u, \qquad (8)$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \qquad (9)$$

- Consider a point release $u(x,0) = \delta(x)$ and $u_s(x,0) = 0$.
- Define the dispersal kernel to be long term settling density $K = u_s(x,\infty)$.
- Integrating (13) yields

$$K(x) = \sigma\int_0^\infty u(x,t)dt$$

- Integrating (12) and applying $u(x,\infty) = 0$ yields

$$-\delta(x) = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - K, \qquad (10)$$

a *modified Helmholtz equation* for the dispersal kernel.

Dispersal kernels: Laplace Kernel

- Laplace kernel comes from random motion plus settling:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - \sigma u, \tag{8}$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \tag{9}$$

- Consider a point release $u(x,0) = \delta(x)$ and $u_s(x,0) = 0$.
- Define the dispersal kernel to be long term settling density $K = u_s(x,\infty)$.
- Integrating (13) yields

$$K(x) = \sigma \int_0^\infty u(x,t)dt$$

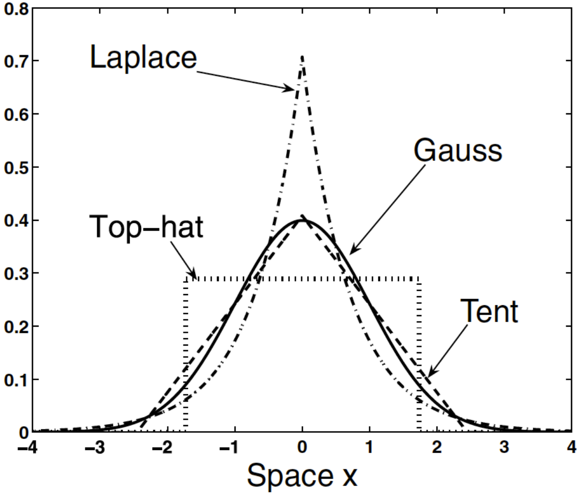
- Integrating (12) and applying $u(x,\infty) = 0$ yields

$$-\delta(x) = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - K, \tag{10}$$

  a *modified Helmholtz equation* for the dispersal kernel.
- The solution is the Laplace (or double-exponential) kernel,

$$K(x) = \frac{\alpha}{2}\exp(-\alpha|x|), \quad \alpha = \sqrt{\sigma/D}. \tag{11}$$

Dispersal kernels



Including advection, settling and mortality

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} - (m+\sigma)u, \tag{12}$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \tag{13}$$

Including advection, settling and mortality

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} - (m+\sigma)u, \quad (12)$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \quad (13)$$

- This yields

$$-\delta(x) = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - \frac{v}{\sigma}\frac{\partial u}{\partial x} - \frac{m+\sigma}{\sigma}K = \mathcal{L}K, \quad (14)$$

Including advection, settling and mortality

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} - v\frac{\partial u}{\partial x} - (m+\sigma)u, \tag{12}$$

$$\frac{\partial u_s}{\partial t} = \sigma u. \tag{13}$$

- This yields

$$-\delta(x) = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - \frac{v}{\sigma}\frac{\partial u}{\partial x} - \frac{m+\sigma}{\sigma}K = \mathcal{L}K, \tag{14}$$

- The solution on a infinite domain is

$$K(x,y) = \begin{cases} \alpha \exp\{\gamma_1(x-y)\}, & x \le y, \\ \alpha \exp\{\gamma_2(x-y)\}, & x \ge y, \end{cases} \tag{15}$$

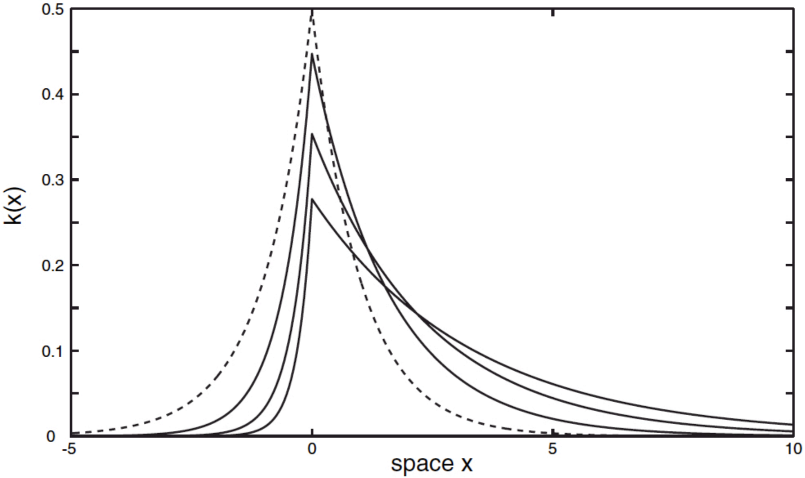
where where

$$\alpha = \frac{\sigma}{\sqrt{v^2 + 4D(m+\sigma)}}, \quad \gamma_{1,2} = \frac{v}{2D} \pm \sqrt{\left(\frac{v}{2D}\right)^2 + \frac{m+\sigma}{D}}.$$

Dispersal kernel for streams

It turns out that, because the process includes mortality as well as settling:

$$\int_{-\infty}^{\infty} K(x,y)dx = \int_{-\infty}^{\infty} K(x,y)dy = \frac{\sigma}{\sigma+m}.$$



Dispersal kernel on a finite domain $(0, L)$

Boundary conditions depend on the biology/physics

- Hostile

$$u(0,t) = 0, \quad u(L,t) = 0.$$

- General

$$\alpha_1 u(0,t) + \alpha_2 u_x(0,t) = 0, \quad \alpha_3 u(L,t) + \alpha_4 u_x(L,t) = 0.$$

Dispersal kernel on a finite domain $(0, L)$

Boundary conditions depend on the biology/physics

- Hostile

$$u(0,t) = 0, \quad u(L,t) = 0.$$

- General

$$\alpha_1 u(0,t) + \alpha_2 u_x(0,t) = 0, \quad \alpha_3 u(L,t) + \alpha_4 u_x(L,t) = 0.$$

- These give boundary conditions for K, eg for hostile boundary conditions we solve

$$-\delta(x) = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - \frac{v}{\sigma}\frac{\partial u}{\partial x} - \frac{m+\sigma}{\sigma}K = \mathcal{L}K,$$

subject to

$$K(0) = \sigma \int_0^\infty u(0,t)dt = 0, \quad K(L) = \sigma \int_0^\infty \sigma u(L,t)dt = 0.$$

Outline

Integrodifference model for zebra mussels in streams

Population dynamics plus dispersal

$$J(x,n+1) = \varphi(J(x,n),A(x,n)) \;\; s_l r \int_\Omega A(y,n)K(x,y)dy,$$
$$A(x,n+1) = \varphi(J(x,n),A(x,n)) \; [s_j J(x,n) + s_a A(x,n)], \tag{16}$$

Competition

$$\varphi(J,A) = \frac{1}{1+\beta[\ell_j J + \ell_a A]},$$

Integrodifference model for zebra mussels in streams

Population dynamics plus dispersal

$$J(x,n+1) = \varphi(J(x,n),A(x,n)) \;\; s_l r \int_\Omega A(y,n)K(x,y)dy,$$
$$A(x,n+1) = \varphi(J(x,n),A(x,n)) \; [s_j J(x,n) + s_a A(x,n)], \tag{16}$$

Competition

$$\varphi(J,A) = \frac{1}{1+\beta[\ell_j J + \ell_a A]},$$

We will use the fact that

$$\int_{-\infty}^{\infty} K(x,y)dx = \int_{-\infty}^{\infty} K(x,y)dy = \frac{\sigma}{\sigma+m}.$$

when deriving the nonspatial model.

Nonspatial model

We consider spatially homogeneous solutions to (16)

$$J(n+1) = \varphi(J(n), A(n))\frac{s_l r\sigma}{\sigma + m}A(n),$$

$$A(n+1) = \varphi(J(n), A(n))[s_j J(n) + s_a A(n)],$$

where

$$\varphi(J, A) = \frac{1}{1 + \beta[\ell_j J + \ell_a A]}$$

Nonspatial model

We consider spatially homogeneous solutions to (16)

$$J(n+1) = \varphi(J(n), A(n)) \frac{s_l r \sigma}{\sigma + m} A(n),$$

$$A(n+1) = \varphi(J(n), A(n)) [s_j J(n) + s_a A(n)],$$

where

$$\varphi(J, A) = \frac{1}{1 + \beta[\ell_j J + \ell_a A]}$$

Linearized about trivial equilibrium:

$$J(n+1) = \frac{s_l r \sigma}{\sigma + m} A(n),$$

$$A(n+1) = [s_j J(n) + s_a A(n)],$$

Nonspatial model

We consider spatially homogeneous solutions to (16)

$$J(n+1) = \varphi(J(n), A(n)) \frac{s_l r \sigma}{\sigma + m} A(n),$$
$$A(n+1) = \varphi(J(n), A(n)) [s_j J(n) + s_a A(n)],$$

where

$$\varphi(J, A) = \frac{1}{1 + \beta[\ell_j J + \ell_a A]}$$

Linearized about trivial equilibrium:

$$J(n+1) = \frac{s_l r \sigma}{\sigma + m} A(n),$$
$$A(n+1) = [s_j J(n) + s_a A(n)],$$

Net reproductive rate:

$$R_0^{\mathrm{loc}}(T) = \frac{s_l(T) s_j(T) r \dfrac{\sigma}{\sigma + m}}{1 - s_a(T)}. \qquad (17)$$

$R_0^{\mathrm{loc}}(T) > 1$ gives zebra mussel survival in the 10–23°C range.

Outline

Critical domain size analysis for zebra mussel model

$$\mathbf{N}(x, n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{18}$$

where $\mathbf{N}(x,n) = (J(x,n), A(x,n))^T$ and

$$\mathbf{A} = \begin{pmatrix} 0 & s_l r \\ s_j & s_a \end{pmatrix}, \quad \mathbf{K}(x,y) = \begin{pmatrix} \delta(x-y) & K(x,y) \\ \delta(x-y) & \delta(x-y) \end{pmatrix}. \tag{19}$$

Critical domain size analysis for zebra mussel model

$$\mathbf{N}(x, n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{18}$$

where $\mathbf{N}(x,n) = (J(x,n), A(x,n))^T$ and

$$\mathbf{A} = \begin{pmatrix} 0 & s_l r \\ s_j & s_a \end{pmatrix}, \quad \mathbf{K}(x,y) = \begin{pmatrix} \delta(x-y) & K(x,y) \\ \delta(x-y) & \delta(x-y) \end{pmatrix}. \tag{19}$$

The eigenvalue problem becomes

$$\lambda \mathbf{N}(x) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y)dy, \tag{20}$$

Critical domain size analysis for zebra mussel model

$$\mathbf{N}(x,n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{18}$$

where $\mathbf{N}(x,n) = (J(x,n), A(x,n))^T$ and

$$\mathbf{A} = \begin{pmatrix} 0 & s_l r \\ s_j & s_a \end{pmatrix}, \quad \mathbf{K}(x,y) = \begin{pmatrix} \delta(x-y) & K(x,y) \\ \delta(x-y) & \delta(x-y) \end{pmatrix}. \tag{19}$$

The eigenvalue problem becomes

$$\lambda \mathbf{N}(x) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y)dy, \tag{20}$$

and the stability condition $\lambda = 1$ yields

$$\begin{aligned} J(x) &= s_l r \int_0^{L^*} A(y,n)K(x,y)dy, \\ A(x) &= s_j J(x) + s_a A(x), \quad \text{or} \end{aligned}$$

Critical domain size analysis for zebra mussel model

$$\mathbf{N}(x, n+1) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{18}$$

where $\mathbf{N}(x,n) = (J(x,n), A(x,n))^T$ and

$$\mathbf{A} = \begin{pmatrix} 0 & s_l r \\ s_j & s_a \end{pmatrix}, \quad \mathbf{K}(x,y) = \begin{pmatrix} \delta(x-y) & K(x,y) \\ \delta(x-y) & \delta(x-y) \end{pmatrix}. \tag{19}$$

The eigenvalue problem becomes

$$\lambda \mathbf{N}(x) = \int_0^L [\mathbf{K}(x,y) \circ \mathbf{A}]\mathbf{N}(y)dy, \tag{20}$$

and the stability condition $\lambda = 1$ yields

$$\begin{aligned} J(x) &= s_l r \int_0^{L^*} A(y,n)K(x,y)dy, \\ A(x) &= s_j J(x) + s_a A(x), \quad \text{or} \end{aligned}$$

$$A(x) = \frac{s_j}{1-s_a} s_l r \int_0^{L^*} A(y)K(x,y)dy. \tag{21}$$

An R_0 approach to critical domain size

- Consider a small adult population density $A(y)$.
- Life time production of larvae from adults at point y is

$$A(y)(1 + s_a + s_a^2 + \ldots)r = \frac{A(y)}{1 - s_a}r. \tag{22}$$

- The density of larvae arriving at point x from all possible y is

$$\int_0^L \frac{A(y)}{1 - s_a} rK(x, y)dy. \tag{23}$$

- New adults produced over the life time of initial distribution of adults is

$$(\Gamma A)(x) = \frac{s_l s_j}{1 - s_a} r \int_0^L A(y)K(x, y)dy. \tag{24}$$

- This is the *next generation operator* and we define $R_0 = \rho(\Gamma)$.
- We can prove that the eigenvector corresponding to R_0 is positive.
- Critical domain size is found by solving $A = \Gamma A$ (i.e., $R_0 = 1$) for $L = L^*$.
- There is a well developed theory for infinite-dimensional next generation operators such as this (Thieme 2009).

Outline

Solving the critical domain size problem

We want to solve

$$A(x) = \frac{s_l s_j r}{1 - s_a} \int_0^{L^*} A(y) K(x, y) dy.$$

$K(0, y) = K(L^*, y) = 0$ yield boundary conditions $A(0) = A(L^*) = 0$.

Solving the critical domain size problem

We want to solve

$$A(x) = \frac{s_l s_j r}{1 - s_a} \int_0^{L^*} A(y)K(x,y)dy.$$

$K(0,y) = K(L^*,y) = 0$ yield boundary conditions $A(0) = A(L^*) = 0$.

Recall

$$\mathcal{L}K = \frac{D}{\sigma}\frac{\partial^2 K}{\partial x^2} - \frac{v}{\sigma}\frac{\partial u}{\partial x} - \frac{m+\sigma}{\sigma}K = -\delta(x-y)$$

Solving the critical domain size problem

We want to solve

$$A(x) = \frac{s_l s_j r}{1 - s_a} \int_0^{L^*} A(y) K(x, y) dy.$$

$K(0, y) = K(L^*, y) = 0$ yield boundary conditions $A(0) = A(L^*) = 0$.

Recall

$$\mathcal{L}K = \frac{D}{\sigma} \frac{\partial^2 K}{\partial x^2} - \frac{v}{\sigma} \frac{\partial u}{\partial x} - \frac{m + \sigma}{\sigma} K = -\delta(x - y)$$

Applying this operator yields

$$\mathcal{L}A = \frac{s_l s_j r}{1 - s_a} \int_0^{L^*} A(y) \left[\mathcal{L}K(x, y)\right] dy = -\frac{s_l s_j r}{1 - s_a} A$$

or

$$A''(x) - \frac{v}{D} A'(x) + \left(\frac{s_l s_j r \sigma}{(1 - s_a) D} - \frac{m + \sigma}{D} \right) A(x) = 0, \quad x \in (0, L^*).$$

with boundary conditions $A(0) = A(L^*) = 0$.

Solving the critical domain size problem

$$A''(x) - \frac{v}{D}A'(x) + \left(\frac{s_l s_j r\sigma}{(1-s_a)D} - \frac{m+\sigma}{D}\right)A(x) = 0, \quad A(0) = A(L^*) = 0. \quad (25)$$

Solving the critical domain size problem

$$A''(x) - \frac{v}{D}A'(x) + \left(\frac{s_l s_j r\sigma}{(1-s_a)D} - \frac{m+\sigma}{D}\right)A(x) = 0, \quad A(0) = A(L^*) = 0. \quad (25)$$

The characteristic equation for (25) is

$$\rho^2 - \frac{v}{D}\rho + \left(\frac{s_l s_j r\sigma}{(1-s_a)D\lambda} - \frac{m+\sigma}{D}\right) = 0,$$

with discriminant

$$\Delta(\lambda) = \left(\frac{v}{D}\right)^2 - 4\left(\frac{s_l s_j r\sigma}{(1-s_a)D\lambda} - \frac{m+\sigma}{D}\right)$$

and solution

$$A(x) = c\exp\left(\frac{v}{2D}x\right)\sin\left(\frac{\sqrt{-\Delta(\lambda)}}{2}x\right).$$

Solving the critical domain size problem

$$A''(x) - \frac{v}{D}A'(x) + \left(\frac{s_l s_j r\sigma}{(1-s_a)D} - \frac{m+\sigma}{D}\right)A(x) = 0, \quad A(0) = A(L^*) = 0. \quad (25)$$

The characteristic equation for (25) is

$$\rho^2 - \frac{v}{D}\rho + \left(\frac{s_l s_j r\sigma}{(1-s_a)D\lambda} - \frac{m+\sigma}{D}\right) = 0,$$

with discriminant

$$\Delta(\lambda) = \left(\frac{v}{D}\right)^2 - 4\left(\frac{s_l s_j r\sigma}{(1-s_a)D\lambda} - \frac{m+\sigma}{D}\right)$$

and solution

$$A(x) = c\exp\left(\frac{v}{2D}x\right)\sin\left(\frac{\sqrt{-\Delta(\lambda)}}{2}x\right).$$

$A(L^*) = 0$ requires

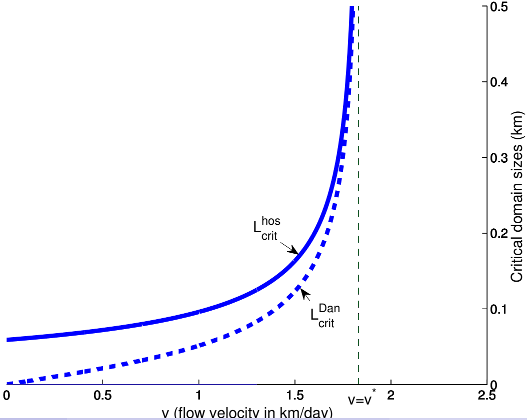
$$\frac{\sqrt{-\Delta(\lambda)}}{2}L^* = \pi.$$

Solving the critical domain size problem

$$L^* = \frac{2\pi D}{\sqrt{4D\left(\frac{s_l(T)s_j(T)r\sigma}{1-s_a(T)} - m - \sigma\right) - v^2}} = \frac{2\pi D}{\sqrt{4D(\sigma+m)\left(R_0^{\mathrm{loc}}(T)-1\right) - v^2}}.$$

Solving the critical domain size problem

$$L^* = \frac{2\pi D}{\sqrt{4D\left(\frac{s_l(T)s_j(T)r\sigma}{1-s_a(T)} - m - \sigma\right) - v^2}} = \frac{2\pi D}{\sqrt{4D(\sigma+m)\left(R_0^{\mathrm{loc}}(T)-1\right) - v^2}}.$$

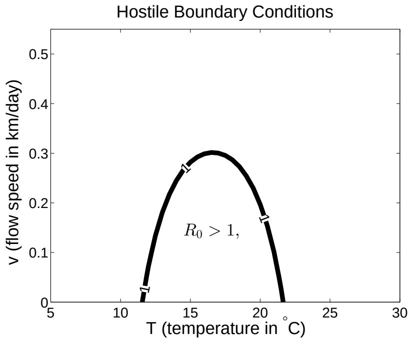


Critical values of other parameters

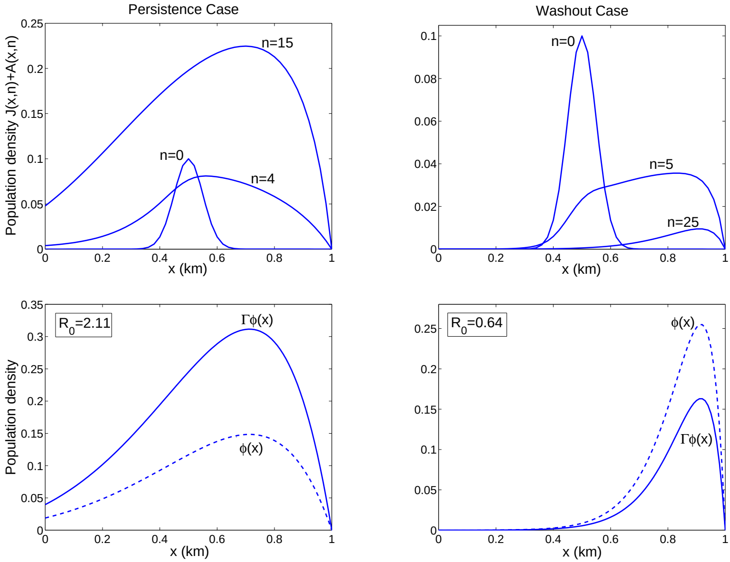
The trivial solution loses stability and a nontrivial solution emerges when

$$L = \frac{2\pi D}{\sqrt{4D(\sigma+m)\left(R_0^{\text{loc}}(T)-1\right)-v^2}}.$$

We can fix the domain size L and calculate the critical values with respect to temperature and advection speed



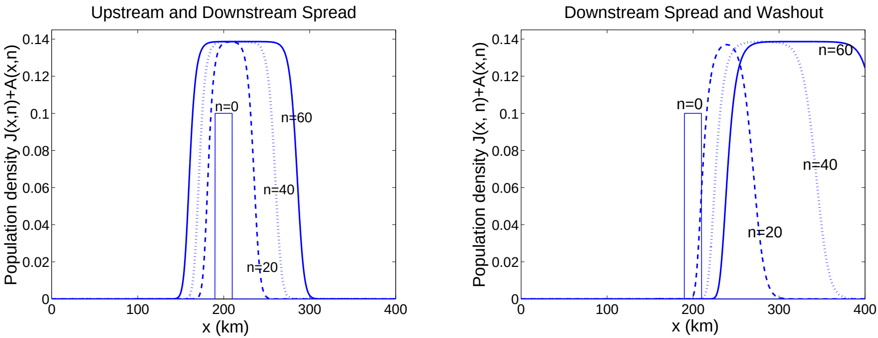
Dynamics below and above critical advection speed



Outline

Upstream and downstream spread

It is possible that, even on an infinite domain, the zebra mussel population could be “washed out” by high advection speeds.

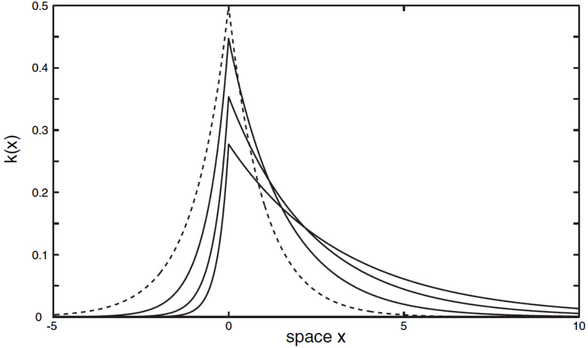


Upstream and downstream spreading speeds

$$\mathbf{N}(x,n+1) = \int_{-\infty}^{\infty} [\mathbf{K}(x-y) \circ \mathbf{A}]\mathbf{N}(y,n)dy, \tag{26}$$

where $\mathbf{N}(x,n) = (J(x,n), A(x,n))^T$ and

$$\mathbf{A} = \begin{pmatrix} 0 & s_l r \\ s_j & s_a \end{pmatrix}, \quad \mathbf{K}(x-y) = \begin{pmatrix} \delta(x-y) & K(x-y) \\ \delta(x-y) & \delta(x-y) \end{pmatrix}. \tag{27}$$



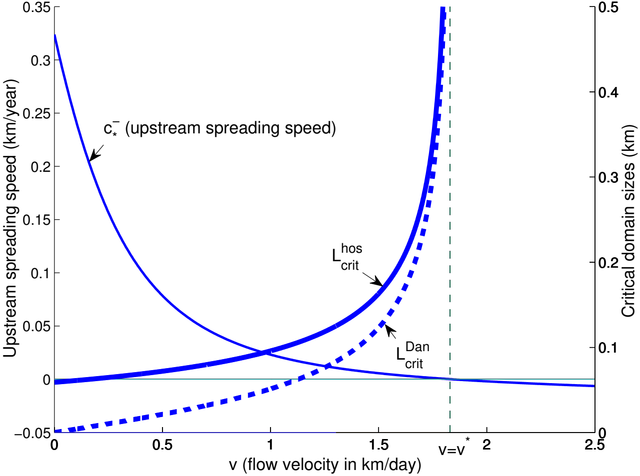
Upstream and downstream spreading speeds

$$c_*^- = \inf_{0<\theta<\gamma_1} \frac{1}{\theta} \ln \rho[\mathbf{H}(-\theta)], \tag{28}$$

$$c_*^+ = \inf_{0<\theta<-\gamma_2} \frac{1}{\theta} \ln \rho[\mathbf{H}(\theta)], \tag{29}$$

$$\mathbf{H}(\theta) = \int_{-\infty}^{\infty} \mathbf{K}(\xi) e^{\theta\xi} d\xi \circ \mathbf{A} = \begin{pmatrix} 0 & s_l r M(\theta) \\ s_j & s_a \end{pmatrix} \tag{30}$$

Upstream and downstream spreading speeds



Outline

Conclusions

- There is a newly emerging theory for critical domain size analysis for systems of integrodifference equations
- The theory discussed today is suited to systems where the linearized dynamics give a primitive matrix (eg, age structured, cooperative dynamics).
- It is possible to look at the problem from perspectives of both classical bifurcation analysis and next generation operator analysis.
- When dispersal has an underlying physical model (PDE), we can use this to our advantage when calculating the critical domain size.
- Critical domain size problems in advective environments can be connected to spreading speed analysis.
- There are several papers that approximate IDEs using a *dispersal success approximation* (Lutscher 2019). These can be very useful.