An invasion dynamics of zebra mussels in rivers and competitive interactions between zebra and quagga mussels

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Invasion of zebra and quagga mussels

Introduced from Europe to North America during the mid-1980s.
“Ecosystem Engineers”: Outcompetes native bivalves, causes large reductions in phytoplankton and zooplankton abundances, modifies the cycling of nutrients, and causes severe damage to waterworks.

Economical Concern: Attach in extremely high numbers to water pipes, boat hulls, and other firm surfaces, causing significant removal costs to individuals, municipalities, and corporations.
0. What is the impact of external environmental features (e.g., flow, water temperature) on river invasibility?
1. What is impact of external environmental features (e.g., flow, water temperature) on river invasibility?

2. When zebra mussels and quagga mussels live in the same environment, how do external environmental features (e.g., temperature, turbidity) impact the competitive interactions?
1. Develop a hybrid continuous/discrete-time model that describes the growth and dispersal of the zebra mussel along a river.
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Introduce three measures of population persistence, study the downstream and upstream spread of the zebra mussel.
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3. The numerical results are presented to understand the influence of temperature and river flow on population persistence.
Outline

1. Develop a hybrid continuous/discrete-time model that describes the growth and dispersal of the zebra mussel along a river.

2. Introduce three measures of population persistence, study the downstream and upstream spread of the zebra mussel.

3. The numerical results are presented to understand the influence of temperature and river flow on population persistence.

4. Develop a stage-structured model that describes the competitive interactions between zebra and quagga mussels.
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2. Introduce three measures of population persistence, study the downstream and upstream spread of the zebra mussel.

3. The numerical results are presented to understand the influence of temperature and river flow on population persistence.

4. Develop a stage-structured model that describes the competitive interactions between zebra and quagga mussels.

5. Use the results of model parameterization to illustrate the interactions between two species under different climate scenarios, assess the impact of spatial heterogeneity and dispersal on competitive outcomes.
\[
\frac{\partial u}{\partial t} = \frac{rA(x, n)}{a(x)} + \frac{1}{a(x)} \frac{\partial}{\partial x} \left[ D(x)a(x) \frac{\partial u}{\partial x} \right] - \frac{Q}{a(x)} \frac{\partial u}{\partial x} - mu - \sigma u,
\]

reproduction  
random movement  
downstream drift  
mortality  
settling

\[
\frac{\partial v}{\partial t} = \sigma a(x)u,
\]
settling

\[
J(x, n + 1) = \phi(v, J, A, T) s_l(T)v(x, \tau),
\]
competition  
larval survival

\[
A(x, n + 1) = \phi(v, J, A, T) \left( s_j(T) J(x, n) + s_a(T) A(x, n) \right),
\]
competition  
juvenile survival  
adult survival
Competition term: $\varphi(v, J, A, T)$

$$
\varphi(v, J, A, T) = \frac{1}{1 + \beta[\ell_l(T)v(x, \tau) + \ell_j(T)J(x, n) + \ell_a(T)A(x, n)]}
$$

$\beta$: the competition coefficient that relates competitive ability to a phenotypic trait

$\ell_l$, $\ell_j$, and $\ell_a$: the average shell lengths of larvae, juveniles and adults, respectively.

$T$: water temperature
Measure 1. Fundamental niche, $R_{\text{loc}}(x)$:

if an individual adult is introduced at location $x$, in the absence of larval dispersal, how many adult offspring will it produce over its lifetime?

$$R_{\text{loc}}(x) = \frac{r(x)s_i(x)s_j(x)\sigma(x)[1 - e^{-(m(x)+\sigma(x))\tau}]}{[1 - s_a(x)][m(x) + \sigma(x)]}.$$

Locations with $R_{\text{loc}}(x) > 1$ correspond to the fundamental niches of the species.
\[
\frac{\partial u}{\partial t} = \frac{r(x)A(x, n)}{a(x)} + \frac{1}{a(x)} \frac{\partial}{\partial x} \left[ D(x) a(x) \frac{\partial u}{\partial x} \right] - \frac{Q}{a(x)} \frac{\partial u}{\partial x} - mu - \sigma u, \]

reproduction  
random movement  
downstream drift  
mortality  
settling  

\[
\frac{\partial v}{\partial t} = \sigma a(x) u, \]
settling  

\[
J(x, n + 1) = \varphi(v, J, A, T) s_l(T) v(x, \tau), \]
competition  
larval survival  

\[
A(x, n + 1) = \varphi(v, J, A, T) \begin{pmatrix} s_j(T) J(x, n) + s_a(T) A(x, n) \end{pmatrix}, \]
competition  
juvenile survival  
adult survival  

\[
x \in (0, L), \ t \in (0, \tau).\]
For a fixed value of $y \in [0, L]$, the probability density that a larval, reproduced at location $y$, will settle at location $x$ is given by $k(x, y) = h(x)\sigma(x)\hat{k}(x, y)$, where $\hat{k}(x, y)$ is the solution of the following ordinary boundary value problem

$$\mathcal{L}\hat{k}(x, y) - [m(x) + \sigma(x)]\hat{k}(x, y) = -\delta(x - y)/h(x), \quad x \in (0, L),$$

$$\alpha_1\hat{k}(0, y) - \alpha_2\hat{k}'(0, y) = 0,$$

$$\alpha_3\hat{k}(L, y) + \alpha_4\hat{k}'(L, y) = 0,$$

where $'$ denotes differentiation with respect to $x$. 


Measure 2. Source-sink distribution: $R_\delta(x)$:

If an individual adult is introduced at location $x$ and undergoes reproduction, larval dispersal and settlement, and the growth of settled larvae and juveniles, how many adult offspring will be contributed by the originally introduced adult over its lifetime?

Adult offspring in the first year:

$$R_\delta(x) = \left[ 1 + s_a(x) + (s_a(x))^2 + \cdots \right] r(x) \int_0^L k(y, x) s_i(y)s_j(y) dy. $$

Adult offspring in the second year:

$$s_a(x)r(x) \int_0^L k(y, x)s_i(y)s_j(y)dy. $$
Measure 3. Net reproductive rate: $R_0$.

For any small initial adult distribution $A(x)$, the associated next generation adults will be distributed according to

$$(\Gamma A)(x) = s_i(x)s_j(x) \underbrace{\int_0^L \frac{r(y)}{1 - s_a(y)} A(y)k(x, y)dy}_{\text{probability that a settled larval grows into an adult}} \underbrace{\int_0^L \frac{r(y)}{1 - s_a(y)} A(y)k(x, y)dy}_{\text{contributions from all location } y \text{ towards the settled larvae at location } x} , \quad x \in [0, L],$$

Define

$$R_0 := \rho(\Gamma),$$

where $\rho(\Gamma)$ is the spectral radius of the linear operator $\Gamma$ on $X$. 
Critical domain size

Find the minimum length of suitable river habitat for a population to persist by analyzing the net generation operator. We solve the eigenvalue problem

\[ \Gamma A(x) = \lambda A(x) = \frac{s_i s_j r}{1 - s_a} \int_0^L A(y) k(x, y) dy, \]

which is equivalent to

\[ \frac{s_i s_j r h \sigma}{1 - s_a} \int_0^L A(y) \hat{k}(x, y) dy = \lambda A(x). \]

Applying the elliptic linear operator in the original hybrid model, we obtain a Sturm-Liouville problem. Then by choosing the threshold value \( R_0 = \lambda = 1 \) and finding the minimum positive solution of the Sturm-Liouville problem, we find that

\[ V < 2 \sqrt{D \left( \frac{s_i s_j r \sigma}{(1 - s_a) \lambda} - m - \sigma \right)} = 2 \sqrt{D \left( \frac{s_i s_j r \sigma}{1 - s_a} - m - \sigma \right)} := V^* \]

is a necessary condition for the population to persist.
When $V < V^*$, the critical domain size, denoted by $L_{\text{crit}}$, under hostile boundary conditions is given by

$$L_{\text{crit}}^{\text{hos}} = \frac{2D}{\sqrt{4D \left( \frac{s_is_j r \sigma}{1-s_a} - m - \sigma \right) - V^2}} \left( \pi - \arctan \sqrt{\frac{4D}{V^2} \left( \frac{s_is_j r \sigma}{1-s_a} - m - \sigma \right)} - 1 \right)$$
First, we are able to find the redistribution kernel in an unbounded domain, $K(x, y)$. Then, at the end of dispersal stage, the settled larvae, will be distributed according to

$$w(x, \tau) = \int_{-\infty}^{\infty} r(y)A(y, n)K(x, y)dy, \quad -\infty < x < \infty.$$ 

Substituting it into the third equation of the original hybrid model, we obtain the following stage-structured integrodifference equation model:

$$J(x, n + 1) = \varphi(x, n)s_l(x) \int_{-\infty}^{\infty} r(y)A(y, n)K(x, y)dy, \quad -\infty < x < \infty,$$

$$A(x, n + 1) = \varphi(x, n)[s_j(x)J(x, n) + s_a(x)A(x, n)], \quad -\infty < x < \infty.$$
the (asymptotic) downstream spreading speed is given by

\[ c^+_* = \inf_{0 < \theta < -\gamma_2} \frac{1}{\theta} \ln \frac{s_a + \sqrt{s_a^2 + 4s_is_j rM(\theta)}}{2}, \]

with \( M(\theta) = \int_{-\infty}^{\infty} K(\xi) e^{\theta \xi} d\xi \), which is referred to as the moment-generating function of the redistribution kernel \( K(\xi) \).

and the (asymptotic) upstream spreading speed is given by

\[ c^-_* = \inf_{0 < \theta < \gamma_1} \frac{1}{\theta} \ln \frac{s_a + \sqrt{s_a^2 + 4s_is_j rM(-\theta)}}{2}. \]

(Neubert and Caswell, Ecology, 2000.)
Numerical results

Model solution, persistence and washout

Persistency Case

Washout Case

\[ R_0 = 2.11 \]

\[ R_0 = 0.64 \]
The effect of interaction between temperature and river flow on $R_\delta$ and $R_0$

Hostile Boundary Conditions

Danckwert’s Boundary Conditions
The effect of flow on the population spread

Upstream and Downstream Spread

Population density \( J(x, n) + A(x, n) \)

Downstream Spread and Washout

Population density \( J(x, n) + A(x, n) \)
Connection between the upstream spreading speed and the critical domain size

- $c^-$ (upstream spreading speed)
- $L_{crit}^{hos}$
- $L_{crit}^{Dan}$
1. How the heterogeneous landscapes affect the successful invasion of zebra mussels?

2. How does the critical domain size for the invasive species depend on the river heterogeneity?

3. How do the seasonal variations in population growth and temporal variations of flow rates affect the successful invasion of zebra mussels?
Quagga replaces zebra: when both species colonize the same water body, quagga mussels outcompete zebra mussels after 9 or more years of coexistence (numerous reports, reviewed in (Karatayev et al. 2011).

Coexistence: In the shallowest western basin of Lake Erie, zebra mussels represented >30% of the combined dreissenid density even after more than 20 years of coexistence (Karatayev et al. 2014). In the Soulanges Canal, Canada, quagga mussels are dominant on the bottom and lower portions of the canal walls, while zebra mussels dominate the upper portions (Ricciardi and Whoriskey 2004).

Zebra dominates: In the Don River, Russia, both species coexisted for over 25 years, and zebra mussels remain dominant (Zhulidov et al. 2010, Zhulidov et al. 2006). In portions of the Mississippi and Ohio Rivers, quagga mussels remain less than 1% of all dreissenids after 12 years of coexistence (Grigorovich et al. 2008).
Competition model

\[ Z^j(t+1) = \varphi(t) \underbrace{b_z Z^a(t)}_{\text{competition}} , \]

\[ Z^a(t+1) = \varphi(t) \left( \underbrace{s^j_z(T, \tau) Z^j(t)}_{\text{juvenile survival}} + \underbrace{s^a_z(T, \tau) Z^a(t)}_{\text{adult survival}} \right), \]

\[ Q^j(t+1) = \varphi(t) \underbrace{b_q Q^a(t)}_{\text{recruit}} , \]

\[ Q^a(t+1) = \varphi(t) \left( \underbrace{s^j_q(T, \tau) Q^j(t)}_{\text{juvenile survival}} + \underbrace{s^a_q(T, \tau) Q^a(t)}_{\text{adult survival}} \right) , \]

\[ T : \text{temperature}, \quad \tau : \text{turbidity (the cloudiness or haziness of water caused by solid particles in suspension)}. \]
\[ \varphi(t) = \frac{1}{1 + \beta \left[ \ell^j_z Z^j(t) + \ell^a_z Z^a(t) + \ell^j_q Q^j(t) + \ell^a_q Q^a(t) \right]} \]

\( \beta \): the competition coefficient that relates competitive ability to a phenotypic trait.

\( \ell^j_z, \ell^a_z \) and \( \ell^j_q, \ell^a_q \): the average shell lengths of juveniles and adults for two species.
Net reproductive values: $R_0^z$ and $R_0^q$

\[
R_0^z(T, \tau) = \frac{b_z s_j^z}{1 - s_a^z} = \frac{b_z s_j^z(T, \tau)}{1 - s_a^z(T, \tau)}
\]

\[
R_0^q(T, \tau) = \frac{b_q s_j^q}{1 - s_a^q} = \frac{b_q s_j^q(T, \tau)}{1 - s_a^q(T, \tau)}
\]

$T$: temperature,

$\tau$: turbidity (cloudiness or haziness of water caused by solid particles in suspension).
Case 1 (both species die out): If $R^z_0 < 1$ and $R^q_0 < 1$, both species die out.

Case 2 (one species excludes the other): If $R^z_0 > 1$ and $R^q_0 < 1$, then the zebra mussel excludes the quagga mussel. If $R^z_0 < 1$ and $R^q_0 > 1$, then the quagga mussels excludes the zebra mussel.
Case 3: Competitive exclusion

If $R_z^0 > 1$ and $R_q^0 > 1$, then each species (living alone) grows. Then when the two species live together, the species that has a higher geometric growth rate excludes the species that has a lower geometric growth rate, that is,

i) if $r_z > r_q$, then the zebra mussel excludes the quagga mussel, 
ii) if $r_q > r_z$, then the quagga mussel excludes the zebra mussel,

where $r_z$ is the geometric growth rate of the zebra mussel, given by

$$r_z = \frac{s_z^a + \sqrt{(s_z^a)^2 + 4b_z s_z^j}}{2},$$

where $b_z$ is fecundity rate of zebra mussels, $s_z^j$ and $s_z^a$ are survival rates of juveniles and adult zebra mussels, respectively.

and $r_q$ is the geometric growth rate of the quagga mussel, given by

$$r_q = \frac{(s_q^a)^2 + \sqrt{(s_q^a)^2 + 4b_q s_q^j}}{2},$$

where $b_q$ is fecundity rate of quagga mussels, $s_q^j$ and $s_q^a$ are survival rates of juvenile and adult quagga mussels, respectively.
Temperature-turbidity space is divided into five regions (environmental niches) by the thresholds: net reproductive values of both species are 1 and both species have the same geometric growth rate.
Both species die out if the turbidity is very high or the temperature is very high or very low.
One species replaces the other.
At low temperature, quagga mussels can survive but zebra mussels cannot.
At high temperature, zebra mussels can survive but quagga mussels cannot.

\[ R_0^z < 1, R_0^q < 1 \]
Both species die out

\[ R_0^z > 1, R_0^q < 1 \]
Q exclude Z

\[ R_0^z < 1, R_0^q > 1 \]
Z exclude Q

\[ R_0^q = 1, R_0^z = 1 \]

\[ r_z = r_q \]

\[ R_0^q = 1 \]

\[ T \text{ (temperature in °C)} \]

\[ \tau \text{ (turbidity in NTU)} \]
Competitive exclusion (each species can survive on its own, but when they are together one species excludes the other).
Suitable environmental ranges for each species
Lower temperatures favour quagga mussels, higher temperatures favour zebra mussels, Generally higher turbidity favours quagga mussels over zebra mussels.
Previous results indicate that when both species live in the same environment (patch), one species includes the other.

Our results support the "competitive exclusion principle"- two similar species living in the same environment and compete for the same resources cannot coexist.

**Question:**
What are the conditions that can lead to the coexistence of zebra and quagga mussels?

How does spatial heterogeneity impact the competitive interactions between these two species?

Single-patch model → two-patch model
A two-patch model (without dispersal)

Patch 1

\[ s_{z_{12}}^i \varphi_1 \]

\[ b_1^z \varphi_1 \]

\[ s_{q_{12}}^i \varphi_1 \]

\[ b_1^q \varphi_1 \]

Patch 2

\[ s_{z_{22}}^i \varphi_2 \]

\[ b_2^z \varphi_2 \]

\[ s_{q_{22}}^i \varphi_2 \]

\[ b_2^q \varphi_2 \]
A two-patch model (with dispersals of zebra)
A two-patch model (with dispersals of both species)

Patch 1

Patch 2

\[ Z^j \]

\[ Z^a \]

\[ Z^j \]

\[ Z^a \]

\[ s^j_{11} \varphi_1 \]

\[ s_{12} \varphi_1 \]

\[ (1 - \alpha^z_{12}) b^z_1 \varphi_2 \]

\[ \alpha^z_{12} b^z_1 \varphi_2 \]

\[ s_{22} \varphi_1 \]

\[ s_{12} \varphi_2 \]

\[ (1 - \alpha^z_{21}) b^z_2 \varphi_2 \]

\[ s^a_{11} \varphi_1 \]

\[ s_{22} \varphi_2 \]

\[ \alpha^z_{21} b^z_2 \varphi_1 \]

\[ s^a_{11} \varphi_1 \]

\[ s_{22} \varphi_2 \]

\[ (1 - \alpha^q_{12}) b^q_1 \varphi_1 \]

\[ \alpha^q_{12} b^q_1 \varphi_2 \]

\[ s^a_{11} \varphi_1 \]

\[ s_{22} \varphi_2 \]

\[ (1 - \alpha^q_{21}) b^q_2 \varphi_2 \]
Full two-patch dispersal model

\[
\begin{align*}
Z_1^j(t + 1) &= \left[ (1 - \alpha_{12}^z) b_1^z Z_1^a(t) + \alpha_{21}^z b_2^z Z_2^a(t) \right] \psi_1(t) \\
&\text{reproduced by adults in patch 1} \quad \text{reproduced by adults in patch 2}
\end{align*}
\]

\[
Z_1^a(t + 1) = [s_{z1}^j Z_1^j(t) + s_{z1}^a Z_1^a(t)] \psi_1(t)
\]

\[
Q_1^j(t + 1) = \left[ (1 - \alpha_{12}^q) b_1^q Q_1^a(t) + \alpha_{21}^q b_2^q Q_2^a(t) \right] \psi_1(t)
\]

\[
Q_1^a(t + 1) = [s_{q1}^j Q_1^j(t) + s_{q1}^a Q_1^a(t)] \psi_1(t)
\]

\[
Z_2^j(t + 1) = \left[ (1 - \alpha_{21}^z) b_2^z Z_2^a(t) + \alpha_{12}^z b_1^z Z_1^a(t) \right] \psi_2(t)
\]

\[
Z_2^a(t + 1) = [s_{z2}^j Z_2^j(t) + s_{z2}^a Z_2^a(t)] \psi_2(t)
\]

\[
Q_2^j(t + 1) = \left[ (1 - \alpha_{21}^q) b_2^q Q_2^a(t) + \alpha_{12}^q b_1^q Q_1^a(t) \right] \psi_2(t)
\]

\[
Q_2^a(t + 1) = [s_{q2}^j Q_2^j(t) + s_{q2}^a Q_2^a(t)] \psi_2(t)
\]

\[Z_1^j: \text{number of juvenile zebra mussels in the patch 1,}\]
\[b_1^z: \text{number of juvenile zebra mussels produced per adult zebra mussel in patch 1,}\]
\[s_{z1}^j: \text{basal survival rate of juvenile zebra mussels in patch 1.}\]
\[\alpha_{12}^z: \text{proportion that juvenile zebra mussels, reproduced by adult zebra mussels in patch 1, live in patch 2 due to dispersal.}\]
\( \psi_1(t) \) and \( \psi_2(t) \) are density-dependent survival terms due to competition.

\[
\psi_1(t) = \frac{1}{1 + Z_1^i(t) + Z_1^a(t) + Q_1^i(t) + Q_1^a(t)},
\]

\[
\psi_2(t) = \frac{1}{1 + Z_2^i(t) + Z_2^a(t) + Q_2^i(t) + Q_2^a(t)},
\]
If the two patches are isolated (all dispersal rates are zero), and quagga mussels exclude zebra mussels in the patch 1 but zebra mussels exclude quagga mussels in the patch 2,

then when the two patches are connect by juvenile dispersal, how do the dispersal rates affect the competitive outcomes?
Stable population levels when the bifurcation parameter (dispersal rate) $\alpha \in [0, 0.1]$. 

![Graph showing stable population levels for Zebra and Quagga in two patches](image)
If the two patches are isolated \((\alpha_{12} = \alpha_{21} = \alpha_q = \alpha^q = 0)\), and quagga mussels exclude zebra mussels in patch 1 while zebra mussels exclude quagga mussels in patch 2, then there exists a positive constant \(\bar{\alpha} \in (0, 1)\) such that:

1) Both species coexist in both patches when \(0 < \alpha < \bar{\alpha}\).

2) Zebra mussels exclude quagga mussels in both patches if \(\alpha > \bar{\alpha}\) and \(r_{z,1} + r_{z,2} > r_{q,1} + r_{q,2}\).

3) Quagga mussels exclude zebra mussels in both patches if \(\alpha > \bar{\alpha}\) and \(r_{q,1} + r_{q,2} > r_{z,1} + r_{z,2}\).
When both species live in the same environment and compete for the same resource, one species excludes the other.
Conclusions

1. When both species live in the same environment and compete for the same resource, one species excludes the other.

2. Spatial heterogeneity may lead to long-term coexistence of two species, in this situation, different species may dominate at different areas due to their different sensitivities to environmental conditions.
Conclusions

1. When both species live in the same environment and compete for the same resource, one species excludes the other.

2. Spatial heterogeneity may lead to long-term coexistence of two species, in this situation, different species may dominate at different areas due to their different sensitivities to environmental conditions.

3. When species live in different local patches and are connected through juvenile dispersals, competitive outcomes in the whole ecosystem and the local areas strongly depend on the dispersal rates.
Future work

1. How do other environmental factors, such as calcium concentration, salinity, pH, impact mussel population dynamics and competitive interactions?

2. How do the environmental conditions impact the competitive interactions between zebra and quagga mussels in rivers?
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