

Temperature- and Turbidity-Dependent Competitive Interactions Between Invasive Freshwater Mussels

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Abstract We develop a staged-structured population model that describes the competitive dynamics of two functionally similar, congeneric invasive species: zebra mussels and quagga mussels. The model assumes that the population survival rates are functions of temperature and turbidity, and that the two species compete for food. The stability analysis of the model yields conditions on net reproductive rates and intrinsic growth rates that lead to competitive exclusion. The model predicts quagga mussel dominance leading to potential exclusion of zebra mussels at mean water temperatures below 20 °C and over a broad range of turbidities, and a much narrower set of conditions that favor zebra mussel dominance and potential exclusion of quagga mussels at temperatures above 20 °C and turbidities below 35 NTU. We then construct a two-patch dispersal model to examine how the dispersal rates and the environmental factors affect competitive exclusion and coexistence.

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1 Introduction

Biological invasion—the spread of non-native species—is recognized as a threat to biodiversity, ecosystem function, and regional economies (Keller et al. 2007; Pimentel et al. 2005). Two invasive Eurasian species that have caused substantial economic and ecological impacts in North America inland waters are the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena rostriformis bugensis*). Both species are fouling pests of municipal and industrial water supply systems, thus incurring substantial management costs (Mackie and Claudi 2010). They are also ‘ecosystem engineers’ that can alter nutrient and contaminant cycling, habitat structure and water quality, so that they disrupt food webs and transform biotic communities of invaded systems (Maclsaac et al. 1992; Madenjian 1995; Ricciardi et al. 1998).

Zebra and quagga mussels possess similar morphologies, life cycles and functional ecologies, and were apparently introduced to the Great Lakes perhaps a few years apart during the mid-1980s (Carlton 2008; Mills et al. 1993). In both Europe and North America, quagga mussels often replace zebra mussels as the dominant bivalve in invaded systems over time (reviewed by Karatayev et al. 2015; Ricciardi and Whoriskey 2004). Typically, the zebra mussel is the first dreissenid species to invade a body of water. When quagga mussels invade the same body of water, they initially colonize soft substrates of deepwater areas and subsequently spread into littoral zones occupied by zebra mussels. After several years, the quagga mussel may become more abundant than the zebra mussel system-wide and may even exclude the zebra mussel from local areas where it was previously dominant (Ricciardi and Whoriskey 2004). There are also bodies of water, and local habitats within bodies of water, in which the two species either coexist, or the zebra mussel persists as the dominant mussel (Ricciardi and Whoriskey 2004; Zhulidov et al. 2006, 2010). For example, in the Soulanges Canal (Quebec, Canada), quagga mussels replaced the zebra mussel on the canal bottom and on lower portions of the canal wall, but zebra mussels remain dominant on the upper wall (Ricciardi and Whoriskey 2004). In the Don River, Russia, both species have coexisted for over 25 years and, after replacing zebra mussels as the dominant mussel, the proportion of quagga mussels declined into a minority (Zhulidov et al. 2006). In portions of the Mississippi and Ohio Rivers, quagga mussels still comprise less than 1 % of all dreissenids after a dozen years of coexistence (Grigorovich et al. 2008). These cases suggest that patterns of relative dominance and competitive exclusion amongst these species may vary over space and time, presumably under the influence of environmental variables.

It is of heuristic and applied importance to understand the factors mediating such interactions, because the two species have some significant ecological differences and impacts (Carlton 2008; Karatayev et al. 2015). The goal of this study is to investigate how the persistence and relative dominance of zebra and quagga mussels are mediated by two critical factors, water temperature and turbidity, which are known to affect dreissenid growth and abundance (bij de Vaate et al. 2014; Diggins 2001; Karatayev

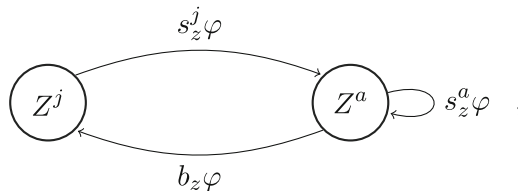
et al. 1998). We develop a stage-structured competition population model, based on the fecundity, survival rates and the proportion of individuals moving from the juvenile stages to adult stages over time. In our model, the population survival rates are functions of temperature and turbidity, and the species compete for food. We use the model to calculate net reproductive values and intrinsic growth rates. The conditions that lead to persistence, extinction, and competitive exclusion among dreissenid species are obtained.

Our competition model assumes that two species occupy the same environment and compete for the same food resource. Both theoretical and numerical results indicate that one species excludes the other; that is, sympatric populations of zebra and quagga mussels cannot coexist. However, as observed in some aquatic ecosystems, both species may coexist in the same ecosystem but different locations (Ricciardi and Whoriskey 2004; Zhulidov et al. 2006), perhaps reflecting the influence of local conditions in heterogeneous systems. This motivates us to extend the single-patch model to a two-patch dispersal model by including two patches of different environmental conditions. Populations in different patches are connected and interact with each other through juvenile dispersal. Based on the two-patch competition model, we examine how different dispersal rates and environmental factors affect the competitive outcomes. The numerical results indicate that indeed the two-patch dispersal model allows for both coexistence and competitive exclusion outcomes.

The rest of the paper is organized as follows. In Sect. 2, we develop a stage-structured model that describes the competitive interactions between zebra and quagga mussels. In Sect. 3, we present a qualitative analysis for the model. We analyze the existence and stability of extinction and coexistence equilibria. In Sect. 4, we connect the model to data via model parameterization. In Sect. 5, the results of model parameterization are used to numerically calculate exclusion results. In Sect. 6, we construct a two-patch competition model and show some numerical results. Finally a brief discussion section completes the paper.

2 A Dreissenid Mussel Competition Model

We begin by formulating a stage-structured competition model based on the shared life cycle of zebra and quagga mussels. Like many aquatic organisms, zebra (Z) and quagga (Q) mussels have a sessile adult (a) stage that reproduces annually and a juvenile (j) stage that disperses before setting and can be represented as follows:



where s_z^j and s_z^a are the basal survival rates for juvenile and adult zebra mussels, respectively, b_z is the number of juveniles produced per adult, and φ is a function accounting for density-dependent survival of juvenile and adults. A stage-structured

model that describes the temperature- and turbidity-dependent competitive interactions between zebra and quagga mussels is given by

$$\begin{cases} Z^j(t+1) = b_z Z^a(t)\varphi(t) \\ Z^a(t+1) = [s_z^j(T, \tau)Z^j(t) + s_z^a(T, \tau)Z^a(t)]\varphi(t) \\ Q^j(t+1) = b_q Q^a(t)\varphi(t) \\ Q^a(t+1) = [s_q^j(T, \tau)Q^j(t) + s_q^a(T, \tau)Q^a(t)]\varphi(t), \end{cases} \tag{1}$$

where $Z^j(t)$ and $Z^a(t)$ are the number of juvenile zebra mussels and the number of adult zebra mussels, respectively at time t , $Q^j(t)$ and $Q^a(t)$ are the number of juvenile quagga mussels and the number of adult quagga mussels, respectively at time t , b_q is the number of juvenile quagga mussels produced per adult, s_q^j and s_q^a are the basal survival rates for juvenile and adult quagga mussels, respectively. The population survival rates are functions of temperature (T) and turbidity (τ). $\varphi(t)$ is a density-dependent survival term due to competition for resources.

Next, we derive a specific expression of the survival term $\varphi(t)$. We assume that individuals compete for food [for example, model simulations link population changes to food limitation in [Strayer and Malcom \(2006\)](#)]. We use $F(\theta, t)$ to represent the food level at time θ ($0 \leq \theta < 1$) in year t . A balance equation for food resource is given by

$$\frac{dF}{d\theta} = F_0 - \gamma F - [c_z^j Z^j(t) + c_z^a Z^a(t) + c_q^j Q^j(t) + c_q^a Q^a(t)] F, \tag{2}$$

where F_0 represents the food input, γ denotes the food decay rate, the food consumption rates by the populations are modeled according to the *Law of Mass Action* and are proportional to both the population levels and the food level, where c_z^j , c_z^a , c_q^j , and c_q^a represent the consumption coefficients by juvenile zebra mussels, adult zebra mussels, juvenile quagga mussels, and adult quagga mussels, respectively.

Setting $dF/d\theta = 0$, we obtain the stable food level

$$\bar{F}(t) = \frac{F_0}{\gamma + c_z^j Z^j(t) + c_z^a Z^a(t) + c_q^j Q^j(t) + c_q^a Q^a(t)}.$$

We assume that the survival rate of juvenile zebra mussels, denoted by $S_z^j(t)$, depends linearly on the stable food level, that is,

$$\begin{aligned} S_z^j(t) &= k_z^j \bar{F}(t) = \frac{k_z^j F_0}{\gamma + c_z^j Z^j(t) + c_z^a Z^a(t) + c_q^j Q^j(t) + c_q^a Q^a(t)} \\ &= \frac{k_z^j F_0 / \gamma}{1 + \frac{1}{\gamma} [c_z^j Z^j(t) + c_z^a Z^a(t) + c_q^j Q^j(t) + c_q^a Q^a(t)]}. \end{aligned}$$

Admittedly, our assumption of linearity is probably simplistic. Mussel survivorship to food limitation may involve threshold effects ([Strayer and Malcom 2006](#)).

We let the basal survival rate of juvenile zebra mussels $s_z^j = k_z^j F_0/\gamma$ and the survival term due to competition for food

$$\varphi(t) = \frac{1}{1 + \frac{1}{\gamma} \left[c_z^j Z^j(t) + c_z^a Z^a(t) + c_q^j Q^j(t) + c_q^a Q^a(t) \right]}. \tag{3}$$

Studies on functionally similar marine mussels demonstrate that mussel growth may be severely impeded by crowding, especially amongst small individuals (Frechette et al. 1992). Moreover, larger individuals have higher filtration capacities (Horgan and Mills 1997) and therefore a food acquisition advantage. We refer to $c_z^j/\gamma, c_z^a/\gamma, c_q^j/\gamma,$ and c_q^a/γ as the competitive abilities of juvenile zebra mussels, adult zebra mussels, juvenile quagga mussels, and adult quagga mussels, respectively. We assume that the competitive abilities are proportional to a phenotypic trait $\ell_z^j, \ell_z^a, \ell_q^j,$ and $\ell_q^a,$ which we take to be the shell lengths of juveniles and adults of both species, hence we let $c_z^j/\gamma = \beta \ell_z^j, c_z^a/\gamma = \beta \ell_z^a, c_q^j/\gamma = \beta \ell_q^j,$ and $c_q^a/\gamma = \beta \ell_q^a,$ where β is the competition coefficient that is assumed to be the same for each species and life-history stage. Hence variation in competitive ability among species and stages is accounted for in $\ell_z^j, \ell_z^a, \ell_q^j$ and $\ell_q^a.$ Thus, we choose the following modified Beverton-Holt density-dependent survival term $\varphi(t)$ in (1)

$$\varphi(t) = \frac{1}{1 + \beta \left[\ell_z^j Z^j(t) + \ell_z^a Z^a(t) + \ell_q^j Q^j(t) + \ell_q^a Q^a(t) \right]}. \tag{4}$$

The authors of Baldwin et al. (2002) conducted laboratory studies to compare the growth, survival, and feeding biology of zebra and quagga mussels and found no significant differences in per capita clearance rate, functional responses, or feeding behavior between zebra and quagga mussels. This is consistent with our assumption that both species have the same survival term $\varphi(t)$ due to competition for food. For simplicity we assume a mass-action functional response in (2) and (3). Moreover, Baldwin et al. (2002) found that at a low food level the assimilation efficiency of quagga mussels was significantly higher than that of zebra mussel. We incorporate this in (3) by assuming that assimilation efficiencies are proportional to their shell lengths. The results of model parameterization in Sect. 4 shows that the average shell length of quagga mussels is longer than that of zebra mussels.

3 Model Analysis

To simplify the problem and facilitate model analysis, in this section we set $s_z^j(T, \tau) = s_z^j,$ and similar notations for other survival rates. We rescale the system (1) as follows. Let

$$\begin{aligned} \tilde{Z}^j &= \beta \ell_z^j Z^j, & \tilde{Z}^a &= \beta \ell_z^a Z^a, & \tilde{Q}^j &= \beta \ell_q^j Q^j, & \tilde{Q}^a &= \beta \ell_q^a Q^a, \\ \tilde{b}_z &= \frac{\ell_z^j}{\ell_z^a} b_z, & \tilde{b}_q &= \frac{\ell_q^j}{\ell_q^a} b_q, & \tilde{s}_z^j &= \frac{\ell_z^a}{\ell_z^j} s_z^j, & \tilde{s}_q^j &= \frac{\ell_q^a}{\ell_q^j} s_q^j, & \tilde{s}_z^a &= s_z^a, & \tilde{s}_q^a &= s_q^a. \end{aligned} \tag{5}$$

Dropping the tildes for notational simplicity, we rewrite the system (1) in the form

$$\begin{cases} Z^j(t+1) = \frac{b_z Z^a(t)}{1+Z^j(t)+Z^a(t)+Q^j(t)+Q^a(t)} \\ Z^a(t+1) = \frac{s_z^j Z^j(t)+s_z^a Z^a(t)}{1+Z^j(t)+Z^a(t)+Q^j(t)+Q^a(t)} \\ Q^j(t+1) = \frac{b_q Q^a(t)}{1+Z^j(t)+Z^a(t)+Q^j(t)+Q^a(t)} \\ Q^a(t+1) = \frac{s_q^j Q^j(t)+s_q^a Q^a(t)}{1+Z^j(t)+Z^a(t)+Q^j(t)+Q^a(t)}. \end{cases} \tag{6}$$

Note that the model (6) has a trivial equilibrium $E_0 = (0, 0, 0, 0)$ at which both species become extirpated. The associated linearized system of model (6) at E_0 is

$$\begin{cases} Z^j(t+1) = b_z Z^a(t) \\ Z^a(t+1) = s_z^j Z^j(t) + s_z^a Z^a(t) \\ Q^j(t+1) = b_q Q^a(t) \\ Q^a(t+1) = s_q^j Q^j(t) + s_q^a Q^a(t). \end{cases} \tag{7}$$

Thus, in the absence of competition, system (7) describes the dynamics of two species that do not interact with each other. The first two difference equations of (7) for zebra mussels are expressed in matrix form as:

$$\begin{pmatrix} Z^j(t+1) \\ Z^a(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b_z \\ s_z^j & s_z^a \end{pmatrix} \begin{pmatrix} Z^j(t) \\ Z^a(t) \end{pmatrix} := M \begin{pmatrix} Z^j(t) \\ Z^a(t) \end{pmatrix}.$$

The dominant eigenvalue of the projection matrix M is the *intrinsic growth rate* (Caswell 2001; Cushing and Zhou 1994; Cushing 1998) of zebra mussels, denoted by r_z . Hence,

$$r_z = \frac{s_z^a + \sqrt{(s_z^a)^2 + 4b_z s_z^j}}{2}. \tag{8}$$

Similarly, we denote the intrinsic growth rate of quagga mussels by r_q , then

$$r_q = \frac{s_q^a + \sqrt{(s_q^a)^2 + 4b_q s_q^j}}{2}. \tag{9}$$

To calculate the *net reproductive value*, we divide the projection matrix M into transition and fecundity components, $M = T + F$, where

$$T = \begin{pmatrix} 0 & 0 \\ s_z^j & s_z^a \end{pmatrix} \quad \text{and} \quad F = \begin{pmatrix} 0 & b_z \\ 0 & 0 \end{pmatrix}.$$

The net reproductive value for zebra mussels, denoted by R_0^z , is the positive, simple, and strictly dominant eigenvalue of the next generation matrix $F(I - T)^{-1}$ (Caswell 2001; Cushing and Zhou 1994; Cushing 1998). Thus, we have

$$R_0^z = \frac{b_z s_z^j}{1 - s_z^a}, \tag{10}$$

Similarly, the net reproductive value for quagga mussels is given by

$$R_0^q = \frac{b_q s_q^j}{1 - s_q^a}. \tag{11}$$

It is well known that $r_z = 1$ if and only if $R_0^z = 1$. The population grows when r_z and R_0^z are greater than 1 and shrinks when r_z and R_0^z are less than 1. Similar results hold for r_q and R_0^q .

In the rest of this section, we study the existence and the local stability of the equilibria of the nonlinear model (6). As we will see, all conditions on the existence and stability are given by the values of the population growth rates, r_z and r_q , or the net reproductive values, R_0^z and R_0^q , which are determined by the linearized system (7).

3.1 Existence of Equilibria

To investigate the long-term behavior of system (6), we look for the steady states (equilibria) where neither, one, or both species survive. An equilibrium of system (6) is a nonnegative solution of the equilibrium system

$$\begin{cases} Z^j = \frac{b_z Z^a}{1 + Z^j + Z^a + Q^j + Q^a} \\ Z^a = \frac{s_z^j Z^j + s_z^a Z^a}{1 + Z^j + Z^a + Q^j + Q^a} \\ Q^j = \frac{b_q Q^a}{1 + Z^j + Z^a + Q^j + Q^a} \\ Q^a = \frac{s_q^j Q^j + s_q^a Q^a}{1 + Z^j + Z^a + Q^j + Q^a}. \end{cases} \tag{12}$$

We first consider the existence of boundary equilibria. Clearly, system (12) always has a trivial solution $(0, 0, 0, 0)$. Hence, system (6) always has an extirpation equilibrium $E_0 = (0, 0, 0, 0)$.

Denote a zebra-only equilibrium by $E_1 = (Z_*^j, Z_*^a, 0, 0)$. Then (Z_*^j, Z_*^a) is a positive solution of the subsystem

$$\begin{cases} Z^j = \frac{b_z Z^a}{1 + Z^j + Z^a} \\ Z^a = \frac{s_z^j Z^j + s_z^a Z^a}{1 + Z^j + Z^a}. \end{cases} \tag{13}$$

From the first equation of (13), we see that

$$1 + Z^j + Z^a = \frac{b_z Z^a}{Z_j}. \tag{14}$$

Substituting (14) into the second equation of (13), we obtain

$$s_z^j \left(\frac{Z^j}{Z^a} \right)^2 + s_z^a \frac{Z^j}{Z^a} - b_z = 0. \tag{15}$$

This quadratic equation with respect to Z_j/Z_a has only one positive solution

$$\frac{Z^j}{Z^a} = \frac{\sqrt{(s_z^a)^2 + 4b_z s_z^j} - s_z^a}{2s_z^j} := \xi_1. \tag{16}$$

Substituting $Z_j = \xi_1 Z_a$ into the first equation of (13), we have

$$b_z - \xi_1 = \xi_1(1 + \xi_1)Z^a. \tag{17}$$

Since $\xi_1(1 + \xi_1) > 0$, (17) has a positive solution $Z_*^a = (b_z - \xi_1)/[\xi_1(1 + \xi_1)Z^a]$ if and only if $b_z - \xi_1 > 0$. Simple calculation shows that $b_z - \xi_1 > 0$ is equivalent to $R_0^z > 1$. Thus, when $R_0^z > 1$, system (6) has a boundary equilibrium $E_1 = (Z_*^j, Z_*^a, 0, 0)$ with

$$Z_*^j = \frac{b_z - \xi_1}{1 + \xi_1} \quad \text{and} \quad Z_*^a = \frac{b_z - \xi_1}{\xi_1(1 + \xi_1)}.$$

Similarly, when $R_0^q > 1$, system (6) has a boundary equilibrium $E_2 = (0, 0, Q_*^j, Q_*^a)$ with

$$Q_*^j = \frac{b_q - \xi_2}{1 + \xi_2} \quad \text{and} \quad Q_*^a = \frac{b_q - \xi_2}{\xi_2(1 + \xi_2)},$$

where

$$\xi_2 = \frac{\sqrt{(s_q^a)^2 + 4b_q s_q^j} - s_q^a}{2s_q^j}.$$

(Note that $R_0^q > 1$ is equivalent to $b_q > \xi_2$.)

Next, we discuss the existence of an interior equilibrium, which is a positive solution of system (12). From the first equation of (12), we see that

$$1 + Z^j + Z^a + Q^j + Q^a = \frac{b_z Z^a}{Z_j}. \tag{18}$$

Substituting (18) into the second equation of (12), again we obtain (15) and (16).

Similarly, from the third and fourth equations of (12) it follows that $Q^j/Q^a = \xi_2$. Substituting this and (16) into the first and third equations of system (12), we have

$$\begin{cases} \frac{b_z}{\xi_1} - 1 = (1 + \xi_1)Z^a + (1 + \xi_2)Q^a \\ \frac{b_q}{\xi_2} - 1 = (1 + \xi_1)Z^a + (1 + \xi_2)Q^a. \end{cases}$$

Table 1 Existence of equilibria of system (6)

Conditions	Equilibria	Biological interpretations
$R_0^z < 1, R_0^q < 1$	$E_0 = (0, 0, 0, 0)$	At E_0 , both species extirpate
$R_0^z > 1, R_0^q < 1$	$E_0, E_1 = (Z_*^j, Z_*^a, 0, 0)$	At E_1 , zebra excludes quagga
$R_0^z < 1, R_0^q > 1$	$E_0, E_2 = (0, 0, Q_*^j, Q_*^a)$	At E_2 , quagga excludes zebra
$R_0^z > 1, R_0^q > 1, b_z/\xi_1 = b_q/\xi_2$	$E_0, E_1, E_2, E_3 = (Z_*^j, Z_*^a, Q_*^j, Q_*^a)$	At E_3 , both species coexist

Note that (13) has a positive solution if and only if $b_z/\xi_1 = b_q/\xi_2 > 1$. (Note that $b_z/\xi_1 > 1$ is equivalent to $R_0^z > 1$ and $b_q/\xi_2 > 1$ is equivalent to $R_0^q > 1$.) Thus, when the conditions $R_0^z > 1, R_0^q > 1$, and $b_z/\xi_1 = b_q/\xi_2$ are satisfied, system (6) has a positive equilibrium $E_3 = (Z_*^j, Z_*^a, Q_*^j, Q_*^a)$ that satisfies $Z_*^j + Z_*^a + Q_*^j + Q_*^a = 1 - b_z/\xi_1$. Note that if E_3 exists, then it is not unique and there is a continuum of interior equilibrium. However, an interior equilibrium of system (6) does not exist in practice because the necessary condition $b_z/\xi_1 = b_q/\xi_2$ rarely holds in reality.

Based on the above discussion, we summarize the existence of equilibria and corresponding conditions required in Table 1.

3.2 Stability of Equilibria

To analyze the stability of an equilibrium, we may use the Jacobian matrix. Setting

$$\psi(t) = \frac{1}{1 + Z^j(t) + Z^a(t) + Q^j(t) + Q^a(t)},$$

the Jacobian of (6) is

$$\mathcal{J} = \begin{pmatrix} \mathcal{J}_{11} & \mathcal{J}_{12} \\ \mathcal{J}_{21} & \mathcal{J}_{22} \end{pmatrix},$$

with

$$\begin{aligned} \mathcal{J}_{11} &= \begin{pmatrix} -b_z Z^a \psi^2 & b_z \psi - b_z Z^a \psi^2 \\ s_z^j \psi - s_z^j Z^j \psi^2 - s_z^a Z^a \psi^2 & -s_z^j Z^j \psi^2 + s_z^a \psi - s_z^a Z^a \psi^2 \end{pmatrix}, \\ \mathcal{J}_{12} &= \begin{pmatrix} -b_z Z^a \psi^2 & -b_z Z^a \psi^2 \\ -(s_z^j Z^j + s_z^a Z^a) \psi^2 & -(s_z^j Z^j + s_z^a Z^a) \psi^2 \end{pmatrix}, \\ \mathcal{J}_{21} &= \begin{pmatrix} -b_q Q^a \psi^2 & -b_q Q^a \psi^2 \\ -(s_q^j Q^j + s_q^a Q^a) \psi^2 & -(s_q^j Q^j + s_q^a Q^a) \psi^2 \end{pmatrix}, \end{aligned}$$

and

$$\mathcal{J}_{22} = \begin{pmatrix} -b_q Q^a \psi^2 & b_q \psi - b_q Q^a \psi^2 \\ s_q^j \psi - s_q^j Q^j \psi^2 - s_q^a Q^a \psi^2 & -s_q^j Q^j \psi^2 + s_q^a \psi - s_q^a Q^a \psi^2 \end{pmatrix}.$$

If at least one of the net reproductive values is less than 1, we could make the following conclusions regarding the stability of equilibria.

- Theorem 1** *i) If $R_0^z < 1$ and $R_0^q < 1$, then the extirpation equilibrium E_0 is globally asymptotically stable.*
ii) If $R_0^z > 1$ and $R_0^q < 1$, then E_0 is unstable and the zebra-only equilibrium E_1 is locally asymptotically stable.
iii) If $R_0^z < 1$ and $R_0^q > 1$, then E_0 is unstable and the quagga-only equilibrium E_2 is locally asymptotically stable.

Proof i) At E_0 , both species become extirpated, and the Jacobian is

$$\mathcal{J}(E_0) = \begin{pmatrix} 0 & b_z & 0 & 0 \\ s_z^j & s_z^a & 0 & 0 \\ 0 & 0 & 0 & b_q \\ 0 & 0 & s_q^j & s_q^a \end{pmatrix}.$$

Notice that since 2×2 matrix in the left-upper corner of the matrix $\mathcal{J}(E_0)$ is non-negative, irreducible, and primitive, the famous Perron-Frobenius Theorem implies that it has a positive, simple, and strictly dominant eigenvalue λ_1 . Since $R_0^z < 1$, we have $\lambda_1 < 1$. Similarly, the 2×2 matrix in the right-lower corner of the matrix $\mathcal{J}(E_0)$ has a positive, simple, and strictly dominant eigenvalue $\lambda_2 < 1$. Hence, the matrix $\mathcal{J}(E_0)$ has a dominant eigenvalue $\lambda = \max\{\lambda_1, \lambda_2\} < 1$. It follows from [Elaydi \(2010\)](#) (Corollary 3.24, p.145) that $\lim_{t \rightarrow \infty} (\mathcal{J}(E_0))^t = 0$. Let $\mathbf{X}(t) = [Z^j(t), Z^a(t), Q^j(t), Q^a(t)]^T$. Then from (6), we find that for any initial value $\mathbf{X}(0) \geq \mathbf{0}$, we have $\mathbf{0} \leq \mathbf{X}(1) \leq \mathcal{J}(E_0)\mathbf{X}(0)$, where the vector and matrix inequalities hold componentwise. Repeating this gives $0 \leq \mathbf{X}(t) \leq (\mathcal{J}(E_0))^t \mathbf{X}(0)$. Since $\lim_{t \rightarrow \infty} (\mathcal{J}(E_0))^t = 0$, we obtain $\lim_{t \rightarrow \infty} \mathbf{X}(t) = 0$. Therefore, $E_0 = (0, 0, 0, 0)$ is globally asymptotically stable.

ii) If $R_0^z > 1$, the dominant eigenvalue of the matrix $\mathcal{J}(E_0)$ is greater than 1, hence E_0 is unstable. At the zebra-only equilibrium E_1 , where zebra mussels replace quagga mussels, the Jacobian is

$$\mathcal{J}(E_1) = \begin{pmatrix} \frac{-b_z Z_*^a}{(1+Z_*^j+Z_*^a)^2} & \frac{b_z(1+Z_*^j)}{(1+Z_*^j+Z_*^a)^2} & \frac{-b_z Z_*^a}{(1+Z_*^j+Z_*^a)^2} & \frac{-b_z Z_*^a}{(1+Z_*^j+Z_*^a)^2} \\ \frac{s_z^j + (s_z^j - s_z^a) Z_*^a}{(1+Z_*^j+Z_*^a)^2} & \frac{s_z^a + (s_z^a - s_z^j) Z_*^j}{(1+Z_*^j+Z_*^a)^2} & -\frac{(s_z^j Z_*^j + s_z^a Z_*^a)}{(1+Z_*^j+Z_*^a)^2} & -\frac{(s_z^j Z_*^j + s_z^a Z_*^a)}{(1+Z_*^j+Z_*^a)^2} \\ 0 & 0 & 0 & \frac{b_q}{1+Z_*^j+Z_*^a} \\ 0 & 0 & \frac{s_q^j}{1+Z_*^j+Z_*^a} & \frac{s_q^a}{1+Z_*^j+Z_*^a} \end{pmatrix}$$

To prove that E_1 is locally asymptotically stable, we show that the eigenvalues of the matrix $\mathcal{J}(E_1)$ are less than 1 in magnitude. Denote the 2×2 matrix in the upper left corner and the 2×2 matrix in the lower right corner of $\mathcal{J}(E_1)$ by $\mathcal{J}_{11}(E_1)$ and $\mathcal{J}_{22}(E_1)$, respectively. Then it suffices to show that the eigenvalues of both $\mathcal{J}_{11}(E_1)$ and $\mathcal{J}_{22}(E_1)$ are less than 1 in magnitude.

We first show that the eigenvalues of $\mathcal{J}_{11}(E_1)$ are less than 1 in magnitude. By Jury test for stability of a discrete-time system, we need to show that the following inequalities hold [see Theorem 2.37 and Eq. (4.3.9) in [Elaydi 2010](#)]:

$$\begin{cases} 1 - \text{tr}(\mathcal{J}_{11}(E_1)) + \det(\mathcal{J}_{11}(E_1)) > 0 \\ 1 + \text{tr}(\mathcal{J}_{11}(E_1)) + \det(\mathcal{J}_{11}(E_1)) > 0 \\ \det(\mathcal{J}_{11}(E_1)) < 1, \end{cases} \tag{19}$$

or, equivalently,

$$|\text{tr}(\mathcal{J}_{11}(E_1))| < \det(\mathcal{J}_{11}(E_1)) + 1 < 2. \tag{20}$$

Simple calculation gives

$$\begin{aligned} \det(\mathcal{J}_{11}(E_1)) &= \frac{-b_z Z_*^a \left[s_z^a + (s_z^a - s_z^j) Z_*^j \right] - b_z (1 + Z_*^j) \left[s_z^j + (s_z^j - s_z^a) Z_*^a \right]}{(1 + Z_*^j + Z_*^a)^4} \\ &= \frac{-b_z s_z^j - b_z s_z^j Z_*^j - b_z s_z^j Z_*^a}{(1 + Z_*^j + Z_*^a)^4} \\ &= -\frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^3} < 0 < 1. \end{aligned} \tag{21}$$

This means that the third inequality in (19) is true. Also, $\det(\mathcal{J}_{11}(E_1)) < 0$ implies that the two eigenvalues of $\mathcal{J}_{11}(E_1)$ are real and of opposite sign. In what follows, we show that the first and second inequalities in (19) are true. Note that $E_1 = (Z_*^j, Z_*^a, 0, 0)$ satisfies (see (13))

$$\begin{cases} b_z Z_*^a = Z_*^j (1 + Z_*^j + Z_*^a) \\ s_z^j Z_*^j + s_z^a Z_*^a = Z_*^a (1 + Z_*^j + Z_*^a). \end{cases} \tag{22}$$

Solving (22) for $Z_*^j + Z_*^a$, we obtain

$$Z_*^j + Z_*^a = \frac{s_z^a + \sqrt{(s_z^a)^2 + 4b_z s_z^j}}{2} - 1 = r_z - 1. \tag{23}$$

Thus, we have

$$\begin{aligned}
 \text{tr}(\mathcal{J}_{11}(E_1)) &= \frac{-b_z Z_*^a + s_z^a + (s_z^a - s_z^j) Z_*^j}{(1 + Z_*^j + Z_*^a)^2} \\
 &= \frac{-Z_*^j (1 + Z_*^j + Z_*^a) + s_z^a (1 + Z_*^j + Z_*^a) - Z_*^a (1 + Z_*^j + Z_*^a)}{(1 + Z_*^j + Z_*^a)^2} \\
 &= \frac{s_z^a - (Z_*^j + Z_*^a)}{1 + Z_*^j + Z_*^a}. \tag{24}
 \end{aligned}$$

From (22), we also find that $Z_*^j + Z_*^a$ satisfies

$$\frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^2} + \frac{s_z^a}{1 + Z_*^j + Z_*^a} = 1. \tag{25}$$

Using (21), (24), and (25), we obtain

$$\begin{aligned}
 &1 - \text{tr}(\mathcal{J}_{11}(E_1)) + \det(\mathcal{J}_{11}(E_1)) \\
 &= \frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^2} + \frac{s_z^a}{1 + Z_*^j + Z_*^a} - \frac{s_z^a - (Z_*^j + Z_*^a)}{1 + Z_*^j + Z_*^a} - \frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^3} \\
 &= \frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^2} \left(1 - \frac{1}{1 + Z_*^j + Z_*^a}\right) + \frac{Z_*^j + Z_*^a}{1 + Z_*^j + Z_*^a} > 0.
 \end{aligned}$$

On the other hand, using (21), (23), and (24), we have

$$\begin{aligned}
 &1 + \text{tr}(\mathcal{J}_{11}(E_1)) + \det(\mathcal{J}_{11}(E_1)) > 0 \\
 &\Leftrightarrow \frac{1 + s_z^a}{1 + Z_*^j + Z_*^a} - \frac{b_z s_z^j}{(1 + Z_*^j + Z_*^a)^3} > 0 \\
 &\Leftrightarrow (1 + s_z^a) (1 + Z_*^j + Z_*^a)^2 > b_z s_z^j \\
 &\Leftrightarrow (1 + s_z^a) \left(\frac{s_z^a + \sqrt{(s_z^a)^2 + 4b_z s_z^j}}{2}\right)^2 > b_z s_z^j \\
 &\Leftrightarrow s_z^a \sqrt{(s_z^a)^2 + 4b_z s_z^j} > 2b_z s_z^j \left(\frac{1}{1 + s_z^a} - 1\right) - (s_z^a)^2,
 \end{aligned}$$

which is true. Therefore, all inequalities in (19) hold. Thus, the eigenvalues of \mathcal{J}_{11} are less than 1 in magnitude.

We now apply Jury test to the 2×2 matrix $\mathcal{J}_{22}(E_1)$. Noting that

$$\text{tr}(\mathcal{J}_{22}(E_1)) = \frac{s_q^a}{1 + Z_*^j + Z_*^a} > 0 \quad \text{and} \quad \det(\mathcal{J}_{22}(E_1)) = -\frac{b_q s_q^j}{(1 + Z_*^j + Z_*^a)^2} < 0,$$

we have

$$\begin{aligned} |\text{tr}(\mathcal{J}_{22}(E_1))| - \det(\mathcal{J}_{22}(E_1)) - 1 &= \frac{s_q^a}{1 + Z_*^j + Z_*^a} + \frac{b_q s_q^j}{(1 + Z_*^j + Z_*^a)^2} - 1 \\ &< s_q^a + b_q s_q^j - 1 < 0, \end{aligned}$$

since $R_0^q = b_q s_q^j / (1 - s_q^a) < 1$. Hence, the inequalities (20) hold. By the Jury test, the eigenvalues of $\mathcal{J}_{22}(E_1)$ are also less than 1 in magnitude. Therefore, the eigenvalues of $\mathcal{J}(E_1)$ are less than 1 in magnitude, hence E_1 is locally asymptotically stable.

iii) Follows by similar arguments as in ii). □

Next, we assume that $R_0^z > 1$ and $R_0^q > 1$ and consider the competitive exclusion. The following theorem indicates that when the net reproductive values of both species are greater than 1, the species that has a higher growth rate excludes the species that has a lower growth rate.

Theorem 2 *Assume that $R_0^z > 1$ and $R_0^q > 1$. Concerning the system (6) we have the following conclusions:*

- i) *If $r_z > r_q$, then E_1 is locally asymptotically stable and E_2 is unstable.*
- ii) *If $r_z < r_q$, then E_2 is locally asymptotically stable and E_1 is unstable.*

Proof i) Since $R_0^z > 1$, it follows by arguments as those in the proof of Theorem 1 that the eigenvalues of $\mathcal{J}_{11}(E_1)$ are less than 1 in magnitude. Also, from Theorem 1, we see that $\det(\mathcal{J}_{22}(E_1)) < 1$ and

$$\begin{aligned} |\text{tr}(\mathcal{J}_{11}(E_1))| - \det(\mathcal{J}_{11}(E_1)) - 1 &= \frac{s_q^a}{1 + Z_*^j + Z_*^a} + \frac{b_q s_q^j}{(1 + Z_*^j + Z_*^a)^2} - 1 \\ &= \frac{s_q^a}{r_z} + \frac{b_q s_q^j}{(r_z)^2} - 1. \end{aligned}$$

Similarly as shown by (25), we have that $Q_*^j + Q_*^a$ satisfies

$$\frac{s_q^a}{1 + Q_*^j + Q_*^a} + \frac{b_q s_q^j}{(1 + Q_*^j + Q_*^a)^2} = \frac{s_q^a}{r_q} + \frac{b_q s_q^j}{(r_q)^2} = 1.$$

Since $r_z > r_q$, we have

$$\frac{s_q^a}{r_z} + \frac{b_q s_q^j}{(r_z)^2} - 1 < \frac{s_q^a}{r_q} + \frac{b_q s_q^j}{(r_q)^2} - 1 = 0.$$

Hence, $|\text{tr}(\mathcal{J}_{11}(E_1))| - \det(\mathcal{J}_{11}(E_1)) - 1 < 0$. Therefore, the eigenvalues of $\mathcal{J}_{22}(E_1)$ are less than 1 in magnitude. Thus, E_1 is locally asymptotically stable.

We now show that E_2 is unstable. At the quagga-only equilibrium E_2 , where quagga mussels replace zebra mussels, the Jacobian is

$$\mathcal{J}(E_2) = \begin{pmatrix} 0 & \frac{b_z}{1+Q_*^j+Q_*^a} & 0 & 0 \\ \frac{s_z^j}{1+Q_*^j+Q_*^a} & \frac{s_z^a}{1+Q_*^j+Q_*^a} & 0 & 0 \\ \frac{-b_q Q_*^a}{(1+Q_*^j+Q_*^a)^2} & \frac{-b_q Q_*^a}{(1+Q_*^j+Q_*^a)^2} & \frac{-b_q Q_*^a}{(1+Q_*^j+Q_*^a)^2} & \frac{b_q(1+Q_*^j)}{(1+Q_*^j+Q_*^a)^2} \\ \frac{-(s_q^j Q_*^j + s_q^a Q_*^a)}{(1+Q_*^j+Q_*^a)^2} & \frac{-(s_q^j Q_*^j + s_q^a Q_*^a)}{(1+Q_*^j+Q_*^a)^2} & \frac{s_q^j + (s_q^j - s_q^a) Q_*^a}{(1+Q_*^j+Q_*^a)^2} & \frac{s_q^a + (s_q^a - s_q^j) Q_*^j}{(1+Q_*^j+Q_*^a)^2} \end{pmatrix}$$

We denote the 2×2 matrix in the left-upper corner of the matrix $\mathcal{J}(E_2)$ by $\mathcal{J}_{11}(E_2)$. Then, we get

$$\begin{aligned} |\text{tr}(\mathcal{J}_{11}(E_2))| - \det(\mathcal{J}_{11}(E_2)) - 1 &= \frac{s_z^a}{1 + Q_*^j + Q_*^a} + \frac{b_q s_q^j}{(1 + Q_*^j + Q_*^a)^2} - 1 \\ &= \frac{s_z^a}{r_q} + \frac{b_z s_z^j}{(r_q)^2} - 1 \\ &> \frac{s_z^a}{r_z} + \frac{b_z s_z^j}{(r_z)^2} - 1 = 0, \end{aligned}$$

which implies that there exists an eigenvalue of $\mathcal{J}_{11}(E_2)$ with magnitude larger than one. Thus, E_2 is unstable.

ii) Follows by similar arguments as in i). □

As we mentioned in Sect. 3.1, the interior equilibrium E_3 hardly exists; hence we are not interested in its stability.

4 Model Parametrization

In this section, we connect model (1) to experimental data via model parametrization. We consider the dependence of population survival rates on temperature (T) and turbidity (τ). The results of model parameteriazation are then used to illustrate the impacts of these two abiotic variables on competitive exclusion in the next section. Although juveniles and adults may have different sensitivities to temperature and

turbidity, we assume that juveniles and adults have the same survival rates because data are lacking.

4.1 Survival Rates: $s_z^j(T, \tau)$, $s_z^a(T, \tau)$, $s_q^j(T, \tau)$, and $s_q^a(T, \tau)$

We assume that the survival rates for zebra mussel are continuous functions with respect to temperature and turbidity, which are given by

$$s_z^j(T, \tau) = s_z^a(T, \tau) = \sigma_z s_z^a(T) s_z^a(\tau)$$

plus our simplifying assumption that $s_z^j = s_z^a$, where $0 < \sigma_z < 1$ is a coefficient that represents the survival rate of population under ideal circumstances (i.e., when $s_z^a(T)$ and $s_z^a(\tau)$ reach their maximum values). Similarly, for quagga mussels, we assume that

$$s_q^j(T, \tau) = s_q^a(T, \tau) = \sigma_q s_q^a(T) s_q^a(\tau),$$

where $0 < \sigma_q < 1$.

The effects of temperatures on survival of zebra and quagga mussels in Lake Erie were studied in [Thorp et al. \(1998\)](#). Therein, the maximum survival rates of zebra and quagga mussels were estimated, which are 0.79 and 0.91, respectively. Thus, we let $\sigma_z/\sigma_q = 0.79/0.91 = 0.87$, and

$$s_z^j(T, \tau) = s_z^a(T, \tau) = 0.87\sigma s_z^a(T) s_z^a(\tau), \quad s_q^j(T, \tau) = s_q^a(T, \tau) = \sigma s_q^a(T) s_q^a(\tau). \tag{26}$$

Next, we estimate the dependence of population survival rates on temperature and turbidity, respectively.

4.1.1 The Dependence of Survival on Temperature: $s_z^j(T)$, $s_z^a(T)$, $s_q^j(T)$, and $s_q^a(T)$

Thermal and turbidity tolerance limits for dreissenid survival were estimated by averaging experimental and empirical data reported in the literature. These data suggest that the lower and upper thermal threshold limits for quagga mussels are below those for zebra mussels, and that the upper thermal limit of the quagga mussel appears to be near 25 °C, whereas that of the zebra mussel is near 30 °C (reviewed by [Mackie and Claudi 2010](#)). The lower threshold limits for zebra mussel survival and quagga mussel survival are 10 and 5 °C, respectively ([Mackie and Claudi 2010](#)). Based on these threshold values, we let

$$s_z^j(10) = s_z^j(30) = 0. \tag{27}$$

We assume that the basal survival rate for juvenile zebra mussels are related to temperature T by the quadratic logistic regression

$$s_z^j(T) = \frac{\exp(a_1 T^2 + a_2 T + a_3)}{1 + \exp(a_1 T^2 + a_2 T + a_3)}. \quad (28)$$

Employing Matlab routine LSQCURVEFIT to fit the function (28) to the data (27), we obtain parameter estimates $a_1 = -0.064$, $a_2 = 2.57$, and $a_3 = -22.52$. Therefore, we assume that the basal survival rates for zebra mussels are related to temperature T by

$$s_z^j(T) = s_z^a(T) = \frac{\exp(-0.064T^2 + 2.57T - 22.52)}{1 + \exp(-0.064T^2 + 2.57T - 22.52)}, \quad (29)$$

plus our simplifying assumption that $s_z^j(T) = s_z^a(T)$.

Similarly, fitting a function (replacing z by q in (28)) for quagga mussels to the data $s_q^j(5) = s_q^j(25) = 0$, we assume that the basal survival rates for quagga mussels are related to temperature T by the quadratic logistic regression

$$s_q^j(T) = s_q^a(T) = \frac{\exp(-0.064T^2 + 1.93T - 11.27)}{1 + \exp(-0.064T^2 + 1.93T - 11.27)}. \quad (30)$$

(left panel of Fig. 1).

4.1.2 The Dependence of Survival on Turbidity: $s_z^j(\tau)$, $s_z^a(\tau)$, $s_q^j(\tau)$, and $s_q^a(\tau)$

Turbidity is the cloudiness or haziness of water caused by solid particles in suspension. The instrument used for measuring it is called a nephelometer or turbidimeter, which measures the intensity of light scattered at 90° as a beam of light passes through a water sample. Kits such as the 2100P Hach Turbidimeter are used to measure turbidity in nephelometric turbidity units (NTU) (Mackie and Claudi 2010). Turbidity is important as a physiological stressor not only because energy is required to process inorganic seston, but also because food quality is diluted by seston (Ricciardi and Whoriskey 2004). Turbidity (suspended particles) limits the filtration capacity of mussels and imposes energetic costs (Baldwin et al. 2002; Stoeckmann 2003). Turbidity levels < 5 NTU are considered optimal for zebra mussel population growth; 5–20 NTU will support moderate population growth; 20–80 NTU will support little growth, whereas 80 NTU are lethal and will not support long-term zebra mussel survival (Mackie and Claudi 2010). Based on these conclusions, in a similar way as we estimate $s_z^j(T)$ in Sect. 4.1.1, we assume that the basal survival rates for zebra and quagga mussels are related to turbidity by the linear logistic regressions

$$s_z^j(\tau) = s_z^a(\tau) = \frac{\exp(-0.11\tau + 3.65)}{1 + \exp(-0.11\tau + 3.65)}. \quad (31)$$

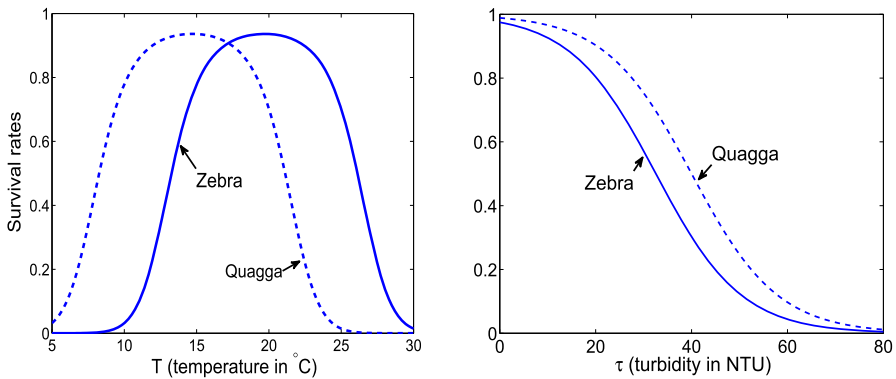


Fig. 1 The dependence of survivor rates for zebra and quagga mussels on temperature (*left panel*) and turbidity (*right panel*) (Color figure online)

As little information exists on the effects of suspended solids on quagga mussel survival or even metabolic activities, some researchers assume that the criteria used for zebra mussels also apply to quagga mussels (Mackie and Claudi 2010). However, although clearance rates of zebra and quagga mussels are reduced when exposed to natural suspended sediments of up to 12mg/L, quagga mussels maintain higher filtration rates than similarly sized zebra mussels, regardless of season (Diggins 2001). Moreover, quagga mussels appear to be better able than zebra mussels to process food when it is diluted by suspended inorganic particles, as they have a higher assimilation efficiency and lower respiration cost (Baldwin et al. 2002; Stoeckmann 2003). Thus, we assume that the survival rates of quagga mussels are slightly higher than those of zebra mussels, and the basal survival rates for quagga mussels are related to turbidity τ by the linear logistic regression

$$s_q^j(\tau) = s_q^a(\tau) = \frac{\exp(-0.11\tau + 4.46)}{1 + \exp(-0.11\tau + 4.46)} \tag{32}$$

(right panel of Fig. 1).

4.2 Fecundity Rates: b_z and b_q

Annually, female zebra mussels can produce up to a million eggs, and males produce up to nearly 10 million sperm (Sprung 1989). Since fertilization occurs externally in the water column, release of eggs and sperm must be concurrent. Our estimate of fecundity is based on a mean number of eggs released by female mussels; given variability in this parameter, we choose a number from 525 to 300,000 eggs per female estimated in Stoeckel et al. (2004). As for the proportion of fertilized zebra mussel eggs, authors of Potapov et al. (submitted) expect values between 0.01 and 0.1. By assuming 1:1 female-male ratio and choosing the mean value of the above quantities, we estimate that the number of larvae produced per adult is 4218. In Krkošek and

Table 2 Parameter estimates for the model (1–4)

Symbols	Definitions	Estimate values
b_z	Reproduction rate of zebra mussels	4.128/year
b_q	Reproduction rate of quagga mussels	4.128/year
ℓ_z^j	Shell length of juvenile zebra mussels	1.25 cm
ℓ_z^a	Shell length of adult zebra mussels	2.5 cm
ℓ_q^j	Shell length of juvenile quagga mussels	1.5 cm
ℓ_q^a	Shell length of adult quagga mussels	3 cm
$s_z^j(T, \tau)$	Survival rate of juvenile zebra mussels	See Eqs. (28), (29), and (31)
$s_z^a(T, \tau)$	Survival rate of adult zebra mussels	See Eqs. (28), (29), and (31)
$s_q^j(T, \tau)$	Survival rate of juvenile quagga mussels	See Eqs. (28), (30), and (32)
$s_q^a(T, \tau)$	Survival rate of adult quagga mussels	See Eqs. (28), (30), and (32)

Lewis (2010), 0.1% of larvae are assumed to survive to settle on the lake bottom. Hence, we estimate that $b_z = 0.001 \cdot 4218 = 4.128$.

Reproduction in sympatric populations of zebra and quagga mussels was compared in western Lake Erie (Stoekmann 2003). The results suggest no difference in the percentage of spawning mussels or the number of sperm released by individuals (Table 3 and Fig. 4 in Stoekmann 2003), although zebra mussels generally released more eggs and a greater mass of gametes than did quagga mussels. Thus, we choose $b_q = b_z$ in this study.

4.3 Shell Lengths: ℓ_z^j , ℓ_z^a , ℓ_q^j , and ℓ_q^a

Adult zebra mussels typically range from 2–2.5 cm in length, whereas adult quagga mussels may grow larger than their congeners and often exceed 3 cm in length (Mills et al. 1993). We choose $\ell_z^a = 2.5$ cm, $\ell_q^a = 3$ cm, $\ell_z^j = 1.25$ cm, and $\ell_q^j = 1.5$ cm.

The parameter estimate for model (1) are listed in Table 2. Based on the above parameter estimates, we are able to calculate the non-dimensional parameters in the model (5–6). Observing that the non-dimensional model (5–6) has the same long-term dynamics as the original model (1), we will make numerical simulations based on model (5–6), instead of model (1). By doing so, we avoid having to estimate the competition coefficient β , for which data are lacking.

5 Numerical Results

In this section, the resulting parameter estimates are used to calculate $R_0^z(T, \tau)$, $R_0^q(T, \tau)$, $r_z(T, \tau)$, and $r_q(T, \tau)$, according to (8–11), for the range of temperatures ($5^\circ\text{C} \leq T \leq 30^\circ\text{C}$) and turbidities ($0 \leq \tau \leq 80$ NTU). We assume that two species share the same environment. We apply the results of stability analysis in Sect. 3 to determine the competitive outcomes in terms of temperature and turbidity (Fig. 2).

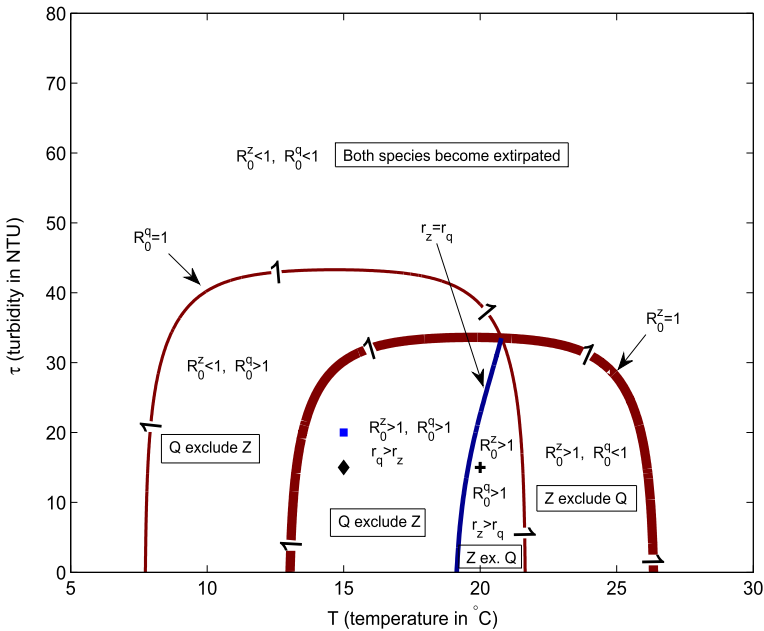


Fig. 2 Results of extirpation and competitive exclusion for different ranges of temperature and turbidity. We choose $\sigma = 0.5$. Three points (square $T = 15$, $\tau = 20$ NTU, diamond $T = 15$, $\tau = 15$ NTU, cross $T = 20$, $\tau = 15$ NTU) which will be chosen as samples in Figs. 3 and 4 are marked (Color figure online)

As shown by Fig. 2, the temperature-turbidity space is divided into five regions by the contour lines $R_0^z = 1$, $R_0^q = 1$, and $r_z = r_q$. In other words, these lines divide the range of temperatures and turbidities into five environmental niches. In the niche where the temperatures are very low or very high, or the turbidities are high, both species become extirpated since their net reproductive values, R_0^z and R_0^q , are both less than 1. In the other four niches, one species excludes the other due to their different tolerances to temperature and turbidity. The results indicate that quagga mussel dominance leading to potential exclusion of zebra mussels at mean water temperatures below 20 °C and over a broad range of turbidities, and a much narrower set of conditions that favor zebra mussel dominance and potential exclusion of quagga mussels at temperatures above 20 °C and turbidities below 35 NTU.

The temperature-turbidity niche space over which quagga mussels are predicted to outcompete zebra mussels is much larger than the space in which they are outcompeted by zebra mussels. This result is in accord with field observations that suggest that the quagga mussel more frequently dominates dreissenid communities, especially in turbid waters (bij de Vaate et al. 2014; Zhulidov et al. 2006).

To see how one species excludes the other when the net reproductive values of both species are greater than 1, as an example, we choose temperature $T = 15$ °C and turbidity $\tau = 20$ NTU (square marked in Fig. 2). Calculation shows that $R_0^z = 1.54$, $R_0^q = 3.02$, $r_z = 1.2$, and $r_q = 1.55$. We consider the case where quagga mussels

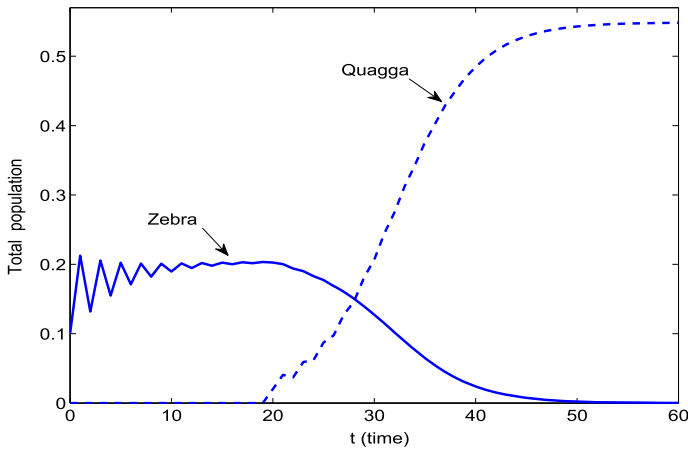


Fig. 3 The total population of zebra mussels $Z^j(t) + Z^a(t)$ (solid line) and the total population of quagga mussels $Q^j(t) + Q^a(t)$ (dashed line). We use the results of parameter estimates in Sect. 4 and choose $T = 15^\circ\text{C}$ and $\tau = 20$ NTU (square marked in Fig. 2) (Color figure online)

invade a body of water already colonized by zebra mussels, and solve the competition model (5–6) (Fig. 3). As observed in some ecosystems, when the zebra mussel is the first species to invade a body of water, it grows up to its carrying capacity. Once the quagga mussel invades the same body of water, it will grow and become more abundant than the zebra mussel, eventually the quagga mussel excludes the zebra mussel.

6 A Two-Patch Dispersal Model

The *Dreissena* competition model (1) assumes that both species share the same living conditions and compete for the same resource (food). It does not consider spatial heterogeneity, and ignores population dispersal. Therefore, both theoretical and numerical results support the “competitive exclusion principle”—that is, two similar species that live in the same environment and compete for the same resources cannot coexist (Cushing et al. 2004). However, it is widely believed that both species exist in ecosystems composed of many local patches with heterogeneous environmental conditions (e.g., Dermott and Munawar 1993; Karatayev et al. 2014). This motivates us to extend the single-patch model (1) to a two-patch dispersal model toward better understanding the effects of environmental heterogeneity and dispersal on the competitive dynamics. As we will see, the two-patch competition model does allow coexistence.

We consider an aquatic ecosystem composed of two patches, say patch 1 and patch 2. A model that describes the competitive dynamics of two species in these two patches is given by

$$\begin{cases}
 Z_1^j(t+1) = [(1 - \alpha_{12}^z) b_1^z Z_1^a(t) + \alpha_{21}^z b_2^z Z_2^a(t)] \psi_1(t) \\
 Z_1^a(t+1) = [s_{z1}^j Z_1^j(t) + s_{z1}^a Z_1^a(t)] \psi_1(t) \\
 Q_1^j(t+1) = [(1 - \alpha_{12}^q) b_1^q Q_1^a(t) + \alpha_{21}^q b_2^q Q_2^a(t)] \psi_1(t) \\
 Q_1^a(t+1) = [s_{q1}^j Q_1^j(t) + s_{q1}^a Q_1^a(t)] \psi_1(t) \\
 Z_2^j(t+1) = [(1 - \alpha_{21}^z) b_2^z Z_2^a(t) + \alpha_{12}^z b_1^z Z_1^a(t)] \psi_2(t) \\
 Z_2^a(t+1) = [s_{z2}^j Z_2^j(t) + s_{z2}^a Z_2^a(t)] \psi_2(t) \\
 Q_2^j(t+1) = [(1 - \alpha_{21}^q) b_2^q Q_2^a(t) + \alpha_{12}^q b_1^q Q_1^a(t)] \psi_2(t) \\
 Q_2^a(t+1) = [s_{q2}^j Q_2^j(t) + s_{q2}^a Q_2^a(t)] \psi_2(t)
 \end{cases} \tag{33}$$

where

$$\begin{aligned}
 \psi_1(t) &= \frac{1}{1 + Z_1^j(t) + Z_1^a(t) + Q_1^j(t) + Q_1^a(t)}, \\
 \psi_2(t) &= \frac{1}{1 + Z_2^j(t) + Z_2^a(t) + Q_2^j(t) + Q_2^a(t)},
 \end{aligned}$$

$Z_1^j(t)$ is the number of juvenile zebra mussels in patch 1 at time t , b_1^z is the number of juvenile zebra mussels produced per adult zebra mussel in patch 1, s_{z1}^j is the basal survival rate of juvenile zebra mussels in patch 1. α_{12}^z is the proportion that juvenile zebra mussels, reproduced by adult zebra mussels in patch 1, live in patch 2 due to dispersal. Similar meanings for other notations (Z, Q represent zebra and quagga mussels, respectively, j, a represent juveniles and adults, respectively, 1 and 2 represent patch 1 and patch 2, respectively). $\psi_1(t)$ and $\psi_2(t)$ are density-dependent competition terms for populations living in patch 1 and patch 2, respectively.

Model (33) assumes that two species compete for food within the patch they live, and populations living in different patches do not compete. The populations in different patches are assumed to be connected and interact with each other through dispersal. Clearly, if $\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$, then model (33) is decoupled into two single-patch models in the form of (6).

We say that two species coexist in the overall ecosystem if each species eventually exists at least one of the two patches, more precisely, if there exists a positive constant δ such that

$$\liminf_{t \rightarrow \infty} \min \left\{ Z_1^j(t) + Z_1^a(t) + Z_2^j(t) + Z_2^a(t), Q_1^j(t) + Q_1^a(t) + Q_2^j(t) + Q_2^a(t) \right\} \geq \delta, \tag{34}$$

where we take the infimum in time, but minimize over the two population sizes.

We say that two species coexist in patch 1 if there exists a positive constant δ_1 such that

$$\liminf_{t \rightarrow \infty} \min \left\{ Z_1^j(t) + Z_1^a(t), Q_1^j(t) + Q_1^a(t) \right\} \geq \delta_1. \tag{35}$$

Similarly, we say that two species coexist in patch 2 if there exists a positive constant δ_2 such that

$$\liminf_{t \rightarrow \infty} \min \left\{ Z_2^j(t) + Z_2^a(t), Q_2^j(t) + Q_2^a(t) \right\} \geq \delta_2. \tag{36}$$

Intuitively, if one species excludes the other in both patches when the two patches are isolated ($\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$), then the first species excludes the second one in both patches for any positive dispersal rates (i.e., $0 < \alpha_{12}^z, \alpha_{21}^z, \alpha_{12}^q, \alpha_{21}^q < 1$) when the two patches are connected through dispersal. We are interested in the following question: if the two patches are isolated ($\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$), and quagga mussels exclude zebra mussels in patch 1 while zebra mussels exclude quagga mussels in patch 2, then when $0 < \alpha_{12}^z, \alpha_{21}^z, \alpha_{12}^q, \alpha_{21}^q < 1$, how do the dispersal rates affect the competitive outcomes? To answer this question, we solve the two-patch dispersal model (33) using the results of model parameterization in Sect. 4. As an example, we consider two patches with the same turbidity level (say $\tau = 15$ NTU) but different temperatures (say temperatures are 15 and 20 °C in patch 1 and patch 2, respectively) (diamond and cross marked in Fig. 2). Then the population survival rates can be calculated according to (26–32). If there is no dispersal ($\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$), calculation shows that, in patch 1, the net reproductive values of zebra and quagga mussels are $R_{0,1}^z = 1.75$ and $R_{0,1}^q = 3.25$, respectively, and the intrinsic growth rates of zebra and quagga mussels are $r_{z,1} = 1.27$ and $r_{q,1} = 1.59$, respectively. Therefore, quagga mussels exclude zebra mussel in the patch 1 (Theorem 2). In patch 2, the net reproductive values of zebra and quagga mussels are $R_{0,2}^z = 2.29$ and $R_{0,2}^q = 2.04$, respectively, and the intrinsic growth rates of zebra and quagga mussels are $r_{z,2} = 1.41$ and $r_{q,2} = 1.34$, respectively. Therefore, zebra mussels exclude quagga mussels in patch 2 (Theorem 2).

To see how the population dispersal affects the competitive outcome, we choose two different dispersal rates and we plot the solutions of the model (33) (Fig. 4). From Fig. 4, we see that different dispersal rates lead to different competitive outcomes. When the dispersal rates are low (top row of Fig. 4), both species coexist in both patches according to (35) and (36), although quagga mussels dominate in patch 1 and zebra mussels are more abundant in patch 2. In other words, both species co-occur and are co-dominant. This pattern of co-dominance reflects different advantages of each species under different environmental conditions. However, if the dispersal rates are high (bottom row of Fig. 4), quagga mussels exclude zebra mussels in both patches, hence quagga mussels exclude zebra mussels in the whole ecosystem, they cannot coexist according to (34). This is because the growth rate of quagga mussels is much higher than that of zebra mussels ($r_{q,1} = 1.59 > r_{z,1} = 1.27$) in patch 1, although the growth rate of quagga mussels is slightly lower than that of zebra mussels ($r_{q,2} = 1.34 < r_{z,2} = 1.41$) in patch 2. Thus, when the dispersal rates are high, the two patches are strongly connected, quagga mussels will ultimately exclude zebra mussels in the whole ecosystem.

We complete this section by making some mathematical conjectures as answers to the above-mentioned questions. To do so, we choose the same parameters, except $\alpha_{12}^z, \alpha_{21}^z, \alpha_{12}^q$, and α_{21}^q as those in Fig. 4. We let $\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q := \alpha$ and

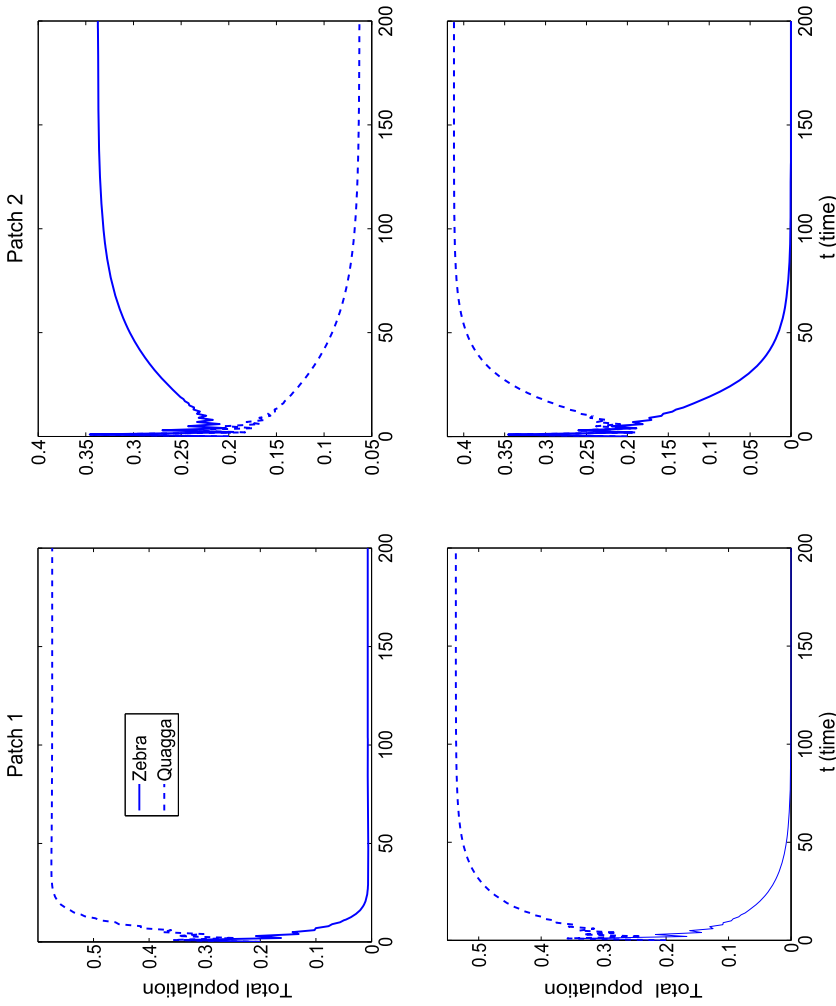


Fig. 4 The solutions of model (33) for different dispersal rates (*Top row* $\alpha_{12}^z = \alpha_{21}^z = 0.01$, *Bottom row* $\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0.2$). Temperatures are 15 and 20 °C in patch 1 and patch 2, respectively, turbidities are the same ($\tau = 15$ NTU) (*diamond* and *cross* marked in Fig. 2). Other parameters are the same as those in Fig. 2 (Color figure online)

plot the bifurcation dynamics of the two-patch dispersal model (33) with respect to α (Fig. 5). Based on the numerical results shown by Fig. 5, we make the following conjectures: if the two patches are isolated ($\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$), 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 $r_{q,1} + r_{q,2} > r_{z,1} + r_{z,2}$.

7 Discussion

In this paper, we developed a dynamic model that describes the competitive interactions between zebra and quagga mussels. The stability analysis of the model yields the conditions on net reproductive rates and intrinsic growth rates that lead to either extirpation of both species or the dominance of one species coupled with the potential competitive exclusion of the other. We then estimated the model parameters by connecting the model to experimental data. The estimates of the dependence of the population survival rates on temperature and turbidity result in temperature- and turbidity dependent net reproductive values and intrinsic growth rates. Combining the theoretical results and numerical ones, we plotted environmental niches in which both species become extirpated or one species excludes the other. As predicted by “competitive exclusion principle”, our single-patch model in which two species compete for food does not lead to coexistence. Extending the single-patch model to a two-patch dispersal model, the numerical results indicate that both competitive exclusion and long-term coexistence may occur, depending on dispersal rates. Moreover, when both species coexist in an ecosystem, they may dominate at different areas (Ricciardi and Whoriskey 2004; Zhulidov et al. 2006, 2010), owing to their different sensitivities to environmental conditions.

Based on the life cycle of the species consisting of a juveniles stage that disperses before settling and an adult stage that reproduces annually, we developed a stage-structured one-patch competition model. On the qualitative side, unlike an unstructured model in which all individuals in a population are treated as identical (hence all individuals have the same reproduction rate and survival rate), our stage-structured models assumed that only adults reproduce and adults and juveniles have different survival rates. Also, we assumed that juveniles and adults have distinct competitive abilities that are proportional to their shell length. On the quantitative side, when we connected the model to data, we assumed that juveniles and adults have the same survival rates because data are lacking. In reality, juveniles and adults may have different sensitivities to temperature and turbidity; therefore, more data is needed to yield more precise quantitative results. It is worth mentioning that having stage structure is clearly crucial in the two-patch model, since only juveniles disperse, in this sense, our stage-structured two-patch model is a natural extension of the stage-structured one-patch model.

In our competition model (1), we chose the same competition-induced survival term with the same competition coefficient for different species and different stages; thus, the resulting dynamics of the model is competitive exclusion, which is analogous to

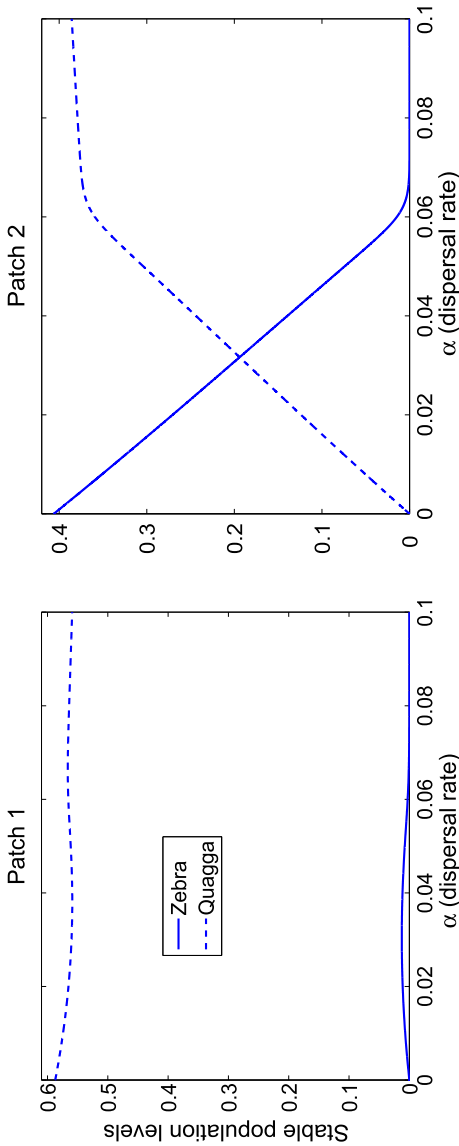


Fig. 5 Stable population levels when the bifurcation parameter $\alpha \in [0, 0.1]$. We let $\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q := \alpha$, other parameters are the same as those in Fig. 4. When $\alpha_{12}^z = \alpha_{21}^z = \alpha_{12}^q = \alpha_{21}^q = 0$, quagga mussels exclude zebra mussels in patch 1 (since $r_{q,1} = 1.59 > r_{z,1} = 1.27$) while zebra mussels exclude quagga mussels in patch 2 (since $r_{q,2} = 1.34 < r_{z,2} = 1.41$). Both species coexist in both patches if $0 < \alpha < 0.065$. Quagga mussels exclude zebra mussels in both patches if $\alpha > 0.06$ (since $r_{q,1} + r_{q,2} > r_{z,1} + r_{z,2}$) (Color figure online)

the classical continuous two-dimensional Lotka–Volterra model (Allen 2007) and to its discrete version studied in Cushing et al. (2004) for the case where the nullclines do not intersect. It is possible to obtain different dynamics, such as coexistence and bistability, if we choose different competition coefficients for different species.

Temperature and turbidity impose important constraints on the growth and abundance of zebra and quagga mussels. Here we assume that reproduction rates and individual shell lengths are constant. More data is needed to estimate the dependence of reproduction rates and shell lengths on temperature and turbidity. In addition, we assume that temperature and turbidity affect the population survival rates independently (for example, $s_z^j(T, \tau) = s_z^j(T)s_z^j(\tau)$). However, there is often a complex co-relationship between the two factors, where temperature can modify the mussel's response to turbidity, thereby changing its turbidity tolerance range, and turbidity can similarly modify the effects of temperature (e.g., Karatayev et al. 1998; Thorp et al. 1998). Moreover, while this study relates competitive interactions to temperature and turbidity, other factors (such as oxygen, calcium, and food quality and quantity) may differentially affect the abundance and distribution of dreissenid mussels (Jones and Ricciardi 2005; Karatayev et al. 1998; Stoeckmann 2003).

It should also be noted that the results of the effects of temperature and turbidity on competitive exclusion are only applicable to habitats where all seasonal temperatures and turbidities are constant or averaged, which would force the net reproductive values to be greater than 1 or less than 1, and the intrinsic growth rate of one species is greater than the intrinsic growth rate of another species. However, we cannot make clear predictions on competition outcomes in habitats where temperature fluctuates seasonally, or daily, forcing the net reproductive rates greater than 1 in one period but less than 1 in another period. Yet, we could presume that a habitat to be more unfavorable to a species when the seasonal fluctuations of a factor forces over a long period of the year, and vice versa. It may be useful to incorporate the effects of short-term and seasonal temperature fluctuations on (see Bacaer 2009; Bacaer and Oufiki 2007).

Steps toward further model development include the following: (1) It is most likely that we are able to prove that the local stabilities (see Sect. 3.2) are indeed global, by using a similar approach as in Ackleh and DeLeenheer (2008), Ackleh and Zhang (2009). (2) Given that the two-patch dispersal model (33) is a system that includes eight difference equations, the theoretical analysis of model (33) is challenging, so we leave this for future mathematical development. (3) We also plan to extend the competition model (1) to a spatially explicit benthic-drift model (Huang et al., accepted) for zebra and quagga mussels in rivers, by including larval dispersal in the drift and juvenile and adult competition on the benthos. We could conceivably use net reproductive rate theory for source-sink dynamics (Krkošek and Lewis 2010) to understand the interactions between growth and dispersal, environmental conditions, and river flow in determining upstream invasion success of zebra and quagga mussels.

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