

## Effects of Heterogeneity on Spread and Persistence in Rivers

Frithjof Lutscher<sup>a,b,\*</sup>, Mark A. Lewis<sup>a,c</sup>, Edward McCauley<sup>b</sup>

<sup>a</sup>*Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E1*

<sup>b</sup>*Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta, Canada T2N 1N4*

<sup>c</sup>*Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E1*

Received: 25 October 2005 / Accepted: 18 January 2006 / Published online: 20 May 2006  
© Society for Mathematical Biology 2006

**Abstract** The question how aquatic populations persist in rivers when individuals are constantly lost due to downstream drift has been termed the “drift paradox.” Recent modeling approaches have revealed diffusion-mediated persistence as a solution. We study logistically growing populations with and without a benthic stage and consider spatially varying growth rates. We use idealized hydrodynamic equations to link river cross-sectional area to flow speed and assume heterogeneity in the form of alternating patches, i.e., piecewise constant conditions. We derive implicit formulae for the persistence boundary and for the dispersion relation of the wave speed. We explicitly discuss the influence of flow speed, cross-sectional area and benthic stage on both persistence and upstream invasion speed.

**Keywords** Aquatic organisms · Persistence · Invasions · Rivers · Spatial heterogeneity · Advection–diffusion equations

### 1. Introduction

Streams and rivers are characterized by a variety of physical, chemical and geomorphological features such as unidirectional flow of water, pools and riffles, bends and waterfalls, floodplains, lateral inflow and hyporheic zones, hierarchical network structure and many more (Allan, 1995). These abiotic conditions give rise to a wide range of qualitatively different habitats for aquatic populations such as periphyton, invertebrates, and fish. Spatio-temporal variations in temperature,

---

\*Corresponding author.  
E-mail address: flutsche@uottawa.ca (Frithjof Lutscher).

light, flow conditions, and nutrient availability particularly affect species who do not possess the ability to actively move between different conditions and thereby choose among or average over these features. These species with limited active mobility in the water column, e.g., periphyton and invertebrates, form the base of a complex food-web, and are indicators of ecosystem health (Hill et al., 2000). Natural and human disturbances may alter these environmental conditions, e.g., through flood events, landslides, dam and channel construction, water extraction, or land-use patterns in the watershed. In order to sustainably manage and maintain riverine ecosystems, it is therefore crucial to understand the effects of heterogeneity on persistence and extinction, invasion potential and invasibility, as well as competition of such populations.

The question how invertebrates in streams can resist wash-out caused by flow, has been termed the “drift paradox” (Müller, 1954, 1982). Recent modeling efforts for the drift paradox identified a “critical flow speed” below which a population can persist on a long enough stretch of a river and also spread upstream in form of a moving front (Speirs and Gurney, 2001; Lutscher et al., 2005; Pachepsky et al., 2005). These models neglect spatial heterogeneities and assume a homogeneous habitat. Spatial heterogeneities have been considered when modeling spread and persistence in terrestrial systems, but typically under the assumption of symmetric dispersal and hence neglecting flow (Shigesada et al., 1986; Cruywagen et al., 1996), but see Weinberger (2002). Lewis et al. (1996) include flow in the model formulation but not in the analysis. Cantrell and Cosner (2003) provide some general results that include flow, but their model formulation is not tied to the geometry of rivers. Since heterogeneities in riverine habitats can frequently be linked to channel geometry, it is important to include an appropriate representation of this geometry into the model. While it is nearly impossible to completely describe the complexity of fluid flow in natural river channels, hydrologists have successfully employed advection–diffusion equations to describe time-series data of conservative tracer injections in rivers and streams (Bencala and Walters, 1983). For a more recent and mathematically detailed theory of transport in hydrology see Logan (2001). Even though the equations are spatially one-dimensional, they implicitly capture some essential aspects of the three-dimensional geometry of the river channel.

The objective of the present work is to analyze the effects of heterogeneity on persistence and spread of a single population in a riverine habitat by synthesizing and extending the approaches and concepts mentioned earlier. We first use the ideas of Bencala and Walters (1983) on representations of transport and flow to derive two models for spatio-temporal dynamics of a population. The first model considers only the pelagic phase and hence simultaneously generalizes the model of Speirs and Gurney (2001) by introducing heterogeneity, and the model of Shigesada et al. (1986) by introducing unidirectional flow. The second model includes a benthic stage of the population and generalizes the system of Pachepsky et al. (2005) by introducing horizontal heterogeneity. The importance of a benthic stage for persistence of populations has been demonstrated frequently (DeAngelis et al., 1995; Dent and Henry, 1999; Mulholland and DeAngelis, 2000; Lutscher et al., 2005; Pachepsky et al., 2005).

For both model equations we study persistence of the population through the “critical domain size” problem and spatial spread through the speed of traveling (periodic) waves. These two concepts have a distinguished history in spatial ecology. For convenience of the reader, we summarize related work in Table 1. The “critical domain size” is the minimal amount of habitat that a population requires to persist (Skellam, 1951). It results from the assumption that a population can grow locally within a bounded habitat, but might be lost from the habitat to uninhabitable exterior by movement across the boundary. The critical domain size has been studied in continuous and discrete time modeling frameworks (Kierstead and Slobodkin, 1953; Kot and Schaffer, 1986), and it provides an important tool in conservation biology and reserve design (Cantrell and Cosner, 1993; Botsford et al., 2001). In unbounded heterogeneous domains, there is a critical fraction of good habitat that guarantees population persistence (Shigesada et al., 1986; Van Kirk and Lewis, 1997).

The invasion speed of a population is a crucial quantity in many cases: some invasions may be intended, e.g. for biological control agents (Baker and Dunn, 1990), others may threaten native species or, in the case of an epidemic disease, human health may be at risk (Medlock and Kot, 2003). Hastings et al. (2005) give a comprehensive overview on ecological aspects of the subject, Xin (2000) provides a summary of mathematical results on front propagation. While several measures of the speed of spread are available (Aronson and Weinberger, 1975; Weinberger, 1982), we focus mostly on the (minimal) speed of a traveling wave (Fisher, 1937) and discuss the relation to other measures in the appendix.

Throughout this paper, we consider flow and advection to be caused by the flowing water in rivers and streams, but many other physical processes induce advective transport of populations, and our modeling framework and results are widely applicable. Most obvious examples are coast lines with dominant currents (Gaylord and Gaines, 2000) where no-fishing zones can create heterogeneity (Botsford et al., 2001), or plug-flow reactors as models for the gut (Ballyk et al., 1998), where pockets in the gut wall give rise to heterogeneities. Somewhat less obvious examples of systems with unidirectional flow are phytoplankton in the water column, sinking due to gravity (Huisman et al., 2002), and terrestrial systems in the presence of moving temperature isoclines (Potapov and Lewis, 2004).

In the next section, we present the two models for population dynamics and movement in heterogeneous domains. In the following we always assume that the habitat consists of periodically varying, alternating patches of good and bad quality. We apply homogenization theory to recover the homogeneous model on a long spatial scale. In Section 3, we derive conditions for persistence of the population in an unbounded domain with alternating good and bad patches. We recover the results from Shigesada et al. (1986) in case of no flow and show how the introduction of flow changes these results. In Section 4, we focus on the minimal speed of a traveling periodic wave in an alternating good–bad habitat. We give conditions under which a population can spread against the flow. Then we turn to conditions for persistence on a bounded patch in Section 5, we focus especially on the question how much heterogeneity is needed for persistence in the case where the homogenized model predicts extinction.

**Table 1** Schematic overview of models and results related to this work

	No Flow		Flow
	Homogeneous	Heterogeneous	
Mobile			
Persistence (unbounded)	×	Shigesada et al. (1986) Cruywagen et al. (1996)	×
Persistence (bounded)	Skellam (1951) Kierstaed and Slobodkin (1953)	Cantrell and Cosner (2001)	Speirs and Gurney (2001)
Invasion	Fisher (1937) Kolmogorov et al. (1937)	Shigesada et al. (1986) Cruywagen et al. (1996)	Fisher (1937) Pachevsky et al. (2005)
Mobile and stationary			
Persistence (unbounded)	×	?	×
Persistence (bounded)	Hadeler and Lewis (2002)	?	Pachevsky et al. (2005)
Invasion	Hadeler and Lewis (2002)	?	Pachevsky et al. (2005)

*Note:* The models in the top section of the table consider only a single pelagic compartment, i.e., all individuals are mobile. The models in the bottom section split the population into a mobile and a stationary compartment, corresponding to a pelagic and a benthic stage. The question of persistence is divided into persistence in unbounded and bounded habitats. The question of persistence in unbounded homogeneous habitats, denoted by ×, is trivial since it reduces to a non-spatial problem. In the present work, we fill in the question mark as well as the entire (missing) column of heterogeneous habitats with flow.

## 2. Modeling

We start by deriving an implicitly three-dimensional conservation law for movement of individuals in rivers and streams. Following [Bencala and Walters \(1983\)](#) and [DeAngelis et al. \(1995\)](#), we partition the river into the flowing water or pelagic zone and the storage or benthic zone. We denote by  $X \in \mathbb{R}$  the longitudinal distance in the river and assume that longitudinal movement occurs only in the pelagic zone. In each cross-section, we assume that the river is well-mixed, and we denote  $A(X)$ ,  $A_s(X)$  as the cross-sectional areas of flowing and storage zone, respectively. The corresponding densities of individuals are denoted by  $U(X)$ ,  $N(X)$ .

### 2.1. Movement dynamics

The two processes that cause longitudinal displacement of individuals are diffusive and advective transport. The temporal change in total mass of pelagic individuals due to these two processes in a given test volume is

$$\begin{aligned} \frac{\partial}{\partial T} \int_{X_0}^{X_1} A(T, X)U(T, X) dX &= \int_{X_0}^{X_1} \frac{\partial}{\partial X} \left( AD \frac{\partial U}{\partial X} \right) (T, X) dX \\ &\quad - \int_{X_0}^{X_1} \frac{\partial}{\partial X} (QU)(T, X) dX. \end{aligned} \tag{1}$$

The change due to the diffusive flux, given by the first integral on the right-hand side of (1) is proportional to the concentration gradient  $U_X$ , by Fick’s law and proportional to the cross-sectional area by the assumption on homogeneous lateral mixing. Similarly to [Shigesada et al. \(1986\)](#), we allow the diffusion constant  $D$  to vary in space. The change due to the advective flux depends on the discharge  $Q = VA$ , where  $V$  is the flow speed at  $X$ . For a more detailed derivation of (1) from a two-dimensional description, see [Appendix A.1](#).

Discharge and cross-sectional area are related by the continuity equation for stream flow ([Eagleson, 1970](#))

$$\frac{\partial A}{\partial T} = - \frac{\partial Q}{\partial X} + (Q_{Lin} - Q_{Lout}), \tag{2}$$

where  $Q_{Lin}$ ,  $Q_{Lout}$  denote lateral flows due to tributaries and groundwater exchange. For the purposes of this study, we assume that there are no lateral flows and that the channel geometry does not change in time, so that the discharge is constant.

### 2.2. Pelagic population

If we consider only the flow compartment and assume that the pelagic population grows logistically, then the earlier mentioned considerations lead to our first model

equation

$$U_T = \frac{1}{A}(DAU_x)_x - \frac{Q}{A}U_x + (F(X) - \mu U)U, \quad (3)$$

where  $F$  is the spatially varying growth rate and  $\mu$  the (spatially constant) factor in the logistic self-limitation term. In Appendix A.1, we derive our model equation (3) again, this time from an individual-based random-walk approach. For constant  $A > 0$  and  $Q = 0$ , this equation is the one studied by Shigesada et al. (1986). For spatially constant coefficients  $D, A, Q, F > 0$ , we obtain the model by Speirs and Gurney (2001).

### 2.3. Benthic–pelagic population

Many populations with benthic stages spend only a small fraction of their lifetime in the free-flowing water and do not reproduce there (Allan, 1995). Therefore, we model logistic growth for the benthic population only and assume a (spatially varying) exchange rate  $K(X)$  between storage and flowing zone. This leads to the system of equations

$$U_T = \frac{1}{A(X)}(D(X)A(X)U_x)_x - \frac{Q}{A(X)}U_x + K(X)(N - U), \quad (4a)$$

$$N_T = K(X)\frac{A(X)}{A_S(X)}(U - N) + (F(X) - \mu N)N. \quad (4b)$$

This model reduces to the one studied by Pachepsky et al. (2005) when all coefficients are assumed constant in space. In the following analysis of the two models, we will usually treat the simpler model (3) first and more explicitly. Details in the analysis of (4) will be omitted when they are not markedly different from the simpler case.

### 2.4. Boundary conditions

In Section 5, we investigate conditions for population persistence in a finite stretch  $[0, B]$  of the river, and hence we have to introduce boundary conditions for  $U$ . Previous studies in flow-through environments have used two different types of such conditions, namely Dirichlet or “hostile” conditions (Speirs and Gurney, 2001; Pachepsky et al., 2005), or Danckwerts conditions (Ballyk et al., 1998; Lutscher et al., submitted for publication). In Appendix A.2 we use a random-walk model to understand the differences between these two approaches. Here, we use a “worst-case” scenario to study persistence, i.e., the hostile boundary conditions. We assume that no individuals leave or enter the stretch at the upstream boundary but all individuals leave and none enter at the downstream boundary. Mathematically, this is expressed by imposing the boundary conditions

$$DAU_x - QU = 0 \quad \text{at} \quad X = 0, \quad \text{and} \quad U = 0 \quad \text{at} \quad X = B. \quad (5)$$

Biological scenarios that correspond to these conditions could be that the top end is the source of the river (stretch), while the bottom end is an abrupt change of conditions. These might include a waterfall, a fast flowing river, a lake or the ocean with different water quality (e.g., saltwater) or human disturbances (e.g., wastewater).

2.5. *Periodic habitat*

As the simplest and most mathematically tractable extension to the constant coefficient case, we consider a periodically varying habitat with piecewise constant coefficient functions (Shigesada et al., 1986; Robbins and Lewis, submitted for publication). This corresponds to a river with a series of pools and riffles, for example. We assume that

$$A(X), D(X), F(X), A_S(X), K(X) = \begin{cases} A_1, D_1, F_1, A_{S1}, K_1, & X \in (0, L_1) + LZ \\ A_2, D_2, F_2, A_{S2}, K_2, & X \in (L_1, L) + LZ \end{cases} \quad (6)$$

where  $L_1 + L_2 = L$ . Without loss of generality, we assume  $F_1 > F_2$  and  $F_1 > 0$ . We refer to the patches where  $F = F_1$  as the “good” patches and the other ones as “bad” patches because of the difference in growth rates. In fact, we will only consider  $F_2 < 0$ , so that the growth rate becomes a death rate in the bad patches. At the boundaries between the two types of habitat we prescribe matching conditions for the density and the flux. For continuity of the density, these conditions are given by

$$\lim_{X \uparrow L_{1j}} U(T, X) = \lim_{X \downarrow L_{1j}} U(T, X), \quad \lim_{X \uparrow L_{2j}} U(T, X) = \lim_{X \downarrow L_{2j}} U(T, X), \quad (7)$$

where  $L_{1j} = L_1 + jL$ ,  $L_{2j} = jL$ ,  $j \in \mathbb{Z}$ . The matching conditions for the fluxes guarantee that total mass is conserved. They are obtained by replacing the density  $U(T, X)$  in conditions (7) with the flux  $J(T, X)$ , given by

$$J(T, X) = D(X)A(X)U_X(T, X) - QU(T, X). \quad (8)$$

2.6. *Non-dimensionalization*

We introduce non-dimensional quantities in lower case letters as follows:

$$T = F_1 t, \quad X = x\sqrt{D_1/F_1}, \quad U(T, X) = F_1 u(t, x)/\mu, \quad N(T, X) = F_1 n(t, x)/\mu, \quad (9a)$$

$$A(X) = A_1 a(x), \quad A_S(X) = A_1 a_S(x), \quad D(X) = D_1 d(x), \quad F(X) = F_1 f(x). \quad (9b)$$

Then the pelagic equation (3) becomes

$$u_t(t, x) = \frac{1}{a(x)} [d(x)a(x)u_x(t, x)]_x - \frac{q}{a(x)} u_x(t, x) + [f(x) - u(t, x)]u(t, x), \quad (10)$$

whereas the benthic–pelagic system (2.4) reads

$$u_t = \frac{1}{a(x)} [d(x)a(x)u_x]_x - \frac{q}{a(x)}u_x + k_u(x)(n - u), \tag{11a}$$

$$n_t = k_n(x)(u - n) + [f(x) - n]n. \tag{11b}$$

The non-dimensional discharge is  $q = Q/(A\sqrt{D_1F_1})$  and the coefficient functions are given by

$$a(x), d(x), f(x), k_u(x), k_n(x) = \begin{cases} 1, 1, 1, \frac{K_1}{F_1}, \frac{K_1A_1}{F_1A_{S1}}, & x \in (0, l_1) + l\mathbb{Z} \\ \frac{A_2}{A_1}, \frac{D_2}{D_1}, \frac{F_2}{F_1}, \frac{K_2}{F_1}, \frac{K_2A_2}{F_1A_{S2}}, & x \in (l_1, l_1 + l_2) + l\mathbb{Z} \end{cases} \tag{12}$$

with  $l_k = L_k\sqrt{F_1/D_1}$ ,  $k = 1, 2$  and  $l = l_1 + l_2$ . For future reference, we will also use subscripts to denote the value of the coefficient functions on the good and bad patches, respectively, i.e.,  $a_1 = 1, a_2 = A_2/A_1$  and so on.

### 2.7. Homogenization

Pools and riffles in a river are examples of heterogeneities that typically occur on much shorter spatial scales than the whole stretch of a river. In this section, we derive spatially homogeneous equations on a large spatial scale by averaging over small-scale heterogeneities. The derivation of these equations follows the general framework of multi-scale expansions and is similar to the work by Othmer (1983), who considered Eq. (10) with  $q = 0$ .

We assume that the period  $l = l_1 + l_2 = \varepsilon \ll 1$  is small and introduce the small space variable  $\varepsilon y = x$ . Assuming that the coefficient functions depend on that small space variable only, we write

$$\bar{d}(y) = d(\varepsilon y) = d(x), \quad \bar{a}(y) = a(\varepsilon y) = a(x), \quad \bar{g}(y, u) = (f(\varepsilon y) - u)u. \tag{13}$$

We assume that the solution of (10) can be expanded as a power series in  $\varepsilon$  as follows

$$u(t, x) = \sum_{k=0}^{\infty} \varepsilon^k u_k(t, z, y) \tag{14}$$

where  $z = x$  is the large space variable, each term  $u_k$  is periodic in  $y$  of period one, and for  $k \geq 1$  the average over a period with respect to  $y$  is zero. The partial derivative with respect to  $x$  translates into the new coordinates as

$$\frac{\partial}{\partial x} = \frac{\partial}{\partial z} + \frac{1}{\varepsilon} \frac{\partial}{\partial y}. \tag{15}$$



We substitute expressions (14), (15) into Eq. (10) and compare powers of  $\varepsilon$ . After lengthy calculations, we find the homogenized form of Eq. (10) to be

$$\frac{\partial}{\partial t} u_0 = \tilde{D} \frac{\partial^2}{\partial z^2} u_0 - \tilde{Q} \frac{\partial}{\partial z} u_0 + \tilde{G}(u_0), \tag{16}$$

where

$$\tilde{D} = \frac{\langle \bar{a}\bar{d} \rangle_H}{\langle \bar{a} \rangle_A}, \quad \tilde{Q} = \frac{q}{\langle \bar{a} \rangle_A}, \quad \tilde{G} = \langle \bar{g} \rangle_W = \frac{\int_0^1 \bar{a}(y)\bar{g}(y, u_0)dy}{\langle \bar{a} \rangle_A}. \tag{17}$$

The harmonic and arithmetic means are denoted by  $\langle \cdot \rangle_H$  and  $\langle \cdot \rangle_A$ , respectively. The term  $\tilde{G}$  is the average growth rate weighted by the cross-sectional area, denoted by  $\langle \cdot \rangle_W$ . Equation (16) is simply Fisher’s equation with advection as studied in Speirs and Gurney (2001). Therefore, the spreading speeds with and against the advection are given by

$$c^\pm = 2\sqrt{\tilde{D}\tilde{G}} \pm \tilde{Q}. \tag{18}$$

Note that the benthic–pelagic system (11) can in general not be homogenized to obtain the corresponding equations (3) in Pachepsky et al. (2005). While the aforementioned homogenization procedure works for the pelagic equation in (11), the spatial scales in the benthic equations do not separate, i.e., the benthic population tracks the small-scale variations in growth rate,  $f$ , and/or exchange rates,  $k_n, k_u$ .

### 3. Persistence in unbounded domains

In a fragmented habitat, persistence of a population depends on there being “enough” good patches. In this section, we derive precise conditions for persistence. We compare the results to the ones obtained by Shigesada et al. (1986) and emphasize the influence of flow, channel geometry, and benthic stage on persistence.

#### 3.1. Pelagic system

Linearizing the pelagic equation (10) at  $u = 0$  and making an exponential ansatz for the eigenvalue  $\lambda$ , we obtain the equation

$$d(x)u'' - \frac{q}{a(x)}u' + (f(x) - \lambda)u = 0, \quad x \in [0, l], \quad l = l_1 + l_2, \tag{19}$$

together with the matching conditions (7) and (8). Thus, the resulting problem is Hill’s equations with piecewise constant coefficient functions  $d, a, f$ . It is known that there is a sequence of eigenvalues of (19) and that the stability of the zero solution is determined by the dominant eigenvalue  $\lambda$  (Magnus and Winkler, 1979).

The zero solution is stable if  $\lambda < 0$  and unstable if  $\lambda > 0$ . The set  $\lambda = 0$  is called the persistence boundary.

**Lemma 3.1.** *If  $q \geq 2$  then Eq. (19) does not have a solution for  $\lambda \geq 0$ , and hence the population cannot persist. For  $0 \leq q < 2$ , the persistence boundary is given implicitly by*

$$\sin(\alpha l_1) \sinh(\delta l_2) \frac{(d_2 a_2 \delta)^2 + \alpha^2}{2 a_2 d_2 \delta \alpha} - \cos(\alpha l_1) \cosh(\delta l_2) + E = 0, \tag{20}$$

where

$$\alpha^2 = (1 - q^2/4), \quad \delta^2 = \left( f_2 - \frac{q^2}{4 a_2^2 d_2} \right) / d_2, \quad E = \cosh \left( \frac{q}{2} \left( l_1 + \frac{l_2}{a_2 d_2} \right) \right). \tag{21}$$

In the original parameters of the model, the extinction condition  $q \geq 2$  reads  $Q/A_1 \geq 2\sqrt{F_1 D_1}$ . Therefore, if the advection speed in the good patches  $Q/A_1$  exceeds the speed of a traveling wave in a homogeneously good environment,  $2\sqrt{F_1 D_1}$ , then the population cannot persist and is washed downstream. Hence, the *critical advection speed* for persistence (Pachepsky et al., 2005) is the same as in the homogeneous model and independent of the conditions in the bad patches. The precise conditions for persistence, however, do depend on the parameters in the bad patch. A proof of Lemma 3.1 and details of the derivation of (20) are given in Appendix A.3. Setting  $q = 0$  and using some trigonometric identities, one obtains condition (13) from Shigesada et al. (1986).

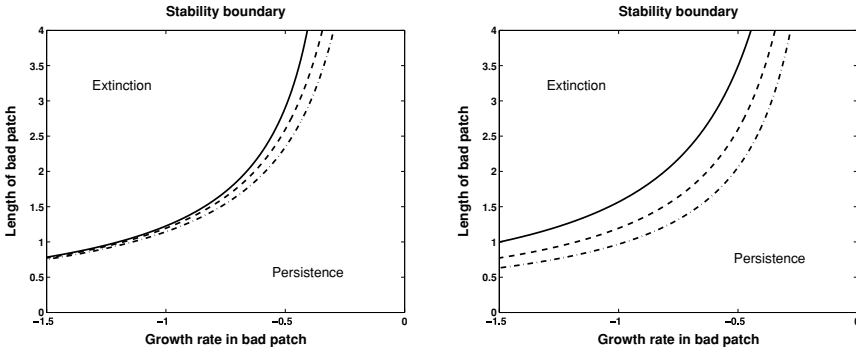
To illustrate the effect of flow and channel geometry on the persistence for a pelagic population, we plot the persistence boundary as given by (20) in Fig. 1. Increasing the flow for fixed channel cross-section reduces the persistence region for the population (left panel). The flow takes individuals from good to bad patches where they die, and hence the population can only persist if the length of the bad patches is shorter or the loss rate in the bad patches is smaller. Increasing the cross-sectional area of bad patches obviously reduces the population’s overall growth rate and hence makes the population more prone to extinction (right panel). Without an additional plot, we report that increasing the diffusion rate in bad patches also reduces the persistence region. Higher diffusion implies again that more individuals are carried to bad patches where they die.

### 3.2. Benthic–pelagic system

Next, we turn to the benthic–pelagic system (11). The linearized problem is given by

$$u_t = \frac{1}{a(x)} [d(x)a(x)u_x]_x - \frac{q}{a(x)} u_x + k_u(x)(n - u), \tag{22a}$$

$$n_t = k_n(x)(u - n) + f(x)n. \tag{22b}$$



**Fig. 1** Stability boundaries of the pelagic equation (10) in the  $f_2$ - $l_2$  plane. The zero solution is stable above the curve and unstable below. The plot on the left shows that the persistence region decreases with increasing flow. The parameters are  $q = 0, 1, 1.9$  for the *solid, dashed, and dash-dot* curve, respectively. Diffusion is held constant at  $d_2 = 1$ , the non-dimensional length of the good patch is  $l_1 = 1$  and cross-sectional area is constant, i.e.,  $a_2 = 1$ . The plot on the right shows that the persistence region decreases with increasing cross-sectional area of bad patches. The parameters are  $a = 0.8, 1, 1.2$  for the *solid, dashed, and dash-dot* curve, respectively. Discharge is fixed at  $q = 1$ ,  $d_2, l_1$  are as mentioned earlier, so that the *dashed* curves in both plots are identical.

If the growth rate on the good patches exceeds the exchange rate, i.e.,  $f > k_n$  then  $n_t > 0$  since  $u \geq 0$ , and hence the benthic population will always grow. In this case, the population can persist, independently of how long or wide the bad patches are and independently of the discharge. Similar parameter regions of unconditional persistence have been found in previous work with stationary and mobile states (Haderler and Lewis, 2002; Lutscher et al., 2005; Pachepsky et al., 2005).

From now on, we assume  $f < k_n$  on good patches. This condition is, of course, always satisfied on bad patches with  $f_2 < 0 < k_n(x)$ . We make an exponential ansatz in (22) and look for the persistence boundary  $\lambda = 0$ . The resulting system of equations can be reduced to the single equation

$$d(x)u'' - \frac{q}{a(x)}u' + g(x)u = 0, \quad x \in [0, l], \quad l = l_1 + l_2, \tag{23}$$

where

$$g(x) = k_u(x) \left( \frac{k_n(x)}{k_n(x) - f(x)} - 1 \right) = \frac{k_u(x)f(x)}{k_n(x) - f(x)}. \tag{24}$$

The function  $g$  is piecewise constant with  $g(x) = g_{1,2}$  on good and bad patches, respectively. On a good patch, we have  $0 < f < k_n$  and therefore,  $g > 0$ . On a bad patch  $f < 0$  implies  $g < 0$ . Hence, Eq. (23) is completely analogous to (19) and can be treated similarly. The following lemma summarizes the results.

**Lemma 3.2.** *If  $f > k_n$  on the good patches, then the zero solution of (11) is unstable and the population can persist independently of the other parameters. If  $f < k_n$  on the good patches and  $q > 2\sqrt{g_1}$ , then the zero solution is stable and the*

population cannot persist independently of the other parameters. Otherwise, the persistence boundary is given by (20), where now the parameter definitions (21) are replaced by

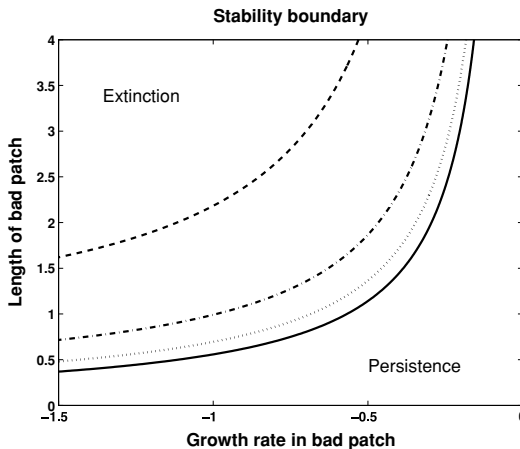
$$\alpha^2 = (g_1 - q^2/4), \quad \delta^2 = \left( g_2 - \frac{q^2}{4a_2^2d_2} \right) / d_2, \quad E = \cosh \left( \frac{q}{2} \left( l_1 + \frac{l_2}{a_2d_2} \right) \right). \quad (25)$$

Just as mentioned earlier in the case without the benthic stage, we can rewrite the persistence condition  $q < 2\sqrt{g_1}$  in dimensional terms as

$$\frac{Q}{A_1} < 2\sqrt{D_1 F_1 \frac{K_1}{K_1 \frac{A_1}{A_{s1}} - F_1}}, \quad (26)$$

which is exactly the critical advection velocity for persistence in homogeneously good habitat as given in Eq. (8) in Pachepsky et al. (2005).

We examine the effect of varying the exchange coefficients  $k_n, k_u$  on the persistence region for Eq. (22). For simplicity, we fix  $k_u = k_n$  to be constant across patches, thereby reducing the problem to only one parameter. In Fig. 2 we plot the stability boundary for increasing values of  $k_n$  and see that the persistence region decreases accordingly. As a comparison, we plot the stability boundary (20) without benthic stage for identical parameter values. As  $k_n$  increases, the stability boundary with benthic stage approaches the one without, in fact for  $k_n = 100$  the two are indistinguishable. Here, we do not explicitly consider possible scalings



**Fig. 2** The stability boundary given by Lemma 3.2 for a population with benthic stage with varying parameter  $k_n = k_u = 2, 4, 10$  for the *dashed, dash-dot, and dotted* curve, respectively. For  $k_n = k_u = 100$ , the curve is virtually indistinguishable from the *solid line* that is obtained from (20) for a population without benthic stage with identical parameter values. These values are  $d_2 = 1, a_2 = 2,$  and  $q = 1$ .

that relate the benthic case to the case without benthic compartment, but refer to Pachepsky et al. (2005), where two approximations were discussed.

Without additional plots, we report that, analogously to the behavior in Fig. 1, fixing all other parameters and increasing  $q$  or  $a_2$ , respectively, results in a decreasing persistence region.

#### 4. Traveling periodic waves

If the persistence condition from the previous section is satisfied, numerical simulations of (10) show that traveling periodic waves evolve from compactly supported initial data. This effect was first observed by Shigesada et al. (1986) in the absence of flow. More recently, Weinberger (2002) proved the existence of traveling periodic waves for a general class of models in periodic habitats. In the presence of flow, the speed of spread is different in the two opposite directions, as illustrated in Fig. 3. In this section, we derive formulae for the minimal upstream and downstream speeds of such waves, and we determine the conditions for the upstream spread to halt.

##### 4.1. Pelagic system

We linearize Eq. (10) at the trivial solution  $u = 0$  and look for traveling periodic waves of the form

$$u(t, x) = u(t + \tau, x + l) = \psi(x - ct)\phi(x), \tag{27}$$

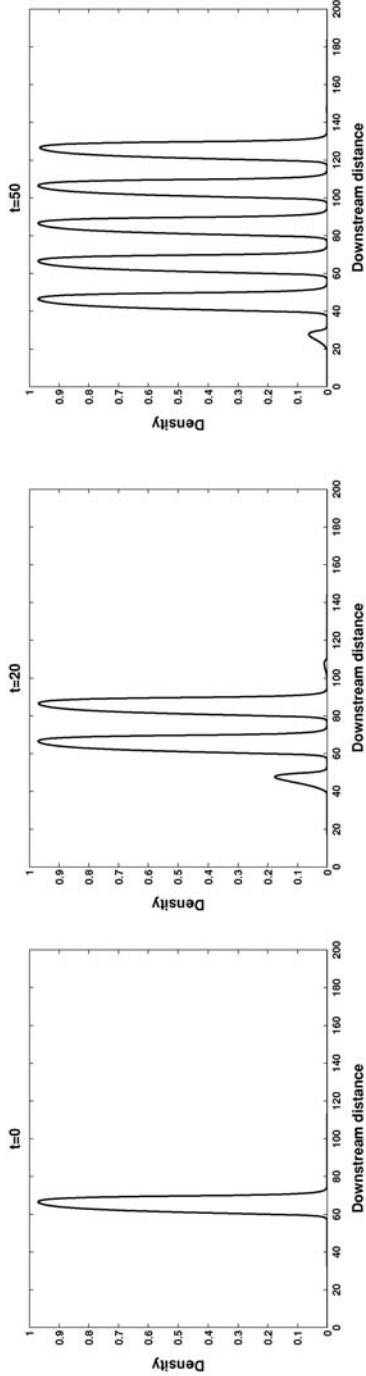
where  $c$  denotes the wave speed, and  $\phi(x) = \phi(x + l)$  is a periodic function. The analysis in Appendix A.4 reveals that  $\psi$  is of the form  $\psi(z) = \exp(-sz)$ , where  $s$  is the shape parameter of the wave front. We collect further results from Appendix A.4 in the following lemma.

**Lemma 4.1.** *If  $q \geq 2$  then there are no upstream traveling periodic waves. If  $q < 2$ , then the dispersion relation between the speed of a traveling periodic wave, upstream or downstream, and its shape parameter is given implicitly by*

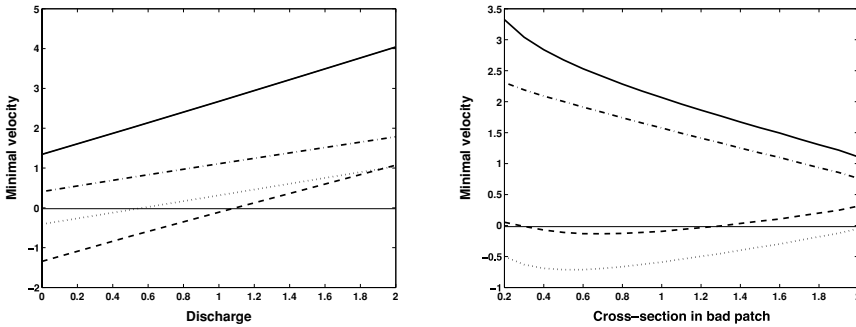
$$\begin{aligned} & \cosh\left(s(l_1 + l_2) + \frac{q}{2}\left(l_1 + \frac{l_2}{a_2 d_2}\right)\right) \\ &= \sinh(\sigma_1 l_1) \sinh(\sigma_2 l_2) \frac{\sigma_1^2 + (d_2 a_2 \sigma_2)^2}{2 a_2 d_2 \sigma_1 \sigma_2} + \cosh(\sigma_1 l_1) \cosh(\sigma_2 l_2), \end{aligned} \tag{28}$$

where

$$\sigma_1 = \sqrt{cs - 1 + \frac{q^2}{4}}, \quad \sigma_2 = \sqrt{\left(cs - f_2 + \frac{q^2}{4a_2^2 d_2}\right) / d_2}. \tag{29}$$



**Fig. 3** Spread of a pelagic population in a periodically varying habitat with advection  $q = 1.5$  going to the right. The other parameters are  $d_s = a_2 = 1$ ,  $f_2 = -3$  and  $l_1 = l_2 = 10$ . Downstream spread is faster than upstream spread. At  $t = 10$ , the population has already reached carrying capacity one good patch downstream from the initial good patch, it has only just begun to colonize the next good upstream patch. The high loss rate in the bad patches leads to near-zero steady-state density there.



**Fig. 4** The minimal wave speeds as a function of discharge for two different values of cross-section in the bad patches (*left panel*) and as a function of cross-sectional area in bad patches (*right panel*). In the left panel, we consider narrow bad patches ( $a_2 = 0.5$ ) and obtain the fast downstream (*solid*) and upstream (*dashed*) speeds. In the same plot, for wide bad patches ( $a_2 = 2$ ) the upstream and downstream speeds are given by the *dash-dot* and the *dotted line*, respectively. In the *right panel*, we consider high discharge ( $q = 1$ ), which results in the *solid* and *dashed line* for downstream and upstream speeds, respectively. Low discharge ( $q = 0.5$ ) results in downstream and upstream speeds given by the *dash-dot* and the *dotted line*, respectively. The other parameters are  $l_1 = l_2 = 1, d_2 = 1, f_2 = -0.5$ . The *horizontal line*  $c = 0$  indicates where upstream waves get stalled.

Note that the condition  $q < 2$  in this lemma implies that the *critical advection speed* for upstream invasion, i.e., the advection speed beyond which no upstream invasion is possible, is identical to the critical advection speed for persistence (see Lemma 3.1). This equality in homogeneous domains was one of the major observations by Pachevsky et al. (2005) and Lutscher et al. (2005).

In Fig. 4 we plot the minimal speed of traveling periodic waves as a function of other parameters in the system. We indicate by  $c > 0$  the speed in the direction of the flow and by  $c < 0$  the opposite direction. Without flow ( $q = 0$ ) the speeds in both directions are exactly the same. With increasing discharge, the downstream speed increases and the upstream speed decreases. The speed is approximately linear as a function of the discharge  $q$ , as could be expected from the homogenized equation (16) and the corresponding speed formula (18). It is instructive to explore the relationship between the minimal wave speeds in the heterogeneous versus homogeneous environments a bit further. Using the parameter values as in Fig. 4, we calculate the values of the homogenized coefficients as given in (17) and compare the behavior of the homogenized to model to the heterogeneous one. For narrow bad patches ( $a_2 = 0.5$ ) we obtain a spreading speed of  $c^\pm = \pm 4/3(1 \pm q)$  from (18) for the homogenized equation, which coincides with the lines plotted in Fig. 4. For wide bad patches ( $a_2 = 2$ ), however, the averaged growth rate is negative. Hence, the population would not spread in the homogenized environment, whereas Fig. 4 shows that it does spread for small enough values of  $q$ .

The right panel in Fig. 4 shows how the wave speed depends on the cross-sectional area in bad patches. The downstream speed is monotonically decreasing with increasing cross-section. As the bad patches get wider, the flow speed decreases there so that individuals move more slowly. At the same time, the larger area of a bad patch incurs higher loss to the population. The situation is different

for the upstream wave. Small cross-sections of bad patches lead to small loss rate but to very high flow velocity, against which the population has to move. Large cross-sections of bad patches imply small flow velocity, which would facilitate upstream invasions, but incur high population loss. The upstream wave moves fastest for intermediate cross-sections.

We can homogenize the dispersion relation (28) by assuming  $l_1 + l_2 \ll 1$  and using the expansions of cosh and sinh up to second order. After some algebra, we obtain

$$c = \frac{(l_1 + l_2)^2 s}{(l_1 + a_2 l_2)(l_1 + l_2/(a_2 d_2))} + \frac{(l_1 + l_2)q}{l_1 + a_2 l_2} + \frac{l_1 + a_2 f_2 l_2}{(l_1 + a_2 l_2)s}. \tag{30}$$

The minimal values of  $c = c(s)$  are given by

$$\begin{aligned} c &= 2\sqrt{\frac{(l_1 + l_2)^2}{(l_1 + a_2 l_2)(l_1 + l_2/(a_2 d_2))} \frac{l_1 + a_2 f_2 l_2}{(l_1 + a_2 l_2)}} \pm \frac{(l_1 + l_2)q}{l_1 + a_2 l_2} \\ &= 2\sqrt{\frac{\langle da \rangle_H}{\langle a \rangle_A} \langle f \rangle_W} \pm \frac{q}{\langle a \rangle_A}, \end{aligned} \tag{31}$$

which is exactly the minimal wave speed (18) for the homogenized Fisher equation (16).

Finally, we look at the conditions for the upstream spread to stop, i.e., we want to characterize  $\max_{s < 0} c(s) = 0$ . Differentiating (28) with respect to  $s$  and substituting the conditions  $c(s) = c'(s) = 0$  leads to

$$1 = \sinh(\sigma_1 l_1) \sinh(\sigma_2 l_2) \frac{\sigma_1^2 + (d_2 a_2 \sigma_2)^2}{2a_2 d_2 \sigma_1 \sigma_2} + \cosh(\sigma_1 l_1) \cosh(\sigma_2 l_2), \tag{32}$$

with  $\sigma_{1,2}$  as mentioned earlier but with  $c = 0$ .

#### 4.2. Benthic–pelagic system

The analysis of traveling periodic waves for the system with benthic stage (11) is, in most parts, a combination of the aforementioned analysis with the idea (24) used to reduce the persistence problem with benthic stage to the one without. Some details are give in Appendix A.4. There are, however, a few differences so that the summary of results in the next lemma is not as complete as could be wished for.

**Lemma 4.2.** *Assume that  $f < k_n$  on good patches. If  $q > 2\sqrt{k_u/(k_n - 1)}$ , then there are no upstream traveling waves. If the reverse inequality holds then the dispersion relation between the wavespeed  $c$  and the shape parameter  $s$  is given by (28) with  $\sigma_{1,2}$  defined by*

$$\sigma_1 = \sqrt{cs - g_1 + \frac{q^2}{4}}, \quad \sigma_2 = \sqrt{\left(cs - g_2 + \frac{q^2}{4a_2^2 d_2}\right) / d_2} \tag{33}$$



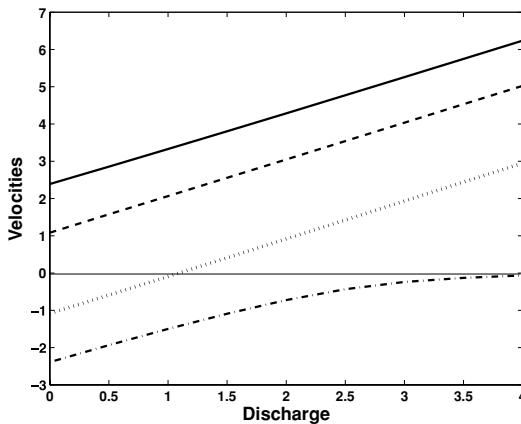
and  $g_{1,2}$  defined as the values on the good and bad patches of  $g(x)$  given by (compare (24))

$$g = \frac{k_u k_n}{cs + k_n - f} - k_u = \frac{k_u(f - cs)}{k_n - (f - cs)}, \quad cs \neq f - k_n. \tag{34}$$

There are no nontrivial traveling periodic wave solutions with  $cs = f - k_n$ .

Solving the dispersion relation from the previous lemma for  $c = c(s)$  numerically reveals that there are several solutions. This was to be expected, since the analysis here contains the case of constant homogeneous environment that was treated in a different way by Lewis and Schmitz (1996), and Pachepsky et al. (2005). There, it could be shown that of the two possible solutions, the larger one is the correct one. The smaller one would lead to oscillatory solutions at the leading edge of the wave, and hence to negative densities. The dispersion relation for  $c(s)$  depends continuously on the length of the bad patch, since it is derived from the determinant of the matrix in (A.31), which depends continuously on  $l_2$ . By continuity then, the larger solution is also the correct wavespeed in our case, at least for small values of  $l_2$ . In Fig. 5 we plot the speeds obtained by the previous lemma, assuming, that the speed with larger absolute value is always the correct one. We compare the speeds to the case without benthic stage. The most notable difference is that the upstream speed is not linear with respect to discharge. The population with benthic stage invades upstream faster than without benthic stage, and the difference increases as  $q$  increases.

For the case missing in Lemma 4.2, namely  $k_n < f$  in good patches, we conjecture that the population can spread upstream independently of the discharge. This conjecture is supported by numerical simulations and by the analogous statement in homogeneous habitats. In addition, it is shown in Appendix A.4 that if  $k_n < f$



**Fig. 5** The figure compares the minimal traveling wave speeds for pelagic only (downstream dashed, upstream dotted) to the speeds with benthic stage (downstream solid, upstream dash-dot). The parameters are  $d_2 = a_2 = 1$ ,  $f_2 = -0.5$  and  $k_n = k_u = 1.1$

then there cannot be a biologically meaningful solution with  $c = 0$ ; hence, an upstream invading wave cannot be stalled by changing parameters. A rigorous proof of this conjecture remains future work.

## 5. Persistence in bounded domains

In this section, we investigate how the graininess of a bounded domain influences persistence on that domain. We consider the domain  $[0, b]$  subdivided into  $2n$  patches, alternating good and bad of length  $l_1$  and  $l_2$ , respectively. Hence, we have the relationship  $b = nl = n(l_1 + l_2)$ . For simplicity, we only present the case of a pelagic species, i.e., we look at Eq. (10), but it is obvious that the treatment of the benthic–pelagic system in Section 3.2 extends to the analysis here. Boundary conditions are given by (5), i.e., no-flux at  $x = 0$  and hostile at  $x = b$ . To find the boundary between persistence and extinction, we linearize (10) at  $u = 0$  and find conditions for the dominant eigenvalue  $\lambda = 0$ . Hence, we study the equation

$$\frac{1}{a}[dau_x]_x - \frac{q}{a}u_x + fu = 0, \quad x \in [0, b], \quad (35)$$

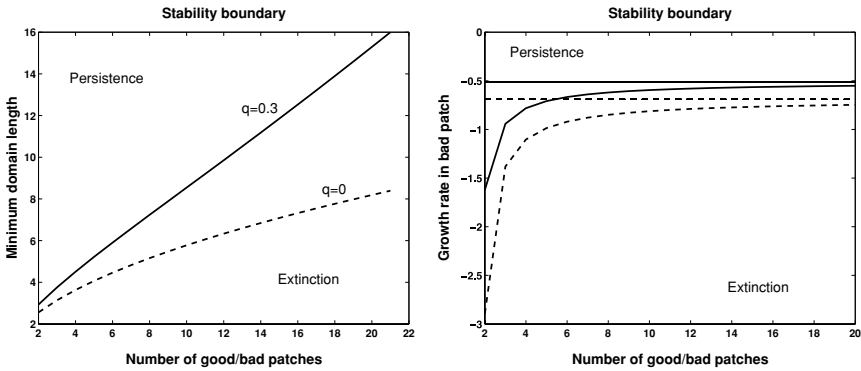
with

$$dau_x - qu = 0 \quad \text{at} \quad x = 0, \quad u(b) = 0. \quad (36)$$

This problem can be fully analyzed, similar to the ones in the two previous sections, but the resulting formulae are somewhat more complicated than the ones for the unbounded domain. The persistence condition is given implicitly as the zero-set of the determinant of a certain  $(4n - 1) \times (4n - 1)$  matrix. Due to the block structure of the sparse matrix, this condition reduces to a condition on certain products of  $2 \times 2$  matrices. We present the details of the analysis in Appendix A.3 and concentrate on the results here.

The critical domain size problem in the presence of flow, i.e., the minimal length of a river that supports a population, was first explicitly addressed by Speirs and Gurney (2001) in homogeneous habitats. A more general treatment of the leading eigenvalue of a reaction–advection–diffusion equation on a homogeneous domain in several space dimensions is given in Murray and Sperb (1983). With heterogeneity, one may ask how the critical domain size depends on the number of subdivisions of the domain. The results are summarized in Fig. 6, left panel. Parameters are chosen in the simplest possible way and such that the spatially averaged growth rate of the population is zero. Hence, in the homogenization limit, the population cannot persist. We see that the minimal domain length increases with the number of subdivisions. For example, whereas a river of length 4 is sufficient to sustain a population if there are only 2 or 3 alternating pairs of good/bad patches, the population will be driven to extinction if there are 6 or more subdivisions. As expected, the case with advection requires a longer domain for persistence.

In the right panel in Fig. 6 we fix the domain length to  $b = 4$  and plot the maximum loss rate in bad patches that a population can tolerate before it goes



**Fig. 6** *Left:* Minimal total domain length for a given number of subdivisions in good/bad patches. *Right:* Possible loss rates (negative growth rates) in bad patches for population persistence on a fixed domain length dependent on number of subdivisions in good/bad patches. See text for details. The parameters are  $d_2 = a_2 = 1$  and we fix the ratio  $l_1/l_2 = 1$ . In the *left panel*, we choose  $f_2 = -1$  so that the average growth rate is zero. In the *right panel*, we fix the total domain length to  $b = 4$ . The *curved lines* are the results from Eq. (A.24). The *straight horizontal lines* indicate the growth rate necessary for population persistence of the homogenized equation (16) on a domain of length 4 according to Speirs and Gurney (2001), Eq. (5). *Solid lines* represent  $q = 0.3$ , whereas *dashed lines* are  $q = 0$ .

extinct. We compare this with the persistence condition as given by Speirs and Gurney (2001) for the homogenization (16). We see that the population can tolerate larger loss rates in the heterogeneous case, but as the patches become small, the persistence condition approaches the one for the homogenization. We want to point out that the case  $f_2 = -1$  corresponds to an average growth rate of zero; hence, if the habitat consists of only two patches, then the population can persist even when the average growth rate is negative. These results are in line with many other studies that confirm that increasing the number of subdivisions into good and bad habitats may lead to extinction of a population, with or without advection, see Cantrell and Cosner (2003) and the discussion therein, and in particular Cantrell and Cosner (1991).

**6. Robustness of results**

There are two loss terms included into the models mentioned earlier: One is related to flow when individuals drift away from a location, the other is mortality given as the negative growth rate in a bad patch. While dependence of the “flow loss” on cross-sectional area is built into the model formulation, it is assumed that the cross-sectional area ( $a_2$ ) and the loss rate ( $f_2$ ) in a bad patch can be chosen independently. In reality, the two parameters may be linked, for example, through nutrient or light levels. One of the results in the previous sections is that persistence is decreasing with increasing cross-sectional area of bad patches. In this section, we discuss whether different biological scenarios satisfy or violate the modeling

assumptions, and we explore how robust the persistence results are with respect to biologically relevant violations of these assumptions.

In the first scenario, we assume that the river is of constant depth, while the width might be changing. We assume furthermore that the input rate of nutrients is constant per surface area of the river, for example nutrient input through upwelling or by rain. Then nutrient concentration, and hence the population growth rate, are independent of cross-sectional area, so that the modeling assumptions are met. The difference between good and bad patches might be caused by physical or chemical features of the river bottom or by harvesting.

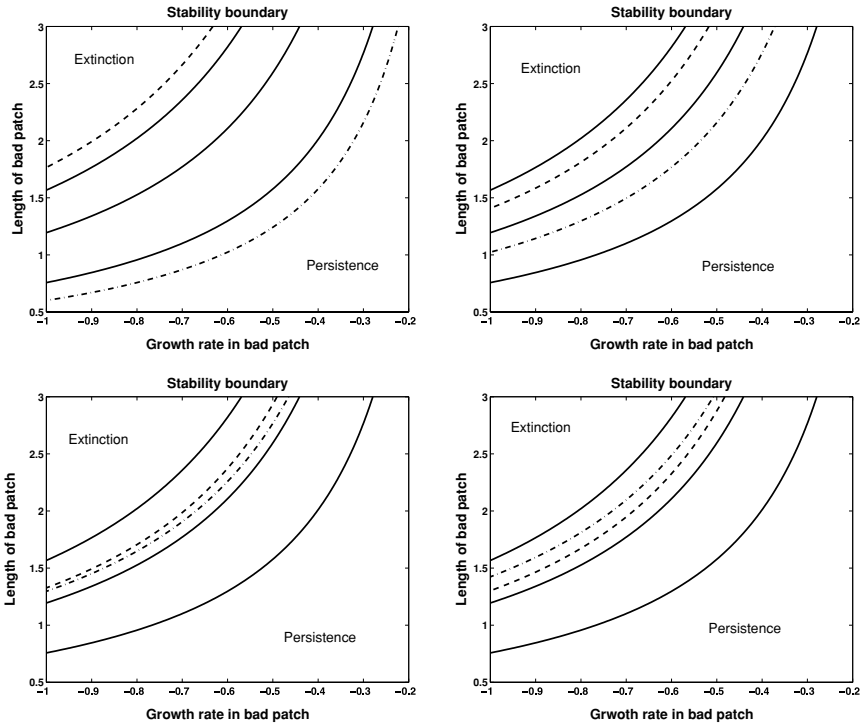
In the second scenario we assume that nutrients enter the river with a constant rate per unit length, for example through lateral run-off. In this case, increasing the cross-sectional area in a bad patch leads to lower nutrient concentration, which implies a higher loss rate. Hence, the two effects combine; increasing loss rate with increasing cross-sectional area of bad patches should reduce the persistence region even further. We explored this scenario by assuming a simple linear relationship between loss rate ( $f_2$ ) and cross-sectional area ( $a_2$ ), at least for values of  $a_2$  close to unity. We set

$$f_2 = (1 - \varepsilon(a_2 - 1)) f_2^*, \quad (37)$$

where  $f_2^*$  is the loss rate for  $a_2 = 1$ , i.e., when the river is of constant cross-sectional area. (We choose parameters in such a way that the factor in front of  $f_2^*$  remains positive.) The result is given in Fig. 7, top left panel, which should be compared to Fig. 1. As expected, the persistence region decreases (compared to the case where  $f_2$  is independent of  $a_2$ ) when  $a_2$  increases above  $a_2 = 1$  and increases when  $a_2$  decreases below unity.

In the next two scenarios, we consider the effect of light levels rather than nutrients. Again, if the river is of constant depth with only the width changing, then the light levels are independent of cross-sectional area so that the modeling assumptions are met. If the depth of the river varies but the width remains constant then light levels decrease with increasing cross-sectional area. If we assume that light is the limiting factor, then bad patches become worse as their depth increases. Hence, the situation is the same as mentioned earlier in the second scenario. Increasing the cross-sectional area in bad patches will decrease the persistence region.

If, however, bad patches are characterized by too high light levels, for example through the effect of photobleaching, then the situation changes. Increasing the depth now decreases the loss rate in the bad patches, which should increase the persistence region. So, increasing the depth generally reduces persistence but in this case might also increase persistence. To explore if and how the two effects balance, we assumed the simple linear relationship as mentioned earlier (37), but this time with  $\varepsilon < 0$ . The results depend on the actual value of  $\varepsilon$  as depicted in Fig. 7. For  $\varepsilon = -0.5$  increasing the cross-sectional area still decreases the persistence region but not as much as with constant  $f_2$ . For  $\varepsilon = -0.8$  the situation is different. The positive effect of reduced light at  $a_2 = 1.5$  compensates for the general negative effect of increased cross-section, and the population is more likely to persist



**Fig. 7** The stability boundary of the pelagic model (10) with  $f_2$  as in (37) for different values of  $a_2$  and  $\epsilon$ . In all four plots, the *solid curves* show the case  $\epsilon = 0$ , where  $f_2 = -0.5$  is independent of  $a_2$  for  $a_2 = 0.8$  (*upper*),  $a_2 = 1$  (*middle*), and  $a_2 = 1.5$  (*lower*). With dependence on  $\epsilon$ , the *dashed lines* represents the case  $a_2 = 0.8$  and the *dash-dot lines* have  $a_2 = 1.5$ . In the *top left panel*, we have  $\epsilon = 0.5$ , the *top right* corresponds to  $\epsilon = -0.5$ , and the *lower panels* are  $\epsilon = -0.8, -0.9$ , respectively.

than for  $a_2 = 1$ . For  $\epsilon = -0.9$  the effect is even stronger, so that the persistence region is even larger than for  $a_2 = 0.8$ .

**7. Discussion**

We studied the effects of flow and heterogeneity on the persistence and invasion of a single population, with or without benthic stage, in a river. We used a hydrodynamic equation to relate the cross-sectional area of a river to the speed of the flow, and hence we implicitly captured the three-dimensional nature of a river in our explicitly one-dimensional model. We incorporated heterogeneity as periodically alternating patches. In our analysis, we generalized previous results from Shigesada et al. (1986) by adding advective flow, and results from Pachepsky et al. (2005) by adding spatial heterogeneity. We derived implicit formulae for the stability boundary for persistence and for the dispersion relation for traveling periodic waves. In addition to previous work, we also considered persistence on bounded

heterogeneous domains. We recovered the threshold character of the *critical advection speed* (Pachepsky et al., 2005) as follows. If the advection speed in good patches is larger than the critical speed, then the population cannot persist nor invade upstream, if it is smaller, then there are parameter values such that the population can persist and invade upstream. We concentrated on the effects of discharge and cross-sectional area. Even in its non-dimensional form, the model still contains too many parameters to explore all the relationships explicitly here, but we gave the general formulae that can be used to explore the specific relationships of interest in applications.

Our mathematical analysis rests on linearization at the trivial solution and stability analysis. It was recently shown by Berestycki et al. (2005) that the linearization at zero does indeed predict the long-term dynamic behavior of the system without benthic stage and without advection. The result that the linearization at zero predicts the correct wavespeed, again without a benthic stage, is due to Weinberger (2002). Generalizing the results to systems with non-mobile stages is future work.

Introducing a benthic stage in the model is biologically reasonable for algae and benthic invertebrates. The effect of the extra compartment is not simply a linear reduction of the advection speed experienced by individuals (Speirs and Gurney, 2001), but introduces the qualitatively different behavior of unconditional persistence and upstream invasion if the local growth rate exceeds the exchange rate, see also Lewis and Schmitz (1996), and Pachepsky et al. (2005).

Intensive research efforts focus on understanding and predicting the dynamics of periphyton and benthic invertebrates in river systems. We discuss the applicability of the results that emerge from this work regarding spatial heterogeneity by considering three cases. The original model assumed that all parameters are independent, whereas in reality some may be related, e.g., the growth rate may depend on cross-sectional area via light availability. We found that the qualitative results obtained for independent parameters are robust for a simple relationship between loss rate and cross-sectional area. This suggests that the general qualitative results hold across a broad range of ecological scenarios, and that they could be found in future experimental work. The results in Section 5 directly apply to channelization and restoration of rivers. Our results indicate a generally negative effect of channelization on (single) species persistence, i.e., the persistence region decreases with increasing homogenization. These findings are supported by recent experimental work on river restoration through increasing spatial heterogeneity, see Giller (2005) and references therein.

Finally, the results in Lemmas 3.1 and 4.1 indicate that a population that can persist in a river can also spread upstream. Biologically, this finding clearly makes sense in a homogeneous environment, but requires extra consideration in the heterogeneous environment considered here. Upstream range limits may be caused by (gradually) changing environmental conditions (Lutscher et al., submitted for publication), which are not captured in the periodic heterogeneity assumed here. However, situations are conceivable where a species can persist in some “good” patches but not spread upstream through a bad patch, e.g., Zebra mussels in chains of lakes in eastern North America. Hence, these species must somehow be dispersal limited, and strong advection could be one limiting factor. The mathematical formulation as a reaction–advection–diffusion equation does not show this effect.

The diffusion operator with its strong positivity properties combined with a growth term that does not have an Allee effect causes the population to spread if it can persist. The result is related to the infinite propagation speed of the diffusion equation, a property that was already criticized by Einstein (1906). We conjecture that corresponding hyperbolic models with finite propagation speed (Haderler, 1999) would be able to capture the phenomenon that a population can persist in some patches but not spread upstream, but we are not aware of such models incorporating advection. Similarly, we would conjecture that a porous-media equation with an additional advective term might be able to capture that phenomenon. Alternatively, we would suggest that certain individual-based stochastic model analogues to our deterministic model may allow for local persistence and downstream, but no upstream, spread. Altogether, we see certain limitations in using the diffusion operator to model spatial spread, certainly when strong spatial heterogeneity is present.

The results obtained earlier extend to other systems where individuals are subject to unidirectional flow coast lines with ocean currents, vertical advection of phytoplankton (Huisman et al., 2002), bacteria in the gut (Ballyk and Smith, 1999), vegetation in sloped terrain (Sherratt, 2005), and effects of climate change (Potapov and Lewis, 2004). In particular, the results can be applied to reserve design along coasts with longshore currents (Botsford et al., 2001).

River ecosystems are, of course, much more complex than the model analyzed here. This model is one more step towards a mechanistic modeling framework for these environments. A strategic model for competition and resource gradients in rivers is presented in Lutscher et al. (submitted for publication). The next steps are to include more ecological interactions, for example model the fate of nutrients explicitly or include a predator into the equations.

## Appendix

### A.1. Derivation of the movement equation

In Section 2, we used heuristics to derive the one-dimensional movement equation (1). Here we present a more detailed derivation from a two-dimensional diffusion equation with coordinates  $X$  (longitudinal) and  $Y$  (transversal). We may assume that the domain is bounded in the  $Y$ -direction by the  $X$ -axis,  $Y = 0$ , and by some positive function  $Y = A(X)$ , the cross-section at  $X$ .

The two-dimensional diffusion equation using Fick's law with drift in the  $X$ -direction is given by

$$B_T = (D_1(X, Y)B_X)_X + (D_2(X, Y)B_Y)_Y - (V(X)B)_X. \quad (\text{A.1})$$

Alternatively, this equation can be interpreted as the probability density of a single individual moving randomly with a bias in the  $X$ -direction (Aronson, 1983). The no-flux boundary conditions are  $B_Y = 0$  at  $Y = 0$  and

$$D_1 B_X n_1 + D_2 B_Y n_2 - V B n_1 = 0 \quad (\text{A.2})$$

at  $Y = A(X)$ , where  $n^T = (n_1, n_2) = (-A'(X), 1)$  is the outward pointing normal.

We integrate (A.1) in the  $Y$ -direction to get

$$\frac{\partial}{\partial T} \int_0^{A(X)} B \, dY = \int_0^{A(X)} (D_1(X, Y)B_X)_X + (D_2(X, Y)B_Y)_Y - (V(X)B)_X \, dY. \quad (\text{A.3})$$

The middle term on the right-hand side can be integrated using the boundary conditions:

$$\int_0^{A(X)} (D_2(X, Y)B_Y)_Y \, dY = [D_1 B_X A' - V B A']_{|Y=A(X)}. \quad (\text{A.4})$$

Now we introduce the assumption of cross-sectional homogeneity by setting  $B(T, X, Y) = \bar{B}(T, X)$  and  $D_j(X, Y) = \bar{D}_j(X)$ . Then (A.3) becomes

$$\begin{aligned} A(X)\bar{B}_T &= (\bar{D}_1 \bar{B}_X)_X A(X) + (\bar{D}_1 \bar{B}_X)A'(X) - (V\bar{B})A'(X) - (V\bar{B})_X A(X) \\ &= (\bar{D}_1 A\bar{B}_X)_X - (VA\bar{B})_X, \end{aligned}$$

which is the movement term in Section 2 with  $Q = AV = \text{constant}$ .

### A.2. Derivation of the boundary conditions

Two different kinds of boundary conditions have been used for the “downstream” boundary of the advection–diffusion model

$$U_t = DU_{XX} - VU_X, \quad X \in [0, b], \quad (\text{A.5})$$

namely, the “hostile” condition  $U(b) = 0$  (Speirs and Gurney, 2001; Pachepsky et al., 2005) and the “Danckwert’s condition”  $U_X(b) = 0$  (Ballyk et al., 1998; Lutscher et al., submitted for publication). We extend the individual random-walk model by Van Kirk and Lewis (1999) to gain insight as to how these two differ in their biological interpretation.

At time steps  $dt$  an individual moves left and right on a grid with step size  $dx$  with probabilities  $L = (D - (Vdx)/2)/2$  and  $R = (D + (Vdx)/2)/2$ , respectively. Expanding the resulting master equation in Taylor series and applying the parabolic scaling  $dt, dx \rightarrow \infty$  while  $(dx)^2/(2dt) = 1$  gives Eq. (A.5), see e.g., Turchin (1998). At the boundary  $X = b$ , the individual moves left, i.e., back into the domain, with probability  $L$  as mentioned earlier. Of the remaining probability  $1 - L$  it leaves the domain with rate  $\alpha dx$  and stays otherwise. Then the master equation at the boundary reads

$$\begin{aligned} U(t + dt, b) &= \frac{1}{2} \left( D + \frac{V}{2} dx \right) U(t, b - dx) \\ &\quad + \left[ 1 - \frac{1}{2} \left( D - \frac{V}{2} dx - \alpha dx \right) \right] U(t, b). \end{aligned} \quad (\text{A.6})$$



Expanding in Taylor series, multiplying by  $dx$  and taking the parabolic limit as described earlier leads to the condition

$$(V - \alpha)U - DU_X = 0. \tag{A.7}$$

When individuals do not leave the domain, then  $\alpha = 0$  and hence we obtain the no-flux boundary conditions used at  $X = 0$ . If individuals leave the domain at the same rate as the advection takes them, then  $\alpha = V$  and we obtain the Danckwert's conditions. If individuals leave the domain at a much faster rate, i.e.,  $\alpha \rightarrow \infty$ , then the "hostile" condition  $U = 0$  results.

### A.3. Derivation of the persistence condition

In this section, we prove Lemma 3.1 and derive in detail the persistence boundary for a single pelagic population as discussed in Section 5 on a bounded domain and in Section 3 on an infinite domain.

To derive the persistence condition for a single pelagic population on a bounded heterogeneous habitat, we study the equation

$$\frac{1}{a}[dau_x]_x - \frac{q}{a}u_x + fu = 0, \quad x \in [0, b], \tag{A.8}$$

with boundary conditions

$$dau_x - qu = 0 \quad \text{at } x = 0, \quad u(b) = 0. \tag{A.9}$$

The habitat  $[0, b]$  is divided into  $2n$  alternating good and bad patches of length  $l_1$  and  $l_2$ , respectively. The parameter values on the good and bad patches are given by (12).

We rewrite the problem as a set of equations, each with constant coefficients and connected through the boundary conditions. On the interval  $[ml, ml + l_1]$  we define  $w_m(x - ml) = u(x)$  for  $m = 0, \dots, n - 1$ . Then each  $w_m$  is defined on  $[0, l_1]$  and satisfies

$$w_m'' - qw_m' + w_m = 0. \tag{A.10}$$

Similarly, we define  $z_m(x - ml) = u(x)$  on  $[ml + l_1, (m + 1)l]$  for  $m = 0, \dots, n - 1$ . Again, each  $z_m$  is defined on  $[l_1, l]$  and satisfies

$$d_2z_m'' - \frac{q}{a_2}z_m' + f_2z_m = 0. \tag{A.11}$$

Since no confusion can arise, we will drop the subscripts on  $d, a, f$  for the rest of this calculation.

The boundary- and matching conditions for  $u$  translate in conditions for  $w_m, z_m$  as follows. At  $x = 0$  and  $x = b$  we have

$$w'_0(0) - qw_0(0) = 0, \quad z_{n-1}(b) = 0. \tag{A.12}$$

At  $x = ml + l_1$  we have the two conditions

$$w_m(l_1) = z_m(l_1), \quad w'_m(l_1) = adz'_m(l_1), \tag{A.13}$$

whereas at  $x = ml$  we get

$$z_m(l) = w_{m+1}(0), \quad adz'_m(l) = w'_{m+1}(0). \tag{A.14}$$

The following transformation turns out to simplify things substantially. We set  $W_m(x) \exp(qx/2) = w_m(x)$  and  $Z_m(x) \exp(qx/(2ad)) = z_m(x)$ . Then (A.10) and (A.11) translate into

$$W''_m + \left(1 - \frac{q^2}{4}\right) W_m = 0, \quad dZ''_m + \left(f - \frac{q^2}{4a^2d}\right) Z_m = 0. \tag{A.15}$$

By assumption, we have  $f < 0$  and hence,  $Z$  is a convex function. If  $q \geq 2$  then  $W$  is also convex. According to the boundary and matching conditions,  $W'_0(0) > 0$  and the signs of the slopes of adjacent  $W_m, Z_j$  are identical. Therefore, each  $W_m, Z_m$  must be an increasing function, and hence the boundary condition  $Z_{n-1}(l) = 0$  cannot be satisfied. From here on, we assume that  $q < 2$  so that  $\alpha^2 = 1 - q^2/4 > 0$ .

The matching conditions (A.12)–(A.14) translate into the following conditions for  $W_m, Z_m$ ,

$$W'_0(0) - \frac{q}{2} W_0(0) = 0, \quad Z_{n-1}(l) = 0 \tag{A.16}$$

$$W_m(l_1)e^{ql_1/2} = Z_m(l_1)e^{ql_1/(2ad)}, \quad W_m(0) = Z_{m-1}(l)e^{ql/(2ad)}, \tag{A.17}$$

$$W'_m(l_1)e^{ql_1/2} = adZ'_m(l_1)e^{ql_1/(2ad)}, \quad W'_m(0) = adZ'_{m-1}(l)e^{ql/(2ad)}, \tag{A.18}$$

where we have used the relations on  $W_m, Z_m$  to simplify the relations for  $W'_m, Z'_m$ . We now make the ansatz

$$W_m(x) = A_m \cos(\alpha x) + B_m \sin(\alpha x). \tag{A.19}$$

Since  $f < 0$ , we may set  $\delta = \sqrt{(q^2/(4a^2d) - f)/d}$  and write

$$Z_m(x) = D_m \cosh(\delta(l - x)) + G_m \sinh(\delta(l - x)). \tag{A.20}$$

The matching conditions mentioned earlier translate into conditions for the coefficients  $A_m, B_m, D_m, G_m$ . After a lot of algebra, these can be conveniently written in matrix form  $M\xi = 0$ , where

$$\xi^T = [A_0, B_0, D_0, G_0, A_1, B_1, D_1, G_1, \dots, A_{n-1}, B_{n-1}, G_{n-1}] \tag{A.21}$$

(note that (A.12) implies  $D_{n-1} = 0$ ) and

$$M = \begin{pmatrix} K_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ M_1 & M_3 & 0 & 0 & 0 & 0 & 0 \\ 0 & M_2 & M_4 & 0 & 0 & 0 & 0 \\ 0 & 0 & M_1 & M_3 & 0 & 0 & 0 \\ \vdots & & & \ddots & \ddots & & \vdots \\ 0 & 0 & 0 & 0 & M_2 & M_4 & 0 \\ 0 & 0 & 0 & 0 & 0 & M_1 & K_2 \end{pmatrix}. \tag{A.22}$$

The entries of  $M$  are matrices of the form

$$K_1 = (q/2, -\alpha), \quad K_2 = \begin{pmatrix} -S_2 E_2 \\ ad\delta C_2 E_2 \end{pmatrix},$$

$$M_1 = \begin{pmatrix} C_1 E_1 & S_1 E_1 \\ -\alpha S_1 E_1 & \alpha C_1 E_1 \end{pmatrix}, \quad M_3 = \begin{pmatrix} -C_2 E_2 & -S_2 E_2 \\ ad\delta S_2 E_2 & ad\delta C_2 E_2 \end{pmatrix},$$

$$M_2 = \begin{pmatrix} E_3 & 0 \\ 0 & ad\delta E_3 \end{pmatrix}, \quad M_4 = \begin{pmatrix} -1 & 0 \\ 0 & \alpha \end{pmatrix},$$

where

$$C_1 = \cos(\alpha l_1), \quad S_1 = \sin(\alpha l_1), \quad C_2 = \cosh(\delta l_2), \quad S_2 = \sinh(\delta l_2)$$

and

$$E_1 = e^{\frac{q}{2}l_1}, \quad E_2 = e^{\frac{q}{2\alpha}l_1}, \quad E_3 = e^{\frac{q}{2\alpha}l_1}.$$

In order for (A.8) and (A.9) to have a solution, we require that the coefficients  $\xi$  be nonzero, which in turn requires that  $\det M = 0$ . The matrix  $M$  has dimension  $(4n - 1) \times (4n - 1)$  so that computation can be time-intensive. However, we use the particular structure of  $M$  to find a simpler way to compute the persistence condition. Note that  $M_1, M_2$  are invertible. If there is a nonzero solution  $\xi$  we may assume  $G_{n-1} = 1$ . Then we can inductively derive the following condition for  $A_0, B_0$  :

$$\begin{pmatrix} A_0 \\ B_0 \end{pmatrix} = (M_1^{-1} M_3 M_2^{-1} M_4)^{n-1} M_1^{-1} K_2 =: \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}. \tag{A.23}$$

With the additional condition for  $A_0, B_0$  from the first row of  $M$ , we arrive at the following formula for the persistence boundary:

$$qv_1 - 2\alpha v_2 = 0. \tag{A.24}$$

The same ideas as mentioned earlier apply to the derivation of the persistence boundary on unbounded domains, in fact, things become easier in that case. Because of the matching conditions, the real line can now be thought of as one good and one bad patch with periodic boundary conditions. The argument that there is no solution for  $q \geq 2$  is even simpler than before because a non-constant periodic function cannot be convex everywhere. The same ansatz for  $W, Z$  leads to the condition that the determinant of the  $4 \times 4$  matrix

$$M_u = \begin{pmatrix} M_1 & M_3 \\ M_4 & M_2 \end{pmatrix} \tag{A.25}$$

be zero. Cofactor expansion of the determinant and rearranging of terms gives formula (20) for the persistence boundary.

If we return to the problem on a bounded domain but now increase the length of the domain by adding patches then we increase  $n$  in (A.23). Then the right-hand side in that equation converges to a multiple of the eigenvector corresponding to the larger eigenvalue. If we want the left-hand side to be neither zero nor infinity, then the matrix in brackets in (A.23) must have 1 as an eigenvalue, while the other eigenvalues must be less than one in absolute value. Indeed, if  $\zeta$  is an eigenvector of  $(M_1^{-1}M_3M_2^{-1}M_4)^{n-1}$  then  $\xi = (\zeta, -M_2^{-1}M_4\zeta)^T$  is a nonzero solution to  $M_u\xi = 0$ . Hence, in the limit  $b \rightarrow \infty$  the persistence condition on the bounded domain becomes the persistence condition on the unbounded domain.

*A.4. Derivation of the minimal wave speeds*

Putting the ansatz (27) into the linearization of (10) and rearranging terms yields the equation

$$d\phi \frac{\psi''}{\psi} + \frac{(da)' - q}{a} \phi \frac{\psi'}{\psi} + c\phi \frac{\psi'}{\psi} + 2d \frac{\psi'}{\psi} \phi' = -d\phi'' - \frac{(da)' - q}{a} \phi' - f\phi. \tag{A.26}$$

Since the right-hand side of that equation is independent of  $\psi$  we conclude that the fractions involving  $\psi$  must be constant, and hence  $\psi$  is an exponential  $\psi(z) = \exp(-sz)$ , where  $s$  is the shape parameter of the wave front. With this we obtain an equation for  $\phi$  alone, namely

$$d\phi'' + \left( \frac{(da)' - q}{a} - 2ds \right) \phi' + \left( f + ds^2 - \frac{(da)' - q}{a} s - cs \right) \phi = 0. \tag{A.27}$$

The matching conditions (7) and (8) translate into

$$\lim_{x \uparrow l_1} \phi(x) = \lim_{x \downarrow l_1} \phi(x), \tag{A.28a}$$

$$\lim_{x \downarrow 0} \phi(x) = \lim_{x \uparrow l} \phi(x), \tag{A.28b}$$

$$\lim_{x \uparrow l_1} (\phi'(x) - s\phi(x)) = \lim_{x \downarrow l_1} da(\phi'(x) - s\phi(x)), \tag{A.28c}$$

$$\lim_{x \downarrow 0} (\phi'(x) - s\phi(x)) = \lim_{x \uparrow l} da(\phi'(x) - s\phi(x)). \tag{A.28d}$$

The equation is linear in  $\phi$  and the coefficients are constant on the two intervals  $[0, l_1]$  and  $[l_1, l]$ . Therefore, we make an exponential ansatz on each of these two subintervals and use (A.28) to match the coefficients. We set

$$\begin{aligned} \phi(x) &= A_1 e^{\alpha_1 x} + A_2 e^{\alpha_2 x}, \quad x \in [0, l_1], \\ \phi(x) &= B_1 e^{\beta_1(l-x)} + B_2 e^{\beta_2(l-x)}, \quad x \in [l_1, l], \end{aligned} \tag{A.29}$$

where

$$\alpha_{1,2} = \frac{q}{2} + s \pm \sigma_1, \quad \beta_{1,2} = -\frac{q}{2ad} - s \pm \sigma_2, \tag{A.30}$$

with  $\sigma_{1,2}$  defined as in (29).

The argument from the previous section that not both arguments  $\alpha_{1,2}, \beta_{1,2}$  can be real at the same time because of periodic matching, carries over to the case at hand. For downstream traveling waves, we have  $c, s > 0$  and for upstream waves, we have  $c, s < 0$ . In both cases, the product satisfies  $cs > 0$ . Therefore,  $\sigma_2$  is always real, and so  $\sigma_1$  must have nonzero imaginary part. This gives the necessary condition  $q < 2$ . The matching conditions (A.28) yield the following linear relationship between the coefficients

$$\begin{pmatrix} 1 & 1 & -1 & -1 \\ e^{\alpha_1 l_1} & e^{\alpha_2 l_1} & -e^{\beta_1 l_2} & -e^{\beta_2 l_2} \\ \frac{q}{2} + \sigma_1 & \frac{q}{2} - \sigma_1 & -(\frac{q}{2} - ad\sigma_2) & -(\frac{q}{2} + ad\sigma_2) \\ (\frac{q}{2} + \sigma_1)e^{\alpha_1 l_1} & (\frac{q}{2} - \sigma_1)e^{\alpha_2 l_1} & -(\frac{q}{2} - ad\sigma_2)e^{\beta_1 l_2} & -(\frac{q}{2} + ad\sigma_2)e^{\beta_2 l_2} \end{pmatrix} \begin{pmatrix} A_1 \\ A_2 \\ B_1 \\ B_2 \end{pmatrix} = 0. \tag{A.31}$$

In order for a nonzero solution to exist, the determinant of the matrix has to vanish. This determinant can be computed explicitly by cofactor expansion. Using some trigonometric identities, one finally arrives at formula (28).

To derive the minimal wavespeed for the benthic–pelagic system (11), we combine the ideas mentioned earlier with a substitution similar to (24). The ansatz  $u(t, x) = \psi_1(z)\phi_1(x)$  and  $n(t, x) = \psi_2(z)\phi_2(x)$  with  $z = x - ct$  first gives the condition  $\psi_j(z) = A_j \exp(-sz)$ . With this information, the benthic equation reads

$$cs\phi_2 - k_n\phi_1 = (f - k_n)\phi_2. \tag{A.32}$$

If  $f(x) > k_n(x)$  on good patches, then this equation does not have a meaningful solution, i.e.,  $\phi_j \geq 0$  for  $c = 0$ . Hence, if there exist upstream traveling periodic waves, then they can never get stalled. Assuming  $cs \neq f - k_n$  we solve for  $\phi_2$  and obtain the following equation for  $\phi_1$ , which is analogous to (A.27):

$$d\phi'' + \left( \frac{(da)' - q}{a} - 2ds \right) \phi' + \left( g + ds^2 - \frac{(da)' - q}{a} s - cs \right) \phi = 0, \quad (\text{A.33})$$

with  $g(x)$  being defined as (compare (24))

$$g = \frac{k_u k_n}{cs + k_n - f} - k_u = \frac{k_u(f - cs)}{k_n - (f - cs)}. \quad (\text{A.34})$$

From here we proceed as mentioned earlier. The condition that one of the exponents in (A.30) have nonzero imaginary part translates into the condition on the good patches that again  $\sigma_1$  be purely imaginary. The critical value for  $q$ , is given by

$$cs - g_1 + q^2/4 = 0, \quad \text{or} \quad q = 2\sqrt{g_1 - cs}. \quad (\text{A.35})$$

The expression under the root is a decreasing function in  $cs$  so that the maximal value is obtained at  $cs = 0$  and given by

$$q = 2\sqrt{\frac{k_u}{k_n - 1}} \quad (\text{A.36})$$

which, in non-dimensional parameters, is the same as (26).

## Acknowledgements

FL gratefully acknowledges partial support as a PIMS postdoctoral fellow during the Period of Concentration in Mathematical Ecology and Evolution. MAL was supported by Collaborative Research Opportunity and Discovery grants from NSERC, and by a Canada Research Chair. EM acknowledges support from NSERC and the Canada Research Chair Program. This research was also supported by grants from the Canadian Water Network and the Alberta Ingenuity Centre for Water Research to EM.

## References

- Allan, J., 1995. *Stream Ecology: Structure and Function of Running Waters*. Chapman & Hall, London.
- Aronson, D., 1983. The role of diffusion in mathematical population biology: Skellam revisited. In: Levin, S. (Ed.), *Mathematics in Biology and Medicine, Lecture Notes on Biomathematics*, vol. 57. Springer-Verlag, Berlin, pp. 2–6.
- Aronson, D., Weinberger, H.F., 1975. Nonlinear diffusion in population genetics, combustion, and nerve pulse propagation. In: Goldstein, J. (Ed.), *Partial Differential Equations and Related Topics, Lecture Notes in Mathematics*, vol. 446. Springer-Verlag, Berlin, pp. 5–49.
- Baker, R., Dunn, P., 1990. *New Directions in Biological Control*. Alan Liss, New York.
- Ballyk, M., Smith, H., 1999. A model of microbial growth in a plug flow reactor with wall attachment. *Math. Biosci.* 158, 95–126.

- Ballyk, M., Dung, L., Jones, D.A., Smith, H., 1998. Effects of random motility on microbial growth and competition in a flow reactor. *SIAM J. Appl. Math.* 59(2), 573–596.
- Bencala, K., Walters, R., 1983. Simulation of solute transport in a mountain pool-and-riffle stream: A transient storage model. *Water Resources Res.* 19(3), 718–724.
- Berestycki, H., Hamel, F., Roques, L., 2005. Analysis of the periodically fragmented environment model: Species persistence. *J. Math. Biol.* 51, 75–113.
- Botsford, L.W., Hastings, A., Gaines, S.D., 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* 4, 144–150.
- Cantrell, R., Cosner, C., 1991. Diffusive logistic equations with indefinite weights: Population models in disrupted environments. II. *SIAM J. Math. Anal.* 22, 1043–1064.
- Cantrell, R.S., Cosner, C., 1993. Should a park be an island? *SIAM Appl. Math.* 53, 219–252.
- Cantrell, R.S., Cosner, C., 2001. Spatial heterogeneity and critical patch size: Area effects via diffusion in closed environments. *J. Theor. Biol.* 209, 161–171.
- Cantrell, R.S., Cosner, C., 2003. *Spatial Ecology via Reaction–Diffusion Equations. Mathematical and Computational Biology.* Wiley, New York.
- Cruywagen, G., Kareiva, P., Lewis, M., Murray, J., 1996. Competition in a spatially heterogeneous environment: Modelling the risk of spread of a genetically engineered population. *Theor. Popul. Biol.* 49(1), 1–38.
- DeAngelis, D., Loreau, M., Neergaard, D., Mulholland, P., Marzolf, E., 1995. Modelling nutrient-periphyton dynamics in streams: The importance of transient storage zones. *Ecol. Model.* 80, 149–160.
- Dent, C., Henry, J., 1999. Modelling nutrient-periphyton dynamics in streams with surface–subsurface exchange. *Ecol. Model.* 122, 97–116.
- Eagleson, P., 1970. *Dynamic Hydrology.* McGraw-Hill, New York.
- Einstein, A., 1906. Zur Theorie der Brownschen Bewegung. *Ann. Phys.* 19, 371–381.
- Fisher, R., 1937. The advance of advantageous genes. *Ann. Eugenics* 7, 355–369.
- Gaylord, B., Gaines, S., 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* 155, 769–789.
- Giller, P., 2005. River restoration: seeking ecological standards. *J. Appl. Ecol.* 42, 201–207.
- Hadeler, K., 1999. Reaction transport systems in biological modelling. In: Capasso, V., Diekmann, O. (Eds.), *Mathematics Inspired by Biology, Lecture Notes Mathematics*, vol. 1714. Springer-Verlag, Heidelberg, pp. 95–150.
- Hadeler, K., Lewis, M., 2002. Spatial dynamics of the diffusive logistic equation with sedentary component. *Can. Appl. Math. Quart.* 10, 473–500.
- Hastings, A., Cuddington, K., Davies, K., Dugaw, C., Elmendorf, A., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B., Moore, K., Taylor, C., Thomson, D., 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecol. Lett.* 8, 91–101.
- Hill, B., Herlihy, A., Kaufmann, P., Stevenson, R., McCormick, F., 2000. Use of periphyton assemblage data as an index of biotic integrity. *J. North Am. Benthol. Soc.* 19(1), 50–67.
- Huisman, J., Arrayás, M., Ebert, U., Sommeijer, B., 2002. How do sinking phytoplankton species manage to persist. *Am. Nat.* 159, 245–254.
- Kierstead, H., Slobodkin, L.B., 1953. The size of water masses containing plankton blooms. *J. Marine Res.* 12, 141–147.
- Kolmogorov, A., Petrovskii, I., Piskunov, N., 1937. A study of the equation of diffusion with increase in the quantity of matter, and its application to a biological problem. *Bjol. Moskovskovo Gos. Univ.* 17, 1–72.
- Kot, M., Schaffer, W.M., 1986. Discrete-time growth-dispersal models. *Math. Biosci.* 80, 109–136.
- Lewis, M., Schmitz, G., 1996. Biological invasion of an organism with separate mobile and stationary states: Modeling and analysis. *Forma* 11, 1–25.
- Lewis, M., Schmitz, G., Kareiva, P., Trevors, J., 1996. Models to examine containment and spread of genetically engineered microbes. *Mol. Ecol.* 5, 165–175.
- Logan, J., 2001. *Transport Modeling in Hydrogeochemical Systems. Interdisciplinary Applied Mathematics.* Springer, New York.
- Lutscher, F., Pachepsky, E., Lewis, M., 2005. The effect of dispersal patterns on stream populations. *SIAM Appl. Math.* 65(4), 1305–1327.
- Lutscher, F., McCauley, E., Lewis, M. Spatial patterns and coexistence mechanisms in rivers. *Theor. Pop. Biol.*, submitted for publication.
- Magnus, W., Winkler, S., 1979. *Hill’s Equation.* Dover, New York.

- Medlock, J., Kot, M., 2003. Spreading diseases: Integro-differential equations new and old. *Math. Biosci.* 184, 201–222.
- Mulholland, P., DeAngelis, D., 2000. Surface–subsurface exchange and nutrient spiraling. In: Jones, J., Jr., Mulholland, P. (Eds.), *Streams and Ground Waters*. Academic Press, New York, pp. 149–166.
- Müller, K., 1954. Investigations on the organic drift in north Swedish streams. Technical Report 34, Institute of Freshwater Research, Drottningholm.
- Müller, K., 1982. The colonization cycle of freshwater insects. *Oecologia* 53, 202–207.
- Murray, J., Sperb, R., 1983. Minimum domains for spatial patterns in a class of reaction diffusion equations. *J. Math. Biol.* 18, 169–184.
- Othmer, H., 1983. A continuum model for coupled cells. *J. Math. Biol.* 17, 351–369.
- Pachepsky, E., Lutscher, F., Nisbet, R., Lewis, M.A., 2005. Persistence, spread and the drift paradox. *Theor. Popul. Biol.* 67, 61–73.
- Potapov, A., Lewis, M., 2004. Climate and competition: The effect of moving range boundaries on habitat invasibility. *Bull. Math. Biol.* 66(5), 975–1008.
- Robbins, T.C., Lewis, M.A. Modeling population spread in heterogeneous environments using integrodifference equations. *SIAM J. Appl. Math.*, submitted for publication.
- Sherratt, J., 2005. An analysis of vegetation stripe formation in semi-arid landscapes. *J. Math. Biol.* 51, 183–197.
- Shigesada, N., Kawasaki, K., Teramoto, E., 1986. Traveling periodic waves in heterogeneous environments. *Theor. Popul. Biol.* 30, 143–160.
- Skellam, J.G., 1951. Random dispersal in theoretical populations. *Biometrika* 38, 196–218.
- Speirs, D., Gurney, W., 2001. Population persistence in rivers and estuaries. *Ecology* 82(5), 1219–1237.
- Turchin, P., 1998. *Quantitative Analysis of Movement*. Sinauer Assoc., Sunderland, MS.
- Van Kirk, R.W., Lewis, M.A., 1997. Integrodifference models for persistence in fragmented habitats. *Bull. Math. Biol.* 59(1), 107–137.
- Van Kirk, R.W., Lewis, M.A., 1999. Edge permeability and population persistence in isolated habitat patches. *Nat. Resource Model.* 12, 37–64.
- Weinberger, H.F., 1982. Long-time behavior of a class of biological models. *SIAM J. Math. Anal.* 13, 353–396.
- Weinberger, H.F., 2002. On spreading speeds and traveling waves for growth and migration models in a periodic habitat. *J. Math. Biol.* 45, 511–548.
- Xin, J., 2000. Front propagation in heterogeneous media. *SIAM Rev.* 42(2), 161–230.