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Seasonal Invasion Dynamics in a Spatially Heterogeneous River with Fluctuating Flows

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Abstract A key problem in environmental flow assessment is the explicit linking of the flow regime with ecological dynamics. We present a hybrid modeling approach to couple hydrodynamic and biological processes, focusing on the combined impact of spatial heterogeneity and temporal variability on population dynamics. Studying

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periodically alternating pool-riffle rivers that are subjected to seasonally varying flows, we obtain an *invasion ratchet* mechanism. We analyze the ratchet process for a caricature model and a hybrid physical–biological model. The water depth and current are derived from a hydrodynamic equation for variable stream bed water flows and these quantities feed into a reaction-diffusion-advection model that governs population dynamics of a river species. We establish the existence of spreading speeds and the invasion ratchet phenomenon, using a mixture of mathematical approximations and numerical computations. Finally, we illustrate the invasion ratchet phenomenon in a spatially two-dimensional hydraulic simulation model of a meandering river structure. Our hybrid modeling approach strengthens the ecological component of stream hydraulics and allows us to gain a mechanistic understanding as to how flow patterns affect population survival.

1 Introduction

Streams and rivers are flow-dominated systems, and it is now widely recognized that variations in the water flow are critically important for the ecosystem integrity of riverine environments (Bunn and Arthington 2002; Poff et al. 1997). Flow regimes can change markedly in time and space, e.g. from daily over seasonal to interannual time scales and from microhabitats over channel units to entire drainage basins (Cooper et al. 1998; Fausch et al. 2002). The impacts of temporal and spatial flow variations are relatively well studied in isolation, but their combined interplay is rarely investigated, and in ecological theory generally little is known on how these two sources of variability can interact. Here, we show that a new phenomenon can arise. By developing a hybrid model that connects spatially heterogeneous river morphology and temporally varying water flow with population dynamics, we also provide a tighter coupling of ecological and hydrological components in environmental flow assessment (EFA).

1.1 Environmental Flow Requirements: The Need for Population Dynamics

There is an increasing concern on how flow regime alterations [due to economic developement, human population growth, climate change, and other factors (Dudgeon et al. 2006; Nilsson et al. 2005; Palmer et al. 2006; Poff et al. 2003; Richter et al. 2003; Vörösmarty et al. 2010)] affect river ecosystems. Moreover, international legislation such as the European Water Framework Directive implement a holistic view of water bodies, emphasizing biological as well as hydromorphological factors in addition to the more traditional physical–chemical aspects. Environmental managers routinely use EFA in water resource planning, with the aim to quantify the flow requirements in space and time that are necessary to sustain desired ecosystem services (Clifford et al. 2006; Pahl-Wostl et al. 2013; Poff et al. 1997; Poff and Zimmerman 2010). This is sometimes also referred to as instream flow need (IFN) assessment Anderson et al. (2006), environmental flow methodologies (EFMs) (Tharme 2003), and instream flow incremental methodology (IFIM) (Stalnaker et al. 1995).

Hence, there are rapidly expanding research activities on how river morphology and water flow affect the ecological status of rivers (Clifford et al. 2006; Poff and Zimmerman 2010). The increasing interest is reflected in recently coined terms such as "ecohydraulics" (Lancaster and Downes 2010), "ecohydrology" (Janauer 2000), "habitat hydraulics" (Stalnaker et al. 1996), and "hydraulic stream ecology" (Statzner et al. 1988). This field of research combines hydraulic aspects such as water depth, velocity, and substrate levels with the aim to identify, record, and design biological habitats, sometimes also called physical biotopes. For instance, the UK Environment Agency uses the River Habitat Survey to catalog and assess the quality of river ecosystems in England and Wales.

However, while the hydraulic side of these approaches are well developed, there is a gap on the ecological side, which has been identified as an "important impediment to progress" (Anderson et al. 2006, p. 311). In essence, existing methodologies rely on habitat suitability models and physical habitat availability as a proxy for population status. Although their limitations are long recognized (Gallien et al. 2010; Ibanez et al. 2013; Lancaster and Downes 2010), they are currently still the "cornerstone" (Shenton et al., 2012, p. 4) in linking flow regimes with ecology. To quote (Lancaster and Downes, 2010, p. 2010), "a lot of work that claims to address problems at the ecology–hydraulics interface lacks a strong ecological context (or, sometimes, even any ecological context) and is often disconnected from ecological theory". As a consequence, good quantitative evidence for impacts of flow alterations on populations is still rare; see the recent review in (Poff and Zimmerman 2010). There remains a lack of framework to integrate ecological dynamics, rather than static habitat descriptions, into water flow assessments (Anderson et al. 2006).

Here, we present a hybrid modeling approach that directly links river hydrology with stream population models. Such a coupling is needed if realistic variations are to be included in river flow models for populations. Ultimately this hybrid physical–biological modeling approach provides a way to analyze the effect of realistic river fluctuations on population processes.

1.2 Spatial and Temporal Variability in Flow Regimes

Spatial heterogeneity in rivers and streams is a result of natural bed structures and water flow as well as anthropogenic modifications of these structures and flows. In natural rivers or streams, the channel shape, channel gradient, bed gravel, flow discharge, and nutrient availability vary from location to location, which in turn greatly affects the growth and spread of a population in the channels. Most mathematical models for stream/river populations assume the habitats to be spatially homogeneous due to the difficulty of modeling and analyzing spatial heterogeneity; see e.g., (Jin and Lewis 2012, 2011; Lutscher et al. 2010). In the few works where spatially heterogeneous habitats are considered in aquatic population models; see e.g., (Lutscher et al. 2006), the stream or river has a simplified structure and is assumed to consist of periodically alternating spatially homogeneous good and bad patches. This simple assumption not only opens the door to study the influences of spatial heterogeneity on the spread of aquatic species but also leaves possibilities for investigations in more realistic streams or rivers.

The pool-riffle sequence is an important feature of river channels that has significant hydrologic and ecological functions; see e.g., (Allan and Castillo 2007; Gregory et al. 1994). Pool-riffle channels consist of alternations between shallow areas of higher velocity and mixed gravel-cobble substrate, called riffles, and deeper areas of slower velocity and finer substrate, called pools. Typically they are found in moderate to low gradient, unconfined, gravel-bed streams (Allan and Castillo 2007). In this work, we will consider a stream or river with a constant bottom slope or with periodically alternating pool-riffle channels.

Temporal heterogeneity is found in temperature, light, flow discharge and velocity, and likely in population life-history parameters and in dispersal rates; see e.g., (Allan and Castillo 2007). These features influence the species' growth and spread in upstream and downstream directions. For instance, early summer water discharge in many rivers/streams is high and flow is fast, which makes it difficult for the population to move to upstream and may decrease the likelihood of persistence of the population. By way of contrast, late summer and possibly fall and winter discharge can be low, with slow flow, which helps provide a stable environment for the population to grow and to move. On the other hand, populations may grow and move more actively in summer than in winter due to warm temperature and abundant food supply. Thus, although it is difficult to generalize as to summer or winter is better for a species to grow or spread, it is clear that the living environment for aquatic species in streams or rivers varies very much in different seasons, and hence the temporal heterogeneity should be taken into account when investigating the growth and invasion of a species in streams or rivers.

Previous work has studied the effects of seasonal variations in population growth and hydrological characteristics on the spreading speeds of population in an infinitely long river (Jin and Lewis 2012) and critical domain size for a finite river or river patch (Jin and Lewis 2011); see also (Lutscher and Seo 2011; Seo and Lutscher 2011). In this work, we will include the temporal variations of flow discharge and hence the flow velocity, water depth, and flow driven diffusion of the population.

While spatial heterogeneity and temporal heterogeneity have been studied separately, we are not aware of any work where their interplay has been investigated. In fact, through their interaction, a new phenomenon can arise. We term this an *invasion ratchet*, where a species can persist in a pool (favorable habitat patch) during adverse times and can traverse riffles (hostile patches) in the upstream direction during more beneficial time periods. In a long term, this type of phenomenon could ensure a population's spread to the upstream and thus invasion and persistence in the whole river. Although the phenomenon of an ecological ratchet has been invoked in the context of climate change impacts on ecosystems (Jackson et al. 2009), the idea of a spatial ratchet phenomenon in rivers is new. In this work, we will study the ratchet phenomenon and analyze the conditions for the phenomenon to occur.

1.3 Spreading Speeds: Indicators of Population Persistence or Wash-Out

The spreading speed (or asymptotic speed of spread) of a population is a crucial quantity that describes the speed of invasion of the population in a spatial habitat; see

Table 1 Overview of reaction-diffusion-advection models related to this work

	Temporally constant	high/low fluctuations
Spatially uniform	Speirs and Gurney and earlier works (Aronson and Weinberger 1975; Fisher 1937; Speirs and Gurney 2001) (EF)	Lutscher and Seo (2011) (EF)
Alternating patches (with piecewise constant water depths)	Lutscher et al. Lutscher et al. (2006) (EF)	In this manuscript (EAS)
Constant bottom slope	In this manuscript (EF)	In this manuscript (EF)
Varying bottom slope	In this manuscript (ES)	In this manuscript (ES)
Two-dimensional hydraulic river models	In this manuscript (S)	In this manuscript (S)

E: proof of existence of a spreading speed; F: explicit formula for a spreading speed;
A: approximation of a spreading speed; S: simulation of a spreading speed

e.g., (Aronson and Weinberger 1975; Jin and Lewis 2012; Liang et al. 2006; Liang and Zhao 2007; Lutscher et al. 2006, 2010; Weinberger 2002). For aquatic species, the calculation of positive spreading speed in the upstream direction has been used to estimate whether it can persist in the habitat or will be washed out; see e.g., (Jin and Lewis 2012; Lutscher et al. 2006, 2010). The solution to the drift paradox problems in terms of spreading speeds says that a population can spread to the upstream if its upstream spreading speed is positive in the upstream direction, and thus can persist if the flow velocity is below some critical flow rate; see e.g., (Lutscher et al. 2005, 2006; Pachepsky et al. 2005).

A conjecture that has been made in (Lutscher et al. 2010) says that "a population can persist at any location in a homogeneous habitat if and only if it can invade upstream". It essentially indicates the mathematical equivalence of the conditions for upstream invasion and for persistence in spatially homogeneous habitats. This conjecture has been verified for many models, including those with temporally varying flows coupled to spatially homogeneous habitats (Jin and Lewis 2012, 2011; Lutscher and Seo 2011). It also holds for some models that relax the assumption of habitat homogeneity but assume constant flow. For example, Lutscher et al. (2006) found that temporally constant flows coupled to spatially heterogeneous habitats yielded identical conditions for upstream invasion and persistence.

The situation we focus on in this paper involves temporally varying flows coupled to spatially heterogeneous habitats. We show that the conjecture regarding the equivalence of the conditions for upstream invasion and for persistence cannot actually be extended to cover this situation. We give numerical evidence that the population will persist in the river, even when it is unable to spread upstream. Here the upstream ratchet mechanism appears to stall well before the population is washed out, and the population persists even though it cannot invade.

Reaction-diffusion-advection models have been used to model population dynamics in streams or rivers. For convenience, we summarize some results about population spread and persistence in Table 1; the results are mainly about spreading speeds and focus on spatial and temporal variability (rows and columns, respectively). In this

work, we fill the gap of combined spatial and temporal heterogeneity. Moreover, we consider more realistic spatial river structures based on channel bed slopes and 2D simulation models.

1.4 Paper Outline

In this paper, we demonstrate the ratchet phenomenon in a suite of increasingly complex models. In Sect. 2, we present stream population models in temporally and spatially homogeneous and heterogeneous habitats as well as the results of spreading speeds for the models. In Sect. 3, we employ a reaction-diffusion-advection model for the density of an aquatic species in a river consisting of alternating good-bad patches (Lutscher et al. 2006). We add temporal fluctuations in the discharge. The simplicity of this model allows us to obtain insightful conditions for an invasion ratchet. In the following Sections, we extend the model by including water depth derived from the hydrologic equation for a periodic pool-riffle river and a river with uniform flow in temporally constant and temporally varying flows.

To this end, Sect. 4 revisits an ordinary differential equation for the water depth of a gradually varied flow in (Chaudhry 1993). In Sect. 5, we substitute the water depth derived from the hydrologic equation into a population model. Considering only temporal variations in flow, we obtain spreading speeds in the upstream and downstream direction in temporally constant and temporally fluctuating flows. In Sect. 6, we additionally introduce spatial heterogeneity. We consider a spatially periodic pool-riffle river, derive the water depth, and substitute it into a population model. This allows us to study the effects of different biological and environmental factors on the spreading of the population. In particular, we show how periodic high/low flow fluctuations lead to the ratchet phenomenon in spatially alternating rivers.

In Sect. 7, we present a spatially two-dimensional hydraulic simulation model (River2D) coupled with a benthic-drift population model. Again, we demonstrate the invasion ratchet phenomenon, this time in a river with "real" hydrology. Finally, Sect. 8 discusses the methodological advances of our modeling approaches and puts them into the context of ecohydrology and environmental flow assessment. Moreover, we relate the invasion ratchet to the existing ecological theories, assess its robustness, and explore empirical evidence.

2 Population Models in Rivers/Streams and Spreading Speeds

In this section, we introduce partial differential equations that have been or can be used to describe population dynamics of stream species in homogeneous or heterogeneous environments. Here, spatial heterogeneity is represented by an idealized hydrodynamic equation that links river's cross-sectional area to flow speed, and temporal variability is taken into account by temporally varying discharges. We begin with a model that is homogeneous in time and space, and then add step-wise spatial and temporal variability. We will use these models throughout this paper, and they will later be made more "realistic" by coupling them to hydrological equations.

2.1 The Model in Temporally and Spatially Constant Environments

The following reaction–diffusion–advection equation was proposed to describe the dynamics of a stream species in a temporally and spatially constant environment (Speirs and Gurney 2001):

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} - v\frac{\partial N}{\partial x} + f(N)N, \tag{1}$$

where $N = N(x, t)$ is the population density at time t and longitudinal downstream location x, D is the diffusion coefficient, v is the flow velocity, and $f(N)$ is the per capita growth rate. Note that if we assume that the population can reside on the benthos and move in the flow, then (1) can be derived by combining a benthic-drift system when the transfer rates between benthos and flow become large [see (Pachepsky et al. 2005) and Appendix 1].

We assume compensatory population growth to a carrying capacity N^*, i.e. $f(N)$ satisfies that $\sup_{N\geq 0} f(N)$ occurs at $N = 0$, $f(N^*) = 0$ for some $N^* > 0$, $f(N) > 0$ for $N < N^*$, and $f(N) < 0$ for $N > N^*$. Let $r = f(0)$ be the intrinsic per capita growth rate when the population is rare. Throughout the paper, we assume that when a growth function f is mentioned it satisfies these conditions. As a particular example, we choose the logistic growth model, $f(N) = r(1 - N/K)$, with intrinsic per capita growth rate r and carrying capacity K.

Assume that the population is introduced locally in a spatial interval of the river. The asymptotic spreading speeds for (1) in the upstream and downstream directions are determined by the linearization of (1) at $N = 0$ (linearly determined spreading speeds) and are given by

$$c^- = 2\sqrt{Dr} - v \quad \text{and} \quad c^+ = 2\sqrt{Dr} + v, \tag{2}$$

respectively [see (Pachepsky et al. 2005)]. Therefore, in a spatially and temporally constant environment, the population spreads asymptotically to the upstream and downstream at constant speeds and never changes spread directions.

2.2 Models in Temporally or Spatially Heterogeneous Environments

The following partial differential equation is based on Bencala and Walters Bencala and Walters (1983) and has been proposed by Lutscher et al. Lutscher et al. (2006) to describe population growth and movement in a spatially heterogeneous river. The idea is to model longitudinal spread in a river while taking account of its spatial variability. This is achieved by linking river's cross-sectional area to flow speed. The idealized hydrodynamic population model reads

$$\frac{\partial N}{\partial t} = \frac{1}{A(x)}\frac{\partial}{\partial x}\left[D(x)A(x)\frac{\partial N}{\partial x}\right] - \frac{Q}{A(x)}\frac{\partial N}{\partial x} + f(N)N, \tag{3}$$

where the diffusion coefficient $D(x)$ depends on the spatial location, Q is the water discharge, and $A(x)$ is the spatially varying cross-sectional area. Similarly as we did for

(1), we can also derive (3) from a benthic-drift model when the transfer rates are very large (see Appendix 1). In (Lutscher et al. 2006), a spatially periodic piecewise river was considered for (3), and constant spreading speeds in the upstream and downstream directions were obtained, which implies that under a temporally constant flow, the population spreads asymptotically at constant speeds to the upstream and downstream directions. Generally, the existence of spreading speeds for (3) in the upstream (c^-) and downstream (c^+) directions follows from the abstract theory for spreading speeds for a semiflow defined in a periodic habitat in (Liang and Zhao 2010) [see also (Berestycki et al. 2005; Weinberger 2002)]. Moreover, the spreading speeds in the upstream and downstream directions are also the minimal wave speeds for spatially periodic traveling waves in corresponding directions. See Appendix 6 for details.

Organisms in streams are involved in two types of diffusion: bio-diffusion $D_b(x)$, which describes the individuals' active mobile ability that may not depend on the flow (Okubo and Levin 2001), and flow driven diffusion $D_f(x)$, which describes the individuals' passive diffusion driven by the water flow (Fischer et al. 1979). Therefore, in this paper, we will use both bio- and flow-driven diffusion

$$D(x) = D_f(x) + D_b(x). \tag{4}$$

Now, we extend model (3) by including water flow $Q(t)$ that varies slowly in time. Then, the diffusion rate and the cross-sectional area of the river may vary accordingly in time. Hence, the conservation of population leads to the following model:

$$
\frac{\partial N}{\partial t} = -\frac{\partial A(t, x)}{\partial t} \cdot \frac{N}{A(t, x)} \\
+ \frac{1}{A(t, x)} \frac{\partial}{\partial x} \left[D(t, x) A(t, x) \frac{\partial N}{\partial x} \right] - \frac{Q(t)}{A(t, x)} \frac{\partial N}{\partial x} + f(N)N. \tag{5}
$$

If the water discharge $Q(t)$ is assumed to vary periodically in time with period T, then $A(t, x)$ and $D(t, x)$ are also time-periodic with period T. We can define a periodic semiflow for (22) and then apply the theories in (Liang et al. 2006; Liang and Zhao 2010; Weinberger 2002) to obtain the existence of spreading speeds and periodic traveling waves (See Appendix 6 for approximations).

3 The Invasion Ratchet in a Parsimonious Model

An invasion ratchet allows species to persist in favorable habitat patches during adverse times and to traverse hostile patches in an upstream direction during beneficial times. In this section, we investigate the invasion ratchet in the model combining both temporal and spatial variability, based on the ideas introduced in the previous section. Precise conditions for the occurrence of the invasion ratchet cannot be derived rigorously, but we obtain approximations for such conditions based on an analysis of asymptotic spreading speeds of the species in constant flows. The aim of this section is therefore to derive ratchet conditions in a model as simple as possible.

3.1 Model Specification

To investigate the interaction between temporal and spatial variability, we simplify Eq. (5) to give a minimal model that still exhibits temporal variability in flow rate $Q(t)$ and spatial variability in cross-sectional area $A(x)$. To this end, we allow the discharge to vary in time (e.g. due to seasonality) and assume the simplest case of a periodic alternation of piecewise constant discharges

$$Q(t) = \begin{cases} Q_1, & \text{if } t \in [0, T_1) + T \, \mathbb{N}, \\ Q_2, & \text{if } t \in [T_1, T) + T \, \mathbb{N}, \end{cases} \tag{6}$$

where $T = T_1 + T_2$. The time intervals $[0, T_1) + T \, \mathbb{N}$ and $[T_1, T) + T \, \mathbb{N}$ represent two different flow seasons that will be used to define temporally fluctuating flows throughout the paper. This simply means that each year can be divided into two seasons of duration T_1 and T_2, and the water discharge is a constant (Q_1 or Q_2) in each season. The habitat is assumed to vary spatially periodically; see also (Lutscher et al. 2006). Each periodic patch consists of two regions with different wetted cross-sectional area $A(x)$. So, $A(x)$ can be written as

$$A(x) = \begin{cases} A_1, & \text{if } x \in (0, L_1) + L \, \mathbb{Z}, \\ A_2, & \text{if } x \in (L_1, L) + L \, \mathbb{Z}, \end{cases} \tag{7}$$

where $L = L_1 + L_2$ is the period length of the habitat, and $[0, L_1) + L \, \mathbb{Z}$ and $[L_1, L) + L \, \mathbb{Z}$ represent the two different habitat types on the infinite domain. Here, $\mathbb{Z}$ and $\mathbb{N}$ represent integers and natural numbers, respectively. Furthermore, we assume that the diffusion rate $D(x)$ is a constant, i.e., $D(x) \equiv D$, and the population growth rate $f(t, x, N)$ is spatially and temporally independent, i.e., $f(t, x, N) \equiv f(N)$. We assume that there are no lateral flows, which implies that the discharge and the cross-sectional area are related as $\partial A(x)/\partial t = -\partial Q/\partial x$. As for the matching conditions, we assume that the population density and the flux are continuous at the boundaries of different types of habitats. That is,

$$\lim_{x \uparrow L_{1j}} N(t, x) = \lim_{x \downarrow L_{1j}} N(t, x), \quad \lim_{x \uparrow L_j} N(t, x) = \lim_{x \downarrow L_j} N(t, x),$$

and

$$\lim_{x \uparrow L_{1j}} J(t, x) = \lim_{x \downarrow L_{1j}} J(t, x), \quad \lim_{x \uparrow L_j} J(t, x) = \lim_{x \downarrow L_j} J(t, x),$$

where $J(t, x) = D(x)A(x)\frac{\partial N}{\partial x} - Q(t)N$ is the flux, $L_{1j} = L_1 + jL$, and $L_j = jL$, $j \in \mathbb{Z}$. With such assumptions, we can define continuous semiflows and hence investigate spreading speeds for (3) and (5).

3.2 Model Analysis

In this subsection, we approximate conditions for the invasion ratchet phenomenon in a pool-riffle habitat under alternating flows. These are based on formulas of upstream

Area	High flow (Q_1)	Low flow (Q_2)
A_1 (pool)	$c_{11}^- = c - \frac{Q_1}{A_1}$	$c_{12}^- = c - \frac{Q_2}{A_1}$
A_2 (riffle)	$c_{21}^- = c - \frac{Q_1}{A_2}$	$c_{22}^- = c - \frac{Q_2}{A_2}$

spreading speeds of a species in infinitely long pool-only and riffle-only habitats under constant flows.

3.2.1 Upstream Spreading Speeds in Pool-Only and Riffle-Only Habitats

Without loss of generality, we assume $A_1 > A_2$ and refer to patches of area A_1 as pools and to patches of area A_2 as riffles. We also assume $Q_1 > Q_2$. Let $c = 2\sqrt{Dr}$ be the spreading speed determined by diffusion coefficient D and intrinsic growth rate r. By using (2) with $v = Q/A$, we can define the upstream spreading speed c_{ij}^- for a species in a spatially constant habitat with cross-sectional area A_i under a temporally invariant flow Q_j. The formulas are given in Table 2.

3.2.2 Approximation of Invasion Ratchet Conditions

In this subsection, we consider a stream with alternating pool-riffle patches and alternating high–low flows as introduced in Sect. 3.1. Recall that the period of the habitat is L with pool length L_1, and riffle length of L_2, and that the time period for flow fluctuation is T with high-flow season length of T_1 and low-flow season length of T_2.

We use the upstream spreading speeds for the different situations obtained in the previous subsection to approximate the speed of spread to the upstream within each patch. That is, we use c_{11}^- to approximate the speed of spread of the species in the pool in the high flow season, c_{12}^- to approximate the speed of spread of the species in the pool in the low flow season, and the other c_{ij}^-s for the other situations. Note that $c_{21}^- < \{c_{11}^-, c_{22}^-\} < c_{12}^-$, which means that upstream invasion is more likely to be observed in pools and for low discharges than in riffles and for high discharges.

Then we approximate conditions for the invasion ratchet phenomenon in such a habitat configuration. The result is only an approximation since the actual speed of spread within each patch is not the same as the spreading speed in an infinitely long habitat.

There are two necessary conditions for the invasion ratchet. The first one is that the population can always persist in the pools, under both high and low flows. This condition is approximated by

$$c_{11}^-, c_{12}^- > 0.$$

In our case, the pools can be regarded as good patches and the riffles as bad patches. The crucial question is now whether the population can traverse the riffle to arrive at the next pool. Therefore, the second condition is that the population cannot survive in riffles at times of high discharge but can invade riffles at times of low discharge. This condition is approximated by

$$c_{22}^- > 0 \quad \text{and} \quad c_{21}^- < 0.$$

If the population invades the riffle during low discharge times, it needs to arrive at the next pool to ratchet upstream. That is, the time of low discharge needs to be sufficiently long to allow the population to traverse the length of the riffle. Mathematically we can express this as

$$T_2 \geq \frac{L_2}{c_{22}^-} =: T_2^*,$$

where T_2^* corresponds to the minimum time length of low discharge for a ratchet step to occur. Note that this criterion only depends on properties of the riffle length and cross-sectional area (L_2, A_2) and the low discharge flow and duration (Q_2, T_2) as well as biological growth rate and diffusion coefficient (r, D) which gives the reaction-diffusion front speed $c = 2\sqrt{rD}$.

Figure 1 shows examples of upstream range expansion (see Appendix 2) for two different time lengths of low discharge, T_2. In Fig. 1a, T_2 is below the critical value T_2^*. Thus, the population starts invading the riffle during low discharges but cannot reach the pool. Hence, the population is washed back to its foothold in the downstream pool where it remains until the next low discharge period. This is a situation where we see the population stalling in the river, but it cannot spread upstream, thus indicating that the conjecture of Lutscher et al. (2010) does not apply here. Fig. 1b displays upstream invasion for a longer period of low discharge $T_2 > T_2^*$. During this time, the population traverses the riffle and arrives at the next pool upstream, where it persists during high discharges and from where it can start to ratchet up the next riffle during the next low discharge period. As already indicated, the critical time length is an approximation. For the simulation shown here, the approximated value is $T_2^* = 120$ and thus somewhat larger than the numerically observed one (103).

The invasion ratchet can also be caused by a number of different mechanisms that are not taken into account here, e.g. seasonality and spatial variability in population growth rather than in the discharge or in the habitat. Also, if there is an Allee effect, the spreading speeds will no longer be linearly determined, although it may still be possible to obtain an approximation of invasion ratchet conditions.

The terminology used here indicates that the organisms we consider in this paper are those preferring to live in slow-moving or still water such as phytoplankton, mayfly nymphs, dragonfly nymphs, damselfly nymphs (Odonata), and water boatman. For these organisms, pools are their favorite habitats but riffles are not. If, instead, one would like to consider organisms preferring fast-moving water, then riffles should be considered as favorable habitats.

4 The Water Depth in Gradual Flows

In this section, we revisit an equation governing the water depth in river hydrology. This takes into account the river morphology and in particular its spatial arrangement. Later on, we will feed the water depth into the population models introduced earlier.
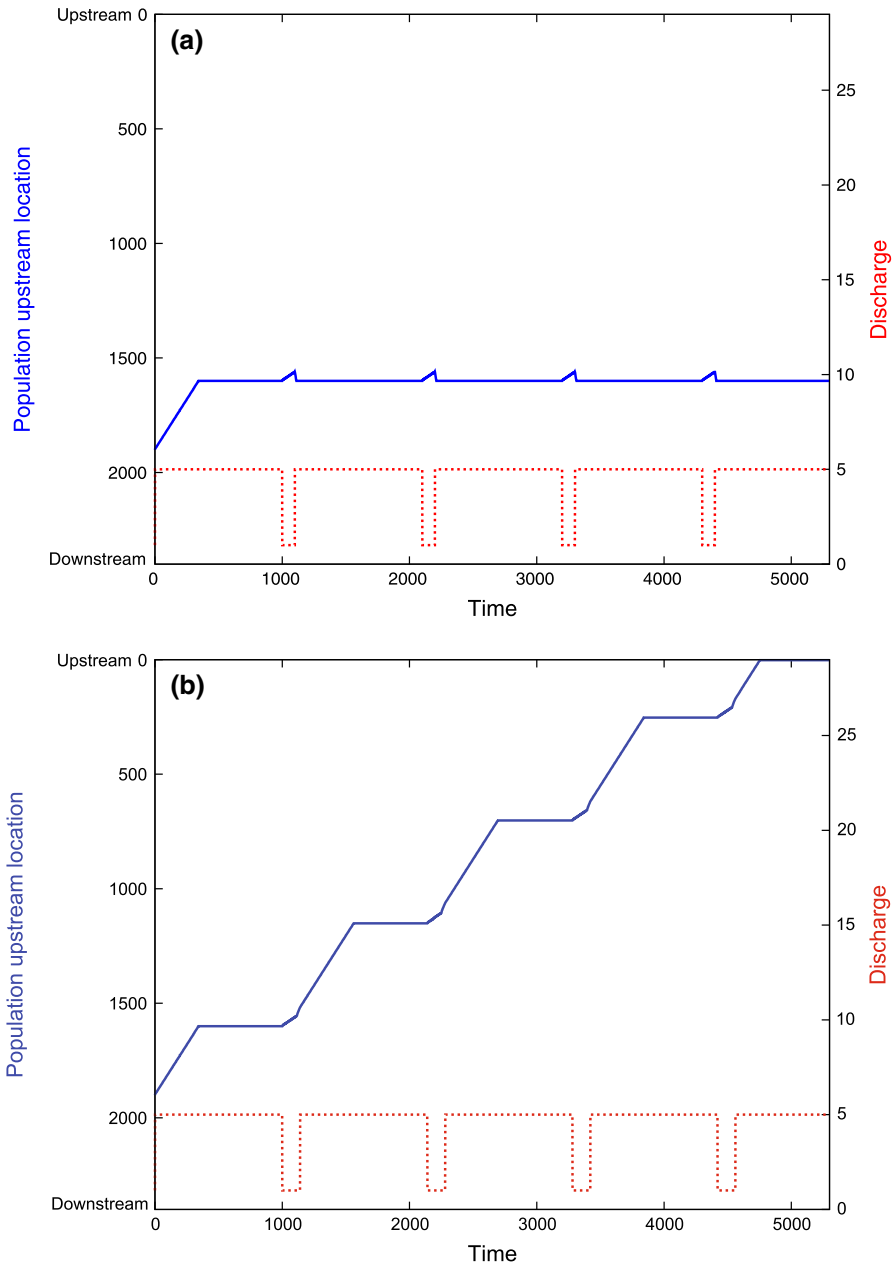
Fig. 1 Upstream range expansion (*solid line*) of a population with logistic growth. The *dotted line* indicates periods of low and high discharges on a different scale. Parameters are: $Q_1 = 5$, $Q_2 = 1$, $T_1 = 1000$, $L_1 = 400$, $L_2 = 50$, $r = 0.5$. The critical value $T_2^* = 120$. **a** $T_2 = 100$, so $T_2 < T_2^*$. **b** $T_2 = 140$ so $T_2 > T_2^*$

Consider a river in a one dimensional space. Let x (unit: m) represent the longitudinal location along the river and $y(x)$ (unit: m) be the water depth at location x. The governing equation for the gradually varied flow is given by

$$\frac{dy}{dx} = \frac{S_0(x) - S_f(y)}{1 - F_r^2(y)} \qquad (8)$$

[see (5–7) in (Chaudhry 1993)], where $S_0(x)$ is the slope of the channel bed at location x, S_f is the friction slope, i.e., the slope of the energy grade line or approximation of the water surface slope, F_r is the Froude number, which is defined as the ratio between the flow velocity and the water wave propagation velocity and is used to determine the resistance of a partially submerged object moving through water. S_0, S_f, and F_r are all dimensionless. Assume that the river has a rectangular cross section with a constant width B (unit: m) and height $y(x)$. By substituting expressions of S_f and F_r into (8) (see Appendix 3 for details), we obtain

$$\frac{dy}{dx} = \frac{g k^2 y^{\frac{10}{3}} S_0(x) - n^2 \left(\frac{Q}{B}\right)^2 g}{k^2 g y^{\frac{10}{3}} - \left(\frac{Q}{B}\right)^2 k^2 y^{\frac{1}{3}}}, \qquad (9)$$

where Q (unit: m^3/s) is the flow discharge, $g = 9.8$ (unit: m/s^2) is the gravitational acceleration, $k = 1$ is a dimensionless conversion factor, and n (unit: s/m$^{1/3}$) is Manning's roughness coefficient, which depends on many factors, including the bed roughness and sinuosity, and represents the resistance to water flows in channels. See (Chaudhry 1993) for more hydrological details.

In the following sections, we assume a subcritical flow in the river, which hydrologically means a flow in which the water velocity is less than the wave velocity in water (Chaudhry 1993). This is equivalent to assuming that the Froude number F_r is less than one in Eq. (8).

5 Population Spread and Persistence in a Spatially Uniform Flow

We now apply the water depth Eq. (9) to a spatially uniform flow in a stream with a constant bed slope. In this section, we ignore spatial heterogeneity, but consider temporally fluctuating flows. However, we begin with a temporally constant flow. Throughtout this section, we will investigate spread and persistence of a species in the different flows by virtue of studying the upstream spreading speed of a related population model with temporally constant or fluctuating habitat.

5.1 The Population Model for Temporally Constant Flow

Consider a river with a constant bed slope S_0. As in the previous Section, we assume that the river has rectangular cross sections with constant width B. The water depth is stabilized at the normal depth

$$y_n = \left(\frac{Q^2 n^2}{B^2 S_0 k^2}\right)^{\frac{3}{10}},\tag{10}$$

and we call the flow in the river a uniform flow; see Appendix 4 and (Chaudhry 1993). Then the wetted cross-sectional area of the river is $A = B y_n$. This is how we feed the water depth into the population model (3). The latter becomes

$$\frac{\partial N}{\partial t} = D\frac{\partial^2 N}{\partial x^2} - \frac{Q}{B y_n}\frac{\partial N}{\partial x} + f(N)N.\tag{11}$$

The spreading speeds for (11) in the downstream and upstream directions are respectively

$$c^\pm = 2\sqrt{Dr} \pm \frac{Q}{B y_n}.\tag{12}$$

From this, we obtain that $c^- \geq 0$ if and only if

$$r \geq \frac{Q^2}{4B^2 y_n^2 D}.\tag{13}$$

Therefore, (13) is the condition for the population to spread upstream in a river under a uniform flow. Note that the flow velocity $v = Q/(B y_n)$. Hence, condition (13) is equivalent to $4Dr \geq v^2$.

Before investigating the condition for population spread in more detail, we need to specify the diffusivity. Assume that the bio-diffusion rate (see Sect. 2.2) is a constant, i.e., $D_b(x) \equiv D_b$. According to the mechanics of dye dilution in water, the flow driven diffusion process is described by

$$D_f(x) \equiv D_f = a y_n u^*\tag{14}$$

[see Sect. 5.2.1 in (Fischer et al. 1979)], where a is a constant that varies in different rivers, and $u^* = \sqrt{y_n S_f g}$ is the shear velocity. We choose $a = 0.5$ in this paper. The expression for S_f can be found in (32). Then the diffusion constant in a uniform flow is

$$D = D_b + D_f = D_b + \frac{0.5 n Q g^{\frac{1}{2}}}{k B y_n^{\frac{1}{6}}}.\tag{15}$$

Substituting (15) into (12) and (13), we obtain

$$c^\pm = 2\sqrt{r\left(D_b + \frac{1}{2}g^{\frac{1}{2}}n^{\frac{9}{10}}S_0^{\frac{1}{20}}\left(\frac{Q}{B}\right)^{\frac{9}{10}}\right)} \pm \frac{S_0^{\frac{3}{10}}}{n^{\frac{3}{5}}}\left(\frac{Q}{B}\right)^{\frac{2}{5}}.$$

Table 3 Influence of different environmental and biological factors on population spread to the upstream

Factor	Effect on upstream spread
Intrinsic growth rate (r)	$+$
Bio-diffusion (D_b)	$+$
Channel slope (S_0)	$-$
Manning's roughness coefficient (n)	$+$
Water discharge per unit width (if $\frac{Q}{B} < q_0$)	$-$
Water discharge per unit width (if $\frac{Q}{B} > q_0$)	$+$

"$-$" means that the factor has a negative effect on the upstream invasion, i.e., when the factor increases, it is harder for the population to spread to the upstream; "$+$" means that the factor has a positive effect on the upstream invasion, i.e., when the factor increases, it is easier for the population to spread to the upstream and hence to persist in the whole river. Here q_0 is the value of q such that c^- attains its minimum when c^- is considered as the function of q_0

Now we are in the position to study the influence of different environmental and biological factors on the spread and persistence of a species in a uniform flow. The results are summarized in Table 3.

As for the biological factors, both the intrinsic growth rate and the bio-diffusion have positive effects on population persistence. The remaining parameters concern environmental and river morphological factors. The steeper the river bottom, the harder it is for the population to persist. Recall that the value of the Manning roughness n depends mainly upon the bottom roughness, amount of vegetation, and channel irregularity, and to a lesser degree, upon stage, scour and deposition, and channel alignment (Chaudhry 1993). n performs as resistance to the washout of the population. Then the larger the Manning roughness n is, the easier it is for the population to spread to the upstream. The parameter combination Q/B represents the water discharge per unit width. The upstream spreading speed c^- decreases and then increases for the increasing Q/B; hence c^- attains its minimum at some q_0. If the water discharge per unit width is low ($Q/B < q_0$), then the water depth is very low, and the flow velocity is relatively large. In this case, when the discharge increases, the increase in diffusion (in terms of $\sqrt{2Dr}$) is less than the increase in downstream advection (in terms of v), so the upstream spreading speed decreases, and hence, it becomes harder for the population to spread to the upstream. However, if the water discharge per unit width is high ($Q/B > q_0$) and increases, then the water depth becomes very high and the increase in downstream advection is less than the increase in diffusion, so the upstream spreading speed increases and the water discharge per unit width becomes a positive factor for population persistence in this case.

5.2 The Population Model for Temporally Fluctuating Flow

Now we replace the temporally constant flow by a water flow that varies periodically and is defined in (6) with Q_1 in high flow seasons of duration T_1 and Q_2 in low flow seasons of duration T_2. Then the normal depths in the different seasons are y_n^1 and y_n^2, which can be defined by replacing Q in (10) with Q_1 or Q_2, respectively. Moreover, if population growth is qualitatively logistic (as described in Sect. 2.1), it follows from

the results in (Lutscher and Seo, 2011, Sect. 3) that if the coefficients in model (11) with temporally constant flow are temporally periodically varying, then the upstream and downstream spreading speeds are given as

$$c^{\pm} = 2\sqrt{r\langle D\rangle} \pm \left\langle \frac{Q}{By_n} \right\rangle, \tag{16}$$

where $\langle\cdot\rangle$ means the arithmetic average of the quantity over a time period with

$$\langle D\rangle = D_b + 0.5\,n^{9/10}\,g^{1/2}\,S_0^{1/20} \cdot \frac{\left(\frac{Q_1}{B}\right)^{9/10} T_1 + \left(\frac{Q_2}{B}\right)^{9/10} (T - T_1)}{T},$$

and

$$\left\langle \frac{Q}{By_n} \right\rangle = \frac{S_0^{3/10}}{n^{3/5}} \cdot \frac{\left(\frac{Q_1}{B}\right)^{2/5} T_1 + \left(\frac{Q_2}{B}\right)^{2/5} (T - T_1)}{T}.$$

Hence, the upstream spreading speed is positive ($c^- \geq 0$) if and only if

$$r \geq \frac{\left\langle \frac{Q}{By_n} \right\rangle^2}{4\langle D\rangle}, \tag{17}$$

which can be considered as the persistence condition for a species in a periodically fluctuating flow. Condition (17) is actually $4\langle D\rangle r \geq \langle v\rangle^2$, where $\langle v\rangle$ is the average flow velocity. Figure 2 shows an example of the relation between c^- and Q_1/B as well as Q_2/B. In the figure, (17) holds in the region below the contour line $c^- = 0$. It is not hard to see from (16) that c^- is an increasing function of D_b and r and that if the ratio between T_1 and T is fixed, then the length of T does not change the value of c^-. Figure 3 also shows the relationships between c^- and other factors. We see that c^- is a decreasing function of the river bottom slope S_0, but is an increasing function of the Manning coefficient n. If the length of a flow period is fixed, then the longer the high flow season is, the smaller the upstream spreading speed is, and hence, the harder the population can spread to the upstream.

6 Population Spread and Persistence in a Spatially Heterogeneous River

In this section, we consider spatial variability in the physical characteristics of the river. To be more precise, we assume a spatially periodic pool-riffle river, which results from spatially varying channel bed slopes. Before studying the population models with both temporally constant and fluctuating flows, we have to derive the water depth for a spatially heterogeneous river.
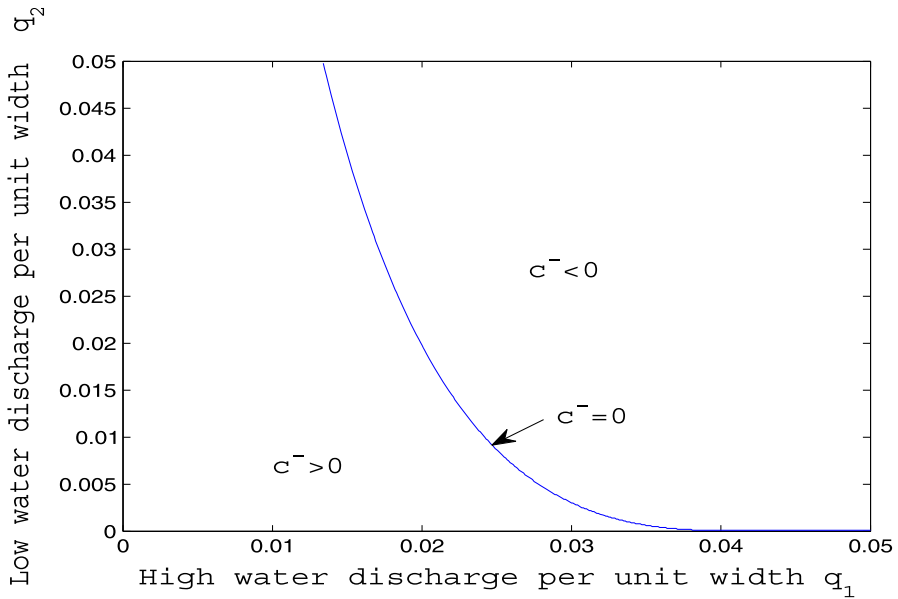
Fig. 2 The relation between upstream spreading speed c^- and high and low discharges per unit width ($q_1 = Q_1/B$ and $q_2 = Q_2/B$, respectively) for a spatially uniform river with constant bed slope. A positive (negative) upstream spreading speed corresponds to population persistence (wash-out). Parameters: $g = 9.8 \, \mathrm{m/s^2}, k = 1, n = 0.1 \, \mathrm{s/m^{1/3}}, S_0 = 0.000004, D_b = 0.5 \, \mathrm{m^2/s}, r = 0.0001982 \, \mathrm{/s}, T = 31536000$ s (i.e., 1 year), $T_1 = 3T/4$

6.1 A Spatially Periodic Pool-Riffle River

Assume that the river has a spatially varying channel bed slope $S_0(x)$ that is a periodic piecewise function:

$$S_0(x) = \begin{cases} S_{0r}, & mL \leq x < mL + L_1, \\ S_{0p}, & mL + L_1 \leq x < (m+1)L, \end{cases} \tag{18}$$

where m is any integer and $S_{0r} > S_{0p}$. Recall that for a pool-riffle river, a pool represents the area with deep water and a riffle represents the area with shallow water (Allan and Castillo (2007)). In this section, for simplicity, we use a riffle to represent a piece of river channel with a steeper bed with slope S_{0r} and a pool to represent a piece of channel with a flatter bed with slope S_{0p}; see Fig. 4. Therefore, the river consists of periodically alternating pool-riffle channels with period L (unit: m), and each periodic patch contains a riffle channel with length L_1 (unit: m) and a pool channel with length L_2 (unit: m) (i.e., $L = L_1 + L_2$).

6.2 The Water Depth in a Spatially Periodic Pool-Riffle River

We now have to consider the water depth Eq. (9) in conjunction with the spatially periodic river structure (18). Mathematically, there exists a unique periodic solution to (9, 18), which is the periodic extension of the solution to
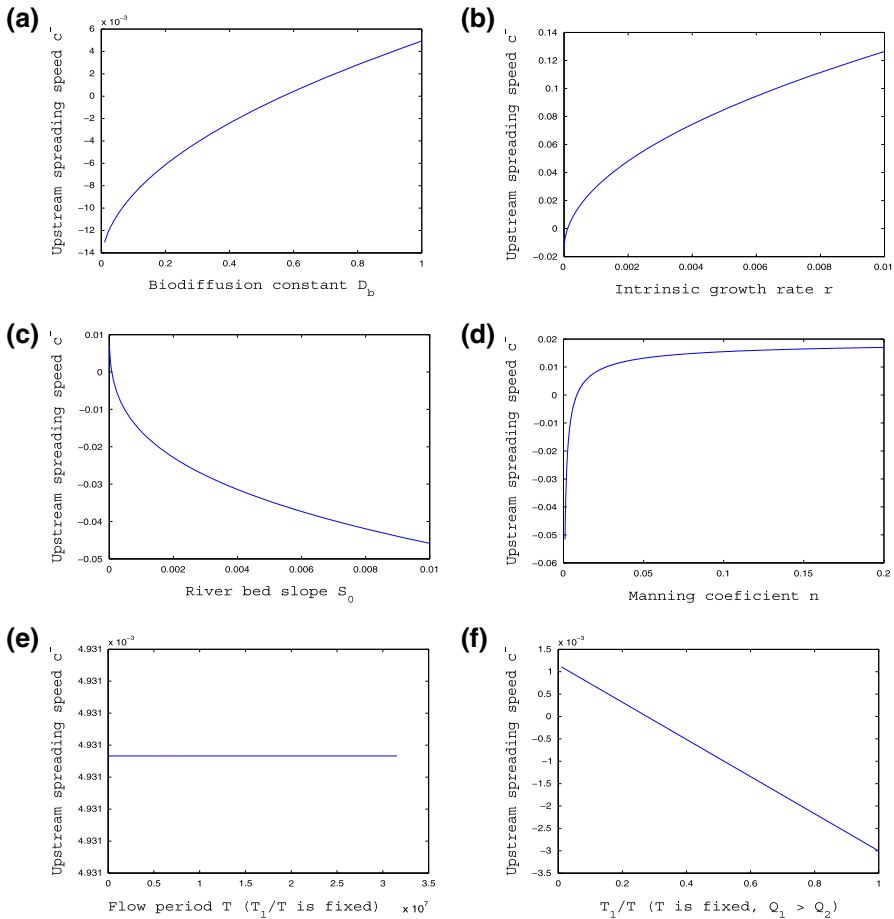
Fig. 3 The relation between upstream spreading speed c^- and various biological and environmental parameters of a spatially uniform river with temporally fluctuating flow. Parameters are: $g = 9.8$ m/s^2, $Q_2/B = 0.0001$ m^2/s, $Q_1/B = 0.0002$ m^2/s, and **a** $r = 0.0001$/s, $n = 0.03$, $T = 31536000$ s, $T_1 = T/2$, $S_0 = 0.0001$; **b** $n = 0.03$, $D_b = 0.5$ m^2/s, $T = 31536000$ s, $T_1 = T/2$, $S_0 = 0.0001$, **c** $n = 0.03$, $D_b = 0.5$ m^2/s, $r = 0.0001$/s, $T = 31536000$ s, $T_1 = T/2$, **d** $D_b = 0.5$ m^2/s, $r = 0.0002$/s, $T = 31536000$ s, $T_1 = T/2$, $S_0 = 0.00002$, **e** $D_b = 0.5$ m^2/s, $r = 0.0002$/s, $n = 0.03$, $T_1 = T/2$, $S_0 = 0.0001$, **f** $D_b = 0.5$ m^2/s, $r = 0.0001$/s, $n = 0.03$, $T = 31536000$ s, $S_0 = 0.0001$

$$
\begin{cases}
\dfrac{\mathrm{d}y}{\mathrm{d}x} = \dfrac{gk^2 y^{\frac{10}{3}} S_0(x) - n^2 (Q/B)^2 g}{k^2 g y^{\frac{10}{3}} - (Q/B)^2 k^2 y^{\frac{1}{3}}}, \quad \text{with} S_0(x) \text{defined in} (6.1), \\
y(0) = y(L).
\end{cases}
\tag{19}
$$

This is a boundary value problem; the existence and uniqueness of its solution and the numerical method to obtain it are included in Appendix 5. Moreover, this periodic solution is stable to perturbations in the downstream flow conditions; see Fig. 11 in Appendix 5. This indicates that the water depth at the far upstream end, which is a large number of channel periods away from the downstream end, asymptotically approaches the periodically varying water depth, i.e., the periodic solution to (9,18).
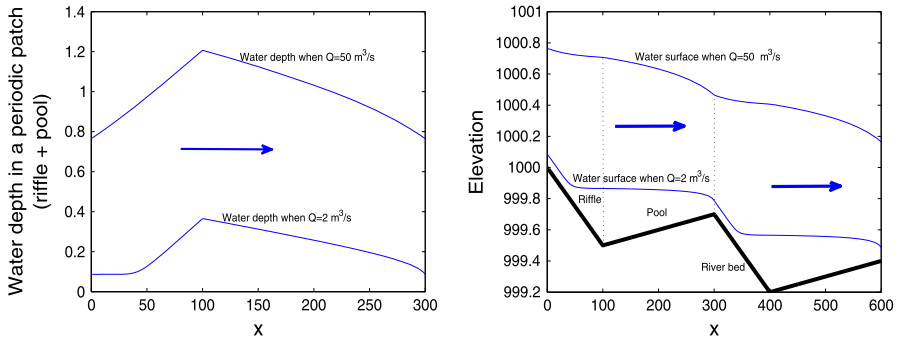
Fig. 4 *Left* the water depth $y(x)$ in a periodic patch of the river in the example. For water discharge $Q = 50 \, \text{m}^3/\text{s}$, $y(0) = y(300) = 0.7652$ m, $y(100) = 1.2071$ m; for $Q = 2 \, \text{m}^3/\text{s}$, $y(0) = y(300) = 0.0867$ m, $y(100) = 0.3654$ m. *Right* the elevation of river bed and water surface in two periodic patches of the river (*longitudinally sectional view*). The riffle region and the pool region are indicated in the first periodic patch

Therefore, we assume that the water depth varies periodically in the river and that in each period it satisfies (19).

Example Assume a spatially periodic pool-riffle river with lateral width $B = 50m$, riffle length $L_1 = 100$ m, pool length $L_2 = 200$ m, riffle bed slope $S_{0r} = 0.005$, and pool bed slope $S_{0p} = -0.001$. We obtain the periodic steady state flow of the river by solving (19). The water depths for different water discharges are shown in Fig. 4a, which indicates that the water depth increases in the riffles and decreases in the pools.

Note that in general, both water depth and velocity increase but the relative variation between the pool and riffle depths and velocities decrease with increasing discharge (see Fig. 4b).

6.3 Population Model for Temporally Constant Flow

We now assume a constant water discharge in the spatially periodic pool-riffle river. We obtain a population model by feeding the solution to the periodic water depth Eq. (9,18) into the idealized hydrodynamic Eq. (3), using that $A(x) = By(x)$. The result is:

$$\frac{\partial N}{\partial t} = \frac{1}{y(x)} \frac{\partial}{\partial x} \left[D(x) y(x) \frac{\partial N}{\partial x} \right] - \frac{Q}{By(x)} \frac{\partial N}{\partial x} + f(N)N, \qquad (20)$$

where f is chosen as the logistic growth and the flow driven diffusion (cf. (15)) is now spatially non-uniform

$$D(x) = D_b + \frac{0.5n Q g^{\frac{1}{2}}}{k B (y(x))^{\frac{1}{6}}}. \qquad (21)$$

In Appendix 6 we show that, even though we can define spreading speeds theoretically, it is difficult to calculate them when there are variations in space and time. Therefore, based on the existence of spreading speeds, we will find numerical solutions for the model (20) and use the upstream extents (see Appendix 2) at different times to approximate the population's upstream invasion. Since we arbitrarily choose

a threshold value 10^{-2} for the range extent, the obtained numerical extents may not be the exact real biological extents, but the qualitative change of upstream extent still indicates whether or not the population spreads to the upstream.

In the following, we give a numerical example to show how different biological and environmental factors affect the upstream invasion of a species in the current model. The river is assumed to occupy the interval $[0, x_L]$. The boundary conditions are assumed to be the zero flux condition at the upstream end and the free flow condition at the downstream end. That is,

$$\left[v(x)N - D(x)\frac{\partial N}{\partial x} \right]\Big|_{x=0} = 0 \quad \text{and} \quad \frac{\partial N}{\partial x}\Big|_{x_L} = 0,$$

where $v(x) = Q/A(x)$ is the flow velocity (Chaudhry 1993). We incorporate the numerical results for the periodic water depth $y(x)$ from (19) into (20) and solve it with the finite difference method with Matlab. The upstream extents for (20) under different parameter conditions are shown in Fig. 5, and the effects of different factors on the population's upstream spread are summarized in Table 4.

The population may be washed out at high flow (high discharge) but can spread to the upstream at sufficiently low flow; see Fig. 5a. The bio-diffusion represents the active movement of individuals, so it helps the population spread to the upstream. The species can be washed out if the bio-diffusion is very small, while it can spread to upstream if its bio-diffusion is sufficiently large; see Fig. 5b. Given a fixed ratio between the lengths of a pool and a riffle, when the length L of a patch period becomes larger, it is easier for the population to spread to the upstream and hence to persist in the whole river; see Fig. 5c. Similarly, if the riffle length is fixed, then the longer the pool length is the easier it is for the population to spread to the upstream. The intrinsic growth rate also helps the population spread to the upstream; see Fig. 5d.

6.4 Population Model for Temporally Varying Flow

Finally, we combine the spatially periodic river structure with water flow that is variable in time. To this end, we feed the water depth into the idealized hydrodynamic Eq. (5) for temporally varying flow. The population model becomes

$$\frac{\partial N}{\partial t} = -\frac{\partial y(t,x)}{\partial t} \cdot \frac{N}{y(t,x)}$$
$$+ \frac{1}{y(t,x)}\frac{\partial}{\partial x}\left[D(t,x)y(t,x)\frac{\partial N}{\partial x} \right] - \frac{Q(t)}{By(t,x)}\frac{\partial N}{\partial x} + f(N)N. \quad (22)$$

Assume that the water flow varies periodically in time and each period consists of a high-flow season and a low-flow season. The water discharge $Q(t)$ is as defined in (6). Then the population model (22) becomes
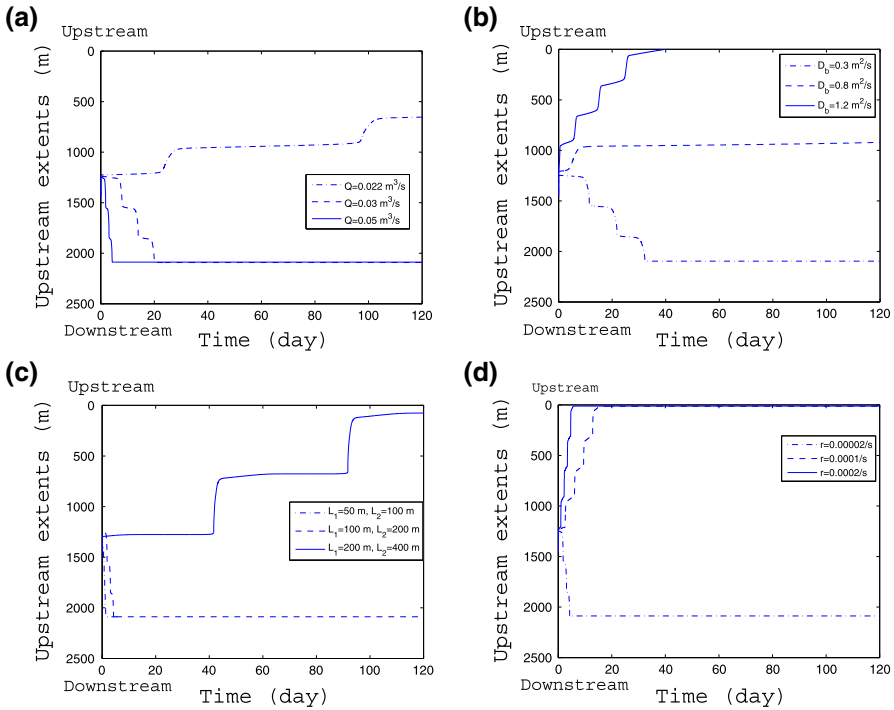
Fig. 5 The upstream extents for (20) under different conditions, where $g = 9.8 \, \text{m/s}^2$, $k = 1$, $B = 50$ m, $n = 0.03 \, \text{s/m}^{1/3}$, $S_{0r} = 0.005$, $S_{0p} = -0.001$, $K = 1000$. The initial value is a point source distribution with $N_0(x) = 1000$ if $x = 1450$ and $N_0(x) = 0$ otherwise. The range threshold is 10^{-2}. Other parameters are as follows. **a** $r = 0.00002$/s, $D_b = 0.5 \, \text{m}^2/\text{s}$, $L_1 = 100$ m, $L_2 = 200$ m, $Q = 0.022, 0.03, 0.05 \, \text{m}^3/\text{s}$. **b** $r = 0.00002$/s, $Q = 0.025 \, \text{m}^3/\text{s}$, $L_1 = 100$ m and $L_2 = 200$ m, $D_b = 0.3, 0.8, 1.2 \, \text{m}^2/\text{s}$. **c** $r = 0.00002$/s, $Q = 0.05 \, \text{m}^3/\text{s}$, $D_b = 0.5 \, \text{m}^2/\text{s}$, $L_1/L_2 = 1/2$, $L = 150, 300, 600$ m. **d** $Q = 0.05 \, \text{m}^3/\text{s}$, $D_b = 0.5 \, \text{m}^2/\text{s}$, $L_1 = 100$ m, $L_2 = 200$ m, $r = 0.00002, 0.0001, 0.0002$/s. Note that the downstream extents reach the downstream end ($x = 2100$) very quickly (in a few hours) in all cases, so when the upstream extent reaches the downstream end, it actually indicates that the population is washed out in that case

Table 4 Influences of different factors on population spread to the upstream

Factor	Effect on upstream spread
Discharge (Q)	−
Intrinsic growth rate (r)	+
Bio-diffusion (D_b)	+
Period of pool and riffle length (L)	+

"−" means that the factor has a negative effect on the upstream invasion, i.e., when the factor increases, it is harder for the population to spread to the upstream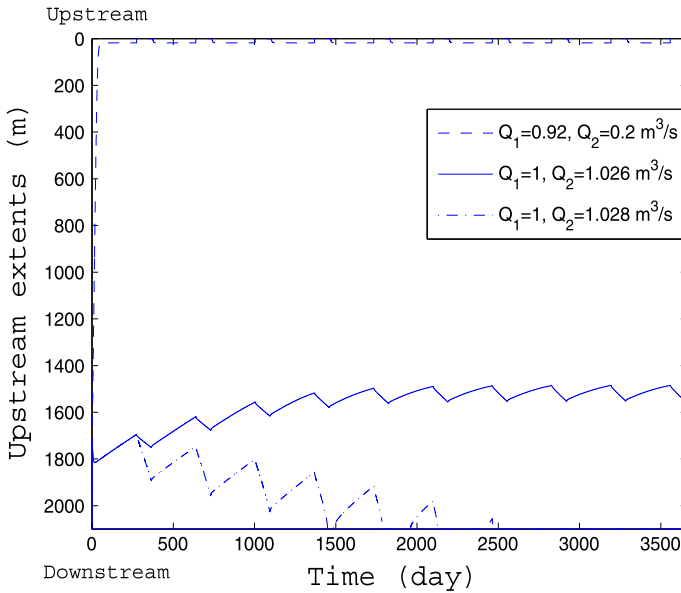 and hence the upstream spreading speed decreases; "+" means that the factor has a positive effect on the upstream invasion, i.e., when the factor increases, it is easier for the population to spread to the upstream and hence the upstream spreading speed increases

Fig. 6 The ranges of the population in the upstream for (23) with $f(N) = 0.0001982(1 - N/1000)$, $g = 9.8$ m/s^2, $k = 1$, $B = 50$ m, $n = 0.1$ s/m$^{1/3}$, $D_b = 0.5$ m^2/s, $L_1 = 50$ m, $L_2 = 200$ m, $X_L = 2, 100$ m, $T = 31, 536, 000$ s (i.e., 365 day), $T_1 = 3/4T$, $S_{0r} = 0.00042$, $S_{0p} = -0.0001$. The initial value is a point source distribution with $N_0(x) = 1000$ if $x = 1950$ and $N_0(x) = 0$ otherwise. The range threshold is 10^{-2}. Note that the downstream extent quickly goes to the downstream end although it is not shown in the figure

$$
\begin{cases}
\dfrac{\partial N}{\partial t} = \dfrac{1}{y_1(x)} \dfrac{\partial}{\partial x} \left[D_1(x) y_1(x) \dfrac{\partial N}{\partial x} \right] - \dfrac{Q_1}{B y_1(x)} \dfrac{\partial N}{\partial x} + f(N)N, \\
\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t \in [mT, mT + T_1), \\
\dfrac{\partial N}{\partial t} = \dfrac{1}{y_2(x)} \dfrac{\partial}{\partial x} \left[D_2(x) y_2(x) \dfrac{\partial N}{\partial x} \right] - \dfrac{Q_2}{B y_2(x)} \dfrac{\partial N}{\partial x} + f(N)N, \\
\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad t \in [mT + T_1, (m + 1)T),
\end{cases}
\tag{23}
$$

for all $m \in \mathbb{N}$, where $D_i(x)$ and $y_i(x)$ are the diffusion coefficient and water depth, respectively, corresponding to the water discharge Q_i for $i = 1, 2$.

6.4.1 Numerical Results

In order to see how the species spreads in such a temporally and spatially varying environment, we solve the population model (23) numerically. Figure 6 shows the resulting upstream extents for a population for three different flow regimes. If the water discharge is sufficiently low in both seasons (e.g., $Q_1 = 0.92$ m^3/s and $Q_2 = 0.2$ m^3/s), then the population consistently spreads to the upstream and will be persistent in the whole river. If the water discharge is sufficiently low in one ("good") season but not too high in another ("bad") season (e.g., $Q_1 = 1$ m^3/s and $Q_2 = 1.026$ m^3/s), then the population retreats to the downstream in the high-flow season but spreads upstream to a larger extent in the low-flow season. As a result, the population will eventually

stall well in a particular range of the habitat before it is washes out, and hence, the population will persist even though it cannot invade to the upstream. However, if the high flow is sufficiently large (e.g., $Q_1 = 1$ m^3/s and $Q_2 = 1.028$ m^3/s), then the population will be washed out even though the population can move upstream to some extent during the first few low flow seasons.

6.4.2 Effects of Spatial Heterogeneity on Population Spread and Persistence

Comparing the preceding results with those for a spatially uniform river under temporally fluctuating flow (Sect. 5.1), we can elucidate the impact of spatial heterogeneity on population spread and persistence. Consider Figs. 2 and 6. The latter figure is for a periodic pool-riffle river; its average channel bottom slope is the same as the constant slope of the spatially uniform river in the former figure. All the other parameters are the same. It is shown in Fig. 2 that in the uniform flow, when the water discharges per width are $Q_1/B = 0.02$ m^2/s and $Q_2/B = 0.0205$ m^2/s in two flow seasons, respectively, the upstream spreading speed is negative and hence the population will be washed out. However, Fig. 6 shows that in the spatially periodic pool-riffle river when $Q_1 = 1$ m^3/s (with $Q_1/B = 0.02$ m^2/s) and $Q_2 = 1.026$ m^3/s (with $Q_2/B = 0.0205$ m^2/s), the population can spread to the upstream and hence persist in the river. Therefore, we can conclude that at least in some cases as in the examples given here, spatial heterogeneity can help the population of a species spread to the upstream and persist in a river.

7 Invasion Ratchet in a 2D Meandering River

In this section, we show an example of an invasion ratchet phenomenon in a two-dimensional meandering river. We use River2D, which is a hydrodynamic and fish habitat model developed specifically for use in natural streams and rivers. It is a Finite Element model, based on a conservative Petrov–Galerkin upwinding formulation. The hydrodynamic component of the River2D model is based on the two-dimensional, depth-averaged St. Venant Equations expressed in conservative form. See http://www.river2d.ualberta.ca/ for more details about River2D.

7.1 Model specification

We consider a species in a spatially two-dimensional river (longitudinal-lateral). The dynamics of the population is governed by the following population model, which is the 2D version of (20),

$$\frac{\partial N(x, y, t)}{dt} = f(N)N + \frac{1}{h(x, y)} \left(v_1(x, y) \frac{\partial N}{\partial x} + v_2(x, y) \frac{\partial N}{\partial y} \right)$$
$$+ \frac{1}{h(x, y)} \left(\frac{\partial}{\partial x} \left(Dh(x, y) \frac{\partial N}{\partial x} \right) + \frac{\partial}{\partial y} \left(Dh(x, y) \frac{\partial N}{\partial y} \right) \right), \quad (24)$$

where the population density $N = N(x, y, t)$ (unit: $1/m^3$) and water depth $h(x, y)$ (unit: m) are functions of two-dimensional space (note that in this section y represents y-coordinate in the $x - y$ plane but not the water depth as in earlier sections). The flow speed in the longitudinal x and lateral y direction are v_1 and v_2, respectively (units: m/s).

The boundary conditions are

$$N|_{x=0} = 0, \quad \frac{\partial N}{\partial x}|_{x=L} = 0,$$

where $x = 0$ is the upstream end, $x = L$ is the downstream end of the river.

Similarly to (1) and (3), model (24) can be derived from a 2D benthic-drift model (see Appendix 1). For the following simulations, we implement Eq. (8.5) in Appendix 1 into River2D to calculate the population density. It has the same form as (24), but rescales the flow dynamics to reflect the approximate proportion of the time spent in the flow.

7.1.1 River Geometry and Discharge

We consider a 2D meandering river with rectangular cross-sectional areas under periodically fluctuating flows. The river channel is represented by a sine generated curve $\theta = \theta_m \sin(2\pi s/L_s)$, where θ represents the angle between the channel and the longitudinal line with the maximum θ_m, s is the length of the river, L_s is a period length of channel, the lateral bed slope is $\tan\alpha$ where $\alpha = \alpha_m \sin(2\pi s/L_s)$ with maximum $|\alpha_m|$. The river is in a seasonally varying environment with time period T, composed of a low-flow season $(kT, kT + T_1)$ and a high-flow season $(kT + T_1, (k + 1)T)$ for some $T_1 > 0$ and for all $k \in \mathbb{N}$. The low flow is Q_1 and the high flow Q_2.

7.1.2 Parameter Values

In simulations, parameters are chosen as follows. The river length is $L = 1,000$ m, the channel period is $L_s = 200$ m, the width is 20 m, the longitudinal slope of the river bottom is $S_0 = 0.001$, $\theta_m = \pi/4$, $\alpha_m = -\pi/200$, $r = 1.92$/day, $K = 1000$, $D = 0.24$ m^2/s. The time period is $T = 365$ days. The low flow season length is $T_1 = 270$ days and the high flow season length is 95 days. The water depth in the river when $Q = 1$ m^3/s and when $Q = 20$ m^3/s is shown in Fig. 7. The constant ς is chosen to be 3599, which makes it possible to consider the time unit as hour in the simulation for Eq. (29) in River2D. The maximal time step for the simulation is 1 hour. Most nodal points inside the numerical domain are uniformly distributed with spacing 5 m between each other, but nodes near the boundary are slightly shifted and the space step on the boundary is smaller than 5 m, for better numerical result.

7.2 Simulation Results

Figure 8 shows an invasion ratchet phenomenon, where the population spreads upstream when the flow is low and retreats when the flow is high, but in the long run it spreads to the upstream as well as to the downstream.
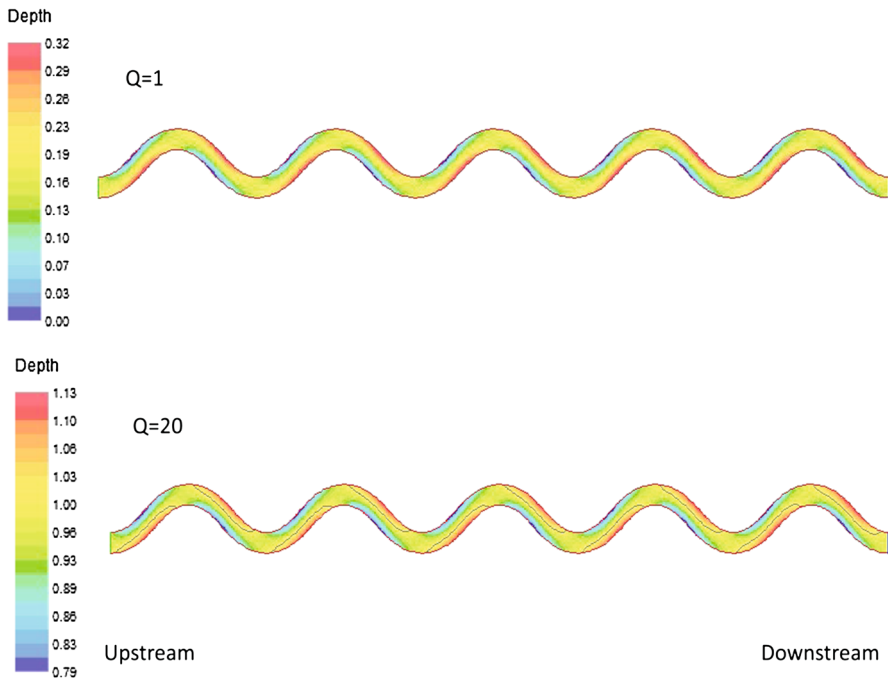
Fig. 7 The water depth (unit: m) in a meandering river with rectangular cross-sectional areas in the cases of $Q = 1$ m^3/s and $Q = 20$ m^3/s, respectively. The total river length is 1, 000 m, the channel period is 200 m, and the width is 20m

8 Discussion and Conclusions

We have used a hybrid physical–biological modeling approach to connect environmental hydrodynamics with ecological dynamics. This methodology allows us to investigate the impact of river morphology and flow patterns on the spatiotemporal dynamics of a population. In the following, we will focus on two major aspects related to our modeling framework. The first one concerns a methodological progress in integrating a dynamic population model into the hydrology–biology interface. This strengthens the ecological component of environmental flow assessments that is currently still lacking.

Second, we found how spatial heterogeneity, in form of different river bed slopes leading to pool-riffle sequences, and temporal fluctuations, in form of seasonally varying discharges, can interact to give rise to the invasion ratchet. This phenomenon has two effects. On the one hand, during adverse times, it functions as a safeguard to the population by providing a toe-hold in favorable habitats. On the other hand, during beneficial times, the population can pass through hostile habitats to arrive at the next stepping stone. As such, the invasion ratchet is an emergent phenomenon of two different sources of (temporal and spatial) variability. It can facilitate not only population invasion of the river, but also population persistence to prevent wash-out if the ratchet stalls.
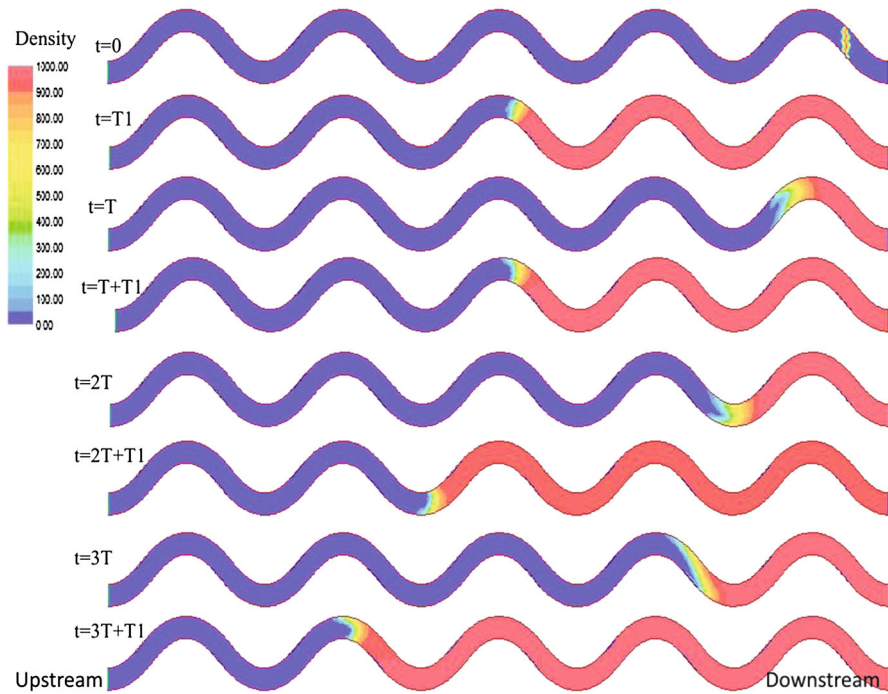
Fig. 8 The population density in the meandering river at different times. Results come from River2D with the population model (29). The total river length is $1,000$ m. The water discharge varies periodically with a period of $T = 365$ days. The low-flow season length is $T_1 = 270$ days with $Q_1 = 1$ m^3/s, and the high-flow season length is 95 days with $Q_2 = 20$ m^3/s. The other parameters are: $f(N) = rN(1 - N/K)$ with $r = 1.92$/day and $K = 1,000$, $D = 0.24$ m^2/s, $\varsigma = 3599$. The *color legend* in the figure shows the population density

The invasion ratchet has important implications for environmental planning and river management from a practical point of view. Flow control and stream restoration schemes can be designed to support the ratchet mechanism or to make use of its safeguarding function. For example, if the aim is to re-introduce a certain species, its spatial colonization can be supported by low-flow periods of sufficiently long duration, for example by controlling dams, or shortening the length of critical riffles. Conversely, if the aim is to prevent the invasion of non-native species or to achieve their eradication, their toe-holds, for example pools, could be targeted. Importantly, the invasion ratchet highlights that both spatial heterogeneity and temporal variability, not only in flow magnitude, but also duration and frequency, are critical for population distribution.

8.1 Methodological Context and Perspectives

Current methods of environmental flow assessment are biased toward the hydrological side; for references, see the Introduction. For example, complex simulation models like PHABSIM (Milhous and Waddle 2012) provide detailed descriptions of the physical habitat, but the link to the biology is based on static habitat suitability models. The ecological limits of hydrologic alteration (ELOHA) framework (Poff and Zimmerman

2010) is also based on categorizing streams and rivers into certain classes, depending on the expected ecological response to hydrological change.

At the other extreme of the spectrum, recent years have seen an increase population dynamic models of fluvial environments (Hilker and Lewis 2010; Lutscher et al. 2005, 2010; Pachepsky et al. 2005; Pasour and Ellner 2010; Speirs and Gurney 2001), but they usually oversimplify the hydrodynamics. Only a few studies take into account flow regimes that vary spatially (Lutscher et al. 2006) or temporally (Jin and Lewis 2012, 2011; Lutscher and Seo 2011; Seo and Lutscher 2011). Moreover, these variations have been modeled only qualitatively to date, and to our knowledge, have not been explicitly linked to the specific riverbed structure or the seasonal flow regime, even though these factors are known to determine the nature of the fluctuating flow (Allan and Castillo 2007).

Overall, there is a conceptual lack in dynamically coupling the hydrology and ecology of river flows. There are only few studies that provide a mechanistic coupling of hydraulic factors to river population models. Hayes et al. (2007) link a hydraulic model (River2D) via a stream-tube model with a drift-transport model of invertebrates and a drift-foraging model of consumers, but their simulations are confined to a single river pool. Anderson et al. (2013) use a detailed hydrological model of a river stretch in central California that is fed into a particle-tracking algorithm to estimate transport and settling parameters for a 1D population model.

Here, we have provided a modeling framework to couple hydrodynamics and ecological dynamics directly. The hydrodynamic component in our hybrid model is based on the water depth in a gradually varying river structure, from which we derive the advective flow. This is fed into a reaction–diffusion–advection model, which integrates the population dynamical component. Hence, this approach links hydraulic features with an ecological model. This opens up the possibility to gain theoretical understanding and make quantitative predictions. For example, we have investigated how different biological and environmental factors, such as discharge, bed slope, Manning coefficient, water flow per unit width, growth rate, biodiffusion, affect the population's spread rate and persistence in the river. For the 2D model, we use the depth-averaged water flow obtained from a complex simulation model and link it with a population model. This is similar to the method used by Anderson et al. (2013), but in oder to account for drift transport we do not fit a diserpersal model to tracking data as in Anderson et al. 2013), but instead use equation (29) stemming from a benthos-drift model.

In the existing literature, another related approach is suggested by Booker (2003). He used a three-dimensional computational fluid dynamics code to simulate flow patterns and compare them with maximum sustainable swimming speeds of fish, which were determined in laboratory experiments and defined as the maximum flow velocity at which a fish can swim for more than 200 min. If the flow velocity is smaller than the maximum sustainable swimming speed, then fish is considered to be able to spread to the upstream. This is, in some sense, similar to the central role of the upstream spread rate in this paper, i.e., when the upstream spreading speed is positive, the population can spread to the upstream. It should be noted, though, that the upstream spread rate is an emergent feature of ecological life-history and dispersal traits. As such, it has a mechanistic foundation and is not restricted to experimental conditions. On the other extreme, Lytle and Merritt (2004) used a matrix population model, in which they

allowed flow to affect vital rates. However, they used hydrograph data, i.e., there is a mechanistic gap in the hydrology.

We have considered river reaches with pool-riffle sequences, which inherently arise from the underlying river morphology in term of channel bed slope. In fact, pool-riffle sequences are the dominant bedforms in gravel and mixed bedded channels of intermediate slope, and they are widely recreated in restoration schemes (Emery et al. 2003). There are various approaches in the literature that classify rivers structures into "patches" according to the spatial and temporal dimensions of their hydrological characteristics (Emery et al. 2003; Thoms and Parsons 2003; Wallis et al. 2012). However, while this can be used to derive physical biotopes, it lacks a link to population dynamics.

The hydrodynamic component used here is probably relatively simple in comparison to other, more hydraulically oriented work. The major methodological progress is the link to the population dynamical component, which has been critically lacking (Anderson et al. 2006; Lancaster and Downes 2010; Shenton et al. 2012). In this paper, we have considered a single-species population without stage structure, but it is straight-forward to extend the framework to more complicated ecological models, for example, taking into account multiple interacting populations or different life stages.

8.2 Variability in Space and Time

In stream ecosystems, it is well established that hydraulic variations in time and space can affect various species, ranging from periphyton (Reid et al. 2006; Simpson et al. 2008) over macrophytes (Biggs 1996; Suren et al. 2000) and macroinvertebrates (Bouckaert and Davis 1998; Lloyd and Sites 2000) to fish (Jungwirth et al. 1995; Labbe and Fausch 2000). Ecological theory predicts that spatial heterogeneity can decrease or increase rates of spatial spread, depending on whether the scale of spatial heterogeneity is greater or smaller than that of dispersal, respectively (Neubert et al. 2000; Schreiber 2010; Shigesada and Kawasaki 1997; With 2002). This has been demonstrated in experimental streams (Simpson et al. 2008). As for temporal variability, ecological theory predicts that fluctuations promote the coexistence of species (Chesson 2000). In spatially extended systems, they are known to produce "shifting mosaics", which can further enhance biodiversity.

Temporal fluctuations and spatial heterogeneity are therefore recurring themes in ecology, because they strongly impact on biodiversity on all levels, from the individuum over populations and communities to the ecosystem level (Goetze et al. 2008). However, similarly to the field of ecohydrology, the field of global change ecology is also largely dominated by correlative niche models. While they are able to reflect the implications of temporal and spatial variability, these statistical models lack the process dynamics of mechanistic models to investigate the interaction of temporal and spatial variability (Gallien et al. 2010; Ibanez et al. 2013). Hence, the combination of these two sources of variability is rarely studied in ecology, and their interplay is much less understood.

As already pointed out in the Introduction, the idea of an invasion ratchet in ecology has been hypothesized by Jackson et al. (2009). While they invoke a number of poten-

tial paleoecological candidate examples, they do not provide any quantification, and the phenomenon we describe is novel in unidirectional flow environments like rivers and streams. Note that Orrock et al. (2010) also use the term "invasion ratchet", but the phenomenon they describe is essentially just an advancing invasion wave. Critically, this wave lacks the backstop mechanism of a ratchet which provides a safeguard for the population during adverse conditions.

In principle, the invasion ratchet is not restricted to river reaches considered here. While it is particularly intriguing in flow-dominated systems (one could also think of ocean currents, wind, and hill-slopes), flow, as such, is not necessary for the ratchet mechanism. The ratchet requires two sources of variability, and the negative spread rates in the "bad" patches during adverse times could also be driven by hostile biotic or abiotic conditions different from flow, e.g., increased predation pressure in certain habitat types or in different seasons. It is also easy to imagine the ratchet on different scales, e.g. within a single pool or entire watersheds, but this will depend critically on the relative spatial and temporal scales as well as on the life-history traits.

The invasion ratchet appears a plausible phenomenon and may occur in ecosystems. However, we are not aware of any explicit reports by field biologists. The most related study we could find is by Labbe and Fausch (2000) who investigated the Arkansas darter (*Etheostoma cragini*), a threatened fish, in plains streams of southeast Colorado. They found seasonal dynamics in pools that provided refuge to the fish and river reaches that allowed dispersal. In fact, pools could dry during droughts or be scoured by large floods. Hence, flow variation between seasons and years could create "intermittent stream habitats" and determine habitat connectivity, thus controlling population growth and dispersal. Another related study is by Stelter et al. (1997). They modeled the metapopulation dynamics of the grasshopper *Bryodema tuberculata*, who occupies gravel bars along braided rivers in the Northern Alps. Catastrophic floods temporarily wash away the habitats of the species. The model predicts that the timing between such floods is critical for the species survival.

One reason why there is little empirical evidence for the invasion ratchet available in the literature may be that field researchers typically monitor invasive spread using field studies at yearly intervals, which amounts to once per periodic cycle in flow. In this case, the ratchet would not be immediately apparent. However, the ratchet phenomenon may become apparent when sampling intensively over fine time intervals. Data sampling at high resolution in both space and time is costly, though, and there is typically a trade-off. But it appears that refined technologies are becoming increasingly available (Fausch et al. 2002; Power et al. 2005).

8.3 Robustness

This paper studies how an invasion ratchet could occur under reasonable biological assumptions. We start by studying this phenomenon for aquatic species in rivers using mathematical modeling analysis and approximate conditions in a simple piecewise river with fluctuating flows. We move to a gradually varying river structure and adopt a mechanistic equation for gradual water flow to derive the water depth in a river. We then use the water depth to calculate the advective flow in a reaction-diffusion-advection

equation model to study population dynamics and invasions in rivers. Here, we include reasonable hydrologic information into population models to obtain conditions under which invasion via a ratchet mechanism may occur as a result of the interplay of periodic spatial variation in the river and temporally varying flow.

Hence, we have established the invasion ratchet phenomenon in a whole suite of different models, ranging from parsimonious reaction-diffusion-advection models over hybrid hydrodynamic-biological models to high-resolution simulation in two dimensions. This provides strong evidence that the invasion ratchet is not an artifact of a particular model type, but appears to be a robust phenomenon. While the high-resolution model of a meandering river is clearly more realistic and relies on numerical simulation, the more conceptual models allowed us to find an explicit formula or approximations of the spreading speeds, or to prove their existence.

8.4 Summary

The modeling framework presented in this paper closely integrates the physical and biotic functioning of water flow and river structures. In particular, it provides a much needed bridge to connect hydraulics with dynamic population modeling and the advances of ecological theory. The invasion ratchet phenomenon illustrates the importance of accounting for spatial and temporal variability simultaneously. Our hybrid modeling approach provides a quantitative and mechanistic framework for the hydraulic and ecological assessment of rivers. This has the potential to guide water resources managers in identifying more accurately the targets for flow regulation.

Note that in cases where an invasion does not occur, a possible outcome is a stalled invasion, where the population may be established in the lower regions of the river, but cannot spread further up the river (Fig. 1a). This contrasts with previously discovered outcomes, applicable to spatially homogeneous river models and fluctuating flows or spatially heterogeneous rivers and constant flows, where invasions either spread up river or get washed down river, and generically do not stall part way up a river. Our results (Fig. 1a) provide a counterexample to the concept that a positive upstream spreading speed is required if a species is to persist in the river (Lutscher et al. 2010).

Appendix 1: Derivation of Single Models from Benthic-Drift Models

(a) Derivation of (1)

Note that in a river or stream, many species of plankton spend most of the time on the benthos and little time in the flow (Walks 2007). We may divide the whole population

into two parts: population on benthos and population in flow, and then describe the population dynamics by the benthic-drift system [(see (Pachepsky et al. 2005))]

$$\frac{\partial N_d}{\partial t} = \mu N_b - \sigma N_d + D\frac{\partial^2 N_d}{\partial x^2} - v\frac{\partial N_d}{\partial x},$$
$$\frac{\partial N_b}{\partial t} = -\mu N_b + \sigma N_d + f(N_b)N_b, \tag{25}$$

where N_b and N_d are population densities on the benthos and in the flow, respectively, D is the diffusion rate, v is the flow velocity, μ is the transfer rate of individuals from the benthos to the flow, and σ is the transfer rate from the flow to the benthos. In a limiting case, when the transfer rates become strong (i.e., $\sigma, \mu \to \infty$ with $\sigma = \tau\mu$), the second equation in (25) yields $N_b = \tau N_d$, and hence, (25) can be combined into a single equation:

$$\frac{\partial N_b}{\partial t} = \tilde{f}(N_b)N_b + \tilde{D}\frac{\partial^2 N_b}{\partial x^2} - \tilde{v}\frac{\partial N_b}{\partial x} \tag{26}$$

with

$$\tilde{f}(N_b) = \frac{f(N_b)}{1 + 1/\tau}, \tilde{D} = \frac{D}{\tau + 1}, \tilde{v} = \frac{v}{\tau + 1},$$

where f, D, and v are the parameters of (25) [see Sect. 6 in (Pachepsky et al. 2005) for details]. Model (1) is of the same form as (26).

(b) Derivation of (3)

In a spatially heterogeneous habitat, the benthic-drift model becomes

$$\frac{\partial N_d}{\partial t} = \mu N_b - \sigma N_d + \frac{1}{A(x)}\frac{\partial}{\partial x}\left(D(x)A(x)\frac{\partial N_d}{\partial x}\right) - \frac{Q}{A(x)}\frac{\partial N_d}{\partial x},$$
$$\frac{\partial N_b}{\partial t} = -\mu N_b + \sigma N_d + f(N_b)N_b, \tag{27}$$

where $A(x)$ is the cross-sectional area at x (see (Lutscher et al. 2006) for the model details). Similarly as above, when the transfer rates $\mu \to \infty$ and $\sigma \to \infty$ with $\sigma = \tau\mu$, (27) can be combined into a single model, which has the same form as (3).

(c) Derivation of (24)

In a two-dimensional habitat, the benthic-drift model becomes

$$\frac{\partial N_d(x, y, t)}{dt} = \frac{\mu(x, y)}{h(x, y)}N_b(x, y, t) - \sigma(x, y)N_d(x, y, t)$$

$$-\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}[v_1(x,y)h(x,y)N_d(x,y,t)]\right.$$

$$+\frac{\partial}{\partial y}[v_2(x,y)h(x,y)N_d(x,y,t)]\right]$$

$$+\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}\left[D(x,y)h(x,y)\frac{\partial N_d(x,y,t)}{\partial x}\right]\right.$$

$$+\frac{\partial}{\partial y}\left[D(x,y)h(x,y)\frac{\partial N_d(x,y,t)}{\partial y}\right]\right],$$

$$\frac{\partial N_b(x,y,t)}{dt}=f(N_b(x,y,t))+\sigma(x,y)N_d(x,y,t)h(x,y)-\mu(x,y)N_b(x,y,t),$$

$$(28)$$

where $h(x,y)$ is the water depth at (x,y), v_1, and v_2 are the flow velocity in the x and y directions, respectively. Similarly as above, when the transfer rates $\mu \to \infty$ and $\sigma \to \infty$ with $\sigma = \tau\mu/h$, where τ is a constant, we approximately have $n_b = \tau n_d$. Then, the summation of the first equation multiplied by τ and the second equation multiplied by a constant $\varsigma \geq 0$ yields

$$\frac{\partial N_b(x,y,t)}{dt}=\tilde{f}(N_b)N_b-\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}\left[\tilde{v}_1(x,y)h(x,y)N_b(x,y,t)\right]\right.$$

$$+\frac{\partial}{\partial y}\left[\tilde{v}_2(x,y)h(x,y)N_b(x,y,t)\right]\right]$$

$$+\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}\left[\tilde{D}(x,y)h(x,y)\frac{\partial N_b(x,y,t)}{\partial x}\right]\right.$$

$$+\frac{\partial}{\partial y}\left[\tilde{D}(x,y)h(x,y)\frac{\partial N_b(x,y,t)}{\partial y}\right]\right],\qquad(29)$$

with

$$\tilde{f}(N_b)=\frac{\varsigma f(N_b)}{1+\varsigma},\ \tilde{D}=\frac{D}{\varsigma+1},\ \tilde{v}=\frac{v}{\varsigma+1}.$$

Model (24) has the same form of (29) if $f(N_b)=rN_b(1-N_b/K)$.

Appendix 2: The Upstream and Downstream Extents

Definition 1 Assume that a species is introduced into the river at $t=0$. The upstream (downstream) extent (or range) x_t^- (x_t^+) at time t is defined to be the most upstream (downstream) position where individuals are observed at this time.

Remark In simulations, x_t^- (x_t^+) is represented by the location where the population reaches a threshold detection density N_{thresh} at time t in the upstream (downstream) direction. That is, the first x in the upstream (downstream) direction such that $N(t,x)=N_{\text{thresh}}$ is defined as x_t^- (x_t^+). See Fig. 9.
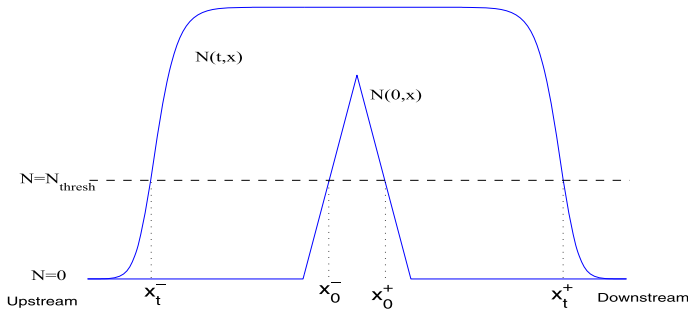
Fig. 9 Upstream and downstream extents of a population with density distribution $N(t, x)$ in a river

Definition 2 Assume that a species is introduced into the river at $t = 0$. The average speeds of spread of the population in the time interval $[0, t]$ are defined as $(x_0^- - x_t^-)/t$ and $(x_t^+ - x_0^+)/t$ in the upstream and downstream directions, respectively.

Remark Note that $(x_0^- - x_t^-)/t \to c^-$ and $(x_t^+ - x_0^+)/t \to c^+$ as $t \to \infty$, where c^- and c^+ are asymptotic spreading speeds as described in Eq. (2). Therefore, we can use $(x_0^- - x_t^-)/t$ and $(x_t^+ - x_0^+)/t$ to approximate the speeds of spread of the population in the upstream and downstream directions. In the simulations in this paper, we simply use the upstream extent x_t^- to describe the upstream invasion.

Appendix 3: The Derivation of the Water Depth Eq. (9)

In a gradually varied flow, the water depth y (unit: m) is non-uniform due to spatially varying slopes of the river bed. The governing equation for the gradually varied flow [see (5–7) in (Chaudhry 1993)] is given as:

$$\frac{dy}{dx} = \frac{S_0(x) - S_f(y)}{1 - F_r^2(y)}. \tag{30}$$

Here, S_0 (unit: m/m) is the slope of the channel bed. It varies in space and is considered as a function of the spatial variable x (unit: m), i.e., $S_0 = S_0(x)$. Generally, the average values of S_0 are between 0.0002 and 0.008 for big rivers and are slightly larger for small streams (see Table 5). S_f is the friction slope, i.e., the slope of the energy grade line, or approximation of the water surface slope. It is also spatially varying and can be determined from the Manning equation

$$S_f = \frac{n^2 v^2}{k^2 R_h^{4/3}}, \tag{31}$$

where n (unit: s/m$^{1/3}$) is Manning's roughness coefficient, varying with basic channel bed mechanism with values in the order of 0.025–0.050 for rivers and representing the resistance to water flows in channels, v (unit: m/s) is the water flow velocity, $k = 1$

Table 5 Parameters in this paper

Parameter	Description	Unit	Typical values
g	The gravitational acceleration	m/s^2	9.8
n	The Manning's roughness coefficient	$s/m^{1/3}$	0.025-0.1 for rivers (Chaudhry 1993)
v	The water flow velocity	m/s	
k	The conversion factor		1 for SI units (Chaudhry 1993)
R_h	The hydraulic radius	m	
A	The wetted area	m^2	
P	The wetted perimeter	m	
F_r	The Froude number		< 1 for subcritical flows (Chaudhry 1993)
S_0	The slope of the channel bed	m/m	0.0002-0.008 for big rivers (Chaudhry 1993)
S_{0r}	The slope of the riffle channel bed	m/m	
S_{0p}	The slope of the pool channel bed	m/m	
S_f	The friction slope	m/m	
B	The width of the river	m	
Q	The flow discharge	m^3/s	
t	The time variable	s	
x	The longitudinally spatial variable	m	
y	The water depth	m	
r	The intrinsic growth rate	/day	
K	The carrying capacity of the species		
L	The length of a river period	m	
L_1	The length of a riffle	m	
L_2	The length of a pool	m	
D_b	The bio-diffusion rate	m^2/s	
D_f	The flow driven diffusion rate	m^2/s	
T	One time period	day	365
T_1	The length of the low flow season	day	
T_2	The length of the high flow season	day	
Q_1	The flow discharge in the low flow season	m^3/s	
Q_2	The flow discharge in the high flow season	m^3/s	

is the conversion factor, R_h (unit: m) is the hydraulic radius, which is the ratio of wetted area A (unit: m^2) and wetted perimeter P (unit: m), i.e., $R_h = A/P$. F_r is the Froude number that is defined as the ratio between the flow velocity and the water wave propagation velocity and is used to determine the resistance of a partially submerged object moving through water. It is a dimensionless parameter. For an arbitrarily shaped channel,

$$F_r = \sqrt{\frac{Q^2 W}{g A^3}},$$

where W (unit: m) is the top width at a particular depth, Q (unit: m³/s) is the flow discharge, and $g = 9.8$ (unit: m/s²) is the gravitational acceleration.

Consider a river (or stream) channel with rectangular cross-sections and fixed width B along one spatial dimension x. Note that for natural rectangular rivers, the width B is much larger than the depth y (i.e., $B \gg y$), and therefore, $R_h = By/(B+2y) \approx y$, so we simply assume $R_h = y$. It then follows that $Q = Av = yBv$, $W \equiv B$,

$$S_f = \frac{n^2 v^2}{k^2 R_h^{4/3}} \approx \frac{n^2 v^2}{k^2 y^{4/3}} = \frac{n^2 Q^2}{k^2 B^2 y^{10/3}} \tag{32}$$

and

$$F_r = \sqrt{\frac{Q^2 W}{g A^3}} = \sqrt{\frac{Q^2 B}{g A^3}} = \frac{Q}{By\sqrt{gy}}. \tag{33}$$

Substituting (32) and (33) into (30), we obtain a first order ODE of the channel depth y:

$$\frac{dy}{dx} = \frac{gk^2 B^2 y^{10/3} S_0(x) - n^2 Q^2 g}{k^2 B^2 g y^{10/3} - Q^2 k^2 y^{1/3}} = \frac{gk^2 y^{10/3} S_0(x) - n^2 (Q/B)^2 g}{k^2 g y^{10/3} - (Q/B)^2 k^2 y^{1/3}}.$$

Appendix 4: The Uniform Flow

Assume that the river has rectangular cross sections and a constant bed slope. If the river channel is long and channel cross sections and the bottom slope do not change with distance, then the flow accelerates or decelerates for a distance until the accelerating and resistive forces are equal (Chaudhry 1993). From that point on, the flow velocity and flow depth remain constant. Such a flow, in which the flow depth does not change with distance, is called a uniform flow, and the corresponding flow depth is called the normal depth, which is actually the critical point of Eq. (9) with a constant bed slope S_0:

$$y_n = \left(\frac{Q^2 n^2}{B^2 S_0 k^2} \right)^{\frac{3}{10}}.$$

As a subcritical flow has downstream control, for any downstream boundary condition, in such a flow, the water depth approximates to the normal depth in the upstream end far away from the downstream (see Fig. 10). Therefore, if we just consider the population
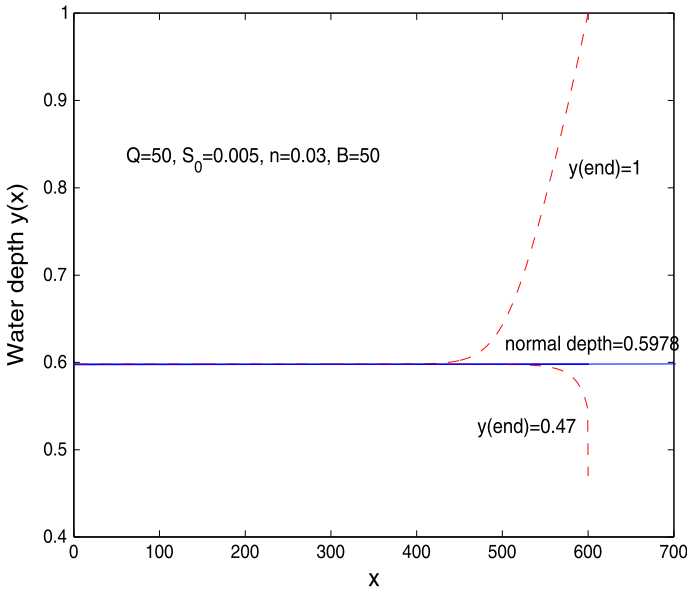
Fig. 10 The water depths in a river with a constant bed slope and with different downstream boundary conditions. The *solid line* represents the normal depth $y_n = 0.5978m$. Parameters: $g = 9.8\ m/s^2$, $k = 1$, $B = 50\ m$, $n = 0.03\ s/m^{1/3}$, $S_0 = 0.005$, $Q = 50\ m^3/s$, channel length $= 700m$

spreading to the upstream end, then we may assume that the water depth stays at the normal depth, and the associated flow is a uniform flow.

Appendix 5: The Periodic Solution to (9)

Existence, Uniqueness and Stability

Note that a periodic solution to (9) with period L corresponds to a solution to (19), and that a flow is subcritical if and only if $F_r < 1$, which implies that $y > y_c = (Q^2/(B^2g))^{1/3}$, where y_c is called the critical depth of the river. We solve the ODE (19) in the half plane of $y > y_c$. When the bed slope $S_0(x)$ is given as in (18), (19) has a solution if and only if there exists some $y_0 > y_c$ such that the solutions to the two problems

$$\begin{cases} \dfrac{dy_1}{dx} = \dfrac{gk^2y_1^{10/3}S_{0r} - n^2(Q/B)^2g}{k^2gy_1^{10/3} - (Q/B)^2k^2y_1^{1/3}} \quad \text{and} \\ y_1(0) = y_0. \end{cases}$$

$$\begin{cases} \dfrac{dy_2}{dx} = -\left(\dfrac{gk^2y_2^{10/3}S_{0p} - n^2(Q/B)^2g}{k^2gy_2^{10/3} - (Q/B)^2k^2y_2^{1/3}} \right), \\ y_2(0) = y_0. \end{cases}$$

satisfy $y_1(L_1) = y_2(L_2)$, which is true if and only if there exists some $y_0 > y_c$ such that the solutions to the two problems

$$\begin{cases} \dfrac{\mathrm{d}y_1}{\mathrm{d}x} = \dfrac{gk^2 y_1^{10/3} S_{0r} - n^2 (Q/B)^2 g}{k^2 g y_1^{10/3} - (Q/B)^2 k^2 y_1^{1/3}} \quad \text{and} \\ y_1(0) = y_0. \end{cases}$$

$$\begin{cases} \dfrac{\mathrm{d}y_3}{\mathrm{d}x} = -\left(\dfrac{gk^2 y_3^{10/3} S_{0p} - n^2 (Q/B)^2 g}{k^2 g y_3^{10/3} - (Q/B)^2 k^2 y_3^{1/3}} \right) \cdot \dfrac{L_2}{L_1}, \\ y_3(0) = y_0. \end{cases}$$

satisfy $y_1(L_1) = y_3(L_1)$.

We actually look for a solution to (19) in the half plane of $y > y_n$, where $y_n = \left(Q^2 n^2 / (B^2 S_{0r} k^2)\right)^{3/10}$ is the normal depth of the river where the bed slope is S_{0r}, because otherwise it is easy to see from the above equivalent relations that we cannot have a solution to (19). Let f_1 and f_2 be the right-hand sides of these two equations, respectively. Then f_1 is an increasing function of y, and f_2 is a decreasing function of y. As $S_{0r} > 0$ and $S_{0p} < 0$, we know that $f_1 < f_2$ for small $y > y_c$ and $f_1 > f_2$ for big $y > y_c$. This results in that the solution $y_1(x, y_0) < y_3(x, y_0)$ at small x and $y_1(x, y_0) > y_3(x, y_0)$ at big x provided that y_0 is not such that $f_1 > f_2$. Therefore, by the continuity of y_1 and y_3 with respect to x, for any $y_0 > y_c$ with $f_1(y_0) < f_2(y_0)$, there exists an x_{y_0} such that $y_1(x_{y_0}, y_0) = y_3(x_{y_0}, y_0)$. By the continuity and monotonicity of f_1 and f_2, there exists a unique $y_0 > y_n$ such that $x_{y_0} = L_1$, which corresponds to a unique solution to (19).

For any solution to (9) with some downstream boundary condition, we can show that the solution approaches the periodic solution at the very upstream periods by iterating the solution backward from the downstream to the upstream. As an illustration, an example is shown in Fig. 11, where the solid curve represents the periodic solution. Therefore, the periodic solution to (9) is stable for solutions to (9) with all downstream boundary conditions.

Numerical Calculation of the Periodic Solution

Recall that subcritical flow has a downstream control, which means that to change the flow conditions in a section, flow conditions must be changed at a downstream location. Consequently, when we solve Eq. (19), we start the computation at a downstream control section and proceed in the upstream direction.

In more details, the idea for solving (19) is as follows. Guessing a boundary value $y^{(0)}(L)$ at the downstream end $x = L$, one calculates backward and obtains all values of y on $[0, L]$, especially $y^{(0)}(0)$ at the upstream end $x = 0$. Then one iterates by taking a new boundary value at the downstream $y^{(1)}(L) = y^{(0)}(0)$ and obtains $y^{(1)}(0)$. Then let $y^{(2)}(L) = y^{(1)}(0)$ and repeat the process till $y^{(n)}(0) = y^{(n)}(L)$ at the n-th step. The reason for integrating backward is that the depth is asymptotic to a constant (called normal depth) proceeding upstream. The fixed point iteration scheme will converge
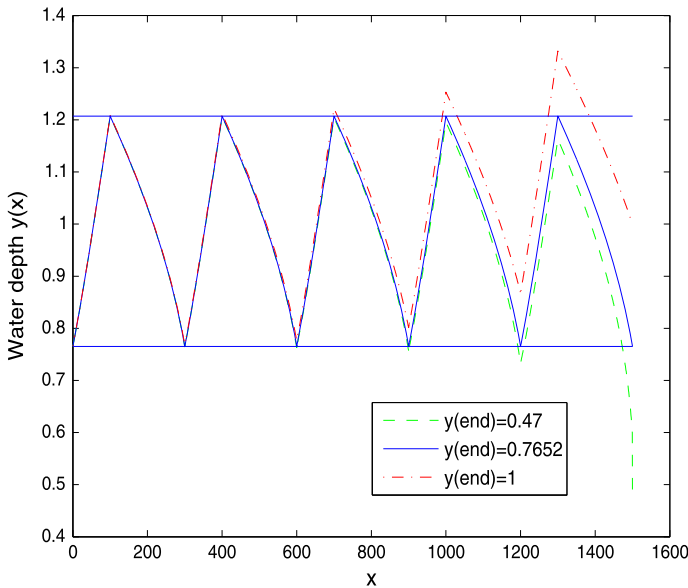
Fig. 11 The water depths in a periodic pool-riffle river with different downstream boundary conditions. The *solid line* is the periodic solution with downstream boundary condition $y(\text{end}) = 0.7652$ m. Parameters: $g = 9.8$ m/s^2, $k = 1$, $B = 50$ m, $n = 0.03$ s/m$^{1/3}$, $L_1 = 100$ m, $L_2 = 200$ m, $S_{0p} = -0.001$, $S_{0r} = 0.005$, $Q=50$ m^3/s, channel length$= 1,500$ m

very quickly integrating upstream, while it will diverge if integrated downstream. In each iteration, the equation is solved by the Runge–Kutta method.

Appendix 6: Spreading Speeds for the Models

Spreading Speeds for the Model in a Temporally Constant Flow

The Existence of Spreading Speeds for (3)

Let $N(t, x)$ be the solution to (3) with initial value $N_0 \in C(\mathbb{R}, \mathbb{R})$. Define the solution map Φ_t of (3) as

$$\Phi_t[N_0](x) = N(t, x), \ t \geq 0.$$

It follows from the standard theory of solutions to (3) that (3) generates a monotone semiflow $\{\Phi_t\}_{t \geq 0}$ in the sense that $\Phi_0[N_0] = N_0$ for all $N \in C(\mathbb{R}_+, \mathbb{R})$, $\Phi_t[\Phi_s[N_0]] = \Phi_{t+s}[N_0]$ for all $t \geq 0$, $s \geq 0$ and $N_0 \in C(\mathbb{R}, \mathbb{R})$, and $Q[t, N_0] := \Phi_t[N_0]$ is continuous in (t, N_0) for all $t \geq 0$ and $N_0 \in C(\mathbb{R}, \mathbb{R})$. As (3) is a standard parabolic equation, Φ_t satisfies all conditions in the abstract theory for spreading speeds for a semiflow defined in a periodic habitat in (Liang and Zhao 2010). Then by (Liang and Zhao 2010, Theorem 5.2), we obtain the existence of the upstream and downstream spreading speeds (c^- and c^+) [see also e.g., (Berestycki et al. 2005; Liang

and Zhao 2007; Weinberger 2002)]. Note that by similar arguments to those in (Lou and Zhao 2010, Lemma 2.10), we have $c^+ + c^- > 0$. The results of spreading speeds are included in the following theorem.

Theorem 1 *Let $N(t, x; \varphi)$ be the solution of (3) with $N(0, x; \varphi) = \varphi(x)$ for all $x \in \mathbb{R}$. The system (3) admits upstream spreading speed c^- and downstream spreading speed c^+ in the following sense.*

(i) *For any $c > c^+$ and $c' > c^-$, if $\varphi \in C_K = \{\psi \in C(\mathbb{R}, \mathbb{R}), 0 \le \psi(x) \le K \text{ for all } x \in \mathbb{R}\}$ with $\varphi(x) = 0$ for x outside a bounded interval, then*

$$\lim_{t \to \infty, x \ge ct} N(t, x; \varphi) = 0, \qquad \lim_{t \to \infty, x \le -c't} N(t, x; \varphi) = 0.$$

(ii) *For any $c < c^+$ and $c' < c^-$, there is a positive number $r \in \mathbb{R}$, such that if $\varphi \in C_K$ and $\varphi(x) > 0$ for x on an interval of length r, then*

$$\lim_{t \to \infty, -c't \le x \le ct} (N(t, x; \varphi) - K) = 0.$$

Moreover, the spreading speeds in the upstream and downstream directions are also the minimal wave speeds for spatially periodic traveling waves, respectively. The following result follows from Theorem 5.3 in (Liang and Zhao 2010).

Theorem 2 *$\{\Phi_t\}_{t \ge 0}$ has an L-periodic rightward traveling wave $V(x - ct, x)$ connecting K to 0 with $V(\xi, x)$ being continuous and non-increasing in $\xi \in \mathbb{R}$ if and only if $c \ge c_+$. $\{\Phi_t\}_{t \ge 0}$ has an L-periodic rightward traveling wave $V(x + ct, x)$ connecting 0 to K with $V(\xi, x)$ being continuous and increasing in $\xi \in \mathbb{R}$ if and only if $c \ge c_-$.*

The Estimation of Spreading Speeds for (20)

We can follow the steps in Example 6.2 in (Weinberger 2002) to derive the spreading speeds for (20). The linearized equation for (20) at $N = 0$ is

$$\frac{\partial N(t, x)}{\partial t} = \frac{1}{y(x)} \frac{\partial}{\partial x} \left[D(x) y(x) \frac{\partial N(t, x)}{\partial x} \right] - \frac{Q}{B y(x)} \frac{\partial N(t, x)}{\partial x} + r N(t, x). \quad (34)$$

Let $N(t, x) = e^{\lambda t - \zeta \rho x} \psi(x)$ with $\zeta > 0$ and $\rho = \pm 1$, and substitute it into (34). We obtain

$$\lambda e^{\lambda t - \zeta \rho x} \psi(x) = \frac{1}{y(x)} \frac{\partial}{\partial x} \left[D(x) y(x) \frac{\partial [e^{\lambda t - \zeta \rho x} \psi(x)]}{\partial x} \right]$$
$$- \frac{Q}{B y(x)} \frac{\partial [e^{\lambda t - \zeta \rho x} \psi(x)]}{\partial x} + r e^{\lambda t - \zeta \rho x} \psi(x),$$

which can be simplified as

$$\lambda \psi(x) = D(x)\psi''(x) + \left[\frac{1}{y(x)} \frac{\partial(D(x)y(x))}{\partial x} - 2\zeta\rho D(x) - \frac{Q}{By(x)} \right] \psi'(x)$$
$$+ \left[D(x)\zeta^2 - \frac{\zeta\rho}{y(x)} \frac{\partial(D(x)y(x))}{\partial x} + \frac{Q\zeta\rho}{By(x)} + r \right] \psi(x). \tag{35}$$

Define L_ρ as

$$L_\rho := D(x)\frac{\partial^2}{\partial x^2} \left[\frac{1}{y(x)} \frac{\partial(D(x)y(x))}{\partial x} - 2\zeta\rho D(x) - \frac{Q}{By(x)} \right]$$
$$+ \frac{\partial}{\partial x} \left[D(x)\zeta^2 - \frac{\zeta\rho}{y(x)} \frac{\partial(D(x)y(x))}{\partial x} + \frac{Q\zeta\rho}{By(x)} + r \right].$$

It follows that L_ρ is compact and strongly positive, and hence, it admits a single principal eigenvalue with a positive periodic eigenfunction. Let $\lambda(\zeta\rho)$ be the principle eigenvalue and ψ be the associated positive periodic eigenfunction. Then $\lambda(\zeta\rho)$ and ψ satisfy (35) with $\psi(0) = \psi(L)$ and $\psi'(0) = \psi'(L)$. Define

$$c^\rho = \inf_{\zeta > 0} \frac{\lambda(\zeta\rho)}{\zeta}.$$

When $\rho = 1$, c^ρ is the downstream spreading speed and when $\rho = -1$, c^ρ is the upstream spreading speed. We can apply the techniques for the principal eigenvalue of Hill's equations to (35) to obtain $\lambda\psi(x)$.

This approximation provides a way to estimate spreading speeds for (20). However, we cannot have explicit expressions and will have to follow numerical calculations. This results in difficulties in finding how different factors affect spreading speeds.

Spreading Speeds for the Model in a Time-Varying Flow Environment (22)

To find the spreading speeds for the model (22) with varying water discharge, let $N(t, x) = V(t, x) \cdot e^{-\eta\rho x}$ and substitute it into the linearized equation of (22) at $N = 0$:

$$\frac{\partial N(t, x)}{\partial t} = -\frac{\partial y(t, x)}{\partial t} \cdot \frac{N(t, x)}{y(t, x)}$$
$$+ \frac{1}{y(t, x)} \frac{\partial}{\partial x} \left[D(t, x)y(t, x)\frac{\partial N(t, x)}{\partial x} \right]$$
$$- \frac{Q(t)}{By(t, x)} \frac{\partial N(t, x)}{\partial x} + f(0)N(t, x), \tag{36}$$

where ρ represents the direction with $\rho = 1$ in the downstream direction and $\rho = -1$ in the upstream direction. We then have

$$
\begin{aligned}
\frac{\partial V(t,x)}{\partial t} = {} & -\frac{\partial y(t,x)}{\partial t} \cdot \frac{V(t,x)}{y(t,x)} + D(t,x)\frac{\partial^2 V(t,x)}{\partial x^2} \\
& + \left[-2\eta\rho D(t,x) + \frac{\partial D(t,x)}{\partial x} + \frac{D(t,x)}{y(t,x)}\frac{\partial y(t,x)}{\partial x} - \frac{Q(t)}{By(t,x)} \right]\frac{\partial V(t,x)}{\partial x} \\
& + \left[\eta^2 D(t,x) - \eta\rho \left(\frac{\partial D(t,x)}{\partial x} + \frac{D(t,x)}{y(t,x)}\frac{\partial y(t,x)}{\partial x} - \frac{Q(t)}{By(t,x)} \right) + f(0) \right] \\
& \times V(t,x),
\end{aligned}
\tag{37}
$$

Let $L_{\eta\rho}^T$ be the Poincaré map of (37), where T is the period of the varying flow. Then the theory in (Weinberger 2002) implies that the spreading speed of $L_{\eta\rho}^T$ is

$$
c_\rho^T = \inf_{\eta > 0} \frac{\ln \lambda(\eta\rho)}{\eta},
$$

where $\lambda(\eta\rho)$ is the principal eigenvalue of $L_{\eta\rho}^T$ corresponding to a positive periodic eigenfunction, and the sign of ρ determines the direction (upstream or downstream). It then follows from the theory in (Liang et al. 2006) that the spreading speed of (22) is

$$
c_\rho = \frac{1}{T} \inf_{\eta > 0} \frac{\ln \lambda(\eta\rho)}{\eta}.
$$

c_1 is the downstream spreading speed, and c_{-1} is the upstream spreading speed.

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