Analysis of spatiotemporal models for stream and river populations

Mark Lewis (Alberta)

Collaborators:
Hannah McKenzie (Alberta Environment),
Yu Jin (Alberta),
Jon Jacobsen (Harvey Mudd),
Peter Steffler (Alberta),
Julia Blackburn

Essential question:

How much water is required to maintain river ecosystems?

What is the impact of changes in flow regimes on ecosystems?

POPULATION DYNAMICS

and

DISTRIBUTIONS

Challenges

Spatial and Temporal

Environmental Heterogeneity

Anthropogenic Inputs

ABIOTIC FORCING

Factors effecting population dynamics in river ecosystems

• Biological factors: growth, biodiffusion, transfer between benthos and water, interspecific interactions.

• Physical factors: water flow, advection, diffusion, channel shape, temperature, ice

Effects of flows on ecosystems

• High flows may wash species downstream.

• Drift paradox: how can species persist in rivers where flow is unidirectional?

• Low flows provide insufficient food for drift feeders.

• They may also allow invaders to thrive, driving out resident species

Mathematical model for river dynamics

- Reaction-diffusion-advection models (Bencala and Walters (1983), DeAngelis et al. (1995), Speirs and Gurney (2001), Pachepsky et al. (2005), Lutscher et al. (2006) etc.).

- Integrodifferential/integrodifference models (Lutscher et al. (2005), Nisbet et al. (2007) etc.).

- Numerical flow models coupled to habitat suitability for target species (Rosenfeld (2003), PHABSIM)

- Numerical flow models coupled to population dynamical equations (uses River2D, Steffler, Blackburn, Jin and Lewis (in prep)).

Mathematical ideas

- Spreading speeds/critical domain size (Spiers and Gurney (2001), Lutscher et al. (2010) etc.).

- Uptake and spiraling lengths (Anderson et al. (2005)).

- Dynamic energy budget models (Nisbet et al. (2000), Kooijman et al. (2000)).

- Habitat heterogeneity and ecological requirements (Rosenfeld (2003)).

Outline

• How can we manage rivers? Biological dynamics and management question.

• Biology meets physics: coupling population dynamics to stream flows

• The stream paradox: spreading speeds and critical domain size

• Is this a good place to live? Niche theory and the net reproductive rate

• Towards realistic stream models

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Water management

• Trade-off between urban, industrial, agricultural and conservation goals for water

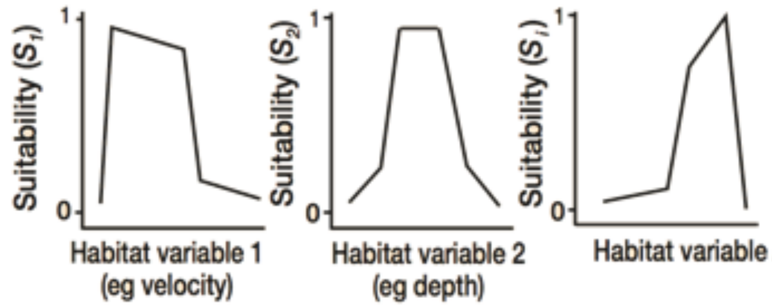
• Flows can be modified, and discharges can be varied and timed

• Successful management requires knowledge of flows required to maintain ecosystem integrity (instream flow needs)

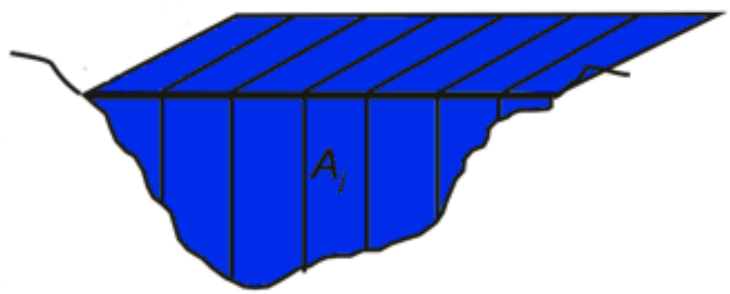
Dickson dam, Red Deer river, AB

Habitat modelling

1. Estimate *habitat suitability curves* from empirical data



2. Run a *habitat simulation model* to determine river characteristics (e.g. River2D)



3. Compute the *weighted usable area* available to species under various flow regimes

$$\mathrm{WUA} = \sum_j \underbrace{A_j}_{\text{Area of section } j} \underbrace{\Pi S_{ij}}_{\text{Suitability of section } j}$$

After Anderson *et al.*, *Frontiers in Ecology*, 2006

Can process-oriented models lead to better instream flow assessment?

• Process-oriented models can potentially include population dynamics, competition, predation, community structure, as interactions with the abiotic environment.

• Ideally they should be able to demonstrate how these factors change with river flow and hence how ecosystem function depends on water flow.

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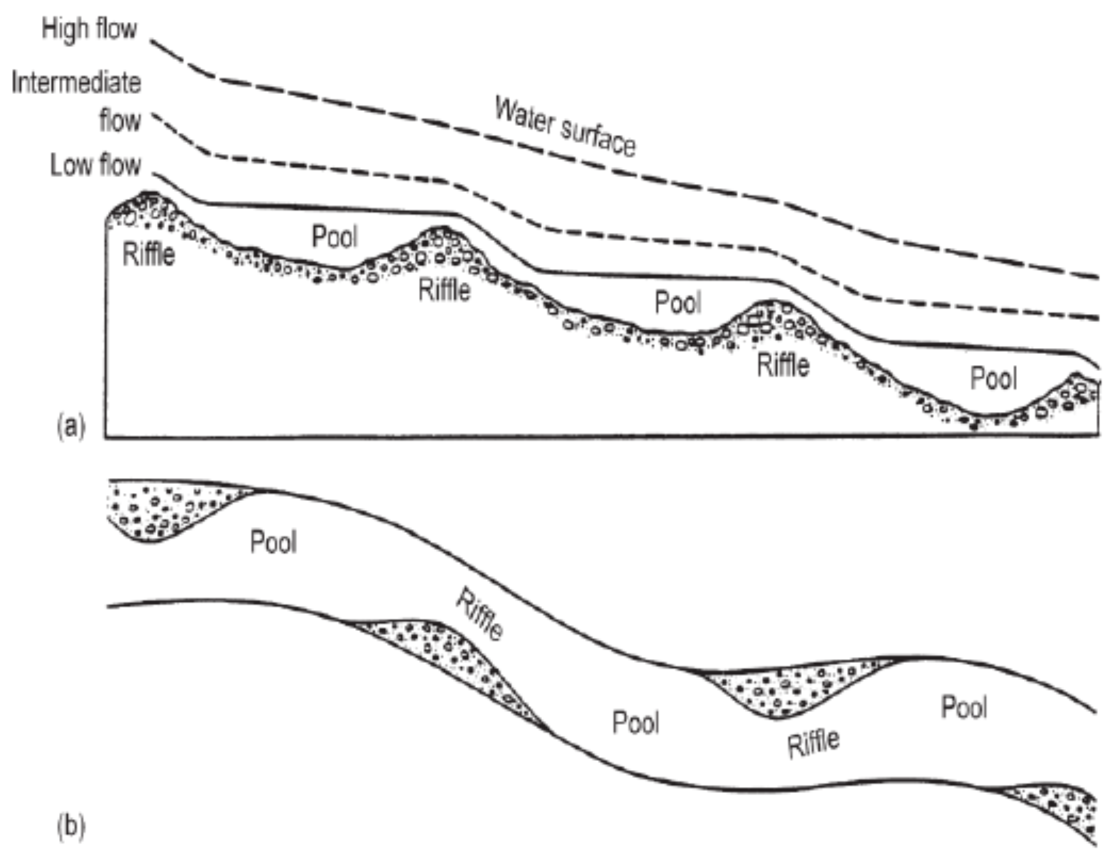
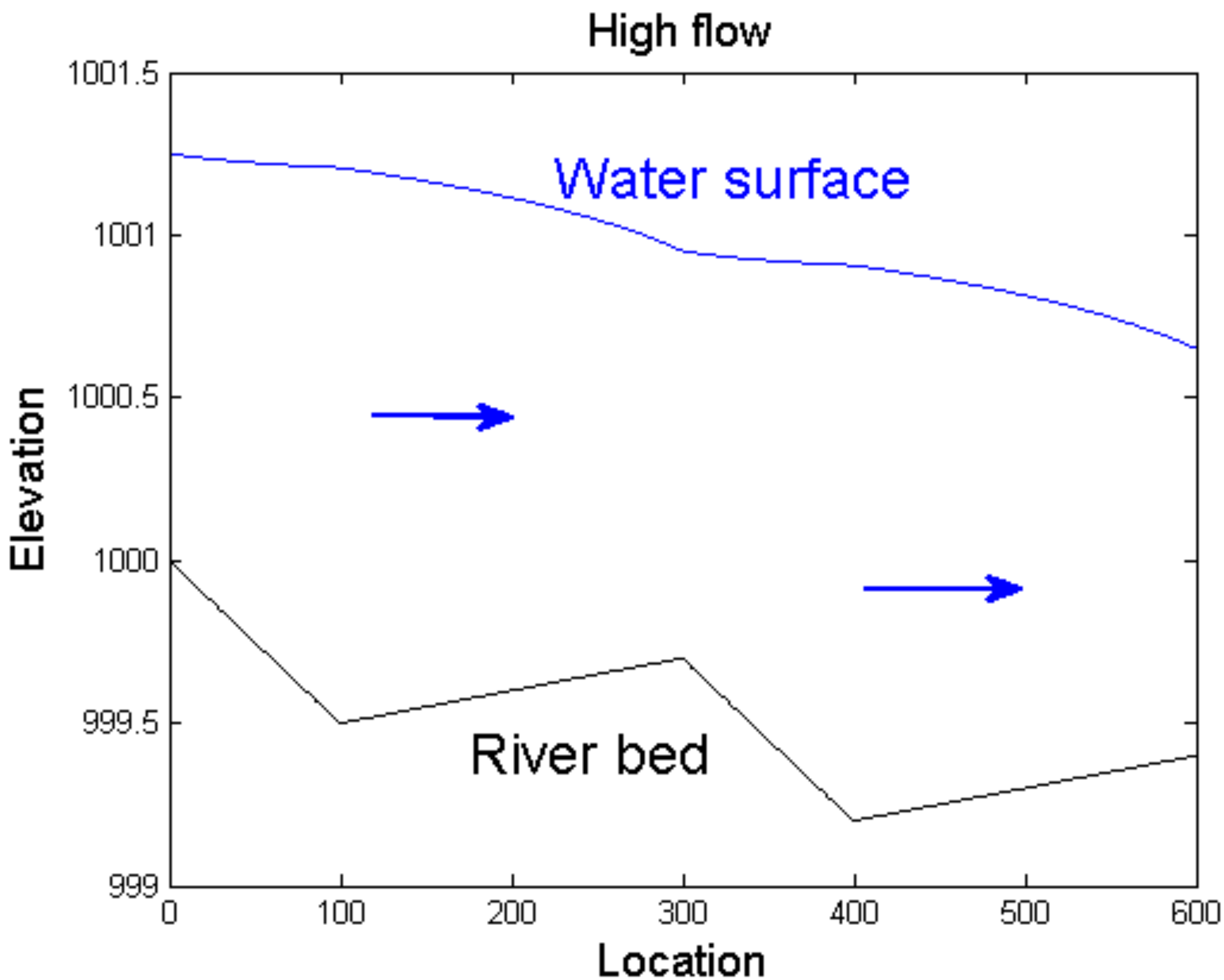


FIGURE 3.5 A longitudinal profile (a) and a plan view (b) of a riffle-pool sequence. Water surface profiles in (a) depict high-, intermediate-, and low-flow conditions. (Reproduced from Dunne and Leopold 1978.)



High flow
Water surface
River bed
Elevation
Location
1001.5
1001
1000.5
1000
999.5
999
0
100
200
300
400
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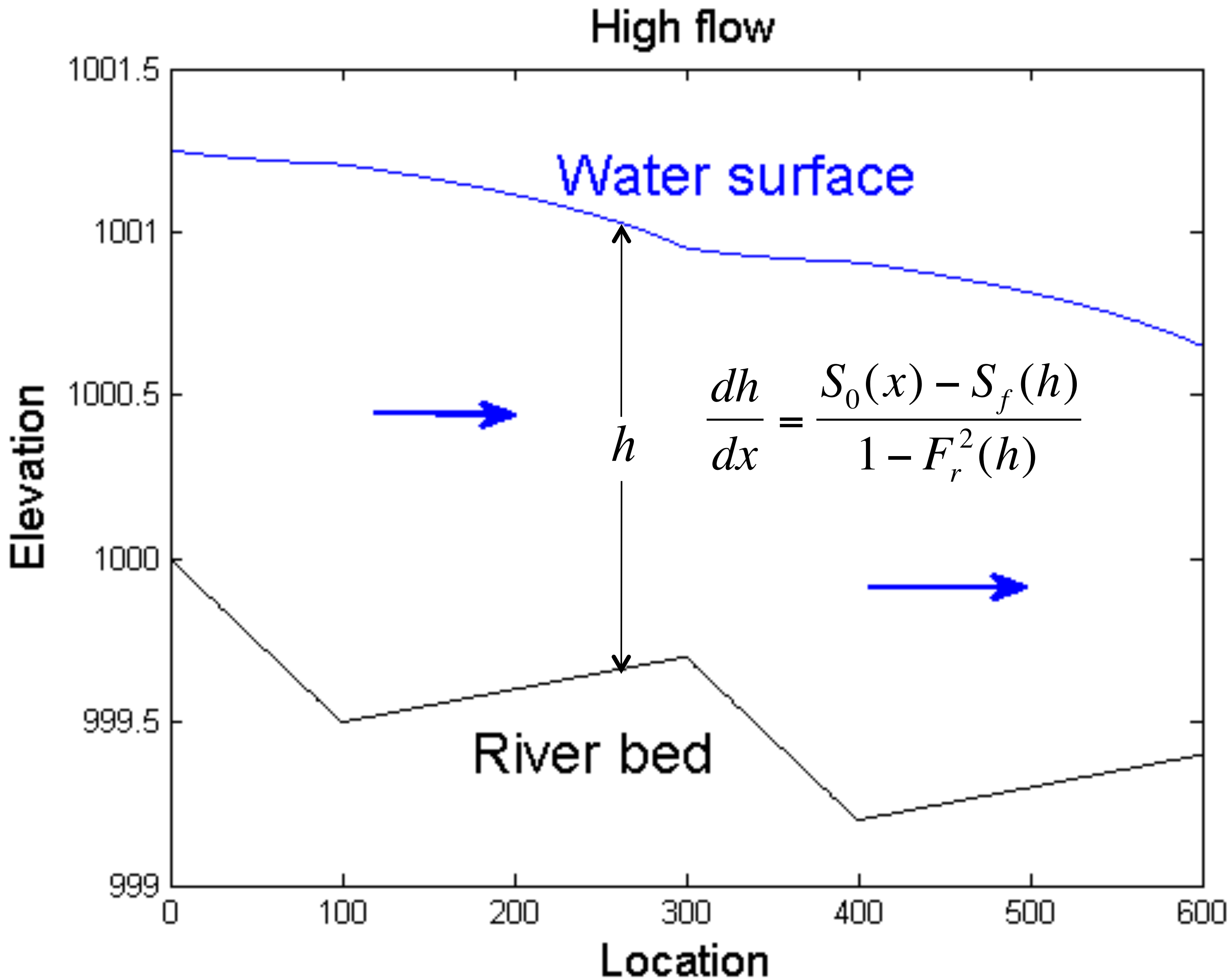
600


High flow
Water surface
River bed
h
$$\frac{dh}{dx} = \frac{S_0(x) - S_f(h)}{1 - F_r^2(h)}$$
Elevation
Location
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1000.5
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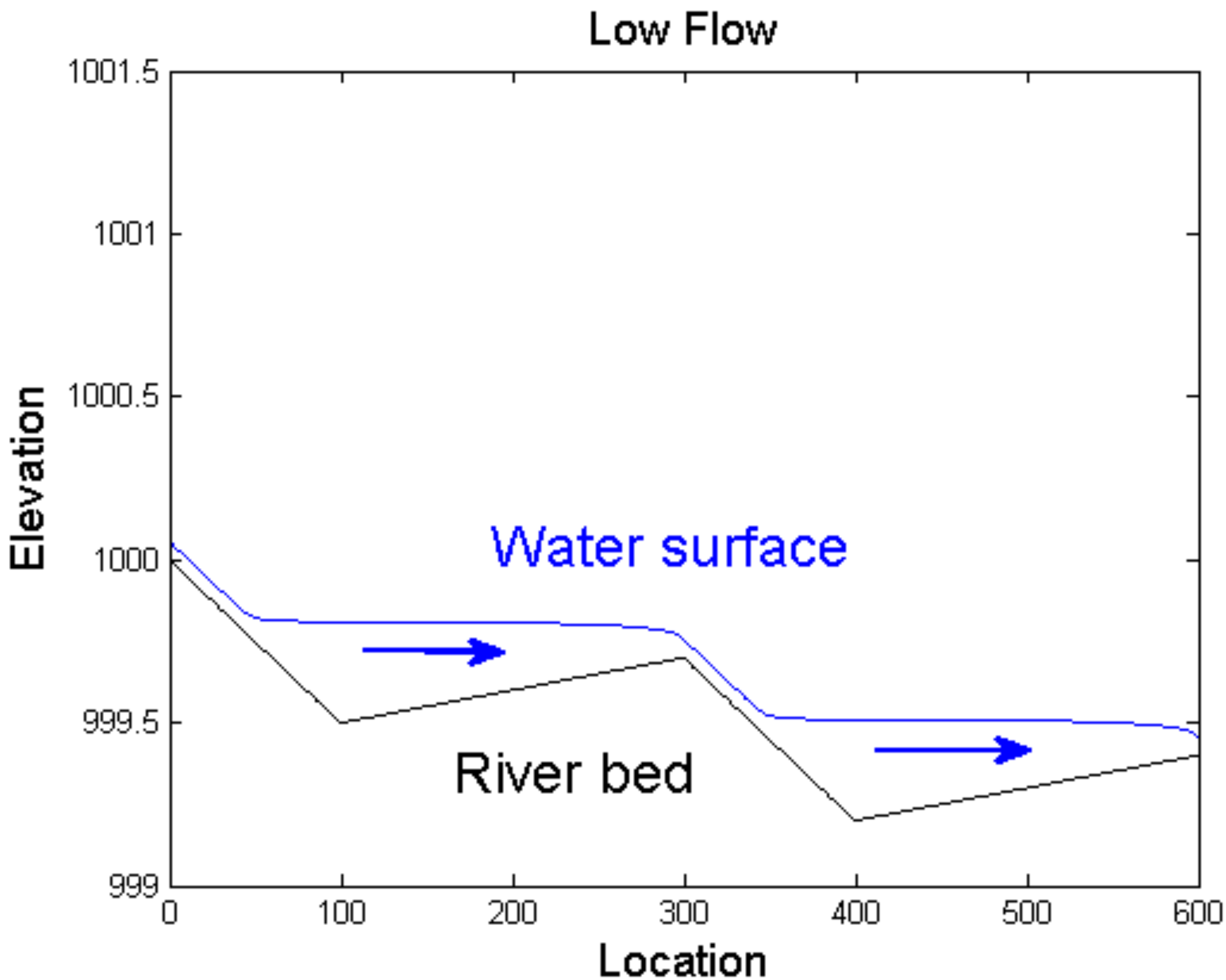
Low Flow
1001.5
1001
1000.5
1000
999.5
999
Elevation
Water surface
River bed
0
100
200
300
400
500
600
Location

Adding a single pelagic population in the drift

$$\underbrace{\frac{\partial n}{\partial t}}_{\text{rate of change of population density}} = \underbrace{\frac{1}{h(x)}\frac{\partial}{\partial x}\left[D(x)h(x)\frac{\partial n}{\partial x}\right]}_{\text{diffusion}} - \underbrace{\frac{1}{h(x)}\frac{\partial}{\partial x}\left[a(x)h(x)n\right]}_{\text{advection}} + \underbrace{g(x,n)n}_{\text{growth dynamics}}$$

where

$$a(x) = \frac{Q}{Bh(x)} = \text{ flow divided by cross-sectional area}$$

and

$$\underbrace{D(x)}_{\text{difusion coefficient}} = \underbrace{D_b}_{\text{biological diffusion}} + \underbrace{D_f(h(x))}_{\text{turbulent and shear dispersion}}$$

with boundary conditions

$$0 = D(x)\frac{\partial n}{\partial x} - a(x)n \quad \text{at x} = 0 \text{ (zero flux) and}$$

$$0 = \frac{\partial n}{\partial x} \qquad \text{at x} = \text{L (free flow)}$$

Bencala and Walters (1983)

Adding a single pelagic population in the drift

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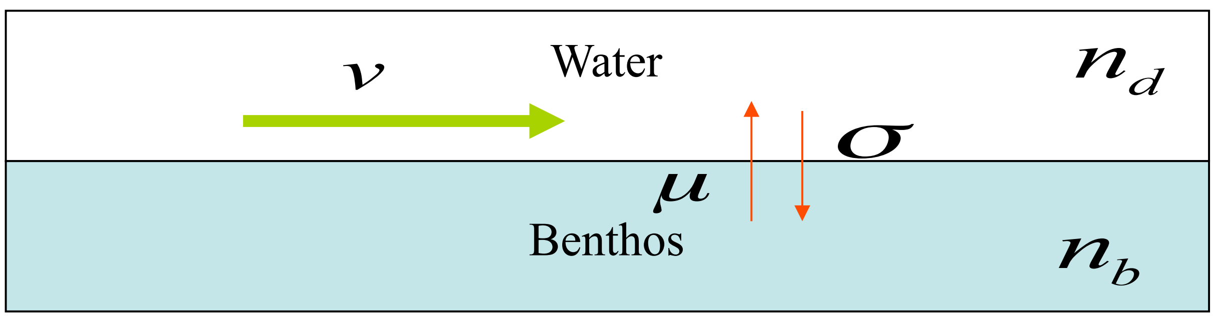
Bencala and Walters (1983)

Model with drift and benthic populations

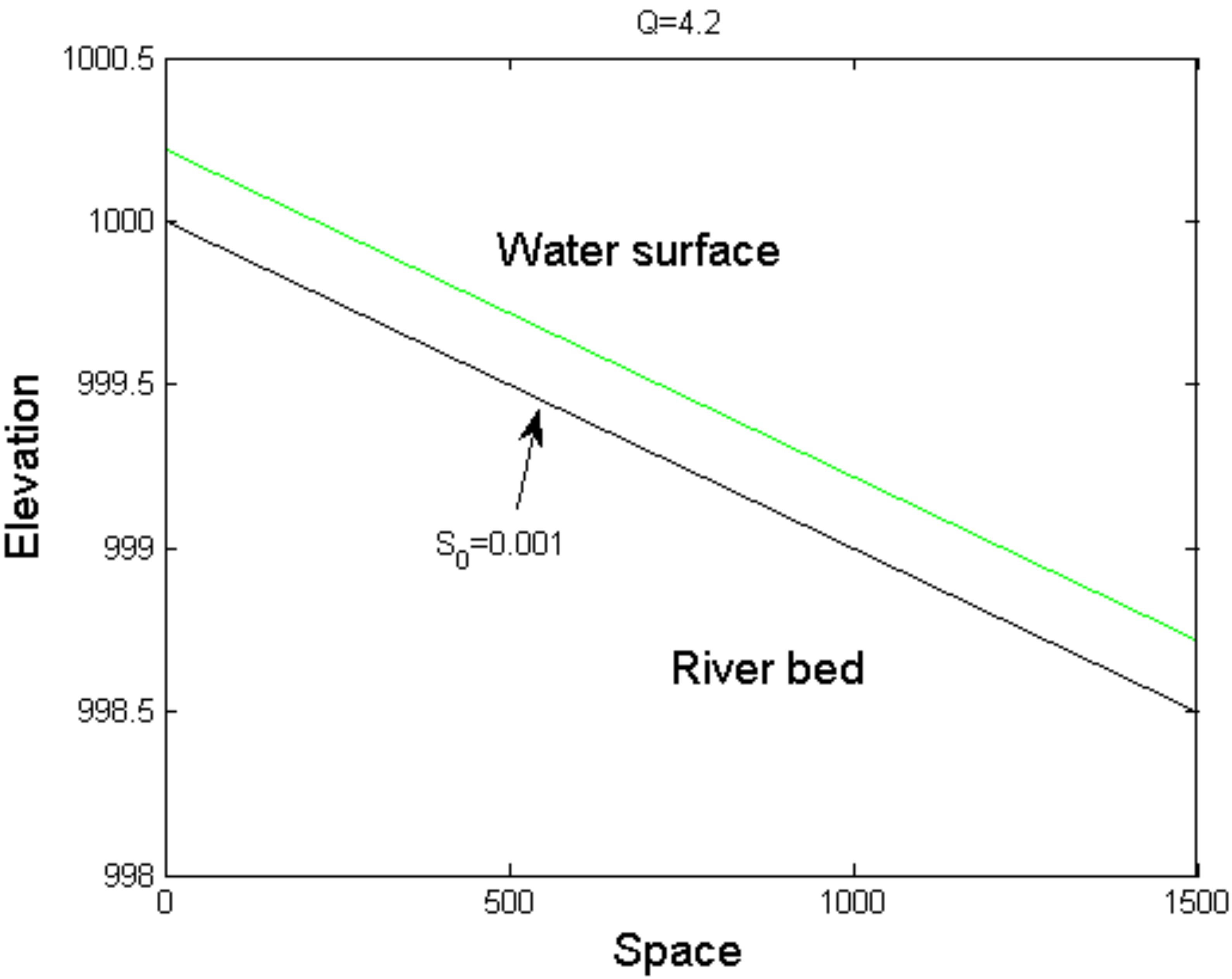
$$\underbrace{\frac{\partial n_d}{\partial t}}_{\text{rate of change of drift population density}} = \underbrace{\frac{1}{h(x)}\frac{\partial}{\partial x}\left[D_d(x)h(x)\frac{\partial n_d}{\partial x}\right]}_{\text{diffusion in drift}} - \underbrace{\frac{Q}{Bh(x)}\frac{\partial n_d}{\partial x}}_{\text{advection}} + \underbrace{\frac{\mu}{h(x)}n_b}_{\text{transfer from benthos}} - \underbrace{\sigma n_d}_{\text{transfer to benthos}}$$

$$\underbrace{\frac{\partial n_b}{\partial t}}_{\text{rate of change of benthic population density}} = \underbrace{-\mu n_b}_{\text{transfer to drift}} + \underbrace{\sigma h(x) n_d}_{\text{transfer from drift}} + \underbrace{g(x, n_b) n_b}_{\text{growth dynamics}} + \underbrace{D_b \frac{\partial^2 n_b}{\partial x^2}}_{\text{diffusion on benthos}}$$

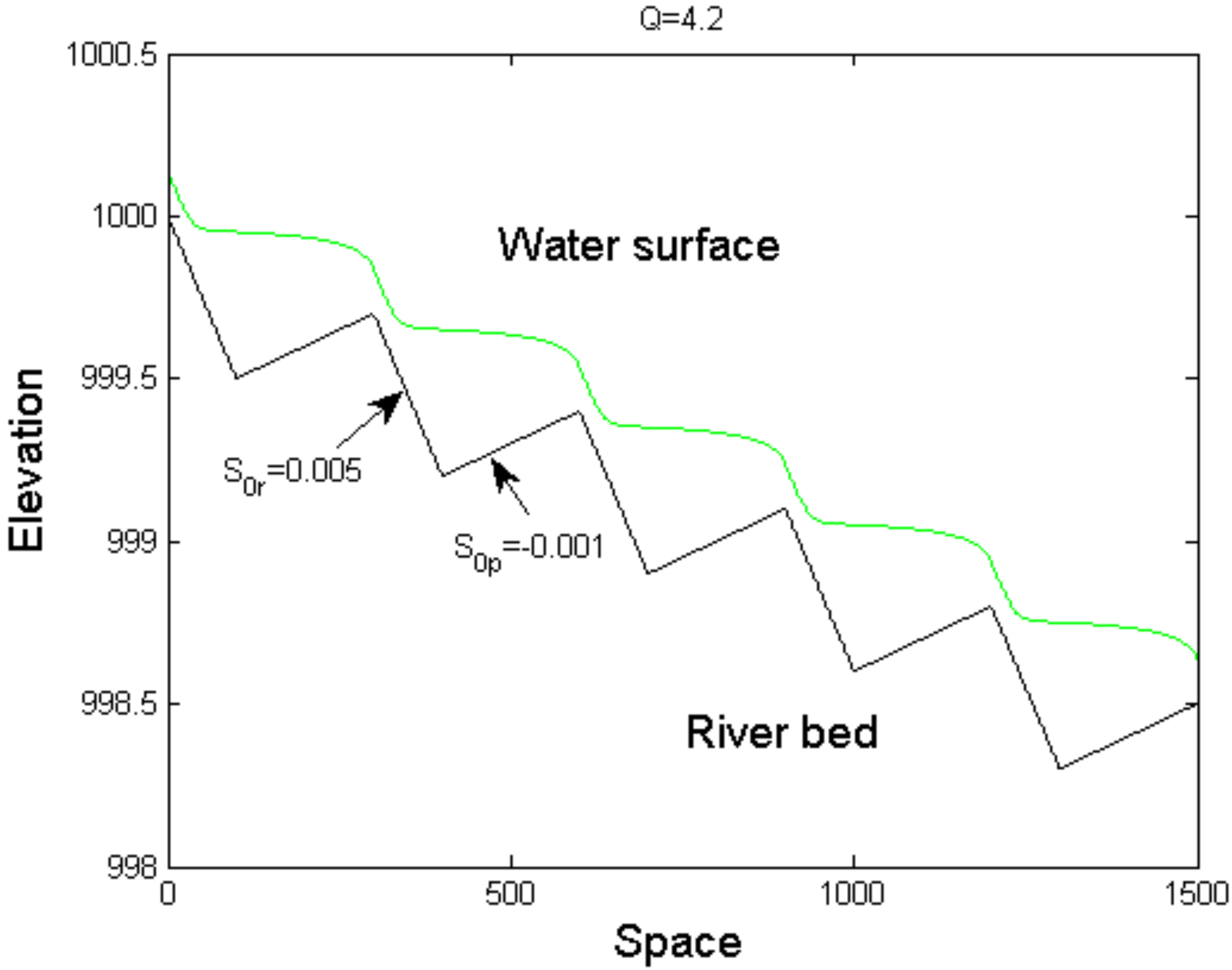


In results given below, it is assumed D_b=0 unless otherwise stated.

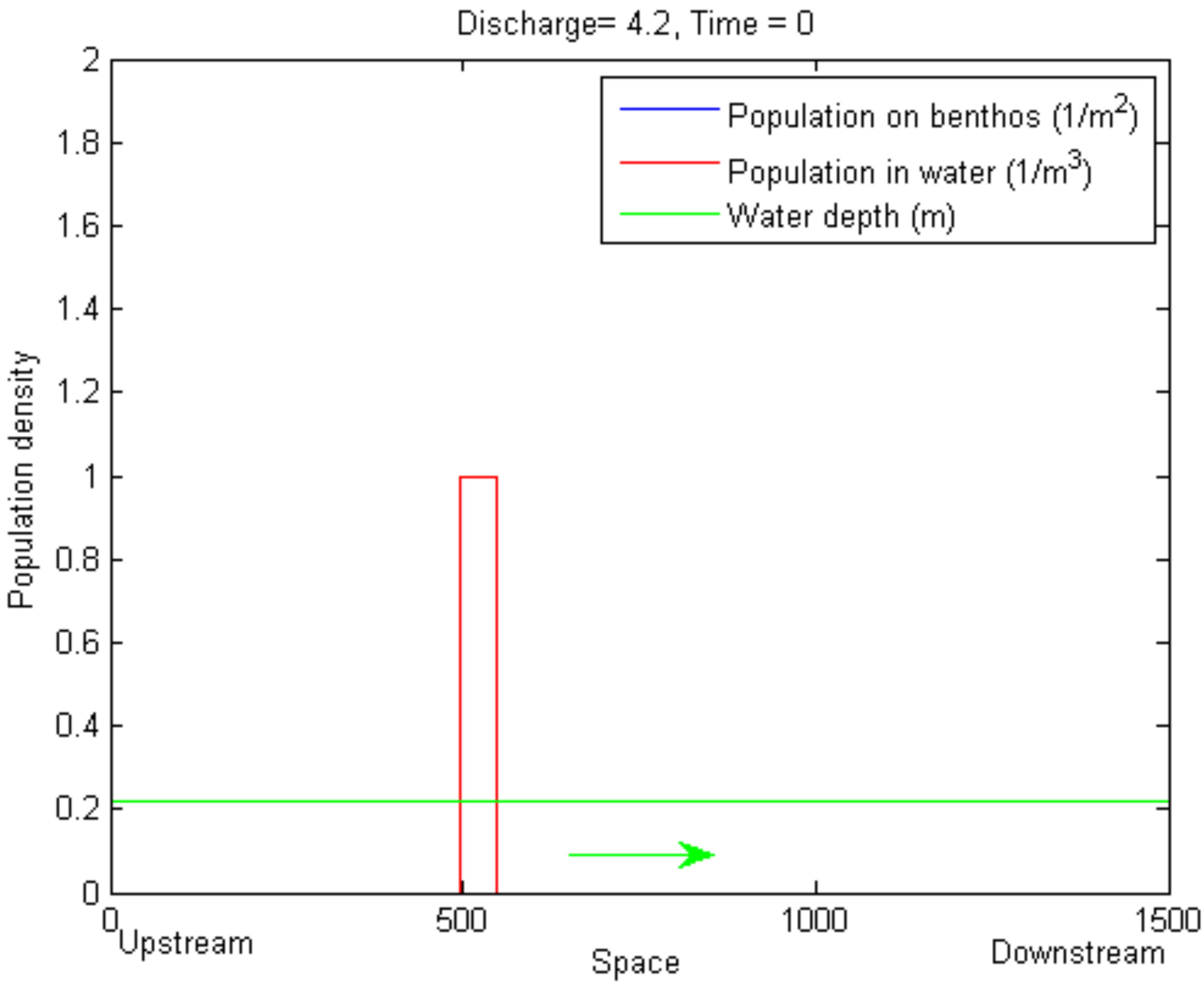
Water depth: spatially uniform, medium flow



Water depth: spatially variable, medium flow



Drift-benthic model: spatially uniform, medium flow



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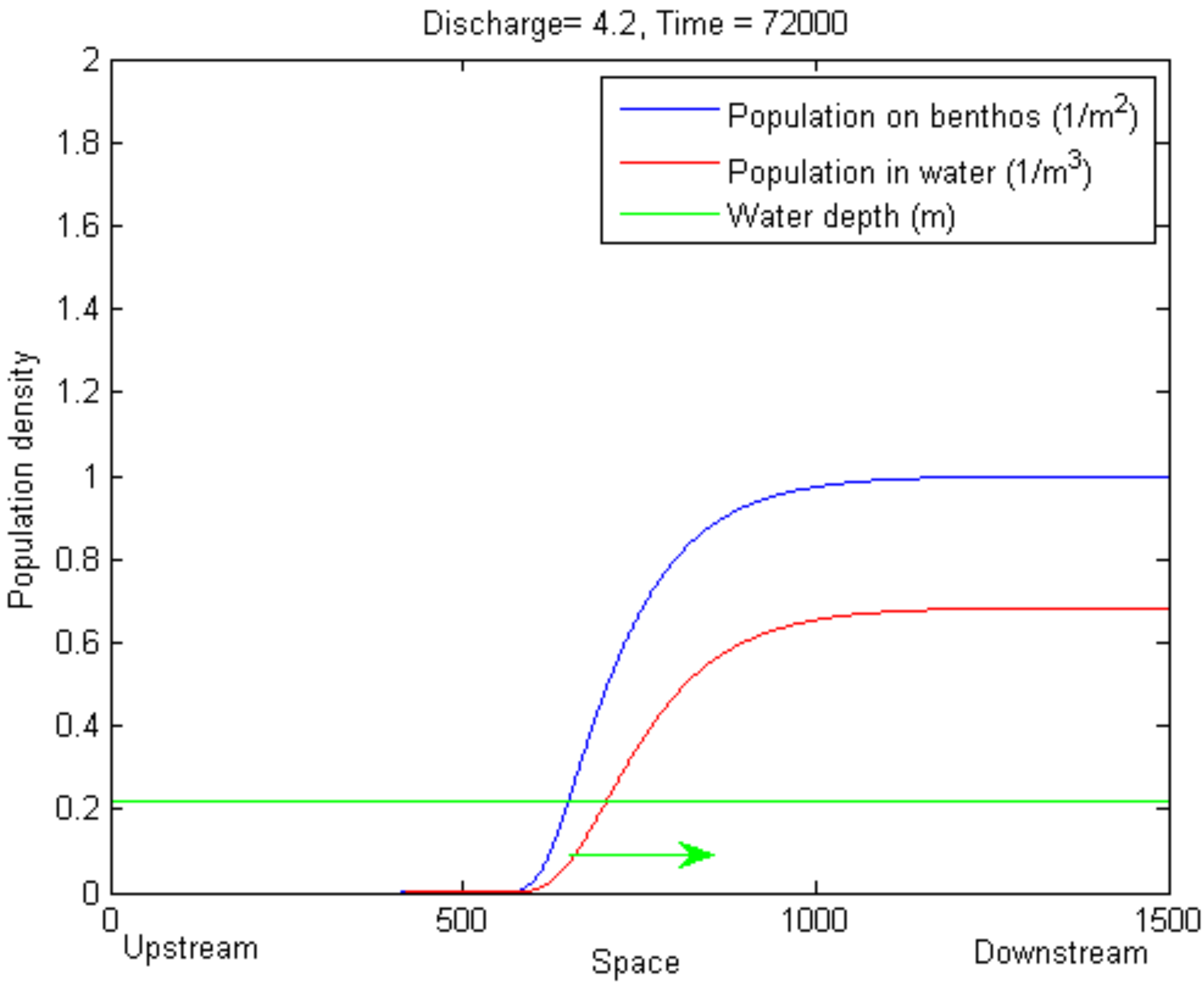

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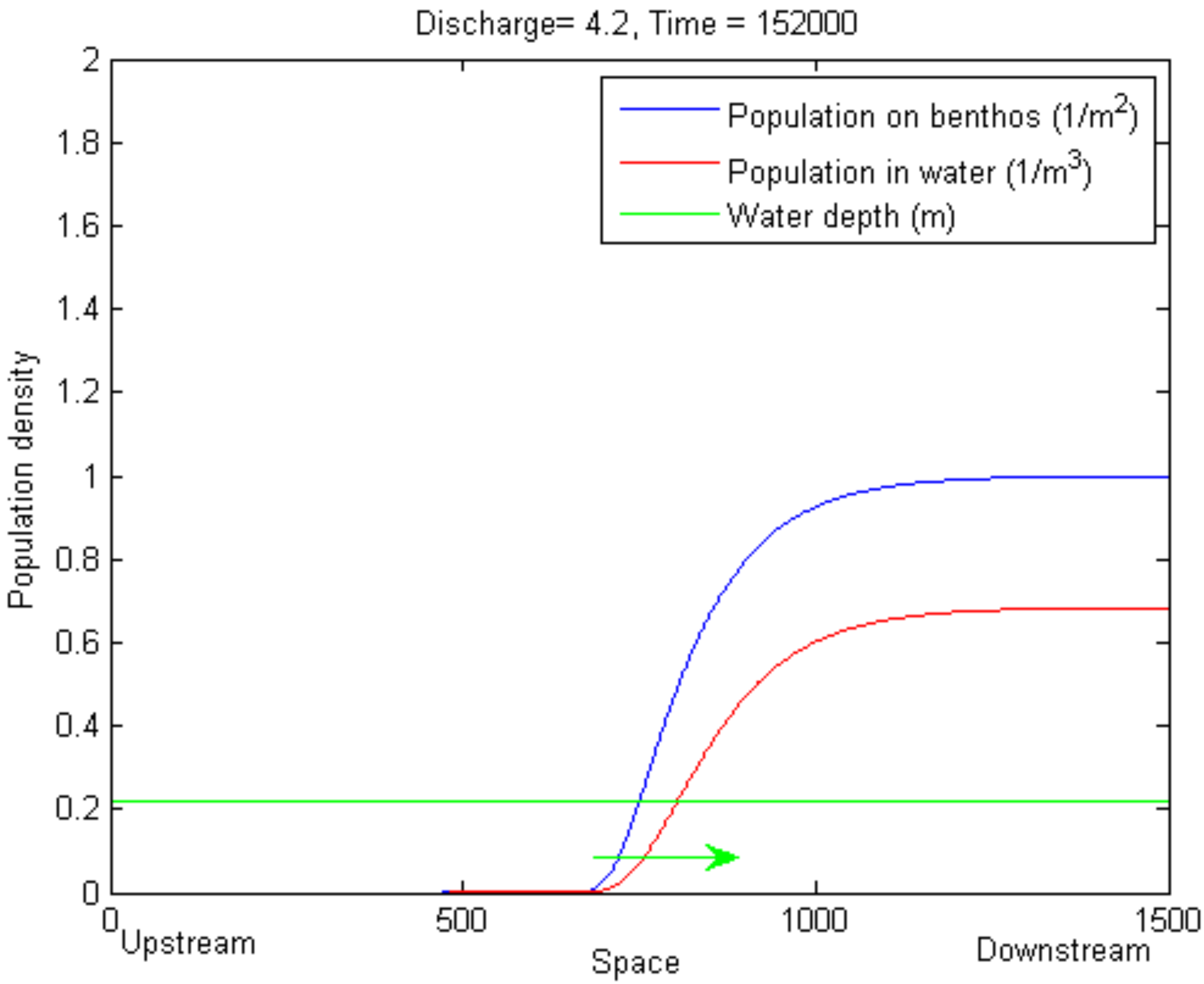

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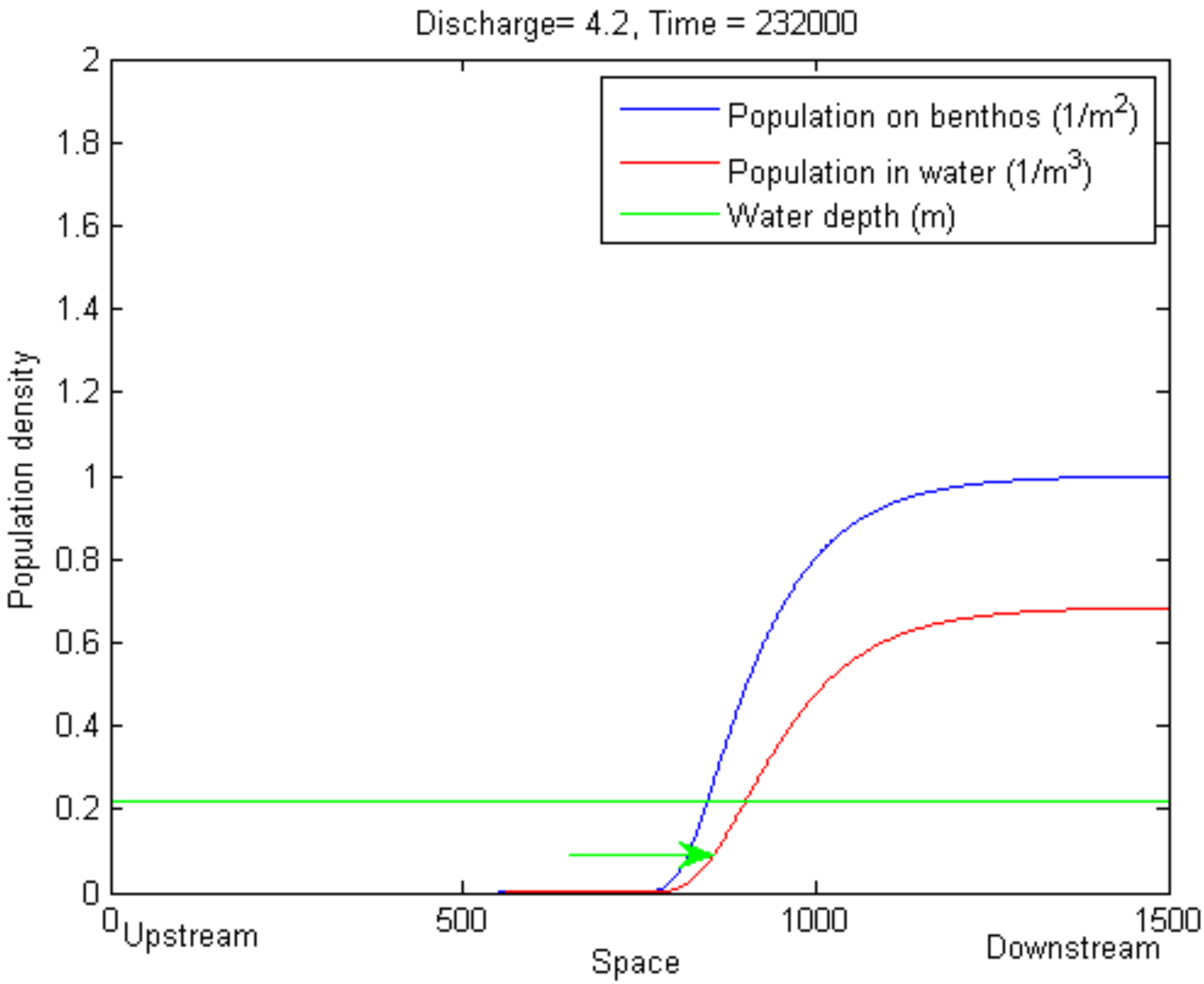

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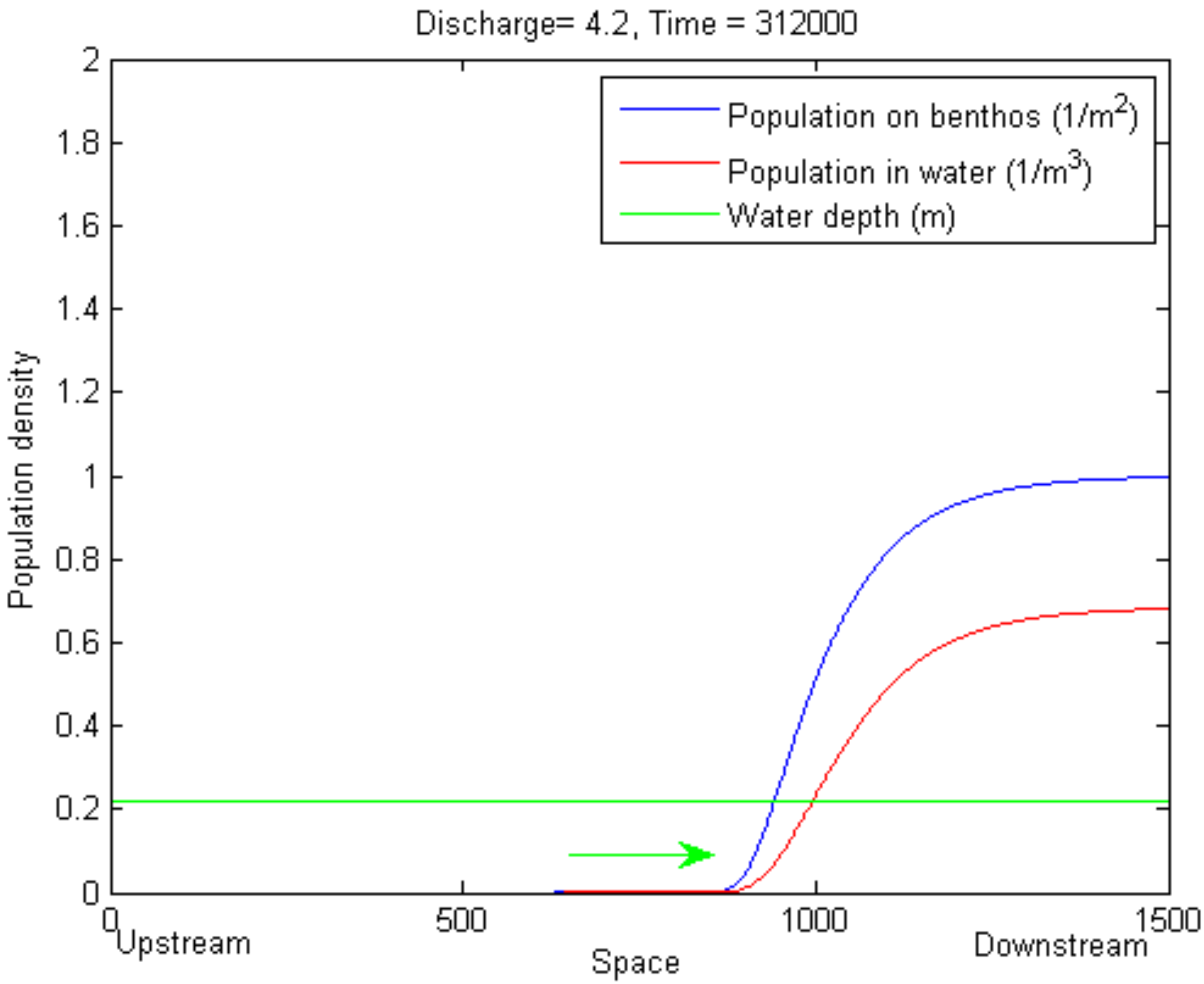

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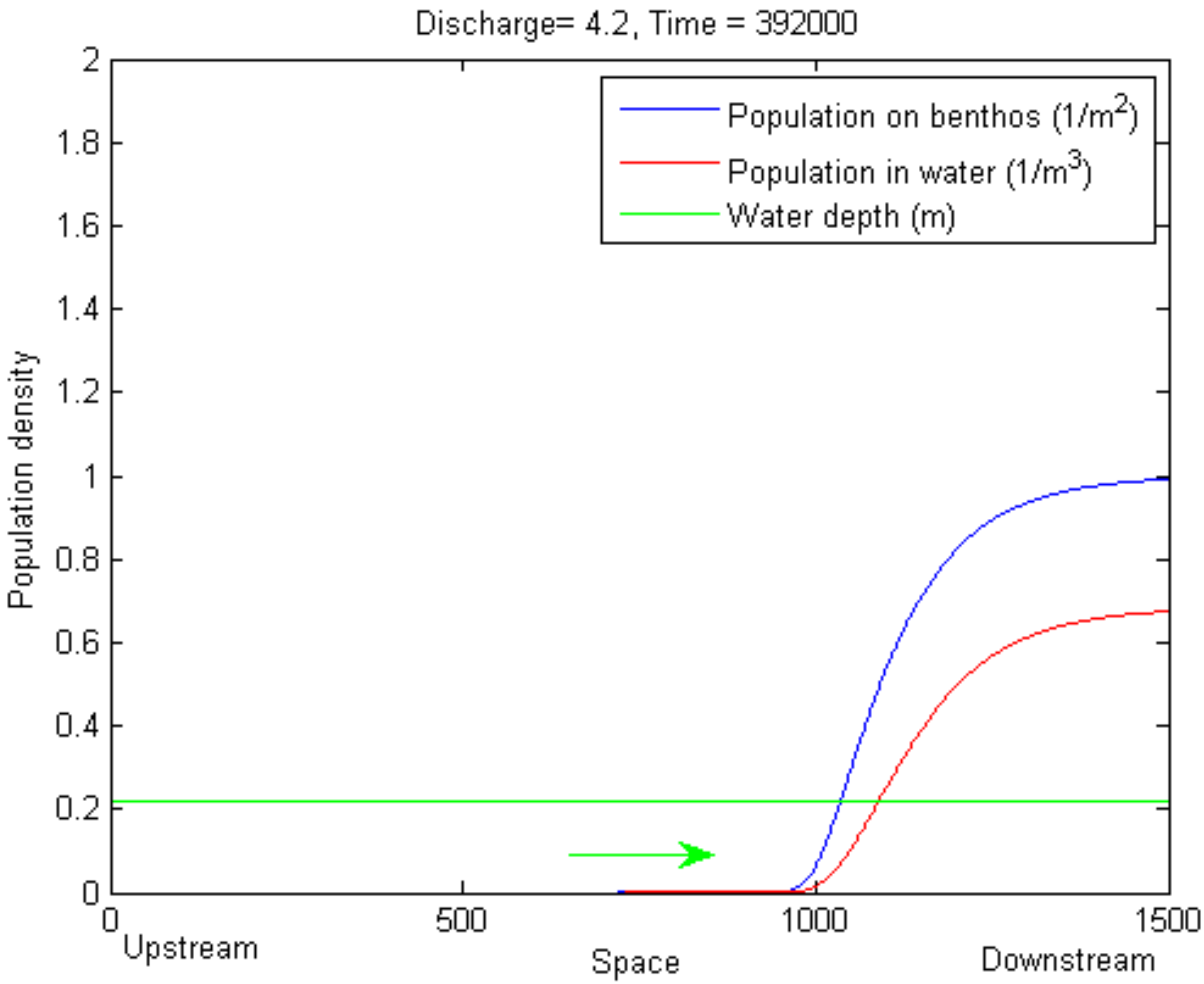

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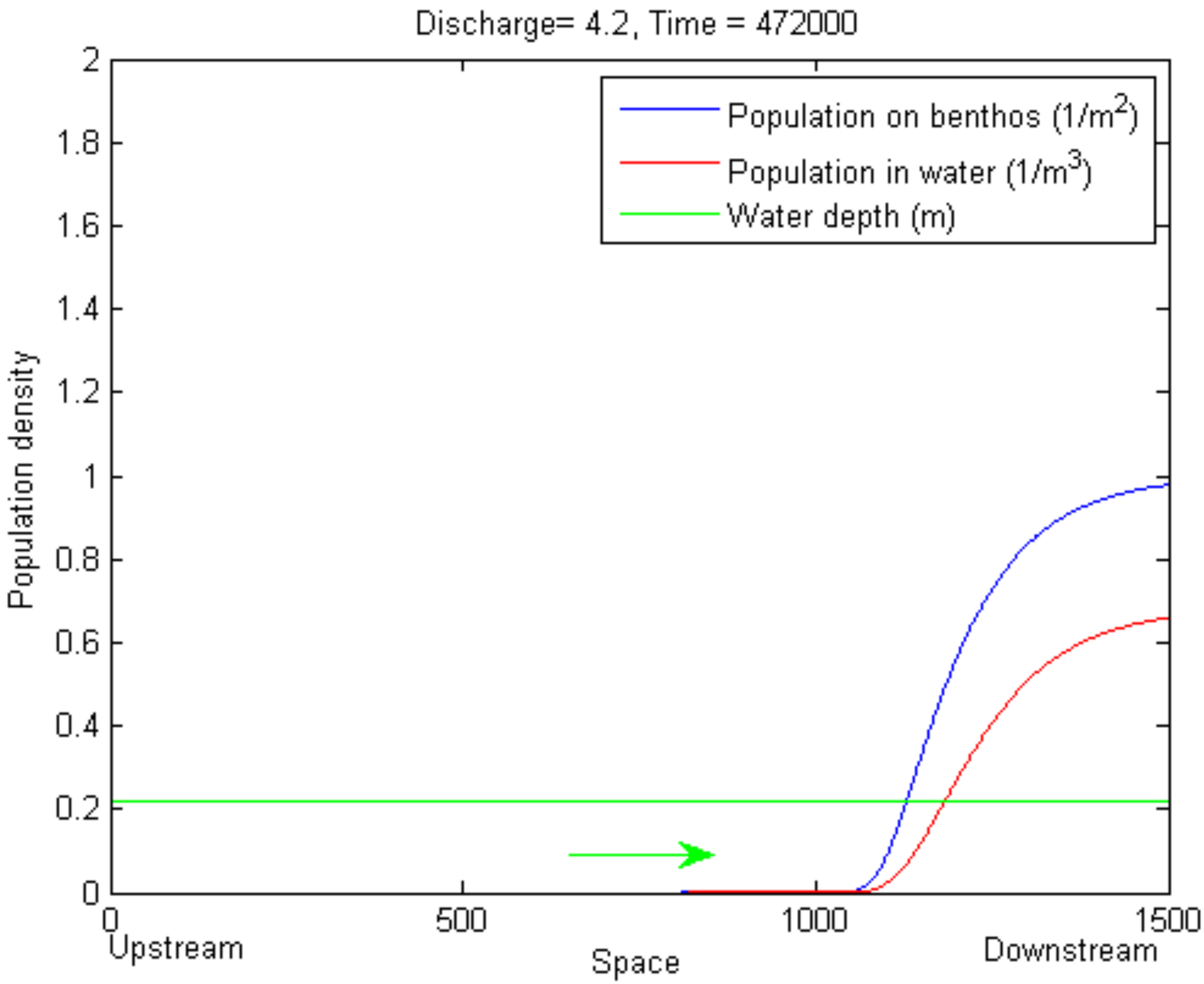

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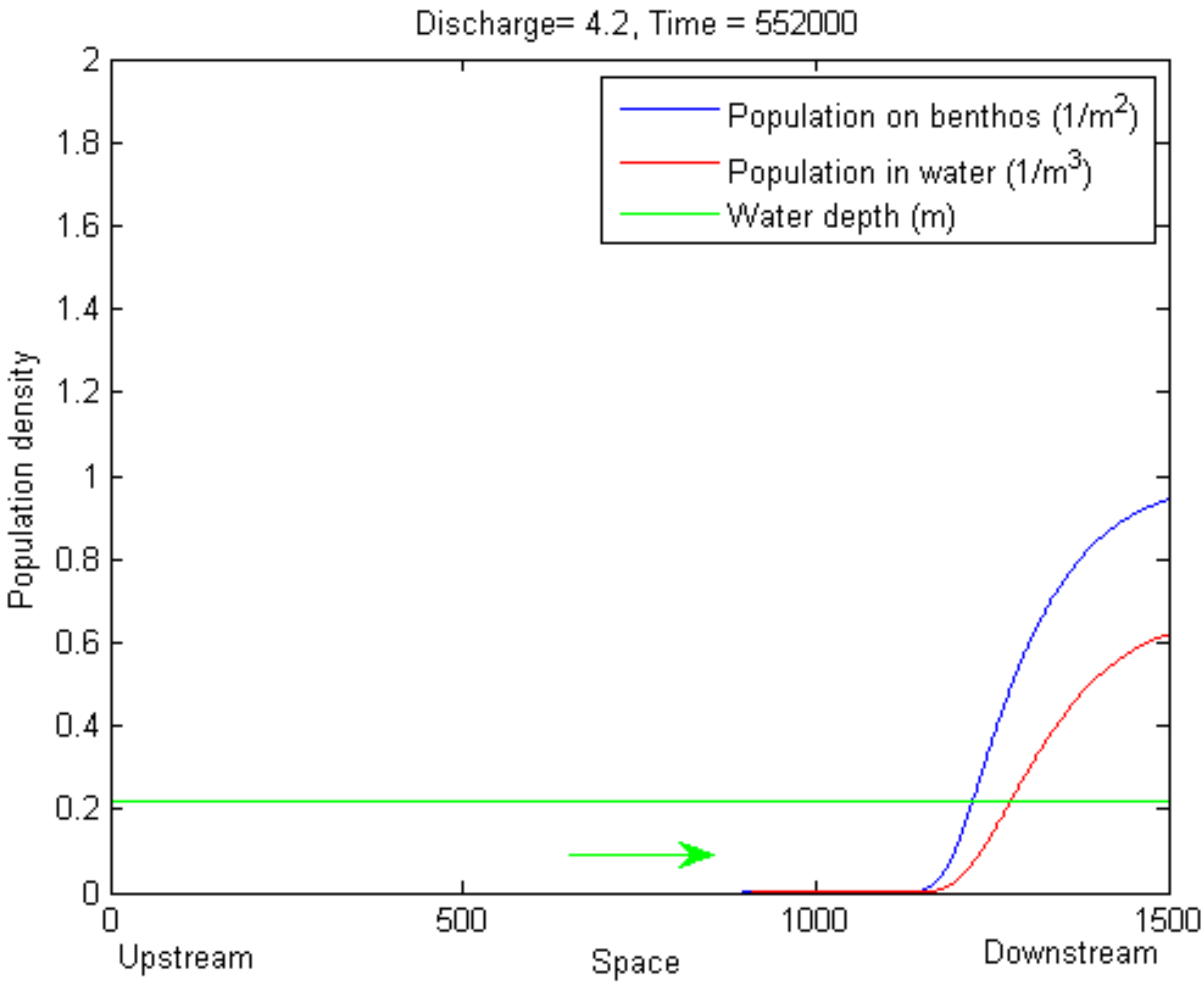

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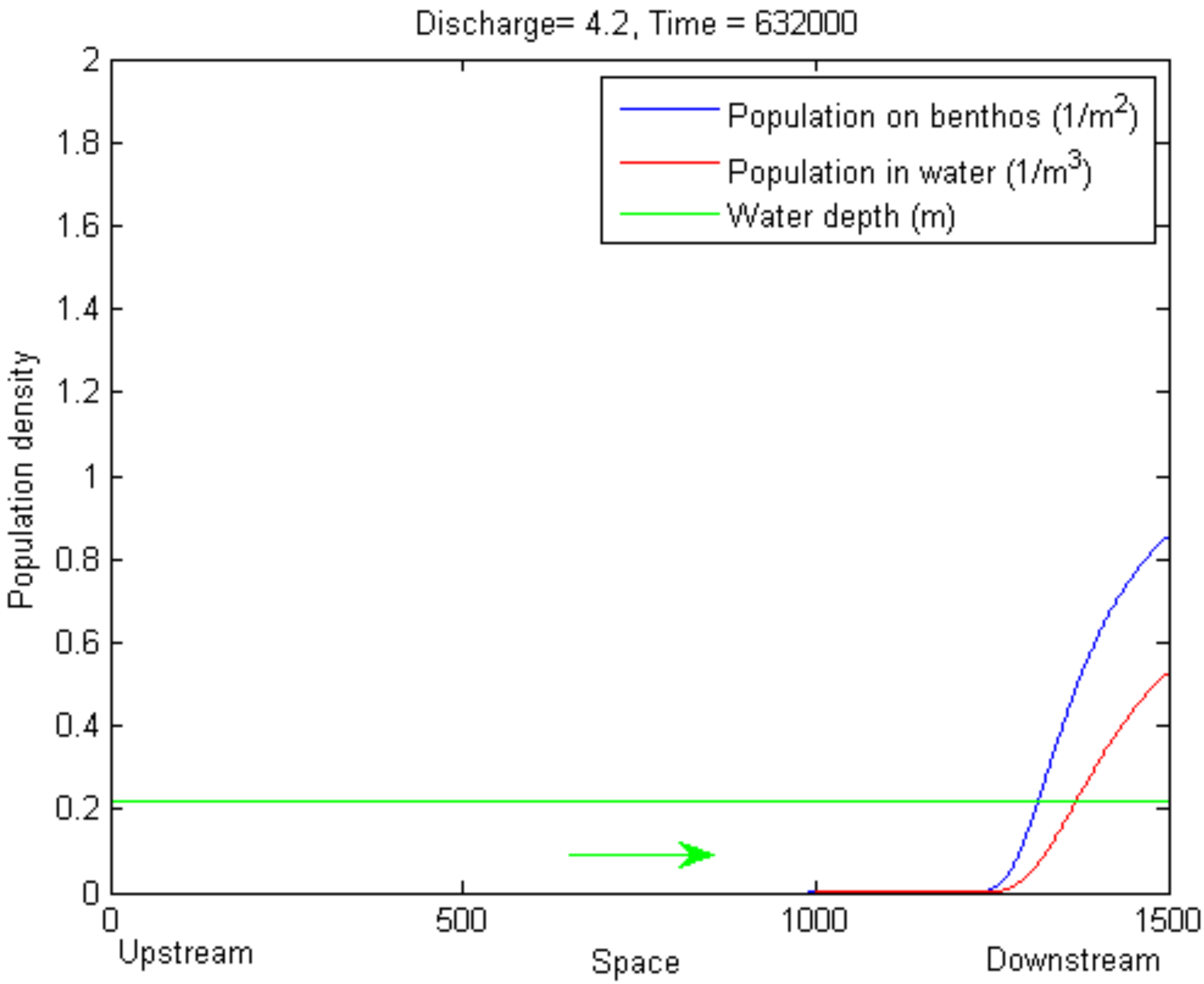

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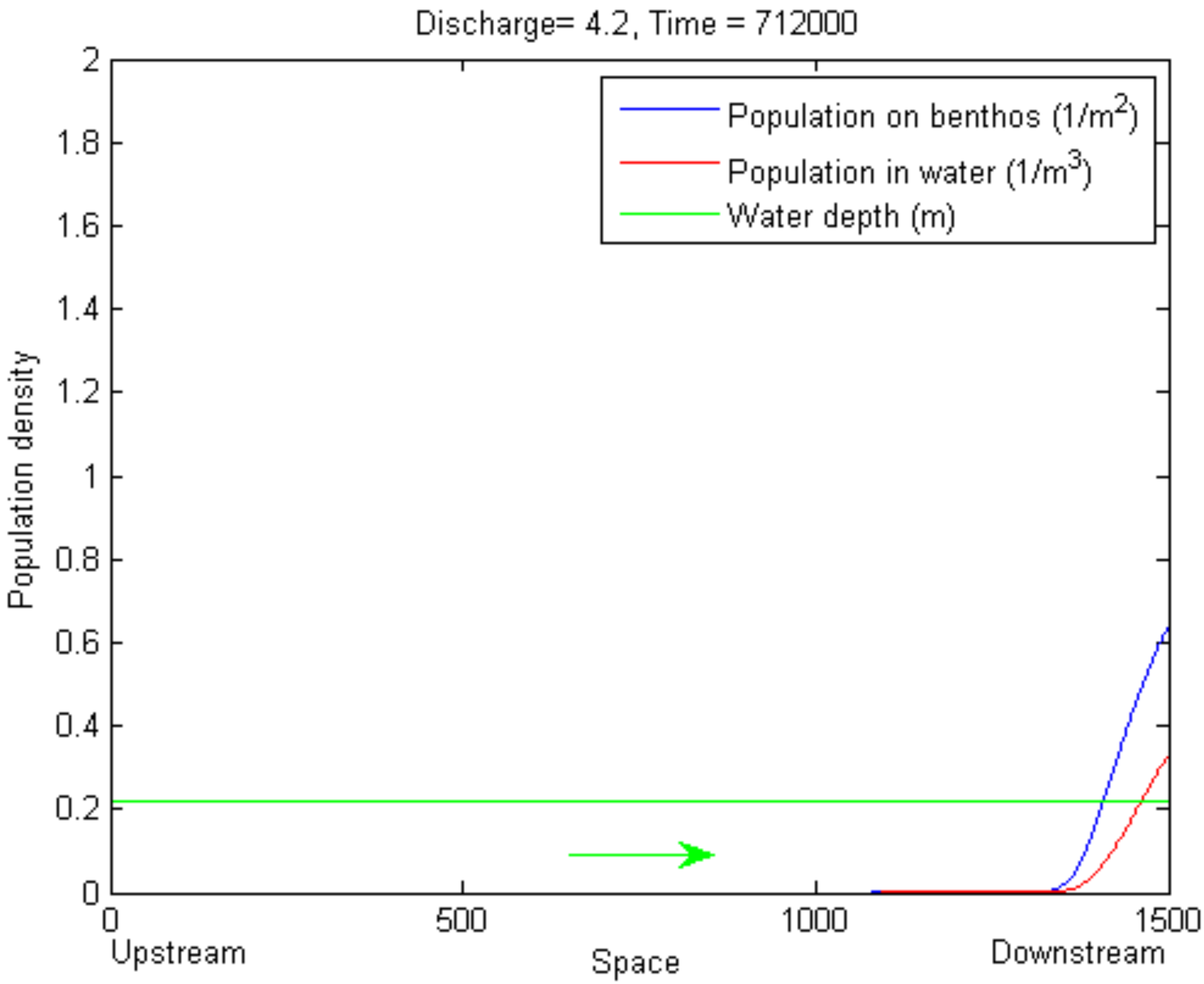

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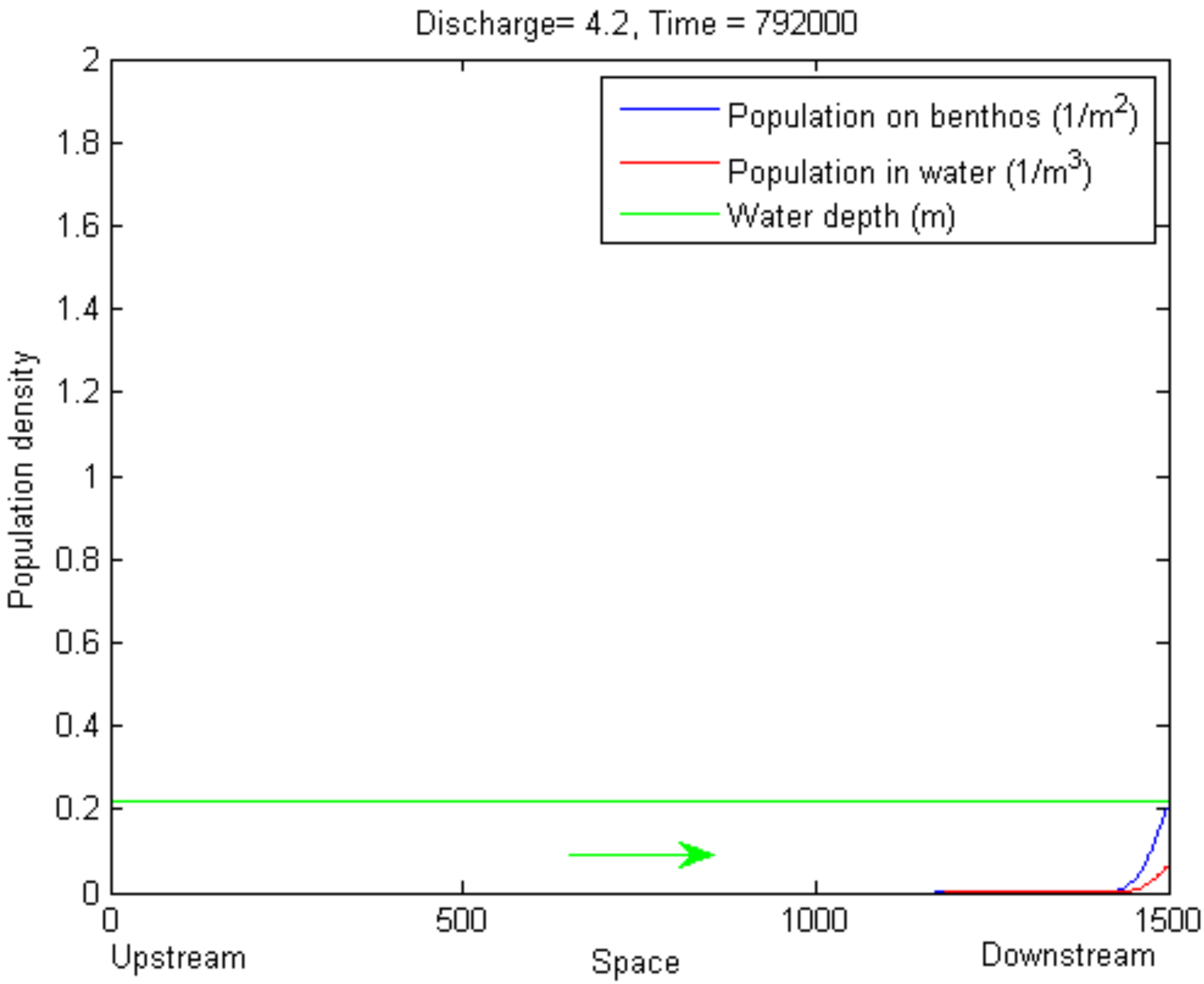

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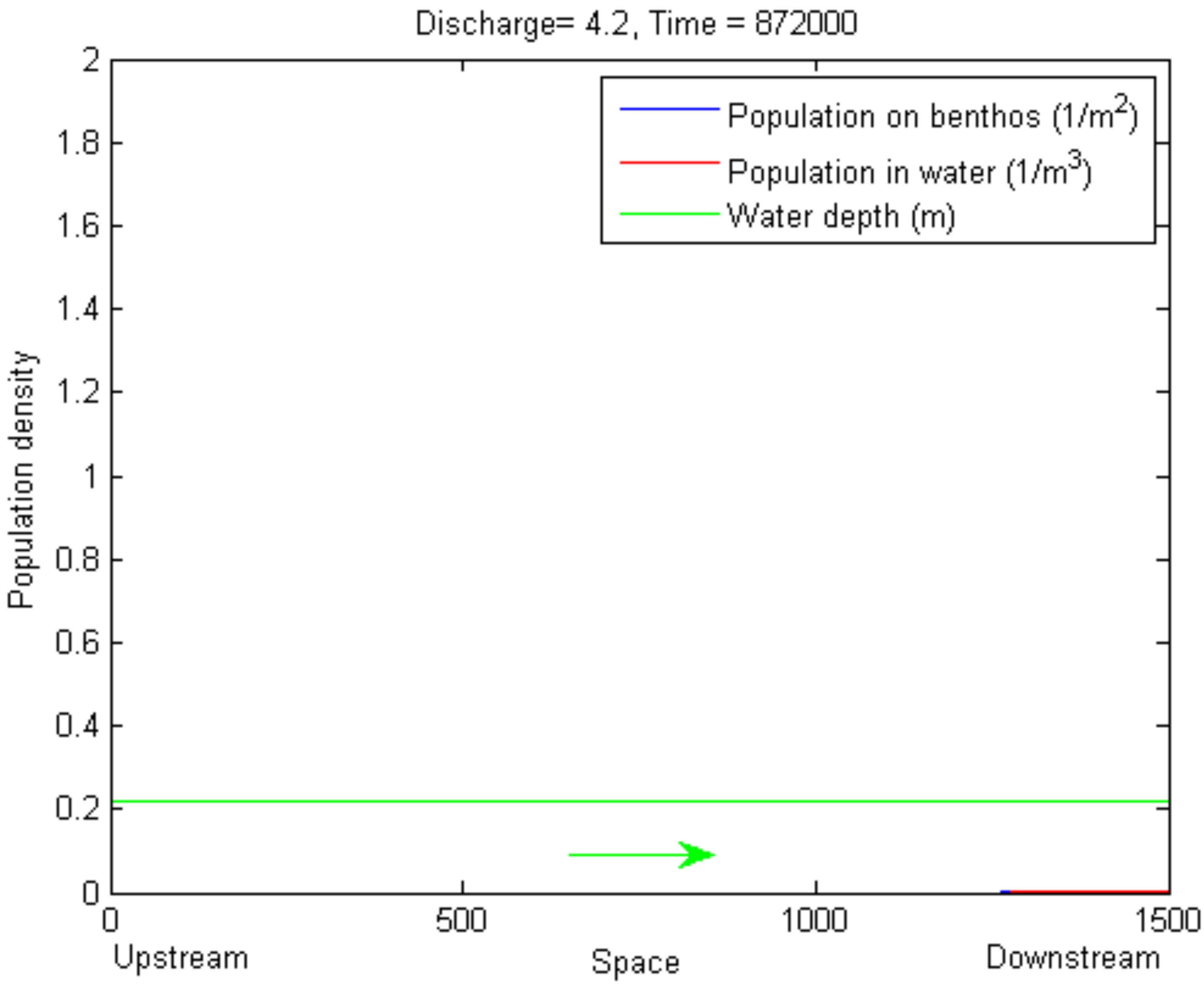
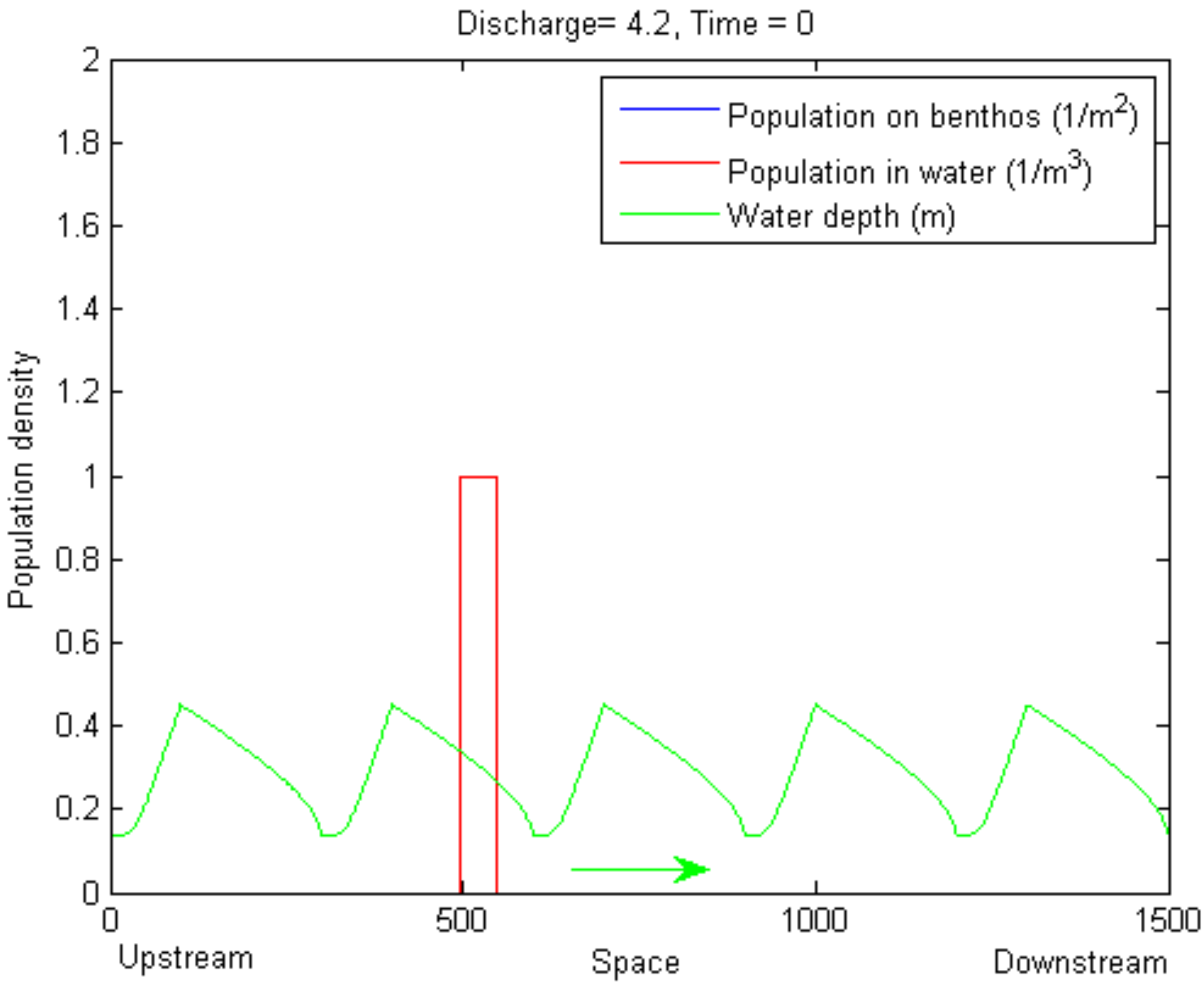


Drift-benthic model: spatially variable, medium flow



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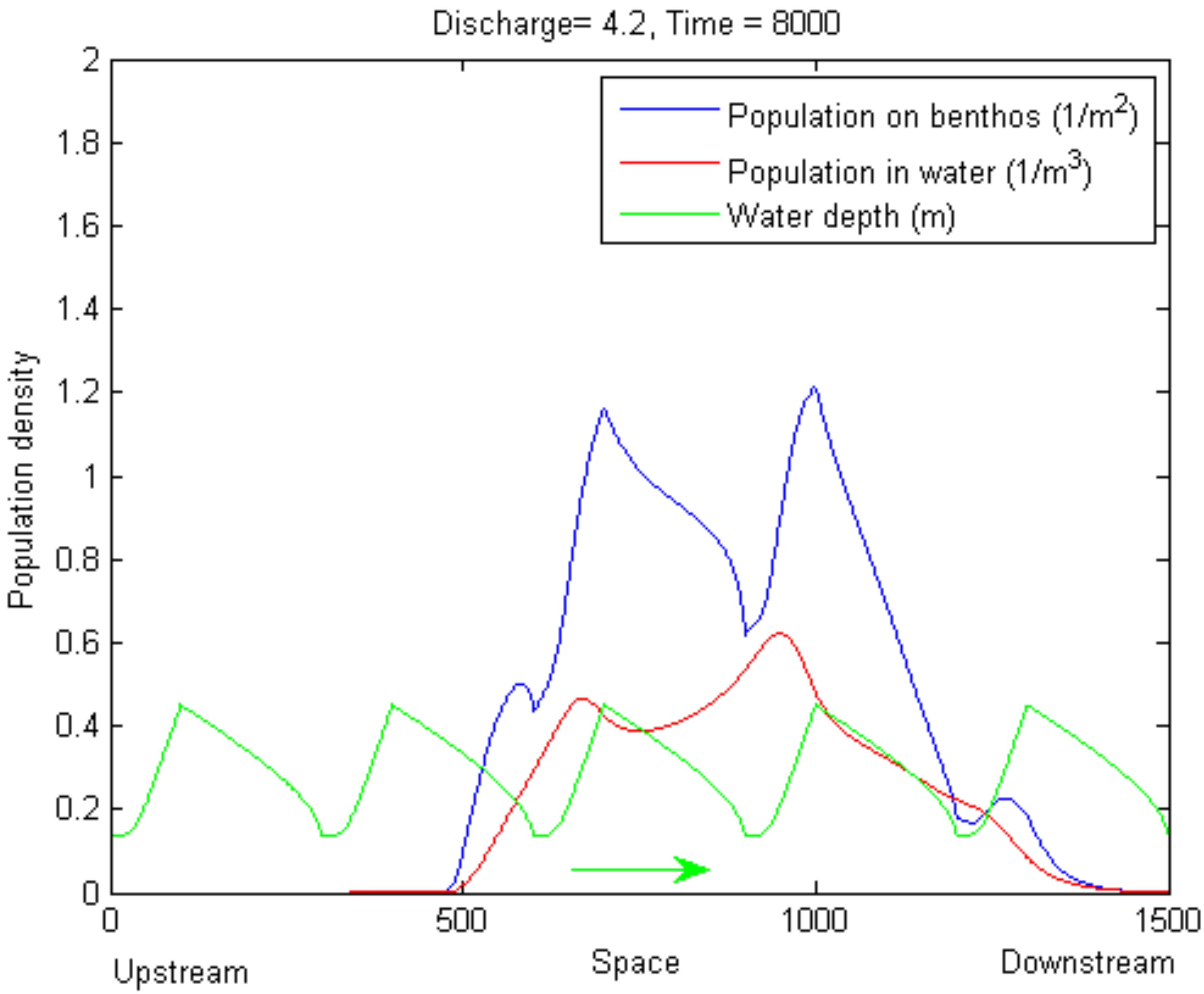

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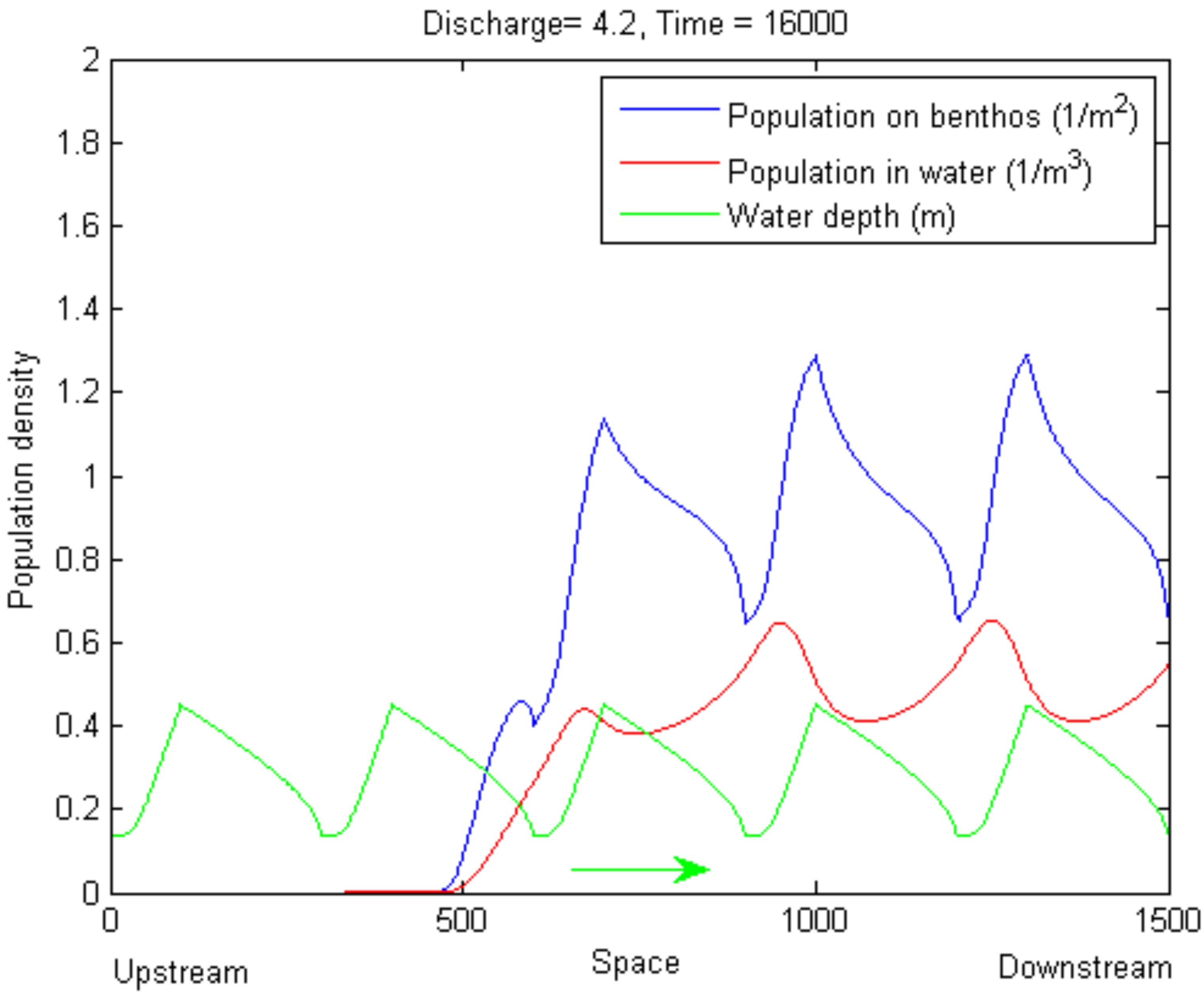

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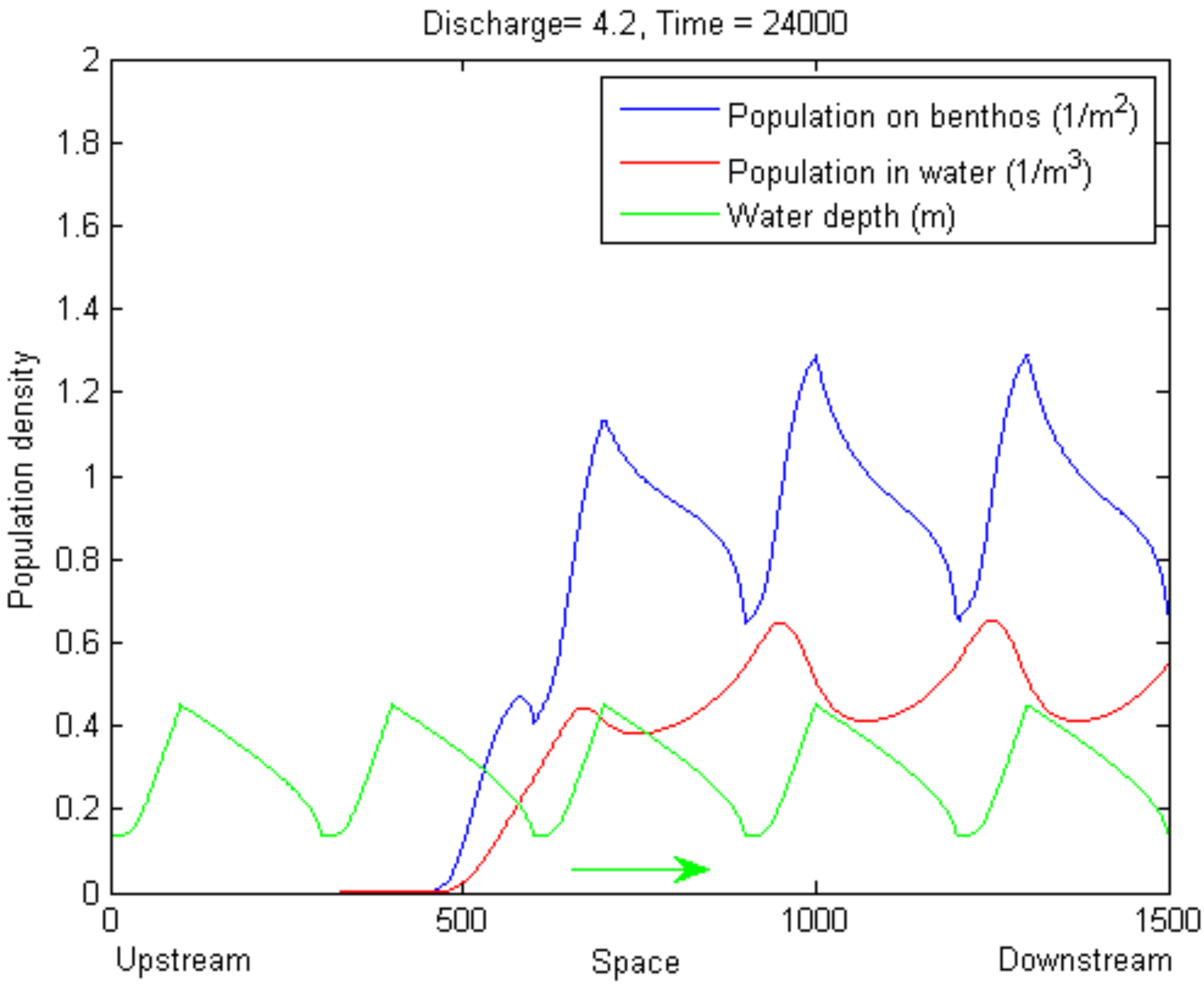

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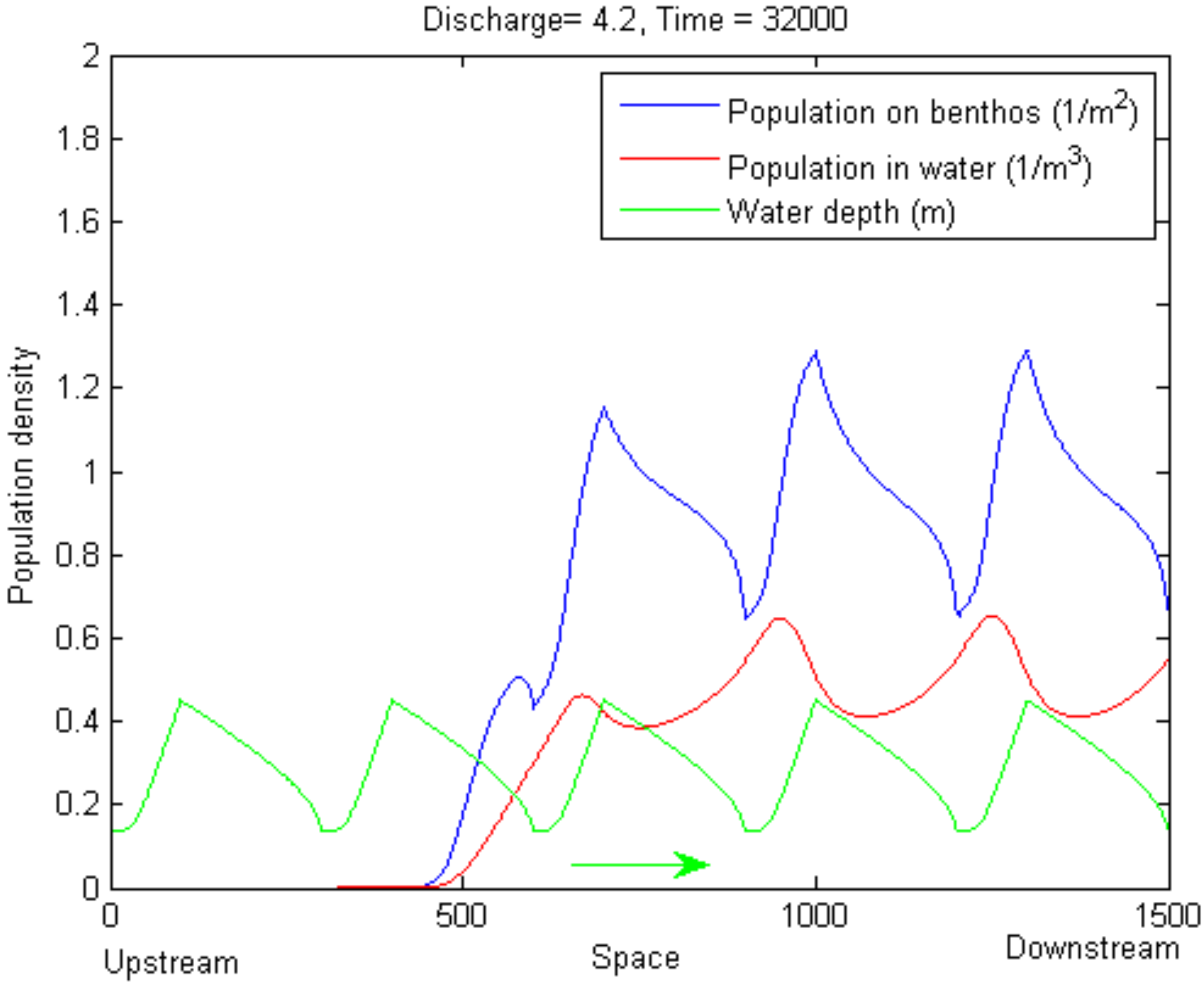

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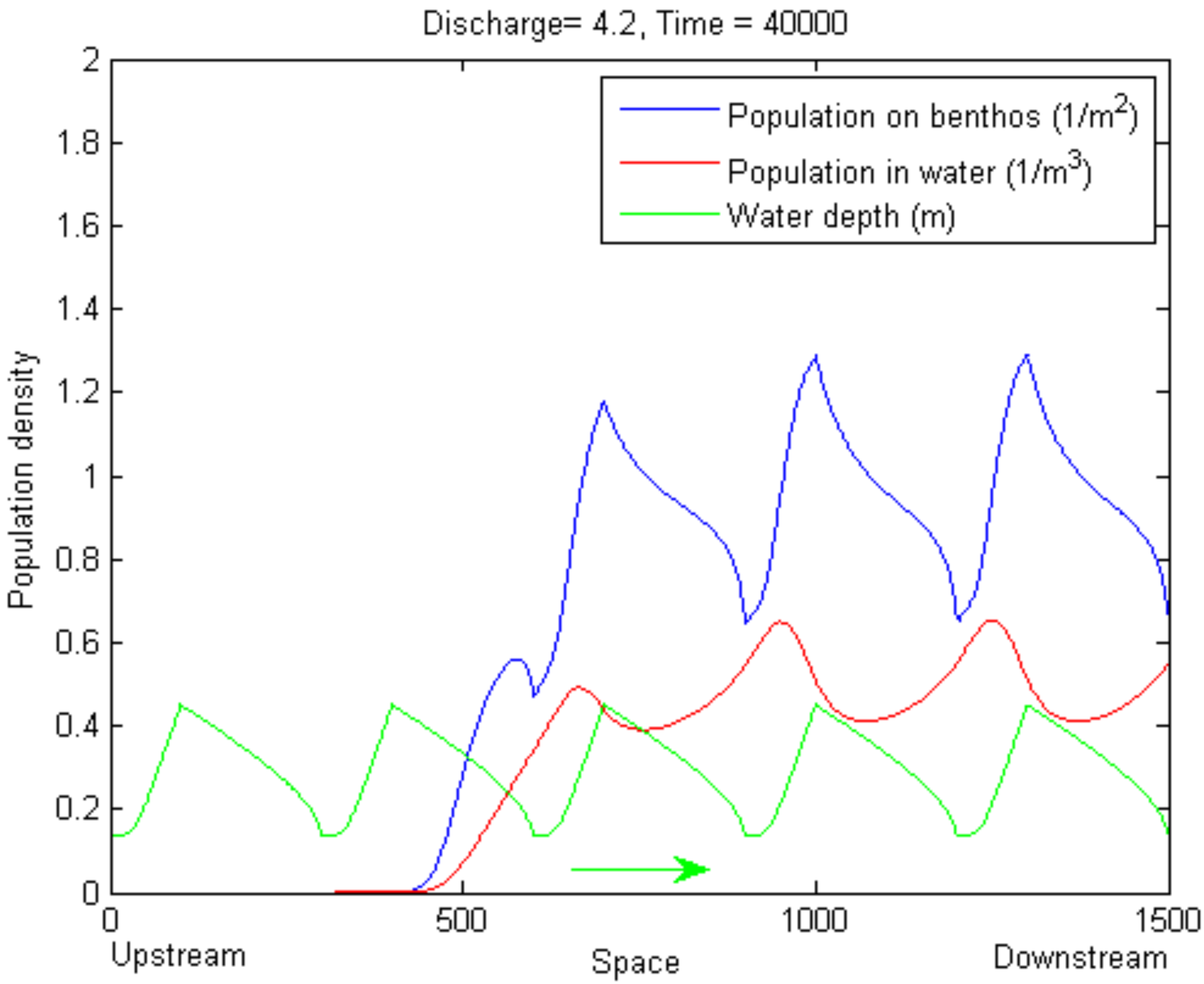

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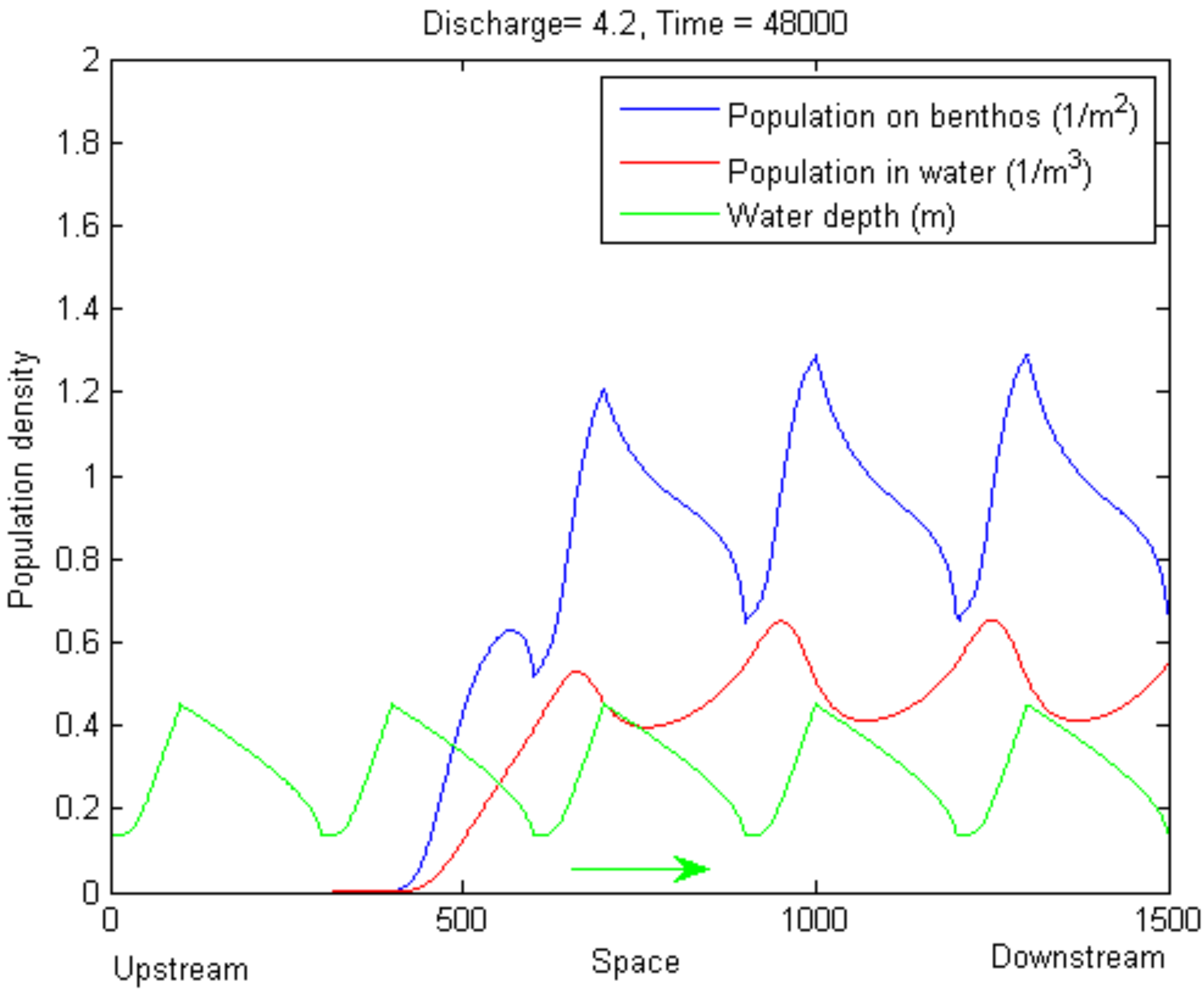

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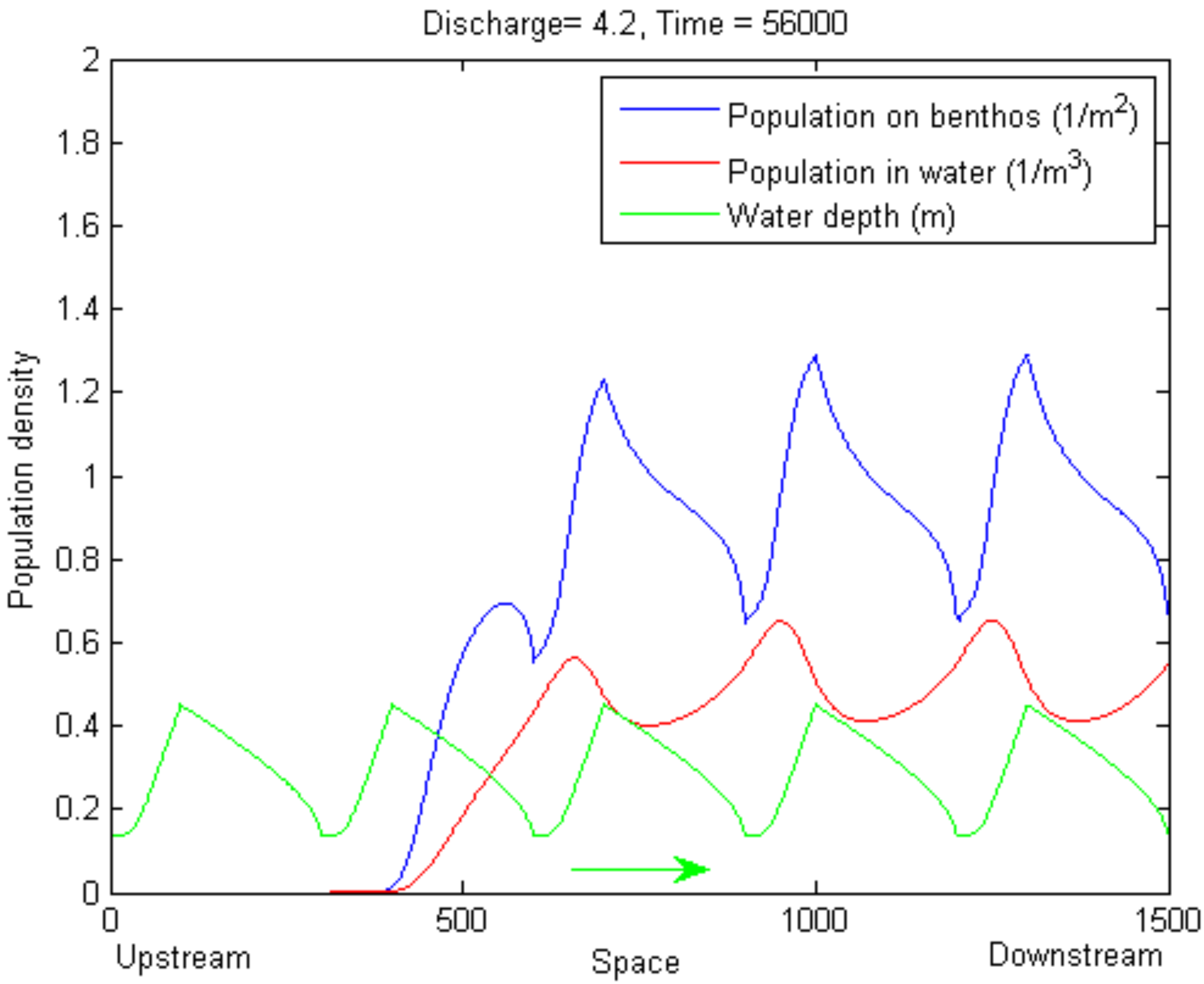

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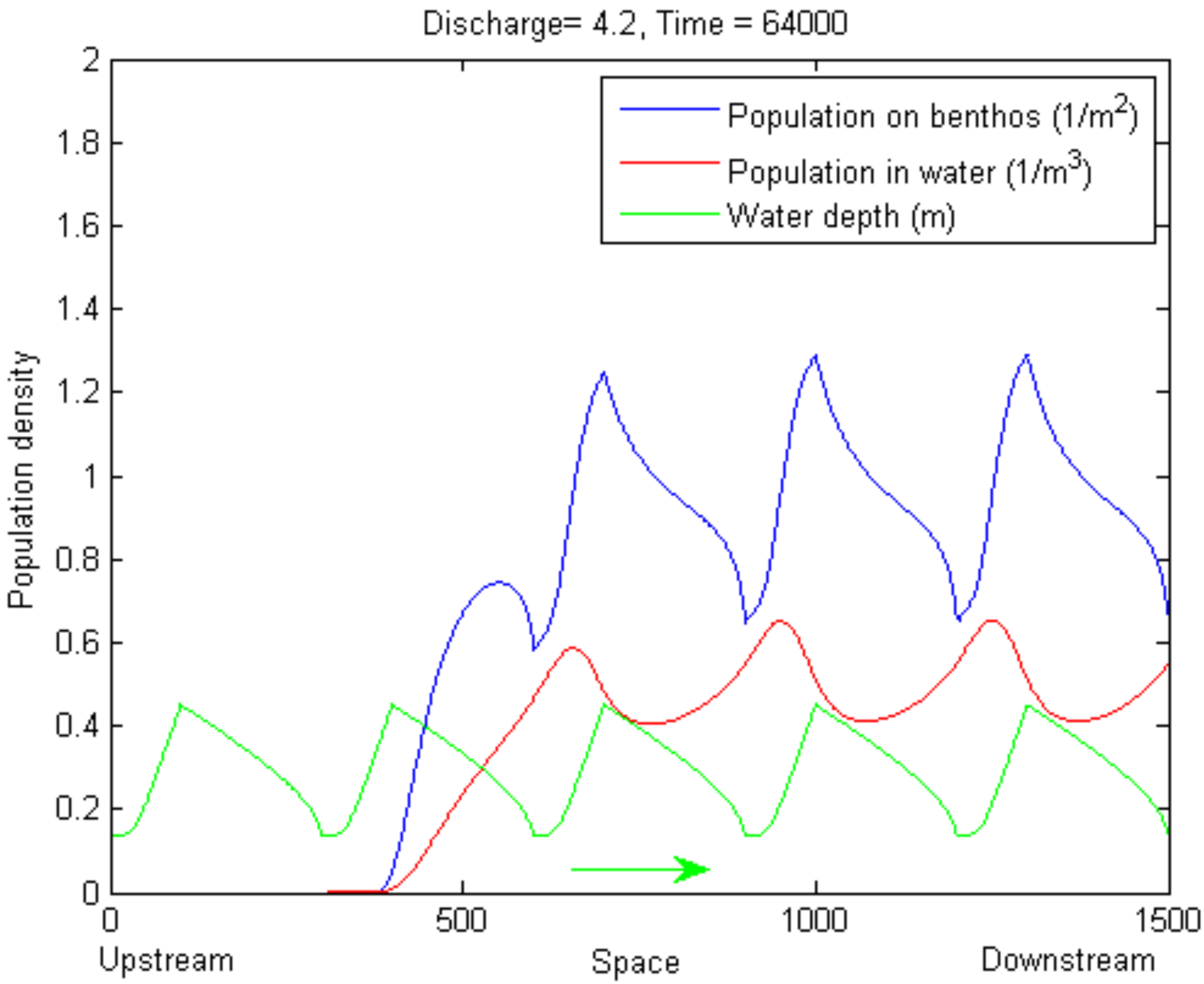

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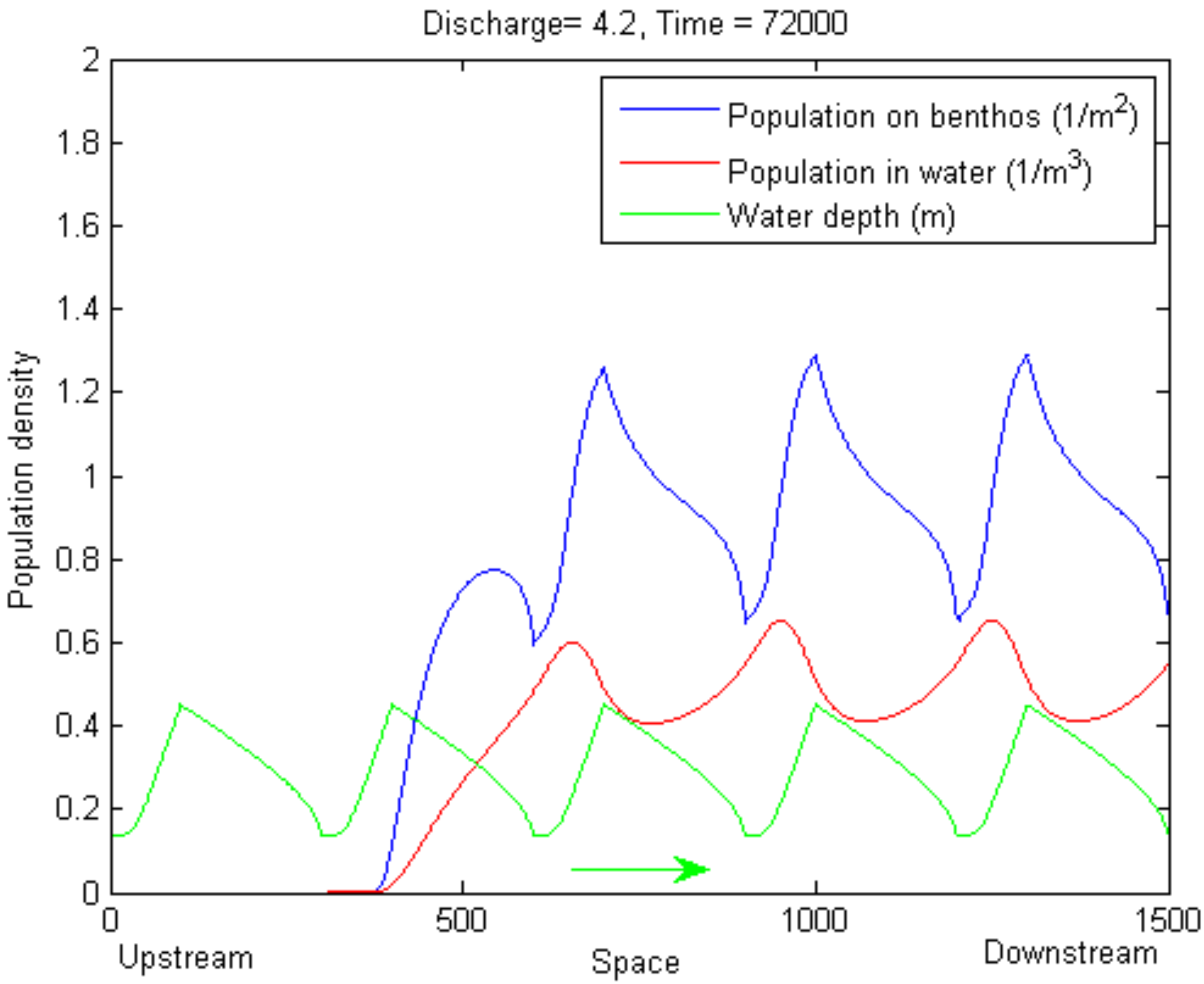

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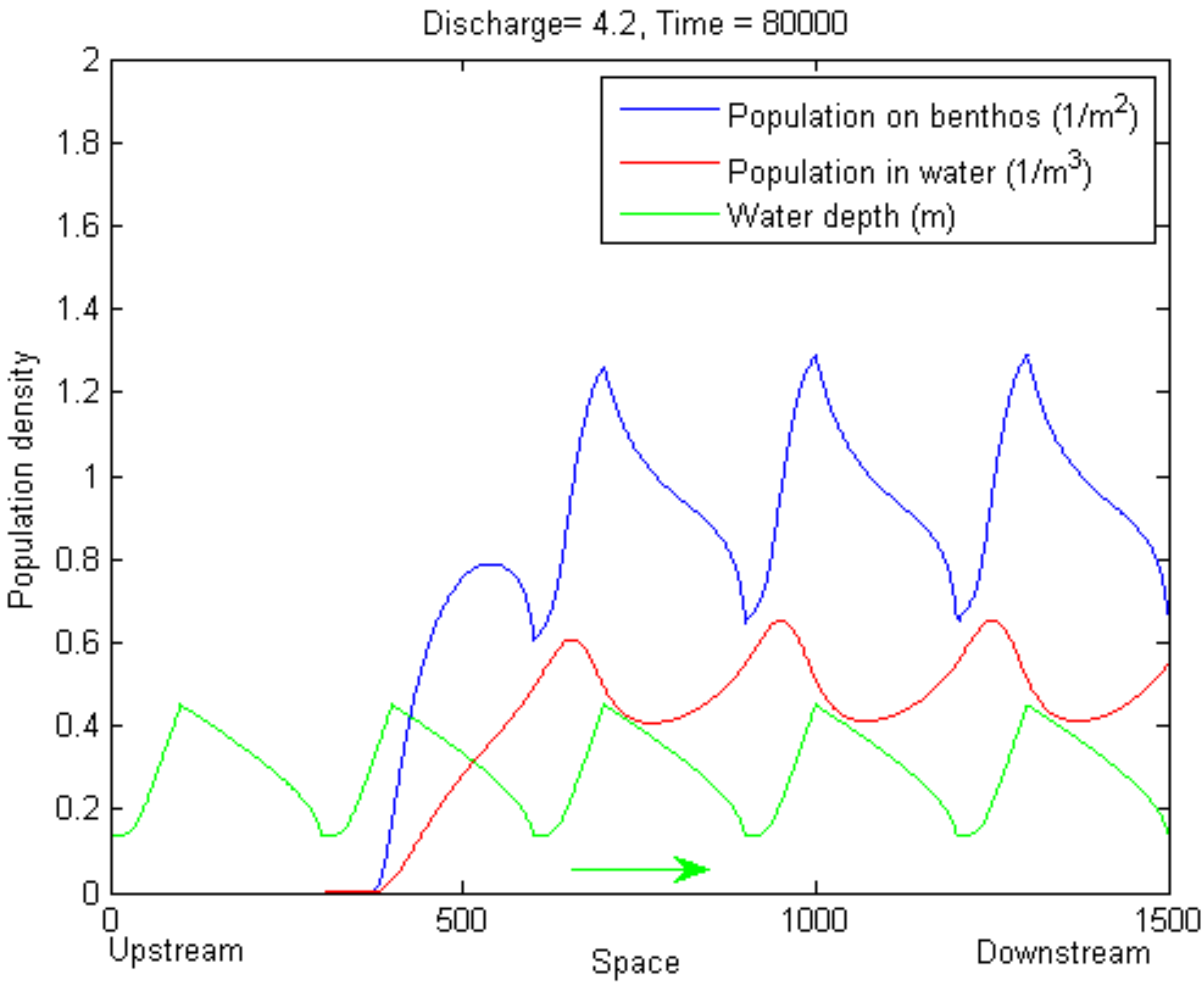

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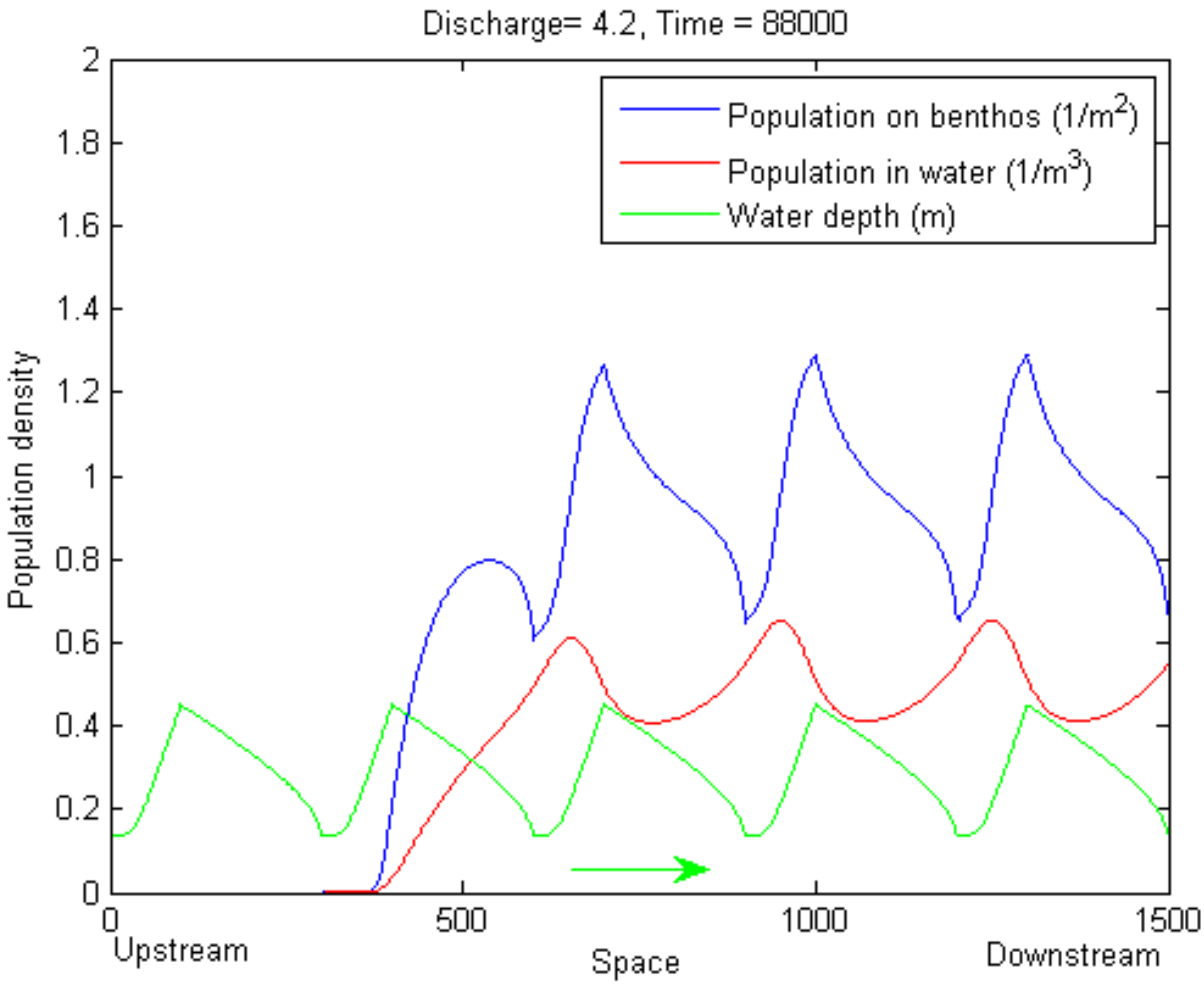

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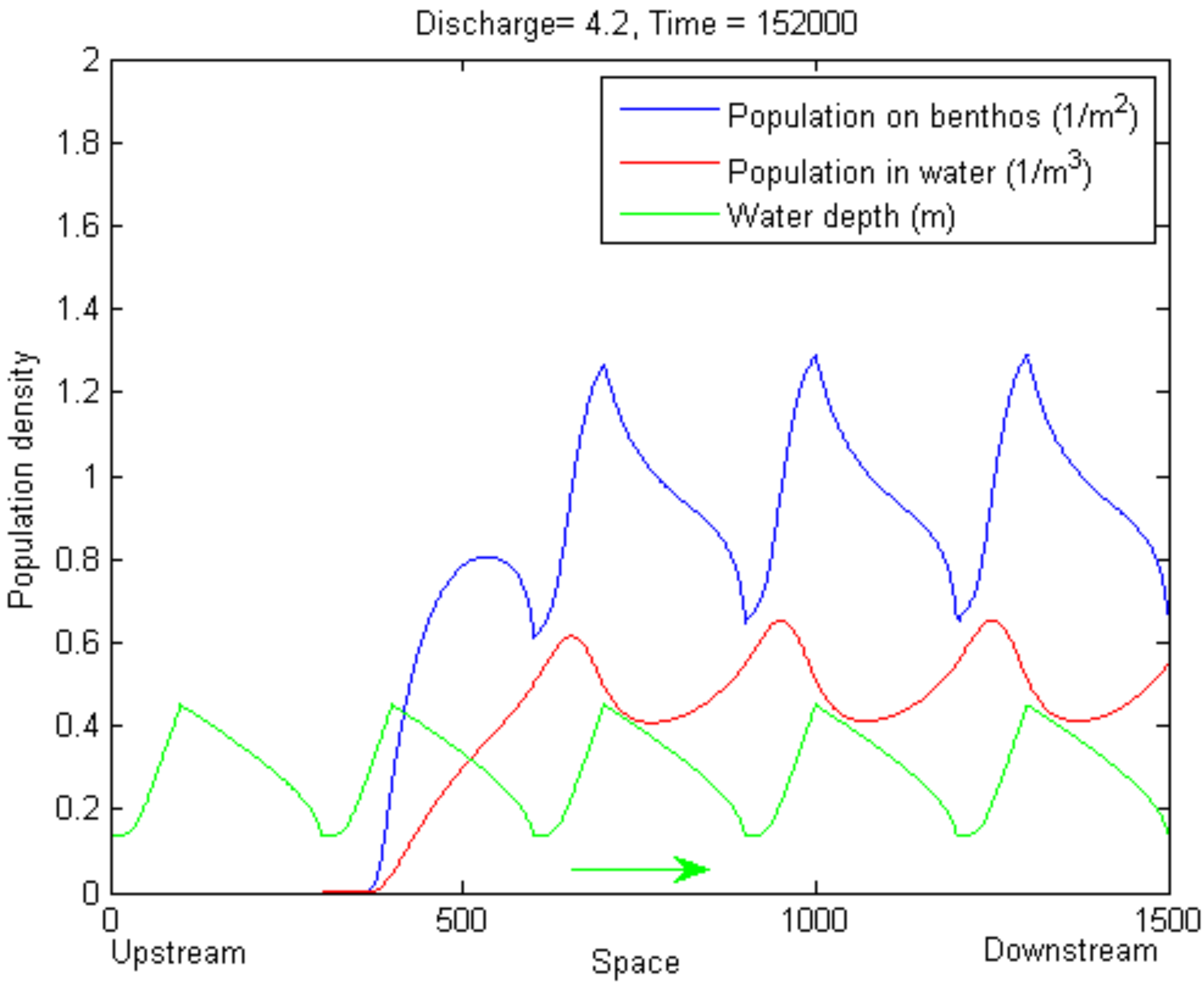

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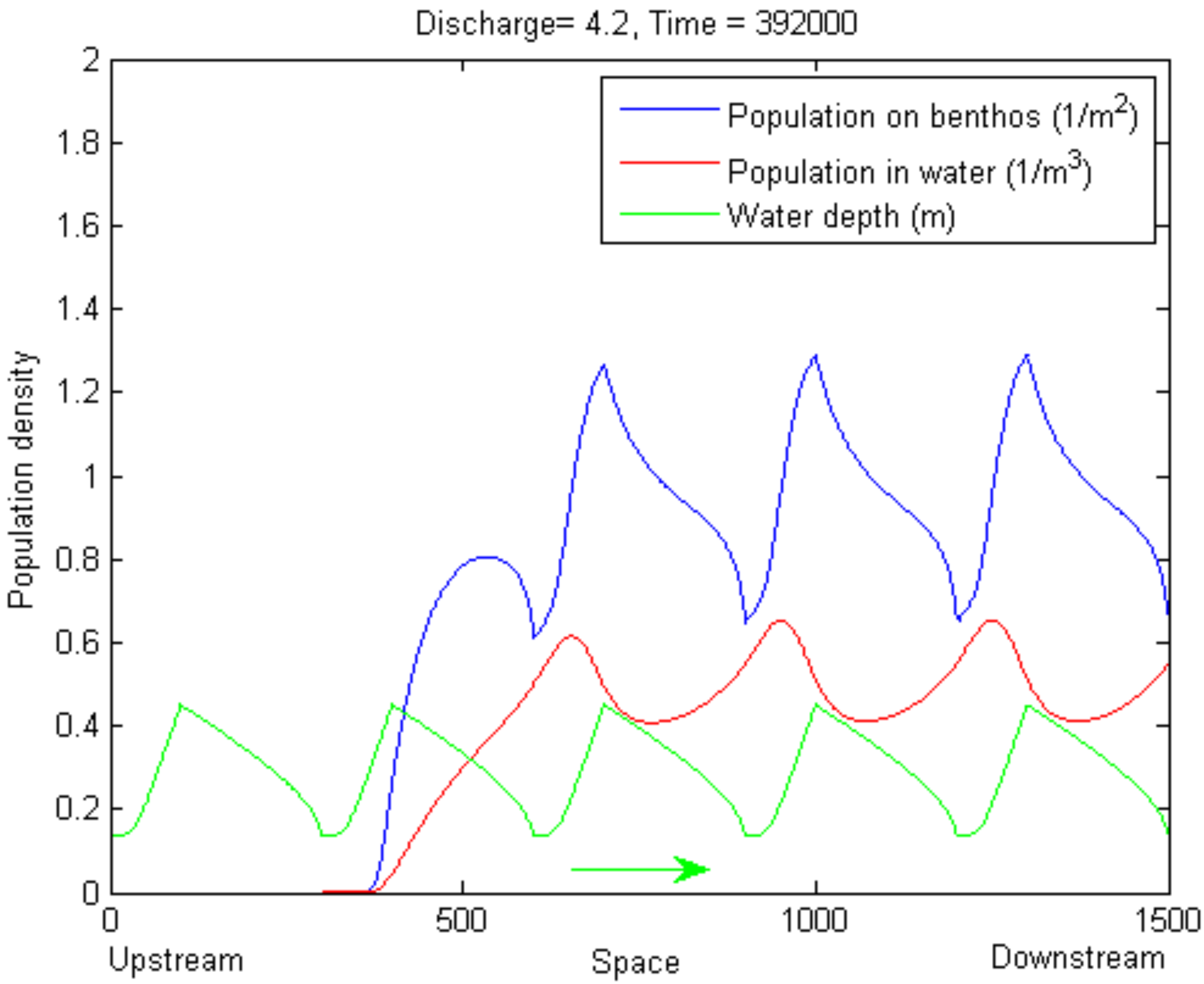

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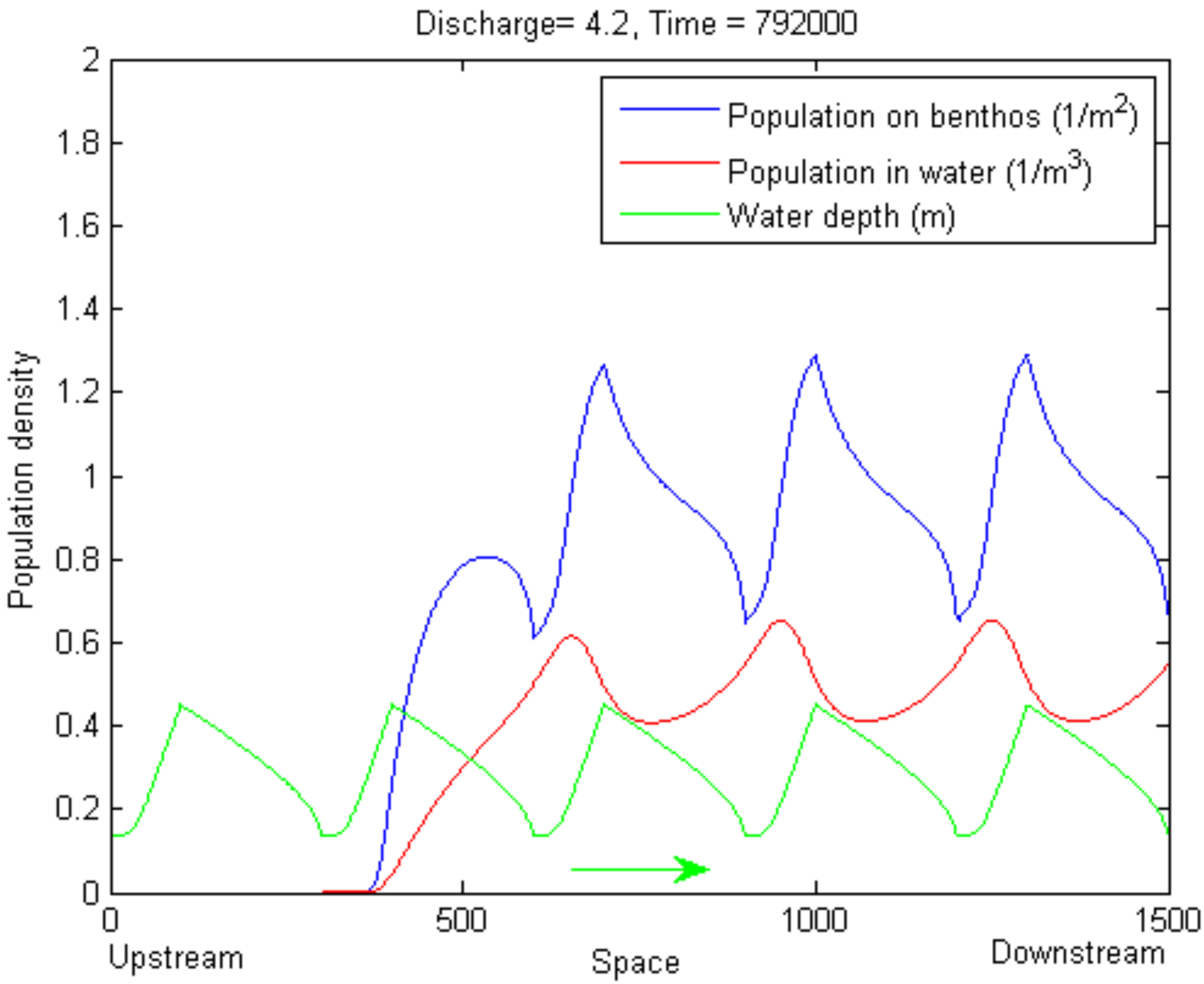
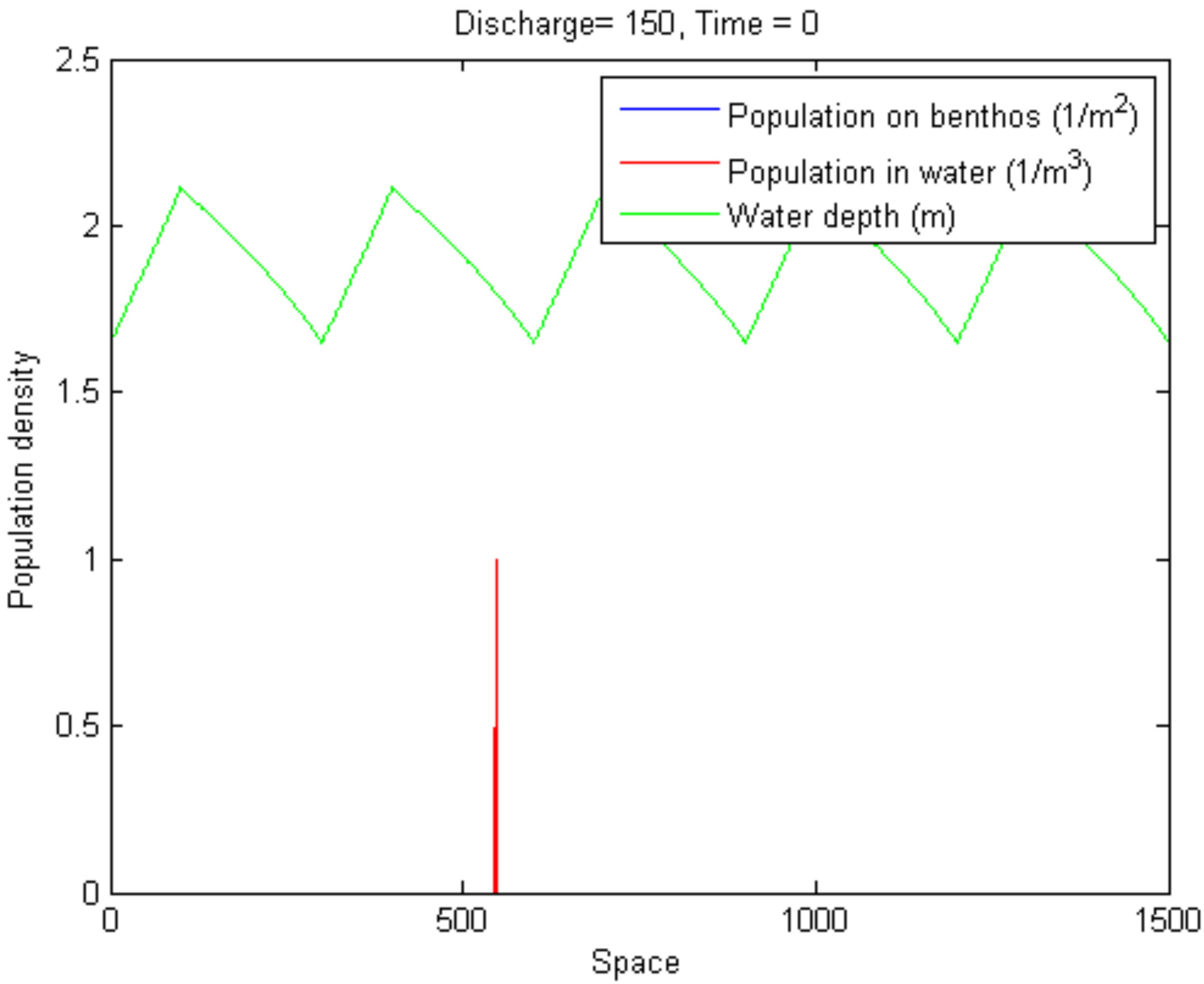


Drift-benthic model: spatially variable, high flow



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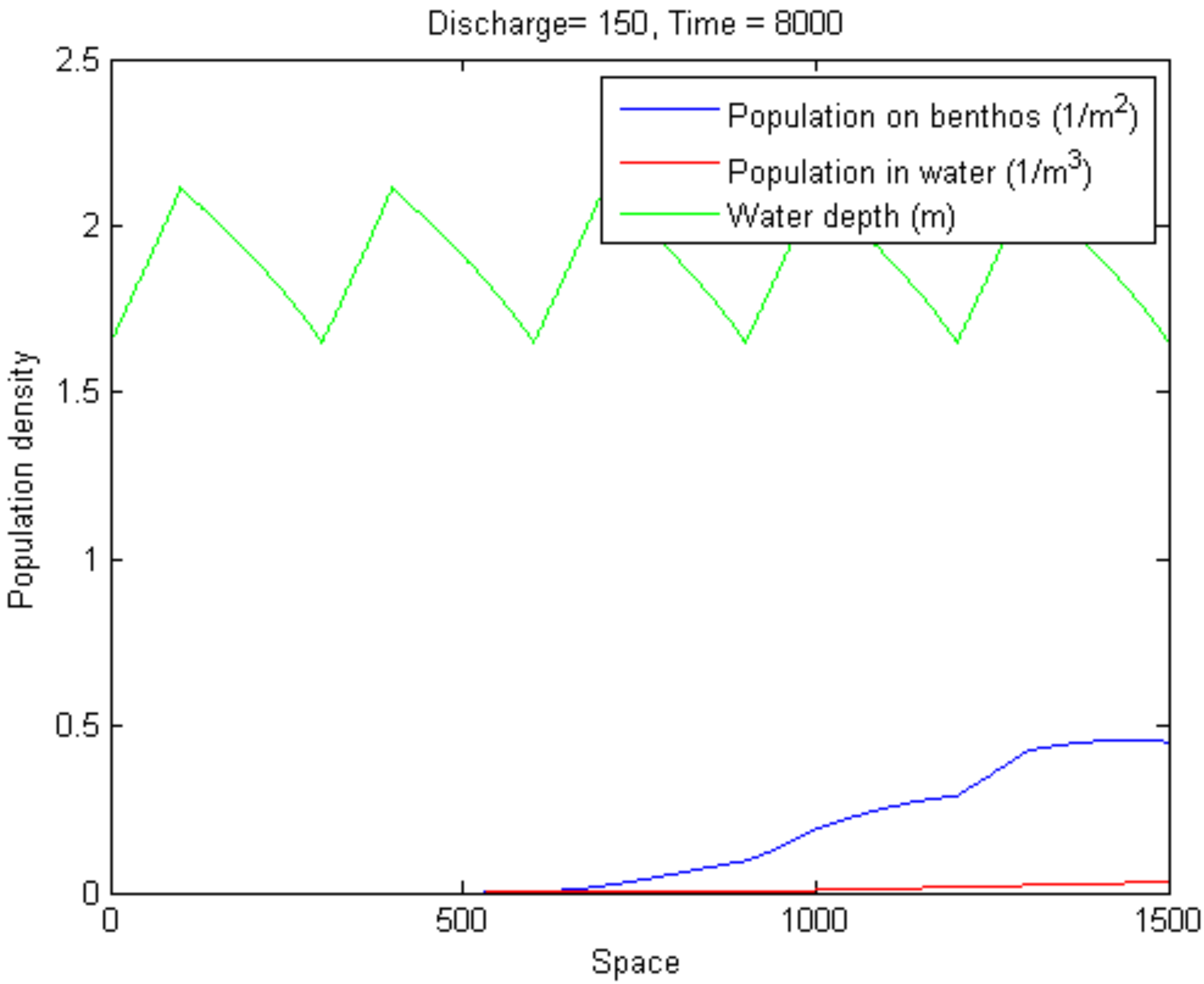

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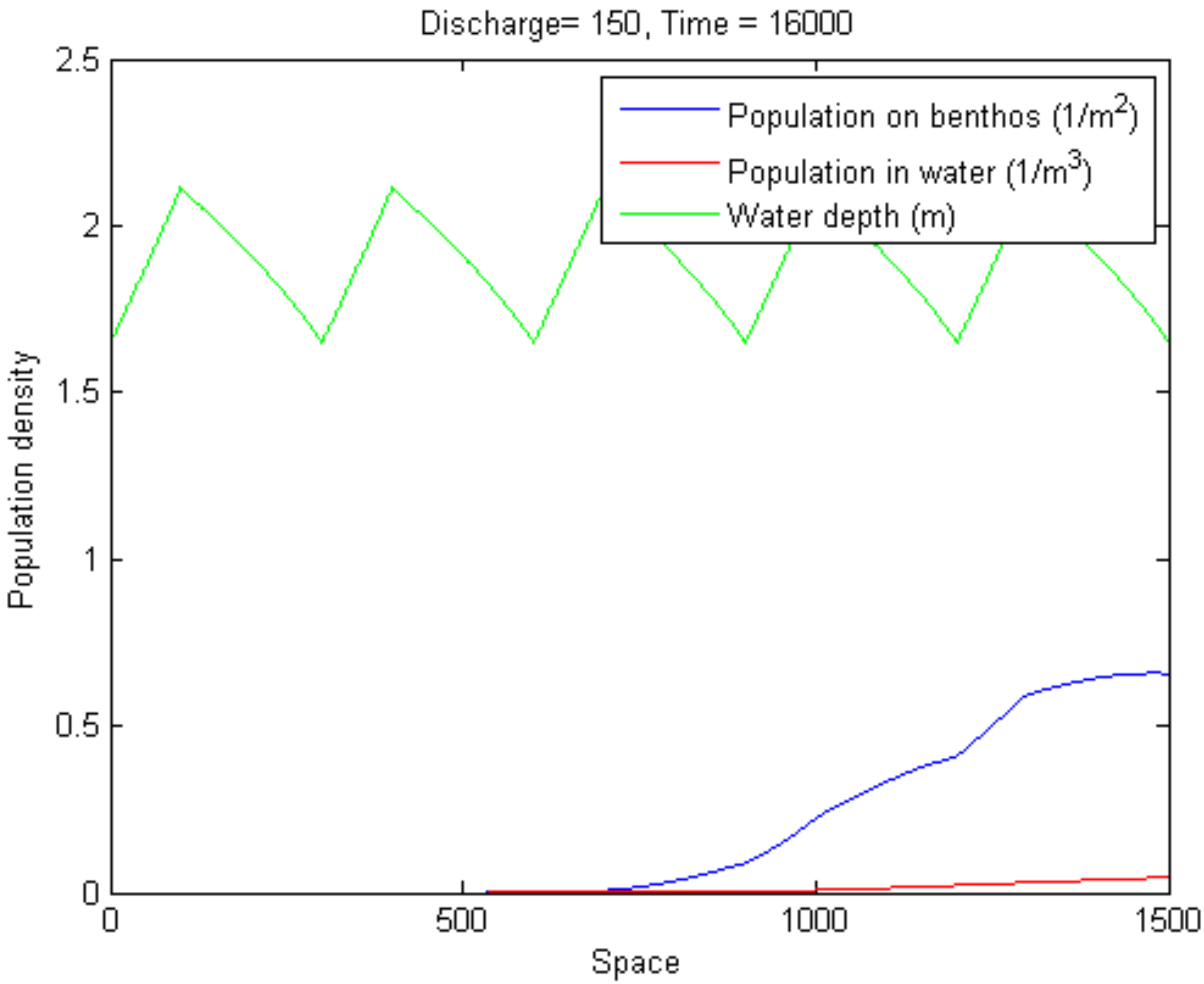

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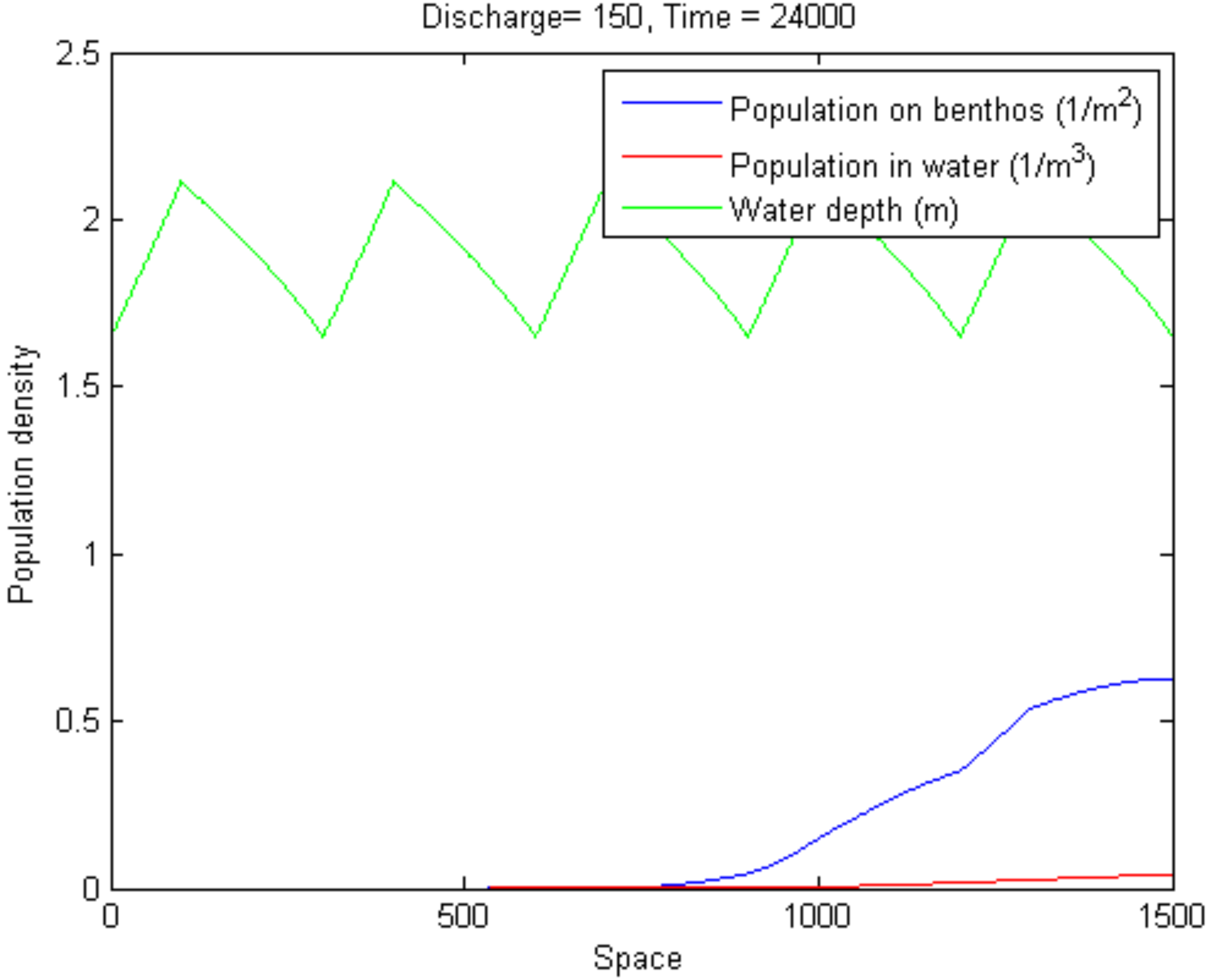

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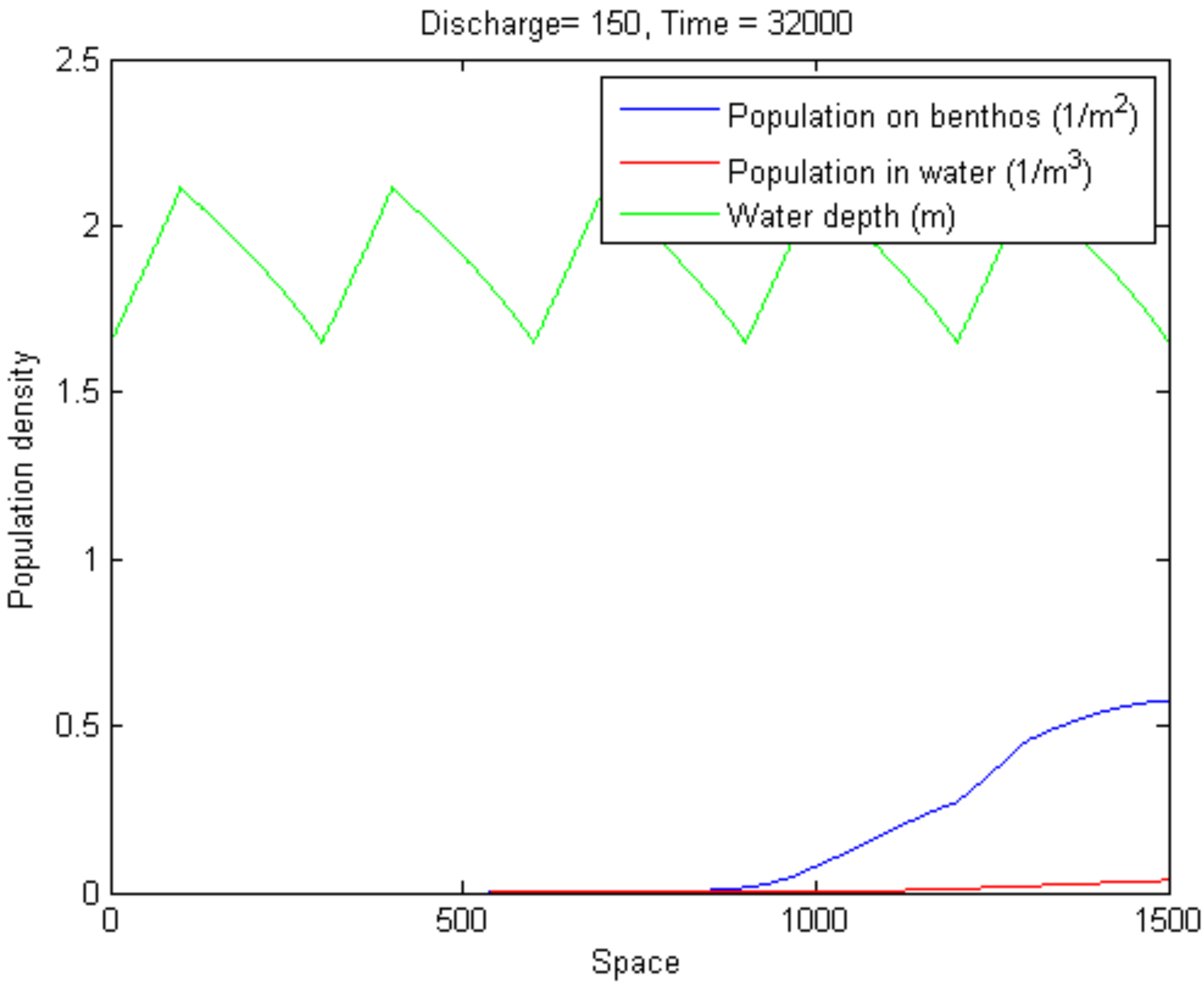

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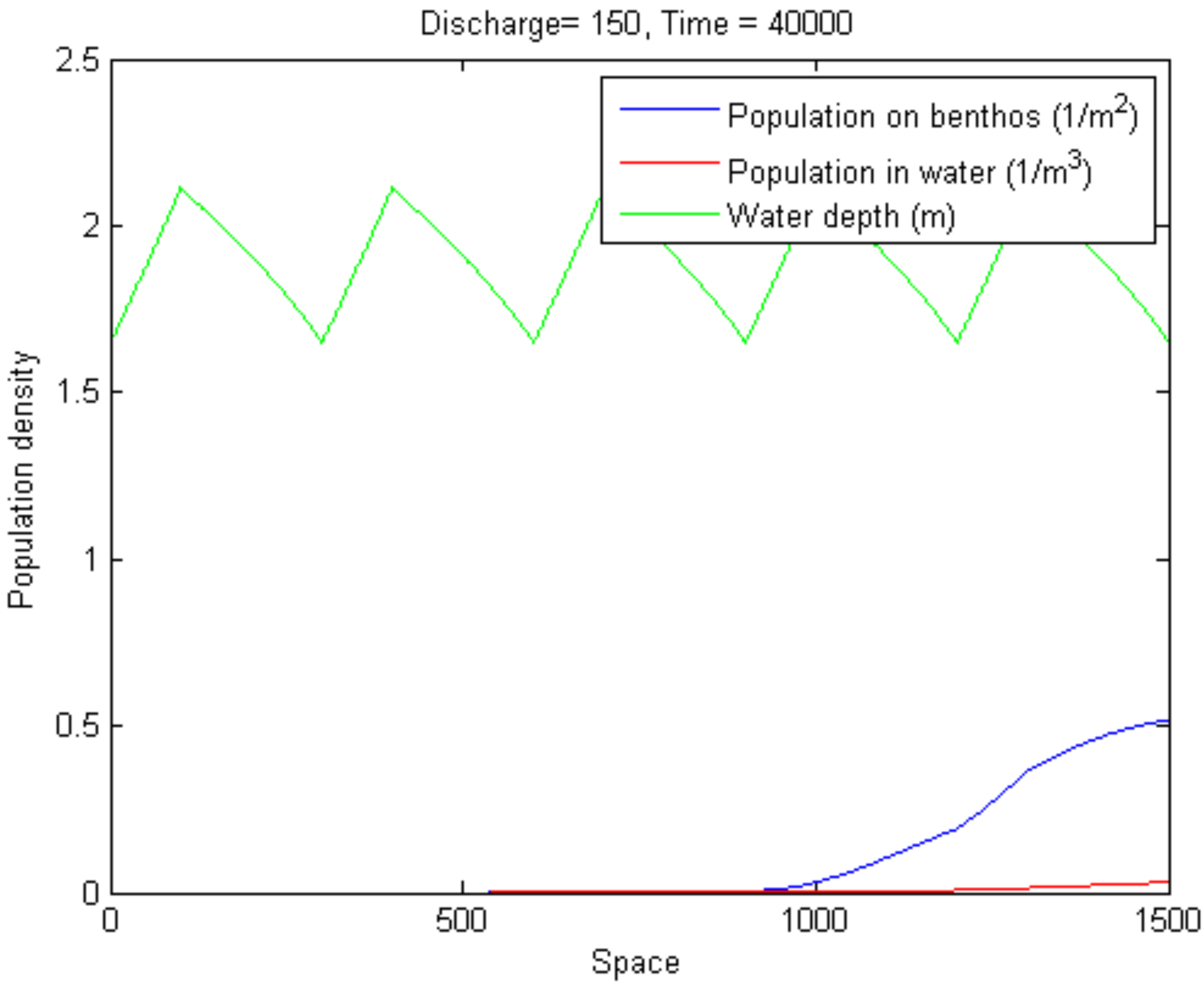

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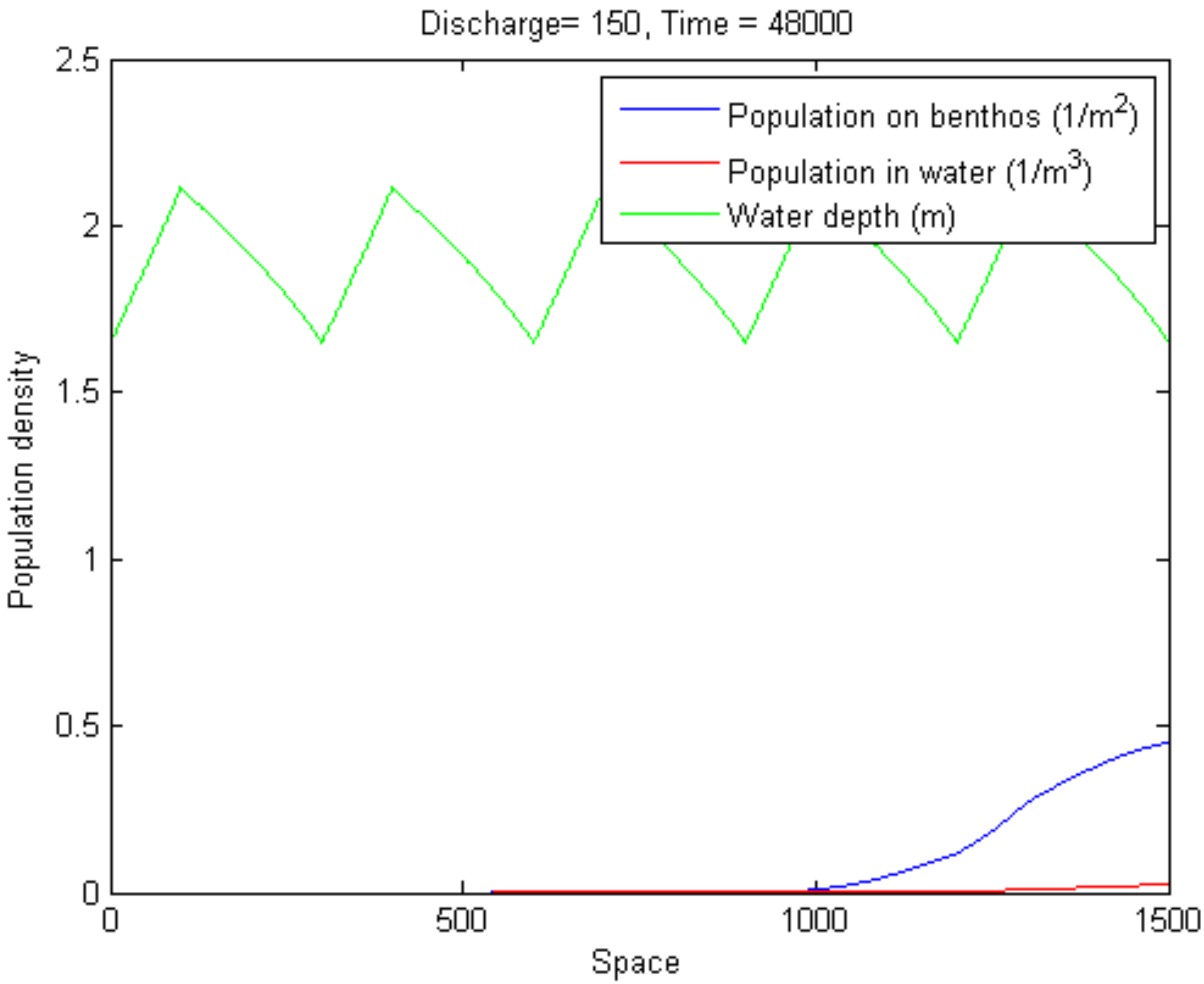

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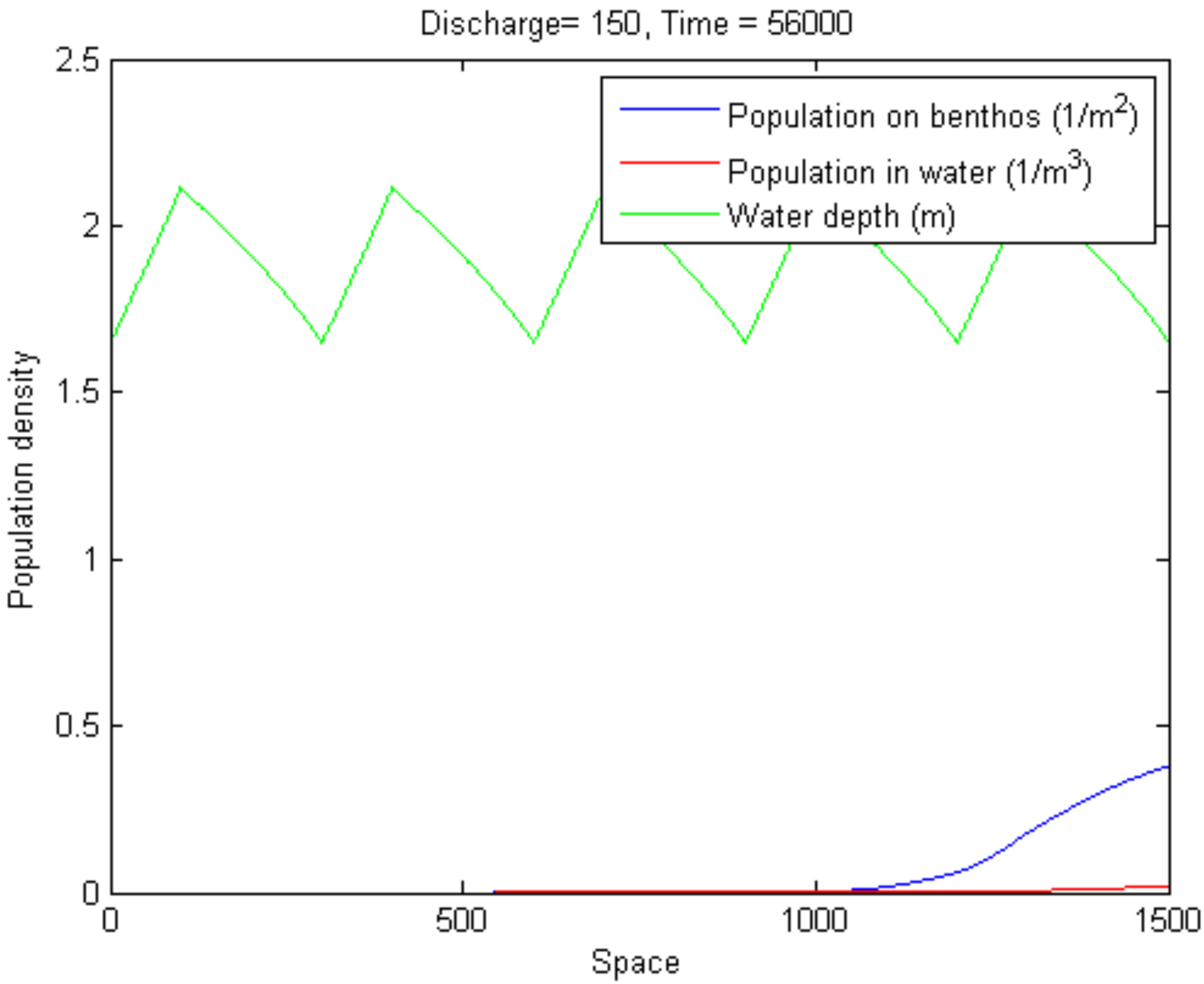

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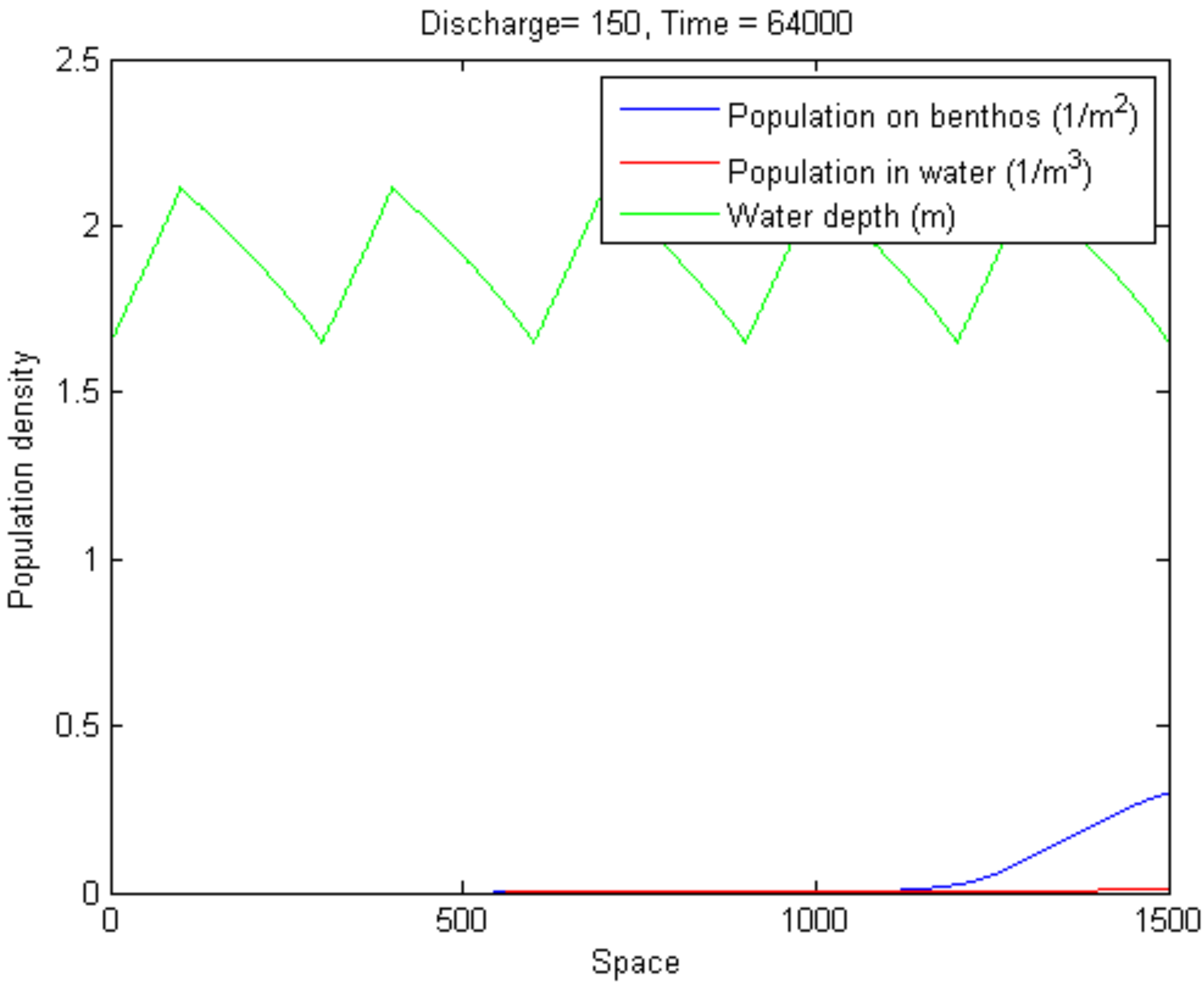

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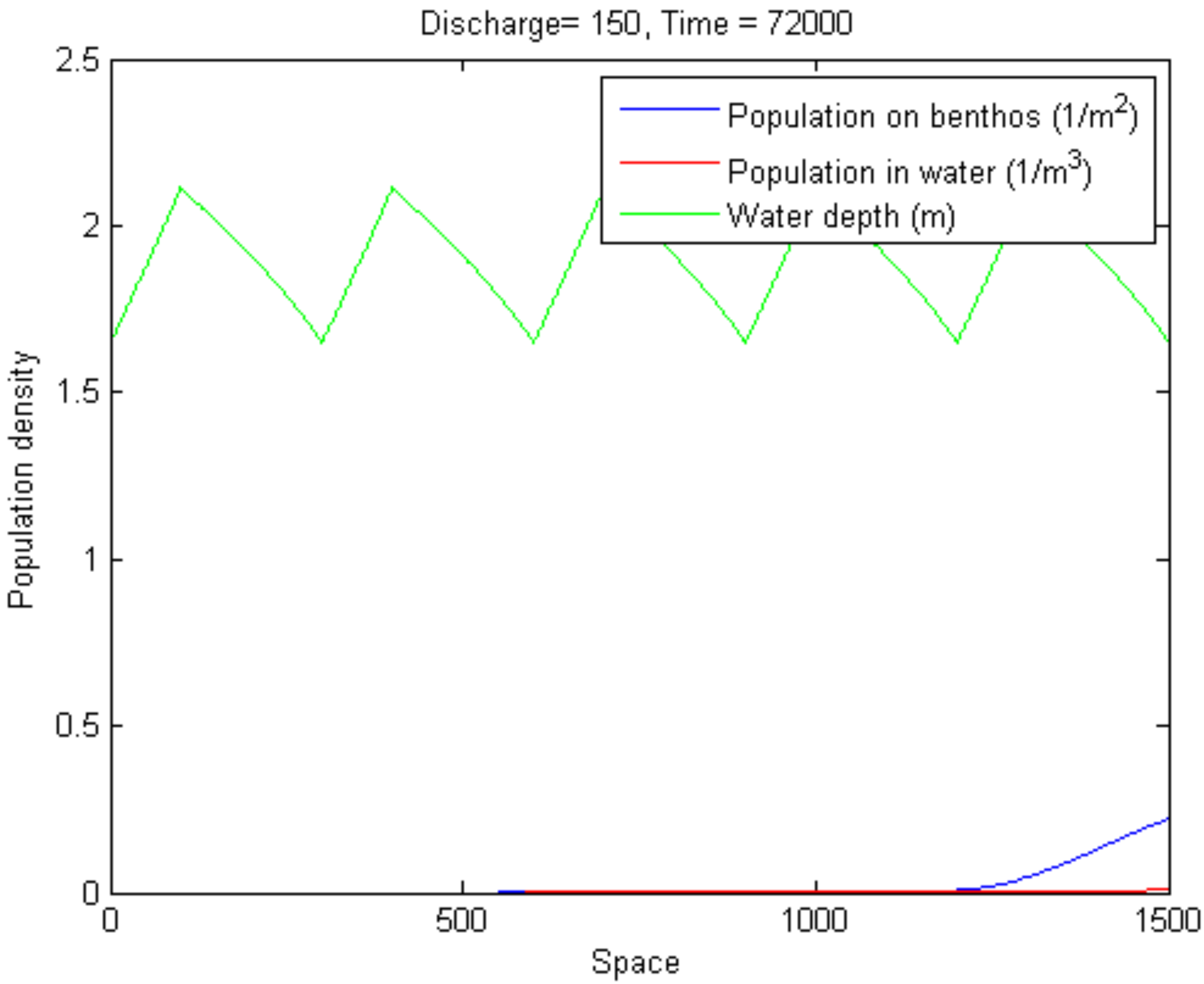

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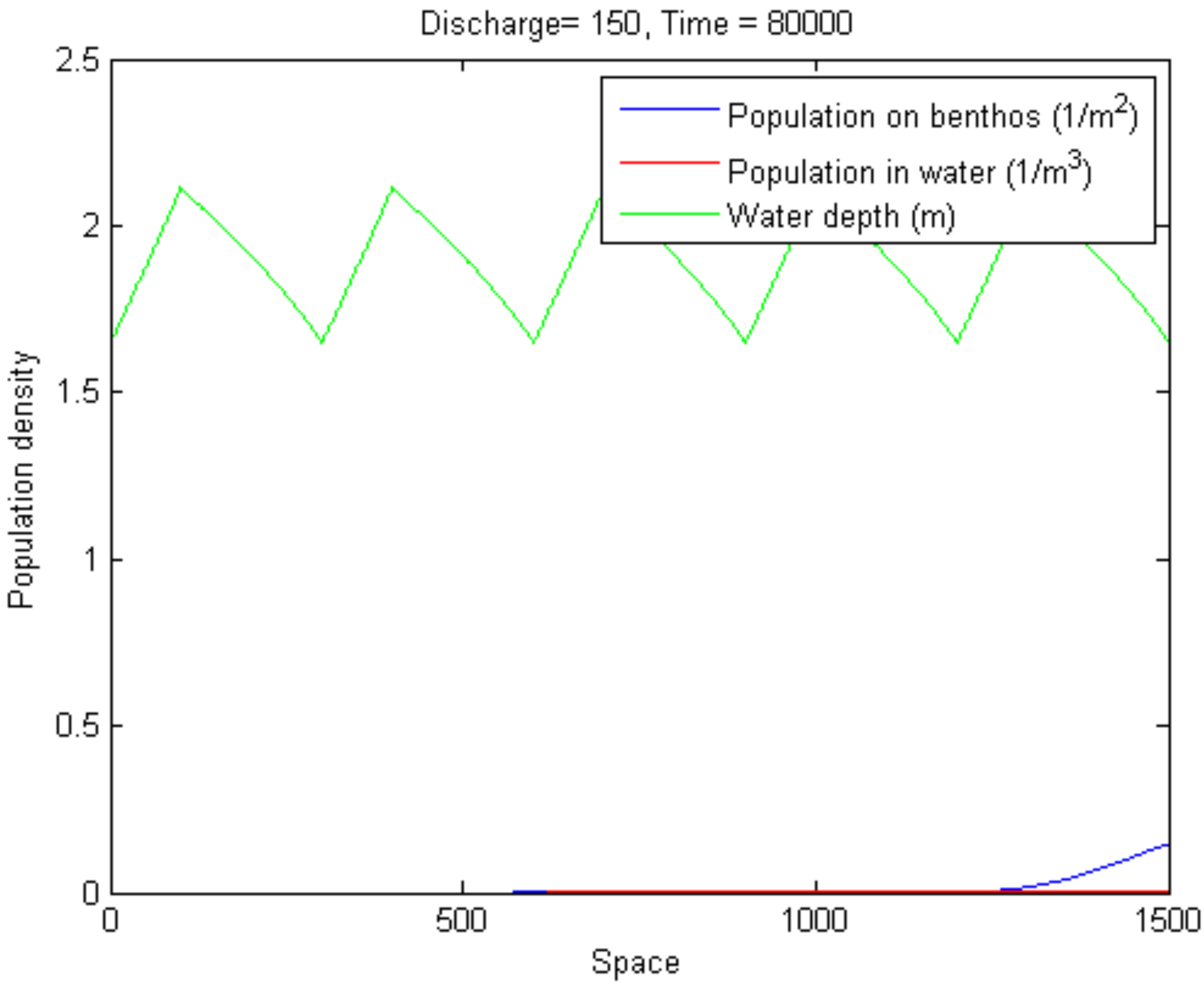

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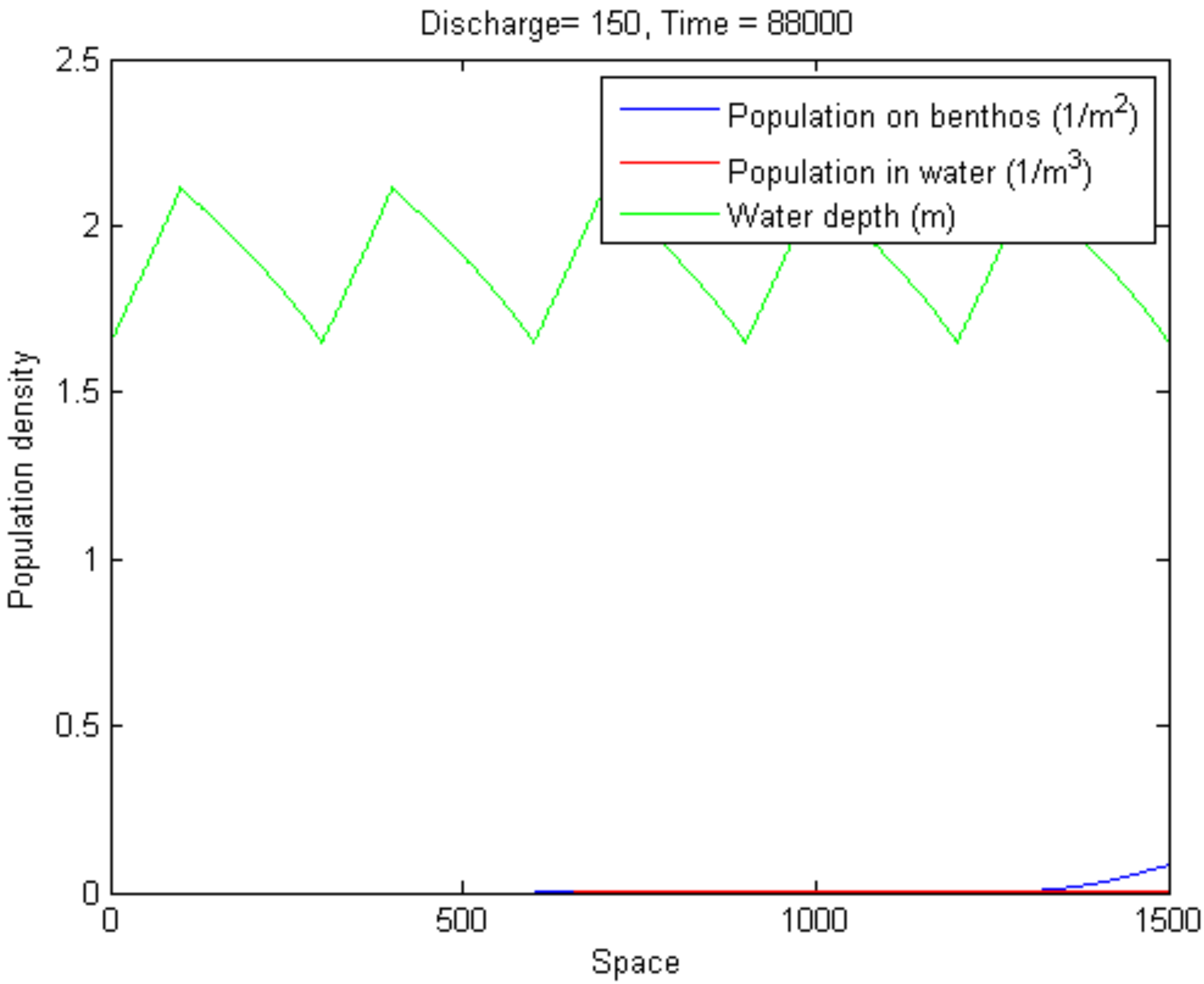

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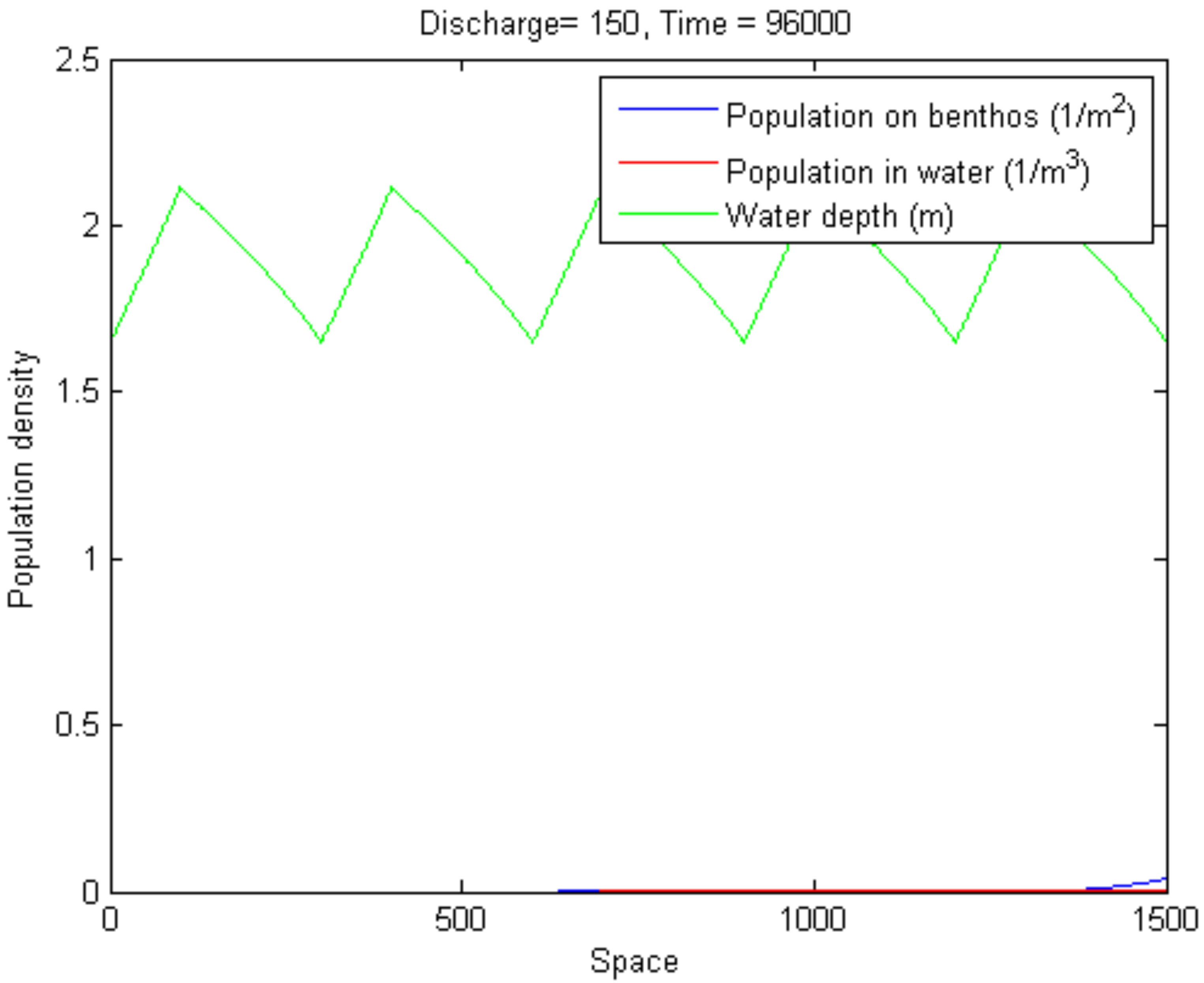

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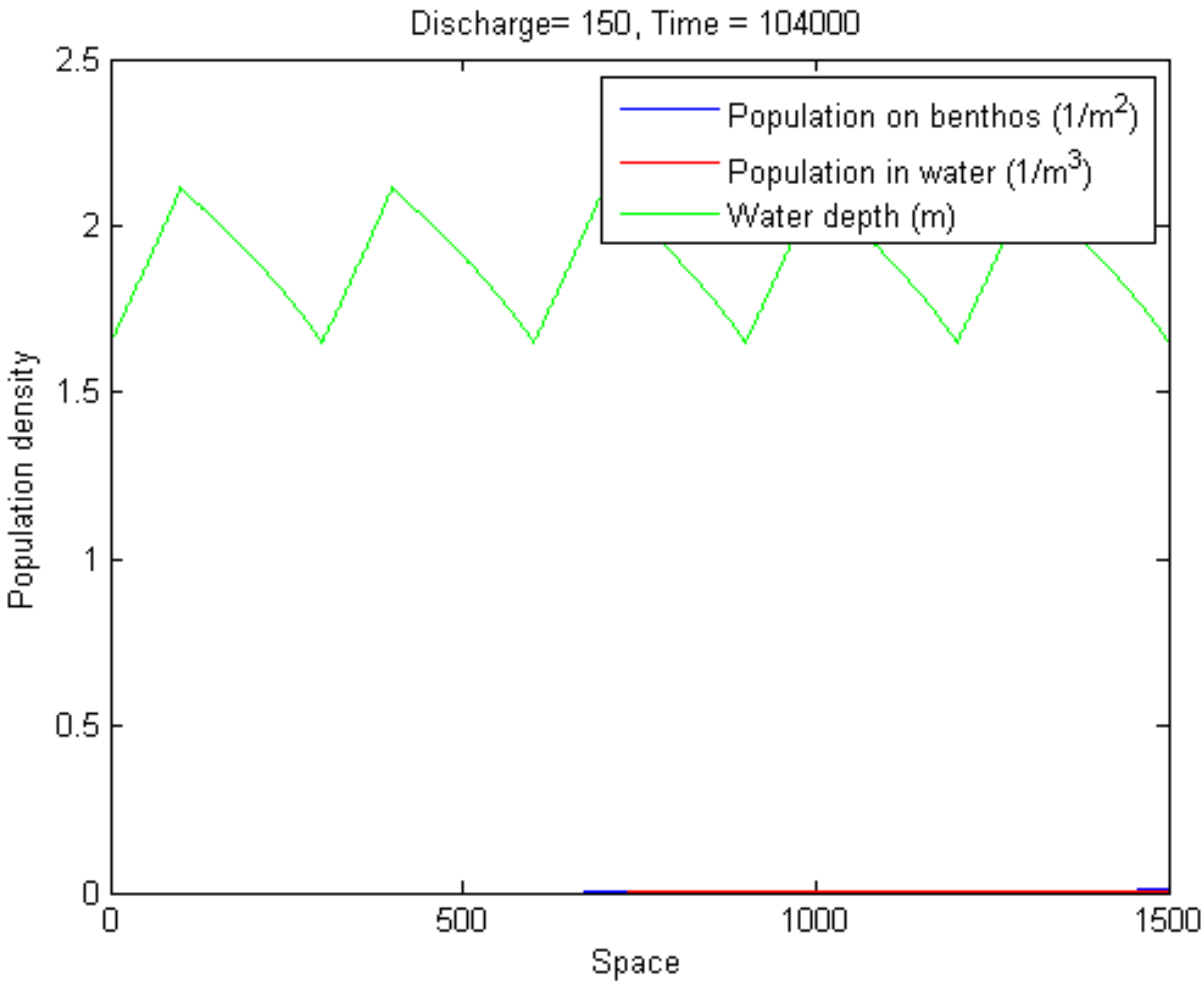


Summary of analytical results for 1D river population

• Analytical results were derived for the case with piecewise constant "good" and "bad" patches, repeating with length scale L in Lutscher et al. (2006).

• For the pelagic model: adding spatial heterogeneity can allow for persistence, when none would be possible in the appropriately homogenized spatially uniform system.

• For the benthic/drift model: if the transfer rate from benthic to drift components is less than intrinsic growth rate in benthic compartment ($\mu < \max_{0 \le x \le L} g(x,0)$) there will be unconditional persistence, independent of flow. When $\mu > \max_{0 \le x \le L} g(x,0)$ persistence is conditional on sufficiently low flow, and spatial heterogeneity also can allow for persistence.

Numerical simulation of a 2D river population

• Water flow in a river is modelled using Reynolds-averaged *Navier-Stokes* methods, with bed friction and with eddy viscosity to define turbulence (River2D).

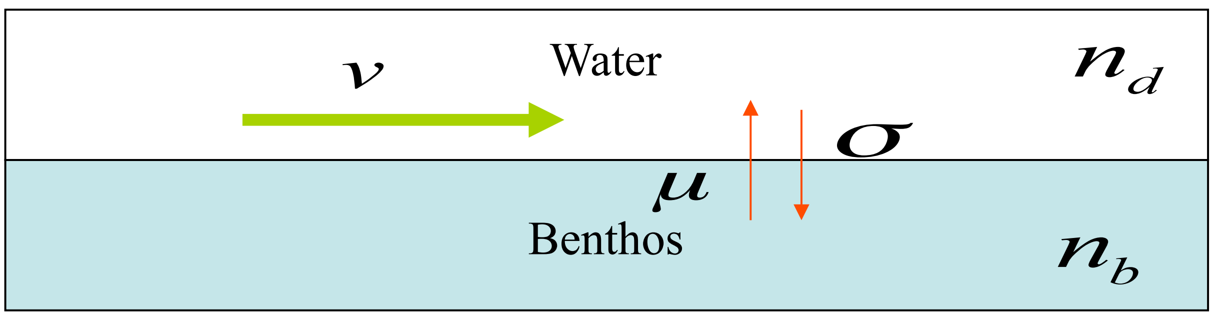
• Equations are solved in 2D (depth averaging), using finite elements, and are run to steady state.

•Physical quantities of velocity $a(x,y)$, depth $h(x,y)$ and turbulent diffusion $D(x,y)$ terms come from River2D calculations.

Steffler, Blackburn.

Benthic-drift model

• Water flow is coupled to a population that grows, dies and moves between the water column and the benthos

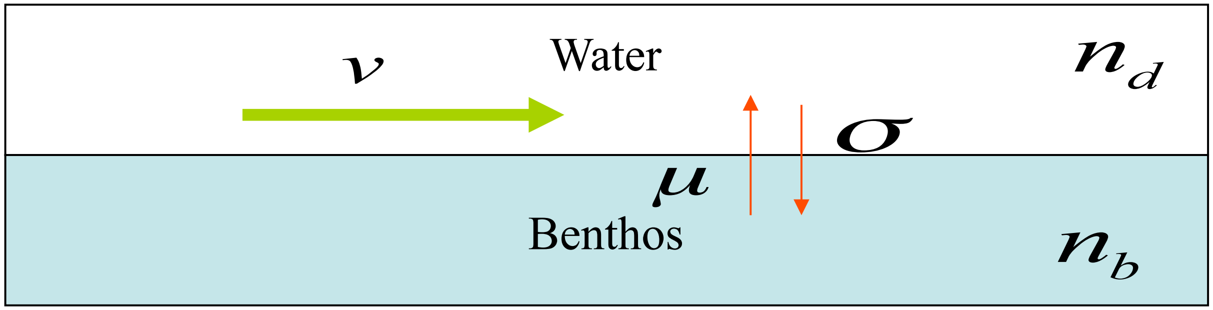


Jin, Lewis, Steffler, Blackburn.

Benthic-drift model

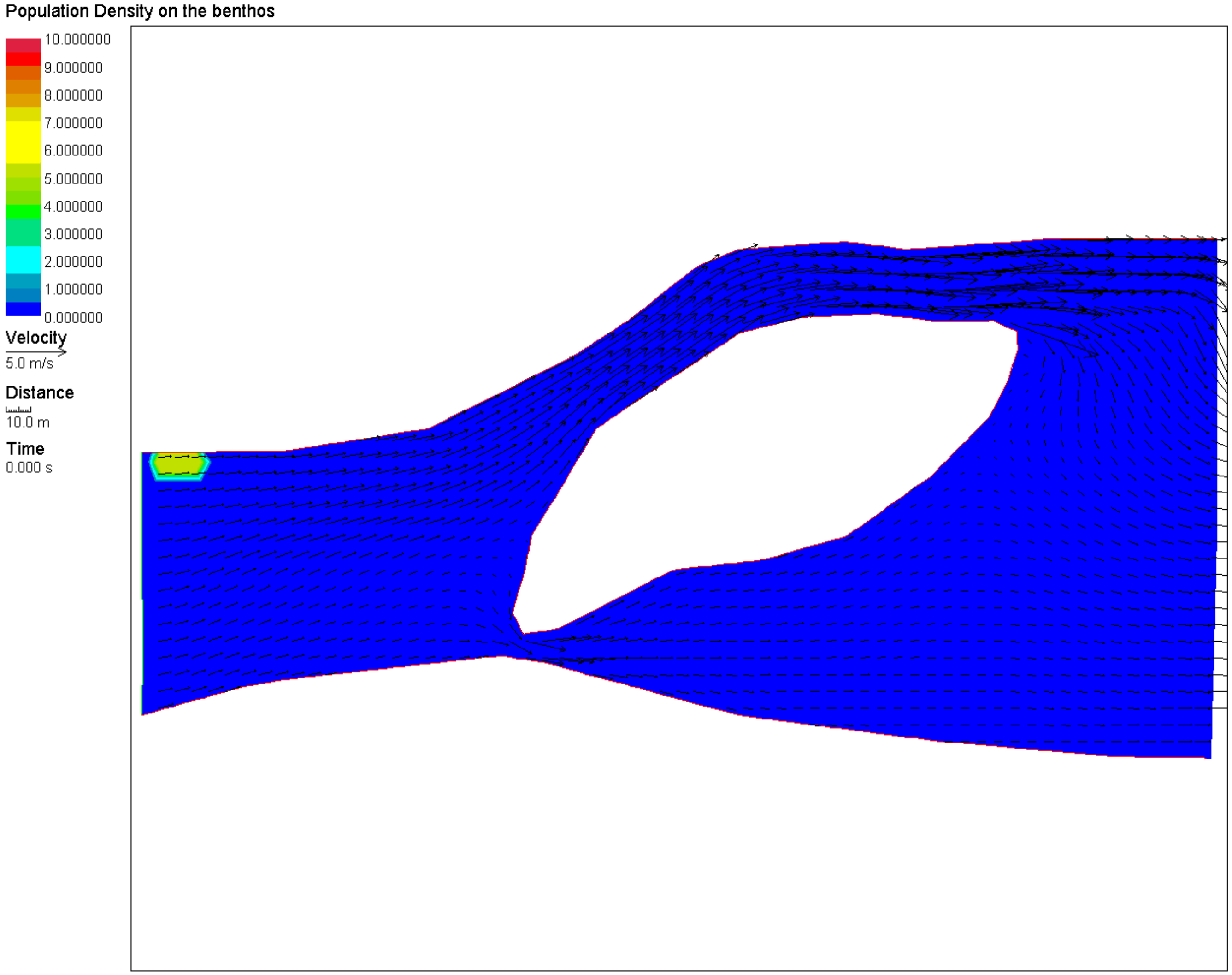
$$\frac{\partial n_d(x,y,t)}{dt} = \underbrace{\frac{\mu}{h(x,y)} n_b(x,y,t)}_{\text{transfer from } N_b} - \underbrace{\sigma n_d(x,y,t)}_{\text{transfer to } N_b}$$
$$\underbrace{-\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}\left[v_1(x,y)h(x,y)n_d(x,y,t)\right] + \frac{\partial}{\partial y}\left[v_2(x,y)h(x,y)n_d(x,y,t)\right]\right]}_{\text{advection}}$$
$$\underbrace{+\frac{1}{h(x,y)}\left[\frac{\partial}{\partial x}\left[D(x,y)h(x,y)\frac{\partial n_d(x,y,t)}{\partial x}\right] + \frac{\partial}{\partial y}\left[D(x,y)h(x,y)\frac{\partial n_d(x,y,t)}{\partial y}\right]\right]}_{\text{diffusion}}$$

$$\frac{\partial n_b(x,y,t)}{dt} = \underbrace{f(n_b(x,y,t))}_{\text{growth}} + \underbrace{\sigma n_d(x,y,t)h(x,y)}_{\text{transfer from } N_d} - \underbrace{\mu n_b(x,y,t)}_{\text{transfer to } N_d}$$



Jin, Lewis, Steffler, Blackburn.

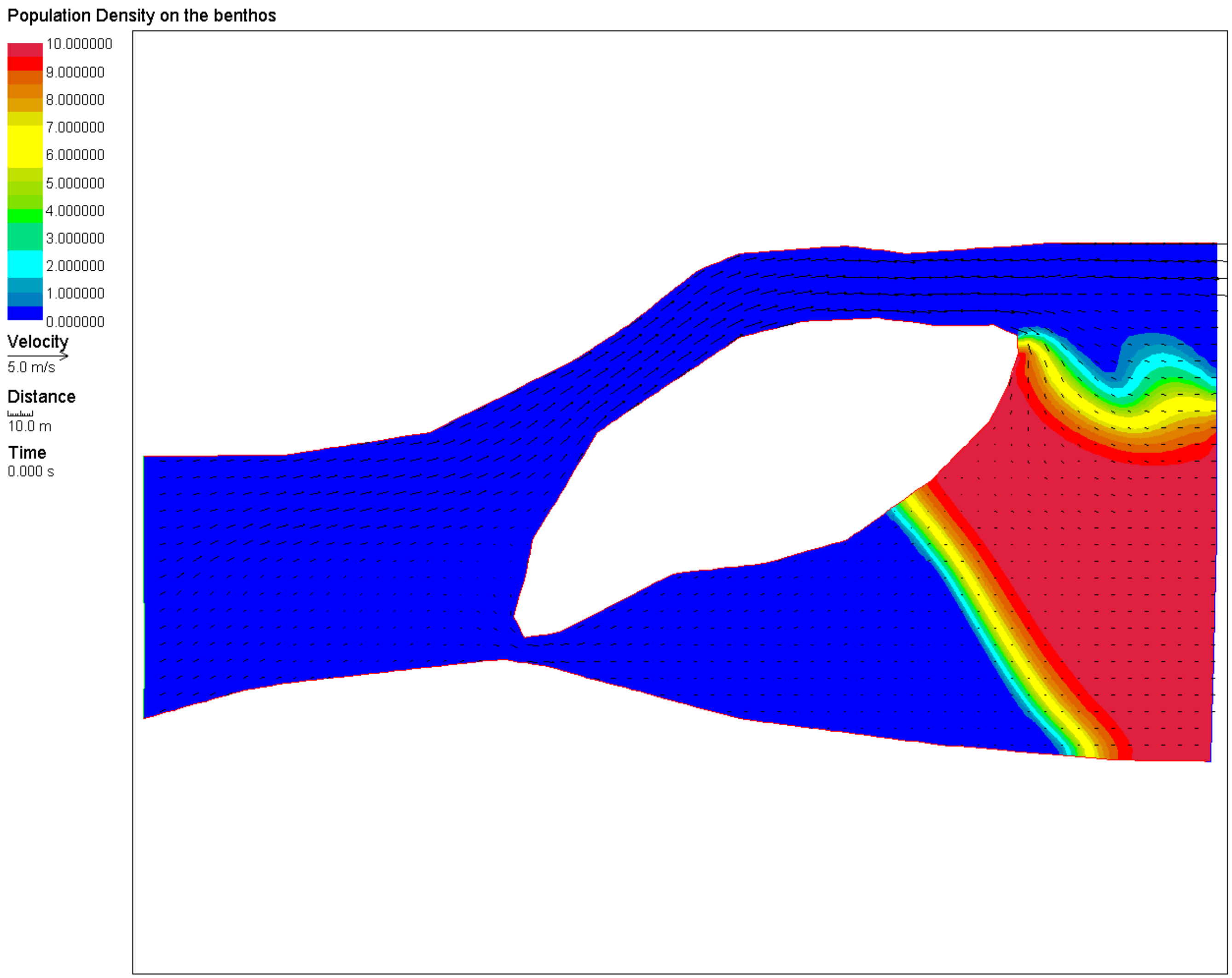
Simulation of benthic-drift model: high flow



Steffler, Blackburn, Jin, Lewis.

Simulation of benthic-drift model: lower flow

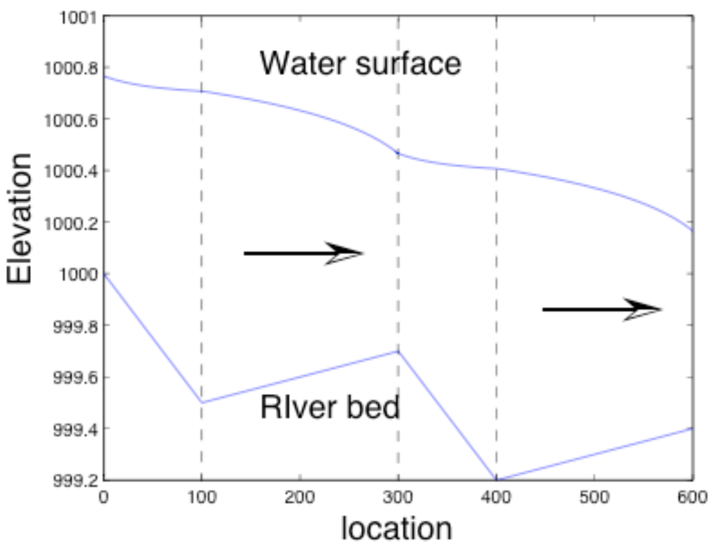
- River2D simulation for the benthic-drift model



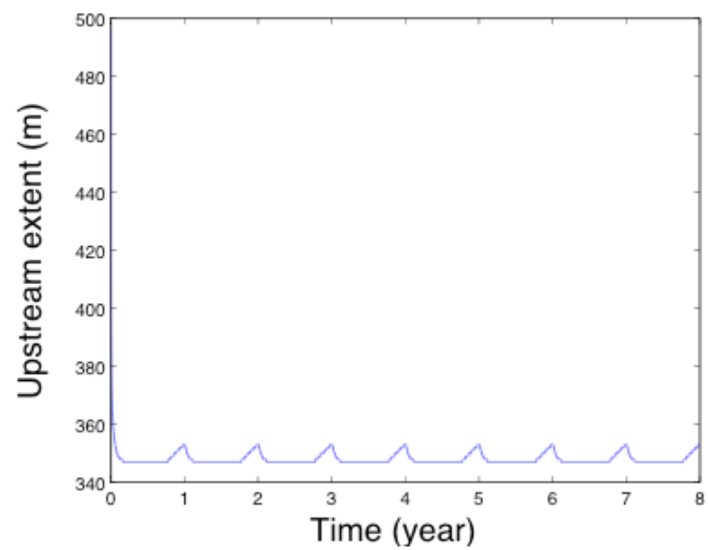
Steffler, Blackburn, Jin, Lewis.

How can flow levels affect invasions? The invasion ratchet

- Flow levels affect environmental conditions (scouring, nutrients, flooding) and hence control of invader (eg., weeds, *Didymo*)
- Reduced flow can enhance upstream spread (eg., zebra mussels).
- Reduced <u>seasonal</u> flow could lead to an *invasion ratchet*



seasonal
\+ fluctuations =
in flow levels



Limited upstream spread

Jin, Lewis, Steffler et al. (in prep)

How can flow levels affect invasions? The invasion ratchet

- Flow levels affect environmental conditions (scouring, nutrients, flooding) and hence control of invader (eg., weeds, *Didymo*)
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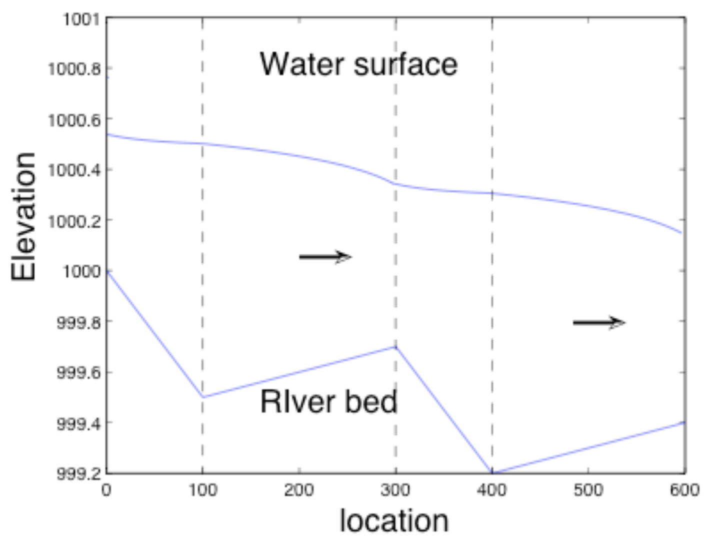
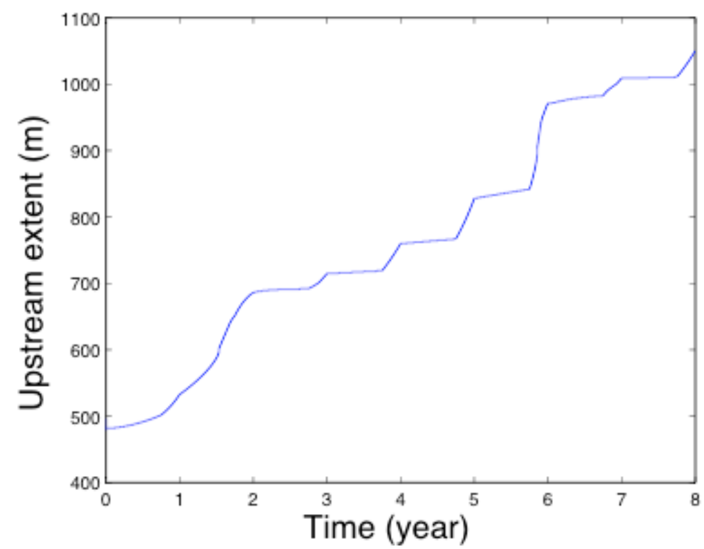


seasonal

\+ fluctuations =

in flow levels



Enhanced upstream spread

Jin, Lewis, Steffler et al. (in prep)

Outline

• How can we manage rivers? Biological dynamics and management question.

• Biology meets physics: coupling population dynamics to stream flows

• The stream paradox: spreading speeds and critical domain size

• Is this a good place to live? niche theory and the net reproductive rate

• Towards realistic stream models

General single species pelagic model

$$\underbrace{\frac{\partial n}{\partial t}}_{\text{rate of change of population density}} = \underbrace{\frac{1}{A(x)}\frac{\partial}{\partial x}\left[D(x)A(x)\frac{\partial n}{\partial x}\right]}_{\text{diffusion}} - \underbrace{\frac{Q}{A(x)}\frac{\partial n}{\partial x}}_{\text{advection}} + \underbrace{g(x,n)n}_{\text{growth dynamics}}$$

with boundary conditions

$$0 = \alpha_1 n(0) + \beta_1 n_x(0)$$

$$0 = \alpha_2 n(L) + \beta_2 n_x(L)$$

Spatially homogeneous model

$$\underbrace{\frac{\partial n}{\partial t}}_{\text{rate of change of population density}} = \underbrace{D\frac{\partial^2 n}{\partial x^2}}_{\text{diffusion}} - \underbrace{a\frac{\partial n}{\partial x}}_{\text{advection}} + \underbrace{g(n)n}_{\text{growth dynamics}}$$

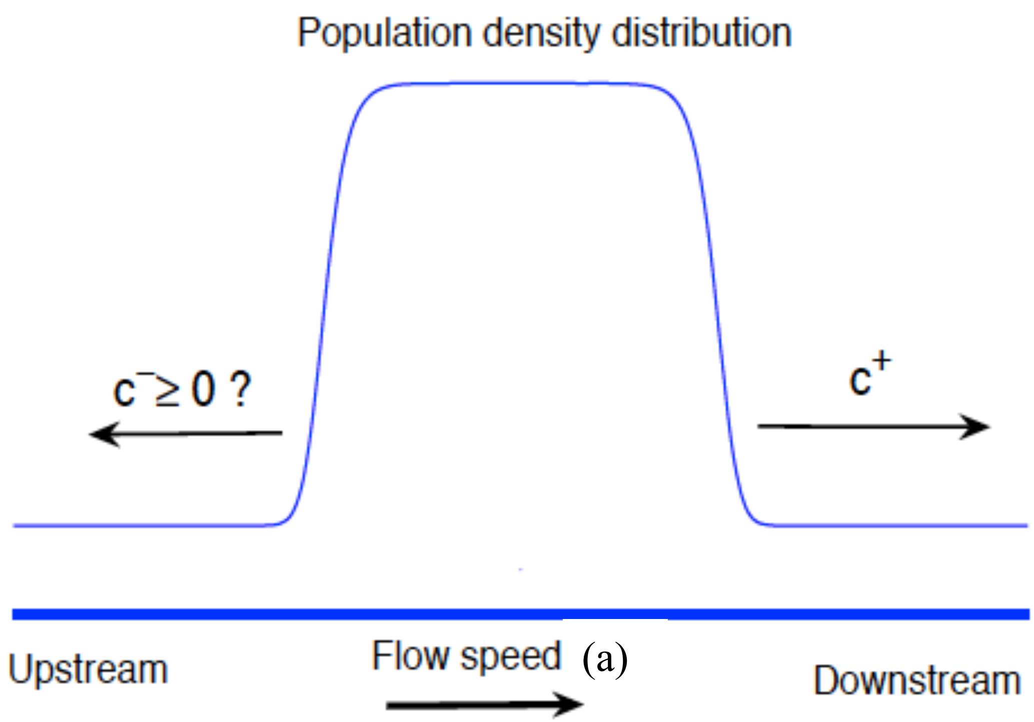
with boundary conditions

$$0 = \alpha_1 n(0) + \beta_1 n_x(0)$$

$$0 = \alpha_2 n(L) + \beta_2 n_x(L)$$

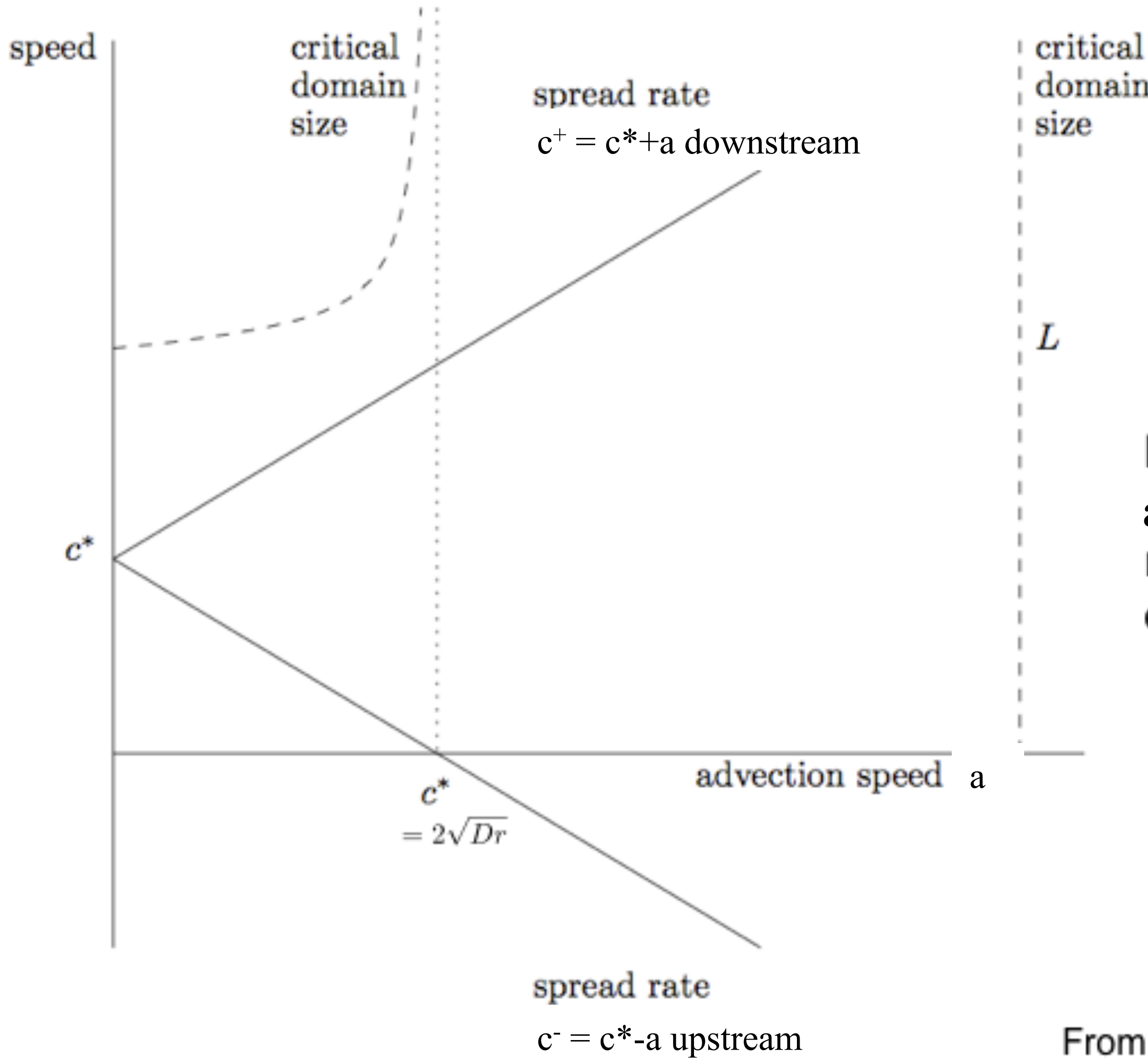
Drift Paradox

- The drift paradox asks how organisms can persist without being washed out, when they are continuously subjected to unidirectional stream flow



- If we assume logistic-type growth dynamics and hostile boundaries then…

Spreading speeds and critical domain size



D diffusion coefficient
a advection coefficient
r growth rate g(0)
c* intrinsic spread rate

From Lewis *et al*, PCMI notes, 2004

Spreading speeds and critical domain size

The connection between the critical domain size and the advection speed at which spread stalls can be extended to account for:

- different boundary conditions (McKenzie et al., 2011).

- long-distance dispersal via integro-difference or integrodifferential equations (Lutscher et al., 2005).

- spatial heterogeneity (Lutscher et al., 2006).

- seasonality in growth and dispersal (Jin and Lewis, 2011).

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

Outline

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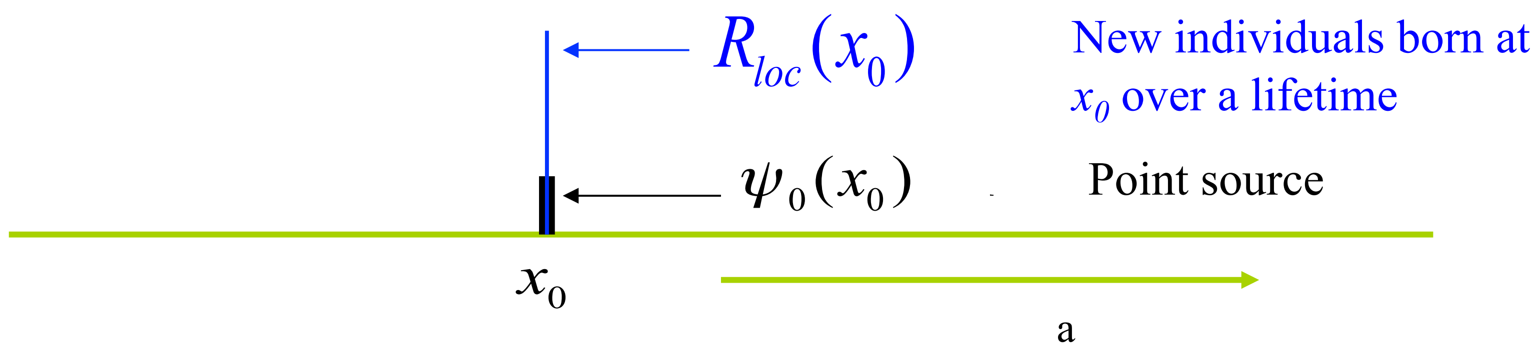
Is this a good place to live?

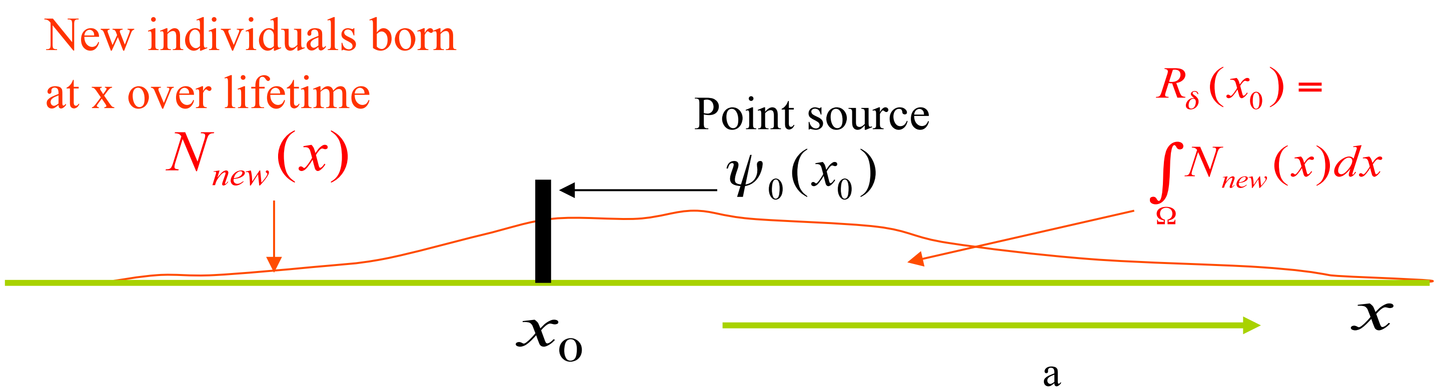
1 $R_{loc}(x)$: number of offspring produced by an individual introduced at x (dispersal excluded), fundamental niche.



Krkosek and Lewis (2010)

Is this a good place to live?

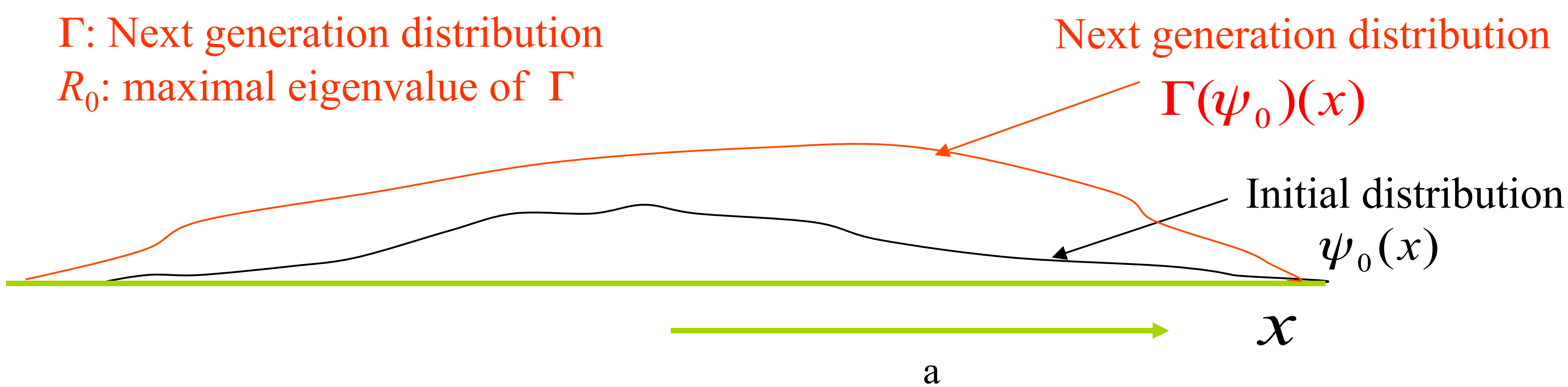
2 $R_\delta(x)$: number of offspring produced by an individual introduced at x (dispersal included), realized niche



Krkosek and Lewis (2010)

Is this a good place to live?

3 R_0: net reproductive rate – number of offspring produced over an individual's lifetime, given that the individual is distributed spatially in a manner appropriate for maximizing long-term growth



$$\text{Global invasion dynamics: } \begin{cases} R_0 < 1, \text{ population extinction} \\ R_0 > 1, \text{ population persistence} \end{cases}$$

Krkosek and Lewis (2010)

Net reproductive rate for the single pelagic species model

$$\underbrace{\frac{\partial n}{\partial t}}_{\substack{\text{rate of change}\\ \text{of population density}}} = \underbrace{\frac{1}{A(x)}\frac{\partial}{\partial x}\left[D(x)A(x)\frac{\partial n}{\partial x}\right]}_{\text{diffusion}} - \underbrace{\frac{Q}{A(x)}\frac{\partial n}{\partial x}}_{\text{advection}} + \underbrace{g(x,n)n}_{\text{growth dynamics}}$$

$$= \mathcal{L}n + g(x,n)n \quad \text{where}$$

$$\mathcal{L} = \frac{1}{A(x)}\frac{\partial}{\partial x}\left[D(x)A(x)\frac{\partial n}{\partial x}\right] - \frac{Q}{A(x)}\frac{\partial n}{\partial x}$$

is a strongly elliptic operator with boundary conditions

$$0 = \alpha_1 n(0) + \beta_1 n_x(0),$$

$$0 = \alpha_2 n(L) + \beta_2 n_x(L)$$

We assume that g is a continuous function of "logistic" form,
and that A > 0 and $D > 0$ are $C^2[0,L]$

Net reproductive rate for the single pelagic species model

Linearized growth term: let $g(x,0) = \underbrace{f(x)}_{\text{birth}} - \underbrace{v}_{\text{mortality}}$

Density of individuals originally present:

$$\begin{cases} \psi_t = -v\psi + \mathcal{L}\psi, & x \in (0,L),\ t > 0, \\ \psi(x,0) = \psi_0(x), & x \in (0,L). \end{cases}$$

Next generation operator $\Gamma : X \to X$ is defined by:

$$\Gamma\psi_0(x) = \int_0^\infty f(x)\psi(x,t)\,dt = f(x)\int_0^\infty \psi(x,t)\,dt,$$

Net reproductive rate for the single pelagic species model

It can alternatively be defined by:

$$\Gamma\psi_0(x) = f(x)\int_0^L k(x,y)\psi_0(y)\,dy,$$

where $k(x,y)$ is the solution of the ordinary boundary value problem

$$\begin{cases} \mathcal{L}k(x,y) - vk(x,y) = -\delta(x-y), & x \in (0,L) \\ \alpha_1 k(0,y) - \beta_1 k'(0,y) = 0 \\ \alpha_2 k(L,y) - \beta_2 k'(L,y) = 0. \end{cases}$$

The function $k(x,y)$ can be considered the lifetime density of space use of an individual originally introduced at y. Then

$$R_0 := r(\Gamma).$$

The next generation operator

$$\Gamma : C([0, L]) \to C([0, L]),$$

$$\underbrace{\Gamma\psi_0(x)}_{\text{density of new individuals produced by } \psi_0(x)} = \underbrace{f(x)}_{\text{birth}} \int_0^\infty \underbrace{\psi(x,t)}_{\text{density of initially introduced individuals still present at time t}} \, dt$$

density of initially introduced individuals still present at time t →

$$\psi_t = -v\psi + \mathcal{L}\psi, \quad x \in (0, L), t > 0$$

$$\psi(x, 0) = \psi_0(x), \quad x \in (0, L)$$

+ BC

$$= f(x) \int_0^L \underbrace{k(x, y)}_{\text{lifetime spatial density of an individual introduced at y}} \psi_0(y) \, dy$$

lifetime spatial density of an individual introduced at y →

$$-vk(x, y) + \mathcal{L}k(x, y) = -\delta(x - y)$$

+ BC

Spectral properties of the next generation operator

(1) Well-defined, compact linear operator

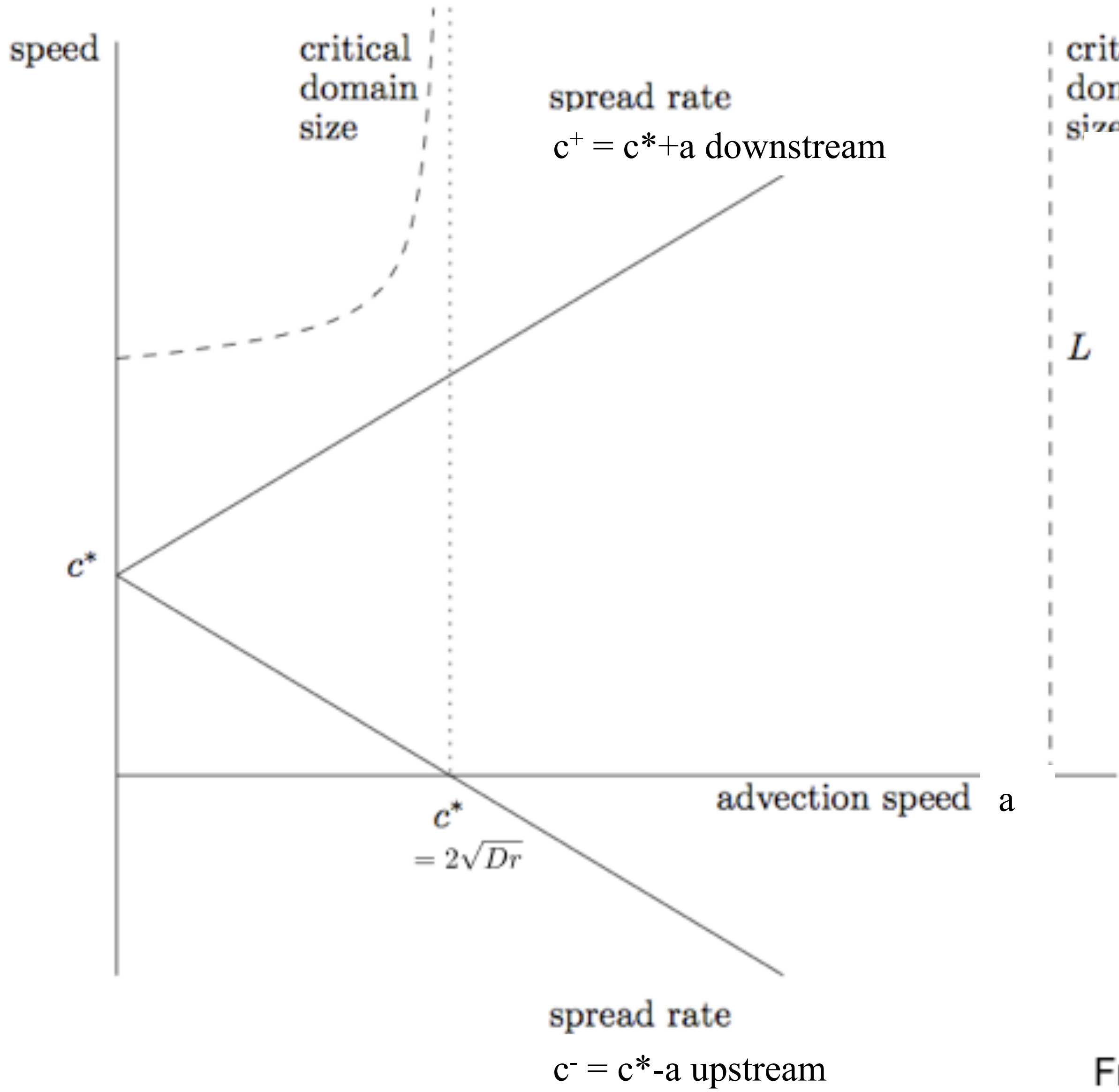
(2) Krein-Rutman Thm: $R_0 = r(\Gamma)$ is a simple eigenvalue and is the dominant eigenvalue of Γ. Furthermore, R_0 is the only eigenvalue with a an eigenvector that is positive on $(0, L)$.

(3) Mckenzie et al. (2011), based on Thieme (2009): The solution $n^*= 0$ is asymptotically stable when $R_0 < 1$ and unstable when $R_0 > 1$. The population is uniformly persistent when $R_0 > 1$.

(4) Chatelin (1981): It is possible to approximate R_0 numerically

Publication:
Hannah McKenzie, Yu Jin, Jon Jacobson, and Mark A. Lewis, R_0 analysis of a spatiotemporal model for a stream population, in review, *SIAM Journal on Applied Dynamical Systems*.

Spreading speeds and critical domain size



D diffusion coefficient
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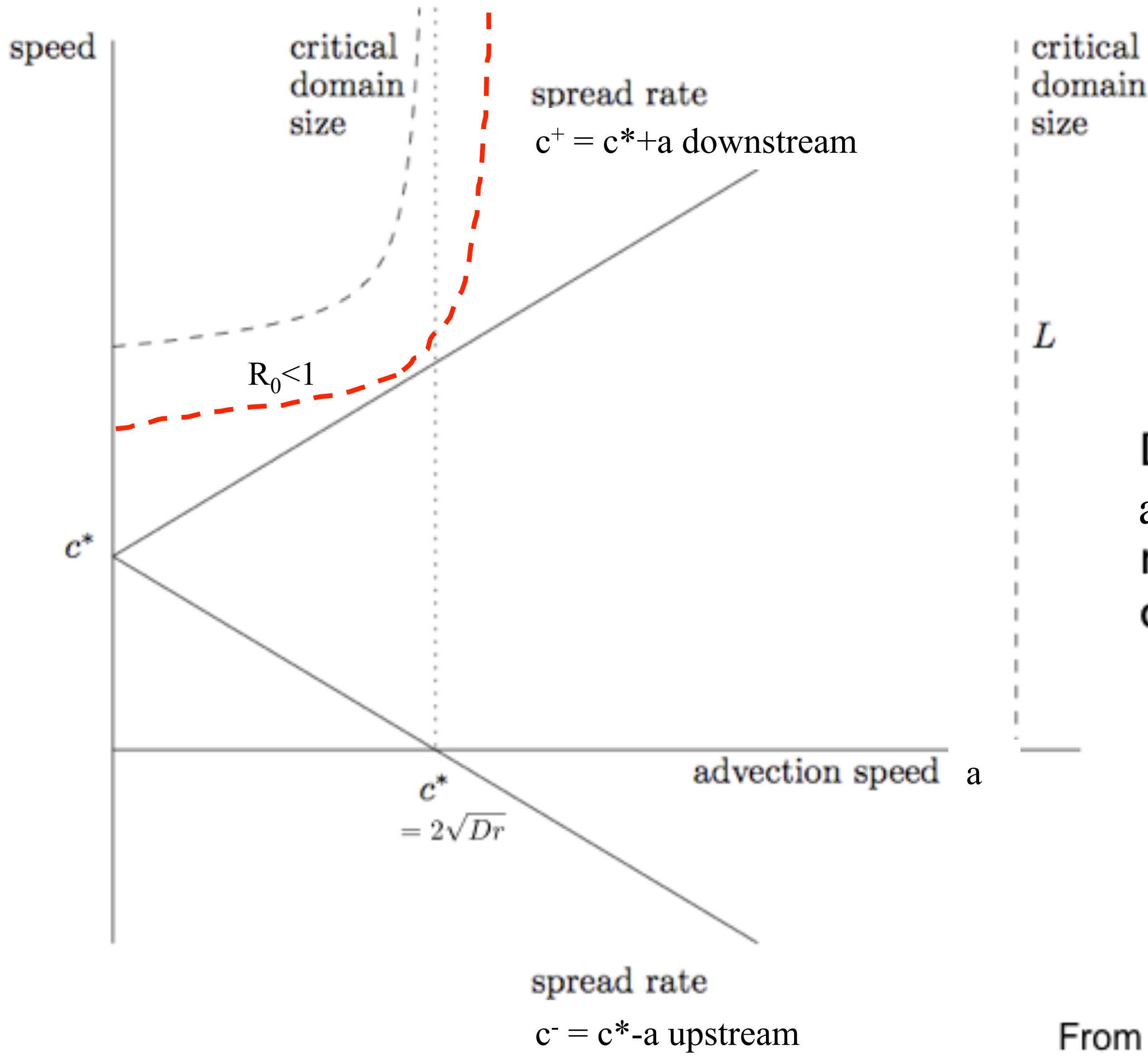
r growth rate g(0)
c* intrinsic spread rate

From Lewis *et al*, PCMI notes, 2004

Spreading speeds and critical domain size



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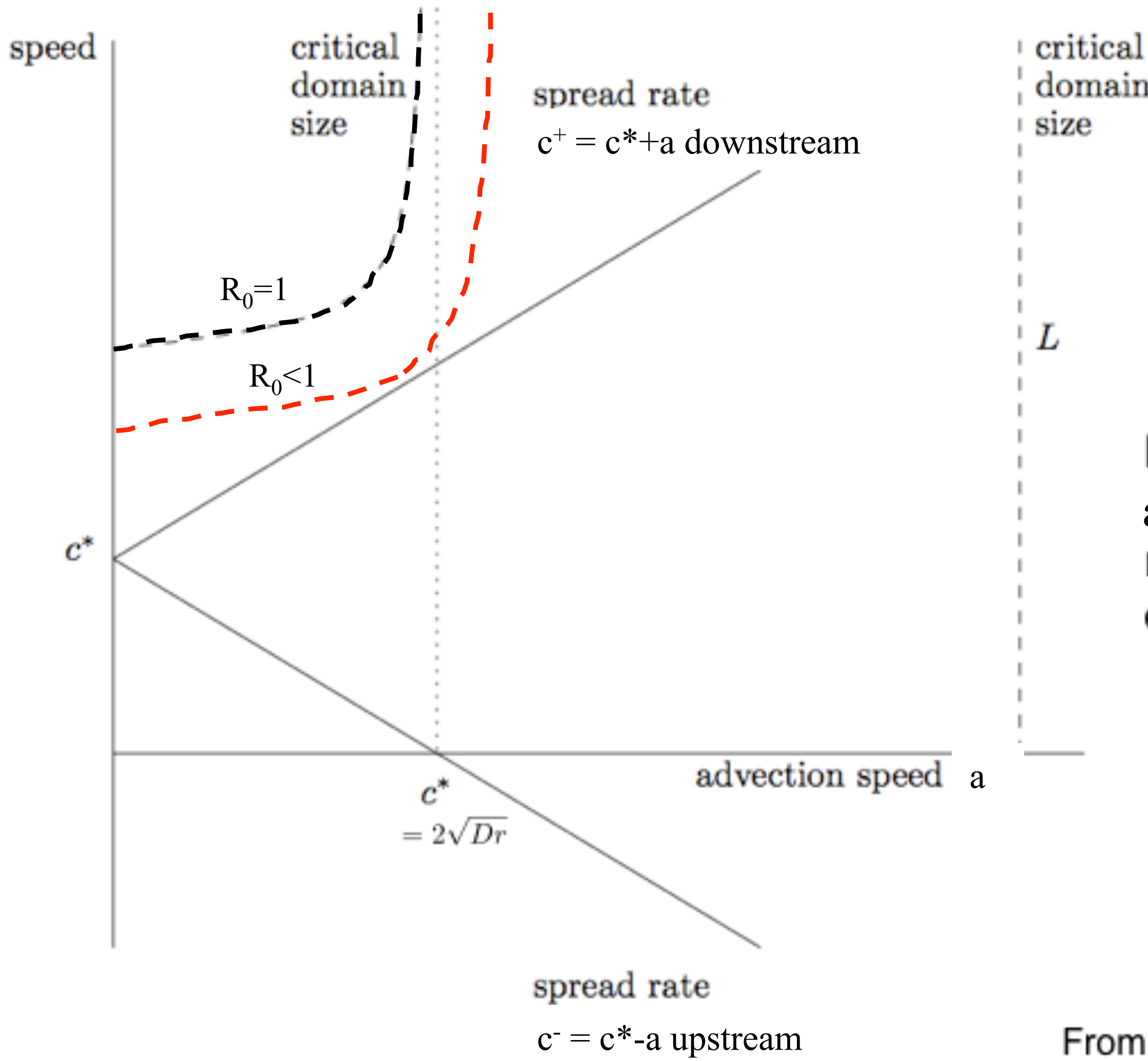
Spreading speeds and critical domain size



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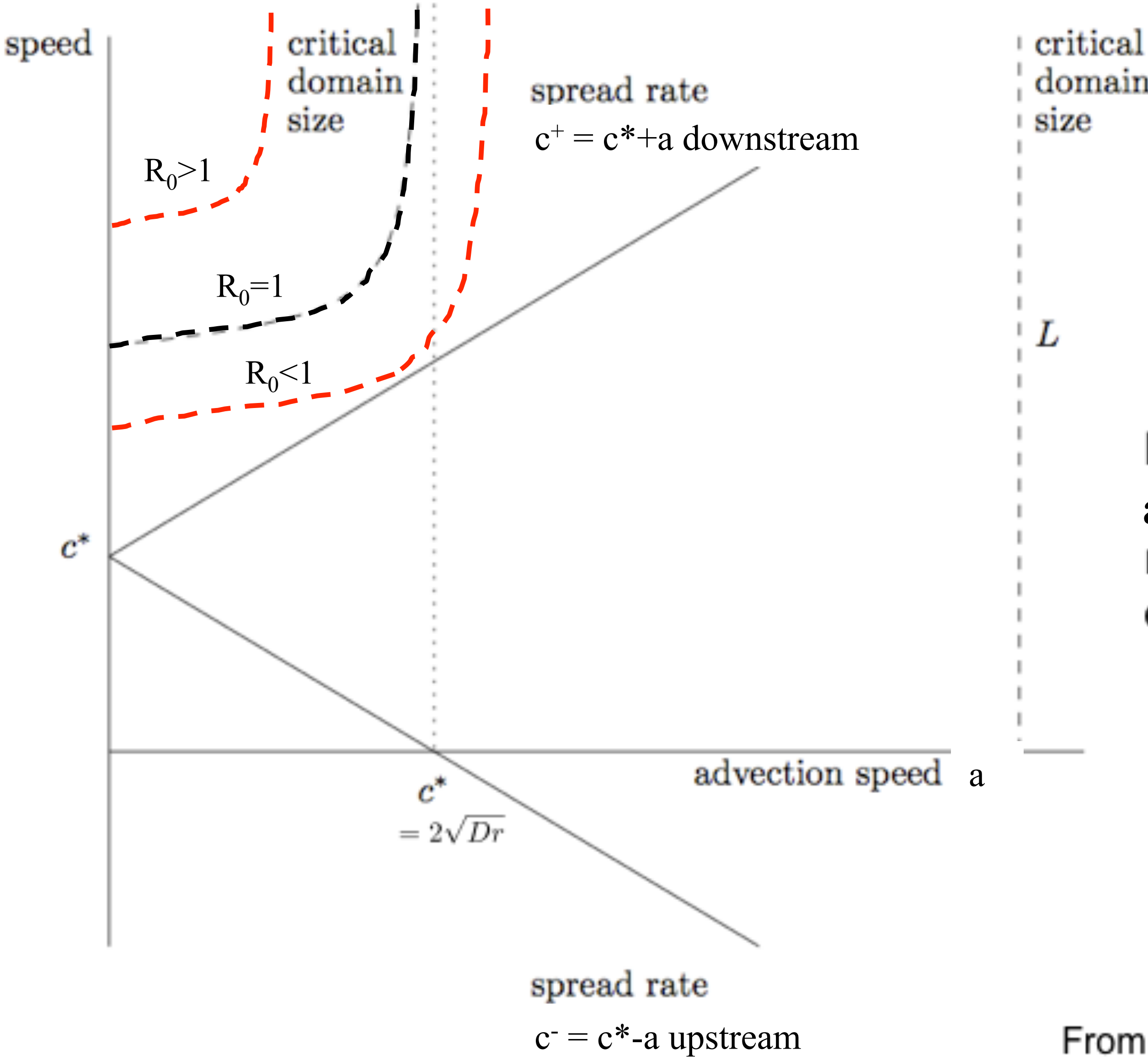
Spreading speeds and critical domain size



D diffusion coefficient

a advection coefficient

r growth rate g(0)

c* intrinsic spread rate

From Lewis *et al*, PCMI notes, 2004

Using math to decide: is this a good place to live?

$R_{loc}(x)$ - What is the spatial distribution of a species' fundamental niche?

$$R_{loc}(x) = f(x)\int_0^\infty \psi(t)\,dt = \frac{f(x)}{v} \qquad \begin{array}{l} \psi_t = -v\psi, \quad t > 0 \\ \psi(0) = 1 \end{array}$$

$R_\delta(x_0)$ Where are the source-sink regions in the habitat?*

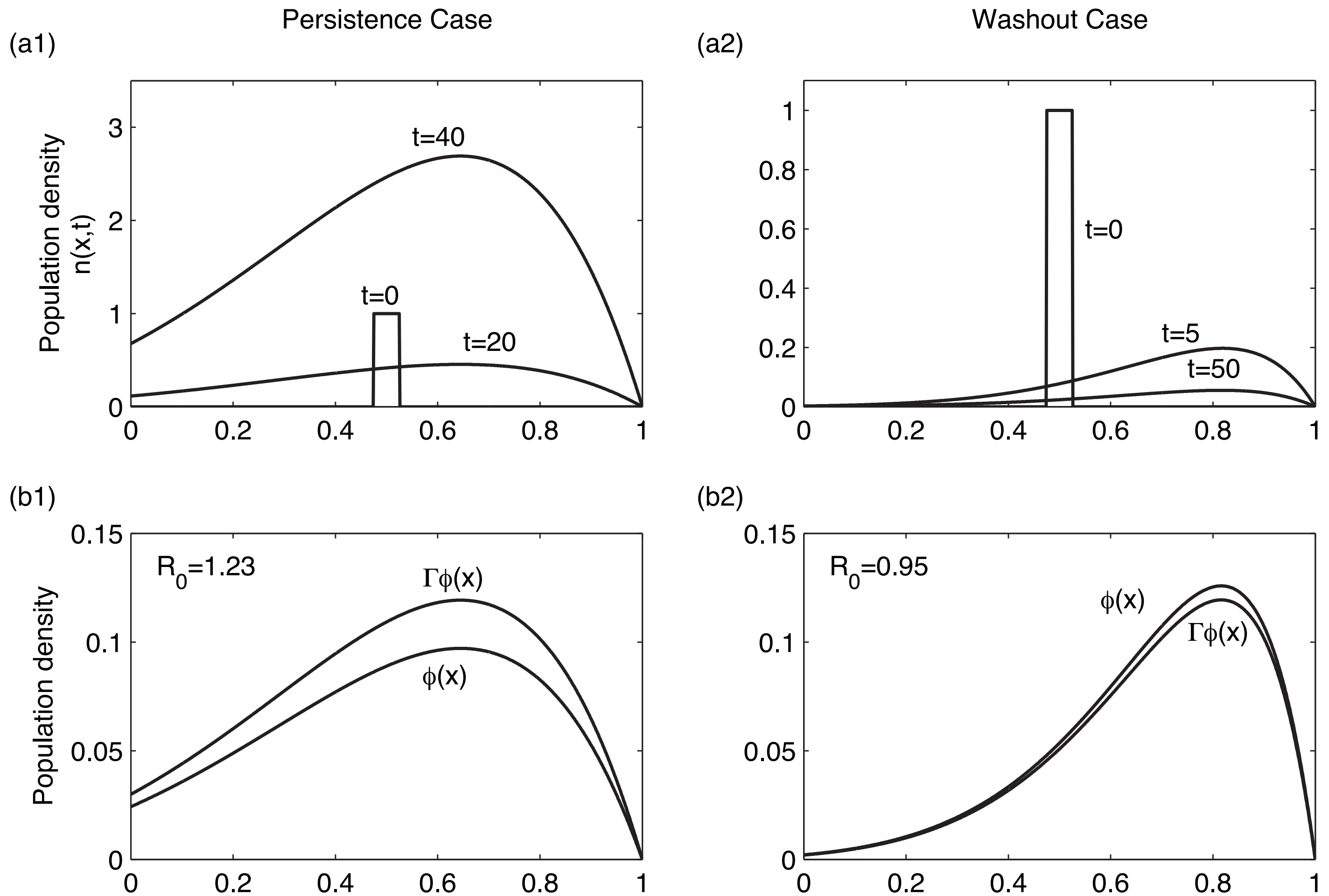
$$R_\delta(x_0) = \int_0^L f(x)\int_0^L k(x,y)\delta(y - x_0)\,dy\,dx = \int_0^L f(x)k(x,x_0)\,dx$$

R_0 - Does the species persist globally?

$$R_0 = r(\Gamma)$$

It is possible to show that R_0 is greater than the spatially averaged value of R_δ

Applying R_0 to river model (spatially homogeneous)

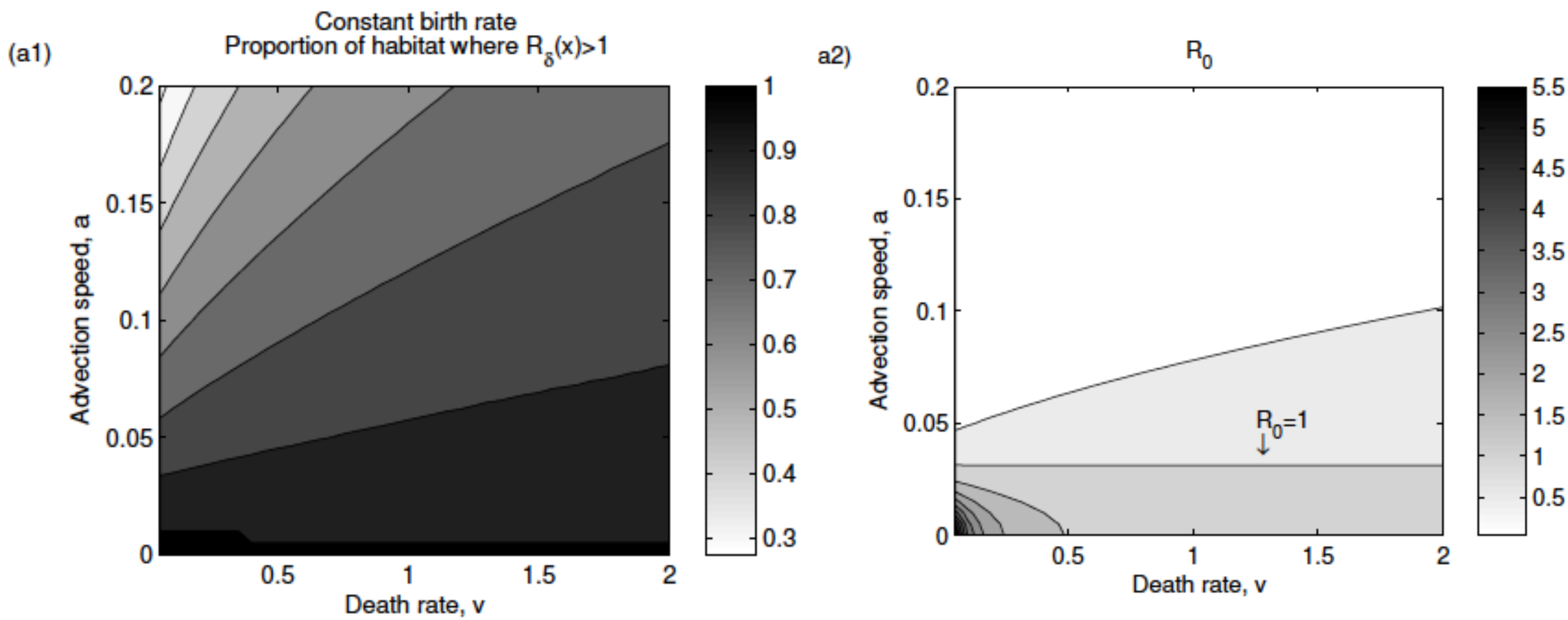


Classical thresholds from critical domain size/spreading speed analysis can be recovered, but R0 analysis can also be easily applied to spatially variable rivers

Applying R_0 to river models

- This type of analysis also provides a useful way to understand persistence in spatially variable rivers.

- The idea can be extended to the benthic-drift model and to two-dimensional environments (detailed analysis still needs to be done).


(a1)
Constant birth rate
Proportion of habitat where $R_\delta(x)>1$
Advection speed, a
Death rate, v
0.2
0.15
0.1
0.05
0
0.5
1
1.5
2
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
a2)
R_0
Advection speed, a
Death rate, v
$R_0=1$
5.5
5
4.5
4
3.5
3
2.5
2
1.5
1
0.5

Outline

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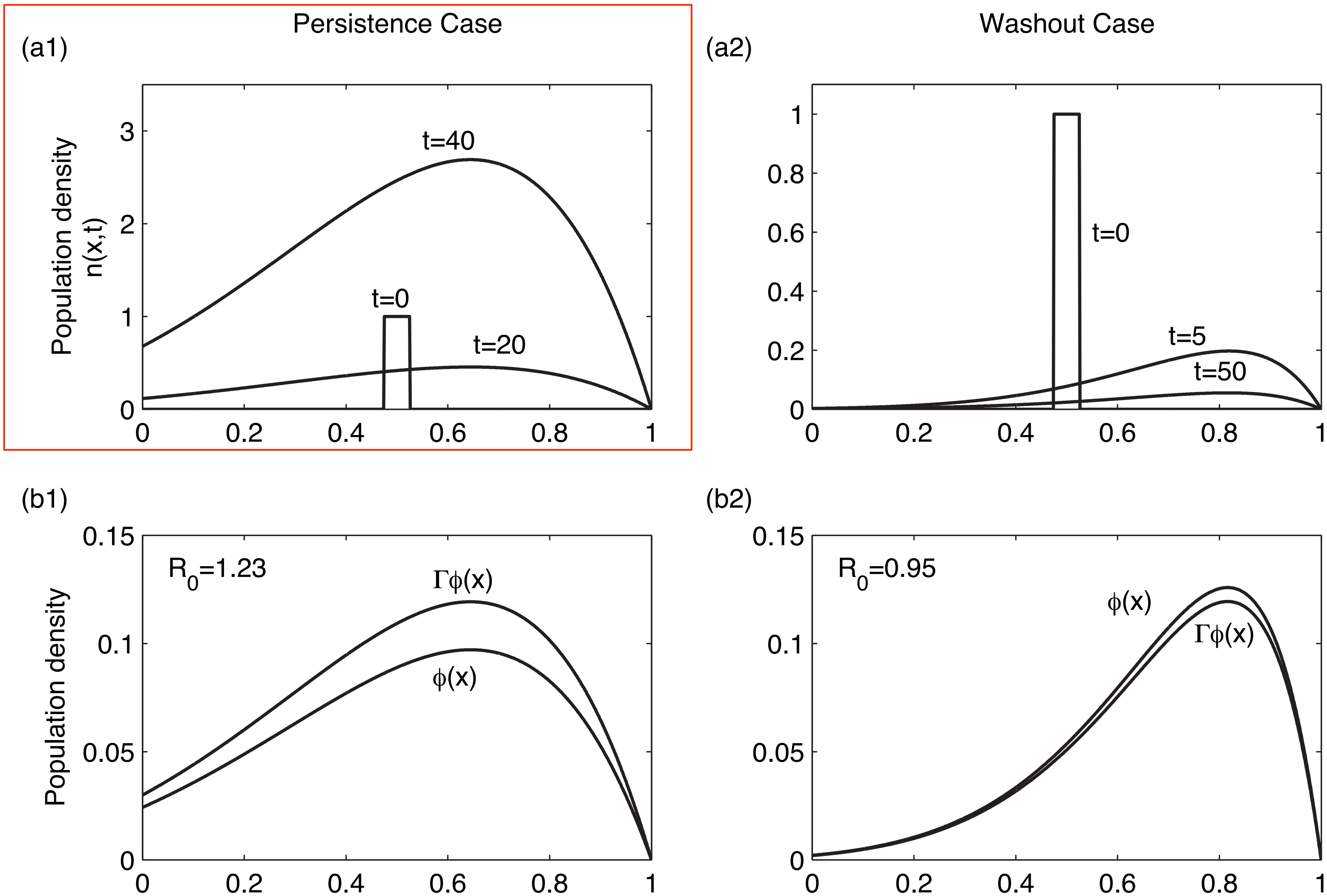
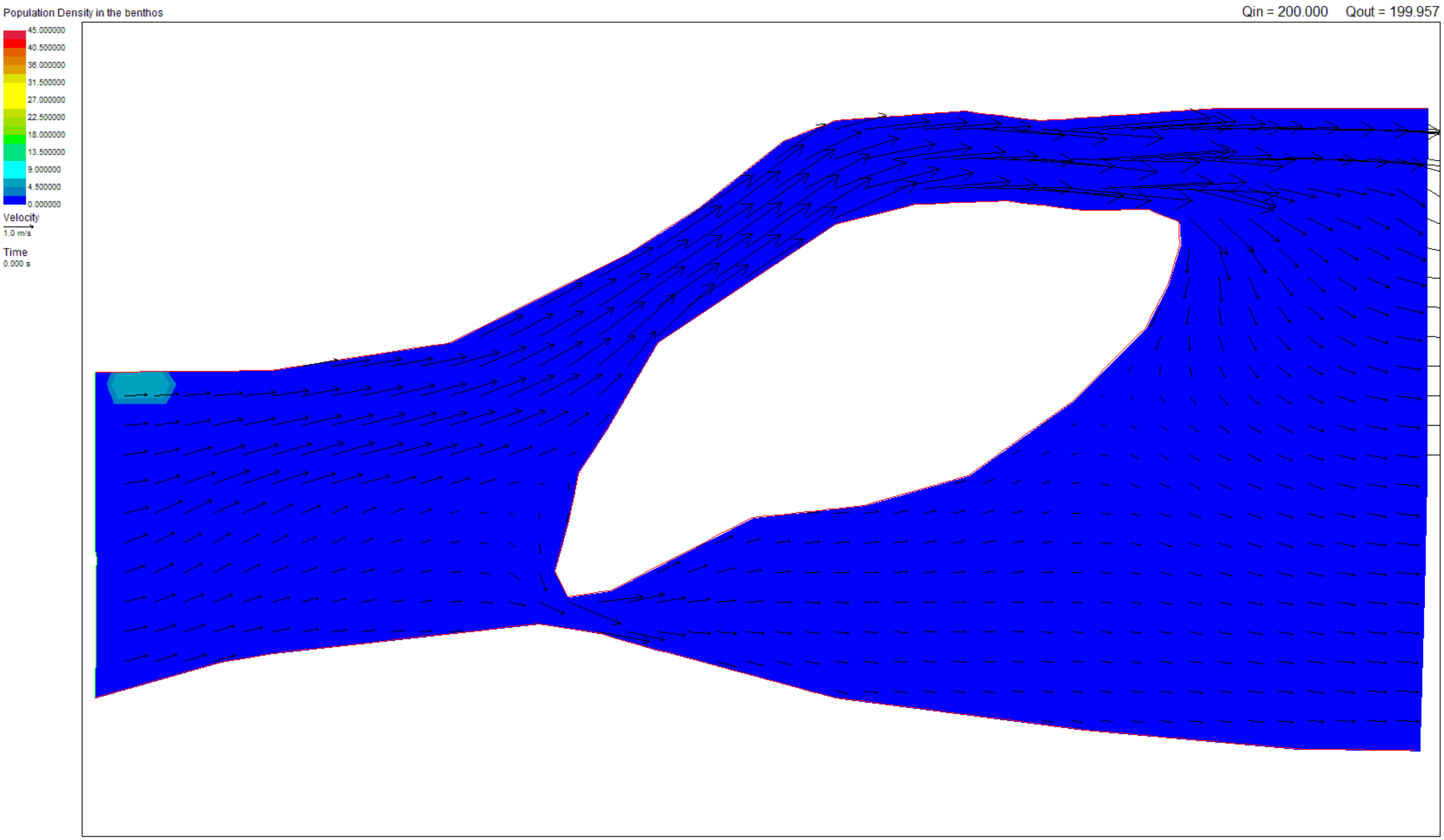
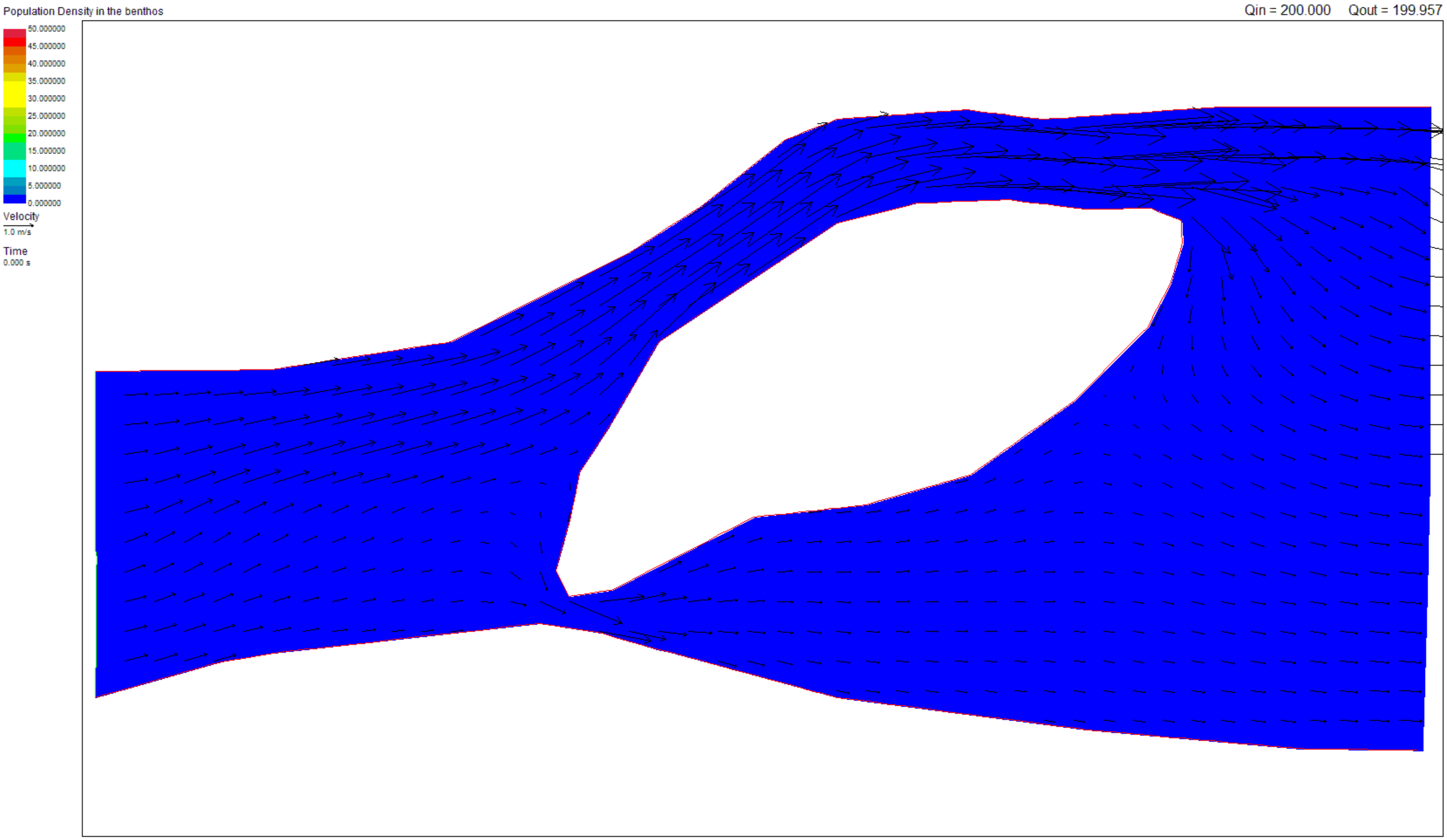
Dynamics of persistence: $R_0 > 1$



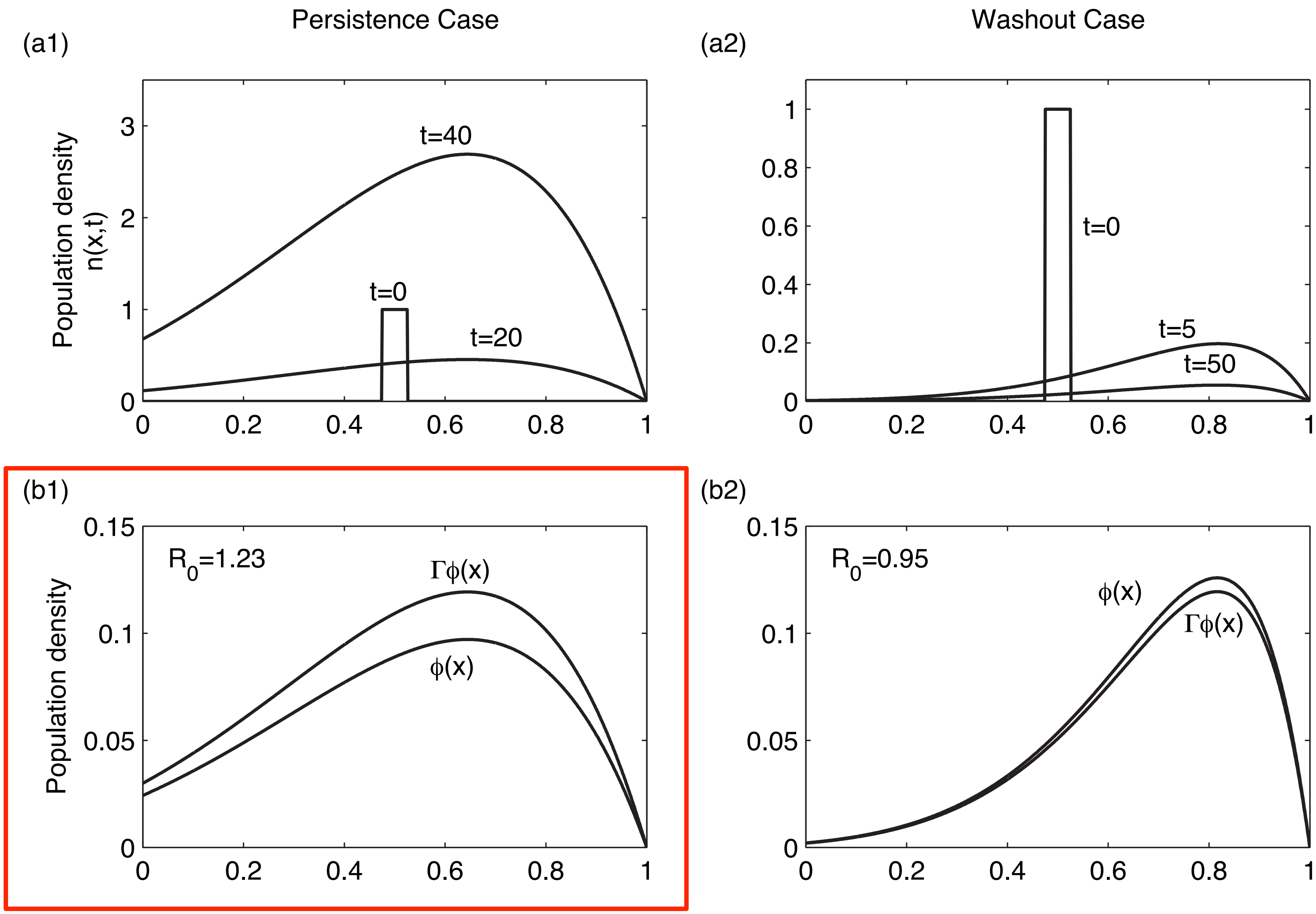
Dynamic 2D Simulation: $R_0 > 1$



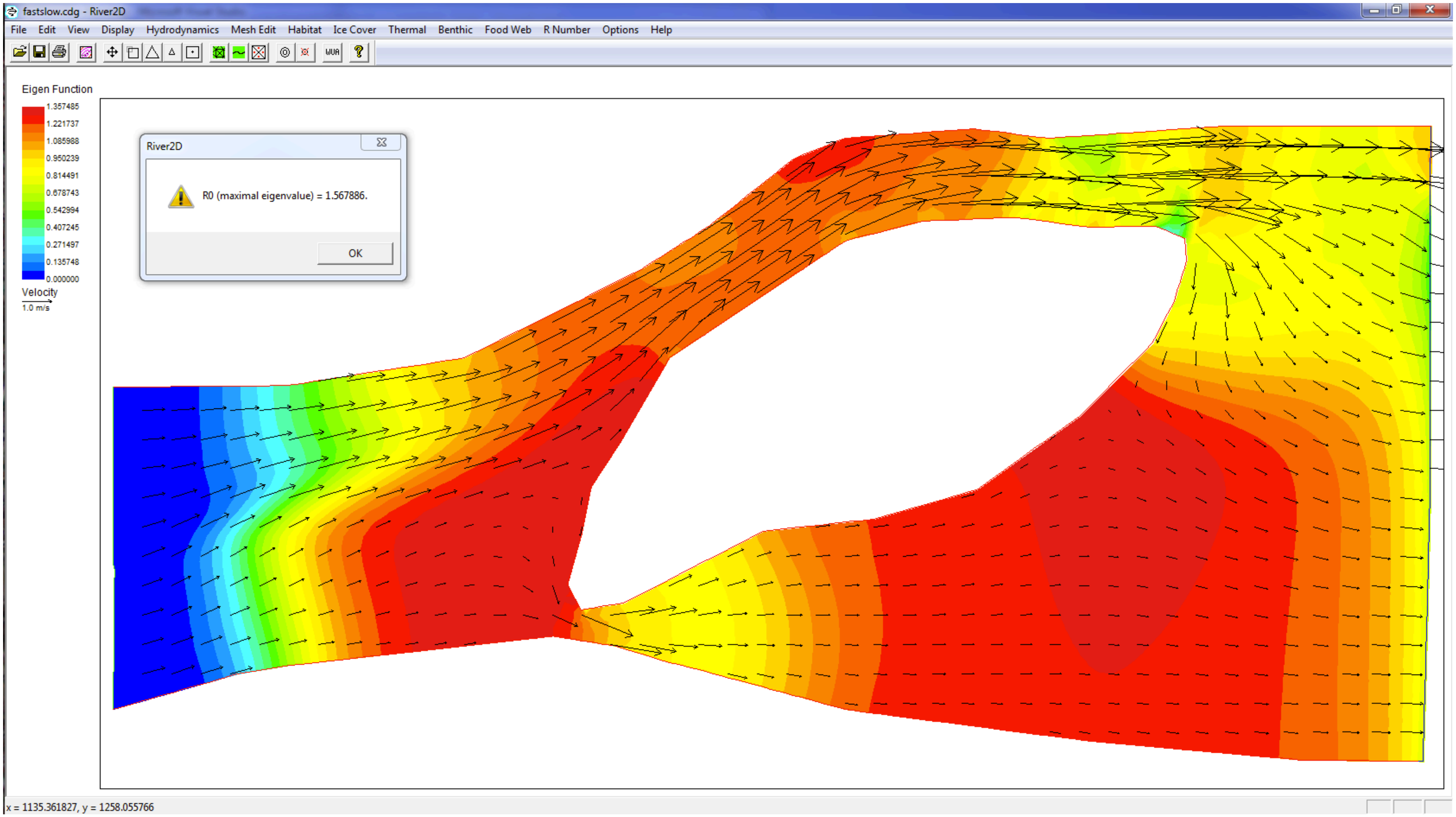
Dynamic 2D Simulation: $R_0 > 1$



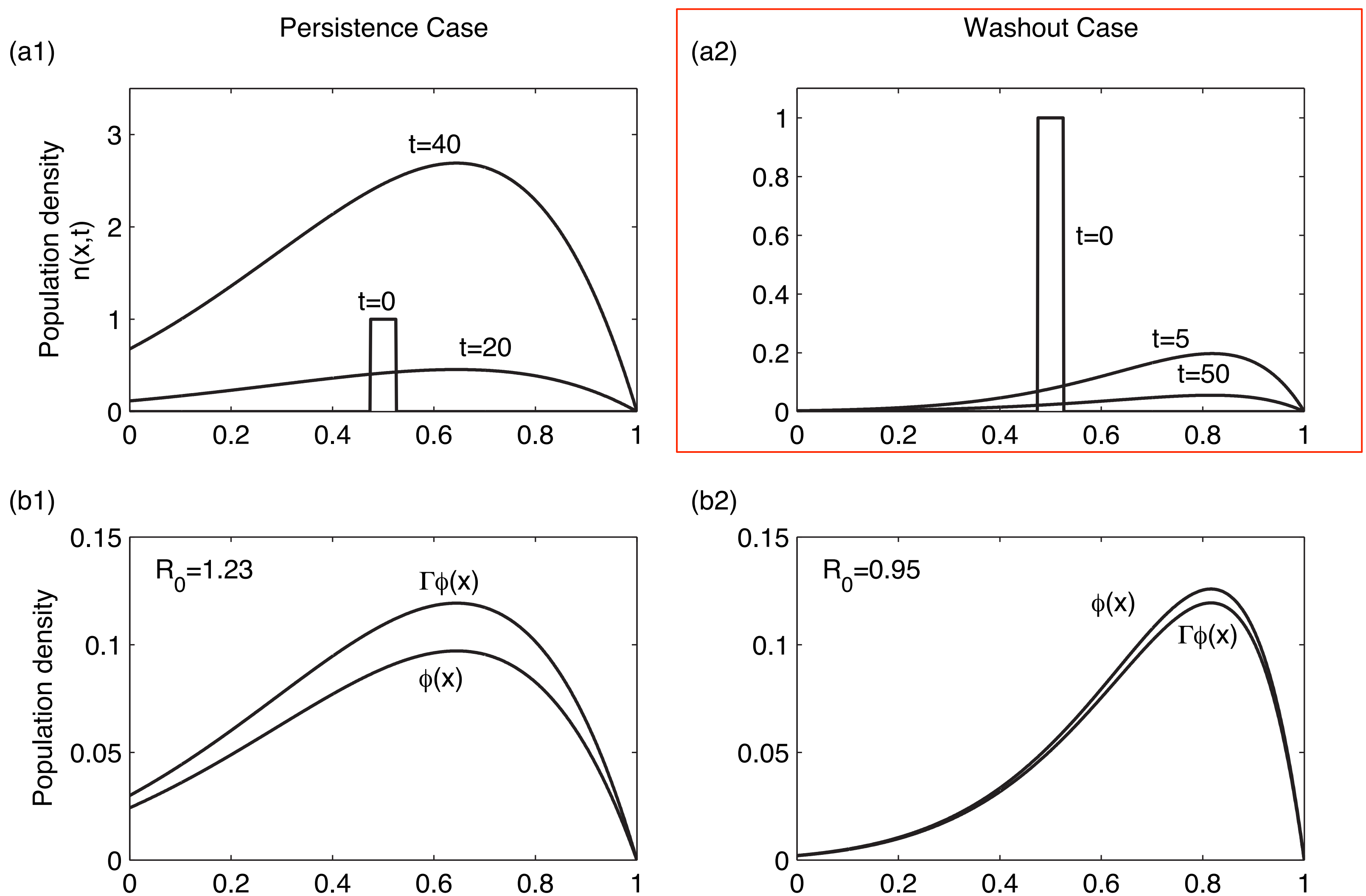
Dominant eigenfunction: $R_0 > 1$



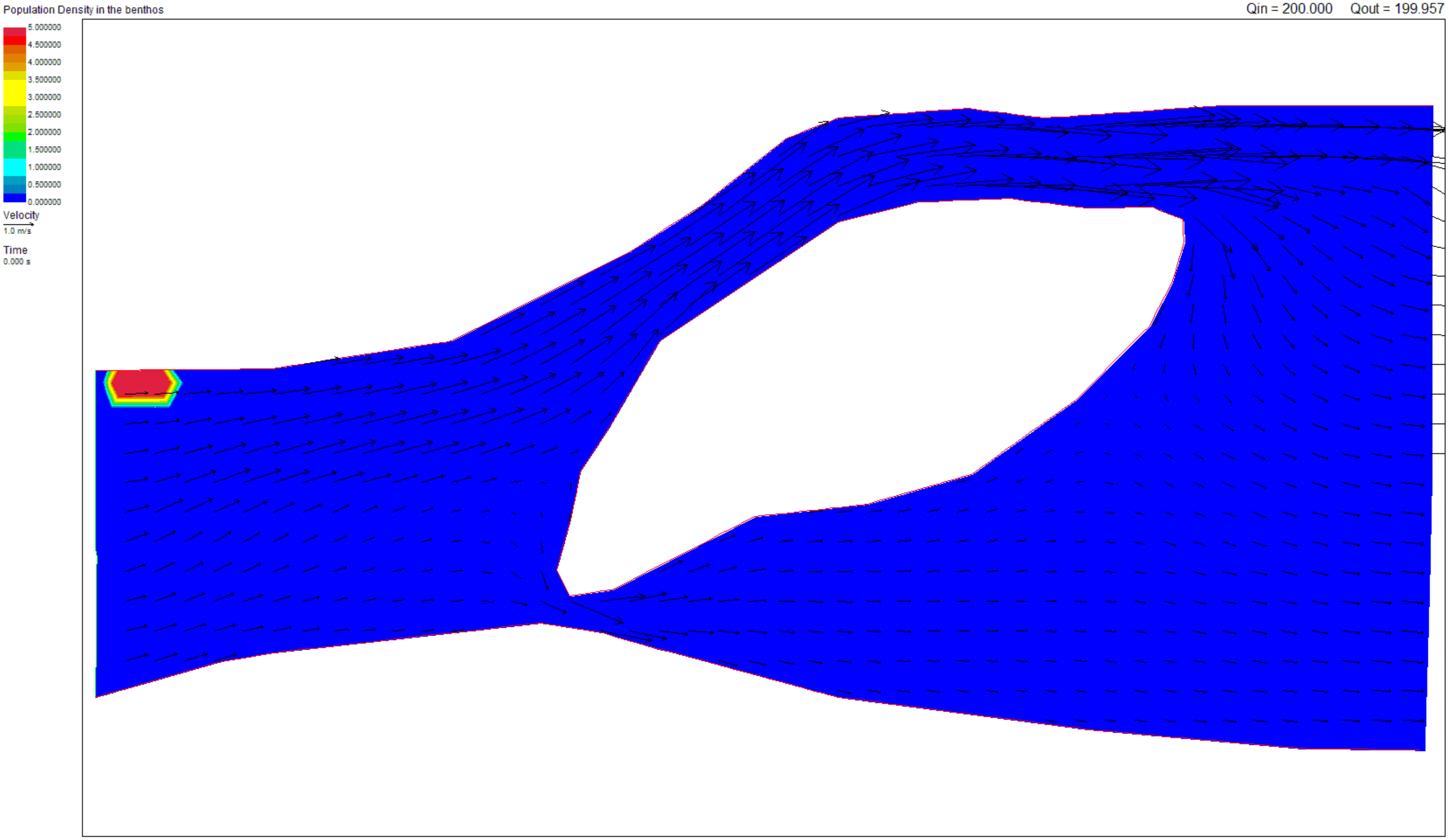
2D Calculation of dominant eigenfunction: $R_0 > 1$



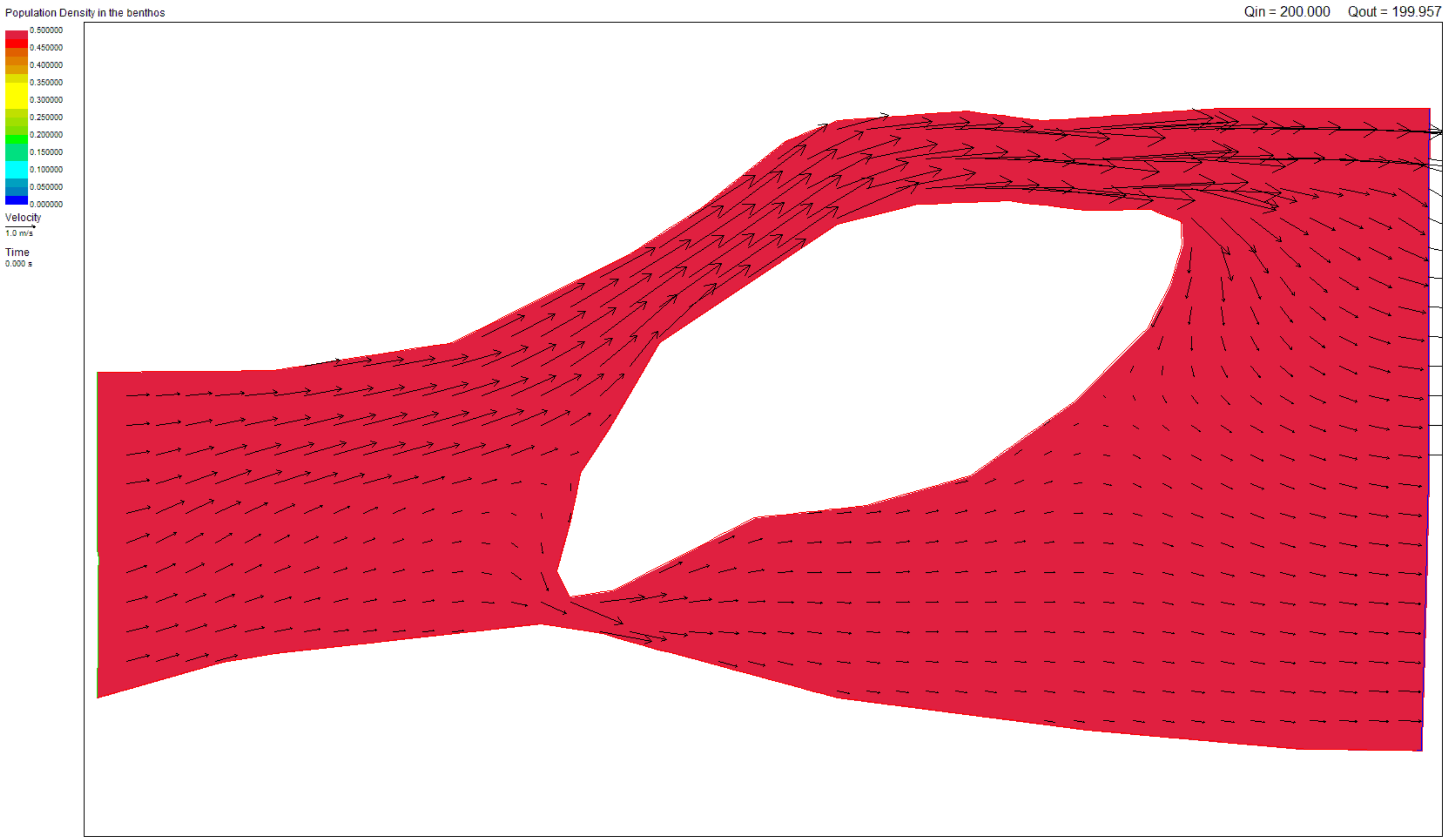
Dynamics of washout: $R_0 < 1$



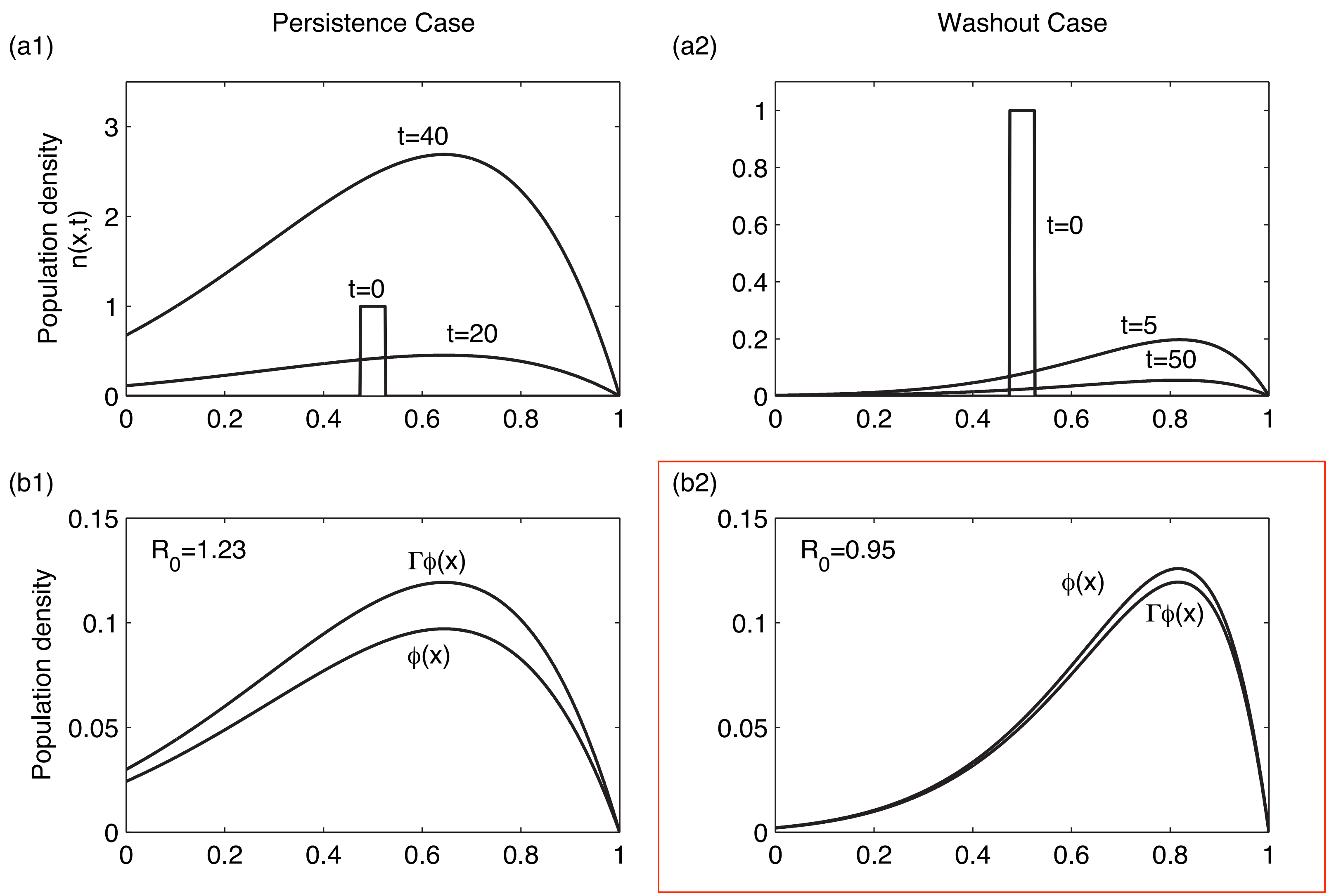
Dynamic 2D Simulation: $R_0 < 1$



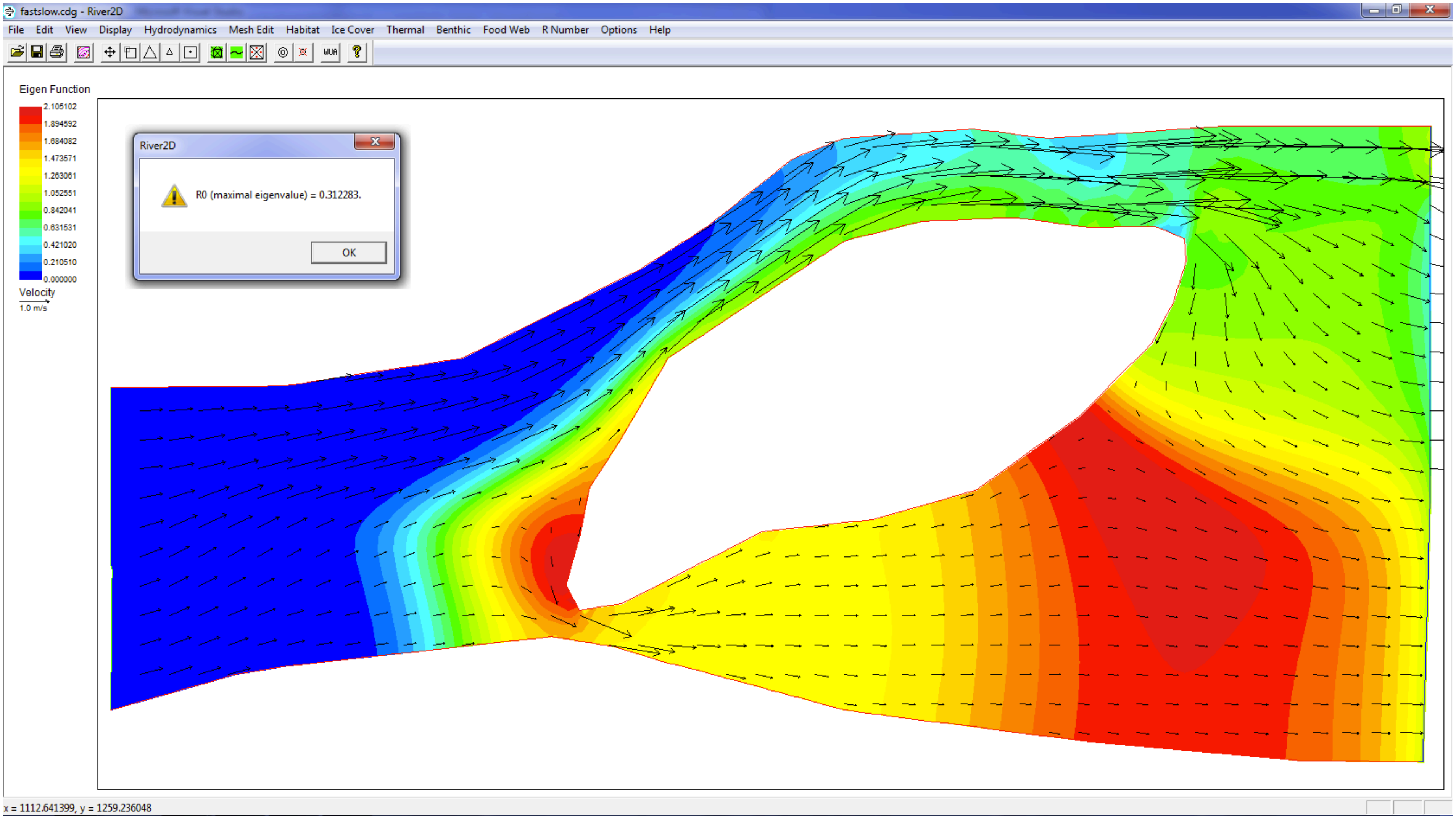
Dynamic 2D Simulation: $R_0 < 1$



Related research: Net Reproductive Rate



Dominant eigenfunction: $R_0 < 1$



Summary

- Spatial R_0 analysis is a powerful approach to understanding persistence in stream habitats, especially when habitats vary spatially, depending upon flow conditions.
- The next step is to prove that this kind of analysis can work for benthic/drift models and in higher dimensions.
- R_{loc} and R_δ are alternative metrics that have biological interpretations.
- Classical mathematical results pertaining to the drift paradox can be recovered with R_0 analysis.
- Hybrid mathematical/numerical methods for R_0 analysis can provide realistic approaches to stream modelling.
- A current project involves extending these methods to multiple trophic levels.

Thanks

- Frank Hilker (Bath)
- Frithjof Lutscher (Ottawa)
- Ed McCauley (Calgary)
- Roger Nisbet (UCSB)
- Lewis Lab (Alberta)

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