



Population persistence in flowing-water habitats: Conditions where flow-based management of harmful algal blooms works, and where it does not



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ABSTRACT

Control of harmful algae in the coves or bays of larger water bodies could be accomplished by hydraulic flushing with algae-free water. This suggestion is examined with a mathematical model of a harmful algal population, parameterized to represent the toxic haptophyte *Prymnesium parvum*, and its limiting nutrient. A small cove with a hydraulic storage zone and longitudinal advection and dispersion is coupled to a larger lake where ongoing or transient blooms serve as a source for the algal population. This population is transported upstream by dispersion and flushed downstream by advection. Morphometry and hydraulics represent a lake in Texas where blooms of *P. parvum* have been problematic. When dispersion and hydraulic storage are low to moderate, available pumping technology is predicted to be capable of suppressing the algal population within a variable portion of the cove, under both steady state and transient conditions. This suppression occurs when temperature-dependent algal growth is low. At temperatures high enough to support more rapid growth, flow augmentation carries a risk of stimulating a bloom under some hydraulic conditions. The model presented here complements similar models without population sources, and contributes to theoretical understanding of population persistence in reservoirs and other flowing-water habitats.

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1. Introduction

How do populations persist and become abundant in flow-dominated habitats, such as rivers, streams, riverine reservoirs, and estuaries? This question is especially pertinent to organisms that do not permanently attach to substrates. Aquatic ecologists have long recognized that immigration and *in situ* growth must combine to overcome the strong advective losses suffered by such populations (Reynolds, 1990). Addressing this matter is important for understanding the persistence of rare species, and the proliferation of invasive or harmful species.

The quantitative challenge thus posed has recently been taken up by theoretical ecologists, for whom partial differential equations with advection terms have been a useful tool (e.g. Lutscher et al., 2005; Grover et al., 2011). Much recent work focuses on habitats where there is no immigration of focal populations. In such

cases, a mathematically elegant analysis addresses population persistence through an eigenvalue problem considering a population's net per capita rate of growth, in the limiting case where abundance approaches zero everywhere within the habitat under steady state conditions (Grover et al., 2009; Grover and Wang, 2013; Hsu et al., 2013). In such theory, populations predicted to persist generally have a high potential to become abundant.

Additional theory is needed, however, to address issues of persistence and abundance in the common circumstance where a flow-dominated habitat is coupled to a source of immigrants. Because migrants penetrate at least part of the habitat, such a source renders useless the mathematical concept of a population vanishing everywhere within the focal habitat, and introduces source-sink population dynamics. In the work presented here, the sharp criterion of positive net growth at near-zero abundance is replaced by a biologically meaningful abundance threshold. We also address transient dynamics (Hastings, 2004) driven by seasonal changes, again focusing on exceedance of a biologically meaningful threshold.

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In this paper, we consider a particular class of flow-dominated habitat, a cove or bay where a stream empties into a larger body of water that serves as a source of the focal population of harmful algae. Dispersion transports this population across the interface at the mouth of the cove, and along the length of the cove, while advection flushes it out. Thus both transport and *in situ* growth affect population dynamics. The physical and biological parameters of the model representing these processes are based on the toxic, fish-killing species *Prymnesium parvum* (Brooks et al., 2011; Granéli et al., 2012; Roelke et al., 2016) and coves characteristic of large reservoirs in the south-central United States where it has bloomed, generally in winter time (Southard et al., 2010; Roelke et al., 2011). Flow is an important determinant of whether blooms occur (Roelke et al., 2011, 2012), and a mechanism whereby blooms terminate (Roelke et al., 2010; Schwierzke-Wade et al., 2011; Jones et al., 2013). Moreover, small-scale experiments (Hayden et al., 2012) and previous modeling (Lundgren et al., 2013) suggest that flow augmentation could be used to control blooms of this species. Thus we seek to clarify further the conditions under which flow prevents the development of blooms, particularly for flows that could be produced with available pump technology. In doing so, we also seek to address general questions of persistence and abundance in such flow-dominated habitats. The analysis proceeds by first examining steady state population distributions, and then examining transient population dynamics under non-steady conditions defined by observations on a lake prone to *P. parvum* blooms.

2. Methods

2.1. Model formulation

The model analyzed here builds upon hydraulic storage zone models (Bencala and Walters, 1983; Martinez and Wise, 2003), which are quasi-two-dimensional models of streams in which the longitudinal dimension of advective flow is resolved continuously. Every point on the continuum representing the main channel of the stream is coupled to a storage zone where no longitudinal transport occurs, which detains dissolved and suspended substances. The biological components of the model are based on prior models of harmful algae in flow-dominated habitats (Grover et al., 2011), representing a single, focal algal population and toxin(s) that it produces. The functions and parameters describing this population are based on prior models for *P. parvum* (Grover et al., 2010, 2012; Lundgren et al., 2013), but neglecting interactions with competitors and grazers to focus on how abiotic factors affect populations unconstrained by biotic factors (i.e. under conditions otherwise favoring abundant, bloom populations). Importantly, the downstream boundary conditions for the governing equations differ from much prior work in which only advective losses occurred. Here, the downstream boundary conditions set population and chemical concentrations to finite source terms representing concentrations in the main lake at the mouth of the cove. Although advection flushes substances towards the mouth, it cannot depress concentrations below the source levels at the boundary.

For general variables $Y_i(x,t)$ and $Y_{Si}(x,t)$, representing concentrations of substance i in the main channel and storage zone, respectively, the governing equations are:

$$\frac{\partial Y_i}{\partial t} = -\frac{F}{A} \frac{\partial Y_i}{\partial x} + \frac{\delta}{A} \frac{\partial}{\partial x} \left(A \frac{\partial Y_i}{\partial x} \right) + \alpha (Y_{Si} - Y_i) + R_i(\mathbf{Y}) \quad (1a)$$

$$\frac{\partial Y_{Si}}{\partial t} = -\alpha \frac{A}{A_S} (Y_{Si} - Y_i) + R_{Si}(\mathbf{Y}_S) \quad (1b)$$

where x is position (m) along main axis of the stream channel ($0 \leq x \leq L$, L = length), t is time (d), F is flow ($\text{m}^3 \text{d}^{-1}$), $A(x)$ is cross-section area of the main channel (m^2), δ is the dispersion coefficient

($\text{m}^2 \text{d}^{-1}$), α is the exchange rate between the main channel and storage zone (d^{-1}), A/A_S is the ratio of main channel cross-section area to storage zone cross-section area, R_i and R_{Si} are local reaction terms in the main channel and storage zone, respectively, and \mathbf{Y} and \mathbf{Y}_S are vectors of concentrations in the main channel and storage zone, respectively. The parameters δ , α , and A/A_S are assumed independent of position and time, while F varies with time but not position, and A varies with position but not time (implying that cove volume is constant).

The general upstream boundary conditions are

$$A(0)\delta \frac{\partial Y_i}{\partial x} \Big|_{x=0} - FY_i(0, t) = -FY_{i,in} \quad (2)$$

where $Y_{i,in}$ is the inflowing concentration of variable i . This inflowing concentration is set to zero for all constituents except the limiting nutrient for algae. The general downstream boundary conditions are

$$Y_i(L, t) = Y_{i,lake}(t) \geq 0, \quad (3)$$

which is the concentration of the variable in the main lake, so that the lake represents a source of constituent i when $Y_i(L, t) < Y_{i,lake}(t)$.

2.2. Reaction terms

To elaborate the reaction terms, denote the variables $Y_i(x,t)$ as $R(x,t)$, $N(x,t)$, and $C(x,t)$ to represent the nutrient resource concentration ($\mu\text{mol m}^{-3}$), algal population density (cells m^{-3}), and toxin concentration ($\mu\text{g m}^{-3}$), and denote $R_S(x,t)$, $N_S(x,t)$, and $C_S(x,t)$ as the respective variables in the storage zone. The reaction term for algae in the main channel specifies population dynamics on a per capita basis:

$$R_N = (\mu(T, R) - m)N, \quad (4)$$

where the mortality rate of algae (m) is constant and the growth rate (μ) depends on temperature (T) and nutrient concentration:

$$\mu(T, R) = \mu_{\max}(T) \left(\frac{R}{K + R} \right). \quad (5)$$

The first factor is a temperature-dependent maximal growth rate, and the second is a Monod nutrient-limitation factor, with half-saturation parameter K . For the temperature-dependent maximal growth rate $\mu_{\max}(T)$, the empirical model of Baker et al. (2009) is adopted:

$$\mu_{\max}(T) = \max \left\{ 0, \mu_{\max}(20) \left[-6.7514 + 14.2792e^{0.7 \left(\frac{T-20}{20} \right)}, -6.5277e^{1.4 \left(\frac{T-20}{20} \right)} \right] \right\} \quad (6)$$

where the originally published parameters are rescaled to a reference growth rate at 20°C , $\mu_{\max}(20)$. Dependence of growth on salinity and light is neglected, implicitly assuming they are near optimal. The maximal growth rate thus displays an asymmetric, unimodal response to temperature with an optimal growth temperature of 22.6°C .

The reaction term for dissolved nutrient in the main channel assumes that nutrient uptake is proportional to algal population growth, and nutrient regeneration is proportional to mortality:

$$R_R = (\mu(T, R) - m)Nq, \quad (7)$$

through a constant quota parameter (q). The reaction term for toxin in the main channel assumes that production increases with algal population density and with the degree that growth is

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