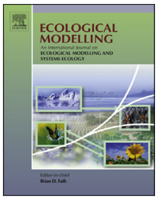
Ecological Modelling xxx (2018) xxx–xxx

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Exploitative competition of invaders differentially influences the diversity of neutral, lumpy and intransitive phytoplankton assemblages in spatially heterogeneous environments

Joydeb Bhattacharyya[a], Daniel L. Roelke[a,b,*], Rika M.W. Muhl[a], Frances G. Withrow[a]

[a] Department of Wildlife and Fisheries Sciences, Texas A&M University, 2258 TAMUS, College Station, TX 77843-2258, USA
[b] Department of Oceanography, Texas A&M University, College Station, TX 77843, USA

ARTICLE INFO

Article history:
Received 18 July 2017
Received in revised form
22 December 2017
Accepted 30 December 2017
Available online xxx

Keywords:
Biodiversity
Species supersaturation
Spatial heterogeneity
Circulation
Invasion

ABSTRACT

Recent theoretical research suggested that species-supersaturated phytoplankton assemblages sustained through neutrality, lumpy coexistence or intransitivity were sensitive to immigration, quickly losing diversity following invasions. The presence of source patches, however, may facilitate persistence of species-supersaturation in the face of invaders. We explore that notion here through simulation analyses of more detailed spatially explicit models depicting one- and two-dimensional systems ("pipe" and "two-eddy" models, respectively) where water circulation is governed over a range of advection and turbulent diffusion. For the pipe model, when advection and turbulent diffusion are low, and when advection is high and turbulent diffusion is low, resident assemblages are more resistant to invaders. But at intermediate rates of advection and with increases to turbulent diffusion, assemblages are more quickly impacted by invaders. For the two-eddy model, when advection and turbulent diffusion are low, resident assemblages are again resistant to invaders, but only for lumpy assemblages. In contrast to the "pipe" model, resistance to invaders of neutral and lumpy assemblages is high when advection and turbulent diffusion are high. For both model configurations, intransitive assemblages were much more sensitive to invaders, suggesting that intransitivity might not be as prevalent a biodiversity-sustaining mechanism in spatially heterogeneous plankton systems.

1. Introduction

In theory, exclusion through exploitative resource competition will lead to a number of co-existing species not greater than the number of limiting resources as systems approach equilibrium. High species richness characteristic of many biological systems challenges this idea, coined the "Paradox of the Plankton" (Hutchinson, 1961). One solution to this paradox occurs due to fluctuations in the environment, thereby preventing equilibrium conditions (Tilman, 1977, 1981, 1982; Sommer, 1984, 1985; Grover, 1989). Environmental fluctuations can arise through various abiotic and biotic processes that change seasonally, contributing to periodic cycling of plankton populations (Smayda, 1985; Nixon, 1995; Roelke and Spatharis, 2015). The effects of these fluctuations can also result in protracted periods of transient population dynamics (Hastings, 2010) or chaotic population dynamics (May and Leonard, 1975). Both of these dynamic types can facilitate species richness. However, there are other mechanisms that are not externally-driven that lead to high species richness (Narwani et al., 2009). For example, competition for nutrients can create internal disequilibria that can sustain high species richness in phytoplankton assemblages (Huisman and Weissing, 1994). In addition, neutrality, lumpy coexistence and intransitive population dynamics, the focus of this research, are biodiversity-sustaining mechanisms which occur in assemblages based on competitive abilities of co-occurring species.

Neutrality refers to the co-occurrence of species within a given trophic level that are nearly identical in their competitive abilities and can be considered ecological equivalents (Hubbell, 2001). With neutrality, multiple species can coexist over ecologically relevant time scales, promoting higher biodiversity. Neutrality was shown for biological systems of wasps (Saez and Lozano, 2005), fungi (Bickford et al., 2007), and trees (McGill, 2003), and might also

---

* Corresponding author at: Department of Wildlife and Fisheries Sciences, Texas A&M University, 2258 TAMUS, College Station, TX 77843-2258, USA.
E-mail address: droelke@tamu.edu (D.L. Roelke).

https://doi.org/10.1016/j.ecolmodel.2017.12.020
0304-3800/© 2018 Elsevier B.V. All rights reserved.

Please cite this article in press as: Bhattacharyya, J., et al., Exploitative competition of invaders differentially influences the diversity of neutral, lumpy and intransitive phytoplankton assemblages in spatially heterogeneous environments. Ecol. Model. (2018), https://doi.org/10.1016/j.ecolmodel.2017.12.020

be a mechanism underlying high species richness in phytoplankton assemblages (Chust et al., 2013; Roelke and Eldridge, 2008).

Where there are co-occurring and competing species clusters along resource gradients, the condition is referred to as lumpy coexistence (Scheffer and van Nes, 2006). With lumpy coexistence, species with very similar competitive abilities co-occur within a cluster. The clusters, however, are sufficiently different from each other so that competition occurs between them. Example communities showing lumpy coexistence include wetland plants in Mediterranean-type ecosystems (Valiente-Banuet et al., 2006), aquatic beetles (Drost et al., 1992) and prairie birds (Holling, 1992). In theory, lumpy coexistence can explain highly diverse phytoplankton systems as well (Scheffer and van Nes, 2006; Roelke and Eldridge, 2008).

When competition for resources between co-existing species is non-hierarchical, intransitive population dynamics can result. With intransitive assemblages, no single species can displace all other species and recurrent, out-of-phase oscillations in population dynamics occur (Huisman et al., 1999; Huisman and Weissing, 2001a,b; Roelke and Eldridge, 2010). Biological systems involving coral reef invertebrates (Jackson and Buss, 1975), side-blotched lizards (Sinervo and Lively, 1996), and herbaceous dicots (Fortner and Weltzin, 2007) are examples of naturally occurring intransitive systems. In theory, intransitivity supports high richness in phytoplankton assemblages as well (Huisman and Weissing, 2001a,b).

In a previous modeling study, Roelke and Eldridge (2008) explored the effect of migration on phytoplankton assemblages whose biodiversity was sustained either by neutrality, lumpy coexistence or intransitivity. They explored a plankton model where the influence of migration was a function of hydraulic mixing. Using a two-patch modeling framework, they found that immigration, even at very low levels, led to global homogenization and species extinctions. From these observations, they questioned the role of neutrality, lumpy coexistence and intransitivity as biodiversity-sustaining mechanisms in natural environments. The two-patch modeling framework used in Roelke and Eldridge (2008), however, might have been too simple to allow for source-sink patches to develop, which are known to facilitate biodiversity (Mouquet and Loreau, 2003).

In this research, we develop two models of greater spatial complexity, thus enabling source-sink patch development. The models employ one-dimensional and two-dimensional horizontal frameworks with various hydrology. The distribution of organisms in our models are subject to advection and turbulent diffusion. In advection, the nutrients and the embedded phytoplankton cells are carried with the movement of water. In turbulent diffusion, the spatial mixing of nutrients and phytoplankton of adjacent patches occurs without a net overall transport of water. Advection and turbulent diffusion were shown to be important to phytoplankton richness and diversity (Codeco and Grover, 2001; Petrovskii and Malchow, 2001; McKiver et al., 2009; Adjou et al., 2012). Here, we explored these over spatial scales >100 km with 10 km^2 areal resolution and at turbulent diffusion rates characteristic of large lakes, bays and coastal oceans. We employ one- and two-dimensional model frameworks. Our one-dimensional model framework is best visualized as two pipes coming together at an outlet where flow through the pipes are advection- and turbulent diffusion-based (Fig. 1). Our two-dimensional model framework is best visualized as two confined eddies that are in contact, rotating in opposite directions, and again with advective and turbulent diffusive flow (Fig. 2). Through simulation analyses, we explore and compare the resistance of phytoplankton assemblage source patches initiated with neutral, lumpy and intransitive phytoplankton assemblages under varied hydraulic conditions.

2. Methods

2.1. One-dimensional model

In our one-dimensional model, $R_{i,k}(t)$ and $P_{j,k}(t)$ represent the concentration of the growth-limiting i-th substrate (μM) and the population density of j-th phytoplankton species ($\times 10^6$ cells L^{-1}), respectively, in the k-th patch at time t. The rate of flushing and the rate of mixing between two adjacent patches are taken as D and d (day^{-1}), respectively (these are discussed in detail further below). The specific growth rate for the j-th phytoplankton species in the k-th patch is determined using the Monod equation (Monod, 1949) and Liebig's law of the Minimum (Liebig, 1840), and is given by

$$\mu_{j,\,k} = \mu_{\max,j}(\min_{i}(\frac{R_{i,k}}{a_{i,j}+R_{i,k}})),$$

where $\mu_{max,j}$ is the maximum specific growth rate (day^{-1}) of species j and $a_{i,j}$ is the half- saturation coefficient (μM) of species j growing on the substrate i. Here, we use the notation "a" instead of the traditional notation "k_S" for convenience with subscript appending. Finally, $Q_{i,j}$ is the fixed cellular content of resource i (μM (10^6 cells)$^{-1}$) for species j.

For our one-dimensional physical framework, we define the system as having an odd number ($2n+1$) of interconnecting patches, out of which the direction of advection in the first and the last patches are pointed towards each other (Fig. 1). In addition, the $(n+1)^{th}$ patch, which receives advection originating from the first and last patches, has an advection rate twice the rate of advection of all the other patches. Also, there is a constant inflow to the first and last patches, bringing new nutrients R_i^{in} to the system. Finally, the first and last patch only contain the initial phytoplankton assemblages (described further below). As the simulation proceeds, these source assemblages disperse by means of advection and turbulent diffusion.

The one-dimensional model is governed by sets of discretized ordinary differential equations necessary for representing both end member patches (1^{st} and $(2n+1)^{th}$), the central patch ($(n+1)^{th}$), and patches in between (2^{nd}–n^{th}, $(n+2)^{th}$–$2n^{th}$). The rate of change of the nutrients in each of the patches is dependent on the advection-driven nutrient input and flushing rate, turbulent diffusion-driven nutrient mixing rate with adjacent patches and nutrient consumption rate by phytoplankton. The rate of change of the phytoplankton density in each of the patches is dependent on the growth rate of phytoplankton, advection-driven hydraulic displacement of phytoplankton and turbulent diffusion-driven exchange rate of phytoplankton.

The governing equations for resources and phytoplankton for the first patch are given by:

$$\frac{dR_{i,1}}{dt} = D(R_i^{in} - R_{i,1}) + d(R_{i,2} - R_{i,1}) - \Sigma_j Q_{i,j}\mu_{j,1}P_{j,1} \tag{1}$$

$$\frac{dP_{j,1}}{dt} = \mu_{j,1}P_{j,1} + d(P_{j,2} - P_{j,1}\ ) - DP_{j,1} \tag{2}$$

The governing equations for resources and phytoplankton for the last patch ($(2n+1)^{th}$) are given by:

$$\frac{dR_{i,2n+1}}{dt} = D(R_i^{in} - R_{i,2n+1}\ ) + d(R_{i,2n} - R_{i,2n+1}\ ) - \Sigma_j Q_{i,j}\mu_{j,2n+1}P_{j,2n+1} \tag{3}$$

$$\frac{dP_{j,2n+1}}{dt} = \mu_{j,2n+1}P_{j,2n+1} + d(P_{j,2n} - P_{j,2n+1}\ ) - DP_{j,2n+1} \tag{4}$$

For each of the patches in between the first and middle patch, designated with $k=2, \ldots, n$, resources and phytoplankton are governed by:

$$\frac{dR_{i,k}}{dt} = D(R_{i,k-1} - R_{i,k}\ ) + d(R_{i,k-1} + R_{i,k+1}\ ) - 2dR_{i,k} - \Sigma_j Q_{i,j}\mu_{j,k}P_{j,k} \tag{5}$$

Please cite this article in press as: Bhattacharyya, J., et al., Exploitative competition of invaders differentially influences the diversity of neutral, lumpy and intransitive phytoplankton assemblages in spatially heterogeneous environments. Ecol. Model. (2018), https://doi.org/10.1016/j.ecolmodel.2017.12.020