



Water column processes differentially influence richness and diversity of neutral, lumpy and intransitive phytoplankton assemblages

Frances G. Withrow^a, Daniel L. Roelke^{a,b,*}, Rika M.W. Muhl^a, Joydeb Bhattacharyya^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

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ABSTRACT

Neutrality, lumpy coexistence and intransitive population dynamics are mechanisms that, in theory, influence biodiversity. In this research, we focus on simulated phytoplankton assemblages that are species-supersaturated because of these mechanisms. We investigate how various water column processes alter mechanism functioning and consequently biodiversity. The water column processes on which we focus are extinguishing light availability with depth, vertical diffusivity, upward diffusive flux of nutrients from lower layers and/or the benthos, particle sinking, and a rescue effect. We explore the influence of these water column processes on phytoplankton biodiversity by characterizing assemblages' α - and β -level richness and diversity. Previous work found that intransitive systems' richness and biodiversity were more sensitive to hydraulic mixing and immigration than those of neutrality and lumpy coexistence. With our expanded modeling framework, our findings are similar in regards to α richness and diversity, but have a more complicated story from the perspective of β richness and diversity where the influence of spatial heterogeneity arising from various water-column processes is dependent upon the phytoplankton assemblage type.

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1. Introduction

Ecologists have long been fascinated with species rich ecosystems with few limiting resources, an interest famously epitomized by the "Paradox of the Plankton" (Hutchinson, 1961). Based on theory, species competition for resources will lead to a number of co-existing species not greater than the number of limiting resources if the system arrives at a steady state (Hardin, 1960). Therefore, a solution to the Paradox of the Plankton occurs when environments fluctuate, thereby preventing steady state conditions from arising and stopping competitive exclusion (Tilman, 1977, 1981, 1982; Sommer, 1984, 1985; Grover, 1989). Environmental fluctuations might arise through various abiotic and biotic processes that change seasonally, contributing to periodic cycling of plankton populations (Smayda, 1980; Ning et al., 2004; Roelke and Spatharis, 2015). Environmental fluctuations can also result in protracted periods of transient population dynamics (Hastings, 2010) or chaotic population dynamics (May and Leonard, 1975). Periodic, transient and chaotic population dynamics can all facilitate species richness.

* 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).

There are, however, other mechanisms leading to high species richness that do not involve environmental fluctuations driven by other processes (Narwani et al., 2009). A condition coined 'supersaturated coexistence' (sensu Schippers et al., 2001) refers to species-rich assemblages that maintain a number of species higher than the number of limiting resources under conditions where external processes do not drive environmental fluctuations. Mechanisms leading to species supersaturation include neutrality, lumpy coexistence, and intransitive population dynamics.

Neutrality refers to the co-occurrence of species within a given trophic level that are nearly identical in their competitive abilities. In other words, they are ecological equivalents (Hubbell, 2001). Because of this competitive near-equality, multiple species can coexist over time scales relevant to ecology, thereby allowing higher biodiversity. Examples of neutral communities in nature include co-occurring species of wasps (Saez and Lozano, 2005), fungi (Bickford et al., 2007), and trees (McGill, 2003). Neutrality might also be a mechanism underlying high species richness in phytoplankton assemblages (Pueyo, 2006; Roelke and Eldridge, 2008; Vergnon et al., 2009).

Lumpy coexistence describes scenarios where there are co-occurring and competing species clusters along resource gradients. Within a cluster, coexisting species are very similar in their competitive abilities (like that of neutrality). But clusters are sufficiently different from each other that competition occurs between them

following traditional niche theory (Scheffer and van Nes, 2006). Examples of “lumpy” communities in nature include plants in Mediterranean-type ecosystems (Valiente-Banuet et al., 2006), aquatic beetles (Drost et al., 1992) and prairie birds (Holling, 1992). Lumpy coexistence might also explain highly diverse phytoplankton systems as well (Havlicek and Carpenter, 2001; Scheffer and van Nes, 2006; Roelke and Eldridge, 2008; Muhl et al., 2017), where recurrent environmental fluctuations may facilitate the formation of species clusters (Sakavara et al. 2017).

Intransitive population dynamics result when competition between co-existing species is non-hierarchical. In such systems, no single species can displace all other species. Instead, recurrent and out-of-phase oscillations in the population dynamics occur (Huisman et al., 1999; Huisman and Weissing, 2001; Roelke and Eldridge, 2010). Because there is no winner over time in this competitive non-hierarchy, this biodiversity sustaining mechanism is often coined ‘rock-paper-scissors’ coexistence. Coral reef invertebrates (Jackson and Buss, 1975), side-blotched lizards (Sinervo and Lively, 1996), and European drylands and agricultural grasslands (Soliveres et al., 2015) are a few examples of naturally occurring systems that experience high species richness through intransitive dynamics. This could be yet another mechanism leading to high richness in phytoplankton assemblages (Huisman and Weissing, 2001).

The effect of migration on simulated phytoplankton assemblages whose biodiversity was sustained by neutrality, lumpy coexistence or intransitivity was studied by Roelke and Eldridge (2008). 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 at very low levels led to global homogenization and species extinctions, with intransitive assemblages being the most sensitive. They suggested that the sensitivity of these supersaturated assemblages to immigration questions the role of neutrality, lumpy coexistence and intransitivity as biodiversity-sustaining mechanisms in spatially heterogeneous 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). Incorporating a more spatially complex modeling framework, one where source patches of immigrants might be maintained, would better enable exploration of these supersaturated assemblage types to immigration.

A more spatially complex modeling framework would also allow for other process to be simulated. For example, in a water column framework (one dimension, vertical), extinguishing light availability with depth, vertical diffusivity of turbulence, nutrient flux from the benthos or from a deeper water mass, particle sinking, and rescue effects from adjacent waters can all be simulated. Light extinction with depth and vertical diffusivity are both known to influence phytoplankton assemblage composition (Huisman and Weissing, 1994, 1995; Weissing and Huisman, 1994; Han et al., 1999; Litchman and Klausmeier, 2001; Flöder et al., 2002; Flöder and Burns, 2005), as are the nutrient gradients that result from vertical mixing and the uptake of resources by phytoplankton (Cullen, 1982; Klausmeier and Litchman, 2001). Some nutrients distributed in the water column originate from the benthos (Rowe et al., 1975; Nowicki and Nixon, 1985) and previous works have explored vertical distribution of phytoplankton as a function of both light and benthic nutrient flux (Mellard et al., 2011; Klausmeier and Litchman, 2001; Huisman et al., 2006). In addition, phytoplankton vary in their sinking rates as a function of their cell size and shape, and physiological condition (Bienfang, 1980; Huisman and Sommeijer, 2002; Padišak et al., 2003) which influences the vertical distribution of cells, and thus the richness and diversity (Huisman et al., 2002; Hsu and Lou, 2010; Peng and Zhao, 2016). Finally,

mixing with adjacent waters have been shown to be important to phytoplankton richness and diversity (Richerson et al., 1970; Codeco and Grover, 2001; Petrovskii and Malchow, 2001; McKiver et al., 2009; Adjou et al., 2012).

As mentioned above, Roelke and Eldridge (2008) suggested that the sensitivity of supersaturated assemblages sustained through neutrality, lumpy coexistence and intransitivity might preclude those mechanisms from being common in spatially heterogeneous environments, with intransitive assemblages being the most sensitive. Roelke and Eldridge's (2008) two-patch modeling framework would not have enabled the development of source and sink patches, whose presence might increase resilience of these species-supersaturated assemblages. In this research, we expand their modeling framework into a one-dimensional water column with the aim to further investigate the sensitivity of phytoplankton assemblages governed by neutrality, lumpy coexistence, and intransitive population dynamics. To this one-dimensional framework, processes of extinguishing light, vertical diffusivity, nutrient flux from a lower boundary, particle sinking, and a rescue effect were added separately and in combination.

2. Methods

2.1. Water-column physical framework

The physical framework of the model is a generic water column, here 10 m. This model domain can either represent shallow waters coming into contact with the benthos at 10 m, or it can represent a surface layer with underlying nutrient rich waters. We keep to a generic physical framework because our focus in this research is on the comparative sensitivities of neutral, lumpy and intransitive assemblages to physical processes, not precise depiction of those physical process in specific systems. Within the model domain phytoplankton compete for three growth-limiting resources. Parameterizations regarding the first resource is based on nitrogen, which included loading, half-saturation coefficient for phytoplankton growth and cellular composition (discussed further below). Parameterizations regarding the other resources are assigned comparable values, and so should be viewed as other growth limiting resources expressed in units of nitrogen-equivalents. The model domain experiences hydraulic flushing that brings new nutrients from an external source and hydraulically displaces resident phytoplankton and dilutes ambient nutrients (e.g., discharge from rivers). From this physical framework, six models are created with the following water column processes added: 1) extinguishing light availability with depth; 2) vertical diffusivity; 3) nutrient flux from a lower boundary combined with vertical diffusivity; 4) particle sinking; 5) rescue effect combined with vertical diffusivity; and 6) all five processes combined.

A conceptual diagram of the 6th model, all processes combined, is shown in Fig. 1. In that diagram, light enters the water column from the surface and diminishes with depth based on, in part, phytoplankton concentration. Interactions between layers include vertical diffusivity and sinking of cells. Rescue effects are from an adjacent water mass (e.g., open ocean source), bringing new phytoplankton cells. Finally, a nutrient source in addition to hydraulic flushing is flux from a lower boundary representing either the benthos or an underlying nutrient rich water mass.

2.2. Phytoplankton assemblages

For this research, we employ 30 phytoplankton assemblages used previously (Roelke and Eldridge, 2008) that self-organized from species rich pools to a species supersaturated state. The high species richness in 10 of these assemblages is sustained through

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