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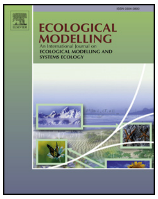

To share or not to share? Phytoplankton species coexistence puzzle in a competition model incorporating multiple resource-limitation and synthesizing unit concepts

Subrata Sarker[a,*,1], Ulrike Feudel[b], Cédric L. Meunier[a], Peter Lemke[c], Partha S. Dutta[d], Karen H. Wiltshire[a]

[a] Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland, Germany
[b] Theoretical Physics/Complex Systems, ICBM, Carl von Ossietzky Universität, PF 2503, 26111, Oldenburg, Germany
[c] Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany
[d] Department of Mathematics, Indian Institute of Technology Ropar, Rupnagar, Punjab, India

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ABSTRACT

The predictions of the competitive exclusion principle about the number of coexisting species not exceeding the number of limiting resources in equilibrium constitute an ecological puzzle for phytoplankton ecosystems. Here we present a synthesizing unit (SU) based competition model taking co-limitation into account, which is the extension of the competition model developed by Dutta et al. (2014).The study aims at understanding the mechanisms of violation of competitive exclusion principle for phytoplankton species with seasonal environmental forcing when multiple resource limitation is taken into account and species growth is formulated based on SU. We also explore the role of changing environmental conditions on species coexistence on a seasonal and a decadal time scale by linking the model forcing to the Helgoland Roads Time Series data sets. For the first time, based on the Helgoland Roads data, we are able to find a realistic parameterization for the phytoplankton competition model where growth is formulated using SU concept. Our study confirms that more species than limiting resources can coexist with seasonal variations of environmental conditions. This supersaturation is related to periodic changes in species' biomass, variation in interspecific competition and niche configuration, nonlinear functional response and the position of resource supply within the convex hull of species' resource uptake rate. Changes in environmental conditions within realistic ranges do not prevent the coexistence of species rather it slightly changes species' biomass and turnover time. This study also confirms that our model with SU based species growth performs better than species competition model where multiple resource limitation is formulated based on the product of several Monod functions. Our study has created a new avenue for phytoplankton coexistence research and the results might be helpful to answer the complex questions on species diversity maintenance in nature.

1. Introduction

Understanding species coexistence is one of the most important fundamental research objectives in community ecology (Hartig et al., 2014; Laird and Schamp, 2006). The mechanisms of species coexistence have long puzzled ecologists (Segura et al., 2011) and the greatest challenge lies in reconciling of coexistence with the competitive exclusion principle (Laird and Schamp, 2006). The competitive exclusion principle (Hardin, 1960) states that the maximum number of coexisting species cannot exceed the number of limiting resources in equilibrium. This claim however contradicts the observations of species number in plankton communities, which led to the formulation of the paradox of plankton (Hutchinson, 1961). Hutchinson (1961) pointed out that in planktonic systems many phytoplankton species can coexist while it seemed that only a few resources (i.e. light and nutrients) are limiting. Since the formulation of the paradox of plankton, many theories (i.e. niche theory, neutral theory and lumpy coexistence) have been proposed to explain species coexistence. Niche theory suggests that multiple species can coexist if the resources they require for growth differ sufficiently (Vandermeer, 1972). However, neutral theory of species

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* Corresponding author at: Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, 27498, Helgoland, Germany.
E-mail addresses: subrata.sarker@awi.de, subratasrk-ocg@sust.edu (S. Sarker).

[1] Current affiliation: Department of Oceanography, Shahjalal University of Science and Technology, Sylhet-3114, Bangladesh.

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coexistence, which deviates from niche theory, suggests that high diversity can be maintained even when life-history traits are very similar (Hubbell, 2001). A reconciliation of niche and neutral theory, termed "lumpy coexistence" (Sakavara et al., 2017), describes the self-organization of assemblages into competing clumps, in which species within clumps have very similar traits and are thus considered nearly neutral (Scheffer and van Nes, 2006). For the number of species to exceed that of resources, termed "supersaturated coexistence" (Schippers et al., 2001), species should differ in their resource-use abilities (Dutta et al., 2014). Since the formulation of the competitive exclusion principle a large number of modelling studies have been conducted to explain the species coexistence taking resource limitation into account.

There are two basic concepts to modelling resource limited species dynamics in the presence of several resources: Liebig's law of the minimum (Liebig, 1840) and the multiple resource limitation hypothesis (Gleeson and Tilman, 1992). Liebig's law of the minimum (Liebig, 1840) states that only a single resource limits species' growth at any given time. However, this idea has been replaced by the realization that phytoplankton growth can be limited by several resources simultaneously. Supersaturated coexistence of species in a multiple resources limited environment based on Liebig's law of the minimum and the product of several Monod functions both lack a good fit to data (Poggiale et al., 2010; Sperfeld et al., 2012). Thus, Dutta et al. (2014) developed a new approach allowing "supersaturated coexistence" of species in a multiple resource-limited ecosystem, based on the concept of a synthesizing unit (SU). This SU converts resources into biomass, fulfilling all stoichiometric requirements for the biomass formation (Kooijman, 2010). A SU forms a product according to the rules prescribed by classical enzyme kinetics, with some modifications: the kinetics is specified in terms of arrival fluxes of the substrate molecules to the enzyme, not in terms of substrate complexes. The enzyme-substrate dissociation rate is assumed to be zero and a SU can bind an arbitrarily large number of substrates and transfer them into products. Moreover, recent experimental results on resource co-limitation theory applied to herbivorous consumers have shown that species growth kinetics based on the concept of SU fits the data better than the product law growth rate (Sperfeld et al., 2012). In addition, this approach obeys mass of conservation. All the nutrient uptake processes are assumed to be irreversible. Such models produce all known possible outcomes of competition (i.e. competitive exclusion, heteroclinic cycles, and equilibrium). As Schippers et al. (2001) pointed out the model of Huisman and Weissing (1999) lacks robustness and supersaturation collapses when parameter are changed only slightly. It is important to note that the re-formulation of this model using the SU-unit overcomes this drawback and exhibits supersaturation in large parameter intervals as demonstrated in Dutta et al. (2014).

Due to the prediction of competitive exclusion principle species coexistence in a limited number of resources has been studied widely (e.g. Roelke et al. (2003), Roelke and Eldridge (2008), Roelke and Eldridge (2008)). However, studies on phytoplankton species coexistence in a multiple resources limited ecosystem based on the concept of a synthesizing unit are rare. The parameterization of the model developed by Dutta et al. (2014) is based on a bacteria-nutrients system and is therefore not suitable to study the competition of phytoplankton species. To test "supersaturation" to be a real possibility for the coexistence of phytoplankton species needs a completely new parameterization of that model, including the check that this new parametrization is robust. Moreover, no previous modelling studies on species coexistence compared the output of species competition with real data sets. Many studies found different behavior in species dynamics in the supersaturated state (e.g. identity of the dominant species changes, cycles in species abundance with peaks every couple of years etc.). These findings might hold true for a real data set. For example, long-term phytoplankton data sets from the Helgoland Roads Time Series also show (Fig. 1) that different species might behave differently on the long-term (i.e. a few species peak in species abundance after few years interval and a few species peak every year). Therefore, comparison of model outputs with the observed data might offer more realistic and exciting insights on species coexistence from the theoretical studies. Here, for the first time, we test the possibility whether the number of coexisting phytoplankton species can exceed the number of known limiting resources in a shallow-sea ecosystem taking the simultaneous co-limitation based on the concept of a SU into account. We also test the behaviour of long-term species coexistence by changing environmental forcing based on the Helgoland Roads Time Series data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). In addition, we discuss our species dynamics produced by the model with the real phytoplankton data (Fig. 1) from the Helgoland Roads Time Series Station.

This study aims to answer the following questions:

(i) Does the number of coexisting phytoplankton species, exceed the number of limiting resources in a multiple resource limited ecosystem modelled by formulating species growth using a SU based approach?
(ii) If yes, then what causes this supersaturated coexistence in an ecosystem where species growth is formulated using a SU?
(iii) What are the consequences of long-term coexistence of species?
(iv) What happens to species coexistence if environmental forcing is changed?
(v) Does the species competition model with SU approach performs better than the model with Monod equations?

2. Materials and methods

2.1. Model description

The main goal of our study is to explain the phytoplankton species coexistence in a multiple resource limited ecosystem by formulating species growth based on the SU concept. More specifically, we aim at understanding how the number of phytoplankton species coexisting can exceed the number of limiting resources. To do so, we based our work on the species competition model developed by Dutta et al. (2014). Dutta et al. (2014) presented a multiple species–multiple resource competition model which is based on the concept of synthesizing unit to formulate the growth rates of species competing for interactive essential resources. They demonstrated that a more mechanistic explanation of interactive effects of co-limitation may lead to the known complex dynamics including non-equilibrium states as oscillations and chaos. This competition model described a community in a chemostat and seasonal forcing was not used. Moreover, no temperature and light dependence of the growth rate of the species was introduced being a necessary condition for using this model to study the competition of phytoplankton species. Therefore, we extended this model for phytoplankton species in a shallow-sea ecosystem. A schematic representation of the model with the flows between variables and parameters is shown in Fig. 2. So, how does our model differ from Dutta et al. (2014)? We considered a shallow sea ecosystem while Dutta et al. (2014) considered the chemostat system where bacteria compete for nutrients. We consider phytoplankton as model organisms and identify a new parameter set which is based on observed data. In addition, seasonal temperature and light forcing is introduced in our case which were absent in Dutta et al. (2014). Species growth rates are formulated as a function of nutrients, temperature and light in our model. We use four phytoplankton species, and SiO_2, PO_4 and NO_3 as three resources in the model. We take their initial conditions from the Helgoland Roads Time Series data sets.

The model considers interactive effects of three essential nutrients (SiO_2, PO_4 and NO_3), temperature and light on the phytoplankton species dynamics. The model equations for n species and k nutrients in a shallow-sea system are described as: