

# Supersaturated coexistence of plankton species is unstable in changing environments

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# Abstract

Plankton is the base of aquatic food production, and plays a major role in the control of the global climate. Plankton ecologies have the puzzling property that many species coexist on a few basic resources, in contradiction to the competitive exclusion principle. Recently, plankton coexistence was explained in a theory that is based on finely-tuned competitive abilities of plankton species and a perfectly stable environment. (The mode of coexistence in this theory has been termed “supersaturated”, to indicate that the number of species exceeds the number of resources). We show here that supersaturated coexistence is unstable and that excess species go extinct if resource availability is not constant, but undergoes small fluctuations. Because such fluctuations are commonplace in natural ecosystems, we conclude that supersaturated coexistence is not a biologically plausible explanation of the plankton paradox.

## 1 Introduction

Plankton forms the basal layer of aquatic food webs, and is a major consumer of atmospheric carbon dioxide. Despite extensive research, an important aspect of phytoplankton ecologies remains ill-understood: Many plankton species coexist and thrive on only a few basic resources (Hutchinson 1961; Scheffer et al. 2003). This coexistence runs contrary to the competitive exclusion principle, according to which no two species can depend predominantly on the same resource (Hardin 1960; Armstrong & McGehee 1980). In a recent article, Huisman & Weissing (1999) proposed an explanation of this phenomenon (also known as the plankton paradox) in terms of supersat-

urated coexistence in a standard resource competition model (Tilman 1977; Grover 1997). Supersaturated coexistence allows for the survival of many species on few resources through oscillations in the species' abundance.

Huisman & Weissing (1999) model species coexistence with a set of differential equations that keep track of the abundance of all species and resources. Resources are assumed to have an abiotic origin, and to flow into the system at a constant rate. Species consume the resources, and there are no direct species–species interactions. For certain parameter values and at least three species, this model produces oscillations in the species' abundance (see Fig. 1). Through these oscillations, many species can coexist on a small number of resources. This apparent violation of the competitive exclusion principle is possible because the species exclude each other in a cyclic fashion, so that no single species can ever become the dominant consumer of a particular resource. Similar results have also been found in a number of models with biotic resources (Armstrong & McGehee 1980; Koch 1974; Armstrong & McGehee 1976; Lundberg et al. 2000).

One weakness of the model by Huisman and Weissing as a robust explanation of the plankton paradox is that stable species oscillations require finely-tuned parameter values, and are unstable under introduction or removal of species (Schippers et al. 2001). Nevertheless, while such fine-tuning may be rare, physiological constraints and ecological trade-offs have been invoked to account for it (Huisman et al. 2001). Here we examine the stability of species oscillations under perturbations in resource availability. Our results show that even for a perfectly tuned system, naturally occurring external variations in resource availability ruin the necessary oscillatory balance and lead to the extinction of species.

## 2 Methods

Simulations were run using the same parameters and methods as given by Huisman & Weissing (1999), unless noted otherwise. Numerical integration was carried out using a stochastic second order Runge-Kutta algorithm (Helfand 1979), with additive Gaussian noise with standard deviation of between 1% and 20% of the average daily influx added to each resource.

We considered systems in which plankton species had to coexist on three distinct resources. The resource influx was 10 units every four days for all three resources, except in the case of Figs. 1 and 3. There, as in (Huisman & Weissing 1999), the resource influx was 6, 10, and 14 units per four days, respectively, for the three resources. Growth rates for all species were assumed to be dependent on only the most limiting resource. We considered a species extinct if its abundance fell below an extinction threshold of 0.1 units, which corresponds to roughly 0.2% of the abundance of a typical single stable species.

We generated supersaturated systems as described by Huisman & Weissing (2001): We randomly assigned resource requirements  $K_{ij}$  to each species in such a way that each species had a strong requirement for one resource, an intermediate requirement for another resource, and a low requirement for the remaining resource. The resource-consumption parameters  $C_{ij}$  were distributed similarly, but shifted and scaled such that each species preferentially consumed the resource for which it had an intermediate requirement. We generated control systems of three species stably coexisting on three resources in the same way, except that resource consumption was chosen such that species were preferentially consuming the resource for which they had the largest requirement.

We tested  $n = 100$  supersaturated and  $n = 100$  control systems for species extinctions after 10,000, 100,000, and 1,000,000 simulated days and various levels of resource fluctuations. All systems were first tested for the maximum simulation time without resource fluctuations, to ensure that the extinctions were due to the noise, and not to instabilities inherent in the deterministic equations.

The simulation programs were written in C++ and run on a Beowulf cluster of 64 Pentium III PCs running Linux. The code is available upon request.

### 3 Results and Discussion

First, we replicated the simulations of (Huisman & Weissing 1999), but added Gaussian noise with a standard deviation of 5% of the daily inflow rate to each resource (see Fig. 1). This relatively moderate amount of noise led to oscillations with increasing amplitude and eventually to the extinction of several of the species living off of these oscillations. We considered a species extinct if its abundance fell below a cutoff value (see Methods).

Second, in order to study more generally the dynamics of supersaturated coexistence under noise, we randomly generated systems showing supersaturated coexistence of four species on three resources, with trade-offs between competitive abilities and a cyclic relationship between competitive ability and resource preference. We then tested these systems for stability in the long term under varying amounts of noise. After 10,000 simulated days, we found that 45% of the systems ( $n=100$ ) had three or fewer surviving species (of the initial four) at a 5% fluctuation in resource availability (a level that seems conservative when compared to biological ecosystem (Sommer 1984)).

After 100,000 simulated days, 67% of the systems had one or more of the oscillating species gone extinct. When we allowed for a 20% fluctuation in resource availability, we saw 95% of the systems lose one or more species after 100,000 simulated days (see Fig. 2).

We performed control simulations with only three species coexisting on three fluctuating resources. After 1,000,000 simulated days at 5% fluctuations in resources, less than 10% of the systems showed any extinctions, while with 20% fluctuations less than 25% of the systems lost any species. Ecological systems with only three species surviving on three resources thus are considerably more stable compared to the systems in supersaturated coexistence, which we attribute to the instability of species oscillation. We found similar results for systems of more than four species coexisting on three resources (data not shown).

The instability we observe occurs because the noise destroys the fine balance that is responsible for the regular oscillations, and pushes the system out of its stable trajectory. More formally, we have found that beyond the standard global attractor (the periodic orbit), many of the supersaturated systems exhibit a heteroclinic cycle, which is a pseudo-orbit that will bring the species arbitrarily close to extinction (see Fig. 3). Adding noise to a system can cause it to switch from the periodic orbit to the heteroclinic cycle (see, e.g, Fig. 1), which—despite the potentially stabilizing effect of the noise as reported by some studies (Stone & Holmes 1990; Hansel et al. 1993)—will eventually push species abundance below the extinction threshold and thus lead to extinction.

We conclude that the oscillations in the supersaturated coexistence model, as interesting as they are from a theoretical viewpoint, cannot solve the plankton problem, because the supersaturated regime is ultimately unstable

if the environment is not constant. Alternative explanations that have been proposed to explain the plankton paradox are based on spatial separation of species due to locally stable patterns of vortices (Bracco et al. 2000) or due to fluctuations in resource abundance (Sommer 1984). Spatial separation can also be caused by the interplay of turbulent diffusion and plankton consumption by predators (Vilar et al. 2003).

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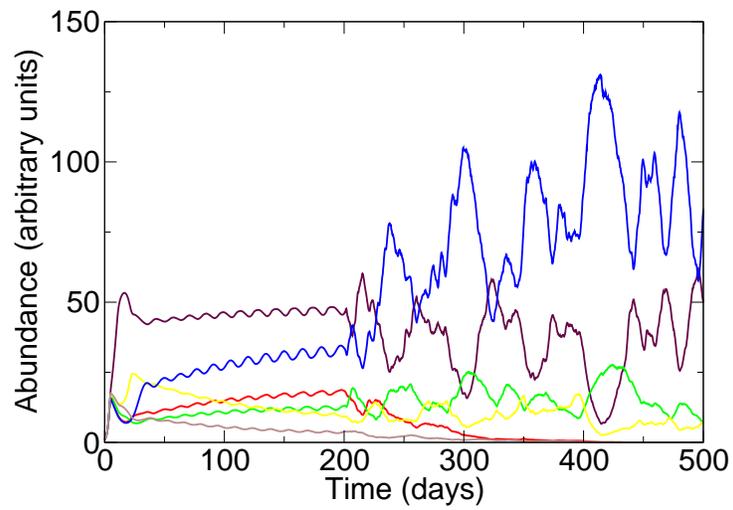


Figure 1: Species abundance as a function of time in a typical system of six coexisting species. All species have an initial abundance of 1 unit. Starting with day 200, 5% noise is added to the resource inflow every day. All other parameters are identical to those of (Huisman & Weissing 1999).

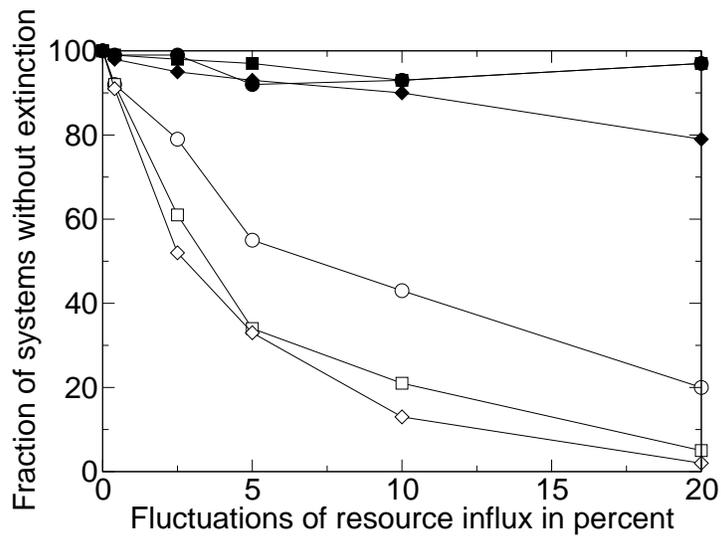


Figure 2: Percentage of systems in which no species have gone extinct after 10,000 days (circles), 100,000 days (squares) and 1,000,000 days (diamonds), as a function of the magnitude of fluctuations in resource availability (in percent). Open symbols correspond to supersaturated oscillating systems; filled symbols correspond to the control systems in which the number of species equals the number of resources.

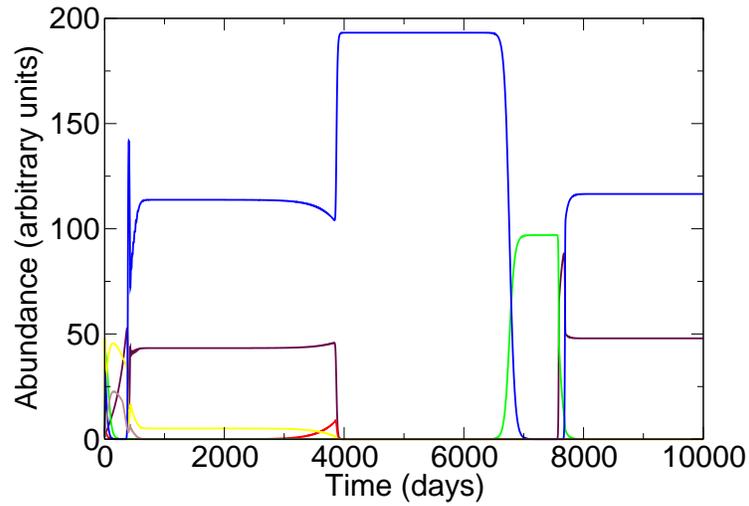


Figure 3: Heteroclinic orbit of a supersaturated system of six species on three resources without resource fluctuations or extinctions. Apart from the initial abundance of species, parameters are identical to those of Fig. 1. The initial abundance is 1 unit for all species but species 4, which has an initial abundance of 10 units. This initial advantage of species 4 pushes the system into a heteroclinic orbit rather than the stably oscillating orbit. If we let species of low abundance go extinct, all but three species would go extinct by day 1000.