

# Disturbance characteristics determine the timescale of competitive exclusion in a phytoplankton model



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## ABSTRACT

The way in which disturbance shapes phytoplankton diversity is still subject to much debate. Various disturbance–diversity relationships have been proposed, with diversity increasing or decreasing with the intensity or frequency of disturbance, or peaking at intermediate levels. A key problem in this discussion is the use of different concepts of “disturbance”, which can encompass both positive and negative effects on phytoplankton. To investigate how different modes of disturbance affect phytoplankton diversity, we subject populations of modelled phytoplankton to different frequencies and intensities of three different disturbance modes: a positive, a negative and a combined positive and negative disturbance mode. A chemostat system, considered undisturbed, is used for comparison. We show that (1) disturbance increases phytoplankton coexistence, (2) the disturbance–diversity relationship depends on the type of disturbance and (3) the effect is transient and disturbances predominantly affect the timescale of competitive exclusion.

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## 1. Introduction

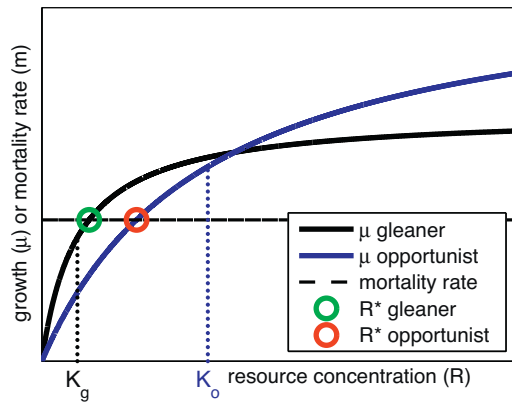
Numerical models used to simulate past, present and future ocean biogeochemistry commonly include a description of marine pelagic ecosystems. A key component of such descriptions is phytoplankton, which is responsible for roughly 50% of global photosynthesis and which, via photosynthetic CO<sub>2</sub> uptake, drives the marine biological carbon pump. Whenever environmental conditions change, as is the case with the current rise of CO<sub>2</sub> levels and temperatures, the ability of the pelagic ecosystem to (1) adapt to the changes and (2) continue its biogeochemical functioning becomes an issue. It is generally assumed that the ability of the planktonic system to adapt depends on how diverse the population is (McCann, 2000; Ptacnik et al., 2008). Phytoplankton diversity is, however, not generally represented well in current numerical models that typically use rigid parameter sets for one or very few model phytoplankton types.

In an attempt to make marine ecosystem models appear more realistic, some recent models have split the phytoplankton compartment into various functional types such as diatoms, non-diatoms, small phytoplankton and N<sub>2</sub>-fixing organisms (Dutkiewicz et al., 2009; Monteiro et al., 2010; Shorsh et al., 2008; Sinha et al., 2010). Yet in many biogeochemical models, the initial diversity is quickly reduced through competitive exclusion until one or few species outcompete most or all of the others (Gregg et al., 2003; Follows et al., 2007; Sinha et al., 2010). This mimics the famous paradox of the plankton (Hutchinson, 1961), which states that competitive exclusion should, in the rather uniform environment of the pelagic zone, lead to dominance of a single phytoplankton species. Possible explanations for the seemingly paradoxical high phytoplankton diversity in the real ocean include externally or internally generated variation, switching or density-dependent predation, life histories and differential resource use (Roy and Chattopadhyay, 2007). This study focuses on externally generated variation, also known as disturbance, as a means of maintaining phytoplankton diversity in biogeochemical models.

In a recent study (Barton et al., 2010a), the drivers of phytoplankton diversity were investigated in a global model with a self-assembling phytoplankton community (Follows et al., 2007; Dutkiewicz et al., 2009): Following the paradigm that “everything is everywhere but the environment selects” (Baas-Becking 1934, cited in Follows and Dutkiewicz, 2011), a global biogeochemical

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**Fig. 1.** Solid lines: growth rate as a function of resource availability for a gleaner and an opportunist, respectively, calculated according to the Monod function:  $\mu = \mu^{\max} R / (K + R)$ . The gleaner has a low half-saturation constant  $K_g$  and a low maximum growth rate  $\mu^{\max}$  and is hence superior under low resource levels. The opportunist has a high half-saturation constant  $K_o$  and a high maximum growth rate and is hence superior under high resource conditions. Dashed line: common mortality rate, e.g. dilution rate.  $R^*$  is the resource concentration of zero net growth and is reached in equilibrium, e.g. under chemostat conditions.

model was seeded with 78 phytoplankton species with randomly assigned parameters from pre-defined ranges, and the emergent biogeography and diversity was analysed after 10 years of simulation. The species were categorised as being either large, with high maximum growth rates and high nutrient requirements (hereafter called “opportunist”), or small, with lower maximum growth rates and lower nutrient requirements (hereafter called “gleaners”). Gleaners dominated equilibrium or near-equilibrium systems in the low latitudes, while opportunists dominated the more dynamic systems in the higher latitudes. Diversity was highest in the low latitudes, based on coexistence of several gleaners with equal or very similar competitive abilities. In this context, the competitive ability of a given species is determined via its  $R^*$ , the concentration of the limiting resource where growth equals losses, hence net growth of this species is zero. A low  $R^*$  determines a strong competitor under nutrient limitation, since the species, under equilibrium conditions, will reduce the resource concentration to its  $R^*$ , thereby competitively excluding all species with a higher  $R^*$ . The opportunists as the contrasting ecotype have a higher  $R^*$  and are therefore competitively excluded under equilibrium conditions, but also have a higher maximum growth rate and can therefore better utilise temporary increases of resource concentration than gleaners. The differences between the two types in growth rate as a function of resource availability are illustrated in Fig. 1.

Under constant low-resource conditions, competitive exclusion of similar gleaner species can take hundreds of years (Barton et al., 2010a), which is much longer than typical periods phytoplankton can stay in relatively homogeneous marine environments, e.g. in the subtropical gyres, thereby essentially leading to persistent coexistence of the respective gleaner species.

The Barton et al. (2010a) explanation of their simulated diversity pattern and its underlying assumption of competitive equivalence, was challenged (Huisman, 2010) on the grounds of the “Intermediate Disturbance Hypothesis” (IDH, Grime, 1973; Connell, 1978), which states that diversity should be highest under intermediate frequency and/or intensity of disturbance. Huisman criticised the occurrence of identical or nearly identical  $R^*$ s for different species and the resulting high diversity based on neutral coexistence as being unlikely. According to the IDH, moderately disturbed rather than undisturbed systems should sustain highest diversity. The diversity-generating mechanism behind these contrasting postulates are different: Neutral coexistence of several gleaners in

equilibrium relies on negligible differences in individual fitness and is hence an equalising mechanism (Chesson, 2000; Huisman, 2010). The IDH in turn relies on differential responses to disturbance by different ecotypes, i.e. significant fitness differences between ecotypes that reverse under changing conditions, realised here through different relative nonlinearities in growth rates. This stabilising mechanism (Chesson, 2000; Huisman, 2010) is seen in the trade-off between competitive ability at low nutrients and maximum growth rate in the gleaners and opportunists. Without trade-offs, disturbance can only delay competitive exclusion, whereas when different species are superior competitors at different points in time, disturbance is thought to prevent competitive exclusion (Chesson, 2000).

One key problem underlying the disturbance–diversity relationships and corresponding discussion is the lack of a common definition of disturbance. Both Barton et al. and Huisman use gradual changes in resource supply by adding a sine curve to the otherwise constant resource concentration in the inflow medium of their chemostat models (Barton et al., 2010a; Huisman, 2010). Other types of disturbance include sudden events of dilution with fresh medium in an otherwise undiluted culture, i.e. semi-continuous culture at different dilution intervals (Gaedeke and Sommer, 1986; Sommer, 1995) or artificial deepening of the mixed layer (Flöder and Sommer, 1999; Elliott et al., 2001), which is comparable to semi-continuous culture. Furthermore, sudden mortality events at distinct intervals (Violle et al., 2010) or modification of seed yield (Miller et al., 2011) have been employed as disturbance. Reynolds et al. (1993) defines disturbance as

“primarily non-biotic, stochastic events that result in distinct and abrupt changes in the composition and which interfere with internally driven progress towards self-organization and ecological equilibrium.” (p. 178)

This definition includes disturbances with positive and negative effects on the individual species, in line with the examples listed above. In this study we investigate how different modes of disturbance affect phytoplankton diversity. For this purpose, we subject populations of modelled phytoplankton – consisting of both gleaners and opportunists – to different modes, frequencies and intensities of disturbance. We create three disturbance modes that encompass both negative and positive aspects of disturbance as well as a combination of the two and compare the outcomes with a simulated chemostat system that is considered undisturbed.

It is shown for a model system with resource-controlled phytoplankton growth and linear mortality that (1) both within-group and between-group coexistence, i.e. coexistence of different gleaners and of gleaners and opportunists, respectively, can be strengthened by disturbance; (2) the disturbance–diversity relationship depends strongly on the type of disturbance; and (3) disturbance-induced diversity is transient and the impact of different disturbance modes mainly comprises changes of the timescale to competitive exclusion. This, eventually, allows us to reconcile the apparently contradictory inferences of Barton et al. (2010a) and Huisman (2010) who report highest diversity for lowest disturbance and highest diversity for intermediate disturbance, respectively.

## 2. Methods

### 2.1. Model

The model used is a version of the widely used Petersen (1975) model of resource competition, modelling each resource and phytoplankton species individually (Eqs. (1)–(3)). Fig. 2 shows a conceptual diagram of the model for one phytoplankton species

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