



Diel light cycle as a key factor for modelling phytoplankton biogeography and diversity



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ABSTRACT

Understanding the mechanisms driving species biogeography and biodiversity remains a major challenge in phytoplankton ecology. Using a model of two phytoplankton species with a gleaner-opportunist trade-off and competing for light and a limiting nutrient, we show that the diel light cycle may be an essential factor to explain large-scale ecological patterns. When only the seasonal light cycle is considered (control scenario) the model predicts that, independently of the nutrient supply, gleaners should dominate across all latitudes and opportunists can obtain a temporal niche only at high latitudes. However, the diel light cycle makes the competition outcome also a function of nutrient supply by affecting the amplitude of diel nutrient oscillations, with gleaners dominating when nutrient supply is low, opportunists when nutrient supply is high, and both species coexisting at intermediate levels of nutrient supply. The combined effects of seasonal and diel light cycles (diel scenario) shape a latitudinal diversity gradient with decreasing diversity towards higher latitudes and a unimodal dependence of diversity on nutrient supply and, therefore, on ecosystem productivity. The proposed mechanism can help interpret the biogeography of major phytoplankton functional groups in the global ocean and link them with large-scale biodiversity patterns.

1. Introduction

In order to understand mechanisms that govern biodiversity ecologists have focused on large-scale patterns of biodiversity along environmental gradients. Two of the most studied global biodiversity patterns are the latitudinal biodiversity gradient and the productivity-diversity relationship. For many marine and terrestrial taxa, there is evidence for biodiversity declining towards high latitudes (Willig et al., 2003; Hillebrand, 2004), supporting the hypothesis of a global biodiversity decline from tropical to polar regions (Pianka, 1966). The productivity-biodiversity relationship, although still under debate (Strong, 2010; Adler et al., 2011), has been suggested to be either increasing diversity with productivity or unimodal with a maximum of diversity at intermediate productivity (Mittelbach et al., 2001; Gillman and Wright, 2006; Fraser et al., 2015). Understanding whether and why such global biodiversity patterns exist is of great importance, as an increasing number of empirical studies supports a strong association of biodiversity with ecosystem functioning (Tilman et al., 2014).

Phytoplankton, the base of plankton food webs, play a major role for global ocean productivity and biogeochemical cycles. Although it has

been suggested that the composition of microbial communities should be driven by similar rules as that of macro-organisms (Martiny et al., 2006), whether phytoplankton diversity follows consistent patterns on a global scale is not clear. A latitudinal diversity gradient with decreasing diversity towards higher latitudes has been observed in freshwater phytoplankton (Stomp et al., 2011) while measurements of marine phytoplankton diversity did not reveal any pattern (Cermeño et al., 2008). The productivity-diversity relationship in phytoplankton has been found to be unimodal, peaking at intermediate productivity levels (Li, 2002; Irigoien et al., 2004; Stomp et al., 2011). However, no such relationship has been observed by Cermeño et al. (2013), indicating that more extensive observations are needed.

The complexity of ecological systems has led to a great number of hypotheses to explain the latitudinal diversity gradient (Pianka, 1966; Rohde, 1992; Colwell and Lees, 2000; Allen et al., 2002; Barton et al., 2010) and the productivity-diversity relationship (Connell, 1978; Huston, 1979; Wright, 1983; Tilman, 1985; Palmer, 1994; Abrams, 1995; Leibold, 1996; Cardinale et al., 2009; Vallina et al., 2014). Trait-based ecology aims to disentangle this complexity by linking functional traits of organisms with ecological patterns (Lavorel and Garnier, 2002;

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Table 1
Model parameters.

Parameter	Symbol	Gleaner	Opportunist	Reference
Maximal growth rate	μ_{max}	1 d ⁻¹	2 d ⁻¹	(Edwards et al., 2015)
Nutrient half saturation constant (nitrate)	K_N	0.1 $\mu\text{mol l}^{-1}$	0.5 $\mu\text{mol l}^{-1}$	(Edwards et al., 2012)
Affinity for nutrient uptake: $A_N = \mu_{max}/K_N$	A_N	10 l $\mu\text{mol}^{-1} \text{d}^{-1}$	4 l $\mu\text{mol}^{-1} \text{d}^{-1}$	
Affinity for light	A_L	0.01 $\mu\text{mol}^{-1} \text{photons m}^2 \text{s}$	0.01 $\mu\text{mol}^{-1} \text{photons m}^2 \text{s}$	(Edwards et al., 2015)
Dilution rate	d	0.25 d ⁻¹		(Edwards et al., 2012)
Nutrient supply (nitrate)	N_{in}	0.1–17.1 $\mu\text{mol l}^{-1}$		(Marañón et al., 2014)
Latitude	L	0°–70°N		
Light attenuation coef.	k	0.1 m ⁻¹		(Kirk, 1994)
Depth	z	5 m		

Kneitel and Chase, 2004; Litchman and Klausmeier, 2008) and to define the key trait trade-offs that are necessary to explain patterns of biodiversity (Willig, 2011).

Phytoplankton might be the best example to link functional traits with biodiversity patterns. Satellite observations have revealed consistent biogeographic patterns of phytoplankton functional types along the latitudinal and productivity gradients. Phytoplankton cell size, a ‘master trait’ of phytoplankton physiology (Litchman and Klausmeier, 2008; Finkel et al., 2010; Marañón et al., 2013; Marañón, 2015), increases on average with increasing productivity and latitude: Smaller phytoplankton cells dominate in oligotrophic environments and low latitudes (e.g., oligotrophic subtropical gyres), while larger cells dominate in eutrophic environments (e.g. upwelling areas) and high latitudes (Kostadinov et al., 2009; Brewin et al., 2010; Hirata et al., 2011; Roy et al., 2013). This pattern is likely related to two important taxonomic groups of phytoplankton: cyanobacteria (*Prochlorococcus* sp.) and diatoms. Small *Prochlorococcus* sp. dominate in oligotrophic environments and at low latitudes, while larger-size diatoms are dominant in eutrophic conditions and at high latitudes (Bracher et al., 2009; Hirata et al., 2011; Flombaum et al., 2013; Vogt et al., 2013; Soppa et al., 2014).

In phytoplankton models, the dynamics of these two functional groups is often explained by the so called gleaner-opportunist trade-off, i.e., a trade-off between affinity for nutrient uptake and maximal growth rate (Follows et al., 2007). Small phytoplankton, such as *Prochlorococcus* sp., can be characterized as gleaners, as their high surface to volume ratio gives them the ability to grow faster under low nutrient concentrations (Marañón et al., 2013). By contrast, larger phytoplankton species like diatoms are considered opportunists, due to their higher maximal growth rates (Marañón et al., 2013). The existence of the gleaner-opportunist trade-off in phytoplankton is supported by models of cell functioning (Klausmeier et al., 2004; Arrigo, 2005), resource competition theory (Grover, 1990) and experimental observations (Edwards et al., 2012, 2013; Marañón, 2015).

Resource competition theory posits that the competitive interaction between gleaners and opportunists is tightly related with temporal variations of resources: In the presence of resource variations phytoplankton species can coexist by sharing temporal niches (Sommer, 1984; Grover, 1990; Cermeño et al., 2011). Gleaners are at an advantage during phases of low resource concentrations, whereas opportunists perform better during phases of high resource concentrations. The most important natural factor for this mechanism of coexistence is the seasonality of light. The seasonal light cycle induces oscillations of limiting nutrients, as phytoplankton nutrient uptake and growth are higher during spring-summer and lower during winter (Falkowski and Raven, 2013). This process leads to a general pattern of phytoplankton seasonal succession, with opportunistic species dominating during the spring-bloom period and gleaners during the post-bloom period (Harris, 1986; Taylor et al., 1993; Alvain et al., 2008).

Another factor potentially affecting the dynamics of gleaners and opportunists is the diel light cycle. Similarly to seasonality, the diel light cycle induces oscillations of limiting nutrients because

phytoplankton nutrient uptake is generally higher during the day than at night (DiTullio and Laws, 1986; Harrison and Denman, 1991; Johnson et al., 2006; Heffernan and Cohen, 2010). Experimental and modelling work has shown that the diel light cycle can delay competitive exclusion, thus constituting a stabilizing mechanism, and affect competition outcomes between gleaners and opportunists through light-induced nutrient oscillations (Litchman, 1998, 2003; Litchman and Klausmeier, 2001; Litchman et al., 2004). Thus, phytoplankton gleaners dominate at no or only weak diel oscillations of resources, as they are better competitors under constant conditions, while opportunistic species dominate in the presence of stronger resource oscillations. However, in spite of the potential effects of the diel light cycle on the gleaner-opportunist competition, its potential role to understand large-scale ecological patterns has not been explored.

Here we use a zero-dimensional (local) resource competition model to investigate the potential effects of the diel light cycle on gleaner-opportunist dynamics and biodiversity along latitudinal and nutrient supply gradients. Comparing simulations with and without diel light cycles, we show that gleaner-opportunist competition under diel light oscillations might be an important factor contributing to the large-scale patterns of phytoplankton biogeography and diversity.

2. Methods

We simulate competition for light I and a limiting nutrient N between two phytoplankton species, a gleaner P_1 and an opportunist P_2 (Table 1). The model assumes chemostat-like conditions with nutrient concentration N_{in} in the supply and dilution rate d in a zero-dimensional system, so the model simulations represent the results of local resource competition in a well-mixed environment. Thus, the inflow rate of nutrient equals dN_{in} and the outflow rates are dN for nutrients and dP_i for species populations.

The specific growth rate μ_i of population P_i is modelled as the product of limitations by nutrient and light using the Monod and Poisson models, respectively (Eq. (1)) (Monod, 1950; Dubinsky et al., 1986). Here μ_{max} is the maximal growth rate and A_N is the nutrient affinity; $A_N = \mu_{max}/K_N$ where K_N is the half-saturation constant of phytoplankton growth. The two competitors have a trade-off between affinity for nutrient uptake and maximal growth rate: Gleaners have higher A_N and opportunists have higher μ_{max} (Fig. 1). Gleaners compared to opportunists reach a higher growth rate when $N < N_{crit}$, while opportunists grow faster when $N > N_{crit}$ (the level of N_{crit} is indicated by the red dashed line in Fig. 1). The growth parameters used are within the ranges of measured values in nitrate-limited phytoplankton cultures (Table 1). Dynamics of populations are described as the balance between population specific growth and loss through outflow (Eq. (2)), while the limiting nutrient N changes as the difference between the gain of the nutrient from the supply and loss through phytoplankton nutrient uptake and outflow (Eq. (3)).

$$\mu_i(N, I) = \mu_{max,i} \frac{A_N N}{A_N N + \mu_{max,i}} (1 - e^{-A_L I}) \quad (1)$$

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