Size-related effects of physical factors on phytoplankton communities

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ABSTRACT

Phytoplankton communities are influenced by light availability. Therefore, one factor promoting phytoplankton species persistence is their ability to stay within the euphotic zone. This ability is determined by the interplay between species mass, buoyancy and dispersion, which are driven by physical factors. In this study, we investigate how these physical factors and light-use efficiency, all correlated with cell size, influence species persistence. Our model shows, first, that species can persist only within a size-dependent range of turbulence strength. The minimal level of turbulence required for persistence increases drastically with cell size, while all species reach similar maximal levels of turbulence. Second, the maximal water column depth allowing persistence is also size-dependent: large cells show a maximal depth at both low and high turbulence strength, while small cells show this pattern only at high turbulence strength. This study emphasizes the importance of the physical medium in ecosystems and its interplay with cell size for phytoplankton dynamics and bloom condition.

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1. Introduction

Light is an essential resource for primary producers. Light distribution over the planet controls primary production over large tracts of the planet's oceans and lakes. Especially, light is a limiting resource during spring blooms. Since these blooms are responsible for a disproportionate fraction of the annual aquatic primary production (Parsons et al., 1984), and of the carbon pump (Watson et al., 1991; Sanders et al., 2014), their study is of primary importance. However, despite decades of studies, the conditions and factors affecting the onset, magnitude and species composition of spring blooms are still debated (Townsend et al., 1994; Behrenfeld and Boss, 2014; Daniels et al., 2015). Indeed, the phytoplankton requires light for growth, but light availability in the sea and in lakes decreases with depth. To persist, phytoplankton populations must stay in the upper region of the water column, known as the euphotic zone, where light availability is sufficiently high to sustain positive population growth rates.

Early work identified turbulent mixing of the water column (or turbulence) as a key factor contributing to the persistence of phytoplankton populations (Riley et al., 1949) and described the interplay of turbulence and light-dependent growth in sinking-prone phytoplankton species (Shigesada and Okubo, 1981; O'Brien et al., 2003). Indeed, the density of many phytoplankton species is higher than that of the surrounding medium, which means they are prone to sinking under the effects of gravity (Smayda, 1970; Reynolds, 2006). Hence, phytoplankton species need to passively or actively counteract the effects of gravity. Several phytoplankton species can actively decrease their body density and increase their buoyancy, e.g., through gas vacuoles or lipids (Waite, 1992; Waite et al., 1992), which especially allows large phytoplankton species to persist in the water column (Villareal, 1992). Margalef (1978) studied how sinking velocity, turbulence, grazing, nutrients and light availability can constrain phytoplankton adaptations, and Sverdrup (1953) argued that systems deeper than a critical depth cannot sustain algal blooms. More recently, Huisman et al. (2002) proposed a model that includes turbulence, sinking velocity and light-dependent growth of the phytoplankton. They demonstrated that only intermediate turbulence allows sinking phytoplankton species to persist. If turbulence is too low, individuals sink too fast, whereas if turbulence is too strong, individuals do not spend enough time in the euphotic zone. In both cases, the population cannot persist.

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Therefore, it seems clear now that hydrodynamical forces may play a major role in the size structure of phytoplankton (Rodríguez et al., 2001). Hence, the ability of a phytoplankton species to grow under light limitation depends on the complex interplay between its growth rate, mortality rate, photosynthetic capacities, sinking properties and turbulent diffusivity. However, these properties are quite disparate and often hard to measure, particularly *in situ*. Some studies investigated the interplay between sinking velocity and persistence (Huisman and Sommeijer, 2002a), but growth and sinking velocity were totally decoupled, while they should be related to each other, as indicated by recent works showing that most of these properties are underlined by a master trait: size (Edwards et al., 2015). Yet, it should be possible to derive estimates for most of these properties based on the cell size of organisms and on the physical properties of the medium in which they live. The laws of physics dictate that cell size in interaction with turbulence and gravity will be key factors for phytoplankton persistence. For example, a large, heavy phytoplankton individual will be more prone to sinking than a small, light one because of differences in the interplay between gravity, medium density, body density and drag. Effects of differential sedimentation due to size differences have been investigated for particles in marine waters (Li et al., 2004), but not for living cells.

In this study, we investigate the importance of body size on phytoplankton species persistence, determined by (a) the interplay between a species' physical and biological properties, and (b) the properties of the medium in which this species lives. Our work is the first to include size as the master trait in a vertically structured, dynamical model of phytoplankton growth under light limitation. Moreover, whenever possible, we derive the size-dependence of traits from primary physical laws, and not empirical allometries, in order to increase the generality of our approach and make it adaptable to different physical conditions. We will use the generic term "body" throughout, acknowledging the fact that the functional unit of phytoplankton in water can be a single cell or a multitude of cells forming a colony. Our first objective is to extend and generalize previous findings on phytoplankton persistence and vertical distribution to a wider range of body sizes, and thereby, to gain a more differentiated understanding of the physical conditions allowing phytoplankton species persistence. The second objective is to investigate the role of physical factors on species persistence by coupling species-specific properties (i.e., growth and motion) to physical factors of high relevance.

Many phytoplankton species show specific adaptations (e.g., gas vacuoles, mucilage) that allow them to control buoyancy (Reynolds, 2006). To avoid unnecessary complexity and keep our model tractable we decided not to consider buoyancy-related adaptations in the present study. First, buoyancy control might not be the only function of traits that decrease density (Reynolds, 2006). Second, species can modify their buoyancy through time, and the relationship between these adaptations and body size is complex (Moore and Villareal, 1996a,b). Third, buoyancy-related adaptations have costs (Walsby, 1994) that are not negligible. In the absence of reliable empirical data on these relationships we felt that the inclusion of buoyancy-related structures would not provide any reliable insight into which species would benefit from these adaptations. As it stands, our model considers species slightly denser than water and, thus, predicts the spatial structure of phytoplankton communities with non-actively buoyant species; as such, the model can be used to identify species that would benefit most from increasing their buoyancy.

More importantly, our model focuses on light limitation and ignores nutrient limitation. Nutrients are known to influence phytoplankton growth (Marañón et al., 2013; Wirtz, 2013), and competition (Ryabov and Blasius, 2011, 2014; Kerimoglu et al., 2012). However, light is an important factor and a special resource.

Indeed, light is essential for photosynthesis, and its distribution through the water column is inverted compared to nutrients. During blooms light but not nutrients is most often the limiting resource. Moreover, some lakes seem to be permanently light-limited rather than nutrient-limited (Karlsson et al., 2009). Last, our model assumes complete mixing of the water column. Thus, it is best suited to represent a phytoplankton species in a lake or coastal area with no thermocline, and at a time when a bloom is likely to occur.

As key physical factors of the medium, we consider light absorption, density, viscosity and turbulence, which are classical factors usually used to define the physical properties of a medium (Lampert and Sommer, 1997). Key properties of phytoplankton species living in the water column are photosynthetic rate (which, via light availability, controls their population growth rate); body density (whose relationship to medium density determines their buoyancy); and cross-sectional area (which interacts with the medium's viscosity to create the drag forces that phytoplankton face when moving). Finally, body size is included as an explicit master trait affecting all the rates of organisms, i.e., photosynthesis, metabolic loss, natural mortality and sinking rates. This study gives new insight into the conditions allowing phytoplankton blooms at a specific cell size and turbulent regime. This work is a contribution towards a better prediction of phytoplankton growth in light-limited environments.

2. Model description

2.1. General description

The model describes a phytoplankton population, in a mixed water column of depth Z_{max}. Three different processes occur. (i) The first process represents biological mechanisms (such as photosynthesis, metabolism or death). These mechanisms are included in a reaction term. (ii) Second, due to the interplay between the species' weight and its buoyancy, individuals are submitted to an oriented motion either toward the bottom, if they are denser than the medium, or toward the top, if they are naturally buoyant. This motion can be represented by an advection term. (iii) Last, turbulence adds a new component to individual motion. However, turbulence is by definition unpredictable and unoriented. This is why turbulence is represented by a diffusion term. Therefore, the model is written as a reaction–advection–diffusion model (see Table 1 for a list of parameters)

$$\frac{\partial \omega}{\partial t} = R(z, t)\omega - \nu \frac{\partial \omega}{\partial z} + D \frac{\partial^2 \omega}{\partial z^2} \tag{1}$$

where ω is the population abundance at depth z, R is the overall growth rate per capita (the reaction), ν is the sinking velocity (the advection), and D is the diffusion due to turbulence. Each term is calculated according to the biological and physical properties of the species, and their interplay with physical factors of the medium.

2.2. The reaction term

The reaction term represents the growth rate *per capita*, and it depends on four different mechanisms. The first one is photosynthesis (P), which varies according to light availability (I_z) at each depth. It describes the amount of energy gained by photosynthesis. However, photosynthesis has a cost, due to pigments synthesis, which is represented by the second term (P_c). The third term represents loss through basic metabolism (m). The last term represents loss though natural death of the organisms (l_d).

$$R(z, t) = P(I_z) - P_c - m - l_d \tag{2}$$