



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)

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

where ω is the population abundance at depth z , R is the overall growth rate per capita (the reaction), v 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 through natural death of the organisms (I_d).

$$R(z, t) = P(I_z) - P_c - m - I_d \quad (2)$$

Table 1
Parameters used in the model.

Symbol	Meaning	Value	Units	References
Variables:				
ω	Population abundance		ind m ⁻³	
I	Light intensity		mol photons m ⁻² s ⁻¹	
Physical parameters:				
g	Acceleration due to gravity	9.81	m s ⁻²	
ρ_m	Medium density	1000	kg m ⁻³	
μ	Dynamic viscosity	0.00131	N s m ⁻²	
Re	Reynolds number		dimensionless	
C_d	Drag coefficient		dimensionless	
Z_{max}	Water column depth		m	
I_0	Incident light intensity	3.5×10^{-4}	mol photons m ⁻² s ⁻¹	
K_{bg}	Background absorption	0.2	m ⁻¹	Kirk (1994)
v	Advection (sinking velocity)		m s ⁻¹	
D	Diffusion (turbulent diffusion)		m ² s ⁻¹	
Biological parameters:				
R	Reaction (per capita net growth rate)		s ⁻¹	
$P(I_z)$	Gross photosynthetic rate at depth z		mg C s ⁻¹	
P_c	Photosynthetic cost		mg C s ⁻¹	
P_{max}	Maximal gross photosynthetic rate		mol C s ⁻¹	
k_{max}	Maximal gross photosynthetic rate at reference size (<i>Chlorella</i> cell)	7.75×10^{-18}	mol C s ⁻¹	Reynolds (1990)
V_{Op}	Volume at reference size for photosynthetic rate (<i>Chlorella</i> cell)	3.35×10^{-17}	m ³	Reynolds (1990)
a	Absorption cross-section		m ²	
a^*	Absorption surface per unit of chlorophyll a		m ² mg chla ⁻¹	
α_s^*	<i>in vitro</i> absorption coefficient	0.04	m ² mg chla ⁻¹	Finkel et al. (2004)
Q_p and ρ	Packaging effect		dimensionless	
c	Chlorophyll a content		mg chla m ⁻³	
C_0	Carbon content at reference size	2.6×10^{-13}	g C	Menden-Deuer and Lessard (2000)
V_{Oc}	Volume at reference size for carbon content	1	μm^3	Menden-Deuer and Lessard (2000)
ϕ	Quantum yield of photosynthesis	0.1	mol C mol photon ⁻¹	Kirk (1994)
ζ	Cost of photosynthetic apparatus	7×10^{-4}	mol photon mg chla ⁻¹	Raven (1984)
τ	Average lifetime of photosynthetic apparatus	24	h	Riper et al. (1979)
m	Metabolic loss		J s ⁻¹	
l_d	Death rate		ind s ⁻¹	
l_{od}	Death rate at reference size	1.58×10^{-6}	s ⁻¹	McCoy and Gillooly (2008)
V_{Od}	Volume at reference size for death rate	1.08×10^3	μm^3	McCoy and Gillooly (2008)
E	Energy content		J ind ⁻¹	
R_{dw}	Dry ash-free mass over wet mass ratio	0.16	dimensionless	
E_{dw}	Energy over dry mass ratio	23,000	kJ kg ⁻¹	
M_b	Body mass (wet)		kg	
V_b	Body volume		m ³	
S_b	Body section surface		m ²	
L_b	Body length		m	

The first term, the photosynthesis rate (P), is a saturating function of the rate of photons captured by an organism (Finkel et al., 2004)

$$P(I_z) = P_{max} \tanh\left(\frac{a\phi I_z}{P_{max}}\right) \quad (3)$$

where I_z is the irradiance at depth z and time t , P_{max} is the maximal photosynthetic rate, a is the absorption cross-section, and ϕ is the quantum yield of photosynthesis. It appears that $P(I_z)$ is a saturating function of I_z .

Both maximal photosynthetic rate (P_{max}) and absorption cross-section (a) are functions of body size (Finkel and Irwin, 2000)

$$P_{max} = k_{max} \left(\frac{V_b}{V_{Op}}\right)^{0.75} \quad (4)$$

where k_{max} is the maximal photosynthetic rate at reference size (7.75×10^{-18} mol C s⁻¹), V_b is body volume, and V_{Op} is the volume at reference size (3.35×10^{-17} m³). k_{max} and V_{Op} are estimated for a *Chlorella* cell (Reynolds, 1990). The absorption cross-section (a) is calculated following Finkel et al. (2004) (see Appendix A for details). It increases with body size.

The second term of the reaction equation is the photosynthetic cost term (P_c)

$$P_c = \frac{cV_b\zeta\phi}{\tau} \quad (5)$$

where ζ is the cost of photosynthetic apparatus, τ is the average lifetime of this apparatus over which the cost of this apparatus is amortized, V_b is cell volume, and c is chlorophyll a content *per cell* (see Appendix A for details).

Units for the photosynthetic rate (P) and photosynthetic cost (P_c) are mol C s⁻¹. In order to transform these molar rates into *per capita* rates, both values are multiplied by the molar weight of carbon (12 g mol C⁻¹). Then, they are divided by the amount of carbon needed to produce one individual (C_b) (Menden-Deuer and Lessard, 2000).

$$C_b = C_0 \left(\frac{V_b}{V_{Oc}}\right)^{0.88} \quad (6)$$

where C_0 is carbon content at reference size (set at 2.6×10^{-13} g C), and V_{Oc} is volume at reference size (set at 10^{-18} m³). Hence, the net *per capita* growth due to photosynthesis decreases when body size increases.

The third term is the metabolic rate (m), which increases with body size (Peters, 1986)

$$m = 0.01 M_b^{0.75} \quad (7)$$

where M_b is body mass (in kg) and m is the metabolic loss (in $J s^{-1}$). This energetic rate is then divided by the amount of energy contained within one individual (E).

$$E = M_b R_{dw} E_{dw} \quad (8)$$

where M_b is the body mass (wet mass), R_{dw} is the ratio between the dry ash-free mass and the wet mass, and E_{dw} is the ratio of energy to dry mass. Overall, *per capita* metabolic rate increases with body size.

The last term is *per capita* loss by natural death (l_d). This natural death rate, excluding external source of death (e.g., predation), is assumed to be the inverse of life span, which scales with body size (McCoy and Gillooly, 2008)

$$l_d = l_{0d} \times \left(\frac{M_b R_{dw}}{V_{0d}} \right)^{-0.22} \quad (9)$$

where l_{0d} is death rate at reference size (set at $1.58 \times 10^{-6} s^{-1}$), and V_{0d} is reference size (set at $1.08 \times 10^{-15} m^3$). The overall *per capita* growth rate calculated is in accordance with empirical observations (Finkel et al., 2010).

An overview of the four parameters considered (i.e., photosynthetic gain, photosynthetic cost, metabolic cost, death loss) leads to the following conclusion: for a given size, the costs (P_C , m , and l_d) are constant, and the reaction term varies with light availability (I_z) at each depth. Light availability follows a Beer–Lambert's law (Huisman et al., 2004), and therefore, depends on light absorption by populations above the considered depth z and the background absorption (i.e., water turbidity)

$$I_z = I_0 \exp \left\{ - \int_0^z a\omega(\sigma, t) d\sigma - K_{bg} z \right\} \quad (10)$$

where I_0 is the initial irradiance received on the top of the system (in mol photon s^{-1}), a is absorption cross-section (defined above), σ is an integration variable, and K_{bg} is the background absorption by water and other components than phytoplankton (in m^{-1}).

2.3. The advection term

The advection term represents the average sinking velocity of a single organism. It evaluates the relative importance of an organism's weight and buoyancy. Therefore, it is oriented either downwards, if the species is denser than the medium, or upwards, if the species is naturally buoyant. Due to their small size, phytoplankton species are usually assumed to be located below the Kolmogorov scale, so that sinking velocity can be calculated using Stokes' law (Davey and Walsby, 1985; Fogg, 1991). However, some phytoplankton species are large enough to face conditions above the Kolmogorov scale (Lazier and Mann, 1989), where Stokes' law is not valid anymore (Almedeij, 2008). Therefore, we use a more general method that can be used either below or above the Kolmogorov scale. A sinking force (F) is calculated, including as its terms three forces that act constantly on organisms. The first term represents weight (i.e., the effect of gravity on the body) and is oriented downwards. The second term represents buoyancy (i.e., Archimedes' force) and is oriented upwards. Considering that motion does not occur in a vacuum, the viscosity of the medium also plays a role. Hence, the last term represents drag (i.e., the effect of medium viscosity) and is always opposed to motion. This model considers only one component of drag, which is surface drag

$$F = gM_b - V_b \rho_m g - \frac{1}{2} S_b v^2 \rho_m C_d \quad (11)$$

where g is acceleration due to gravity, ρ_m is medium density, v is speed, S_b is the body section surface, and C_d is the drag coefficient. Then, this equation allows the calculation of an equilibrium

speed, which is the sinking velocity (see Appendix B for details). Sinking velocity increases with body size, which is in accordance with empirical observations (Kjørboe, 2008). If Reynolds number becomes very low (i.e., $Re \ll 1$), the last term of Eq. (B.2) dominates (see Appendix B), which leads to similar results as with Stokes' drag coefficient. However, while Stokes' law is valid only for very low Reynolds numbers, our approach is more general and allows prediction of sinking velocity for bigger cells or colonies that can face conditions beyond Stokes' law conditions.

2.4. The diffusion term

Turbulence is neither predictive nor oriented. This is why turbulence effects are represented as a diffusion process. The current of fluid produces a force on cells, leading to motion. This motion can be easily included into a diffusion parameter. In order to avoid confusion with other definitions of diffusion (e.g., molecular diffusion), we will use the term "turbulent diffusion" throughout. However, calculating the effect of current speed on the diffusion parameter value according to organism body size remains challenging. Moreover, turbulence is a complex phenomenon that occurs at different scales. Thus, the relationship between turbulence and diffusion related to body size remains difficult to describe precisely. Many studies have investigated the effects of turbulence on predation rate (Lewis and Pedley, 2000, 2001), nutrient uptake (Metcalf et al., 2004; Hondzo and Wüest, 2008), or phytoplankton patchiness (Seuront, 2005). Although the effects of turbulence on plankton settling rate have been studied (Ruiz et al., 2004), it is challenging to disentangle the relative effects of turbulence and gravity in these studies. So far, we are not aware of any study, either empirical or theoretical, that calculates the turbulent diffusion of planktonic cells according to the attributes of turbulent currents, and the relationship between this turbulent diffusion and cell body size. Previous studies considering turbulence set the turbulent diffusion parameter at a constant *ad hoc* value (Huisman et al., 1999b, 2002; Yoshiyama et al., 2009; Mellard et al., 2011), implicitly assuming that turbulence has similar effects on phytoplankton cells of different body sizes. For a lack of a better alternative, we use a similar approach. However, studies have emphasized the importance of considering the relationship between turbulence and body size (Zhang et al., 2014).

2.5. Implementation

The system represents the mixed layer of a water column. It is assumed that no individual can enter or leave the system at the top (0) and bottom boundary layers (Z_{max}), which is a zero flux boundary condition. This case happens in lakes and shallow coastal waters during spring or fall, and this condition was used in several studies (Huisman et al., 1999b, 2002; Huisman and Sommeijer, 2002b).

$$v\omega - D \frac{\partial \omega}{\partial z} \Big|_{z=0} = v\omega - D \frac{\partial \omega}{\partial z} \Big|_{z=Z_{max}} = 0 \quad (12)$$

The model is solved numerically by using a finite volume method by Crank–Nicolson's scheme, which is known to be a very stable scheme for reaction–advection–diffusion equations in one dimension (Najafi and Hajinezhad, 2008). Finite volume methods and the Crank–Nicolson scheme are commonly used in physics. Moreover, in order to check the validity of applying our method to an integro–reaction–advection–diffusion model, we also did some tests using a scheme combining the method of lines, a third order upwind scheme and the trapezoid rule, as described in detail in Huisman and Sommeijer (2002b). Both methods give similar results. However, the method we use is computationally lighter.

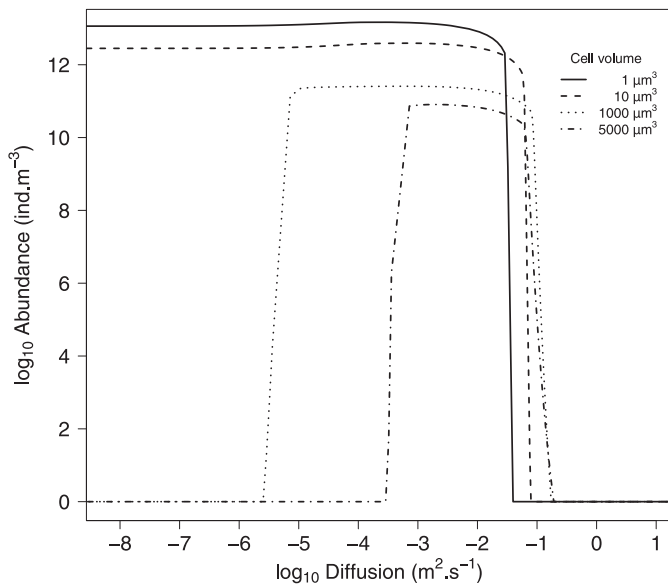


Fig. 1. Total abundance according to turbulent diffusion rate ($Z_{max} = 60$ m). Small species are able to persist at very low turbulence strength, while bigger species need stronger turbulence for persistence. All populations disappear when turbulence is too strong. However, differences between species at high turbulence are quite small.

Numerical model's simulations were performed with Matlab (8.0.0.783) and Java (1.6.0.65); figures were made using the R software (R Core Team, 2013).

3. Results

In this study, species body density is set at 1080 kg m^{-3} , which is the mean density value for biological organisms (Denny, 1993). Individuals are slightly denser than their surrounding medium, and therefore they are prone to sinking. Light availability decreases with depth, and growth is maximal close to the surface. Below a given depth (compensation depth), the remaining light does not allow photosynthetic gains to compensate for the costs, which leads to a negative growth rate. In our model, when body size increases, the maximal per capita growth rate decreases, and the sinking velocity increases. Furthermore, following Huisman et al. (2002), incident light intensity is set at $3.5 \times 10^{-4} \text{ mol photons m}^{-2} \text{ s}^{-1}$, which is assumed to be a saturating condition at the surface.

3.1. Relationship between persistence and turbulence

According to several studies (Denman and Gargett, 1983; MacIntyre, 1993; Huisman et al., 2002), phytoplankton turbulent diffusion in lakes or oceans, varies from $10^{-7} \text{ m}^2 \text{ s}^{-1}$ to $10^{-1} \text{ m}^2 \text{ s}^{-1}$. In this study, turbulent diffusion varies from $10^{-8} \text{ m}^2 \text{ s}^{-1}$ to $1 \text{ m}^2 \text{ s}^{-1}$, which allows the model to include the usual conditions in natural ecosystems as well as potential extreme cases. By looking at the interplay between light availability, sinking velocity and body size, for a wide range of turbulent diffusion values, several important results appear (Fig. 1). First, at low levels of turbulence (i.e., small turbulent diffusion values), small species can persist, while larger species cannot. As body size increases, the minimal turbulence strength required for persistence increases. Second, when turbulence strength increases, part of the population is present at shallower depth, and the maximal depth reached by the population increases with turbulence strength (Fig. 2). Individuals are present deeper when turbulence increases. When the system reaches a critical depth at high turbulence, the population is mostly located in the dark zone. Therefore, it cannot persist. Above an

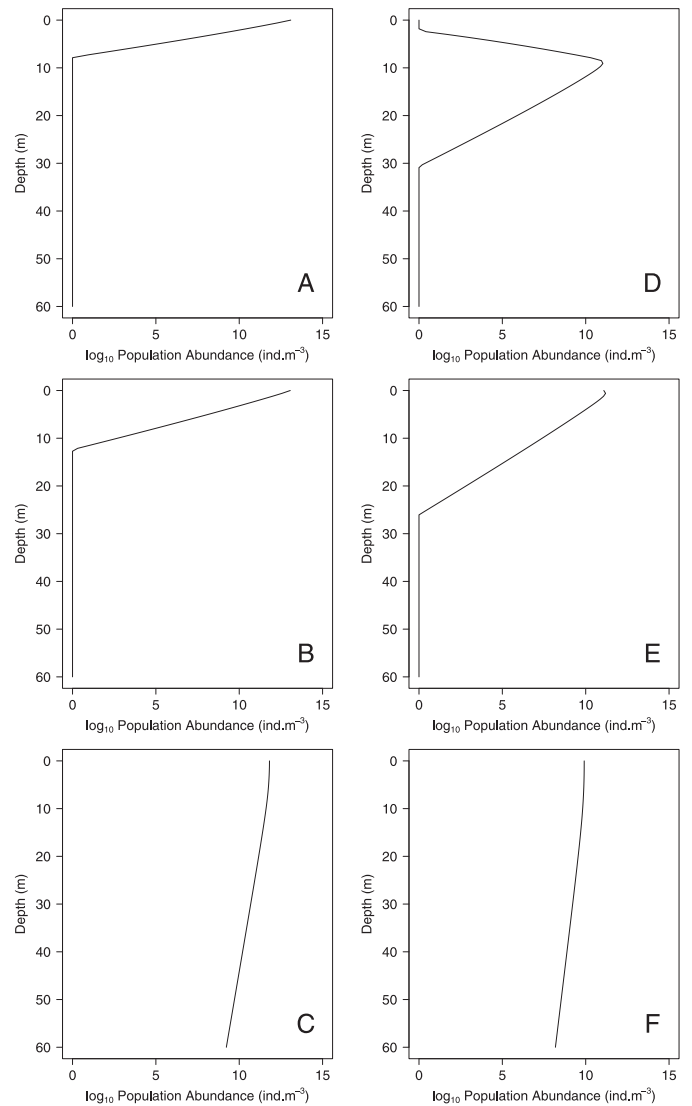


Fig. 2. Depth profiles at steady state for three turbulent diffusion values. The left column represents a small species ($1 \mu\text{m}^3$) at respectively 10^{-10} (A), 10^{-6} (B) and $10^{-3} \text{ m}^2 \text{ s}^{-1}$ (C). The right column represents a large species ($650 \mu\text{m}^3$) at respectively 10^{-10} (D), 10^{-8} (E) and $10^{-5} \text{ m}^2 \text{ s}^{-1}$ (F). The small species maintains a population close to the surface at low turbulence. When turbulence increases, the population diffuses over the whole column. The large species maintains a population below the surface at low turbulence. When turbulence increases, the population has its maximum upwards. If turbulence increases more, the population spreads over the water column.

upper threshold, the population is unable to persist. Therefore, a given species can persist only within an optimal range of turbulence.

Third, the breadth of the optimal range of turbulence allowing persistence becomes narrower with increasing body size (Fig. 1). Small species are able to persist from very low to very high diffusion rates. When body size increases, a lower limit of turbulent diffusion first appears, and this limit increases with body size. However, if strong differences exist among species at low turbulence, all species seem to reach similar upper turbulence thresholds. Last, by looking at the depth profile of the population, the model leads to a fourth interesting result. When the population persists at low levels of turbulence, individuals are located very close to the surface (Fig. 2A). However, with increasing body size, this pattern is altered, and the depth of maximal abundance is located deeper (Figs. 2D and 3).

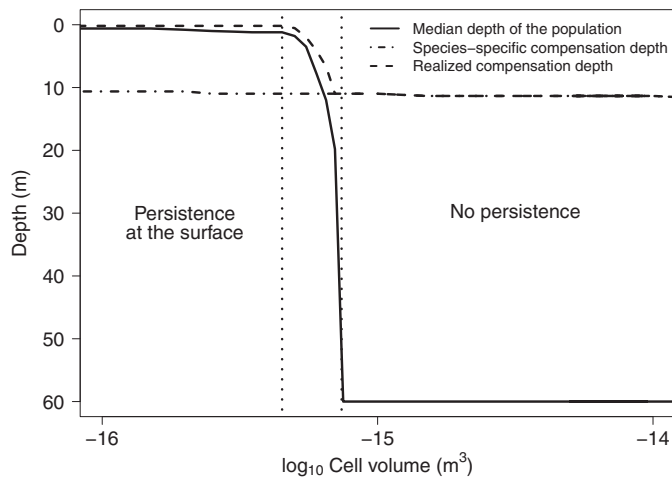


Fig. 3. Median depth of the population at low turbulence according to cell size. When turbulent diffusion is very low ($D = 10^{-10} \text{ m}^2 \text{ s}^{-1}$), the median depth of the population (solid line) of small cells is located close to the surface. Cells shade the light, and the realized compensation depth (dashed line) is located above the species-specific compensation depth (dashed-dotted line). Larger cells sink to fast and cannot maintain a population at the surface. Thus, the median depth of the population is at the bottom. For intermediate-sized cells (between the two vertical dotted lines), the median depth of the population is located below the surface. Since fewer cells are located close to the surface, light can reach deeper water, which allows cell growth below the surface, but above the species-specific compensation depth.

3.2. Relationship between depth and persistence

The critical depth concept (Sverdrup, 1953) can be applied – if the water column is deep enough that the dark zone is non negligible. Under a realistic range of turbulent strength, patterns for small and large species are different (Fig. 4). As the population is located at the surface at low turbulence strengths, a small species is not affected by ecosystem depth. On the other hand, when turbulence strength increases to a very high level, the population is able to persist only in a relatively shallow system. Beyond a critical depth, the population cannot persist above an upper threshold of turbulence for the same reason as suggested by Sverdrup (1953). Because high turbulence strength increases population spread, cells are transported into the dark zone too fast. For large species, similarly to small species, a critical depth is observed at high turbulence strength. However, a critical depth is also observed at low turbulence strength. Moreover, the critical depth at low turbulence strength is shallower than the critical depth at high turbulence strength and is close to the compensation depth. Cells that are too big to be resuspended by mixing, stay outside the euphotic zone.

4. Discussion

4.1. Size-mediated relationship between persistence and turbulence

A number of previous studies investigated the relationship between sinking velocity, turbulence, and phytoplankton persistence (Huisman et al., 2002; Huisman and Sommeijer, 2002a,b). However, in these studies cell growth and sinking velocity were treated as totally independent parameters, while our model considers one master trait (body size) that links all these parameters together. Thus, our model leads to two important new results. First, small species are able to persist at low turbulence, while larger species are unable to do so, which is in accordance with empirical observations (Fogg, 1991). Second, all species are unable to persist beyond an upper turbulent diffusion threshold. All species seem

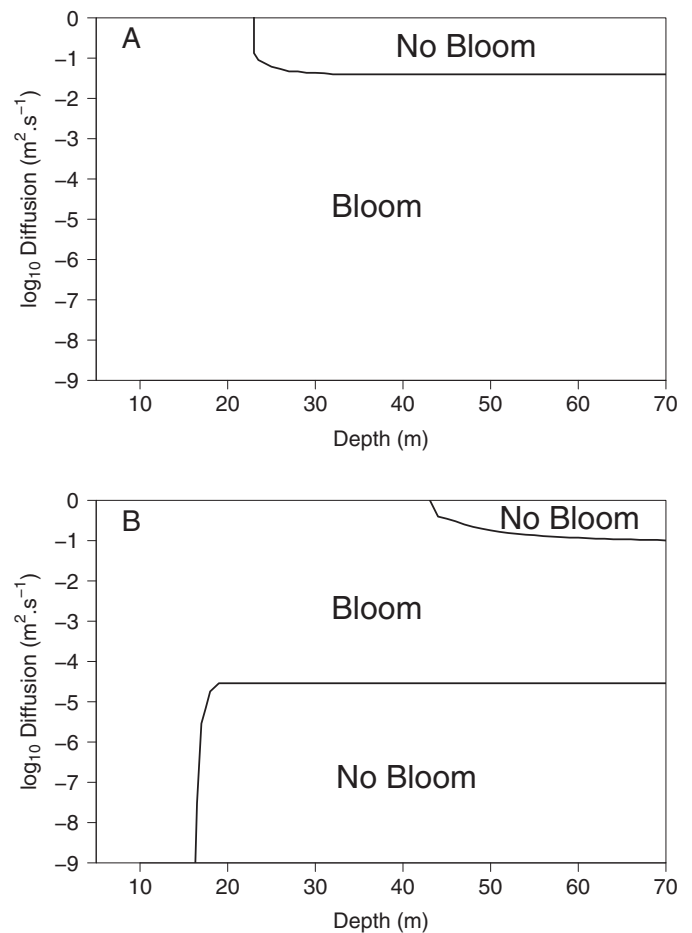


Fig. 4. Water column depth (Z_{max}) and turbulent diffusion interplay on algal bloom. For a small species ($1 \mu\text{m}^3$), turbulence does not allow persistence beyond an upper threshold if the medium is too deep (A). On the other hand, a large species ($1000 \mu\text{m}^3$) cannot maintain a population if turbulence is either too low or too strong, and if the medium is too deep (B). The critical depth for the largest species is shallower at low turbulence strength.

to reach similar upper thresholds. However, this upper threshold seems to be maximal for intermediate size species. Whether these small differences are important for community structure at high turbulences is an open question. This finding can be understood by considering species' growth rate, their sinking velocity, and their compensation depth. Small species have (i) a high *per capita* population growth rate, (ii) a relatively low sinking velocity, but (iii) a relatively shallow compensation depth (i.e., depth at which production from photosynthesis is equivalent to the costs). When turbulent diffusion is very low, individuals can stay in the euphotic zone during a long period of time, which allows them to multiply before sinking. In other words, reproduction overcompensates for the sinking loss, even if individuals are not naturally buoyant. This result is consistent with other studies demonstrating that small cells are able to remain at the surface of the water column due to medium viscosity (Pedrós-Alió et al., 1989). The minimal level of turbulent diffusion allowing a small species to persist is very low: we found $10^{-11} \text{ m}^2 \text{ s}^{-1}$ for a $1 \mu\text{m}^3$ cell using the classical formula given by Riley et al. (1949), which is far below the lowest diffusion rate measured in aquatic ecosystems (Daly and Smith, 1993). Hence, one can assume that small cells can persist in even the calmest water.

At the other end of the size spectrum, large species face inverted conditions (i.e., a relatively low *per capita* population growth rate and a relatively high sinking velocity). Therefore, in

the absence of turbulence, individuals sink out of the euphotic zone too fast to allow growth to compensate for the sinking loss. These populations need turbulence to maintain individuals within the euphotic zone. Indeed, turbulence increases species motion in and out of the euphotic zone and their spread over the water column, and the strength of this process increases with turbulence strength. As a result, large cells are able to spend more time in the light zone at intermediate turbulence than at very low turbulence, which allows persistence of the population. Because growth decreases with body size, while sinking velocity increases with body size, a higher turbulent diffusion rate (i.e., a higher turbulence) is necessary to keep large cells within the euphotic zone. This is why the minimal strength of turbulence increases with body size.

However, if turbulence is too strong, individuals are mixed into the dark zone too fast and do not spend enough time in the euphotic zone to allow the persistence of the population. This process operates on all species and explains the presence of an upper threshold of turbulence above which species cannot persist. High turbulence increases individual turnover between euphotic and dark zones. Since large species have a low growth rate, these species need to spend more time in the light. However, since large species have a deeper compensation depth (i.e., a deeper euphotic zone), they show an upper threshold at higher turbulence than smaller species. But, sinking velocity increases with size faster than compensation depth does. Therefore, for larger species, this upper threshold occurs between small and intermediate size species' thresholds. Nonetheless, it should be noticed that differences between species are quite small and might not have a strong impact in real ecosystems. Indeed, some field studies have shown that smaller phytoplankton species tend to dominate when turbulence is strong (Ward and Waniek, 2007), while other studies show that highly mixed systems tend to be dominated by large species (Kjørboe, 1993).

Another interesting result comes from the study of the depth profile given by the model. The model predicts that, at low turbulence, small species should have their maximal abundance at the surface, while species with large body size, provided they are able to survive, should reach their maximum abundance below the surface. Indeed, population growth is maximal at the surface, and this is where the majority of cells of the population accumulates, provided that reproducing cells get to stay sufficiently long in this zone. The accumulation of these cells close to the surface shades the light. Thus, growth becomes impossible below the surface. The depth of median population abundance (the depth where half of the population is located above and the other half below) is close to the surface (Fig. 3). The realized compensation depth is located close to the surface and above the species-specific compensation depth (i.e., the compensation depth in the absence of shade). However, when body size increases, sinking velocity becomes more and more important in the overall dynamic. This means that individuals are unable to stay close to the surface. Since fewer cells are located at the surface, light can reach deeper water. Thus growth is possible below the surface, and the depth of median population abundance is located below the surface (Fig. 3). For even larger cells, sinking velocity is too strong. The cells sink below their species-specific compensation depth and disappear. This pattern of maximum density below the surface observed for intermediate-size species is usually interpreted as a consequence of either nutrient limitation (Klausmeier and Litchman, 2001), photoinhibition (Worrest et al., 1978), or zooplankton grazing (Cullen et al., 1992). Here, this pattern results only from the interplay between growth, shade, and sinking velocity (Huisman et al., 2002). Our model shows that this pattern can be explained by the interplay between gravity, body density, medium density, and light, without involving any other biological mechanism.

According to the model, phytoplankton cells larger than $10,000 \mu\text{m}^3$ cannot survive because they sink too fast at all turbulence levels. In real ecosystems, large phytoplankton cells usually increase their buoyancy by modifying their body density (Waite, 1992), so that even very large diatom species (e.g., *Ethmodiscus* species) can persist when turbulence is weak (Villareal, 1992).

The abundances that our model predicts for small species (around 10^8 cells mL^{-1}) can be quite high. Although population growth is usually limited by several factors, the present study focuses on light limitation during bloom conditions, and nutrients are assumed to be non-limiting. However, once a phytoplankton bloom is beyond its peak, cells will have consumed the available nutrients, which in turn should become limiting, and population growth will sharply decrease (Boyd et al., 2004; Elser et al., 2007). As a consequence, real populations do not usually experience levels of abundance predicted by the model. Nonetheless, several empirical studies reported similar or even higher abundances (Agusti et al., 1987; Miyazono et al., 1992).

4.2. Size-mediated relationship between depth and persistence

The model predicts that a critical depth is observed only at high turbulence for small species, while it is observed at both low and high turbulence for large species. Considering first, small species at low turbulence, their population is close to the surface. Below the surface, light availability is very low and does not allow growth. Any loss by sinking can easily be compensated by new growth. This phenomenon is independent of water column depth. Therefore, there is almost no critical depth for small species at low turbulence. However, at high turbulence, the population diffuses through the whole column. Hence, the population cannot persist for depths above Sverdrup's critical depth. This is why a critical depth is observed only at high turbulence for small species.

Considering now large-bodied species, at low turbulence, individuals sink too fast compared to their growth rate (see above). In a shallow system, light availability is still high at the bottom, and, even if individuals sink fast, the population can thrive on the bottom. In this case, the maximal abundance is located at the bottom of the system, and even large species are able to persist in absence of turbulence. On the other hand, in a deep system, individuals sink into the dark zone before multiplying, and the population disappears. This is why a critical depth close to the compensation depth is observed at low turbulence. Considering now high turbulence, a Sverdrup's critical depth is observed for large as well as for smaller species. One can notice that the critical depth at high turbulence moves to deeper layers when body size increases, which is a consequence of the deeper light compensation depth of large-bodied species. Larger phytoplankton species are therefore expected to be able to grow in deeper systems than smaller species at high turbulence.

4.3. Importance of body size on phytoplankton community structure

A major insight from this study is that effects of turbulence vary depending on both turbulence strength and species body size. The interplay between sinking velocity, body size and turbulent diffusion is the corner stone of population persistence. In the present study, size is considered as a master trait for growth and sinking velocity, which provides a more realistic interplay between these two features of phytoplankton cells. The model assumes that species are denser than the surrounding medium, and therefore are prone to sinking. Hence, it appears that large-bodied species should not be able to thrive in calm water. Indeed, several species have specific adaptations that increase their buoyancy (e.g., gas vacuoles), which allows some larger species (such as *Microcystis*, *Anabaena*,

Aphanizomenon, *Trichodesmium* or buoyant diatoms) to be abundant in relatively calm waters, while our results show that they should not persist in such conditions. According to our model, on the one hand, large species would benefit more than small species from an increase of buoyancy, because it would increase their optimal range of turbulence, especially toward low turbulence values. On the other hand, in deep and highly turbulent systems, all species would benefit from evolving traits that decrease turbulent diffusion because it would allow them to escape Sverdrup's critical depth constraint.

Our model assumes zero-flux boundary conditions at the top and the bottom, an assumption that was used in several other studies (Huisman et al., 2002, 2004; Ryabov and Blasius, 2014). However, other studies have used different boundary conditions or incompletely mixed systems (Huisman et al., 1999b; Mellard et al., 2011). Our model represents relatively shallow systems during spring mixing conditions and is best suited to study phytoplankton spring blooms that occur under such conditions. Boundary conditions under which cells are allowed to leave the system at the bottom of a thermocline are less realistic for this type of situation, and the combination of having a thermocline in a deep system with high turbulence may lead to the disappearance of all species from the system (Huisman and Sommeijer, 2002a).

Similarly it is known that shear stress from water mixing is another factor that potentially affects phytoplankton cells and can cause cell destruction, cell collision or agglomeration (Hondzo and Lyn, 1999). Because it is very difficult to quantify this shear stress and to define a clear relationship between this effect and cell size, we followed other studies (Shigesada and Okubo, 1981; Huisman et al., 2002; O'Brien et al., 2003) and did not consider the effect of shear stress in our study.

All simulations were done using incident light intensity at 3.5×10^{-4} mol photons $m^{-2} s^{-1}$, which is assumed to be a saturating condition at the surface. Robustness of the results has been tested using higher and lower light intensity. On the one hand, for higher irradiance, all species show a deeper compensation depth. Therefore, phytoplankton species are able to thrive deeper, which displaces the upper threshold of turbulence towards stronger turbulence values, while the lower threshold of turbulence occurs at lower turbulence. Furthermore, critical depth occurs deeper at high turbulence for all species. On the other hand, for lower irradiance, all species show a shallower compensation depth, which leads to an upper threshold of turbulence occurring at lower turbulence values, a lower threshold of turbulence occurring at higher turbulence, and a shallower critical depth. Overall, any change in incident light intensity creates quantitative but not qualitative changes in the results.

The present study provides new insight on phytoplankton bloom conditions. However, after the bloom period, other limiting factors (such as nutrients) will play an important role. Usually, nutrients are more abundant at the bottom of the system, while light is more available at the surface. Therefore, species requirement and uptake for nutrients and light create a trade-off that can lead to coexistence for some range of conditions (Huisman and Weissing, 1995; Diehl, 2002; Yoshiyama et al., 2009). The population should be located close to the surface if light is more limiting, and deeper if nutrients are more limiting (Klausmeier and Litchman, 2001). Moreover, turbulence can also play a role by mixing cells as well as nutrients, therefore having an influence on species total biomass (Dutkiewicz et al., 2009; Jäger et al., 2010). A few studies considered interplay between light, nutrient and mixing, and their results are consistent with real observations (Valenti et al., 2012, 2015; Denaro et al., 2013).

Nutrients might also play another role because in our model, the *per capita* population growth rate is supposed to be a decreasing function of body size, in accordance with a number of empirical

studies (Fenchel, 1974) and the metabolic theory of ecology (Brown et al., 2004). However, this pattern can be altered by nutrient availability. Small species might be limited by nutrient uptake, as it is assumed to be an increasing function of body size, while large species might be limited by nutrient conversion into biomass, as it is assumed to be a decreasing function of body size. Therefore, the optimum for this trade-off should occur at intermediate size, leading to a unimodal relationship between growth and body size (Marañón et al., 2013; Wirtz, 2013). This should have an effect on competition as species with an intermediate body size would be more productive than smaller species but deeper below the surface.

Nutrient limitation would also affect competition among phytoplankton species after the bloom period. Our model considers only one resource (light). According to the resource-ratio theory (Grover, 1997) as well as to niche theory (Chase and Leibold, 2003), competition between two species for only one resource should lead to the exclusion of the weaker competitor. Spatial segregation can sometimes allow species coexistence. In our model, a spatial segregation might transiently occur since a large-bodied species is able to thrive below the surface, and a smaller one thrives at the surface. However, as light comes from the surface, it means that the largest species tries to thrive in its competitor's shade, which is not sustainable (Huisman et al., 1999b), unless nutrient limitation is included and traded off against light limitation.

Although a large number of studies considered the effect of nutrient limitation on phytoplankton competition (e.g., Ryabov and Blasius, 2011, 2014; Kerimoglu et al., 2012), considering size as a master trait for light requirement, nutrient requirement, and sinking velocity over a wide range of body size remains challenging because species may have different trade-offs according to the nutrients considered (Litchman et al., 2007). Nonetheless, we think that inclusion of nutrient limitation should be the next step to undertake.

Last, it should be noticed that the relationship between size and turbulence is not totally understood. Previous studies (Huisman et al., 1999a, 2002; Klausmeier and Litchman, 2001; Mellard et al., 2011) considered (often implicitly) that the turbulent diffusion rate is the same for all species. Nonetheless, this assumption remains to be fully explored. Indeed, this might be a gross oversimplification given that the size and mass of phytoplankton species may differ by several orders of magnitude (e.g., a small cyanobacterium such as *Synechococcus* has a volume of $18 \mu m^3$, whereas a dinoflagellate such as *Ceratium hirundinella* has a volume of $44,000 \mu m^3$). Mainstream theory (Kemp and Mitsch, 1979; Landahl and Mollo-Christensen, 1992; Ross and Sharples, 2008; Delhez and Deleersnijder, 2010) argues that because of their small size, phytoplankton cells live below the Kolmogorov scale. Therefore, cells are embedded within eddies and move with them, all at the same rate. However, studies on particle motion tend to demonstrate that particles diffuse more below Kolmogorov scale as their size decreases (Friedlander, 2000). Experiments demonstrated that planktonic cells show different response to shear according to their size (Stocker and Stocker, 2006). Last, some physical studies revealed the existence of sub-Kolmogorov scale velocity fluctuations (Zeff et al., 2003; Schumacher, 2007). Hence, investigation of the relationship between size and turbulence should be an important step toward our understanding of phytoplankton community structure.

5. Conclusion

Our study provides new insights into the conditions allowing algal blooms. It highlights that big and small phytoplankton species experience very different physical constraints in light-limited environments, potentially resulting in very different contributions to primary production depending on habitat depth and turbulence

strength. In the future, the model may be extended to include nutrient limitation, which could allow the study of competition between phytoplankton and size-based food web dynamics.

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Appendix A. Absorption cross-section

The absorption cross-section a is calculated as the following (Finkel et al., 2004):

$$a = a^*cV_b \quad (\text{A.1})$$

where a^* is the absorption surface per unit of chlorophyll a , and c is the chlorophyll a content *per cell*. This quantity is size-dependent (Finkel, 2001; Baird and Suthers, 2007).

$$c = 0.03 V_b^{0.69} \quad (\text{A.2})$$

The absorption per unit of chlorophyll a includes the packaging effect, which also depends on body size (Morel and Bricaud, 1981)

$$a^* = \frac{3}{2} a_s^* \frac{Q_\rho}{\rho} \quad (\text{A.3})$$

where a_s^* is the in vitro (unpacked) absorption coefficient of chlorophyll a . Q_ρ and ρ are dimensionless numbers accounting for the packaging effect

$$Q_\rho = 1 + \frac{2e^{-\rho}}{\rho} + \frac{2e^\rho - 1}{\rho^2} \quad (\text{A.4})$$

$$\rho = a_s^*cd \quad (\text{A.5})$$

where d is body diameter.

Appendix B. Sinking velocity

Sinking velocity is determined by three forces: weight, Archimedes' force, and drag.

$$F = gM_b - V_b\rho_m g - \frac{1}{2}S_b v^2 \rho_m C_d \quad (\text{B.1})$$

where g is the acceleration of gravity, ρ_m is the medium density, v is speed, S_b is the body section surface, and C_d is the drag coefficient. The drag coefficient (C_d) is calculated according to an empirical rule (Turton and Levenspiel, 1986).

$$C_d = \left[0.352 + \left(0.124 + \frac{24}{Re} \right)^{0.5} \right]^2 \quad (\text{B.2})$$

where Re is the Reynolds number, which is calculated as the following:

$$Re = \frac{\rho_m v L_b}{\mu} \quad (\text{B.3})$$

where L_b is body length, and μ is the medium dynamic viscosity. Hence, considering Newton's second law, force divided by mass represents acceleration, which is the first derivative of speed by time.

$$\frac{dv}{dt} = g - \frac{V_b \rho_m g}{M_b} - \frac{1}{2} \frac{S_b v^2 \rho_m C_d}{M_b} \quad (\text{B.4})$$

The sinking velocity is assumed to be an equilibrium speed, when all the three forces compensate each other (i.e., acceleration is null). Due to the recursive relationship between speed and drag, the sinking velocity at steady state is calculated by numerical approximation using the bisection method.

References

- Agustí, S., Duarte, C.M., Kalf, J., 1987. Algal cell size and the maximum density and biomass of phytoplankton? *Limnol. Oceanogr.* 32 (4), 983–986.
- Almedeij, J., 2008. Drag coefficient of flow around a sphere: matching asymptotically the wide trend? *Powder Technol.* 186 (3), 218–223.
- Baird, M.E., Suthers, I.M., 2007. A size-resolved pelagic ecosystem model? *Ecol. Model.* 203 (3–4), 185–203.
- Behrenfeld, M.J., Boss, E.S., 2014. Resurrecting the ecological underpinnings of ocean plankton blooms. *Ann. Rev. Mar. Sci.* 6, 167L 194.
- Boyd, P.W., Law, C.S., Wong, C.S., Nojiri, Y., Tsuda, A., Levasseur, M., Takeda, S., Rivkin, R., Harrison, P.J., Strzepek, R., Gower, J., McKay, M., Abraham, E., Arychuk, M., Barwell-Clarke, J., Crawford, W., Crawford, D., Hale, M., Harada, K., Johnson, K., Kiyosawa, H., Kudo, I., Marchetti, A., Miller, W., Needoba, J., Nishioka, J., Ogawa, H., Page, J., Robert, M., Saito, H., Sastri, A., Sherry, N., Soutar, T., Sutherland, N., Taira, Y., Whitney, F., Wong, S.-K.E., Yoshimura, T., 2004. The decline and fate of an iron-induced subarctic phytoplankton bloom? *Nature* 428 (6982), 549–553.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology? *Ecology* 85 (7), 1771–1789.
- Chase, J., Leibold, M., 2003. *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press.
- Cullen, J.J., Lewis, M.R., Davis, C.O., Barber, R.T., 1992. Photosynthetic characteristics and estimated growth rates indicate grazing is the proximate control of primary production in the equatorial Pacific. *J. Geophys. Res.: Oceans* 97 (C1), 639–654.
- Daly, K.L., Smith Jr., W.O., 1993. Physical–biological interactions influencing marine plankton production. *Ann. Rev. Ecol. Syst.*, 555–585.
- Daniels, C.J., Poulton, A.J., Esposito, M., Paulsen, M.L., Bellerby, R., St John, M., Martin, A.P., 2015. Phytoplankton dynamics in contrasting early stage North Atlantic spring blooms: composition, succession, and potential drivers. *Biogeosciences* 12 (8), 2395–2409.
- Davey, M., Walsby, A., 1985. The form resistance of sinking algal chains? *Brit. Phycol. J.* 20 (3), 243–248.
- Delhez, E.J.M., Deleersnijder, E., 2010. Residence time and exposure time of sinking phytoplankton in the euphotic layer? *J. Theor. Biol.* 262 (3), 505–516.
- Denaro, G., Valenti, D., La Cognata, A., Spagnolo, B., Bonanno, A., Basilone, G., Mazzola, S., Zgozi, S., Aronica, S., Brunet, C., 2013. Spatio-temporal behaviour of the deep chlorophyll maximum in Mediterranean Sea: Development of a stochastic model for picophytoplankton dynamics. *Ecol. Complex.* 13, 21L 34.
- Denman, K., Gargett, A., 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean? *Limnol. Oceanogr.* 28 (5), 801–815.
- Denny, M., 1993. *Air and Water: The Biology and Physics of Life's Media*. Princeton University Press.
- Diehl, S., 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: theory. *Ecology* 83 (2), 386–398.
- Dutkiewicz, S., Follows, M., Bragg, J.G., 2009. Modeling the coupling of ocean ecology and biogeochemistry. *Global Biogeochem. Cycl.* 23 (4).
- Edwards, K.F., Thomas, M.K., Klausmeier, C.A., Litchman, E., 2015. Light and growth in marine phytoplankton: allometric, taxonomic, and environmental variation. *Limnol. Oceanogr.* 60 (2).
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10 (12), 1135–1142.
- Fenchel, T., 1974. Intrinsic rate of natural increase: the relationship with body size? *Oecologia* 14 (4), 317–326.
- Finkel, Z.V., 2001. Light absorption and size scaling of light-limited metabolism in marine diatoms? *Limnol. Oceanogr.* 46 (1), 86–94.
- Finkel, Z.V., Beardall, J., Flynn, K.J., Quigg, A., Rees, T.A.V., Raven, J.A., 2010. Phytoplankton in a changing world: cell size and elemental stoichiometry? *J. Plankton Res.* 32 (1), 119–137.
- Finkel, Z.V., Irwin, A.J., 2000. Modeling size-dependent photosynthesis: light absorption and the allometric rule? *J. Theor. Biol.* 204 (3), 361–369.
- Finkel, Z.V., Irwin, A.J., Schofield, O., 2004. Resource limitation alters the 3/4 size scaling of metabolic rates in phytoplankton. *Mar. Ecol. Prog. Ser.* 273, 269L 279.
- Fogg, G., 1991. The phytoplanktonic ways of life? *New Phytol.* 118 (2), 191–232.
- Friedlander, S.K., 2000. *Smoke, Dust, and Haze*, vol. 198. Oxford University Press, New York.
- Grover, J., 1997. *Resource Competition*. Chapman and Hall, New York.
- Hondzo, M., Lynn, D., 1999. Quantified small-scale turbulence inhibits the growth of a green alga? *Freshw. Biol.* 41 (1), 51–61.
- Hondzo, M., Wüest, A., 2008. Do microscopic organisms feel turbulent flows? *Environ. Sci. Technol.* 43 (3), 764–768.
- Huisman, J., Arrayas, M., Ebert, U., Sommeijer, B., 2002. How do sinking phytoplankton species manage to persist? *Am. Nat.* 159 (3), 245–254.
- Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M., Sommeijer, B., 2004. Changes in turbulent mixing shift competition for light between phytoplankton species? *Ecology* 85 (11), 2960–2970.

- Huisman, J., Sommeijer, B., 2002a. Maximal sustainable sinking velocity of phytoplankton. *Mar. Ecol. Prog. ser.* 244, 39–48.
- Huisman, J., Sommeijer, B., 2002b. Population dynamics of sinking phytoplankton in light-limited environments: simulation techniques and critical parameters? *J. Sea Res.* 48 (2), 83–96.
- Huisman, J., van Oostveen, P., Weissing, F.J., 1999a. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms? *Limnol. Oceanogr.* 44 (7), 1781–1787.
- Huisman, J., van Oostveen, P., Weissing, F.J., 1999b. Species dynamics in phytoplankton blooms: incomplete mixing and competition for light? *Am. Nat.* 154 (1), 46–68.
- Huisman, J., Weissing, F.J., 1995. Competition for nutrients and light in a mixed water column: a theoretical analysis? *Am. Nat.* 146 (4), 536–564.
- Jäger, C.G., Diehl, S., Emans, M., 2010. Physical determinants of phytoplankton production, algal stoichiometry, and vertical nutrient fluxes. *Am. Nat.* 175 (4), E91–E104.
- Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems? *Nature* 460 (7254), 506–509.
- Kemp, W., Mitsch, W., 1979. Turbulence and phytoplankton diversity: a general model of the “paradox of plankton”? *Ecol. Model.* 7 (3), 201–222.
- Kerimoglu, O., Straile, D., Peeters, F., 2012. Role of phytoplankton cell size on the competition for nutrients and light in incompletely mixed systems. *J. Theor. Biol.* 300, 330L 343.
- Kjørboe, T., 1993. Turbulence, phytoplankton cell size, and the structure of pelagic food webs. *Adv. Mar. Biol.* 29 (1), 72.
- Kjørboe, T., 2008. *A Mechanistic Approach to Plankton Ecology*. Princeton University Press.
- Kirk, J., 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge, UK.
- Klausmeier, C.A., Litchman, E., 2001. Algal games: the vertical distribution of phytoplankton in poorly mixed water columns? *Limnol. Oceanogr.* 46 (8), 1998–2007.
- Lampert, W., Sommer, U., 1997. *Limnology. The Ecology of Lakes and Streams*. Oxford University Press, New York.
- Landahl, M.T., Mollo-Christensen, E., 1992. *Turbulence and Random Processes in Fluid Mechanics*. Cambridge University Press, Cambridge, UK.
- Lazier, J., Mann, K., 1989. Turbulence and the diffusive layers around small organisms? *Deep-Sea Res. A – Oceanogr. Res. Pap.* 36 (11), 1721–1733.
- Lewis, D.M., Pedley, T.J., 2000. Planktonic contact rates in homogeneous isotropic turbulence: theoretical predictions and kinematic simulations? *J. Theor. Biol.* 205 (3), 377–408.
- Lewis, D.M., Pedley, T.J., 2001. The influence of turbulence on plankton predation strategies? *J. Theor. Biol.* 210 (3), 347–365.
- Li, X.-y., Zhang, J.-j., Lee, J.H., 2004. Modelling particle size distribution dynamics in marine waters? *Water Res.* 38 (5), 1305–1317.
- Litchman, E., Klausmeier, C.A., Schofield, O.M., Falkowski, P.G., 2007. The role of functional traits and trade-offs in structuring phytoplankton communities: scaling from cellular to ecosystem level? *Ecol. Lett.* 10 (12), 1170–1181.
- MacIntyre, S., 1993. Vertical mixing in a shallow, eutrophic lake: possible consequences for the light climate of phytoplankton. *Limnol. Oceanogr.* 38 (4), 798–817.
- Marañón, E., Cermeño, P., López-Sandoval, D.C., Rodríguez-Ramos, T., Sobrino, C., Huete-Ortega, M., Blanco, J.M., Rodríguez, J., 2013. Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use? *Ecol. Lett.* 16 (3), 371–379.
- Margalef, R., 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment? *Oceanol. Acta* 1 (4), 493–509.
- McCoy, M.W., Gillooly, J.F., 2008. Predicting natural mortality rates of plants and animals? *Ecol. Lett.* 11 (7), 710–716.
- Mellard, J.P., Yoshiyama, K., Litchman, E., Klausmeier, C.A., 2011. The vertical distribution of phytoplankton in stratified water columns? *J. Theor. Biol.* 269 (1), 16–30.
- Menden-Deuer, S., Lessard, E.J., 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnol. Oceanogr.* 45 (3), 569–579.
- Metcalfe, A.M., Pedley, T., Thingstad, T., 2004. Incorporating turbulence into a plankton foodweb model? *J. Mar. Syst.* 49 (1), 105–122.
- Miyazono, A., Odate, T., Maita, Y., 1992. Seasonal fluctuations of cell density of cyanobacteria and other picophytoplankton in Iwanai Bay, Hokkaido, Japan. *J. Oceanogr.* 48 (3), 257–266.
- Moore, J.K., Villareal, T.A., 1996a. Buoyancy and growth characteristics of three positively buoyant marine diatoms? *Mar. Ecol. Prog. Ser.* 132 (1), 203–213.
- Moore, J.K., Villareal, T.A., 1996b. Size-ascent rate relationships in positively buoyant marine diatoms? *Limnol. Oceanogr.* 41 (7), 1514–1520.
- Morel, A., Bricaud, A., 1981. Theoretical results concerning light-absorption in a discrete medium, and application to specific absorption of phytoplankton. *Deep-Sea Res. A – Oceanogr. Res. Pap.* 28 (11), 1375–1393.
- Najafi, H.S., Hajinezhad, H., 2008. Solving one-dimensional advection-dispersion with reaction using some finite difference methods? *Appl. Math. Sci.* 2 (53), 2611–2618.
- O'Brien, K.R., Ivey, G.N., Hamilton, D.P., Waite, A.M., Visser, P.M., 2003. Simple mixing criteria for the growth of negatively buoyant phytoplankton? *Limnol. Oceanogr.* 48 (3), 1326–1337.
- Parsons, T.R., Takahashi, M., Hargrave, B., 1984. *Biological Oceanographic Processes*, (3rd ed.), Pergamon, Oxford.
- Pedros-Alí, C., Mas, J., Gasol, J.M., Guerrero, R., 1989. Sinking speeds of free-living phototrophic bacteria determined with covered and uncovered traps? *J. Plankton Res.* 11 (5), 887–905.
- Peters, R., 1986. *The Ecological Implications of Body Size*, vol. 2. Cambridge University Press, Cambridge, UK.
- Raven, J.A., 1984. A cost-benefit-analysis of photon-absorption by photosynthetic unicells? *New Phytol.* 98 (4), 593–625.
- Reynolds, C., 1990. Temporal scales of variability in pelagic environments and the response of phytoplankton? *Freshw. Biol.* 23 (1), 25–53.
- Reynolds, C.S., 2006. *The Ecology of Phytoplankton*. Cambridge University Press, Cambridge, UK.
- Riley, G.A., Stommel, H.M., Bumpus, D.F., 1949. *Quantitative Ecology of the Plankton of the Western North Atlantic*. Bingham Oceanographic Laboratory, New Haven, CT.
- Riper, D.M., Owens, T.G., Falkowski, P.G., 1979. Chlorophyll turnover in *Skeletonema costatum*, a marine plankton diatom. *Plant Physiol.* 64 (1), 49–54.
- Rodríguez, J., Tintoré, J., Allen, J.T., Blanco, J.M., Gomis, D., Reul, A., Ruiz, J., Rodríguez, V., Echevarría, F., Jimenez-Gómez, F., 2001. Mesoscale vertical motion and the size structure of phytoplankton in the ocean? *Nature* 410 (6826), 360–363.
- Ross, O.N., Sharples, J., 2008. Swimming for survival: a role of phytoplankton motility in a stratified turbulent environment? *J. Mar. Syst.* 70 (3–4), 248–262.
- Ruiz, J., Macías, D., Peters, F., 2004. Turbulence increases the average settling velocity of phytoplankton cells? *Proc. Natl. Acad. Sci. U. S. A.* 101 (51), 17720–17724.
- Ryabov, A.B., Blasius, B., 2011. A graphical theory of competition on spatial resource gradients? *Ecol. Lett.* 14 (3), 220–228.
- Ryabov, A.B., Blasius, B., 2014. Depth of the biomass maximum affects the rules of resource competition in a water column? *Am. Nat.* 184 (5), E132–E146.
- Sanders, R., Henson, S.A., Koski, M., De La Rocha, C.L., Painter, S.C., Poulton, A.J., Riley, J., Salihoğlu, B., Visser, A., Yool, A., Bellerby, R., Martin, A.P., 2014. The biological carbon pump in the North Atlantic. *Prog. Oceanogr.* 129, 200L 218.
- Schumacher, J., 2007. Sub-Kolmogorov-scale fluctuations in fluid turbulence. *Europhys. Lett.* 80 (5), 54001.
- Seuront, L., 2005. Hydrodynamic and tidal controls of small-scale phytoplankton patchiness. *Mar. Ecol. Prog. Ser.* 302, 93L 101.
- Shigesada, N., Okubo, A., 1981. Analysis of the self-shading effect on algal vertical-distribution in natural waters? *J. Math. Biol.* 12 (3), 311–326.
- Smayda, T.J., 1970. The suspension and sinking of phytoplankton in the sea. *Oceanogr. Mar. Biol. Ann. Rev.* 8, 353–414.
- Stocker, M., Stocker, R., 2006. Microorganisms in vortices: a microfluidic setup. *Limnol. Oceanogr.*: Methods 4, 392L 398.
- Sverdrup, H., 1953. On conditions for the vernal blooming of phytoplankton? *Journal du Conseil Permanent International pour l'Exploration de la Mer* 18 (3), 287–295.
- Townsend, D.W., Cammen, L.M., Holligan, P.M., Campbell, D.E., Pettigrew, N.R., 1994. Causes and consequences of variability in the timing of spring phytoplankton blooms? *Deep Sea Res. I: Oceanogr. Res. Pap.* 41 (5–6), 747–765.
- Turton, R., Levenspiel, O., 1986. A short note on the drag correlation for spheres? *Powder Technol.* 47 (1), 83–86.
- Valenti, D., Denaro, G., La Cognata, A., Spagnolo, B., Bonanno, A., Basilone, G., Mazzola, S., Zgozi, S., Aronica, S., 2012. Picophytoplankton dynamics in noisy marine environment? *Acta Phys. Pol.-Ser. B Element. Part. Phys.* 43 (5), 1227–1240.
- Valenti, D., Denaro, G., Spagnolo, B., Conversano, F., Brunet, C., 2015. How diffusivity, thermocline and incident light intensity modulate the dynamics of deep chlorophyll maximum in tyrhenian sea. *PLOS ONE* 10 (1), e0115468.
- Villareal, T.A., 1992. Buoyancy properties of the giant diatom *Ethmodiscus*? *J. Plankton Res.* 14 (3), 459–463.
- Waite, A.M., 1992. *Physiological control of diatom sedimentation*. University of British Columbia (Ph.D. thesis).
- Waite, A.M., Thompson, P.A., Harrison, P.J., 1992. Does energy control the sinking rates of marine diatoms? *Limnol. Oceanogr.* 37 (3), 468–477.
- Walsby, A.E., 1994. Gas vesicles? *Microbiol. Rev.* 58 (1), 94–144.
- Ward, B.A., Waniek, J.J., 2007. Phytoplankton growth conditions during autumn and winter in the Irminger Sea, North Atlantic. *Mar. Ecol. Prog. Ser.* 334, 47L 61.
- Watson, A.J., Robinson, C., Robinson, J.E., le, B., Williams, P.J., Fasham, M.J.R., 1991. Spatial variability in the sink for atmospheric carbon dioxide in the North Atlantic? *Nature* 350 (6313), 50–53.
- Wirtz, K.W., 2013. Mechanistic origins of variability in phytoplankton dynamics: Part I: Niche formation revealed by a size-based model? *Mar. Biol.* 160 (9), 2319–2335.
- Worrest, R.C., Dyke, H.V., Thomson, B.E., 1978. Impact of enhanced simulated solar ultraviolet radiation upon a marine community? *Photochem. Photobiol.* 27 (4), 471–478.
- Yoshiyama, K., Mellard, J.P., Litchman, E., Klausmeier, C.A., 2009. Phytoplankton competition for nutrients and light in a stratified water column? *Am. Nat.* 174 (2), 190–203.
- Zeff, B.W., Lanterman, D.D., McAllister, R., Roy, R., Kostelich, E.J., Lathrop, D.P., 2003. Measuring intense rotation and dissipation in turbulent flows? *Nature* 421 (6919), 146–149.
- Zhang, L., Thygesen, U.H., Banerjee, M., 2014. Size-dependent diffusion promotes the emergence of spatiotemporal patterns. *Phys. Rev. E* 90 (1), 012904.