Can we predict phytoplankton community size structure using size scalings of eco-physiological traits?

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ABSTRACT

Cell size is an important determining factor for predicting the physiological and ecological properties of phytoplankton. Size dependencies in eco-physiological properties are in general reported as log–log linear scaling relationships. Considerable uncertainty in these allometries, hence, limits our ability to link them to observed changes in phytoplankton community structures. In this study, we develop a size-based multi-species phytoplankton model and assess the sensitivity of the predicted community size structure to variations in allometric coefficients. The model describes the nutrient–phytoplankton–detritus dynamics within the upper mixed layer for a matrix of habitats, which are characterized by the deep layer nutrient concentration and mixing frequency. Predicted diatom community mean cell size becomes maximal at intermediate mixing frequencies, which confirms the importance of storage capacity (relative to the subsistence demand) at intermittent nutrient supplies. Smaller subsistence demand of large diatoms makes a critical factor in shaping the community size structure, while in environments with either short or long nutrient replenishment periods, maximum growth rate gains similar or more importance. Notably, in these environments, the diatom community converges towards unrealistically small species when we assumed a uniform (log–log linear) allometry in maximum growth rate. Independent theoretical and empirical arguments motivated the usage of non-uniform growth scaling, with which the minimal diatom cell size actually observed in nature is realized in long-term simulations. Using allometries parameterized for the entire phytoplankton community, the subsistence advantage of the larger species becomes insignificant, leading to a ubiquitous dominance of smaller species, even when assuming non-uniform scaling in maximum growth rate. This finding corresponds with the observed dominance of pico-phytoplankton in many parts of the ocean. All combinations of physiological allometries for diatom or mixed communities, however, underestimate both the mean cell size of the community and also size diversity. This may indicate a significant role of other ecological selection mechanisms, such as arising from size-selective grazing. The approach outlined in this paper helps to better assess the limits and the potential of size based phytoplankton models as an increasingly important tool in plankton research.

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1. Introduction

Unicellular photosynthetic organisms in the ocean are responsible for roughly half of the primary production on Earth (Field et al., 1998), therefore, making a prominent subject of environmental research. Phytoplankton communities display high diversity with regard to the size of individual organisms, with cell volumes spanning more than nine orders of magnitude, from smallest cyanobacteria ($\sim$0.1 μm^3) to the largest diatoms (>10^8 μm^3) (Finkel et al., 2010). Phytoplankton cell size influences a large number of physiological traits as reviewed below and therefore plays a key role in ecological functioning and biogeochemical cycling of major elements such as carbon, nitrogen and phosphorous in aquatic ecosystems (Guidi et al., 2009).

Given the importance of phytoplankton community structure in functioning of marine ecosystems, a better understanding of the factors controlling the structure of those communities is needed. Whereas earlier work on phytoplankton resource competition focused on individual species or phytoplankton types, trait-based representations of phytoplankton communities are becoming increasingly popular (Follows et al., 2011). Empirical studies suggest that the competitive abilities of species are constrained by various trade-offs (Litchman et al., 2007; Edwards et al., 2012). A significant portion of such relationships between traits are

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predicted by the phytoplankton cell size as a 'master trait' (Finkel et al., 2010; Litchman et al., 2010; Marañòn, 2015), as it has a very large influence on the individual eco-physiological traits. For major physiological traits such as maximum growth rate (μ_{max}), maximum uptake rate (v_{max}), nutrient uptake affinity (A), and minimum and maximum intracellular nutrient quotas (Q_{min}, Q_{max}), power law functions of cell volume had been fitted based on collected data (e.g., Litchman et al., 2007; Edwards et al., 2012):

$$y = \beta V^{\alpha} \tag{1}$$

where y represents the physiological trait, V phytoplankton cell volume (μm^3), β the intercept (minimum or maximum value for the smallest cell size) and α the scaling exponent describing the size dependency of the trait. Using cell size for predicting eco-physiological traits in ecosystem models (e.g., Ward et al., 2012; Wirtz, 2013; Terseleer et al., 2014; Acevedo-Trejos et al., 2015) helps reducing the parameterization complexity considerably. However, high uncertainties exist regarding the quantitative, and in some cases, qualitative form of these allometric relationships. For example, major uncertainties exist related to size scaling of maximum growth rate (μ_{max}). For μ_{max} reported size scaling exponents range from; -0.32 (Schlesinger et al., 1981), -0.25 (Edwards et al., 2012) similar to a specific metabolic rate (Brown et al., 2004), -0.13 for diatoms (Sarthou et al., 2005), -0.17 for dinoflagellates (Banse, 1982), -0.08 for Antarctic phytoplankton (Sommer, 1989) to small values such as -0.06 for all marine phytoplankton (Finkel et al., 2010). In contrast to these fitted linear relationships between μ_{max} and cell size, theoretical work by Wirtz (2011), in agreement with the data compilation by Finkel et al. (2010), proposed a unimodal function of μ_{max} over cell size. Also, the recent experimental work of Marañòn et al. (2013) supports a unimodal, thus non-uniform allometry, with size scaling exponent of 0.19 for species with cell volume less than 300 μm^3 and -0.15 for the ones with cell volume larger than 40 μm^3.

Until now, no modeling study has performed a systematic investigation of the impact of uncertainties in allometric relationships on the prediction of the community composition and dynamics. It is also unclear to what extent physiological aspects can explain the observed size structure; or when other (ecological) aspects become major determinants. The purpose of the model study presented here is, first, to investigate the influence of various μ_{max} size scalings (linear/non-linear) on the predicted community size structure in typical environments characterized by different nutrient availability and disturbance frequencies. Second, we extend our analysis to assess the importance of size scalings in other physiological traits (v_{max}, A, Q_{min} and Q_{max}) for phytoplankton community dynamics. This sensitivity study should from a methodological point of view reveal the importance of each size scaling relationship for assembling size-based ecosystem models.

To address these objectives, we describe a size-based multi-species model where to each species a cell size is assigned, which in turn determines the resource competition abilities of each species according to various allometric relationships regarding the diatoms only and the entire community of unicellular autotrophs. We then systematically assess the relative importance of size scaling of each eco-physiological trait under consideration.

2. Model

2.1. Model description

Our model describes phytoplankton community dynamics within a 0-dimensional box representing the surface layer of marine system. The model resolves the interactions between nutrient (Nut), detritus (Det), and multiple phytoplankton species (Phy$_i$)
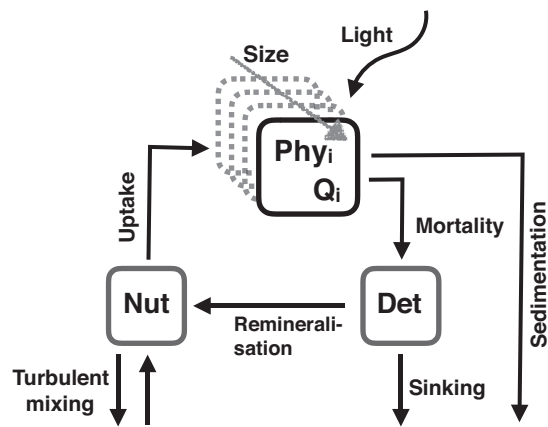

Fig. 1. Schematic representation of the size-based multi-species model for the surface ocean, which resolves: phytoplankton (Phy), intracellular nutrient quota (Q), nutrient (Nut) and detritus (Det).

Table 1
Model equations and major functions. Parameters are described in Tables 2 and 3.

1. $\frac{dPhy_i}{dt} = \mu_i(Q_i, \bar{I})Phy_i - (m + D)Phy_i$

2. $\frac{dQ_i}{dt} = V_i(Nut, Q_i) - \mu_i(Q_i, \bar{I})Q_i$

3. $\frac{dNut}{dt} = D(Nut_{in} - Nut) + \phi Det - \sum_{i=1}^{n} V_i(Nut, Q_i)Phy_i$

4. $\frac{dDet}{dt} = \sum_{i=1}^{n} mPhy_i Q_i - (\phi + D + \frac{v_{Det}}{z})Det$

5. Growth : $\mu_i(Q_i, \bar{I}) = (\frac{\mu_{max,i} Q_{max,i}}{Q_{max,i} - Q_{min,i}})(1 - \frac{Q_{min,i}}{Q_i})(\frac{\bar{I}}{K_I + \bar{I}})$

6. Average light intensity : $\bar{I}(z) = \frac{1}{z}\int_0^z I_0 e^{-kz'} dz' = \frac{I_0}{kz}(1 - e^{-kz})$, $k = \kappa + \epsilon \sum_{i=1}^{n}(Phy_i Q_i)$

7. Nutrient uptake : $V_i(Nut, Q_i) = (\frac{v_{max,i} Nut A_i}{v_{max,i} + Nut A_i})(\frac{Q_{max,i} - Q_i}{Q_{max,i} - Q_{min,i}})$

Table 2
Model variables and allometric parameters.

Symbol	Value	Unit	Description
State variables			
Phy$_i$		mmol-C m^{-3}	Phytoplankton biomass
Q_i		mol-N mol-C^{-1}	Intracellular nutrient quota
Nut		mmol-N m^{-3}	Nutrient concentration
Det		mmol-N m^{-3}	Detritus concentration
Physiological parameters[a]			
μ_{max}	Allom. scaled	d^{-1}	Maximum growth rate
Q_{min}	Allom. scaled	mol-N mol-C^{-1}	Minimum internal cell quota
Q_{max}	Allom. scaled	mol-N mol-C^{-1}	Maximum internal cell quota
v_{max}	Allom. scaled	mol-N (mol-C d)$^{-1}$	Maximum nutrient uptake rate
A	Allom. scaled	m^3 (mmol-C d)$^{-1}$	Nutrient affinity
Q_c	Allom. scaled	pgC cell^{-1}	Cell carbon content

[a] see Table 4.

and the variability of the internal nutrient store of each phytoplankton species (Q_i) (Eqs. (1)–(4)) (Fig. 1 and Table 1). The model box is assumed to be perturbed at certain frequencies to describe the loss of phytoplankton form, and incorporation of the nutrient-rich deep water to the surface layer during mixing events (e.g., Gargett, 1991). The mixing frequencies and the nutrient concentration at the bottom layer (Nut$_{in}$) were considered here as environmental sensitivity parameters.

Phytoplankton is further subdivided into n species, according to a standard approach of modeling intra-compartment changes (Rose et al., 1988; Ebenhoeh, 1992; Kohyama, 1992). To each phytoplankton (Phy$_i$ with $i = 1, \ldots, n$) a certain cell size is assigned, which in turn determines the parameters for growth and nutrient uptake kinetics following allometric relationships (see Tables 2 and 4).