



# Influence of light in the mixed-layer on the parameters of a three-component model of phytoplankton size class



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## ABSTRACT

Phytoplankton size structure is an important indicator of the state of the pelagic ecosystem. Stimulated by the paucity of *in situ* observations on size structure, and by the sampling advantages of autonomous remote platforms, new efforts are being made to infer the size-structure of the phytoplankton from oceanographic variables that may be measured at high temporal and spatial resolution, such as total chlorophyll concentration. Large-scale analysis of *in situ* data has revealed coherent relationships between size-fractionated chlorophyll and total chlorophyll that can be quantified using the three-component model of Brewin et al. (2010). However, there are variations surrounding these general relationships. In this paper, we first revise the three-component model using a global dataset of surface phytoplankton pigment measurements. Then, using estimates of the average irradiance in the mixed-layer, we investigate the influence of ambient light on the parameters of the three-component model. We observe significant relationships between model parameters and the average irradiance in the mixed-layer, consistent with ecological knowledge. These relationships are incorporated explicitly into the three-component model to illustrate variations in the relationship between size-structure and total chlorophyll, ensuing from variations in light availability. The new model may be used as a tool to investigate modifications in size-structure in the context of a changing climate.

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## 1. Introduction

Phytoplankton cell size influences many processes in marine biogeochemistry and marine ecology (Chisholm, 1992; Finkel et al., 2010; Marañón, 2009). Photosynthesis by phytoplankton, the primary source of energy for marine plants and animals, is dependent upon the absorption of available light and the uptake of available nutrients, both of which vary according to the size of the phytoplankton (Chisholm, 1992; Ciotti, Lewis, & Cullen, 2002; Devred et al., 2006; Morel & Bricaud, 1981; Prieur & Sathyendranath, 1981; Probyn, 1985; Raven, 1998). Cell size influences physiology, growth and metabolic rates in marine phytoplankton (Geider, Platt, & Raven, 1986; Platt & Denman, 1976, 1977, 1978; Sunda & Huntsman, 1997), the export of carbon to the deep-ocean (Briggs et al., 2011; Guidi et al., 2009; Laws, Falkowski, Smith Jr., Ducklow, & McCarth, 2000), and the structure of the marine food chain (Legendre & Le Fèvre, 1991; Moloney & Field, 1991). For these reasons,

many marine biogeochemistry models use a size-based partitioning for phytoplankton (Aumont, Maier-Reimer, Blain, & Monfray, 2003; Blackford, Allen, & Gilbert, 2004; Kishi et al., 2007; Marinov, Doney, & Lima, 2010; Ward, Dutkiewicz, Jahn, & Follows, 2012).

Observations on phytoplankton size, well resolved in time and space, are required to address key questions pertaining to our understanding of marine biogeochemistry and marine ecology, and how they are likely to be influenced by climate variability (Brewin et al., 2012; Finkel et al., 2010; Kostadinov, Siegel, & Maritorea, 2010; Siegel et al., 2014). These observations may be used directly or indirectly to address such questions, through the validation of, or assimilation into, size-based marine biogeochemistry models (Hirata et al., 2013; Holt et al., 2014; Ward et al., 2012; Xiao & Friedrichs, 2014). A common method to infer phytoplankton size structure *in situ* is through measurements of phytoplankton biomass (typically indexed through the chlorophyll concentration, the principal photosynthetic pigment in phytoplankton), partitioned into key size classes (Sheldon, 1972; Sieburth, Smetacek, & Lenz, 1978; Uitz, Claustre, Morel, & Hooker, 2006). However, demand for observations on phytoplankton size is not met by the sparse *in situ* data currently available. To address issues of data availability, renewed

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efforts are being made to relate the size-structure of the phytoplankton to other oceanographic properties that can be measured at high temporal and spatial resolution.

Large-scale analysis of *in situ* data has revealed coherent patterns describing how the fractional contribution of different size classes to total chlorophyll varies with total chlorophyll concentration (Brewin, Sathyendranath, Tilstone, Lange, & Platt, 2014; Brewin et al., 2010; Hirata et al., 2011; IOCCG, 2014; Marañón, Cermeño, Latasa, & Tadonlélé, 2012; Uitz et al., 2006). Once quantified, these relationships may be applied to total chlorophyll concentration measured at a high temporal or spatial resolution (using *in situ* or remote-sensing methods). Using a large database of High Performance Liquid Chromatography (HPLC) measurements, Uitz et al. (2006) associated the proportions three commonly-used size classes (micro- [ $>20 \mu\text{m}$  in diameter], nano- [ $2\text{--}20 \mu\text{m}$  in diameter] and picoplankton [ $<2 \mu\text{m}$  in diameter]), determined using biomarker pigments (Vidussi, Claustre, Manca, Luchetta, & Marty, 2001), to class intervals in chlorophyll concentration, for samples partitioned into those from stratified and those from mixed waters. Based on the work of Sathyendranath et al. (2001), Brewin et al. (2010) developed a model describing how the proportions of phytoplankton size-classes change with chlorophyll concentration in the Atlantic Ocean. Hirata et al. (2011) used a suite of empirical functions to describe how the fractional contributions of the three phytoplankton size classes to total chlorophyll (also derived from HPLC data) varies with the total chlorophyll.

Despite the emergence of coherent patterns on the dependence of size structure on total chlorophyll concentration, there still remain large variations surrounding these general relationships (Brewin et al., 2010; Mouw & Yoder, 2010; Uitz et al., 2006). To improve models that describe these patterns, research must focus on quantifying and accounting for the unexplained portion of variability. For example, changes in the contribution of phytoplankton communities to total chlorophyll have been observed with changes in optical depth (Brewin et al., 2010; Brotas et al., 2013) and other easily accessible environmental variables, such as sea-surface temperature and wind stress (Devred, Sathyendranath, & Platt, 2009; Palacz, St. John, Brewin, Hirata, & Gregg, 2013; Raitos et al., 2008). One such environmental variable likely to influence size structure is the availability of light, a key environmental resource for phytoplankton and a property that may be monitored at high temporal or spatial resolution. The acclimation of phytoplankton to various ambient light conditions, through changes in photosynthetic pigmentation (Brunet et al., 2013; MacIntyre, Kana, Anning, & Geider, 2002), may vary among taxonomic communities.

In this paper, we revise the three-component model of Brewin et al. (2010) using a large dataset of surface HPLC measurements collected throughout the global ocean and compare retrieved model parameters with those from previous studies. Using co-located estimates of surface photosynthetically-active radiation (PAR), mixed-layer depth and diffuse attenuation, we estimate the average irradiance in the mixed-layer for each sample in the dataset. We then investigate the influence of light in the mixed-layer on the parameters of the three-component model, with the goal of improving our understanding of the relationship between size-structure and total chlorophyll under varying environmental conditions.

## 2. Data and methods

### 2.1. Statistical tests

To compare the *in situ* and modelled chlorophyll concentrations, we used the Pearson linear correlation coefficient ( $r$ ) and the root mean square error ( $\Psi$ ). The value of  $\Psi$  was computed according to

$$\Psi = \left[ \frac{1}{N} \sum_{i=1}^N (X_i^E - X_i^M)^2 \right]^{1/2}, \quad (1)$$

where  $X$  is the variable (chlorophyll concentration) and  $N$  is the number of samples. The superscript  $E$  denotes the estimated variable from the model and  $M$  the measured variable. All statistical tests were performed in  $\log_{10}$  space, considering that the chlorophyll concentration is approximately log-normally distributed over the global ocean (Campbell, 1995).

### 2.2. Global High Performance Liquid Chromatography (HPLC) dataset

Some 5841 HPLC samples collected in the global ocean were used in this study (Fig. 1). Only samples collected within the top 10 m of the water column (or within the 1st optical depth as in the case of the NASA NOMAD dataset) were used, so as to ensure the data are representative of the first penetration depth of the ocean colour satellite signal, and that the data were within the surface mixed-layer depth (rarely  $<10 \text{ m}$ ; de Boyer Montégut, Madec, Fischer, Lazar, & Iudicone, 2004). Only HPLC data for which the total chlorophyll concentration was greater than  $0.001 \text{ mg m}^{-3}$  (Uitz et al., 2006), and the difference between the total chlorophyll concentration and the total accessory pigments was less than 30% of the total pigment concentration (Aiken et al., 2009), were used. These strictures were designed to control the quality of the pigment data, by removing data with unrealistically low chlorophyll concentrations and data in which chlorophyll and the sum of the concentrations of the major accessory pigments did not covary in a predictable manner (Trees, Clark, Bidigare, Ondrusek, & Mueller, 2000). Only samples with corresponding estimates of the average irradiance in the mixed-layer ( $E$ ) were used (see Section 2.4 for computation of  $E$ ). ETOPO2v2c 2-minute gridded global relief data were downloaded from the NOAA National Geophysical Data Centre (<http://www.ngdc.noaa.gov/mgg/fliers/01mgg04.html>) to estimate the bathymetric depth at the location of each sample, using a simple spatial (latitude and longitude) match-up procedure. Samples in waters with a bathymetric depth  $<30 \text{ m}$  were not included in the analysis. The majority of remaining samples ( $\sim 91\%$ ) were located in waters with a bathymetric depth  $>200 \text{ m}$ , with the remaining measurements ( $\sim 9\%$ ) located on the continental shelf. The geographical distribution and the sources of the 5841 HPLC samples used in this study are provided in Fig. 1. These samples include data collected between 1992 and 2012 and contain data collected during each calendar month.

Samples were also matched to daily, level 3 (4 km sinusoidal projected) satellite chlorophyll data, from version 1.0 of the Ocean Colour Climate Change Initiative (OC-CCI, a merged MERIS, MODIS-Aqua and SeaWiFS product available at <http://www.oceancolour.org/>), between 1997 and 2012. Each *in situ* sample was matched in time (daily temporal match-up) and space (latitude and longitude) with the satellite data. Following standard methods (Bailey & Werdell, 2006) we used a multi-pixel box ( $3 \times 3$  pixel window), to increase the possibility of an *in situ* measurement being available for comparison with the OC-CCI data, and computed the coefficient of variation (median coefficient of variation for  $R_{rs}$  bands between 412 and 555 nm) for each box of nine pixels. The median chlorophyll concentration of the nine pixels was considered as the satellite estimate, and only match-ups with a coefficient of variation  $<0.15$ , and  $>50\%$  of the nine pixels, were included, to ensure homogeneity and good quality match-ups (Bailey & Werdell, 2006). Following this criteria, 598 satellite match-ups were available. The correlation coefficient ( $r$ ) and the root mean square error ( $\Psi$ ) between OC-CCI (reflectance-based estimates) and *in situ* chlorophyll ( $C$ ) was 0.88 and 0.25 respectively, comparable with other studies (Bailey & Werdell, 2006; Brewin et al., 2015; Werdell & Bailey, 2005).

### 2.3. Estimation of size structure from HPLC data

To estimate the fractions of chlorophyll in the three phytoplankton size classes ( $F_p$ ,  $F_n$  and  $F_m$ , for pico-, nano- and microplankton respectively), we used the method of Vidussi et al. (2001) and Uitz et al.

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