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Size-partitioned phytoplankton carbon and carbon-to-chlorophyll ratio from ocean colour by an absorption-based bio-optical algorithm

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ABSTRACT

The standing stock of phytoplankton carbon is a fundamental property of oceanic ecosystems, and of critical importance to the development of Earth System models for assessing global carbon pools and cycles. Some methods to estimate phytoplankton carbon at large scales from ocean colour data rely on the parameterisation of carbon-to-chlorophyll ratio, which is known to depend on factors such as the phytoplankton community structure, whereas other methods are based on the estimation of total particulate organic carbon (POC), and rely on the assumption that a known fraction of POC is made up of phytoplankton carbon. The carbon-to-chlorophyll ratio is also used in marine ecosystem models to convert between carbon and chlorophyll, a common requirement. In this paper we present a novel bio-optical algorithm to estimate the carbon-to-chlorophyll ratio, and the standing stocks of phytoplankton carbon partitioned into various size classes, from ocean colour. The approach combines empirical allometric relationships of phytoplankton size structure with an absorption-based algorithm for estimating phytoplankton size spectra developed earlier. Applying the new algorithm to satellite ocean colour data from September 1997 to December 2013, the spatio-temporal variations of carbon-to-chlorophyll ratio and phytoplankton carbon across various size classes are computed on a global scale. The average annual stock of phytoplankton carbon, integrated over the oceanic mixed-layer depth, is estimated to be ~0.26 gigatonnes, with the size-partitioned stocks of 0.14 gigatonnes for picoplankton, 0.08 gigatonnes for nanoplankton and 0.04 gigatonnes for microplankton. The root-mean-square error and the bias in the satellite-derived estimates of picoplankton carbon, when compared with corresponding *in situ* data, are found to be 36.23 mgC m^{-3} and −13.53 mgC m^{-3}, respectively, on individual pixels. The regional uncertainties in the estimates of phytoplankton carbon are calculated to be less than the relative uncertainties in other satellite-derived products, for most parts of the global ocean, and can amplify only for certain oceanographic regions. Although the new estimates of phytoplankton are of the same order of magnitude as those based on existing models, our study suggests that a consensus is yet to be built on the accurate sizes of the phytoplankton carbon pools; improved satellite chlorophyll products, and better estimates of inherent optical properties would be essential pre-requisites to minimising the uncertainties.

1. Introduction

Although the standing stock of the autotrophic biomass (phytoplankton) in the ocean is only a small fraction (less than 1%) of the Earth's photosynthetic biomass, approximately half (~50 gigatonnes C) of the global annual carbon-fixation is accounted for by the oceanic autotrophs through primary production (Falkowski, 2012; Field et al., 1998). Therefore, for understanding, estimating and monitoring the carbon dynamics in the ocean, it is important to be able to make accurate measurements of the standing stocks of phytoplankton carbon. However, major complexities in carbon estimation arise from phytoplankton community composition; for example, the carbon content of a phytoplankton cell varies with species and its morphological characteristics (*e.g.*, large *vs* small cell size); it also depends on the ambient light and nutrient conditions (Marañón, 2008; Marañón et al., 2013; Menden-Deuer and Lessard, 2000). Another level of complexity in estimating phytoplankton carbon accurately arises from uncertainties in parameterising the carbon-to-chlorophyll ratio (χ), which is used to convert phytoplankton-carbon biomass to chlorophyll biomass in ecosystem models for comparison with satellite-derived chlorophyll data, and also in

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satellite algorithms for estimating phytoplankton carbon from chlorophyll data (Sathyendranath et al., 2009). A standard product from ocean colour remote sensing is chlorophyll concentration (*e.g.*, http://oceandata.sci.gsfc.nasa.gov/; https://www.oceancolour.org/). Marine biogeochemical and ecosystem models (*e.g.*, http://pft.ees.hokudai.ac.jp/maremip/index.shtml), on the other hand, deal with phytoplankton biomass in carbon units and use a carbon-to-chlorophyll ratio. The magnitude of carbon-to-chlorophyll ratio can vary over two orders of magnitude depending on phytoplankton community composition and environmental conditions (Geider, 1987; Geider et al., 1998; Sathyendranath et al., 2009), and hence it may lead to significant uncertainties in the conversions between the two measures. Furthermore, the retrieval of phytoplankton carbon from remote sensing of ocean colour is also affected by the presence of particulates, other than phytoplankton that contribute to the water-leaving radiance captured by the sensors. Dissolved constituents such as coloured dissolved organic materials (CDOM) that absorbs strongly in the blue wavelengths can also affect the remotely-sensed ocean colour and interfere with chlorophyll-*a* retrievals, particularly in coastal and high latitudes. Owing to these complexities, the estimation of phytoplankton carbon from remote sensing is recognised as a non-trivial task, and it is essential to improve satellite-based algorithms for use in carbon-cycle research (Behrenfeld et al., 2005; Kostadinov et al., 2016; Sathyendranath et al., 2009).

Nevertheless, algorithms have been developed to compute particulate organic carbon (POC) in the ocean from remotely-sensed ocean colour. For example, Stramski et al. (2008) derived a band-ratio algorithm that uses the blue-to-green band ratio of remote-sensing reflectance to calculate the concentration of POC. This algorithm can then be used to compute phytoplankton carbon by assuming a constant ratio of phytoplankton carbon to POC in the ocean (Stramski et al., 2008). Behrenfeld et al. (2005) derived an empirical relationship to compute phytoplankton carbon from particulate backscattering coefficients by assuming a fixed ratio of 30% between phytoplankton carbon and POC. More recently, Kostadinov et al. (2016) developed an algorithm to compute phytoplankton carbon from particulate backscattering coefficient using allometric relationships for the POC particle size distribution and assuming that the fraction of carbon in the living phytoplankton relative to that of POC is 1/3. Kostadinov et al. (2016) also computed the absolute and the fractional carbon biomass in three size classes of phytoplankton, *i.e.*, picoplankton (with diameter 0.5 –2 μm), nanoplankton (with diameter 2–20 μm) and microplankton (with diameter 20–50 μm), under these assumptions. Although the existing algorithms may provide a mutually comparable estimate (in order of magnitude) of total phytoplankton carbon in the global ocean, the underlying assumption of a constant ratio of phytoplankton carbon and POC imposes significant uncertainties in regional estimates of phytoplankton carbon and its spatial distributions. This is important because the ratio of phytoplankton carbon to POC varies over a wide range, from 14% to 85%, across a variety of oceanographic regions (Behrenfeld et al., 2005; DuRand et al., 2001; Eppley et al., 1992; Gundersen et al., 2001; Kostadinov et al., 2016; Oubelkheir et al., 2005; Redalje and Laws, 1981; Stramski et al., 2008). Furthermore, with the exception of Kostadinov et al. (2016), current algorithms are limited in their ability to retrieve the carbon-based classification of phytoplankton functional types (PFT) or phytoplankton size classes (PSC), though many methods are available to estimate the fractional chlorophyll distribution across PFTs and PSCs (*e.g.*, IOCCG, 2014). Given the importance and wide applications of satellite-based PFTs, it is important to improve our understanding on phytoplankton carbon stocks in various PSCs and PFTs, through developing new algorithms based on complementary bio-optical variables.

In this paper, we present a new bio-optical algorithm to estimate phytoplankton carbon from remotely-sensed ocean colour data, designed by targeting the photosynthetic phytoplankton cells directly. The algorithm builds on Roy et al. (2013), where we developed a semi-analytical method to compute the exponent of the phytoplankton size spectrum from the specific-absorption coefficient of phytoplankton (which depends on chlorophyll concentration and total absorption by phytoplankton), and derived the equivalent spherical diameter of phytoplankton cells and the fractions of chlorophyll in any size class of phytoplankton, in particular, those for picoplankton, nanoplankton and microplankton. Here, the method is extended for computing carbon-to-chlorophyll ratio from ocean colour applicable to any size class of phytoplankton, by combining analytically the allometric relationships between phytoplankton cell size and carbon content with the size-spectrum algorithm of Roy et al. (2011, 2013), and implementing them to estimate phytoplankton carbon in any size class. The method is applied to ocean colour data for the period 1997–2013, and is validated using the available *in situ* data. Results are discussed in relation to the applicability of this method to obtain independent remote-sensing-based measurements of phytoplankton carbon, and the carbon budget, according to phytoplankton size. The results pave the way to improved implementation of carbon-based growth models using satellite data for computation of primary production in various PSCs.

2. Data

We used a continuous time series of ocean colour data on global scale produced by the European Space Agency's Ocean Colour Climate Change Initiative (OC-CCI) project (http://www.esa-oceancolour-cci.org) through systematically merging the available satellite data from three major sensors: NASA-SeaWiFS, NASA-MODIS-Aqua and ESA-MERIS. For temporal consistency of OC-CCI products, and for algorithms selected for processing them, please see Belo Couto et al. (2016), Brewin et al. (2015), Müller et al. (2015). We used the global 4-km, level-3 mapped products from OC-CCI, the details of which can be found in http://www.esa-oceancolour-cci.org (also in, Sathyendranath et al., unpublished manuscript). Further, to validate the new algorithm we used a global dataset on pico-phytoplankton carbon compiled by Buitenhuis et al. (2012) that included flow cytometry data obtained since the late 1980s during cruises throughout most of the world ocean, as a contribution to the MAREDAT World Ocean Atlas of Plankton Functional Types database. The details of the database can be found in Buitenhuis et al. (2012) and in http://doi.pangaea.de/10.1594/PANGAEA. We extracted a subset of this database to cover the time period from September 1997 to December 2013, over which the satellite-based ocean colour data were available. We further obtained mixed-layer depths from Monthly Isopycnal & Mixed-layer Ocean Climatology (MIMOC, Schmidtko et al., 2013, http://www.pmel.noaa.gov/mimoc/), and remapped those to OC-CCI 4-km grids using nearest-neighbour interpolation (using MATLAB2015b interpolation routine).

3. Development of the bio-optical algorithm

3.1. Exponent of phytoplankton size spectra (ξ) from their absorption coefficients $a_{ph}(\lambda)$ following Roy et al. (2013)

The exponent of the phytoplankton size spectrum (ξ) can be computed from the absorption coefficient of phytoplankton at 676 nm, $a_{ph}(676)$, using a method developed by Roy et al. (2013). For the completeness of the methodology of this paper, we briefly describe below the