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Remote sensing of assimilation number for marine phytoplankton

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ABSTRACT

Estimating primary production at large spatial scales is key to our understanding of the global carbon cycle. Algorithms to estimate primary production are well established and have been used in many studies with success. One of the key parameters in these algorithms is the chlorophyll-normalised production rate under light saturation (referred to as the light saturation parameter or the assimilation number). It is known to depend on temperature, light history and nutrient conditions, but assigning a magnitude to it at particular space-time points is difficult. In this paper, we explore two models to estimate the assimilation number at the global scale from remotely-sensed data that combine methods to estimate the carbon-to-chlorophyll ratio and the maximum growth rate of phytoplankton. The inputs to the algorithms are the surface concentration of chlorophyll, sea-surface temperature, photosynthetically-active radiation at the surface of the sea, sea surface nutrient concentration and mixed-layer depth. A large database of in situ estimates of the assimilation number is used to develop the models and provide elements of validation. The comparisons with in situ observations are promising and global maps of assimilation number are produced.

1. Introduction

An important application of ocean-colour data has been the computation of marine primary production at the global scale (Antoine, André, & Morel, 1996; Antoine & Morel, 1996; Behrenfeld & Falkowski, 1997; Chavez, Messié, & Pennington, 2011; Friedrichs et al., 2009; Longhurst, Sathyendranath, Platt, & Caverhill, 1995). Typically, these computations use chlorophyll concentration derived from ocean colour as the state variable, although alternate approaches that use phytoplankton carbon rather than chlorophyll concentration have also been proposed (Behrenfeld, Boss, Siegel, & Shea, 2005). All these models require auxiliary information on light available at the sea surface, which is then combined with light-penetration models to compute the light available at depth for photosynthesis. A key step in the computations, and a non-trivial one, is the assignment of the model parameters required to estimate the photosynthetic response of phytoplankton to available or absorbed light.

Longhurst et al. (1995) and Platt and Sathyendranath (1999) proposed delineation of ecological provinces in the ocean as a template for extrapolating sparse in situ measurements of photosynthesis–irradiance parameters to the global ocean. Platt et al. (2008) developed the so-called nearest-neighbour methodology to assign, for each pixel (characterised by chlorophyll concentration and temperature), values of these parameters representative of similar local environmental conditions. Both of these methodologies rely on the availability of a database of photosynthesis–irradiance parameter measurements on which the extrapolation is based.

In the remote sensing context, the methods described above can be placed in a more generic categorisation of different options for parameter assignment for primary-production models (Platt & Sathyendranath, 1999). Specifically, the ecological-province-based approach may be termed as a piecewise-constant approach to parameter assignment (Longhurst et al., 1995). There are however alternative approaches which include the continuous method, where the assignments are based on some other empirical or parametric relation to other variables amenable to remote sensing (as in the case of the nearest-neighbour method, Platt et al., 2008). Another approach is the piecewise-continuous method, which is a combination of the two previous approaches (e.g. Huot, Babin, & Bruyant, 2013). In the current paper we consider a method that falls in the category of the continuous approach for estimating the assimilation number. Each method has its own inherent advantages and disadvantages. In the case of the continuous approach the advantages lie in its applicability in more dynamic regions, where the piecewise approach would lead to discontinuities in the production field, and its applicability at regional and basin scales, so long as the proposed approach is valid over the dynamic range of variability represented in the regions considered.

Some authors have linked the assimilation number to temperature (Eppley, 1972) and have shown that it is possible to use a temperature relationship in some particular conditions (shallow coastal and estuarine areas) as a basis for assigning it. The assimilation number has also been shown to be correlated with the available light (Finenko, Churilova, Sosik, & Basturk, 2002; Geider, 1987), nutrients (Harrison &

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Platt, 1980) and depth (Marañón & Holligan, 1999), which may be a proxy for both light and nutrient.

In this study we explore two options to estimate the assimilation number from combinations of easily-measured environmental variables. The first one is a global implementation of the model of Cloern, Grenz, and Vidergar-Lucas (1995). The second is based on the model of Sathyendranath et al. (2009) for estimating the carbon-to-chlorophyll ratio of phytoplankton, which is extended here to estimate the assimilation number. The choice of the two approaches was dictated by the goal of applying the methods globally, preferably using satellite data: both approaches presented here require only a small set of input variables that are readily available at the global scale. From the perspective of implementation, both models require temperature and light as inputs. The main difference between them is that the Cloern et al. (1995) model requires nitrate fields, whereas the other approach presented here requires chlorophyll fields instead of nitrate fields.

2. Material and methods

2.1. Approach

Marine primary production at a particular time and depth can be computed using photosynthesis-light models, which incorporate the parameters of the photosynthesis–irradiance curve (P–E curve). Integration over time and depth enables estimation of daily water column production. Although a number of variants of photosynthesis–light models exist in the literature, and regardless of the formalism adopted to describe the dependence of photosynthesis on available light, the relationships may all be expressed in the general form:

$$P^B(t,z) = P^B\left(E(t,z);\alpha^B,P^B_{\mathrm{m}}\right), \tag{1}$$

where P stands for primary production, E is irradiance, t is time and z is depth. The parameters of the model are α^B, the initial slope of the photosynthesis–irradiance curve as light tends to zero, and P^B_{m}, the assimilation number, which is a measure of the asymptotic maximum production under light-saturating conditions. Superscript B indicates normalisation to chlorophyll biomass B. The above equation states simply that chlorophyll-normalised production at a particular depth and time can be computed if we know the light available and the two parameters of the P–E curve. A third parameter would be needed under conditions of photo-inhibition. In photosynthesis-light experiments, dark respiration is corrected for, such that the model yields net primary production.

The photosynthesis–irradiance parameters have a central role in primary production models, and this study focuses on one of the parameters: the assimilation number, P^B_{m}, which may be defined as the asymptotic maximum rate of change in phytoplankton carbon due to net primary production, per unit chlorophyll concentration:

$$P^B_{\mathrm{m}} = \frac{1}{B}\frac{\mathrm{d}C_p}{\mathrm{d}t}\Big|_{\max}, \tag{2}$$

where C_p is the phytoplankton carbon concentration. It is useful to establish the relationship between P^B_{m} and maximum realised growth rate, μ_{m}, defined as:

$$\mu_{\mathrm{m}} = \frac{1}{C_p}\frac{\mathrm{d}C_p}{\mathrm{d}t}\Big|_{\max}. \tag{3}$$

Comparing Eqs. (2) and (3) we see that:

$$P^B_{\mathrm{m}} = \chi\mu_{\mathrm{m}}, \tag{4}$$

where χ is the carbon-to-chlorophyll ratio of phytoplankton.

The objective of our work is to establish methods to estimate P^B_{m} from environmental variables that are readily available, preferably through remote sensing. We explore two options here: both are based on existing methods to estimate χ and μ_{m}.

2.1.1. Model of assimilation number based on light, temperature and nutrients (LTN model)

This approach combines the chlorophyll-to-carbon model developed by Cloern et al. (1995) and the maximum growth rate as a function of temperature proposed by Eppley (1972).

Cloern et al. (1995) provided an empirical relationship linking the chlorophyll-to-carbon ratio (in phytoplankton) to temperature, average daily irradiance in the mixed layer and nutrient-limited growth rate:

$$B:C_p = \frac{1}{\chi} = 0.003 + 0.0154exp(0.05T)exp(-0.059E)\mu', \tag{5}$$

where T is the temperature (°C), E is the daily irradiance (photosynthetically-active radiation, PAR) averaged over the mixed-layer depth (mol quantan $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$) and $\mu' = N/(N+k_N)$ is the nutrient-limited growth rate, with N being the concentration of the most limiting nutrient (taken here to be nitrate) and k_N the half-saturation constant for that nutrient.

Combining Eqs. (4) and (5), the LTN model for the assimilation number can be expressed as:

$$P^{B,\mathrm{LTN}}_{\mathrm{m}} = \left[0.003 + 0.0154exp(0.05T)exp(-0.059E)\mu'\right]^{-1}\mu_{\mathrm{m}}. \tag{6}$$

This model can be implemented if we know the maximum growth rate μ_{m}, the temperature, the nutrient concentration, the average light in the mixed layer and the half-saturation constant k_N, for which Cloern et al. (1995) have used a value of 1 μM in their computations. On the other hand, Harrison, Harris, and Irwin (1996) have reported that k_N is positively correlated with nitrate concentration, with a lower limit around 0.01 to 0.02 μM. Combining these, k_N may be modelled as:

$$k_N = \begin{cases} 0.01, & N \le 0.01 \\ N, & 0.01 < N \le 1 \\ 1, & 1 < N \end{cases}. \tag{7}$$

To compute the maximum growth rate, we use the maximum temperature-dependent growth rate defined by Eppley (1972), μ^E_{m}, multiplied by a nutrient-limitation term, μ':

$$\mu_{\mathrm{m}} = \mu^E_{\mathrm{m}}\,\mu' = 0.851\left(1.066^T\right)\frac{\ln 2}{24}\left[\frac{N}{N+k_N}\right], \tag{8}$$

where the factor ln 2/24 accounts for the transformation from doubling time to hourly growth rate.

2.1.2. Model of assimilation number based on light, temperature and chlorophyll biomass (LTB model)

Nutrients are not directly observable by satellites, and for remote sensing of P^B_{m} we seek other options for a predictive environmental variable. Here we explore the use of chlorophyll biomass B instead of nutrients. Several studies have highlighted the relationship between chlorophyll concentration and phytoplankton cell size (see for example Brewin et al., 2010; Hirata, Aiken, Hardman-Mountford, Smyth, & Barlow, 2008), which is an important determinant of physiological rates. We begin with the expression for χ, the carbon-to-chlorophyll ratio, proposed by Sathyendranath et al. (2009):

$$\chi = \frac{1}{B}10^{(1.81+0.63log_{10}(B))}. \tag{9}$$

This expression, as pointed out by the authors, yields an upper bound on the phytoplankton carbon concentration, but does not