



## Models for estimating photosynthesis parameters from *in situ* production profiles



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### ABSTRACT

The rate of carbon assimilation in phytoplankton primary production models is mathematically prescribed with photosynthesis irradiance functions, which convert a light flux (energy) into a material flux (carbon). Information on this rate is contained in photosynthesis parameters: the initial slope and the assimilation number. The exactness of parameter values is crucial for precise calculation of primary production. Here we use a model of the daily production profile based on a suite of photosynthesis irradiance functions and extract photosynthesis parameters from *in situ* measured daily production profiles at the Hawaii Ocean Time-series station Aloha. For each function we recover parameter values, establish parameter distributions and quantify model skill. We observe that the choice of the photosynthesis irradiance function to estimate the photosynthesis parameters affects the magnitudes of parameter values as recovered from *in situ* profiles. We also tackle the problem of parameter exchange amongst the models and the effect it has on model performance. All models displayed little or no bias prior to parameter exchange, but significant bias following parameter exchange. The best model performance resulted from using optimal parameter values. Model formulation was extended further by accounting for spectral effects and deriving a spectral analytical solution for the daily production profile. The daily production profile was also formulated with time dependent growing biomass governed by a growth equation. The work on parameter recovery was further extended by exploring how to extract photosynthesis parameters from information on watercolumn production. It was demonstrated how to estimate parameter values based on a linearization of the full analytical solution for normalized watercolumn production and from the solution itself, without linearization. The paper complements previous works on photosynthesis irradiance models by analysing the skill and consistency of photosynthesis irradiance functions and parameters for modeling *in situ* production profiles. In light of the results obtained in this work we argue that the choice of the primary production model should reflect the available data and these models should be data driven regarding parameter estimation.

### 1. Introduction

Phytoplankton inhabit the uppermost, well illuminated, portion of the ocean within which the sunlight required for photosynthesis is readily available, and by assimilating carbon dioxide dissolved in sea water play an important role in the global carbon cycle (Falkowski and Raven, 2007; Williams and Follows, 2011). The ecological term used for carbon assimilation by phytoplankton is primary production (Williams, 1993). On the annual time scale, phytoplankton primary production is comparable in magnitude to the production of terrestrial plants (Field, 1998; Prentice et al., 2001). It has been estimated that around 8% of the global annual phytoplankton primary production is required to sustain

global fisheries catches (Pauly and Christensen, 1995). These are significant numbers in the context that phytoplankton biomass accounts for only one percent of the overall carbon stored in the biosphere (Falkowski, 2002; Le Quere et al., 2005). Compared with land plants, the growth of phytoplankton is rapid, with the biomass turnover time on the order of one week (Vermet and Smith, 2007; Behrenfeld et al., 2008). This makes phytoplankton extremely sensitive to changes in the physical environment. On longer time scales, the high flux of carbon through phytoplankton populations makes it a regulator of that same physical environment. A portion of the organic carbon that gets stored in the products of photosynthesis (phytoplankton) sink to the sea floor, contributing to the diminution of atmospheric carbon concentration

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(Sarmiento and Gruber, 2006; Williams and Follows, 2011). It is for these reasons that quantification of primary production is of interest in marine ecosystems research, fisheries, climate change studies, and to society at large.

In contemporary oceanography, models are used to quantify primary production, an activity that has developed over the last half century. As primary production is a fundamental flux in the pelagic ecosystem, it would be difficult to imagine any ocean ecosystem model without a suitable representation of primary production. The way primary production enters ecosystem models is via the light dependent carbon assimilation term in the phytoplankton growth equations (Franks, 2002). Over time, models with varying degrees of complexity have been proposed, ranging from simple models with few components (Fasham et al., 1990), to complex multi phytoplankton models (Dutkiewicz et al., 2009; Levy et al., 2015). Whether simple or complex, single species or multi species, all such models use the advection-diffusion-reaction type of partial differential equations (Ryabov and Blasius, 2008). In these equations the terms that are specific, and crucial, for primary production modeling are the reaction terms, which are light dependent (Huisman and Weissing, 1994). It is well known that in the ocean light is a strong function of depth, and given that phytoplankton absorb and scatter light, light intensity at depth itself depends on the vertical distribution of phytoplankton (Kirk, 2011). Once formulated mathematically, the advection–diffusion–reaction model transforms into a system of integro-differential equations and analysis becomes complex (Huisman et al., 2002). In this formulation, the light dependent reaction term, the driver of phytoplankton dynamics in models, is also the source of nonlinearities and associated mathematical complexity. The dependence of production on light also makes the system non-autonomous.

Many authors have studied the dynamics of phytoplankton caused by the interplay of phytoplankton distribution in the sea and the underwater light climate. The pioneering work on this topic dates back to 1949 and is concerned with the existence of stationary biomass profiles (Riley et al., 1949). Although Riley et al. (1949) were the first to model phytoplankton light interactions as a dynamical system, in their model they disregarded the vertical dependence of the growth rate and thereby lost control over the maximum sustainable biomass in the water column. Steele and Yentsch (1960) extend Riley's model by including phytoplankton sinking, which they considered responsible for the formation of the deep maximum in biomass. Shigesada and Okubo (1981) provided the first systematic analysis of the feedback between biomass and light, but they disregarded the effect of light attenuation by sea water as the optical medium. Ishii and Takagi (1982) generalized former results by including light attenuation caused by sea water. Models of this type were studied and discussed thoroughly, resulting in an extensive literature: Huisman et al. (2002), Kolokolnikov et al. (2009), Hsu and Lou (2010), and Du and Mei (2011), to name but a few authors. A good review of the topic, with a historical outlook, is provided by Gentleman (2002).

In all the models mentioned above, the growth of phytoplankton is represented by a light-dependent reaction term. It is modelled with the photosynthesis-irradiance (light-saturation) function. There are many functions in use, some with clear physiological interpretation, and some are used solely for empirical reasons (Platt and Jassby, 1976). The first model was introduced by Blackman in 1905, who assumed a linear dependence of primary production on light and a sudden jump to a fixed value at saturation (Blackman, 1905). Baly later employed the rectangular hyperbola (Baly, 1935) and Smith (1936) the modified rectangular hyperbola. Platt and Jassby (1976) introduced the hyperbolic tangent and made the first systematic comparison of the various photosynthesis irradiance functions. Webb et al. (1974) introduced the exponential function for higher plants, which Platt et al. (1980) were the first to use for representing the photosynthetic response of phytoplankton.

At implementation, models require parameter values to be assigned.

All of the above-mentioned functions have the same parameters, referred to as the photosynthesis parameters. These can be arbitrarily set, or otherwise estimated from measurements, the latter being the preferred way. Once estimated from measurements, the parameter values form the bridge between the model and the phytoplankton population, being representative of the ocean region in question at the time the ocean was sampled. In standard oceanographic practice the values of photosynthesis parameters are estimated from results of *in vitro* experiments, under controlled light conditions (Platt and Jassby, 1976). The values of parameters depend on the choice of photosynthesis irradiance function and are not interchangeable amongst the functions (Frenette et al., 1993). Lack of agreement in photosynthesis irradiance functions for estimating the photosynthesis parameters is known and has been studied (Jassby and Platt, 1976; Frenette et al., 1993), but modelers often disregard these apparently subtle discrepancies.

Just how subtle they are for modeling production measured at sea, has not yet been explored. This is unfortunate, given that the ultimate goal of primary production modeling is to come close to what we observe by measurements at sea. The preferred approach for measuring primary production in this case is the so called *in situ* approach. Phytoplankton samples enriched with  $^{14}\text{C}$  are submerged at specified depths, remain incubated during daylight hours, yielding finally estimates of the production profile and watercolumn production. Recently, a new approach to estimating photosynthesis parameters from *in situ* measurements was developed and implemented by Kovač et al. (2016a,b). In this approach a model of the production profile, formulated with photosynthesis-irradiance functions, is compared with the *in situ* production profile and the parameter values estimated, for which the residual error in the model is minimized.

Here we follow this approach and build upon it by extending the model to include various photosynthesis-irradiance functions. We use these functions to model production at depth and to recover photosynthesis parameters from *in situ* production profiles. We then compare recovered parameter distributions and demonstrate that both parameters can be estimated with differing degrees of accuracy. The paper further explores the effect of parameter interchange on the accuracy of modeling production at depth and watercolumn production. The results demonstrate that a systematic bias is introduced into model predictions when parameters estimated with one function are used in a model which employs another function. We extend the model further by deriving an analytical solution for daily production at depth with spectral dependence of production taken into account. We then demonstrate how the production profile is altered when biomass is allowed to accumulate with time due to primary production. Finally, we demonstrate how to recover the values of photosynthesis parameters from the information on watercolumn production by using a linear and a nonlinear solution for watercolumn production.

## 2. Photosynthesis irradiance functions

Phytoplankton primary production  $P$  ( $\text{mg C m}^{-3} \text{h}^{-1}$ ) is defined as the rate of assimilation of inorganic carbon by phytoplankton (Platt et al., 1977) and concentration of chlorophyll *a* is used as an index of phytoplankton biomass  $B$  ( $\text{mg Chl m}^{-3}$ ). Primary production normalized to biomass  $P^B$  ( $\text{mg C (mg Chl)}^{-1} \text{h}^{-1}$ ) is defined as the rate of carbon assimilation per unit biomass and is in first order determined by available light (Platt and Gallegos, 1980). The amount of light energy passing perpendicularly through a unit surface in unit time, called irradiance  $I$  ( $\text{W m}^{-2}$ ), is used as a measure of available light. Normalized production is treated as a function of irradiance and we write  $P^B = P^B(I)$ . The dependence of normalized production on irradiance is expressed with the aid of the photosynthesis-irradiance function  $p^B(I)$  (Jassby and Platt, 1976). The shape of the photosynthesis irradiance function reflects biophysical, biochemical and metabolic processes which regulate photosynthesis (Falkowski, 1992; Falkowski and Raven, 1997).

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