



PERGAMON

Deep-Sea Research II 48 (2001) 2005–2035

DEEP-SEA RESEARCH  
PART II

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# Variability of the effective quantum yield for carbon assimilation in the Sargasso Sea

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## Abstract

The effective quantum yield for carbon assimilation,  $\phi_c$  (mol C Einstein<sup>-1</sup>), quantifies the efficiency by which phytoplankton use absorbed light energy to photochemically fix and store carbon. A five-year time series from the Sargasso Sea shows a high degree of variability in estimated values of  $\phi_c$ . A significant seasonal cycle is found as  $\phi_c$  values are reduced in summer. However, this seasonal cycle explains only a small fraction of the total variance in  $\phi_c$ , and very few environmental parameters correlate with  $\phi_c$ . Significant correlation is observed between  $\phi_c$  and the flux of photosynthetically active radiation,  $Q_{PAR}$ , and between  $\phi_c$  and the rate at which phytoplankton absorb quanta,  $AQ_{PAR}$ . Near-surface  $\phi_c$  values also are correlated with concentrations of the photoprotectant pigment zeaxanthin, where  $\phi_c$  values are depressed when zeaxanthin concentrations are elevated. Four previously published  $\phi_c$  models are assessed using these data. The predictive skill for each of these  $\phi_c$  models indicates that they behave as good data interpolators, but poor predictors of  $\phi_c$  variability. The prognostic capability of these models does not improve when seasonal mean parameters are applied. The present results demonstrate the difficulties in modeling primary production, as we have yet to develop a predictive understanding of the important photophysiological, ecological and methodological processes regulating primary production. © 2001 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

Primary production quantifies the input of externally derived energy into an ecosystem via photosynthesis. Fueled by the absorption of solar energy, photosynthesis reduces CO<sub>2</sub> to produce

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chemical energy in the form of organic carbon. This net energy source for an ecosystem may be further utilized by heterotrophic organisms supporting the complex, marine food web, or exported from the euphotic zone. Because of the processes of carbon fixation, exchange and export, the ocean acts as a dynamic storehouse for atmospheric carbon dioxide (e.g., Sarmiento and Toggweiler, 1984). Hence, the determination of primary production and its time and space variations will have important implications for the understanding of the marine carbon budget and its changes due to anthropogenic CO<sub>2</sub> emissions. In this paper, we start at the beginning of the oceanic carbon cycle and describe the temporal- and depth-dependent variability in the efficiency by which solar energy enters the marine ecosystem, the quantum yield of carbon assimilation.

Chlorophyll- and light-based primary production models were developed more than four decades ago (e.g., Ryther and Yentsch, 1957; Talling, 1957; Steele, 1962) and have been used in recent times to provide estimates of carbon fixation over a wide range of spatial and temporal scales (cf. Bidigare et al., 1987, 1992; Cullen, 1990; Morel, 1991; Balch et al., 1992; Platt et al., 1995; Longhurst et al., 1995; Antoine and Morel, 1996; Behrenfeld and Falkowski, 1997; Siegel et al., 2001). Although primary production models differ in detail, nearly all predict primary production,  $P$ , as the product of the rate at which light quanta are absorbed by phytoplankton,  $AQ_{ph}$ , and the efficiency with which that absorbed light energy is converted to stored carbon,  $\phi_c$ , or

$$P = AQ_{ph} \phi_c. \quad (1)$$

Considerable research efforts in primary production modeling have focused on the accuracy of the phytoplankton absorption expression,  $AQ_{ph}$ , producing accurate methods for its in situ and remote determination (e.g., Morel, 1978, 1991; Smith and Baker, 1978; Prieur and Sathyendranath, 1981; Bidigare et al., 1985, 1989a; Kishino et al., 1985; Sathyendranath et al., 1989). However, generalized refinements in estimating quantum efficiency expressions have been elusive, proving to be the most significant, least understood and ultimately controversial part of the primary production estimate (Bidigare et al., 1992; Dickey and Siegel, 1993). Part of this difficulty arises because the regulating physiological, photochemical and ecosystem processes are complex, making it extremely difficult to derive a globally applicable expression for quantum efficiency.

To avoid these complexities, models for primary production rates make many simplifying assumptions to parameterize the quantum efficiency. Often  $\phi_c$  is assumed constant for a given region and/or season. These regions are termed biogeochemical “provinces” (e.g., Platt and Sathyendranath, 1988; Mueller and Lange, 1989; Platt et al., 1992, 1995; Longhurst et al., 1995; Longhurst, 1998). These approaches require that the spatial and temporal variability in any efficiency expression behave in a consistent and predictable manner either constrained within specific geographic regions and/or seasons — assumptions which must be validated. This is especially true for physiological parameters such as  $\phi_c$ .

Estimates of quantum yield will vary depending on the duration and method of the measurement. This is due to the fact that quantum yields are not only variable through out the day (e.g., Kishino et al., 1986; Prézélin et al., 1986), but also that <sup>14</sup>C uptake methods commonly used are invariably time averaged and include varying degrees of respiratory and grazing losses (e.g., Peterson, 1980; Carpenter and Lively, 1980; Platt et al., 1984; Williams, 1993). Hence, a distinction must be made among determinations of quantum yield made over different time scales. Over short time scales (order milliseconds to several hours),  $\phi_c$  estimates are representative of an instantaneous or physiological yield and should quantify the gross rates of photosynthesis with little

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