Carbon-based ocean productivity and phytoplankton physiology from space

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Abstract: Ocean biogeochemical and ecosystem processes are linked by net primary production (NPP) in the ocean’s surface layer, where inorganic carbon is fixed by photosynthetic processes. Determinations of NPP are necessarily a function of phytoplankton biomass and its physiological status, but the estimation of these two terms from space has remained an elusive target. Here we present new satellite ocean color observations of phytoplankton carbon (C) and chlorophyll (Chl) biomass and show that derived Chl:C ratios closely follow anticipated physiological dependencies on light, nutrients, and temperature. With this new information, global estimates of phytoplankton growth rates (μ) and carbon-based NPP are made for the first time. Compared to an earlier chlorophyll-based approach, our carbon-based values are considerably higher in tropical oceans, show greater seasonality at mid- and high latitudes, and illustrate important differences in the formation and demise of regional algal blooms. This fusion of emerging concepts from the phycological and remote sensing disciplines has the potential to fundamentally change how we model and observe carbon cycling in the global oceans.

1. Introduction

Marine net primary production (NPP: mg C m$^{-2}$) is a key metric of ecosystem health and carbon cycling and is commonly estimated as the product of plant biomass, incident solar flux, and a scaling parameter that accounts for variations in plant physiology (Behrenfeld et al. 2001). Satellite measurements now routinely provide global chlorophyll biomass (Chl) and incident light (I$_0$) data, but the remote determination of phytoplankton carbon (C) biomass and physiological status has proven elusive. Present-day ocean NPP estimates consequently use chlorophyll as an index of phytoplankton biomass and rely on stylized empirical descriptions of physiological variability (e.g., Longhurst, A. 1995; Behrenfeld & Falkowski 1997a) that perform poorly when compared to local field measurements (Siegel et al. 2001; Campbell et al. 2002; Behrenfeld et al. 2002). Far more is known, however, regarding the nature of phytoplankton physiology than reflected in these empirical relationships. In particular, laboratory studies have long shown that phytoplankton respond to changes in light, nutrients, and temperature conditions by adjusting cellular pigment levels to match their new demands for photosynthesis and that this response is well quantified by changes in the ratio of chlorophyll to carbon biomass (Chl:C) (e.g., Geider 1987; Sakshaug et al. 1989; MacIntyre et al. 2002). It follows, therefore, that a remote sensing index of Chl:C may provide a path for assessing phytoplankton physiology from space.

Optical scattering coefficients in marine waters covary with the suspended particle load (see review by Babin et al. 2003). Indeed, the particulate beam attenuation coefficient at 660 nm (c$_p$) (an inherent optical property that is dominated by scattering) has been repeatedly shown in the field to covary with the particulate organic carbon concentration (POC) (Gardner et al., 1993, 1995; Walsh et al., 1995; Loisel and Morel, 1998; Bishop, 1999; Bishop et al., 1999; Claustre et al., 1999). Behrenfeld and Boss (2003) suggested that c$_p$ should likewise be well correlated with phytoplankton carbon biomass, particularly since the particle size domain dominating c$_p$ more closely matches that of phytoplankton than POC. Accordingly, they proposed the c$_p$:Chl ratio as an index of phytoplankton C:Chl and subsequently demonstrated a first-order correspondence between c$_p$:Chl and independent $^{14}$C-tracer measures of physiological condition (Behrenfeld & Boss 2003). Thus, the ratio of chlorophyll to light scattering appears to provide an optical index
of phytoplankton physiology.

Currently, \( c_p \) is not a remote sensing product. However, recent advances in satellite ocean color data analysis now permit the separation of light absorbing and scattering components in seawater, yielding simultaneous estimates of Chl and particulate backscattering coefficients (\( b_{bp} \)) (Maritorena et al. 2002; Siegel et al. 2002; Stramski et al. 1999; Loisel et al. 2001). While \( b_{bp} \) is likely more influenced by particles outside the phytoplankton size domain than \( c_p \) (Morel & Ahn 1991; Stramski & Kiefer 1991), a relationship between \( b_{bp} \) and phytoplankton carbon is nevertheless anticipated so long as the abundance of non-algal particles contributing to \( b_{bp} \) covaries with phytoplankton biomass. Such covariability in components of the particle assemblage is evidenced by the relatively constant slope of the particle size spectrum in open ocean waters (Bader 1970; Stramski & Kiefer 1991; Kiefer & Berwald 1992; see also discussion in Twardowski et al. 2001) and is responsible for reported correlations between satellite \( b_{bp} \) and field measurements of POC (Stramski et al. 1999; Loisel et al. 2001).

Here we proceed through a sequence of steps that lead from satellite Chl and \( b_{bp} \) determinations to global carbon-based estimates of ocean NPP. From \( b_{bp} \), we estimate phytoplankton carbon biomass (C) and then demonstrate that regional satellite Chl:C ratios behave in a manner consistent with well established physiological dependencies on light, nutrients, and temperature. We then use Chl:C data to estimate phytoplankton growth rates (\( \mu \)) and, finally, calculate NPP from the product of \( \mu \) and C. In this manner, closure on the productivity equation is achieved through remote sensing, yielding a new view of global ocean productivity and its variation over space and time.

2. Methods

2.1 Global Data

Chlorophyll concentrations (Chl: mg m\(^{-3}\)) and \( b_{bp} \) at 440 nm (m\(^{-1}\)) were estimated using the Garver-Siegel-Maritorena (GSM) semi-analytical algorithm (Garver & Siegel 1997; Maritorena et al. 2002; Siegel et al. 2002) and monthly satellite water-leaving radiances for the September 1997 to January 2002 period from the 4\(^{th}\) reprocessing of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) data set. Comparison with coincident open ocean observations indicates that the Chl product from the GSM algorithm is statistically indistinguishable from the standard SeaWiFS Chl product (Siegel et al. 2004). For this analysis, we also used coincident SeaWiFS cloud-corrected surface PAR data (\( I_0 \); moles photons m\(^{-2}\) h\(^{-1}\)), SeaWiFS mixed layer light attenuation coefficients at 490 nm (\( k_{490} \); m\(^{-1}\)), 8 km Advanced Very High Resolution Radiometer (AVHRR) sea surface temperature data (SST; °C) from the Physical Oceanography Distributed Active Archive Center (PODAAC) (http://podaac-www.jpl.nasa.gov), and monthly mean regional mixed layer depths (MLD: m) from the Fleet Numeric Meteorology and Oceanography Center (FNMOC) (7 Grace Hopper Avenue, Stop 1, Monterey, California, U.S.A. 93940). While FNMOC and climatological MLD data compare favorably over large space and time scales, the FNMOC model assimilates coincident field and satellite temperature and salinity data and thus provides information on interannual variability in MLDs. \( I_0, k_{490}, \) and MLD data were used to calculate monthly median mixed layer light levels (\( I_g \)) following: \( I_g = I_0 \exp^{k_{490} \times \text{MLD}/2}. \)
2.2 Regional Binning
Arctic and coastal regions were excluded from our analysis and the remaining data (89% of the global oceans) were partitioned into 28 regional bins, defined by ocean basin and the degree of seasonal variability in chlorophyll. Standard deviations in Chl (s.d.\textsubscript{Chl}) provide a means to coarsely separate functionally different ocean regions (e.g., oligotrophic versus seasonal bloom areas) (Esaias et al. 1999; Doney et al. 2003). For the current study, five chlorophyll variance bins (L0 to L4) were used and defined as: \( L0 = 0 < \text{s.d.}_{\text{Chl}} < 0.018 \text{ mg Chl m}^{-3} \), \( L1 = 0.018 < \text{s.d.}_{\text{Chl}} < 0.026 \text{ mg Chl m}^{-3} \), \( L2 = 0.026 < \text{s.d.}_{\text{Chl}} < 0.09 \text{ mg Chl m}^{-3} \), \( L3 = 0.09 < \text{s.d.}_{\text{Chl}} < 0.4 \text{ mg Chl m}^{-3} \), \( L4 = \text{s.d.}_{\text{Chl}} > 0.4 \text{ mg Chl m}^{-3} \). The precise cutoff values for these bins are not critical and were simply chosen to yield regions consistent with large-scale ocean circulation and pigment features. All data for the Southern Ocean were grouped into a single bin because >90% of the data fell into L2 and L3 variance levels and the seasonal patterns in these bins were nearly identical.

2.3 Phytoplankton Carbon
To constrain our satellite-based phytoplankton carbon estimates, we analyzed laboratory data compiled by Behrenfeld et al. (2002) on light- and nutrient-dependent changes in cellular pigmentation from published studies between 1946 and 1987. This data set yielded Chl:C values ranging from 0.001 to > 0.06 mg mg\(^{-1}\), with a median value of 0.010 mg mg\(^{-1}\) for light levels between 0.7 and 1.4 moles photons m\(^{-2}\) h\(^{-1}\). The median mixed layer light for our remote sensing data set was 1.2 moles photons m\(^{-2}\) h\(^{-1}\).

As an additional constraint, satellite-based POC concentrations were calculated from \( b_{bp} \) data using relationships developed for the Mediterranean (POC = 37550 \( b_{bp}(550) + 1.3 = 29769 \)) (Loisel et al. 2001) and the Antarctic Polar Front Zone (POC = 17069 \( b_{bp}(510)^{0.859} = 14726 \)) (Stramski et al. 1999), where the first equation is the original published relationship and the second equation is the converted relationship for use with \( b_{bp}(440) \) data. We then calculated phytoplankton carbon:POC ratios for our remote sensing data and compared these to field-derived values. Specifically, Eppley et al. (1992) reported phytoplankton carbon:POC ratios of 29% to 49%, Durand et al. (2001) found a relatively constant value of 33% throughout the year near Bermuda, Gundersen et al. (2001) reported a value of 32%, and Oubelkheir (2001) measured values ranging from 19% to 21% in regions spanning from oligotrophic to eutrophic. It is noteworthy that this restricted variability observed in the field includes methodological differences for estimating phytoplankton carbon.

2.4 Productivity Calculations
For comparative purposes, global ocean NPP was calculated using our new carbon-based approach and a common chlorophyll-based algorithm, the Vertically Generalized Production Model (VGPM) (Behrenfeld & Falkowski 1997a). The depth-integrated VGPM equation is:

\[
\text{NPP} = \text{Chl} \cdot Z_{eu} \cdot f(I_0) \cdot d.l. \cdot P_{\text{opt}},
\]

where \( Z_{eu} \) is the depth of the photosynthetically active surface layer and physiological variability (\( P_{\text{opt}} \)) is described by an empirical polynomial function of SST that increases from 0 to 20 °C and then decreases at higher temperatures (Behrenfeld & Falkowski 1997a). For both the chlorophyll- and carbon-based calculations, the light-dependent function was described as: \( f(I_0) = 0.66125 \frac{I_0}{(I_0 + 4.1)} \) (Behrenfeld & Falkowski 1997a), \( Z_{eu} \) was calculated as: \( Z_{eu} = \ln(0.01)/k_{400} \) (which gives slightly higher NPP values than earlier VGPM
estimates), and the same GSM satellite chlorophyll estimates were used.

3. **Results**

3.1 **Satellite-based phytoplankton carbon biomass**

Comparison of monthly $b_{bp}$ and Chl data revealed two distinct regimes; one where $b_{bp}$ is relatively constant and one where $b_{bp}$ covaries with Chl (Fig. 1). In the most unproductive ocean regions, $b_{bp}$ varies by only a factor of 1.6 (from 0.0010 to 0.0016 m$^{-1}$) while Chl ranges from 0.03 to 0.14 mg m$^{-3}$ (i.e., a factor of 4.6), with no correlation between the two variables (Fig. 1). In more productive regions where chlorophyll concentrations exceed ~0.14 mg Chl m$^{-3}$, $b_{bp}$ and Chl are well correlated ($r^2 = 0.74$) (Fig. 1). Our interpretation of this bilinear pattern is that Chl variability is largely due to intracellular changes in pigmentation (i.e., physiology) in impoverished ocean regions, while in more enriched regions first-order changes in Chl and $b_{bp}$ are predominantly due to changes in phytoplankton biomass (i.e., abundance).

To estimate phytoplankton carbon biomass (mg m$^{-3}$) from $b_{bp}$, we first subtracted a background value of 0.00035 m$^{-1}$ and then multiplied by a scalar of 13,000 mg C m$^{-2}$ [i.e., phytoplankton C = 13,000 $\cdot$ ($b_{bp}$ - 0.00035)]. The background value was estimated from least squares regression analysis of the linear portion of the Chl-$b_{bp}$ relationship (Fig. 1A - solid line) and it represents a global estimate of backscattering by the stable heterotrophic and detrital components of the surface particle population. For comparison, a similar independent estimate of 0.00017 m$^{-1}$ is calculated using backscattering coefficients from Stramski and Kiefer (1991) and a field-based background heterotrophic bacterial concentration of $7 \times 10^{11}$ m$^{-3}$ from Cho & Azam (1990; their Fig. 1). The scalar of 13,000 mg C m$^{-2}$ was chosen to give satellite Chl:C values (average = 0.010, range = 0.002 to 0.030) consistent with laboratory results and an average phytoplankton contribution to total particulate organic carbon of ~30% (range: 24% to 37%), which is consistent with field estimates from a variety of ocean regions (Eppley et al. 1992; DuRand et al. 2001; Gundersen et al. 2001; Oubelkheir 2001) (see Methods, Section 2.3).

Restating the above in more general terms, we assume that the particle population contributing to $b_{bp}$ is comprised of a stable non-algal ‘background’ component and a second component that includes phytoplankton and other particles that covary with phytoplankton. We then subtract the ‘background’ component and directly relate the remaining $b_{bp}$ to phytoplankton biomass using a simple scalar that gives reasonable values for both Chl:C and the phytoplankton carbon to POC ratio. We do not assume that the remaining $b_{bp}$ is entirely due to backscattering by phytoplankton, only that it correlates with phytoplankton abundance. This conversion of $b_{bp}$ to phytoplankton carbon will clearly be compromised by significant shifts in the composition of the particle assemblage (e.g., prominent inorganic particulate component) or by large deviations in the slope of the particle size spectrum. The influence of local-scale variability in such factors has been minimized in the current analysis by integrating over large areas and omitting coastal waters where suspended inorganic particle loads can be particularly high (see Methods, Section 2.2).

In the next two sections, we describe how regional variability in satellite Chl:C is consistent with anticipated changes in phytoplankton physiology. Importantly, these results are quite insensitive to the $b_{bp}$-to-carbon conversion parameters described above, such that the same
degree of correspondence with mixed layer growth conditions is found with unaltered Chl:$b_{bp}$ ratios as with our converted Chl:C values.

### 3.2 Five basic seasonal patterns in phytoplankton biomass and physiology

Analysis of regional phytoplankton Chl, C, and Chl:C ratios revealed seasonal patterns related to basic ocean circulation and ecosystem features. Parallel changes in Chl and C biomass reflect changes in phytoplankton abundance caused by shifts in the balance between phytoplankton growth and losses (e.g., sinking, predation). Divergent patterns in Chl and C (i.e., changes in the Chl:C ratio) result from physiological acclimations to changing growth conditions. Quite specifically, decreases in Chl:C are associated with increases in growth irradiance ($I_g$), decreases in nutrients, and decreases in temperature (Geider 1987; Sakshaug et al. 1989; Cloern et al. 1995; Geider et al. 1998; MacIntyre et al. 2002; Behrenfeld et al. 2002).

From our 28 regions, five basic seasonal patterns emerged (Fig. 2) (see SUPPLEMENTAL FIGURE 1 for all 28 regional graphs). In eight of the lowest production regions (see Fig. 2 legend), stable environmental conditions foster stable C concentrations through a tight coupling between phytoplankton growth and consumption, while seasonal changes in light cause smooth seasonal cycles in Chl, and thus Chl:C (Fig. 2B). In other words, phytoplankton biomass is essentially constant throughout the year in these unproductive waters, but chlorophyll still varies notably from physiological responses to seasonally changing growth conditions [i.e., intracellular chlorophyll increases during winter months in response to generally deeper mixed layers, lower light levels, and possibly higher nutrient levels (Winn et al. 1995; McClain et al. 2004)]. In four other low production regions, the coupling between phytoplankton growth and consumption is not so tight and this imbalance causes moderate changes in C and Chl biomass (Fig. 2C). Physiological responses to changing light and nutrient stress in these regions cause additional variability in Chl that leads to somewhat dampened Chl:C cycles with both spring and fall peaks (Fig. 2C). Together, these 12 regions contribute most of the Chl-$b_{bp}$ pairs in Figure 1 at $< 0.14$ mg Chl m$^{-3}$, where chlorophyll variability is predominantly due to changes in physiological state.

In five moderately productive regions, temporally offset seasonal cycles of Chl and C biomass are found, with the rise in Chl preceding the rise in C (Fig. 2D). We interpret this pattern as a seasonal cycle where initial cell ‘greening’ is followed by increased growth and biomass, and later culminates in nutrient- and light-dependent reductions in pigmentation and growth. Nine other moderate- and high-production areas exhibit seasonal cycles in both Chl and C biomass that are dominated by large spring-summer blooms in phytoplankton abundance (Fig. 2E). Despite this first-order influence of biomass, physiological adjustments during the seasonal cycle are still registered by coherent second-order changes in Chl:C ratios that increase during low-light and early bloom conditions and decrease just prior to the biomass peak and crash (Fig. 2E). These qualitative results thus indicate that scatter in the Chl-$b_{bp}$ relationship at $> 0.14$ mg Chl m$^{-3}$ (Fig. 1) is indeed associated with seasonal changes in phytoplankton physiology.

The fifth temporal pattern revealed by this analysis was unique to the two equatorial upwelling regions of the central Pacific [i.e., CP-L2, CP-L3 (Fig. 2A)] and characterized by a strong shift in Chl:C during the 1997-98 El Niño to La Niña transition (Chavez et al. 1999; Behrenfeld et al. 2001), followed by an extended period of low-level, correlated variability in Chl and C (Fig. 1F). This pattern is consistent with the regions’ low amplitude variability in mixing
depths and surface light (therefore, $I_g$) and the dominating influence of El Niño-La Niña shifts in nutrient availability on phytoplankton physiology (Fig. 1F).

### 3.3 Satellite-derived physiology registers light-, nutrient-, and temperature effects

It is well established from decades of laboratory studies that phytoplankton Chl:C ratios decrease from low to high light (e.g., Geider 1987; Sakshaug et al. 1989; Geider et al. 1998; MacIntyre et al. 2002; Behrenfeld et al. 2002). This phenomenon, known as ‘photoacclimation’, reflects physiological responses aimed at minimizing the influence of light variability on growth (Fig. 3A). The relationship between Chl:C and light has a low-light maximum ($\text{Chl:C}_{\text{max}}$) that increases with increasing temperature (Geider 1987; Cloern et al. 1995) (Fig. 3B) and a light-saturated minimum ($\text{Chl:C}_{\text{min}}$) that decreases with increasing nutrient stress (Laws & Bannister 1980; Sakshaug et al. 1989; Cloern et al. 1995; Geider et al. 1998) (Fig. 3C). These adjustments in cellular pigmentation function to balance light harvesting with temperature- and nutrient-dependent changes in growth. The dependency of Chl:C on light can be modeled for a range of growth conditions as an exponential function of light (Cloern et al. 1995; Behrenfeld et al. 2002), such as:

$$\text{Chl:C} = \text{Chl:C}_{\text{min}} + \left[\text{Chl:C}_{\text{max}} - \text{Chl:C}_{\text{min}}\right] \exp^{-3 I_g r}.$$

To more quantitatively link satellite Chl:C data with phytoplankton physiology, we compared regional changes in Chl:C with corresponding changes in mixed layer light levels ($I_g$) and found clear relationships that closely followed equation 1 (median $r^2 = 0.85$) in all regions with significant seasonal variability in $I_g$ (Fig. 3D) (Table 1). In other words, regional Chl:C values varied with $I_g$ precisely as expected from the laboratory (compare Fig. 3A & 3D). Overall, equation 1 captured 94% of the global variability in satellite Chl:C. Moreover, fits of equation 1 to the regional Chl:C data yielded Chl:C$_{\text{max}}$ values that increased with increasing sea surface temperature (SST) ($r^2 = 0.79$) in a manner consistent with laboratory trends (Geider 1987; Cloern et al. 1995) (Fig. 3E). Differences of scale in these relationships indicate that the nutrient-saturated, exponential growth conditions used in laboratory monoculture studies (Fig. 3A,B) are rarely replicated for all members of any natural phytoplankton community (Fig. 3D,E).

While nutrient concentrations are not directly measured from space, the global tendency is for surface nutrients to decrease with increasing SST (Kamykowski et al. 2002; Switzer et al. 2003). Accordingly, we found that fits of equation 1 yielded regional values for the nutrient-dependent term, Chl:C$_{\text{min}}$, that decreased with increasing SST in 21 of our 28 regions ($r^2 = 0.83$) (Fig. 3F, solid circles). The seven remaining regions were all areas where SST is a poor surrogate for nutrient stress. For the six high-temperature outliers (Fig. 3C, open triangles), equatorial or monsoon-driven upwelling sustains elevated nutrients and productivity. In these regions, annual mean Chl is a more robust index of nutrient input and indeed is well correlated with Chl:C$_{\text{min}}$ ($r^2 = 0.93$). The single low temperature outlier (Fig. 3C, open circle) corresponds to the Southern Ocean region, where macronutrients ($\text{NO}_3$, $\text{PO}_4$) are abundant, but phytoplankton growth is limited by iron availability and temperature (annual mean $= 1.6 \, ^\circ\text{C}$).

Analysis of our satellite Chl:C data thus reveals (i) seasonal patterns consistent with regional ecology (Fig. 2B-F), (ii) strong dependencies on mixed layer light levels (median $r^2 =$
0.85) that are consistent with laboratory studies (compare Fig. 3A with 3D), and (iii) estimates of Chl:C\(^{\text{max}}\) and Chl:C\(^{\text{min}}\) that follow anticipated relationships with SST (compare Fig. 3B,C with 3E,F) and have minimum values (0.0155 and 0.0037, respectively) indistinguishable from laboratory-based estimates (0.0154 and 0.0030, respectively) (Cloern et al. 1995) (Fig. 3B,C). Taken together, these findings strongly support a link between satellite Chl:C and phytoplankton physiology, and thus a path from ocean color to phytoplankton growth rates (\(\mu\)).

### 3.4 Phytoplankton growth rates from space

The growth rate of a natural phytoplankton community (\(\mu\): divisions d\(^{-1}\)) is a function of light, nutrients, and temperature and can be described by:

\[
\mu = \mu^{\text{max}} \cdot f(N, T) \cdot g(I_g)
\]  

(2)

where, \(f(N, T)\) accounts for reductions in growth rate due to nutrient and temperature limitation at a given light level (range: 0 to 1), \(g(I_g)\) accounts for reductions in growth rate due to light limitation (range: 0 to 1), and \(\mu^{\text{max}}\) is the maximum potential community growth rate under optimal conditions. Equation 2 is applied here to estimate community carbon-specific phytoplankton growth rates and does not provide information on growth of specific algal groups (e.g., the bulk growth rate of an oligotrophic community may be low despite a picoplankton fraction dividing nearly once per day).

As a first attempt at estimating \(\mu\) from satellite Chl:C data, we assigned \(\mu^{\text{max}}\) a value of 2 divisions d\(^{-1}\), based on the highest phytoplankton community growth rates reported in the extensive field data set compiled by Banse (1991). We then assumed that increases in nutrient and temperature stress cause decreases in phytoplankton growth rates that are paralleled by proportional decreases Chl:C ratios (Geider 1987; Sakshaug et al. 1989; Cloern et al. 1995). This response [which is the \(f(N, T)\) function in equation 2] was quantified by dividing satellite Chl:C data (Chl:C\(^{\text{sat}}\)) by a maximum potential community chlorophyll:carbon value for a given \(I_g\) (Chl:C\(^{\text{N,T-max}}\)):

\[
\mu = \mu^{\text{max}} \cdot \frac{\text{Chl:C}\(^{\text{sat}}\)}{\text{Chl:C}\(^{\text{N,T-max}}\)} \cdot g(I_g).
\]  

(3)

Chl:C\(^{\text{N,T-max}}\) was then defined by a parameterization of equation 1 that enveloped > 99% of our satellite Chl:C data, specifically: Chl:C\(^{\text{N,T-max}}\) = 0.022 + (0.045 - 0.022) \exp(-3I_g) (Fig. 4A - blue line). This description of Chl:C\(^{\text{N,T-max}}\) has a Chl:C\(^{\text{min}}\) value (0.022) that is somewhat higher than the fitted curves for our 28 regions (Fig 4A), implying that high light environments are generally associated with suboptimal growth conditions at the regional scale (note that at the pixel scale, near-maximum values are frequently observed). Finally, decreases in \(\mu\) at low light result because physiological adjustments in pigmentation are insufficient to maintain constant levels of light absorption (Geider 1987; Sakshaug et al. 1989; Cloern et al. 1995; Geider et al. 1998). With the dependence of Chl:C on \(I_g\) described by (1), this relationship between \(\mu\) and light is given by: \(g(I_g) = 1 - \exp(-3I_g)\). In summary, \(\mu\) was estimated as:

\[
\mu = 2 \cdot \text{Chl:C}\(^{\text{sat}}\) / [0.022 + (0.045 - 0.022) \exp(-3I_g)] \cdot (1 - \exp(-3I_g))
\]  

(4)
Equation 4 was then applied uniformly to all 28 regions, including the 7 outliers identified in Figure 3F (since these regions correspond to areas where SST is not a good predictor of nutrient stress, while Chl:C still tracks changes in physiology).

Representing the first direct estimates of $\mu$ from space, we found mixed layer phytoplankton growth rates to be persistently elevated in the upwelling-enriched tropical oceans, chronically suppressed in the stratified central ocean gyres, and strongly seasonal at higher northern and southern latitudes (Fig. 4B,C). In the equatorial Pacific, $\mu$ peaked along the upwelling axis near the equator and then diminished to the north and south (Fig. 4B,C), as often suggested by field $^{14}$C-uptake measurements (Lindley et al. 1995; Behrenfeld & Boss 2003). At high southern latitudes where easterly circumpolar currents prevail, enhanced summertime growth rates were largely restricted to the leeward eastern margins of continents and islands (Fig. 4C), consistent with sources of growth-limiting micronutrients (i.e., iron) (Boyd et al. 1999; Sullivan et al. 1993). In the north Atlantic and western Pacific, spring and summer growth rates were broadly elevated across mid- and high-latitudes, reflecting a shoaling of surface mixing depths and elevated sunlight (Fig. 4B). The markedly lower summer growth rates in the eastern subarctic Pacific are consistent with this region’s restriction by iron availability (Boyd et al. 1996; Harrison et al. 1999) (Fig. 4B). Globally, satellite-based phytoplankton community growth rates exhibited a smooth, peaked distribution with a median around 0.5 divisions d$^{-1}$ (Fig. 4D).

3.5 Global ocean productivity

The product of phytoplankton carbon biomass and growth rate is net primary production. Water column NPP can be estimated from surface satellite C and $\mu$ by additionally accounting for changes in photosynthesis with depth:

$$NPP = C \cdot \mu \cdot Z_{eu} \cdot h(I_0)$$ (5)

where $Z_{eu}$ is the depth (m) of the photosynthetically active surface layer and $h(I_0)$ describes how changes in surface light influence the depth-dependent profile of carbon fixation. Equation 5 is of the same form as earlier NPP models (Behrenfeld & Falkowski 1997b), with the exception that Chl is replaced by C and the empirical estimate of chlorophyll-specific photosynthesis ($P_{opt}^b$) is replaced by $\mu$ (where C and $\mu$ are now directly estimated from remote sensing - see above). To illustrate the impact of this new carbon-based approach, we now compare NPP calculated from (5) and a common Chl-based algorithm, the Vertically Generalized Production Model (VGPM) (Behrenfeld & Falkowski 1997a) (see Methods, Section 2.4).

Annual total global ocean productivity averaged 67 Pg C y$^{-1}$ (Pg = 10$^{15}$ g) for the C-based model and 60 Pg C y$^{-1}$ for the Chl-based model over the 1997 to 2002 period, a difference that scales directly with the value of $\mu_{max}$. Far more striking (and independent of $\mu_{max}$) are the spatial and seasonal differences in NPP between models (Fig. 5A-D). The carbon model yielded 40% and 49% higher annual NPP for the central Atlantic and central Pacific regions (see Fig. 2 for regional boundaries) and an increase from 1.6 to 2.6 Pg C y$^{-1}$ in the north Indian region (Fig. 5E-F). It is interesting to note that the two models are in better agreement in these areas when an exponential model for $P_{opt}^b$, following Antoine et al. (1996), is used in the VGPM. This
exponential expression performs better at low latitudes than the standard VGPM model based on comparisons with $^{14}$C data (Campbell et al. 2002)]. Carbon-based NPP was also higher by 9% in the south Indian, 7% in the north Pacific, and 2% in the south Pacific regions (Fig. 5E-F). The opposite trend was found for the north and south Atlantic, where NPP was 21% and 18% lower for the C model than the Chl model, respectively (Fig. 5E-F). In the Southern Ocean, the relationship between C- and Chl-based NPP was patchy (particularly in summer months) (Fig. 5F), but overall the C model gave a 20% lower estimate for this region.

Without exception, the C-based and Chl-based models yielded different seasonal cycles in NPP, and often dramatically so (see Supplemental Figure 2 to view time-series for all 28 regions). While each region exhibited unique differences, the general trend over variance levels was for the C model to give dampened cycles relative to the Chl model in low variance regions, and often stronger and delayed seasonal cycles in higher variance regions (see Supplemental Figure 2).

When viewed by ocean basin (i.e., combining all variance levels), the C model typically gave stronger seasonal cycles in NPP at high latitudes (Fig 6A,C,D,F) and persistently higher NPP at tropical latitudes (Fig. 6B,E,G). For the North Indian region, the C model indicated enhanced NPP (0.21 - 0.25 Pg C month$^{-1}$) in the spring (March - late May) and fall (October - December), while the Chl model yielded only a single peak (0.16 Pg C month$^{-1}$) between September and November (Fig. 6G). Both models gave similar magnitude (0.8 to 1.0 Pg C month$^{-1}$), single-peaked annual cycles in NPP for the South Indian region, but the C-based cycle was offset later by roughly 2 months (Fig. 6H). The two models also gave similar magnitude mid-summer maxima in NPP (0.4 to 0.5 Pg C month$^{-1}$) and nearly identical fall declines for the North and South Atlantic, but summer highs for the C model were slower to develop and more sharply peaked than the broad maxima given by the Chl model (Fig. 6A,D). A similar delay in the time of the spring bloom was also indicated for the Southern Ocean by the C model (Fig. 6I). In contrast, timing of the seasonal cycle and annual integrated production were similar for the two models in the North Pacific, but the C model gave a 25% higher summer peak (0.96 Pg C month$^{-1}$) and 27% lower winter minimum (0.12 Pg C month$^{-1}$) in NPP than the Chl model (Fig. 6D). In all northern and southern regions of the Atlantic and Pacific and in the Southern ocean, the C-based model gave lower winter minima in NPP than the Chl-based model (Fig. 6A,C,D,F).

4. DISCUSSION

Quantification of areal net primary production from a limited set of surface observations has been a long standing quest that can arguably be said to have roots in a 1957 paper by John H. Ryther and Charles S. Yentsch. In that seminal contribution, NPP was related to the product of chlorophyll biomass, daily integrated surface solar radiation, an average extinction coefficient for visible light in the water column, and a constant chlorophyll-specific assimilation efficiency of 3.7 g C (g Chl h$^{-1}$) (Ryther & Yentsch 1957). In their approach, which has been progressively developed and expanded upon ever since, chlorophyll functioned as a measure of phytoplankton biomass. An attractive aspect of chlorophyll is that it is uniquely associated with plant material, while a critical drawback is that its relation to carbon is strongly influenced by the physiological state of the phytoplankton assemblage. This later dependency is expressed as changes in the
assimilation efficiency and its importance was already recognized by Ryther and Yensch:

“Probably the weakest point in the foregoing treatment is the photosynthesis-chlorophyll factor. There is little reason to assume that this must be constant under all conditions” (pg 285)

While these authors proposed potential regulating factors for the ‘photosynthesis-chlorophyll’ term (i.e., temperature, light, species composition, season, and time of day), a clear path for globally modeling or remotely observing variability in chlorophyll-specific photosynthesis has even to this day never been identified. Indeed, contemporary physiological descriptions employed in satellite NPP algorithms exhibit little improvement over the assumption of a constant assimilation efficiency (Siegel et al. 2001; Campbell et al. 2002; Behrenfeld et al. 2002).

Here we propose an alternative to chlorophyll-based NPP modeling that builds upon recent field-based evidence that scattering:chlorophyll ratios track changes in phytoplankton physiology (Behrenfeld & Boss 2003). A particularly attractive aspect of this new approach is that each of the four primary variables in the NPP equation (5) can now be linked to satellite observations. This closure is achieved by associating the variable component of $b_{p}$ to changes in the abundance of particles functionally associated with (thus correlated to) phytoplankton carbon biomass. Strong support for this proposition is provided by the ecologically coherent temporal patterns found in Chl, C, and Chl:C ratios for our 28 regions (Fig. 2, SUPPLEMENTAL FIG. 1) and by the remarkable agreement between laboratory- and satellite-based dependencies of Chl:C on light, temperature, and nutrient stress (Fig. 3).

An important point emphasized by our results is that chlorophyll concentration is a poor proxy of phytoplankton biomass over large areas of the ocean. Particularly in low-biomass oligotrophic regions, chlorophyll variability can be dominated by, if not exclusively due to, adjustments in physiological state (i.e., changes in Chl:C resulting from changes in growth conditions). This decoupling between phytoplankton biomass and pigmentation has been indicated in the vertical dimension of the water column (e.g., Kiefer & Kremer 1981; Kitchen and Zaneveld, 1990; Mitchell and Kiefer, 1988; Mitchell and Holm-Hansen, 1991; Fennel and Boss, 2003) and here is simply extended on a global scale to the horizontal dimension. In both the vertical and horizontal dimensions, however, the physiological underpinning for this independent behavior in carbon and chlorophyll biomass is the same: acclimation to changing light, nutrient, and temperature conditions.

The link between satellite Chl:C and phytoplankton physiology established here has benefitted from a variety of factors. For example, excluding optically complex coastal regions and integrating open ocean data over large time (monthly) and space (regional) scales undoubtedly helps remove local-scale variability in the $b_{p}$:C ratio. The wide range of growth conditions in the global oceans also helps create a dynamic range in Chl:C that is sufficient to overcome optically-based changes in the $b_{p}$ to phytoplankton C relationship. Perhaps the most important factor, though, is the apparent compositional stability of natural particle assemblages. Indeed, field studies suggest that over seasonal cycles (DuRand et al. 2001) and across oligotrophic to eutrophic conditions (Oubelkheir 2001) phytoplankton contribute a relatively consistent fraction to POC, although exceptions to this rule certainly exist. For the planktonic
contributors to $b_{bp}$, this relationship may be particularly tight because the rapid potential growth rates of the heterotrophic component allow for a close correspondence between their biomass and phytoplankton abundance.

The quest to quantify areal net primary production over regional to global scales is certainly not over yet, but our results suggest that an important step has been taken in this direction. Already, the carbon-based approach has revealed some unexpected and fascinating temporal patterns in regional NPP (Fig. 6, SUPPLEMENTAL FIG. 2) and raised important questions regarding the functioning of planktonic communities. One particularly intriguing observation has been the bilinear relationship between Chl and $b_{bp}$ (Fig. 1). This pattern suggests that, at least at the regional scale, a minimum exists to which the heterotrophic community is ‘willing’ to graze the phytoplankton (Lessard and Murrell 1998). Is there an energetic justification for this apparent ‘floor’ in phytoplankton abundance? If not, what is the basis for this ‘hinge-point’ between physiologically-dominated and biomass-dominated systems? Another interesting observation has been the organization of regional Chl, C, and Chl:C data into five basic temporal patterns (Fig. 2). Are these patterns simply due to ocean circulation and other physical constraints, or are they also associated with dominant ecosystem modes? Certainly, there is much left to be done here and much left to learn.

4.1 Future directions

A multitude of future research needs and exciting potential applications emerge with this first indication of a space-based optical index of phytoplankton physiology. Clearly of foremost importance is the continued development and validation of derived satellite products, including $b_{bp}$, phytoplankton pigment and carbon biomass, $\mu$, and NPP. These developments will require new field measurements (as there is currently a paucity of such data) and an evolution in satellite ocean color technology that allows better separation of optically-active in-water constituents (e.g., utilizing ultraviolet wavebands to better separate phytoplankton and colored dissolved organic material absorption) and improved atmospheric corrections (e.g., characterization of absorbing aerosol column thickness and heights).

Improvements in the carbon-based approach can also be made in the many steps leading from satellite Chl and $b_{bp}$ to NPP. For example, in (3) we assume that nutrient-dependent changes in Chl:C are paralleled by equivalent changes in $\mu$. However, laboratory studies indicate that when $\mu = 0$ division day$^{-1}$, Chl:C is $> 0$. In addition, we have not yet considered potential taxonomic influences on the relationship between Chl:C and $\mu$, nor have we attempted to adjust the $b_{bp}$ to phytoplankton carbon relationship to account for changes in particle size distributions (often associated with features such as high-latitude spring diatom blooms) or the occurrence of high concentrations of inorganic particles (e.g., coccoliths, suspended sediments). Calculations of NPP might also benefit from expanding the current depth-integrated model (5) into a time-, depth-, and wavelength-resolved model. Relating $\mu$ to phytoplankton absorption:C rather than Chl:C may also be worthwhile, as the former is physiologically more relevant and absorption is operationally closer to ocean color than chlorophyll. Alternative relationships between Chl:C and $\mu$ might additionally be considered for physiologically unique growth conditions, such as in iron-limited high-nutrient, low-chlorophyll (HNLC) waters.
One of the simplifying assumptions in our current estimates of $\mu$ from Chl:C is that surface phytoplankton assemblages are in a state of balanced growth; that is, all cellular constituents (particularly carbon and chlorophyll) are in a fully acclimated state (i.e., growing at the same rate). This assumption allows the use of basic physiological expressions and may very well be valid for the large spatial and temporal scales considered here. However, when physical perturbations to mixed layer growth conditions occur on time scales similar to or shorter than times scales of acclimation, transient episodes of unbalanced growth can ensue. Under such conditions, relationships between Chl:C and $\mu$ become complicated and can require more complex ‘dynamic’ physiological models (e.g., Gießer et al. 1998; Flynn 2001; Flynn et al. 2001) to unravel. This issue of accounting for balanced versus unbalanced growth will be one of the challenges faced in extending the carbon-based approach to smaller space ($< 1 \text{ km}^2$) and time (daily) scales.

A potentially important application for our phytoplankton carbon biomass and growth rate data, beyond quantifying ocean production and detecting its change, is for the development of prognostic ocean circulation-ecosystem models (i.e., ‘coupled models’). In such models, phytoplankton carbon (or nitrogen) biomass and growth rates are primary derived variables. In the past, no remote sensing data has been available to directly test modeled growth rate fields and broad assumptions have been necessary regarding Chl:C ratios (often assumed constant) to compare modeled phytoplankton carbon biomass with satellite chlorophyll data. It will now be possible with the new carbon-based approach to directly compare satellite and model estimates of phytoplankton carbon biomass and growth rates.

5. **Perspective**

Photosynthesis is the primary conduit through which inorganic carbon enters the living components of the biosphere. In addition to linking ecosystem and biogeochemical processes, terrestrial and ocean productivity is functionally dependent on climate and is thus an indicator of temporal change in environmental forcings. Remote sensing is a route through which prohibitive space-time gaps in surface measurements of photosynthesis can be overcome; but photosynthesis is not directly amenable to satellite detection. For the oceans, empirical conversion factors employed to relate satellite data products (i.e., chlorophyll) to production have entailed such large uncertainties that any hope of detecting global change has been compromised.

Here we present a path for retrieving the ‘missing piece’ of the productivity equation from space. Our approach is rooted in well developed physiological dependencies on light, nutrients, and temperature and in a solid understanding of the light scattering and absorption properties of ocean waters. Our resultant carbon-based NPP estimates provide a dramatically different view of how ocean productivity is distributed over space and time and point to the importance of this new development. With future improvements in ocean color remote sensing (i.e., expanded wavebands, improved atmospheric corrections) and algorithm development, the full potential of this carbon-based approach will be realized and, through the resultant closure on the productivity equation, NPP estimates will be achieved with higher fidelity and an improved capacity for detecting real trends in global ocean carbon cycling.
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References


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**Figure Legends**

**Fig. 1** Regional monthly mean particulate backscattering coefficients at 440 nm ($b_{bp}$) and surface chlorophyll concentrations (Chl) for the September 1997 to January 2002 period. Data are from the 28 regional bins identified in Figure 2A. The solid line represents a linear fit to data with Chl > 0.14 mg m$^{-3}$. The dashed line indicates the mean $b_{bp}$ value of 0.0012 m$^{-1}$ for data where Chl < 0.14 mg m$^{-3}$ (i.e., the realm where Chl and $b_{bp}$ are uncorrelated).

**Fig. 2** (A) The 28 regional bins determined by ocean basin and chlorophyll variance. Variance levels ($L_0$ to $L_4$) are indicated by color. Low-production, central ocean gyres with the lowest chlorophyll variance ($L_0$, $L_1$) are outlined in white and separated into northern and southern components. All variance levels in the Indian ocean are also separated into northern and southern components. Moderate- to high variance levels ($L_2$ to $L_4$) in the Atlantic and Pacific are separated into northern, central, and southern components. A single bin was used for all Southern Ocean data (see Methods). Basin designations are: NA = North Atlantic, CA = Central Atlantic, SA = South Atlantic, NP = North Pacific, CP = Central Pacific, SP = South Pacific, NI = North Indian, SI = South Indian, and SO = Southern Ocean. Black = Land. Grey = Arctic and coastal areas not included. (B-F) Examples of the five basic temporal patterns in regional phytoplankton chlorophyll (Chl; ○) and carbon (C; ⬤) biomass and Chl:C ratios (●; mg mg$^{-1}$). Left axis = Chl and C concentration (mg m$^{-3}$), where C has been multiplied by the following factors to scale with chlorophyll: B = 0.004, C = 0.008, D = 0.010, E = 0.014, F = 0.013. Right axis = Chl:C (mg mg$^{-1}$). (B) Pattern observed in regions NA-$L_0$, NA-$L_1$, NA-$L_2$, SA-$L_1$, NP-$L_2$, SP-$L_0$, SP-$L_1$, SI-$L_1$. (C) Pattern in regions CA-$L_2$, SA-$L_0$, NP-$L_0$, NP-$L_1$. (D) Pattern in regions SA-$L_2$, SP-$L_2$, SP-$L_3$, SI-$L_2$, SI-$L_3$. (E) Pattern in regions NA-$L_3$, NA-$L_4$, CA-$L_3$, SA-$L_3$, NP-$L$, NP-$L_4$, NI-$L_2$, NI-$L_3$, SO. (F) Pattern in regions CP-$L_2$, CP-$L_3$. The specific region shown is indicated at the top right of each panel and identified in this legend by **bold blue type** (e.g., panel B = south Pacific, variance level 0). Please refer to Supplemental Figure 1 to view Chl, C, and Chl:C time series for all 28 regions.

**Fig. 3** Changes in phytoplankton Chl:C ratios in response to changes in light, nutrients, and temperature as (A-C) observed in the laboratory and (D-F) derived from satellite ocean color data. (A) Chl:C values measured in monocultures of the marine chlorophyte, *Dunaliella tertiolecta*, grown over a range of light levels (I$g$) at 20 °C and with replete nutrients. (B) Temperature dependence of Chl:C$^{\text{max}}$ for 16 cultured phytoplankton species as reported by Gieder (1987). ○ = Diatoms. ▲ = all other species. (C) Influence of nutrient stress on Chl:C$^{\text{min}}$ in the diatom, *Thalassiosira fluviatilis* (Laws & Bannister 1980). Nutrient stress is quantified by changes in growth rate (x axis). ● = NO$_3$ limited cultures. ○ = NH$_4$ limited cultures. ▼ = PO$_4$ limited cultures. (D) Satellite Chl:C estimates versus I$g$ for 4 of the regions defined in Figure 2A. ● = SP-$L_1$. ▲ = SA-$L_1$. ▼ = SP-$L_2$. ▲ = SA-$L_1$. Fitted curves for all 28 regions are shown in Figure 4A and fit statistics are provided in Table 1. (E) Relationship between sea surface temperature (SST: °C) and fitted values of Chl:C$^{\text{max}}$ for all 28 regions. Solid line = fit to data (Chl:C$^{\text{max}}$ = 0.0155 + 0.00005 exp $^{0.215\ \text{SST}}$) ($r^2 = 0.79$). (C) Relationship between sea
surface temperature (SST; °C) and fitted values of Chl:C_{min} for all 28 regions. Solid line = fit to • data (Chl:C_{min} = 0.017 - 0.00045 SST) (r² = 0.83). ▼ = the six high-temperature outliers (L2 and L3 data from the North Indian, Central Pacific, Central Atlantic). ○ = low-temperature outlier (Southern Ocean). These ‘outliers’ are anticipated based on regional relationships between SST and constraints on phytoplankton growth (see text). Solid line in (A) and (D) = fit of (1). Solid line in (B) = fit of exponential model as in (E). Solid line in (C) = linear regression fit to all data.

Fig. 4. (A) Phytoplankton chlorophyll to carbon (Chl:C) ratios versus mixed layer growth irradiance (I_g). Blue line = modeled maximum Chl:C. Gray lines = fits of (1) to the 28 regions (see Fig. 2A). (B,C) Seasonal mean mixed layer phytoplankton growth rates (µ: divisions d⁻¹) calculated from satellite Chl:C using (2). (B) Boreal summer (June to August). (C) Boreal winter (December to February). (D) Frequency histogram of annual mean satellite-based phytoplankton growth rates.

Fig. 5 Seasonal mean water column net primary production (mg C m⁻² d⁻¹) calculated from (A,B) satellite phytoplankton carbon and growth rate estimates and (C,D) a conventional chlorophyll-based model (the VGPM). The difference between these model NPP estimates (E = A-C, F = B-D) has significant implications on regional carbon cycling. (A,C,E) Boreal summer (June to August). (B,D,F) Boreal winter (December to February).

Fig. 6 Seasonal cycles in net primary production for the nine ocean basins (labeled at the top of each panel) identified in Figure 2A. • = NPP calculated from satellite phytoplankton carbon and growth rate estimates. ○ = NPP calculated using a conventional chlorophyll-based model (the VGPM). Seasonal cycles are based on monthly averages for the 1997 to 2002 period. Data were combined for all chlorophyll variance bins within a given ocean basin. Full temporal patterns in carbon-based and chlorophyll-based NPP for each of the 28 regional bins is provided in Supplemental Figure 2.
Table 1. Mean surface chlorophyll biomass (mg m$^{-3}$), mean sea surface temperature (SST: °C), and range in median mixed layer light levels ($I_g$: moles photons m$^{-2}$ h$^{-1}$) for each region (see Fig. 2 in manuscript) during the September 1997 to January 2002 period. Also provided is Chl:C$_{\text{min}}$, Chl:C$_{\text{max}}$, and correlation coefficients for regional fits of equation 1. Chl:C$_{\text{min}}$ and Chl:C$_{\text{max}}$ [mg Chl (mg C)$^{-1}$] are all significant at p < 0.0005. n.s. = not significant.

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<th>Chl:C$_{\text{max}}$</th>
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Figure 1
Figure 5

Net Primary Production (mg m$^{-2}$) vs Difference (mg m$^{-2}$)

Boreal Winter

B

D

F

Boreal Summer

A

C

E

Carbon-based

Chlorophyll-based

Difference