Phytoplankton Absorption and Assimilation Numbers

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Phytoplankton pigment absorption: A strong predictor of primary productivity in the surface ocean

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Abstract

Over a range of trophic conditions in the ocean, we argue that variations in productivity are more closely related to variations in phytoplankton absorption than to variations in the chlorophyll-*a* (Chl-*a*) concentration. Our analysis suggests that environmental variability is expressed through the absorption properties of phytoplankton pigments rather than their quantity, and that productivity normalized to absorption is relatively invariant in the world ocean. The relationship between primary productivity and phytoplankton absorption makes possible a more direct approach to the estimation of ocean productivity from satellite sensors.

Keywords: Assimilation number; Ross Sea; Arabian Sea; Equatorial Pacific; Package effect; Biogeochemical provinces; Absorption; Quantum yield

1. Introduction

Nearly 50 years ago, Ryther and Yentsch (1957) proposed a method whereby the productivity of the ocean could be calculated from the assimilation number (AN), the light-saturated rate of photosynthesis, or near-surface productivity, normalized to chlorophyll-*a* (Chl-*a*) (e.g., Cullen et al., 1992). To arrive at water-column productivity, Ryther and Yentsch (1957) used AN scaled to a relative photosynthesis rate based on irradiance and the light extinction coefficient. Using data from the literature, they calculated a mean value for the AN of $3.7\,\mathrm{g\,C\ (g\,Chl)^{-1}\,h^{-1}}$. One of their conclusions was that much of the observed variability in AN is "undoubtedly due to errors in the measurement," although they recognized that a number of environmental factors could influence its value. The AN relates the rate of primary production to an index of the autotrophic biomass, specifically, chemically extracted Chl-*a*, providing an indication of the growth rate and turnover time. The residual variability may be examined with respect to environmental factors, light, nutrients, temperature, etc.

Ryther and Yentsch's (1957) conclusions stimulated a major effort to study how AN might be

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regulated by these environmental factors (see Cullen et al., 1992), as well as efforts directed at the mechanisms of photoadaptation in phytoplankton. Since that time, AN has been found to vary from <0.5 to about 25, almost two orders-of-magnitude (Glover, 1980; Falkowski, 1981). Eppley (1972) used AN to calculate growth rates in phytoplankton, by employing the ratio of carbon to Chl-*a* (C/Chl). Platt and Gallegos (1980) introduced the 'scaled rate' of photosynthesis, or P^B, which is dimensionally equivalent to AN, and later Behrenfeld and Falkowski (1997) defined a variant of this, P^B_{opt}, to represent a near-surface value of P^B for use in remote sensing studies. With satellite ocean color expressed as Chl-*a*, productivity can be easily calculated from knowledge of AN (or P^B). Despite its limitations, Chl-*a* has been widely used as an index of phytoplankton abundance. The method of deriving areal productivity from Chl-*a* integrated over the euphotic zone (Eppley et al., 1985) was subsequently used, for example, by Campbell and O'Reilly (1988) and Antoine et al. (1996). AN also underlies models for phytoplankton growth that which are based on the C/Chl ratio (e.g., Geider et al., 1998).

Here we further explore the utility of AN using a comprehensive suite of measurements taken during the Joint Global Ocean Flux Study (JGOFS), an international program designed to improve understanding of the ocean's carbon cycle (Hanson et al., 2000). 'Process studies' were carried out in JGOFS for a variety of trophic conditions and included extensive observations of primary productivity, phytoplankton pigments and absorption characteristics, and ocean optical properties. Furthermore, the program was carried out using consistent measurement protocols (JGOFS, 1996). Thus, the JGOFS data permitted a contemporary analysis of the relationship among productivity, pigments, and absorption, with a goal to improve algorithms for estimating productivity from satellite ocean color or shipboard observations.

JGOFS Process studies were conducted from 1989 to 1998, and the US participated in the North Atlantic Bloom Experiment, the Equatorial Pacific Process Study (EqPac), the Arabian Sea Expedition (ASE), and the Antarctic Ecosystem and Southern Ocean Process Study (AESOPS). We examined data from the last three of these, in which phytoplankton absorption measurements were routinely determined, and where the methods for measuring phytoplankton pigments had matured. Most of the data were contemporaneous samples for (1) measurements of primary productivity based on the assimilation of ^{14}C in in situ incubations (Knudson et al., 1989; Barber et al., 1996), (2) phytoplankton absorption spectra (see below) and (3) phytoplankton pigments via high-performance liquid chromatography (Bidigare et al., 2002). [Most of these data (and their contributors) are available at the website: http://usjgofs.whoi.edu.]

2. Primary productivity and Chl-*a*

Fig. 1 shows daily productivity plotted against Chl-*a*. These data are from the near surface (<10 m) because of the importance of evaluating productivity from passive satellite ocean color sensors. The slope of these data is AN. Interestingly, in samples from the equatorial Pacific, the Arabian Sea, and the Southern Ocean (south of New Zealand, February–March), the values for AN are relatively constant. For the Ross Sea (NBP97-1), on the other hand, the Chl-*a* data are widely scattered and estimates of AN are much lower than for the other areas. We have plotted example line segments on the graph corresponding to AN's of 5, 1.5, and 0.9 to show the variability that can be observed. There have been many explanations for why AN's from the Ross Sea (and other areas of the Southern Ocean) are much lower than those observed in other ocean regions, including low temperatures (Tilzer et al., 1986), low irradiances (Mitchell and Holm-Hansen, 1991), or a low rate of supply of a trace element such as iron (Smith et al., 2000). We will show, however, that the variability in the relationship between primary production and phytoplankton pigments observed for these data may be much less, or non-existent, if the absorption properties of intact phytoplankton cells are considered instead of the extracted pigments. That is, an optical biomass index is better than a chemical index of biomass for scaling photosynthesis. Before proceeding to an analysis of absorption and productivity, we briefly review methods used to measure phytoplankton absorption properties.

3. Phytoplankton absorption methods

There are two commonly used methods for estimating absorption by pigments in phytoplankton cells and both have ambiguities. In the first method, called the 'filter pad technique' (FPT), particulate matter (including phytoplankton) is

concentrated on a filter and scanned in a spectrophotometer to produce an absorption spectrum over visible wavelengths (Yentsch, 1962; Mitchell and Kiefer, 1988; Mueller and Austin, 1995). The filter is then washed in hot methanol to remove the pigments (Kishino et al., 1985) and re-scanned. What remains on the filter is assumed to be detrital material. The difference between detrital and particulate spectra, therefore, gives an estimate of phytoplankton pigment absorption. A correction is applied to the spectra to account for the increased scattering caused by the interaction of the particles and the glass-fiber filter. There are other variations to this method, for example the filter-freeze-transfer method (Allali et al., 1995), and the use of NaClO instead of a hot methanol wash (Tassan and Ferrari, 1995), but these will be subject to some of the same issues as the FPT.

In the second method, called 'pigment reconstruction' (PIG), pigments from the filtered particulate material are chemically extracted into an organic solvent (e.g., acetone), and then separated and quantified by high performance liquid chromatography (HPLC). The phytoplankton absorption spectrum is reconstructed from the quantity of pigments and the pigment-specific absorption coefficients as a function of wavelength (Bidigare et al. 1990), using the equation

$$a_{\mathrm{ph}}(\lambda) = \sum a_i^*(\lambda) C_i,$$

where $a^*(\lambda)$ is the specific absorption coefficient for pigment (or pigment group) i and C is the concentration of pigment i.

Neither the FPT nor the pigment reconstruction method gives a true measure of phytoplankton absorption in the ocean, although both have their advantages. In the filter pad technique, colored compounds from sources other than phytoplankton are typically included in the particulate spectra, and are washed out with the methanol extraction (Nelson et al., 1993). The additional particulate absorption thus leads to an overestimation of the phytoplankton component (Bricaud et al., 2004).

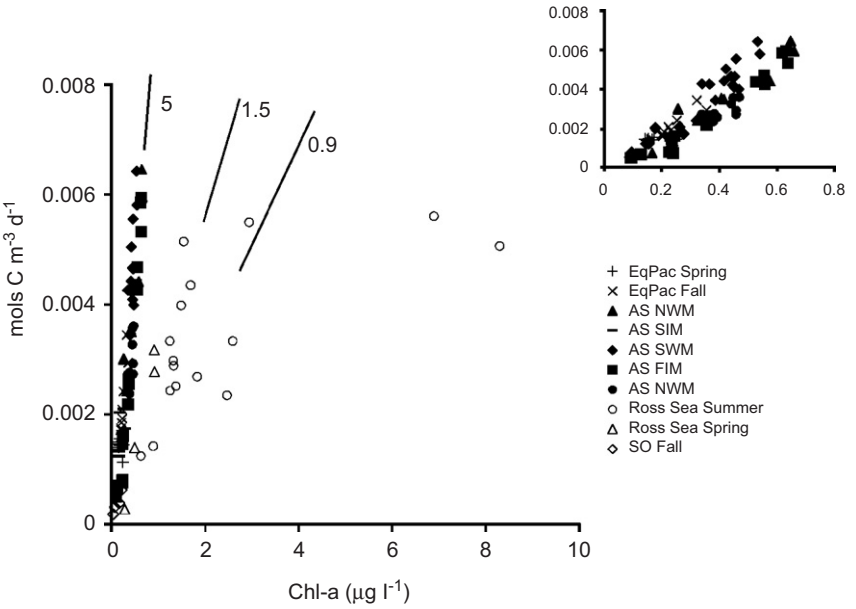

Fig. 1. Near-surface primary productivity (y-axis) plotted against Chl-a (measured by HPLC) using data from the equatorial Pacific [EqPac Spring (TT008) and Fall (TT012)], the Arabian Sea [AS Northwest Monsoon (NWM; TTN043, TTN054), Spring Intermonsoon (SIM; TTN045), Southwest Monsoon (SWM; TTN049), Fall Intermonsoon (FIM; TTN053)], the Ross Sea (Summer, NBP97-1) and the Southern Ocean south of New Zealand [SO Fall (RR-kiwi-9)]. The line segments correspond to assimilation numbers (AN's) or near-surface P^{B}'s, of 5, 1.5, and 0.9 mg C (mg Chl)$^{-1}$ h^{-1}. (To improve visualization of these data, three high data points from TT049 are not plotted, but correspond to an AN$\approx$5). The linear regression of the low-latitude data (EqPac, Arabian Sea) in units of AN, is $y = 4.76(\pm 0.54)x - 0.22(\pm 0.19)$, where the errors are the 95% confidence intervals, and $r^2 = 0.78$. The inset shows data for Chla $< 0.8\ \mu g\ l^{-1}$. The productivity data are the means of two replicate incubations at each depth. HPLC analyses for Chl-a are based on single samples collected simultaneously with the productivity samples (Arabian Sea, Southern Ocean) or on adjacent hydrographic casts (EqPac). Documentation regarding these data can be found at the US JGOFS website, http://usjgofs.whoi.edu.

We have evaluated the overestimate empirically by comparing the spectrally averaged absorption using the pigment reconstruction method with the FPT. Using data from the ASE, the overestimate of the FPT over pigment reconstruction can be as high as a factor of two (Fig. 2). In theory, absorption based on pigment reconstruction should equal or exceed absorption from the FPT, thus Fig. 2 shows clearly the artifact of the method.

The pigment reconstruction method, which measures only phytoplankton pigments, avoids artifacts associated with the FPT, but suffers from two other problems. First, not all pigments are soluble in acetone or methanol, e.g., water-soluble phycobiliproteins in cyanobacteria. Second, the absorption coefficients for many pigments are not known or well quantified (Bidigare et al., 1990). The advantage with the filter pad technique is that absorption is measured from pigments as they exist within the intact cells, giving a more accurate representation of absorption as it occurs in situ. The advantage of using pigment reconstruction is that only phytoplankton pigments are included in the spectra. Pigment reconstruction, therefore, can have an advantage over the FPT, but important information is lost as to how pigments might affect absorption of irradiance and subsequent photosynthesis.

In summary, current methods only approximate the portrayal of phytoplankton absorption. Despite these shortcomings in absorption methods, we now show that phytoplankton absorption is a more appropriate quantity than Chl-*a* for use in normalizing productivity, especially where biomass is high. Over the large range of trophic conditions present in the global ocean, variations in productivity are more closely related to variations in phytoplankton absorption than to variations in the Chl-*a* concentration. To understand the variability in productivity in the ocean and the relationships between this variability and environmental factors, we would be better served by examining productivity normalized to absorption rather than productivity normalized to Chl-*a*.

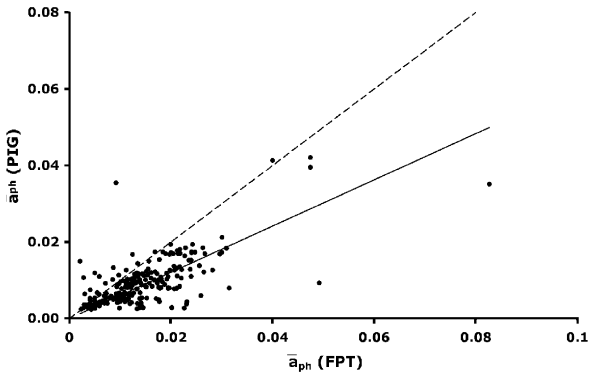

Fig. 2. A comparison between spectrally averaged absorption by phytoplankton (a_{ph}), based on pigment reconstruction (PIG) and the filter-pad technique (FPT), from near-surface values. The solid line is a trend-line, with an intercept at zero, and where $y = 0.62x$; the dashed line is the 1:1 relationship. Theoretically, a_{ph}(PIG) should always be greater than a_{ph}(FPT) because of the package effect, indicating that, on average, the FPT method is biased high by about 38%.

4. Productivity, absorption, and packaging

Fig. 3 shows data similar to Fig. 1, except that now, a_{ph} (spectrally averaged) is on the *x*-axis instead of Chl-*a*. For clarity, we have shortened the *x*-axis so as not to include the points corresponding to the two highest Chl-*a* values in Fig. 1. We have also incorporated a linear regression line, representing surface ocean data for EqPac and ASE. Data from the Ross Sea (NBP97-1) is plotted in three ways. First, the dark open circles are a_{ph} values from pigment reconstruction. Since they are a reflection of pigment concentration, they show about the same relationship to the low latitude data as in Fig. 1. The lighter shaded open circles are a_{ph} values from the FPT. There is a large difference

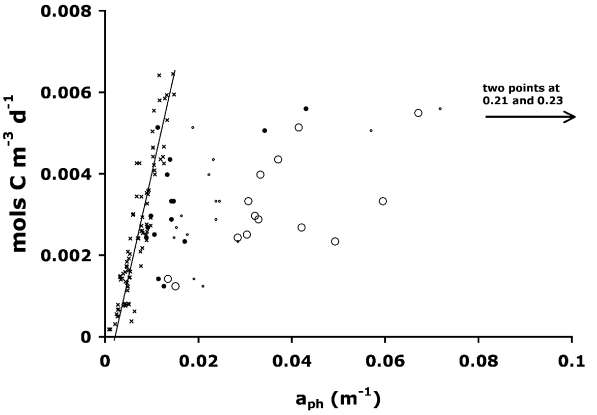

Fig. 3. Primary production (*y*-axis) plotted against a_{ph}. The *x*-axis has been truncated to $a_{ph} = 0.1\ m^{-1}$ for clarity, omitting two high data points. The data (*x*'s) from the equatorial Pacific and Arabian Sea is described by the Model II linear regression ($\pm$std. dev.), $y = 0.51(\pm 0.023)x - 0.0011(\pm 0.0001)$ ($r^2 = 0.84$). The open circles are a_{ph} from pigment reconstruction. The smaller open circles are a_{ph} data from the FPT method. The filled circles are a_{ph}(FPT) data corrected for excess absorption, according to Fig. 2 (i.e., a reduction of 40%). The data needed for the PIG/FPT comparisons were only available for NBP97-1.

between the pigment reconstruction (PIG) and FPT values, with the FPT values closer to the regression line. Above we showed how FPT values *overestimate* phytoplankton pigment absorption (see Fig. 2). Correcting the FPT values by a factor (40%) representing the overestimate gives the smaller filled circles in the graph. These data are now even closer to the low-latitude data.

The difference between the pigment reconstruction and FPT values for a_{ph} is from pigment packaging. Pigment packaging (the 'package effect') arises from intracellular shading of the chloroplasts on one another, and is revealed by the ratio between the absorption of pigments in solution (using pigment reconstruction), and pigments inside cells in suspension (using the FPT) (Kirk, 1986). This ratio will always be <1. Kirk (1986) further shows that packaging will be a factor for cell diameters greater than 10 μm, thus pigment reconstruction should give a fairly accurate expression of absorption for low latitude regimes where cell sizes are typically small. The Arabian Sea and equatorial Pacific have communities of small cells, while the communities in the Ross Sea and other areas of the Southern Ocean are usually characterized by large-cell species, such as diatoms. For the Southern Ocean, the importance of pigment packaging has been known for some time (Mitchell and Holm-Hansen, 1991), but to our knowledge, its relationship to primary productivity has not been previously appreciated.

Based on the data from Fig. 3, we hypothesize that primary productivity normalized to phytoplankton absorption is conserved in the surface ocean, regardless of the oceanic regime. The absorption measurements based on corrected FPT data from the Ross Sea are still higher, on average than the low latitude data; comparing the mean and standard deviation values of the productivity:a_{ph} ratio for Ross Sea data with the mean of the same ratio for the low-latitude data shows a significant difference (t-test, $n = 15$, 95% probability). The difference in the means for productivity:a_{ph} data weakens support for our hypothesis. We point out, however, that the overestimate in the FPT data, which we use for correction, is based on an average itself (from Fig. 2). In Section 6, below, we present other arguments to support our hypothesis. However, one other explanation for the higher absorption in the Ross Sea data relative to productivity could be because of increased absorption by pigments that do not contribute to photosynthesis, the so-called 'photoprotectant carotenoids.' The largest concentration of these carotenoids (relative to photosynthetic pigments; data not shown) occurs in the Arabian Sea during the intermonsoon periods (the SIM and FIM data in Fig. 1). The Ross Sea data have the same proportion of photoprotectant carotenoids as occurs during the Arabian Sea monsoon cruises (NWM, SWM). Thus, the variability in a_{ph} caused by acclimation to high irradiances is within the variability observed for the low-latitude data in Fig. 3.

5. Rate of absorption of irradiance

Knowing absorption and productivity allows an examination of the quantum efficiency of photosynthesis through the rate of absorption of irradiance. The rate of absorption of irradiance can be thought of as the ultimate limiting step in photosynthesis (Kirk, 1994, p. 261), and can be expressed as

$$a_{ph}(z)E_0 \exp(-k_{PAR}z),$$

where E_0 is the surface scalar irradiance (mols photons $m^{-2}d^{-1}$), k_{PAR} is the attenuation coefficient (m^{-1}) for PAR, and z the depth in meters below the sea surface. Fig. 4 illustrates this relationship between phytoplankton irradiance absorption and productivity for the surface layer of the ocean, where there are data available. The ratio of these two variables provides an estimate of the quantum efficiency of photosynthesis. Because we are introducing another

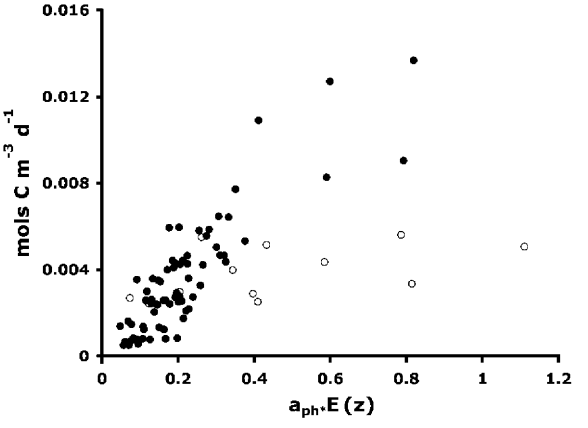

Fig. 4. Primary productivity vs. the rate of absorption by irradiance (x-axis). The slope of this line will be an estimate of the quantum efficiency. The closed symbols are from data from the ASE; open symbols are from the Ross Sea (AESOPS; NBP97-1). Absorption values used to calculate the rate of absorption are a_{ph}(PIG) for ASE and a_{ph}(FPT) for the Ross Sea.

variable, the data in Fig. 4 are more scattered. Most of the data, however, suggest a quantum efficiency of 0.020 ± 0.004, or about one-sixth the maximum value (Kirk, 1994). Oliver et al. (2004) suggest a mean quantum efficiency of 0.025 for temperate waters, while their reported quantum efficiency estimates for areas around the Antarctic Peninsula are much higher. The quantum efficiency estimates from the Ross Sea (NBP97-1) are below what might be expected. The reason for this departure is unclear, except that we note that this cruise took place at the end of the seasonal growth period (see Smith et al., 2000).

6. Discussion

Our main hypothesis is that productivity normalized by phytoplankton absorption is constant in the surface ocean and can be supported by the following argument.

Conditions in the ocean drive phytoplankton community structure (Margalef, 1978). Phytoplankton community structure can be defined in terms of its pigment composition (Mackey et al., 1996; Vidussi et al., 2001). In addition to being an important determinant of phytoplankton taxonomy, pigment composition is the determinant of phytoplankton absorption properties. Therefore, the absorption properties of phytoplankton are a response to environmental factors (Claustre et al, 2005), and perhaps govern, or at least indicate their physiological rates (Cullen, 1990). If our hypothesis can be corroborated with further measurements, it has great significance for biological oceanography. It means that near-surface productivity can be expressed in terms of phytoplankton absorption regardless of the temperature, nutrient, or irradiance regime.

To be sure, we have not been able to support our hypothesis statistically. We have done a retrospective analysis of a limited data set. For example, our data for significant package effect comes exclusively from the summertime Ross Sea. Nonetheless, we can present indirect evidence from other environments that support the idea that absorption may be the more useful property to explain the variations in productivity in the surface ocean.

It is generally true that when Chl-*a* increases, cell size also increases (e.g., Bricaud et al. 1995; Ciotti et al. 2002). When the mean cell size of a population increases, packaging increases, and absorption efficiency decreases along with decreases in AN. Thus, if Chl-*a* increases in a particular region, we should see a decrease in AN if pigment packaging is affecting primary productivity. We have researched the literature and found several instances where increases in Chl-*a* are accompanied by decreases in AN, and offer the following examples from at-sea programs.

Example 1: Muller-Karger et al. (2001) present a summary of productivity data from the program 'Carbon Retention in a Colored Ocean (CARIACO). CARIACO is a time series project with a station in the Cariaco Basin, north of Venezuela. The annual cycle is divided into periods of upwelling (January–May) and stratified (June–December) conditions. Sea surface temperatures range from 21 to 29 °C. During the upwelling period, Chl-*a* typically increases to 6–10 $\mathrm{mg\,m^{-3}}$ (their Fig. 5). At the same time, the AN declines from about 10 to 2 (their Fig. 7). Other data from the time series indicate that diatoms are dominant during the upwelling period. Thus, these changes suggest, indirectly, that the package effect may be influencing the AN.

Example 2: Mitchell-Innes and Walker (1991) report a 3-week occupation of station in the Benguela upwelling area, off Namibia. During that time, they show time series data of Chl-*a*, productivity, the productivity index (which at the surface is AN), and the dominant phytoplankton species (their Fig. 2). Early in the station occupation, they show a bloom of *Coscinodiscus* sp., a large diatom. As the bloom develops to values of 20 $\mathrm{mg\,m^{-3}}$ of Chl-*a*, productivity also increases, but AN remains relatively constant at 2. Later on, 'microflagellates' dominate the phytoplankton community, and Chl-*a* increases, along with increases in AN to values of around 6. In each case, the AN reflects more the change in the species composition than environmental changes. These authors recognize that pigment packaging might have been a factor in causing the lower AN's during the *Coscinodiscus* bloom. AN (or PI, as they indicate it) is lowest where Chl-*a* is highest (*Coscinodiscus* sp. bloom). On the other hand, PI increases with the increase in Chl-*a* during the period when small phytoplankton dominate the autotrophic community.

Example 3: Malone (1971) is a study of the dynamics of net- and nano-plankton in the California Current system, where netplankton are defined as those retained on a 20 μm mesh screen. Netplankton, on average, had AN's about half that of the nanoplankton, and this difference he explains

through biomass export and grazing. For example, netplankon are more likely to sink, and nanoplankton more likely to be grazed and to be exported out of the system. Grazing and export are adequate explanations, but they do not exclude differences in physiology (Parsons and Takahashi, 1975). It is possible that the netplankton have lower absorption efficiencies from greater pigment packaging than is the case for nanoplankton. The package effect becomes significant for cell sizes $>10\,\mu m$ (Kirk, 1986), which is the effective size separation for the $20\,\mu m$ mesh screen used to separate the populations (Malone et al., 1979).

Example 4: Montecino and Quiroz (2000) report a thorough analysis of the size structure of productivity, the AN, and Chl-*a* for the phytoplankton community in the Chilean upwelling system. In a plot of productivity against Chl-*a*, for example, when Chl-*a* exceeds $1\,mg\,m^{-3}$, the productivity values fall below that which might be predicted from lower Chl-*a* values. These authors conclude that AN (or, P^B) of the smaller phytoplankton is significantly higher than the larger-sized phytoplankton fraction.

Other examples include data found in Table 1 of Ruttlant and Montecino (2002) and Medina-Gomez and Herrera-Silviera (2006). For Ruttlant and Montecino (2002), Chl-*a* data are reported as areal values; nevertheless, there is a decline in AN with greater Chl-*a* standing crops closer to the Chilean coast and coastal upwelling. The data of Medina-Gomez and Herrera-Silviera (2006) show a large increase in Chl-*a* coinciding with a decrease in AN in a coastal lagoon in Mexico.

Again, our hypothesis is that for the open ocean, near-surface, daily primary production can be estimated from a relatively simple parameter: phytoplankton absorption. The relationship suggests a new, perhaps more direct approach to estimating productivity from earth-orbiting satellites, provided that phytoplankton absorption can be retrieved from surface ocean reflectance (Lee et al., 2002; see also Lee et al., 1996). In a sense, the relationship in Fig. 3 suggests that AN or P^B for marine phytoplankton anywhere in the surface ocean varies within a small range, and thus functional expressions relating AN to temperature (Behrenfeld et al., 2002) (for example) may not be necessary. The reason for the commonly observed low ANs in the Southern Ocean and Ross Sea (Fig. 1) is not, in a proximate sense, because of low temperatures or low irradiance (e.g., Tilzer et al., 1986), but because of pigment packaging and community structure.

Cullen (1990) has re-examined the analysis of Ryther and Yentsch (1957) concluding that AN depends on irradiance and Chl-*a*. He also has updated the model of Ryther and Yentsch (1957), based on the overestimate of Chl-*a* with earlier spectrophotometric methods, and finds an average AN of $4.8\,g\,C\,(g\,Chl)^{-1}\,h^{-1}$, which is similar to the value we show for areas of the ocean where the quantity of Chl-*a* itself (and not the absorption) can be used to estimate productivity (Fig. 1). Furthermore, like Cullen (1990), our results suggest that variation in productivity normalized to absorption does not depend directly on the nutrient concentration or supply. The data (see http://usjgofs.whoi.edu) encompass a range of regimes with variations in the potential limiting nutrient and in nutrient supply. We extend Cullen's (1990) analysis in three ways. First, we find that the absorption properties are more important predictors of daily productivity in some environments than the quantity of chemically extracted Chl-*a*. Second, temperature may not be useful in predicting productivity; the data from the Antarctic, at least, are consistent with data from low-latitude waters if pigment packaging is taken into account. Third, we have been able to establish relationships with field data from very different environments. We agree with Cullen (1990) on one point: that simple models of photosynthesis in the ocean may be as powerful as those that are more complicated.

There are several cautions to our analysis. First, we have not been able to find comparable data from the temperate ocean, where we can expect strong seasonality and which often exhibits phytoplankton blooms. Nor do we have the appropriate kinds of data from the ocean's central gyres. However, for temperate oceans, the phytoplankton species characteristic of blooms (e.g., diatoms, *Phaeocystis*) are also common to the Southern Ocean. Second, although the ^{14}C method is the most commonly used standard by which to evaluate algorithms for calculating productivity from space (Campbell et al., 2002), the method necessitates holding the samples at particular depths during incubations. The ^{14}C method may (Chipman et al., 1993), or may not (Marra et al., 1995) represent the daytime drawdown of CO_2 in situ, depending on the dynamics of the mixed layer. Third, there is no standardized method available for the analysis of the phycobiliproteins, a pigment group associated

with a component of the pico-phytoplankton community (cyanobacteria) in tropical, near-surface waters (Waterbury et al., 1979). Fourth, we have not yet extended our analysis to deeper depths in the euphotic zone, but we expect the ratio of primary productivity to absorption to decline in regular manner with optical depth.

Our findings have implications for future studies of the productivity of the ocean by affording a simple means for calculating productivity from space, as well as estimating the daily rate of productivity from shipboard. Our results also have ecological ramifications. We can regard the phytoplankton pigment absorption to be the cumulative response to environmental factors such as irradiance, temperature, and nutrients (Claustre et al., 2005). In this sense, phytoplankton near the surface may have the same relationship to daily primary productivity whether they are growing in the Antarctic at 0 °C and low irradiances, or at the high irradiances and high temperatures of the equatorial Pacific or Arabian Sea. Thus, it is not temperature or irradiance that indicate the low productivity in, for example, the Ross Sea, as much as these environmental factors selecting for phytoplankton species and their absorption characteristics. While our finding of a reasonable relationship (Fig. 3) between absorption and production among three distinct oceanic regimes is encouraging, there is certainly a need for more data, and which should be examined with regard to variations across oceanographic or biogeochemical provinces (Longhurst et al., 1995).

Acknowledgments

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