An optical index of phytoplankton photoacclimation and its relation to light-saturated photosynthesis in the sea

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AN OPTICAL INDEX OF PHYTOPLANKTON PHOTOACCLIMATION AND ITS RELATION TO LIGHT-SATURATED PHOTOSYNTHESIS IN THE SEA

ABSTRACT:

In relation to understanding ocean biology at the global scale, one of NASA's primary foci has been measurements of near-surface concentrations of phytoplankton chlorophyll. Chlorophyll is an important light-absorbing pigment in phytoplankton. The absorbed light energy is used to fix carbon in the process of photosynthesis. Photosynthesis, in turn, is critical to the growth of phytoplankton and the function of entire marine ecosystems. Thus, the use of satellite surface chlorophyll data to estimate primary production in the ocean has been a key focus of much biological oceanography research. One of the major challenges in this research is to develop relationships that allow a given chlorophyll concentration (a standing stock) to be interpreted in terms of carbon fixation (a rate). This problem centers on the description of the light-saturated photosynthetic rate, Pbmax. In this paper, we describe how optical measurements of light attenuation provide information on particulate organic carbon (POC) concentrations. We then show how the ratio of POC to chlorophyll (θ) provides critical information on variability in Pbmax. We then test this relationship between θ and Pbmax using field data from a variety of open ocean ecosystems.

SIGNIFICANCE:

The significant finding of this research is that remote sensing data on chlorophyll and particulate backscattering may provide important information on physiological variability in mixed layer phytoplankton. Specifically, the optically-derived ratio of particulate organic carbon concentration to chlorophyll concentration is related to first order to variability in the light-saturated photosynthetic rate, Pbmax. Variability in Pbmax is one of the primary uncertainties in quantifying oceanic photosynthesis at the global scale and detecting its temporal change. Thus, the results of this study are relevant to NASA's interest in improving our ability to understand primary production in the sea.

ABSTRACT

The characterization of physiological variability in phytoplankton is a primary source of uncertainty in estimates of global ocean primary production. While remote sensing data has provided critical information on the distribution of phytoplankton chlorophyll biomass, the conversion of such data into photosynthetic rates has largely remained dependent on empirical relationships derived from a limited pool of field and laboratory observations. Here we investigated the relationship between field measurements of chlorophyll-normalized, light-saturated photosynthesis (P^b_{max}) and optically-derived estimates of the phytoplankton carbon to chlorophyll ratio (θ). For a variety of ocean regions, P^b_{max} and θ exhibited a remarkable degree of covariance. Using laboratory data for two marine diatom species, this first-order correlation between P^b_{max} and θ was shown to result from a shared influence of photoacclimation. The significance of these results is that they document a relationship between a bio-optical parameter that can be retrieved from space (θ) and a physiological parameter that is critical for estimates primary production in the sea.

INTRODUCTION

Historical estimates of global phytoplankton photosynthesis have ranged from 20 to ~100 Pg C y^{-1} (Pg = 10^{15} g) (Barber & Hilting 2002). Remote sensing retrievals of near-surface phytoplankton chlorophyll concentrations now constrain global estimates to between ~30 and 60 Pg C y^{-1} (Longhurst 1995, Antoine et al. 1996, Field et al. 1998, Behrenfeld et al. 2001). A primary uncertainty remains, however, in the characterization of phytoplankton assimilation efficiencies (i.e., the chlorophyll-specific efficiency of carbon fixation). At the center of this problem is the description of variability in the light-saturated, chlorophyll-normalized photosynthetic rate, P^b_{max} (Behrenfeld & Falkowski 1997a,b; Behrenfeld et al. 2002a).

Photoacclimation is a primary determinant of P^b_{max} in nature, due to associated changes in cellular pigmentation (Behrenfeld et al. 2002b). Photosynthesis at light saturation (P_{max}) is limited by the carbon fixing reactions 'downstream' of the light harvesting electron transport chain (Kok 1956, Stitt 1986; Sukenik et al. 1987; Orellana and Perry 1992, Behrenfeld et al. 1998); specifically, by the reactions of the Calvin cycle. Phytoplankton can respond to a decrease in growth irradiance by increasing light harvesting (thus, cellular chlorophyll) without necessarily changing their Calvin cycle capacity (Sukenik et al. 1987). Normalizing P_{max} to chlorophyll (denoted by the superscript 'b') thus causes P^b_{max} to decrease with decreasing light (Behrenfeld et al. 2002b). Increases in pigmentation resulting from low-light acclimation also cause a decrease in cellular carbon to chlorophyll ratios (θ) (Geider 1987, Anning et al. 2000, MacIntyre 2001). Consequently, we can anticipate P^b_{max} and θ to covary to some degree because of the common influence of photoacclimation. From a productivity modeling perspective, this correlation between θ and P^b_{max} is significant because θ, unlike P^b_{max}, can be estimated from optical measurements alone (Morel 1988, Chung et al. 1996, Claustre et al. 1999) and thus may be accessible from remote sensing (Stramski et al. 1999; Loisel et al. 2001).

In the field, particulate organic carbon concentrations (POC) are highly correlated with red-light (~660 nm) beam attenuation (c) measured with a transmissometer (e.g., Bishop 1999,

Bishop et al. 1999). At 660 nm, dissolved substances (such as chromophoric dissolved organic material, CDOM) do not significantly contribute to beam attenuation, so c can be expressed as the sum of two components: attenuation by water (c_w) and suspended particles (c_p) (i.e., $c = c_w + c_p$ (Pak et al. 1988)). Since c_w is a constant for pure seawater, the relationship between c and POC or particulate matter concentration (PMC) can be simplified to a correlation with c_p alone. A variety of, generally linear, relationships have been described between c_p and POC (or PMC) (e.g., Gardner et al. 1993,95, Siegel et al 1989, Walsh et al. 1995, Loisel & Morel 1998, Claustre et al. 1999). Differences between these relationships largely reflect variability in particle quality (e.g., shape, refractive index, & size distribution (Gardner et al. 1993)) and methodological differences in transmissometer and POC measurements (Bishop 1999).

For oceanic particle size distributions with a Junge-like differential slope of ~4, the 0.5 to 20 μm particulate size fraction contributes greatest to c_p variability (Morel 1973, Stramski & Kiefer 1991, Boss et al. 2001). This range encompasses a bulk of the phytoplankton size distribution in the open ocean and makes c_p a potential optical measure of phytoplankton carbon biomass. To first order, c_p and chlorophyll covary because both are dependent on the numerical abundance of phytoplankton (Morel 1988, Loisel & Morel 1998). However, c_p is relatively insensitive to variability in intracellular chlorophyll (Kitchen & Zaneveld 1990, Loisel & Morel 1998), so the ratio of c_p to chlorophyll (i.e., θ_{cp}) has been used as an index of θ (Pak et al. 1988, Morel 1988, Chung et al. 1996, Claustre et al. 1999).

In stratified water columns, vertical changes in θ_{cp} appear consistent with light-dependent changes in cellular chlorophyll (Kitchen & Zaneveld 1990). If the dominant causative mechanism for this vertical structure is indeed photoacclimation, it follows that horizontal and temporal variability in mixed layer θ_{cp} will likewise register changes in surface irradiance, day length, light attenuation, and mixing depth. However, a direct comparison between θ_{cp} and an independent, photoacclimation-sensitive measure of algal physiology has not yet been made. Consequently, the utility of θ_{cp} as an index of physiological variability remains unverified. Here, we describe the relationship between θ_{cp} and light-saturated photosynthesis. Published laboratory data are used to discuss how θ and P^b_{max} vary with growth irradiance (I_g), photoperiod, and growth rate (μ). Historical field data are then used to compare spatio-temporal variability in θ_{cp} and light-saturated photosynthesis. Our results indicate that θ_{cp} can provide critical information on physiological variability in mixed layer phytoplankton and, if accurately retrieved from remote sensing data, could significantly improve global estimates of oceanic productivity.

METHODS

Laboratory Studies

Laboratory data were from continuous culture experiments with the marine diatom, *Thalassiosira fluviatilis* (Laws & Bannister 1980) and semi-continuous culture experiments with the marine diatom, *Skeletonema costatum* (Sakshaug et al. 1989). In the former study, *T. fluviatilis* was limited by either NO_3, NH_4, PO_4, or light, daylength was constant at 12 h, μ ranged from 0.05 to 1.15 d^{-1}, I_g ranged from 0.016 to 0.752 mole quanta m^{-2} h^{-1}, and θ varied from 18 to 336. During the later study, *S. costatum* was grown in NO_3-limiting or N:P-balanced

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medium, daylength ranged from 6 to 24 h, μ ranged from 0.10 to 1.4 d^{-1}, I_g ranged from 0.043 to 4.33 mole quanta m^{-2} h^{-1}, and θ varied from 22 to 786. For both studies, measurements were always made after a given culture reached steady state for its particular set of growth conditions.

Field Studies

Field data were assembled from the 5 oceanographic studies described below. For each study, light-saturated photosynthesis was determined by ^{14}C-uptake measurements, chlorophyll concentrations (*chl*: mg m^{-3}) were measured by high-performance liquid chromatography (HPLC), and beam attenuation (*c*) was measured with a Sea Tech 25 cm pathlength transmissometer (660 nm). θ_{cp} was calculated as: $\theta_{cp} = s_1 \times c_p \times chl^{-1}$, where s_1 is a single scalar (10 mg C m^{-2}) applied to all 5 data sets and $c_p = c - c_w$. The appropriate value for c_w is influenced by instrument calibration, fouling, and drift. The attenuation coefficient at 660 nm is ~0.41 m^{-1} for pure seawater (Pope & Fry 1997) and is little affected by variations in salinity or temperature (Pegau et al. 1997). However, Sea Tech transmissometers are factory calibrated to give a value for c_w of 0.364 m^{-1} in deep, clear waters. Thus, the c_w values applied here were generally close to or equal to this value of 0.364 m^{-1}, as detailed below.

Hawaii Ocean Time-series (HOT) — Depth profiles of c_p, chlorophyll, and photosynthesis collected at Station Aloha (22°45' N, 158° W) between September 1989 and December 1999 were extracted from the web site: http://hahana.soest.hawaii.edu/hot/hot_jgofs.html. Primary production measurements were conducted on samples collected from 8 depths and involved both *in situ* and simulated *in situ* incubations (sunrise to sunset) between 1989 and 1990, and *in situ* incubations only thereafter. For each productivity profile, the maximum photosynthetic rate (P$^b_{opt}$) measured in the upper 4 sampling depths was taken as an estimate of P$^b_{max}$. As described by Behrenfeld & Falkowski (1997a,b) and Behrenfeld et al. (2002a,b), the prolonged nature of such incubations causes P$^b_{opt}$ to approximate, but always be slightly less than, P$^b_{max}$.

From the 10 year HOT record, 106 P$^b_{opt}$ and corresponding chlorophyll values were extracted. Unfortunately, beam attenuation measurements were terminated after 1995. However, analysis of data collected between 1989 and 1995 indicated that c_p was relatively constrained. We therefore used monthly mean c_p values for all θ_{cp} calculations after 1995. A c_w value of 0.364 m^{-1} was applied to the HOT data. Protocols for all HOT measurements have been described previously and can be found on the above web site.

Bermuda Atlantic Time Series (BATS) and Bermuda BioOptics Program (BBOP) — Depth profiles of c_p, chlorophyll, and photosynthesis collected during the BATS/BBOP program between January 1992 and November 1997 at 31° N, 64° W were extracted from the web site: http://www.bbsr.edu/cintoo/bats/bats.html. BATS and BBOP measurement protocols have been described previously (Knap et al. 1993; Michaels and Knap 1996; Siegel et al. 1995a,b, 2000). Primary production measurements were conducted on samples collected from 8 depths and incubated *in situ* from sunrise to sunset. P$^b_{opt}$ values were determined according to Behrenfeld et al. (2002b). c_w was calculated as the average difference between *c* measured at ~200 m and the expected value for c_w of 0.364 m^{-1}.

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<u>North Atlantic Bloom Experiment (NABE)</u> — c_p, chlorophyll, and P^b_{opt} data for Legs 4 and 5 of the NABE experiment on the R.V. Atlantis (April 25 to June 6, 1989) (Gardner et al. 1993) were extracted from the web site: http://usjgofs.whoi.edu/jg/dir/jgofs/. Primary production measurements were conducted on samples collected from 6 to 8 depths and incubated for 24 h *in situ* (during Leg 4, samples were incubated onboard in the dark from sunset to sunrise). P^b_{opt} was taken as the maximum photosynthetic rate measured in the upper 4 sampling depths. c_w was assigned a value of 0.364 m^{-1}.

<u>Equatorial Pacific (EqPac) Study</u> — c_p, chlorophyll, and P^b_{opt} data for EqPac were extracted from the web site: http://usjgofs.whoi.edu/jg/dir/jgofs/eqpac/. The 1992 EqPac study entailed 4 separate components: Transect TT007 (February 4 to March 7; 12°N, 140°W to 12°N, 140°W), Station TT008 (March 23 to April 9; 0°, 140°W), Transect TT011 (August 10 to September 14; 12°N, 140°W to 12°N, 140°W), and Station TT012 (October 1 to October 20; 0°, 140°W). Primary production measurements were conducted on samples collected from 8 depths and incubated *in situ* for ~24 h. P^b_{opt} was taken as the maximum photosynthetic rate measured in the upper 4 sampling depths. From Walsh et al. (1995) and Chung et al. (1996), c_w was taken as the minimum value for c measured in the upper 400 m. For our EqPac analysis, surface mixed layer depths (MLD) were also required and taken from Gardner et al. (1995). EqPac measurement protocols have been described previously and can be found on the above web site.

<u>Oligotrophic Pacific (OliPac) Study</u> — The OliPac study was conducted during November 1994 as part of the international Joint Global Ocean Flux Study (JGOFS) (Dandonneau 1999). Samples were collected along 150°W longitude from 16°S to 1°N latitude, which is close to the EqPac study area (140°W). Primary production measurements were conducted on samples collected from 8 to 10 depths between the surface and the 0.1% light depth. Unlike the long-term incubations used during the other 4 studies, photosynthesis-irradiance measurements were conducted during OliPac. For each depth, 50 ml subsamples were dispensed into 12 polystyrene tissue culture flasks, inoculated with 0.5 μCi ml^{-1} $H^{14}CO_3^-$, and incubated for 120 to 180 min in a radial photosynthetron (Babin et al. 1994). The incubation irradiance gradient ranged from 5 to 400 μmol quanta m^{-2} s^{-1} (integrated from 400 to 700 nm) and was created by stacking the 12 culture flasks in front of a 250 W arc lamp (Osram, HQI-T250WD). Following incubation, samples were passed through a 25 mm glass fiber filter (Whatman GF/F), acidified with concentrated HCl to remove inorganic carbon, and total ^{14}C activity (counts min^{-1}) determined by liquid scintillation counting. Carbon fixation was calculated from the measured total activity, after correcting for scintillation counter background and quenching (Parsons et al. 1984). The light-limited slope (α^b) and light-saturated rate (P^b_{max}) of chlorophyll-normalized photosynthesis was determined for each sampling depth and station by fitting the model of Jassby and Platt (1976) to measured carbon fixation as a function of incubation irradiance. The light saturation parameter (E_k) was calculated as: $E_k = P^b_{max} / \alpha^b$. c_w was taken as the average value for c measured between 300 and 400 m and was generally close to 0.364 m^{-1} (Claustre et al. 1999).

RESULTS AND DISCUSSION

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Growth rate (μ), growth irradiance (I_g), and daylength (d.l.) have a predicable effect on θ. Consider first the influence of light in the absence of growth limitation. If μ and respiration (r) are constant at all light levels, then photosynthesis (P: mg C m^{-3} d^{-1}) will also be constant, since:

$$P = C\,(\mu + r),$$ (Eq. 1)

where C = phytoplankton carbon (mg m^{-3}) and μ and r have units of d^{-1}. P is proportional to light absorption at low light, so maintaining a constant photosynthetic rate with decreasing irradiance requires light harvesting to change inversely with I_g. If chlorophyll is the primary light harvesting pigment, this relationship can be expressed as:

$$d\text{Chl}/dI_g = I_g^{-1}.$$ (Eq. 2)

With increasing light, cellular chlorophyll does not approach zero, as suggested by equation 2, but instead asymptotically approaches a value significantly greater than zero (e.g., see Figure 1 in Behrenfeld et al. 2002b). Consequently, light harvesting exceeds photosynthetic requirements at very high light. The physiological basis for this chlorophyll minimum is that functional photosynthetic units (PSU) require at least ~1000 to 2000 chlorophyll molecules each (Falkowski 1981, Behrenfeld et al. 2002b) and have a minimum potential turnover time (τ^*_{PSU}) of ~1 to 2 ms (Falkowski 1981, Behrenfeld et al. 1998). Thus, if all PSUs are operating at a maximum rate, the minimum number of PSUs (therefore chlorophyll) is limited by the ratio of carbon fixation to τ^*_{PSU}. The ratio of chlorophyll to carbon fixation at very high light (b_{min-C}) is thus a function of τ^*_{PSU} and should be relatively constrained.

Dividing P by the light-dependent changes in chlorophyll described above, the growth-rate-independent effect of photoacclimation on daily, chlorophyll-normalized photosynthesis (P^b) can be described by:

$$P^b = \frac{d.l}{b_{min-C} + (I_g \times \alpha^b)^{-1}},$$ (Eq. 3)

where I_g = mol quanta m^{-2} h^{-1}, b_{min-C} = mg Chl mg C^{-1} h, and α^b (mg C mg Chl^{-1} mol quanta^{-1} m^2) has been included in the denominator to account for species-dependent differences in chlorophyll-specific photosynthetic efficiencies. If we now drop the assumption of a constant growth rate, the description of θ as a function of μ, I_g, and d.l. can be derived by dividing equation 1 by chlorophyll and combining with equation 3:

$$\theta = \frac{d.l}{b_{min-C} + (I_g \times \alpha^b)^{-1}} \times \frac{1}{(\mu + r)}.$$ (Eq. 4)

Equation 4 does not encompass every environmental factor influencing θ, but does include the three primary factors manipulated in the steady-state experiments of Laws and Bannister (1980) and Sakshaug et al. (1989). Applying equation 4 to these two data sets required parameter values for b_{min-C}, r, and α^b. For both *Thalassiosira fluviatilis* and *Skeletonema costatum* we assigned b_{min-C} a value of 0.12 mgChl h mgC^{-1} (~1.6 moles chlorophyll per mole of carbon fixed per hour) and estimated r at 0.001 d^{-1}. α^b was estimated at 7.5 and 10 mgC m^2 mgChl^{-1} mol quanta^{-1} for *S. costatum* and *T. fluviatilis*, respectively. With these parameter values, equation 4 explained 94% of the observed variance in θ for *T. fluviatilis* (Fig. 1A) and 93% of the variance for *S. costatum* (Fig. 1B).

Our goal in this section is to provide a physiological justification for anticipating P^b_{max}

and θ to covary in natural mixed layer phytoplankton assemblages. Equation 4 clearly captures the primary influence of μ and I_g on θ (Fig. 1) and, from equation 1, should likewise apply to P^b. The question remaining is thus, to what extent does the Calvin cycle capacity (P_{max}) vary with μ and I_g? Sukenik et al. (1987) found that P_{max} and the cellular concentration of ribulose-1,5-bisphospate-carboxylase (Rubisco: an index of P_{max}) was invariant in the marine chlorophyte, *Duneliella tertiolecta*, over a range in I_g (0.29 to 6.84 mol quanta m^{-2} h^{-1}) that was not strongly limiting to growth. In contrast, Falkowski et al. (1989) observed a significant decrease in Rubisco concentration with NO_3-limited growth in the marine haptophyte, *Isochrysis galbana*, exposed to constant I_g. These results therefore suggest that the growth-independent component of photoacclimation (Eq. 3) will have a similar effect on P^b_{max} as it does on θ, whereas growth-dependent changes in chlorophyll will have a limited influence on P^b_{max} compared to θ because of coincident changes in P_{max}.

In the following section, temporal and spatial variability in P^b_{max} and P^b_{opt} are compared to coincident changes in θ_{cp} for the 5 field studies described in the Methods section. From the above laboratory-based discussion, the occurrence of a first-order correlation between θ_{cp} and light-saturated photosynthesis is interpreted as reflecting a dominant influence of the growth-independent component of photoacclimation. The differential influence of μ on P^b_{max} and θ is assumed to play a central role in observed divergences between θ_{cp} and P^b_{opt} or P^b_{max}. We recognize, however, that temperature (Geider 1987), non-steady-state growth, and other factors may have also contributed to these divergences.

Field Studies

<u>Ocean Time Series Results (HOT & BATS)</u>: Of the 5 field studies examined, the HOT record is most representative of a low-production, temporally-stable ecosystem; although long-term shifts in community structure and nutrient cycling have even been reported for Station Aloha (Karl et al. 1995). Between September 1989 and December 1999, P^b_{opt} fluctuated between 1.55 and 14.3 mg C mg Chl^{-1} h^{-1} and exhibited a weak seasonal cycle of variable amplitude (Fig. 2). During this period, c_p varied from 0.012 to 0.15 m^{-1} and chlorophyll ranged from 0.04 to 0.18 mg m^{-3}, with no correlation between c_p and chlorophyll ($r^2 < 0.01$). Basic features in the temporal progression of P^b_{opt} were paralleled by similar changes in θ_{cp}, indicating that both variables were being strongly influenced photoacclimation (Fig. 2).

Mixed layer phytoplankton growth rates (μ_{cp}) during the HOT record can be estimated by solving equations 1 and 4 for μ:

$$\mu_{cp} = P^b_{opt} \times chl \times d.l. \times (194 \times c_p)^{-1} - 0.001 , \qquad \text{(Eq. 5)}$$

where 194 is an approximate conversion factor for phytoplankton carbon based on the average POC:c_p ratios of Bishop (1999) and Bishop et al. (1999) and r is estimated at 0.001 d^{-1} based on the laboratory data discussed above. Equation 5 simply states that growth rate equals daily photosynthesis per unit phytoplankton carbon minus the carbon-specific respiration rate. For Station Aloha, applying measured values of P^b_{opt} and c_p to equation 5 yielded a mean value for μ of 0.62 d^{-1} (range: 0.14 to ~1.24), which is consistent with independent growth rate estimates for open-ocean, picoplankton-dominated populations (Vaulot et al. 1994, 1995, Vaulot & Marie 1999).

At the BATS site, phytoplankton dynamics are dominated by a strong seasonal cycle of deep winter mixing and summer stratification. Consequently, large amplitude changes in I_g give rise to pronounced seasonal cycles in photoacclimation (Behrenfeld et al. 2002b). For the 1992 to 1997 period, P^b_{opt} varied from 1.82 to 14.7 mg C mg Chl^{-1} h^{-1} (Fig. 3), c_p ranged from 0.012 to 0.068 m^{-1}, and chlorophyll varied from 0.026 to 0.42 mg m^{-3}. Changes in c_p and chlorophyll were again uncorrelated ($r^2 < 0.01$). As with HOT data, primary temporal features in the BATS P^b_{opt} record were paralleled by similar changes in θ_{cp} (Fig. 3). Divergences between θ_{cp} and P^b_{opt} were greatest during the annual spring bloom, when equation 5 yielded growth rates that generally exceeding 1 d^{-1}. During the summer stratification period, μ_{cp} averaged 0.55 d^{-1} and varied between ~0.32 and 0.72 d^{-1}.

The first-order correspondence between θ_{cp} and P^b_{max} observed in the HOT and BATS records (Fig. 2,3) clearly indicates that θ_{cp} registers the physiological effects of photoacclimation and can provide critical information on P^b_{max} variability in oligotrophic waters. But does this correlation hold in other oceanographic regions?

North Atlantic Bloom Experiment: Conditions during the North Atlantic Bloom Experiment were very much different than those during HOT and BATS. During the NABE, surface nitrate levels were elevated and an early shoaling for the mixed layer from ~125 m to < 20 m gave rise to a phytoplankton bloom that increased surface chlorophyll concentrations from 0.55 to 3.0 mg m^{-3} and increased c_p from 0.17 to 0.89 m^{-1} (Gardner et al. 1995). Unlike BATS and HOT, changes in chlorophyll during Legs 4 and 5 of NABE were generally dominated by changes in phytoplankton abundance, rather than photoacclimation. Despite the resultant covariation between c_p and chlorophyll ($r^2 = 0.73$), θ_{cp} retained information about physiological variability during the bloom. During Leg 4, chlorophyll biomass increased steadily from 0.55 to 1.72 mg m^{-3}, while P^b_{opt} exhibited only a modest increase from 2.5 to 4.8 mg C mg Chl^{-1} h^{-1} that was paralleled by similar changes in θ_{cp} ($r^2 = 0.68$) (Fig. 4A). Chlorophyll biomass continued to increase during Leg 5 until May 25th, then decreased to 0.57 mg m^{-3} by June 6th. P^b_{opt} varied inversely with chlorophyll concentration during Leg 5 and was highly correlated with θ_{cp} ($r^2 = 0.82$) (Fig. 4A), indicating that phytoplankton biomass was significantly influencing I_g and thus, photoacclimation.

P^b_{opt} was consistently lower than θ_{cp} during Leg 5 when a scalar of $s_1 = 10$ mg C m^{-2} was applied to the NABE data (Fig. 4A). It is not clear whether this offset is due to methodological differences between Legs 4 and 5, or a true physiological change during the 10 day gap separating the two cruises. Assuming the nature of this offset is not methodological, we applied equation 5 to the NABE data to estimate temporal changes in μ_{cp}. Resultant growth rates exhibited an increase from 0.65 d^{-1} on April 26th to a peak of 0.96 d^{-1} on May 20th (Fig. 4B), which is significantly earlier than the maximum in either chlorophyll or c_p. After May 20th, μ_{cp} decreased steadily at a rate of ~2% d^{-1} ($r^2 = 0.86$) to a minimum of 0.41 d^{-1} on May 27th, then increased slightly to 0.60 d^{-1} by June 6th (Fig. 4B). From these temporal changes in μ_{cp}, we might speculate that the phytoplankton bloom experienced an increasing level of light-limitation shortly after stratification. Upon further increases in biomass, light-stress increased and was exacerbated by a deepening of the mixed layer from ~15 to ~30 m between May 25th and 26th. Subsequently, phytoplankton biomass decreased and mixing depths shoaled to 14 m, resulting in an increase in

I_g, and thus P^b_{opt} and θ_{cp}, until June 6th.

Equatorial Pacific Results (EqPac & OliPac): Environmental conditions during the 4 EqPac studies varied widely, from an El Nino (TT007 & TT008) to a La Nina (TT011 & TT012) and from oligotrophic to equatorial upwelling systems (Gardner et al. 1995; Walsh et al. 1995; Chung et al. 1996, 1998). P^b_{opt} varied from 2.67 to 9.91 mg C mg Chl^{-1} h^{-1} during the El Nino period and from 2.58 to 15.30 mg C mg Chl^{-1} h^{-1} during the La Nina (Fig. 5A). Chlorophyll ranged from 0.06 to 0.37 mg Chl m^{-3} and c_p varied from 0.034 to 0.138 m^{-1} during the 4 studies. Chlorophyll largely varied as a function of phytoplankton abundance and thus exhibited a significant correlation with c_p ($r^2 = 0.67$). Based on our results for HOT, BATS, and NABE, the remaining, independent variations in chlorophyll and c_p were anticipated to yield θ_{cp} values that tracked observed changes in P^b_{opt}. However, θ_{cp} and P^b_{opt} were not correlated ($r^2 < 0.01$). Instead, P^b_{opt} covaried with c_p (Fig. 5A), particularly during TT007, TT011, and TT012 ($r^2 = 0.69$). A defendable explanation for these parallel changes in P^b_{opt} and c_p can not yet be offered.

One potential explanation for the decorrelation between θ_{cp} and P^b_{opt} is that variability in P^b_{opt} was dominated by factors other than light. If this were the case, then θ_{cp} may still have reliably recorded changes in photoacclimation during EqPac. As an initial test of this hypothesis, we compared surface θ_{cp} values with corresponding mixed layer depths (MLD) estimated by Gardner et al. (1995). Indeed, primary features in θ_{cp} were also evident in the MLD profiles (Fig. 5B), suggesting that θ_{cp} was tracking changes in photoacclimation. We therefore turned to the OliPac data to gain additional insight into processes taking place during EqPac.

EqPac and OliPac data were collected from a similar region of the Pacific ocean and, like P^b_{opt} data for EqPac, P^b_{max} exhibited little correlation with θ_{cp} during OliPac ($r^2 = 0.23$) (Fig. 6A). An important difference between the EqPac and OliPac studies is that photosynthesis-irradiance (P-E) experiments were conducted during OliPac, rather than 24 h *in situ* incubations. These P-E measurements allowed the light-saturation index, E_k, to be calculated for each population sampled in the water column. E_k can vary independently of P^b_{max}, and thus provides an alterative measure of photoacclimation when variability in P^b_{max} is dominated by factors other than light. For the OliPac data, a clear correlation emerged ($r^2 = 0.76$) when θ_{cp} was compared to E_k (Fig. 6B). Obviously, θ_{cp} retained information on photoacclimation despite the lack of correlation with P^b_{max}. By inference and considering the correspondence between θ_{cp} and MLDs (Fig. 5B), it seems likely that θ_{cp} also reliably recorded variability in photoacclimation during EqPac.

So, why was θ_{cp} not correlated with P^b_{max} and P^b_{opt} during OliPac and EqPac? We do not yet have an answer, but closer inspection of the OliPac data provides some clues. When OliPac data were sorted into optical depth bins (o.d. = $k_d \times z$, where k_d is the mean attenuation coefficient for 400 to 700 nm light and z = depth), station-to-station variability in P^b_{max} for a given bin was largely matched by equivalent changes in α^b. Consequently, α^b and P^b_{max} were highly correlated within each optical depth bin ($0.68 < r^2 < 0.97$) and exhibited greater variability than E_k. Similar positive correlations between α^b and P^b_{max} have been described for a variety of ocean regions (Platt & Jassby 1976, Li et al. 1980, Harding et al. 1981, Cote and Platt 1983, Harding et al. 1987, Platt et al. 1992, Claustre et al. 1997, Moline et al. 1998). These parallel, equal-magnitude changes in α^b and P^b_{max} can not be attributed to light-dependent changes in cellular chlorophyll (i.e., classic photoacclimation). One mechanism related to photoacclimation

that can cause α^b and P^b_{max} to covary is a change in optical absorption cross sections ($a*$) due to self-shading or accessory pigments. However, light-limited and light-saturated photosynthetic rates remained highly correlated ($0.69 < r^2 < 0.95$) when OliPac P-E data were normalized to $a*$, rather than chlorophyll. Thus, variability in $a*$ was not the primary mechanism responsible for the observed parallel changes in α^b and P^b_{max}.

Taken collectively, all 5 field studies discussed above indicate that θ_{cp} provides a robust index of photoacclimation in mixed layer phytoplankton assemblages. The HOT, BATS, and NABE data demonstrate that photoacclimation is also a primary source of variability in P^b_{max}. This common influence of light results in a first-order covariance in θ_{cp} and P^b_{max} (Fig. 2-4). Data from the equatorial Pacific, however, indicate that the imprint of photoacclimation on P^b_{max} can, at least regionally, be overwhelmed by a second factor that decouples variability in θ_{cp} and P^b_{max}. The physiological mechanism involved in this second factor and the environmental conditions required for its expression remain unresolved, but clues provided by the OliPac study indicate that it is: 1) unrelated to photoacclimation, 2) inconsequential to θ_{cp}, and 3) equally influential on α^b and P^b_{max}. These three characteristics should help foster a focused research effort on this problem by restricting the number of candidate mechanisms that need to be considered.

Remote Sensing Application

There is no known quantitative optical signature of aquatic photosynthesis. Estimates of ocean productivity therefore rely on global remote sensing fields of phytoplankton chlorophyll biomass and empirical descriptions of physiological variability. Current models for P^b_{max} have large uncertainties that translate directly into the confidence intervals that can be placed on productivity model results. Development of a remote sensing index that furnishes synoptic global information on P^b_{max} variability in mixed layer phytoplankton can contribute significantly toward reducing these uncertainties. Photoacclimation is clearly one of the primary physiological processes causing variability in chlorophyll-specific photosynthetic efficiencies (Behrenfeld et al. 2002b) and here we have demonstrated that θ_{cp} provides a measure of photoacclimation.

θ_{cp} is a bio-optical parameter that can potentially be retrieved from space, with a primary challenge being the assessment of c_p. While an active approach to measuring c_p has not yet been developed, regional estimates of c_p have been made using passive remote sensing data (e.g., Stramski et al. 1999, Loisel et al. 2001). This passive approach involves inverting a water-leaving radiance model to solve for the particulate backscattering coefficient (b_{bp}), and then relating c_p to b_{bp}.

Although total particulate scattering (b_p) is highly correlated with c_p ($r^2 > 0.9$) (Chung et al. 1998), the difficult step in relating b_{bp} to c_p is the conversion of b_{bp} to b_p. The ratio, $B = b_{bp}/b_p$, is dependent primarily on the bulk index of refraction for the ensemble of particles in the water column (Twardowski et al., 2001). In most open ocean waters, B is relatively low and varies with the size distribution of the phytoplankton, ranging from ~0.5% for populations dominated by large cells to ~0.8% for picoplankton-dominated populations (Ulloha et al. 1994, Twardowski et al., 2001). B is considerably larger (~2% to 3%) when the suspended particulate pool includes a significant inorganic component or when the particle size distribution is steep (Junge-like differential slope > 4.1). These situations occur in near-shore waters (Case II) where benthic

sediments are resuspended, in regions with large coccolithophorid blooms, and in ultra-oligotrophic waters.

Retrieving accurate estimates of phytoplankton carbon (POC_{ph}) is critically dependent on the size distribution and composition of the particulate pool. Published within-study correlations between b_{bp}-, c_p-, and filtration-based estimates of POC (e.g., Loisel et al 2001, Bishop 1999) are remarkable considering that the b_{bp} signal is dominated by non-algal, submicron particles (Stramski & Kiefer 1991, Morel & Ahn 1991, Ulloa et al. 1994, Loisel et al 2001), the c_p signal is dominated by 0.5 to 20 μm particles (Morel 1973, Stramski & Kiefer 1991, Boss et al. 2001), and filtration data represent POC in all particles over a particular filter pore size. These results imply that the algal to non-algal ratio and the size distribution of the particulate pool are relatively constrained. However, comparison of results between studies indicates that the ratio of POC to c_p can vary from 180 to ~500 mg C m^{-2} (Cullen et al. 1992, Walsh et al. 1995, Loisel & Morel 1998, Bishop 1999, Bishop et al. 1999, Claustre et al. 1999). Bishop (1999) suggested that much of this inconsistency is due to methodological issues related to small volume POC determinations. Nevertheless, a degree of regional variability can be expected and must be considered when relating θ_{cp} to algal physiology (Cullen & Lewis 1995).

One approach to the c_p:POC_{ph} conversion problem might be to regionally constrain θ_{cp} to a predetermined distribution. For example, carbon to chlorophyll ratios in phytoplankton monocultures have been routinely measured in the laboratory and a tremendous volume of literature is available describing how θ varies with daylength, growth irradiance, nutrient stress, temperature, species, and growth rate (*reviewed by* Geider 1987). Figure 7 shows a distribution of steady-state θ values for a compilation of 9 published laboratory studies (Falkowski & Owens 1980, Laws and Bannister 1980, Schlesinger & Shuter 1981, Raps et al. 1983, Geider et al. 1985, 1986, Dubinski et al. 1986, Sakshaug & Andresen 1986, Sakshaug et al. 1989). For the 16 species and 214 observations represented by this data set, θ ranged from 8.6 to 785 and exhibited a skewed distribution with a median of 42 and ~95% of the data falling below 220 (Fig. 7). A similar distribution (range = 8.3 to 461, median = 73, 95% of the data < 205) was achieved for our 415 field c_p values by applying a scaling factor of 194 mg C m^{-2} (from Bishop 1999, Bishop et al. 1999) (Fig. 7). In contrast, applying a scaling factor closer to 500 mg C m^{-2} (Loisel & Morel 1998, Claustre et al. 1999) resulted in a θ distribution that was too high, while a factor much lower than 200 gave θ values less than the expected minimum of ~6 (Geider 1987). Laboratory data can thus provide a constraint on field c_p:POC_{ph} conversion factors. A comprehensive review of the literature could similarly yield a set of θ distributions that can be applied regionally to global remote sensing retrievals of θ_{cp}.

Summary

With respect to ocean biology, remote sensing technology has largely focused on quantifying near-surface phytoplankton chlorophyll concentrations (C_{sat}). C_{sat} data have been used to revise global estimates of ocean photosynthesis (e.g., Longhurst 1995, Antoine et al. 1996, Field et al. 1998, Behrenfeld et al. 2001), investigate broad-scale nutrient limitation (e.g., Sullivan et al. 1993, Boyd et al. 2000), and detect climate-related, interannual changes in productivity (Behrenfeld et al. 2001). Chlorophyll, however, is neither a direct measure of

photosynthesis or phytoplankton carbon biomass. Conversion factors that relate C_{sat} to primary production have largely been developed from a limited pool of field and laboratory observations. The resultant empirical models introduce uncertainties that are difficult, if not impossible, to evaluate at the global scale and thus require assumptions regarding error distributions and biases. If information on physiological variability could instead be retrieved remotely, then uncertainties in the C_{sat}-derived products would inevitably be reduced. The central objective of this study was to take a step forward in this direction.

Results presented here provide a link between a physiological parameter that is crucial to productivity estimates (P^b_{max}) and a bio-optical parameter (θ_{cp}) readily measured *in situ* and accessible from remote sensing. While this study has not found a single global relationship between these two parameters, we have shown them to be related in several distinctly different oceanic ecosystems over time-scales of months to years (Fig. 2-4). We have also proposed that variability in P^b_{max} is dominated by two physiological processes: photoacclimation and a separate, unresolved mechanism that leads to a positive correlation between α^b and P^b_{max}. Remote sensing retrievals of θ_{cp} will improve the characterization of P^b_{max} by addressing the effects of photoacclimation. As for the unresolved process, empirical parameterizations may remain necessary until further field and laboratory studies can reveal its physiological basis and environmental dependence. In the mean time, development of global θ_{cp} fields alone will contribute to improved ocean productivity estimates and a refinement in our understanding of phytoplankton photoacclimation in the sea.

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FIGURE LEGENDS

Fig.1   Carbon to chlorophyll ratios (θ) measured by (A) Laws & Bannister (1980) for *Thalassiosira fluviatilis* and (B) Sakshaug et al. (1989) for *Skeletonema costatum* versus θ values modeled with equation 4. For (A), growth conditions (where $\mu = d^{-1}$ and I_g = mol quanta m^{-2} h^{-1}) were: $\bullet$ = NO$_3$-limited (μ = 0.152 to 0.938, I_g ~0.86). $\lozenge$ = NH$_4$-limited (μ = 0.174 to 0.938, I_g ~0.86). $\bigcirc$ = PO$_4$-limited (μ = 0.178 to 0.916, I_g ~ 0.82). $\blacklozenge$ = light-limited (μ = 0.054 to 1.15, I_g = 0.016 to 0.752). Photoperiod (d.l.) for all treatments was 12 h d^{-1}. Growth conditions in (B) were: $\blacksquare$ = (I_g = 4.33, d.l. = 24, μ = 0.22 to 1.4). $\blacktriangle$ = (I_g = 2.17, d.l. = 14, μ = 0.27 to 1.4). $\triangle$ = (I_g = 2.17, d.l. = 6, μ = 0.33 to 0.87). $\bigcirc$ = (I_g = 0.358, d.l. = 24, μ = 0.24 to 1.4). $\circledast$ = (I_g = 0.358, d.l. = 14, μ = 0.22 to 1.1). $\bullet$ = (I_g = 0.358, d.l. = 6, μ = 0.24 to 0.61). $\lozenge$ = (I_g = 0.254, d.l. = 24, μ = 0.19 to 1.2). Solid hexagon = (I_g = 0.146, d.l. = 14, μ = 0.1 to 0.56). $\blacktriangledown$ = (I_g = 0.043, d.l. = 24, μ = 0.24 to 0.52). $\triangledown$ = (I_g = 0.043, d.l. = 14, μ = 0.1 to 0.28).

Fig. 2   Comparison of light-saturated photosynthesis (P^b_{opt} = $\bullet$) and the particulate attenuation-based estimate of the phytoplankton carbon to chlorophyll ratio (θ_{cp} = $\bigcirc$) for the 10 year Hawaii Ocean Time-series (HOT) record. Data are plotted by sequential observations during the time-series (September 1989 and December 1999), with corresponding year indicated at the top. P^b_{opt} = mg C mg Chl^{-1} h^{-1}. θ_{cp} = mg C mg Chl^{-1}.

Fig. 3   Comparison of light-saturated photosynthesis (P^b_{opt} = $\bullet$) and the particulate attenuation-based estimate of the phytoplankton carbon to chlorophyll ratio (θ_{cp} = $\bigcirc$) measured during the Bermuda Atlantic Time Series (BATS) program January 1992 and November 1997. Data are plotted by sequential observations during the time-series, with corresponding year indicated at the top. P^b_{opt} = mg C mg Chl^{-1} h^{-1}. θ_{cp} = mg C mg Chl^{-1}.

Fig. 4   (A) Comparison of light-saturated photosynthesis (P^b_{opt} = $\bullet$) and the particulate attenuation-based estimate of the phytoplankton carbon to chlorophyll ratio (θ_{cp} = $\bigcirc$) measured during Legs 4 and 5 (labeled at top) of the North Atlantic Bloom Experiment (NABE) on the R.V. Atlantis between April 25 to June 6, 1989. P^b_{opt} = mg C mg Chl^{-1} h^{-1}. θ_{cp} = mg C mg Chl^{-1}. (B) Mixed layer phytoplankton growth rates (μ_{cp}) during NABE calculated with equation 5. μ_{cp} = d^{-1}.

Fig. 5   (A) Comparison of light-saturated photosynthesis (P^b_{opt} = $\bullet$) and particulate beam attenuation (c_p = $\bigcirc$) measured during the 4 studies (labeled at top) of the Equatorial Pacific (EqPac) program between February 4 and October 20, 1992. Left axis = P^b_{opt} (mg C mg Chl^{-1} h^{-1}). Right axis = c_p (m^{-1}). (B) Comparison of the particulate attenuation-based estimate of the phytoplankton carbon to chlorophyll ratio (θ_{cp} = $\bullet$) and mixed layer depths (MLD = $\bigcirc$) calculated according to Gardner et al. (1995) for the 4 studies of the EqPac program (labeled at top). First-order correspondence between θ_{cp} and MLD results because θ_{cp} varies with growth irradiance (I_g) and I_g is dependent on MLD. Left axis = θ_{cp} (mg C mg Chl^{-1}). Right axis for each study = MLD (m). For both (A) and (B), data

are plotted according to the sequential observation for a given study.

Fig. 6 (A) Light-saturated photosynthesis (P^b_{max}: mg C mg Chl^{-1} h^{-1}) versus the particulate attenuation-based estimate of the phytoplankton carbon to chlorophyll ratio (θ_{cp}: mg C mg Chl^{-1}) for the November 1994 Oligotrophic Pacific (OliPac) study ($r^2 = 0.23$; n = 161). Samples were collected at 17 stations from 8 depths between the surface and 150 m. (B) The light saturation parameter ($E_k = P^b_{max} / \alpha^b$) versus θ_{cp} for the OliPac study ($r^2 = 0.76$; n = 161).

Fig. 7 Comparison of frequency distributions for carbon to chlorophyll ratios (θ) measured in laboratory monocultures of 16 phytoplankton species (black bars) and in the field (gray bars). θ were sorted into 10 unit bins and then normalized to 1 at the highest frequency for each data set. Field θ values were calculated as: $\theta = 194 \times c_p \times$ chl^{-1}. Data sources are described in the text.
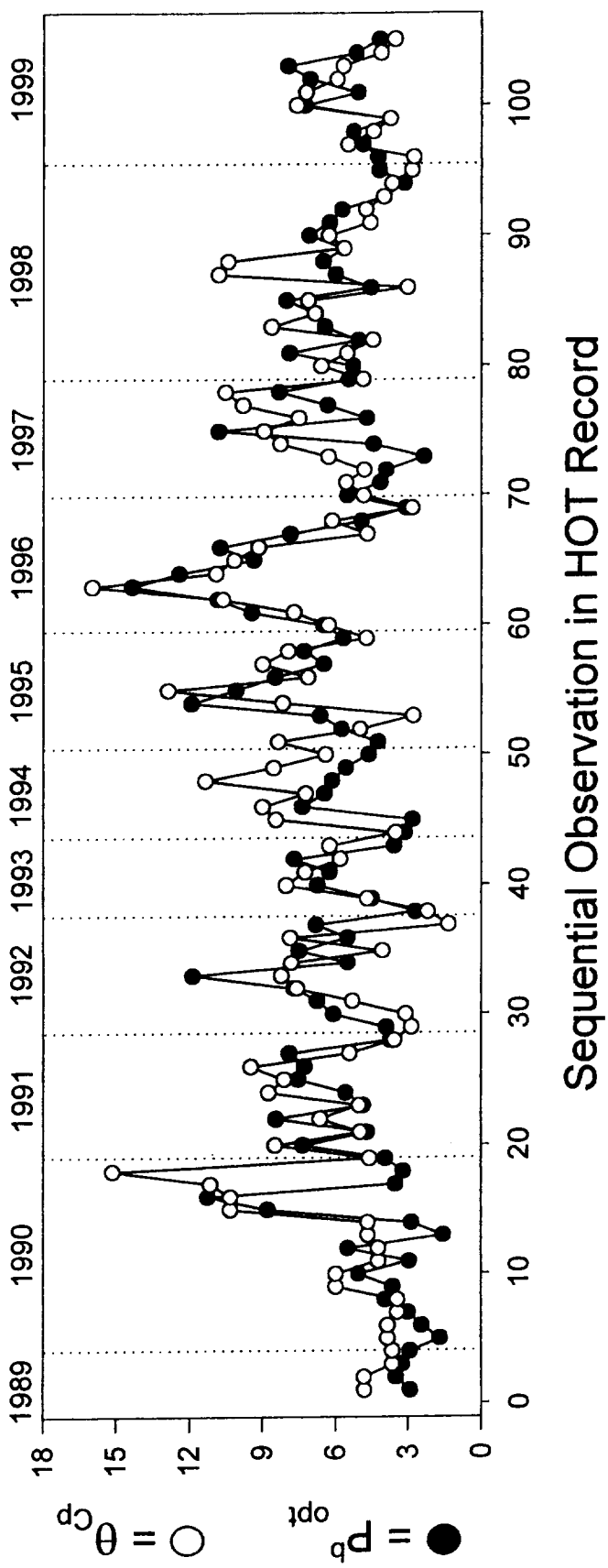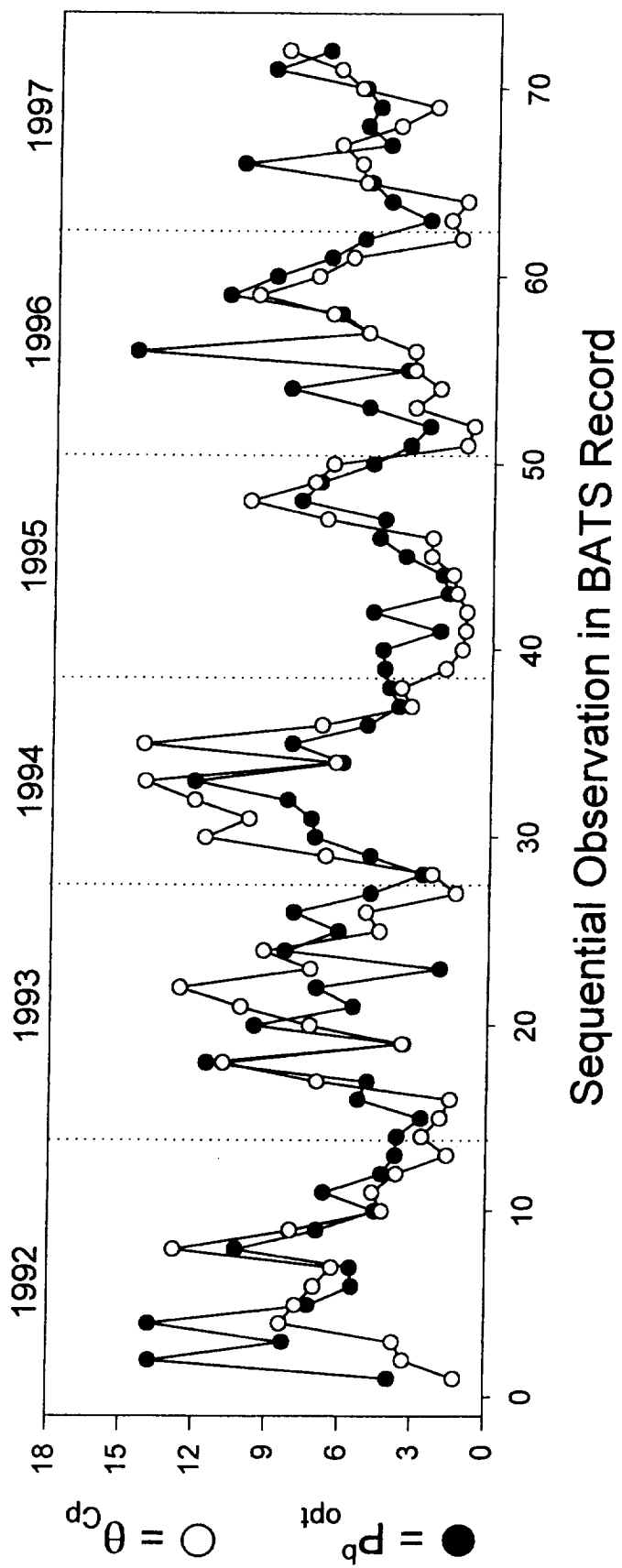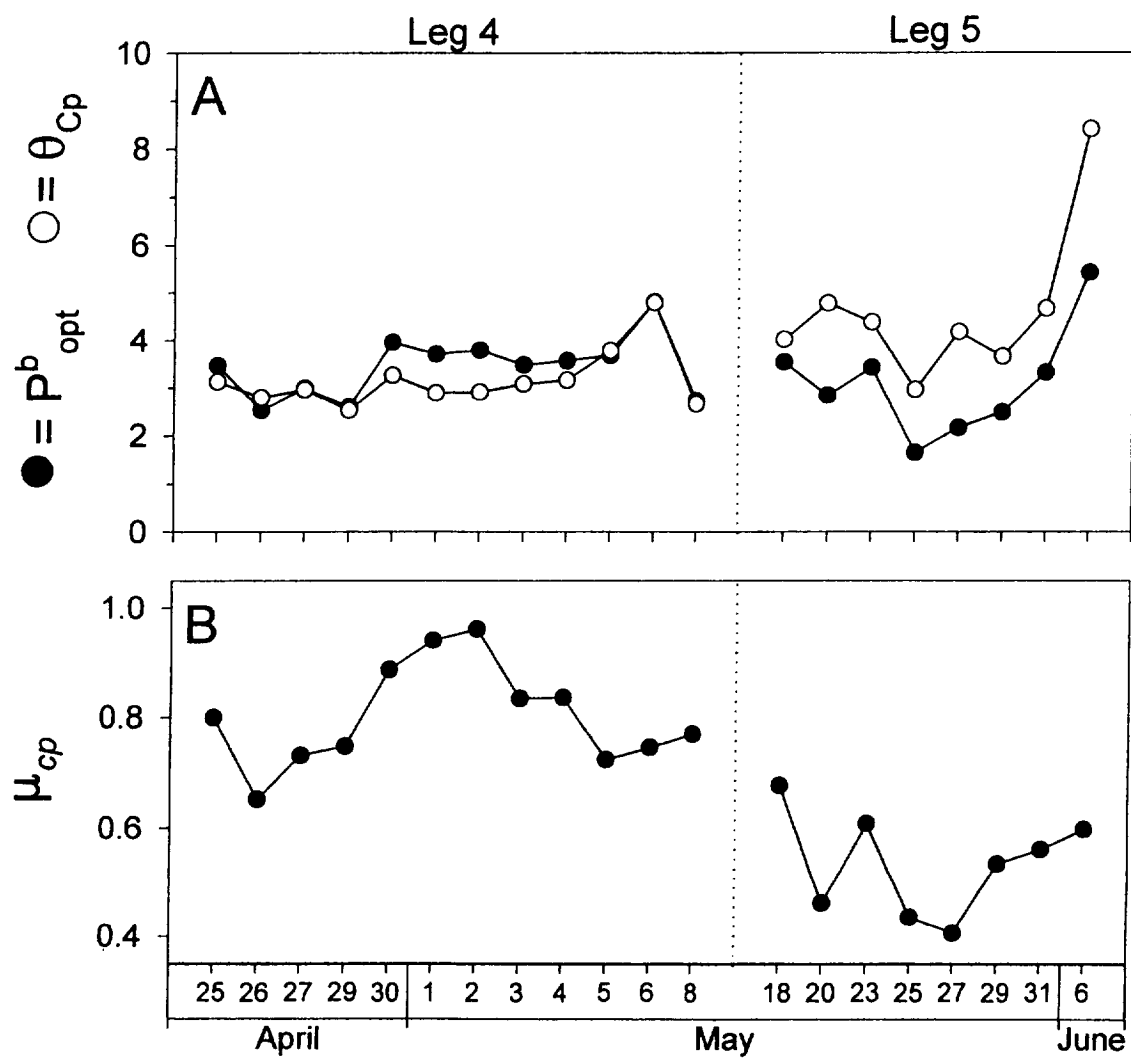
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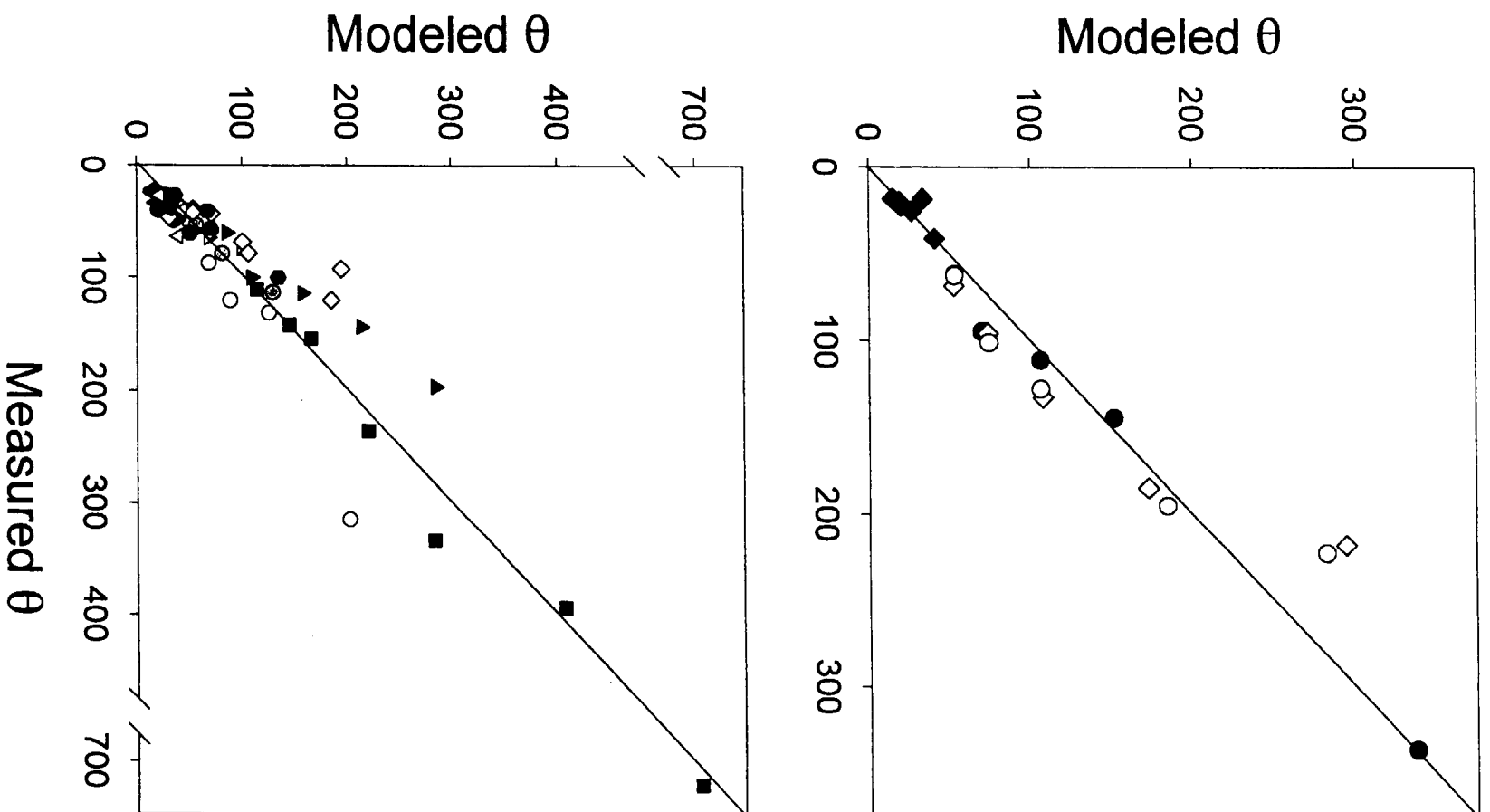
Figure 2

Figure 3

Figure 4

NABE Time Series

Figure 5

Figure 6

Figure 7