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Biogeosciences Discussions

Interactive comment on "Does chlorophyll *a* provide the best index of phytoplankton biomass for primary productivity studies?" *by* Y. Huot et al.

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Measurements of phytoplankton biomass for estimating ocean producitivity: A review of a manuscript by Hout et al. (2007) for Biogeosciences

by Michael Behrenfeld

The current manuscript by Huot et al. describes variability in a range of ocean properties influenced by the abundance of particles. While I found the data set interesting and the primary results of potential value, there are currently significant problems with the presentation, interpretation of the results, and the treatment of different approaches for estimating ocean productivity. Substantial revision and additional review will be necessary before this material is ready for publication. The broader issue addressed in this

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manuscript is important, however, and the current contribution clearly has a potential to advance our understanding of phytoplankton biomass and productivity.

Before continuing, I would like to point out that this is my first opportunity to review for *Biogeosciences*. I think that the new web-based open format for reviewing is a great idea and I've put considerable effort into making this review not only beneficial to the authors, but also the outside science community that may contribute to the discussion of this paper. Consequently, my review is rather lengthy, as I wanted to be clear on a number of points. Also, this review is partitioned into two parts. Part I is a set of comments to help improve the paper from the Introduction to the end of Section 4.2. I believe this initial part of the manuscript can be suitably revised. Part II of this review concerns all material from Section 4.3 to the end. This later part of the manuscript was poorly prepared and should be dropped completely and replaced with a more useful analysis and discussion.

PART I

1) An important issue that permeates this entire manuscript is that phytoplankton biomass and photosynthetic parameters are not the same thing, and this difference confounds attempts to evaluate the former through comparison with the later. This point is so central to the evaluation of the current manuscript that it requires elaboration. . .

To start, what exactly do the authors mean by 'biomass'? In the first paragraph of the introduction we find the statement, *". . . due to the pronounced variability of its cellular content and its ratio with respect to phytoplankton carbon, the concentration of Tchla is a biased estimator of phytoplankton biomass as organic carbon."* From this statement, we conclude that what the authors mean by 'phytoplankton biomass' is 'phytoplankton carbon concentration' in seawater. Indices of 'biomass' are then to be evaluated by comparison with photosynthesis-irradiance variables (specifically, Pmax and alpha), so we must next consider what these variables mean.

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Pmax is the light saturated rate of photosynthesis and it is equal to the phytoplankton carbon concentration (i.e., biomass) *times the light saturated growth rate*. The accuracy of optical indices for assessing phytoplankton biomass(i.e., bp and bbp) can not be rigorously evaluated by comparison with Pmax without first either (1) correcting Pmax for variability in phytoplankton light saturated growth rates or (2) correcting the optical indices for growth rates. To do this, one needs measurements of 24 h growth rates for the entire phytoplankton community as determined under the *incubation conditions* used to determine Pmax. If the authors have such data, by all means they should try and incorporate this information in their evaluation. If not, an alternative is to use Chl:C ratios to assess the growth rate component. To do this, we must next consider what factors influence Chl:C ratios.

The three first-order factors controlling chlorophyll concentrations are phytoplankton abundance (i.e., biomass), growth rate, and light (i.e., photoacclimation). Other secondary factors include species composition and the importance of assessory photosynthetic pigments. In the current study, the authors suggest that assessory pigments truly are 'secondary' features at best, since accounting for them does little for improving relationships with light limited photosynthetic rates (i.e., compare regression between alpha and chlorophyll, total pigment absorption, and photosynthetic pigment absorption). Coming back to the first order factors then, we see that chlorophyll concentration and Pmax share two of the three factors, such that a relationship between them should be found once the photoacclimation term is accounted for. Photoacclimation can be factored out in surface samples by considering mixed layer depth, incident PAR, and Kd or for deeper samples by replacing MLD with the actual depth of sampling. Once the photoacclimation component is removed, the residual chlorophyll (Chl_{res}) is essentially only dependent on biomass and growth rate, leaving its relationship to Pmax dependent on how changes in growth rate are expressed by changes in chlorophyll concentration. So, we now need to consider this issue. . . .

We can get a sense of this relationship by looking at results from a 1980 paper

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by Laws and Bannister (Limnology & Oceanography). In their study, they reported Chl:C ratios for light-saturated phytoplankton grown under PO4, NH4 and NO3 limiting conditions (see Figure at http://science.oregonstate.edu/~omalleyr/natascha.otto/ – note y-axis has units of mg per gram). What we see is that Chl:C varies linearly with growth rate (i.e., dilution rate). If this relationship had an intercept of zero and could be applied to field samples, we could conclude that Chl_{res} varies in *direct proportion* to Pmax, but we could not distinguish what fraction of Chl_{res} was due to biomass and what fraction was due to growth rate without additional information.

So now we can return to the approach that employs optical indices of biomass (lets call this the 'carbon-based approach'). In its simplest form, Pmax can be estimated in the carbon-based approach by calculating carbon biomass from cp or bbp and *then multiplying by a function of* Chl_{res} : C.If we assume a linear Chl:C vs growth relationship with intercept equal to zero, then the calculation can be simplified to:

$$Pmax = C * Chl_{res}/C = Chl_{res}$$

Thus, assuming that Chl_{res} is calculated in the same way as in the analysis of chlorophyll alone and that this simple version of the carbon approach is employed, both treatments will have *exactly the same performance* when evaluated through comparisons with Pmax data. However, the carbon-based approach has a major advantage: it provides an estimate of the fraction of chlorophyll variability that is due to biomass changes and that due to physiological changes. This is important for two reasons. First, it provides information on physiological variability that is simply not available by looking at chlorophyll alone. Second, if the relationship between cellular chlorophyll concentration and growth rate does not have an intercept of zero (as is shown in the Laws and Bannister figure and as is intuitively obvious when one considers that phytoplankton are never completely absent of chlorophyll when growth is arrested) then it allows this phenomenon to be accounted for by adjusting the 'physiological component' of chlorophyll for its true relationship with growth rate and thus Pmax. Again, the

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'chlorophyll approach' does not allow this adjustment because it can not distinguish biomass- and growth-rate-dependent contributions to Chl_{res}.

From this discussion so far we can conclude that: (1) comparison of chlorophyll, cp, and bbp to Pmax does not provide a rigorous assessment of which index is the better measure of phytoplankton biomass without accounting for the growth rate dependence of Pmax, (2) direct comparison of cp or bbp with Pmax is inconsistent with the construct of the carbon-based approach, and (3) a thorough evaluation of chlorophyll, Pmax, and cp or bbp should provide useful information on the relative importance of photoacclimation and growth rate variability – since (1) Pmax is proportional to *biomass and growth rate*, (2) chlorophyll is proportional to *biomass, growth rate, and photoacclimation*, and (3) cp or bbp are taken as proportional to *biomass alone*.

One of the assumptions of the current manuscript is that the influence of physiology (i.e., photoacclimation and growth rate) can be minimized by comparing Pmax, chlorophyll, cp, and bbp (and the other properties measured) over a wide enough range of environments to insure that biomass is the dominant source of variability. The problem, however, is that this predominant influence of biomass is expressed in all of the variables compared to Pmax, such that differences in performance collapse again to the realm expected for the physiological terms. With respect to figures 1 and 3 of the manuscript, we find cp outperforms chlorophyll in accounting for variability in Pmax (fig 3) and that cp is better correlated with biovolume than any of the pigment and absorption measures (fig 1). The simplest interpretation of this result is that (1) biomass is the predominant control on cp and biovolume, (2) variability in phytoplankton growth rates makes a significant contribution to the scatter observed when Pmax is compared to cp and biovolume, (3) photoacclimation is having a significant influence on relationships between Pmax and chlorophyll, and (4) that the relative influence of photoacclimation is greater than that of variability in growth rates. This later conclusion is clearly demonstrated in Figure 4, where chlorophyll is by far the better predictor of the light limited slope, alpha, compared to biovolume or the optical indices of biomass.

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Continuing now from this last statement, we need to turn our attention to the light limited slope of the PI curve. The current manuscript is purportedly aimed at assessing the suitability of various ocean properties for quantifying phytoplankton carbon biomass. Alpha is not an appropriate variable for such an evaluation. The quantum yield of carbon fixation at low light is a minor contributor to alpha variability compared to pigment concentration, especially over the range of environments sampled during the current study. This is clearly demonstrated in panels 1, 4, 5, and 6 of Figure 4. Focusing for the moment on chlorophyll, we must consider again the factors controlling its variability; namely, phytoplankton abundance, growth rate, and photoacclimation. These are precisely the same variables controlling alpha (neglecting the secondary contributions of variations in the maximum quantum yield for carbon fixation). So exactly what is the reader suppose to learn regarding indices of phytoplankton biomass from a demonstration that one measure of light absorption (alpha) is better correlated with other measures of light absorption (chlorophyll, aps, aphyt, fluorescence) than with measures of phytoplankton abundance (cp, bbp, biovolume)?

When figures 1, 3, and 4 are taken together, it seems to me that the story told by the data is: (1) alpha is correlated with light absorption, (2) Pmax is correlated with biomass and growth rates, and (3) cp and bbp are correlated with biomass. This later conclusion is emphasized by the observation that the *only variable examined* that actually represents a direct measurement of phytoplankton abundance, biovolume (although its relationship to the true total phytoplankton biomass is influenced by the applied conversion from volume to carbon and the fact that large phytoplankton are not well represented by the flow-cytometry data), is best correlated with cp.

From the above considerations, it is clear that alpha is not an appropriate measure for evaluating indices of phytoplankton biomass. But perhaps this isn't the intended objective of the study after all. So lets look more carefully at the Introduction and Background to see if we can find out better what the objective is. . . .

In the Introduction, we are first told that *"the main question we wish to address in this*

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paper is: Does Tchla provide the best index of ***phytoplankton biomass*** *for primary productivity studies?"* So at this point it appears that the goal is to assess phytoplankton biomass proxies, not primary production, and we are then told that 'biomass' means 'phytoplankton carbon'. However, in the paragraph following equations 4 & 5, we are told that *"the best measures of* ***photosynthetic biomass*** *are. . . ."* Importantly, 'photosynthetic biomass' in the context of this paragraph no longer means 'phytoplankton biomass'. At light saturation, 'photosynthetic biomass' means the *carbon fixing capacity* of the phytoplankton assemblage (i.e., the capacity of the carbon fixing machinery downstream of the light reactions). At low light, 'photosynthetic biomass' has a different meaning and is the capacity of the light reaction (i.e., the front end of the photosynthetic electron transport chain) to absorb light for carbon fixation. Thus, 'photosynthetic biomass' is a vague term that is defined differently under different conditions. Interestingly, this section of the manuscript is then followed by two paragraphs discussing optical indices of biomass, but in this case we are back to the original context of carbon biomass and not carbon fixation capacity. We then proceed on to page 713 where we learn that *"We will examine here both* b_{bp} *and* c_p *(approximated as* b_p*) as potential alternatives to Tchla for the estimate of* ***photosynthetic parameters***". Now we are really in trouble because 'photosynthetic parameters' are strongly influenced by physiology, no longer a reliable measure of biomass, and not the characteristic of the phytoplankton assemblage that the optical indices of biomass are trying to achieve.

So what is it that the authors are really after? If its *carbon biomass*, then they have no data on carbon biomass to truly evaluate the performance of the different indices and comparisons with PI variables must take into account all the issues raised above. If it is *photosynthetic parameters* than the optical indices of biomass must not be taken out of context and can only be used in the construct of the carbon-based approach. In other words, the performance of the approach can only be evaluated when chlorophyll and bbp or cp are considered *together*. Just to be clear, let me go through this again. . . .

Photosynthesis is calculated using the carbon based approach as the product of phyto-

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plankton carbon and growth rates. Growth rate is calculated from Chl:C data after correction for photoacclimation (i..e., Chl_{res}). For Pmax, the simple version of the carbon-based approach (i.e., assuming an intercept of zero for the relationship between Chl:C and growth rate) will give *exactly* the same result as a chlorophyll-only approach if the later accounts for photoacclimation in the same way (see above). Alternatively, one could compare the two approaches without accounting for photoacclimation in the later, but then we have to assume that photoacclimation is a negligible phenomenon. This presumption, however, is in direct conflict with the data. Indeed, in the current study the only way the authors were able to get chlorophyll to outperform the optical indices at predicting Pmax was by accounting for depth-dependent changes in photoacclimation (Fig. 5). One might also argue that the photoacclimation model employed in the carbon-based approach is incorrect. However, if a different model of photoacclimation is employed to correct chlorophyll data, it could be equally employed in the carbon model, so this doesn't help. In the end, the chlorophyll-only approach can not outperform the carbon-based approach at estimating Pmax, but the carbon approach does have the potential of outperforming the chlorophyll approach if the relationship between Chl:C and growth rate does not have an intercept of zero or is nonlinear.

But what about alpha? Well again, the carbon based approach employs both chlorophyll and carbon. While it has not been used to directly estimate alpha before, it assumes that light absorption is directly proportional to chlorophyll content and thus will give the *exact same relationship* between chlorophyll and alpha as the chlorophyll-only approach. Any deviation from proportionality between chlorophyll concentration and light limited carbon fixation that might be employed to improve the chlorophyll-only description of alpha could be equally effectuated in the carbon-based approach. So, once again, the chlorophyll-only approach can not outperform the carbon-based approach.

So, we must come back to the question "What is the goal of this paper?" Is it to evaluate indices of biomass or photosynthesis? If it is the former, then the current treatment is incomplete. If it is the later, then the current treatment is incomplete.

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2) The chosen equation for Pmax (equation 3) is rather obscure. I don't think it is beneficial to introduce '$n_{slowest}$' and '$t_{slowest}$' because most readers are not going to understand what you're talking about and this division is not an effective way of separating the 'biomass' and 'physiology' components of Pmax. Let me explain. . . .

Pmax is the carbon fixing capacity at light saturation and it is dependent not only on biomass, but growth rate as well. The '$n_{slowest}$' term represents the concentration of the carbon fixing machinery that is rate limiting at light saturation. For a given temperature, the turnover time (i.e., '$t_{slowest}$') of this enzyme or electron transport complex can be taken as a constant. Therefore, given two phytoplankton communities of the same total carbon biomass but different growth rates (therefore different Pmax), it is '$n_{slowest}$' that will be different, not '$t_{slowest}$' - thus the former is both biomass and physiology dependent. In same manner, if the slowest component for carbon fixation at light saturation is an enzyme, we can be confident that '$t_{slowest}$' will be temperature dependent. Thus, for two phytoplankton communities growing at the same rate and of equal biomass, we can expect Pmax to be the same (by definition) and this can only occur if the temperature effects on turnover times of the rate limiting component are perfectly compensated by changes in the concentration of these rate limiting elements (in other words, '$n_{slowest}$' and '$t_{slowest}$' are not independent terms).

My recommendation for this section is that a careful explanation is prepared so that the reader is clear on what is meant by 'photosynthetic biomass' at light saturation. I suggest using an equation with more comprehensible terms, such as:

Pmax = phytoplankton carbon biomass times light saturated growth rate.

3) (pg 712) In the discussion of optical indices of biomass we are told:

"*Though it has long been known that the beam attenuation coefficient is a good proxy of the total particulate organic carbon (POC) in case 1 waters (Morel 1988; Gardner et al. 2006 and references therein), the suggestion of Behrenfeld and Boss (2003) that*

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it represents an accurate proxy of phytoplankton carbon merits further research. In a similar way, the particulate backscattering coefficient (b_{bp}, m^{-1}), which can be obtained from satellite remote sensing, has been used to estimate the concentration of POC (Stramski et al. 1999). More recently, Behrenfeld et al. (2005) proposed the utilization of the backscattering coefficient to estimate the phytoplankton carbon over large space and time scales. Because of its implications, the idea has already garnered significant attention (e.g. Smith 2005). However, based on Mie theory calculations, backscattering is expected to be mostly influenced by non-phytoplanktonic, submicron particles (Morel and Ahn 1991; Stramski et al. 2004), albeit the sources of backscattered light in the ocean remains controversial. Thus, it would appear a priori *that there is little basis for it being a good proxy of phytoplankton carbon."*

This text boils down to the following statements:

1. Beam-c has long been know to be a good proxy of POC in case 1 waters
2. Beam-c as a measure of phytoplankton carbon merits further research
3. bbp has been used to estimate POC
4. bbp has been suggested as a measure of phytoplankton carbon
5. Mie theory says that bbp is dominated by submicron particles (which include the very small phytoplankton, but are dominated by non-phytoplankton)
6. It appears that there is no a priori basis for relating bbp to phytoplankton carbon

So let's take a look at this in greater detail. . . . When the authors state that cp is a good proxy of POC, they are talking about POC as measured on filter pads, usually 0.7 um nominal pore size filters. Scattering by all particles influences cp, but its peak sensitivity is around 1 – 2 um in natural samples. It has also been shown that variability in cp is

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tightly coupled to variability in phytoplankton abundance (see citations in Behrenfeld and Boss 2003, 2006) and that the ratio of cp:chl often tracks variability in chlorophyll-normalized light saturated carbon fixation rates. So, we can conclude that the 'long known good relationship between cp and POC' is due to the close covariation of all other scattering particles collected on a filter with phytoplankton.

The problem with bbp is that its peak contribution comes from particles around 0.5 um – in other words, outside the size domain of phytoplankton and outside the size domain of POC as measured using filter pads. If we now think about the constitution of the particle size domain of POC data, we can anticipate that the grazing community will be a greater *fraction* of POC in the larger size bins (grazers are generally larger than prey) and will be particularly weak contributors to bbp. Phytoplankton, on the other hand, will contribute more to bbp due to their smaller average size, greater abundance, and significant deviation from the erroneous assumption of "homogeneous spherical particles" (i.e., Mie). In addition, in case 1 waters, phytoplankton production is what is fueling the ecosystem, so it would not be surprising if a significant fraction of the bacterial community and other heterotrophic components covaried with phytoplankton abundance. But, we are left with a very interesting conundrum. . . .what exactly is dominating bbp in the open ocean and what controls the concentration of these backscattering particles?

If we begin by assuming that Mie theory is correct, then our conclusion must be that submicron (dominated by non-phytoplankton) particles are the drivers of bbp variability. These might be small bacteria, detritus, and minerals. While there may not be an *a priori* reason based on physics alone to assume that bbp will covary with phytoplankton, there is *even less of an a priori reason* to believe that bbp will covary in any significant way with the sum of all $>$0.7 um bacteria, $>$0.7 detrital particles, phytoplankton, zooplankton, and every other particle bigger than 0.7 microns that gets captured on a filter – in other words, POC. What we observe, however, is that bbp and POC are correlated, so any retrieval of the later from the former is not based on physics but simple empirical evidence. Therefore, we must turn to empirical evidence for reason to think that bbp

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and phytoplankton carbon might be correlated. Of course, there are hardly any measurements available on phytoplankton carbon concentrations compared to POC data and those that are available are based on a range of techniques that all give different results. So, we need to consider less direct evidence. For example, variations in phytoplankton abundance dominate cp variability ♢ ratios of cp:chl track variability in Pbmax ♢ cp is well correlated with POC ♢ POC is correlated with bbp ♢ therefore, bbp should be correlated with phytoplankton abundance. So there really is empirical evidence to think that bbp and phytoplankton carbon might be correlated.

In the end, the truth of the matter is that there is no *a priori* reason to believe that either phytoplankton carbon or POC should be related to either cp or bbp – assuming that '*a priori*' means a physical basis absent of all empirical evidence. Observations that provide evidence for such relationships, however, include information on the conserved nature of the particle size spectrum, POC measurements, investigations on dominant factors controlling variability in cp, comparisons between cp data and Pmax data, comparisons of cp and chlorophyll in an ocean region where physiological variability is greatly constrained, and satellite analyses of bbp relationships with both POC and phytoplankton carbon. Nevertheless, one of the biggest problems we face in evaluating relationships between scattering coefficients and phytoplankton carbon is that that we simply have so little data on phytoplankton carbon and that there is no consensus on the best technique for routinely measuring it in the field. What has been done so far involves comparisons with more indirect proxies and behaviors, which is exactly what the current study does.

4) **Some comments on the Methods section. . .**

1. **PI curves**: It is not clear to me exactly what Pmax data are being used. If you used equation 2, then the Pmax retrieved is not actually the observed Pmax, but deviates from the observed Pmax in a manner dependent on the extent of photoinhibition. If this equation gives an accurate estimate of the true Pmax, then

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we must assume that the samples that yielded the observed maxima in carbon fixation suffered from some degree of photoinhibition over the course of the incubation. Is there any reason to believe this? Is it not possible that the samples giving the maximum rates were actually at a light level where their repair capacities were able to keep up with PSII turnover and that the 'photoinhibited' samples simply represent the light levels where these repair mechanisms could no longer keep up? If this were the case, then how would your results (e.g., performance metrics) be influenced? In other words, if you didn't use the 'potential Pmax' values that equation 2 gives you, but rather employed the actually observed values, how would it affect your results? Perhaps not at all, but I was just wondering. . .

Also, in your analysis and discussion of results, you have not discussed the issue that PI data have uncertainties as well. How might these uncertainties influence your interpretation? Is it possible that the biomass indices are actually doing better than suggested by the regressions because the PI data are not perfect?

1. **Fluorescence**: Did you try to make any corrections for nonphotochemical quenching to improve the performance of the fluorescence data? Huot and colleagues have discussed this issue in their earlier papers.

2. **Scattering and Backscattering**: Did you actually calculate bp from the AC-9 data or are you using cp as a proxy of bp? If the former, say this in the methods. If the later, you need to change bp throughout the text with cp.

5) (first few sentences of Results and Discussion – comments in **bold**)

An overview of the biomass data collected during the BIOSOPE cruise shows that most variables follow the trends expected as a function of chlorophyll a for case 1 waters (***Error! Reference source not found.***)−−**expected based on what? –**. *Indeed, relationships between surface measurements of* b_p, b_{bp}, *and* a_{phy} *and Tchla concentration*

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are consistent with statistical relationships previously established for case 1 waters. **– add a reference here to point the readers to the lines in Figure 1 –** *It is interesting to note the resemblance between panels A and H showing respectively b_p and the phytoplankton biovolume obtained from the flow cytometry measurements as a function of the Tchla concentration* **– why is this interesting? Tell the reader what you mean.**

6) (line 12, pg 722) units are wrong for Pmax normalized to bp

7) (page 723– comments in **bold**)

Indeed, for values of $P_{max} <$ ~0.1, b_{bp}continues to decrease while P_{max} remains constant. In these waters with low concentrations of particulate matter, b_{bp} is particularly difficult to measure given the low signal available to in situ instruments. – **So, can we trust the bbp data at the lower end? Did you have problems retrieving good bbp data? If so, what were they and how did you deal with them? Was bbp measured with multiple instruments during the cruises and if so how do results compare? A very recent paper by Boss et al. (2007 Hydrobiologia 574:149) reported bbp values from multiple instruments and analysis techniques for the extremely clear waters of Crater Lake and found that bbp did not go below 0.0005 m^{-1} from the surface to 300 m. Does it seem reasonable that your own data approach values of zero at even shallower depths? The bottom line is, how do we know your values of bbp are correct?**

8) (last paragraph on pg 723) Reiterating a point from above, what is the point of comparing scattering coefficients and biovolumes to alpha? Would *anyone* who works on photosynthesis suggest that alpha would be better correlated with biomass than light absorption or pigment concentration?

9) (line 8 on page 724) Rather than saying, “On the other hand, the results concerning P_{max} are more surprising: b_p, despite not being specific to phytoplankton, provides a better estimate of P_{max} than the traditional measure of Tchla”, would it not be more appropriate to say “On the other hand, we found bp to provide a better estimate of

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Pmax than chlorophyll, as consistent with recent results of Behrenfeld and Boss (2003, 2006)". I'm not trying to be self serving here, but your result really isn't as big a 'surprise' as it might have been 5 or more years ago.

10) (page 724) In this paragraph describing the performance of cp and bbp in capturing variability in Pmax, you could also mention that the remaining scatter in these relationships include the effects of variable growth rates that are registered in Pmax but not cp or bbp. This would suggest that the optical indices may be doing even better at getting biomass than Pmax.

11) Other comments:

a) The paper lacks self consistency checks. For example, bbp from different instruments on the cruise, bbp vs bp, bp vs. POC, POC vs chl, cp vs biovolume, all of which are important to establish confidence in the data.

b) When regressions are done with log transformed data the (hidden) assumption is that the uncertainty divided by the measurement is a constant. With optical data this is usually never the case when the values are low. Rather, the uncertainty is usually constant for low values of optical parameters. This can be included in the regression by weighting points according to their uncertainties.

c) The analysis is very empirical. Do the relationships really make sense? For example, is it reasonable that Tchl is actually better than aps for estimating alpha? How can this be a robust conclusion? If it were true, it would mean that packaging is never an issue? Perhaps the underlying issue is that the difference between Tchl and aps is not significant if real measurement uncertainties are taken into account.

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