

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

Y. Huot et al.

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Response to Michael Behrenfeld review

Firstly, we would like to thank Michael Behrenfeld for taking the time to write such a complete and thorough review. We believe his comments and suggestions have led to an improved manuscript. In our response, we address all of the points raised in his review. We begin with a summary of the study to address some of the general comments followed by a point-by-point reply in response to his specific comments. In order to answer adequately Dr. Behrenfeld's review, we will need to clarify some important differences between our approaches. However, we would like to highlight here that the main purpose of this response and in our manuscript is not to address the approach proposed by Behrenfeld et al. in 2005. While the topic of our manuscript makes it relevant to compare our results to the approach they proposed, it is not possible to test

their method with our dataset. The paper has been clarified to make this point very clear to the reader.

General response

The objective of our paper is to evaluate which index of phytoplankton biomass is best suited for estimating primary production. Our aim is *not* to estimate phytoplankton carbon or to verify the carbon-based model published by Behrenfeld et al. (2005). To reach our objective, we follow a two-step approach to compare several indexes of phytoplankton biomass with measured photosynthetic parameters (P_{\max} and α). First, a regression analysis is carried out between the photosynthetic parameters and the different indexes of biomass. Second (sections 4.3 and higher), to identify the remaining sources of variability in the relationships described above, we include a series of potentially relevant environmental variables in a multiple linear (stepwise) regression analysis. *The approach is not mechanistic and purely empirical, but we believe it achieves its aims: we identify the proxy of biomass that allows the photosynthetic parameters to be retrieved with the least error.* The main findings are:

1. if taken alone, the scattering coefficient provides a better estimate of P_{\max} , and the chlorophyll concentration a better estimate of α .
2. when environmental variables are accounted for (mostly accounting for the effect of light on photoacclimation and photoadaptation), chlorophyll concentration is the best estimator of both P_{\max} and α .

Before the publication in 2005 of the “carbon-based model” of Behrenfeld et al. (and surely after), many studies were conducted to evaluate the dependence of P_{\max} (usually normalized to chlorophyll a) on environmental factors. The goal was typically to evaluate what governs and dominates this variability, and efforts focused mostly on light, nutrient status (evaluated in different ways) and species composition. This

was represented either by functional relationships or by identifying geographic regions where the environmental factors were sufficiently similar to allow a given value of P_{\max} to be used. With the aim of improving models of primary productivity, Behrenfeld et al. (2005) proposed a model based on the estimate of phytoplankton carbon using backscattering. While, in its published version (Behrenfeld et al. 2005, combining their equations 4 and 5), carbon is not used to estimate primary production, it is used to calculate the carbon-specific growth rate of phytoplankton in the ocean. There are two important assumptions in this model:

1. there exists a universal relationship between the C/chl ratio of phytoplankton and the light-saturated carbon-specific growth rate (due to effects other than photoacclimation), and
2. backscattering measurements provide accurate estimates of the phytoplankton carbon concentration. This assumption has been referred to as “a big leap of faith” by E. Boss, the second author on the study, in the press release following the publication of the article (http://www.umaine.edu/News/article.asp?id_no=416).

Neither can be formally evaluated in our paper but, as emphasized above, this is not our intent (indirect evidence, however, arises from our analysis and will be discussed).

Our intent instead is to assess, using *in situ* data, the possibility raised by MacIntyre et al. (2002, and references therein), that when normalized to phytoplankton carbon P_{\max} is less variable (in particular in response to photoacclimation). In an operational sense, however, phytoplankton carbon can only be estimated using scattering based measurements. This method was suggested by Behrenfeld et al. (2003, 2005) on the basis that phytoplankton carbon appear to be well correlated with the scattering coefficient. We thus evaluated these proxies (scattering and backscattering coefficients) and

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compared them with others. Furthermore, we wanted to evaluate if using these proxies would lead to improved estimates of the photosynthetic parameters compared to chlorophyll a , when used in a regression against environmental variables. As opposed to the carbon-based model of Behrenfeld, we evaluate an approach where carbon estimated from scattering based measurements is *directly used to predict variability in the photosynthetic parameters*.

Based upon the literature on physiological parameters, a logical argument can be built that growth rates (physiological state) of phytoplankton should be linked to environmental forcing (this is in fact how the carbon-based model is “validated”, see Behrenfeld et al. 2005, Figure 3). Therefore, while functions of the ratio chl/C retrieved from optical proxies may prove useful for estimating the growth rate directly (an aspect which, in our opinion, still requires verification), other correlative or mechanistic approaches to evaluate the physiological variability in P_{\max} must not be discarded. *We therefore strongly disagree with the reviewer’s suggestion that sections 4.3 and higher should all be dropped or are “thoughtless”, nor do we share his opinion that a more “sane” treatment is preferable.* In fact, we firmly believe some of these sections contain the most important results of our study and are an important contribution for, as the reviewer puts it, “. . . improving our understanding of phytoplankton biomass, productivity, and ecology”. Improving the presentation, structure, and performing additional analyses are a better alternative than discarding these sections. To shorten the paper and keep the focus on our most important findings we have, however, dropped sections 4.4 and 4.6. Section 4.4 provided an error analysis to extrapolate our results to remotely sensed data, while section 4.6 discussed our results for particulate backscattering and compared it with the results obtained by Behrenfeld et al. (2005).

Note also that for the revised version of the manuscript, the b_{bp} datasets have been reprocessed by M. Twardowski following his paper submitted to the same special issue and we subsequently repeated our analysis. In addition further quality control were applied to the b_p dataset. While this did not change any of our conclusions, all regression

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coefficients and fit statistics have been modified accordingly .

We now present a point-by-point response to the reviewer's comments, however this proved somewhat difficult with the structure of the review.

Part I.

1) The reviewer says:

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,

This is true, but in this statement the reviewer is referring to phytoplankton carbon. As we have already emphasized, this was not our objective; see the General Response section above. We apologize, if this was unclear. We have completely rewritten the introduction and background section, such that the objectives are indisputably to examine which proxies of biomass allow the best estimation of photosynthetic parameters.

(2) direct comparison of cp or bbp with Pmax is inconsistent with the construct of the carbon-based approach,

Again, while this is true it is not central to the context of our study. See General Response section above.

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*.

This is addressed with an empirical analysis in sections 4.3 and above (the sections that the reviewer suggested should be dropped).

-Later the reviewer makes the following statements about our results:

The simplest interpretation of this result is that (1) biomass is the predominant control on c_p and biovolume,

Yes! The biomass of the primary producers varies by roughly two orders of magnitude in this dataset. It is expected to be the *predominant* control on phytoplankton biovolume. It is probably true of c_p , though, strictly, the influence of covarying material cannot be excluded.

(2) variability in phytoplankton growth rates makes a significant contribution to the scatter observed when P_{max} is compared to c_p and biovolume,

As the reviewer pointed out earlier in his review, we do not have any information about growth rates, thus in our opinion this conclusion cannot be made. With our results the only way to reach this conclusion is to assume that c_p retrieves phytoplankton carbon biomass without error — it probably doesn't — even if biomass is the predominant driver of c_p , the origin of the variability is unknown.

(3) photoacclimation is having a significant influence on the relationships between P_{max} and chlorophyll,

Yes.

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, α , compared to biovolume or the optical indices of biomass.

This is probably true, however, we do not follow the reviewer's logic.

-The reviewer later writes:

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 P_{max} , chloro-

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phyll, cp, and bbp (and the other proper ties 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 P_{max} , such that differences in performance collapse again to the realm expected for the physiological terms.

This assumption is only relevant to section 4.2. We remove this assumption in section 4.3 by replacing it by the generally accepted and used assumption that physiological changes can be predicted from environmental forcing (see General Response section).

The reviewer further writes:

The current manuscript is purportedly aimed at assessing the suitability of various ocean properties for quantifying phytoplankton carbon biomass.

Again, this is not the case. We have greatly clarified the objectives of the paper to avoid this confusion.

The reviewer asks also:

So exactly what is the reader suppose to learn regarding indices of phytoplankton biomass from a demonstration that one measure of light absorption (α) is better correlated with other measures of light absorption (chlorophyll, aps, aphyt, fluorescence) than with measures of phytoplankton abundance (cp, bbp, biovolume)?

In the manuscript, we submit α to exactly the same analysis as P_{max} and our results are as expected: absorption-based measures of phytoplankton biomass are better than scattering-based measurements to retrieve α .

We find this exercise valuable for several reasons:

1. We find that all indexes of absorption performed well, even chlorophyll fluorescence.

2. It allows a cross-verification of our PvsE dataset.
3. Since photoacclimation is driving much of the variability, if scattering is a good estimate of phytoplankton carbon, this implies that correcting for growth irradiance should also allow us to obtain good estimates using scattering-based measurements.

- The reviewer makes the following conclusion about the carbon-based model.

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.

This is an opinion, not a fact. The reviewer probably arrives at this conclusion by making the assumptions stated earlier regarding the carbon-based approach (see General Response section). These are unverified assumptions! It is not our intention to test the published version of the carbon-based model, and our study does not invalidate, nor support these assumptions.

2) The chosen equation for Pmax (equation 3) is rather obscure. I don't think it is beneficial to introduce 'nslowest' and 'tslowest' 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. . . .

We have evaluated this suggestion seriously. In the end, we decided to keep the original representation. Firstly, we are confident that readers will be capable of understanding what this equation means. Secondly, it is fully compatible with our approach (but it may not be the most convenient representation for the carbon-based approach). Using our representation, for the scattering based estimate to perform better than the Tchl_a approach at saturating irradiance, it has to provide the best estimate of $n_{slowest}$ (whether or not it is considered "a physiological index"). Environmental

variables must account for the remaining variability. We now provide in the text the suggested representation of P_{\max} and this allows the reader to link the two easily; $P_{\max} = C\mu_{\max} = C\frac{1}{C}\frac{dC}{dt} = C\frac{1}{C}cte\frac{n_{slowest}}{\tau_{slowest}} = cte\frac{n_{slowest}}{\tau_{slowest}}$. By showing that to predict P_{\max} , C is not essential, we emphasize that what we really care about is $n_{slowest}$ and $\tau_{slowest}$. To us, the main advantage of using C in the representation of P_{\max} is that it allows us to use a representation that describes P_{\max} in terms of commonly measured variables, which can be parameterized based on previous lab experiments (such as in the carbon-based approach). Since this was not our intent, we do not feel that this representation provides a clearer description for the objectives of our paper.

The reviewer wrote:

“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.”

We removed the term photosynthetic biomass throughout the text. We hope that this has clarified this issue.

3) We wrote in the original version of the paper:

“Thus, it would appear a priori that there is little basis for it being a good proxy of phytoplankton carbon.”

The reviewer argues that the statement is incorrect and writes:

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.

It is always stressed in classes on statistics that “correlation” does not imply “causation”. We do not argue that b_{bp} and phytoplankton carbon are not correlated. What we suggest is that there is not a clear causal link and *that the sources of variability*

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between the two are unknown and, thus, difficult to interpret. This section has been rewritten and shortened.

4) a) PI curves : We were not clear on this point. The P_{\max} used in the manuscript are those corresponding to $P_{\max} = P_S \left(\frac{\alpha}{\alpha+\beta} \right) \left(\frac{\beta}{\alpha+\beta} \right)^{\alpha/\beta} + P_O$. We updated the manuscript to describe this aspect more clearly. Generally, surface samples did not suffer any photoinhibition. For deep samples, inhibition was noted at the highest irradiances. We do not understand exactly what the reviewer calls the “retrieved”, and the observed “ P_{\max} ”. Our values will include the effect of photoinhibition, if it is present. We are not too inclined to use potential values (P_s) as these are not necessarily correct; they assume an exponential increase of photoinhibition with irradiance which may or may not be consistent with reality at all irradiance levels. Using P_{\max} as calculated above provides the “maximum of the measured (fitted) value”.

Yes, PvsE data have relatively large uncertainties, compared with the other measurements, but we believe that the quality of our data is equal to the best found in the literature. We attempted to reduce the influence of the uncertainties originating from the fitting procedure and within sample variability (different light levels) by rejecting photosynthetic parameters where the errors were high (see PvsE curve section). Human error and other errors due to the handling of samples, are also present, these cannot be excluded, unless obvious outliers are present in a PvsE curve. In any case, these errors are present in all regressions used in the paper equally so they do not affect the comparisons of the different biomass proxies. Random errors will lead to a lower r^2 than would be obtained without errors, but this is the case for any regression. As for our interpretation, we believe it is correct. When we look for statistical differences, the tests account for the fact that errors in the PvsE curve exist.

b) Fluorescence. We did not account for nonphotochemical quenching (NPQ) because we did not have simultaneous irradiance data with the CTD casts (unfortunately, there was no irradiance sensor placed on the rosette). Irradiance data was collected continuously on deck, but at low frequency. Since the timescales for induction are ~ 5

minutes, any variability in the light during the cast would have an effect. The effect of not accounting for NPQ, likely increases the variability in the relationship between photosynthetic parameters and fluorescence.

c) Scattering and Backscattering. The b_p used was measured using the ac9. The text has been clarified.

5) We now explain why this is of interest. We write: “Despite (or because of) the lack of *Prochlorococcus* in the biovolume dataset and the upper limit of 3 μm , and unless strongly covarying particles are present, this suggests that variability in b_p is in large part influenced by the biovolume (similar to carbon concentration) of phytoplankton.”

6) Corrected.

7) Our b_{bp} data do not show trends with chlorophyll concentration that would lead us to believe that they would be incorrect. The updated Figure 1 with the b_{bp} panel in loglog format, which the reviewer requests later in the review shows that the b_{bp} does not go to near 0 (a somewhat subjective criterion though). Instead it shows that b_{bp} follows a similar distribution to b_p . We have also changed the vertical scale on the g anel showing the relationship between P_{max} and α , which further highlights the resemblance with the b_p and b_{bp} vs chl plots. As for comparing with the Crater Lake data, the BIOSOPE waters are arguably the clearest waters on earth, their attenuation coefficients are below those of Crater Lake (Morel et al. 2007, L&O), the backscattering coefficient is also lower than Crater Lake (See Twardoski et al. this issue). The center of the gyre has the lowest chlorophyll a concentration of the global ocean and is thousands of kilometers away from land influences (thus reducing any aerosols reaching this area). We also provide below (see response to comment #11) the measured values of b_{bp}/b_p , which do not show inconsistent trends at low values of b_{bp} (as with the figures in the manuscript, colors coding refers to depth). A comparison of the backscattering data measured with the bb3 (used in the present paper) and Hydroscat-6 data measured by Dariusz Stramski is also provided below. The latter figure, which will appear in the

paper by Twardowski et al. in the same BIOSOPE issue is not presented in our paper.

8) (last paragraph on pg 723). We have already answered this question previously ; we believe there is value in it. We don't believe anyone would use b_p instead of $Tchl_a$ to normalize α . However, this is the type of comparison that if it is not done, it will be requested, and if it is done someone else will say it doesn't make sense. We believe it is interesting, even if it doesn't change current practices in oceanography.

9) We changed this sentence. One must be careful though, Behrenfeld et al. never really made such a comparison. This finding appears to us "stronger" for demonstrating that b_p or b_{bp} are interesting proxies for P_{max} than those of Behrenfeld et al. because the comparison is made directly with other proxies. In contrast, Behrenfeld et al. showed that c_p/chl predicted P_{max}/chl well without comparison to other proxies.

10) Yes, we included this point. Using our formalism, this comment is essentially covered when we say: "Since the variability in $\bar{\tau}_{slowest}$ and the measurement errors on P_{max} are equal for all panels, this suggests that $b_p(650)$ is the best single measure of $n_{slowest}$."

11) a) To give more confidence in the data, we provide below a graph for b_{bp}/b_p , b_p vs POC, POC vs chl and b_p vs biovolumes. The comparison between the two backscattering instruments was provided previously in this response. Only very few POC data points were taken during the BIOSOPE cruise and even less are simultaneous with the PvsE database. Nevertheless for all the graphs below there is nothing that suggests that the data is incorrect. We do not provide these graphs in the paper as they do not add much to the problem addressed. These relationships will be examined by others in the BIOSOPE special issue. The dataset of backscattering will be treated separately by Twardowski et al. (same issue). The comparison between the biovolumes and c_p will be discussed by Grob et al. Finally, the analysis of the POC will be made by Claustre et al. (same issue).

b) Yes, with any regressions, the variance of the residual must be constant. If the

uncertainty is not proportional to the measurement, as suggested by the reviewer, it means that in a loglog plot representation the points should appear more dispersed at low values than at high values, this is not obvious from our dataset for a_{phy} , b_p and b_{bp} (looking only at a given depth interval, of course).

c) The difference between Tchla and a_{ps} is not significant. Perhaps this was not originally clear, and we have clarified this in the text. Despite being empirical, we believe the results are robust. However, if better methods or better experimental practices lead to lower errors on the determination of the different biomass proxies this will impact the significance tests. For example, with perfect measurements, it is likely that a_{ps} would become significantly better than Tchla. The analysis is indeed influenced by the errors made during the implementation of the methods for obtaining the data. We took great care in collecting and manipulating the samples and used methods that are state of the art. Note also, that if packaging covaries with Tchla, the second order fits can account for at least part of this variability.

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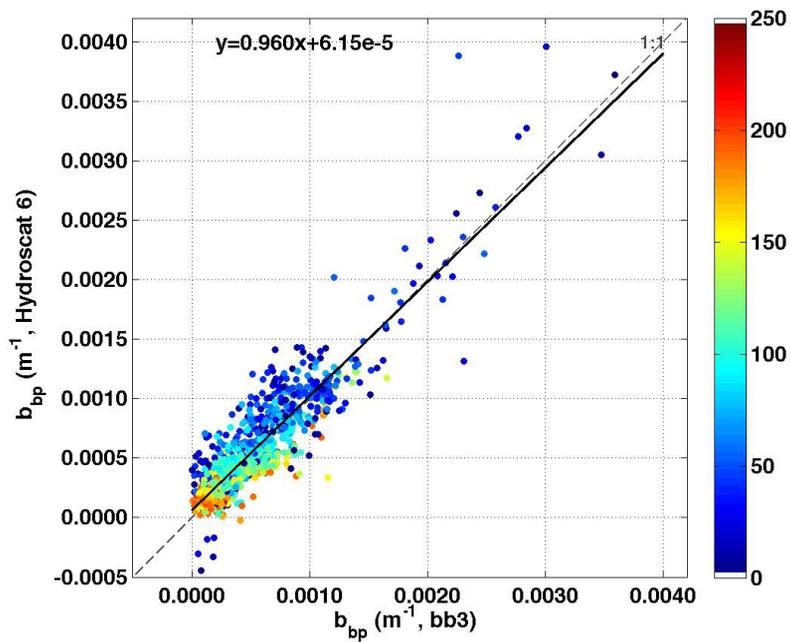


Figure 1:

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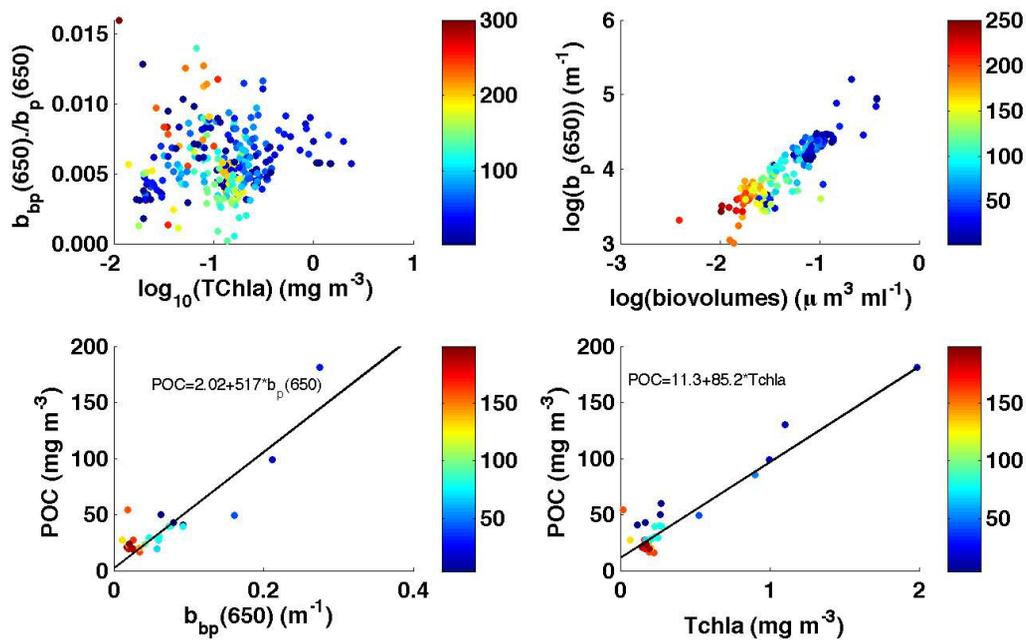


Figure 2:

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