

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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PART II

From the Introduction section through section 4.2, I found the analysis presented in this manuscript interesting, although requiring some significant modification as per the comments made above. From section 4.3 to the end of this manuscript, the quality of the work and presentation is very poor indeed. It is neither constructive nor unbiased, and the conclusions and statements made are incorrect. *My recommendation is to throw this later part of the manuscript out completely and try again* – aiming for something more constructive and forward looking that provides direction for improving our understanding of phytoplankton biomass, production, and ecology.

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Interactive Discussion

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1) (section 4.3) At the end of section 4.2, your conclusion is that cp is the best estimator of P_{max} and that bbp matches $Tchl$ in estimating P_{max} . Why then do you continue from this point on to invalidate the value of the optical indices and, to this end, your own findings? I am at a loss to explain this drastic change in the nature of the manuscript.

Section 4.3 is the first problem. Here, the authors take a selected set of additional variables and throw them into a thoughtless stepwise regression to improve the performance of $Tchl$ in explaining P_{max} variability. The variables included “log-ten of biomass squared”, “depth squared”, “temperature squared”, “log-ten of incident PAR for a cloud-free atmosphere squared”, and “log-ten of Nitrate concentration”. What could possibly be the justification for this? This is simply grasping at straws.

So instead of this approach, I would recommend a more sane treatment. Let's start with $Tchl$. The primary factor contributing to scatter in the relationship between $Tchl$ and P_{max} is photoacclimation. Once the photoacclimation term is removed, we are left with chlorophyll variability from biomass and growth rate. P_{max} is likewise a function of biomass and growth rate. Why not present this more process-oriented and logical discussion of the relationship between Chl_{res} and P_{max} , rather than employing a brute force statistical treatment with variables and relationships that are difficult to defend at best?

Next, the authors need to consider the pertinent variables necessary to improve relationships between cp or bbp and P_{max} . It is important to recognize that these are not the same variables as those necessary to improve the chl - P_{max} relationship, so throwing together a set of variables (and variables-squared) that improve the chlorophyll fit but not the scattering fit is far from adequate. As discussed earlier, cp and bbp (and biovolume) are estimators of biomass, not P_{max} . The key difference is growth rate. If the appropriate community growth rate data are available, then such an analysis should be undertaken. If they do not, then the problem lies in their data set, not in the scattering approach for estimating phytoplankton biomass. It is also noteworthy that without the growth rate data, they cannot also covert their chlorophyll data (corrected

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for photoacclimation) to biomass and can therefore make no claims as to the accuracy with which phytoplankton biomass can be assessed from chlorophyll.

2) (section 4.4) This section begins with the following statement:

“In summary, simple functions of Tchl_a along with information about the irradiance or depth appear more accurate for estimating photosynthetic parameters (and eventually primary productivity) than scattering based methods.”

I am hoping that this statement simply reflects a complete misunderstanding of the scattering based approach. So, for the sake of the authors and others in the community that might be reading this discussion on *Biogeosciences Discuss*, let me try to provide a simple description. . .

The “scattering-based method” is the same as the “carbon-based approach” discussed above (Behrenfeld & Boss 2003, 2006, Behrenfeld et al. 2005). The motivation for the approach is to utilize the new information coming from satellite inversion algorithms to improve NPP estimates and our understanding of phytoplankton ecology. These ‘improvements’ are (1) separation of absorption by colored dissolved organic matter and phytoplankton pigments to give better estimates of light absorption by phytoplankton and (2) the simultaneous retrieval of backscattering coefficients (bbp) and chlorophyll concentrations. The later of these is particularly critical.

The idea is that both bbp and chlorophyll covary with phytoplankton biomass, but differences in bbp and chlorophyll behavior contain information on phytoplankton physiology (i.e., growth rates and photoacclimation). *At no point in time has it ever been suggested (aside from the current manuscript) that bbp (or cp) **alone** provides a better measure of **productivity** than chlorophyll.* Rather, the suggestion is that these two variables *in combination* can lead to not only better estimates of production (NPP), but new and important information on biomass and physiology that simply is not available from chlorophyll alone.

In its simplest form (Behrenfeld et al. 2005), the basic relationship is:

$$\text{NPP} = \text{phytoplankton carbon} * \text{growth rate}$$

Where phytoplankton carbon is estimated from bbp and growth rate is determined from chlorophyll:carbon ratios. If one were to use this approach to estimate Pmax, then the first step is to partition chl:c variability into that due to photoacclimation and that due to variability in growth rate. To understand why this is important, consider two surface phytoplankton populations of equal biomass and growth rate and with equal incident PAR, but in one case mixing depths are very shallow and in the other case very deep. In the later, cellular pigmentation levels will be much higher than in the former, even though they will have the same Pmax. After correcting for this photoacclimation component, both populations will have the same $\text{Chl}_{res}:\text{C}$ ratio, giving the same Pmax.

$$\text{Pmax} = \text{phytoplankton carbon} * f(\text{Chl}_{res}:\text{C})$$

As described above, if the relationship between growth rate and Chl:C is linear and has an intercept of zero, then

$$\text{Pmax} = \text{phytoplankton carbon} * \text{Chl}_{res}:\text{C} = \text{Chl}_{res}$$

Thus, after correcting for photoacclimation, this simple version of the carbon-based model gives exactly the same result as a chlorophyll-only model that includes photoacclimation.

However,... we also need to reconsider this critical assumption about growth rate.

If the relationship between growth rate and Chl:C is linear with an intercept of zero, then what this means is that as nutrient stress increases and growth rate goes down,

the change in growth rate will be *precisely matched* by changes in chlorophyll and, consequently, there can be no relationship between nutrient stress and chlorophyll-normalized light-saturated carbon fixation rates (P_{bmax}) for a given incident light level. Let me say that again... this simple approach requires that P_{bmax} is unaffected by nutrient stress. I think you will find it difficult to convince the scientific community of this. . . .

The more likely scenario is that the relationship between Chl:C and growth rate is not so simple. At the very least it does have an intercept $> \text{zero}$. Once you introduce this complication, the carbon-based approach can no longer be simplified to $P_{max} = \text{Chl}_{res}$. A more complex relationship between Chl:C and growth rate is easily introduced in the carbon-based approach and has been included in a revised version of the carbon-based model by Westberry et. al. (2007), but it is not so straight forward to do in a chlorophyll-only model because the separate contributions of biomass and physiology can not be distinguished.

In conclusion, when the 'scattering based' approach is accurately portrayed, no evidence has been provided from the beginning of the manuscript to section 4.4 that supports any statement that T_{chl} provides a more accurate estimate of photosynthesis.

3) (remainder of section 4.4) The later part of the second paragraph of section 4.4 is as follows and is accompanied by Appendix A:

"... unless the estimate of the backscattering coefficient from remote sensing is much more accurate than that of phytoplankton absorption or chlorophyll a, there is little opportunity to improve the determination of photosynthetic biomass from space using scattering or backscattering based algorithms. However, estimates of the backscattering coefficient tend indeed to be more accurate than those of T_{chl} from remote sensing. To test the possibility that backscattering could improve estimates of photosynthetic biomass at light saturation, we conducted the same analysis by stepwise

regression as previously done for P_{max} but restricted the depth range to the first optical depth at 490 nm (obtained as $1/K_d(490)$, leaving 45 points). We thus obtained two regression equations for the estimate of P_{max} using $Tchl a$ or b_{bp} as the phytoplankton biomass proxy. From these equations, we can use standard theory for the propagation of errors to test if we can obtain lower dispersion using the backscattering coefficient. This analysis is presented in Appendix A, and shows that for realistic values of the error on backscattering and $Tchl a$, it is not possible to improve estimates of the photosynthetic parameters for the BIOSOPE region in the context of the regression equations developed here.”

Here are two comments that pretty much invalidate this paragraph and Appendix A:

(i) The relative accuracy of bbp retrievals from space compared to chlorophyll is not the relevant question. Again returning to the carbon-based relationships above, one can see that *production* estimates are rather insensitive to bbp retrieval errors because if bbp is underestimated (overestimated), phytoplankton carbon biomass will be underestimated (overestimated) but growth rates will be overestimated (underestimated), such that production will be little effected (particularly if we assume the simple relationship between $Chl:C$ and growth rate). The carbon-based approach is, however, just as sensitive to chlorophyll errors as the chlorophyll-only approach.

(ii) This section is supposed to be about remote sensing applications and it is stated here that “BIOSOPE waters [are] probably representative of many open ocean conditions”, but this statement is only true *if all the data surface and deep water samples are included*. From a remote sensing perspective, the deep water samples are akin to ocean areas with deep mixing or low ambient light or both. As discussed above, scatter in the $Chl:P_{max}$ relationship is dominated by photoacclimation. This major effect of photoacclimation on $Chl:P_{max}$ relationships is also expressed across the global ocean surface layer and exhibits strong seasonal variability. So what then is the value of assessing errors only in the surface samples where you have thrown out nearly all of the variability due to photoacclimation? Even if this were an appropriate approach,

you would also have to correct the bbp:chl relationship for variability in growth rates.

4) (section 4.5) The first paragraph of this section is as follows:

*“An important question remains: Given the regression using $Tchl_a$, can scattering based variables allow us to improve estimates of P_{max} and α ? In other words, is there supplementary information in the scattering based proxies? This question can also be addressed by a stepwise regression analysis, by verifying if adding scattering based measures improves the fit significantly. We tested the addition of the following variables: $b_p(650)$, $b_p(650)^2$, and $Tchl_a/b_p(650)$. None of them provided significant improvements in the regression of P_{max} (all had values of $p > 0.17$) or α (all had values of $p > 0.14$). We therefore conclude that, for the waters studied, which are probably representative of many open ocean waters, bulk scattering measurements cannot be used to improve estimates of photosynthetic biomass (or parameters), once basic information regarding chlorophyll concentration and irradiance at depth is available (see **Error! Reference source not found.** and 3.)”*

What this is saying is that, once photoacclimation is taken out of Tchl, throwing bp, bp-squared, or Tchl/bp into the stepwise regression soup doesn't improve the regression between Chl and Pmax (forget the alpha part because it is not a valid analysis, as described above). But why would it? I'm not going to go through the whole argument yet again, but there is no reason to think that this approach will help. The way to improve the Chl:Pmax relationship after accounting for photoacclimation is to also address any nonlinearities or intercepts in the chl:C and growth rate relationship. Simply adding cp or bbp to a stepwise regression is not expected to help.

5) The difference in the bbp to chlorophyll relationship between the satellite data set (Behrenfeld et al. 2005) and the BIOSOPE data set is interesting. One possibility that has not been raised in the manuscript is that the BIOSOPE data is the problem. This is not a criticism of the investigators, only recognition that getting good bbp data from the open ocean is difficult and the current study included some of the clearest waters in the

world – this is very impressive!. Having attempted bb measurements myself in the open ocean, I'm wondering how the current investigators dealt with instrument corrections? Did they find that when numbers got low that a simple correction for backscattering by water actually yielded negative values for bbp? If so, how was this dealt with? Perhaps it would be worthwhile to show ratios of bbp:bp to see if the numbers are reasonable.

One thing that is clear from your data set is that there is a lot of variability in the intracellular chlorophyll concentration, since this is what's driving much of the variability in your Chl:Pmax relationship. Another issue is that the data shown in the satellite study represent integrations over very large areas and if you do a plot showing all the satellite pixels, the range of variability allows for a wide range of relationships between bbp and chlorophyll but this does not represent any particular problem with retrieving phytoplankton carbon from bbp.

The bigger problem is that your data do not suggest an intercept significantly greater than zero, as the satellite data do. Again, this could be a problem with bbp data in clear waters, but it could also be a problem with the satellite retrievals. You state in the manuscript *"Regarding these low-chlorophyll waters, we note that the recent comparison of semi-analytical models using IOCCG synthetic data set has only 11 out of 500 points below $bb = 0.001$, and is therefore of little help in resolving the issue. . ."*, but I would also note that in this IOCCG report, the GSM tends to **underestimate** bbp at very low concentrations rather than overestimate them.

Finally, in Figure 1 all of the panels are log-log plots except the bbp vs chlorophyll plot. You should plot all figures in a consistent way.

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