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Biogeosciences Discussions

Interactive comment on "Inferring phytoplankton carbon and eco-physiological rates from diel cycles of spectral particulate beam-attenuation coefficient" *by* G. Dall'Olmo et al.

G. Dall'Olmo et al.

gdal@pml.ac.uk

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Reviewer 1

We thank the reviewer for his helpful and constructive review, which we believe has significantly improved the original manuscript.

Below we present the reviewer's comments in blue and our answers in plain text. Our answers follow the order of the reviewer's comments.

Size-dependent model of cell growth – Sosik and colleagues (2003) (hereafter S03) published a comprehensive and very well described study of the population dynam-

ics of coastal phytoplankton determined from time-series measurements using a submersible flow cytometer. A model of cell size transitions figures prominently. Their Figure 5 shows their matrix population model for growth and cell division in Synechococcus. The elements of the figure are directly comparable to Figures 1 and 2 and Equations 3 and 4 in D11, but in my opinion, the schematics in S03 describe the model elements much more clearly. Further, I feel that the presentation of equations and choice of notation in S03 are much easier to follow than those in D11. More importantly, the similarities between the model of cell growth in D11 and that in S03 greatly exceed the differences; to me, they look essentially the same. DallÊijOlmo and colleagues appropriately cite the studies on which their model is based, and they cite S03 to support one of their assumptions and to recognize a difference in observed size distributions, but they do not acknowledge the existence of the S03 model and thus seem to imply that the D11 model is novel in this oceanographic application. To satisfy the BG Evaluation Criterion, "Do the authors give proper credit to related work and clearly indicate their own new/original contribution?" the authors should add some serious consideration of the S03 model, which may have been developed independently but which is applied to an oceanographic problem very closely related to what is studied in D11. When the authors review the content of S03, it might be helpful for them to check a complementary publication by Green et al. (2003) that might help in reconciling optical estimates.

The main concerns of the reviewer here are: 1)the presentation of our model equations and notation is not clear; 2)the S03 model should be better acknowledged and the differences with the model employed in this work should be clarified; 3)we should consider the `[Green_etal_2003]` paper to reconcile our optical estimates.

We respectfully disagree with the reviewer that the S03 model is identical to the model employed in this study, which was initially developed by `[Gage_etal_1984]` and extended by `[Smith_1996]` and `[Arino_etal_2002]` (GSA94, for brevity). Although both models are discrete and based on a transition matrix approach, there are signifi-

cant mathematical differences that make the GSA94 self-consistent and more realistic, which is why it was selected for this study.

One of the most important differences is that the GSA94 model allows cell division only after cells reach a critical size. Cells in this critical size class have a mean volume that is twice the minimum cell volume. Thus, the model conserves biomass and the cell population remains within its original size range, even after many generations. On the contrary, the S03 model allows cell division in any size class. As a consequence, the cell population would reach progressively smaller minimum sizes with time, if [Sosik_etal_2003] did not prevent this unnatural behaviour by forcing new-born cells smaller than the imposed minimum size to acquire such minimum size. In practice, therefore, the S03 model does not conserve biomass.

Another important difference between the GSA94 and S03 model is that the former links growth rate, number of classes and iteration time. Thus, unlike the S03 model, the GSA94 model is self-consistent and does not need to set the iteration time to a short enough time to avoid cells from one class to grow, in one iteration, to a size larger than that of the next size class.

Finally, the S03 model simulates the relative distribution of cells, while the one we employed is based on absolute concentrations.

We further respectfully disagree with the reviewer that the presentation of equations in clearer in the S03 paper. The S03 paper requires 13 equations (their eqs. 2-14) to present essentially the same information that is presented in our paper in about 8 equations. By exploiting the previous publications of [Gage_etal_1984], [Smith_1996] and [Arino_etal_2002] we believe we can better focus on the novelty of our study (the interpretation of the spectral dependence of cp by means of a size-structured population model), rather than on details that have been already published.

Nevertheless, in the revised manuscript, we have 1)modified the notation to make the

symbols more clear (although we are limited by having two models in our manuscript, which reduces the number of symbols available); 2)prepared a new table with a detailed list of symbols and units and 3)added text in the discussion that clearly acknowledges that the S03 paper employed a discrete, size-structured model of population dynamics to interpret in-situ flow cytometric measurements of Synechococcus.

With respect to the paper by [Green_etal_2003], it is not clear how we should be using it to reconcile our optical estimates. The Green et al. paper presents a method to invert carefully calibrated flow cytometric data to derive size and refractive index of cells. The difficulty in employing the methodology proposed by Green et al. is that the flow cytometer that we used to derive cell counts and side scatter data was not calibrated in the manner required by the study by [Green_etal_2003]. Therefore, only relative measurements of side scatter can be extracted, and we cannot estimate size and refractive index from our flow cytometry data. A reference to the [Green_etal_2003] paper has been added in the section of the manuscript where future studies are discussed.

Comparison with previous studies of diel variability in the beam attenuation coefficient — The authors do a good job reviewing relevant research going back to the pioneering study by Siegel et al. (1989), and their examination supports assertions about the particular advantages of their new approach. They did miss at least one relevant study, however. Years ago, Cullen and Lewis (1995) addressed problems that were recognized in the early studies, bringing up most of the issues that are discussed in D11. These include diel changes in cell size and chemical composition, assumptions about carbon-specific attenuation and the attenuation of light by particles besides phytoplankton, the effects of light-induced changes in refractive index (cf. Ackleson et al. 1993, Ackleson et al. 1990), and assumptions involved in comparing estimates of productivity from beam attenuation with those from incubations. They also presented calculations to reconcile cp-derived estimates of growth rates and chemical composition with independent estimates of the ratio of phytoplankton carbon to chlorophyll and

measurements of primary productivity. A physiological-optical model produced results consistent with available knowledge, eliminating a major issue with the estimation of growth rate highlighted in D11 (p3024: 25-26). The assumptions could not be confirmed, but the analysis and its results are relevant to D11.

We thank the reviewer for pointing out this problem. We have removed the part indicated in this comment and added references to [Cullen_Lewis_1995].

Simulation of optical properties – As I mentioned briefly in the overview, the computational demands for the Mie calculations limit the utility of this approach, not only because only one day at one depth at one location is modeled and validated, but also because others are unlikely to try to replicate the analysis. A simple question arises, "Could this analysis be done using the anomalous diffraction approximations, e.g., as used by Morel and Bricaud (1986)?", If so, perhaps new horizons would unfold: thorough sensitivity analyses could be performed and results could be validated (or not) by applying the model inversions to different depths in different environments, including some where phytoplankton divide more than once per day. The answer to my question may be obvious to some, but I do not know what it is – if this is due to my ignorance, I apologize. If the answer is "no" on first principles, the authors can improve the paper by explaining why, in a brief statement. If the answer is unclear, I feel that the authors should conduct a parallel analysis using the approximations and determine if they can substitute for the Mie calculations in this particular application. To me, this would be important to the ultimate fate of this research.

Unfortunately, the Mie calculations are not the rate-limiting step that determines the long computation times (as clarified in the revised text, we employed a look-up table to minimize computation time). The execution of one model run is relatively fast (on the order of 0.005 seconds) and its duration is dominated mostly by calculations relative to the population model, not the optical model.

Typically, one full optimization of the model presented in the Biogeosciences Discus-

sion manuscript (i.e., one of the points in figures 6-8) required on the order of 1e5 iterations and lasted about 7 minutes on a 2.66GHz cpu. To be able to assign confidence intervals to our parameters and to test the robustness of our results, however, we carried out multiple (3000) optimizations. This resulted in a very large computation time that was subdivided among approximately 40 processors connected on a grid. Thus, the main time-limiting step is the need to repeat the optimization multiple times.

Potential future improvements, that are out of the scope of this work, could be 1) fine tuning the optimization algorithm and 2) rewriting the original Octave code in a lower-level language such as C, which is likely to result in an significant decrease in computation time (but a considerable investment in terms of debugging the new code).

Following the reviewer's suggestion, we have added clarifications regarding this issue in the discussion.

1) There is a fairly extensive literature on phased cell division in microalgae, and by no means is all cell division phased and confined to the nighttime (e.g., see Chisholm and Costello 1980). Many microscopic algae divide more than once per day, and such high estimated rates are not uncommon in a global assessment presented by some of the authors of D11 (Behrenfeld et al. 2005). How are these facts reconciled with the assumption of division only during the dark period? The answer should include some specific references to studies showing cell division dynamics of phytoplankton growing at more than 1 division per day; in my opinion it is not adequate to cite a study suggesting synchronized cell division in diatoms (p3013:3) without acknowledging that they divide during the day (Chisholm and Costello 1980).

We have answered this reviewer's question by relaxing the original hypotheses that cells divide only once per day and only during the night. The new version of the model, presented in the revised manuscript, admits division also during the day and, as a consequence, allows for more than one division per day.

2) How important to the analysis is the assumption of constant refractive index? Basing

their analysis on known processes that lead to short-term changes in refractive index of phytoplankton (cited therein), Cullen and Lewis (1995) modeled plausible changes in the optical properties of phytoplankton during the day, speculating about their influence on diel patterns of cp and their interpretation. It would be helpful for the authors to comment on these possible influences, based on their own quantitative analysis and access to more recent research results.

As mentioned in the introduction, experimental results have demonstrated that the refractive index of several phytoplankton cultures can be relatively constant during the diel cycle [DuRand_etal_2002];[Stramski_etal_1995], although other studies (e.g., [Stramski_Reynolds_1993]) concluded that variations in the refractive index were the primary driver of the observed diel changes in cp for T. pseudonana. Thus, it is still unclear whether m or D (or both) are responsible for the diel variations of cp.

Regardless, our results show that the inferred average cellular diameter is directly related to the assumed value of the refractive index, indicating that our model cannot independently infer m and D from our data. This is one of the limitations of our study. However, we have also found that other inferred parameters ($\mu_{\max}, k_{PAR}, \zeta, \delta_{\max}, c_{p0}, \xi_0$) are robust with respect to the refractive index chosen.

We have added text in the limitation section of the discussion to better acknowledge this issue.

3) The authors assign considerable significance to their results showing much lower grazing rates in the day as compared to the night. (Note that their proposed dismissal of the assumption by Cullen et al. (1992) of light-independent grazing [p3026:20] did not take into account the reanalysis presented by Cullen and Lewis (1995), in which the anomalous result was resolved.) Regardless, the proposal that nanoplankton are grazed at a much lower rate during the day should be evaluated much more thoroughly based on what is already known about diel patterns of grazing on very small

phytoplankton. Are the flow cytometer results for this study definitive? What do other records show? What is the evidence that large organisms (2 cm) are the dominant grazers on nanoplankton as implied on p 3026(line 25)? What about other research? For example, Smith et al. (1984) assumed light-independent grazing rates and obtained internally consistent results. There is a great deal more relevant information available, and I am not familiar with much that suggests very high grazing impact on nanoplankton at night and very low during the day. I may have missed the key papers, however. More support from the literature would help the authors' argument.

We have added a paragraph (with several new references) in the discussion section "Growth and loss rate estimates" to expand on this issue.

4) How are the comparisons of cp-based productivity with measured productivity influenced by the under-representation of picoplankton in the optically based estimates? Is C-bicarbonate uptake by picoplankton an insignificant part of total uptake in this oligotrophic environment? That would be a surprise, but if the data show it, fine: please report the results to the readers.

The production contributed by picoplankton (< 2.0 um) near the depth sampled by our system (9 m) was a significant fraction of the total particulate primary production (77% at 5.1 m and 47% at 12.2 m depth, unpublished data). We have added this comparison in the discussion section "Productivity estimates".

I feel that the presentation is fairly clear, but could be improved during revision. For example, the presentation of equations and the schematic depiction of the model are in my opinion not to the standard of Sosik et al. (2003), which I consider to be exemplary. The appendix describing the parameter selection procedure is terse, and I found it difficult to fully comprehend the corresponding figures 8-10, the legends of which did not help me much. Consequently, it is not clear to me that they are needed.

Following the reviewer suggestion we have removed the appendix and added text in the methodology to describe the parameter selection procedure.

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