Interactive comment on "Inferring phytoplankton carbon and ecophysiological rates from diel cycles of spectral particulate beamattenuation coefficient," by G. Dall'Olmo et al.

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1 Overview

This study, hereafter referred to as D11, addresses a scientifically important challenge that has received steady, but perhaps not intensive, attention for more than 20 years: describing the dynamics of phytoplankton on the diel time scale based on measurements of the particulate beam attenuation coefficient ($c_{\rm n}$; m⁻¹). The innovation presented here, well described in the title of the paper, is the analysis of attenuation coefficients at multiple wavelengths to retrieve information on changes in particle size spectra that could not be obtained in prior studies using measurements at one wavelength alone. The authors use a model of particle dynamics as one of their analytical tools. It describes cell growth and division, and predicts the optical consequences of changes in the sizes and numbers of cells for assumed constant values of the real part of the index of refraction. Applying a number of other assumptions about the nature of particle dynamics - for example, exponential rates of biovolume increase but no cell division during the day, and two constant loss rates (one for the light period and one for the dark) - the authors use a computationally intensive optical model inversion to minimize the difference between observations of spectral c_n and the model predictions, thereby retrieving estimates of rates of growth (net and gross) and parameters of cellular size. Further calculations yield estimates of phytoplankton carbon. Some of the products of this analysis are important for describing primary production and particle dynamics and are very difficult to obtain using established approaches; the conclusions of this study, if validated, are thus substantial.

The analysis is supported with observations using flow cytometry, and there is a fair degree of comparison of results to previously published observations or estimates. However, the authors do not discuss some relevant research, including prior modeling of cell populations that is very similar. Because the procedure requires a great deal of computing time, it was applied to only one example near the surface in oligotrophic waters. Questions about the generality of the model and the suitability of its assumptions — that might be readily answered by analyzing results from other environments (e.g., deeper, more eutrophic) — can therefore not be addressed. Further, it is unlikely that the method will be readily adopted by others or subjected to direct critical examination, since it is so computationally intensive. By no means does this invalidate the scientific contribution, but in my opinion it does reduce its general utility. As suggested below, if some simplifications can be applied, the method would be more practical for general application.

2 Comments on components of the presentation

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

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 c_p -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.

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.

Summary – The paper meets many of the Evaluation Criteria for BG, but there are some weaknesses and unresolved issues. Also, some questions should be addressed.

3 Questions

Questions that arise – I feel that the presentation — and the reader's ability to evaluate it — could be strengthened if the following questions were answered, either in the revised text or the response:

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).

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 c_p 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.

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.

4) How are the comparisons of c_p -based productivity with measured productivity influenced by the underrepresentation of picoplankton in the optically based estimates? Is ¹⁴C-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.

4 Additional comments

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.

5 Summary and conclusion

The analysis of attenuation coefficients at multiple wavelengths to retrieve information on changes in particle size is a great idea, and this analysis is an interesting start. I hope that it could be done using a simpler approach employing less computation, and I think that the presentation should include more consideration of the relevant literature. The assumptions of the model should be very carefully considered; some are not fully supported, and they may have led to misleading results, such as very low rates of grazing loss during the day. The questions raised in this review should be addressable, and the paper could be improved in the process.

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