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Discussions

Interactive comment on "Seaglider observations of variability in daytime fluorescence quenching of chlorophyll-*a* in Northeastern Pacific coastal waters" *by* B. S. Sackmann et al.

J. Cullen (Referee)

John.Cullen@Dal.CA

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John J. Cullen
Department of Oceanography
Dalhousie University
Halifax, Nova Scotia
Canada B3H 4J1

This is a very well presented quantitative examination of the variability of chlorophyll fluorescence as observed with an autonomous glider. The authors focus on the light-dependent depression of fluorescence near the surface – a phenomenon that has been recognized for decades (Kiefer 1973b, Loftus and Seliger 1975) but which continues to evade widespread appreciation by non-biologists.

As summarized in their conclusions, the authors “(i) used a unique bio-optical time series collected from an autonomous underwater glider to characterize variability in daytime fluorescence quenching; (ii) confirmed that daytime fluorescence quenching can be detected in waters off the Washington coast at all times of the year; and (iii) determined that the relationship between daytime fluorescence quenching and incoming solar radiation in phytoplankton off the Washington coast was remarkably similar to observations made in other oceanographic regimes, suggesting a degree of universality for the observed relationship.” I think that the authors’ summary is fully justified: the presentation is clear, the analyses are honest, and the conclusions are conservative. This study is solid indeed. However, the authors failed to impress upon Anonymous Reviewer #1 the scientific significance of their work. I agree with Reviewer #1 that on this count the paper falls short. But, I feel that this deficiency can be fairly easily corrected in a revised version if the authors can show more clearly the potential applications of their analyses.

A central theme, stimulated by work in the sixties (Lorenzen 1966, Strickland 1968), developed in the seventies (Kiefer 1973a, Kiefer 1973b, Loftus and Seliger 1975, Vincent 1979), and reviewed in the early eighties (Cullen 1982), is that physiological and taxonomic influences on fluorescence yield are sources of both errors and useful information. We should measure and interpret the variability of fluorescence yield in nature, not only to correct for the sources of error, thereby obtaining more robust estimates of chlorophyll concentration (Cullen and Lewis 1995, Holm-Hansen et al. 2000), but also to infer environmental influences on the physiology and taxonomic status of phytoplankton assemblages. The goals are no less than autonomous and non-invasive assessment of the bottom-up controls on phytoplankton dynamics on scales from meters (or less) to ocean basins.

Ocean gliders provide the opportunity to characterize with unprecedented resolution

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the distributions and dynamics of phytoplankton in relation to the physical and chemical environment in the ocean interior. The correction of fluorescence records to account for nonphotochemical quenching near the surface is extremely important for obtaining estimates of near-surface chlorophyll for comparison with remote sensing and with increasingly realistic models that describe vertical structure of phytoplankton. Sackmann et al. show how this correction can be made, and they demonstrate as well as can be expected that the method works. Similar irradiance-dependent corrections for nonphotochemical quenching have been presented before (Cullen and Lewis 1995, Holm-Hansen et al. 2000), but I believe that this analysis, based on diel variability and unable to rely on direct measurements of chlorophyll, is a novel contribution. The contribution is important, but as Reviewer #1 points out, largely methodological.

In my opinion, the scientific significance of the approach is its potential for being used to describe spatial and temporal variability in fluorescence quenching in relation to irradiance and the physical/chemical environment. That is, the information value of the relationship between quenching and irradiance is not in its universal generality, but in its variability in relation to environmental forcing. Where, when and why is quenching more pronounced? What does this tell us about environmental influences on photosynthetic physiology? The authors allude to the importance of these questions, but they need to be more specific about how they can be addressed (e.g., at the end of section 1). To do so, they need to delve further into the relevant literature (as suggested by Reviewer #1), including just a bit of what is written on variability of sun-induced fluorescence yield, the process that is more commonly assessed near the sea surface. Several studies can be consulted to describe hypotheses about physiological influences on sun-induced fluorescence yield as a function of irradiance (Babin et al. 1996, Kiefer et al. 1989, Laney et al. 2005, Letelier et al. 1997, Schallenberg et al. 2008). Of course, there are others.

Both Referee #1 and I feel that the authors need to describe better the scientific significance of their work. Further, as I describe below, the authors should re-

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solve some uncertainties about how background corrections were applied to measurements of backscatter, and what the implications are for the estimation of fluorescence:backscatter ratios.

Specific comments:

1) p 2841, lines 15-16: This definition of quantum yield is one of several possible definitions, and it is a bit fuzzy. Light emitted from pigments or from the cell? Why do you define it using light absorbed by photosynthetic pigments rather than by the cell? Relative quantum yield as estimated with a fluorometer is probably more closely approximated by fluorescence emitted from the cell divided by light absorbed by the cell. This is not the same as physiological quantum yield. Some distinctions among definitions are discussed by Huot et al. (2005).

2) The discussion of types of nonphotochemical quenching could be tightened up a bit:

a) The discussion of quenching on p. 2841 might be a bit more formal to avoid confusion (e.g., photoinhibition is not defined precisely so “photoinhibitory” can have different meanings). It would be useful to introduce the terms qE and qI and how they are defined and interpreted (e.g., Horton et al. 1996, Müller et al. 2001).

b) Be careful about the use of the term “photon-dose”, which refers to cumulative exposure and has implications that may not be intended here (see, e.g., Cullen and Lesser 1991).

c) Recognize the protective potential of qI (mentioned in the review by Müller et al. 2001).

3) p 2842 lines 10-21. Here is where you can make a better case for interpreting variation in fluorescence yield. See the general comments above.

4) Data and methods (section 2.2):

a) Clarify (if it is the case) that even though the glider descended to 1000 m, optical

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measurements were made only in the upper 150 m.

b) If you can, document that pressure (rather than darkness for example) is a major factor in reduced fouling. Otherwise, revise.

c) Clarify implementation of the clean-water background: i) was it determined for each profile and subtracted from values for that profile only, or was some average used? ii) Was this background subtracted from the backscatter measurements? If so, consider carefully if it is an appropriate "blank" for backscatter due to phytoplankton. Perhaps the authors should consider using special notation to refer to backscatter corrected for non-phytoplankton scatter.

5) Seaglider-satellite comparison: It might be useful to append a sentence to Section 2.3 stating the central assumption of the comparison, that the chlorophyll field estimated on one day by the satellite is static over the 7 d period. I know that this is mentioned later, but maybe it would be better to state it up front. A matter of choice.

6) Section 2.4, characterizing daytime fluorescence quenching: It appears that a modest amount of subjectivity was involved in the analysis. Perhaps the authors could be a bit more clear about their criteria (e.g., "if values of F:b_{bp}(700) were constant throughout most of the deeper portion of the mixed layer"), and how objectively they were applied. Also they should discuss the extent to which their results are sensitive to their criterion for depth of the mixed layer; other definitions could have been applied.

7) p 2846 line 27; DFQ is "sensor independent": In principle, DFQ is sensor independent if the sensor has the same specifications and the only differences are in sensitivity and blank (calibration). But as pointed out by Referee #1, since fluorometers differ greatly in their excitation characteristics (e.g., Neale et al. 1989) we cannot assume that all fluorometers (or satellite sensors) would detect the same degree of diel quenching.

8) p 2847, line 15; depth of quenching is related to the attenuation coefficient, Kd: Here

and elsewhere the authors refer to the attenuation of sunlight, but they do not attempt to quantify it even though in this sentence they say it is high. This is a conservative and acceptable approach, I suppose, but they could try to estimate light penetration using a standard chlorophyll-based case 1 model or a remote-sensing algorithm for Kd, at least for comparison of different regimes.

9) p 2847 line 24; bubbles: I believe that the prediction is that, even though bubbles may be found well below the surface, their influence on scatter would decline with depth so that if bubbles were an important factor, backscatter could not be uniform in a deep mixed layer. I agree with Referee #1 that this issue should be discussed, with reference to appropriate publications.

10) p 2848 line 10; influence of resuspended sediments on backscatter: Assessment of this statement depends on an explicit description of how the backscatter measurements were corrected for background. Using the measurements at 150 m for each profile could introduce a bias. But the figure seems to show non-zero scatter at 150 m in some parts (I can't tell for sure). Please clarify.

11) p 2849 line 9; "Vertical distribution of phytoplankton can be non-uniform, even in a so-called "mixed layer": This statement is not supported by a definition of mixed layer, and no citations are provided. The concepts should be discussed. You might go to Lewis et al. (1984) and work your way forward in time to Dusenberry et al. (2000).

12) p 2849 final paragraph; Discussion of fluorescence:backscatter: More citations are needed to provide perspective, and don't forget Mitchell and colleagues (Mitchell and Holm-Hansen 1991, Mitchell and Kiefer 1988).

13) p 2849; Interpretation of Figure 4a: It is very important to recognize that the ratio, F:b_{bp}(700), is sensitive to the background correction (c.f., Cullen and Davis 2003) and a positive correlation of the ratio of fluorescence to backscatter and fluorescence alone (compare Figs. 4a and 4b) can arise from an inappropriate background offset being applied to backscatter (Fig. 1, see `http://www.cmep.ca/jcullen/Cullen_`

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Biogeosciences_Fig_1.jpg).

14) Further, the assumption of a constant background for the calculation of ratios is problematic, as was well established in the pre-pdf era (Banse 1977, Eppley et al. 1977). A brief mention of this problem and perhaps some additional consideration of its implications may be helpful.

15) p 2850 paragraph 2; calculation of DFQ: Consider replacing “true negative values of DFQ” with “true negative values of diel quenching”. Also, try to improve the paragraph, which is a bit confusing. Since variation of biomass is a potential problem and backscatter is considered to represent biomass, why not calculate an alternate DFQ using F:b_{bp}(700) during the night and day, rather than F_N and F_D? Maybe I am missing something. Also (p 2851 line 8), why not use F_N from the middle of the night to minimize uncertainties about residual quenching near dusk?

16) p 2851 line 2; persistence of “photoinhibitory quenching”: See Morrison (2003) for an example of day-to-day changes in qI that may be due to persistent quenching. This was considered to be a cause of event-scale variability of what appears to be qI in a records of fluorescence from the Bering Sea (Schallenberg et al. 2008).

17) p 2851; discussion of daytime quenching: Old-timers would be gratified to see recognition of the studies by Kiefer (1973b) and Loftus and Seliger (1975), showing daytime quenching.

18) p 2852, top; parameterization of quenching as a function of irradiance: Using comparisons of measured fluorescence with extracted chlorophyll, both Cullen and Lewis (1995) and Holm-Hansen et al. (2000) parameterized quenching as a function of irradiance. The function presented by Cullen and Lewis (1995) is similar to the ones presented by the authors and Behrenfeld and Boss ...(2006), although the earlier study was cited in neither (Figure 2, see http://www.cmep.ca/jcullen/Cullen_Biogeosciences_Fig_2.jpg). There are similarities and differences between sets of observations (and fluorometers used), and the differences may be informative.

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19) p 2852; discussion of patterns in DFQ as related to light and nutrient stress: I agree with Reviewer #1 that the discussion of these issues is shaky and must be shored up with support from a number of relevant references. See Review #1 and the general comments above for references, and take a look at the recent paper by Ragni et al. (2008).

20) p 2853 lines 4-13; discussion of fluorescence profiles: Refer to Holm-Hansen et al. (2000) and replace "photoadaptation" with "photoacclimation". I agree with Referee #1 that this paragraph needs a bit of improvement.

21) p 2853 lines 12-20; vertical mixing and photoacclimation: I agree with Referee #1 – there is a great deal of relevant literature to consider.

Technical corrections:

22) p 2851 lines 10-11; causes of variability in quenching: Replace "due to" with "associated with". Causality has not been established.

23) Figure 3 legend: Explain the horizontal dashed lines.

24) Figure 5: I do not understand what "Median: 0.16 / 0.02" means. The first value is the median, but what does 0.02 represent?

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