Biogeosciences Discuss., 9, C3763–C3775, 2012
www.biogeosciences-discuss.net/9/C3763/2012/

Biogeosciences Discussions

Interactive comment on "Nutritive and photosynthetic ecology of subsurface chlorophyll maxima in the Canadian Arctic waters" *by* J. Martin et al.

J. Martin et al.

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Received and published: 5 September 2012

1) Comment: *General Comments: The manuscript presents an extensive analysis of 13C, NO3 and NH4 -uptake versus irradiance experiments for the Arctic subsurface chlorophyll maxima (SCM). NO3 and NH4 – uptake versus irradiance experiments are rarely conducted alongside traditional "P vs E" curves, so the paper includes some novel information on the rates of NO3 and NH4 uptake compared to carbon fixation for a range of irradiances and locations in the Canadian Arctic. Some observations, such as variability in the f-ratio with light and nitrogen availability, have wider implications for ocean biogeochemistry, but on the whole the paper is of local interest. My main*

concern is that there is no mention of a spectral correction to account for spectral difference between experimental and in situ light fields, or to account for variability in the absorption spectra of phytoplankton. Large errors will likely be present in a significant amount of the analysis presented in the paper if a spectral correction was not performed. I have given more detail on this below.

Response: We thank referee #3 for insightful comments and for appreciating the novelty of the study. Yet we think our study is much more than "local" in scope – since it deals with an area representing nearly a third of the Arctic Ocean, the most understudied and most affected (by climate change) ocean on Earth. Moreover it highlights fundamental differences in SCM ecology and function between the Arctic Ocean and subtropical/tropical domains. We slightly modified the text to place our result in this larger context.

Specific Comments:

2) Comment: *A spectral correction ought to be performed in order to account for spectral difference between experimental and in situ light fields, as well as for variability in the absorption spectra of phytoplankton. The importance of spectral corrections is well documented (Babin et al. 1993; Morel et al. 1996; Sugget et al. 2001) and relevant for the Arctic (Shakshaug and Slagstad 1991; Brunelle et al. 2012). With relevance to the current paper, the spectral correction is important, at least in my view, for the following reasons: 1) The initial slope (alpha), light saturation parameter (Ek) are spectrally dependent - their magnitudes are experiment-specific (relative) unless the experimental light spectra is accounted for, 2) Large and variable differences between the spectra of the experimental lamps and insitu light field are likely (particularly in coastal, case II, regions) so that experimental parameters cannot be accurately used to estimate in situ primary production without a spectral correction. 3) Phytoplankton*

BGD

9, C3763–C3775, 2012

light absorption varies with species composition and with depth, contributing significant variability in light-response curve parameters. Unfortunately, these issues are not acknowledged in the paper and, if a correction was not performed, I cannot see how any estimates made by combining experimental parameters and insitu irradiance can be valid. Similarly, if spectra differed between experimental light sources, then paramteres obtained from different experiments cannot be directly compared without a correction (e.g. such as comparison of NO3, NH4 and C13 response curves to estimate the f-ratio). I feel this is a fundamental problem that needs to be addressed as it could potentially undermine much of the data presented in the paper.

Response: This comment is very valid and we recognize that spectral corrections of the parameter alpha (and consequently of calculated Ek) are important, especially when the spectrum of the light source differs greatly from the *in situ* light field. We did not perform these corrections systematically. This is now specified in the text, which also includes a caveat on the accuracy of absolute alpha an Ek estimates. Before we discuss this further, however, it must be stated the main conclusions and arguments developed in the discussion are based on PBm values, and so are not affected by spectral issues. Another part of our analysis is based on relative differences in Ek for the uptake of carbon and different N sources. This analysis is not biased by the lack of spectral correction since the light source and incubator was the same for all stations, years and substrates (as previously stated in Methods). Since the photochemical dependency of N uptake pathways cannot be assumed to be as straightforward as for C fixation, we did not feel justified to apply corrections.

The comparisons of alpha and Ek made between the surface and the SCM, as well as the reconstruction of vertical profiles of C uptake, are more susceptible to spectral effects. We now acknowledge that uncorrected values can potentially introduce minor biases in the comparison between the surface and the SCM, with consequences for

BGD

9, C3763–C3775, 2012

the estimated contribution of the SCM layer to water-column primary production. We deal with these two issues separately in the next paragraphs.

Based on a thorough survey of the Arctic literature, none of the studies using laboratory incubations (Gallegos et al., 1983; Lewis and Smith, 1983; Gosselin et al., 1986; Harrison, 1986; Hirche et al., 1991; Kristiansen and Lund, 1989; Kristiansen and Farbrot, 1991; Kristiansen et al., 1994; Cota et al., 1996; Carmack et al. 2004; Palmer et al., 2011) that can be compared with ours performed spectral corrections of alpha (and Ek). Babin et al. (1994) argued that spectral effects have a minor impact on the assessment of primary production and vertical differences in photosynthetic parameters when full spectral lamps are used in conjunction with light-gradient incubators and when cyanobacteria are in low abundance (which was the case here – see Tremblay et al. 2009, AME 54, for cyanobacteria). We also used blue filters (Blue 118 Lee Filters Ltd.) in order to better simulate the underwater light of coastal environment (Harrison, 1977; Carmack et al., 2004; Hill and Cota 2005). While it is true that spectral absorption varies with depth below the surface, Shakshaug and Slagstad (1991) found small differences in alpha values ($\pm$ < 0.001 mg C (mg Chla)-1 h-1 (μmol m-2 s-1)-1; Fig 9) over the depth interval considered here. This difference falls within range of the statistical error attached to uncorrected estimates of alpha as determined with the 13C method ($\pm$11% for a mean value of 0.027). Moreover, this difference is one order of magnitude smaller than the variability observed in our data set (SD observed on the mean; 0.027 $\pm$ 0.014). Working in the same sampling regions during fall 2007 and spring 2008, Brunelle et al. (2012) concluded to a lack of difference in the spectral absorption coefficient of phytoplankton between the surface and the SCM in Amundsen Gulf for fall 2007 and a difference lower than regional variability elsewhere. We therefore conclude that the statistical analyses and interpretations presented in the paper are valid.

BGD

9, C3763–C3775, 2012

For the reconstructed profiles of primary production, the spectral issue is somewhat alleviated by the fact that near-surface communities operate at PBmax most of the time. Below, the prescription of an approximate alpha value may either underestimate or overestimate the contribution of the SCM, but this uncertainty is largely drowned by the biomass effect – i.e. the biomass differential between the SCM and the surface is so large that the conclusions would hold even if alpha values were overestimated for the SCM. Finally spectral corrections generally increase the value of alpha, which would only reinforce our conclusions that SCM layers account for a large share of productivity.

3) Comment: *Pg 6447 Ln 11: You could also reference Taylor et al. 1986.*

Response: Added.

4) Comment: *Pg 6450 Ln 26: Change "Detail" to "Detailed"*

Response: Done

5) Comment: *Pg 6450 Ln 26 – Pg 6451 Ln 1-2: "The depths (Z) of the SCM, pycnocline and nitracline were identified as those where the vertical gradients of in vivo fluorescence, N2 and NO3- had the highest values, respectively." Is the maximum gradient in chlorophyll concentration a reliable method for identifying the SCM? Why not use the depth of maximum in vivo fluorescence? Using this criterion, it seems possible that the maximum gradient in Chl-a could be either above or below the actual Chl-a maxima, thus unpredictably over- or under- estimating ZSCM for different profiles?*

BGD

9, C3763–C3775, 2012

Response: The SCM depth is actually defined by the depth of the maximum *in vivo* fluorescence. We reworked the text to clarify this point.

6) Comment: *Pg 6451 Ln 6: "Daily-averaged irradiance at the SCM (EÂËĞnSCM) and a continuous record of incident PAR above the sea surface (Kipp Konen; PAR-Lite) to estimate E0." Was any correction made for the transmittance of irradiance through the sea surface? If not, in situ irradiance could be quite significantly overestimated due to low solar angles and high surface reflectance in the polar regions (e.g. see Kirk 1994, Sakshaug Slagstad 1991).*

Was there any evidence of carbon fixation in the dark (as would be expected for the 14C radioisotope method)? If so, how was it accounted for? Since the dark uptake of NO3 and NH4 is discussed at length, it would be helpful to mention dark carbon fixation as well.

It would be helpful to mention whether or not the experiments were conducted at the same time each day. Was there evidence of diel variability in photophysiological parameters?

Response: A correction was indeed performed for E0. Sakshaug Slagstad (1991) indicated that surface reflectance accounts for a loss of 5 to 10

We did not observed C dark uptake in our incubation (i.e. the intercept of the initial slope of the photosynthesis-irradiance relationship was not statistically different from 0).

With respect to the timing of incubations most samples were taken during the local

BGD

9, C3763–C3775, 2012

morning, but keeping to an exact time was not possible due to logistical constraints (duration of the day, timing and duration of stations).

7) Comment: *Pg 6452 Ln 2-5. It is unclear what these standard errors represent? Are they errors or variability in the data?*

Response: The error on irradiance-uptake parameters is the standard error estimated by SigmaPlot for the fitting of the empirical exponential models (Platt et al. 1980 or Webb et al. 1974). Added.

8) Comment: *Please use different symbols for the light saturation parameter and initial slope of the NO3 and NH4 –uptake vs. irradiance parameters. Ek and alpha are accepted photosynthesis – irradiance parameters, but in this manuscript they have multiple meanings. If there are no standard symbols for "Ek" and "alpha" for NO3- and NH4 –uptkae versus irradiance curves, I suggest simply using subscripts, EkNO3, alphaNO3, EkNH4, alphaNH4 to make things clearer. I would also suggest doing this to distinguish DBNO3 and DBNH4.*

Response: Changed.

9) Comment: *Section 3.1 General Results in the sampling area. More information on the water column structure in the region would be very helpful here. What is the typical water depth? Is the water column stratified all year? The authors reference Martin et al. 2010 for details, but I feel information in the current manuscript is needed for the reader to put the SCM into context. A figure showing density, Chl-a, NO3, NH4 profiles for a representative station would help greatly.*

BGD

9, C3763–C3775, 2012

Response: We added the bathymetry to Fig. 1 and stratification information to the introduction section. We added NO3 and NH4 profile to Fig. 3.

10) Comment: *Pg 6453 Ln 15-18. ". . . and their vertical positions were significantly correlated with the SCM (ZPNM = 0.50 x ZSCM + 39.23, r2 = 0.12, n=201; ZPAmM = 0.72 x ZSCM + 25.75, r2 = 0.20, n=96)." What is the significance level of these relationships? The r2 values are very low, with ZSCM only representing < 20% of the variability in ZPNM and ZPAmM. To me, these do not seem like strong relationships?*

Response: Given the inclusion of all regions and seasons, a lot of variability was expected in these relationships - which is reflected in the modest r2 value. Yet the correlations are highly significant ($p < 0.0001$). When the analysis is restricted to near-synoptic oceanographic sections for the fall, the correspondence between the ZSCM, ZPNM and ZPAmM is very tight as showed by Martin et al. (2010). We added the "*p*" statistic to the text.

11) Comment: *Pg 6455 Ln 2-5: "On order to assess the contribution of the SCM layer to daily primary production and NO3- uptake during 2006, we combined uptake-irradiance parameters with measurements of daily mean irradiance and detailed vertical profiles of Chl-a. . . ." Some additional information on how the calculations described in this section were done would be helpful. I have a number specific questions: 1) what were the criteria for defining the surface layer and SCM (how was the 'top of the pycnocline and top of SCM defined?)? 2) Given the non-linear nature of the 13C and NO3 –uptake vs irradiance curves, an estimate of daily uptake based on the mean daily irradiance will not be the same as an estimate based on the integrated daily irradiance (i.e. that accounts for the change in irradiance during the day). Is the assumption of mean irradiance likely to lead to a large error? 4) The authors assuming NO3- uptake parameters measured on the SCM sample are*

BGD

9, C3763–C3775, 2012

representative of the region from the top of the SCM to the base of the pycnocline. This assumption consequently assumes no change in the NO3- uptake parameters across the nitracline (since the nitracline and SCM are coupled). This assumption is, presumably, backed up by the observation that the parameters were not altered by NO3- additions. However, this is an important assumption and I feel it would be helpful to make it clear to the reader.

Response: 1) The bottom of the surface layer was defined as the top of the SCM (which was estimated as the first depth where the mean vertical gradient *in vivo* fluorescence (d(*in vivo* fluorescence)/dz) was zero over 5 consecutive depth bins). It was a coincidence that both depths corresponded at station 303. 2) This assumption could lead to important error in the case where the irradiance available during the day exceeds the light level where photoinhibition is observed. In the present study, no photoinhibition was observed in surface communities and photoinhibition in the SCM layer is very unlikely (see sections 3.2 and 3.9). 4) Actually, we did not assume that NO3- uptake parameters measured on the SCM sample were representative of the region from the top of the SCM to the base of the pycnocline (see comment # 11.1). But we assumed constant parameters for the whole SCM (from the top of the SCM to the bottom of the euphotic zone). As the referee mentions, this is based on the facts that experimental NO3- additions did not induce changes in uptake parameters (section 3.7) and that no correlation was found between uptake parameters and NO3- concentrations for the surface-SCM data set (Table A2). We clarified these points in the text.

12) Comment: *Pg 6456 Ln 2: Change "station" to "stations".*

Response: Changed.

BGD

9, C3763–C3775, 2012

13) Comment: *Pg 6456 Ln 13: Change "was" to "were".*

Response: Changed.

14) Comment: *Pg 6457 Ln 7-10: ". . . a detailed analysis of PBm versus temperature (T) showed a significant, positive linear relationship during late summer- fall (Fig 5. . .)." It looks to me that only the surface (solid triangles) samples show a linear relationship, the values from the SCM (solid circles) do not appear to not conform to this statement.*

Response: We specified that the PPMC analysis at the beginning of section 3.5 considered data from the SCM only (and was significant; $p < 0.001$) and included data from station NR24. This station has a disproportionate influence on the correlation since it is the only one where water at the SCM was distinctively warm. The station was removed from the analysis presented in figure 7 – where the correlation indeed appears to be weak for the SCM. However we argue that this is caused by the very small range (ca. 1°C) of temperatures actually observed at the SCM. The superimposed surface data, which are characterized by a much broader temperature range, are coherent with those of the SCM at low temperature (where PBm values from the surface and SCM overlap). We use this as a justification to propose a determinant role of temperature on PBm after the bloom.

15) Comment: *Pg 6460 Ln 26: ". . . because it can be mediated by heterotrophic bacteria and the portion taken up by phytoplankton is not necessarily constitutive (i.e. not assimilated or, more precisely, not leading to amino acid synthesis) since photosynthesis does not occur in the dark (e.g. N may be stored in cell vacuoles)." Please include references for these statements.*

BGD

9, C3763–C3775, 2012

Response: We added Kirchman and Wheeler 1998, Allen et al., 2002 for bacterial uptake and Dortch 1982 for non-constitutive uptake.

16) Comment: *Pg 6464 Ln 18: ". . .because the strong SCM there abolished the separation that different Ek values would otherwise impart." The wording could do with some work here.*

Response: Reworded

17) Comment: *Pg 6464 Ln 21-26: "In the reconstructed profiles (Fig. 3) the depth of maximum productivity occurred at the SCM and the 'classical' decrease in primary production with depth was not observed. . .". Please make clear that the water-column estimates were made only at a minority of stations during Sept-Nov 2006 - they are not representative of the whole region or of changes over time. It would be helpful to identify stations where profiles were estimated on Fig 1.*

Response: Actually, these stations are representative of the different regions of the Canadian Arctic (Table 1, Column 1). We also acknowledge the lack of spring data as a caveat in our conclusion. The impact of this shortcoming may be very limited however since Palmer et al. (2011) observed a continuous and rapid acclimation (within 4 to 10 days) of the phytoplankton during the initiation of the growth season (mentioned P6467 L1-6). We can thus reasonably assume that our observations apply to most of the productive period.

18) Comment: *Pg 6466 Ln 20-22: "When considering spring-early summer only, PBm*

BGD

9, C3763–C3775, 2012

can be approximated as a function of day of the year and temperature (e.g. PBm = 8.417 – 0.0229 DY + 2.742 T). Otherwise PBm can be estimated as a function of temperature only (e.g. PBm = 0.178 T + 0.538; Fig 5)." Please include statistics for these relationships so the reader has a clear idea of how much of the variability in PBm is described by T and DY. There is rather a lot of unexplained variability in the data (for these relationships as well as others in the manuscript) that is not currently acknowledged. It seems rather misleading particularly when promoting these relationships for remote sensing or ecosystem modeling applications.

Response: To ease the reading and avoid repeating numbers, we provided the statistics of this relationship only in the Result section (e.g. section 3.5 for relationship between temperature and the day of the year and PmB). As with all field data it is generally impossible to explain all the variability – but even partial explanations are a step forward. We believe that the relationships we offer are reasonably robust and represent an improvement over current approaches employed in some models and remote-sensing algorithms for the Arctic: which is to use an average PBm value established before climate change affected the region and apply this value blindly irrespective of season, region and depth.

19) Comment: *Table 1: Please define 'n/d' in the caption. Also, please describe how the correction for ice cover was performed and specify what the Mean and SD at the bottom of the two parts of the table represent.*

Response: Added.

Additional references quoted above:
Taylor AH, JRW Harris, J Aiken (1986) The interaction of physical and biological pro-

BGD

9, C3763–C3775, 2012

cesses in a model of the vertical distribution of phytoplankton under stratification. Elsev Oceanogr Ser 42: 313-330.
Babin M, JC Therriault, L Legendre, A Condal (1993) Variations in the specific absorption coefficient for natural assemblages: Impacts on estimates of primary production. Limnology and Oceanography, 38:154-177.
Brunelle CB, P Larouche, M Gosselin (2012) Variability of phytoplankton light absorption in Canadian Arctic seas. Journal of Geophysical Research. 117:17
Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press.
Morel A, D Antoine, A Babin, Y Dandonneau (1996) Measured and modeled primary production in the northeast Atlantic (EMULI JGOFS program): the impact of natural variations in photosynthetic parameters on model predictive skill. Deep-Sea Research 43:1273-1304.
Sakshaug E, D Slagstad (1991) Light and productivity of phytoplankton in polar marine ecosystems: a physiological view. Pp. 6S-85 in E Sakshaug, CCE Hopkins NA Britsland (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology. Trondheim. 12-16 May 1990. folur Research 10(1).
Sugget D, G Kraay, P Holligan, M Davey, J Aiken, R Geider (2001) Assessment of photosynthesis in a spring cyanobacterial bloom by use of a Fast Repitition Rate Fluorometer. Limnology and Oceanography 46:802-810.

Interactive comment on Biogeosciences Discuss., 9, 6445, 2012.