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Biogeosciences Discussions

Interactive comment on "Gross community production and metabolic balance in the South Pacific Gyre, using a non intrusive bio-optical method" *by* H. Claustre et al.

H. Claustre et al.

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We would like to thank both Dr. Marra and Dr. Williams for their in depth review which show that the topics and the method proposed are of significant interest for them.

Response to Dr. Marra

Your review was organized according to general and more specific comments. In what follows your comments (or part of your comments) are identified in bold and our response follows.

General comments

"**Their text implies that they see this as the first use of this method. . .**"

In the Introduction section (line 27), the paper by Siegel et al. was quoted as the first one to have highlighted diurnal cycle in c_p and to have concluded from this observation "that particle production is balanced at the diel scale". Thus it was not our intend to have the reader believe that we were the first one to describe this kind of method. We rather believe that this false impression was likely due to the lack of a literature review on what had been achieved with the use of c_p cycle since the first seminal paper by Siegel. This obviously was lacking and is now corrected by strengthening the introduction section by referring to a significant number of important papers in this respect.

"**The criticisms for using cp as a proxy of productivity are (1) that the carbon attenuation cross-section (essentially, C:cp) is not constant on a diurnal basis, and (2) that cell division cycles will confound any analysis.**"

We believe that we had addressed these criticisms (especially the second one : possible influence of cell division on the analysis) in the supplementary information section that was associated with the main paper. We still refer to this supplementary section in the revised version. This section has now been strengthen by adding a review / analysis of the laboratory studies that have addressed the diel change in the carbon specific attenuation coefficient (first criticisms of the method.)

"**Marra (2002) also show good agreement between O2, 14C, cp and diurnal CO2 drawdown. . . .These authors cannot make that claim**".

We agree and were not aware of the comparison performed by Dr. Marra. The agreement between the various techniques reported for the NABE experiment is now quoted in the introduction section.

However, we would like to point out that the North Atlantic bloom experiment Dr. Marra is referring to and where diverse methods (including optical ones) converge is a com-

BGD
4, S2298–S2311, 2008

pletely different system which appears to be a net autotrophic system at the time of the study. The issue of metabolic balance (net heterotrophy vs net autotrophy) is not a general global ocean issue, but essentially an issue specific to sub-tropical gyres. We wanted to test the c_p method in the very oligotrophic waters of the SPG (here defined as those waters with Ze $>$100m) essentially for two reasons. First the SPG is likely the most oligotrophic waters of the global ocean and it is arguably the best location to compare optical and in vitro methods in the context of the debate related to the metabolic balance of such systems. Secondly we believe that the optical method can be especially reliable in 1D system where lateral advection is negligible (this point is in agreement with the specific comment (7) of Dr. Marra). In other oceanic environments, the optical method can be applied (Marra, 2002) and compare well with other production measurement, only if there is a way to make a lagrangian study of a water parcel or if the analysis is restricted to mixed layer (Marra, 2002). In some other places the cp method does not work, likely because of lateral advection during the period of investigation. This was for example the case at the EGY station in our study where obvious changes in water masses did occur. In summary, addressing only the oligotrophic, highly stratified waters provide some kind of guarantee of water stability to investigate $c_p$diel cycle free of "noise" due to lateral advection.

specific comments of Dr. Marra

1 p. 3092, near top. Hansell et al. (2004, Limnol. Oceanogr., 49(4), 2004, 1084–1094) is also a 'large scale geochemical analysis' of the North Atlantic, and they find that the metabolic balance is autotrophic but very close to 1.

OK reference added

2. p. 3098, lines 7-10. This is a new definition of gross community production. Gross production is supposed to include respiration losses, and diurnal cp will have losses built in, whether they are respiration or grazing.

We agree with this statement. The rate that we define here as gross community pro-

BGD
4, S2298–S2311, 2008

duction is closely linked to its optical determination and is not the strict equivalent (or an exact estimator) of the classical production terms. But we recall that we wrote "*the GCP seen by a transmissiometer is here defined as*" to specify that it was a definition pertinent to optical measurements. Thus, to avoid any ambiguities, all optically-resolved rates we define here will be referred with a Opt prefix (e.g. ^{Opt}GCP for optically resolved Gross Community Production). To help the reader assess the method, we now further detail the meaning of ^{Opt}NCP and the potential implications of these differences with standard definitions [see text after eq (1)].

3. p. 3098, lines 15-17. It looks as if CL is constant day or night. Is there evidence for this?

Admittedly there is no evidence for this. Here, we make the same assumption as the one generally used for the O_2 technique, where it is considered that night and day respiration are the same (see also your comment 5). This assumption is now provided in the ms ([before eq (2)].

4. p. 3098, line 25. I'm not at all sure what 'net carbon stock' is.

NCS definition was essentially the net POC accumulation in the water column over a period of time (g C m^{-2}). We, however, decided to remove this definition from the text as it was not necessary to explain the method.

5. p. 3100, lines 5-15. First, this analysis (like all O2 based incubations) assumes that the dark bottle gives an accurate representation of the actual respiration rate during the day. This might not be true, and often, comparisons of GPP from dissolved O2 analyses with ^{18}O incubations shows significant differences. The correct comparison with cp should be the increase in O2 in the light bottle during the day, the only unambiguous measurement of the dissolved oxygen method.

You are right however, we have only two O_2 incubation experiment simultaneous to diel c_p measurements at the GYR station. This is not sufficient to establish any (rigorous)

BGD
4, S2298–S2311, 2008

comparison. The 473 value presented in Table 1 correspond to an average between 315 (day 1, very cloudy) and 631 (day 3, sunny). For the same periods, the corresponding ^{O}GCP were 618 and 692, respectively in the 0-Ze layer (vs 663 and 911 in the 0-1.5 Ze layer). No, conclusion can be drawn from these comparisons.

6. p. 3100, lines 18-19. I don't think you can make the categorical statement that GPP will be less in the South Pacific Central Gyre. Light penetration is also greater, so there is a deeper euphotic zone, and more depth over which to integrate production.

We do not agree. The SPG is likely the oceanic end member of oligotrophy and it is thus expected that the rates are lower. Yes, light penetration is greater and so deeper is the euphotic zone. Actually it is the deepest for open ocean waters (see also Morel et al., 2007, L & O). But this deep euphotic zone is mainly the consequence of Chla within this layer being more "dilute". Actually the integrated Chla (including DV-Chla) content within within 0-Ze is around 8 mg m^{-2}, to our knowledge the lowest ever reported for an oceanic area. Thus low biomass in this layer should expectedly convert into low production.

7. p. 3100, lines23-24. Too bad there are no geochemical methods to use in the comparison. It might be wise to point out that they don't always work at these time scales because of the variability in mixed layer depths, and other confounding factors. It is interesting that the most stable water column is best for this analysis, and incubation techniques do the same thing by hold samples at prescribed depths.

We agree, the technique based on diel cp is relevant only for stable stratified, expectedly 1D systems. See our response in "general comment"

8. p. 3101, p. 3102. I would like to be sure, for the discussion of deep productivity, that the water column was stable for these measurements. That is, there were no internal waves or intrusions that contaminated the cp signal. I don't see

BGD
4, S2298–S2311, 2008

EGU

any hydrographic data to go along with Fig. 3.

There was no internal wave. We provide a figure of the density field (over the five days of investigation at GYR) here.

See Fig. 1.

9. p. 3103, lines 22-23. I think the 'light shock' they mention is unlikely in current practice. Not to say it hasn't happened before, but it has become well-recognized that keeping the samples in Niskin bottles is ok, and storing until filtration in dark nalgene bottles is ok, too.

We partly agree. What we were referring in the ms was not a light shock after the 24 hours incubation : these shocks have likely no influence on the already labelled living particles. We are rather referring to light shocks possibly occurring during sampling from the Niskin bottles into "light" bottle, during the adjunction of tracers (generally in the lab under so called "dim" light) and during deployment at sea of the production moorings which can sometimes occur, for unavoidable reasons on ships, a little bit after sunrise. In such conditions, the light shock for these deep phytoplankton population adapted to extremely weak photon flux ($<$1 μmole quanta m^{-2} s^{-1} at noon) might be irreversible.

10. p. 3105. The psi models deserve a further look. It was always difficult to determine to what depth you integrate to. That is, if the Chl-max is beneath the 1%E(0), it is difficult to see that it is a productive layer.

The last part of the section related to the PSI models was developed in order to highlight the possible potential of the optical technique in supporting the validation of carbon-based production model rather than Chla-based. We believe that, at least for stratified oligotrophic ocean (which represents a significant part of the global ocean) there is a great potential for this techniques. The various panel of Figure 9 correspond to various integrated layer. We believe and we try to demonstrate that even below the 1% depth,

BGD
4, S2298–S2311, 2008

EGU

in this highly stratified environment, there is the potential for significant production.

Response to Dr. Williams

Although you globally agree with our conclusions and rate estimation (introduction of your review), you addressed two main criticisms that we summarize here.

1. the first one is linked to the fact that we might have started on false conceptual basis (GCP underestimated by a factor of 2, comment 2) or spurious assumptions (phytoplankton responsible for only 20% of the POC increase, your comment 4). Both of these are not correct and seemed to have arisen from a misunderstanding of our manuscript.

2. the second one concerns our interpretation of the significant presence of photoheterotrophs as a possible explanation for metabolic balance . We agree with your arguments.

In what follows your comments (or part of them) are identified in bold and precede our response.

Comment (1)

Section 3097, l. 10-12. They start with a definition of NCP as NCP=GP-CL, where CL (community losses) is the sum of grazing, viral lysis and respiration. Now, NCP has a very clear meaning in the literature as the difference between Gross production and Respiration, i.e. it is the balance of organic material and organic energy in the system. Grazing, for example, gives rise to growth, which is part of community production and thus not wholly a loss term. (Of course, it would be if they were determining net primary production – but the discussion is of NCP.) Thus, their definition of NCP is at variance with the common and longstanding usage (a recent set of definitions can be found in Karl, 2002). Maybe they are

BGD

4, S2298–S2311, 2008

just considering net small particle production, but that is not NCP as there is a comparable flux of DOC – as they will be aware

We agree that the rates that we define in the present study are closely dependant on their (optical) determination. There are indeed not the strict equivalent (or estimator) of the classical production terms (by reference for example to Karl's et al. definitions). Thus, to avoid any ambiguities, all optically-resolved rates we define in this paper will be referred with a Opt prefix (e.g. ^{Opt}GCP for optically resolved Gross Community Production).

Here, grazing is considered as a loss term. Thus, the reviewer is right when he says that our measurement is not a strict estimation of NCP because additional loss terms are likely superimposed on respiration. This point is now clearly acknowledged in the manuscript [after eq(1)]. However these additional terms are weak, if any, given the method and the environment studied. Indeed, the present study was conducted in hyper-oligotrophic conditions where most grazers are expected to be small (and hence still detected by the transmissiometer) and sinking to be negligible. Additionally viral lysis likely does not contribute (as initially postulated in the first version) to the removal of particles from optical detection (by products of particle viral lysis are still seen by the transmissiometer), furthermore, the low concentration of organisms reduces the potential importance of viral lysis. Thus we believe (and now detail in the manuscript why) that ^{opt}NCP is only a slight underestimation of true NCP.

Comment (2)

Section 3097, l. 20 onwards. They seem to argue (line 20 onwards) that, as there the rate of day-time rise in POC equals the night-time loss rate (Eq 5), then GCP will equal the time-corrected day-time rise or night-time loss (Eq 6). This would only be the case if there were no particle removal during the day.

Maybe this is their conceptual model – but it is at variance with their proposal (Section 3097, sentence starting line 2) "heterotrophic biomass thus appears

BGD
4, S2298–S2311, 2008

also stimulated (. . .) to photo-autotrophic processes". They also should note, see (4) below and Section 3096, line 21, that they acknowledge day-time flux of particles. The conventional assumption is that the night-time removal processes continue during the day. This being the case, day-time gross production is the sum of the particulate production and removal. If there is no net production then in the simple case of the day and night-time periods being equal in length, GPP is 2*night-time loss not 1*night-time loss, as their calculation. This is the principal used for all O2 GPP rate determinations. In the case of the O2 approach, some authors contend there is greater flux during the day-time period, this would give a multiplier greater than 2. The uncertainties over the scale of heterotrophic processes in the light means that multiplier probably falls in the range between 1 and 3. Given equal day and night rates of particle removal the calculated rates of GPP and losses are essentially twice the reported ones, i.e. circa 1600 mgC/m2.d – that's high, twice those reported at the HOT site in the North Pacific Gyre but that is not grounds to conclude they are wrong.

We agree with all the conceptual statements / assumption (the important one being night-time removal processes continue during the day) of the reviewer but disagree with his conclusion that our rates are underestimated by a factor of 2. First of all Eq (5) [now eq (4)] does not deal with rate but with stocks (see also Figure 5) and it is likely the reason why the reviewer misinterpreted our rate estimation. Our calculation is indeed approximately equal to 2* night time loss. The factor 2 the reviewer is referring to was in the denominator of eq (6) [now eq(5)] where it was stated that GCP (not GPP) is equal to the night decrease in POC (NδPOC) divided by the night period ($\sim$0.5 d). Thus the calculated GCP (and losses rates) we have initially reported are right. There are not $\sim$1600 mg m^{-2}d^{-1} but $\sim$ 800 mg m^{-2}d^{-1} a value which actually remains very high compared with other in vitro measurements.

It is likely that the text was not clear enough with this respect. In particular the denomi-

BGD
4, S2298–S2311, 2008

EGU

nator of eq 6 [now eq(5)], (1 –Nt), was misleading, although valid in such systems with a roughly 12:12 day-night cycle. This part has been now reworked and clarified (see eq 5 and text after).

There was a mistake in our eq (6) where

Comment (3)

These higher calculated rates mean however, that the argument (Section 3099, l.13) based on Table 1 of the comparability of the optical and O2-determined losses would no longer stand and gets worse when we consider the implications of (4) below.

Given the above response to comment 2, the argument of the reviewer is not correct. The loss rates estimated through O2 and optical method are compatible.

Comment (4)

"**I presume this refers to the POC increase**". . . .

No we do not refer to POC increase, solely to POC concentration and this has very important implication regarding the arguments of the reviewer in this section and the final statement of his review. It is likely that the text was not clear enough with this respect. This point has been now rewritten and clarified in the section "*3.2.1 The various terms of the budget*"

"if my arguments are correct, the present analysis is flawed and need a hard looking at. My intuition is that their observation that phytoplankton only give rise to 20% of the particle increase will turn out to be a major headache"

What we say here (and initially stated in Claustre et al. (1999) is that phytoplankton alone (20% of POC) can not explain the daily increase in POC. This means that other players (likely heterotrophs) would potentially have to intervene (but see below). But we never state that other heterotrophic players explains 80% of the cp increase.

BGD
4, S2298–S2311, 2008

EGU

Note that the following is also included in the supplementary information of the paper to demonstrate that a carbon budget closure can be achieved.

Let us try to provide a rough estimate the respective contribution of phytoplankton and "others" in shaping the daily cycle of cp-POC: In the euphotic layer (0-Ze) of the Gyre, the average POC standing stocks is 2.1 gm^{-2} (Figure 6, central panel) of which ∼20% (0.42 g m^{-2}) is phytoplankton POC (Claustre et al., 1999; Grob et al., this issue). If we look for an estimation of the part of POC increase that is due to phytoplankton let us take a gross growth rate value of 0.69 d^{-1} (1 division per day, typical for *Prochlorococcus*, an important organism of subtropical gyres, Vaulot et al., 1995). The POC increase due to phytoplankton is thus 0.420 g m^{-2} (one doubling) which has to be compared to an average gain of 0.730g m^{-2} over the same period (Table 1). Thus phytoplankton would be responsible for ∼60% of POC increase leaving the remaining 40% (310 mg m^{-2}) for other, non-phytoplankton organisms. If the phytoplankton growth rate was 1 j^{-1} (a value reported by Laws et al. 1984) for the North pacific subtropical gyre), POC increase would be totally explained by phytoplankton.

Thus phytoplankton contribute between 60 and 100% of the daily increase. Lets use, for the sake of this calculation an intermediate value of 80% for phytoplankton (580 mg C m^{-2}) and 20% (150 mg C m^{-2}) for the others (say heterotrophic bacteria). Dividing 150 mg C m^{-2}by 0.15 (bacteria growth efficiency), we end up with a bacterial carbon demand of 1g m^{-2} per day. At this stage, we recall that for the North pacific Gyre (less oligotrophic than here), Karl et al. (1998) reported that phytoplankton production is partitioned between 50% particulate (580 mg C m^{-2}) and 50% dissolved (580 mg C m^{-2}). Using these findings, there is clearly a "missing DOC" of 1-0.580, i.e. ∼0.4 g m^{-2} for covering the organic requirements of the heterotrophic production. Furthermore, let us remark that a picture of more DOC release during photosynthetic processes is likely possible in such an exceptionally nitrogen depleted environment, where DOC content is the highest ever reported (Raimbault et al. , 2008). While there are several plausible ways to balance this computation (i.e changing the growth efficiency of bacteria,

BGD
4, S2298–S2311, 2008

EGU

increasing phytoplankton contribution), another is simply by assuming that dissolved production percentage is greater than 50%. Indeed if it is 65 % the dissolved phase would be sufficient to cover all the bacterial carbon demand.

In summary we believe that, although the reasoning of reviewer was correct the starting point of this reasoning (part of GCP due to phytoplankton production) was wrong and misinterpretation of our manuscript which referred to phytoplankton carbon standing stocks and not to the fraction of GCP due to phytoplankton production. Based on this and following the reasoning of the reviewer with the correct starting values and some reasonable assumptions we show that a closure of the different terms of a carbon budget are attainable from our optical measurements.

Comment (5)

The various comments/arguments of the reviewer regarding anoxygenic photosynthesis can be summarized as "**Thus the notion that anoxygenic photosynthesis can reconcile the net heterotrophy. . . doesn't hold. . . "**

We agree with the reviewer's demonstration and we do not suggest anymore that anoxygenic photosynthesis can explain the oxygen unbalance. The text has been largely simplify and in particular the sentence "*We therefore suggest that part of the apparent metabolic unbalance reported for the euphotic zone of SPG and more generally of subtropical oligotrophic gyres based on in vitro oxygen techniques could be due to unaccounted photoheterotrophic processes, including anoxygenic carbon fixation processes*." has been deleted. However, we keep the anoxygenic photosynthesis idea as a potentially important process of POC formation (in the same way as heterotrophic bacteria) in such N depleted system where (very) high DOC release during photosynthesis could be the rule.

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BGD

4, S2298–S2311, 2008

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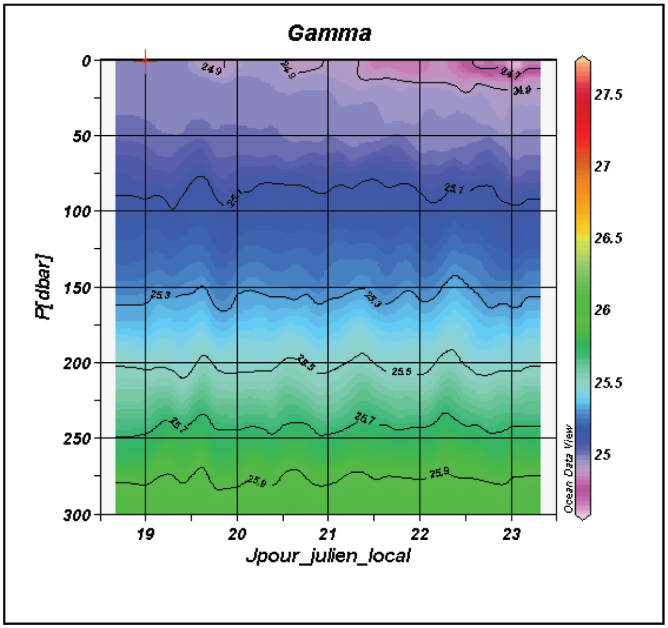

Figure 1:

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