Editor
Biogeoscienes

Sir/Madam,

Attached, please find the author's response along with the corresponding revised version of the manuscript "*Phytoplankton lysis predicts dissolved organic carbon release*" (previously entitled "*Rapid carbon cycling in the oligotrophic ocean*") to be considered for publication in *Biogeosciences*.

After careful consideration of the reviewers' comments and examination of the raw data for the time-series ^{14}C uptake experiments and the associated uncertainty, we acknowledge a basis for the reviewer's criticisms and conclude that the confidence of the results derived from the time-series experiments and the associated modelling is as yet insufficient to support the conclusions derived from these data. These results need to be verified with more robust experimental evidence, including more extensive replication. Hence, we will remove these results from the revised manuscript until they can be verified with additional experimental results.

As a result, the revised manuscript is greatly modified and focusses on the relationship between lysis rates and DOC release rates across communities, which reviewer #1 found to be the most interesting results presented. Hence, the title has changed, the order of authors has changed and the manuscript has been thoroughly rewritten to focus on these results. We provide additional rationale for this change in focus along with detailed replies to the reviewer's comments below.

Sincerely,

Carlos M. Duarte
Profesor de Investigación, CSIC

Actions taken to accommodate the comments of Reviewer #2

Reviewer #1: This study examined the release over time of dissolved 14C during standard 14CO2 primary production measurements in several oceanic regions visited over the years. The authors relate this release to a measure of phytoplankton lysis and then analyzed their results using a simple model of carbon flow between phytoplankton, DOC, and bacteria. The writing style of the paper is very compelling and engaging, and the topic the authors address is important.

Comment: We agree with this summary of the originally submitted paper.

Reviewer #1: But the paper has lots of problems. It is very difficult to see what is actually new about the study, other than the interesting observation about a positive correlation between lysis and extracellular release. As the authors acknowledge, extracellular release has been examined extensively (albeit not recently), starting with studies published back in the 1970s.

Comment: We agree, and have thoroughly revised the manuscript to focus on the positive correlation between lysis and extracellular release.

Action: We have removed the time-series ^{14}C uptake experiments and re-written the manuscript accordingly, highlighting the novel aspects of the results presented..

Reviewer #1: Likewise, several studies have examined the dependence of 14C primary production estimates on incubation times. The authors mention briefly some of these previous studies, but they don't mention John Marra's work on the topic. A couple of his papers are cited below. (Overall, the reference list of this paper is very short, especially after the authors' papers are subtracted out.)

Comment: We agree that time-series ^{14}C uptake experiments have been reported and discusses extensively earlier, and that our experimental results added little, to the existing body of literature, particularly considering the uncertainties in the estimates, which we have now evaluated.

Action: We have now removed these experiment and the associated model and discussion and focused on the relationship between lysis rates and DOC release rates..

Reviewer #1: The authors have to identify which specific problem has not been adequately examined before and how they will shed new light on it.

Comment: We agree.

Action: We now focus the paper in the role of phytoplankton lysis in accounting for the variability in DOC release rates among communities, the most novel aspect of the study.

Reviewer #1: Another overall problem with the paper is that too often it is hard to understand what is going on. Specific examples are discussed below. One big one is that the authors talk about DOC, TOC, and particulate carbon, but in fact the authors have measured none of these things. They have data "only" about 14C. So, their terms and language need to reflect that, as discussed below in more detail.
Specific comments

Comment: We agree.

Action: We have revised the ms. to avoid such confussion and to use terms accurately and consistently.

Reviewer #1: P11662, bottom: In this short review in the Introduction, the authors don't say exactly what they mean by "high" bacterial carbon demand; they do not give any percentages or ratios relative to primary production. Models may or may not need to have a large fraction of primary production released into the DOC pool, depending on what "high" is. Models by Nagata (2000) and Anderson and Ducklow (2001) (none all models in Anderson and Ducklow) assume that only 10% of primary production is excreted, yet in these models bacteria processing a "high" fraction of primary production, supported by DOC release by other components of the food web.
The importance of this paper does not rest on the reader believing that bacterial carbon demand is really high, perhaps unreasonably high. Understanding extracellular release would be important regardless of whether the emperor has clothes or not.

Comment: We agree.

Action: We have removed all of the models and discussion on bacterial carbon demand.

Reviewer #1: Somewhere here, the authors should cite Fouilland and Mostajir (2010), one of the
most recent data synthesis studies of bacterial carbon demand and primary production. Also, Williams (1990) is still one of the most complete reviews on phytoplankton excretion.

Comment: We have removed the discussion on bacterial carbon demand altogether. Unfortunately, we have been unable to find a copy of Williams (1990), since the journal was discontinued and is not available in the libraries we have access to, nor we have been able to find it in pdf form.

Reviewer #1: P11665, line 24: What was the level of 14C-DOC in the original 14CO2 stocks? Since the authors criticize a bit the "traditional 14C method", they need to

assure readers that they minimized all possible artifacts which have been identified over the years.

Comment: We have removed the results and discussion on 14C time series and no longer question the 14C method.

Reviewer #1: Another one that comes to mind is trace metal contamination. It can both inhibit and stimulate 14CO2 uptake.

Comment: We have removed the results and discussion on 14C time series and no longer question the 14C method.

Reviewer #1: P11666, line 10: What kind of “membrane” filters? Polycarbonate, nitrocellulose, mixed esters of cellulose or what? Actually, the text already gives probably the most important detail: that the pore size of these filters is 0.22 um. This is a significant difference from the vast majority of 14CO2 primary production studies which use GF/F filters. This is worth pointing out and discussed briefly.

Comment: We agree that this should be specified. Evaluation of the precision of dissolved primary production showed that 0.22 µm filters yield superior results to the use of GF/F filters, as adsorption of 14C-DOC onto glass fiber filters may overestimate particulate production, and understimate dissolved production, by up to 30% (Karl et al. 1998), and recommended that 0.22 µm filters be used for these measurements.

Action: We now specify that the filters used were cellulose membrane filters, the text now reads “The remaining volume was filtered through 0.22 µm cellulose membrane filters for determination of the total labelled particulate carbon (POC > 0.22 µm) retained in the filters, as use of glass fibber filters has been reported to overestimate particulate primary production (Karl et al. 2001).”

Reviewer #1: P11666, line 22: The description of the methods for assessing phytoplankton lysis, which is now buried in the middle of this paragraph, should be put into its own paragraph.

Comment: We agree.

Action: We have now described the methods for assessing phytoplankton lysis in a dedicated paragraph.

Reviewer #1: P11667, line 10: The left side of the equation is incorrect; the volume units (uL) should not be in it.

Comment: The equation did not contain volume units. μ_L is the notation for lysis rates, not µL.

Action: We have now changed the notation to μ_{lysis} , to avoid confusion with μL, and clarified the meaning of μ_{lysis}, the text now reads “The phytoplankton cell lysis rate μ_{lysis}, h^{-1}) was calculated from the decrease in PEA with time (t) due to the production of dissolved EA during cell lysis.
”.

Reviewer #1: Better would be to either say “specific lysis rate” (or something like that) or give a symbol for this parameter in the equation.

Comment: We agree.

Action: We now use specific lysis rates and have changed the notation to μ_{lysis} to avoud confusion.

Reviewer #1: More importantly, this equation would be more useful if it explicitly included the actual measured parameter, the dissolved esterase activity.

Comment: We agree.

Action: We now provide an equation linking PEA_t to the measured parameters, which is (Agustí et al. 1998). The methods section now reads “The initial particulate esterase activity () was calculated from the measured Chl a concentration using a ratio of PEA to Chl a derived from phytoplankton cultures (Agustí et al. 1998). The specific phytoplankton cell lysis rate (μL, d-1) was calculated from the decrease in PEA with time (t = 1 d) due to the production of dissolved EA during cell lysis.

$$\mu_{lys} (d^{-1}) = \frac{\ln\left(\frac{PEA_0}{PEA_t}\right)}{t}$$

where PEA0 represents the initial particulate esterase activity, estimated as described above, and PEAt, is the particulate esterase activity expected after a time interval t in days. PEA was calculated as PEA0 minus the production of dissolved EA, EA(Prod), calculated as,

$$EA_{(Prod)} = \frac{\frac{1}{2} EA}{T_{\frac{1}{2}}}$$

where EA is the measured estarase activity and is the half life of esterases, calculated from the rate of loss of the activity of the enzyme measured in experiments conducted in parallel to sampling (Agustí et al. 1998).”

Reviewer #1: P11667, line 20: “POC production” is not accurate and misleading here. A more precise, informative, and commonly used phrase is “particulate primary production” or even better “particulate 14C-primary production”.

Comment: We agree.

Action: We now refer to particulate primary production.

Reviewer #1: P11667, line 23: The authors report a negative correlation here between phytoplankton lysis rates and phytoplankton biomass. First, they give an rˆ2, but r should be reported because this is a correlation problem, not a regression problem; note that rˆ2 will always be positive even for negative correlations.

More importantly, the analysis is suspect because chlorophyll is used for calculating both lysis rates and phytoplankton biomass, meaning that the relationship between the two may be an artifact of the analysis; one cannot compare X and Y when B is used to calculate both X and Y.

Comment: We agree.

Action: We now just refer to table 1 and have removed the correlation analysis, which is not essential.

Reviewer #1: The analysis would be much more convincing and statistically valid if the authors analyzed the original dissolved esterase activity versus chlorophyll.

Comment: We have removed the statistical analysis of the relationship between specific lysis rates and chlorophyll since this could lead to artifacts and is not necessary here. We now focus on independent traits, particulate and dissolved primary production and specific lysis rates.

Reviewer #1: p11668, line 4 and elsewhere: The terms “TOC” and “POC” are inaccurate and very misleading. The authors did not measure TOC or POC or changes in these two pools. They measured the movement of 14C, so their terms should reflect that.

Comment: We now refer to particulate and dissolved primary production, as recommended by the reviewers.

Reviewer #1: p11671: This section is very difficult to wade through and understand. It may help to put the results of the modeling efforts in the Results section and to separate description of the model results from their interpretation and discussion. A table or two could be used to summarize what combinations of parameters were tested. There are discrepancies among the text, Table 2 and Figure 6. Table 2 does not summarize all values that were examined and tested.

Comment: This section has been removed altogether.

Reviewer #1: P11673, line 10: The authors here say that “cycling of carbon in the microbial food web occurs at a characteristic time scale of 10–15 min”. First, it is not clear where “10-15 min” comes from. But more important, if the authors mean all carbon, this is very hard to believe and is inconsistent with virtually everything known about microbes and carbon cycling in the oceans. Perhaps some free amino acids cycle on this time scale, but certainly not the entire pool of carbon. That implies incredibly high growth rates or extremely low growth efficiencies or some combination of both.

Comment: The reviewer’s concerns are correct. This section has been removed altogether for the reasons indicated in the cover letter and below. Analysis of the variability and uncertainty indicated that the rates derived from short-term incubations involved considerable error and uncertainty. Accordingly, we opted to remove this section, and the corresponding modeling study, waiting for the opportunity to verify the results with new experiments using a higher number of replicated providing greater statistical power.

Reviewer #1: p11674, bottom: The authors have to mention viruses as one possible mechanism accounting for the observed lysis. It doesn’t change their argument. But more troublesome, they really can’t discount grazing on phytoplankton, or even that some of the esterase activity may come from bacteria or other organisms.

Comment: The authors is correct that virus could account for some of the observed lysis (in fact we do not discuss the various mechanisms conducive to lysis, since we did not measure them). However, Agustí et al. (1998) report experiments that showed that grazing is not a significant source of dissolved esterases and that bacteria, and other heterotrophs, are not significant sources of dissolved esterase, as their specific esterase contents are much lower than those of autotrophs. Hence, Agustí et al. (1998) conclude that the estimates of specific lysis rates are not significantly affected by possible contributions by heterotrophs.

Action: We have now acknowledged the various processes that lead to phytoplankton lysis in the discussion section, which now reads “Phytoplankton cell lysis results from a number of processes including viral infections, UVB damage and light and nutrient stress (Suttle et al. 1990, Agustí et al. 1998, Berges and Falkowski 1998, Agustí 2004, Llabrés and Agustí 2006, Llabrés et al. 2011).”.

Reviewer #1: Table 2: The information in this table should be combined somehow with Figure 5 or 6. It is likely that Table 2 and the figures will not be on the same page (or computer screen), making it difficult for readers to go back and forth between them.

Action: The table and figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: Some of the values here are very extreme and are not the same as those actually discussed in the main text. The extreme ones include the assumption that percent extracellular release is 90% for all panels where in fact the caption for Figure 6

says 40%. Table 2 gives a bacterial growth efficiency (BGE) of only 2%, but it seems others were tested. Although BGE can be as low as 2%, the grand average for the oceans is closer to 10%. What happens when that value is assumed?

Action: The table and figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: Table 3: The time frame for these slopes is not clear. Are they the slopes of the initial part of the time course experiments? If the time courses were divided up, then the actual time frame should be given.

Action: The table and figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: The number of time points for each experiment should be given. If the same for all, the number can be put into the table caption. The column with "Experiment" does not give any information (readers can simply count the lines of the data to deduce this) and should be deleted. Rather than the slope for "TOC" (again, the wrong term), the slope for DOC should be given. Errors on all slopes should be given. The location of the column with p-values implies that they apply to only the TOC data. Why is that? If errors are given, then the p-value column isn't as necessary. And now the values (only 0 or 1??) look truncated.

Action: The table and figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: Figure 1: The orientation of this figure is weird, with lysis rate constants on the y-axis (and the label orientated the wrong way). The orientation gives the impression of a depth profile, which isn't what the data are about. The lysis rate constants should be on the x-axis, as in Figure 4. The difference between Figures 1 and 4 (the same type of data are plotted) is not clear.

Action: The panels in Fig. 1 have been separated and the

Reviewer #1: Figure 2: The authors should give the dissolved 14C data, in place of the total 14C (dissolved and particulate data). Also, the time zero values are not given, and the methods don't say anything about time zero. Were time zeros measured? Or they assumed to be background?

Action: The figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: Figure 3: This figure is hard to understand, mostly because the y-axis label is inconsistent with the figure caption.

Action: The figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Reviewer #1: Also, the micron sign is missing from the axes labels.

Action: The figures referred have been removed, for the reasons provided above, as these experiments and the models are no longer reported.

Actions taken to accommodate the comments of Reviewer #2

Reviewer 2: The study is built upon the basis that the discrepancy between bacterial carbon demand (BCD) and phytoplankton dissolved primary production is paradoxical. However, there is nothing paradoxical in this discrepancy: 14C-based dissolved primary production need not be equal, or even close to, bacterial carbon demand. The reason is that the 14C-labelling technique only measures a fraction of all DOC production within the planktonic food web. Release of 'older' (e.g. not recently fixed, therefore unlabelled) phytoplankton carbon, excretion from protists, DOC production from zooplankton sloppy feeding, breakage of fecal pellets, and other processes, all contribute to the release of dissolved organic substrates that can be used by bacteria. This has been shown conceptually by Nagata et al (2000) and in a steady-state model by Anderson and Ducklow (2001), among others. These studies show that high values of BCD are compatible with low rates of primary production and moderate (e.g. 20-30%) PER values.

Comment: The reviewer is correct.

Action: We have thoroughly revised the manuscript to focus on the relationship between dissolved primary production and specific cell lysis rates, and the time-series ^{14}C experiments (and the associated modeling) need to be verified further by additional experiment with increased replication to constraint the uncertainty and add confidence to the analyses.

Reviewer 2: The rates of short-term primary production measured by the authors in oligotrophic waters (e.g. Figs. 2a,b,c) are extraordinarily high, and deserve further scrutiny. Let us examine these rates, calculating the resulting hourly and daily rates, and compare them to relatively well-known quantities pertaining to plankton standing stocks and metabolic activity in the open ocean. In several oligotrophic locations (see Figs 2a,b,c) the amount of total organic carbon (TOC) produced during a 15-min period was in the range 10-28 mgC m-3. Assuming, conservatively, this activity is sustained during only 8 hours per day, the resulting daily rate of primary production would be ca. 320-900 mgC m-3 d-1. This rate exceeds the commonly reported rates of primary

production by more than 1 order of magnitude. Typical rates of particulate primary production in surface waters of the oligotrophic ocean (excluding blooms) are around 2-6 mgC m-3 d-1 (Steinberg et al. 2001). Assuming a high PER of 50%, total primary production would be 4-12 mgC m-3 d-1. Typical Chla concentrations in surface waters of the oligotrophic ocean are 0.1-0.2 mg m-3 or lower. Assuming surface Chla was 0.2 mg m-3 in the case of the samples shown on Fig. 2, the resulting carbon fixation to chla ratios (assimilation numbers) would range between 200-560 mgC mgChla-1 h-1. The maximum theoretical value, calculated taking into account the composition and turnover of photosystems, is 25 mgC mgChla-1 h-1 (Falkowski 1981). Typical values of phytoplankton C biomass in surface waters of oligotrophic regions are 5-15 mgC m-3 (Caron et al 1995, Buck et al 1996). Assuming a value of 10 mgC m-3 for phytoplankton C biomass, the rates reported here would imply biomass turnover times of 32-90 d-1. These values are clearly impossible: maximum biomass turnover rates for phytoplankton are 1-3 d-1.

Comment: The reviewer is correct and we concur that the rates measured are too high. We have gone back to the raw data, conferred the errors associated with the measurements and blanks and propagated the errors to assess the uncertainty associated with the estimates of accumulated ^{14}C in TOC. Whereas ^{14}C POC estimates were robust, ^{14}C TOC values involved considerably uncertainty, particularly at low sampling times, so that the results reported were flawed by very large errors. Whereas we believe these errors are unlikely to account for the very large rates measured, these are not as robust - because of the large associated error - as they should be to hold them against arguments that they are too large. We have, therefore, decided to remove these experiments, and the associated modeling, and conduct additional time series with increased replication to constraint errors to further verify the results of the time-series experiments originally reported.

Action: We have thoroughly revised the manuscript to focus on the relationship between dissolved primary production and specific cell lysis rates, as the time-series ^{14}C experiments (and the associated modeling) need to be verified further by additional experiment with increased replication to constraint the uncertainty and add confidence to the analyses.

Reviewer 2: The rates of TOC produced over a 15-min period are likely to be close to phytoplankton gross primary production (GPP). Converting C into O2 units by using a PQ of 1, the resulting GPP values are 27-75 mmolO2 m-3 d-1. Typical GPP rates in surface,oligotrophic waters, measured with the O2-evolution technique, are 1-3 mmolO2 m-3 d-1 (Robinson et al 2002, Williams et al. 2004).

Comment: We agree.

Action: We have thoroughly revised the manuscript to focus on the relationship between dissolved primary production and specific cell lysis rates, and the time-series ^{14}C experiments (and the associated modeling) need to be verified further by additional

experiment with increased replication to constraint the uncertainty and add confidence to the analyses.

Reviewer 2: The sharp decrease in accumulated DO14C, observed by the authors in oligotrophic waters, must be the result of bacterial respiration. The observed decrease, which is thus equivalent to bacterial respiration, is 8-25 mgC m-3 during a 45-min. period (Fig 2a,b,c). Even assuming that bacteria do not respire during the night, this rate translates (using a RQ of 1) into a daily rate bacterial respiration of ca. 7-22 mmolO2 m-3 d-1. For comparison, typical rates of total, community respiration (e.g. including the respiration of all heterotrophs) in the oligotrophic ocean are 0.5-5 mmolO2 m-3 d-1 (Robinson et al 2002, Williams et al. 2004).

In summary, it seems fair to conclude that the extraordinarily high values of primary production in oligotrophic waters reported here are not possible, which renders the authors' arguments and conclusions invalid.

Comment: We agree that the time series experiments need be verified further to confirm the (extraordinary) high rates reported. However, the relationship between dissolved primary production and specific cell lysis rates is novel and important, and is worth reporting. Conclusions need be focussed on this relationship alone.

Action: We have thoroughly revised the manuscript to focus on the relationship between dissolved primary production and specific cell lysis rates, and the time-series ^{14}C experiments (and the associated modeling) need to be verified further by additional experiment with increased replication to constraint the uncertainty and add confidence to the analyses.

Reviewer 2: Throughout the ms, the authors refer to bacterial use of carbon, rapid bacterial respiration, etc. However, none of these variables has actually been measured. Rather, they are inferred from the temporal dynamics of DO14C disappearance, which is attributed to bacterial use. This should be made clear throughout the ms.

Action: These statements are now removed

Reviewer 2: The ms does not refer to previous measurements of DOC production over short-time scales (e.g. <1 h). However, in their seminal paper on phytoplankton DOC production, Mague et al. (1980) included a time-series experiment (conducted in relatively low production waters, Gulf of Maine in summer) which had measurements during the first 15 min. Lancelot (1979) and Jensen (1983), among others, also reported DOC production measurements over time scales of ca. 30 min. None of these studies reported major departures from linearity in DO14C accumulation over time.

Action: The time-series experiments have been removed.

Reviewer 2: Pages 11665-6. More details should be given regarding the 14C incubations, including sampling time, time elapsed between end of incubation and filtration, handling of DPMs from black bottles (e.g. were they subtracted from DPMs measured in the light bottles?), difference in DPM counts between light and dark bottles at each incubation time.

Action: The time-series experiments have been removed (see reasons above).

Reviewer 2: Page 11668, line 14. This sentence doesn't work – should be: ': : :shallower than that for TOC, at: : :.'

Action: The time-series experiments have been removed (see reasons above).

Reviewer 2: Page 11671 The model should be described with more detail – this description should be included in the Methods section.

Action: The model has been removed, since the time-series experiments are no longer presented (see reasons above).

Reviewer 2: Table 3. From the legend, it seems as tough there are missing columns in this table.

Action: The time-series experiments have been removed (see reasons above).

Reviewer 2: P-values should have some decimal digits.

Action: The table has been removed (see reasons above).

Reviewer 2: Fig. 3 The legend and the label to the Y-axis seem contradictory – please re-write.

Action: The figure has been removed since time-series experiments have been removed (see reasons above).

Reviewer 2: Fig. 4. Y-axis labels are missing the micro- symbol.

Action: The figure has been removed since time-series experiments have been removed (see reasons above).

Actions taken to accommodate the comments of Reviewer #3

Reviewer 3: C5653 The conceptual model of the cycling of carbon in the microbial food web used (as pre- sented in figure 5) is incomplete, which together with the assumption

of steady-state leads to misleading conclusions. Firstly, microzooplankton may graze on both phyto- plankton and bacteria and respiration by auto- and heterotrophic eukaryotes are sig-nificant loss processes. This means that the assumption that the loss of accumulated TOC produced must derive from respiratory losses mediated by bacteria (p.11669) is not correct.

Comment: We agree.

Action: The figure has been removed since time-series experiments have been removed (see reasons below).

Reviewer 3: Secondly and most important, local or allochthonous DOC (and not only recently produced DO14C) is an important contribution to the heterotrophic res- piration in oligotrophic oceans (e.g., Duarte and Agustí 1998, del Giorgio and Duarte 2002). This implies that bacterial carbon use and respiration cannot be calculated from a steady-state model that only includes instantaneous primary production as organic matter source.

Comment: We agree.

Action: The model has been removed since time-series experiments have been removed (see reasons below).

Reviewer 3: From the large difference between total and particulate 14C primary production after short incubations in oligotrophic habitats, and the rapid loss of only total 14C PP (Fig.2), the paper concludes a very high DOC release and rapid respiration by bacteria. According to the authors, such a high DOC release can only be accounted for by an important cell lysis (L15, p.11670), which does not occur with healthy cells (L10, p.11670). At the same time, the extremely high 14C primary production rates after 15 minutes incubations are interpreted as representative of the high rates of photosyn-thesis in the oligotrophic ocean, previously undetectable by conventional methods. I find it difficult to reconcile the required prevalence in the phytoplankton of cells that are dead or compromised (L6, p.11670) on the one hand, with such a high photosynthetic activity on the other.

Comment: We agree.

Action: The model has been removed since time-series experiments have been removed (see reasons below), and rapid cycling is no longer invoked.

Reviewer 3: In addition, the conclusion that the extremely high rates of 14C primary production measured after 15 minutes incubations are representative of the oligotrophic ocean, would demand an explanation to a new suitable mechanism supplying the required large amount of inorganic nutrients to the surface of the stratified open ocean. Calculations of nutrient supply mechanisms to the upper oligotrophic ocean, including nitrogen fixation, diffusive transport and vertical entrainment, are insufficient to support

even standard primary production estimations (Johnson et al. 2010). Given the magnitude of the proposed new high flux of carbon in the oligotrophic ocean, a discussion on this issue is necessary.

Comment: We agree.

Action: The time-series experiments and the associated interpretations and models have been removed (see reasons below).

Reviewer 3: Such high primary production rates also contravene published independent evidence. Given that the paper sustains that conventional rates of 14C primary production in oligotrophic waters are severely underestimated, we need to compare the proposed GPP rates (after 15 min 14C incubations) with direct GPP measurements from changes in O2 concentration after incubations. In the N Atlantic subtropical Gyre, the range and mean for O_2 GPP rates in the dataset at www.amt-uk.org/data/respiration.xls, are 10- 201 and 69 mmol O2 m-2 d-1, respectively (Gist et al. 2009). Assuming 100 m of photic depth and a PQ of 1, these data become 1.2 - 24.1 mgC m-3 d-1 and a mean of 8.3 mgC m-3 d-1, respectively. The surface 14C PP data presented here (after 15 minutes incubation) are ca. 27 and 10 mgC m-3 15min-1 (Fig.2), that is, assuming 10 hours light, they are 1080 and 400 mgC m-3 d-1. This is 17 to 45 times larger than the highest value in the range of Gist et al (2009), and a discrepancy > two orders of magnitude with the mean published evidence based on a large database. These extremely high data would require extremely solid evidence and a very solid justification.

Comment: The reviewer calculations and arguments are compelling and indeed indicate that the rates measured at short-time scales appear much too high. We have gone back to the raw data, conferred the errors associated with the measurements and blanks and propagated the errors to assess the uncertainty associated with the estimates of accumulated ^{14}C in TOC. Whereas ^{14}C POC estimates were robust, ^{14}C TOC values involved considerably uncertainty, particularly at low sampling times, so that the results reported were flawed by very large errors. Whereas we believe these errors are unlikely to account for the very large rates measured, these are not as robust - because of the large associated error - as they should be to hold them against arguments that they are too large. Hence, we do not feel that the evidence provided by the time-series measurements conform to the requirement of providing extremely solid evidence, which - we agree with the reviewer - are necessary to underpin the extremely high rates reported. We have, therefore, decided to remove these experiments, and the associated modeling, and conduct additional time series with increased replication to constraint errors to further verify the results of the time-series experiments originally reported.

Action: We have thoroughly revised the manuscript to focus on the relationship between dissolved primary production and specific cell lysis rates, as the time-series ^{14}C experiments (and the associated modeling) need to be verified further by additional

experiment with increased replication to constraint the uncertainty and add confidence to the analyses.

Reviewer 3: And this is a critical issue in the manuscript, because the entire discussion rests on these data: time course data in Figure 2, support both the high GPP rates and the inference of high phytoplankton cell lysis and bacterial uptake and respiration. Yet the paper does not provide any argument supporting the possibility of such high GPP data in the upper oligotrophic ocean. And moreover, I have some difficulties not only with the magnitude but also to asses the validity of the data themselves. According to the Methods (p.11665) and Table 3, 20 time course experiments were carried out. However, only 6 out of these 20 time courses are presented in the key Figure 2. Why? Also according to the Methods, 2 dark and 2 light bottles were incubated, which is a very limited number of replicates that may compromise any statistical test of differences. And yet, data in figure 2 are presented without either their corresponding standard deviations or standard errors. Altogether, this means that the patterns sustaining the entire discussion rest on one (Fig.2.a) or at best 2 (Figs.2.b and 2.c) extremely improbable high data points based on just two replicates and whose variance we ignore, from 6 selected experiments out of 20 performed.
In my opinion, resolving these issues is necessary before we can start a critical debate about the ecological an biogeochemical implications of the observations and conclusions presented in the manuscript.

Comment: We agree with the reviewer and will go back at sea to conduct new experiments included much greater replication to derive the solid results required to verify the rates reported here (see above).

Action: We now focus on the relationship between specific lysis rates and particulate primary production.