

RESPONSE to REVIEWER #3 (130315)
BGD
11, C8710–C8713, 2015 Interactive Comment

Biogeosciences Discuss., 11, C8710–C8713, 2015 www.biogeosciences-discuss.net/11/C8710/2015/

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Biogeosciences Discussions

Interactive comment on “Peru upwelling plankton respiration: calculations of carbon flux, nutrient retention efficiency and heterotrophic energy production” by T. T. Packard et al.

Anonymous Referee #3 Received and published: 13 February 2015

This is a very interesting, well written and thought provoking manuscript that pursues the estimation of important and difficult to measure biogeochemical variables such as organic carbon flux and nutrient retention efficiency from estimates of plankton respiration derived from measurements of the ETS activity. Both the concept, calculations and results are novel, clearly presented and relevant for Biogeosciences. However I have some questions that would like to see discussed.

Comment #1: The model to estimate F_c from R (Eq.(1), Page 16184) is one-dimensional, which has several implications.

1.1. Lateral inputs of organic matter are assumed negligible for R compared to vertical fluxes (Page 16183, line 17). This goes against abundant observations of relevant lateral POC and DOC transport in upwelling systems, which should be important here given the dynamics of the upwelling during the sampling, described in section 3. Even in less dynamic and less heterogeneous systems, the horizontal scale of the region supplying organic carbon to a water column should depend on the depth of the water column, which varies here from 63 to 4755 m. It is not clear which is the top area of the seawater cube where F_c is estimated (Page 16183, line 15), nor if it is different for shallow and deep stations. I think that it is important that the horizontal domain of the model is stated. The consequences of the assumption of irrelevance of lateral inputs should be discussed, and if possible quantified.

Authors' response: A priori, we thought as does the reviewer, but it seems that even in the dynamic waters of an upwelling system the vertical dynamics dominate horizontal ones. Using particulate protein (PP) as a proxy for particulate organic carbon (POC) and drawing on the analyses in Fig. 4 of Garfield et al. (1979) we find that the strongest horizontal gradient is in the offshore direction in the upper 130 m of the water column. This is 5.51×10^{-5} microgram PP per meter in the offshore direction. In the vertical direction we draw on Fig. 3 and Table 1 from Garfield et al. (1978) to calculate a vertical gradient of 326 microgram/l over 500m or 0.652 microgram/l per meter. Accordingly, the ratio of the vertical to horizontal gradient is $0.652 / 5.51 \times 10^{-5} = 0.119 \times 10^5 = 1.2 \times 10^4$, ten thousand fold greater! This means that in the strongest case for a horizontal gradient, in the upper 130 m of the water column the vertical protein gradient is ten thousand times greater than the horizontal gradient. In the deeper parts of the water column the horizontal gradients become

even smaller, and the long-shore gradients are even smaller than the offshore gradients (Garfield et al., 1978). Thus we feel justified in using a vertical model to calculate carbon flux.

As for the top of the seawater cube where carbon flux is estimated, it is the bottom of the euphotic zone (E_z).

On page 16183, line 16-17, as proposed previously the text now reads. ”

Conceptually, planktonic RCO_2 in a seawater cube is considered as equivalent to the difference between the total FC_1 through the top of the cube and total FC_2 through the bottom of the cube, where total carbon flux refers to the sum of the DOC and the POC carbon flux. We deduce, on the basis of (Craig, 1971; Carlson et al., 2010; Hansell et al., 2012), that R based on DOC and lateral POC flux, compared to the R based on the vertical flux of labile POC, is less than 30% of the total R . Note that if organic matter, in any form, is resistant to oxidation (Arrieta et al., 2015) its flux through the water column will not be detected by respiration measurements. The flux will be transparent to our ETS measurements. However, the dissolved organic matter in the ocean, at least, appears to be oxidizable (Arrieta et al., 2015). In all cases, to a first approximation, one can express our conceptual model by the expression, $RCO_2 = FC_1 - FC_2$. In other words, in the vertical, one dimensional case, the changes in the FC between depths in a water column are equal to the RCO_2 between those depths.

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Comment #2: The assumption that DOC-based R is negligible (Page 16183, line 17) also goes against abundant empirical evidence, and hence requires an analysis of the error introduced in F_c estimations. This analysis should include potential biases in terms of both magnitude and variation because surely the relative contribution of DOC and POC to R will vary in space and time.

In reviewing the DOC literature by Reiner Schlitzer, Dennis Hansell, Craig Carlson and others we feel that our first-approximation-model for carbon-flux-from-respiration is valid. It is true that the calculations by this model will overestimate vertical carbon flux by the amount of respiration based on DOC oxidation, but Hansell et al. (2012) state that “...POC export fluxes will far exceed water column integrated rates of DOC removal in equatorial and coastal upwelling areas.” This means that to a first-approximation focusing on POC is valid. Furthermore, Santinelli et al. (2013) point out that, “DOC concentrations are low in the upwelling regions, where water with high nutrients and low DOC are mixed with surface waters..”. Earlier Schlitzer (2002) in a modeling study of global DOC distributions comments that, “...globally the relative size of downward DOC fluxes compared to particle fluxes decreases rapidly with depth, from about 30% at the base of the euphotic zone to 5% at 1078 m depth...”. These percentages could be used as error estimates (on the high side) associated with our decision to focus on the POC flux.

Proposed change in the manuscript: We used our response to comment #1 here.

Comment #3 The one-dimensional model assumes that the relation between F_c and R is time independent, or that the system is in steady state. However the temporal scales of F_c and R are not the same, and connection does not need to be instantaneous. The derived time dependence may be particularly important here, not only because of the dynamic upwelling, but because R is derived from ETS

measurements where accumulated biomass (whose response to organic carbon inputs is slower than that of metabolic rates) may play a higher role than in situ activity. In a highly dynamic upwelling, high heterotrophic biomass may be related to previous organic carbon inputs, while a large F_c may occur together with low biomass. Given that the F_c should vary in time (and space) with productivity pulses, and that biomass evolution is not instantaneous, the potential limitations in estimating F_c from instantaneous vertical profiles of R should be discussed.

Authors response: As with all ocean properties temporal and spatial scales are critical to understanding the meaning of any measurement, calculation, or model. Carbon flux calculations here are based on the particulate matter trapped inside a Niskin Bottle the moment it is tripped. It took about an hour to get that sample back on deck, filtered, and frozen in liquid nitrogen and 20 minutes to obtain the ETS activity reading. An ETS activity measurement is not as instantaneous as a CTD or transmissometer reading, but it is much closer to being instantaneous than a Winkler-based respiration, a C-14 based- or N-15 based- productivity measurement. The time and space scale for an invitro-based chlorophyll measurement on a filtered phytoplankton sample is a rough equivalent. Compared to a sediment trap measurement an ETS activity measurement is instantaneous. It should be comparable to the thorium-POC method for calculating carbon fluxes. We should state here that this use of respiration to calculate carbon flux goes back a long way (Riley, 1951), is fundamental in the development of Eppley and Peterson's (1979) Nature paper and is a logical extension of the thinking in Suess (1980) and Martin et al, (1987). With this conceptual relationship between carbon flux and respiration, we calculated a deep-sea carbon sequestration rate of 22 Gt C per year below 200m in Packard et al.(1988). In Packard and Christensen (2004) we developed the idea in detail. In Packard and Codispoti (2008) we applied it to calculating carbon flux in the Nansen Basin, in Packard and Gómez, 2013 we applied it to zooplankton carbon flux, and in Osma et al (2014) we applied it to calculating carbon flux in the Namibian upwelling. Proposed changes by the authors: In a revision we have added, on page 16184, line 5, the following sentence. "Note that these carbon-flux calculations represent the flux at the time the CTD-Niskin cast was made. They are fine scale calculations of C-Flux."

Comment #4: *The model rests conceptually in the progressive consumption of organic carbon associated to its vertical flux. However, this progressive consumption carries with it changes in composition and lability of organic matter. The composition of organic carbon should also vary along the horizontal scale. How these changes in composition and lability reflect on the relation between F_c and R along the vertical and horizontal axes?*

Authors' original response: ETS activity, in the ocean will not sense variability in the composition and lability variations in the POC or DOC. The posited variations mentioned by the reviewer could be reflected in physiological measures of the CO_2 production rate, the electron flux connecting organic carbon oxidation and the consumption of the terminal electron acceptor, the reduction rate of the terminal electron acceptor, and the ATP production rate. However, as far as we know, these physiological rates in the deep-sea can not be measured by current technology. That is why we have used ETS activity measurements as proxies for these rates.

We have recently read the new paper by Arrieta et al (2015) in which it is shown that low concentration rather than recalcitrance to oxidation retards DOC utilization in the deep ocean. Deep sea ETS activity reflects the biomass and the potential respiration of the deep-sea microbial community. Whether the metabolism

of the community is limited by the concentration of organic matter or its resistance to oxidation will not change the measurement nor the carbon-flux calculations. However, it does change our thinking about the fraction of fluxing carbon that is being influenced by respiration. The paper in several places now reflects this new awareness and Arrieta et al is cited.

[Dilution limits dissolved organic carbon utilization in the deep ocean Jesús M. Arrieta, Eva Mayol, Roberta L. Hansman, Gerhard J. Herndl, Thorsten Dittmar, and Carlos M. Duarte Science 1258955 Published online 19 March 2015
[DOI:10.1126/science.1258955]]

Comment #5: A single equation is used to convert ETS measurements to RO_2 though the water column, however I would expect this relationship to change with the composition and activity of the plankton community along the water column (e.g. with the relative abundance of auto/heterotrophic organisms, eu/prokaryotes, etc.), especially between the phytoplankton rich euphotic zone and the bathypelagic waters. This equation derives from the ETS: RO_2 regression in Packard and Christensen (2004), which is based on 14 paired measurements from 4 stations in the Gulf of Maine (Packard and Williams 1981), where subsurface chlorophyll a maxima of 1.1 to 3.2 g Chla/L were found between 25 and 40 m depth, and surface values ranged 0.17 to 0.77 g Chla/L. Both the magnitude and distribution of Chla in the euphotic zone here (Figure 1b) are very different to those in the Gulf of Maine. Moreover, in Packard and Williams (1981) RO_2 measurements were only made in the upper 10, 10, 9 and 25 m of each station, thus always excluding the DCM, and at depths where Chla concentration ranged from 0.09 to 0.94 $\mu\text{g/L}$. I feel that the use of this regression to convert ETS measurements to RO_2 throughout the euphotic zone, mesopelagic and bathypelagic waters of the Peru upwelling needs to be justified. Are there other regressions available that may cover the spectrum of ecosystems, or at least the ranges of biomass included in this study? 3) The ranges of ETS activity in the regression of Packard and Christensen (2004) is 293 to 919 $\text{g O}_2 \text{ L}^{-1} \text{ d}^{-1}$, however the range of ETS measurements here is 0.06 to 532 $\text{g O}_2 \text{ L}^{-1} \text{ d}^{-1}$ (calculated from Table 3). 88 out of 102 measurements (Table 3) are out of the range in the regression, and all the data deeper than 100 m (29 measurements) are at least two to four orders of magnitude below the minimum value in the regression. The validity of the regression outside its range needs to be defended.

RESPONSE- In the Nansen Basin we compared profiles of oxygen utilization rates down to 500 m as calculated from the Apparent Oxygen Utilization (AOU) and ^3H - ^3He ages according to Zheng et al. (1997), and from ETS-based oxygen utilization rates (OURs) using the factor 0.26 from Packard and Christensen (2004) and Packard and Williams (1980). The rates compare well (Fig. 3 from Packard and Codispoti (2007) attached below). We argue that because the ETS-based OURs compared well with the OURs calculated from the AOU/(^3H - ^3He age) -based OUR, this is the best available way to calculate water respiration from our ETS measurements. We would like to point out that regardless of the way the respiration is calculated, the major contributions of this paper are: the use of water column respiration to calculate ocean sections of carbon flux, nutrient retention deficiency, and heterotrophic energy production as well as the recognition of the role in the exponent, b, in determining carbon-flux transfer efficiency and the NRE.

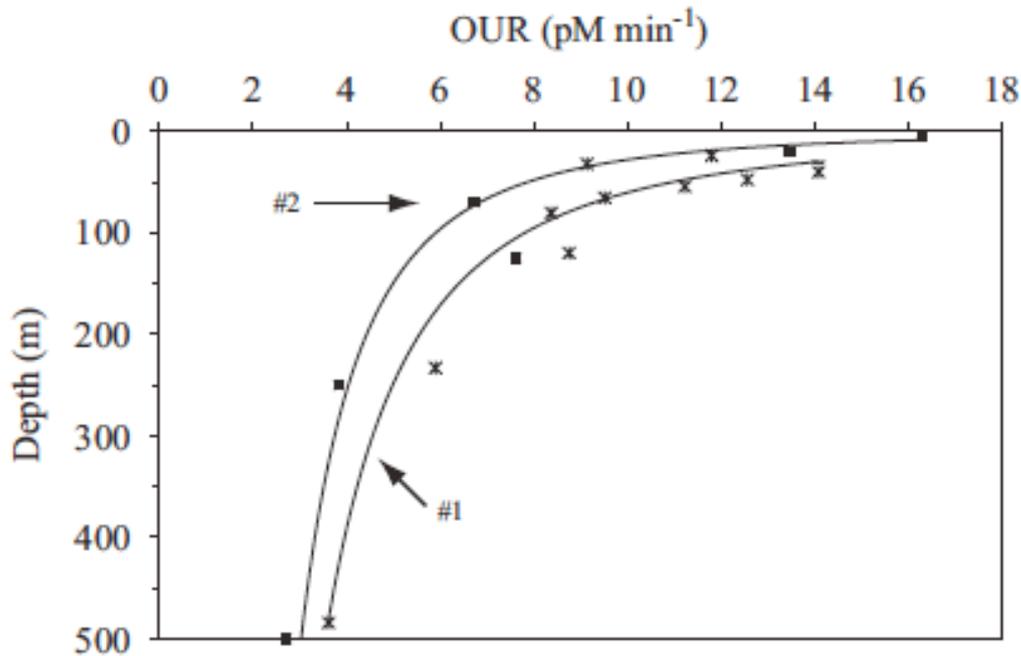


Fig. 3. Comparison between oxygen utilization rates in the Nansen Basin as calculated by two different methods. (1) OUR from AOU and ^3H - ^3He ages according to Zheng et al. (1997, $\text{OUR} = 52.155Z^{-(0.4058)}$, $r^2 = 0.8274$ (stars)). (2) ETS-based R_{O_2} s from absorbances in Fig. 2 according to Table 1 [$R_{\text{O}_2} = 67.477Z^{-(0.5534)}$, $r^2 = 0.6924$ (squares)]. The latter is a composite of measurements taken under the Arctic ice cap north of the Yermak Plateau between 13 and 15 April 1981 as the ice station drifted 6.3 km/day from $83^\circ03.85'\text{N}$, $7^\circ14.40'\text{E}$ to $82^\circ57.93'\text{N}$, $6^\circ58.97'\text{E}$ (Hunkins, 1986). Sonic depth ranged from 4024 to 3982 m. Note that changes over months are required for the measurements of profile #1, whereas changes over minutes are sufficient for measurements of profile #2.

Change in the manuscript: We have explained our respiration calculations as follows. Section 2.3 now reads: “Respiratory ETS activity in the euphoric zone (Ez) was measured according to Kenner and Ahmed (1975) as described in Packard and Williams (1981). In deeper waters it was measured according to (Packard et al., 1971) and multiplied by 3.35 to render the two data sets comparable as explained in Christensen and Packard (1979). Potential respiration and respiration were calculated from the combined ETS data set according to Packard and Christensen (2004) and Packard and Codispoti (2007). Tables 2 and 3 explain the calculations in detail. Table 3 presents the calculations as RO_2 in units of $\mu\text{mol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ for oxic waters.

Using ETS activity as a proxy for RO_2 requires selection of a ratio of potential respiration (Φ) to RO_2 . Since direct measurements of RO_2 can not be made below the euphoric zone, a true calibration can not be made. The Φ to RO_2 ratio should

range around 0.5 if Φ represents V_{max} of the ETS and standard physiological rates, governed by enzyme activities, operate close to 1/2 their potential capacity (Cleland, 1967). In our hands (sense Schatteman et al. (1988); Sigman et al. (1997)), with our methodology (Packard and Williams, 1981), and by our analysis (Packard and Christensen, 2004) we calculated a Φ to RO_2 ratio, 0.26 (Table 2), that successfully predicted RO_2 in the epipelagic and the mesopelagic waters of the Nansen Basin of the Arctic Ocean (Packard and Codispoti, 2007). In that study, RO_2 was a long-term average RO_2 calculated by the AOU-He-tritium method of Jenkins (1982, 1984) as used by W. Roether in Zheng et al. (1997). We have chosen to use the same Φ to RO_2 ratio of 0.26 here (Table 2 and 3). RCO_2 (Fig. 2a) was then calculated from RO_2 using a Redfield ratio (C/O₂) of 0.71 from Takahashi et al. (1985). This is the best available way to calculate water respiration from our water column ETS measurements.

Comment #6: Minor comments: Page 16179, line 2, rather than net primary production, I think it should be net community production.

Authors' response: We agree, especially since we are citing the Ducklow and Doney (2013) reference where this is particularly the case..

*Proposed change: On page 16179, line 2, we have changed the text to read: **Plankton community respiration is a key variable in calculating net community productivity (Ducklow and Doney, 2013)***

Comment #7: If ETS measurements and RO_2 calculations were made throughout the water column, why in Fig.2.a only R in the EZ is based directly on the ETS measurements while the R in the aphotic zone below is based on the R models in Table 4 (Page 16183, line 8)? Are these modelled R estimates or the actual data what are used to estimate F_c from integrated R?

Author' response: We could have used the respiration models given in Table 4 throughout the water column. However, since we had abundant direct ETS-based respiration measurements in the euphotic zone (Table 3) we decided to use them in Fig. 2a. We feel that this is the best way to prepare the section on respiration in Fig. 2a. We have made changes (including the following ones) to explain this procedure through the text.

Proposed change in the text: On page 16183, lines 7-10, after Charland (2002) would replace the existing text with the following. "These R models at each station (Table 4) along with the euphotic zone respiration data (Table 3), were used to create Fig. 2a. Note that R in the Ez of these sections is based on the respiration calculations in Table 3 while the R in the aphotic zone below is based on the R models in Table 4."

Comment #8: This manuscript makes a solid statement of the central position of plankton R in the connection of ecological and biogeochemical fluxes of energy, carbon and nutrients in the ocean, and from there explores new modes of estimating difficult to measure biogeochemical rates. This is important and timely, and a difficult undertaking because of the complexity of those connections across time and space. Although I ask the authors to explore and discuss these difficulties, and limitations derived from the necessary simplification in their model, their original approach is insightful and potentially important.

Interactive comment on Biogeosciences Discuss., 11, 16177, 2014.

Authors' response: We have tried to conscientiously to answer each of the reviewer's comments in a substantive way. Should our responses be found wanting, we will reconsider our answers and proposed changes.

REFERENCES (The ones in red are now in the paper)

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