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Interactive comment on "Chemometric perspectives on plankton community responses to natural iron fertilization over and downstream of the Kerguelen Plateau in the Southern Ocean" *by* T. W. Trull et al.

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Anonymous Referee #2

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In this manuscript results from the KEOPS2 survey in the vicinity of the Kerguelen Islands are presented. The purpose of the study is the understanding of the impact of natural iron fertilization on productivity and biogeochemistry of the Southern Ocean. These studies are highly relevant to our understanding of the impact of changes in the

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Interactive Discussion

Discussion Paper

SO biological pump on past (Glacial/Interglacial) and future atmospheric pCO2. Here results on the size-fractionated composition of particulate organic matter (BSi, POC, PON, ∂13C and ∂15N) as well as estimates on nutrient utilization and, by comparison with standing stocks, export are presented. Further, ∂13C and ∂15N of particulate size fractionated organic matter is used to estimate growth rates and f-ratios of the different size classes in the community. Results are interpreted to infer the impact of different intensities in iron fertilization (based on hydrography and location) on community structure, and the impact of community structure on biogeochemistry.

********** I commend the authors on their effort to interpret the data, but must confess that I am not too convinced by the manuscript. Most of the data interpretation is based on indirect evidence itself based on assumptions that are possibly not valid (see also comments below).

AUTHOR RESPONSE

We consider that this statement is a fair assessment for one of our chemometric methods (growth rates estimated from 13C, for which we provide further discussion below and have added a large section of new text regarding the associated caveats in the paper), but not for the others. Specifically, our measurements of the size distribution of POC, PN, and BSi do provide direct quantification of some of the most important characteristics of pelagic microbial ecosystems: i) size structure, which more than 50 years of measurements and models has placed at the centre of the understanding of ecosystem function, ii) the possibility of the presence of significant levels of detritus with higher C/N than autotrophs (not strongly present in this case), and iii) the extent of nitrogen recycling as estimated from the 15N natural abundance contents of the community (this can be argued to be indirect, but neither reviewer raised any specific objections to this approach and in this paper and in previous work over the Kerguelen plateau (Trull et al., 2008) we have shown excellent correlation with the more time-consuming 15N-tracer incubation approach to determining f-ratios). Nutrient depletion methods are also well tested to estimate export, especially in the Southern Ocean where the presence of the

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winter mixing derived temperature minimum provides a good guide to the initial water column inventory (see references in Sweeney et al., 2000). Yes, we also examined a salinity based estimate of the winter inventory, which is more uncertain (and we have added further discussion of this uncertainty in the revised paper), but we did not do this lightly and we do cite careful previous assessments of the scope of the probable biases from this approach (up to 2x, but more typically 30%, Wang et al., 2003).

********** Further, there are better and more direct methods to study both community composition and export.

AUTHOR RESPONSE

We agree that community composition is most directly and precisely studied by microscopy, and that other methods such as pigment analyses can also, in some cases, be more powerful than size-fractionated bulk chemical measurements (although we note with irony that the main use of pigment analyses from the KEOPS1 experiment was to estimate the size structure of the community, in keeping with the importance of size in assessing ecosystem function, Uitz et al.,2009). Microscopic study and pigment analyses were also pursued during KEOPS2, and we have cited the components of that work that are available (Lasbleiz et al, 2014 and L. Armand personal communication). But we don't agree that this knowledge necessarily makes it any easier to quantitatively connect community composition to export, because conversion of biovolumes to units of elemental concentrations for biomass quantification (and its subsequent comparison to dissolved nutrient fields) also has large uncertainties. Direct measures of export using free-drifting and gel-filled sediment traps were also carried out during KEOPS2, with this effort led by lead author Trull and published by his PhD student Laurenceau (Laurenceau et al., 2014). But this time consuming method could only be carried out at 6 sites (whereas our work examined 33) and has its own large uncertainties regarding trap collection efficiencies. In summary, and as is well known, evaluating ecosystem controls on export requires the application of multiple methods, (as many as possible!), and we have provided a large suite in this paper, and also cite and discuss many others

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from additional papers in this special volume, including the indirect method of 234Th inventories.

********** Although I concur with the main conclusions of the study (i.e. high biomass and productivity does not necessarily lead to high export and is depen- dent on the community composition), this is already well known and the use of bulk parameters (as presented here) adds little to our understanding.

AUTHOR RESPONSE

In a broad sense we agree that this is well known, but we think that understanding this under the mesoscale varying conditions of iron fertilization in the Southern Ocean is far from resolved. For example, the high biomass over the Kerguelen plateau does correlate well with enhanced carbon export (both in autumn and for the full season, Blain et al, 2007; Jouandet et al., 2008; Ebersbach and Trull, 2008). But here we show that this does not necessarily extend to the downstream plume, and that this is not necessarily true in springtime. .

********** Finally, when study- ing export (highly dependent not only on whole community but possibly on behavior of individual species), there is a temporal component not taken into account (i.e. most of the export does generally not occur during the growth phase of a bloom) and is possibly masked by the large spatial variations in the area of study.

AUTHOR RESPONSE

Yes, we agree, and we addressed these temporal and spatial aspects in great detail by providing i) a full annual animation of the bloom development as seen by satellite surface Chla image, ii) 4 images detailing the stages of the bloom at the times of shipboard sampling, ii) two temporal metrics: time since Fe fertilization and time since onset of surface Chla accumulation. We suspect the reviewer means to imply that our assessment of spatial variations may not hold over the whole season, and of course

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that is true and we have added text to make this very explicit in the revised version in section 3.5:

MODIFIED TEXT

Of course observation of these variations in spring does not mean that they would have persisted into summer, and it is possible that over the full season the extent of nutrient depletion was significantly different, either towards homogeneity across the region or towards larger variations.

ADDITIONAL AUTHOR RESPONSE

[As an aside, we do not agree with the reviewers statement that "most of the export does generally not occur during the growth phase of a bloom". Our view is that most of the time ∼90% of the production is removed by grazing (with a component of this sinking as fecal pellets each day) or aggregate sinking, and that even during the rapid build up of biomass at the start of a bloom this probably only drops to ∼50% (indeed for our case this is the approximate value suggested by this reviewer in the last paragraph below) and thus at best the accumulation of biomass during the bloom might represent half the total seasonal export if it is all exported in autumn. This perspective of the autumn export being important but not dominant is consistent with results from the vast majority of deep ocean sediment trap time series (e.g. the reviews of Lampitt and Antia, 1997 and Lutz et al, 2007)]. .

********** As the paper seems somewhat to be an attempt at synthesising results from the whole study, I would recommend the authors incorporate in their results and discussion other measurements (submitted in separate papers in this issue) in a more explicit manner.

AUTHOR RESPONSE

Our paper is focused on the chemometric results, which (as both reviewers have requested), requires detailed explanation of their uncertainties and their implications,

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and thus is not the right place for a broader synthesis (although we do cite and discuss comparisons to many other results from KEOPS2).

Additional comments:

********** Lines 311-318: In the description of the community how were non-diatom protists (in- cluding heterotrophs important in the < 210μm size fractions) assessed? These tend to be more delicate and probably damaged during filtration.

AUTHOR RESPONSE

We added text as follows:

MODIFIED TEXT

These microscopic assessments of the materials present on the filters are rather limited, and may well have missed significant contributions from autotrophs and heterotrophs without frustules or carapaces, but other studies during KEOPS2 of bacterial abundances (Christaki et al., 2014), phytoplankton (Georges et al., 2014; Lasbleiz et al., 2014), diatom species (L. Armand, personal communication), and zooplankton (Carlotti, 2014) are consistent with our chemometric interpretation that detritus, bacteria, and phytoplankton contributed to the 1 um fraction; phytoplankton and especially diatoms dominated the 5, 20, and 50 um fractions; a mix of large diatoms and copepods were present in the 210 um fraction and copepods, isopods, and occasionally krill were the primary contributions to the 300 um fraction.

********** Growth rates estimates from ∂13C of POC are based on the assumption that cells do not use bicarbonate. From previous laboratory studies, bicarbonate use is common and highly variable at a species-specific level (also dependent on light regime). I am not sure that any of the growth rates estimates given here are reliable. Also the au- thors failed to refer to the studies on this topic: Burkhardt et al. (1999) Geochimica et Cosmochimica Acta, 63: 3729-3741, Burkhardt

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et al. (1999) Marine Ecology Progress Series, 184: 31-41; Rost et al. (2002) Limnology and Oceanography, 47(1): 120-128. I also fail to see large differences in growth rate estimates for the different groups (Fig. 5).

AUTHOR RESPONSE

We share the reviewers' concerns regarding the fidelity of our transformation of the 13C-POC values into growth rates (and not only because of the issue of CO2 versus bicarbonate use), and we acknowledge that our introduction to the associated issues and uncertainties was too brief. We have completely rewritten the introduction to this section to cite these and many other works and to provide a clearer explanation of the influences of bicarbonate and CO2 uptake. In this regard, we note that while the Popp et al (1998) model fit to observed 13C dependencies on growth rate did assume uptake was solely of CO2, this assumption is not necessary (as shown by the modeling work of Keller and Morel, 1999).

MODIFIED TEXT

Controls on the 13C composition of phytoplankton are complex, and have been explored in hundreds of papers since an early survey of the variability in marine carbon isotopic compositions (Craig, 1953), with occasional significant advances and reviews, e .g. (Farquhar et al., 1982; Goericke et al., 1994; Laws et al., 1995; Laws et al., 2002; Rau et al., 1996; Schulz et al., 2007; Tortell et al., 2008) In brief, there are two main causes for 13C variations of any given phytoplankton cell. Firstly, the cell 13C content depends on the chemical form of DIC that is assimilated, because the less abundant aqueous molecular CO2 form contains much less 13C than the bicarbonate anion form which makes up more than 90% of the total DIC. At the temperatures pertaining during the KEOPS study, this equilibrium fractionation lowers the 13C content of aqueous molecular CO2 by ∼11‰ (Rau et al., 1997): 13C-CO2 = 13C-DIC +23.644 -9701.5/Tkelvin (1) Secondly, the cell 13C-POC content depends on the extent to which the enzymatic kinetic discrimination against 13C during photosynthetic carbon fixation

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(of 20-30 ‰ varying with the specific metabolic pathways) is expressed. It is only fully expressed when inorganic carbon flow into and out of the cell (supply) is faster than fixation (demand). Both these effects often lead to higher 13C contents in faster growing cells, because faster growth favours use of the more abundant bicarbonate form of DIC and also leads to less expression of the kinetic fractionation. Thus the association of higher 13C contents with faster growing cells is very strongly justified for any particular phytoplankton species, from both metabolic understanding and the plethora of batch and chemostat experimental studies. Despite this understanding, inferring growth rates for communities of phytoplankton from field measurements of 13C-POC is fraught with difficulties. The magnitudes of these two main isotopic effects vary strongly among different phytoplankton (and with their conditions of growth including temperature, nutrient and trace metal availability, light levels, specific enzymatic pathways, etc. (Burkhardt et al., 1999b; Burkhardt et al., 1999c; Fontugne et al., 1991; Schulz et al., 2007)), and there is no universal quantitative relationship between growth rate and phytoplankton 13C content. In particular, cell size is a key variable in the control of 13C contents (Popp et al., 1999; Rau et al., 1996; Rau et al., 1997; Rau et al., 1990), and the global range of surface water 13C-POC values can be observed within a single Southern Ocean sample, simply via its size fractionation (Trull and Armand, 2001). Good correlations between growth rates and 13C contents when cell size is expressed in terms of the surface/volume ratio suggest this results from the balance of supply versus demand (Popp et al., 1998b), of either or both aqueous CO2 and bicarbonate forms (Burkhardt et al., 1999a; Keller and Morel, 1999; Schulz et al., 2007), and with further modulation by other environmental controls such as the availability of light and other nutrients (Burkhardt et al., 1999c; Gervais and Riebesell, 2001; Schulz et al., 2004). This complexity means that our observed 13C-POC variations, even within a given size fraction, could arise by multiple mechanisms. Higher 13C contents could reflect faster growth rates (via either greater use of bicarbonate or an increase of fixation of all DIC chemical forms relative to supply), or might instead reflect changes in species with inherently different uptake and assimilation metabolisms, or changes in

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metabolism driven by other controls such as light or iron availability. Our chemometric methods cannot distinguish among these possible causes, and thus our expression of the 13C-POC variations in terms of growth rate variations can only be viewed as an indicative exercise. To pursue this, we chose a model fit to chemostat data (Popp et al., 1998b): 13C-POC = (13Csource – ÉŻf) + k demand-rate/supply-rate (2) in which the first term expresses the lowest possible 13C contents of the cell as growth rate approaches zero, and the second term describes the linear (constant k) dependence of isotopic composition on the relative rates of CO2 supply into the cell and it's cellular fixation. Popp et al. (1998) assumed the chemical form was aqueous molecular CO2, but further evaluation showed that the data could also be fit by a model allowing either or both CO2 and bicarbonate uptake (Keller and Morel, 1999). Both models assume that the, supply rate depends linearly on its external concentration modulated by the surface area of the cell, and thus while the fitting constants we use here are from Popp et al (1998), the scaling to the surface/volume ratio (S/V) of the cell is independent of the chemical form of uptake): 13C-POC = (13C-CO2 – 25) + 182 μ/([CO2] S/V) (3) Rewriting this equation for growth rate, μ, and our measured 13C-DIC and 13C-POC values yields an indicative path to possible growth rates for our size fractions: μ = S/V [CO2] [13C-POC – (13C-CO2 - 25)]/182 (4) with 13C-CO2 calculated using equation (1), [CO2] obtained from underway pCO2 observations (Lo Monaco et al., 2014) and Henry's Law (Weiss, 1974). In this expression, growth rate μ is in d-1, S/V in μm-1, and [CO2] in umol kg-1. This expression provides growth rates that we compare to other estimates. Of course, comparison of these rates is very sensitive to S/V estimates, as well as to all the other possible sources of variations in 13C contents summarized above. For example, a 30% increase in the mean size of cells, such as could occur within a given size fraction, would yield a 69% increase in the model growth rate (for spherical cells). For this reason, our growth rate estimates must be viewed with great caution, not only in terms of their absolute magnitudes, but also in terms of their relative magnitudes across the different stations.

ADDITIONAL AUTHOR RESPONSE

In addition to this revised text regarding our growth rate estimates we have added caveats at several places in the Results and Discussion sections to emphasize that the growth rates are not quantitative and that our conclusions are not based solely upon them:

MODIFIED TEXT in Results Section 3.3:

This provides a useful cautionary note that the apparent growth rate variations have no real quantitative validity; at best they provide indicative information on the relative intensities of CO2 assimilation across the Groups. Indeed, it is possible that the variations among the Groups results from other issues such as species metabolic differences, or light and trace element availability (as discussed in detail in the Methods section). Thus it is important to emphasize that the overall view of ecosystem responses developed in the Discussion section does not depend only on these potential growth rate estimates from the 13C-POC observations, but also draws on biomass accumulation rates from the POC concentrations, their distribution across size fractions, and other indicators as discussed below.

ADDITIONAL MODIFIED TEXT in Discussion Section 4.1.:

Both of the more strongly iron fertilised offshore regions (the Group 3 central plateau and the Group 5 Polar Front bloom, Table 1.) exhibited increased 13C model growth rates in comparison to HNLC waters (elevated by $\sim$0.05 d-1), but their community structures were quite different (emphasizing caution regarding the 13C model growth rates, although the incubation results also indicated increased growth rates; (Cavagna et al., 2014)).

********** I am not sure of the logic in separating some of the stations in 2 groups (groups 1 and 2) as they are in a similar location and could be used to infer temporal development.

AUTHOR RESPONSE

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This was done largely for convenience to have a manageable number of stations in each of these two groups, and the temporal aspect is discussed in just the way the reviewer recommends – as an evolution from the status observed in Group 1 towards that observed in Group 2, and then with additional consideration of the temporal evolution within Group 2 which was specifically carried out as a time series.

********** Lines 685-690: I am not sure I agree with the authors on the method used: estimating nutrient consumption from nutrient profiles is valid under the assumption that there is no significant impact of lateral transport. If there is horizontal exchange (or mixing), especially in an area with strong horizontal gradients such as in this study, nutrient consumption estimates are highly uncertain. Using the Tmin as a criterion, helps to at least constrains the temporal scale of the estimate (i.e. from previous winter), while using other criteria does not. Hence robustness of the estimates given here can hardly be assessed and I doubt values for the different groups can be compared.

AUTHOR RESPONSE

Because all nutrient profiles do show surface depletions, they clearly contain information on export (from either local and recent export, or remote and prior export). Extracting the desired local and recent contribution information is difficult for just the reasons the reviewer mentions, and this is why we have pursued two criteria: the traditional temperature minimum based estimate of winter values, and a salinity threshold method designed to evaluate the possibility that this Tmin approach overestimates export when the surface depletion is associated with the overlaying of warm salty waters above the Tmin layer (via horizontal mixing). We have taken care to emphasize that this makes the depletion estimates uncertain, and to explain how this affects our conclusions, including adding new text:

MODIFIED TEXT

This analysis underlines the importance of appropriate winter nitrate (and silicic acid) surface nitrate concentration estimates to the assignment of export magnitudes. We

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believe the Sthreshold approach is the most appropriate given the observed salinity stratification, especially for the relatively weak subsurface thermal stratification observed in the Group 5 stations near the Polar Front.

********** Given the robustness of the different estimates and the variability (which might be re- lated to both temporal and spatial patterns) I could also argue that there are no sig- nificant differences in organic matter (based on N) export between systems. When looking at figure 8 roughly half of the N uptake is lost (either through grazing or sink- ing). This is consistent with the fact that growth estimates are in the order of roughly one doubling every 3 days while biomass accumulation (from satellite Chla) indicates a doubling very week (between 28/10 and 6/11).

AUTHOR RESPONSE

We thank the reviewer for this insightful comment, and we have incorporated it in the revised text, in Results Section 3.5:

********** Firstly, given the uncertainties regarding the estimation of nutrient depletions from the profiles, it could be argued that the most robust conclusion is that all the Groups exhibit similar depletions, with roughly half of the N uptake exported and half remaining as accumulated biomass. This is consistent with the growth estimates of roughly one doubling every 3 days and the satellite biomass observations indicating slower doubling approximately each week.

AUTHOR RESPONSE

Importantly, we also note that the Abstract emphasizes only this most robust conclusion, that all regions exported similarly:

MODIFIED TEXT

Comparison of these communities to surface water nitrate (and silicate) depletions as a proxy for export shows that the low biomass recirculation feature had exported similar amounts of nitrogen to the high biomass blooms over the plateau and north of the Polar

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Front.

REFERENCES CITED IN AUTHOR RESPONSE TO REVIEWER2 Sweeney, C., Hansell, D. A., Carlson, C. A., Codispoti, L., Gordon, L. I., Marra, J., Millero, F. J., Smith, W. O., and Takahashi, T.: Biogeochemical regimes, net community production and carbon export in the Ross Sea, Antarctica, Deep Sea Research Part II: Topical Studies in Oceanography, 47, 3369-3394, 2000.

Uitz, J., Claustre, H., Griffiths, B., Ras, J., and Sandroni, V.: A phytoplankton class-specific primary production model applied to the Kerguelen Islands region (Southern Ocean), Deep Sea Research I, 56, 541–560, 2009.

Lasbleiz, M., Leblanc, K., Blain, S., Ras, J., Cornet-Barthaux, V., Hélias Nunige, S., and Quéguiner, B.: Pigments, elemental composition (C, N, P, Si) and stoichiometry of particulate matter, in the naturally iron fertilized region of Kerguelen in the Southern Ocean, Biogeosciences Discuss., 11, 8259-8324, 10.5194/bgd-11-8259-2014, 2014.

Wang, X., Matear, R. J., and Trull, T. W.: Nutrient utilization ratios in the Polar Frontal Zone in the Australian sector of the Southern Ocean: a model, Global Biogeochemical Cycles, 17, 1009, doi:1010.1029/2002GB001938, 2003.

Laurenceau, E. C., Trull, T. W., Davies, D. M., Bray, S. G., Doran, J., Planchon, F., Carlotti, F., Jouandet, M. P., Cavagna, A. J., Waite, A. M., and Blain, S.: The relative importance of phytoplankton aggregates and zooplankton fecal pellets to carbon export: insights from free-drifting sediment trap deployments in naturally iron-fertilised waters near the Kerguelen plateau, Biogeosciences Discuss., 11, 13623-13673, 10.5194/bgd-11-13623-2014, 2014.

Blain, S., Quéguiner, B., Armand, L., Belviso, S., Bombled, B., Bopp, L., Bowie, A., Brunet, C., Brussaard, C., Carlotti, F., Christaki, U., Corbière, A., Durand, I., Ebersbach, F., Fuda, J. L., Garcia, N., Gerringa, L., Griffiths, B., Guigue, C., Guillerm, C., Jacquet, S., Jeandel, C., Laan, P., Lefèvre, D., Lomonaco, C., Malits, A., Mosseri, J.,

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Obernosterer, I., Park, Y.-H., Picheral, M., Pondaven, P., Remenyi, T., Sandroni, V., Sarthou, G., Savoye, N., Scouarnec, L., Souhaut, M., Thuiller, D., Timmermans, K., Trull, T., Uitz, J., van-Beek, P., Veldhuis, M., Vincent, D., Viollier, E., Vong, L., and Wagener, T.: Impacts of natural iron fertilisation on the Southern Ocean, Nature, 446, 1070-1074, doi:1010.1038/nature05700, 2007.

Ebersbach, F., and Trull, T. W.: Sinking particle properties from polyacrylamide gels during the KErguelen Ocean and Plateau compared Study (KEOPS): Zooplankton control of carbon export in an area of persistent natural iron inputs in the Southern Ocean, Limnology and Oceanography, 53, 212-224, 10.4319/lo.2008.53.1.0212, 2008.

Jouandet, M. P., Blain, S., Metzl, N., Brunet, C., Trull, T. W., and Obernosterer, I.: A seasonal carbon budget for a naturally iron-fertilized bloom over the Kerguelen Plateau in the Southern Ocean, Deep-Sea Research Part Ii-Topical Studies in Oceanography, 55, 856-867, 10.1016/j.dsr2.2007.12.037, 2008.

Lampitt, R. S., and Antia, A. N.: Particle flux in deep seas: regional characteristics and temporal variability, Deep-Sea Research I, 44, 1377-1403, 1997.

Lutz, M. J., Caldeira, K., Dunbar, R. B., and Behrenfeld, M. J.: Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump global ocean, Journal of Geophysical Research, 112, C10011, doi:10010.11029/12006JC003706, 2007.

Keller, K., and Morel, F. M. M.: A model of carbon isotopic fractionation and active carbon uptake in phytoplankton, Marine Ecology-Progress Series, 182, 295-298, 1999.

Popp, B. N., Laws, E. A., Bidigare, R. R., Dore, J. E., Hanson, K. L., and Wakeham, S. G.: Effect of phytoplankton cell geometry on carbon isotopic fractionation, Geochimica et Cosmochimica Acta, 62, 69-77, 1998.

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