

Interactive comment on “Estimates of micro-, nano-, and picoplankton contributions to particle export in the northeast Pacific” by B. L. Mackinson et al.

B. L. Mackinson et al.

bmackinson@my.uri.edu

Received and published: 30 January 2015

We would like to thank the reviewer for the careful review and thoughtful comments. The reviewer's comments are included here with our responses.

In this manuscript Mackinson et al. use phytoplankton pigments combined with large volume pump sampling, ^{234}Th deficiency measurements, and two sediment trap deployments to address the relative contributions of pico-, nano-, and microplankton to passive (sinking) carbon export in the northeast Pacific. This is an important topic, given the hypothesis proposed by Richardson & Jackson (2007) that production stemming from picoplankton may dominate the flux of particulate material in the ocean. To

C8364

date, there have only been (to my knowledge) three published field studies specifically designed to address this hypothesis, thus this new dataset is quite valuable. There are some methodological issues with the authors' approach (as there will be with any approach to tackling this difficult problem) that I would like to see the authors address more directly and succinctly. However, I believe that this is a nice manuscript overall, and is certainly worthy of being published (with moderate revision). Below please find some major and minor issues that I believe should be dealt with:

Major Concerns:

There is no perfect way to address the contribution of picoplankton to particle export, because (1) there is no perfect way to measure export and (2) the source of the exported material is often obscured by grazing, aggregation, physical breakdown, and microbial remineralization processes. The authors have chosen to use a combination of ^{234}Th and pigments as their primary methods for this study. It is very important that they succinctly outline the problems with these methods:

1) ^{234}Th – The two primary methods for measuring vertical carbon fluxes in the field are ^{234}Th and sediment traps. Each has issues (hydrodynamic and degradation for sediment traps; steady-state assumptions and variable C: ^{234}Th ratios for ^{234}Th). For practical reasons, the authors rely very heavily on ^{234}Th measurements for this manuscript (although it is very nice that they have two sediment trap deployments that largely agree with the ^{234}Th -based results). Unfortunately, for their particular question ^{234}Th is inferior to sediment traps. It is incredibly important to note that, when determining the relative contributions of pico-, nano-, and microplankton to export using the authors' approach, the ^{234}Th measurements are COMPLETELY IRRELEVANT. The relative contribution of different size classes to export is completely determined by their pigment ratios in the >50-micron large-volume samples. This needs to be explicitly stated. The authors make the (defensible) assumption that these large particles (likely aggregates) collected by the pump at depth are representative of sinking material. As the authors note at the end of their discussion, however, the pumps do not sample

C8365

fecal pellets effectively, and fecal pellets may both contribute significantly to export and represent different ratios of micro/nano/picoplankton than the aggregates sampled by the authors.

***The reviewer correctly recognized that while the flux of ^{234}Th is required to determine the overall pigment flux, the relative contributions of pico-, nano-, and microplankton are, dependent only on the pigment ratios found on the $>53\text{-}\mu\text{m}$ particles. An explicit statement noting this has been added to the results section. In addition, we do acknowledge that the relative contributions of pico-, nano-, and microplankton to fecal pellet export likely differ from their relative contributions to algal aggregate export and noted that in our original manuscript (page 12648, lines 8 – 20).

2) Pigments – the other half of the authors' primary methodology is pigment analysis to determine the composition of the sinking material. There are a few issues with using pigments for this question (though nucleic acids, the other primary option, may have even greater issues). One issue that the authors have is that indicator pigments do not map perfectly into size classes. It would be nice to see the authors discuss the correlation between different pigments and size-fractionated chlorophyll. Another significant issue is differential pigment degradation. There is no a priori reason to assume that different indicator pigments are degraded at the same rate, especially when considering that picoplankton (primarily grazed by protozoans) and microplankton (largely grazed by mesozooplankton) likely undergo significantly different processes prior to being incorporated in aggregates or fecal pellets. C:pigment ratios may vary significantly with depth and inconsistently between taxa.

***While it is true that pigments are not a perfect proxy for cell size, we did find a statistically significant correlation between microplankton pigment concentrations and the $>5\text{-}\mu\text{m}$ size-fractionated chlorophyll concentrations for small-volume samples from the photic zone (page 12641, lines 18-20). We believe this justifies the use of indicator pigments as proxies for plankton size class for broad-level analysis.

C8366

Other Issues:

One of the strengths of this study is that the authors measured export and the contribution of pico-/nano /microplankton at multiple stations and several different seasons. Given these measurements, it would be nice to see them discuss whether or not there are correlations between export and the contributions of pico/microplankton to surface biomass. Ultimately the Richardson & Jackson hypothesis is important because it pertains to the question of whether or not we would expect export to decrease in a more oligotrophic future ocean. In addition to looking directly at the proportion of picoplankton in export, the authors can also look at whether or not a picoplankton dominated ocean has less export than a microplankton dominated ocean.

***No clear relationship was observed POC export, e-ratio, or NPP and the contribution of different phytoplankton size classes (as determined by pigment ratios) to integrated photic zone biomass. This is somewhat surprising, as the classical theory would suggest a strong correlation between microplankton pigments and e-ratio.

It would be nice to see the authors use pigment:carbon estimates to put together a back-of-the-envelope calculation of the ratio of phytoplankton carbon: total carbon in the deep LV pump samples and sediment trap samples. Do the pigments that the authors measured comprise most of the organic carbon that is being exported or is a significant amount of the sediment trap material unaccounted for?

***Following the reviewer's suggestion, Chl a:POC ratios were calculated for all in situ pump samples. Assuming that the shallowest samples (30 m) were comprised entirely of healthy phytoplankton, the amount of exported phytoplankton carbon (pigment supported carbon) can be estimated by multiplying this ratio by the Chl a concentration of deeper samples. Ratios phytoplankton carbon:total POC were calculated at 100 m (roughly the base of the photic zone) for all stations sampled. Results varied widely, ranging from 0.8% - 232% and averaging 69%.

On a similar note, although the authors do not give any methodological details for their

C8367

fluorometric chlorophylls (this is an oversight that should be corrected – did they use the acidification method of Strickler & Parsons?) if they used the acidification method, they can get an estimate of phaeopigment concentration in the sediment trap as well. Although chlorophyll is not quantitatively converted to phaeopigments in mesozooplankton guts, phaeopigment concentration can still give an estimate of the proportion of flux that may be due to mesozooplankton fecal pellets and hence likely originating from microplankton but not showing up as microplankton indicator pigments.

***Unfortunately, phaeopigment data is not available for the small-volume fluorometric chlorophyll samples. The in situ pump and sediment trap samples were analyzed by HPLC, which also did not yield phaeopigment data.

Since the authors talk about standing stocks sampled by SV and LV (and these two measurements do not agree) it is very important that they explicitly state when they are using standing stocks derived from SV or LV samples both in the text and in figures.

***Standing stocks are always determined by integrating small-volume pigment concentrations over the photic zone due to our belief that these measurements more accurately reflect the community composition due to the pumps missing cells < 1 μm in size as noted in the original manuscript (page 12642, line 18 – 21). Explicit statements clarifying this have been added to the text.

Figure 8 shows microplankton indicator pigments often dominating even the 1-10 micron size fraction. This should probably be discussed since it clearly illustrates the issues with using phytoplankton pigments as indicators of size.

***As noted earlier, the correspondence of indicator pigments with particular plankton size-classes is an imperfect one. Diatoms and dinoflagellates (as indicated by fucoxanthin and peridinin pigments) are counted as microplankton regardless of actual cell size. Given that significant numbers of small diatoms (< 5 μm) have been observed at OSP, it is not surprising to find microplankton pigments in the 1 – 10- μm size-fraction (Boyd and Harrison, 1999). However, for all cruises in this study, the highest concen-

C8368

tration of pigments was found in the 10 – 53- μm size-class. The 1 – 10- μm size-fraction generally represented a small percentage of overall pigments, and therefore, we do not feel the presence of microplankton indicator pigments in the 1 – 10- μm size-fraction indicates a major flaw in our methodology. The presence of microplankton indicator pigments in the smallest size-fractions could also result from the collection of cell fragments or from the rupture of cells leading to a loss of material from larger screens during the pumping process. Finally, it should be noted that the presence of diatoms and dinoflagellates in the <53 size-fractions would lead to an underestimate of the small cell contribution to export.

This paper uses a lot of non-standard abbreviations. I would recommend that the authors add a table at the beginning of the manuscript that lists all their abbreviations so that readers don't have to hunt through the text to find out what mPF or PTh mean. Also, PTh is a strange choice for Th flux, since it could easily be mistaken to mean particulate thorium.

***To address this, abbreviations have been defined at their first use in the text so the reader should not need to hunt for their definitions. Furthermore, PTh is a common abbreviation for the loss rate of thorium on sinking particles while ThP is typically used to represent particulate thorium (e.g. Coale and Bruland, 1985).

p. 12633 line 6 – Stukel & Landry 2010, and Lomas & Moran 2011 do not state that picoplankton export is proportional to biomass, but rather that its proportional contribution to export is less than to biomass, but still significant. Amacher et al. (2009, DSR I 56(12): 2206-2215) and Stukel et al. (2013, PinO 112-113: 49-59) should probably be cited as other studies that have attempted to directly assess the proportion of picoplankton in export. Amacher used nucleic acids and found a significant role for picos at ESTOC and Stukel used pigments and found a less than proportional role for picos in the Costa Rica Dome.

***The relationship between biomass and export found by Stukel & Landry 2010, and

C8369

Lomas & Moran 2011 has been corrected and the additional references have been added.

p. 12636 line 5 – Although there is nothing the authors can do about it at this point (and it probably isn't a huge problem), best practices with thorium involve an acidification step with HNO₃ to bring pH < 2 before spiking with the tracer Th-230 (Pike et al. 2005, *Journal of Radioanalytical and Nuclear Chemistry* 263(2) 355-360). This brings all the naturally particle-associated Th-234 into the dissolved phase so that it can equilibrate with the added Th-230. Without this step it is possible that the yield of Th-234 (initially bound to naturally occurring particles and colloids) and the yield of Th-230 tracer will be different. Also, no methods for yield analysis are mentioned.

***The methods used in this study follow Buesseler et al. 2001 where there is no acidification. Previous studies by the Moran lab have consistently found ²³⁰Th recoveries of >95% for small volume samples using chemical separation and alpha counting. Furthermore, Moran lab results from the ²³⁴Th GEOTRACES Intercalibration experiment fell well within the group mean, indicating that acidification does little, if anything, to improve thorium recovery.

p. 12636 line 10 – “drying over” should be “drying oven”

***The typo has been corrected.

p. 12636 line 25 - I do not see how mPF, nPF, and pPF are calculated. Is it simply the ratio of the summed indicator pigments that are believed to be responsible for each size class? This seems to be implied by Figure S2 which shows a 1:1 correlation between total indicator pigment and Chl a. This is not, however, the best way to estimate mPF, nPF, and pPF, since different taxa of phytoplankton will have different ratios of indicator pigment : Chl a. A better approach would probably be to multiply each indicator pigment by a pigment:C ratio for the taxa that it represents and then summing these carbon contributions (perhaps using a CHEMTAX approach – e.g. Mackey et al. 1996; *MEPS* 144: 265-283). Note that this should not change their primary results (the com-

C8370

parison of the proportions of picoplankton to biomass and export), but it would change the total proportion of picoplankton in biomass and export.

***The indicator pigment PFs are calculated following the method outlined in Hooker et al. 2005. As the reviewer surmises, the indicator pigment concentrations for each size-class are summed and divided by the total indicator pigment concentration. While this is an admittedly simple approach, more complex methods (like CHEMTAX) still report taxonomic/size group data as a percentage of Chl a containing particles, and would still suffer from the issue of imperfect correlation between pigments and cell size. Furthermore, as the reviewer notes, the choice of method would not change the results of the comparison between contribution to biomass and contribution to export, which is the focus of this paper. Given this, we feel that our method is sufficient for this study. The reviewer also suggested determining taxon-specific carbon export as a means for comparing the contributions of different phytoplankton size-classes to export. This paper is focused on pigment analysis and not on the determination of carbon export by different phytoplankton size-classes. We did not determine taxon-specific carbon in this study, and therefore, we are unable to calculate POC:pigment ratios. Given that POC:pigment ratios are strongly dependent on phytoplankton growth conditions, the use of literature values would be problematic. Given these complexities, an analysis of small cell carbon export is left for companion works.

p. 12643 line 23 – The authors have not stated how they determined ²³⁸U concentrations. Did they use the Owens et al. (2011 *MarChem* 127(1-4):31-39) or Chen et al. (1986, *EarthPlanSciLett* 80: 241-251) relationships or did they actually measure it directly?

***The relationship established by Chen et al., 1986 was used in this study, following the method outlined by Baumann et al. 2013. A reference and statement clarifying this have been added to the text.

p. 12644 equation 1 – The equation shown neglects the effects of upwelling or down-

C8371

welling which can (at times) lead to a significant error in simple thorium export models (see Savoye et al. 2006, *MarChem* 100(3-4): 234-249). Since the authors (like most who study thorium) have no way of estimating upwelling it is acceptable that they have neglected it, however, this term should definitely be included in equation 1 and the rationale behind ignoring it should be given.

***Open ocean scavenging models typically do not include a term for vertical advection or do not distinguish between vertical and horizontal advection and diffusion for the reasons noted by the reviewer (e.g. Coale and Bruland, 1985, Charette et al. 1999.) Furthermore, vertical advection has been found to be important only in areas of high upwelling or downwelling velocity (Buesseler, 1998). The northeast Pacific is not a region known for strong upwelling or downwelling.

p. 12645 line 19 – “decreasee” should be “decrease”

***The typo has been corrected.

p. 12645 line 25 – the POC/234Th ratio in traps is substantially higher than the ratio of particles collected by pumps. This is significant since it suggests that there may be a substantial amount of sinking material that is not being collected by the pumps. Such a situation could arise if there is a rapidly sinking particle fraction (perhaps fecal pellets) that has a high C:Th ratio that is similar to the higher bulk C:Th ratio found in surface water as well as a slowly sinking particle fraction that has time to equilibrate with lower bulk C:Th ratios at depth. This should be discussed as it bears on the question of whether or not the pump samples pigment ratios are representative of all sinking material.

***We agree that the collection of a rapidly sinking particle fraction (fecal pellets) by the traps and not the pumps is a plausible explanation for the differing POC:Th ratios between the two methods and comment on this at length in the discussion section. The higher POC:Th and POC:Pigment ratios observed in the material collected by the traps relative to material collected by the in situ pumps implies that a significant proportion

C8372

of the exported material could be carbon-rich, pigment-depleted fecal pellets.

p. 12646 line 4 – I cannot find a Fig. 11c

***The typo has been corrected. The figure being referred to was Fig. 12c.

p. 12648 lines 15-20 – the authors point out that much of picoplankton production will be grazed and that the grazing pathway will not show up with their methodology. This is true. However, they then suggest that this may lead to an underestimate of the role of picoplankton by their methodology. This is not true. While picoplankton can certainly be exported by grazing pathways, they are most likely exported after transfer through one (or two) protozoan grazing steps which will degrade a significant fraction of their carbon before the protozoans are grazed by large fecal pellet-producing mesozooplankton. Microplankton, by contrast are much more likely to be grazed directly by mesozooplankton, hence contributing a significantly greater fraction of their biomass to export. Thus the grazing pathway (which was not assessed by the methodology used by the authors) is actually much more likely to underestimate the contribution of microplankton than picoplankton. This is particularly important since, as the authors note at the end of the discussion, fecal pellet export is substantially greater than algal aggregate export in their study region.

***As the reviewer noted, the classic paradigm for carbon export suggests that large phytoplankton are grazed by mesozooplankton leading to efficient export via fast sinking fecal pellets while smaller plankton are grazed by microzooplankton, leading to less efficient export and enhanced recycling through the microbial loop. However, in the northeast Pacific mesozooplankton are known to be omnivorous and are not thought to exhibit a strong grazing control on large phytoplankton such as diatoms, which are instead subject to bottom-up control due to iron limitation (Stoecker and Capuzzo, 1990, Dagg, 1993, Gifford, 1993, Goldblatt, et al. 1999, Harrison, 2002). Direct sinking is therefore a more likely fate for diatoms and other large phytoplankton. In contrast, small phytoplankton are tightly controlled by grazing in the northeast Pacific and are

C8373

thus less likely to sink directly. In addition, recent studies have shown that indirect export can be an important pathway for small cell export due to grazing of individual pico- and nanoplankton by salps and grazing of small cell aggregates by mesozooplankton such as copepods (Richardson et al., 2004; Richardson and Jackson, 2007; Stukel and Landry, 2010).

Table 1 – I find this table to be slightly confusing. It might be easier to read if there were borders around the cells to show which samples go with which cruises.

***Horizontal borders have been added between cruises in order to clarify which samples correspond to which cruise.

Table 2 – Please define all abbreviations so readers don't have to hunt through the text.

***All abbreviations have been defined at their first use in the text and in the captions of figures and tables.

Figure 2 – I would recommend only showing plots down to 200 m (since I believe that is the deepest depth of the authors' samples) in the interest of making upper water column patterns more visible.

***Hydrography and ^{234}Th activity data extends down to 500 m, and profiles were shown down to 300 m in an effort to show upper water column data clearly while still showing the $^{234}\text{Th}/^{238}\text{U}$ activity ratio reaching/approaching ~ 1 at depth, indicating secular equilibrium.

Figure 9 – This is an important figure with a lot of data crammed into it. Is it possible to make it a bit larger so that patterns are more visible?

***The figure is already at the maximum size permitted by the journal. Data for the figure is also included in the appendices.

Figure 10 - legend and figure, there is no symbol for Harrison, 2002

***As noted in the figure caption, NPP data from Harrison, 2002 and POC fluxes from C8374

Wong et al., 1999 are combined as one data point. The symbol has been moved in between Wong et al., 1999 and Harrison, 2002 in the figure legend in an effort to reduce confusion.

Please also note the supplement to this comment:

<http://www.biogeosciences-discuss.net/11/C8364/2015/bgd-11-C8364-2015-supplement.pdf>

Interactive comment on Biogeosciences Discuss., 11, 12631, 2014.