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Interactive comment on “Seasonal variation in marine C:N:P stoichiometry: can the composition of seston explain stable Redfield ratios?” by H. Frigstad et al.

Anonymous Referee #2

Received and published: 17 August 2011

I think this paper shows some useful and interesting data, but it oversells itself and spends far too much space on issues unrelated to the data presented. The Discussion is too long and does not for the most part address the deficiencies of the methods used. The Introduction and Discussion consist mostly of unnecessary literature review and largely unsupported claims to have advanced the state of the art in ecological stoichiometry in some important way. It is somewhat disquieting to read the rather lengthy discussion of the importance of variation in elemental ratios to ecosystem dynamics and then view the actual data which show very little variation. The freshwater and marine literature are largely treated as if the same processes were in play which I do not think is the case. The Redfield ratios are a specifically marine phenomenon and there

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are good reasons why C/P or N/P ratios are more variable in lakes.

The key conclusion - that diverse contributions of different organisms tend to drive the bulk community elemental composition towards a mean (Redfield) value rather than phytoplankton physiology being a key driver - is basically sound, but more speculative than the authors acknowledge. Given that they observed little deviation from Redfield stoichiometry in this environment, this mechanism can be invoked to explain the results presented. But that is different from saying that the results presented provide evidence that this is an important process governing elemental ratios in planktonic ecosystems, which in fact they do not. At best one can say that fairly constant ratios were observed in an environments where the (estimated) autotroph fraction was low enough that autotroph physiology as the main governing mechanism seems implausible. There are a number of possible explanations of why this might occur, and these data do not specifically provide evidence in support of the one advocated here.

The regression intercept as a means of estimating the autotrophic/heterotrophic or living/nonliving fractions is based on some fairly tenuous assumptions. Even within specific seasons I would expect autotrophic biomass, heterotrophic biomass, and non-living detritus concentrations to be positively correlated. It isn't obvious to me how one estimates the errors these correlations induce and the authors make little or no effort to do so. I was pleased to see that the problems with this approach are at least acknowledged in the Discussion, but I think it could be given a good deal more space especially given that much of the text is more or less superfluous.

I have two significant issues of terminology. Firstly I question whether the term 'seston' should be used at all. It seems to me to be more an archaism than anything else, a term that has been superceded by more precise, if somewhat inelegant, terms like "suspended particulate organic matter". These terms are somewhat jargonish but they allow us to define very precisely which fractions were are discussing. Seston is imprecise and I don't really see the use of retaining it. Secondly I do not believe there is such a thing as "Particulate Organic Phosphorus" in the sense that the method used mea-

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sure total phosphorus and not just the organic fraction. The same is true of carbon and nitrogen but not to nearly the same degree since (a) the CHN analyzer works by combustion and (b) common inorganic nitrogen compounds are not strongly surface active, and authigenic N minerals do not normally form in seawater. Not so for P (see e.g. Fu et al 2005 L+O 50: 1459). In any case it might be prudent to drop the word “organic” in all cases unless some measures were taken to actually isolate the organic fraction, e.g., to correct for carbonate carbon (although I note that “PC” is already used, for principal components).

When seasonal cycles of elemental ratios are presented in 3.1 it sounds like they are all independent quantities rather than algebraic rearrangements of the same data. If C/P and N/P doesn't vary much, what does this say about the statistical significance of the variation in C/N ($= (C/P)/(N/P)$)? It isn't clear to me that any of the observed deviations from the Redfield ratios have actually been tested for significance. The 3X lower P quota for heterotrophs (6236/17) seems quite remarkable and implausible given the sort of heterotrophic organisms one would expect to have sampled; some effort should be made to establish its statistical significance. When reading this paper I often get the feeling that when the authors say “heterotrophs” they envision primarily crustacean zooplankton (e.g., 6240/16-17), which I think is not the case given the sampling methods employed (see also 6238/1-2 below).

I do not think the principal components analysis is well presented. The independent variables include both things that are actually drivers of the underlying biological processes (temperature, nutrient concentrations) and things that are merely correlative, or are themselves part of the ecosystem response (chlorophyll), and the implications of combining the two should at least be discussed. The role of freshwater inputs should be discussed a bit more: if the fluvial component contains refractory DON isn't it likely that some of this is adsorbed onto the particulates thereby increasing the N/P in the seasons with higher river flow.

The figure captions are sometimes lacking essential details and should all be reviewed

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carefully. In Figs 2-4 there is no definition of the lines, boxes and symbols used ("panel" is not very informative). In Fig 6 the location is not specified. Figs 9-11 should specify which method of calculating these quantities was used.

Some specifics:

6229/26 I have no idea what "expansion" means in this context. Not sure what the right word is here but this isn't it.

6232/28 same goes for "deviance" here (deviation). If you have any native English speakers around your lab ask them why this is so funny.

6230/9-12 Does this sentence make sense? What does "this approach" refer to?

6234/13 and 23 seasonal trend or seasonal cycle?

6234/19-22 If PN doubles from 1 to 2 μM but DIN declines by 10, where did the rest go? Has it all been lost to sedimentation?

6237/5-6 vague

6237/12-13 This is not a proper sentence (deleting "showing that" should fix it).

6238/1-2 I don't see why this is counterintuitive. As far as I know most heterotrophic microorganisms have elemental ratios similar to those of autotrophs, except when growth conditions drive autotrophs to the extremes of their range of variability. But the assertion here is that it is counterintuitive that heterotrophs would approximate the RR.

6239/11-15 It seems like a big leap from the methods considered here to inferences from satellite data. It seems to me that there are many other potential approaches that are overlooked, e.g., possibilities for using microscopy or flow cytometry (e.g., Campbell et al., 1994, L+O 39: 954, Heywood et al., 2006, DSR-II 53: 1530), other biochemical indicators (see e.g. chapter by Karl and Dobbs in KE Cooksey, ed., Molecular approaches to the study of the ocean (Chapman and Hall, 1998)), and in situ optical instrumentation that uses the same models of light absorption and scattering as the

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satellite methods but can give more accurate results for a specific location.

6240/19-21 "The discrepancies between the two estimates could also rely on that the statistical model does not efficiently catch the reversal of growth trends" The discrepancies between the two estimates could also result from the failure of the statistical model to efficiently capture the reversal of growth trends

6240/24 log-linear

6241/25-29 "Previous studies of suspended particulate matter in the western North Atlantic has shown that Chl-a and P from dead phytoplankton cells were quickly remineralized in the euphotic zone, while C and N were more refractory, and gradually build up in the detritus pool (Menzel and Ryther, 1964)". There are several things wrong with this assertion. Firstly the chlorophyll is not remineralized. It is degraded to some other compound but those compounds are actually quite refractory. Secondly, only organic compounds or organic fractions (e.g., POC, DON) can accurately be referred to as refractory to decomposition, not the elements themselves. Finally this is a very far-reaching assertion to make based on a very old reference. Obviously chlorophyll is degraded to phaeopigment very rapidly, but the idea that P generally remineralizes faster than C and N has been around a long time without much actual data to substantiate it. I believe that this is partially true but is by no means a robust generalization for all times and places. If there are more up-to-date references please cite them. There is a brief note by Clark et al (1998, Nature 393: 426) that is suggestive, but note that it deals only with DOM not POM.

6242/9-14 "The traditional understanding is that in marine pelagic systems the contribution from detritus is minor, or at least substantially smaller than that in freshwater systems, and the elemental composition is not very different from that of phytoplankton" I don't understand this statement at all. I thought almost all estimates of the nonliving fraction of POM are on the order of 50% or more. I have never heard it said that the conventional wisdom among oceanographers is that detritus in small compared to

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plankton biomass.

6243/3-5 "Detritus will, for obvious reasons, serve as poor food for most grazers due to its low content not only of essential elements, but also its deficiency in essential macromolecules like amino acids and polyunsaturated fatty acids." How do you know this? No references are cited. Again these compounds might be remineralized somewhat more rapidly than some others but I wouldn't assume you can generalize too much.

6243/13-14 "Traditionally phytoplankton are modeled as an organic pool of N and P (cf. Weber and Deutsch, 2010)" I have no idea what this means. Traditionally, phytoplankton are modeled as a pool of organic matter whose currency may be C, N, P, or more than one of these, but I would say that models with both N and P pools in phytoplankton are still relatively rare.

Interactive comment on Biogeosciences Discuss., 8, 6227, 2011.

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