Biogeosciences Discuss., 8, C2969–C2980, 2011
www.biogeosciences-discuss.net/8/C2969/2011/

Biogeosciences Discussions

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.

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Received and published: 9 September 2011

Final Author Comment.

Reviewer #1

In the Author Comment posted on the 8th of August (AC C2366) we address many of the issues that were raised. We will therefore only address the remaining comments by this reviewer in the Final Author Comment.

The reviewer writes that "they use this dataset to first analyze for any relationship between C:N:P and season or environmental conditions. This part of the paper is great

and will be of broad interest. An added discussion of inter-annual trends would be of interest too". We thank the reviewer for the positive comment. We felt the that including inter-annual trends to this paper would make it too wide in scope, and limit the possibility to discuss the seasonal variations amply. We have therefore chosen focus on seasonal variations in the present manuscript.

The reviewer continues: "this part of the paper (2nd part) is more controversial as it builds on several assumptions, e.g. constant POC/chlA ratio that we clearly know does not exist. The authors are well aware of these assumptions per their discussion in section 4.3". We discussed the assumptions and validation of the method in the previous author comment. However, we stress that considerations of the uncertainties inherent in the method will be included in the abstract and in the discussion of the implications of the results.

The reviewer suggests that "a sensitivity analysis of the assumptions in this model could be one way to quantify the effect of various ways of analyzing the results". As mentioned above the main assumption of the regression model is that there is a constant POM:Chla ratio throughout the year. This is an assumption we know to be highly questionable, due to variatons in for example light, temperature, species succession, stratification etc. In addition the method assumes that phytoplankton C (or N/P) does not covary with detrital or zooplankton C (Banse 1977). We state in the method section that: "We have divided the data into seasons to limit the errors introduced by these correlations, however this assumption is admittedly disputable". One could argue that dividing the data into seasons is one way of testing the assumptions in the model. We see that there is indeed different POM:Chla slopes and intercepts throughout the year (ie. not constant POC:Chla), which is illustrated in the different estimates for different seasons in Figs. 9 – 11. This shows that different intercept and slopes in the regression model for different seasons leads to different results, both in the percentage of autotrophs (Fig. 9) and ratios of live autotrophs (Fig. 10) and non-autotrophs (Fig. 11). Therefore this procedure is also a test of the ability of the regression model to reproduce the trends that we expect in autotrophic percentage and elemental ratios of sestonic fractions. An expectation would be that the share of phytoplankton in seston is higher during the productive season, and lower in winter when the non-autotrophic fraction is higher. This is what we estimate with the regression model in Fig. 9 for arendal, while for Jomfruland there is no seasonal signal in autotrophic percentage, which is attributed to an allochthonous source of suspended matter (as also disussed below). In general for the live phytoplankton (Fig. 10) we see that the C:nutrient increases over the productive period, as has been shown in the literature due to "carbon overconsumption". In addition we see in Fig. 11 that the C:nutrient is higher in the non-autotrophic fraction than the live phytoplankton fraction, as would be expected from preferential remineralization. We believe that the ability of the regression model approach to reproduce the expected signals, despite the underlying assumptions, together with reasonable correspondence with phytoplankton carbon (Fig. 8) shows that this is a valid approach.

Minor comments:

6228 / 9 We will rephrase to: A generalized linear model was used to differentiate between the live autotrophic and non-autotrophic sestonic fractions, for both stations the non-autotrophic fractions dominated with respective annual means of 76 and 55%.

6235 / 18 Correct, we will change the wording to: " the C:N ratios were oriented along PC2 . . .".

Figure 2. We will plot the nutrient on a log scale as the reviewer suggests.

Figure 3. There is a statistically significant effect of month on POC, PON and POP (using a linear model of log(POC/N/P) on factor(month)) for both stations. No effect of seasonality (mainly caused by biology) would be surprising. However, the seasonal effect due to biology is less for Jomfruland, due to the high concentrations of POC and PON found throughout the year. The reason for these high (presumably mostly non-autotrophic) material is largely unknown, however investigations by the Coastal

Monitoring Programme suggests it is caused by advected waters from the nearby Frierfjorden, which is high in suspended material (Norderhaug et al., 2009).

Reviewer #2

We acknowledge the thorough inputs from referee #2, which will improve the revised manuscript. However there are certain aspects of the review in which we disagree and these will be discussed together with the general response below.

The reviewer states: "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". We felt it necessary to introduce the background and references of variable stoichiometry. Our argument point is however, that despite a large literature on strong stoichiometric responses, especially in autotrophs, our analysis shows that the actual seasonal variability is small in the two stations we examine. Then we move on to discuss why this may be so. We also state in 6234/17-20 that: "The relatively stable seasonal patterns in seston elemental ratios observed in this study do not contradict variable stoichiometry in phytoplankton, precisely because phytoplankton responses can be masked by other sestonic fractions."

Further the reviewer comments: "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". We do not spend much space on freshwater systems, but simply refer to the fact that the method applied here has been applied also for freshwaters (Hessen et al., 2003). Clearly the Redfield ratio for dissolved nutrients has dominant marine origin, yet we cannot see any fundamental differences between freshwater and marine systems when it comes to the regulation of particulate elements.

The reviewer finds our key conclusion basically sound, "but more speculative than the authors acknowledge". We may very well stress that there are several assumptions behind our estimates (we believed we had done so). However, our main point is that currently there is no easy way to separate the compartments of particulate matter. We suggest one approach that clearly is not perfect, but where we nevertheless believe that this approach is a valid approach. The reviewer is pleased to see that we that we discuss the assumptions and limitations with the regression model approach in section 4.3. Banse (1977) pointed out the correlations between the sestonic fractions and its impact on the results of a regression model of POC on Chla. We are well aware of these limitations, and discuss them in the aforementioned section. Given the assumptions inherent in the method, we compared the estimates of autotrophic percentage from the model with data of phytoplankton carbon (from microscopic counts and biovolume conversions) taken for the Arendal stations over the 20-year period. The results of this are shown in Fig. 8, and the two estimates shows similar seasonal cycles and are in the same range. By comparing these two independent estimates of autotrophic percentage of seston we believe we provide the best test of the validity of our method, with the data we have available.

The reviewer further argues that "within specific seasons I would expect autotrophic biomass, heterotrophic biomass, and nonliving detritus concentrations to be positively correlated". This is a dubious assumption assuming little or no seasonal dynamics. Most studies suggest seasonal fluctuations in these, with typically spring blooms of autotrophs followed by post bloom increases in detritus and grazers, and typically winter dominance of detritus.

On the terminology: Seston is a widely used concept, and we do not see the problem with using this when it is properly defined (as we do in the first sentence of the article). The wide use of this term is exemplified by Google Scholar giving 1 190 hits for suspended particulate organic matter, against 20 000 for seston. We believe that it is well understood what is meant by this term by the people who work in this field. Regarding Particulate Organic Phosphorus (POP) it has been used as an operational definition here; it simply refers to the P bound in (or attached to) particles trapped on a GFF-filter. The standard analytical approach can/will include inorganic P bound to particles as the

reviewer point out and we will change POP to Particulate P (PP).

The reviewer writes "it isn′t clear to me that any of the observed deviations from the Redfield ratio have actually been tested for significance". The aim of the study was not to test if the elemental ratios at the two stations did or did not have a statistical significant difference from the Redfield ratios, but to investigate the natural variability and try to understand what were the drivers behind this variability.

At the Jomfruland station we estimated an almost 3X increase in C:P and N:P ratios from the live autotrophic to the non-autotrophic fraction (see Figs. 10 and 11), and the reviewer writes that this "seems quite remarkable and implausible given the sort of heterotrophic organisms one would expect to have sampled". The reviewer seems to have misunderstood our meaning of the term of non-autotrophic, and interprets it to be the same as heterotrophs. In the method section we stress that the use of the term non-autotrophic in this context: "does not imply that the material cannot have an autotrophic origin, since it will include recently dead phytoplankton (where Chla has decomposed), bacteria and other small heterotrophs, as well as detritus of both allochthonous and autochthonous origin". It is therefore not for the heterotrophs we have estimated a 3X lower P quota, but for this pool of matter, for which we state (in 6242/20-23) "the higher C:P and N:P of the non-autotrophic compared to the live autotrophic fraction at Jomfruland suggests that detritus is a substantial component in this pool, because of the abovementioned high influence of local river run-off for this station".

The reviewer continues "when reading this paper I often get the feeling that when the authors say "heterotrophs" they envision primarily crustacean zooplankton". The reviewer refers to a paragraph where we discuss the discrepancies in autotrophic percentage estimated by the regression model and phytoplankton carbon in June (see Fig. 8), and we write (in 6240/16-17) "this was caused by a high POC:Chla intercept in the regression, which could be related to the post-bloom build-up of zooplankton (which will be included in the non-autotrophic fraction) frequently recorded in June for this station". The samples are routinely screened using a cloth with a mesh size of 180 μm (we will add description of this to the method section), and therefore only copepodite stages of zooplankton and microzooplankton will be included in the POM analyses. It is correct that in this paragraph we are referring to a post-bloom build-up of copepodite stages, however also higher densities of ciliates and microzooplankton will be present at this time. It is also likely that particles with a terrestrial origin from local river run-off contribute to the non-autotrophic pool in early June, as this often coincides with snow melting in the mountains. This does not mean that we believe that it is ALWAYS this croup of heterotrophs that contribute to the non-autotrophic fraction, and this will naturally vary throughout the year.

Regarding the Principal Component Analysis (PCA), the reviewer expresses concerns that we include both variables like temperature and nutrient concentrations and variables that are correlated and driven by these, like Chla and Total N and P, and feels that "the implications of combining the two should at least be discussed". To include variables that are correlated in a PCA is partly the point, because then the potential overlap or redundancy in the multivariate dataset is reduced to orthogonal principal components, representing the two (or more) axis (which should be uncorrelated) that explain as much of the variance as possible. The principal components shown in Fig. 5 are uncorrelated (R2= -0.02).

The reviewer asks "if the fluvial component contains refractory DON isn't it likely that some of this absorbed onto the particles thereby increasing the N/P in the seasons with higher river flow?" It is reasonable that this process might occur, however it would be difficult to quantify to which extent. The question is if this process would be large enough to influence the N/P, which we believe is questionable, however it would be impossible to conclude on this matter without detailed investigations.

Figures: the reviewer comments that the figure captions are "lacking essential details". In the BG guidelines for manuscript preparation (http://www.biogeosciences.net/submission/manuscript_preparation.html) it says: "visual clues should appear on the figure itself, rather than verbal explanation in the

legend (e.g. "dashed line" or "open green circles")". We have tried to accommodate this guideline, and have left these details out of the figure captions. The reviewer also asks for a definition of the "lines, boxes and symbols" in Figs. 2-4. These plots are standard box-and-whisker plots, and in the method section (6232/8) we state this and provide a reference where these are explained in detail. However we will change the wording in the figure captions from "Panel" to "Box-and-whisker plots". In Fig. 6 the location is lacking and we will specify the station at the top of the plot, as is done for the other figures. In Figs 9-11 we will change the wording in the caption to include the method. Response to specific comments:

6229/26 In this sentence we want to emphasize that including the concept of variable stoichiometry deals with a more fundamental change in how we perceive the Redfield ratio, than just changing the mere numbers of the ratio. We will change the word "expansion" with "development".

6232/28: Reviewer states: "same goes for "deviance" here (deviation). If you have any native English speakers around your lab ask them why this is so funny." We point out that one of the co-authors is a native English speaker, and we do not see a problem with this term. It is a standard statistical term, see for example http://en.wikipedia.org/wiki/Deviance_%28statistics%29.

6230/9-12 "this approach" refers to representation of variable stoichiometry in models. We will change the wording to "It has been shown that including variable stoichiometry in ocean biogeochemistry models better represent important processes, especially those related to vertical and seasonal C cycling, than using a fixed C:N:P proportionality".

6234/13 and 23 We will rephrase to "seasonal cycle".

6234/19-22 The reviewer asks: "If PN doubles from 1 to 2 uM, but DIN declines by 10, where did the rest go? Has it all been lost to sedimentation?" The observations are not taken from a closed system, but from two stations in the Norwegian Coastal Current, where horizontal (i.e. advection) and vertical (i.e. sinking of organic matter) transport will play significant roles. In addition there will be production (and break-down) of PON and production of larger zooplankton (and higher trophic levels) that will not be included in the measured PON fraction.

6237/5-6 We will rephrase to: "In addition Chla fell along this axis, which indicates that the timing of the spring bloom and the level of productivity are important drivers as well".

6237/12-13 We will replace "showing that" with "and".

6238/1-2 The term heterotrophs will of course include organisms that are widely different both in size and phylogeny. However a basic concept in ecological stoichiometry, and indeed the concept of consumer-driven nutrient recycling, is that there, due to the strict homeostasis of consumers, is the potential for an elemental imbalance in the interactions between phytoplankton and its consumers (e.g. Sterner and Elser, 2002). This elemental imbalance is founded on the lower C:nutrients often found in heterotrophic bacteria and zooplankton (see section 4.5, and references cited therein) compared with their food source. With the opposite situation (ie. high C:nutrient) often detected in detritus, due to preferential remineralization of N and P over C. The meaning of our statement in this paragraph is not that it is counterintuitive that heterotrophs should ever approximate the Redfield ratio. The reviewer's statement also emphasizes that he/she has misunderstood our meaning of non-autotrophs with heterotrophs, as described regarding P- quotas and Figs. 10 and 11 above. What we discuss in in this paragraph is that the observation of an annual median for this stations identical to Redfield was surprising, given the fact that our statistical model (and other investigations discussed in the annual reports of the Coastal Monitoring Program, as detailed in Norderhaug et al., (2009)) reveals that this stations has a high fraction of non-autotrophic material.

6239/11-15 We merely wanted to show that methods using widely different approaches

give similar results. We will also incorporate the suggestions of the review to this section.

6240/19-21 We will change the wording as suggested by the reviewer.

6240/24 We will change the wording to "log-linear".

6241/25-29 We will change the wording as suggested. However preferential remineralization of C over N and P and P over N has been demonstrated for the HOT data set in the Subtropical Pacific Gyre (Li et al., 2000) and recently for the Baltic Sea (Jilbert et al., 2011). We will rewrite the paragraph and include these references.

6242/9-14 In this paragraph we do not mean to say that all oceanographers believe that detritus is an insubstantial fraction of seston. However we believe it is it is a common belief (an rightfully so) that freshwater systems have a higher load of terrestrial matter (excluding coastal areas with high river loading), adding to the more refractory pool of detritus.

6243/3-5 Deficiency of P and N in detritus, as a result of preferential remineralization as discussed above, will have consequences for the growth of consumers. As reviewed in Hessen (2008), P is especially important for biosynthesis (ie. ribozyme synthesis, however also important for building phospholipids in the cell wall), while N (and C) are more important as "building blocks" both for protein synthesis and lipids. Generally, N and P are important for consumers in active growth, while they are less important in maintenance metabolism. We will rewrite the paragraph in question to be more explicit on this matter and include the appropriate references.

6243/13-14 The misunderstanding comes from our use of the word "traditionally", which is confusing in this case. However, increasingly models incorporating variable stoichiometry include both N and P, as is the case with the study we reference in this paragraph (Weber and Deutsch, 2010) and others (Flynn, 2001). Our meaning of this sentence is however not whether the models include N or P or both, but the fact that they are modeled as a dissolved organic pool of an element, which is interpreted as consisting solely of phytoplankton. We will revise the sentence to make this point more clear.

References

Banse, K.: Determining the Carbon-to-Chlorophyll Ratio of Natural Phytoplankton, Mar. Biol., 41, 199-212, 1977.

Flynn, K. J.: A mechanistic model for describing dynamic multi-nutrient, light, temperature interactions in phytoplankton, J. Plankton Res., 23, 977-997, 2001.

Hessen, D. O., Andersen, T., Brettum, P., and Faafeng, B. A.: Phytoplankton contribution to sestonic mass and elemental ratios in lakes: Implications for zooplankton nutrition, Limnol. Oceanogr., 48, 1289-1296, 2003.

Hessen, D. O.: Efficiency, energy and stoichiometry in pelagic food webs; reciprocal roles of food quality and food quantity, Freshwater Reviews, 1, 43-57, 2008.

Jilbert, T., Slomp, C. P., Gustafsson, B. G., and Boer, W.: Beyond the Fe-P-redox connection: preferential regeneration of phosphorus from organic matter as a key control on Baltic Sea nutrient cycles, Biogeosciences, 8, 1699-1720, 2011.

Li, Y. H., Karl, D. M., Winn, C. D., Mackenzie, F. T., and Gans, K.: Remineralization ratios in the Subtropical North Pacific Gyre, Aquatic Geochemistry, 6, 2000.

Norderhaug, K. M., Moy, F., Aure, J., Falkenhaug, T., Johnsen, T., Lømsland, E., Magnusson, J., Omli, L., Rygg, B., and Trannum, H. C.: Long-term monitoring of environmental quality in the coastal regions of Norway. Report for 2008 (In Norwegian), Norwegian Institute for Water Research (NIVA Report 5796), 2009.

Sterner, W. R., and Elser, J. J.: Ecological Stoichiometry : the Biology of Elements from Molecules to the Biosphere, Princeton University Press, 2002.

Weber, T. S., and Deutsch, C.: Ocean nutrient ratios governed by plankton biogeogra-

phy, Nature, 467, 550-554, Doi 10.1038/Nature09403, 2010.

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