Biogeosciences Discuss.,
https://doi.org/10.5194/bg-2020-314-RC2, 2020

Biogeosciences Discussions

Interactive comment on "Modelling Silicate – Nitrate - Ammonium co-limitation of algal growth and the importance of bacterial remineralisation based on an experimental Arctic coastal spring bloom culture study" *by* Tobias R. Vonnahme et al.

Anonymous Referee #2

Received and published: 27 October 2020

Review of: "Modelling Silicate – Nitrate - Ammonium co-limitation of algal growth and the importance of bacterial remineralisation based on an experimental Arctic coastal spring bloom culture study" by Vonnahme et al.

Summary

This manuscript presents an interesting combined laboratory and modelling study of the nutrient dynamics of a diatom species common in the Arctic. The laboratory component uses two experimental set-ups: 1. axenic cultures of the diatom species; 2.

cultures of the diatom species that include associated bacteria. Short incubations (∼2 weeks) of these cultures take them from exponential phase through to stationary phase, with the cultures sampled throughout to measure cell counts, nutrient concentrations, etc. After an initial period of diatom cell number growth (week 1) in both cultures, this stops as NOx and dSi concentrations approach limiting concentrations. However, NH4 is consistently higher in the non-axenic cultures, and the bacterial cell counts in these cultures increase exponentially during the latter period of the incubations (week 2). The authors interpret the presence of bacteria as being conducive to supplying the diatoms with regenerated nutrients. The modelling component uses a base model, G98, and an extended model based on this that includes a number of additional processes with relevance to the laboratory setting and the hypothesised role of bacterial remineralisation in supporting phytoplankton growth. The models are tuned to fit the laboratory data, with a manual phase to retain consistent parameter values between the models. The authors conclude with a discussion on the application of their results to the real Arctic and its expected future state.

I have listed a number of significant general comments below, followed by more specific and often minor comments. Overall, my assessment is that the manuscript requires major revision to clarify and amend the work described.

General comments

Upfront, my modelling background means that I cannot comment directly on the details of the laboratory work in the study. However, I note that the experiments conducted exhibit anomalies that are not addressed in the manuscript. In Figure 1c, phosphate in bacterial cultures exhibits a strong spike upwards at day 8 that persists and shows high variability. In Figure 3d, chlorophyll in bacterial cultures shows a marked but temporary spike downward at day 8. While the latter is likely a replication or measurement issue, the former is harder to understand, and the manuscript does not discuss its scale or variability. It would be useful to know what the authors believed happened here, particularly in the case of phosphate where bottle concentrations approximately double

against a backdrop of slowly declining phytoplankton and rising bacteria concentrations. The model may even be able to help on this point.

The manuscript's model description appears incomplete, with equations for terms such as those for dSi omitted. More generally, the manuscript would be improved by simply making clear which models are being run – while the text refers to model G98 and "the extended model", the plots shown refer instead to "model + excr" and "model - excr". What might be helpful is to have some sort of diagram of the two main models being used (G98 and Extended) to help illustrate the main connections between state variables, and make clear the differences between the two models.

The description of the model tuning needs to be clearer. It's unclear why some parameters were picked for tuning while others weren't (e.g. remineralisation parameters were not tuned), or what the rationale for picking the training data streams was (e.g. model ammonium was "loosely constrained" to observations). The text mentions several R packages used, but these are presented without any information about what they do, how they work, or what assumptions they make. For instance, is parameter space sampled by latin hypercube, genetic algorithm, or via local misfit gradient? There's also an unclear distinction made around a "manual" component of this tuning exercise.

On a point related to tuning, I noted that the model has a key parameter for restricting phytoplankton growth (by 80%) in the absence of silicate, but that this parameter is not included in the tuning, which seems something of an omission (and, on a more presentation level, is hard-wired into the equations as a number rather than a parameter).

Finally, the authors identify three central hypotheses in their study:

1. Bacterial regeneration of ammonium will extend a phytoplankton growth;

2. Silicate or nitrogen limitations have different physiological responses;

3. A simple experiment can adequately represent Arctic spring bloom dynamics.

On the first, the model has a very poor performance replicating the time history of

ammonium concentrations. On the second, this study would be more convincing if the concentrations of Si and N had been experimentally manipulated to enhance / diminish limitation of each. On the third, the model's inconsistent fit with observations, and its omission of significant real world factors (e.g. zooplankton) make it difficult to evaluate whether this is true. And because the model is only being run for the short incubation period (i.e. rather than beyond the incubation period, or in some mode investigating more realistic or extrapolated settings), it's not clear how it behaves when "unleashed".

Overall, I very much like the combined laboratory and modelling approach, but judge that the modelling component in particular needs to be made much clearer, and evaluated more critically.

Specific comments

Pg. 1, ln. 20: "neglect" or "simplify"?; the distinction is important

Pg. 1, ln. 23: surplus "and"

Pg. 1, ln. 25: regarding the importance of organic matter excretion, was this based on observational evidence?

Pg. 1, ln. 26: "model complexity is comparable to other ecosystem models" – this is misleading as the model here is really an incubator model and not an ecosystem model; it's missing most of the components that such models include (e.g. detritus, zooplankton)

Pg. 2: maybe be a little clearer on the distinction between autotrophic and heterotrophic bacteria throughout; cyanobacteria, for instance, are unlikely to play the role that's described as "bacterial" here

Pg. 2: also, you should probably say something about the role of zooplankton; they graze phytoplankton and excrete some of the nitrogen they acquire; how quantitatively important is this here?; (I've added a cite to a paper that hints that they might not be all that important)

Pg. 2, ln. 36: "marine phytoplankton *are*"?

Pg. 2, ln. 41: predictions of what?

Pg. 2, ln. 47: you might want to cite something like doi:10.1016/j.dsr.2012.10.003 as evidence of the reduced role of mesozooplankton in controlling / terminating blooms

Pg. 2, ln. 48: remineralisation of what?; a bit of clarity would be helpful; dead diatoms, TEP, faecal material, etc.?

Pg. 2, ln. 57: heterotrophic bacterioplankton?

Pg. 2, ln. 60: regarding “neglected”, do you mean omitted or simplified?; most models include remineralisation of detrital material, and this implicitly bacterial

Pg. 2, ln. 63: cultivation experiments normally provide parameter values for things like maximum rates of processes, half-saturations, etc., so it’s not clear this is problematic; if model tuning is using cultivation experiments at equilibrium then this might be more of an issue

Pg. 3, ln. 72: this process was well-known long before this citation (Flynn, 1997); dig a bit deeper

Pg. 3, ln. 72: “iron has a strong control on silicate uptake” - I’m not sure that this is quite right; Si:C ratios are affected by Fe availability, but this is through continuing Si uptake but reduced C/N uptake and no cell division; my understanding is that Si *uptake* (within a certain range of Si:C) is not immediately affected by Fe; also the recent source given for this statement, Hohn et al., 2009, is a modelling PhD thesis

Pg. 3, ln. 75: “ultimately too complex” - they add computational expense to large-scale ecosystem models; it’s not clear that they are "too complex" (or even what is meant by this)

Pg. 3, ln. 79: is phosphate limiting in the Southern Ocean?; in parts of its northern extent, yes, but in the south its concentrations are high, no?

Pg. 3, ln. 79: "coastal"?; is there a distinction to be drawn with deep Arctic locations?

Pg. 3, ln. 81: yes and no; if simple lab experiments exclude factors such as zooplankton excretion which might help fuel phytoplankton growth in parallel with bacterial remineralisation, then it is questionable that they are demonstrating something that’s important in the real ocean

Pg. 3, ln. 86: how "associated" is this?; is it something that lives in direct physical contact or shares the same waters?

Pg. 3, ln. 87: again, what specifically is the issue with complexity?; is it model cost, or is there some other aspect of complexity that disfavours inclusion in large-scale models?

Pg. 3, ln. 93: good hypotheses!; however, you do not clearly return to them (e.g. “Regarding the hypotheses framed for this study . . .”)

Pg. 4: this all sounds good, but my expertise in laboratory work is very limited

Pg. 4, ln. 111: just for simplicity in the labelling, you might want to come up with nice short names for these experiments; e.g. BACT- (for the axenic) and BACT+ (for the non-axenic), or similar; this will make it easier to refer to the experiments in clear, non-wordy ways later on

Pg. 5, ln. 143: the origin of the f-ratio should be cited so that less familiar readers can understand what it is

Pg. 5, ln. 144-146: this is a little confusing; perhaps spell it out with equations?

Pg. 5, section 2.2: I don’t think it ever hurts to have a schematic of a model’s dynamics to supplement equations and (especially) verbal description

Pg. 5, section 2.2: similarly, this section would be a lot clearer if you spelled out which models you were using, and ensured that the later plots use the same nomenclature; I initially misread the work ; I reckon it’s: 1. G98; 2. Extended; 3. G98 – excretion; 4. Extended – excretion

Pg. 5, section 2.2: stating up front an outline about the modelling strategy might help (i.e. two models, tuned to the lab work, DOM addition, etc.)

Pg. 5, ln. 149: some model equations by the looks of things; the model description appears incomplete

Pg. 6, ln. 164: equation for dSi seems missing in appendix

Pg. 6, ln. 166: “80% reduction” - is this where the 0.2 in the equations comes from (i.e. 1 - 0.8 = 0.2)?

Pg. 6, ln. 167: some syntheses would suggest that N dynamics *are* coupled to Si dynamics: e.g. Martin-Jezequel, V., M. Hildebrand, and M. A. Brzezinski, Silicon metabolism in diatoms: Implications for growth, J. Phycol., 36, 821 – 840, 2000.

Pg. 6, ln. 171: make it clear here that your model has labile and refractory DON

Pg. 6, ln. 173: it seems unlikely that the bacteria would simply "give up" on remineralisation if the C:N ratio is too high; perhaps expand on why Tezuka suggests this is happening

Pg. 6, ln. 175: this is unclear; when you say "substrate" what do you mean?; typically substrate is used to indicate a resource consumed by an organism; here you’re talking about phytoplankton, so DIN and DIC would appear to be meant - but DIC will likely be much higher than 10x DIN

Pg. 6, ln. 177: does this mean that bacteria won’t remineralise material with a C:N > 10?; that seems a little unlikely

Pg. 6, ln. 178: as the paper makes a fuss earlier about other models glossing over bacterial remineralisation, this simplified form is surprising

Pg. 6, ln. 185: Table A6 - it looks to me like some equations are missing

Pg. 6, ln. 186: which order of RK?; e.g. 3 or 4 (or higher)

Pg. 6, ln. 185-191: this description of model tuning is far too brief; I’m not sure what’s going on here; readers unfamiliar with R (I am one) will not understand what these different packages are doing or what their underlying assumptions are; this aspect of the modelling is too important to be glossed over so quickly; in general, to avoid the appearance of having just used the first package that occurred to you, expanding on the detail of the tuning (tools, approach, goal) would greatly benefit this description (hence and on Pg. 7)

Pg. 6, ln. 192: the text should be clear on which observed variables were used to fit the model, why these were favoured, and whether any weighting was made to account for those judged better observed or more important; I would naively expect nutrient concentrations to be of prime importance but it’s unclear what criteria the authors are using here (see my later remark about ammonium)

Pg. 7, ln. 197: this seems rather unsatisfactory; I would expect parallel runs with the same parameter values to be performed for axenic and not-axenic simulations, with an automated process (e.g. a genetic algorithm) to evaluate cost (i.e. misfit) before somehow generating new parameter values and iterating; having a manual component seems odd

Pg. 7, ln. 198: what are these "known limitations"?; also, it’s noticeable in the plots that the model solutions inflect strongly around the lag/stationary phase time point - is the model somehow different either side of this division?

Pg. 7, ln. 202: “Colinearlity” - do you mean that you’re looking for linkages between parameters here?

Pg. 7, ln. 205: ammonium was "constrained loosely" - perhaps given later results this was a mistake?

Pg. 7: ecosystem models have notoriously non-linear misfits in their parameter space; when this is highly multidimensional (as here) it can be difficult for optimisation to find

the global minimum misfit; how has this been achieved here?

Pg. 7, ln. 220: “stationary phase” - how exactly defined here?; particularly in the context of Figure B3c, which shows chlorophyll concentrations peaking ∼2 days later in the bacterial incubations

Pg. 8, ln. 234: can you explain if these values are meaningful, or is it just the relative values between phases that’s important?

Pg. 8, ln. 279: This seems a pretty serious deficiency given the focus of this paper; I would interpret this as potentially a problem at the tuning stage; did you consider weighting fitting ammonium more heavily?

Pg. 9, ln. 283: "complexity" is an unusual way to describe a lack of sensitivity (which is what you seem to be suggesting); also, given the extended model performs no better (worse?) than the G98 model is this not to be expected?; i.e. you’ve added a means for the model to be different, but this means is far less powerful than what the model already has

Pg. 9, section 4: this discussion seems far too long for what’s quite a simple set of experiments

Pg. 10, section 4.1: there’s nothing in here about the (hard-wired!) 80% adjustment to growth rates caused by low silicate; this appear to be an unchangeable assumption

Pg. 10, ln. 310: do values of the f-ratio from bottle experiments relate well to those measured from the open ocean?; I can’t think of any reason to suspect that they will, not least because there are no nitrifying bacteria including in the cultures here

Pg. 11, ln. 357: ah-ha, computational cost is finally mentioned

Pg. 11, ln. 351: I don’t think it’s ever made clear why there may be a preference for NH4 over NO3; it would be good to include mention of this so that readers understand why this aspect may be important in the work here

Pg. 12, ln. 360: the authors note different conceptual models for the Si:N relationship in this section, but stick instead with a highly simplified approach from a review almost 40 years old; and also remove this relationship from the tuning exercise undertaken; I would expect to see more justification for this - or potentially some form of model sensitivity analysis to evaluate how important it is

Pg. 12, ln. 375: is a biofilm something one might expect in the natural system?; it doesn’t seem to be the sort of thing that would form in free water; also, it’s unclear from the methods whether there’s any agitation of the cultures to mimic ocean mixing

Pg. 13, ln. 392: the value of the f-ratio has been questioned as the wider role of nitrifying bacteria has been recognised; perhaps rephrase talking instead about the balancing roles of export and remineralisation?

Pg. 13, ln. 406: consider: Kamatani, A., Dissolution rates of silica from diatoms decomposing at various temperatures, Mar. Biol., 68, 91– 96, 1982

Pg. 14, ln. 426: model availability?; might be good to include the code too - it’s simple enough

Pg. 21, Figure 1: presumably the gap between (NOx + NH4) in the two experiments is due to N getting stuck in (dead) organic matter?; bar PON / POC, was anything about this recorded in the experiments?

Pg. 21, Figure 1: the span of PO4 at day 14 (5-55) seems implausible given its narrow span at day 11 (30-35); especially as it narrows again at day 15 (5-18)

Pg. 22, Figure 2: not so axenic, eh?; is this contamination in the axenic incubations from repeatedly opening the vessels?

Pg. 23, Figure 3: so as well as having less NOx and NH4, the axenic experiments have less PON; where is the N going?

Pg. 24, Figure 4: it’s idle curiosity, but what happens if you extend your model runs

past the time point that the laboratory cultures ran?; the model should permit this

Pg. 24, Figure 4: the inflections on some of the model plots here look rather artificial; can you explain why there are such sharp transitions around the 8-day mark?

Pg. 24, Figure 4: the spikes in chlorophyll in the cultures seem difficult to believe; do you think they are perhaps artifacts / measurement error?

Pg. 25, Figure 5: given that the key is the same in all of the plots, it would be better to not use it in plots where it interferes with the data (e.g. 5c)

Pg. 25, Figure 5: why are the fits without the excretion term all flat?; that's not what I'd expect at all; actually, I now realise that you're using two sets of dotted lines on this plot; one for the model output, one for the limiting concentration of the nutrients; this should be changed as it's a very confusing presentational choice

Pg. 26, Table 1: the text reads as if these crosses denote both (a) remineralisation, and (b) variable stoichiometry?; that seems a lot for one cross to bear!; however, in the table, it looks like you separate out the stoichiometry - I think this sentence needs rewording

Pg. 26, Table 1: as a stylistic aside, a cross is not necessarily the best way to denote that a model includes something; conventionally, ticks are used, with ticks and crosses meaning opposite things

Pg. 26, Table 1: where other models are presented, these are often older versions of these models; might it be better to report their current versions?

Pg. 27, Table A1: this is confusing; why not have separate columns for G98 and the extended model?; also, this table implies that some properties are not in the model, but you seem to have equations for them; meanwhile, there are other properties, e.g. dSi, for which no equation is presented

Pg. 27, Table A1: you appear to be using underscores rather than minus signs in units

at the base of this table

Pg. 30, Table A4: what do all of the columns mean here?; some explanation would be useful

Pg. 31, Table A5: please choose a table size that doesn't line-break your units

Pg. 32, Table A6: maybe pull the ODEs together in one place then follow-up with the separate terms afterwards?; it's a little difficult to parse the equations otherwise

Pg. 33, Equation 1: if there's a conditionality on a single term in an equation (as here) better to have a single ODE and put the conditionality inside this term (i.e. it's this value if X, zero if Y); this is easier to follow and makes it much easier to see where the important parts of the model's behaviour lie; duplicating the equations for the sake of a single term in them does not make things clear

Pg. 33, Equation 1: you should note somewhere that organic C is removed from an unmodelled reservoir of DIC; unmodelled because it's always in excess of the ecosystem model's requirements

Pg. 35, Equation 15: the presentation of equations 14 and 15 around the 14e3 divisor is different; this is an unnecessary confounding factor that makes the equations less readable

Pg. 35, Equation 16: why is this a hard-wired number (0.2) and not a parameter?; even if it's not something you change in your study (which seems a little strange given what you do change), having this as a clearly parameter rather than an undescribed constant is important

Pg. 36, Figure B1: I don't understand what this plot is showing; please explain what it means for a line to deviate from zero here; also, why is sensitivity time-variable in any case?; and why is it not monotonically variable in time?; I also note that it looks like DIN is super-sensitive compared to the other properties - is that a correct interpretation of this plot?

Pg. 37, Figure B2: a full explanation for what this plot is showing is critical; it is very difficult to understand what's being shown; also does the frequent occurrence of "NA" imply that some parameters should be excluded from this analysis?

Pg. 38, Figure B3: the key seems to omit reference to the bacterial model

Pg. 38, Figure B3: the failure of the model to capture the observed behaviour of the PON seems quite significant, but is not well-described in the text; it is also noticeably different from that of POC, which suggests interesting POM dynamics in the model that I would not expect; do the authors know what is going on here?

Pg. 38, Figure B3: would quartile or decile range be better here?; this may make your experiments look more messy than they actually are (i.e. it looks like you may have an outlier experiment); this may not be possible given the number of replicates

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