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Interactive comment on "A numerical analysis of the role of the microbial loop in regulating nutrient stoichiometry and phytoplankton dynamics in a eutrophic lake" *by* Y. Li et al.

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Authors response to review comments by B Robson.

The authors would like to sincerely thank Dr Robson for her constructive comments and suggestions made regarding our manuscript. A detailed response to each of the comments is given below.

GENERAL COMMENTS:

COMMENT: I was pleased to receive this paper for review, as the degree to which representation of microbial processes in biogeochemical and ecological models makes a

difference is currently an open question, and an important one as explicit incorporation of bacteria in these models is just beginning to emerge as a theme. Direct comparisons of alternative model formulations is required to advance the field, and that is the subject of this paper. I would like to see it published ultimately, but do think it has some weaknesses in its current form.

RESPONSE: Thank you for the positive comments about the usefulness of this modelling study. It is our view that the direct comparisons of alternative model formulations has been useful to highlight that inclusion of bacteria and the role of flexible C:N:P stoichiometry within the microbial food web can impact model predictions significantly.

COMMENT: There are a few points on which the analysis and the discussion around the model could be improved. Most importantly: 1) It is not clear from the paper whether the model has been validated, or whether the results shown are for the calibration period. I.e. did you use the entire simulation period for model calibration?

RESPONSE: The model period presented here (1997-2001) covers both the model validation and calibration period, though that has not been discussed in this manuscript. The previous study (Gal et al., 2009) that we cited had a detailed manual calibration of the model for the period 1997-1998, with presentation of the model results over the full period in that publication. Several other variants of the model have also been published (Bruce et al., 2006; Makler-Pick et al., 2011; Li et al., 2013) that present the calibration of different model state variables against the same data. Because the model was assessed in Gal et al., 2009, we have made a point to not present in detail the calibration/validation results in this paper and focus on the internal dynamics of the model. The methods applied in this study and reference to previous studies will be made clear in the revised version of the manuscript.

COMMENT: 2) What calibration procedure was followed? Was it a manual calibration, or did you use some formal method? Which parameters were calibrated? Only those relating to the microbial interactions, or was the whole model recalibrated to adjust for

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the impacts of the different formulations on other parts of the model?

RESPONSE: Again, we did not intend for the calibration of the model to become a focus of the paper as it was covered previously in Gal et al., 2009. The procedure adopted (as documented in the Gal et al., 2009 analysis for BAC+DIM), was essentially based on parameters assigned from field or laboratory derived estimates. Most of these parameters (eg: phytoplankton growth rates, zooplankton grazing rates etc) were not merely assigned from the values generally reported in literature but from the composite of many analyses conducted by the Kinneret Limnological Laboratory scientists over several decades (see Table 2 in Gal et al. 2009). A sub-set of these coefficients were subject to some manual fine tuning to improve the seasonal patterns of the microbial species and chemical concentrations. An earlier version of the model Bruce et al. 2006 applied a Levenberg-Marquant method of optimisation (Marquardt 1963) to determine local parameter space optima for the Lake Kinneret model coefficients.

From the base calibration performed in Gal et al. 2009, we did need to adjust some parameters in the alternate model configurations (BAC-DIM and NOBAC) to make sure the model structure was functionally equivalent to BAC+DIM as much as possible (these changes are outlined in Table 4). In the revised version of the paper these parameters will be highlighted in bold for clarity. However the majority of parameters in the model (for example related to mixing, phytoplankton and sediment) were unchanged between configurations in order to isolate the ecological influence of model components relevant to this study, rather than to assess which model configuration performs best against observed data.

Since a similar comment was also raised by the 2nd reviewer, we have proposed to add the following statement to our introduction to more clearly define the context and motivation for this paper: "Earlier versions of the model were thoroughly calibrated to field data and process measurements (Gal et al., 2009, Li et al 2013). Here we use the best-calibrated model version to explore the impact of changes in bacterial dynamics on the ecological system. Within a well-validated set of core ecological process parameters determined elsewhere, we vary the structure and function of the microbial loop to assess how these changes would

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impact broader ecosystem biogeochemistry. While this is essentially a theoretical study, it remains nested in a robust modelling framework that rests on strong process understanding of the Kinneret system."

COMMENT: 3) I'd like to see some formal model evaluation metrics. r2 and RMSE are the most commonly used. A range of other options are presented by Bennett et al. (2013) "Characterising the performance of environmental models".

RESPONSE: We are happy to provide a summary in a revised submission, though again it is important to keep in mind that several of the metrics highlighted in the Bennet paper have been used to assess the BAC+DIM simulation in Gal et al (2009). Interestingly, the errors for the alternate simulations were not very different for many state variables, highlighting the challenges of validating complex models of this nature – equivalent model error values between simulations can be achieved even if the underlying models are functioning differently and that is one of the points we feel this analysis highlights.

Since our focus is to explore the significance of microbial loop mechanisms, we propose to add the required information as supplementary material so as not to make the validation and error assessment a focus of the analysis, but to be available if necessary to allow readers to judge how the alternative model configurations perform against a real ecosystem.

COMMENT: A few points could do with further discussion in the manuscript: 1) Do you have any observational data for observational abundance and biomass? If so, how much do you think this affects the validity of your results?

RESPONSE: Yes – we have used weekly species level biomass data taken from multiple depths and sites to validate that the model is structurally sound from an ecosystem process point of view (again this is the focus of Gal et al., 2009). Note our discussion of this in Section 4.1 – where we aimed to justify the model was structurally sound in general terms for the purposes of demonstrating the microbial loop dynamics.

2) I'd like to see some discussion in the introduction regarding the strength of physiological evidence in the literature supporting formulation (3). How strong is the evidence for bacterial uptake of DIN and PO4, and is there a different metabolic cost to this versus uptake of DOP and DON?

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RESPONSE: In the manuscript (introduction, 2nd para) we cited the following papers that have all documented evidence of inorganic nutrient uptake by bacterial communities:

Barsdate, R.J., Prentki, R.T. & Fenchel, T. (1974) Phosphorus cycle of model ecosystems: Significance for decomposer food chains and effect of bacterial grazers. Oikos, 25, 239-251.

Bratbak, G. & Thingstad, T.F. (1985) Phytoplankton-bacteria interactions-an apparent paradox-analysis of a model system with both competition and commensalism. Marine Ecology-Progress Series, 25, 23-30.

Stone, L. (1990) Phytoplankton-bacteria-protozoa interactions - a qualitative model portraying indirect effects. Marine Ecology-Progress Series, 64, 137-145.

Kirchman, D.L. (1994) The uptake of inorganic nutrients by heterotrophic bacteria. Microbial Ecology, 28, 255-271.

Caron, D.A. (1994) Inorganic nutrients, bacteria, and the microbial loop. Microbial ecology, 28, 295-298.

Joint, I., Henriksen, P., Fonnes, G. A., Bourne, D., Thingstad, T. F., Riemann, B. (2002) Competition for inorganic nutrients between phytoplankton and bacterioplankton in nutrient manipulated mesocosms. Aquatic Microbial Ecology, 29, 145-159.

Danger, M., Oumarou, C., Benest, D. & Lacroix, G. (2007) Bacteria can control stoichiometry and nutrient limitation of phytoplankton. Functional Ecology, 21, 202–210.

It has also been experimentally demonstrated in Lake Kinneret, for example:

Berman, T. (1985) Uptake of (32P)orthophosphate by algae and bacteria in Lake Kinneret. Journal of Plankton Research, 7, 71-84.

Regarding the potential extra metabolic cost of inorganic vs organic nutrient supplementation we have assumed that bacteria primarily get the N and P via DOM intake as a first step during their metabolic process and supplement as required by PO4 and DIN. The uptake of DIM is not rate limited and the metabolic rate of the bacteria is not reduced once DIM supplementation is engaged within the model. There is some literature evidence for rapid PO4 uptake by bacteria and as stated in 19755 of the manuscript, "Bacteria generally have faster P uptake rates relative to phytoplankton (Berman, 1985), which in our model was captured by not limiting the rate of

uptake of PO4 by bacteria".

3) Similarly, is the metabolic cost of uptake of C from DOC the same as that for uptake of POC?

RESPONSE: This point is different from above since in the model representation adopted here, the bacteria are themselves NOT gaining C from POC directly. POC is subject to enzymatic hydrolysis to DOC, which is then able to be consumed. The hydrolysis parameterisation depends on the amount of bacteria (f(B) in the model), however, this is a proxy for the rate of enzyme production by the bacterial population and bacteria are not "choosing" between POC and DOC.

4) It is briefly mentioned in the discussion, but I'd like to see a little more on how stoichiometry affects the rate of breakdown of DOM. It would also be worth mentioning recent work on the affect of HUFA and fatty acids in general on food quality. E.g. Perhar et al. 2013 Modeling zooplankton growth in Lake Washington: A mechanistic approach to physiology in a eutrophication model.

RESPONSE: Thanks for the suggestion, we will highlight potential complicating factors and limitations in our model related to food quality in the revised discussion.

5) I'd also like to see discussed the implications of POM as a bacterial substrate. Smaller particles will have more surface area and, presumably, a higher grazing efficiency than larger particles for the same concentration of POM. Do bacteria specialise on consumption of DOC vs POC? Will a high concentration of POM, by providing more substrate, increase the efficiency of bacteria grazing on DOC? At higher local concentrations, do bacteriophages become important? I'm not asking for these points to be added to the model, only discussed.

RESPONSE: The model is not resolving the different size fractions of POM and as pointed out above the model assumes bacteria are ingesting DOM only for terminal metabolism. Indeed POM will vary whether it is generated from smaller or larger microbes and in the model these sources are lumped into a common pool. As above, we are grateful for this suggestions and we will consider expanding this point in the revised discussion.

6) Another point for discussion: Given that this is a lake prone to blooms of buoyant cyano species such as Microcystis, it would be interesting to consider the role of surface blooms and accumulation of organic carbon in the surface film layer. This can produce a very high

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local concentration of both particulate and labile dissolved organic material at the surface, which is likely to increase bacterial efficiency as well as the potential for cyanophages and bacteriophages to become important. If the bloom is toxic, zooplankton grazing efficiency will be reduced, and if not, it may be increased due to increased concentration of food and substrate for eggs.

RESPONSE: These are interesting points raised by the reviewer that were considered in model development. In Lake Kinneret, surface blooms do occur, however, whilst developing our model simulations we kept in mind: 1. We have no good estimate of the surface biomass as all quantitative sampling occurs below the surface.

2. Because of the size of the lake, the wind and current regime, the surface accumulation of the microcystis are highly patchy. And indeed these patches may be rich in cyanophages and bacteriophages.

3. Toxicity is generally low in the lake though when it occurs the spatial patchiness is large enough to prevent a major decline in zoop grazing. Furthermore the zooplankton are not set up to consume microcystis in the model given empirical evidence that grazing on microcystsis is a small component of the zooplankton diet.

In general we feel that these details are relevant at a higher level of spatio-temporal detail than what is the focus of this model application; as such we may underestimate the intense cycling that periodically occur during such events, however the model reasonably captures the seasonal trends that are predicted for microcystis over the period simulated.

7) ANOVA may not be a good statistical test for comparison of different model runs, as the frequency of model output is arbitrary and consecutive points in a time-series are not independent samples. I am led to understand that this gives an arbitrary apparent "n" and can give a misleading p value.

RESPONSE: We will revisit the approach to assessing the model differences. Also, in light of earlier comments about providing validation information, in the revised submission we will remove this component and replace with summary data and error metrics of the three simulations, provided as supplementary material so as to not dilute the main aim of the investigation. Note, the aim of this component of the paper was to highlight significant difference in the state variables between the simulations, and we will aim to achieve this through comparing state

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variable means and the error assessment.

8) I haven't checked the sensitivity analysis method given by Bruce et al. (2006), but it may be worth referring to the Environmental Modelling & Software position paper, "How to avoid a perfunctory sensitivity analysis".

RESPONSE: Thankyou for this suggestion – we felt that the paper already dedicated to the sensitivity analysis of the model (see Makler-Pick et al 2010) meant that we did not want to focus on SA in the present analysis, but nonetheless were interested to highlight microbial loop specific parameters that were important in the three simulations. The approach we used is simple (+/-20% each parameter individually or one-factor-at-a-time (OAT)), to provide insights into the main parameters where empirical work could be prioritised, and we refer the reader to Makler-Pick et al (2010) for a detailed global sensitivity analysis of the entire BAC+DIM simulation including the microbial loop parameters if they have a specific interest in the parameter interactions and non-linearites that are present.

9) (This ties in with my opening remarks about model validation): the more complex model produces a better match to observations, but to what extent is this attributable to a greater number of parameters allowing a better fit, versus the relative virtues of the model? A point for discussion, at least.

RESPONSE: The DYRESM-CAEDYM model has previously been applied to Lake Kinneret using a more simple model configuration (eg. Bruce et al., 2006) and the Gal et al. 2009 simulation has also been extended to include fish (Makler-Pick et al. 2011). The evolution of the model structure as we have presented it in this analysis is the product of trying to resolve problems with the calibration that could not be simply solved by "better calibration" of a more simple counter-part and this is to some degree is the genesis of this analysis. The NOBAC was the starting point used in Bruce et al. 2006 and is consistent with many approaches currently being published by lake ecosystem modellers. This configuration however, failed to accurately represent the competition between zooplankton groups so that the micro-grazers were under predicted. Furthermore by short-circuiting the microbial loop, the NOBAC configuration missed a crucial process-limiting step in nutrient cycles. Adding bacteria was the next logical step to capture the more dynamic variability in mineralisation and a specific food source for micrograzers, but in doing so we found the BAC-DIM sim was less efficient in recycling DOM and with implications for nutrient cycling and availability to phytoplankton. By putting the last mecha-

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nism (DIN/DIP uptake) in we were able to balance both uptake and release of nutrients in the microbial loop and achieved an optimal prediction of the micro-zooplankton group. To summarise whilst it is likely possible to recalibrate the NOBAC and BAC-DIM configurations to get reasonable error metrics, we feel the level of model complexity and processes presented in the BAC+DIM simulation is necessary to fully resolve the microbial loop and the important influence it has on pelagic nutrient cycling. We will edit the discussion to include an overview of this point in the revision.

10) You mention that bacteria become N and P limited. Is there a role of N fixation in your model? I hope it is already included in your model for N-fixing cyanophytes, but some heterotophic bacteria are also capable of fixing N, so this could be a point for future refinement (supported by process studies in the lake).

RESPONSE: The hetertrophic bacteria in the model are primarily P limited (as evidenced by the small DIN uptake by bacteria in Figure 4) and this fits the observations made in the lake.

The model does include N-fixation in the 3rd phytoplankton group (outlined in Table 1), but not in the bacteria. Whilst we acknowledge N fixing heterotrophs also could be at play there is minimal empirical support for this at the moment and it is most likely a minor flux, but agree it could be the subject of further studies aimed at refining our understanding the ecosystem and mentioned in the discussion.

MINOR POINTS:

1) What did you use for model initialisation? p 19738, li 11: the mineralisation rates in this formulation aren't really constant, as they are affected by f(T) and f(DO).

RESPONSE: Field data was used to initialise the vertical profiles of all major state variables. You are correct the mineralisation rates are not constant, we had meant to imply they were constant for a given temperature and redox (oxygen) condition, and will reword accordingly.

2) Equation (3): Is this actually respiration or mortality? Is respired carbon not mostly lost as DIC?

RESPONSE: Thanks for highlighting this inconsistency – the Eq 3 is correctly summarised as respiration but we had mistakenly omitted the mortality term ("M") from the Z3 balance equations. We will update accordingly.

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3) Equation (7): It would be worth referring to papers that discuss the implications of alternative zooplankton grazing functions, e.g. the difference between this simple MM function and a function that considers zooplankton clearance rates, which are affected by swimming strategies and speed, etc. Also, the impacts of zooplankton size distribution.

RESPONSE: Suggestion noted – we feel this in itself would warrant an investigation similar to what we have done here for the microbial loop, and will endeavour to mention this to our recommendations for further work.

4) Given that the focus is on the microbial loop, I will note only in passing that the representation of NH4/NO3/DON preferences is fairly blunt and does not consider the different metabolic costs that underly this preference. See e.g. my recent MODSIM2013 paper on modelling Trichodesmium for one way to implement this.

RESPONSE: Thankyou for this information, we will include your suggestion when discussing future improvements for the model.

5) Section 3.4: some of this would be easier to follow if presented as bar graphs instead of as text.

RESPONSE: We had put in Fig 4 as a summary of this text which we feel portrays the relationships as well as the magnitudes (compared to a bar graph), but will also aim to make the text more succinct to point the reader to essential aspects of the Figure.

Typos: p 19735, li 19: "there" should be "their". p 19736, li 8: "loop on" should be "loop for" p 19741, li 3: inconsistent spelling of "mineralization"/"mineralisation"

RESPONSE: Thank you for noting these – we will address during the revision.

Interactive comment on Biogeosciences Discuss., 10, 19731, 2013.