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Interactive comment on "Modeling the impact of riverine DON removal by marine bacterioplankton on primary production in the Arctic Ocean" *by* V. Le Fouest et al.

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We first would like to thank the referee for her/his relevant comments and suggestions. The constructive comments of the referee were very helpful to improve the quality of the manuscript. In what follows, the referee's comments are reminded in bold and italic police of character, whereas our responses are given in normal police character. Note that the line numbers mentioned in our response refer to those of the submitted version of the manuscript. New references cited in our responses are given at the end of each comment.

1. "In the model it is assumed that bacteria prefer (take up faster) DON compared

to ammonia (eqns A19-A22; P 16974, L 10-12). This may indeed be the case with small nucleotides and amino acids, as is shown in the article referred in the ms to justify the above assumption (Kirchman et al. 1989). However, these compounds form a small part of released DON (dDON; Fig. 1), and their share must be minimal in the bioavailable riverine RDON pool, being processed by bacteria during transport from drainage area. Ammonia is readily taken up, but bulk RDON compounds need to be broken down exoenzymatically before transport into cells (accordingly, the authors define bioavailable RDON as the fraction of total DON degradable within one month; P 16965, L 4-7)!"

Response #1: Dissolved organic matter (DOM) is a complex bacterial substrate representing a source of nitrogen (DON) and carbon (DOC). As nitrogen is the sole currency of the model, the simulated DONl is made a proxy of DOC for bacterioplankton uptake. It means that bacterioplankton in the model obtain all their carbon and some of their nitrogen from the usable fraction of RDON and from detrital DON (dDON) that form the DONl pool. This assumes that all the DOC required for growth is in N-containing forms. By contrast, the simulated ammonium uptake supplements the bacterioplankton N requirements for growth. We modified the original text to clarify this point according to the reviewer comment. The sentence "DONl (i.e. the sum of dDON and usable RDON) is the preferred substrate for bacterial uptake (d-1) (Kirchman et al., 1989) represented by a Michaelis–Menten model:" (page 16973, L 16) was replaced by "Dissolved organic matter (DOM) is a complex bacterial substrate representing a source of nitrogen (DON) and carbon (DOC). As nitrogen is the sole currency of the model, the simulated DONl is made a proxy of DOC for bacterioplankton uptake. It means that bacterioplankton in the model obtain all their carbon and some of their nitrogen from the usable fraction of RDON and from detrital DON (dDON). This assumes that all the DOC required for growth is in N-containing forms. By contrast, the simulated ammonium uptake supplements the bacterioplankton N requirements for growth. The DONl uptake is represented by a Michaelis-Menten model:". The sentence "such a mechanistic behavior is consistent with the preferential uptake of DONl relative to NH4 (Kirchman, 1990)."

(page 16974, L 11) was also removed. In addition, we added two sentences in the discussion section: Page 16966, L 8: “Single explicit pools of DOC and DON represented as two different state variables, as well as a distinction between readily usable molecules (turnover within days) and more complex ones (turnover within a month) would also make the model more realistic.”. Page 16966, L 12: “Appropriate values for the maximum uptake rates and half-saturation constants may not be easily obtained from existing data in the Arctic.”

2. “Finally, why can’t bacteria take up nitrate, like they in reality do (P16973, L 14)?”

Response #2: We agree that bacterioplankton can take up nitrate. During spring blooms, nitrate uptake can be significant (4-14%; Kirchman et al., 1994), but it is an energetically expensive process so that bacterioplankton usually account for more ammonium than nitrate uptake (Lipschultz, 1995). In sub-Arctic and Arctic waters, a substantial nitrate uptake by bacterioplankton has been observed, but in very specific environments such as in high nitrate low chlorophyll waters (Kirchman and Wheeler, 1998) or low chlorophyll waters dominated by cyanobacteria (Fouilland et al., 2007). In the model, the fact that such conditions are not achieved motivated our choice not to account for nitrate uptake by bacterioplankton at this stage of development of the model. According to referee’s comment, we will add sentences to justify the lack of nitrate as a nitrogen source for bacterioplankton (page 16974, L13): “Bacterioplankton cannot grow on nitrate in the model. Nitrate uptake is an energetically expensive process so that bacterioplankton usually account for more ammonium than nitrate uptake (Lipschultz 1995). Furthermore, although a substantial nitrate uptake by bacterioplankton was reported at high latitudes, it occurred in very specific conditions such as in high nitrate low chlorophyll waters (Kirchman and Wheeler, 1998) or in low chlorophyll waters dominated by cyanobacteria (Fouilland et al., 2007). Such conditions are not achieved in the model.”.

Fouilland, E., M. Gosselin, R. B. Rivkin, C. Vasseur, and B. Mostajir (2007), Nitrogen uptake by heterotrophic bacteria and phytoplankton in Arctic surface waters, J. Plankton Res., 29, 369-376; Kirchman, D. L. (1994), The uptake of inorganic nutrients by heterotrophic bacteria, Microb. Ecol., 28, 255-271; Kirchman, D. L., and P. A. Wheeler (1998), Uptake of ammonium and nitrate by heterotrophic bacteria and phytoplankton in the sub-Arctic Pacific, Deep-Sea Res. I, 45, 347-365; Lipschultz, F. (1995), Nitrogen-specific uptake rates of marine phytoplankton isolated from natural populations of particles by flow cytometry, Mar. Ecol. Prog. Ser., 123, 245-258.

3. “The nutrient uptake efficiency or affinity (α) of osmotrophs for nutrients can be given as α = maximum nutrient uptake rate / half-saturation constant of uptake. In this study (Table 2) α for bacterial ammonia uptake is 1/0.1 m3/(mmol-N*d), being smaller than α for small phytoplankton (SP, = 1.4/0.1 m3/(mmol-N*d)); and even large algae (LP) show similar α as bacteria (= 1.4/0.5 m3/(mmol-N*d)). This contradicts with the theoretical and empirical results that smaller cells are more efficient in taking up nutrients than large ones, showing a quadratic penalty with respect to size (radius, though adjustments like diatom cell vacuoles devoid of nutrients can diminish this penalty; e.g. Fenchel 1987; Ecology – potentials and limitations, Oldendorf-Luhe; Thingstad & Rassoulzadegan 1999, Prog. Oceanogr. 44: 271–286; Lignell et al. 2013, Limnol. Oceanogr. 58: 301–313). Thus, more than an order of magnitude smaller α would seem more appropriate for <5 μm SP compared to bacteria.”

Response #3: As mentioned in page 16974 (L4) of the original manuscript, the maximum growth rate for bacterioplankton (Ubactmax = 1 d-1) is temperature normalized. At 5°C, Ubactmax reaches a value of ~1.7 d-1, whereas at 10°C it reaches a value of ~3 d-1. Hence the specific affinity for ammonium varies within the range 17-30 m3/(mmol-N*d) that is up to 2-fold higher than the affinity for ammonium of small phytoplankton (14 m3/(mmol-N*d)). However, we acknowledge that α for bacterioplankton is less than one order of magnitude higher compared to small phytoplankton (e.g. Baltic Sea, Table 3 in Lignell et al., 2013) as mentioned by the referee. Nevertheless, it is comparable to what is observed in the Isefjord (Table 3 in Lignell et al., 2013). Finally, the parameterization used in the model does not contradict with the theoretical and empirical results that show that smaller cells are more efficient than larger ones. Moreover, we would like to stress out that the half-saturation constants for nutrients uptake can vary for bacterioplankton hence leading to some inherent uncertainty.

4. “The above 2 issues rise the question, have the authors tested a stand-alone version of their nutrient flow model (Fig. 1)? That is, has the model been verified with appropriate time-course data from enclosed or semi-enclosed systems (e.g. plankton nutrient treatment responses in mesocosms), where uncertainties arising from hydrodynamics are minor.”

Response #4: The biological model was applied in a one-dimension (i.e. water column) framework in the Beaufort Sea (Le Fouest et al., 2013). It was run in steady state during summer conditions, when the ocean column was well stratified and with limited advection, and successfully compared to in-situ and coincident measurements. The model reproduced satisfactorily scalars such as nitrate and ammonium concentration, bacterioplankton biomass, size–fractionated chlorophyll, mesozooplankton biomass, and PON concentration, as well as nitrogen fluxes including primary and bacterioplankton production, ammonium and nitrate uptake, and ammonium regeneration. Because of the very oligotrophic conditions of the Beaufort Sea, the model in Le Fouest et al. (2013) differed slightly from the version used in the present study with regards to a limited number of biological constants and processes (e.g. parameterization of DON photoammonification, but no bacterioplankton temperature dependence or RDON flux). Nevertheless, it is same as the model used in this study in terms of structure (biological state variables) and functions controlling nitrogen flows. To that respect, we are confident on the consistency of the nutrients flows simulated by the model.

Le Fouest, V., Zakardjian, B., Xie, H., Raimbault, P., Joux, F., and M. Babin (2013), Modeling plankton ecosystem functioning and nitrogen fluxes in the oligotrophic waters of the Beaufort Sea, Arctic Ocean: a focus on light-driven processes, Biogeosciences, 10, 4785-4800.

5. “Something seems to be missing from eqn A20, and judging from text (P 16974) it should read S = (NH4, 0.6DONl)min (bold ‘min’ added, right or?). Authors should carefully check the equations, as also eqn A23 seems incomplete (below); this also concerns parameter Table 2 (e.g. LP sinking rate unit should probably read md-1 instead of m-1)!.”

Response #5: Equations in the Appendix, as well as tables 1 and 2 will be carefully checked for typesetting errors.

6. “Due to above problems (issues 1 and 2) evaluation of model functioning is not straightforward. i) The model seems to function so that phytoplankton grow on ammonia (and nitrate) and bacteria grow mostly on DONl (RDON+dDON, ammonia uptake appearing to be redundant, especially since it’s further constrained with DONl availability; denominator in eqn A22). ii) Bacteria cannot become N-limited in substrate (dissolved organic matter, DOM) uptake. iii) Labile dissolved organic carbon flow is not explicitly included, but bacteria fulfill their C needs along with DON uptake (DON pool is estimated from DOC with fixed C:N ratio of 40), and maximal bacterial ammonia uptake is constrained by DONl availability (eqns A19-A22). In summary, with the temporal (annual) and spatial (AO) scales applied, and with the order of decade residence time of AO water body (P16958, L 21-22) it seems that the model may be able to reproduce reasonably well annual average PP and BP values as long as bacteria are C-limited. This is also because most of the N incorporated into bacterial biomass is subsequently recycled in the planktonic grazing processes.”

Response #6: As nitrogen is the sole currency of the model, the simulated DONl is made a proxy of DOC for bacterioplankton uptake. It means that bacterioplankton in the model obtain all their carbon and some of their nitrogen from the usable fraction of RDON and from detrital DON (dDON). By contrast, the simulated ammonium uptake only supplements the nitrogen requirements for growth. As pointed out by the referee, it results that ammonium uptake by bacterioplankton is constrained by the concentration of DONl that is the main N- and C-containing substrate for growth. It means that DONl in the model must contain enough nitrogen to meet the nitrogen requirements of bacterioplankton. In the discussion section of the original manuscript, the third paragraph (page 16965, L 19 to 16966, L 15) was modified to discuss the referee's comments as follows: "In the biogeochemical model, the usable RDON, dDON, and NH4 produced by the plankton components are taken up by bacterioplankton to build up biomass. The synthesis of cell proteins requires at least carbon and nitrogen. Bacterioplankton obtain all their carbon and some of their nitrogen from DONl (usable RDON + dDON). The simulated NH4 uptake supplements their nitrogen requirements. The growth function is formulated using the Fasham et al. (1990) model. It assumes that in a balanced growth situation, where N and C assimilation occurs simultaneously and where bacterioplankton have fixed stoichiometry, the ratio of NH4 uptake to DONl uptake is constant (0.6, see Appendix A) to ensure that biomass of the required C:N ratio is produced from DONl with a given C:N ratio. If there is not enough NH4 available, the uptake rate of both DONl and NH4 decreases allowing both N and energy limitation. In Arctic waters, the inhibition of DOC uptake by bacterioplankton under inorganic nitrogen limitation was shown by Thingstad et al. (2008). However, as DONl in the model is made a proxy of DOC, the C:N ratio of the substrate is assumed constant. As a consequence, any explicit stoichiometric treatment of the simulated bacterioplankton metabolism is precluded as well as any stoichiometric coupling between DOC and inorganic nutrients (e.g. Thingstad et al., 2008). In addition, the implicit treatment of DOC in the model implies that all the DOC required for growth is in N-containing forms. Hence it assumes that bacterioplankton cannot be N-limited in substrate. However, N-limitation of bacterioplankton production was observed in summer in surface waters of the Beaufort Sea (Ortega-Retuerta et al., 2012). This pattern contrasts with the organic carbon limitation observed in the Yenisei and Mackenzie River plumes and adjacent Kara and Beaufort seas (Meon and Amon, 2004; Vallières et al., 2008), hence highlighting the difficulty to draw a general pattern at the AO scale. Nevertheless, making the C:N ratio of substrates of terrigeneous and marine origin vary in a realistic way in biogeochemical models would farther be required. Single explicit pools of DOC and DON repre-

sented as two different state variables, as well as a distinction between readily usable molecules (turnover within days) and more complex ones (turnover within a month) would also make the model more realistic. The parameterization of variable C:N ratios is not trivial as it requires large in-situ datasets (see Letscher et al., 2014) and, in Arctic river-influenced shelf seas, a good knowledge on the characteristics of the terrigenous dissolved organic matter flowing into the coastal ocean (e.g. Mann et al., 2012). Appropriate values for the maximum uptake rates and half-saturation constants may not be easily obtained from existing data in the Arctic. As a result, the coupled model that is used in the present study is an interesting compromise to more complex (in terms of number of biological equations and parameters) models of bacterioplankton growth applied to shelf waters (e.g. Auger et al., 2011; Anderson and Williams, 1998)."

Ortega-Retuerta E., W. H. Jeffrey, J. F. Ghiglione, and F. Joux (2012), Evidence of heterotrophic prokaryotic activity limitation by nitrogen in the Western Arctic Ocean during summer, Polar Biol., 35, 785-794; Meon B, and R. M. W. Amon (2004), Heterotrophic bacterial activity and fluxes of dissolved free amino acids and glucose in the Arctic rivers Ob, Yenisei and the adjacent Kara Sea, Aquat. Microb. Ecol., 37, 121-135.

7. Related to point 5, can the authors come up with any empirical data (or reference) on C vs. N limitation of bacteria in AO?

Response #7: A discussion on that topic with new references is given in our answer to point 6 above.

8. Basically two model runs (with and without RDON inputs) are reported in the ms, resulting in point estimates of annual PP and BP averages of the deterministic model (P 16960, L 12-18; Fig. 5). It is unfortunate, that no uncertainty analyses are included in in model examinations (cf. comments above), also hampering trend evaluations! The ms deals with the impact of RDON inputs on AO system, and the authors report percentage labile RDON range of 8-24% (of total RDON) as annual averages in loads of different rivers (P 16965, mean of 15% has been applied). Thus, the labile RDON

range would be a natural candidate for initiating model sensitivity analysis. Not the least, because the authors seem to feel that way themselves (P 16965, L 13-15)!

Response #8: We agree with this comment, which is discussed in the original manuscript (page 16965, L 10-18). In line 16, we mention that the model provides a first order estimation of the RDON contribution to BP and PP. To be accurate in the methods, a sensitivity analysis should be performed taking into account the variability amongst rivers and seasons as estimates of RDOC lability are given in the study of Wickland et al. (2012). Furthermore, we explain in page 16968 (L 8) that to obtain more robust predictions of the microbial food web functioning and mass fluxes, the model would require improvements in the parameterized land-ocean fluxes in terms of spatial and temporal variability of the freshwater discharge. In the Mackenzie River, strong interannual variations of the freshwater discharge in terms of peak of discharge and maximum spring flow were observed in the last decades by Yang et al. (in press). We consider that sensitivity analyses on RDON lability should be combined with sensitivity analyses on the freshwater discharge to provide robust scenarios. This work would make by itself another new manuscript. The text has been modified to take the referee's comment into account (page 16965, from L13 in the original manuscript):"Sensitivity analyses with different parameterizations of the usable RDON fraction set amongst river and seasons would hence be informative on the amplitude of the PP and BP response to spatial and temporal variations of the usable RDON flux. To be robust, they should be combined with sensitivity analyses on the freshwater discharge to better constrain the RDON flux. In the Mackenzie River, strong interannual variations in terms of peak of discharge and maximum spring flow were observed in the last four decades (Yang et al., in press). Nevertheless, the use a constant fraction of usable RDON as preformed in the present study provides a first order estimation of its contribution to BP and PP that is consistent with the average state of knowledge on the RDON inputs."

Yang, D.,Shic, X, and P. Marsh (in press), Variability and extreme of Mackenzie River daily discharge during 1973–2011, Quaternary International, DOI:

10.1016/j.quaint.2014.09.023.

9. Finally some small questions and comments: i. Why is nutrient/food limited growth formulated differently with different functional plankton groups, instead of using consistently one Monod/Michaelis-Menten/Holling type expression? The latter alternative would improve model transparency and evaluation of parameter set used.

Response #9i: Different mathematical expressions are used for the different biological compartments as they allow for specific behaviors with respect to known ecological/physiological processes. For instance, a sigmoidal formulation is used for small zooplankton, because it has been observed that protozooplankton exert a control on small phytoplankton biomass only beyond a threshold (Lancelot et al., 1997). By contrast, a Michaelis-Menten function is usually preferred for phytoplankton. In the model, we use for the two size fractions of phytoplankton the substitutable model of O'Neill et al. (1989), because it allows for an inhibitory effect of ammonium on nitrate uptake as often observed (Dorch, 1990).

ii. Why does large zooplankton not release dDON via sloppy feeding in model like small zooplankton – and like experimental studies suggest?

Response #9ii: We agree that sloppy feeding can fuel the DOM pool in marine waters. Laboratory experiments showed that copepods grazing on algae promoted bacterial growth (Strom et al., 1997). In contrast, Vargas et al. (2007) showed that C losses mediated through sloppy feeding significantly promoted bacterial growth in oligo-mesotrophic waters but not in coastal waters. To that respect, and in order to limit the uncertainty related to the process parameterization including the assignment of the biological constants, we made the choice not to include sloppy feeding in the model at this stage, or other known sources of DOM as phytoplankton lysis whose parameterization is not easy.

Strom, S. L., Benner, R., Ziegler, S., and M. J. Dagg (1997), Planktonic grazers are a potentially important source of marine dissolved organic carbon, Limnol. Oceanogr., 42, 1364-1374; Vargas, C. A., Cuevas, L. A., Gonza, H. E., and G. Daneri (2007), Bacterial growth response to copepod grazing in aquatic ecosystems, J. Mar. Biol. Ass. U.K., 87, 667-674.

iii. The dPON sedimentation loss term includes a strong quadratic penalty for increasing dPON concentrations, mimicking aggreagate formation and subsequent fast sedimentation (eqn A23 should probably read sed_dpondPON, with bold 'd' added, or?). The authors need to give a reference or show data to justify this formulation!

Response #9iii: According to the Stokes's Law, the settling velocity of particles increases with the particle size and with excess density, and is reduced with increasing porosity. The biological model does not account for detrital PON quality (e.g. density, porosity) but only for concentration. Hence we consider detrital PON concentration as a proxy of size. The formulation we use in the biological model finds support with the study of Guidi et al. (2008), which showed that the size distribution of aggregates could be related to the mass and PON flux measurements. The reference to Guidi et al. (2008) was added in the original text (page 16974, L 16): "The sedimentation loss term (d-1) is expressed as a quadratic function allowing for increasing implicit aggregation of particles with increasing dPON concentration (see Guidi et al., 2008):".

Guidi, L., Jackson, G. A., Stemmann, L., Miquel, J. C., Picheral, M., and G. Gorsky (2008), Relationship between particle size distribution and flux in the mesopelagic zone, Deep-Sea Res. I, 55, 1364-1374.

iv. Protozooplankton (SZ) shows maximum grazing rate of 1 d-1 and growth efficiency of 30% (Table 2), which translates to maximum SZ growth rate of 0.3 d-1. This value sounds low to me – do the authors have empirical proof for it?

Response #9iv: The growth efficiency of 30% set in the model finds support with the studies of Straile (1997) and Chen and Liu (2011) that give an average value between 20% and 30%. With respect to the maximum grazing rate (1 d-1), the value set in the model lies within the range given by Sherr et al. (1-2 d-1, in average; 2013) for Arctic

waters. The maximum growth rate set in the model (0.3 d-1) is consistent with the average potential growth rate given by Sherr et al. (2013) for non-bloom (0.33 d-1) and bloom (0.43 d-1) conditions in Arctic waters. Potential growth rates over 1 d-1 were observed but for a limited number of stations (Sherr et al., 2013).

Chen, M., and H. Liu (2011), Experimental simulation of trophic interactions among omnivorous copepods, heterotrophic dinoflagellates and diatoms, J. Exp Mar. Biol. Ecol., 403, 65–74; Sherr, E. B., Sherr, B. F., and C. Ross (2013), Microzooplankton grazing impact in the Bering Sea during spring ice conditions, Deep-Sea Res. II, 94, 57-67; Straile, D. (1997), Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group, Limnol. Oceanogr., 42, 1375-1385.

v. The ms would benefit from a linguistic check.

Response #9v: A linguistic check will be performed.

10. To conclude, despite its weaknesses this ms is in my opinion a worthy first step towards evaluating the effects of labile RDON inputs on AO biogeochemistry, including recent development of PP vs. BP balance. However, one can be question the value or potential of the present model in projecting AO system responses to temperature increase and permafrost thaw due to global change, if this leads to increased riverine inputs of humic compounds with high C:N ratio. To forecast AO ecosystem responses to these scenarios, mechanistically more sound models, allowing for flexible stoichiometry and N-limitation of bacterial substrate uptake are probably needed.

Response #10: We agree with the referee on that point. We modified the last sentence at the end of the conclusion (page 16968, L 16) accordingly: "Finally, model predictions of future trajectories of PP (e.g. Vancoppenolle et al., 2013) would probably gain in considering riverine nutrients fluxes as an important driver of PP on Arctic shelves for the next decades. However, to forecast AO ecosystem responses to climate change scenarios, mechanistically more sound models allowing for flexible stoichiometry and

N-limitation of bacterial substrate uptake are probably needed".

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