Review of « Accumulation of DOC in Low Phosphate Low Chlorophyll (LPLC) area: is it related to higher production under high N-P ratio? by Mauriac et al., 2010.

The manuscript presents a mathematical model for describing the interactions between phytoplankton, bacteria and DOC in the Mediterranean Sea. Phytoplankton and bacterial content in carbon, nitrogen and phosphorus is described and three pools of DOC with different degradability levels are included. The model is used to investigate the interactions and dynamics of phytoplankton and bacteria considering different initial contents of Total Phosphorus and Nitrogen. Model results are widely discussed in terms of growth rates, limitation, N/P ratios. ..

I have a lot of quite serious concerns about the methodology used in this paper: hypotheses, equations, model structure, units, calibration validation, type of simulations...

First, there are some inconsistencies in the units and dimensions of the different terms of the equations (see details below). These inconsistencies make me worried about the use of the model. Then, a lot of hypotheses are made in the manuscript (hardly justified), sometimes these hypotheses can be highly criticized and no analysis of the sensitivity of model results to these hypotheses is made in the manuscript (although the model is quite simple allowing sensitivities studies). For instance, grazing is totally ignored and is represented as a fixed fraction of the mortality rate. What is the sensitivity to the imposed 50 % for the input of DOC from grazing and mortality (page 4, line 16), what is the sensitivity to the partitioning of this grazing into semi- refractory and labile form (LDOC). The authors use the same half saturation constants for phosphate and nitrogen uptake although usually these constants are very different by ~one order of magnitude (more below). Some symbols/variables are not defined, some symbols are used with different meaning (σ is the phosphate content and after this is a cross section, ϕ is phytoplankton biomass or the quantum yield),

I would have hoped to have a validation exercise before to have a long interpretation of model results. It is quite easy to run a model, the most difficult part is the criticism/error assessment of his results.

Here below are my detailed comments on the manuscript:

Comments on the model structure:

Before to be available for bacteria, SRDOC and SLDOC have to be hydrolysed. I am surprised that there is not transformation of SLDOC and SRDOC into LDOC. I do not understand why SRDOC can be assimilated by bacteria. Besides, it is well know (Anderson and Ponhaven, 2003) that a part of PER is labile DOC. I am also surprised that bacteria uptake of N and P does not involve a part of DOP and DON that may be deduced from the uptake of DOC. Indeed, the main source of nitrogen and phosphorus for bacterial growth is first DOM and not inorganic nutrients. This assimilation should be considered.

Page 5: eq. 10 and 12: you mention that only 50%of the mortality of phytoplankton and bacteria goes to the DOC compartment. What about the other 50 %?

It seems that finally, the uptake of nitrogen/phosphate is not influenced by the availability of phosphate/nitrogen, there is no minimum in eq. 17 between the different elements. It means that nitrogen and phosphate are taken independently by phytoplankton and bacteria. Please clarify.

Model description

I found the description of the model equations very difficult to understand and I suggest improving it. A suggestion would be to add a table defining ALL the variables used in eqs 1-14. This is absolutely necessary to allow understanding the equations. Like it is now, this is not understandable; we have to search through all the paper and tables in order to find some information about the meaning and units of the variables.

Eqs. 1 and 6 are strange, what is f_{β}^{μ} and f_{ϕ}^{μ}? They appear as production and destruction terms, in the equation for cellular abundance as well as in the equation for biomass they are mortality terms (very unclear) (I understand after and I suggest removing these two equations since we are told that the cellular abundance of bacteria and phytoplankton is maintained contant throughout the experiment. They are thus not state variables of the model). In eq. 10 and 12, I would use parameters to represent the percentage of grazing that is going to LDOC and SRDOC (instead of directly values).

Sometimes phosphate is denoted by PO_4 and sometimes it is P (compare eq. 5, 9 with eq. 14).

Eq. 15 describes the computation of f^{μ} as a growth term. If I understand well, this term is just use to compute the mortality since the cell abundance is maintained constant! So eq 15 represent the mortality of bacteria and phytoplankton!! Very unusual representation. Please clarify.

Line 6, we are told that: "Since we assumed that for every element *Q*max is 2.5 times greater than *Q*min, the maximum achievable growth rate $\hat{\mu}$ is equal to 0.6 $\bar{\mu}$. The value of 2.5 was chosen in order to stay within a reasonable range compared to literature data". Please give references and more justifications for this choice? Is it sensitive parameters?

Units:

It would be helpful to use the same convention for units. Sometimes, the authors used fmol or µmol or nM. It is messy and need uniformisation. Some units are inconsistent and this makes me worried. Some examples among others: in table 2 the max. growth rate is expressed per day while the maximum uptake rate of nutrients listed in table 3 are expressed per hour, the diffusion rate is per second. The same in eq.19, the units of all the terms are different: diffusion rate is in m2/sec while the cell radius is in µm, p is in mol/cell and finally α is in lnmol/hour! Page 8, line 10, we are told that "This maximum potential uptake rate is associated with a maximum theoretical affinity α which represents the volume of water cleared for nutrients per unit of biomass per hour." Looking at the units of α in Table 3, it appears that this quantity is not per unit of biomass.

I also have a very serious concern about the units used of f^{upt}. Indeed, according to eq. 16, this term is expressed in the same units as V_X^{max} (since f^{Qx} is adimensional) and thus it is expressed in fmol/cell/hour (according to Table3). Also, it means that in eqs. 3, 4, 7 , 8 ,9, the units of the first term in the right hand side are fmol/cell/hour*mol/m3, you understand that this is totally inconsistent. The dimension of this term should be a biomass/time.

Page 11, eq. 25: Once again, I think that there is a problem of Units in this formulation. Indeed, fresp has to be a rate (since it is multiplied by ϕ in eq. 2) however, it has the units of Qc*w4 it means fmolC/cell/s. Same remark for eq. 26. By the way what about the activity respiration of phytoplankton? What is Q_{vC} in eq. 26? Besides, if the activity respiration of bacteria is a fraction of the DOC uptake, I think that $f_{\square}^{Qc}$ is missing in eq. 26

Others:
Page 6, line 4-6: we are told that the model is described by 4 biogeochemical processes: growth, nutrient uptake primary production, respiration. The authors forgot mortality.
What is the difference between "growth" and "primary production"?
Besides, we are told that "bacterial and phytoplanktonic biomass are described in term of cellular abundance and …" Cellular abundances are not state variables of the model (see below, they are maintained constant).
I would say chlorophyll concentration rather than biomass.

Equation 15, page 6, fμ is computed as a minimum but I do not understand what are exactly the factors entering this minimum law?
Please clarify this sentence: "It should be noted that using explicit maximum intracelullar quota implies that $\bar{\mu}$ is never achieved". What do you mean by using **explicit maximum** intr-cellular ratio? I would say "imposing"

Page 7, The value of 2.5 was chosen in order to stay within a reasonable range compared to literature data. Please give a reference.

Page 8, line 16, σ is the internal nutrient concentration (phosphate/nitrogen) what is the link between σ and Q?

Table 2 is a mess: 1) Qx is not a parameter but a variable (if I am right), 2) the authors use once again different types of units (fmol and mol) 3) I would suggest to put the values of the parameters in both columns (for μ and Qmax).
Same remark for Table 3: 1)what are the units of alpha P and alphaN? 2)What is the number between the second and third columns? 3) Different units 4) why do not you have molecular diffusion rates for bacteria?
I do not agree to use the same value for the uptake of SLDOC and SRDOC, this is not justifiable.
Page 8, eq 16: f^{upt}_X appears in eqs. 3 and 4, and thus have to be expressed in molP or N/m3. However, it is not clear what are the units of V_x^{max} because looking at eq. 21, it seems that V_x^{max} is expressed /cell.

Page 9, lines 8-10, In Eq. 22, the assumption is that under extremely low nutrient concentrations, the slope of the Michaelis Menten relationship is equal to the diffusion rate of the molecules. Please give a reference.

Page 9, line 15, the sentence has not to end there but has to continue.

Page 9, lines 14-15: "… on the fact that we wanted bacteria to be more competitive than phytoplankton in terms of nutrient acquisition". Please justify why you made this assumption. How the results are sensitive to it. What does it mean, which parameters are concerned?

Page8, if I am right p is in fact Q, so why do you use different symbols? It increases the confusion. Besides, this section is also very confusing. You start to describe f^{upt} and then a long paragraph about the computation of α, we are wondering why until the next page. I would suggest to put eq. 21 and 22 after 17 in order to allow the reader to follow your

reasoning. Eq. 20, put “max” as indices for clarity. I do not understand how you derive α_{max} from eq. 19.
Page 9, line 3, we are told that “In Eq. 20, V_X is the maximum uptake rate obtain at the population level (molm−3 s−1) and [cell], the cellular abundance (cellm−3).” However, once again, in Table 3, the units defined for V (fmol/cell/hour) are totally different. Besides if in eq. 20 V is the max uptake you should write it for clarity. Please clarify how you obtain eq. 21, and give a reference for eq. 22 and explain where is V_X used.

Table 3, it is strange that you have the same half saturation constant for phosphate and nitrogen, usually this is very different by ~one order of magnitude. The same with the uptake rate. This illustrates the lot of very critical hypotheses that are made and are never validated. The authors say ” In addition, since we did not see any reason for assuming differences in the maximum gross uptake of both nutrients, the model assumes that the uptake parameters are identical for both P and N,”. The reason is experimental evidence.

Page 9, lines 20-22: “For DOC uptake, we set *V* max 20 *X* and *KX* values **arbitrarily** to obtain maximum affinity constants one and two orders of magnitude lower than for inorganic nutrients for LDOC and SLDOC & SRDOC respectively.” There are values in the literature for these parameters; you can not fix them arbitrarily!

What is the meaning of “X”? Sometimes it is used to represent ϕ or β (eq. 16) and sometimes it is used to represent N,C or P.(eg. Eq. 17). Again very confusing

Page 10, line 4-5, What do you mean by “The most reliable DOC source for bacterial growth being LDOC..”? It is not reliable but directly usable.

Page 10, line 7-10, we are told that : “The photosynthesis model is based on the idea that the quantum yield of carbon fixation is proportional to the probability of photosystem II being open and was originally presented by Han (2002)”. This sentence is for me not understandable, please extend the description.

Eqs. 23 and 24, Why do we have a superscript “i” for Q?

Do you have arguments to use the physiological model proposed by Han 2002) instead of classic model of photosynthesis? Did you compare the different approaches? What about the parameters? In the Han (2002) paper, parameters values are not given and he concluded that “ It must be argued that in natural conditions, variations in the model parameters can be found. The variations characterize phytoplankton adaptation to different light regimes » So do you test the sensitivity to the values of parameters used? and validate the approach?

Page 12, eq. 27 I think that t is not the time in seconds but in day.

Page 12, line 7, the authors say: “Since we set the mortality rate equal to the cellular growth rate at all time, cellular abundance is always constant and was fixed to 5 10^8 cell l−1 and 2.5 107 cell l−1 for bacteria and phytoplankton respectively” So I suggest that you remove eq. 1 and 6 from the list of eq. as well as the state variables ϕ and β because they are maintained constant throughout the simulations! They are not computed dynamically. Besides, why do you choose these two values?
We are told that : “This choice was made in order to obtain similar carbon biomass for both functionnal groups” Why do you want to have similar carbon biomass?

Page 13, lines 16-17, we are told that "This particular feature for heterotrophic bacterial growth is the result of a higher affinity for phosphate associated with high DOC availability". I do not agree with this justification because this process is not taken into account in the model equations.

Page 12, line 20, what do you mean by arbitrarily distributed? You mean between TP and TN?

Page 12, line 22, I do not think that the aim of the model is to estimate the fluxes between variables in order to maintain both bacteria and phytoplankton. Rather, the model estimates the concentrations and fluxes under scenarios of concentrations in DIP And DIN.

Page 13, line 6, I would say " represents N-limited as well as P-limited environment". Could you please give justification for the values chosen for TN, TP, inorganic N and inorganic P. Does it refer to real environmental conditions changes? Besides, what do you mean by "Within the range of TN and TP used in this study, inorganic nutrient concentrations range from 0 to 15nM and from 0 to 370nM for phosphate and nitrogen respectively » are there model results or the partitioning of the initial conditions? What are the initial conditions of the different variables? From fig 2b, we have the impression that the values given are model results rather than initial conditions. Please clarify.

Page 13, line 10-11: give the exact meaning of phytoplankton and bacterial growth rate? To which variables of the equations does it refer? The growth rate is expressed in div/day, once again, use the same units as in the Table.

Figure 2: I do not understand this figure and its aim. The isolines in fig 2a illustrate different ratios for TN/TP. First, we do not need a figure for that, second I do not understand why the isolines are not straight lines! We are told that the diamonds markers are model results, since it seems from the equations (from eq. 3, 8 and 13 and from eqs. 4,9 and 14, it appears that nitrogen and phosphorus is just transferred from the inorganic box to bacteria and phytoplankton and then it returns to inorganic form through mortality) that the model is conservative, meaning that TN and TP has to remain constant in the system, TN and TP are just the initial conditions! Fig2b: does it mean that for instance, inorganic nitrogen remains constant at steady state when TN is fixed whatever is TP is the system? It means that the initial content of phosphate has no impact on the nitrogen dynamics? And conversely, the TN cntent in the system has no impact on the dynamics of inorganic phosphate?

Fig.3: What are the white curves on the two plots (visible in the dark part of the figure? IS it isolines of growth rates? If yes, I do not understand how isolines can cross each other.

Minor

Abstract, line 2, please clarify what do you mean by "the interaction between C,N and P at the cell level"

Line 5 "impact the overall stock and dynamics of organic carbon"" I would add .. and inorganic nutrients

line 4, "interactions" instead of "interaction"

line 8 "intends" instead of "intend".

line 10, "gives us" instead of "give us".

Page 3, line 21, correct "scale"

Page 4, line 9, please clarify what do you mean by “implicit in our model”
Page 4, line 12, please clarify what are the three detritus compartments.
Page 4, eq. 1, page 6 eq. 12: please use different symbols for the mortality and growth f^{μ}.
Page 5, eq. 12, parenthesis error: Bc should go inside the parenthesis.

Page 6, line 5, remove an “and”.
Page 6, Line 15: “Qmin can be interpreted as the amount of element used in cellular structure and machinery and everything else can be seen as storage for future growth”. I would say something like” … and the nutrients consumed in excess to this minimal threshold are stored …”.
Page 6, eq. 15: you mean f^{QN} instead of f^{μ} ll
Table 1: correct the units of “phytoplankton phosphate biomass”.
Page 8, line 17: as follows and not as follow, last line the and not The
Page 9, lines 12 and 16, it is table 3 and not table2.