Author Comment on behalf of all Co-Authors

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December 18, 2010

General

First of all, we would like to thank the referee for is thorough investigation on the methodology used in this paper. His comments helped us improve the content of the present study. For many aspects we agree with the reviewer that the description of the model as well as the choice of the parameters values could be clarified. We took the referee comments into consideration and modified the model description in our paper (modifications are reported throughout our response). We admit that too many errors have escaped our attention. These errors have make the referee's work much harder and we deeply apologize for that matter. As a result, we will respond in two parts, first we will provide the new set of equations corrected for the inconsistencies pointed out by the authors (we will refer to this set of equation in the second part of our response). Then we will respond in detail to each comment made by the referee.

Corrected Equations

The author pointed out inconsistencies between the state equations and the equation for uptake (Eq. 16) and respiration (Eq. 25 and Eq. 26). We modify the equations to correct these inconsistencies and provide below the new equations (we kept the numbering unchanged for comparison). We would like to point out that these inconsistencies in the manuscript where not present in numerical model, therefore the results presented in the paper are not affected. Simulation were re-checked for conservativity and dimensions and no error could be found.

State equations

Phytoplankton

$$\frac{d\varphi}{dt} = f_{\varphi}^{\mu} \,.\, \varphi \,-\, f_{\varphi}^{m} \,.\, \varphi \tag{1}$$

$$\frac{d\varphi_C}{dt} = f_{nr}^{PP} \,.\, h_{\varphi}^{Q_C} \,.\, \varphi \,-\, f_{\varphi}^{resp} \,.\, \varphi \,-\, f_{\varphi}^{m} \,.\, Q_C^{\varphi} \,.\, \varphi \tag{2}$$

$$\frac{d\varphi_N}{dt} = f_{\varphi}^{upt_N} \,.\, h_{\varphi}^{Q_N} \,.\, \varphi \,-\, f_{\varphi}^{m} \,.\, Q_N^{\varphi} \,.\, \varphi \tag{3}$$

$$\frac{d\varphi_P}{dt} = f_{\varphi}^{upt_P} \,.\, h_{\varphi}^{Q_P} \,.\, \varphi \,-\, f_{\varphi}^{m} \,.\, Q_P^{\varphi} \,.\, \varphi \tag{4}$$

$$\frac{d\varphi_{Chl}}{dt} = f^{PChl} \,.\, \varphi_N \,-\, f_{\varphi}^{\mu} \,.\, Q_{Chl}^{\varphi} \,.\, \varphi \tag{5}$$

Bacteria

$$\frac{d\beta}{dt} = f_{\beta}^{\mu} \,.\, \beta \,-\, f_{\beta}^{m} \,.\, \beta \tag{6}$$

$$\frac{d\beta_C}{dt} = (f_{\beta}^{upt_{LDOC}} \,+\, f_{\beta}^{upt_{SLDOC}} \,+\, f_{\beta}^{upt_{SRDOC}}) \,.\, h_{\beta}^{Q_C} \,.\, \beta \,-\, f_{\beta}^{resp} \,.\, \beta \,-\, f_{\beta}^{m} \,.\, Q_C^{\varphi} \tag{7}$$

$$\frac{d\beta_N}{dt} = f_{\beta}^{upt_N} \,.\, h_{\beta}^{Q_N} \,.\, \beta \,-\, f_{\beta}^{m} \,.\, Q_N^{\beta} \,.\, \beta \tag{8}$$

$$\frac{d\beta_P}{dt} = f_{\beta}^{upt_P} \,.\, h_{\beta}^{Q_P} \,.\, \beta \,-\, f_{\beta}^{m} \,.\, Q_P^{\beta} \,.\, \beta_P \tag{9}$$

Dissolved organic carbon

$$\frac{dLDOC}{dt} = \omega_5 \,.\, (f_{\varphi}^{m} \,.\, Q_C^{\varphi} \,.\, \varphi \,+\, f_{\beta}^{m} \,.\, Q_C^{\beta} \,.\, \beta_C) \,-\, f_{\beta}^{upt_{LDOC}} \,.\, h_{\beta}^{Q_C} \,.\, \beta \tag{10}$$

$$\frac{dSLDOC}{dt} = f_{nr}^{PP} \,.\, (1 \,-\, h_{\varphi}^{Q_C}) \,.\, \varphi \,-\, f_{\beta}^{upt_{SLDOC}} \,.\, h_{\beta}^{Q_C} \,.\, \beta \tag{11}$$

$$\frac{dSRDOC}{dt} = \omega_6 \,.\, (f_{\varphi}^{m} \,.\, Q_C^{\varphi} \,.\, \varphi \,+\, f_{\beta}^{m} \,.\, Q_C^{\beta} \,.\, \beta_C) \,-\, f_{\beta}^{upt_{SRDOC}} \,.\, h_{\beta}^{Q_C} \,.\, \beta \tag{12}$$

Nutrients

$$\frac{dN}{dt} = f_{\varphi}^{m} \,.\, Q_N^{\varphi} \,.\, \varphi \,+\, f_{\beta}^{m} \,.\, Q_N^{\beta} \,.\, \beta \,-\, f_{\beta}^{upt_N} \,.\, h_{\beta}^{Q_N} \,.\, \beta \,-\, f_{\varphi}^{upt_N} \,.\, h_{\varphi}^{Q_N} \,.\, \varphi \tag{13}$$

$$\frac{dP}{dt} = f_{\varphi}^{m} \,.\, Q_P^{\varphi} \,.\, \varphi \,+\, f_{\beta}^{\mu} \,.\, Q_P^{\beta} \,.\, \beta \,-\, f_{\beta}^{upt_P} \,.\, h_{\beta}^{Q_P} \,.\, \beta \,-\, f_{\varphi}^{upt_P} \,.\, h_{\varphi}^{Q_P} \,.\, \varphi \tag{14}$$

Intracellular quota and growth

$$f^{\mu} = \bar{\mu} \,.\, min\,[(1 \,-\, \frac{Q_C^{min}}{Q_C}); ((1 \,-\, \frac{Q_N^{min}}{Q_N}); (1 \,-\, \frac{Q_P^{min}}{Q_P})] \tag{15}$$

Uptake of carbon and nutrients

$$f^{upt_X} = V_X^{max} \,.\, \frac{[X]}{[X] \,+\, K_X} \tag{16}$$

$$h^{Q_X} = \frac{Q_X^{max} \,-\, Q_X}{Q_X^{max} \,-\, Q_X^{min}} \tag{17}$$

$$\alpha_{max} = \frac{3D}{\sigma r^2} \tag{18}$$

$$\alpha_{max} = \frac{4\,.\,\pi\,.\,D\,.\,r}{Q_X^{min}} \tag{19}$$

$$\alpha_{max} = \frac{V_X^{max}}{K_X\,.\,Q_X^{min}} \tag{20}$$

this equation no longer exist in the reviewed version of the manuscript (21)

$$\frac{V_X^{max}}{K_X} = 4\,.\,\pi\,.\,D\,.\,r \tag{22}$$

Photosynthesis and chlorophyll production

$$f_{nr}^{PP} = \frac{\phi_{max}^{C}\,.\,\bar{a}^{*}\,.\,E\,.\,Q_{Chl/C}^{\varphi}}{1+\sigma_{PSII}\,.\,E\,.\,\tau+(k_d^H/k_r)\,.\,(\sigma_{PSII}\,.\,E)^2\,.\,\tau} \tag{23}$$

$$f^{PChl} = \frac{\bar{\mu}_{\varphi}\cdot(Q_{Chl/N}^{\varphi})_{max}\cdot f_{nr}^{PP}}{\bar{a}^{*}\,.\,\phi_{max}^{C}\cdot Q_{Chl/C}^{\varphi}\,.\,E}\cdot\frac{1-Q_{Chl/N}^{\varphi}/(Q_{Chl/N}^{\varphi})_{max}}{(1-Q_{Chl/N}^{\varphi}/(Q_{Chl/N}^{\varphi})_{max})+0.05} \tag{24}$$

Respiration rate

$$f_{\phi}^{resp} = (Q_C - Q_C^{min})\,.\,\omega_4 \tag{25}$$

$$f_{\beta}^{resp} = (1-\omega_1)\,.\,f_{\beta}^{upt_{LDOC}} + (1-\omega_2)\,.\,f_{\beta}^{upt_{SLDOC}} + (1-\omega_3)\,.\,f_{\beta}^{upt_{SRDOC}} \tag{26}$$

Detailed response on the referee comments

Response to the comments on the model structure

Before answering to the referee's concerns on our description of DOC in the model, we propose to add in the manuscript, the following figure (Fig. 1) to clarify what LDOC, SLDOC and SRDOC represent. In our model, SRDOC and SLDOC are assumed to have similar sizes above the critical size for direct assimilation (an hydrolysis step is thus required). Since we associated different assimilation efficiencies with each two pool, SLDOC and SRDOC differ in terms of lability. LDOC was associated with the highest assimilation efficiency (0.7) and a size below the critical size for direct cell uptake (no hydrolysis required prior to assimilation and thus higher V^{max} and Ks compared to SLDOC and SRDOC).

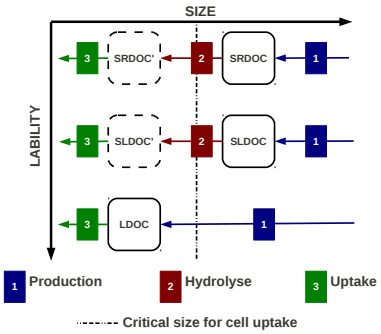

Figure 1: Diagram representing dissolved organic matter in the model. Each pool is discriminated based on size and lability assumptions. Two pools (SLDOC and SRDOC) are considered similar in size and above the critical size of particle that can pass through bacterial cell wall (thus they need an hydrolyzis step before being assimilated). LDOC on the other hand is considered to be directly assimilable. In terms of lability, each DOC pool is associated with an assimilation efficiency of 0.7, 0.5 and 0.3 for LDOC, SLDOC and SRDOC respectively.

Referee's comment: **"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."**

Since SRDOC and SLDOC are larger in size than LDOC, we agree that these compounds need to be hydrolyzed before being assimilated by bacteria. However, we assumed that the products of the hydrolysis of SLDOC and SRDOC (denoted SLDOC' and SRDOC' in Fig 1) are not LDOC but molecules of lower benefit for heterotrophic bacteria. In other words, the net budget between the carbon assimilated and the carbon respired is different for each DOC compartment. The net budget correspond to the parameters ω_1, ω_2 and ω_3. For example, for SRDOC only 30% of the gross SRDOC uptake can be stored within the cell, assuming that the remaining 70% is lost through respiration. Based on the parameters chosen for SRDOC, SLDOC and LDOC, bacterial growth efficiency (BGE) cannot exceed 0.7 and could in theory reach zero when growth rate is null. The fact that BGE will vary with substrate supply and inorganic nutrient availability without exceeding 0.7 concur with in-situ observation ([9]).

Referee's comment: **"I do not understand why SRDOC can be assimilated by bacteria."**

SRDOC can be assimilated by bacteria after an hydrolysis step. The products of the hydrolysis are small molecules that can pass through the cell wall, but with a different energetic content than LDOC.

Referee's comment: **"It is well known (Anderson and Pondaven, 2003) that a part of PER is labile DOC."**

The model proposed by Anderson et Pondhaven ([1]) is a C/N model applied to the Sargasso Sea and was derived from an earlier model applied to the English Channel ([2]). In their studies, the DOM compartments are divided between a labile (turnover time of days) and semi-labile (turnover time of month) compartments. One of the source for labile and semilabile carbon is phytoplankton exudation which is assumed in their model ([1]) as a fix fraction of photosynthesis. This choice was made despite the fact that in most studies, phytoplankton photosynthetic extracellular release (PER) is consider highly variable and is linked to the growth conditions of the phytoplankton ([25]). In addition, their PER flux was then divided into labile and semi-labile DOC using fix parameter values. We found no justification concerning the values for these parameters. In their original publication ([2]), two approaches concerning phytoplankton excretion were tested: directly proportional to photosynthesis or proportional to the difference between nutrient limited and nutrient saturated growth (which is similar to our approach). Parameters for both approaches were adjusted to fit particular DOC dynamics in the English Channel. The authors argue that they cannot conclusively assert that either of the two equations for production of "extra" carbon is better than the other. But acknowledge the fact that:" Ideally, the simulation of phytoplankton excretion as a photosynthetic overflow process could take account of diel variations in light intensity, and the associated balance between internal pools of fixed carbon and nutrients within algal cells.".

It thus appears to us that the second approach is more relevant in our case. We tried to simplify our approach by having a DOC compartment dedicated for DOC excretion by phytoplankton (SLDOC). Since PER is mainly composed of long carbohydrate chains, in our model, we assumed that it was the only type of DOC exuded by phytoplankton.

Referee's comment: 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".

The statement that the main source of N and P for bacterial growth is first DOM and not inorganic nutrients is not entirely true and has been challenged by several authors over the past decades. For DOP, several papers show that in low P environment, dissolved organic phosphorous is hydrolyzed resulting in the release of inorganic P which in turn induce algal-bacterial competition ([30], [6], [23], [7]). For nitrogen a similar pathway can be considered in low N environment. Most of the nitrogen requirements of heterotrophic bacteria is met through the uptake of dissolved free amino acids and NH4 ([22]), two forms of nitrogen that are also assimilated by phytoplankton ([22], [8]). As a result, it did not appear necessary to us to explicitly represent the labile fraction of DOP and DON in our model, the labile part being instantaneously remineralized into the inorganic form resulting in algal-bacterial competition for both N and P.

Referee's comment: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 %?".

The remaining 50% are either transfered higher in the food chain or respired by predators. In all cases, it is lost for our system ([16]).

Referee's comment:"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."

It should be noted that while the gross uptake rate of nutrients only depends on external concentrations, the net uptake rate is mediated by a quota function. The minimum the referee is expecting in Eq. 17 is in fact in Eq. 15. The general idea in the model is that the net uptake rate depends on nutrient external concentration ($[P]$), intracellular quota (Q_P) and cell abundance ($[Cell]$).

$$f_P^{upt} = V^{max} \cdot \left(\frac{Q_P^{max} - Q_P}{Q_P^{max} - Q_P^{min}}\right) \cdot \frac{[P]}{[P] + K_P} \cdot [Cell] \tag{27}$$

In the previous equation, the intracellular quota (Q_P) can be influenced by the availability of N since:

$$\frac{dQ_P}{dt} = V^{max} \cdot \left(\frac{Q_P^{max} - Q_P}{Q_P^{max} - Q_P^{min}}\right) \cdot \frac{[P]}{[P] + K_P} \; - \; f^{\mu} \cdot Q_P \tag{28}$$

with:

$$f^{\mu} = \bar{\mu} \cdot min\left[\left(1 - \frac{Q_C^{min}}{Q_C}\right); \left(\left(1 - \frac{Q_N^{min}}{Q_N}\right); \left(1 - \frac{Q_P^{min}}{Q_P}\right)\right)\right] \tag{29}$$

Thus uptake of nitrogen/phosphate is influenced by the availability of phosphate/nitrogen through the growth function (f^{μ}). In general, when a given element limits growth, the non limiting elements tend to accumulate in the cell and their net uptake decrease as a result of the quota function (h^Q).

Response to the comment on Model Description

Referee's comment:"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."

In the reviewed version of the manuscript we have change the model description and added a table defining all the variables and parameters.

Referee's comment:"Eq. 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 constant throughout the experiment. They are thus not state variables of the model)."

In order to clarify the model description, we differentiated the growth function from the mortality function (cf Eq. 1 and Eq. 6). We kept cell abundance as a state variable in the model and mentioned that in this study we only considered the steady state solution for the particular case where mortality rate is equal to growth rate at all time.

Referee's comment:"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)."

This has been modified in the revised version of the manuscript, the percentage of grazing going to LDOC and SRDOC are now denoted ω_5 and ω_6

Referee's comment:"Sometimes phosphate is denoted by PO4 and sometimes it is P (compare eq. 5, 9 with eq. 14)."

This has been modified in the revised version of the manuscript only PO4 was used.

Referee's comment:"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."

Please refer to the previous response concerning eq. 1 and 6 (page 6) and the corrected equations (page 1 and 2).

Referee's comment:"Line 6, we are told that: "Since we assumed that for every element Qmax is 2.5 times greater than Qmin, the maximum achievable growth rate μ is equal to 0.6 μ_{max}. 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?"

For phytoplankton, Table 1 compares the range of conversion factors in $fg.\mu m^{-3}$ found in the literature with the values chosen for our model (assuming fixed diameter of 1 μm). Table 3 compares our intracellular quota values to studies that directly provided intracellular contents in $fg.cell^{-1}$ for synechococcus species. For heterotrophic bacteria, the equivalent is found respectively in Table 2 and Table 4 assuming a cell diameter of 0.36 μm. Considering all the information together we considered that we were within a reasonable range compared to literature data.
Concerning the factor 2.5 between Q^{min} and Q^{max}, if we assume that an individual cell needs at least to double its biomass before being able to divide into two cells, then $Q^{max} = 2 \,.\, Q^{min}$ appears as a minimum value for Q^{max}. The value 2.5 which has been used in the present study is a compromise between (i) the fact that an element can be stored in excess of what is required for one cell division, (ii) the fact that our values should be within the range of reported values in the literature.

Table 1: Comparison between the range of conversion factors found in the literature for small phytoplankton ($\oslash : 0-5\mu m$) and our values for the model, all data are provided in $fg.\mu m^{-3}$. These data are derived from a literature review of C,N,P conversion factors for osmotrophs which is currently in preparation (Mauriac et al. in prep.)

Groups	Range
C .vs. V	
Phyto (literature)	123 - 429
Phyto (model)	157 - 392
N .vs. V	
Phyto (literature)	15 - 75.5
Phyto (model)	27.7 - 69.3
P .vs. V	
Phyto (literature)	1.63 - 5.16
Phyto (model)	3.8 - 9.5

Table 2: Comparison between the range of conversion factors found in the literature for heterotrophic bacteria and our values for the model, all data are provided in $fg.\mu m^{-3}$. These data are derived from a literature review of C,N,P conversion factors for osmotrophs which is currently in preparation (Mauriac et al. in prep.)

Groups	Range
C .vs. V	
Bacteria (literature)	32 - 964
Bacteria (model)	85.6 - 214
N .vs. V	
Bacteria (literature)	3.0 - 200.4
Bacteria (model)	20 - 50
P .vs. V	
Bacteria (literature)	0.23 - 242.7
Bacteria (model)	4.4 - 11.1

Table 3: Values for intracellular quota ($fg.cell^{-1}$) in the literature for Synechococcus sp.

Species	Q	reference
C .vs. cell		
Synechococcus WH8012	92.4 - 132	[5]
Synechococcus WH8103	213 - 244	[5]
Synechococcus WH7803	120 - 200	[18]
Synechococcus WH8103	150 - 250	[18]
Phytoplankton (Model)	82 - 205	**This study**
N .vs. cell		
Synechococcus WH8012	20.0 - 20.6	[5]
Synechococcus WH8103	50.2 - 39.8	[5]
Synechococcus WH7803	17 - 26	[18]
Synechococcus WH8103	18 - 36	[18]
Phytoplankton (Model)	14.5 - 36.3	**This study**
P .vs. cell		
Synechococcus WH8012	1.84 - 0.47	[5]
Synechococcus WH8103	3.34 - 0.81	[5]
Synechococcus WH7803	3.1 - 7.9	[18]
Synechococcus WH8103	2.2 - 3.6	[18]
Synechococcus NIBB 1071	0.65 - 2.1	[19]
Phytoplankton (Model)	2.0 - 5.0	**This study**

Table 4: Values for intracellular quota ($fg.cell^{-1}$) in the literature for heterotrophic bacteria

Species	Q	reference
C .vs. cell		
Heterotrophic Bacteria	7 - 31	[12]
Heterotrophic Bacteria	5.9 - 23.5	[14]
Heterotrophic Bacteria (Model)	9.68 - 24.2	**This study**
N .vs. cell		
Heterotrophic Bacteria	2.2 - 5.0	[12]
Heterotrophic Bacteria	1.2 - 3.9	[14]
Heterotrophic Bacteria (Model)	2.26 - 5.65	**This study**
P .vs. cell		
Heterotrophic Bacteria	0.46 - 1.04	[12]
Heterotrophic Bacteria (Model)	0.5 - 1.25	**This study**

Response on the comments for Units

Concerning the dimensions and units of the model, we would like to precise that although parameters appear in different units in the presentation of the model, the numerical simulation were all performed using standardized units system of mole, meters and second and all dimensions were re-checked and no error could be found. In the paper, our first intention was to present parameter values in the unit most commonly found in the literature. This was intended to help the reader but we acknowledge that it was not the most suitable choice. In the new version of the manuscript we propose to use the same standardized units system than the one we used in our numerical simulations.

Response on the comments for Others

Referee's comment: 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.

Mortality has been added because it was indeed lacking in this sentence.

Referee's comment: What is the difference between "growth" and "primary production"?

Growth refers to cell production while primary production refers to organic carbon production by phytoplankton, in our model net primary production correspond to the growth rate multiplied by the carbon biomass ($f^{\mu}_{\varphi} \,.\, Q^{\varphi}_{C} \,.\, \varphi$) while gross primary production under nutrient repleted conditions corresponds to the term (f^{PP}_{nr}).

Referee's comment: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).

The fact that bacterial and phytoplankton abundances are maintained constant is a particular case of our general dynamical model. In the present study, and for the sake of simplicity, we focus on this particular case to highlight bottom up effect on DOC dynamics. However, the model can also be used with variable abundances. That's why we preferred to maintain the cell abundances as state variables. However, we have clarified and generalized the conservation equations for cells by introducing different names for the growth (f^{μ}) and the mortality rates (f^{m}).

Referee's comment:I would say chlorophyll concentration rather than biomass.

This has been modified in the new version of the manuscript.

Referee's comment:Equation 15, page 6, f is computed as a minimum but I do not understand what are exactly the factors entering this minimum law?

In order to clarify what parameters are involved in the growth function, in the reviewed version, Eq. 15 has been rewritten as follow:

$$f^{\mu} = \mu_{max} \,.\, min[(1 - \frac{Q_P^{min}}{Q_P}); (1 - \frac{Q_N^{min}}{Q_N}); (1 - \frac{Q_C^{min}}{Q_C})] \tag{30}$$

Referee's comment:Please clarify this sentence: "It should be noted that using explicit maximum intracelullar quota implies that μ_{max} is never achieved". What do you mean by using explicit maximum intra-cellular ratio? I would say "imposing"

The sentence has been clarified as follows: "It should be noted that imposing an explicit maximum intracellular quota with the Droop formulation implies that μ_{max} is never achieved"

Referee's comment: 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.

Please refer to the previous answer concerning Q^{min} and Q^{max} values found in the literature (page 7 -9).

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

This part of the model description has been modified to include a description of the relationship that links Q and σ: "σ is the internal nutrient concentration ($mol.m^{-3}$) or the so called conversion factor. Q is the intracelullar elemental content ($mol.cell^{-1}$). To convert σ into Q and reciprocally, one would need to know the cell volume of the organism. During cell growth, both the cell volume and Q can vary more or less independently from each other. We assume in our model that the volume is constant and that only Q can vary.

Referee's comment: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 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?

As suggested by the referee, all tables except Table 1 have been merged into a new table where all the parameters values are now given in mole, meter, s. An additional table containing all the terms used in Eq. 1 to Eq. 14 is also added.

Referee's comment:I do not agree to use the same value for the uptake of SLDOC and SRDOC, this is not justifiable.

These two compartments (SLDOC and SRDOC) represent two types of DOC molecules, similar in size but with different assimilation cost and origins. Following this idea, we further assumed that SLDOC, which is entirely composed of carbohydrate chains produced by phytoplankton, was less costly to transform into bacterial biomass than most of the DOC associated with mortality processes (SRDOC). Given our size assumption concerning SLDOC and SRDOC we assume that they were hydrolyzed and assimilated at the same rate (V^{max} and K_s are equal). However, their transformation into bacterial biomass would occur at different rates since they have a different respiration costs associated with their uptake (ω_2 and ω_3). In a C-limited system, and at a given DOC concentration, heterotrophic bacteria would then grow 1.6 times faster when growing on SLDOC compared to SRDOC.

Referee's comment: Page 8, eq 16: f_X^{upt} 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 Vxmax because looking at eq. 21, it seems that Vxmax is expressed /cell.

Please refer to the corrected equations section (page 1-2).

Referee's comment: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. Uptake of nutrient is a process that can be described as a Michaelis Menten relationship:

$$V = V^{max} \cdot \frac{[X]}{Ks + [X]} \tag{31}$$

At very low concentrations ($[X] << Ks$), the term $Ks + [X]$ can be approximated by Ks and the resulting flux is:

$$V = \frac{V^{max}}{Ks} \cdot [X] \tag{32}$$

For a spherical cell, when nutrient concentration is very low, the limiting step for the uptake of a given molecule is diffusion and the corresponding flux (mol.s-1) is given by (i.e. [21]):

$$V = 4 \cdot \pi \cdot D \cdot r \cdot [X] \tag{33}$$

In Eq. 33, D represents diffusion coefficient and r cell radius. Since Eq. 32 and Eq. 33 both described the same process (i.e uptake at very low nutrient concentration), we assume that:

$$4 \cdot \pi \cdot D \cdot r = \frac{V^{max}}{Ks} \tag{34}$$

we have re-written the sentence: "the slope of the Michaelis Menten relationship is equal to the diffusion rate of the molecules (Thingstad et Rassoulzadegan (1999) [29])".

Referee's comment: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?

Several studies have looked at the competition between phytoplankton and heterotrophic bacteria both for phosphorous and nitrogen, most of these studies show that heterotrophic bacteria are better competitors than phytoplankton (including picophytoplankton) for the acquisition of N and P at low concentrations ([22], [20], [15], [10]). From a bottom up point of view, the competitive ability of an osmotrophic organism can be seen as the result between its uptake ability (how fast an organism can take up an element) and its requirements for growth (how much of this element is needed to produce a new cell). The competition is often expressed in terms of maximum affinity. Maximum affinity is calculated by considering the ratio between the maximum specific uptake rate and the minimum requirement for growth (cf .Eq. 19). Saying that bacteria are more competitive than phytoplankton is the same than saying that $\alpha^{\beta}_{max} > \alpha^{\varphi}_{max}$. In our model the competitive ability is defined using Eq. 19 to Eq. 22. α_{max} was inferred from our choice of size (r), growth requirements (Q^{min}) and diffusion coefficient. V^{max} was chosen based on literature values for uptake of [PO4] ([13], [19]) and Ks was derived from Eq. 22.

Referee's comment:Page8, if I am right p is in fact Q, so why do you use different symbols? It increases the confusion.

We agree and only use Q in the reviewed version of the manuscript.

Referee's comment: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 ($mol.m^{-3}.s^{-1}$) and $[cell]$, the cellular abundance ($cell.m^{-3}$)." However, once again, in Table 3, the units defined for V ($fmol.cell^{-1}.h^{-1}$) 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 VX used.

Please refer to the equations (page 1 and 2) and our answer concerning Eq. 22 (page 12). Eq. 22 is put after Eq. 17 in the revised version of the manuscript.

Referee's comment: 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.

Since we made the assumption that the diffusion coefficient for NH4 and PO4 are the same this implies that:

$$\frac{V_N^{max}}{Ks_N} = \frac{V_P^{max}}{Ks_P} \tag{35}$$

We have found in several studies that Ks values for [PO4] and [NH4] are not so different (Table 5)

Table 5: Half saturation constants for NH4 and PO4 found in the litterature for small phytoplankton

Ks_{NH4}	Ks_{PO4}	Reference
$mol.m^{-3}$	$mol.m^{-3}$	
$8\ .\ 10^{-5}$	$5.1\ .\ 10^{-5}$	[24]
$1.8 - 2.4\ .\ 10^{-4}$	$3.4 - 4.4\ .\ 10^{-4}$	[27]
	$2 - 4\ .\ 10^{-4}$	[13]
	$4 - 10\ .\ 10^{-5}$	[19]

For the sake of simplicity, we therefore chose $Ks_N = Ks_P$ which combined with Eq. (35) leads to $V_N^{max} = V_P^{max}$. We are aware that this is a simplification of reality but this simplification is not wholly unreasonable as it maintains a difference between the maximum affinity for P and the maximum affinity for N (by a factor 16 for phytoplankton and 10 for heterotrophic bacteria) similarly to what is reported in the litterature (cf. [27] and reference within).

<u>Referee's comment:</u> 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 and SRDOC respectively." There are values in the literature for these parameters; you can not fix them arbitrarily!

We agree that the term arbitrarily was a bad choice. If we consider glucose as a proxy of LDOC, then we are left with a wide range of values for both Ks and V^{max} ([28] and reference within). Since we are interested in describing the uptake rate of an organisms strongly C-limited, we chose our Ks values for LDOC in the lower range of reported values $Ks = 40nM$. Assuming a diffusion rate of $3\ .\ 10^{-10} m^2.s^{-1}$ ([26]), the resulting V^{max} based on Eq. 22 is $5\ .\ 10^{-20}\ mol.cell^{-1}.s^{-1}$ ($0.18\ fmol.cell^{-1}.h^{-1}$). For SLDOC and SRDOC, we assume that the V^{max} was lower than for LDOC (assuming the hydrolysis step as the limiting step). We therefore set their V^{max} to half the value chosen for LDOC. We also tried to take into account the slower diffusion rate of these larger molecules by reducing the diffusion coefficient to $6\ .\ 10^{-11} m^2.s^{-1}$. Thus our choice is an extrapolation based on literature values for diffusion coefficient and

uptake kinetics of labile DOC compounds such as glucose. We scaled SLDOC and SRDOC uptake kinetics based on the previous consideration.

Referee's comment: What is the meaning of "X"? Sometimes it is used to represent or (eq. 16) and sometimes it is used to represent N,C or P.(eg. Eq. 17). Again very confusing

We agree, X should only represent C, N or P (please refer to the corrected equation)

Referee's comment: 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.

This sentence has been changed to "For bacterial growth, highest growth efficiency is achieved when using LDOC followed by SLDOC and SRDOC"

Referee's comment: 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.

The basic idea of Han ([17]), an other mechanistic model (e.g. [11]), is that the reactionary centers of PSII can be found in three different states, namely open (and therefore reactive for photosynthesis), close (that means already occupied) or photodamaged. In these models, the primary production rate is therefore proportional to n_o, the ratio of PSII in the open state. In terms of equations, this means that the carbon-specific primary production rate (in s^{-1}) can be written :

$$P = \bar{a}^* \phi^C E \theta \tag{36}$$

where:

- $\bar{a}^*$ is the spectrally integrated chlorophyll a-specific absorption coefficient over the [400; 700] nm range, in m^2 $(gChl)^{-1}$
- ϕ^C is the quantum yield of carbon fixation, (mol O_2) (μmol quanta)$^{-1}$
- E is the scalar irradiance, (μmol quanta) m^{-2} s^{-1}
- θ the Chl:C ratio in phytoplnakton, mol C $(gChl)^{-1}$,

In Han (2002) model, ϕ^C is set to $n_o \cdot \phi^C_m$ where ϕ^C_m is the maximum quantum yield of carbon fixation and that's why it is written in the text that: "the quantum yield of carbon fixation is proportional to the probability of photosystem II being open". We however acknowledge that this was not sufficiently clear in the original text and this has been clarified in the revised version of the manuscript.

Referee's comment: Eqs. 23 and 24, Why do we have a superscript "i" for Q?

This superscript has been removed from the equations

Referee's comment: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?

An extensive work on the phototosynthesis formulations used in biogeochemical models, and especially on Han ([17]) formulation has been done in ([4],[3]). First, the choice of Han model has been made precisely because of its mechanistic basis and its use of measurable physiological parameters. This seemed to us more rigorous and more robust than the classical empirical formulations available in literature. In ([4]) a sensitivity study on the photosynthetic parameters has been undertaken. In addition, a validation with chemostat experiments on the diatom *Thalassiossira Weissflogii* has been performed. Parameters specific to this species have been taken from literature. This allowed not only to validate the phytoplankton model, but to illustrate its ability to reproduce the photoacclimation process since the model was also able to reproduce the variations in the Chl:C ratio due to different light regimes, using a single set of parameter values extracted from the literature.

Referee's comment:Page 12, eq. 27 I think that t is not the time in seconds but in day.

We maintained the time in second. We do not see any error in eq. 27

Referee's comment: 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 510^8 cell l^{-1} and 2.510^7 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 and 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?

Our choice of running the model for similar carbon biomass is based on the fact that during the stratified period, the ratio of heterotrophic bacteria to phytoplankton carbon biomass ($\frac{\beta_C}{\varphi_C}$) is usually equal or below 1 (Pedros-Alio et al. 1999). If we consider the ratio of $\frac{\beta_C}{\varphi_C}$ in the model it ranges between 0.12 and 0.94. The cell abundance values where chosen as typical values found for the Mediterranean Sea during summer.

Referee's comment: 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.

We modified the sentence to:"This particular feature for heterotrophic bacterial growth is the result of the high affinity for phosphate associated with higher DOC production". However we are not entirely sure that we correctly understood this particular comment.

Referee's comment: Page 12, line 20, what do you mean by arbitrarily distributed? You mean between TP and TN?

The sentence :*"Given a total amount of nitrogen (TN) and phosphate (TP) arbitrarily distributed, the model calculates the distribution of N and P among the different compartments and displays the biogeochemical fluxes and concentrations required in order to maintain a given population under a fix amount of nutrients (N and P)"* has been modified to: "The model gives an estimate of the C,N,P fluxes under various growth conditions assuming constant cell abundances. This is achieved by considering that the sum of living and non living N and P which is denoted TN and TP is conservative. By doing so we highlight the potential bottom up effect that N and P could have on the cycling of carbon in the system"

Referee's comment: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.

We modified our sentence as suggested by the referee (see previous comment).

Referee's comment:Page 13, line 6, I would say " represents N-limited as well as P-limited environment".

This has been modified in the revised version

Referee's comment: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.

TP was chosen in order to obtain steady state concentrations of PO4 in the range of what is measured in the surface layer of the Mediterranean Sea during summer. TN values were chosen in order to represent a realistic range of inorganic nitrogen concentrations for surface water in the Mediterranean Sea but also in order to create growth environments with realistic TN:TP ratio. Since we only consider the steady state solution in this study, the initial partitioning between living and inorganic compartments does not affect the steady state results. Initial conditions are described in the section simulation setup.

Referee's comment: 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.

Please refer to the response concerning the difference between growth and primary production (page 10). The function f^{μ} represents growth (s^{-1}) depending on which variable it is applied to (cell abundance, carbon biomass), it will represent the growth rate in terms of cell production or carbon production.

Referee's comment: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!

The main purpose of Figure 2 was to present the different TN and TP values used for each simulation and to show the resulting steady state concentration of NH4 and PO4. The referee is right when saying that TN and TP are initial conditions and that in our steady state assumption the model is conservative for N and P.

Referee's comment: 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?

We have seen that P dynamics can be affected by the N dynamics under N limited conditions and that N dynamics can be affected by P dynamics under P-limited conditions. However, in our simulations limitation by N or P is rarely observed (given the high maximum affinity values for N and P) and thus in

most simulations C is the most limiting resource (even for phytoplankton). As a result, N and P dynamics appear as relatively uncoupled from each others.

Referee's comment: 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.

The white lines appear as an artifact from conversion of png file into pdf. We will resolve this issue in the revised version of the manuscript.

References

[1] T. R. Anderson and P. Pondaven. Non-redfield carbon and nitrogen cycling in the sargasso sea: pelagic imbalances and export flux. *Deep Sea Research Part I: Oceanographic Research Papers*, 50(5):573–591, May 2003.

[2] T. R. Anderson and P. J. le B. Williams. Modelling the seasonal cycle of dissolved organic carbon at station e1in the english channel. *Estuarine, Coastal and Shelf Science*, 46(1):93–109, January 1998.

[3] M. Baklouti, F. Diaz, C. Pinazo, V. Faure, and B. Queguiner. Investigation of mechanistic formulations depicting phytoplankton dynamics for models of marine pelagic ecosystems and description of a new model. *Progress In Oceanography*, 71(1):1–33, October 2006.

[4] M. Baklouti, V. Faure, L. Pawlowski, and A. Sciandra. Investigation and sensitivity analysis of a mechanistic phytoplankton model implemented in a new modular numerical tool (eco3m) dedicated to biogeochemical modelling. *Progress In Oceanography*, 71(1):34–58, October 2006.

[5] S. Bertilsson, O. Berglund, D. M. Karl, and S. W. Chisholm. Elemental composition of marine prochlorococcus and synechococcus: Implications for the ecological stoichiometry of the sea. *Limnology And Oceanography*, 48(5):1721–1731, September 2003.

[6] K. M. Bjorkman and D. M. Karl. Bioavailability of inorganic and organic phosphorous-compounds to natural assemblages of microorganisms inorganic hawaiian coastal waters. *Marine Ecology Progress Series*, 111(3):265–273, 08 1994.

[7] K. M. Bjorkman and D. M. Karl. Bioavailability of dissolved organic phosphorus in the euphotic zone at station aloha, north pacific subtropical gyre. *Limnology and Oceanography*, 48(3):1049–1057, 2003.

[8] D. A. Bronk, J. H. See, P. Bradley, and L. Killberg. Don as a source of bioavailable nitrogen for phytoplankton. *Biogeosciences*, 4:283–296, 2007.

[9] P. A. del Giorgio and J. J. Cole. Bacterial growth efficiency in natural aquatic systems. *Annual Review of Ecology and Systematics*, 29:503–541, 1998.

[10] S. Drakare. Competition between picoplanktonic cyanobacteria and heterotrophic bacteria along crossed gradients of glucose and phosphate. *Microbial Ecology*, 44(4):327–335, 2002.

[11] P. H. C. Eilers and J. C. H. Peeters. A model for the relationship between light intensity and the rate of photosynthesis in phytoplankton. *Ecological Modelling*, 42(3-4):199–215, September 1988.

[12] K. M. Fagerbakke, M. Heldal, and S. Norland. Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria. *Aquatic Microbial Ecology*, 10(1):15–27, March 1996.

[13] F. X. Fu, Y. H. Zhang, Y. Y. Feng, and D. A. Hutchins. Phosphate and atp uptake and growth kinetics in axenic cultures of the cyanobacterium synechococcus ccmp 1334. *European Journal Of Phycology*, 41(1):15–28, February 2006.

[14] R. Fukuda, H. Ogawa, T. Nagata, and I. Koike. Direct determination of carbon and nitrogen contents of natural bacterial assemblages in marine environments. *Applied And Environmental Microbiology*, 64(9):3352–3358, September 1998.

[15] J. P. Grover. Resource competition and community structure in aquatic micro-organisms: experimental studies of algae and bacteria along a gradient of organic carbon to inorganic phosphorus supply. *Journal of Plankton Research*, 22(8):1591–1610, August 2000.

[16] A. Hagstrom, F. Azam, A. Andersson, J. Wikner, and F. Rassoulzadegan. Microbial loop in an oligotrophic pelagic marine ecosystem - possible roles of cyanobacteria and nanoflagellates in the organic fluxes. *Marine Ecology-Progress Series*, 49(1-2):171–178, November 1988.

[17] B. P. Han. A mechanistic model of algal photoinhibition induced by photodamage to photosystem-ii. *Journal of Theoretical Biology*, 214(4):519–527, February 2002.

[18] M. Heldal, D. J. Scanlan, S. Norland, F. Thingstad, and N. H. Mann. Elemental composition of single cells of various strains of marine prochlorococcus and synechococcus using x-ray microanalysis. *Limnology And Oceanography*, 48(5):1732–1743, September 2003.

[19] T. Ikeya, K. Ohki, M. Takahashi, and Y. Fujita. Study on phosphate uptake of the marine cyanophyte synechococcus sp nibb 1071 in relation to oligotrophic environments in the open ocean. *Marine Biology*, 129(1):195–202, July 1997.

[20] I. Joint, P. Henriksen, G. A. Fonnes, D. Bourne, T. F. Thingstad, and B. Riemann. Competition for inorganic nutrients between phytoplankton and bacterioplankton in nutrient manipulated mesocosms. *Aquat Microb Ecol*, 29(2):145–159, 2002.

[21] T. Kiorboe. *A mechanistic approach to plankton ecology*. Princeton University Press, 2008.

[22] D. L. Kirchman. The uptake of inorganic nutrients by heterotrophic bacteria. *Microbial Ecology*, 28(2):255–271, 1994.

[23] M. W. Lomas, A. L. Burke, D. A. Lomas, D. W. Bell, C. Shen, S. T. Dyhrman, and J. W. Ammerman. Sargasso sea phosphorus biogeochemistry: an important role for dissolved organic phosphorus (dop). *Biogeosciences*, pages –, 2009.

[24] T. Lovdal. *Competition between marine osmotrophs for phosphorus and nitrogen : implications for the microplanktonic food web*. PhD thesis, The University of Bergen, 2007.

[25] S.M. Myklestad. Release of extracellular products by phytoplankton with special emphasis on polysaccharides. *Science of The Total Environment*, 165(1-3):155–164, April 1995.

[26] E. Nimer, R. Schneiderman, and A. Maroudas. Diffusion and partition of solutes in cartilage under static load. *Biophysical Chemistry*, 106(2):125–146, November 2003.

[27] R. Riegman, W. Stolte, AM. Noordeloos, and D. Slezak. Nutrient uptake and alkaline phosphatase activity of emiliania huxleyi (prymnesiophyceae) during growth under n and p limitation in continuous cultures. *Journal of Phycology*, 36(1):87–96, 2000.

[28] F Schut, EJ. de Vries, JC. Gottschal, BR. Robertson, W Harder, RA. Prins, and DK. Button. Isolation of typical marine bacteria by dilution culture: Growth, maintenance, and characteristics of isolates under laboratory conditions. *Applied and Environmental Microbiology*, pages 2150–2160, 1993.

[29] T. Frede Thingstad and Fereidoun Rassoulzadegan. Conceptual models for the biogeochemical role of the photic zone microbial food web, with particular reference to the mediterranean sea. *Progress In Oceanography*, 44(1-3):271–286, August 1999.

[30] TF. Thingstad, EF. Skjoldal, and RA. Bohne. Phosphorus cycling and algal-bacterial competition in sandsfjord, western norway. *Marine Ecology Progress Series*, 99:239–259, 09 1993.