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Biogeosciences Discussions

Interactive comment on "Growth and specific P-uptake rates of bacterial and phytoplanktonic communities in the Southeast Pacific (BIOSOPE cruise)" *by* S. Duhamel et al.

S. Duhamel et al.

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All suggestions made by this referee have been taken into account and are include in the revised version of the manuscript. Specific comments

Introduction. The authors refer to a parameter μ that is not clearly defined. This leads to some confusion (at least for the reader) between specific growth rates (which I assume is what the authors mean by μrelated to cell division rates and cell specific or biomass specific uptake of C, N or P (specific uptake rates). These two parameters can be related to each other but are not equal (as an example specific C uptake does not directly reflect specific growth rates as some C is respired by the cells and not incorporated into cell biomass). A clear definition of these too parameters and how they

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relate to each other for the different elements would be helpful.

In the introduction we have now defined parameters (μ and Vsp) and explained how they relate to each other. We have made it clear that the production estimators have to be biomass production estimators (particulate primary production for autotrophic biomass and thymidine or leucine incorporation converted into C-biomass with appropriate conversion factors of biomass for bacterial biomass).

§ 1: "An assessment of the ecological role of both autotrophic and heterotrophic marine micro-organisms depends, to a significant extent, on estimates of their specific growth rate (μ) (Azam et al., 1983). Bacterial or primary production is the synthesis of bacteria or phytoplankton biomass, respectively. Production can be expressed as the rate of synthesis of cells or cell mass: production = μ x biomass, where μ is the specific growth rate of the population expressed in units of inverse time t-1 (Ducklow, 2000)."

§ 2: "According to Kirchman (2002), the most appropriate approach for estimating μ of microbial assemblages is the simplest, that is, to divide the production rate by the estimate of biomass (B). This ratio called the "specific uptake rate" (Vsp) is a C,N or P-based measurement of μ corresponding to the cell specific or biomass specific uptake of C, N or P (Lipschultz, 1995; Dickson and Wheeler, 1995; Ducklow, 2000). Vsp is an expression of the μ. These two parameters are not necessarily equal and Vsp must be considered as an estimator of μ. Both μ and Vsp are determined by resource limitation, temperature and predation (Brock, 1971; Thingstad, 2000)."

§ 2: "In such equations, AP is deduced from the NaH14CO3 incorporation rate measurements (Steemann-Nielsen, 1951) in the particulate fraction (i.e. biomass production) which do not include significant losses from respiration or excretion, when short term incubations are processed."

§ 2: "In such equations, HBP is generally deduced from the incorporation of 3H-thymidine (Fuhrman and Azam, 1980, 1982) and 3H-leucine (Kirchman et al., 1985) into DNA and proteins, respectively, with appropriate conversion factors of biomass

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production."

1) Abstract, line 8: μ has dimension 1/time nothing to do with carbon units. Be more precise. What is meant is that estimates of μ are based on C incorporation and C biomass measurements?

Yes, estimates of μ are usually based on C incorporation and C biomass measurements. To be clear, we have changed the sentence "Most of the methods using this approach are expressed using carbon (C) data." to: "Most of the methods using this approach to estimate μ are based on carbon (C) incorporation rates and C biomass measurements"

2) Introduction, § 1: The introduction begins with the symbol μ without mentioning what μ really stands for. I would suggest first explaining what is meant by μ (specific growth rate I suppose).

We changed the sentence line 1-3 in: "An assessment of the ecological role of both autotrophic and heterotrophic marine micro-organisms depends, to a significant extent, on estimates of their specific growth rate (μ) (Azam et al., 1983)."

3) Introduction, § 1: "The determination of heterotrophic bacterial ...". This seems to be a repetition of the first sentence in the introduction. It is not clear what the additional message is here. Be more precise or leave this sentence out.

We removed this sentence.

4) Introduction, § 2, lines 10-13: "and is an expression of μ as it is modified by ..." μ is not modified but rather determined by environmental conditions.

We rephrased the sentence line 10-13 in: "Both μ and Vsp are determined by resource limitation, temperature and predation (Brock, 1971; Thingstad, 2000)."

5) Introduction, § 4, line 6: "Contrary to C and N, P is more quickly liberated from dead material...". Should be rather "In contrast to C and N, P is quickly released from

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decaying material...". Can the authors give a time scale for that?

We didn't find any time scale for the C, N, P liberation from decaying material. Most authors who showed that P is quickly released from decaying material based their reasoning on variations in C, N, P stoichiometric ratios, in dissolved organic matter (DOM) or in particulate matter, with depth. As an example, Clark et al. (1998, 1999) examined changes in P concentration and C/N/P ratios in marine DOM from depth profiles in the Pacific Ocean in order to understand the mineralization of C, N and P from HMW DOM. Loh and Bauer (2000) examined such changes in both DOM and particulate matter. Both showed that P is more efficiently released from decaying material. Menzel and Ryther (1964) used another method: they studied the relationships between particulate C, N, P and Chlorophyll a. They made regressions of PartP or Chla on PartN or PartC. When extrapolated toward the origin, they indicated appreciable but variable amounts of PartN and PartC in the absence of PartP and Chla. The regression of PartP on Chla, on the other hand, had its intercept at the origin. These authors concluded that Chla and PartP are decomposed or mineralized at essentially the same rate, while PartC and PartN are more refractory.

We changed the sentence to: "PartP is released from decaying material more efficiently than C and N (Loh and Bauer, 2000) and seems to be decomposed or remineralized essentially at the same rate as chlorophyll (Menzel and Ryther, 1964)."

6) Introduction, § 5, line 6-9. Should be rather something like this "This area presents a gradient in trophic conditions from the extremely oligotrophic South East Pacific gyre, the largest and most poorly investigated province of the world ocean, to the high productivity Chilean upwelling region"

We agree with the referee and changed the sentence as suggested "This area presents a gradient in trophic conditions from the extremely oligotrophic Southeast Pacific gyre, the largest and most poorly investigated province of the world ocean (Claustre and Maritorena, 2003; Claustre et al., this issue), to the highly productive Chilean upwelling

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region."

Materials and methods

7) MM, section 2.1, lines 4-8: rephrase: "Temperature, conductivity, salinity, oxygen and fluorescence high resolution profiles were obtained using a CTDO profiler (Seabird 911 Plus) between 0 and 500 m depth...Seawater samples were collected at 6 different depths corresponding to levels of 50, 25, 15, 7, 3 and 1

We rephrased the sentence as suggested by the referee: "Temperature, conductivity, salinity, oxygen and fluorescence high resolution profiles were obtained using a CTDO profiler (Seabird 911 Plus) between a depth of 0 and 500 m (See Claustre et al. and Ras et al., this issue, for hydrodynamical entities, hydrographic conditions and pigment distribution). Seawater samples were collected at 6 different depths corresponding to levels of 50, 25, 15, 7, 3 and 1

8) Why is the max. irradiance for measurements 50

The 6 percentages enabled us to obtain a relatively well-balanced discontinuous repartition of the samples in the productive layer, which provided a good estimation of integrated primary production. The 50

9) MM, section 2.4, lines 1-6: rephrase " Specific uptake rates (Vsp) have been calculated by dividing heterotrophic bacterial production (HBP), C uptake rates (VDIC) or P uptake rates (VDIP) by bacterial biomass (HBB), phytoplankton biomass (AB) and particulate P (PartP), respectively."

We rephrased the sentence as suggested by the referee: "Specific uptake rates (Vsp) have been calculated by dividing heterotrophic bacterial production (HBP), C uptake rates (VDIC) or P uptake rates (VDIP) by heterotrophic bacterial biomass (HBB), phytoplankton biomass (AB) and particulate P (PartP), respectively."

10) MM, section 2.4: It would be more elegant if HBB was expressed as VLeuC or something similar.

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We understand that referee 1 suggests expressing HBP as VLeuC or something similar. It is true that VLeuC is more widely used than HBP. Nevertheless, in our opinion, it would be easier for the reader if we keep HBP. Indeed, we chose the abbreviation A, HB, B and P for autotrophic, Heterotrophic bacterial, biomass and production, respectively, throughout the manuscript: Autotrophic production: AP Autotrophic biomass: AB Heterotrophic bacterial production: HBP Heterotrophic bacterial biomass: HBB

We are convinced that it is more homogeneous this way. We have added a list of the principal abbreviations at the end of the introduction to make it clearer for the reader:

"List of principal abbreviations: Autotrophic production: AP Autotrophic biomass: AB Heterotrophic bacterial production: HBP Heterotrophic bacterial biomass: HBB Particulate phosphate: PartP specific uptake rate: Vsp DIP specific uptake rate: DIC specific uptake rate: Specific growth rates: μ"

Results

11) Results, section 3.1, lines 8-11: rephrase "Flow cytometry measurements showed that over the whole transect...cells had an average size of 0.68ś0.08 μm, 0.86ś0.1 μm and 1.74ś0.13 μm, respectively. Average cells size of Synechococcus in the upwelling stations was 1.16ś0.2μm."

We rephrased the sentence as suggested by the referee: "Flow cytometry measurements showed that over the whole transect Prochlorococcus (when detectable), Synechococcus and Picoeucaryotes cells had an average size of 0.68 ś 0.08 μm; 0.86 ś 0.1 μm and 1.74 ś 0.13 μm, respectively (Results from Grob et al., this issue). Average cells size of Synechococcus in the upwelling stations was 1.16 ś 0.02 μm."

12) Results, section 3.2: In order to evaluate the methods comparisons between Chla, PartP and POC measurements are presented (figures 2 and 3), but no mention is made of biomass estimates based on cell counts. Why is that? It seems to me that biomass estimates based on cell counts is still the most reliable method to separate detritus

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from living organisms as well as to estimate biomass of different living groups (even if one has to use conversion factors to estimate C), instead only "proxy" measurements (POC, Chla, and even PartP) are considered.

We did not mention biomass estimates based on cell counts as the main purpose of figures 2 and 3 was to compare Chla (the most widely used parameter in estimating autotrophic biomass) and PartP. In figure 2, we showed that contrary to Chla, PartP does not have a deep concentration maximum suggesting that in areas limited by light, phytoplankton accumulate pigments which thus complicates the estimation of phytoplankton biomass based on C:Chla conversion factors. We also showed that the variation of PartP is similar to those of total cell counts (flow cytometry data). Thus we agree that it would be interesting to add biomass estimates based on cell counts. We had data for total biomass (AB+HBB) determined from cell counts by flow cytometry and Campbell et al (1997) conversion factors for the different group of organisms (heterotrophic bacteria, Prochlorococcus, Synechococcus and picoeukaryotes).

We modified the section 3.2 §1 as follows: "Figure 2 shows a typical example of the vertical distribution of PartP and Chla concentrations compared to the vertical distribution of cell counts by flow cytometry and total C biomass estimate based on cell counts (AB+HBB). In the upper 80 m, PartP concentrations were fairly constant, varying between 10.0 and 10.4 nmol L-1 from surface to the depth of 7

13) Results, section 3.2, §2, lines 10-12: rephrase "This indicates that 69

We rephrased the sentence as suggested by the referee: "This indicates that 69

14) Results, section 3.2, §3: The differences between C and P uptake ratios (57 which incidentally is much lower than Redfield: 106/1) and particulate matter ratios (349) is used to derive differences in residence times. I am not sure how that works. Residence times can also be roughly estimated (assuming no vertical or horizontal export) from the measurements as the ratio between the concentration in particulates (nmol l-1)/Uptake (nmol l-1 d-1). What is the residence times using this formula for C and P?

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Does it vary depending on region and depth?

As reported, in response to question 5, Menzel and Ryther (1964) determined the detrital proportion of PartP by a regression of particulate phosphorus on particulate carbon for the same group of samples. Thus we first made such comparisons with our dataset. Because we thought this was not sufficient to prove that P was more rapidly mineralized from dead material than C, we also compared the slope of the regression between POC and PartP concentration and C and P uptake rates to show the significant difference between these 2 values.

We modified section 3.2 §3 as follows: "Menzel and Ryther (1964) determined the detrital proportion of PartP using a regression between Part P, particulate carbon and Chla, for the same group of samples. We made such comparisons (Fig 4A,C,D; eutrophic stations have been omitted to avoid regressions being drawn by high values.). The correlation between Chla and PartP concentration data was better ($r = 0.87$, $p < 0.001$, Fig 4C) than that between Chla and POC ($r = 0.51$, $p < 0.05$, Fig 4D), supporting the idea that PartP is a better indicator of living biomass than POC. As previously found by Menzel and Ryther (1964), the regressions of PartP on POC, when extrapolated toward the origin, indicate appreciable amounts of C in the absence of P while the regression of PartP on Chla intercepted at the origin, indicating that Chla and PartP was decomposed or mineralized at essentially the same rate, while POC was more refractory. The comparison of the regression slope between POC and PartP concentration and between VDIC and VDIP (Fig 4A, B) also supports the hypothesis that P is more rapidly mineralized from dead material than C. Indeed, if POC and PartP are representative of C and P living biomass, then the C to P incorporation rate ratio is expected to be in the range of POC to PartP ratio. The regression slope between POC and PartP concentration was 3489 (Fig 4A) while between VDIC and VDIP was 57 (Fig 4B). Such a difference can be explained by longer turnover rates of POC than those of PartP."

For the same samples as those represented on figure 4, the ratio between the concentration in particulate P (nmol l-1) and uptake rates of P (nmol l-1 d-1) and between the

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concentration in POC (nmol l-1) and uptake rates of C (nmol l-1 d-1) was 8.9 ś 5.8 d and 43.3 ś 31.9 d, respectively. These ratios vary with depth and region (with higher values in depth and oligotrophic area).

15) Results, section 3.2, §3: I understand that data from high productivity (a few high values) will significantly influence the regression. I find it, therefore, commendable that the authors show results for the oligotrophic regions separately. It would be, however, relevant to this study that an analysis including all the data is also shown (additional figures maybe).

The results taken from all stations are not so different from those found in oligotrophic regions (we will add additional files). Thus we chose to remove these particular stations from the analysis to show the reader that our analysis was not influenced by high values of POC, PartP, Chla or VDIC, VDIP. We therefore choose not to show all data and oligotrophic regions separately because it would provide too much information in one figure. Moreover, the idea we develop through this figure does not necessitate the study of all stations.

NB: we found a conversion error for the values of POC (nM) previously reported on figure 4 and corrected it in the final version of the manuscript. We apologise for this inconvenience.

16) Results, section 3.3: rephrase "Vsp DIP<0.6 values were 1.2 to ... HBP:HBB values in the productive areas (MAR-STB6 and STB15-UPX, respectively)..."

We rephrased the sentence as suggested by the referee: "VspDIP <0.6 values were 1.2 to 9.5 times higher than HBP:HBB values in productive areas (MAR-STB6 and STB15-UPX, respectively) while in the centre of the gyre (STB7-STB14), VspDIP <0.6 values were 1.2 to 2.2 times lower than HBP:HBB values."

17) Results, section 3.3: From the cell counts and Chla measurements what would the C:Chla ratio be as compared to the values from Veldhuis and Kraay (2004). Why not

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use conversion factors derived from data in this study?

As the determination of C:Chla ratios from cell counts and Chla measurements requires the use of cell-to-biomass conversion factors the comparison of our data with that of Veldhuis and Kraay (2004), estimated using a different method, would prove difficult. We calculated the C:Chla ratio from our dataset using phytoplankton cell counts and Chla concentrations from the >0.6 μm fraction and then used the conversion factors of Campbell et al (1997) for Prochlorococcus, Synechococcus and picoeukaryotes. We found C:Chla values of 98 ś 35 gC gChla-1 and 55 ś 18 gC gChla-1 at 50

In most of studies, authors choose their conversion factors from the literature. Our purpose was to show that this is a crucial choice, since results of can vary strongly depending on this choice. For this reason we didn't use conversion factors derived from data in this study.

If the biomass estimates from cell counts are too high, how do they compare with measured POC values?

POC concentration was only measured in the total fraction. Specific P uptake rate of phytoplankton must be evaluated in the >0.6 μm fraction supposedly free of bacteria. Thus to compare VspDIP>0.6 with VSPDIC>0.6 (=DIC incorporation rate to DOC ratio), we should have measured POC values in the >0.6 μm fraction. Consequently we can't make such a comparison.

And since the C:cell convertion factors are so variable (Table 1) why not simply try using a better one and then compare with the P-based estimates? We made such comparisons with Veldhuis and Kraay (2004) Chla-to-biomass conversion factors. Reading the text we concede that it is not apparent. Thus, we have modified the text to avoid confusions, changing: "With this Chla-to-biomass conversion factor, VspDIC >0.6 values were 1 to 4 and 0.6 to 1.8 times higher than VspDIP >0.6 in the gyre and in the meso- and eutrophic areas, respectively (Fig 5B)." to: "Using the Chla-to-biomass conversion factors of Veldhuis and Kraay (2004), VspDIC>0.6 values were 1 to 4 and 0.6

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to 1.8 times higher than VspDIP>0.6 in the gyre and in the meso- and eutrophic areas, respectively (Fig 5B)."

Discussion

18) Discussion, §1: It is growth-mortality that controls population dynamics or assemblage composition, not growth alone.

We modified sentence 1 as follows: "Quantifying heterotrophic bacteria and phytoplankton μ in the ocean is vitally important for understanding many oceanographic processes since μ and mortality of individual populations control the ultimate composition of the assemblage (Banse, 1991)."

19) Discussion, §1: rephrase "We measured DIP ... in order to assess in-situ specific growth rates of bacteria and two size classes of phytoplankton".

We rephrased the sentence as suggested by the referee: 8220;We measured DIP uptake rates and PartP concentrations in three size fractions: 0.2-0.6, 0.6-2 and >2 μm in order to assess in-situ specific growth rates of bacteria and two size fractions of phytoplankton8221;

20) Discussion, Section 4.1,§1: There seems to be a mix-up between Table 1 and Table 2. Also, from the text Table 1 should be Table 2 and vice-versa. I am also not sure that Table 2 is very useful. Since variability in C:Chla ratios is well known, couldn't the authors simply give the range of C:Chla variability with relevant references? I would also remove the large parenthesis describing variability in C cellular content since they are given in Table 1.

The mix-up between Table 1 and Table 2 has been corrected. Table 2 has been removed so Table 3 becomes Table 2.

The variability in C:Chla ratio has been cited in the text : 4.1,§1 : "C:Chla values vary over a wide range even at species level. As an example, in the subtropical Atlantic ocean, Veldhuis and Kraay (2004) found C:Chla ratios ranging from 450 at the surface

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to 15 gC gChla-1 at 150 m, for Prochlorococcus populations and a C:Chla ratio of 30-80 gC gChla-1 in surface waters for the collective eukaryotic phytoplankton varying by a factor of 3-7 fold with depth. Nevertheless, in most studies, authors use values ranging between 30 and 55 gC gChla-1 to convert their Chla data into C biomass (Gasol et al., 1997; Lequéré et al., 2005; Houlbrèque et al., 2006)."

The large parenthesis has been removed as follows: "For phytoplankton, cell-number-to-C conversion factors can vary significantly even at the species level (Table 1)."

21) Discussion, section 4.1, §1: rephrase "So although the use of a single conversion factor is the rule in field studies, it probably leads to significant errors in biomass estimates. Conversely, using appropriate cell or Chla to carbon conversion factors would demand complex data analysis"

We rephrased the sentence as suggested by the referee.

22) Discussion, section 4.1, §2: rephrase "It is found in a variety of molecules with different cellular roles, ranging from...If the contribution of detrital P to PartP standing stocks is small enough, than PartP can be considered to reflect standing stock of living material."

We rephrased the sentence as suggested by the referee: "It is found in a variety of molecules with different cellular roles, ranging from storage of genetic information (nucleic acids: DNA, RNA) and energy (ATP, ADP, AMP) to structural composition (phospholipids). If the contribution of detrital P to PartP standing stocks is small enough, then PartP can be considered to reflect the standing stock of living material."

23) Discussion, section 4.2: Is there no measurements of DOP in these or similar regions. I was under the impression that DOP could be an important P source and sink in oligotrophic regions.

DOP has been measured in this area (see Moutin et al., this issue). DOP can be an important source of P in P-depleted regions which is not the case here. In any case,

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direct uptake of DOP is "negligible" in comparison to P uptake of DIP coming from the extracellular liberation from DOP hydrolysis.

Moutin, T., Karl, D., Duhamel, S., Rimmelin, P., Raimbault, P., Van Mooy, B., and H. Claustre. 2007. Phosphate availability and the ultimate control of new nitrogen input by nitrogen fixation in the tropical Pacific Ocean. Biogeosciences Discussion 4, 2407-2440.

24) Discussion, section 4.3, §1: Why aren't the results of Perry and Eppley (1981) and of Thingstad et al. (1996) given in Table 3? How can the detrital proportion of PartP be estimated?

The results of Perry and Eppley (1981) and of Thingstad et al. (1996) have been added to Table 3. The detrital proportion of PartP can be estimated by the Menzel and Ryther (1964) method (see answer to question 5). Labelling with propidium iodide (PI) enables living cells to be separated from dead cells (Grégori et al., 2001). Assuming that the mineral part of PartP is negligible in oligotrophic areas, it would be possible to separate the detrital proportion of PartP by flow cytometry using cell sorting of PI-labelled cells (supposed to be dead cells) and of nonPI-labelled cells (supposed to be living cells). Nevertheless the subsequent analysis of PartP in each fraction would require high volumes (1L) which would be time consuming.

Grégori G., Citterio S., Ghiani A., Labra M., Sgorbati S., Brown S.Denis M. 2001. Resolution of viable and membrane-compromised bacteria in freshwater and marine waters based on analytical flow cytometry and nucleic acid double staining. Applied and Environmental Microbiology 67, 4662-4670.

25) Discussion, section 4.3, §2: replace "rich areas"; with "productive areas".

We replaced "rich areas" with "productive areas" as suggested by the referee.

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