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Biogeosciences Discussions

Interactive comment on "Heterotrophic bacterial production in the South East Pacific: longitudinal trends and coupling with primary production" *by* F. Van Wambeke et al.

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We are thankful to the two referees for their objective and clear review. We have addressed below most of their comment and suggestions:
- Figure 5 has been changed and now shows IBP=f(IPP) relationship. This figure is commented and discussed in the revised version of the ms.
- Published empirical relationships relating dissolved organic production and particulate primary production were used as an alternative way to estimate the percentages of DOC excretion.
- The requested information about figures/discussions on chlorophyll and primary production has not been added in the revised version, because beyond the scope of this study and because such information is now available on other papers of the

special issue.

Response to anonymous referee 2

The sentence: such imbalance being impossible
This sentence has been suppressed from the abstract and the last sentence corrected (see also response to referee 3)

The fact that only at 2 occasions DCR was compared to BR. The assumption that most of all DCR is BR is probably a source of error.
This remark has been also made by the other reviewer (see response to referee 3).

I do not think it is proper to compare O_2 derived GCP with ^{14}C derived PP as a way to estimate dPP.
First, the range of dPP percentage cited in the text page 2776-line 19 (37-68%) was wrong. For the GYR station based on different assumptions on PQ and the choice of IPP (IPPdeck or IPPin situ) the range, calculated as (GCP-IPP)/GCP was 37-52%. We apologize for this error. If photorespiration is properly corrected from dark community respiration rates, and assuming no biases in estimation of photosynthetic quotient, then the difference between gross community production (GCP, derived from oxygen measurements) and particulate primary production (IPP, measured by ^{14}C measurement) represents the sum of respiration losses and dissolved organic carbon production (through lysis, grazing, excretion).
Consequently, as we considered that the difference could be dissolved production only, the percentages that we calculated in our ms, with the formula (GCP-IPP)/GCP were only potential maximum values.
Teira et al. (2003), exploring oligotrophic area in the North Atlantic, estimated a mean budget of the fate of radiolabelled bicarbonate during a 12h light incubation period (see their figure 6). In this budget, autotrophic respiration loss was assumed to represent 20% of particulate primary production. Maranon et al. (2007) considered that such

BGD
4, S2210–S2219, 2007
Interactive Comment

EGU

losses represented 20% to 40% of daylight 14C uptake, the 40% value consisting in an upper limit.

If we apply this range of percentage to our data of Table 2 and 3, then maximum dPP percentages will decrease from the range 37-52% to 24-42% using a percentage of autotrophic respiration loss of 20% (i.e. GCP-1.2xIPP)/GCP and 12-33% using a percentage of autotrophic respiration loss of 40% (GCP-1.4xIPP)/GCP. In addition most percentage of excretion in the literature are not expressed relative to GCP, but rather to total net primary production (i.e. totPP= IPP + dPP). Percentages of extracellular release, relative to total net primary production, i.e., PER = dPP/(IPP+dPP), would be 28-47% and 16-41% according the choice of the percentage of autotrophic respiration loss (20%, 40%, respectively).

We recognize that trying to estimate DOC loss through comparison with GCP and IPP is not simple due to the biases related to 1) the estimate of the respirations fluxes for all microbial groups (Maranon et al., 2007, Moran et al. in press), 2) scales of measurements of respiration (Briand et al., 2004), 3) assumptions about equal respiration rates in the light and dark conditions (Pringault et al., 2007).

However, even with our assumptions which provide upper limits of PER we found values in the range of those cited in the literature for particularly low oligotrophic regions where picoplankton dominate autotrophs. For instance Teira et al. (2003) found a PER of 37% in their most oligotrophic station (where IPP was 129 mgC m^{-2} d^{-1}). And PER is assumed to increase in autumn situation in NW Iberian coast when picoautotrophs dominates (33%, Teira et al., 2001), confirming what was obtained in SW Mediterranean (Fernandez et al., 2004).

We explored also, like suggested by the referee literature showing empirical relationships between particulate production (PP) and dissolved organic carbon production (dPP). Some of them were the following:

Baines Pace (1991) in Marine and Estuarine samples:

log (dPP) = -0.88 + 1.03 x log (PP), with a range of PP 0.1-200 mgC m^{-3} h^{-1}, and with

BGD

4, S2210–S2219, 2007

Interactive Comment

no correction for bacterial DOC uptake

Moran et al. (2001), in offshore Antarctic waters, with no correction for bacterial DOC uptake
log (dPP) = -0.92 + 1.00 x log (PP), with a range of PP 0.1-2 mgC m^{-3} h^{-1}, n = 18

Moran et al. (2002), in Southern Ocean and NE Atlantic, with correction for bacterial DOC uptake during the experiments
log (dPP) = -1.03 + 0.62 x log (PP), with a range of PP 0.1-20 mgC m^{-3} h^{-1}, n = 40

Teira et al. (2001), in NW Iberian coastal transition zone
log (dPP) = -0.54 + 0.37 x log (PP), range of PP 0.2-40 mgC m^{-3} h^{-1}, n = 31.
These authors noticed that the relationship between dPP and PP is different and less significant in autumn when more interference with lysis and grazing is expected (relative importance of photosynthetic pico-eukaryotes in autumn):
log (dPP) = -0.45 + 0.43 x log (PP), range of PP 0.2-6 mgC m^{-3} h^{-1}, n=15

Because all these relationships were established only on hourly volumetric rates, we took all corresponding data along our profiles to compute dPP from these empirical relationships. Because the rate of particulate primary production obtained between stations STB6 and 15, in the centre of the SPG was very low (means $\pm$ sd was 0.12 $\pm$ 0.09 mgC m^{-3} h^{-1}, n = 63), and because phytoplankton populations were largely composed by pico-autotrophs, we found more relevant to use relationships of Moran et al (2002) and that of Teira et al (2001) in autumn.
Percentage of extracellular release, PER%=dPP/(dPP+PP)x100, were calculated from data of volumetric rates per hour between stations STB6 and STB15. Means $\pm$ sd of PER from these 2 empirical relationships were 20% $\pm$ 6% and 58% $\pm$ 11% (n = 63) according Moran et al. (2002) or Teira et al. (2001) relationships. Such high percentages are in the same range than those estimated by comparison of GCP and IPP. In fact, the extrapolation of the empirical relationships to our very low range of

BGD
4, S2210–S2219, 2007

Interactive Comment

EGU

particulate primary production suffers also some biases. They were established on other oceanic regions, they were estimated on a range of PP higher than ours, and finally the PER estimated from hourly rates are difficult to extrapolate on a daily basis (Teira et al. 2003). However, although both approaches (comparison GCP-IPP and empirical relationships) are not satisfying for the reasons explained above, we found in both cases high PER.

Then I can t buy tour argument that the fact that BP is maximum around midnight indicates that bacteria are using the large fraction of dPP an equally likely explanation8230;. Detrimental effect of light.

The daily variability of BP is discussed in a companion paper for this special issue BIOSOPE in BGD (Van Wambeke at al., submitted). We agree with the referee about effects of daily variability of UVB, UVA and PAR radiations. We explain in this ms that the delay before BP growth is probably due to inhibition by UVB.

Response to anonymous referee 3

The last pat of the abstract . metabolic balance.

We apologize for this error in the abstract. In fact, it was clearly stated in the BGD version of the ms (page 2770, lines 17-18) what the referee said, i.e. Net community production was not statistically different from zero at GYR, was negative at UPX.
We corrected the abstract accordingly.

The other aspect of the paper is the reporting of bacterial growth efficiencies.

As the referee wrote, we made only on 2 occasions direct measurements of bacterial respiration using size fractionation. We extrapolated these results to the whole data set because we wanted to compare bacterial carbon demand and primary production for the whole transect. We are aware that such extrapolation is risky. However, we calculated the incidence of computing different values of BGE, notably that bacterial respiration could represent half of the DCR. In such a way we examined the whole

BGD
4, S2210–S2219, 2007

range of possible values of BGE. In fact, as discussed in the paper (end page 2771), the biases due to estimate of BR after confinement of 24h in a glass bottle is very large. In addition, a large part of the heterotrophic bacterial production (on average 36 %) is retained by a 0.6 μm filter in this oligotrophic system and the respiration of the heterotrophic bacteria associated to this high-size fraction was not taken into account.

The authors should consider adding more discussion and a figure or table about phytoplankton (primary production and chlorophyll).

Primary production (based on carbon but also on nitrogen) is discussed in details in Raimbault and Garcia (2007), see their figure 4, and chlorophyll in Ras et al. (2007) see their figure 3 (total chlorophyll a) and 4 (pigments). We focused on bacterial heterotrophic production and secondly to its potential link with primary production so we don t think that it is necessary to go deeper in these fields in our ms.

Specific comments

1 Page 2772 line 3-4 a decrease in the BCD/IPP ratio from 2.1 to 8.6

This is the range of BCD/IPP ratio for 9 stations: STB6 to STB15
With BGE 7%, the range is 3.7-14 (lines 16-17 page 2271 of the BGD ms), and this range switch to 2.1-8.6 with a BGE set to 12% (line 3-4 page 2772). The sentence in the text was modified in the revised version to help the reader.

2. Table 3 BGEs, RQ and PQ
The table 3 was constructed in such a manner that all biases in the estimation of BGE, and then IPP/GCP and BCD/GCP ratio are considered. As the reviewer 3 noticed, the choice of the fraction of DCR attributable to bacteria has higher influence on the BGE estimate than the choice of RQ. Finally, the choice of PQ modify largely (up to 50% change) the IPP/GCP ratio when this ratio is low (see MAR1, where the values switch from 0.16 to 0.31) and thus we feel interesting to consider simultaneously the consequences of all these choices.
Finally, as all such biases can accumulate, we explored the whole range possible which

are important to compare BCD and GCP in these hyper-oligotrophic regions. For all these reasons, we prefer to keep Table 3 as it is.

Table 3 how GCP was calculated
GCP from table 3 is expressed in carbon units (mgC m^{-2} d^{-1}) and that of table 2 is expressed in oxygen units (mmole O_2 m^{-2} d^{-1}). Both are related with PQ, i.e.: GCP in C units = GCP in O_2 units x PQ
Typewriting errors in the legend of Table 3 were corrected (IGCP instead of GCP, gross primary production instead of gross community production) and we apologize because this might have been confusing.

3 A table with examples of chlorophyll and PP.
Dealing on chlorophyll, all relevant information is in Ras et al. (2007).

For primary production, we did not insisted that much because due to the varying ways to incubate (in situ on mooring lines, on deck with screens, several hours to 24h incubation duration), we choose to compare data only reporting estimates obtained using in situ moored lines as a reference. Most relevant references were included in the text for corresponding temperate areas (lines 29 page 2774 to lines 4 page 2776). Other papers describe precisely autotrophic activities and are now available in BGD (Raimbault et al., 2007).

Is the South Pacific the more oligotrophic ocean ?
The GYR station (114°W, 26°S) is extremely close to the location (115°W, 26°S) of the most oligotrophic area of the global ocean identified from an historical analysis of SeaWiFS ocean colour data (see http://earthobservatory.nasa.gov/Newsroom/NewImages/images.php3?img_id=16409).

See also supplementary material in Claustre et al. (2007a) and introduction paper by Claustre et al. (2007b).

Many biological/physical variables that could help for responding to this question, as well as the manner to consider them. For instance, it has been shown that volumetric concentration of chlorophyll a could be considered as absolute records of minimum values (Ras et al., 2007). However, because the transparency of water masses in the SPG reached absolute records (Morel et al., 2007), chlorophyll was detected down to particularly deep layers (depth of 1.5 times the euphotic zone). Consequently, because euphotic zone included a large layer, often integrated values, although low, were not absolute records (Ras et al., 2007).

In terms of primary production with simulated in situ incubations data (on board both ^{14}C technique, and ^{13}C technique were used). Means $\pm$ sd of maximum values along each profile for oligotrophic stations STB6 to STB15 were 1.29 $\pm$ 0.36 mgC m^{-3} d^{-1} (n = 9) for ^{14}C data and 1.52 $\pm$ 0.64 mgC m^{-3} d^{-1} (n = 12) for ^{13}C data. Mean $\pm$ sd of integrated values for these stations were 134 $\pm$ 42 mgC m^{-2} d^{-1} (n = 9) with ^{14}C data (this ms, range 76 to 219 mgC m^{-2} d^{-1}, Figure 5); and 156 $\pm$ 60 with ^{13}C technique: (range 74-275 mgC m^{-2} d^{-1}, Raimbault et al., 2007, in revised version to be submitted). Dealing on new primary production and f ratios we reached also particularly low values (Raimbault and Garcia, 2007; Raimbault et al., 2007). All these means are very low and are within the limits of values reported in other oligotrophic temperate oceans. A more general interpretation on the aspect of absolute record in term of primary production would need a careful examination of other published data, in terms of methodology, seasonal variability and so on, and we think that is beyond the scope of our paper dealing mainly on bacterial production.

4. Contours plots of chlorophyll and PP.
Such figures are available in Ras et al. (2007) and Raimbault et al. (2007).

5 Figure 5
As the referee suggested, we modified figure 5. The data are now presented in a scatter diagram log IBP = f(log IPPdeck). We added also 3 lines for BCD equalling primary production, with BGEs values set to 7, 12, and 24 %. We added also data points log IBP=f(log GCP). The comparison of data points and lines confirms what was

BGD
4, S2210–S2219, 2007

described in the ms: using IPPdeck data and low BGE (7, 12%), BCD is always higher than IPPdeck, and only with a BGE at 24 % for 1/5 of the data set, BCD is lower than IPPdeck. By plotting our 7 GCP data, however, BCD can be lower than GCP for BGEs values around those estimated in our study : with BGE 7%, 3 data, with BGE 12%, 4 data and for BGE 24% all the 7 data.

We plotted also the canonical Cole et al (1988) log-log relationship between IBP and IPP:
Log IBP=0.746 log (IPP) + 0.093 (n=36, p<0.0001) as well as that obtained from our data: Log IBP=0.542 log (IPP) + 0.615 (n=24, p<0.0001).

Because in this scatter diagram the longitudinal trend is not visible anymore, we added the IBP and IPP data in Table 1.

References cited not listed in the revised version of the ms.

Maranon, E., et. al.: Planktonic carbon budget in the eastern subtropical North Atlantic. Aquatic Microbial Ecology, 48, 261-275, 2007.

Moran, X. A., Perez, V., and Fernandez, E.: Mismatch between community respiration and the contribution of heterotrophic bacteria in the NE Atlantoc open ocean: What causes high respiration in oligotrophic waters? J. Mar. Res., 65, in press, 2007.

Pringault, O., Tassas, V., and Rochelle-Newall, E.: Consequences of respiration in the light on the determination of production in pelagic systems. Biogeosciences, 4, 105-114, 2007.

Raimbault, P., and Garcia, N.: Carbon and nitrogen uptake in the South Pacific Ocean: evidence for efficient dinitrogen fixation and regenerated production leading to large accumulation of dissolved organic matter in nitrogen-depleted waters. Biogeosciences Discuss., 4, 3531-3579, 2007.

Teira, E., Pazo, M. J., Quevedi, M., Fuentes, M. V., Niell, F. X., and Fernandez, E.:

BGD
4, S2210–S2219, 2007

Rates of dissolved organic carbon production and bacterial activity in the eastern North Atlantic Subtropical Gyre during summer. Mar. Ecol. Prog. Ser, 249, 53-67, 2003.

PS: There was an editing error that we did not see in the proof of our BGD ms in Table 2. For UPX1, DCR is 245 mmol O_2 m^{-2} d^{-1}, not 24 mmol O_2 m^{-2} d^{-1}

Interactive comment on Biogeosciences Discuss., 4, 2761, 2007.

BGD

4, S2210–S2219, 2007

Interactive Comment