Growth and specific P-uptake rates of bacterial and phytoplanktonic communities in the Southeast Pacific (BIOSOPE cruise)

S. Duhamel, T. Moutin, France van Wambeke, B. van Mooy, P. Rimmelin, Patrick Raimbault, Hervé Claustre

Biogeosciences Discuss., 4, 2027–2068, 2007
www.biogeosciences-discuss.net/4/2027/2007/

Biogeosciences Discussions

Biogeosciences Discussions is the access reviewed discussion forum of *Biogeosciences*

Growth and specific P-uptake rates of bacterial and phytoplanktonic communities in the Southeast Pacific (BIOSOPE cruise)

S. Duhamel[1,2], T. Moutin[1], F. Van Wambeke[2], B. Van Mooy[3], P. Rimmelin[1], P. Raimbault[1], and H. Claustre[4]

[1]Aix-Marseille Université, Laboratoire d'Océanographie et de Biogéochimie, LOB-UMR 6535 CNRS, OSU/Centre d'Océanologie de Marseille, 13288 Marseille, Cedex 09, France
[2]Aix-Marseille Université, Laboratoire de Microbiologie, Géochimie et Ecologie Marines, LMGEM-UMR 6117 CNRS, OSU/Centre d'Océanologie de Marseille, 13288 Marseille, Cedex 09, France
[3]Woods Hole Oceanographic Institution, Mailstop 4 Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
[4]Observatoire Océanologique de Villefranche, Laboratoire d'Océanographie de Villefranche, UMR7093, B.P. 08, 06238 Villefranche-sur-mer, France

Received: 15 June 2007 – Accepted: 15 June 2007 – Published: 27 June 2007

Correspondence to: S. Duhamel (solange.duhamel@univmed.fr)

Abstract

Predicting heterotrophic bacteria and phytoplankton growth rates (μ) is of great scientific interest. Many methods have been developed in order to assess bacterial or phytoplankton μ. One widely used method is to estimate μ from data obtained on biomass or cell abundance and rates of biomass or cell production. According to Kirchman (2002), the most appropriate approach for estimating μ is simply to divide the production rate by the biomass or cell abundance estimate. Most of the methods using this approach are expressed using carbon (C) data. Nevertheless it is also possible to estimate μ using phosphate (P) data. We showed that particulate phosphate (PartP) can be used to estimate biomass and that the phosphate uptake rate to PartP ratio can be employed to assess μ. Contrary to other methods using C, this estimator does not need conversion factors and provides an evaluation of μ for both autotrophic and heterotrophic organisms. We report values of P-based μ in three size fractions (0.2–0.6; 0.6–2 and >2 μm) along a Southeast Pacific transect, over a wide range of P-replete trophic status. P-based μ values were higher in the 0.6–2 μm fraction than in the >2 μm fraction, suggesting that picoplankton-sized cells grew faster than the larger cells, whatever the trophic regime encountered. Picoplankton-sized cells grew significantly faster in the deep chlorophyll maximum layer than in the upper part of the photic zone in the oligotrophic gyre area, suggesting that picoplankton might outcompete >2 μm cells in this particular high-nutrient, low-light environment. P-based μ attributed to free-living bacteria (0.2–0.6 μm) and picoplankton (0.6–2 μm) size-fractions were relatively low ($0.11\pm0.07\,d^{-1}$ and $0.14\pm0.04\,d^{-1}$, respectively) in the Southeast Pacific gyre, suggesting that the microbial community turns over very slowly.

1 Introduction

A fundamental aim in ecology and hence, biological oceanography and limnology, is to understand and predict the abundance of organisms and their temporal change

BGD

4, 2027–2068, 2007

(Banse, 2002). An assessment of the ecological role of both autotrophic and heterotrophic marine micro-organisms depends, to a significant extent, on estimates of their μ (Azam et al., 1983). Phytoplankton μ estimates vary widely from values of around 0.1–0.3 d^{-1} (Letelier et al., 1996; Maranon et al., 2000, 2005) to 1–2 d^{-1} (Laws et al., 1987; Quevedo and Anadon, 2001). Bacterial μ estimates also vary widely, from very low values 0.004–0.25 d^{-1} (Sherr et al., 2001; Van Wambeke, 2007b[1]) to higher values of around 2–10 d^{-1} (Ducklow, 1983; Jones et al., 1996). Studies comparing bacterial and phytoplankton μ are scarce and show significant differences between these organisms (Jones et al., 1996). The determination of heterotrophic bacterial and phytoplankton μ is critical in order to predict the responses of the planktonic ecosystem to potential changes in nutrient supply to the upper ocean.

Numerous methods have been developed to measure μ (Brock, 1971). In order to estimate phytoplankton and heterotrophic bacterial μ, authors have used various direct or indirect methodologies of varying accuracy. The two most common direct methods, applicable to both heterotrophic bacteria and phytoplankton, are the frequency of dividing cells (Hagstrom et al., 1979) and the dilution technique (Landry and Hassett, 1982; Quevedo and Anadon, 2001). Direct methods are difficult to set up on board so microbial growth rates are commonly calculated from production and standing stock data. According to Kirchman (2002), the most appropriate approach to estimate μ of microbial assemblages is the simplest, that is, to divide the production rate by the estimate of biomass (B) or cell abundance. This ratio is called the "specific uptake rate" (V^{sp}) (Lipschultz, 1995; Dickson and Wheeler, 1995) or specific growth rate (Laws et al., 1984; Marañon et al., 2003; Holl and Montoya, 2005) and it is an expression of the μ, as it is modified by resource limitation, temperature and predation (Brock, 1971). The most common indirect methods to measure phytoplankton μ are ^{14}C-pigment labelling (Redalje and Laws, 1981; Welschmeyer et al., 1991; Jones et al., 1996; Cailliau

[1]Van Wambeke, F., Obernosterer, I., Moutin, T., Duhamel, S., Ulloa, O., and Claustre, H.: Heterotrophic prokaryotic production in the South East Pacific: longitudinal trends and coupling with primary production, Biogeosciences Discuss., in preparation, 2007b.

et al., 1996), cell cycle analysis (Vaulot, 1992; Liu et al., 1999) and the use of equations linking autotrophic production (AP) and autotrophic cell abundance or biomass (AB) (Smith et al., 2000; Maranon, 2005). In such equations, AP is deduced from the $NaH^{14}CO_3$ incorporation uptake rate measurements (Steemann-Nielsen, 1951). The most common indirect method for studying heterotrophic bacterial μ, is the use of equations that link heterotrophic bacterial production (HBP) and heterotrophic bacterial cell abundance or biomass (HBB). In such equations, HBP is generally deduced from the incorporation of ^{3}H-thymidine (Fuhrman and Azam, 1980, 1982) and ^{3}H-leucine (Kirchman et al., 1985) into DNA and proteins respectively. More recently, measurements of the incorporation rates of $^{33}PO_4$ into phospholipids (particularly phosphatidylglycerol: PG and phosphatidylethanolamine: PE) specific to bacterioplankton have been used (Van Mooy et al., 2006).

In numerous studies, authors have estimated phytoplankton μ by dividing AP, measured using the ^{14}C method, by various AB estimators such as Chlorophyll a (Chla), particulate organic carbon (POC) and carbon (C) content estimated from microscopy or flow cytometry measurements (Eppley, 1972; Vadstein et al., 1988; Malone et al., 1993; Maranon et al., 2000, 2005; Moreira-Turcq, 2001). The use of Chla and POC as AB proxies is debatable (Le Floc'h et al., 2002; Sobczak et al., 2002; Huot et al., this issue) and C content estimates are dependant on conversion factors. These conversion factors can vary greatly between studies. In the same way, the evaluation of bacterial μ based on the HBP to HBB ratio requires several conversion factors (to convert the incorporation of ^{3}H-leucine or ^{3}H-thymidine to C equivalents and to convert cell number to biomass equivalents) varying with different studies (Riemann et al., 1990). Furthermore, method comparisons can show significant differences between μ estimates (Laws et al., 1984).

If μ = production/biomass, then there is a direct relationship between incorporation rate per cell and μ (Kirchman, 2002). Although biomass and production estimators are usually expressed in terms of C, it is also possible to express them in terms of nitrogen (N) or phosphate (P) as C, N and P are major cellular constituents linked via the

"Redfield ratio" (Redfield, 1963; Berman, 1980; Laws et al., 1984). Contrary to C and N, P is more quickly liberated from dead material (Menzel and Ryther, 1964; Knauer et al., 1979; Minster and Boulahdid, 1987; Clark et al., 1999). As a consequence, in the open ocean, the proportion of detrital P in PartP is low (Faul et al., 2005). Phosphate uptake rates are commonly measured using the ^{32}P or ^{33}P method and quantifies the amount of P that is taken up by both heterotrophic and autotrophic cells. Measuring the dissolved inorganic P (DIP) uptake rates provides an estimate for planktonic production, assuming DIP is the sole source of P and there is no, or negligible luxury uptake (Thingstad et al., 1996). Thus, particulate P (PartP) and P uptake rate can be used as estimators of planktonic biomass and production, respectively.

We estimated μ from production to biomass ratios expressed in terms of P and discussed the bias associated with using C and P-based μ estimations. Combining P uptake rates and PartP measurements with size fractionations, we determined the DIP specific uptake rate (V^{sp}_{DIP}) in three size fractions corresponding to heterotrophic bacteria, picophytoplankton and nano-microphytoplankton (0.2–0.6; 0.6–2 and >2 μm, respectively), following an east-west transect along the Southeast Pacific ocean. Yet, this area present an interesting diversity of trophic conditions among which the Southeast Pacific gyre which is the largest, least described and most oligotrophic anticyclonic gyre of the ocean (Claustre and Maritorena, 2003; Claustre et al., 2007[2]). The measurement of V^{sp}_{DIP} in the different compartments enabled us to compare bacterial to phytoplankton μ using the same method and to study the variability of dynamics among 2 major groups of phytoplankton.

[2]Claustre, H., Sciandra, A., and Vaulot, D.: Introduction to the special section: bio-optical and biogeochemical conditions in the South East Pacific in late 2004 – the BIOSOPE cruise, Biogeosciences Discuss., in preparation, 2007.

2 Materials and methods

2.1 Station locations, sample collection and hydrological characteristics

This work was conducted during the BIOSOPE (BIogeochemistry and Optics SOuth Pacific Experiment) cruise in the Southeast Pacific Ocean (between 146.36° W and 72.49° W; Fig. 1). The cruise was carried out aboard "l'Atalante" from October to December 2004. High vertical resolution environmental data was produced using a conductivity temperature-depth-oxygen profiler (CTDO, Seabird 911 Plus), from 0 and 500 m, measuring external temperature, conductivity, salinity, oxygen, fluorescence and depth (see Claustre et al., 2007[2]; Ras et al., 2007[3], for hydrodynamical entities, hydrographic conditions and pigment distribution). Seawater samples were collected at 6 predetermined depths corresponding to 6 levels of the Photosynthetically Active Radiations (PAR – 50, 25, 15, 7, 3 and 1% of surface irradiance). Samples were collected in 12 L Niskin bottles attached to a rosette CTD system, at 09:00 a.m. (local time). Subsamples were collected directly, without pre-filtration, into clean, sample-rinsed polycarbonate bottles.

2.2 Analytical methods

Particulate phosphate (PartP) was measured using the Strickland and Parsons procedure (1972) for standard DIP, following high-temperature persulfate wet-oxidation at 120°C and 1 bar (Pujo-Pay and Raimbault, 1994). Sequential filtration was carried out on 1 to 1.2 L samples through different porosity polycarbonate filters (0.2, 0.6, and 2 μm; 47 mm) using Sartorius systems and very low vacuum (drop by drop). The 0.2 and 0.6 μm filters in the lower Sartorius system were separated by a nylon separator (NY8H04700, Millipore) previously treated by persulfate wet-oxidation to lower blank values. Immediately after filtration, the filters (and the separator for the 0.2 μm filter)

[3] Ras, J., Uitz, J., and Claustre, H.: Spatial variability of phytoplankton pigment distribution in the South East Pacific, Biogeosciences Discuss., in preparation, 2007.

BGD
4, 2027–2068, 2007

were put into 20 mL Teflon bottles. 2.5 mL of reagent (140 ml of NaOH 1.5 M, 30 g of H_3BO_3, 360 ml of demineralised water) was added and the mineralization processed (autoclave 30 min, 1 bar). After cooling down to ambient temperature, DIP was measured in the same bottles as for mineralization. All reagents were prepared with pro analysis MerckTM Reagent Grade chemicals and with Milli-QTM high purity demineralised water. All utensils were washed with 10% hydrochloric acid and rinsed three times with demineralised water.

Particulate organic carbon concentration was determined by the wet-oxidation procedure (Raimbault et al., 1999), following the filtration of 1.2 L of seawater through 0.2 μm teflon membranes.

Chlorophyll a (Chl a) concentration was determined by the serial filtration of 1 to 1.2 L samples following the same filtration method as for PartP. Immediately after filtration, the filters were put in cryotubes with 5 mL of methanol for pigment extraction (30 min, 4°C) (Herbland et al., 1985). The fluorescence was measured using a Turner designs 10-AU-005-CE fluorimeter equipped with a chlorophyll a Kit (F4T45.B2 lamp) according to Welschmeyer (1994).

Picophytoplankton (*Prochlorococcus*, *Synechococcus* and picophytoeukaryotes) and bacterial abundances were determined according to Grob et al. (2007) using a FACSCalibur (Becton Dickinson) flow cytometer. Picophytoplankton abundances were determined in situ on fresh samples while bacterioplankton samples were fixed with either paraformaldehyde at 1% or glutaraldehyde at 0.1% final concentration and frozen in liquid nitrogen. Samples were then processed according to Marie et al. (2000a, b). At each sampling depth, corresponding to the Chla and P and C uptake rates measurements, 2 mL samples were filtered through 0.6 μm polycarbonate filters. The filtrate was then analysed using flow cytometry and compared to the total in the corresponding sample.

Carbon and phosphate uptakes were determined using the $^{33}P/^{14}C$ dual labeling method (Duhamel et al., 2006). Duplicate samples (300 ml) were collected into sample-rinsed, polycarbonate bottles (Nalgene) for each sampling depth. An additional dupli-

cate sample (300 ml) of surface water was incubated with 300 μl of $HgCl_2$ (20 g L^{-1}) to act as a control for non-biological assimilation (Kirkwood 1992). The samples were inoculated with 1080 kBq carrier-free ^{33}P (<40 pmol L^{-1} final concentration – orthophosphate in dilute hydrochloric acid; Amersham BF 1003; half-life 25.383±0.040 days; Duhamel et al., 2006), and 3.7 MBq ^{14}C (bicarbonate aqueous solution; Amersham CFA3; half-life 5700±30 years; Duhamel et al., 2006). Samples were incubated under simulated conditions for 4 to 5 h. Incubation boxes equipped with light filters (nickel screens) were used to reproduce the light level at the appropriate sample depths (50, 25, 15, 7, 3, 1% of transmitted light). Following incubation, 600 μL of KH_2PO_4 (10 mmol L^{-1}) was added to each flask in order to stop labelled DIP assimilation. Samples were kept in the dark to stop DIC uptake. Fractions of 50 mL were filtered through 25 mm polycarbonate membranes (0.2, 0.6 and 2 μm) which had been placed on GF/F filters soaked with saturated KH_2PO_4, using a low-pressure suction (<0.2 bars). When all samples were filtered, the pressure was increased to 0.6 bars for 5 s in order to eliminate un-incorporated ^{33}P. Filters were placed into scintillation vials (Wheaton low-potassium 6 mL glass-clear vials with screw-cap foil liner) with 150 μl of HCl (0.5 mol L^{-1}) in order to eliminate any un-incorporated ^{14}C. After 12 h, 6 ml of scintillation liquid (Ultimagold MV scintillation liquid, Packard) was added to each vial before the first count. Counting (count per minute – cpm) was carried out on a Packard Tri-Carb® 2100TR scintillation counter. In order to separate the activity due to ^{33}P from that of ^{14}C, we applied the method using the different half-lives of the two isotopes (For more details, see Duhamel et al., 2006). A second count was made after a year, samples having been preserved in the dark at room temperature. C and P uptake rates measurements in each size fraction (0.2–0.6; 0.6–2 and >2 μm) were obtained using difference calculations.

Bacterial production was determined by [^{3}H]-leucine incorporation using the centrifugation method (Smith and Azam, 1992) according to Van Wambeke et al. (2007b)[1]. A factor of 1.5 kg C mol leucine^{-1} was used to convert the incorporation of leucine to carbon equivalents, assuming no isotopic dilution (Kirchman, 1993).

2.3 Daily rates

The daily C uptake rates have been calculated using the method of Moutin et al. (1999). The model enables a conversion factor to be calculated which permits net hourly DIC uptake rates (nmol L^{-1} h^{-1}) to be transformed into net daily rates (nmol L^{-1} d^{-1}). The model takes into account the geographical position (latitude and longitude), the sampling date, the time of dawn, incubation start time and the time the incubation ended (GMT). The model of Moutin et al. (1999) that previously took theoretical solar radiation into account has been modified to take into account the surface irradiance measured on board.

Daily P uptake rates may be calculated simply by multiplying the hourly rate by 24. Indeed, in several studies (Perry and Eppley, 1981; Moutin et al., 2002), P uptake was shown to be constant over 24h.

2.4 Specific uptake rate estimates

Specific uptake rates (V^{sp}) have been calculated by dividing the estimators of production (heterotrophic bacterial production – HBP, C uptake rates – V_{DIC} or P uptake rates – V_{DIP}) by estimators of biomass (Phytoplankton and/or bacteria cytometric counts converted in AB and HBB, respectively, or particulate P – PartP). V^{sp}_{DIP} corresponds to the V_{DIP} to PartP ratio, V^{sp}_{DIC} corresponds to the V_{DIC} to AB ratio, HBP:HBB corresponds to the HBP to HBB ratio. A conversion factor of 10 fg C $cell^{-1}$ (Christian and Karl, 1994; Caron et al., 1995) has been used to convert heterotrophic bacterial abundance (counted by flow cytometry) to C equivalent. AB has been calculated using two methods. The first one uses a cell-number-to-biomass conversion factor. We chose the Campbell et al. (1997) estimates for *Prochlorococcus*, *Synechococcus* and Picoeukaryotes (Table 1). The second method uses a Chla-to-biomass conversion factor. For stations outside the gyre, we chose 70 g C g $Chla^{-1}$, the average value found for subtropical Atlantic Ocean total phytoplankton (Veldhuis and Kraay, 2004). For sta-

tions inside the gyre, we used values of Chla-to-biomass conversion factor varying with PAR: 185, 120, 90, and 20 g C g Chla^{-1} for 50 and 25%, 15%, 7%, and 3 and 1% of PAR, respectively. These factors were chose according to the results found by Veldhuis and Kraay (2004) at the most oligotrophic station of their transect in the Atlantic tropical gyre.

The V^{sp}_{DIP} have been calculated for four size fractions: 0.2–0.6; 0.6–2; >2 and >0.6 μm. We will develop arguments to show that they correspond to heterotrophic bacteria ($V^{sp}_{DIP<0.6}$), picophytoplankton ($V^{sp}_{DIP0.6-2}$), nano-micophytoplankton ($V^{sp}_{DIP>2}$) and total phytoplankton ($V^{sp}_{DIP>0.6}$), repectively. The V^{sp} are expressed as daily rates (d^{-1}) so they are comparable with values found in the literature.

3 Results

3.1 Cytometry data

We chose to separate bacteria from phytoplankton by filtrating through 0.6 μm filters. In this way, we determined bacteria V^{sp}_{DIP} in the 0.2–0.6 μm fraction. To verify the accuracy of our results, we counted the percentage of bacterial cells that passed through a 0.6-μm-filter using flow cytometry. On comparing the total and <0.6 μm sample counts, we found that on average, 91±10% of the heterotrophic bacteria passed through the 0.6-μm-filter whatever the trophic regime (n=90; all euphotic-layer depth included). This value was in the same range as values obtained in other studies (~80%; Obernosterer et al., 2003). Cytometry data showed that *Prochlorococcus* (when detectable), *Synechococcus* and Picoeucaryotes cells had an average size of 0.68±0.08 μm; 0.86±0.1 μm (1.16±0.02 μm for the upwelling stations) and 1.74±0.13 μm all over the transect, respectively (Results from Grob et al., 2007). Nevertheless, cytometry counts showed that 34±24% of the *Prochlorococcus* cells and 3±5% of the *Synechococcus* cells were found in the <0.6 μm fraction.

BGD
4, 2027–2068, 2007

3.2 Evaluation of using particulate phosphate as an estimator of living biomass

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. 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% PAR. PartP concentrations decreased to 5.3 nmol L^{-1} at the depth of 1% PAR while Chla concentrations increased from 0.05 to 0.19 μg L^{-1} from the surface waters down to 1% of PAR, respectively. So, contrary to Chla, PartP did not show a deep concentration maximum (Fig. 2). Phytoplankton cell counts by flow cytometry showed an increase from 1.1×10^5 to 2.8×10^5 cells mL^{-1} from surface water to the depth of 3% of PAR and a decrease to 1.3×10^5 cells mL^{-1} at the depth of 1% of PAR. In the same way, total cytometric counts (bacteria + phytoplankton) showed an increase from 6.8×10^5 to 8.5×10^5 cells mL^{-1} from the surface water to the depth of 15% of PAR and a decrease to 6.5×10^5 cells mL^{-1} at the depth of 1% of PAR. Variations in PartP concentration throughout the euphotic zone are closer to that of cell concentration than to Chla concentration.

Chla is largely used to estimate phytoplankton biomass (Trembaly and Legendre, 1994; Uitz et al., 2006). Nevertheless, as illustrated by Fig. 2, the C:Chla ratio is subjected to variations depending on light (Taylor et al., 1997). For this reason, only data between 50 and 15% of transmitted light are considered for the comparison of biomass estimates to Chla concentration, to avoid any biases associated with photoacclimatation. In order to check whether PartP below 0.6 μm is representative of bacteria and PartP above 0.6 μm is representative of phytoplankton biomass, data in terms of PartP and Chla were compared in the two fractions (Fig. 3). The relation between Chla and PartP in the 0.2–0.6 μm fraction was less significant than in the >0.6 μm fraction (r^2=0.31, P<0.001; and r^2=0.86, P<0.001, respectively; Fig. 3). This indicates that 69% and 14% of the dispersion can not be explained by the regression in the fractions between 0.2–0.6 μm and above 0.6 μm, respectively. The contribution of *Prochlorococcus* to PartP in the 0.2–0.6 μm fraction drives the correlation to Chla,

BGD
4, 2027–2068, 2007

but this correlation is comparatively weak and suggests the contributor to PartP are organisms that do not contain Chla. In other words, it is mainly free-living bacteria that contribute to PartP in the 0.2–0.6 μm fraction. In the same way, the essential part of the PartP in the >0.6 μm fractions was correlated to Chla, supporting the hypothesis that it corresponds essentially to phytoplankton biomass.

The regression slope between POC and PartP concentration was 349 (Fig. 4a) while between V_{DIC} and V_{DIP} was 57 (Fig. 4b). This indicates that the turnover rates of POC and PartP were different, and supports the hypothesis that P is more rapidly mineralized from dead material than C. The correlation between Chla and PartP concentration data was also 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 was a better indicator of living biomass than POC. Eutrophic stations have been omitted to avoid regressions being drawn by high values.

3.3 Evaluation of the use of V^{sp}_{DIP} as an estimator of bacteria and phytoplankton growth rates

We compared euphotic-layer averaged values of V^{sp} obtained from different methods (Fig. 5). For bacteria, we compared the values of $V^{sp}_{DIP<0.6}$ and of HBP:HBB (Fig. 5a). $V^{sp}_{DIP<0.6}$ values were 1.2 to 9.5 times higher than HBP:HBB values in rich areas (MAR to STB6 and STB15 to UPX) while in the centre of the gyre (STB7 to STB14), $V^{sp}_{DIP<0.6}$ values were 1.2 to 2.2 times lower than HBP:HBB values. Between MAR and STB21 stations, HBP:HBB values were quite low and constant (0.11±0.04) while $V^{sp}_{DIP<0.6}$ values varied widely from 0.04 to 1.11 d^{-1} depending the trophic regime encountered. As a consequence, the correlation between HBP:HBB ratio and $V^{sp}_{DIP<0.6}$ values, even excluding the "original" upwelling sites, was not significant (r^2=0.08, p>0.05). For phytoplankton, we compared the values of $V^{sp}_{DIC>0.6}$ and of $V^{sp}_{DIP>0.6}$. $V^{sp}_{DIC>0.6}$ can be obtained using a Chla-to-biomass or cell-number-to-biomass conversion factor. Using cell-number-to-biomass conversion factors according to Campbell et al. (1994, 1997)

we found V^{sp}_{DIC} values on average 2 and 12 times higher than using a Chla-to-biomass conversion factors. Highest differences were found in meso- and eutrophic areas. With this Chla-to-biomass conversion factor, $V^{sp}_{DIC>0.6}$ values were 1 to 4 and 0.6 to 1.8 times higher than $V^{sp}_{DIP>0.6}$ in the gyre and in the meso- and eutrophic areas, respectively (Fig. 5b). The major bias linked with the determination of V^{sp}_{DIC} is the choice of the conversion factor. Indeed, considering extreme values of the C:Chla ratio found in literature for surface layer of the equatorial Pacific ocean (40 and 200 g C Chla^{-1}, Chavez et al., 1996), values of V^{sp}_{DIC} can vary up to a factor 5. In the same way, we calculated V^{sp}_{DIC} using different cell-number-to-biomass conversion factor. Using conversion factors provided by Campbell et al. (1997) or by Bertilsson et al. (2003) for *Prochlorococcus*, *Synechococcus* and picoeucaryotes (see Table 1), we found that V^{sp}_{DIC} values were on average 20% higher with Campbell's value.

3.4 Estimates of bacteria and phytoplankton V^{sp}_{DIP} in the Southeast Pacific gyre

The different size fractions showed significant vertical and longitudinal variations of V^{sp}_{DIP} along the transect (P<0.001; Fig. 6). Highest values were found in rich areas while lower values were found in the upper part of the photic zone in the gyre area. In rich areas, the 0.2–0.6 μm fraction, assumed to be composed mostly of free-living heterotrophic bacteria, showed the highest euphotic zone averaged values of V^{sp}_{DIP} (0.6±0.3 to 3±1 d^{-1}) while in the gyre area, the 0.6–2 μm fraction, assumed to consist of picophytoplankton cells, showed the highest euphotic zone averaged values of V^{sp}_{DIP} (0.10±0.04 to 0.20±0.11 d^{-1}). Whatever the station, the >2 μm fraction had the lowest V^{sp}_{DIP} euphotic zone averaged values (0.02±0.07–0.6±0.2 d^{-1}). The variation of V^{sp}_{DIP} with depth in the 0.6–2 μm fraction was quite different from that of the >2 μm fraction, particularly in the west part of the gyre area. In the gyre area, while the >2 μm fraction showed quiet constant V^{sp}_{DIP} values with depth (no significant difference was found between V^{sp}_{DIP} values in the deep chlorophyll maximum layer (DCML) and the upper

BGD
4, 2027–2068, 2007

EGU

layer of the euphotic zone, P=0.161), the 0.6–2 μm fraction showed significantly higher values of V_{DIP}^{sp} in the DCML (P<0.001). The smaller size fraction (0.2–0.6 μm) showed quite low values throughout the euphotic zone in the oligotrophic area ($0.11 \pm 0.07\,d^{-1}$) and no significant tendency with depth was observed (P<0.001).

4 Discussion

Quantifying heterotrophic bacteria and phytoplankton μ in the ocean is of critical importance to understand many oceanographic processes since μ of individual populations control the ultimate composition of the assemblage (Banse, 1991). This, in turn, controls a large number of ecosystem properties, such as export of organic matter, nutrients utilization and production patterns. Knowledge of μ is critical to our understanding of the biotic responses to environmental forcing. The physiological responses are an integral component in mechanistic models to predict ecosystem trophodynamics. Nevertheless, studies of heterotrophic bacteria and phytoplankton assemblages are still scarce, especially in the Southeast Pacific. 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 both heterotrophic bacteria and two size fractions of phytoplankton μ. First, we discuss the production and biomass estimators; second, we discuss the P-based μ estimates obtained in the Southeast Pacific.

4.1 Biomass estimators

The distribution of phytoplankton is commonly described in terms of Chla (Huot et al., 2007). Because the Chla content varies between species and with light and nutrients (Philips et al., 1995; Sciandra et al., 1997; Finkel et al., 2004; Pérez et al., 2006; Moore et al., 2006), it is not an ideal biomass estimator (Breton et al., 2000; Le Floc'h et al., 2002). POC cannot be used directly because it contains a high proportion of detrital matter (Sobczak et al., 2002; Figs. 4a and d). The AB in terms of C is never directly

determined but derived from other variables: Chla, biovolumes or cell numbers which are then transformed using appropriate conversion factors. This entails a critical step in the estimation of AB: the choice of conversion factor. C:Chla values vary over a wide range (Table 2). For phytoplankton, cell-number-to-C conversion factor can vary significantly (Table 2) even at a species level (*Prochlorococcus* CCMP 1378: considering C is independent of light = 49±9 fg C cell^{-1} and considering C content varies with light = 65±67 and 48±10 fg C cell^{-1}, for cultures switched from low light to high light and from high light to low light, respectively – Cailliau et al., 1996; *Prochlorococcus* PCC 9511 grown in turbidostat under a daily light cycle = 27±6 fg C cell^{-1} – Clautre et al., 2002; *Synechococcus* WH8102 grown under continuous white light in batch cultures = 279.1±84.2 fg C cell^{-1} – Six et al., 2004). We found significant differences ($P<0.001$) in V^{sp}_{DIC} estimates according to the choice of phytoplankton cell-number-to-C or C:Chla conversion factors. So, although the employ of conversion factors is still largely used, it is difficult to choose the appropriate one. Because they vary with in situ conditions and species composition, it should be necessary to use different factors for all samples. This would result in a complex data analysis. Studies on heterotrophic bacterial communities have shown that the C cell content changes in relation to natural conditions and the physiological state of the bacterial assemblages (Table 2). Gundersen et al. (2002) showed that the outcome of HBB assessments is highly dependant on the choice of cell-specific conversion factors. In the same way, La Ferla and Leonardi (2005) demonstrated that the quantification of HBB based solely on abundance must be considered with caution because of the variability in cell volumes and morphotypes. Therefore, there is great uncertainty surrounding the estimate of C-based phytoplankton and heterotrophic bacterial μ, whatever the choice of biomass estimator.

P is an essential element required for life, used by all organisms. It is found in a wide range of molecules with varying cellular roles, going from storage of genetic information (nucleic acids: DNA, RNA) and energy (ATP, ADP, AMP) to structural composition (phospholipids). If participation of detrital P is low in the PartP stock, then it would represent cellular P content. Our results showed that PartP contained less detrital ma-

BGD
4, 2027–2068, 2007

terial than the POC (Fig. 4). This was indicated by significantly higher turnover rates of PartP compared to those of POC and a significant correlation between PartP and Chla concentrations. Similar observations have shown that P is preferentially released into the water column relative to other elements such as C and N (Menzel and Ryther, 1964; Knauer et al., 1979; Minster and Boulahdid, 1987; Loh and Bauer, 2000; Paytan et al., 2003). The use of PartP as a living biomass indicator is particularly well adapted to the open ocean. Indeed, in such areas, low values of detrital P are commonly found (~1% in equatorial Pacific Ocean, Faul et al., 2005). Nevertheless, even if the fraction of detrital P is negligible in the whole fraction, the size distribution of detrital P is not known and can affect the measurement of V^{sp}_{DIP} in each size fraction. It has been shown that the more the size of the organic matter decreases, the more refractory it is (the size-reactivity continuum hypothesis; Amon and Benner, 1996; Mannino and Harvey, 2000), therefore we can hypothesis that there is also a size-reactivity continuum in detrital matter that engender higher concentration of detrital matter in the smallest fraction. In this way, $V^{sp}_{DIP<0.6}$may be underestimated. The proportion of detrital P in PartP is high in coastal areas (Faul et al., 2005). Consequently, V^{sp}_{DIP} is more likely to be underestimated in the upwelling area. The other main advantage of using P instead of Chla is that PartP takes both bacteria and phytoplankton into account. So if it is possible to separate bacterial P from phytoplankton P in PartP, then it would be possible to estimate bacterial and phytoplankton V^{sp}_{DIP} in the same sample. Size fractionation was an adequate method for separating heterotrophic bacteria from phytoplankton since more than 90% of bacterial cells passed through the 0.6 μm-filters. However, an increasing fraction of *Prochlorococcus* cells passed through this filter when water became ultra-oligotrophic (in the centre of the gyre). Consequently, values of heterotrophic bacteria V^{sp}_{DIP} in the gyre may be biased due to the influence of *Prochlorococcus* cells. Nevertheless, it was shown that DIC uptake in the 0.2–0.6 μm fraction was negligible (data not shown) and therefore the phytoplankton production in this fraction was negligible. Thus, production in terms of P in the 0.2–0.6 μm fraction can be mainly attributed to free-living heterotrophic bacteria. Therefore, $V^{sp}_{DIP<0.6}$ gives a good representation of the

bacterial μ. In >0.6 μm size fractions, the nano and microzooplankton can account for a fraction of the PartP concentration values. Gasol et al. (1997) showed that zooplankton C-biomass (protozooplankton + mesozooplankton) could account for 13–21% and 15–65% of the total C-biomass in coastal and open ocean areas, respectively. Consequently, this could be a non negligible source of phytoplankton V^{sp}_{DIP} underestimation, particularly for the >2 μm size fraction.

4.2 DIP uptake rate measurements

Assuming the DIP to represent biologically available orthophosphate, we measured P uptake rates (V_{DIP}) in three size fractions. Daily P uptake rates were calculated by multiplying the hourly rate by 24. P uptake is generally shown to be constant over 24 h (Perry and Eppley, 1981; Harrison, 1983; Moutin et al., 2002) but diurnal variations in P uptake have been observed in some studies (Eppley et al., 1971; Harrison et al., 1977; Currie and Kalff, 1984). For the majority of stations, time course experiments for ^{33}P uptake were linear over 24 h, however there were some variations in P uptake rates at some stations along the BIOSOPE transect (Duhamel et al., 2006). The methodological problems associated with 24-h incubation experiments can be significant (Nalewajko and Garside, 1983; Harrison and Harris, 1986), especially in terms of losses. However, short incubation experiments are supposed to reduce the bias linked to such losses (see discussion in Duhamel et al., 2006). Nevertheless, it is important to stress that even if the <0.6 μm fraction is composed of solely heterotrophic bacteria, our data set does not prove that P is turning over at the same rate as the cells. Indeed, Nalewajko and Lean (1978) measured net phosphate uptake and influx rates in batch cultures of three algal cells. They showed that short-term P fluxes always exceeded the net increase in P biomass, indicating that the cells release P compounds back into the medium. To the best of our knowledge, the study of Nalewajko and Lean (1978) has not been repeated, so it would be necessary to repeat this experiment in a variety of field samples in order to verify that this phenomenon is not exclusively observed in cultures. C-based μ estimations are also submitted to such error type. Indeed, the re-

lease of assimilation products is common to C measurements. Claustre et al. (2007)[2] propose that the release of DOC in the Southeast Pacific should be a major process which could explain the high community (bacteria + phytoplankton) production rates. So, the release of DOC by phytoplankton cells produces bias in the evaluation of C production (Wood et al., 1992) and subsequently for C-based μ estimations.

4.3 Growth rates estimates

In 1981, Perry and Eppley used the ^{33}P uptake rate to PartP ratio to estimate the growth rate of phytoplankton making the statement that DIP assimilation was mediated by phytoplankton (their data indicating low heterotrophic activity). In 1996, Thingstad et al. used the ^{32}P uptake rate to PartP ratio to evaluate both heterotrophic bacteria and phytoplankton growth rates using 1 μm size fractionations. From these different studies, where the proportion of detrital matter in the PartP was negligible, it was possible to put forward the hypothesis that DIP was the sole source of P and so V_{DIP}^{sp} estimates could be used to assess bacteria and/or phytoplankton μ. Thus the idea of using P-based estimates of μ is not new. In this study we provide information on the variations in P-based μ values in a gradient of oligotrophy where the waters where P-repleted (DIP concentration and turnover time minimum values: 120 nmol L^{-1} and 7 d^{-1}, respectively; Moutin et al., 2007[4]). Most estimates for C-based heterotrophic bacterial growth rates in the open ocean fall into a wide range from zero to 10 d^{-1}, whilst phytoplankton appears to grow at rates of no more than 2 d^{-1} (Tables 1 and 3). We report a wide range in μ estimates ranging from 0 to 7 d^{-1} for heterotrophic bacteria and from 0 to 2 d^{-1} for phytoplankton. This range of values reflects the wide range of trophic status encountered during the BIOSOPE cruise.

Estimates of the production to the biomass ratio, based on the leucine incorpora-

[4]Moutin, T., Karl, D., Duhamel, S., Rimmelin, P., Raimbault, P., Van Mooy, B., and Claustre, H.: Phosphate availability and the ultimate control of nitrate input by nitrogen fixation in the Pacific Ocean, Biogeosciences Discuss., in preparation, 2007.

tion technique and C conversion of bacterial abundance (HBP:HBB) were significantly lower than those estimated by $V^{sp}_{DIP<0.6}$ in rich areas (MAR to STB6 and STB15 to UPX). Applying various methods (measurements of the natural abundance of nucleoid-containing cells by combined epifluorescence and phase-contrast microscopy; Detection of the reduction of the fluorogenic dye, 5-cyano-2,3-ditolyl tetrazolium chloride; Nucleic acid double staining (SYBR Green + propidium iodide); determination of membrane integrity by confocal laser-scanning microscopy), it has been shown that at any given time, a significant fraction of the bacterioplankton community has minimal or no metabolic activity (Zweifel and Hagström, 1995; Sherr et al., 1999; Gregori et al., 2001; Pirker et al., 2005). For this reason, μ estimates based on the HBP:HBB ratio could be underestimated. Our $V^{sp}_{DIP<0.6}$ values were significantly higher in the rich areas (MAR to STB6 and STB15 to UPX, $P<0.001$) than in the gyre area. In the same way, Morgan et al. (2006) found that bacterial growth rates (with μ=HBP/bacterial abundance, HBP deduced from ^{3}H-Thymidine method using conversion factor of 2×10^{18} cells × [mol TdR]$^{-1}$) were significantly greater on the shelf (0.8–1.8 d^{-1}) compared to the gyre (0.1–0.3 d^{-1}) in the western Black Sea.

Studies comparing bacterial and phytoplankton μ are scarce (Jones et al., 1996; Almeida et al., 2002). Measurements of V^{sp}_{DIP} in the 0.2–0.6, 0.6–2 and >2 μm fractions have enabled us to make such comparisons. In oligotrophic environments, heterotrophic bacterial μ can be higher or lower than that of phytoplankton. For example, Pérez et al. (2006) showed that in the upper water (mixed layer) of the subtropical Atlantic gyres, phytoplankton growth rates were 0.17 d^{-1} (from daily AP and picoplankton abundance transformed to B with the empirical conversion factors obtained by Zubkov et al. (2000), see Table 1). While in the same area, Zubkov et al. (2000) found that heterotrophic bacterial growth rates were 0.12 d^{-1} (using a conversion factor of 11.5 fg C per heterotrophic bacteria). In the upper 40 m of the North Pacific subtropical gyre, Jones et al. (1996) found 0.7 d^{-1} and ~1 d^{-1} for phytoplankton (estimated from the Chla-labelling technique) and heterotrophic bacteria (estimated from the incorporation of ^{3}H-adenine into DNA), respectively. We showed that picophytoplank-

BGD
4, 2027–2068, 2007

ton μ (0.14±0.04 d^{-1}) were higher that heterotrophic bacteria μ (0.11±0.07 d^{-1}) in the Southeast Pacific gyre and found values in the range than those found in the Atlantic and North pacific gyres by Pérez et al. (2006) and Zubkov et al. (2000), suggesting the existence of a microbial community that turns over very slowly. These relatively low values of μ for both phytoplankton and heterotrophic bacteria in the oligotrophic gyre area must be the result of the limitation of both bacterial and primary production by nitrogen (Bonnet et al., 2007[5]; Van Wambeke et al., 2007a[6]). Slow phytoplankton μ in the subtropical Atlantic have been explained in terms of the observed assimilation numbers and C:Chl-a ratios in a review by Marañon (2005). The light-saturated, chlorophyll normalised photosynthesis rate necessary to support phytoplankton μ of 1 d^{-1} would be well above those reported in the subtropical Atlantic (156±16 and 205±17 mg C m^{-2} d^{-1}, in the North and South Atlantic subtropical gyres, respectively; Pérez et al., 2006) which were in the range of those measured in the Southeast Pacific gyre (134±82 mg C m^{-2} d^{-1}; Van Wambeke et al., 2007b[1]). In coastal areas heterotrophic bacterial μ are often found to be lower than that of phytoplankton (Laws et al., 1984; Revilla et al., 2000). In the Southeast Pacific, we found that organisms in the <0.6 μm fraction had higher V^{sp}_{DIP} values than organisms in the >0.6 fraction in the rich areas (MAR to STB6 and STB15 to UPX), while in the hyperoligotrophic gyre, organisms in the 0.6–2 μm fraction yielded the highest V^{sp}_{DIP} values. Thus it may be deduced that the picophytoplankton was more efficient than nano-microphytoplankton and free living heterotrophic bacteria for growing in such hyperoligotrophic conditions.

There are relatively few studies comparing μ for different size fractions of natural phy-

[5]Bonnet, S., Guieu, C., Bruyant, F., Prasil, O., Raimbault, P., Gorbunov, M., Zehr, J. P., Grob, C., Masquelier, S., Garczareck, L., Moutin, T., Van Wambeke, F., and Claustre, H.: Nutrients controlling primary productivity in the South East Pacific, Biogeosciences Discuss., in preparation, 2007.

[6]Van Wambeke, F., Bonnet, S., Moutin, T., Raimbault, P., Alarçon, G., and Guieu, C.: Factors limiting heterotrophic prokaryotic production in the Southern Pacific Ocean, Biogeosciences Discuss., in preparation, 2007a.

toplanktonic communities (Pérez et al., 2006). In coastal eutrophic ecosystems, large phytoplankton have been reported to have faster growth rates than the small-sized phytoplankton (Cermeno et al., 2005 – C-specific photosynthetic rates). Nevertheless, in the Chilean upwelling area, there was no significant difference between V^{sp}_{DIP} for the two size-fractions of phytoplankton (0.5±0.3 and 0.4±0.2 d^{-1} for picophytoplankton and nano-microphytoplankton respectively, $p>0.05$). We found that picophytoplankton (0.6–2 μm) was growing 1 to 15 times faster than the nano-microphytoplankton (>2 μm) between the Marquesas Islands and Chile, with maximal differences in the gyre area. Differences in growth rates have been reported to be related to the specific composition of the planktonic community (Furnas, 1990). So the differences we observed could be related to differences between the taxonomic groups encountered along the BIOSOPE transect. Indeed, flow cytometry data showed high variations in the relative composition of picophytoplankton populations along the BIOSOPE transect (Grob et al., 2007). In the hyperoligotrophic region, the DCM corresponded to *Prochlorococcus* and picophytoeukaryotes maxima (Grob et al., 2007) as well as the maximum growth rates values of the picophytoplankton size fraction (Fig. 6).

In most of the oligotrophic area, phytoplankton μ were found to be higher in the upper mixed layer than within the proximity of the DCML (Malone et al., 1993 – with AP deduced from the ^{14}C labelling method and AB deduced using a C:Chla ratio or ^{14}C-Chla experiments ; Quevedo and Anadon, 2001 – dilution method). We found that picophytoplankton grew significantly faster at the DCML than in the upper part of the photic zone in the hyperoligotrophic gyre area (from STB7 to STB14; $P< 0.001$). Pérez et al. (2006) found the same trends in the subtropical Atlantic gyres with μ in the <2 μm fraction of 0.17±0.01 d^{-1} in the mixed layer and 0.25±0.02 d^{-1} in the DCML. Neverthelees, they found that large size fraction (>2 μm) was growing faster in the mixed layer than in the DCML while we found no statistical difference for $V^{sp}_{DIP>2}$ ($P=0.161$). Our results support the hypothesis of Pérez et al. (2006) that picoplankton might outcompete large cells in high-nutrient, low-light environment of the DCML.

The evaluation of μ is still a subject of debate (Marañon, 2005). It is not possible

to judge which technique is the best for measuring μ, if indeed any one technique is capable of doing such as each method measures a different aspect of growth. P-based μ estimates are one of the many ways to assess μ and comparing the results obtained using the different existing methods can help to understand how fast the cells grow in relation to the area of ocean under study (Christian et al., 1982; Laws et al., 1984; Jespersen et al., 1992).

5 Conclusions

Growth rate is a fundamental property of all organisms and is especially informative about the activity of microbial populations. The relative activity of bacteria and phytoplankton in oligotrophic oceans has significant implications for the food-web structure, nutrient cycling pathways and for sinking flux of organic matter. Contrary to C-based approaches, the P-based approach allows to assess bacterial and phytoplankton μ on the same sample, to the extend that size fraction can isolate efficiently both heterotrophic and phytoplanktonic fractions. We have characterized the vertical and longitudinal variability of P-based μ in three size fractions of plankton. Picophytoplankton (0.6–2 μm) grew faster than the large phytoplankton (>2 μm) all over the Southeast Pacific transect and particularly in the centre of the gyre. Thus, cells smaller than 2 μm were better adapted for growing in a wide range of trophic conditions than those greater than 2 μm. Heterotrophic bacteria (0.2–0.6 μm) showed higher variations in P-based μ with maximum rates in rich areas. Picophytoplankton grew faster than heterotrophic bacteria in the Southeast Pacific gyre with values in the range than those found in the Atlantic and North pacific gyres by Pérez et al. (2006) and Zubkov et al. (2000), suggesting the existence of a microbial community that turns over very slowly.

Acknowledgements. We express our gratitude to O. Ulloa, G. Alarcon and C. Grob for providing us cytometry data. We thank T. Bentley for help with improving the English. We also thank the crew of the R/V L'Atalante for outstanding shipboard support operations. D. Tailliez and C. Bournot are warmly thanked for their efficient help in CTD rosette management and

data processing. This is a contribution to the BIOSOPE project of the LEFE-CYBER program. This research was funded by the Centre National de la Recherche Scientifique (CNRS), the Institut des Sciences de l'Univers (INSU), the Centre National d'Etudes Spatiales (CNES), the European Space Agency (ESA), The National Aeronautics and Space Administration (NASA) and the Natural Sciences and Engineering Research Council of Canada (NSERC). This work is funded in part by the French Research and Education council.

References

Almeida, M. A., Cunha, M. A., and Alcântara, F.: Seasonal change in the proportion of bacterial and phytoplankton production along a salinity gradient in a shallow estuary, Hydrobiol., 475/476, 251–262, 2002.

Amon, R. M. W. and Benner, R.: Bacterial utilization of different size classes of dissolved organic matter, Limnol. Oceanogr., 41, 41–51, 1996.

Arin, L., Moran, X. A. G., and Estrada, M.: Phytoplankton size distribution and growth rates in the Alboran Sea (SW Mediterranean): short term variability related to mesoscale hydrodynamics, J. Plankton Res., 24, 1019–1033, 2002.

Aristegui, J., Hernandez-Leon, S., Montero, M. F., and Gomez, M.: The seasonal planktonic cycle in coastal waters of the Canary Islands, Sci. Mar., 65, 51–58, 2001.

Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A., and Thingstad, F.: The ecological role of water-column microbes in the sea, Mar. Ecol. Prog. Ser., 10, 257–263, 1983.

Banse, K.: Rates of phytoplankton cell division in the field and in iron enrichment experiments, Limnol. Oceanogr., 36, 1886–1898, 1991.

Banse, K.: Should we continue to measure ^{14}C-uptake by phytoplankton for another 50 years?, Limnol. Oceanogr.: Bull., 11, 45–46, 2002.

Becquevort, S., Bouvier, T., Lancelot, C., Cauwet, G., Deliat, G., Egorov, V. N., and Popovichev, V. N.: The seasonal modulation of organic matter utilization by bacteria in the Danube–Black Sea mixing zone, Estuar., Coast. Shelf Sci., 54, 337–354, 2002.

Berman, T.: Multiple isotopic tracer methods in the study of growth, dynamics and metabolic processes in marine ecosystems, in: Primary Productivity in the Sea, edited by: Falkowski, P., p. 213–229, Plenum Publishing, 1980.

Bertilsson, S., Berglund, O., Karl, D. M., and Chisholm, S. W.: Elemental composition of marine

Prochlorococcus and Synechococcus: Implications for the ecological stoichiometry of the sea, Limnol. Oceanogr., 48, 1721–1731, 2003.
Björkman, K. M. and Karl, D. M.: Bioavailability of dissoved organic phosphorus in the euphotic zone at Station ALOHA, North Pacific Subtropical Gyre, Limnol. Oceanogr., 48, 1049–1057, 2003.
Breton, E., Brunet, C., Sautour, B., and Brylinski, J. M.: Annual variations of phytoplankton biomass in the Eastern English Channel: comparison by pigment signatures and microscopic counts. J. Plankton Res., 22, 1423–1440, 2000.
Brock, T. D.: Microbial growth rates in nature, Bacteriol. Rev., 35, 39–58, 1971.
Buck, K. R., Chavez, F. P., and Campbell, L.: Basin-wide distributions of living carbon components and the inverted trophic pyramid of the central gyre of the North Atlantic Ocean, summer 1993, Aquat. Microb. Ecol., 10, 283–298, 1996.
Cailliau, C., Claustre, H., Vidussi, F., Marie, D., and Vaulot, D.: Carbon biomass and gross growth rates as estimated from 14C pigment labelling method during photoacclimation in Prochlorococcus CCMP1378), Mar. Ecol. Progr. Ser., 145, 209–221, 1996.
Campbell, L., Liu, H., Nolla, H. A., and Vaulot, D.: Annual variability of phytoplankton and bacteria in the subtropical North Pacific Ocean at Station ALOHA during the 1991–1994 ENSO event, Deep-Sea Res. Part I., 44, 167–192, 1997.
Campbell, L., Nolla, H. A., and Vaulot, D.: The importance of *Prochlorococcus* to communitu structure in the central North Pacific Ocean, Limnol. Oceanogr., 39, 954–961, 1994.
Caron, D. A., Dam, H. G., Kremer, P., Lessard, E. J., Madin, L. P., Malone, T. C., Napp, J. M., Peele, E. R., Roman, M. R., and Youngbluth, M. J.: The contribution of microorganisms to particulate carbon and nitrogen in surface waters of the Sargasso Sea near Bermuda, Deep-Sea Res., 42, 943–972, 1995.
Cermeno, P., Maranon, E., Rodriguez, J., and Fernandez, E.: Large-sized phytoplankton sustain higher carbon-specific photosynthesis than smaller cells in a coastal eutrophic ecosystem, Mar. Ecol. Progr. Ser., 297, 51–60, 2005.
Chavez, F. P., Buck, K. R., Coale, K. H., Martin, J. H., DiTullio, G. R., Welshmeyer, N. A., Jacobson, A. C., and Barber, R. T.: Growth rates, grazing, sinking, and iron limitation of equatorial Pacific phytoplankton, Limnol. Oceanogr., 36, 1816–1833, 1991.
Chavez, F. P., Buck, K. R., Service, S. K., Newton, J., and Barber, R. T.: Phytoplankton variability in the central and eastern tropical Pacific, Deep-Sea Res., 43, 835–870, 1996.
Christian, R. R., Hanson, R. B., and Newell, S. Y.: Comparison of methods for measurement

of bacterial growth rates in mixed batch cultures, Appl. Environ. Microbiol., 43, 1160–1165, 1982.
Christian, J. R. and Karl, D. M.: Microbial community structure at the U.S. -Joint Global Ocean flux Study Station ALOHA: Inverse methods for estimating biochemical indicator ratios, J. Geophys. Res., 99(C7), 14 269–14 276, 1994.
Clark, L. L., Ingall, E. D., and Benner, R.: Marine organic phosphorus cycling: Novel insights from nuclear magnetic resonance, Amer. J. Sci., 2999, 724–737, 1999.
Claustre, H., Kerherve, P., Marty, J. C., Prieur, L., Videau, C., and Hecq, J. H.: Phytoplankton Dynamics Associated with a Geostrophic Front – Ecological and Biogeochemical Implications, J. Mar. Res., 52, 711–742, 1994.
Cloern, J. E., Alpine, A. E., Cole, B. E., and Heller T.: Seasonal changes in the spatial distribution of phytoplankton in small, temperate-zone lakes, J. Plankton Res., 14, 1017–1024, 1992.
Cochlan, W.: The heterotrophic bacterial response during a mesoscale iron enrichment experiment (IronEx II) in the eastern equatorial Pacific Ocean, Limnol. Oceanogr., 46, 428–435, 2001.
Cotner, J. B. and Biddanda, B. A.: Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems, Ecosystems, 5, 105–121, 2002.
Currie, D. J. and Kalff, J.: The relative importance of bacterioplankton and phytoplankton in phosphorus uptake in freshwater, Limnol. Oceanogr., 29, 311–321, 1984.
Dickson, M.-L. and Wheeler, P. A.: Nitrate uptake rates in a coastal upwelling regime: A comparison of PN-specific, absolute, and Chl a-specific rates, Limnol. Oceanogr., 40, 533–543, 1995.
Ducklow, H. W.: Production and fate of bacteria in the oceans, Bioscience, 33, 494–501, 1983.
Duhamel, S., Zeman, F., and Moutin, T.: A dual-labeling method for the simultaneous measurement of dissolved inorganic carbon and phosphate uptake by marine planktonic species, Limnol. Oceanogr. Meth., 4, 416–425, 2006.
Eppley, R. W.: Temperature and phytoplankton growth in the sea, Fish. Bull., 70, 1063–1085, 1972.
Eppley, R. W., Carlucci, A. F., Holm-Hansen, O., Kiefer, D., McCarthy, J. J., Venrick, E., and Williams, P. M.: Phytoplankton Growth and Composition in Shipboard Cultures Supplied with Nitrate, Ammonium, or Urea as the Nitrogen Source, Limnol. Oceanogr., 16(5), 741–751, 1971.

Eppley, R. W.: Relations between nutrient assimilation and growth rate in phytoplankton with a brief review of estimates of growth rate in the ocean, in: Physiological Bases of Phytoplankton Ecology, edited by: Platt, T., Can. Bull. Fish. Aquat. Sci., 210, 251–263, 1981.
Fabricius, K., Yahel, G., and Genin, A.: In situ depletion of phytoplankton by an azooxanthellate soft coral, Limnol. Oceanogr., 43, 354–356, 1998.
Faul, K. L., Paytan, A., and Delaney, M. L.: Phosphorus distribution in sinking oceanic particulate matter, Mar. Chem., 97, 307–333, 2005.
Finkel, Z. V., Irwin, A. J., and Schofield, O.: Resource limitation alters the 3/4 size scaling of metabolic rates in phytoplankton, Mar. Ecol. Progr. Ser., 273, 269–279, 2004.
Fuhrman, J. A. and Azam, F.: Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: Evaluation and field results, Mar. Biol., 66, 109–120, 1982.
Fuhrman, J. A. and Azam, F.: Bacterioplankton secondary production estimates for coastal waters of British Colombia, Antarctica and California, Appl. Environ. Microbiol., 39, 1085–1095, 1980.
Fukuda, R., Ogawa, H., Nagata, T., and Koike, I.: Direct determination of carbon and nitrogen contents of natural bacterial assemblages in marine environments, Appl. Environ. Microbiol., 64, 3352–3358, 1998.
Furnas, M. J.: In situ growth rates of marine phytoplankton: approaches to measurement, community and species growth rates, J. Plankton Res., 12, 1117–1151, 1990.
Gasol, J. M., Del Giogio, P., and Duarte, C. M.: Biomass distribution in marine planktonic communities, Limnol. Oceanogr., 42, 1353–1363, 1997.
Gasol, J. M., Del Giogio, P., Massana, R., and Duarte, C. M.: Active versus inactive bacteria: size-dependence in a coastal marine plankton community, Mar. Ecol. Progr. Ser., 128, 91–97, 1995.
Goericke, R.: Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda, Limnol. Oceanogr., 43, 921–935, 1998.
Grégori, G., Citterio, S., Ghiani, A., Labra, M., Sgorbati, S., Brown, S., and Denis, M.: Resolution of viable and membrane-compromised bacteria in freshwater and marine waters based on analytical flow cytometry and nucleic acid double staining, Appl. Environ. Microbiol., 67, 4662–4670, 2001.
Grob, C., Ulloa, O., Claustre, H., Huot, Y., Alarcon, G., and Marie, D.: Contribution of picoplank-

ton to the total particulate organic carbon (POC) concentration in the eastern South Pacific, Biogeosciences Discuss., 4, 1461–1497, 2007, http://www.biogeosciences-discuss.net/4/1461/2007/.
Gundersen, K., Heldal, M., Norland, S., Purdie, D. A., and Knap, A. H.: Elemental C, N, and P cell content of individual bacteria collected at the Bermuda Atlantic Time-series Study (BATS) site, Limnol. Oceanogr., 47, 1525–1530, 2002.
Hagstrom, A., Larsson, U., Horstedt, P., and Normark, S.: Frequency of dividing cells, a new approach to the determination of bacterial growth rates in aquatic environments, Appl. Environ. Microbiol., 37, 805–812, 1979.
Harrison, W. G. and Harris L. R.: Isotope dilution and its effects on measurements of nitrogen and phosphorus by oceanic microplankton, Mar. Ecol. Progr. Ser., 27, 253–261, 1986.
Harrison, W. G.: The time-course of uptake of inorganic and organic nitrogen compounds by phytoplankton from the Eastern Canadian Arctic: A comparison with temperate and tropical populations, Limnol. Oceanogr., 28, 1231–1237, 1983.
Harrison, W. G., Azam, F., Renger, E. H., and Eppley, R. W.: Some experiments on phosphate assimilation by coastal marine plankton, Mar. Biol., 40, 9–18, 1977.
Herbland, A., LeBouteiller, A., and Raimbault, P.: Size structure of phytoplankton in the Equatorial Atlantic Ocean, Deep Sea Res., 32, 819–836, 1985.
Holl, C. M. and Montoya, J. P.: Interactions between nitrate uptake and nitrogen fixation in continuous cultures of the marine diazotroph Trichodesmium (Cyanobacteria), J. Phycol., 41, 1178–1183, 2005.
Houlbrèque, F., Delesalle, B., Blanchot, J., Montel, Y., and Ferrier-Pagès, C.: Picoplankton removal by the coral reef community of La Prévoyante, Mayotte Island, Aquat. Microb.Ecol., 44, 59–70, 2006.
Huot, Y., Babin, M., Bruyant, F., Grob, C., Twardowski, M. S., and Claustre, H.: Does chlorophyll a provide the best index of phytoplankton biomass for primary productivity studies?, Biogeosciences Discuss., 4, 707–745, 2007, http://www.biogeosciences-discuss.net/4/707/2007/.
Jespersen, A.-M., Nielsen, J., Riemann, B., and Sondergaard, M.: Carbon-specific phytoplankton growth rates: a comparison of methods, J. Plankton Res., 14, 637–648, 1992.
Jones, D. R., Karl, D. M., and Laws, E. A.: Growth rates and production of heterotrophic bacteria and phytoplankton in the North Pacific subtropical gyre, Deep Sea Res. Part I, 43, 1567–1580, 1996.

Kirchman, D. L.: Calculating microbial growth rates from data on production and standing stocks, Mar. Ecol. Progr. Ser., 233, 303–306, 2002.
Kirchman, D., K'nees, E., and Hodson, R.: Leucine incorporation and its potential as a measure of protein synthesis by bacteria in natural aquatic systems, Appl. Environ. Microbiol., 49, 599–607, 1985.
Kirchman, D. L.: Leucine incorporation as a measure of biomass production by heterotrophic bacteria, in: Handbook of methods in aquatic microbial ecology, edited by: Kemp, P. F., Sherr, B. F., Sherr, E. B., and Cole, J. J., Boca Raton: Lewis, pp. 509–512, 1993.
Kirkwood, D. S.: Stability of solutions of nutrient salts during storage, Mar. Chem., 38, 151–164, 1992.
Knauer, G. A., Martin, J. H., and Bruland, K. W.: Fluxes of particulate carbon, nitrogen, and phosphorus in the upper water column of the northeast Pacific, Deep-Sea Res., 26, 97–108, 1979.
Krell, A., Schnack-Schiel, S. B., Thomas, D. N., Kattner, G., Zipan, W., and Dieckmann, G. S.: Phytoplankton dynamics in relation to hydrography, nutrients and zooplankton at the onset of sea ice formation in the eastern Weddell Sea (Antarctica), Polar Biol., 28, 700–713, 2005.
La Ferla, R. and Leonardi, M.: Ecological implications of biomass and morphotype variations of bacterioplankton: an example in a coastal zone of the Northern Adriatic Sea (Mediterranean), Mar. Ecol., 26, 82–88, 2005.
Landry, M. R. and Hassett, R. P.: Estimating the grazing impact of marine micro-zooplankton, Mar. Biol., 67, 283–288, 1982.
Laws, E. A., Ditullio, G. R., and Redalje, D. G.: High phytoplankton growth and production rates in the North Pacific subtropical gyre, Limnol. Oceanogr., 32, 905–918, 1987.
Laws, E. A., Redalje, D. G., Haas, L. W., Bienfang, P. K., Eppley, R. W., Harrison, W. G., Karl, D. M., and Marra, J.: High phytoplankton growth and production rates in oligotrophic Hawaiian coastal waters, Limnol. Oceanogr., 29, 1161–1169, 1984.
Le Floc'h, E., Gilbert, M., and Sciandra, A.: An automatic device for in vivo absorption spectra acquisition and chlorophyll estimation in phytoplankton cultures, J. Appl. Phycol., 14, 435–444, 2002.
Le Quéré, C., Harrison, S., Prentice, I. C., Buitenhuis, E. T., Aumont, O., Bopp, L., Claustre, H., Cotrim Da Cunha, L., Geider, R., Giraud, X., Klass, C., Kohfeld, K. E., Legendre, K. L., Manizza, M, Platt, T., Rivkin, R. B., Sathyendranath, S., Uitz, J., Watson, Y. J., and Wofl-Glaro, D.: Ecosystem dynamics based on plankton functional types for global ocean

biogeochemistry models, Global Change Biol., 11, 1–25, 2005.
Lee, S. and Fuhrman, J. A.: Relationships between biovolume and biomass of naturally derived marine bacterioplankton, Appl. Environ. Microbiol., 53, 1298–1303, 1987.
Letelier, R. M., Dore, J. E., Winn, C. D., and Karl, D. M.: Seasonal and interannual variations in photosynthetic carbon assimilation at Station, Deep Sea Res. Part II, 43, 467–490, 1996.
Lipschultz, F.: Nitrogen-specific uptake rates of marine phytoplankton isolated from natural populations of particles by flow cytometry, Mar. Ecol. Progr. Ser., 123, 245–258, 1995.
Liu, H. B., Landry, M., Campbell, L., and Vaulot, D.: Prochlorococcus growth rates in the central equatorial Pacific: an application of the f_{max} approach, J. Geophys. Res.-Ocean., 104,, 3391–3399, 1999.
Loh, A. N., Bauer, J. E., and Druffel, E. R. M.: Variable ageing and storage of dissolved organic components in the open ocean, Nature, 430, 877–881, 2004.
Macedo, M. F. and Duarte, C. M.: Phytoplankton production modelling in three marine ecosystems – static versus dynamic approach, Ecol. Model., 190, 299–316, 2006.
Malone, T. C., Pike, S. E., and Conley, D. J.: Transient variations in phytoplankton productivity at the JGOFS Bermuda time series station, Deep Sea Res. Part I, 40, 903–924, 1993.
Mannino, A. and Harvey, H. R.: Biochemical composition of particles and dissolved organic matter along an estuarine gradient: Sources and implications for DOM reactivity, Limnol. Oceanogr., 45, 775–788, 2000.
Maranon, E., Holligan, P., Varela, M., Mourino, B., and Bale, A. J.: Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean, Deep Sea Res. Part I, 47, 825–857, 2000.
Maranon, E.: Phytoplankton growth rates in the Atlantic subtropical gyres, Limnol. Oceanogr., 50, 299–301, 2005.
Marie, D., Partensky, F., Simon, N., Guillou, L., and Vaulot, D.: Flow cytometry analysis of marine picoplankton, in: Living Colors: Protocols in Flow Cytometry and Cell sorting, edited by: Diamond, R. A. and DeMaggio, S., 421–454, 2000a.
Marie, D., Simon, N., Guillou, L., Partensky, F., and Vaulot, D.: DNA, RNA analysis of phytoplankton by flow cytometry, in: Current Protocols in Cytometry, John Wiley & Sons, Inc., 11.12.1–18, 2000b.
Menzel, D. W. and Ryther, J. H.: The composition of particulate organic matter in the western north Atlantic, Limnol. Oceanogr., 9, 179–186, 1964.
Minster, J. F. and Boulahdid, M.: Redfield ratios along isopycnal surfaces – a complementary

study, Deep-sea Res. Part I, 34, 1981–2003, 1987.
Moore, C. M., Ostrowski, M., Scanlan, D. J., Feren, K., and Sweetsir, T.: Phytoplankton photoacclimation and photoadaptation in response to environmental gradients in a shelf sea, Limnol. Oceanogr., 51(2), 936–949, 2006.
Moreira-Turcq, P. F., Cauwet, G., and Martin, J. M.: Contribution of flow cytometry to estimate picoplankton biomass in estuarine systems, Hydrobiol., 462, 157–168, 2001.
Morgan, J. A., Quinby, H. L., and Ducklow, H. W.: Bacterial abundance and production in the western Black Sea, Deep Sea Res. Part II, 53, 1945–1960, 2006.
Moutin, T., Raimbault, P., and Poggiale, J.-C.: Production primaire dans les eaux de surface de la Méditerranée occidentale, Calcul de la production journalière, C. R. Acad. Sci., 322, 651–659, 1999.
Moutin, T., Thingstad, T. F., Van Wambeke, F., Marie, D., Slawyk, G., Raimbault, P., and Claustre, H.: Does competition for nanomolar phosphate supply explain the predominance of the cyanobacterium Synechococcus?, Limnol. Oceanogr., 47, 1562–1567, 2002.
Mulholland, M. R., Floge, S., Carpenter, E. J., and Capone, D. G.: Phosphorus dynamics in cultures and natural populations of Trichodesmium spp., Mar. Ecol.Progr. Ser., 239, 45–55, 2002.
Nalewajko, C. and Garside, C.: Methodological problems in the simultaneous assessment of photosynthesis and nutrient uptake in phytoplankton as functions of light intensity and cell size, Limnol. Oceanogr., 28, 591–597, 1983.
Nalewajko, C. and Lean, D. R.: Phosphorus kinetics-algal growth relationships in batch cultures, Mitt. Int. Ver. Theor. Angew. Limnol., 21, 184–192, 1978.
Paytan, A., Cade-Menun, B. J., Mclaughlin, K., and Faul, K. L.: Selective phosphorus regeneration of sinking marine particles: evidence from 31P-NMR, Mar. Chem., 82, 55–70, 2003.
Pérez, V., Fernandez, E., Maranon, E., Moran, X. A. G., and Zubkov, M.: Vertical distribution of phytoplankton biomass, production and growth in the Atlantic subtropical gyres, Deep-Sea Res. I, 53, 1616–1634, 2006.
Perry, M. J. and Eppley, R. W.: Phosphate uptake by phytoplankton in the central North Pacific Ocean, Deep-Sea Res., 28A, 39–49, 1981.
Perry, M. J. and Eppley, R. W.: Phosphate uptake by phytoplankton in the central North Pacific Ocean, Deep-Sea Res., 28, 39–49, 1981.
Philips, E. J., Aldridge, F. J., Schelske, C. L., and Crisman, T. L.: Relationships between light availability, chlorophyll a, and tripton in a large, shallow subtropical lake, Limnol. Oceanogr.,

40(2), 416–421, 1995.
Pirker, H., Pausz, C., Stoderegger, K. E., and Herndl, G. J.: Simultaneous measurement of metabolic activity and membrane integrity in marine bacterioplankton determined by confocal laser-scanning microscopy, Aquat. Microb. Ecol., 39, 225–233, 2005.
Pujo-Pay, M. and Raimbault, P.: Improvement of the wet-oxidation procedure for simultaneous determination of particulate organic nitrogen and phosphorus collected on filters, Mar. Ecol. Progr. Ser., 105, 203–207, 1994.
Quevedo, M. and Anadon, R.: Protist control of phytoplankton growth in the subtropical noth-east Atlantic, Mar. Ecol. Progr. Ser., 221, 29–38, 2001.
Raimbault, P., Diaz, F., and Boudjellal, B.: Simultaneous determination of particulate forms of carbon, nitrogen and phosphorus collected on filters using a semi-automatic wet-oxidation procedure, Mar. Ecol. Progr. Ser., 180, 289–295, 1999.
Redalje, D. G. and Laws, E. A.: A new method for estimating phytoplankton growth rates and carbon biomass, Mar. Biol., 62, 73–79, 1981.
Redfield, A. C., Ketchum, B. H., and Richards, F. A.: The influence of organisms on the composition of seawater, p. 26–77, in: The Sea, edited by: Hill, M. N., Wiley, 1963.
Revilla, M., Iriarte, A., Madariaga, I., and Orive, E.: Bacterial and phytoplankton dynamics along a trophic gradient in a shallow temperate estuary, Est. Coast. Shelf Sci., 50(3), 297–313, 2000.
Riemann, B., Bell, R. T., and Jorgensen, N. O. G.: Incorporation of thymidine, adenine and leucine into natural bacterial assemblages, Mar. Ecol. Prog. Ser., 65, 87–94, 1990.
Rodier, M., Eldin, G., and Le Borgne, R.: The Western Boundary of the Equatorial Pacific Upwelling: Some Consequences of Climatic Variability on Hydrological and Planktonic Properties, J. Oceanogr., 56, 463–471, 2000.
Saunders, P. A., Deibel, D., Stevens, C. J., Rivkin, R. B., Lee, S. H., and Klein, B.: Copepod herbivory rate in a large arctic polynya and its relationship to seasonal and spatial variation in copepod and phytoplankton biomass, Mar. Ecol. Progr. Ser., 261, 183–199, 2003.
Sciandra, A., Gostan, J., Collos, Y., Descola-Gros, C., Leboulanger, C., Martin-Jézéquel, V., Denis, M., Lefèvre, D., Copin-Montégut, C., and Avril, B.: Growth-compensating phenomena in continuous cultures of Dunaliella tertiolecta limited simultaneously by light and nitrate, Limnol. Oceanogr., 42(6), 1325–1339, 1997.
Sherr E. B., Sherr, B. F., and Sigmon, C. T.: Activity of marine bacteria under incubated and in situ conditions, Aquat. Microb. Ecol., 20, 213–223, 1999.

Sherr, E., Sherr, B., and Cowles, T.: Mesoscale variability in bacterial activity in the Northeast Pacific Ocean off Oregon, USA, Aquat. Microb. Ecol., 25, 21–30, 2001.
Six, C., Thomas, J. C., Brahamsha, B., Lemoine, Y., and Partensky, F.: Photophysiology of the marine cyanobacterium Synechococcus sp. WH8102, a new model organism, Appl. Environ. Microbiol., 35, 17–29, 2004.
Smith, D. C. and Azam, F.: A simple, economical method for measuring bacterial protein synthesis rates in seawater using 3H-leucine, Mar. Microb. Food Webs, 6(2), 107–114, 1992.
Smith, J. W., Marra, O. J., Hiscock, M. R., and Barber, R. T.: The seasonal cycle of phytoplankton biomass and primary productivity in the Ross Sea, Antarctica, Deep Sea Res. Part II, 47, 3119–3140, 2000.
Sobczak, W. V., Cloern, J. E., Jassby, A. D., and Muller-Solger, A. B.: Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources, Proc. Natl. Acad. Sci., USA 99, 8101–8105, 2002.
Steeman-Nielsen, E.: Measurement of production of organic matter in the sea by means of carbon-14, Nature, 267, 684–685, 1951.
Strickland, J. D. H. and Parsons, T. R.: A practical handbook of seawater analysis, Bull. Fish. Res. Board of Canada, 1972.
Taylor, A., Geider, R., and Gilbert, F.: Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll a ratios: results of a modelling study, Mar. Ecol. Prog. Ser., 152, 51–66, 1997.
Thingstad, T. F., Riemann, B., Havskum, H., and Garde, K.: Incorporation rates and biomass content of C and P in phytoplankton and bacteria in the Bay of Aarhus (Denmark) June 1992, J. Plank. Res., 18, 97–121, 1996.
Tremblay, J. and Legendre, L.: A model for the size-fractionated biomass and production of marine phytoplankton, Limnol. Oceanogr., 39, 2004–2014, 1994.
Uitz, J., Claustre, H., Morel, A., and Hooker, S. B.: Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll, J. Geophys. Res., 111, C08005, doi:10.1029/2005JC003207, 2006.
Vadstein, O., Jensen, A., Olsen, Y., and Reinertsen, H.: Growth and phosphorus status of limnetic phytoplankton and bacteria, Limnol. Oceanogr., 33, 489–503, 1988.
Van Mooy, B. A. S., Rocap, G., Fredricks, H. F., Evans, C. T., and Devol, A. H.: Sulfolipids dramatically decrease phosphorus demand by picocyanobacteria in oligotrophic marine environments, Proc. Natl. Acad. Sci., 103, 8607–8612, 2006.

Vaulot, D.: Estimate of phytoplankton division rates by the mitotic index method: The f_{max} approach revisited, Limnol. Oceanogr., 37(3), 1992, 644–649, 1992.
Veldhuis, M. J. W. and Kraay, G. W.: Phytoplankton in the subtropical Atlantic Ocean: towards a better assessment of biomass and composition, Deep-Sea Res., 51, 507–530, 2004.
Watson, S. W., Novitsky, T. J., Quinby, H. L., and Valois, F. W.: Determination of bacterial number and biomass in the marine environment, Appl. Environ. Microbiol., 33, 940–946, 1977.
Welschmeyer, N. A., Goericke, R., Strom, S., and Peterson, W. T.: Phytoplankton growth and herbivory in the subarctic Pacific: a chemotaxonomic analysis, Limnol. Oceanogr., 36, 1631–1649, 1991.
Welschmeyer, N. A.: Fluorimetric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments, Limnol. Oceanogr., 39, 1985–1992, 1994.
Wood, A. M., Rai, H., Garnier, J., Kairesalo, T., Gresens, S., Orive, E., and Ravail, B.: Practical approaches to algal excretion, Mar. Microb. Food Webs, 6, 21–38, 1992.
Zubkov, M. V., Sleigh, M. A., Burkill, P. H., and Leakey, R. J. G.: Picoplankton community structure on the Atlantic Meridional Transect: a comparison between seasons, Prog. Oceanogr., 45(3–4), 369–386, 2000.
Zubkov, M. V., Sleigh, M. A., Tarran, G. A., Burkill, P. H., and Leakey, R. J. G.: Picoplanktonic community structure on an Atlantic transect from 50° N to 50° S, Deep Sea Res. Part I, 45, 1339–1355, 1998.
Zweifel, U. L. and Hagstrom, A.: Total Counts of Marine Bacteria Include a Large Fraction of Non-Nucleoid-Containing Bacteria (Ghosts), Appl. Environ. Microbiol., 61, 2180–2185, 1995.

Table 1. Review of values of biovolume-to-biomass and cell-number-to-biomass conversion factors.

Biovolume-to-biomass conversion factor		
Biovolume:B (g of C cm^{-3})	Organisms – location	Reference
0.121	Bacteria seawater or cultures	Watson et al. (1977)
0.38±0.05	Heterotrophic bacteria – pebble beach (Long Island) or culture	Lee and Fuhrman (1987)
Cell-number-to-biomass conversion factor		
Cell:B (fg of C $cell^{-1}$)	Organisms – location	Reference
20±0.8	Heterotrophic bacteria – pebble beach (Long Island) or culture	Lee and Fuhrman (1987)
5.9 to 47.9	Heterotrophic bacteria – coastal environments	Fukuda et al. (1998)
13	Heterotrophic bacteria – subtropical Pacific Ocean	Fukuda et al. (1998)
12.4	Heterotrophic bacteria – Oceanic environments	Fukuda et al. (1999)
10	Heterotrophic bacteria – subtropical Pacific Ocean	Christian and Karl (1994)
15	Heterotrophic bacteria – Sargasso Sea	Caron et al. (1995)
5.83	Heterotrophic bacteria – Northern Adriatic Sea (warm period)	La Ferla and Leonardi (2005)
42.17	Heterotrophic bacteria – Northern Adriatic Sea (cold period)	La Ferla and Leonardi (2005)
20	Heterotrophic bacteria – Station ALOHA	Campbell et al. (1997)
53	Prochlorococcus – Station ALOHA	Campbell et al. (1997)
46	Prochlorococcus – cultures *Prochlorococcus* MED4	Bertilsson et al. (2003)
29	Prochlorococcus – Atlantic transect from 50° N to 50° S	Zubkov et al. (1998)
279.1±84.2	Synechococcus – cultures *Synechococcus* WH8102	Six et al. (2004)
250	Synechococcus – Station ALOHA	Campbell et al. (1997)
92	Synechococcus – cultures *Synechococcus* WH8012	Bertilsson et al. (2003)
100	Synechococcus – Atlantic transect from 50° N to 50° S	Zubkov et al. (1998)
2108	Picoeukaryote – Station ALOHA	Campbell et al. (1997)
1500	Picoeukaryote – Atlantic transect from 50° N to 50° S	Zubkov et al. (1998)

Table 2. Review of values of growth rate (d^{-1}) and of C:Chla ratio (gC $gChla^{-1}$). The first part of the table illustrates examples of C-based growth rates values and corresponding measured C:Chla conversion factors values. The second part illustrates examples of values of C:Chla ratio chose by the authors for growth calculations.

Growth rate	C:Chla	Organisms – location	Reference
d^{-1}	gC $gChla^{-1}$		
		Values calculated in the study	
0.5	80	Cyanobacteria, Cryptophytes, flagellates	Claustre et al. (1994)*
0.2	200	Dinoflagellates	Claustre et al. (1994)*
0.7	30	Diatoms	Claustre et al. (1994)*
0.64–0.74	57–81	Natural phytoplankton populations – equatorial Pacific surface waters	Chavez et al. (1991)
0.55–0.7	40–120	Natural phytoplankton (surface values) – equatorial Pacific surface waters	Chavez et al. (1996)
0.03–0.53	14–50	Natural phytoplankton populations – Alboran Sea	Arin et al. (2002)
0.01–0.25	47–51	Phytoplankton in small-temperate-zone lakes	Cloern et al. (1992)
	172±51	Natural phytoplankton populations – Tropical regions – North Atlantic	Buck et al. (1996)
	180±39	Natural phytoplankton populations – Subtropical regions – North Atlantic	Buck et al. (1996)
	82±42	Natural phytoplankton populations – Subarctic regions – North Atlantic	Buck et al. (1996)
	63.9–75.3	Whole water column phytoplankton – Subtropical Atlantic Ocean	Veldhuis and Kraay (2004)
	93–122	Whole water column *Prochlorococcus* – Subtropical Atlantic Ocean	Veldhuis and Kraay (2004)
	200–450	*Prochlorococcus* (surface values) – Subtropical Atlantic Ocean	Veldhuis and Kraay (2004)
	20–>160	Modelling study	Taylor et al. (1997)
	40–200	Natural phytoplankton (surface values) – central and eastern tropical Pacific	Chavez et al. (1996)
	77±6 and 17±2	Upper layer and deep chlorophyll maximum <2 μm phytoplankton – Atlantic subtropical gyres	Perez (2006)
	186±21 and 58±10	Upper layer and deep chlorophyll maximum >2 μm phytoplankton – Atlantic subtropical gyres	Perez (2007)
		Values selected by authors for growth calculations	
	30	Pico- and nanoplankton in a lagoon reef – Mayotte island	Houlbrèque et al. (2006)
	30	Pico- and nanoplankton in a coral reef – Coast of Eilat	Fabricius et al. (1998)
	30	Phytoplankton – Antarctica	Krell et al. (2005)
	50	Microphytoplankton – Model	Lequéré et al. (2005)
	50	Phytoplankton – North Water Polynya	Sanders et al. (2003)
	50	Phytoplankton – coastal area of canary Islands	Aristegui et al. (2001)
	35	Phytoplankton 150° W – Model	Macedo and Duarte (2006)
	90	Phytoplankton – Model – equatorial Pacific upwelling	Rodier et al. (2000)
	55	Review	Gasol et al. (1997)

* and cited references.

Table 3. Review of values of surface water phytoplankton and bacteria growth rate (d^{-1}).

Growth rate (d^{-1})	Technique	Organisms – location	Reference
0.76 (0.57–1.07)	Dilution tehcnique	Phytoplankton – North-east Atlantic	Quevedo and Anadon (2001)
0.26 (0.19–0.36)	^{14}C method	Phytoplankton – eastern North Atlantic subtropical gyre	Maranon (2005)
0.51 (0.42–0.62)	^{14}C method	Phytoplankton – western North Atlantic subtropical gyre	Maranon (2005)
0.17 (0.13–0.22)	^{14}C method	Phytoplankton – South Atlantic subtropical gyre	Maranon (2005)
0.21±0.02	^{14}C method	Microphytoplankton – oligotrophic area – Atlantic ocean	Maranon et al. (2000)
0.1–>1.5	Review	Phytoplankton – poor water of the open ocean	Eppley (1981)
0.0–2.9	Review	Phytoplankton assemblages	Furnas (1990)
0.3–0.53	^{14}C method	Phytoplankton – Station ALOHA – 22°45′ N; 158°00′ W	Letelier et al. (1996)
1	Pigment labeling with ^{14}C	Phytoplankton – North Pacific subtropical gyre	Laws et al. (1987)
0.3–0.6	Pigment labeling with ^{14}C	Cyanobacteria – Sargasso Sea off Bermuda	Goericke (1998)
0.06–0.99	Specific DIP uptake rate	Picophytoplankton – Southeast Pacific 146.36° W, 72.49° W	This study
0.02–0.83	Specific DIP uptake rate	Nano-microphytoplankton – Southeast Pacific 146.36° W, 72.49° W	This study
1.44	Seawater culture	Bacteria – North western Atlantic Ocean	Ducklow and Hill (1985)
0–0.45	Dilution tehcnique	Bacteria – Gulf of Mexico	Jochem et al. (2004)
2–10	Review	Bacteria	Ducklow (1983)
4.7	^{3}H-adenine method	Bacteria – North pacific subtropical gyre	Jones et al. (1996)
0.2–1.5	^{3}H-Thymidine method	Bacteria – western Black Sea	Morgan et al. (2006)
0.03–1.1	^{3}H-Thymidine method	Bacteria – Danube – Black Sea	Becquevort et al. (2002)
0.004–0.25	^{3}H-Leucine method	Bacteria – review	Van Wambeke et al. (2007b)[1]
0.31±0.09	^{3}H-Leucine method	Bacteria – Northeast Pacific Ocean 44°38.3′ N, 124°18.5′ W	Sherr et al. (2001)
0.03±0.01	^{3}H-Leucine method	Bacteria – Northeast Pacific Ocean 44°38.3′ N, 124°48.0′ W	Sherr et al. (2001)
0.02±0.01	^{3}H-Leucine method	Bacteria - Northeast Pacific Ocean 44°38.65′ N, 127°10′ W	Sherr et al. (2001)
0.1–0.45	^{3}H-Leucine method	Bacteria – eastern equatorial Pacific Ocean 4.6° S, 105° W	Cochlan (2001)
0.06–4.28	Specific DIP uptake rate	Bacteria – Southeast Pacific 146.36° W, 72.49° W	This study

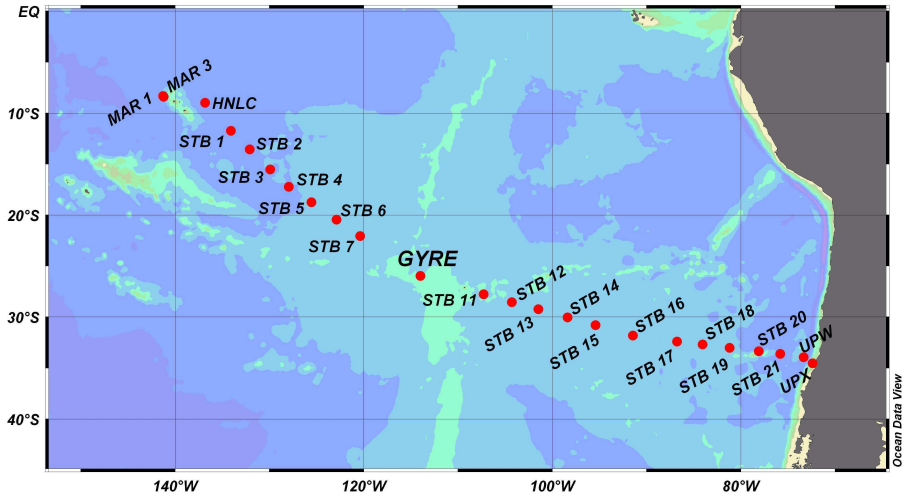

Fig. 1. Station names and locations of the BIOSOPE cruise transect in the South East Pacific Ocean (October–December 2004). MAR 1 and MAR 3 (in the vicinity of Marquesas Islands), HNLC (High Nutrient Low Chlorophyll area), GYRE (the central part of the Southeast Pacific gyre), and UPW and UPX (the Chilean upwelling) are long stations (3–4 days) abbreviated according their location; STB1-21 are short stations (1 day).

BGD
4, 2027–2068, 2007

EGU

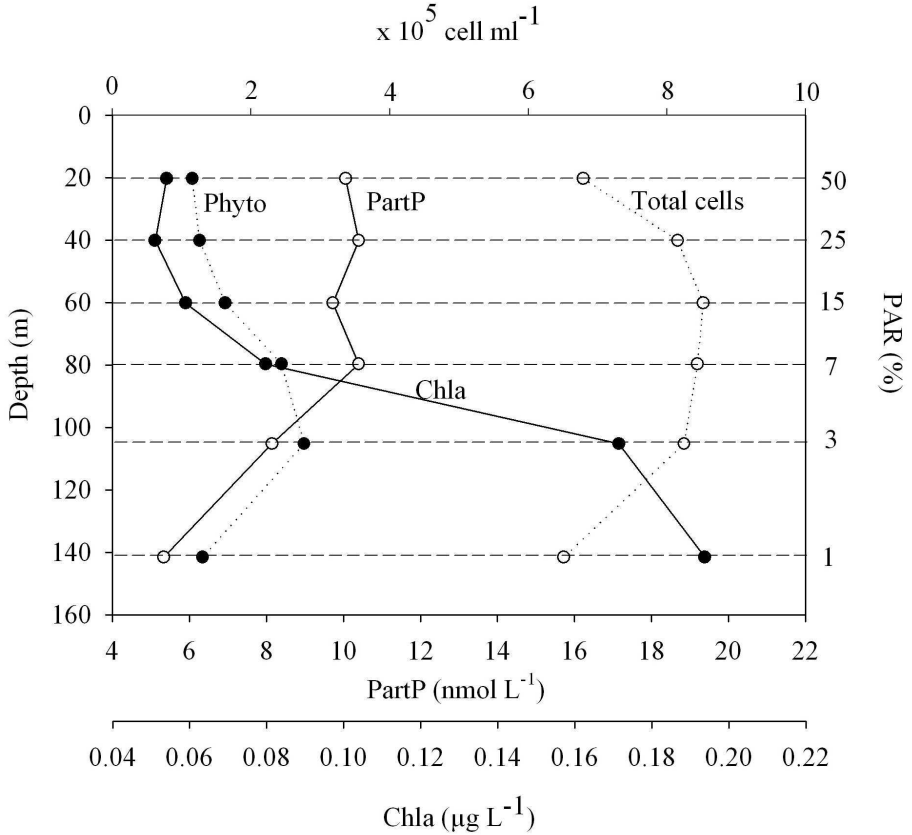

Fig. 2. Example of vertical distribution of biological properties at station STB4 (127.97° W; 17.23° S): particulate phosphate (PartP), chlorophyll a (Chla), total phytoplankton counted by flow cytometry: *Prochlorococcus* + *Synechococcus* + picoeucaryotes (phyto) and total cells (heterotrophic bacteria + phytoplankton) counted by flow cytometry (Total cells).

BGD
4, 2027–2068, 2007

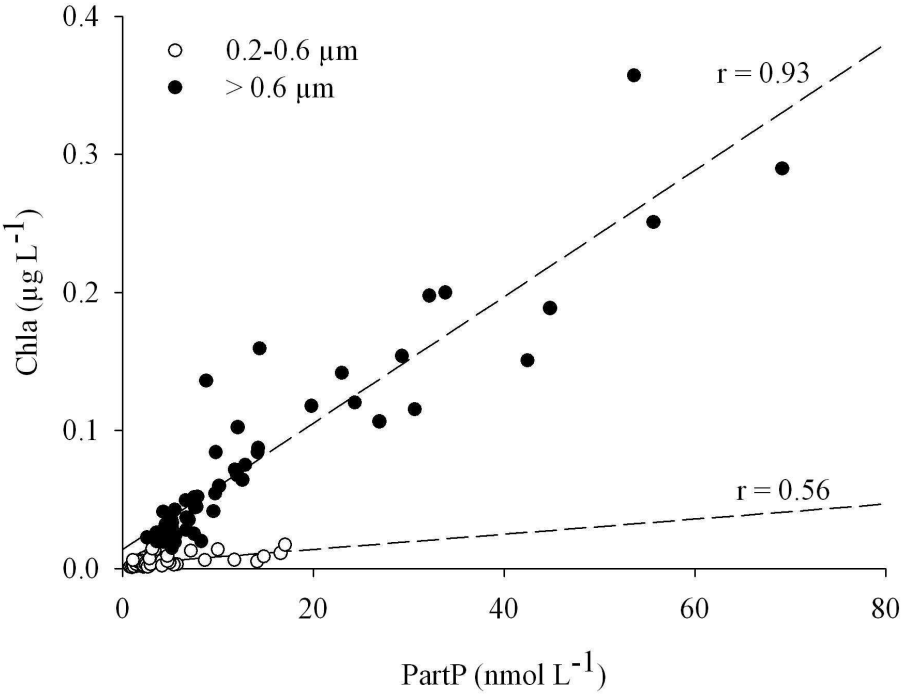

Fig. 3. Relations between Chlorophyll a (Chla) and particulate phosphate (PartP) at depth corresponding to a range of PAR levels between 50% and 15%, for two size fractions: 0.2–0.6 μm and >0.6 μm.

BGD
4, 2027–2068, 2007

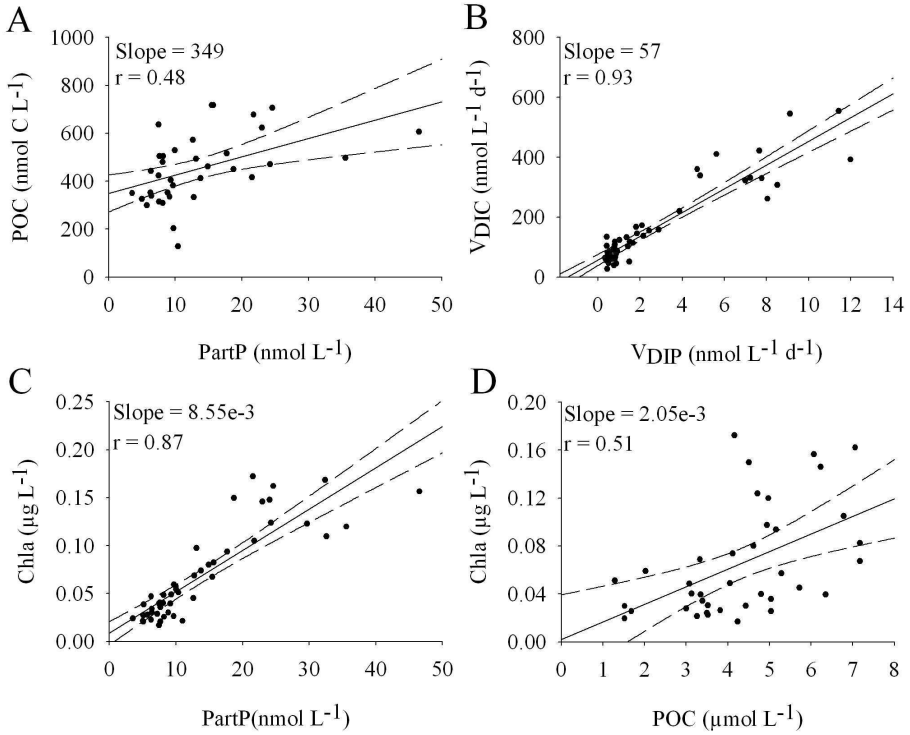

Fig. 4. Relations between particulate carbon (POC) and phosphate (PartP) **(A)**, between carbon (V_{DIC}) and phosphate (V_{DIP}) uptake rates **(B)** between chlorophyll a (Chla) and PartP **(C)** and between Chla and POC **(D)**. Data from 50 to 15% of PAR and between HNLC and STB18 stations. "slope" and "r" corresponds to the slope and the regression coefficient, respectively. The dotted lines correspond to the 95 % confident range of the regression line (full line).

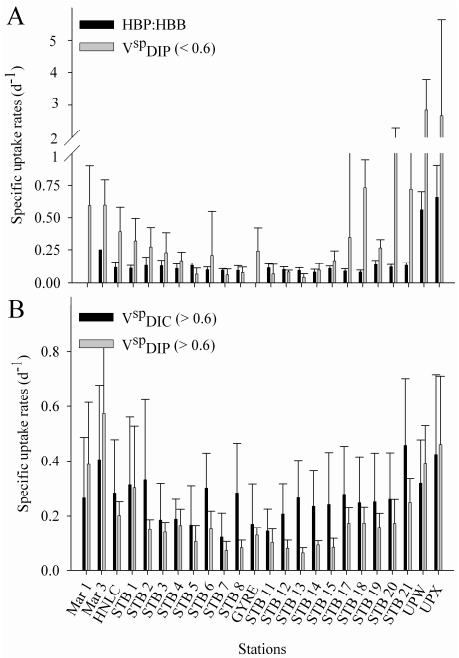

Fig. 5. (A) Bacterial specific uptake rates calculated from HBP:HBB ratio and V^{sp}_{DIP} in the fraction <0.6 μm. **(B)** Phytoplankton specific uptake rates calculates from V^{sp}_{DIC} and V^{sp}_{DIP} in the fraction >0.6 μm. Average specific uptake rates values on the photic zone. Autotrophic biomass calculated from Chla using C:Chla conversion factors as describe in the Materials and Methods section. Heterotrophic bacterial biomass calculated from bacterial cells abundance converted to C equivalent using a conversion factor of 10 fgC cell^{-1}.

BGD
4, 2027–2068, 2007

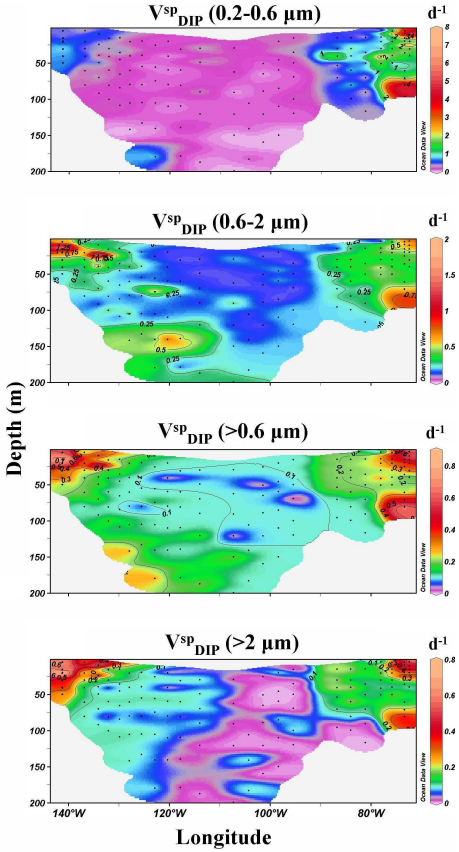

Fig. 6. Vertical and longitudinal distribution of the daily specific uptake of DIP (V^{sp}_{DIP}) along the BIOSOPE transect for four size classes: 0.2–0.6; 0.6–2; >0.6 and >2 μm.