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# Heterotrophic bacterial production in the South East Pacific: longitudinal trends and coupling with primary production

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## Abstract

Spatial variations of heterotrophic bacterial production and phytoplankton primary production were investigated across South East Pacific Ocean ( $-141^{\circ}$  W,  $-8^{\circ}$  S to  $-72^{\circ}$  W,  $-35^{\circ}$  S) in November–December 2004. Bacterial production ( $^3\text{H}$  leucine incorporation) integrated over the euphotic zone encompassed a wide range of values, from 43  $\text{mg C m}^{-2} \text{d}^{-1}$  in the hyper-oligotrophic South Pacific Gyre to 392  $\text{mg C m}^{-2} \text{d}^{-1}$  in the upwelling off Chile. Within the gyre ( $120^{\circ}$  W,  $22^{\circ}$  S) records of low phytoplankton biomass ( $7 \text{ mg TChla m}^{-2}$ ) were obtained and in situ  $^{14}\text{C}$  based particulate primary production rates were as low as  $153 \text{ mg C m}^{-2} \text{d}^{-1}$ , thus equal to the value considered as a limit for primary production under strong oligotrophic conditions. In the South Pacific gyre average rates of  $^3\text{H}$  leucine incorporation rates, and leucine incorporation rates per cell ( $5\text{--}21 \text{ pmol L}^{-1} \text{ h}^{-1}$  and  $15\text{--}56 \times 10^{-21} \text{ mol cell}^{-1} \text{ h}^{-1}$ , respectively), were in the same range as those reported for other oligotrophic sub tropical and temperate waters. Rates of dark community respiration, determined at selected stations across the transect varied in a narrow range ( $42\text{--}97 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ), except for one station in the upwelling off Chile ( $245 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ). Bacterial growth efficiencies varied between 5 and 38% and bacterial carbon demand largely exceeded  $^{14}\text{C}$  particulate primary production across the South Pacific Ocean. Net community production also revealed negative values in the South Pacific Gyre ( $-13 \pm 20$  to  $-37 \pm 40 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ). Such imbalances being impossible in this area far from any external input, we discuss the techniques involved for determining the coupling between primary production and bacterial heterotrophic production.

## 1 Introduction

Over a broad range of aquatic systems, heterotrophic bacterial biomass varies less than phytoplankton biomass (Cole et al., 1988). The magnitude, variability and control of bacterial heterotrophic production is well studied in the northern hemisphere (Duck-

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low, 2000; Landry and Kirchman, 2002), including the Arctic (Sherr et al., 2003; Kirchman et al., 2005). By contrast, the oceans in the southern hemisphere have been less explored, except along coasts and margins, and the Indian and the Antarctic Ocean. In the Pacific Ocean, results for heterotrophic bacterial production were mainly acquired in tropical and subtropical regions (20° N–20° S, Landry and Kirchman, 2002). The North Pacific Central gyre has been intensively studied, particularly the long term station HOTS (Hawai Ocean Time Series, Karl et al., 2001). Overall, oligotrophic regions of the ocean are clearly the least well studied.

On the basis of remotely sensed ocean color, the South East Pacific gyre is suggested to be the most oligotrophic and stable water body (Claustre and Maritoner, 2003). To date, however, no investigation on the biogeochemistry of this water body has taken place. The aim of the BIOSOPE (Biogeochemistry and Optics South Pacific Experiment) project was to conduct a pluridisciplinary exploration of this gyre as well as their eastern (Chilean upwelling) and western (Marquesas plateau) borders, allowing the examination of a very large range of trophic conditions. Hyperoligotrophic conditions were observed in the centre of the gyre, with the clearest waters ever described (Morel et al 2007) and a deep chlorophyll maximum reaching 180 m. In oligotrophic environments it has been often discussed the issue that ocean respiration could exceed production (del Giorgio et al., 1977; Steinberg et al., 2001; Williams et al., 2004; Mourino-Carballido and McGillicuddy, 2006). Thus, in this study, we will discuss levels of bacterial production rates reached in comparison to other open ocean environments, compare bacterial carbon demand to primary production and reevaluate the interpretation of such comparison in the frame the of metabolic balance of these open ocean waters.

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## 2 Materials and methods

### 2.1 Strategy of sampling

The BIOSOPE cruise was conducted from 24 October to 11 December 2004 aboard R/V Atalante across the South East Pacific Ocean (Fig. 1). Stations of short (<5 h, 21 stations) and long (3 to 6 days, 6 stations) duration were sampled (Table 1). Stations occupied for less than 5 h were abbreviated chronologically (station type STB1 to STB20 and STA21, Fig. 1, Table 1). The stations of long duration were abbreviated according to their location: MAR (in the vicinity of Marquise Islands), HNL (High Nutrients Low Chlorophyll waters in North Eastern area far from Marquise Islands), GYR (the central part of the South Pacific gyre), EGY (the Eastern part of the South Pacific gyre) and, UPW and UPX (2 sites chosen in the upwelling of Chile). At the short stations we systematically sampled at 09:00 h local time to avoid possible biases due to daily variability in heterotrophic bacterial abundance and activity. At the long stations, we checked the validity of our routine bacterial production protocols by time series and concentration kinetics. All samples were collected from a CTD rosette fitted with 20 12-L Niskin bottles equipped with Teflon rings. Samples were processed within 1 h of collection. Water samples used for in situ – simulated primary measurements (IPP<sub>deck</sub>) came from the same rosette as that used for BP (the 09:00 a.m. CTD cast). However some measurements of PP using the JGOFs protocol (in situ moored lines immersed for 24 h from dusk to dusk, IPP<sub>in situ</sub>) were also performed for some time at the long stations. In that case, samples were taken on a rosette before dusk. Besides measurements of bacterial abundance and production and primary production described below, other data included in this paper includes hydrographic properties (Claustre et

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al., 2007a<sup>1</sup>) and Total chlorophyll *a* (TChl*a* = Chl*a*+Divinyl-Chl*a*, Ras et al., 2007<sup>2</sup>).

## 2.2 Bacterial abundance

Water samples for flow cytometric analyses of heterotrophic bacterial populations were fixed with paraformaldehyde at 1% and preserved in liquid nitrogen for further analysis in the laboratory. The protocol is fully described in Grob et al. (2007). Briefly, bacterial samples were counterstained with SYBR-Green I and counted on a FACS Calibur (Becton Dickinson) flow cytometer.

## 2.3 Bacterial production

Bacterial production was determined by [<sup>3</sup>H] leucine incorporation applying the centrifugation method (Smith and Azam, 1992). Duplicates 1.5 mL samples were incubated with a mixture of [4,5-<sup>3</sup>H]leucine (Amersham, specific activity 160 Ci mmol<sup>-1</sup>) and nonradioactive leucine at final concentrations of 7 and 13 nM, respectively for active waters (>10 pmol leu L<sup>-1</sup> h<sup>-1</sup>) and the opposite (7 nM cold, 13 nM labeled) for low activity waters. Samples were incubated in the dark at the respective in situ temperatures for 1–7 h according to expected activities, period during which we preliminarily checked that the incorporation of leucine was linear with time (e.g. in the centre of the gyre we incubated on average 2 h surface waters and the activity in dark incubated samples was linear up to 8 h, data not shown). Incubations were stopped by the addition of trichloroacetic acid (TCA) to a final concentration of 5%. To facilitate the precipitation of proteins, bovine serum albumin (BSA, Sigma, 100 mg L<sup>-1</sup> final concentration) was added prior to centrifugation at 16 000 g for 10 min. After discarding the super-

<sup>1</sup>Claustre, H., Sciandra, A., Vaulot, D., and Raimbault, P.: Introduction to the special section: bio-optical and biogeochemical conditions in the South East Pacific in late 2004 – the BIOSOPE program, Biogeosci. Discuss., in preparation, 2007a.

<sup>2</sup>Ras, J., Uitz, J., and Claustre, H.: Spatial variability of phytoplankton pigment distribution in the South East Pacific. Biogeosci. Discuss., in preparation, 2007.

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natant, 1.5 ml of 5% TCA were added and the samples were subsequently vigorously shaken on a vortex and centrifuged again. The supernatant was discarded and 1.5 ml of PCS liquid scintillation cocktail (Amersham) were added. The radioactivity incorporated into bacterial cells was counted in a Packard LS 1600 Liquid Scintillation Counter on board the ship. We checked effects of ethanol rinse and BSA addition in our protocol, because in most published studies BSA is not added and ethanol rinse is often used to remove unspecific  $^3\text{H}$  labelling (Wicks and Robarts, 1998; Ducklow et al., 2002; Kirchman et al., 2005) although sometimes ethanol rinse did not change the results (Van Wambeke et al., 2002; Granéli et al., 2004). There was no significant difference among the different treatments (+ or – ethanol, + or – BSA added, data not shown). As we managed also some size-fractionated bacterial activity measurements on some selected samples, we were also able to compare the filtration technique (20 ml incubated with 1 nM  $^3\text{H}$ -leucine +19 nM cold leucine, filtered through Millipore GS 0.2  $\mu\text{m}$  filters, no ethanol rinse), with the centrifugation technique (BSA addition, no ethanol rinse). The model II regression was applied to compute the relationships between both techniques. With the whole data set ( $n=88$ , BP ranged 5–578  $\text{ng C L}^{-1} \text{h}^{-1}$ ), the slope of “filtration” versus “centrifugation” was  $1.04 \pm 0.02$ , and with only the  $<50 \text{ ng C L}^{-1} \text{h}^{-1}$  data set ( $n=77$ ), the slope was  $0.93 \pm 0.04$  (figure not shown). In both cases, the Y intercept was not significantly different from 0. We felt thus confident in comparison of our measurements of leucine rates compared to other protocols (centrifugation with no BSA or filtration technique).

A factor of  $1.5 \text{ kg C mol leucine}^{-1}$  was used to convert the incorporation of leucine to carbon equivalents, assuming no isotopic dilution (Kirchman, 1993). Indeed, isotopic dilution ranged from 1.04 to 1.18 as determined on 4 occasions on concentration kinetics. Error associated to the variability between replicate measurements (half the difference between the two replicates) averaged 13% and 6% for BP values less and more than  $10 \text{ ng C L}^{-1} \text{h}^{-1}$ , respectively.

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## 2.4 Particulate primary production

Primary production was determined (1) by 24 h- in situ incubations according to the experimental protocol detailed in Moutin and Raimbault (2002) and (2) by short-term (<5 h) on-deck incubations using incubators equipped with Nickel screens (50, 25, 15, 7, 3 and 1% of incident irradiance) (Duhamel et al., 2006). Rates of daily particulate primary production were obtained using 2 incubation methods: i) in situ moored lines immersed during 24 h, and in that case daily rates were directly measured ( $PP_{in\ situ}$ ) and ii) using the conversion factors  $\tau_{(T_i;T)}$  according to Moutin et al. (1999) to calculate normalized (dawn-to-dawn) daily rates from the hourly rates measured in the on-deck incubators ( $PP_{deck}$ ). The conversion factors were calculated based on incident irradiance measured aboard.

## 2.5 Gross community production, dark community respiration and net community production

Rates of gross community production (GCP), dark community respiration (DCR) and net community respiration (NCP) were estimated from changes in the dissolved oxygen ( $O_2$ ) concentration during light/dark incubations of unfiltered seawater (24 h) carried out in situ on moored lines. Seawater was collected at 6 depths in the euphotic zone and transferred to 9-L polycarbonate bottles. The biological oxygen demand (BOD) bottles (125 ml) were filled by siphoning, using silicon tubing. For DCR, the BOD bottles were placed in black bags. All BOD bottles were incubated in situ at the respective depth layers under natural irradiance levels from dusk to dusk using the same mooring line as for  $PP_{in\ situ}$ . The concentration of oxygen was determined by Winkler titration of whole bottles. Titration was done with an automated potentiometric end-point detection system (Metrohm DMS 716), following the recommendations of Carignan et al. (1998). DCR and NCP were calculated as the difference between initial and final  $O_2$  concentrations in dark and light bottles, respectively. GCP was calculated as the difference between NCP and DCR. On two occasions (St 3 5 m, 125 m), respiration rates were

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also determined on filtered (0.8  $\mu\text{m}$ ) water samples.

## 2.6 Bacterial growth efficiency

The bacterial growth efficiency (BGE) was calculated from bacterial heterotrophic production and rates of DCR, assuming that bacterial respiration represented a constant proportion (f) of DCR and applying a respiratory quotient (RQ) to convert  $\text{O}_2$ - based measurements to carbon units:

$$\text{BGE} = \text{BP} / (\text{BP} + (f \times \text{RQ} \times \text{DCR}))$$

The choices of RQ and f are developed in the results section. The BGE were estimated from data of daily BP and DCR integrated over the euphotic zone. Vertical profiles for both parameters are available at the long stations MAR, HNL, GYR, UPW and UPX where moored lines were deployed for 24 h in situ.

## 3 Results

### 3.1 Spatial variation

Bacterial abundances ( $0.8\text{--}20.7 \times 10^5$  bacteria  $\text{ml}^{-1}$ ) and leucine incorporation rates ( $0.34\text{--}400$   $\text{pmol leu L}^{-1} \text{h}^{-1}$ ) revealed large variations across the 8000 km of the BIOSOPE transect (Fig. 2). Both parameters were strongly correlated (relation  $\log - \log$ ,  $n=249$ ,  $r=0.85$ ,  $p<0.001$ ) over these large range of data. The gradients of bacterial abundances and leucine incorporation rates were particularly pronounced off Chile. Highest leucine incorporation rates were obtained in the upwelling area ( $250$   $\text{pmol L}^{-1} \text{h}^{-1}$  at UPW at 35 m, Fig. 3;  $400$   $\text{pmol L}^{-1} \text{h}^{-1}$  at UPX at 15 m, profile not presented) and in the northwestern zone of the transect, close to the Marquesas Islands ( $60$   $\text{pmol L}^{-1} \text{h}^{-1}$ , at MAR at 10–50 m). Substantially lower rates were obtained between Stations 8 and 14 (maximum  $15$   $\text{pmol L}^{-1} \text{h}^{-1}$ ). A similar pattern

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was detectable for phytoplankton biomass (Tchl<sub>a</sub>, Ras et al., 2007<sup>2</sup>) and nitrate concentrations (Raimbault et al., 2007<sup>3</sup>). At MAR, sea surface temperature was 27.5°C and the mixed layer reached 70 m (Fig. 3). A large peak of leucine activity developed between 10 and 50 m (59±8 pmol L<sup>-1</sup> h<sup>-1</sup>) coinciding with the layer of maximum primary production (20 m, 13 μg C L<sup>-1</sup> d<sup>-1</sup>) and maximum TChl<sub>a</sub> (50 m, 0.4 μg L<sup>-1</sup>). At UPW, characterized by a reduced mixed layer (20 m) and lower surface water temperature (15.9°C), maximum rates of primary production (50 μg C L<sup>-1</sup> d<sup>-1</sup>) and leucine incorporation (250 pmol L<sup>-1</sup> h<sup>-1</sup>) were higher than at the MAR site. Maximum leucine incorporation coincided with a narrow, high TChl<sub>a</sub> peak (2.6 μg L<sup>-1</sup>) at 35 m depth (Fig. 3). At the GYR site, leucine incorporation was homogenous (mean ± SD: 9.3±1.9 pmol L<sup>-1</sup> h<sup>-1</sup>) down to 120 m depth, similarly to primary production (0.9±0.3 μg C L<sup>-1</sup> d<sup>-1</sup> between 20 and 160 m). Below 120 m, leucine incorporation progressively decreased to 1.4 pmol L<sup>-1</sup> h<sup>-1</sup> at 250 m depth. No clear association with the deep, very low peak of TChl<sub>a</sub> (0.16 μg L<sup>-1</sup>) at 185 m depth was detectable at this site. At EGY, leucine incorporation rates were still very low but exhibited a subsurface maximum around 40 m, coinciding with a peak of primary production around 3 μg C L<sup>-1</sup> d<sup>-1</sup>.

By contrast to bulk fluxes of heterotrophic bacterial production, specific leucine incorporation rates varied within a rather low range (10–70×10<sup>-21</sup> mol cell<sup>-1</sup> h<sup>-1</sup>), except for the Chilean coast, where values reached up to 200×10<sup>-21</sup> mol cell<sup>-1</sup> h<sup>-1</sup> (Fig. 4). From MAR to STB4, a sub-surface maximum was visible around 20–30 m with values ranging from 30 to 70×10<sup>-21</sup> mol cell<sup>-1</sup> h<sup>-1</sup> (Fig. 4). Within the gyre (stations 5 to 15) the vertical distribution of specific leucine incorporation rates were rather constant down to the deep Tchl<sub>a</sub> maximum at around 160 m (13–56×10<sup>-21</sup> mol cell<sup>-1</sup> h<sup>-1</sup>) with slightly higher values in the subsurface and around 110 m depth.

BP integrated over the euphotic zone (IBP) ranged from 43 to 392 mg C m<sup>-2</sup> d<sup>-1</sup> during the BIOSOPE Cruise (Fig. 5). These data reflect the large range of trophic conditions encountered, with integrated stocks of TChl<sub>a</sub> within the euphotic zone ranging

<sup>3</sup>Raimbault, P., Garcia, N., and Cerutti, F.: Distribution of organic and inorganic nutrients in the south Pacific Gyre, Biogeosci. Discuss., in preparation, 2007.

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between 7 and 59 mg m<sup>-2</sup> (Table 1) and integrated fluxes of particulate primary production (IPP<sub>deck</sub>) between 76 and 1446 mg C m<sup>-2</sup> d<sup>-1</sup> (Fig. 5). As for volumetric values, highest values of IBP were obtained in the upwelling off Chile (226–392 mg C m<sup>-2</sup> d<sup>-1</sup>) corresponding roughly to the IBP fluxes obtained by Cuevas et al. (2004) – based on thymidine technique- in the upwelling area off Concepcion in October 1999 (268–561 mg C m<sup>-2</sup> d<sup>-1</sup> for their coastal station 73° W). At stations STB6 to STB15, encompassing the GYR sites, IBP was as low as 58±11 mg C m<sup>-2</sup> d<sup>-1</sup> (mean ± SD). Similarly IPP<sub>deck</sub> revealed lowest values in this region (134±42 mg C m<sup>-2</sup> d<sup>-1</sup>). Stations MAR and HNL, on the western part of the transect, presented intermediary values of IBP (86–140 mg C m<sup>-2</sup> d<sup>-1</sup>) and IPP<sub>deck</sub> (318–683 mg C m<sup>-2</sup> d<sup>-1</sup>). IPP<sub>in situ</sub>, determined only on a limited number of stations across the transect reflected the trends of IPP<sub>deck</sub> (r=0.89, n=5) with higher values at MAR and UPW (1146 and 1344 mg C m<sup>-2</sup> d<sup>-1</sup>, respectively) and lower values at GYR (154 mg C m<sup>-2</sup> d<sup>-1</sup>, Table 2). Both estimates of <sup>14</sup>C particulate primary production were very close, with IPP<sub>in situ</sub> being, on average 1.3 fold higher than IPP<sub>deck</sub> (range 0.92–1.67). GCP ranged from 29 to 505 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> and was well correlated also with IPP<sub>deck</sub> (r=0.89, n=7). Net community production was not statistically different from 0 at GYR, was negative at UPX (–38±23 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and reached up to 429 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> at UPW. The ratio of IBP to IPP<sub>deck</sub> was not constant, ranging from 0.19 to 1.04 and presented higher values in the oligotrophic area (mean ± SD for stations 6 to 15: 0.48±0.24) and lower on the boundaries of the transect (for the eastern part, stations EGY to UPX: 0.24±0.05, for the western part, stations MAR to 1: 0.25±0.03).

### 3.2 Dark community respiration and Bacterial growth efficiencies

Rates of DCR varied within a narrow range (42–97 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) except for the high rates obtained at UPX (245 mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>). The BGE was calculated assuming i) that heterotrophic bacterial respiration accounts entirely for DCR (BGE<sub>100</sub>), or that it represented half of it (BGE<sub>50</sub>, Table 3). For all stations considered, BGE<sub>100</sub> ranged

between 7 and 24% and  $BGE_{50}$  ranged between 14 and 38%. DCR rates in  $<0.8 \mu\text{m}$  fractionated sea water was not different from DCR ( $0.62 \pm 0.22$  and  $0.52 \pm 0.25 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$  for the  $<0.8 \mu\text{m}$  size fraction and unfiltered seawater, respectively, at 5 m and  $0.46 \pm 0.12$  and  $0.58 \pm 0.24 \mu\text{mol O}_2 \text{ L}^{-1} \text{ d}^{-1}$  for the  $<0.8 \mu\text{m}$  size fraction and unfiltered seawater, respectively at 125 m). This suggests that the estimate of  $BGE_{100}$  is appropriate for the oligotrophic region visited in the present study. The application of respiratory quotients (RQ) for a given contribution of bacterial to community respiration resulted in minor changes of BGEs, differing only by 2 to 7% when RQs of 0.8 and 1.1 are applied. Hence, the assumption on the fraction of DCR attributable to bacterial respiration has a greater impact on the variability of the BGE than the choice of the respiratory quotient (RQ). With both assumptions on the RQ, however, lower BGEs were obtained at site GYR (5–15%) and BGEs increased in the upwelling area (UPW: 14–38%) and in the western part, at the MAR and HNL sites (12–28%). Keeping an average BGE of 7% as a correct estimate for the more oligotrophic sites, the ratio of the integrated bacterial carbon demand (BCD) to  $^{14}\text{C}$ -Primary production ( $\text{IPP}_{\text{deck}}$ , data from Fig. 5) in the gyre would range between 3.7 (STB15) to 14 (STB7) (median for stations STB6 to STB15: 5.7,  $n=9$ ).

The calculation of the BGE is commonly based on bacterial heterotrophic production determined prior to the 24 h incubation. During the size fractionation experiment at station STB3 as well as during bioassays experiments (Van Wambeke et al., 2007a<sup>4</sup>), we observed, however, an increase in bacterial heterotrophic production during the incubation period. The median value of the increase at stations STB6 to STB15 was  $\times 3.2$  in 24 h (Van Wambeke et al., 2007a<sup>4</sup>). Such increases during DCR measurements were reported previously (Pomeroy et al., 1994). Estimates of BGE can be corrected from this bias by assuming an exponential increase in bacterial production during the 24 h incubation as follows:  $(BP_{24} - BP_0) / (\text{Ln}(BP_{24}) - \text{Ln}(BP_0))$ . Applying this

<sup>4</sup>Van Wambeke, F., Bonnet, S., Moutin, T., Raimbault, P., Alarçon G., and Guieu, C.: Factors limiting heterotrophic prokaryotic production in the southern Pacific Ocean, *Biogeosci. Discuss.*, in preparation, 2007a.

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correction, BGEs at the GYR sites range from 10 to 15% (Table 3). Thus the average BGE of 7% used for the oligotrophic site increases to 12%, resulting in a decrease in the BCD/IPP<sub>deck</sub> ratios from 2.1 to 8.6 (median 3.3 for stations STB6 to STB15, n=9) according to locations.

## 4 Discussion

The South Pacific Gyre is the most oligotrophic water body in the global ocean, a description that is up to date mainly based on satellite observations (Claustre and Maritoner, 2003; Longhurst, 1998). Several parameters determined during the BIOSOPE-cruise, such as water clarity (Morel et al., 2007) and phytoplankton biomass (7 mg TChla m<sup>-2</sup> within the euphotic zone, Table 1, Ras et al., 2007<sup>2</sup>) confirm the hyper-oligotrophic character of this area. One question that we addressed in the present study was to determine whether bacterial production is also the lowest ever reported for open seas and oligotrophic areas? For surface layers, most reported rates of leucine incorporation in oligotrophic areas do not decrease below a threshold of ~10 pmol L<sup>-1</sup> h<sup>-1</sup> (Table 4). Lower leucine incorporation rates were only obtained in the Eastern Mediterranean Sea (Levantine and Ionian Sea, range 0.4–17, mean 6.6±4.9 pmol L<sup>-1</sup> h<sup>-1</sup>, Table 4), and in our study between STB5 and STB14 (range 5–21 mean 10.8±2.9 pmol L<sup>-1</sup> h<sup>-1</sup>). Both cases correspond to marine environments where the depth of deep TChla maximum exceeds 150 m. Bacterial abundance varies less than bacterial heterotrophic production, thus the lowest specific activities are again obtained for the Levantine Basin in the Mediterranean Sea (1–49×10<sup>-21</sup> mole cell<sup>-1</sup> h<sup>-1</sup>) and cell specific activities were in the same order of magnitude (10–60×10<sup>-21</sup> mole cell<sup>-1</sup> h<sup>-1</sup>) in the centre of the south Pacific Gyre, the western Mediterranean Sea, or the equatorial Pacific Ocean (Table 4).

Bacterial community turnover rates (the ratio of bacterial heterotrophic bacterial production to bacterial biomass ratio = BP/BB ratio) allows a comparison among studies independent of the technique (leucine or thymidine incorporation), but it requires the

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application of conversion factors for bacterial biomass and production. In the present study, we used 1.5 kg C per mol leu assuming no isotopic dilution, and a low carbon per cell conversion factor more specific for oligotrophic environments (10 fg C per cell, Christian and Karl, 1994; Fukuda et al., 1998). The application of these conversion factors allowed us to compare our bacterial community turnover rates (0.05–0.21 d<sup>-1</sup>, Table 4, mean 0.11±0.03 d<sup>-1</sup>, n=63) with many previous studies that used 3.1 kgC per mol leu and 20 fg C per cell (Li et al., 1993, Kirchman et al., 1995). Lowest bacterial community turnover rates are still obtained for the Eastern Mediterranean Sea (0.003-0.123 d<sup>-1</sup> based on leucine incorporation, Table 4 and 0.005–0.11 d<sup>-1</sup> based on thymidine incorporation, Robarts et al., 1996). In the tropical, subtropical and temperate Pacific and Atlantic oceans a bacterial community turnover rate of 0.02–0.04 d<sup>-1</sup> (Table 4) appears to be a minimum threshold based on theoretical leucine-carbon conversion factors. However, a recent investigation of empirical conversion factors along a coast-offshore transect in the Atlantic (Alonso-Saez et al., 2007) suggests a bias related to high respiration of leucine in off shore stations (60–80%) which lead to very low conversion factors when using <sup>3</sup>H leucine (0.02–0.36 kg C per mole leucine in off-shore stations). Applying the mean of these empirical conversion factors (0.17 kg C per mole leucine) in the gyre, our bacterial growth rates would decrease and range from 0.005 to 0.02 d<sup>-1</sup>. On the other hand, based on microautoradiographic observations, it has further been shown that only 25% of prokaryotic cells within surface waters in the gyre are taking up leucine (Obernosterer et al., 2007<sup>5</sup>), suggesting that a low percentage of the prokaryotic heterotrophic community is active. Thus the growth rate of the active population based on leucine incorporation would be 4 fold higher. All these corrections would lead to a possibly very large range of bacterial community growth rates, varying between 0.005 d<sup>-1</sup> (0.17 kg C per mole, no correction for active frac-

<sup>5</sup> Obernosterer, I., Catala, P., Lami, R., Caparros, J., Ras, J., Bricaud, A., Dupuy, C., Van Wambeke, F., and Lebaron P.: Biochemical characteristics and bacterial community structure of the sea surface microlayer in the south Pacific Ocean, in preparation, Biogeoscience Discuss., 2007.

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tion) to  $0.8 \text{ d}^{-1}$  (1.5 kg C per mole, 25% bacteria active). The fact that the bacterial community turnover rate is often low compared to that of phytoplankton is presently a subject of debate (Duhamel et al., 2007, and references therein). Development of alternative techniques to estimate turnover of heterotrophic bacterial cells have recently been used, based on the examination on the turnover of a particular chemical pool or compound of the cell. For instance, the turnover rate of the phosphate (P) pool has been examined in different size fractions during the BIOSOPE cruise (Duhamel et al., 2007). Based on the hypothesis that detrital particulate P is mostly negligible, and assuming that the P assimilation rates and the P biomass in the  $<0.6 \mu\text{m}$  fraction are mainly related to heterotrophic prokaryotes, these authors found a bacterial P-based turnover time of  $0.11 \pm 0.07 \text{ d}^{-1}$  within the gyre. This value is in accordance with the mean range of BP/BB ratio that we obtained in the centre of the gyre using theoretical conversion factors. Unexpected high turnover rates of bacteriochlorophyll a have been detected in the Mediterranean and Atlantic seas (Koblizek et al., 2007) a pigment characteristic of aerobic anoxygenic phototrophs which have been also observed during BIOSOPE cruise (Lami et al., 2007). Such turnover rates derived from analysis of a given chemical pool, if in close relation to the whole cell turnover (Koblizek et al., 2007), suggest also that some components of the heterotrophic (including mixotrophs) bacterial community might have higher turnover rates than the whole consortium.

Our measurements of bacterial production, though among the lowest reported for the open ocean – excluding high latitude, cold waters-, clearly do not represent minimum values. If bacterial activity is similar among open ocean oligotrophic environments, is this also the case for primary production? A comparison among studies is not simple due to differences in the incubation conditions. Our IPP<sub>deck</sub> values were generally lower than those obtained by “standard” in situ incubations (IPP<sub>in situ</sub>, Table 2). It is well known that it is difficult to reproduce the natural irradiance conditions on board and thus, for the comparison with IPP from other studies, we will only refer to primary production determined from the in situ moored lines. It appears that considerably higher rates of IPP<sub>in situ</sub> were obtained in the North Pacific Gyre at ALOHA ( $200\text{--}900 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,

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Karl et al., 2001), and in the Sargasso Sea at BATS (312–520 mg C m<sup>-2</sup> d<sup>-1</sup> and 340–530 mg C m<sup>-2</sup> d<sup>-1</sup>, Steinberg et al., 2001 and Mourino-Carballido and McGillicuddy, 2006, respectively) as compared to the measurements of IPP<sub>in situ</sub> in the centre of the South Pacific Gyre (154–203 mg C m<sup>-2</sup> d<sup>-1</sup>). These previous estimates were derived from in situ dawn to dusk incubations whereas our results are from 24 h incubations. As previously reported for the eastern Mediterranean Sea, an integrated primary production of about 150 mg C m<sup>-2</sup> d<sup>-1</sup> may appear as a lower limit for primary production rates estimated by 24 h in situ incubations under strong oligotrophic conditions (Moutin and Raimbault, 2002). Thus the rates of primary production determined in the centre of the south Pacific gyre appear to be among the lowest reported.

We explored the phytoplankton-bacterial coupling by comparing the bacterial carbon demand (BCD) to primary production (IPP) and gross community production (GCP). These comparisons are often used to determine the potential fate of primary production through the microbial food web, but also to discuss the metabolic balance, presently a subject of debate in oligotrophic waters (del Giorgio et al. 1997; Kirchman, 1997; del Giorgio and Duarte, 2002; Williams, 2004, Mc Andrew et al., 2007; Claustre et al., 2007b<sup>6</sup>). We paid particular attention to the methodological biases related to these different estimates.

As suggested previously (Ducklow et al., 2000), we assumed linearity when converting hourly rates of bacterial heterotrophic production to daily rates. Taking into account the diurnal variability we observed at selected stations (Van Wambeke et al., 2007b<sup>7</sup>), this resulted in differences in the daily rates by 4% to 19% as compared to the linear increase over 24 h. The error introduced by not taking into account the daily variability is

<sup>6</sup>Claustre, H., Huot, Y., Obernosterer, I., Gentili, B., Taillez, D., and Lewis, M.: Revisiting production budget in oligotrophic and mesotrophic system using a non intrusive bio-optical method: a case study in the south East Pacific. *Biogeosci. Discuss.*, in preparation, 2007b.

<sup>7</sup>Van Wambeke, F., Duhamel, S., Tedetti, M., and Claustre, H.: Heterotrophic prokaryotic production in the South East Pacific: daily variability. *Biogeosci. Discuss.*, in preparation, 2007b.

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in the same order of magnitude as the precision of bacterial production measurements in oligotrophic areas (13% for BP values lower than  $10 \text{ ng C L}^{-1} \text{ h}^{-1}$ , see methods).

Considering all possible biases related to the estimate of BCD (daily variability, BGE estimates), bacterial carbon demand could exceed  $^{14}\text{C}$  based IPP estimates inside the gyre by factors varying between 2 to 8 fold (median 3.3,  $n=9$ ). There are two aspects to examine about these results: first, the fact that BCD always exceeded PP at all stations and second, the fact that a large variability of this ratio is obtained. Particulate PP based on  $^{14}\text{C}$  measurements is generally 40–50% of gross photosynthesis (Karl et al., 1998; Moutin et al., 1999; Bender et al., 1999). For the present study, the comparison between these fluxes is possible at some selected stations (Table 3). The ratio IPP/GCP (including the whole set of IPP<sub>deck</sub> and IPP<sub>in situ</sub> cited Table 2) was  $0.47 \pm 0.25$  (mean  $\pm$  SD), which confirms this notion. Thus the question arises how adequate the comparison between the bacterial carbon demand and  $^{14}\text{C}$ -particulate primary production is? In fact, the ratio BCD/IPP was for most stations within the gyre  $>1$ , while the ratio BCD/ GCP is  $<$  or close to 1 (Table 3). Even in the centre of the gyre the two fluxes were close to balance (Table 3), as also observed for net community production (NCP  $-13 \pm 20 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ , Table 2). Considering photorespiration as negligible, this would suppose that DOC excreted during the incubation time represented a maximum of 37–68% of GCP, which is in the upper range of “gross” excretion values acquired in oligotrophic situations (Fernandez et al., 1994). More recently, the percentage of DOC release was assumed to represent a constant fraction of 22% across wide trophic levels (Maranon et al., 2005). However, this percentage has to be considered as “net”, as bacterial reassimilation of the DOC released during the incubation period was not taken into account. In addition, none of these studies examined the amount of DOC release that is respired by bacteria during  $^{14}\text{C}$  incubations devoted to determine primary production, even though this fraction is likely to be high given the low BGEs in oligotrophic environments. During laboratory studies it has been shown that DOC excretion increases under nutrient limited conditions (Myklestad, 1995; Obernosterer and Herndl, 1995). The South Pacific Ocean gyre represents an end member of

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oligotrophic conditions and an exceptional percentage of DOC release by phytoplankton cannot be ruled out. A marked diurnal pattern in bacterial production determined from high-frequency sampling at three stations (MAR, GYR and EGY) support this hypothesis (Van Wambeke, 2007b<sup>7</sup>). Bacterial production was highest around midnight, decreased until the early afternoon, and then rapidly increased again. This pattern reflects a rapid response of heterotrophic bacteria to in situ primary production. These results suggest that the coupling between primary production and heterotrophic bacterial activity is particularly pronounced in the South Pacific Ocean.

The variability in the BCD/IPP ratio observed in the present study is more driven by the variability in IPP than the variability in IBP (percentage of variation 32% for IPP<sub>deck</sub> data, versus 19% for IBP data at stations 6 to 15 considered as oligotrophic, Fig. 5). The strong variability in IPP was not only related to the position of the station. At station GYR, IPP<sub>deck</sub> and GCP varied both considerably during our visit, and this variability was linked to surface irradiance. Day-to-day fluctuations of primary production and thus variability in the ratio of BCD/IPP are also reported from a Lagrangian experiment (Ducklow, 1999). At station ALOHA, it was also observed that the variability in production is higher than that in respiration (Williams et al., 2004). The lack of synchronicity between PP and BP has been proposed as an explanation for punctual high BCD/IPP ratios (Kirchman, 1997). Our results appear to support the hypothesis that short-term variability in PP frequently occurs, but that it is rarely determined due to the time scale on which oceanographic cruises are taking place (Williams et al., 2004). Indeed, rapid (<1 week) bursts of net autotrophy, decoupled from respiration, could appear consequently to mesoscale physical processes, as shown by recent investigation on the effects of deep sea water enrichment in nutrient-limited surface waters of the North Pacific subtropical Gyre (Mc Andrew et al., 2007). The question on the metabolic balance in the South Pacific Gyre was also investigated applying an optically based method to determine gross primary production (Claustre et al., 2007b<sup>6</sup>). These authors conclude that the South Pacific Gyre is in metabolic balance. The acquisition of high-frequency signals (Emerson et al., 2002) are necessary to provide valuable

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insights into the temporal variability of PP and respiration in open oceans.

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**Table 1.** Main physical and biological characteristics of longitudinal stations sampled during BIOSPE cruise. SST: sea surface temperature, Ze: depth of the euphotic zone (1% PAR), Z<sub>10%</sub>(UV-B): the 10% UV-B irradiance depth (at 305±2 nm) as determined in Tédetti et al (2007), I TChl *a*: integrated Total chlorophyll *a*.

station	Longitude °W	Latitude °S	date	SST °C	Ze m	Z <sub>10%</sub> (UVB) m	I TChl <i>a</i> mg m <sup>-2</sup>
MAR1	-141.24	-8.40	26-Oct	27.8	66	10	24
MAR3	-141.28	-8.33	28-Oct	27.8	70		21
HNL1	-136.85	-9.00	31-Oct	27.8	90	10	16
STB1	-134.10	-11.74	3-Nov	27.8	99	12	17
STB2	-132.11	-13.55	4-Nov	27.4	124		17
STB3	-129.93	-15.53	5-Nov	27.1	134	12	16
STB4	-127.97	-17.23	6-Nov	26.5	136	17	16
STB5	-125.55	-18.75	7-Nov	25.7	142	19	11
STB6	-122.89	-20.45	8-Nov	24.5	157		5
STB7	-120.38	-22.05	9-Nov	24.3	167	28	8
STB8	-117.89	-23.55	10-Nov	23.4	144		7
GYR2	-114.01	-25.97	12-Nov	22.1	160	21	11
STB11	-107.29	-27.77	20-Nov	21.3	152		8
STB12	-104.31	-28.54	21-Nov	21.2	152	19	7
STB13	-101.48	-29.23	22-Nov	20.0	145		8
STB14	-98.39	-30.04	23-Nov	19.8	136		10
STB15	-95.43	-30.79	24-Nov	18.7	108		12
EGY2	-91.46	-31.82	26-Nov	18.1	92	12	14
STB17	-86.78	-32.40	1-Dec	17.3	96	10	15
STB18	-84.07	-32.68	2-Dec	17.4	87	9	15
STB19	-81.20	-33.02	3-Dec	17.2	107		12
STB20	-78.12	-33.35	4-Dec	17.6	48		21
STA21	-75.83	-33.61	5-Dec	16.8	56		21
UPW2	-73.36	-33.93	7-Dec	15.9	34	3	59
UPX1	-72.41	-34.54	9-Dec	13.3	38		39

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**Table 2.** Gross community production (GCP), dark community respiration (DCR), net community production (NCP), particulate primary production 14C based (IPP<sub>deck</sub> and IPP<sub>in situ</sub>) at some selected stations where all these parameters were available. Data are integrated over the euphotic zone (Ze). Errors corresponds to standard deviation for GCP, DCR and NCP (quadruplicate samples available at each depth) and for IPP<sub>in situ</sub> (triplicate samples) whereas, for IBP, IPP<sub>deck</sub> errors represents only integration of variability within duplicate measurements, as only 2 duplicate were used at each depth sampled. Note that the units used are not the same for all data (mmol O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> and mgC m<sup>-2</sup> d<sup>-1</sup>).

	Ze m	IBP mgC m <sup>-2</sup> d <sup>-1</sup>	DCR mmol O <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>	NCP mmol O <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>	GCP mmol O <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>	IPP <sub>deck</sub> <sup>1</sup> mgC m <sup>-2</sup> d <sup>-1</sup>	IPP <sub>in situ</sub> <sup>1</sup> mgC m <sup>-2</sup> d <sup>-1</sup>
MAR 1	66	131±4	71±18	193±32	264±37	457±17	702±136
MAR 3	70	171±10*	97±13	227±16	324±20	683±29	1146±123
HNL 1	90	86±4	42±17	44±21	86±28	318±33	518±28
GYR 1	160	50±3	66±19	-37±40	29±45	159±19	154±23
GYR 4	160	65±3*	74±30	-13±20	61±37	nd	203±15
UPW 2	34	226±9	76±12	429±19	505±24	nd	4362±306
UPX 1	38	392±3	24 ±21	-38±23	207±34	1446±46	1344±46

<sup>1</sup> IPP<sub>deck</sub>: as in Fig. 5 (on-deck measurements), IPP<sub>in situ</sub>: 24 h in situ moored lines as standard JGOFS protocol (see methods).

\* The daily IBP were calculated cumulating data of different profiles measured every 3 h along a diel cycle (Van Wambeke et al., 2007b<sup>7</sup>). In other cases, daily BP was calculated from the 09:00 CTD cast assuming daily rates = 24 times hourly rates.

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**Table 3.** Bacterial growth efficiencies (BGE), gross primary production (IGCP, in carbon units), IPP/GCP and BCD/GCP ratio at some selected stations where these estimations were possible. BGEs were calculated using the following formula:  $BGE = BP / (BR + BP)$ , where BR (bacterial respiration) was assumed to be equal to DCR ( $BGE_{100}$ ) or half of it ( $BGE_{50}$ ). DCR and IBP data considered are those of Table 2.  $BGE_{corr}$ :  $BGE_{100}$  corrected for exponential growth in the flask during incubation.

	$BGE_{50}^1$ %	$BGE_{100}^1$ %	$BGE_{corr}^1$ %	$GCP^2$ $mgC\ m^{-2}d^{-1}$	$IPP/GCP^3$ ratio	$BCD/GCP^3$ ratio
MAR 1	22–28	12–16	21–27	2259–2876	0.16–0.31	0.16–0.47
MAR 3	21–27	12–16	20–26	2778–3536	0.19–0.41	0.18–0.52
HNL 1	24–30	13–17	23–29	738–939	0.34–0.7	0.31–0.87
GYR 1	10–14	5.4–7.4	10–13	252–320	0.48–0.63	1.2–3.7
GYR 4	12–15	6.2–8.3	11–15	525–669	0.30–0.39	0.63–2.0
UPW 2	31–38	18–24	30–37	4328–5509	0.22–1	0.11–0.29
UPX 1	20–25	10–14	19–24	1774–2258	0.6–0.81	0.69–2.0

<sup>1</sup> The range considers variability of Respiratory Quotients from 0.8 to 1.1.

<sup>2</sup> The range considers variability of photosynthetic quotient from 1.1 to 1.4.

<sup>3</sup> The range considers minimum – maximum values obtained according to the choice of BGEs, RQ and PQ.

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**Table 4.** Review of leucine incorporation rates, specific leucine incorporation rates (SA leu) and bacterial turnover rates (TR) in most oligotrophic mid-latitudes to equatorial areas. Temperature (T), conversion factors used to compute TR (leu CF), bacterial biomass conversion factor (BB CF) and Leucine concentration used are also indicated. Empty case: data not available. CK: concentration kinetic.

T <sup>1</sup> °C	Area		leu conc nM	Leu rate pmol L <sup>-1</sup> h <sup>-1</sup>	SA leu 10 <sup>-21</sup> mol cell <sup>-1</sup> h <sup>-1</sup>	leu CF kgC mole <sup>-1</sup>	BB CF fgC cell <sup>-1</sup>	TR d <sup>-1</sup>	reference
20–25	South East Pacific, center of the Gyre <sup>1</sup>	Nov–Dec 04	20	5–21	13–56	1.5	10	0.05–0.21	This study
30	South West pacific (Tuamotou Arch. 148°15'W, 14°55'S)	91–94	CK	36	71	1.7	15.3	0.13–0.19	Torréron and Dufour (1996a)
18	Northwestern Med, inshore off-shore transect	June 93 & June 95	20	8–70	3.4–101	0.3–2.1			Gasol et al. (1998)
22–24	Med longitudinal transect, ionian+levantine <sup>2</sup>	June 99	20	0.4–17	1–49	1.5	15	0.003–0.123	Van Wambeke
21–22	western			3–36	8–68			0.02–0.17	et al 2002
26–27	Med longitudinal transect, ionian <sup>3</sup>	September 99	20	10–26	18–49	1.5	15	0.04–0.123	Van Wambeke
23–25	western			15–48	14–63			0.03–0.15	et al 2002
25–28	Arabian Sea	Jan–Dec 95		15–202	40–100				Ducklow et al. (2001)
15	Atlantic NABE 40° N 45° N	April–May 89	10	20–100	66–136*	1.1	20	0.08–0.1	Li et al. (1993)
20	Sargasso Sea, BATS	spring	21	20–200		3.4	20	0.2–0.4	
25–26	(31°50'N, 64°10'W)	summer		10–40		0.3–0.6	4.2–7.2	0.096	Carlson et al. (1996)
24–26		autumn		10–30				0.079	
18–21		winter		10–25				0.057	
18	North East Pacific, gyre edge off Oregon	summer 97,98	20	10–20	14–21	0.4	20	0.07	
28	Equatorial Pacific along 140° W	Feb, Oct 92		15–33	60–70**	3	20	0.109–0.163	Kirchman et al. (1995)
28	Equator, Pac 140° W during El Nino	March 92	10	25–55		2.3	20	0.15–0.25	Ducklow et al. (1995)
25	Equator, Pac 140° W during non El Nino	oct-92	10	20–40		2.3	20	0.05–0.1	

<sup>1</sup> Only surface temperatures are indicated when stratification is important, <sup>2</sup> values from profiles down to depth of TChla maximum, <sup>3</sup> values from surface layers, <sup>4</sup> for our study, values have been indicated for stations 5 to 14 within euphotic layer (down to Ze), \*from related reference Ducklow et al. (1992), \*\* from related reference Kirchman et al. (2005).

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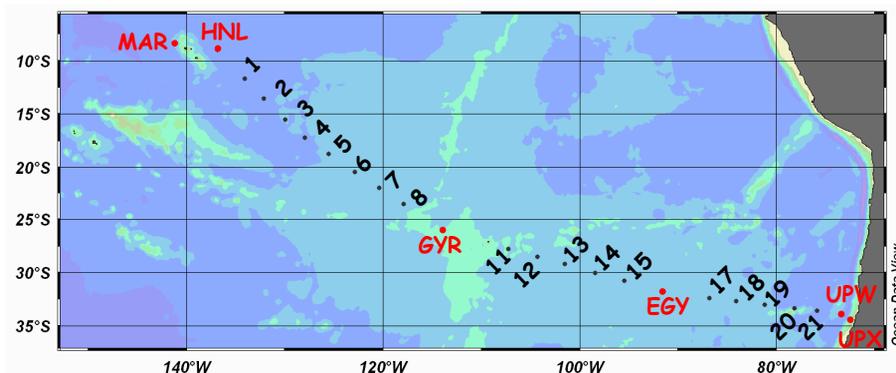
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**Fig. 1.** Transect of the BIOSOPE cruise from the Marquesas Islands to Chile. Long-term process stations are indicated in red. Numbers indicates short-term stations, for which only numbers have been indicated to simplify presentation, not the complete code as in Table 3. For instance 1 is STB1 and 21 is STA21.

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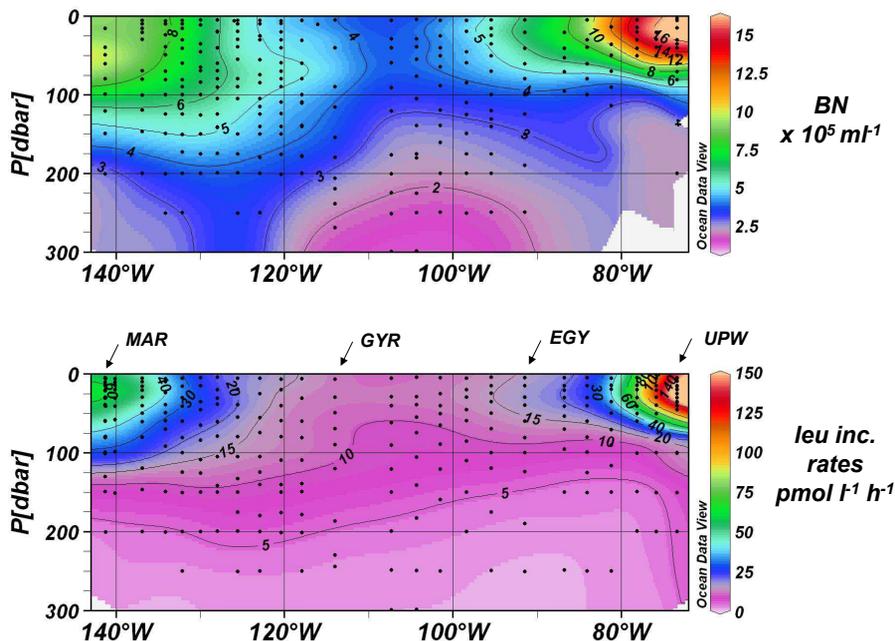
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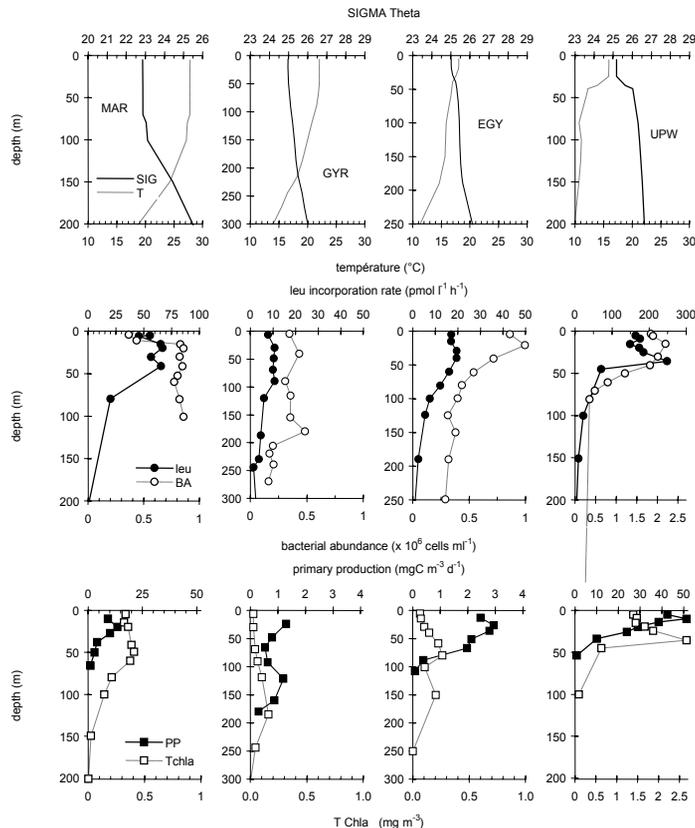


**Fig. 2.** Distribution of bacterial abundances and leucine incorporation rates along the BIOSOPE cruise transect. All CTD casts performed around 09:00. The main characteristics of the stations sampled are presented Table 1. The scale of leucine incorporation rate was stopped at  $150 \text{ pmol L}^{-1} \text{ h}^{-1}$  but higher values were obtained in the upwelling (see Fig. 3). Interpolation between sampling points in contour plots was made with Ocean Data View program (VG gridding algorithm, Schlitzer, 2004).

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**Fig. 3.** Example of vertical distribution of some physical (temperature, sigma theta) and biological (Tchl<sub>a</sub>, bacterial abundance, leucine incorporation rates, primary production – PP<sub>deck</sub>, see methods -) variables at stations meso to eutrophic MAR (26 November) and UPW (7 December), and oligotrophic to hyperoligotrophic EGYR (26 November) and GYR (12 November). All variables came from the 09:00 CTD cast except bacterial abundance (the following 12:00 CTD cast).

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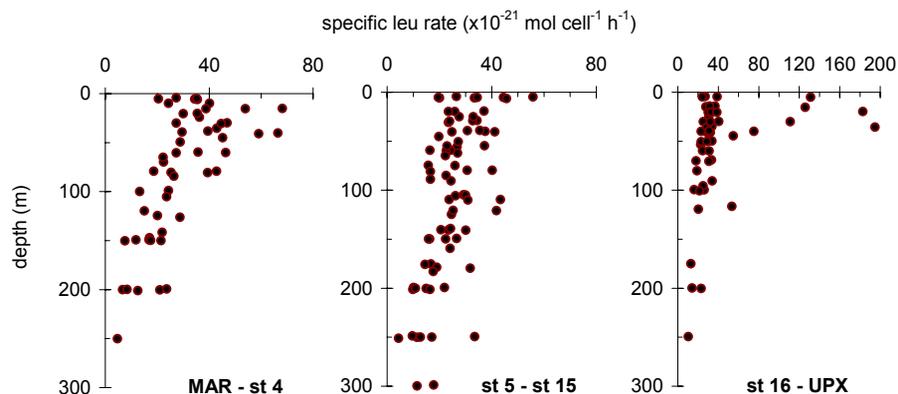
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**Fig. 4.** Vertical distribution of specific leucine incorporation rates ( $\times 10^{-21}$  mol leucine cell $^{-1}$  h $^{-1}$ ). Bacterial abundance and leucine incorporation rates were measured on water samples coming from the same CTD cast. MAR-st 4: MAR 3, HNL1, STB1, 2, 3, 4; st5-st15: STB5, 6, 7, 8, 11, 12, 13, 14; st16-UPW: STB15, 17, 18, 19, 20, 21, UPW2, UPX1. All these casts were sampled at 09:00 local time.

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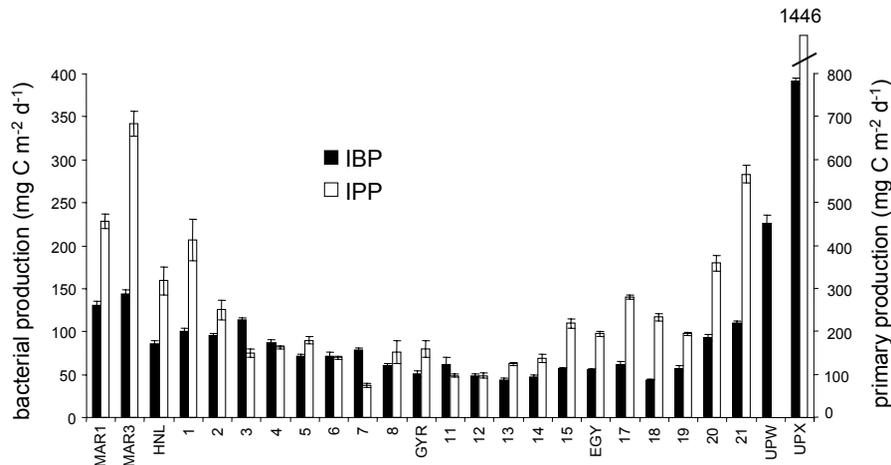
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**Fig. 5.** Integrations to the euphotic zone depth. IBP: integrated bacterial production, IPP<sub>deck</sub>: integrated primary production from deck incubation technique (see methods). BP and PP samples came from the same CTD cast sampled around 09:00 a.m. local time. Error bars corresponds to integration of the variability of volumetric rates within duplicate samples. Note that the scales for IBP and IPP are different.

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