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

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Abstract. Spatial variation of heterotrophic bacterial production and phytoplankton primary production were investigated across the eastern South Pacific Ocean (−141° W, −8° S to −72° W, −35° S) in November–December 2004. Bacterial production (^{3}H leucine incorporation) integrated over the euphotic zone encompassed a wide range of values, from 43 mg C m^{-2} d^{-1}in the hyper-oligotrophic South Pacific Gyre to 392 mg C m^{-2} d^{-1} in the upwelling off Chile. In the gyre (120° W, 22° S) records of low phytoplankton biomass (7 mg Total Chl*a* m^{-2}) were obtained and fluxes of in situ ^{14}C-based particulate primary production were as low as 153 mg C m^{-2} d^{-1}, thus equal to the value considered as a limit for primary production under strong oligotrophic conditions. Average rates of ^{3}H leucine incorporation rates, and leucine incorporation rates per cell (5–21 pmol l^{-1} h^{-1} and 15–56×10^{-21} mol cell^{-1} h^{-1}, respectively) determined in the South Pacific gyre, were in the same range as those reported for other oligotrophic subtropical and temperate waters. Fluxes of dark community respiration, determined at selected stations across the transect varied in a narrow range (42–97 mmol O_2 m^{-2} d^{-1}), except for one station in the upwelling off Chile (245 mmol O_2 m^{-2} d^{-1}). Bacterial growth efficiencies varied between 5 and 38%. Bacterial carbon demand largely exceeded ^{14}C particulate primary production across the South Pacific Ocean, but was lower or equal to gross community production.

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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 has been well studied in the northern hemisphere (Ducklow, 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 much less explored, except along several 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 (Hawaii 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 Pacific central gyre appears to be the most oligotrophic and

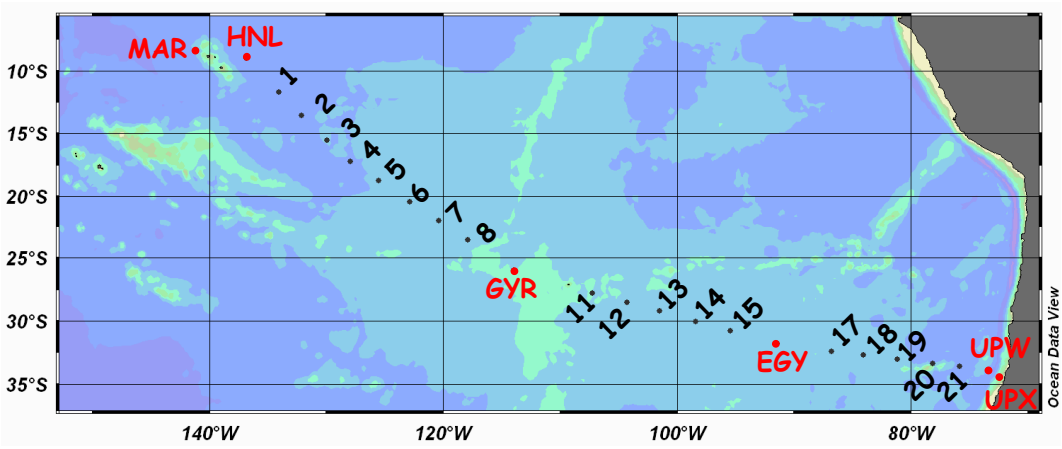

Fig. 1. Transect of the BIOSOPE cruise from the Marquesas Islands to Chile. Long-term process stations are indicated in red. Numbers indicates short-term stations, for which only numbers have been indicated to simplify presentation, and not the complete code as in Table 3. For instance 1 is STB1 and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

stable water body (Claustre and Maritonera, 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 coastal upwelling) and western (Marquesas plateau) borders, allowing the examination of a very large range of trophic conditions. Hyperoligotrophic conditions were observed at the centre of the gyre, with the clearest natural waters ever described (Morel et al., 2007), and a deep chlorophyll maximum reaching 180 m (Ras et al., 2007). The aim of the present study was to determine the abundance and activity of heterotrophic bacteria across the South Pacific Ocean, and to relate bacterial heterotrophic activity to phytoplankton primary production. We further discuss the techniques involved for determining the coupling between primary and bacterial heterotrophic production.

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 eastern South 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 Marquesas 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 (two sites chosen in the coastal upwelling region of central 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 system 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_{deck}) came from the same rosette cast as that used for bacterial production (the 09:00 a.m. CTD cast). However some measurements of PP using the JGOFs protocol (in situ moored lines immerged for 24 h from dusk to dusk, IPP_{insitu}) were also performed sometimes 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 presented in this paper include hydrographic properties (Claustre et al., 2008) and Total chlorophyll *a* (TChl*a*=Chl*a*+Divinyl-Chl*a*, Ras et al., 2007).

2.2 Bacterial abundance

Water samples for flow cytometric analyses of non-chlorophyllous bacterioplankton populations, asssumed to be mainly heterotrophic bacteria in the upper ocean, 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, bacterioplankton samples were stained with SYBR-Green I and counted on a FACS Calibur (Becton Dickinson) flow cytometer.

2.3 Bacterial production

"Bacterial" production (BP – sensus stricto referring to heterotrophic prokaryotic production –) was determined by [^{3}H]

Table 1. Main physical and biological characteristics of the stations sampled during the BIOSPE cruise. SST: sea surface temperature, Ze: depth of the euphotic zone (1% PAR), $Z_{10\%}$(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*, IPP_{deck}: integrated particulate primary production (based on on-deck incubations, see methods), IBP_{Ze}: integrated bacterial heterotrophic production. All stocks and fluxes are integrated from the surface to the euphotic depth.

station	Longitude ° W	Latitude ° S	date	SST °C	Ze m	$Z_{10\%}$ (UVB) m	I TChl *a* mg m^{-2}	IPP_{deck} mgC m^{-2} d^{-1}	IBP_{Ze} mgC m^{-2} d^{-1}
MAR1	−141.24	−8.40	26 October	27.8	66	10	24	457	131
MAR3	−141.28	−8.33	28 October	27.8	70		21	683	144
HNL1	−136.85	−9.00	31 October	27.8	90	10	16	335	86
STB1	−134.10	−11.74	3 November	27.8	99	12	17	414	101
STB2	−132.11	−13.55	4 November	27.4	124		17	250	96
STB3	−129.93	−15.53	5 November	27.1	134	12	16	150	114
STB4	−127.97	−17.23	6 November	26.5	136	17	16	164	87
STB5	−125.55	−18.75	7 November	25.7	142	19	11	142	71
STB6	−122.89	−20.45	8 November	24.5	157		5	139	72
STB7	−120.38	−22.05	9 November	24.3	167	28	8	76	79
STB8	−117.89	−23.55	10 November	23.4	144		7	152	61
GYR2	−114.01	−25.97	12 November	22.1	160	21	11	159	50
STB11	−107.29	−27.77	20 November	21.3	152		8	97	62
STB12	−104.31	−28.54	21 November	21.2	152	19	7	98	49
STB13	−101.48	−29.23	22 November	20.0	145		8	125	43
STB14	−98.39	−30.04	23 November	19.8	136		10	138	47
STB15	−95.43	−30.79	24 November	18.7	108		12	219	57
EGY2	−91.46	−31.82	26 November	18.1	92	12	14	196	55
STB17	−86.78	−32.40	1 December	17.3	96	10	15	280	61
STB18	−84.07	−32.68	2 December	17.4	87	9	15	233	44
STB19	−81.20	−33.02	3 December	17.2	107		12	195	57
STB20	−78.12	−33.35	4 December	17.6	48		21	359	93
STA21	−75.83	−33.61	5 December	16.8	56		21	566	110
UPW2	−73.36	−33.93	7 December	15.9	34	3	59		226
UPX1	−72.41	−34.54	9 December	13.3	38		39	1446	392

leucine incorporation applying the centrifugation method (Smith and Azam, 1992). Duplicate 1.5 mL samples were incubated with a mixture of [4,5-^{3}H]leucine (Amersham, specific activity 160 Ci mmol^{-1}) and nonradioactive leucine at final concentrations of 7 and 13 nM, respectively for active waters (>10 pmol leu l^{-1} h^{-1}) 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. at the centre of the gyre we incubated surface waters on average for 2 h, and the activity in dark incubated samples was linear up to 8 h, data not shown). Incubations were stopped by the addition of trichloracetic acid (TCA) to a final concentration of 5%. To facilitate the precipitation of proteins, bovine serum albumin (BSA, Sigma, 100 mg l^{-1} final concentration) was added prior to centrifugation at 16 000 g for 10 min. After discarding the supernatant, 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}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 also managed some size-fractionated BP measurements on some selected samples, we were also able to compare the filtration technique (20 ml incubated with 1 nM ^{3}H-leucine +19 nM cold leucine, filtered through Millipore GS 0.2 μm 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 range 5–578 ng C l^{-1} h^{-1}), the slope of "filtration" versus "centrifugation" was 1.04±0.02,

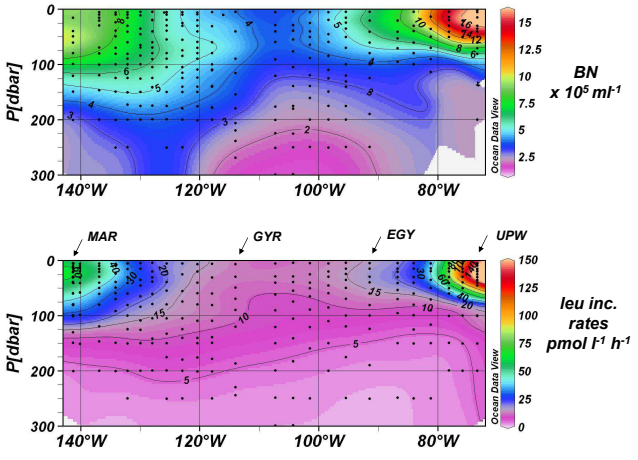

Fig. 2. Distribution of bacterial abundances (upper panel) and leucine incorporation rates (lower panel) along the BIOSOPE cruise transect. All CTD casts were performed around 09:00. The main characteristics of the stations sampled are presented in Table 1. The scale of leucine incorporation rates is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

and with only the $<$50 ng C l^{-1} h^{-1} data set (n=77), the slope was 0.93±0.04 (figure not shown). In both cases, the Y intercept was not significantly different from 0. We felt thus confident in comparing our measurements of leucine rates to results obtained with other protocols (centrifugation with no BSA or filtration technique).

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). Indeed, isotopic dilution ranged from 1.04 to 1.18 as determined on four occasions on concentration kinetics. Errors associated with the variability between replicate measurements (half the difference between the two replicates) averaged 13% and 6% for BP values less and more than 10 ng C $l^{-1}h^{-1}$, respectively.

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 two incubation methods: (i) in situ moored lines immerged during 24 h, and in that case daily rates were directly measured (PP_{insitu}) and (ii) using the conversion factors $\tau_{(Ti;T)}$ 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 six 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 (quadruplicate in the dark, quadruplicate in the light at each layer) 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_{insitu}. 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 also determined on filtered (0.8 μm) water samples.

2.6 Bacterial growth efficiency

The bacterial growth efficiency (BGE) was calculated from BP and DCR, assuming that bacterial respiration represented a constant proportion (f) of DCR, and applying a respiratory quotient (RQ) to convert O_{2-} based measurements to carbon units:

BGE = BP / (BP + (f × RQ ×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 Horizontal and vertical variation of bacterial production

Bacterial abundances (0.8–20.7×10^5 cells ml^{-1}) and leucine incorporation rates (0.34–400 pmol leu l^{-1} h^{-1}) varied over a large range across the 8000 km of the BIOSOPE transect (Fig. 2) and both variables were strongly correlated (relation log–log, n=249, r=0.85, $p<0.001$) . The gradients of

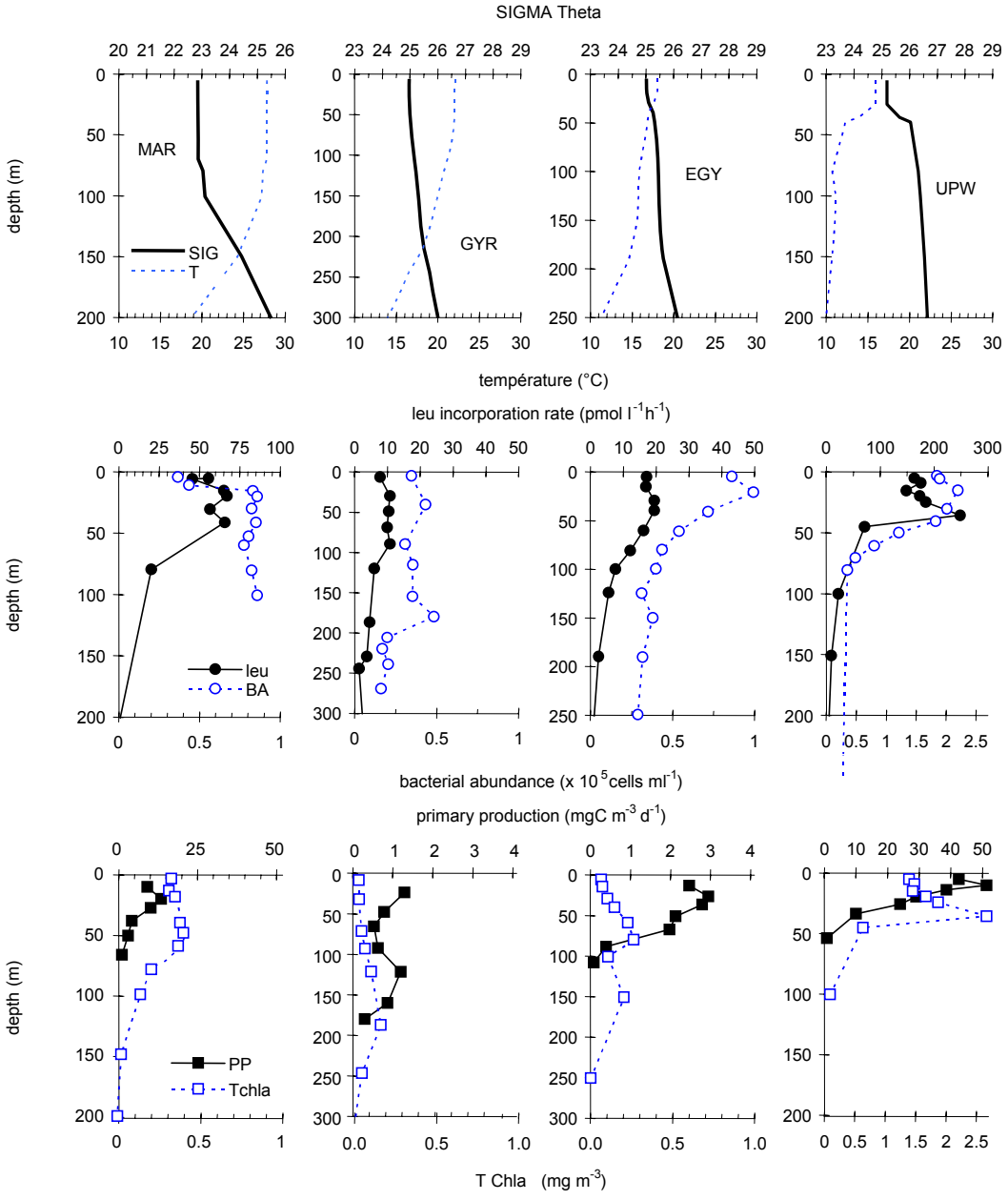

Fig. 3. Vertical distributions of temperature, sigma theta (upper panel), bacterial abundance, leucine incorporation rates (middle panel), Tchl*a*, primary production (PP_{deck}, see methods, lower panel), at stations mesotrophic MAR (26 October), hyperoligotrophic GYR (12 November), oligotrophic EGYR (26 November), and eutrophic UPW (7 December). All variables are from the 09:00 CTD cast, except for bacterial abundance (the following 12:00 CTD cast).

bacterial abundances and leucine incorporation rates were particularly pronounced off Chile. Highest leucine incorporation rates were obtained in the coastal upwelling area (250 pmol l^{-1} h^{-1} at UPW at 35 m, Fig. 3; 400 pmol l^{-1} h^{-1} at UPX at 15 m, data not shown) and in the northwestern zone of the transect, close to the Marquesas Islands (60 pmol l^{-1} h^{-1} at MAR at 10–50 m). Leucine incorporation rates were substantially lower between STB6 to STB15 representing the gyre stations (maximum 15 pmol l^{-1} h^{-1}). A similar pattern was detectable for chlorophyll (Ras et al., 2007) and concentrations of inorganic nutrients (Raimbault et al., 2007).

At the mesotrophic site MAR, sea surface temperature was 27.5°C and the mixed layer reached 70 m (Fig. 3). Leucine incorporation rates were highest between 10 and 50 m (59±8 pmol l^{-1} h^{-1}) coinciding with the layer of

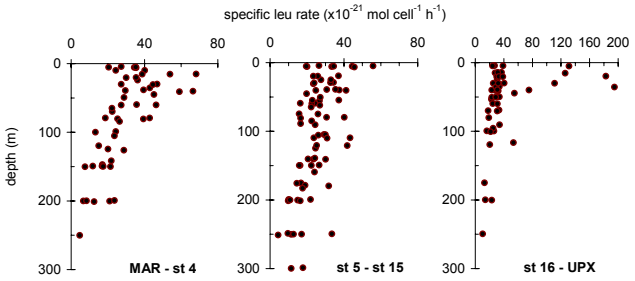

Fig. 4. Vertical distribution of specific leucine incorporation rates ($\times 10^{-21}$ mol leucine cell^{-1} h^{-1}). Bacterial abundance and leucine incorporation rates were measured on water samples coming from the same CTD cast. MAR-st 4: MAR 3, HNL1, STB1, 2, 3, 4; st5-st15: STB5, 6, 7, 8, 11,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

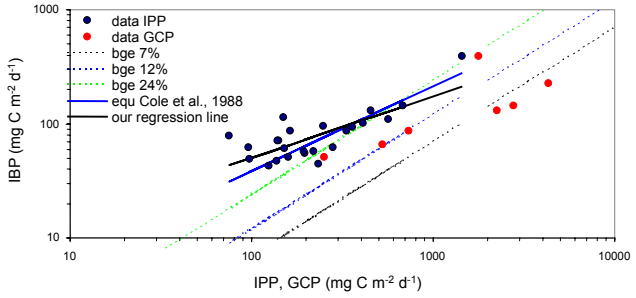

Fig. 5. Relation between bacterial production (IBP; y axis) and primary production (IPP, x axis), both expressed on an integrated basis for the euphotic zone (black dots). Relation between IBP and gross community production (GCP) are also indicated (red dots). Black line: regression line (Log IBP=0.542 Log IPP+0.615) for all our data set (n=24, r^2=0.59, p<0.0001). Red line: regression line (Log IBP=0.746 Log IPP+0.093) from Cole et al. (1988) calculated for pelagic systems. We used ordinary least square regression for comparison purposes, and also for the reasons evoked in Teira et al. (2001). The three dotted lines are relying on a couple of IBP, IPP points such that BCD equals IPP, (BCD=IBP/BGE=IPP), with assumed BGEs values of (from left to the right) 7% (green), 12% (blue), 24% (black).

maximum primary production (20 m, 13 μg C l^{-1} d^{-1}) and maximum TChl*a* (50 m, 0.4 μg l^{-1}). At the eutrophic site UPW, characterized by a shallow mixed layer (20 m) and relatively low surface water temperature (15.9°C), the maximum rates of leucine incorporation (250 pmol l^{-1} h^{-1}) and primary production (50 μg C l^{-1} d^{-1}) were higher than those at the MAR site. Maximum leucine incorporation coincided with a narrow, high TChl*a* peak (2.6 μg l^{-1}) at 35 m depth (Fig. 3). At the hyperoligotrophic GYR site, leucine incorporation was homogenous (mean ±SD: 9.3±1.9 pmol l^{-1} h^{-1}) down to 120 m depth, similarly to primary production (0.9±0.3 μg C l^{-1} d^{-1} between 20 and 160 m). Below 120 m, leucine incorporation progressively decreased to 1.4 pmol l^{-1} h^{-1} at 250 m depth. No clear association with the deep, very small peak of TChl*a* (0.16 μg l^{-1}) at 185 m depth was detectable at this site. At the oligotrophic site 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^{-1} d^{-1}.

In contrast to bulk leucine incorporation rates, cell-specific leucine incorporation rates varied within a rather narrow range (10–70$\times 10^{-21}$ mol cell^{-1} h^{-1}), except for the Chilean coast, where values reached up to 200$\times 10^{-21}$ mol cell^{-1} h^{-1} (Fig. 4). From MAR to STB4, a sub-surface maximum was visible around 20-30 m with values ranging from 30 to 70$\times 10^{-21}$ mol cell^{-1} h^{-1} (Fig. 4). Within the gyre (stations STB6 to STB15), specific leucine incorporation rates were rather constant down to the deep Tchl*a* maximum at around 160 m (13–56$\times 10^{-21}$ mol cell^{-1} h^{-1}).

Bacterial production (BP) integrated over the euphotic zone (IBP) ranged from 43 to 392 mg C m^{-2} d^{-1} during the BIOSOPE cruise (Table 1). The large range of trophic conditions encountered is reflected by the integrated stocks of TChl*a* in the euphotic zone ranging between 7 and 59 mg m^{-2} (Table 1) and the integrated fluxes of particulate primary production (IPP$_{deck}$) varying between 76 and 1446 mg C m^{-2} d^{-1} (Table 1). As for volumetric values, highest values of IBP were obtained in the upwelling region off Chile (226–392 mg C m^{-2} d^{-1}) corresponding roughly to the IBP obtained by Cuevas et al. (2004) – based on the thymidine technique – in the upwelling area off Concepcion in October 1999 (268–561 mg C m^{-2} d^{-1} for their coastal station at 73° W). At stations STB6 to STB15, encompassing the GYR sites, IBP was as low as 58±11 mg C m^{-2} d^{-1} (mean ±SD). Similarly, IPP$_{deck}$ revealed lowest values at these stations (134±42 mg C m^{-2} d^{-1}). Stations MAR and HNL, on the western part of the transect, presented intermediary values of IBP (86–140 mg C m^{-2} d^{-1}) and IPP$_{deck}$ (318–683 mg C m^{-2} d^{-1}). IPP$_{insitu}$, determined only on a limited number of stations across the transect reflected the trend in IPP$_{deck}$ (r=0.89, n=5) with higher values at MAR and UPX (1146 and 1344 mg C m^{-2} d^{-1}, respectively) and lower values at GYR (154 mg C m^{-2} d^{-1}, Table 2). IPP$_{insitu}$ was, on average, 1.3 fold higher than IPP$_{deck}$ (range 0.92–1.67, n=5). There was a significant log-log relationship between IBP and IPP$_{deck}$ when all data were pooled (Log IBP=0.551 Log IPP+0.594, n=36, r^2=0.59, p<0.0001) (Fig. 5). The ratio IBP to IPP$_{deck}$, however, was highly variable, ranging from 0.19 to 1.04 (n=24) across the cruise transect. For the GYR sites (STB 6 to STB15), the ratio IBP to IPP$_{deck}$ was, on average, 0.48±0.24, and it was 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 STB1: 0.25±0.03).

Gross community production (GCP) integrated in the euphotic zone ranged from 29 to 505 mmol O$_2$ m^{-2} d^{-1} (Table 2) and was well correlated with IPP$_{insitu}$ (r=0.88, n=7).

Table 2. Measured gross community production (GCP), dark community respiration (DCR), net community production (NCP), ^{14}C based particulate primary production (IPP_{deck} and IPP_{insitu}) at stations where all these parameters were available. Data are integrated over the euphotic zone (Ze). Errors correspond to water-column integrated standard deviations for GCP, DCR and NCP (quadruplicate incubations at each depth) and for IPP_{insitu} (triplicate samples at each depth). For IBP and IPP_{deck} errors represent water column integrated values of the variability between duplicate measurements per depth. Note that the units vary according the variable (mmol O_2 m^{-2} d^{-1} and mgC m^{-2} d^{-1}).

	Ze m	IBP mgC m^{-2} d^{-1}	DCR mmol O_2 m^{-2} d^{-1}	NCP mmol O_2 m^{-2} d^{-1}	GCP mmol O_2 m^{-2} d^{-1}	IPP^1_{deck} mgC m^{-2} d^{-1}	IPP^1_{insitu} mgC m^{-2} d^{-1}
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 2	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	245±21	−38±23	207±34	1446±46	1344±46

[1]IPP_{deck}: as in Table 1 (on-deck incubations), IPP_{insitu}: from 24 h in situ moored lines.

* The daily IBP were calculated cumulating data of different profiles measured every 3 h along a diel cycle (Van Wambeke et al., 2008). In other cases, daily BP was calculated from the 09:00 CTD cast assuming daily rates = 24 times hourly rates.

Integrated net community production (NCP) was again highest at the upwelling site UPW (429±19 mmol O_2 m^{-2} d^{-1}) and at the stations close to the Marquesas islands (mean 210 mmol O_2 m^{-2} d^{-1}). Integrated fluxes of NCP were negative at UPX (−38±23 mmol O_2 m^{-2} d^{-1}) and were close to balance at the GYR site (−13±20 mmol O_2 m^{-2} d^{-1} and −37±40 mmol O_2 m^{-2} d^{-1}).

3.2 Dark community respiration and bacterial growth efficiency

Rates of dark community respiration (DCR) varied within a narrow range (42–97 mmol O_2 m^{-2} d^{-1}) except for the high rates obtained at UPX (245 mmol O_2 m^{-2} d^{-1}). Respiration in 0.8 μm filtered seawater was determined only at station STB5. Respiration rates in the <0.8 μm size fraction and unfiltered seawater amounted to 0.62±0.22 and 0.52±0.25 μmol O_2 l^{-1} d^{-1}, respectively, at 5 m and to 0.46±0.12 and 0.58±0.24 μmol O_2 l^{-1} d^{-1}, respectively, at 125 m. Such comparison was made only in two occasions, and since it is risky to generalize these results, to determine the BCD we assume the following: (i) that heterotrophic bacterial respiration accounts entirely for DCR (BGE_{100}), (ii) or that it represents half of it (BGE_{50}, Table 3). For all stations considered, BGE_{100} and BGE_{50} ranged between 7 and 24% and between 14 and 38%, respectively. The application of respiratory quotients (RQ) reported in the literature (0.8–1.1; Robinson and Williams, 1999; Lefevre et al., in press) resulted in minor changes in the BGE for a given contribution of bacterial to community respiration (by 2 to 7%). 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). Considering both assumptions (i.e. different contributions of bacterial to community respiration and RQs), the lowest 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%, Table 3).

Table 3. Calculated bacterial growth efficiency (BGE), integrated gross community production (GCP, in carbon units), the ratio of IPP_{insitu}/GCP and BCD/GCP at stations where all the parameters were available. 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 given in Table 2. BGE_{corr}: BGE_{100} corrected for exponential growth in the flask during incubation.

	BGE^1_{50} %	BGE^1_{100} %	BGE^1_{corr} %	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 2	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

[1]The range considers minimum – maximum values when applying Respiratory Quotients of 0.8 and 1.1.

[2] The range considers minimum – maximum values when applying Photosynthetic Quotients of 1.1 and 1.4.

[3]The range considers minimum – maximum values obtained according the BGEs, RQ and PQ used.

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[1] °C	Area		leu conc nM	Leu rate pmol l^{-1} h^{-1}	SA leu 10^{-21} mol $cell^{-1}$ h^{-1}	leu CF kgC $mole^{-1}$	BB CF fgC $cell^{-1}$	TR d^{-1}	reference
20–25	South East Pacific, center of the Gyre[4]	Nov–Dec 2004	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	Torréton and Dufour, 1996a
18	Northwestern Med, inshore offshore transect	June 1993 & June 1995	20	8–70	3.4–101	0.3–2.1			Gasol et al., 1998
22–24	Med longitudinal transect, ionian+levantine [2]	June 1999	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 [3]	Sep 1999	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 1995		15–202	40–100				Ducklow et al., 2001
15	Atlantic NABE 40° N	April–May 1989	10	20–100	66–136*	1.1	20	0.08–0.1	Li et al., 1993
	45° N		10	20–200		3.4	20	0.2–0.4	
20	Sargasso Sea, BATS	spring	21	10–40		0.3–0.6	4.2–7.2	0.096	Carlson et al., 1996
25–26	(31°50 N, 64°10 W)	summer		10–30				0.079	
24–26		autumn		10–25				0.057	
18–21		winter		10–20				0.07	
18	North East Pacific, gyre edge off Oregon	summer 1997, 1998	20	15–33	14–21	0.4	20	0.02–0.04	Sherr et al., 2001
28	Equatorial Pacific along 140° W	Feb, Oct 1992			60–70**	3	20	0.109–0.163	Kirchman et al., 1995
28	Equator, Pac 140° W during El Niño	March 1992	10	25–55		2.3	20	0.15–0.25	Ducklow et al., 1995
25	Equator, Pac 140° W during non El Niño	Oct 1992	10	20–40		2.3	20	0.05–0.1	

[1]Only surface temperatures are indicated when stratification is important, [2]values from profiles down to depth of TChl*a* maximum, [3] values from surface layers, [4]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).

Keeping an average BGE of 7% as an estimate for the more oligotrophic sites, the ratio of the integrated bacterial carbon demand (BCD) to ^{14}C-Primary production (IPP_{deck}, given in Table 1) in the gyre would range between 3.7 (STB15) and 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 bioassay experiments (Van Wambeke et al., 2007), we observed, however, an increase in bacterial heterotrophic production during the 24 h incubation period (median factor of increase ×3.2, n=9, STB6 to STB15, Van Wambeke et al., 2007). Such increases during DCR measurements were reported previously (Pomeroy et al., 1994). Estimates of the BGE can be corrected from this bias by assuming an exponential increase in bacterial production during the 24 h as follows: $(BP_{24}-BP_0)/(Ln\,(BP_{24})-Ln\,(BP_0))$. Applying this correction, BGEs at the GYR sites range from 10 to 15% (Table 3). Consequently, the average BGE of 7% given above for the hyper-oligotrophic sites increases to 12%, resulting in a decrease in the range of the ratio BCD/IPP to 2.1–8.6 (median 3.3 for stations STB6 to STB15, n=9).

4 Discussion

The South Pacific Gyre is probably the most oligotrophic water body of the global ocean, a description that is up to date mainly based on satellite observations (Claustre and Maritonera, 2003). Several parameters determined during the BIOSOPE-cruise (Claustre et al., 2008), such as water tranparency (Morel et al., 2007) and phytoplankton biomass (7 mg TChl*a* m^{-2} in the euphotic zone, Table 1, Ras et al., 2007) confirm the hyperoligotrophic character of this area. One question that we addressed in the present study was whether bacterial production rates are also the lowest 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^{-1} h^{-1} (Table 4). Lower leucine incorporation rates were measured in the eastern Mediterranean Sea (Levantine and Ionian Sea, range 0.4–17, mean 6.6±4.9 pmol l^{-1} h^{-1}, Table 4), and in our study between STB6 and STB15 (range 5–21 pmol l^{-1} h^{-1}, mean 10.8±2.9 pmol l^{-1} h^{-1}). Both cases correspond to marine environments where the depth of the deep TChl*a* maximum exceeds 150 m. Bacterial abundance varies less than bacterial heterotrophic production, thus the lowest cell-specific activities are again obtained for the Levantine Basin in the Mediterranean Sea (1–49×10^{-21} mol $cell^{-1}$ h^{-1}), and cell specific activities were in the same order of magnitude (10–60×10^{-21} mol $cell^{-1}$ h^{-1}) in the centre of the South Pacific Gyre, the western Mediterranean Sea, or the equatorial Pacific Ocean (Table 4).

The bacterial community turnover rate (the ratio of bacterial production (BP) to bacterial biomass (BB) allows a comparison among studies independent of the technique (leucine or thymidine incorporation) used, but it requires the application of conversion factors for bacterial biomass and production. In the present study, we used 1.5 kg C per mol leucine incorporated, assuming no isotopic dilution, and

a low carbon per cell conversion factor 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^{-1}, Table 4, mean 0.11±0.03 d^{-1}, n=63) with many previous studies that used 3.1 kgC per mol leucine 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^{-1} based on leucine incorporation, Table 4 and 0.005–0.11 d^{-1} 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^{-1} (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 the high respiration of leucine (60–80%), in off shore stations leading to very low conversion factors (0.02–0.36 kg C mol leu^{-1}). Applying the mean of their empirical conversion factors (0.17 kg C mol leu^{-1}, Alonso-Saez et al., 2007) to our data set, bacterial turnover rates would range between 0.005 and 0.02 d^{-1} in the South Pacific Gyre. Based on microautoradiographic observations, the fraction of bacteria taking up leucine was determined to account for 19 to 33% of the bacterioplankton cells in surface waters in the gyre (Obernosterer et al., 2007). Assuming that this fraction represents the active bacterioplankton community, the turnover rate of the active population would be four-fold higher than any estimate based on the total counts. Considering all these assumptions, would lead to a possibly very large range of bacterial community growth rates, varying between 0.005 d^{-1} (0.17 kg C per mole, no correction for the active fraction) to 0.8 d^{-1} (1.5 kg C per mole, 25% of the bacteria active).

The fact that the bacterial community turnover rate is often low compared to that of phytoplankton is presently subject of debate (Duhamel et al., 2007 and references therein). Alternative techniques based on the turnover of a particular chemical pool or a cell compound were recently proposed to estimate turnover rates of heterotrophic bacterial cells. The turnover rate of the phosphate (P) pool in different size fractions, for instance, was examined during the BIOSOPE cruise (Duhamel et al., 2007). Based on the hypothesis that detrital particulate P is negligible, and assuming that the P assimilation rates and the P biomass in the $<0.6\,\mu$m fraction are mainly related to heterotrophic prokaryotes, these authors found a bacterial P-based turnover time of 0.11±0.07 d^{-1} in the gyre. This value compares well with the mean bacterial turnover rate that we obtained in the centre of the gyre using theoretical conversion factors. Unexpected high turnover rates of bacteriochlorophyll-a were reported for the Atlantic (0.7–1.1 d^{-1} in gyres centers, Koblizek et al., 2007). This pigment is characteristic for aerobic anoxygenic phototrophic bacteria, which were also abundant in the South Pacific Gyre (Lami et al., 2007) at the time of the cruise. Such turnover rates derived from the analysis of a given chemical pool, if representative for cell turnover (Koblizek et al., 2007), further suggest that some components of the heterotrophic (including mixotrophs) bacterioplankton 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_{deck} values were generally lower than those obtained by "standard" in situ incubations (IPP_{insitu}, Table 2). It is well known that it is difficult to reproduce 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_{insitu} were obtained in the North Pacific Gyre at ALOHA (200–900 mg C m^{-2} d^{-1}, Karl et al., 2001), and in the Sargasso Sea at BATS (312–520 mg C m^{-2} d^{-1} and 340–530 mg C m^{-2} d^{-1}, Steinberg et al., 2001 and Mourino-Carballido and McGillicuddy, 2006, respectively) as compared to the measurements of IPP_{insitu} in the centre of the South Pacific Gyre (154–203 mg C m^{-2} d^{-1}). 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^{-2} d^{-1} 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-bacteria 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 they often represent also the basis for defining the metabolic balance, presently a subject of debate (del Giorgio et al., 1997; Kirchman, 1997; del Giorgio and Duarte, 2002; Williams, 2004; Mc Andrew et al., 2007; Claustre et al., 2007a). 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 bacterial heterotrophic production from hourly to daily rates. Taking into account the diurnal variability of BP we observed at selected stations (Van Wambeke et al., 2008), real daily rates were, on average, by 18% higher than those calculated from one single measurement made at 09:00 a.m. and assuming linearity over 24 h. The error introduced by not taking into account the diurnal variability is in the same order as the precision of the

bacterial production measurement in oligotrophic areas (13% for BP values lower than 10 ng C l^{-1} h^{-1}, see methods).

Considering all these biases (e.g. diurnal variability in BP, BGE estimates), BCD could exceed ^{14}C based IPP in the gyre by factors varying between 2 to 8 (median 3.3, n=9). This is illustrated in Fig. 5 where most of our data points (IBP, IPP) are on the left side of the theoretical lines corresponding to situations where BCD equals IPP (Fig. 5), in particular with an assumed BGE of 7% and 12%. Two aspects should be considered about these results: first, BCD exceeded IPP at all stations, and second, a large variability of this ratio was obtained. Particulate PP based on ^{14}C measurements accounts for about 40–50% of gross photosynthesis (Karl et al., 1998; Moutin et al., 1999; Bender et al., 1999). In the present study, the ratio IPP/GCP (including the whole set of IPP_{deck} and IPP_{insitu} as given in Table 2) was 0.47±0.25 (mean ±SD) (Table 3), which confirms previous studies. Thus, the question arises how adequate the comparison between the BCD and ^{14}C-particulate primary production is? The present data set allowed us to compare the BCD to GCP, indicating that the ratio BCD/GCP is <1 or close to 1 (Table 3). Even in the centre of the gyre the two fluxes were close to balance. The same conclusion can be drawn from the fluxes of NCP (Table 2).

Processes like DOC production (by excretion, lysis, grazing processes) and respiratory losses are the main contributors to the difference between GCP and particulate PP. Estimates on the percent of primary production released as DOC vary largely among studies. Although some studies report a percentage of excretion constant across trophic gradients (Maranon et al., 2005); both laboratory (Myklestadt, 1995; Obernosterer and Herndl, 1995) and field studies (Teira et al., 2001; Moran et al., 2002; Fernández et al., 2004), indicate an increase of the percent of primary production released as DOC in nutrient-limited environments. In the South Pacific Gyre primary production was strongly limited by nitrogen (Bonnet et al., 2007). We attempted to estimate DOC excretion by using empirical equations on DOC production and particulate primary production obtained in field studies (Baines and Pace, 1991; Moran et al., 2001; Teira et al., 2001; Moran et al., 2002). This approach is, however, limited because the rates of primary production analyzed are higher than those encountered in the South Pacific Ocean. Applying on our data set relationships which were obtained in oligotrophic conditions as close as possible as ours: southern Ocean – NE Atlantic (Moran et al., 2002) or NW Iberian coastal transition zone (Teira et al., 2001), the percentage of extracellular release would vary between 20%±6% and 58%±11% (n=63) in the South Pacific Gyre, respectively. This approach does not take into account the amount of DOC released that is respired by bacteria during the incubation period. This fraction is likely to be high given the low BGEs in oligotrophic environments. This suggests potentially high percentages of DOC production rates in the South Pacific Gyre.

A marked diurnal pattern in bacterial production determined from high-frequency sampling at three stations (MAR, GYR and EGY) was observed (Van Wambeke, 2008). Bacterial production was highest around midnight, decreased until the early afternoon, and then rapidly increased again. This pattern reflects an adjustment of heterotrophic bacterial production to in situ primary production and DOC production. Heterotrophic bacterial production is likely to be delayed by a few hours from that of phytoplankton due to inhibition by UV radiation around noon. Apart from this short time-lag, these results suggest a strong coupling between primary production and heterotrophic bacterial production.

The variability in the ratio BCD/IPP observed in the present study is more driven by the variability in IPP than by the variability in IBP (percentage of variation 32% for IPP_{deck} data, versus 19% for IBP data at stations 6 to 15 considered as oligotrophic, Table 1). The strong variability in IPP was not related to the position of the station only. At station GYR, IPP_{deck} and GCP varied both considerably during our visit, and this variability was linked to surface irradiance (Claustre et al., 2007). 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). Larger variability in primary production as compared to respiration was also observed during a one year study at station ALOHA (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 as a consequence of 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). During the BIOSOPE-cruise the balance between autotrophic and heterotrophic processes was also determined applying an optically based method to determine gross primary production (Claustre et al., 2007). These authors conclude that the South Pacific Gyre is in metabolic balance. Observations based on alternative techniques and higher frequency (Emerson et al., 2002) are probably required to provide valuable insights into the temporal variability of autotrophic and heterotrophic processes in the open ocean.

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