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Gross community production and metabolic balance in the South Pacific Gyre, using a non intrusive bio-optical method

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Abstract

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The very clear waters of the South Pacific Gyre likely constitute an end-member of oligotrophic conditions which remain essentially unknown with respect to its impact on carbon fixation and exportation. We describe a non-intrusive bio-optical method 5 to quantify the various terms of a production budget (Gross Community Production, community losses, net community production) in this area. This method is based on the analysis of the diel cycle in Particulate Organic Carbon (POC), derived from high frequency measurements of the particle attenuation coefficient c_p . We report very high integrated rates of Gross Community Production within the euphotic layer (average of 10 $846 \pm 484 \text{ mg C m}^{-2} \text{ d}^{-1}$ for 17 stations) that are far above any rates determined using incubation techniques for such areas. Furthermore we show that the daily production of POC is essentially balanced by the losses so that the system cannot be considered as net heterotroph. Our results thus agree well with geochemical methods, but not with incubation studies based on oxygen methods. We stress to the important role of 15 deep layers, below the euphotic layer, in contributing to carbon fixation when incident irradiance at the ocean surface is high (absence of cloud coverage). These deep layers, not considered up to now, might fuel a part of the heterotrophic processes in the upper layer, in particular through dissolved organic carbon release. We further demonstrate that, in these extremely clear and stratified waters, integrated Gross Community 20 Production is proportional to the POC content and surface irradiance via an efficiency index ψ_{GCP}^* , the water column cross section for Gross Community Production. We finally discuss our results in the context of the role of oligotrophic gyre in global carbon budget and of the possibility of using optical proxy from space for the development of gross community rather than primary production global models.

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1 Introduction

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Subtropical gyres are vast oceanic oligotrophic biomes representing 60% of the global ocean. Their metabolic state (magnitude of carbon fixation vs. respiration rates) and, consequently, their role in the global oceanic carbon cycle is still being debated (del 5 Giorgio et al., 1997; Williams, 1998) which finds its roots in early discussions about the magnitude of carbon fixation in these systems (Jenkins, 1982; Lewis et al., 1986; Jenkins, 1988). On one hand, and based on in vitro biological techniques performed in the euphotic zone and having characteristic time scales of \sim 1 day, it is generally concluded that the ocean is in a net heterotrophic state: rates of carbon fixation are low and the 10 whole community respiration rate (R) exceeds the gross primary production (GPP) (del Giorgio et al., 1997; del Giorgio and Duarte, 2002), so that the so-called Net Community Production (NCP=GPP-R) is always negative. On the other hand, studies based on geochemical tracer distributions with larger relevant space/time scales support net production and export rates one order of magnitude higher (Jenkins, 1982; Jenkins, 1988; Lewis et al., 1986). As a result, the upper ocean ecosystems are considered 15 on average to be autotrophic which suggests that in vitro experiments are affected by biases or not representative of larger space or time scales. Modelling studies conclude that mesoscale activity and the so-called eddy-pumping processes cannot explain the discrepancies between both approaches (Oschlies, 2002), and that unaccounted biological processes, such as N_2 -fixation (Gruber, 2005), export of dissolved organic 20 carbon (Dietze and Oschlies, 2005) or episodic primary production events generally missed by classical sampling strategies (Karl et al., 2003; Williams et al., 2004), may be responsible. It has been suggested that primary production rates are as much as 3–5 times higher in these vast ocean regions than what has been estimated using classical 25 strategies/methods (Karl et al., 2003). Given the vast extent of the oligotrophic gyres, the implications for carbon dynamics at the global scale are profound.

Siegel et al. (1989) presented the first data of a daily cycle in the attenuation coefficient, c_p , a proxy of particle load, in the upper layers (>100 m) of the oligotrophic

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waters of the North Pacific Gyre. Increase of particle load was observed during day-time, while a decrease of similar amplitude was observed during nighttime, allowing the conclusion that particle production was balanced at the daily scale. At the western border of the South Pacific Gyre (SPG, precisely at 150° W, 16° S), similar observations 5 were obtained by Claustre et al. (1999) down to 160 m. Furthermore, as c_p can be calibrated into Particulate Organic Carbon (POC) concentration (e.g. Gardner et al., 1993; Loisel and Morel, 1998; Claustre et al., 1999), daily cycle in c_p likely embeds information into the various terms involved in the upper ocean carbon budget. Thus, 10 the first aim of the present study is to develop a method, based on the analysis of the daily cycle in optically-resolved POC, allowing to quantify the various terms of the production budget in an oligotrophic area.

The South Pacific Gyre (SPG) is likely the most oligotrophic oceanic area (Claustre and Maritorena, 2003) of the global ocean with the clearest waters ever reported (Morel et al., 2007) associated with undetectable surface nitrate and the deepest nitracline (Raimbault et al., 2007). Obviously, any conclusion reached about the carbon 15 production terms in this oligotrophic condition end-member might constitute a reference for subtropical gyres as a whole. Therefore, as part of the BIOSOPE cruise (Claustre et al., 2007¹) which was carried out in the South East Pacific and crossed the SPG in its most oligotrophic part, we here focus on the analysis and interpretation of the 20 diel cycle in c_p for a ~3000 km subset of the transect where the oligotrophic conditions appeared to be the most extreme.

¹Claustre, H., Sciandra, A., and Vaulot, D.: Introduction to the special section: bio-optical and biogeochemical conditions in the South East Pacific in late 2004 – the BIOSOPE program. Biogeosciences Discuss., in preparation, 2007.

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2 Methods

2.1 Cruise description and station selection

The BIOSOPE cruise onboard RV Atalante took place during austral summer from 26 October to 11 December 2004 from Marquesas Island toward the Chilean coast. The ~8000 km transect encompassed a wide range of hydrodynamic and trophic conditions (Claustre et al., 2007¹). Two types of stations were investigated (Fig. 1), the so-called long (more than 2 days of occupation) and short (less than one day of occupation) stations (Claustre et al., 2007¹). For the present study we will mainly focus on the most oligotrophic waters. They are here defined as those waters for which the euphotic zone depth (the depth where the Photosynthetically Available Radiation (PAR, in the visible range 400–700 nm) is reduced to 1% of its surface value) is greater than 100 m. Actually such criteria delineates waters with surface Chlorophyll a (Chla) concentration lower than ~0.08 mg m⁻³ (Morel et al., 2007, equation in the legend of their Fig. 9). Such waters represent ~30% of the global ocean (Antoine et al., 2005, their Fig. 8). In the area investigated during BIOSOPE, these oligotrophic stations include the long station GYR (Fig. 1), west of Easter Island. We will focus on this station to develop our approach and apply it elsewhere. From the real-time ocean color images, this station was selected as having the lowest surface Chla concentration (see also supplementary information <http://www.biogeosciences-discuss.net/4/3089/2007/bgd-4-3089-2007-supplement.pdf>). The GYR station was occupied for five days and eight casts a day were performed. Additionally, 13 “oligotrophic” short stations (St2 to St15 and St19, Fig. 1) were investigated and at least three casts were performed during the day period.

2.2 Particle attenuation coefficient : treatment and significance

The attenuation coefficient, c (m⁻¹) was determined using a Wetlabs C-star transmissiometer (25 cm path length, 660 nm wavelength) attached to the CTD rosette. Each

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cast was performed down to 500 m. Data treatment was performed as described in Loisel and Morel (1998) and Claustre et al. (1999). Briefly, in order to take into account any possible variation due to changes in the cleanliness of the optical window, attenuation coefficient profiles were corrected assuming that deep waters are optically stable and close to pure water ($c=0.364 \text{ m}^{-1}$). The average attenuation coefficient between 450 and 500 m was thus taken as a reference for each cast.

In open ocean waters, the beam attenuation coefficient at 660 nm measured by a transmissiometer, once corrected for absorption by pure water, is essentially a measurement of the attenuation coefficient by particles, c_p (m^{-1}), because absorption coefficients by dissolved material is negligible at this wavelength (Loisel and Morel, 1998). Furthermore, the absorption by particles (detrital and vegetal) is also negligible so that c_p is equivalent to the particle scattering coefficient. Thus, the main source of variation in c_p is the numerical abundance and size of particles while second order sources are refractive index and shape of particles (Gardner et al., 1993). For a standard particle size distribution (Junge type with a -4 exponent), the particles to which the transmissiometer is most sensitive lie in the $0.5\text{--}10 \mu\text{m}$ size range (Stramski and Kiefer, 1991) which typically corresponds to the size domain of the living (pico- and nanophytoplankton, cyanobacteria, heterotrophic and photo-heterotrophic bacteria pico- and nano-zooplankton,) and non-living particles (detritus). It has been suggested (Morel, 1988) and subsequently verified (e.g. Gardner et al., 1993 ; Loisel and Morel, 1998; Claustre et al., 1999) that c_p is linearly related to POC (mg m^{-3}). Some significant regional differences in this relationship have been reported. In particular a relationship with a slope of $502 \text{ mg C m}^{-3} \text{ m}^{-1}$ was reported for the North western part of South Pacific gyre (Claustre et al., 1999) which was at least twice as large as those found for other oceanic regions (Siegel et al., 1989; Walsh et al., 1995). As part of the present study and using 35 simultaneous c_p and POC measurements, the high slope was confirmed ($\text{POC}=502 c_p + 10$) and also recently corroborated by new regional relationships obtained for the North Pacific Gyre (slope = 560) and the equatorial Pacific (slope = 552) (Gardner et al., 2006). Therefore, the slightly rounded relationship $\text{POC} = 500 c_p$ pro-

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posed by Claustre et al. (1999) is adopted for the present study. This conversion factor is equivalent to an attenuation cross section of $2\text{ m}^2\text{ gC}^{-1}$.

2.3 Other measurements

Total sun radiation was measured onboard (every min) using an Eppley pyranometer.

5 PAR (in energy units) was subsequently derived, assuming it represents 43% of the total irradiance at the ocean surface.

For the pigment analysis, 5.6 L of seawater were filtered onto GF/F filters which were subsequently stored in liquid nitrogen. Within 3 months after collection, pigments were extracted in methanol and analyzed by HPLC using a method dedicated for low concentration samples (Ras et al., 2007²). The HPLC absorbance detector was also set at 770 nm to detect bacteriochlorophyll *a* (Bchl_a) (limit of quantitation of 0.0004 mg m^{-3}). The euphotic zone limit, *Ze* (m) was derived from in situ radiometric measurements using an LICOR irradiance profiler (Morel et al., 2007). On some occasions, when irradiances measurements were not performed, *Ze* was derived from the vertical profile of Chla (Ras et al., 2007²).

For the determination of POC, up to 8.2 L of seawater were collected from Niskin bottles and filtered onto precombusted GF/F filters. Carbon analysis was performed using a CEC 440HA Organic Elemental Analyzer after the filters had been treated with 0.25 ml of 10% HCl to remove inorganic carbon (Stramski et al., 2007³).

20 On two occasions at the GYR station (12 November and 14 November), net community production and community respiration were measured using 24-h light and dark incubations, respectively, of unfiltered seawater in 120-ml biological oxygen demand

²Ras, J., Uitz, J., and Claustre, H.: Spatial variability of phytoplankton pigment distribution in the South East Pacific, *Biogeosciences Discuss.*, in preparation, 2007.

³Stramski, D., Reynolds, R. A., Babin, M., Claustre, H., Kaczmarek, S., Lewis, M. R., Rottgers, R., Sciandra, A., Stramska, M., and Twardowski, M. S.: Relationships between the particulate organic carbon concentration and optical properties of surface waters in the South East Pacific and Atlantic Oceans, *Biogeosciences Discuss.*, in preparation, 2007.

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(BOD) bottles. Seawater was collected at six depths in the upper 200 m and in situ incubations started at 06:00 a.m. The BOD bottles were filled by siphoning the seawater from 10-L acid-rinsed polycarbonate (PC) carboys, using silicon tubing and allowing the BOD bottles to overflow. Prior to sampling, the BOD bottles were rinsed with 1N 5 HCl, Milli-Q water and seawater (3x) from the respective depth layer. Measurements of net community production and respiration were performed in five replicate BOD bottles. Gross primary production and community respiration were calculated as the difference between the initial and final dissolved oxygen concentrations in the light and dark incubations, respectively. The concentration of dissolved oxygen was determined by 10 Winkler titration of whole bottles. Titration was done with an automated potentiometric end-point detection system (Metrohm DMS 716). The mean standard error of the oxygen concentration determination was $0.15 \mu\text{mole O}_2 \text{ L}^{-1}$ (coefficient of variation of 0.061%).

3 Results and discussion

15 3.1 Main patterns observed along the transect

The main hydrodynamic patterns crossed along the BIOSOPE transect are described elsewhere (Claustre et al., 2007¹). The distribution in c_p (Fig. 2) is in accordance with these patterns. At both extremities, in the vicinity of Marquesas islands (west) and associated with the Peru Chile Current (east), high c_p values are recorded in the 20 upper layers (up to 0.5 m^{-1} in the upwelling conditions off the Chilean coast). In the central part of the transect (~km 2000 to km 4500), associated with undetectable nitrates in the 0–150 m layer (Raimbault et al., 2007), low surface Chla and the presence of a pronounced deep Chla maximum (DCM, sometimes extending to 180 m and below), c_p takes its lowest values, especially at st7 and st8. St7 indeed represents the 25 clearest waters (Morel et al., 2007) with the euphotic zone depth extending down to ~170 m. From the GYR station to St14 there is a weak, but significant, relative maxi-

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mum in c_p around ~ 100 m. The distribution of c_p in this layer roughly parallels that of BChla, an indicator of photoheterotrophs performing anoxygenic photosynthesis. Eastwards, outside the core of the oligotrophic part of the Gyre, station 19 still presents oligotrophic characteristics with an euphotic zone depth of ~ 105 m, surface Chla of $\sim 0.06 \text{ mg m}^{-3}$ and $c_p < 0.06 \text{ m}^{-1}$ in the upper layer. Actually, nutrient distribution at this station ($\sim 2.8 \text{ mM}$ at the surface) reveals that it corresponds to a High Nutrient Low Chla situation (Raimbault et al., 2007; Claustre et al., 2007¹).

3.2 POC budget at the daily cycle: case study at the GYR station

3.2.1 The various terms of the budget

10 At the GYR station, high frequency CTD transmissiometry measurements allow the variations of c_p to be highlighted at the daily scale (Fig. 3). The c_p measurements displayed conspicuous daily variations with a sunrise minimum and sunset maximum, an observation previously reported for other oligotrophic and mesotrophic areas (Siegel et al., 1989; Claustre et al., 1999). While this cycle was detectable down to 220–240 m, 15 there are two zones in the upper layer where it is stronger: the zone of the DCM and the layer around ~ 100 m (zone of BChla maximum, see Fig. 2). Once calibrated in terms of POC and integrated over pre-defined layers (Fig. 4), the clear increase of POC during the day followed by a decrease of roughly similar amplitude during nighttime, suggests that production and loss of POC are balanced over 24 h (see also supplementary information). 20 In a less oligotrophic part of the South Pacific Gyre ($16^\circ \text{ S } 150^\circ \text{ W}$, with surface concentration of $\sim 0.07 \text{ mg Chla m}^{-3}$), it was demonstrated that phytoplankton does not contribute to more than 20% of the c_p -derived POC (Claustre et al., 1999). As part of BIOSOPE, this value was confirmed by Grob et al. (2007) throughout the gyre. If phytoplankton alone would be responsible of the daily change in POC, this would imply uncomfortably high growth rates (Claustre et al., 1999). Therefore, it is suggested that the increase in POC reported here not only reflects the sole photo-autotrophic production of POC but also the POC production by other heterotrophic components 25

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of the microbial community (actually the production of living particles that are seen by a transmissiometer). Given that the increase in POC occurs during the day, the increase of heterotrophic biomass thus appears also stimulated (positively related) to photo-trophic processes. We thus propose that a budget of the various production and loss terms can be derived from the variations in the integrated content in POC at the daily scale (Fig. 5).

Over a given oceanic layer, the light stimulated Gross Community Production (GCP, $\text{mg C m}^{-2} \text{ d}^{-1}$) seen by a transmissiometer, is here defined as the sum of Gross Primary Production (GPP, excluding dissolved production) and of the production by the microbial (heterotrophic) community. The Net Community Production (NCP, $\text{mg C m}^{-2} \text{ d}^{-1}$) represents the difference between GCP and community losses (CL, $\text{mg C m}^{-2} \text{ d}^{-1}$, the consequence of grazing, viral lysis, settling, and respiration rates).

$$\text{NCP} = \text{GCP} - \text{CL} \quad (1)$$

For the duration of the night period (Nt , d), the Gross Community Production is null, so the night time decrease in POC, $N\delta\text{POC}$ (mg m^{-2} , taken as a positive number), can be considered as an estimation of CL :

$$\text{CL} = \frac{N\delta\text{POC}}{Nt} \quad (2)$$

rearranging Eq. (1) and (2):

$$\text{GCP} = \text{NCP} + \frac{N\delta\text{POC}}{Nt} \quad (3)$$

At this stage, another constraint can be imposed, which is derived from the observation of Fig. 4. Actually, over a full day, the daily increase in POC, $D\delta\text{POC}$ (mg m^{-2}) roughly balances $N\delta\text{POC}$. NCP presents slight positive and negative variations from day to day at station GYR (Fig. 4). However, over the 4 days of investigation the average NCP is not significantly different from zero. Defining the Net Carbon Stock (NCS, mg m^{-2}) (Fig. 5) as the product of NCP by a given time interval (day), null NCP implies:

$$\text{NCS} = D\delta\text{POC} - N\delta\text{POC} \quad (4)$$

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It comes that :

$$D\delta\text{POC} = N\delta\text{POC} \quad (5)$$

Applying this new constraint, the equation can be finally rewritten as:

$$\text{GCP} = \frac{D\delta\text{POC}}{1 - Nt} = \frac{N\delta\text{POC}}{Nt} \quad (6)$$

5 Thus, only the increase (decrease) in POC during day (night) time and the night (day) length are required to estimate GCP.

3.2.2 Model development

The sampling frequency at the GYR station was sufficient to encompass the full range of day-night variations in POC. This was not the case for other stations (see Fig. 2) 10 which were sampled only 3 times during daytime. To obtain GCP from these data, we need to provide additional information in the form of simple model. We base this model on the rather regular daily variations in POC observed at the GYR station, which suggests that they can be accurately modelled using an empirical formulation. A polynomial of third degree was chosen with the following constraints. The rates of change 15 of POC are equal to zero at sunrise (t_{sr} , h) and sunset (t_{ss} , h), respectively, and maximal (inflection point) at noon (t_{no} , h). Using these constraints, the time variation in POC, POC(t), can be modelled as:

$$[\text{POC}(t)] = [\text{POC}_{t_{no}}] + \text{RPOC}_{t_{no}} (t - t_{no}) \left[\frac{1 - (t - t_{no})^2}{3(t_{sr} - t_{no})^2} \right] \quad (7)$$

where $[\text{POC}_{t_{no}}]$ (mg m^{-2}) and $\text{RPOC}_{t_{no}}$ ($\text{mg m}^{-2} \text{ h}^{-1}$) represents the [POC] content 20 and the instantaneous production in [POC] at noon (t_{no} , h), respectively. Actually, $\text{RPOC}_{t_{no}}$ represents the maximal instantaneous rate of change in POC. Equation (7) was fitted to the GYR data using the Gauss-Newton method. The model performs well

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for the four days of investigation and for the 3 layers investigated (Fig. 6). Actually fitted GCP compares well with measured GCP estimated from the difference between the minimal and maximal values (Fig. 7).

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3.3 Gross and net community production in oligotrophic regimes

5 The average GCP within the euphotic zone over four diel cycles is ~ 734 (± 97) $\text{mg C m}^{-2} \text{d}^{-1}$ (Table 1). This production is balanced by losses [721 (± 159) $\text{mg C m}^{-2} \text{d}^{-1}$], and average NCP (over 4 days) is not significantly different from zero.

On days 1 and 3, using classical measurements of O_2 changes in light/dark bottles incubated over a 24-h period, Gross Primary Production (O_2 -GPP) and Community

10 Respiration (O_2 -CR) were determined in the euphotic zone. O_2 -GPP, once converted to carbon units with a photosynthetic quotient of 1.1 (Laws, 1991), is significantly lower [473 (± 223) $\text{mg C m}^{-2} \text{d}^{-1}$] than GCP (Table 1). By contrast, and assuming a respiratory quotient of 1.1, the CR of 768 (± 65) $\text{mg C m}^{-2} \text{d}^{-1}$ is in the same range as the loss rates determined by the optical method.

15 The net community production computed solely using O_2 measurements leads to the usual conclusion that the upper ocean is in metabolic deficit (O_2 -NCP = -295 (± 158) $\text{mg C m}^{-2} \text{d}^{-1}$) (Table 1). Being the most oligotrophic oceanic region, it is not surprising that our O_2 based production rates are lower than those previously reported for the less oligotrophic North Pacific Gyre [O_2 -GPP = 657 (± 52) $\text{mg C m}^{-2} \text{d}^{-1}$; O_2 -CR =

20 920 (± 39) $\text{mg C m}^{-2} \text{d}^{-1}$]. Our O_2 -NCP values for the SPG are however essentially equivalent to those for the North Pacific Gyre [-270 (± 49) $\text{mg C m}^{-2} \text{d}^{-1}$]. Contrary to incubation methods, our optical method is non-intrusive as are geochemical approaches. In addition, unlike geochemical observations, we integrate over the same time scales (hours to day) as incubation measurements.

25 When the model is applied to all oligotrophic stations (using only three measurements a day), the high GCP values recorded at GYR are confirmed (Fig. 8). On average, GCP amounts 452 ± 264 , 846 ± 484 and 1093 ± 520 $\text{mg C m}^{-2} \text{d}^{-1}$ for $0-0.5 \text{ Ze}$,

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0-Ze and 0–1.5 Ze layers, respectively. These high *in situ* estimates are comparable to the very high values of GPP (greater than $1 \text{ g m}^{-2} \text{ d}^{-1}$) reported at station ALOHA using an *in situ*, non-intrusive technique based on triple oxygen isotope measurements (Juranek and Quay, 2005). Our results, when compared to other BIOSOPE results, 5 remain, however, higher than primary production rates measured at the GYR station using O_2 *in vitro* techniques. Furthermore these rates are much higher than the average rates derived for all the oligotrophic stations, using *in vitro* incubation with either ^{13}C labelling (Raimbault and Garcia, 2007) ($180 \pm 60 \text{ mg C m}^{-2} \text{ d}^{-1}$) or ^{14}C labelling (Van Wambeke et al., 2007) ($153 \pm 48 \text{ mg C m}^{-2} \text{ d}^{-1}$). It should be noted, that contrarily to 10 the O_2 -based method, those measurements based on isotope labelling do not take into consideration Dissolved Organic Carbon (DOC) excretion, a process which can be of major significance in such systems (see below).

While optical measurements indicate that POC production is roughly balanced over five days, consistent with geochemical approaches, the oxygen measurements imply 15 net heterotrophy. We argue that photosynthetic processes occurring in extremely dim light conditions could explain the missing $\sim 300 \text{ mg C m}^{-2} \text{ d}^{-1}$ estimated with O_2 measurements (Table 1) to obtain the balanced production observed by the optical approaches.

Significant production rates were recorded in the deep layer (160–240 m) where the 20 remaining light represents between 1% and 0.1% of surface radiation, i.e. below the so called euphotic zone (Table 2). A diurnal trend was not observed in this layer during our first day on this station, which had experienced overcast conditions for at least 2 days (Fig. 4). A clear cycle became apparent, however, in the last three days (13 to 15 November). SPG surface waters are the clearest of the global ocean (Morel et al., 25 2007); thus short term fluctuations in surface irradiance are reflected in the 160–240 m layer. They undoubtedly impact photosynthesis (and hence GCP) at these depths. This process was previously suggested for highly stratified oligotrophic systems (Karl et al., 2002) but had been never evidenced. Actually in this deep layer, the GCP increased by a factor of seven over the four days of investigation (from 45 mg to $319 \text{ mg C m}^{-2} \text{ d}^{-1}$)

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(Table 2). Over the same period, GCP in the euphotic zone increased by 34% reflecting to some extent saturation of photosynthesis at high light intensities. Furthermore, on some days (e.g. cycle 4, 15 November), production in the deep layer could account for more than the average discrepancy between the oxygen and optical method observed for the 0–160 m layer. Over the 4 days of investigation, the mean GCP in this deep layer ($176 \text{ mg C m}^{-2} \text{ d}^{-1}$, Table 2) accounts for ~60% of this discrepancy. About 40% of this discrepancy remains to be explained.

The concentration of dissolved organic carbon (DOC) in the euphotic layer (~120 μM) is the highest ever reported (Raimbault et al., 2007) for a subtropical gyre. It is indeed about 20% higher than maximal values reported for the North Pacific Gyre (Church et al., 2002), and values as high as 90 μM were still recorded at the 0.1% of surface radiation. Most of this DOC is likely of refractory nature and given the shape of the profile, these high concentrations must result from local production accumulating over time. For the North Pacific Gyre, it has been advanced that phototrophic production of DOC could represent up to 50% of GPP (Karl et al., 1998). The optical method does not measure this dissolved fraction. However, in a tightly coupled system with a rapid turnover, the fraction of this dissolved production is labile and can fuel heterotrophic and photo-heterotrophic production in the SPG, especially during the daylight period (Church et al., 2004; Karl et al., 1998).

We observed a peak in c_p at ~100 m that is not associated with any Chla features (Fig. 2), and which shows clear daily oscillations and thus contribute to GCP. This c_p maximum is collocated with the BChla maximum lying 80 m above the Chla maximum, a feature present throughout a large part of the SPG. BChla-containing bacteria can use both light and dissolved organic material to sustain their growth and carbon requirements (Sieracki et al., 2006). However, their photosynthesis is anoxygenic (Sieracki et al., 2006; Kolber et al., 2001), and thus not accounted for by measurements based on changes in oxygen. Furthermore, besides photoheterotrophy performed by these BChla-containing bacteria, it is very likely that other photoheterotrophic organisms might intervene in POC build-up (Church et al., 2004; Beja et al., 2001). These

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processes might be particularly important in the nutrient impoverished environments of subtropical gyres (Karl, 2002). We therefore suggest that part of the apparent metabolic unbalance reported for the euphotic zone of SPG and more generally of subtropical oligotrophic gyres based on *in vitro* oxygen techniques could be due to 5 unaccounted photoheterotrophic processes, including anoxygenic carbon fixation processes. These processes would be sustained by deep (below the euphotic zone) photosynthesis intracellular products, which would represent the required organic source that is often referred to when trying to understand the metabolic unbalance of these systems (e.g. del Giorgio et al., 1997).

10 The fact that, in these extremely clear oligotrophic waters, processes below the so-called euphotic zone (1% depth) have not to date received much attention, might be surprising. Indeed, even if it is widely recognized that the deep chlorophyll maximum prevailing in oligotrophic gyres might be in large part the result of photo-adaptation processes, its presence nevertheless remains a clear indication that oxygen photosynthesis 15 does occur in deep layers. Actually, at the GYR station, more than 60% of the water Chla content was located in the layer comprised between the euphotic depth (Ze) and $1.5 Ze$. Other studies did not succeed to measure production (O_2 , ^{14}C) in very deep layer (below Ze). This is very likely linked to the difficulty of keeping “deep samples” in extremely dim light (not to say dark) conditions during sample processing 20 at sea. We suggest here that in most cases, deep populations receive unavoidable light damage during their sampling, manipulation and bottle deployment at sea. Our optical method, operating at the same time scale than *in vitro* measurements, is not intrusive (like geochemical ones) and thus avoid any light hazard of that sort.

25 During the present investigation, surface irradiance varied tremendously, by a factor of 6 (more than the seasonal variation in surface irradiance) over 6 days. Nevertheless, the investigated area remained in metabolic balance (even in slight autotrophic state) which means that such highly stratified systems have a large capacity to adapt and to stabilize their metabolic status under strongly variable environmental conditions (here light, which is likely the most important forcing variable in subtropical oligotrophic

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3.4 Potential extrapolation of our observations

The estimations based on the bio-optical method presented here were conducted at a location and a period representative for the most extreme oligotrophic conditions of

5 the global ocean (see supplementary information). In this context, the rates estimated for this maximum of oligotrophy can be considered as a minimum reference for oligotrophic gyres in general (60% of the global ocean). From the GCP rates measured (846±484 mg C m⁻² d⁻¹) the annual carbon fixation rates for subtropical gyres are thus estimated to be at least 67 Pg for the euphotic layer. These values are equivalent or
10 higher than estimates derived from bio-optical models for the global ocean (Antoine et al., 1996; Behrenfeld et al., 2005). The subtropical gyres, therefore, might have a much
15 larger impact than anticipated on ocean carbon cycle.

Furthermore, we believe that the method presented here is potentially useful in the context of bio-optical modelling of production. Bio-optical models for the estimation of depth integrated primary production are of the general form :

$$P = PAR(0^+) \times B \times \Psi \quad (8)$$

which expresses that the carbon fixation rate P (g C m⁻² d⁻¹) is proportional to the product of the column integrated content of the biomass (B) of phototrophic organism by the irradiance at the ocean surface, PAR(0+). B is generally depicted by areal Chla

20 (mg Chla m⁻²). Ψ is an efficiency term which convolves the irradiance absorption capability of B together with its efficiency in converting absorbed photons into chemical energy. Depending on the units chosen for PAR(0+) (quanta- or energy based), different ways of expressing Ψ have been proposed (Falkowski, 1981; Malone, 1987; Morel, 1991). The most simple expression of Ψ is achieved when B is expressed in terms of
25 integrated Chla concentration and PAR(0+) is expressed in MJ m⁻² d⁻¹ and converted into reduced carbon equivalent (39 kJ gC⁻¹), so that that equation (8) can be rewritten

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as :

$$\Psi^* = 39P/[PAR(0^+)Chla] \quad (9)$$

Ψ^* ($m^2 \text{ g Chla}^{-1}$) is here defined as the Chla specific water column photosynthetic cross section. For the global ocean, within the layer comprised between the surface and 1.5 Ze, Ψ^* varies within a relatively narrow range around a central value of $\Psi^* = 0.070 \pm 0.035 \text{ m}^2 \text{ gChla}^{-1}$. This means that 7% of the incident PAR is converted into stored chemical energy when 1g of Chla is present in the upper lit layers.

All the studies investigating such bulk water column efficiency indexes have only considered the biomass of photo-autotrophic organisms depicted by Chla. The present study clearly demonstrates that phytoplankton alone cannot explain the daily increase in particulate carbon; heterotrophs (bacteria and possibly pico and nano-heterotrophs) as well as photo-heterotrophs also participate in this process. From Fig. 8, it is clear that GCP in all investigated layers appear to be reduced in the vicinity of 120° W, when surface irradiance was drastically reduced ($2 \text{ MJ m}^{-2} \text{ d}^{-1}$ vs an average value over 10 $\text{MJ m}^{-2} \text{ d}^{-1}$ for the other stations). Figure 9 provides an analyses, for each layer, of the possible dependency of GCP with respect to biomass (here expressed in POC) and surface irradiance. Clearly GCP appears proportional to the product of POC and surface irradiance. This coupling suggests that, in the same way that a photosynthetic cross section was defined earlier, the Gross Community Production cross section with respect to carbon can be defined, Ψ^*_{GCP} :

$$\Psi^*_{GCP} = 39GCP/[PAR(0^+)POC] \quad (10)$$

Actually the slopes of the regression presented in Fig. 9 have units of $\text{m}^2 \text{ MJ}^{-1}$. Using the conversion factor (between energy and carbon), Ψ^*_{GCP} is estimated to 2.28×10^{-3} , 1.63×10^{-3} and $1.63 \times 10^{-3} \text{ m}^2 \text{ g C}^{-1}$ for 0–0.5 Ze, 0-Ze and 0–1.5 Ze layers, respectively. In other words, ~0.2% of the surface irradiance is converted to chemical energy when 1 g of POC is present. If the values are normalized by the generic $0.07 \text{ m}^2 \text{ g Chla}^{-1}$ for photosynthetic cross section a reasonable POC/Chla ratio of ~40 is esti-

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mated within the 0–1.5 Ze layer. This represents, at least, a partial validation of the estimations.

Beside the estimation of a carbon- rather than a Chla-based water column efficiency for production, the present approach has also a potential interest for the bio-optical modelling of production. Recently, it has been proposed that carbon-based, rather than Chla-based, models could be an improved way to estimate the rate of ocean carbon fixation from remote sensing data (Behrenfeld et al., 2005). The premise of carbon-based models is that the particle backscattering coefficient, b_{bp} , retrieved from space is an (accurate) estimation of phytoplankton carbon. This assumption is, however, questionable. Indeed, optical proxies (either c_p or b_{bp}) derived either from space or in situ measurements are primarily related to the particle load (POC content in oceanic waters). This includes, together with phytoplankton, heterotrophic components (bacteria, flagellates) and also bio-detritus; thus, their relationship to phytoplankton carbon is not straightforward, if any exists. Therefore, because community production likely integrates the contribution of all organisms depicted by b_{bp} , the proper rate of carbon fixation that should be associated with this optical proxy of particle load would better be the community production rather than the sole primary production.

It is interesting to note that using the carbon-based model, Behrenfeld et al. (2005) ends up with much higher primary production rates for the tropical ocean than using a Chla-based model, while the discrepancies are much lower for other oceanic areas. One possibility for such discrepancies is that phytoplankton carbon derived from space would be overestimated in tropical environments; some dedicated studies have indeed clearly shown that the contribution of phytoplankton to c_p can be low in such oligotrophic environment (Claustre et al., 1999). The production rates derived for these environments would possibly be more closely related to gross community (phytoplankton and small heterotrophs) rather than to primary production rates.

Based on the use of optical proxies of biogenic particles (not exclusively phytoplankton) from space, we thus believe that bio-optical model of Gross Community Production (GCP) would thus likely provide a more reliable estimate of carbon fixation, especially

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in oligotrophic tropical environments where microbial communities play an essential role. Indeed, GCP is a photo-driven process which, besides the POC formation by phytoplankton, also integrates DOC excretion and its subsequent use by microbial organisms. DOC release is certainly a key process (see Karl et al., 1998) that would require much more attention in view of implementing such models.

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Table 1. Comparative carbon production and loss rates in the South Pacific Gyre.

Process measured		Rate obtained		
	Oxygen method	Optical method	Oxygen method	Optical method
Gains	O ₂ -GPP	GCP	473±223	734±97
Losses	O ₂ -CR	CL	768±65	721±159
Balance	O ₂ -NCP	NCP	-295±158	14±73

Measurements were obtained using two techniques in the euphotic zone (0–160 m) at the GYR station. Values are expressed in $\text{mg C m}^{-2} \text{ d}^{-1} \pm$ one standard deviation. A photosynthetic and respiratory quotient of 1.1 is assumed (Laws, 1991).

CR: Dark community respiration.

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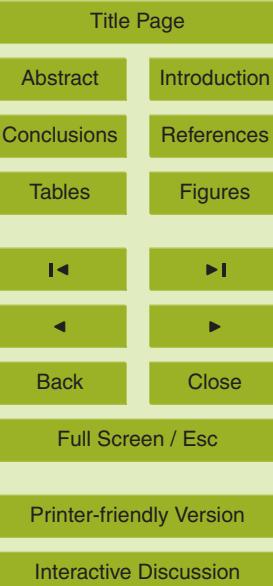
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Table 2. Day-to-day variations in the carbon production and loss rates in the South Pacific Gyre.

	GCP (0–240 m)	CL (0–240 m)	NCP (0–240 m)	GCP (160–240 m)	Surface irradiance
Cycle 1	663	607	56	45	26.6
Cycle 2	920	881	39	123	44.5
Cycle 3	911	888	23	219	38.4
Cycle 4	1148	1211	-63	319	44.4
Mean	910±198	897±247	14±53	176±119	

The 240 m depth corresponds to 1.5 times the euphotic depth as traditionally defined, and is a depth where 0.1% of surface irradiance is available. Production terms are expressed in $\text{mg C m}^{-2} \text{ d}^{-1} \pm$ one standard deviation and surface irradiance in $\text{moles quanta m}^{-2} \text{ d}^{-1}$.



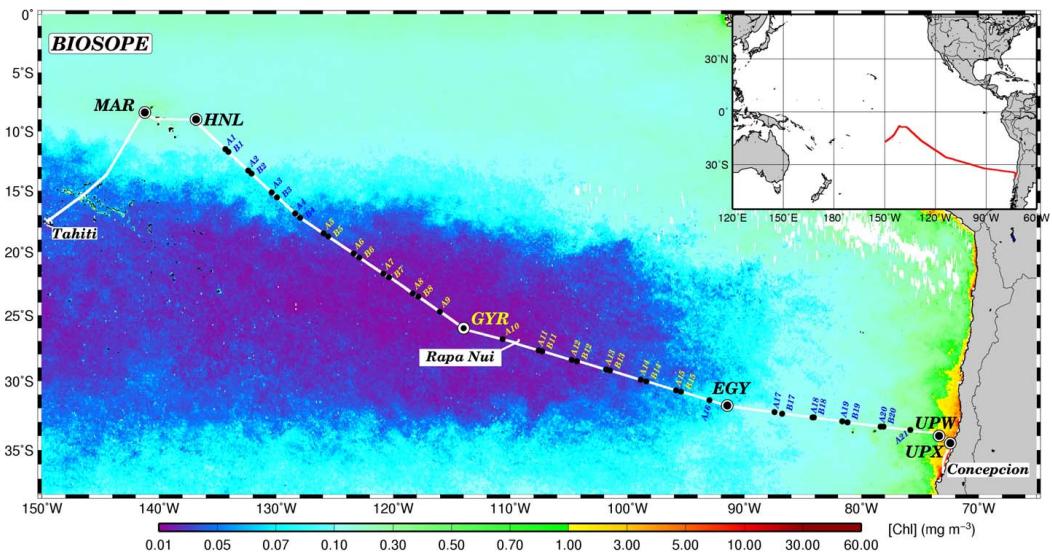


Fig. 1. Transect of the BIOSOPE cruise superimposed on a SeaWiFS composite image of Chla concentration in the upper layer for November–December 2004.

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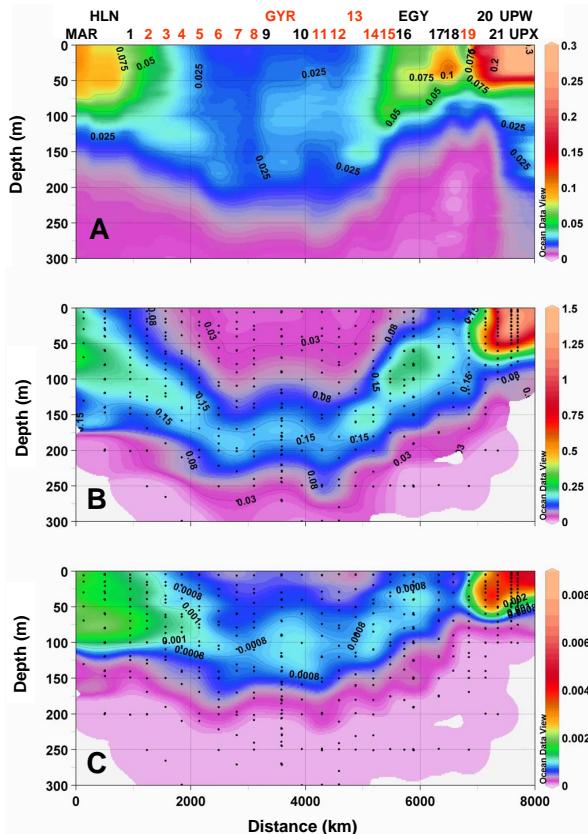


Fig. 2. Distribution of key biogeochemical quantities along the BIOSOPE transect. **(A)** The attenuation coefficient, c_p . **(B)** the concentration in Chla (sum of mono- and Divinyl-Chla) **(C)** the concentration in bacteriochlorophyll a (mg m^{-3}). On the upper part of panel (A) are reported the positions of stations (see also Fig. 1). The “oligotrophic stations” examined in this study are identified in red.

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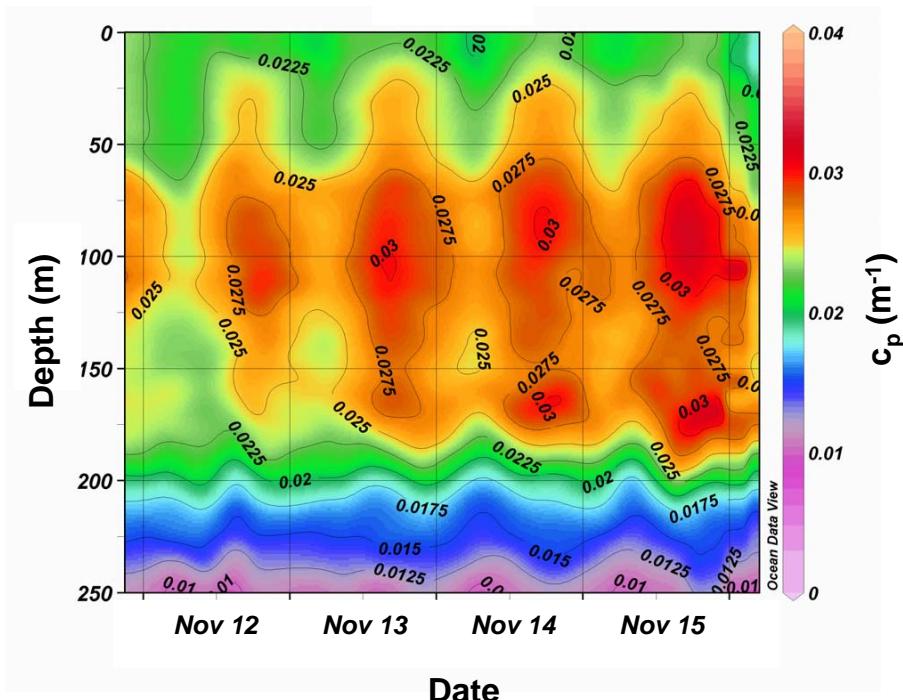


Fig. 3. Daily variations in the vertical distribution of c_p within the 0–300 m layer at the GYR station.

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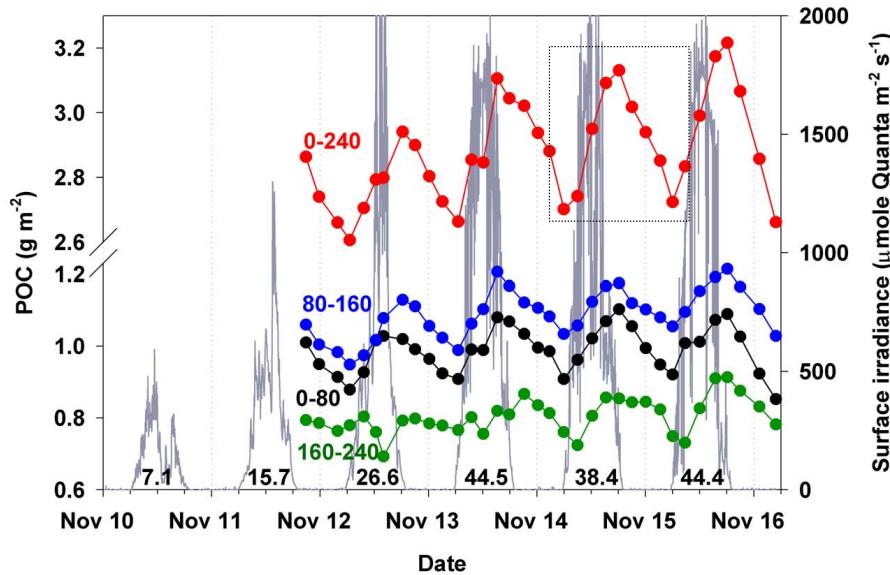


Fig. 4. Daily variations in integrated particulate organic carbon content, derived from c_p measurements, over various optical depth intervals. Red: 0–240 m corresponds to the range of 100%–0.1% of surface irradiance; Blue: 80–160 m (10%–1%); Black: 0–80 m (100%–10%); Green: 160–240 m (1%–0.1%). Surface irradiance is plotted as a grey line and the number inside each daily irradiance cycle refers to the daily dose of photons (moles quanta m^{-2}). The dotted square identifies the portion of the cycle which is used for the schematic presented in Fig. 5.

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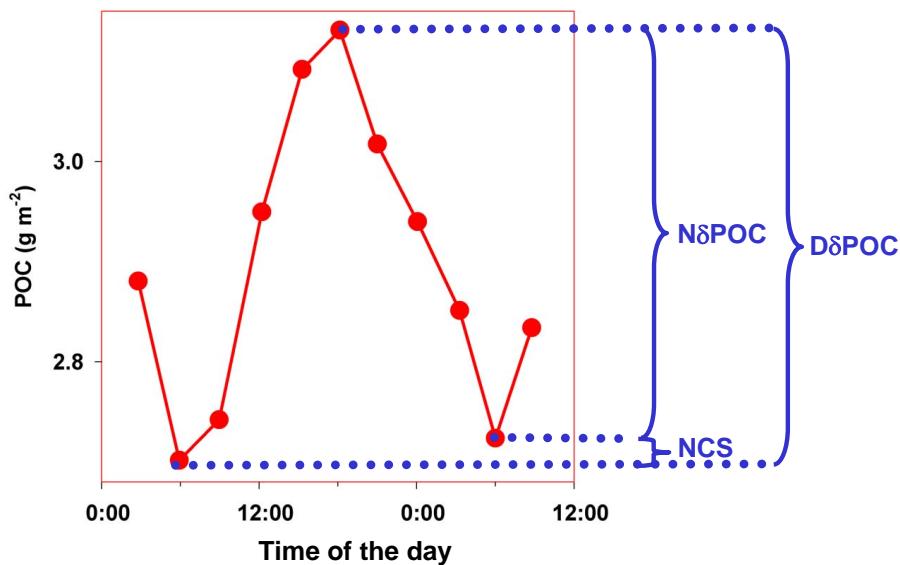


Fig. 5. Schematic of the various terms of the metabolic balance that can be inferred from the diel change in c_p or POC. See text for definition. The data corresponds to the third cycle presented in Fig. 4 (dotted square).

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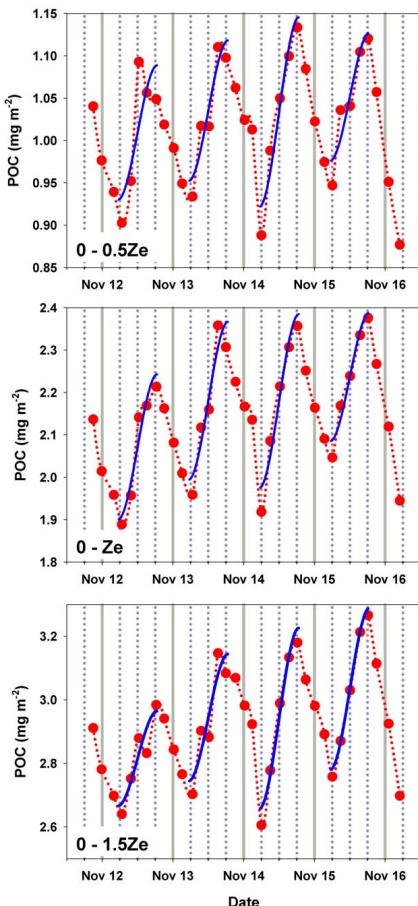


Fig. 6. Modelling diurnal variations in optically determined POC in various optical layers (0–0.5Ze, 0-Ze, 0–1.5Ze) at the GYR station. The red dot corresponds to the original data while the blue line represents the fitting of Eq. (7) to the data.

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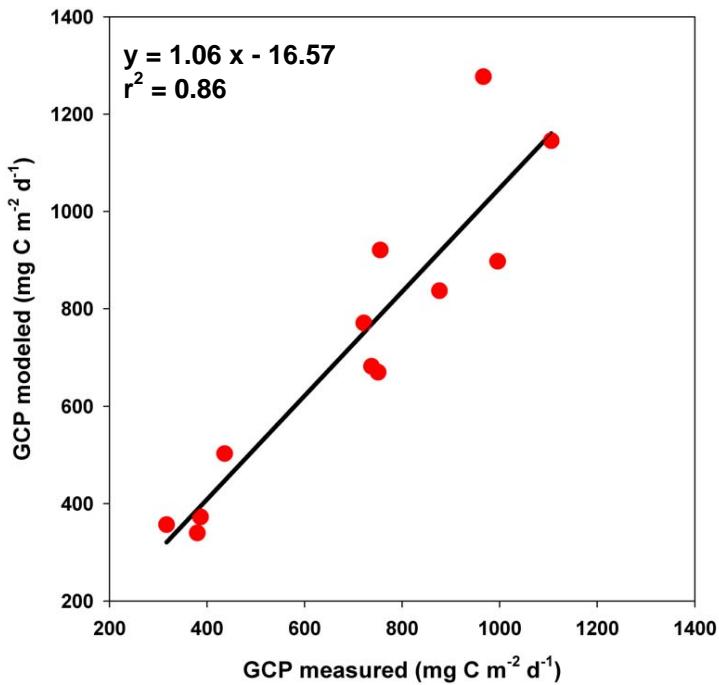


Fig. 7. Comparison of fitted (using the polynomial model) and measured GCP at the GYR station.

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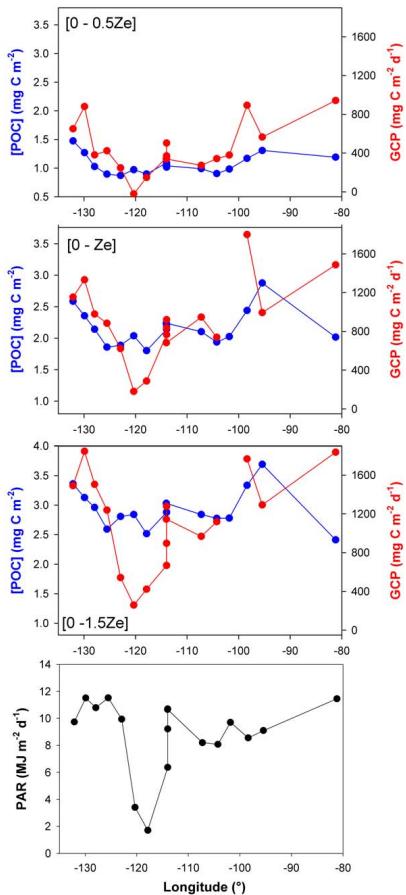


Fig. 8. Variations in POC and GCP in oligotrophic stations along the BIOSOPE transect. Only oligotrophic stations reported in red in Fig. 2 are here considered. The three upper panels correspond to three optical layers (0–0.5 Ze, 0-Ze, 0–1.5 Ze). The lower panel presents daily dose of PAR.

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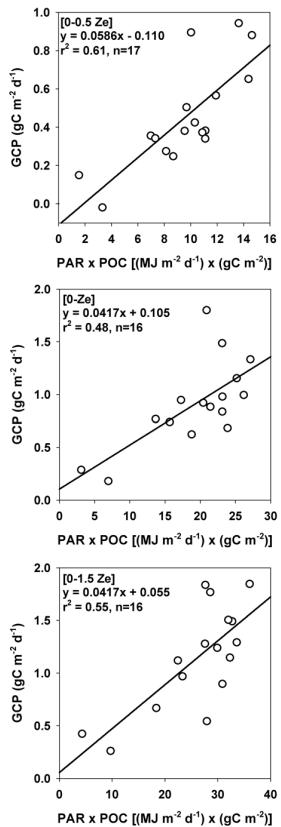


Fig. 9. The Estimation of ψ^*_{GCP} , the cross section for Growth Community Production in oligotrophic regime. ψ^*_{GCP} represents the slope of the regression between GCP and the product of surface irradiance by the carbon content. Data from station 13 have been excluded from this analysis for the 0-Ze and 0–1.5 Ze layer because internal waves have made the DCM (and the associated c_p peak) shift from above Ze to below Ze between consecutive casts.

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