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Response of heterotrophic and autotrophic microbial plankton to inorganic and organic inputs along a latitudinal transect in the Atlantic Ocean

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Abstract

Atmospheric nutrient deposition into the open ocean increased over the past decades as a result of human activity and water-soluble organic nitrogen accounts for up to 30% of the total nitrogen inputs. The effects of inorganic and/or organic nutrient inputs on phytoplankton and heterotrophic bacteria have never been concurrently assessed in open ocean oligotrophic communities over a wide spatial gradient. We studied the effects of potentially limiting inorganic (nitrate, ammonium, phosphate, silica) and organic nutrient (glucose, aminoacids) inputs on microbial plankton biomass, community structure and metabolism in five microcosm experiments conducted along a latitudinal transect in the Atlantic Ocean (from 26° N to 29° S).

Primary production rates increased up to 1.8-fold. Bacterial respiration and microbial community respiration increased up to 14.3 and 12.7-fold, respectively. Bacterial production and bacterial growth efficiency increased up to 58.8-fold and 2.5-fold, respectively. The largest increases were measured after mixed inorganic-organic nutrients additions. Changes in microbial plankton biomass were small as compared with those in metabolic rates. A north to south increase in the response of heterotrophic bacteria was observed, which could be related to a latitudinal gradient in phosphorus availability. Our results suggest that organic matter inputs associated with atmospheric deposition into the Atlantic Ocean will result in a predominantly heterotrophic versus autotrophic response and in increases in bacterial growth efficiency, particularly in the Southern Hemisphere. Subtle differences in the initial environmental and biological conditions are likely to result in differential microbial responses to inorganic and organic matter inputs.

1 Introduction

Atmospheric nutrient deposition into the open ocean has increased over the last decades as a result of human activities. Changes in land use and in hydrologic and

global biogeochemical cycles are known to significantly alter the fluxes of matter entering into the ocean (Duce et al., 2008). Atmospheric nitrogen deposition over the oceans is expected to double in the next 50 yr, and recent studies suggest that atmospheric water-soluble organic nitrogen entering central ocean regions accounts for up to 30% of the total atmospheric nitrogen inputs into these marine areas (Cornell et al., 1995; Duce et al., 2008 and references therein). Increases in atmospheric nutrient inputs have been shown to change the structure and metabolism of coastal microbial planktonic communities (Paerl, 1997; Peierls and Paerl, 1997; Seitzinger and Sanders, 1999) and similar effects may be expected over open ocean microbial communities. Thereby, the circulation of organic matter in the upper ocean, a key process in the global carbon cycle, might also be altered. However, the magnitude and nature of these changes is uncertain given the complex interactions and feedback mechanisms governing the dynamics of autotrophic and heterotrophic planktonic microbial communities.

Atmospheric inputs have been recognized as an important source of nutrients for upper ocean microbial communities (Baker et al., 2007), being responsible for the supply of significant amounts of inorganic and organic nitrogen (N), phosphorus (P), silica (Si) and micronutrients such as iron (Fe), zinc (Zn) or cobalt (Co), to the surface oceanic layer. Nitrate and ammonium atmospheric deposition is mainly related to industrial and agriculture practices (Galloway et al., 2004) and it is still under study whether atmospheric organic nitrogen is derived from natural or anthropogenic sources (Cornell et al., 1995). Saharan dust and biomass burning are considered the main sources of phosphorus to the atmosphere (Mahowald et al., 2005; Baker et al., 2006).

The stoichiometric ratios of these inputs notably differ from those of the nutrient uptake ratios of primary producers. In this context, Baker et al. (2003, 2007) reported inorganic N:P and N:Si ratios in atmospheric deposition in the Atlantic Ocean from 20 to 2200 and from 34 to 830, respectively, well above phytoplankton uptake ratios, even for organisms with relatively high N:P ratios such as *Prochlorococcus* and *Synechococcus* (Bertilsson et al., 2003).

The nature of nutrient limitation of phytoplankton and bacterial production is known to vary over spatial and temporal scales (Cullen et al., 1992; Arrigo, 2005; Church, 2008; Saito et al., 2008). Nitrogen is the proximal limiting nutrient of phytoplankton growth in the oligotrophic tropical and subtropical Atlantic over physiological and/or ecological time scales (Graziano et al., 1996; Mills et al., 2004, 2008; Moore et al., 2008), whereas P and Fe, as limiting nutrients for N_2 fixation (Falkowski, 1997; Tyrrell, 1999) are responsible for N-limitation of primary production at geological time scales. It has also been suggested that enhanced atmospheric inputs together with enhanced nitrogen fixation rates may lead to phosphorus limitation in the tropical North Atlantic Ocean (Wu et al., 2000; Ammerman et al., 2003; Mather et al., 2008).

Some nutrient enrichment bioassays have demonstrated that N and P are co-limiting heterotrophic bacterial metabolism in oligotrophic environments (Thingstad and Rassoulzadegan, 1995; Rivkin and Anderson, 1997; Joint et al., 2002; Mills et al., 2008); whereas many others report organic carbon as the limiting or co-limiting factor (Church et al., 2000; Carlson et al., 2002; Alonso-Sáez et al., 2007; Van Wambeke et al., 2008; among others).

Although organic nitrogen constitutes a relevant fraction of the total atmospheric nitrogen deposition into the surface ocean, the effects of inorganic and/or organic nitrogen inputs on both phytoplankton and heterotrophic bacteria remain poorly studied. To the best of our knowledge, only the study by Davidson et al. (2007) have concurrently addressed the differential effect of inorganic versus organic nitrogen inputs on both phytoplankton and bacteria in coastal waters.

The aim of our study was to assess the response of microbial planktonic communities to inorganic and/or organic nutrient loading over a large spatial scale, in order to determine general patterns in the linkage between the type of input, the initial biotic and abiotic conditions, and the interactions between microbial components. Specifically, we tested the differential effect of inorganic versus organic nitrogen inputs on autotrophic and heterotrophic microbial communities along a latitudinal gradient in the upper oligotrophic Atlantic Ocean.

2 Materials and methods

Five enrichment microcosm experiments were performed during cruise Trynitrop I on board "BIO-Hespérides" from 16 November to 16 December 2007 (Fig. 1 and Table 1). Water for the experiments was collected along a latitudinal transect in the Atlantic Ocean (approximately from 26° N to 29° S latitude) (Fig. 1).

At each sampling station, vertical profiles of temperature, salinity and in situ fluorescence were obtained using a Conductivity-Temperature-Depth sensor (CTD) attached to a rosette down to 300 m.

Water samples were collected before dawn from 10–15 m into 15-l acid-clean Niskin bottles and filtered through 150 µm pore size net to remove larger zooplankton. Subsequently, eight 12-l acid-washed polycarbonate bottles were gently filled under dim light conditions.

2.1 Experimental design

Following sample collection, nutrients were added to the experimental bottles. The experimental design included duplicates for a series of four treatment levels: 1. Control: no additions made; 2. Inorganic Addition Treatment: 0.5 µmol l^{-1} nitrate (NO_3^-), 0.5 µmol l^{-1} ammonium (NH_4^+), 0.05 µmol l^{-1} phosphate (PO_4^{3-}) and 0.1 µmol l^{-1} silicate (SiO_4^{2-}); 3. Organic Addition Treatment: 0.5 µmol l^{-1} glucose and 0.5 µmol l^{-1} of an equimolar mixture of 18 aminoacids; 4. Mixed Addition Treatment: combination of inorganic and organic additions. Inorganic nitrogen and phosphorous additions concentrations fell within the ranges reported for dissolution experiments conducted with collected aerosols (Herut et al., 2005) and Saharan soils (Bonnet et al., 2005). The ratio N:Si:P of the additions performed was 20–30:2:1 depending on the addition made (inorganic or mixed addition treatment). No trace metal-clean techniques were available to collect the required sample volume, thus we decided not to include Fe in the experimental design. Organic nitrogen additions were performed to simu-

late previously reported increases in atmospheric bioavailable water-soluble organic nitrogen inputs (Seitzinger and Sanders, 1999; Mace et al., 2003; Duce et al., 2008). Glucose was also included as atmospheric depositions can contain non-nitrogenous organic constituents (Jurado et al., 2008; Pulido-Villena et al., 2008; Reche et al., 2009). Pulido-Villena et al. (2008) reported an increase of dissolved organic carbon (DOC) of ca. 3 µmol C l^{-1} after a dust deposition event in the surface mixed layer of the Western Mediterranean. Therefore, our addition of ca. 5 µmol C l^{-1} in the form of amino acids and glucose, compare reasonably well, in terms of DOC concentration, with the observed DOC increases associated with a natural event of dust deposition.

Experimental bottles were maintained in an in-door incubation chamber which simulated in situ irradiance (photoperiod=12–14 h, and constant light intensity=240 µE m^{-2} s^{-1}) and temperature. Using the measured values of incident irradiance and vertical extinction coefficient, we determined that the irradiance used during the experiments was similar (within 20%) to the mean irradiance reaching the sampling depth in situ over the light period (from dawn to dusk). Experiments lasted 3 d and samples were taken every 24 h to monitor changes in microbial community structure and function.

2.2 Chemical and biological analysis

2.2.1 Nutrients

The concentration of nitrate and ammonium was determined on-board on fresh samples with a Technicon segmented-flow auto-analyser and using modified colorimetric protocols that allow to lower the detection limit to 2 nmol l^{-1} (Kerouel and Aminot, 1997; Raimbault et al., 1990). The concentration of phosphate was determined using standard procedures (Tréguer and Le Corre, 1975).

2.2.2 Size-fractionated chorophyll-*a*

Size-fractionated chlorophyll-*a* (chl-*a*) concentrations were measured in 250 ml water samples which were filtered sequentially through 2 and 0.2 µm polycarbonate filters. After extraction with 90% acetone at 4 °C overnight at dark, chlorophyll-*a* fluorescence was determined with a TD-700 Turner Designs fluorometer calibrated with pure chl-*a*.

2.2.3 Primary production (PP)

Four 75 ml acid-cleaned polystyrene bottles (3 light and 1 dark) were filled and inoculated with 277–740 kBq (7.5–20 µCi) $NaH^{14}CO_3$. Samples were incubated for 12–14 h in the same incubation chamber as the experimental bottles. After the incubation period, samples were sequentially filtered through 2 and 0.2 µm polycarbonate filters at very low vacuum (<50 mm Hg). Filters were processed to assess ^{14}C incorporation as described in Marañón et al. (2001).

2.2.4 Bacterial heterotrophic production (BP)

The [^{3}H]leucine incorporation method (Kirchman et al., 1985), modified as described by Smith and Azam (1992), was used to determine Leu incorporation rates (LIR). Samples were incubated for 1.5 to 2 h in the same incubation chamber as the experimental bottles. Dilution experiments in order to determine the in situ leucine to carbon conversion factors (CF) were performed with enrichment water following the methods detailed elsewhere (Calvo-Díaz and Morán, 2009). The CFs obtained at the station where the enrichment microcosm experiments were performed (or an average between the CF values from the nearest available stations) were used to calculate bacterial biomass production rates from Leu uptake rates (CF range: 0.17–0.21 kg C mol Leu^{-1}).

2.2.5 In vivo electron transport system (ETS)

ETS activity rate was used as estimator of community respiration (CR). Size-fractionated in vivo ETS activity rates were measured using the in vivo INT method (Martínez-García et al., 2009). Four 250 ml dark bottles were filled from each microcosm bottle. One bottle was immediately fixed by adding formaldehyde (2% w/v final concentration) and used as killed-control. Samples were incubated at the same temperature that the microcosm bottles and in dark conditions. After incubation (4–6 h), samples were filtered sequentially through 0.8 and 0.2-µm pore size polycarbonate filters. Bacterial respiration (BR) was operationally defined as ETS activity of the <0.8 µm size-fraction following the extensive review by Robinson (2008). In order to transform ETS activity in carbon respiration a R/ETS ratio of 12.8 (Martínez-García et al., 2009) and a respiratory quotient (RQ) of 0.8 (Williams and del Giorgio, 2005) were used.

2.2.6 Flow cytometry

The abundance of *Synechococcus*, *Prochlorococcus*, picoeukaryotes and heterotrophic bacteria was determined on board on 0.6 ml fresh and 0.4 mL frozen samples (autotrophic and heterotrophic groups, respectively) using a Becton Dickinson FACSCalibur flow cytometer equipped with a laser emitting at 488 nm (Gasol and del Giorgio, 2000). Samples for heterotrophic bacteria were preserved with 1% paraformaldehyde+0.05% glutaraldehyde and frozen at −80 °C until analysis on board. Prior to analysis, heterotrophic bacteria were stained with 2.5 mM SybrGreen DNA fluorochrome. Picoplankton groups were identified on the basis of their fluorescence and light side scatter (SSC) signatures. *Synechococcus* and *Prochlorococcus* cyanobacteria and eukaryotic cells were identified in plots of SSC versus red fluorescence (FL3, >650 nm), and orange fluorescence (FL2, 585 nm) versus FL3, whereas three groups of heterotrophic bacteria were distinguished by their green fluorescence (FL1, 530 nm) after SybrGreen staining: very high (vHNA), high (HNA) and low (LNA) nucleic acid content bacteria.

Two empirical calibrations specific for this dataset between SSC or forward scatter (FSC) and cell diameter, as explained in Calvo-Díaz and Morán (2006), were used to estimate biovolume (BV) for picophytoplanktonic cells (diameter cell=2.14×SSC+0.54; n=30, r^2=0.87) and for heterotrophic bacterioplankton (BV=0.058×FSC+0.013; n=13, r^2=0.60). BV was finally converted into biomass by using the following volume-to-carbon conversion factors for autotrophic groups: 230 fg C µm^{-3} for *Synechococcus*, 240 fg C µm^{-3} for *Prochlorococcus* and 237 fg C µm^{-3} for picoeukaryotes (Worden et al., 2004). Heterotrophic bacterial biomass (BB) was calculated by using the allometric relationship of Gundersen et al. (2002): bacterial biomass (fg C cell^{-1})=108.8×BV$^{0.898}$.

2.3 Statistical analysis

The Pearson coefficient was used to analyse correlations between nutricline depth and biomasses and rates at the sampling stations, as all variables followed normal distributions. Given the low sample size (n=5), a power analysis was conducted using the GPower 3.1.0 software (Faul et al., 2007). We computed the adequate significance level for each slope which balances the likelihood of type I and type II errors. The power of the statistical analysis remained always >0.8 and correlations were considered significant when the p-value was bellow the significance level obtained using GPower 3.1.0.

A repeated measure ANOVA (RMANOVA) was conducted to assess time (within subject factor), treatment (between subject factor, nutrient additions), and experiment (between subject factor, sampling location) effects. All data fitted a normal distribution (Kolmogorov-Smirnov test); however, even after log or arcsine data transformation, the homogeneity of covariance matrices failed for some datasets. For the latter case we applied the Huynh-Feldt adjustment to correct p-values (Scheiner and Gurevitch, 1993). A Bonferroni post-hoc test was conducted to assess the effect of each addition treatment.

In order to compare the effect of different nutrient additions on the biomasses and rates, we calculated response ratios ($_{RR}$) as AT/C, where AT and C are the time inte-

grated value of the variable in the Addition Treatment and the Control, respectively. In the case of/biomasses time-averaged values were used. Values presented in this work were integrated (or averaged in the case of biomasses) from 0 to 72 h incubation since no relevant differences were found between ratios calculated from 0 to 24, 48, or 72 h. The quotient between distinct response ratios (e.g. BP_{RR}/PP_{RR}) was also calculated in order to compare the magnitude of change of heterotrophic (e.g. BP_{RR}) versus autotrophic (e.g. PP_{RR}) variables for each experiment and treatment. A quotient higher than one indicates a larger heterotrophic than autotrophic response.

3 Results

3.1 Initial conditions

Initial conditions for each experiment are presented in Table 1 and Fig. 2. Nitrate, ammonium and phosphate concentrations at the beginning of the experiments were always <125 nM, ≤17 nM and ≤80 nM, respectively. The depth of the nutricline, calculated as the first depth at which nitrate concentration is >0.5 µM, reached 150 and 140 m at 26° N and 12° S, respectively and 80 and 100 m at 18° N and 29° S, respectively. The shallowest nutricline was found at 3° N (50 m). The depth of the nutricline, which is a proxy for nutrient supply into the euphotic layer, was significantly (GPower 3.1.0. correction was applied when necessary as explained in Material and Methods section) and negatively correlated with chlorophyll-*a* concentration ($r=-0.87$, $p=0.06$; $n=5$), primary production ($r=-0.77$, $p=0.13$; $n=5$), bacterial production ($r=-0.94$, $p=0.02$; $n=5$) and community respiration ($r=-0.78$, $p=0.12$; $n=5$). These negative relationships illustrate the role of vertical nutrient fluxes in controlling the biomass and metabolism of microbial plankton (Marañón et al., 2003).

Phytoplankton biomass, estimated as chlorophyll-*a* (chl-*a*) concentration, was lower at those stations located in the center of the gyres (26° N and 12° S), where the deepest nutriclines were found, than at 18° N, 3° N and 29° S (Fig. 2a). Picophytoplankton

(<2 µm phytoplankton) dominated the autotrophic biomass, contributing 57 to 66% of total chl-*a* concentration, except at 29° S (48%) (Fig. 2a). *Prochlorococcus* dominated the picophytoplankton biomass at all sampling stations (Fig. 2b–c). The ratio *Prochlorococcus*:Total Picophytoplankton biomass (Prochl:Total Pico) ranged from 0.60 to 0.92 and was positively correlated with water temperature (r=0.68, p=0.21; n=5).

Primary Production (PP) rates were higher at 18° N and 3° N (0.091 µg C l^{-1} h^{-1}) than at the stations located in the center of the gyres (26° N and 12° S) and the largest PP rate was measured at 29° S (0.12 µg C l^{-1} h^{-1}) (Fig. 2d).

The relative contribution of picophytoplankton to total primary production never exceeded 50%, and was especially low at the northern stations (12% and 25% at 26° N and 18° N, respectively) (Fig. 2d).

The biomass of heterotrophic bacteria (BB) was higher at stations located in the Northern Hemisphere than in the Southern Hemisphere (Fig. 2e). The ratio vHNA/BB ranged from 0.48 (at 26° N) to 0.69 (at 18° N). Higher contributions of vHNA bacteria to total heterotrophic bacterial biomass were found at low latitudes (Fig. 2e–f).

Rates of BP and CR varied one order of magnitude among sampling stations (Fig. 2g–h). The highest BP rates were registered at 18° N and 3° N (0.14 and 0.16 µg C l^{-1} d^{-1}, respectively) coinciding with the shallowest nutriclines, and an extremely low value was measured at 26° N (0.02 µg C l^{-1} d^{-1}), where the deepest nutricline was found (Fig. 2g). The lowest community respiration (CR) rates, estimated as in vivo ETS activity, were also registered at 26° N (0.27 µg C l^{-1} d^{-1}) and largest values at 3° N and 29° S (6.1 and 3.7 µg C l^{-1} d^{-1}). The >0.8 µm microbial plankton fraction dominated CR at all stations except at 12° S, where the contribution of >0.8 µm fraction to total CR was 30%. In all cases, differences in metabolic rates among sampling sites were more pronounced than those in biomass (Fig. 2h).

3.2 Autotrophic responses to nutrient additions

The responses of phytoplankton differed among experiments (Fig. 3a–f). Autotrophic biomass, estimated as chl-*a* concentration, decreased with incubation time in the ex-

periments performed in the Northern Hemisphere (Fig. 3a). At 18° N a slight increase in chl-*a* (mostly due to the >2 µm fraction) was observed in the mixed treatment. In this experiment, picophytoplankton shifted from a *Prochlorocccus* and *Synechococcus* dominated community in the first incubation day to an increase of picoeukaryotic biomass in the last day (data not shown).

In the experiments conducted in the Southern Hemisphere, chl-*a* increased after inorganic additions (inorganic and mixed treatments) at 12° S and after mixed additions at 29° S (Fig. 3a). The relative contribution of <2 µm chl-*a* decreased in the addition treatments relative to the control in the experiments performed at 18° N, 3° N and 29° S (Fig. 3b). In the experiments conducted in the Northern Hemisphere, the Prochl:Total Pico ratio showed a marked decrease with incubation time both in the control and the addition treatments (Fig. 3c). This decrease was less intense at 26° N when organic nutrients were added. The response of the Proch:Total Pico ratio in the Southern Hemisphere showed a rather constant temporal evolution in the control bottles and slightly decreased in the addition treatments. The effect of additions was not significant neither on phytoplankton biomass nor on the relative contribution of <2 µm chl-*a* or on Proch:Total Pico ratio when all the experiments are considered together ($p>0.05$, RMANOVA test) (Table 2). Time and experiment effects on all these variables were found to be significant ($p<0.001$, RMANOVA test) (Table 2).

The response of total primary production (PP) differed between the experiments (Fig. 3d). At 26° N and 3° N, PP decreased in the first 24 h. Thereafter, PP increased in all microcosms at 26° N, whereas at 3° N it remained rather constant or slightly decreased during the rest of the incubation period except in the inorganic treatment, where a slight increase of PP was registered. Enhancements of primary production rates relative to the controls, mostly due to the >2 µm phytoplankton, were found in the nutrient addition treatments in all experiments except at 3° N (Fig. 3d). The highest increases were registered in the mixed treatment bottles. The contribution of <2 µm phytoplankton to primary production (%PP<2 µm) decreased in the addition treatments relative to the control (Fig. 3e).

Primary production to chlorophyll ratios (PP/chl-*a*) also showed different patterns between the experiments (Fig. 3f). At 26° N and 12° S a slight decrease of PP/chl-*a* during the first 24 h and a progressive increase until the end of the incubation period was observed. PP/chl-*a* remained constant or increased with incubation time at 18° N and 29° S. At 3° N a sharp decrease of PP/chl-*a* was measured during the first 24 h, then remaining constant until the end of the incubation except for the inorganic treatment where PP/chl-*a* increased with time.

The effect of the addition treatments on PP and PP/chl-*a* was not significant ($p>0.05$, RMANOVA, Table 2), but significant effects of time and experiment were found on both variables ($p<0.001$, RMANOVA, Table 2). Nutrient addition, incubation time and experiment had a significant effect on the %PP<2 µm ($p<0.05$, $p<0.001$ and $p<0.001$, respectively, RMANOVA, Table 2). A significant decrease of the %PP<2 µm was related to inorganic additions ($p<0.05$, Bonferroni post-hoc test, Table 3).

The response ratios ($_{RR}$) illustrate the direction and magnitude of autotrophic responses observed in the experiments (Fig. 4a–f). A response ratio larger than one entails higher values in the addition treatment than in the control, e.g. a positive response to the addition. No large changes in response ratios were found for phytoplankton biomass and size distribution. *Prochlorococcus* tended to decrease in abundance, relative to the other picophytoplankton groups, when nutrients were added, except at 26° N where Prochl:Tot Pico$_{RR}$ was higher than 1 in the organic nutrients treatment (Fig. 4c). PP$_{RR}$ were slightly higher than those encountered for biomass. Maximum values of PP$_{RR}$ (up to 1.8-fold relative to control) were registered for the mixed treatment bottles at 18°n and 29° S. The relative contribution of <2 µm fraction to total PP decreased after the additions except at 26° N, in which organic nutrients additions resulted in an increase of the relative contribution of <2 µm fraction to total PP (Fig. 4e).

Overall, PP/chl-*a* $_{RR}$ did not differ from 1 except after organic nutrient additions in the experiments conducted at 18° N and 3° N.

3.3 Heterotrophic microbial responses to nutrient additions

Heterotrophic bacteria were greatly stimulated after organic nutrient additions (Fig. 5a–e). BB increased after organic and mixed inputs in all the experiments except at 26° N, where only the mixed addition resulted in an increase in BB relative to the control and at 3° N, where BB increased after the mixed or, to a lesser extent, the organic addition. At 26° N and at 18° N, BB followed the same temporal evolution in the control than in the addition treatments, showing a rapid increase followed by a sharp decrease. At 3° N a slight initial decrease was followed by an increase of BB during the rest of incubation time. In the experiments conducted in the Southern Hemisphere, BB increased in the control and treatment bottles, showing the greatest responses to the organic and mixed treatments (Fig. 5a).

The ratio vHNA/BB increased beyond 0.5 during the first 24 h after organic and mixed additions and remained constant during the rest of the incubation in all experiments (except for experiment at 26° N in which only the mixed addition resulted in a measurable positive response) (Fig. 5b).

The responses of BP and BR to nutrient additions were much stronger than those observed for primary production (Fig. 5c–d). After organic and mixed inputs, BP increased in all experiments during the first 24–48 h and remained constant or even decreased thereafter, except at 26° N, where only the mixed addition resulted in an increase relative to the control. The responses of BP to the additions were of higher magnitude in the southern experiments (Fig. 5c). BGE increased in the addition treatments relative to the control (Fig. 5e) following the pattern of BP responses. CR responses to nutrient additions were higher than those of PP (Fig. 5f). BR (i.e. ETS activity <0.8 µm) and CR always followed the same pattern (Fig. 5d, f). BR accounted for 20 to 40% of CR and this contribution did not significantly change among treatments and experiments (RMANOVA, $p>0.05$). BR and CR largely increased during the first 24 h after organic and mixed inputs in all experiments except at 26° N, where only the mixed addition resulted in an increase relative to the control, decreasing progressively until the end of

the incubation period (Fig. 5d, f).

The effects of the addition treatment, time and experiment on BB, vHNA/BB ratio, BP, BR and CR were all significant (RMANOVA, Table 2) and significant stimulations were registered when organic nutrients were added (Bonferroni post-hoc test, Table 3).

A significant interaction between the treatment and experiment factors, which indicates that the response to treatments varies among experiments, was also found for most variables (RMANOVA, $p<0.001$, Table 2). The effects of the addition treatment and time on BGE were significant (RMANOVA, Table 2) and significant stimulations were registered when organic nutrients were added (Bonferroni post-hoc test, Table 3).

Responses ratios show a north to south gradient in the magnitude of the heterotrophic responses when organic nutrients are added (Fig. 6a–f). BB_{RR} and $vHNA/BB_{RR}$ were higher for organic and mixed additions, especially in the experiments performed in the Southern Hemisphere (up to 2.2 and 9.6-fold increases in BB_{RR} and $vHNA/BB_{RR}$, respectively). BP_{RR} and BR_{RR} in the organic and mixed treatments were considerably higher (up to 58.8 and 11.4-fold increases in BP_{RR} and BR_{RR}, respectively) and followed a more evident north to south gradient than BB_{RR}. BGE_{RR} ranged from 1.2 to 2.5 when organic nutrients were added and was higher in the southern experiments (Fig. 6f). Higher CR_{RR} were also registered at the southern stations (up to 8 and 8.6-fold for experiments at 12° S and 29° S, respectively) although the maximum value was registered in the mixed treatment at the northernmost experiment (12.7-fold).

3.4 Heterotrophic vs. autotrophic responses

Responses of the different variables (BB_{RR}, chl-a_{RR}, BP_{RR}, CR_{RR} and PP_{RR}) were compared to one another for the different addition treatments (i.e. inorganic, organic and mixed) in the five experiments (Fig. 7).

Overall, the magnitude of bacterial and phytoplankton response to the addition of inorganic nutrients was always small (Fig. 7a–c). When both inorganic and organic nutrients were supplied, heterotrophic bacteria responses were higher than phytoplankton responses. Bacterial production to primary production response ratios (BP_{RR}/PP_{RR})

and community respiration to primary production response ratios (CR_{RR}/PP_{RR}) were always higher than 1 and followed an increasing north to south gradient (Fig. 7b and c).

4 Discussion

The response of the autotrophic and heterotrophic microbial compartments to the different additions assessed in this investigation varied greatly, both in direction and magnitude, as a function of latitude and experimental treatment, suggesting that different processes are likely to control phytoplankton and bacterial dynamics in the five sampled locations. Overall, the responses of the heterotrophic compartment were clearly larger than those of autotrophs, suggesting that heterotrophic bacteria outcompeted phytoplankton in the utilization of the added nutrients.

4.1 Initial conditions

The sampling stations visited in this investigation cover a wide range of situations within the low nutrient regions of the central Atlantic Ocean (Table 1 and Fig. 2). The values of the different microbial variables measured at the beginning of the 5 experiments (Fig. 2) are within the ranges reported in previous studies in these areas (Zubkov et al., 1998; Marañón et al., 2000; Morán et al., 2004; Gasol et al., 2009).

Nutricline depth, indicative of the degree of oligotrophy of the different sites, varied among stations and was significantly correlated with initial biological conditions. Sampling stations at 26° N and 12° S showed the deepest nutriclines and very low chl-*a*, PP, BP and CR, indicative of highly oligotrophic conditions, consistently with their location in the central regions of the subtropical gyres (Fig. 1). Samples from 18° N, 3° N and 29° S were collected at stations with relatively shallow nutriclines where nutrient input from deeper waters is expected to be higher. This situation is particularly evident at 3° N, where the equatorial upwelling resulted in a shallow nutricline (50 m) and high biomass and activity of autotrophic and heterotrophic microbial plankton.

Lower autotrophic and heterotrophic biomasses were found at the southern locations (Fig. 2a, e), suggesting either a stronger top-down control or more severe nutrient limitation as compared to the northern stations. The higher rates of nitrogen fixation (Baker et al., 2007; Mather et al., 2008; Moore et al., 2009) and atmospheric deposition (Galloway et al., 2004) reported in the North, as compared to the South Atlantic, could explain a comparatively more severe nitrogen limitation in the South compared to the North Atlantic. By contrast, phosphate concentration was higher in the southern than in the northern stations (Table 1), in agreement with the latitudinal pattern reported by Fanning (1992) and Mather et al. (2008).

As we shall discuss below, the characteristics of the sampling site affecting the initial microbial community (e.g. nutrient availability) proved to be important factors in modulating the microbial community response to the experimental additions.

4.2 Responses of autotrophic communities

The phytoplankton responses to nutrient amendments were small when compared to those of heterotrophic bacteria, although different patterns among the five experiments were found (Figs. 3 and 4).

Phytoplankton communities from 26° N and 3° N experienced a decrease in biomass during the experiment (Fig. 3a), a response that has been observed during previous in vitro experiments in oligotrophic waters (Caron et al., 2000; Lignell et al., 2003; Davey et al., 2008). We do not have a definitive explanation for the decrease of chl-*a* at 26° N and 3° N (Fig. 3a). On one hand, the parallel decrease in PP and PP/chl-*a* ratio during the first 24 h incubation, especially at 3° N, would suggest a poor physiological condition of the phytoplankton assemblages, limitation by micronutrients not studied in this investigation or differential susceptibility of autotrophic communities to the methodological procedure. On the other hand, the PP/chl-*a* ratio increased after the first incubation day (Fig. 3f), which would suggest that the decrease of chl-*a* concentration was caused by top-down control of phytoplankton at these stations. This explanation is reinforced by the higher abundance of heterotrophic flagellates at these two sites (up to 2-fold

relative to the rest, data not shown). The pronounced decreases in Prochl:Total Pico ratio with incubation time observed in northern experiments (Fig. 3c) suggests either a high grazing pressure over this group or a high susceptibility of *Prochloroccus* to handling (Partensky et al., 1999). Similar results have been previously reported by Herut et al. (2005), Davey et al. (2008) and Paytan et al. (2009).

Primary production moderately increased (up to 1.8-fold) after inorganic and mixed additions. Similar enhancements have been previously reported after experimental Saharan surface soils additions (Mills et al., 2004; Bonnet et al., 2005) or collected-aerosols additions (Herut et al., 2005); and also after natural events of dust deposition (Herut et al., 2005). Higher responses were found by Mills et al. (2004) and Moore et al. (2006, 2008) in the subtropical North Atlantic after inorganic (N and P) nutrient additions, possibly due to the higher final concentrations of the nutrients added (2 and 4-fold higher for N and P, respectively).

Enhanced PP was paralleled by changes in the size distribution of phytoplankton populations. The decrease of the picophytoplankton contribution to total PP observed when inorganic nutrient additions were performed (Figs. 3e and 4e), is likely related to a higher growth potential of >2 µm phytoplankton cells, known to be highly efficient when nutrients are available (Thingstad and Sakshaug, 1990; Agawin et al., 2000; Cermeño et al., 2005). At 26° N the contribution of <2 µm cells to PP increased in the organic treatments relative to the control, possibly associated with the presence of mixotrophic picophytoplankton (Figs. 3e and 4e).

4.3 Responses of heterotrophic communities

Heterotrophic microbial responses to the additions significantly differed among experiments (RMANOVA, $p<0.05$, Table 2), being always larger than autotrophic responses. Bacterial biomass and activity were stimulated by organic additions and differences among experiments were observed. Heterotrophic bacterial metabolic rates (BP and BR) responded considerably more than bacterial biomass (BB), likely related to the widely reported strong top-down control (i.e. predation) on microbial populations in

these oligotrophic environments (Weisse and Scheffel-Möser, 1991; Zubkov et al., 2000; Jürgens and Massana, 2008). BB and BP values measured in this work after nutrient additions are within the range of in situ values reported for the central Atlantic Ocean (Zubkov et al., 1998; Morán et al., 2004; Gasol et al., 2009), which support the adequacy of the chosen concentrations of added nutrients in the experimental design adopted in this study.

BB and BP were limited by organic nutrients in all the experiments and co-limited by inorganic and organic nutrients at 26° N (Figs. 5a, c and 6a, c). In the experiment performed at 3° N, the responses of BB and BP were larger in the mixed than in the organic treatment (Figs. 5a, c and 6a, c), suggesting that the additional inorganic nutrients supplied allowed bacteria to utilize more organic matter in the mixed treatment than in the organic treatment. It has been demonstrated that inorganic nutrient limitation prevents bacteria to utilize organic matter and contributes to DOC accumulation in the upper water column (Rivkin and Anderson, 1997; Thingstad et al., 1997; Tanaka et al., 2009). Considering that our organic addition includes N, the bacterial responses observed at 26° N and 3° N are most likely explained by the previously reported phosphorous limitation in the North Atlantic (Fanning, 1992; Mather et al., 2008). Accordingly, BB and BP response to organic additions was much higher in the southern than in the northern stations, possibly associated to the higher inorganic phosphorous availability in the South than in the North Atlantic Subtropical Gyre (Table 1).

The magnitude of the BB and BP responses to nutrient additions (0.8–2.2-fold and 1.4–58.8-fold, respectively) (Fig. 6) is in agreement with previous addition experiments in the Sargasso Sea (Carlson et al., 2002); and with that previously observed after experimental Saharan surface soils additions (Bonnet et al., 2005; Pulido-Villena et al., 2008), collected-aerosols additions (Herut et al., 2005) or after real dust deposition events (Herut et al., 2005; Pulido-Villena et al., 2008). A previous addition experiment in the North Atlantic (Mills et al., 2008) registered considerably higher responses, both in BB and BP, to mixed (inorganic N and P, and DOC) additions than the ones presented in the present work. It is worth mentioning that in that study the final concentrations

of DOC, inorganic N and inorganic P added were 10, 2 and 4-fold higher than the final concentrations tested in the present study. Furthermore, the N:P ratios of the additions performed in those investigations were below Redfield ratio (i.e. N:P=10), which implies an extra P relative to N supply in the P limited North Atlantic Ocean (Fanning, 1992; Mather et al., 2008). Baker et al. (2003, 2007) reported inorganic N:P ratios in dry atmospheric deposition in the Atlantic Ocean ranging from ca. 20 to 2200 and N:P ratios associated with nutrient increases after realistic additions of collected-aerosols are mostly well above the Redfield ratio (N:P=30–50) (Herut et al., 2005). Therefore, the N:P ratios of nutrient additions should be above Redfield (20–30 in the present investigation) if we aim at simulating the effects of atmospheric inputs on the microbial populations.

vHNA bacteria, equivalent to the HNA2 group described by Fernández et al. (2008) in the NE Atlantic Ocean, accounted for a considerable fraction of the total bacterial standing stock when BB and BP enhancements were registered (Figs. 5b and 6b), suggesting the role of vHNA as rapid responders, benefiting from high inorganic (N, P) and organic nutrient concentrations (Jacquet et al., 2002).

BR and CR followed the same pattern as BP. They were greatly stimulated by organic inputs, indicating limitation by organic substrates except for the 26° N experiment where co-limitation by inorganic and organic nutrients was observed (Figs. 5d, e and 6d, e). Only a few nutrient addition studies have included microbial respiration as response variable. Alonso-Sáez et al. (2007) found that BR in the North Atlantic Ocean was generally unaffected by inorganic (nitrate and phosphate) or by organic (glucose and acetate) nutrients. By contrast, the observed increases of BR and CR in the present work (1.3 to 12.7-fold) are comparable to the increases in respiration associated with experimental Saharan surface soils additions (Pulido-Villena et al., 2008; E. Marañón et al., 2010) with collected-aerosols additions (E. Marañón et al., 2010) and with natural dust depositions events (Pulido-Villena et al., 2008).

BGE increased after organic additions in all the experiments and the magnitude of the increases was higher in the southern experiments (up to 2.5-fold). This resulted

in a more efficient utilization of the added organic carbon by heterotrophic bacteria (Zweifel et al., 1993; Pomeroy et al., 1995; del Giorgio and Cole, 1998) in the south (mean BGE_{RR} of 2.1) than in the north (mean BGE_{RR} of 1.3) (Fig. 6e), a latitudinal pattern likely related to the aforementioned higher availability of phosphate in the southern stations. A higher P-availability would explain a higher bacterial growth efficiency (BGE), and also a higher accumulation of BB (Fig. 6a), given the relatively elevated P-content of bacterial biomass (Norland et al., 1995). Actually, the lowest BGE_{RR} was measured in the organic treatment at 26° N suggesting an extreme P limitation at this site. The biogeochemical implications of the BGE enhancement estimated for the south Atlantic, would be an increase of the potential carbon export as a consequence of a higher carbon flow through the microbial food web (Azam et al., 1983; del Giorgio and Cole, 2000; Ducklow, 2000).

4.4 Heterotrophic vs. autotrophic responses

Bacterioplankton clearly outcompeted phytoplankton when both inorganic and organic nutrients were supplied (Fig. 7a–c), thus potentially driving the microbial community towards heterotrophy. In oligotrophic environments, if organic carbon is readily available, heterotrophic bacteria are expected to be more efficient in the uptake of inorganic nutrients than phytoplankton, due to their higher surface area to volume ratio (Cotner and Bidanda, 2002). Furthermore, heterotrophic bacteria requirements of inorganic nutrients are larger than those of phytoplankton due to the lower C:N and C:P ratios of bacteria as compared to phytoplankton (Cotner and Bidanda, 2002).

Community respiration enhancements after organic and mixed treatments were always higher than those of primary production (Fig. 7c). This implies a decrease in the photosynthesis to respiration ratio that was more evident in the South than in the North Atlantic.

The predominantly heterotrophic response consistently observed after mixed additions agree with previous nutrient addition experiments in coastal zones (Joint et al., 2002) and also with observations obtained after Saharan surface soils and after col-

lected aerosols addition experiments in oligotrophic waters (Herut et al., 2005; Reche et al., 2009; E. Marañón et al., 2010). These last studies found a globally higher (up to 8-fold) heterotrophic response compared to phytoplankton response associated with realistic atmospheric inputs.

Given the observed limited response of bacteria to our inorganic additions with a N:P ratio exceeding Redfield (simulating N:P ratios of atmospheric deposition), we speculate that a predominantly heterotrophic response to atmospheric deposition might be at least partially explained by inputs of readily available organic matter. Indeed, several works have shown significant amounts of dissolved organic nitrogen and carbon associated with atmospheric deposition (e.g., Cornell et al., 1995; Pulido-Villena et al., 2008). Thus, our experimental approach, based on the controlled addition of organic and/or inorganic nutrients may help at unveiling the causal processes behind the microbial plankton responses to atmospheric inputs.

Our findings might be also relevant in the context of the recently published projections of future matter inputs into the oceans (Dentener, 2006; Duce, 2008). Increasing amounts of organic matter of atmospheric origin are expecteded to be entering the open ocean in the next decades. A significant fraction of this organic matter might be ready available for microbial utilization (Seitzinger and Sanders, 1999). Our results suggest that the ultimate fate of this organic matter, ie. the relative importance of accumulation in the water column, conversion to potentially exportable microbial biomass or remineralization to CO_2, will depend on the initial environmental and biological conditions of the oceanic region where deposition occurs. Differences between North and South Atlantic microbial plankton community responses to the matter inputs in this investigation appeared to be related to the latitudinal gradient of P availability. The apparently higher efficiency of organic matter utilization by bacteria in the South than in the North Atlantic would ultimately result in a comparatively higher potential for carbon export to deep waters. On the other hand, the expected decrease in the photosynthesis to respiration ratio in the upper tropical and subtropical Atlantic associated with organic matter inputs is likely to affect the CO_2 exchange between the ocean and the

atmosphere.

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References

Agawin, N. S. R., Duarte, C. M., and Agustí, S.: Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production, Limnol. Oceanogr., 45, 591–600, 2000.

Ammerman, J. W., Hood, R. R., Case, D. A., and Cotner, J. B.: Phosphorous deficiency in the Atlantic: An emerging paradigm in oceanography, Econ. Trans. AGU, 84, 165–170, 2003.

Alonso-Sáez, L., Gasol, J. M., Arístegui, J., Vilas, J. C., Vaqué, D., Duarte, C. M., and Agustí, S.: Large-scale variability in surface bacterial carbon demandand growth efficiency in the subtropical Northeast Atlantic Ocean, Limnol. Oceanogr., 52, 533–546, 2007.

Arrigo, K. R.: Marine microorganisms and global nutrient cycles, Nature, 437, 349–355, 2005.

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

Baker, A. R., Kelly, S. D., Biswas, K. F., Witt, M., and Jickells, T. D.: Atmospheric deposition of nutrients to the Atlantic Ocean, Geophys. Res. Lett., 30, 2296, doi:10.1029/2003GL018518, 2003.

Baker, A. R., Jickells, T. D., Biswas, K. F., Weston, K., and French, M.: Nutrients in atmospheric aerosol particles along the Atlantic Meridional Transect, Deep-Sea Res. Pt. I, 53, 1706–1719, 2006.

Baker, A. R., Weston, K., Kelly, S. D., Voss, M., Streu, P., and Cape, J. N.: Dry and wet deposition of nutrients from the tropical Atlantic atmosphere: links to primary productivity and nitrogen fixation, Deep-Sea Res. Pt. I, 54, 1704–1720, 2007.

Bertilsson, S., Berrglund, O., Karl, D. M., and Chisholm, S. W.: Elemental composition of marine *Prochlorococcus* and *Synechococcus*: implications for the ecological stoichiometry of the sea, Limnol. Oceanogr., 48, 1721–1731, 2003.
Bonnet, S., Guieu, C., Chiaverini, J., Ras, J., and Stock, A.: Effect of atmospheric nutrients on the autotrophic communities in a low nutrient, low chlorophyll syatem, Limnol. Oceanogr., 50, 1810–1819, 2005.
Calvo-Díaz, A. and Morán, X. A. G.: Seasonal dynamics of picoplankton in shelf waters of the southern Bay of Biscay, Aquat. Microb. Ecol., 42, 159–174, 2006.
Calvo-Díaz, A. and Morán, X. A. G.: Empirical leucine-to-carbon conversión factors for estimating heterotrophic bacterial production: seasonality and predictability in a temperate coastal ecosystem, Appl. Environ. Microb., 75, 3216–3221, 2009.
Carlson, C. A., Giovannoni, S. J., Hansell, D. A., Goldberg, S. J., Parsons, R., Otero, M. P., Vergin, K., and Wheeler, B. R.: Effect of nutrient amendments on bacterioplankton production, community structure, and DOC utilization in the northwestern Sargasso Sea, Aquat. Microb. Ecol., 30, 19–36, 2002.
Caron, D. A., Lim, E. L., Sanders, R. W., Dennett, M. R., and Berninger, U. G.: Responses of bacterioplankton and phytoplankton to organic carbon and inorganic nutrient additions in contrasting oceanic ecosystems, Aquat. Microb. Ecol., 22, 176–184, 2000.
Cermeño, P., Marañón, E., Rodríguez, J., and Fernández, E.: Large-sized phytoplankton sustain higher carbon-specific photosynthesis than smaller cells in a coastal eutrophic ecosystem, Mar. Ecol.-Prog. Ser., 297, 51–60, 2005.
Church, M. J., Hutchins, D. A., and Ducklow, H. W.: Limitation of bacterial growth by dissolved organic matter and iron in the Southern Ocean, Appl. Environ. Microb., 66, 455–466, 2000.
Church, M. J.: Resource control of bacterial dynamics in the sea, in: Microbial Ecology of the Oceans (2nd edition), edited by: Kirchman, D. L., Wiley-Liss, New York, 335–382, 2008.
Cornell, S., Rendell, A., and Jickells, T.: Atmospheric inputs of dissolved organic nitrogen to the oceans, Nature, 376, 243–246, 1995.
Cotner, J. B. and Biddanda, B. A.: Small players, large role: microbial influence on biogeochemical processes in pelagic aquatic ecosystems, Ecosystems, 5, 105–121, 2002.
Cullen, J. J., Yang, X., and Macintyre, H. L.: Nutrient limitation of marine photosynthesis, in: Primary Productivity and Biogeochemical Cycles in the Sea, edited by: Falkowski, P. G. and Woodhead, A., Plenum, New York, 69–88, 1992.
Davey, M., Tarran, G. A., Mills, M. M., Ridame, C., Geider, R. J., and LaRoche, J.: Nutrient lim-

itation of picophytoplankton photosynthesis and growth in the tropical North Atlantic, Limnol. Oceanogr., 53, 1722–1733, 2008.
Davidson, K., Gilpin, L. C., Hart, M. C., Foilland, E., Mitchell, E., Álvarez-Calleja, I., Laurent, C., Miller, A. E. J., and Leakey, J. G.: The influence of the balance of inorganic and organic nitrogen on the trophic dynamics of microbial food webs, Limnol. Oceanogr., 52, 2147–2163, 2007.
del Giorgio, P. A. and Cole, J. J.: Bacterial energetics and growth efficiency, in: Microbial Ecology of the Oceans (1st edition), edited by: Kirchman, D. L., Wiley-Liss, New York, 289–326, 2000.
Dentener, F., Drevet, J., Lamarque, J. F., Bey, I., Eickhout, B., Fiore, A. M., Hauglustaine, D., Horowitz, L. W., Krol, M., Kulshrestha, U. C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Van Noije, T., Atherton, C., Bell, N., Bergman, D., Butler, T., Cofala, J., Collins, B., Doherty, R., Ellingsen, K., Galloway, J., Gauss, M., Montanaro, V., Müller, F., Pitari, G., Rodriguez, J., Sanderson, M.,. Solmon, F., Strahan, S., Schultz, M., Sudo, K., Szopa, S., and Wild, O.: Nitrogen and sulfur deposition on regional scales: a multimodel evaluation, Global Biogeochem. Cy., 20, GB4003, doi:10.1029/2005GB002672, 2006.
Duce, R. A., LaRoche, J., Altieri, K., Arrigo, K. R., Baker, A. R., Capone, D. G., Cornell, S., Dentener, F., Galloway, J., Ganeshram, R. S., Geider, R. J., Jickells, T., Kuypers, M. M., Langlois, R., Liss, P. S., Liu, S. M., Middelburg, J. J., Moore, C. M., Nickovic, S., Oschlies, A., Pedersen, T., Prospero, J., Schlitzer, R., Seitzinger, S., Sorensen, L. L., Uematsu, M., Ulloa, O., Voss, M., Ward, B., and Zamora, L.: Impacts of atmospheric anthropogenic nitrogen on the open ocean, Science, 320, 893–897, 2008.
Ducklow, H.: Bacterial production and biomass in the oceans, in: Microbial Ecology of the Oceans (1st edition), edited by: Kirchman, D. L., Wiley-Liss, New York, 85–120, 2000.
Falkowski, P. G.: Evolution of the nitrogen cycle and its influence on the biological sequestration of CO_2 in the ocean, Nature, 387, 272–275, 1997.
Fanning, K. A.: Nutrient provinces in the sea: concentration ratios, reaction rate ratios, and ideal covariation, J. Geophys. Res., 97, 5693–5712, 1992.
Faul, F., Erdfelder, E., Lang, A. G., and Buchner, A.: G*Power 3: a flexible statistical power analysis for the social, behavioural, and biomedical sciences, Behav. Res. Methods, 39, 175–191, 2007.
Fernández, C., Thyssen, M., and Denis, M.: Microbial community structure along 18° W (39° N–44.5° N) in the NE Atlantic in late summer 2001 (POMME programme), J. Marine Syst., 71,

46–62, 2008.
Galloway, J. N., Dentener, F. J., Capone, D. G., Boyer, E. W., Howarth, R. W., Seitzinger, S. P., Asner, G. P., Cleveland, C. C., Green, P. A., Holland, E. A., Karl, D. M., Michaels, A. F., Porter, J. H., Townsend, A. R., and Vörösmarty, C. J.: Nitrogen cycles: past, present, and future, Biogeochemistry, 70, 153–226, 2004.
Gasol, J. M. and del Giorgio, P. A.: Using flow citometry for counting natural planktonic bacteria and understanding the structure of planktonic bacterial communities, Sci. Mar., 64, 197–224, 2000.
Gasol, J. M., Vázquez-Dominguez, E., Vaqué, D., Agustí, S., and Duarte, C. M.: Bacterial activity and diffusive nutrient supply in the oligotrophic Central Atlantic Ocean, Aquat. Microb. Ecol., 56, 1–12, 2009.
Graziano, L. M., Geider, R. J., Li, W. K. W., and Olaizola, M.: Nitrogen limitation of North Atlantic phytoplankton: Analysis of physiological condition in nutrient enrichment experiments, Aquat. Microb. Ecol., 11, 53–64, 1996.
Gundersen, K., Heldal, M., Norland, S., Purdie, D. A., and Knap, A. N.: Elemental C, N, and P cell content of individual bacteria collected at the Bermuda Atlantic Time-series Study (BATS) site, Limnol. Oceanogr., 47, 1525–1530, 2002.
Herut, B., Zohary, T., Krom, M. D., Mantourad, R. F. C., Pitta, P., Psarra, S., Rassoulzadeganf, F., Tanaka, T., Thingstadg, T. F.: Response of Mediterranean surface water to Saharan dust: On-board microcosm experiment and field observations, Deep-Sea Res. Pt. I, 52, 3024–3040, 2005.
Jacquet, S., Havskum, H., Thingstad, T. F., and Vaulot, D.: Effects of inorganic and organic nutrient addition on a coastal microbial community (Isefjord, Denmark), Mar. Ecol.-Prog. Ser., 228, 3–14, 2002.
Joint, I., Henriksen, P., Fonnes, G. A., Bourne, D., Thingstad, T. F., and Riemann, B.: Competition for inorganic nutrients between phytoplankton and bacterioplankton in nutrient manipulated mesocosms, Aquat. Microb. Ecol., 29, 145–159, 2002.
Jurado, E., Dachs, J., Duarte, C. M., and Simó, R.: Atmospheric deposition of organic and black carbon to the global oceans, Atmos. Environ., 4, 7931–7939, 2008.
Jürgens, K. and Massana, R.: Protistan grazing on marine bacterioplankton, in: Microbial Ecology of the Oceans (2nd edition), edited by: Kirchman, D. L., Wiley-Liss, New York, 383–441, 2008.
Kerouel, R. and Aminot, A.: Fluorometric determination of ammonia in sea and estuarine waters

by direct segmented flow analysis, Mar. Chem., 57, 265–275, 1997.
Kirchman, D., K'nees, E., and Hodson, R.: Leucine incorporation and its potential as a mesure of protein synthesis by bacteria in natural aquatic systems, Appl. Environ. Microb., 49, 599–607, 1985.
Lignell, R., Seppälä, J., Kuuppo, P., Tamminen, T., Andersen, T., and Gismervik, I.: Beyond bulk properties: responses of coastal summer plankton communities to nutrient enrichment in the northern Baltic Sea, Limnol. Oceanogr., 48, 189–209, 2003.
Mace, K. A., Kubilay, N., and Duce, R. A.: Organic nitrogen in rain and aerosol in the eastern Mediterranean atmosphere: An association with atmospheric dust, J. Geophys. Res.-Atmos., 108, 4320, doi:10.1029/2002JD002997, 2003.
Mahowald, N., Artaxo, P., Baker, A. R., Jickells, T. D., Okin, G., Randerson, J. T., and Townsend, A.: Impacts of biomass burning and land use on Amazonian atmospheric phosphorus cycling and deposition, Global Biogeochem. Cy., 19, GB4030, doi:10.1029/2005GB002541, 2005.
Marañón, E., Holligan, P. M., Varela, M., Mouriño, B., and Bale, A. J.: Basin-scale variability of phytoplankton biomass, production and growth in the Atlantic Ocean, Deep-Sea Res. Pt. I, 47, 825–857, 2000.
Marañón, E., Holligan, P. M., Barciela, R., González, N., Mouriño, B., Pazó, M. J., and Varela, M.: Patterns of phytoplankton size structure and productivity in contrasting open-ocean environments, Mar. Ecol.-Prog. Ser., 216, 43–56, 2001.
Marañón, E., Behrenfeld, M. J., Gonzalez, N., Mourino, B., and Zubkov, M. V.: High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure, Mar. Ecol.-Prog. Ser., 257, 1–11, 2003.
Marañón, E., Fernández, A., Huete-Ortega, M., Mouriño-Carballido, B., Cermeño, P., Chouciño, P., Martínez-García, S., Teira, E., Fernández, E., Calvo-Díaz, A., Morán, X. A. G., Bode, A., Moreno-Ostos, E., Varela, M. M., Patey, M., and Achterberg, E. P.: Patterns in the response of marine microbial plankton to Saharan dust, Limnol. Oceangr., submitted, 2010.
Martínez-García, S., Fernández, E., Aranguren-Gassis, M., and Teira, E.: In vivo electron transport system activity: a method to estimate respiration in marine microbial planktonic communities, Limnol. Oceanogr.-Meth., 7, 459–469, 2009.
Mather, R. L., Reynolds, S. E., Wolff, G. A., Williams, R. G., Torres-Valdés, S., Woodward, E. M. S., Landolfi, A., Pan, X., Sanders, R., and Achterberg, E. P.: Phosphorus cycling in the North and South Atlantic Ocean subtropical gyres, Nat. Geosci., 1, 439–443, 2008.

Mills, M. M., Ridame, C., Davey, M., La Roche, J., and Geider, R. J.: Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic, Nature, 429, 292–294, 2004.
Mills, M. M., Moore, C. M., Langlois, R., Milne, A., Achterberg, E., Nachtigall, K., Lochte, K., Geider, R. J., and La Roche, J.: Nitrogen and phosphorus co-limitation of bacterial productivity and growth in the oligotrophic subtropical North Atlantic, Limnol. Oceanogr., 53, 824–834, 2008.
Moore, C. M., Mills, M. M., Milnes, A., Langlois, R., Achterberg, E. P., Lochte, K., Geider, R. J., and LaRoche, J.: Iron limits primary productivity during spring bloom development in the central North Atlantic, Glob. Change Biol., 12, 626–634, 2006.
Moore, C. M., Mills, M. M., Langlois, R., Milne, A., Achterberg, E. P., La Roche, J., and Geider, R. J.: Relative influence of nitrogen and phosphorus availability on phytoplankton physiology and productivity in the oligotrophic sub-tropical North Atlantic Ocean, Limnol. Oceanogr., 53, 291–305, 2008.
Moore, C. M., Mills, M. M., Achterberg, E. P., Geider, R. J., LaRoche, J., Lucas, M. I., McDonagh, E. L., Pan, X., Poulton, A. J., Rijkenberg, M. J. A., Suggett, D. J., Ussher. S. J., and Woodward, E. M. S.: Large-scale distribution of Atlantic nitrogen fixation controlled by iron availability, Nat. Geosci., 2, 867–871, 2009.
Morán, X. A. G., Fernández, E., and Pérez, V.: Size-fractionated primary production, bacterial production and net community production in subtropical and tropical domains of the oligotrophic NE Atlantic in autumn, Mar. Ecol.-Prog. Ser., 274, 17–29, 2004.
Norland, S., Fagerbakke, K. M., and Heldal, M.: Light element analysis of individula bacteria by x-ray microanalysis, Appl. Environ. Microb., 61, 1357–1362, 1995.
Paerl, H. W.: Coastal eutrophication and harmful algal blooms: importance of atmospheric deposition and groundwater as "new" nitrogen and other nutrient sources, Limnol. Oceanogr., 42, 1154–1165, 1997.
Partensky, F., Hess, W. R., and Vaulot, D.: *Prochlorococcus*, a marine photosynthetic prokaryote of global significance, Microbiol. Mol. Biol. R., 63, 106–127, 1999.
Paytan, A., Mackey, K. R. M., Cheng, Y., Lima, I. D., Doney, S. C., Mahowald, N., Labiosa, R., and Post, A. F.: Toxicity of atmospheric aerosols on marine phytoplankton, P. Natl. Acad. Sci. USA, 106, 4601–4605, 2009.
Peierls, B. L. and Paerl, H. W.: Bioavailability of atmospheric organic nitrogen deposition to coastal phytoplankton, Limnol. Oceanogr., 42, 1819–1823, 1997.
Pomeroy, R., Sheldon, J. E., Sheldon, W. M., and Peters, F.: Limits to growth and respiration of

bacterioplankton in the Gulf of Mexico, Mar. Ecol.-Prog. Ser., 117, 259–268, 1995.
Pulido-Villena, E., Wagener, T., and Guieu, C.: Bacterial response to dust pulses in the Western Mediterranean: implications for carbon cycling in the oligotrophic ocean, Global Biogeochem. Cy., 22, GB1020, doi:10.1029/2007GB003091, 2008.
Raimbault, P., Slawyk, G., Coste, B., and Fry, J.: Feasibility of using an automated colorimetric procedure for the determination of seawater nitrate in the 0 to 100 Nm range – examples from field and culture, Mar. Biol., 104, 347–351, 1990.
Reche, I., Ortega-Retuerta, E., Romera, O., Pulido-Villena, E., Morales-Baquero, R., and Casamayor, E.: Effect of Saharan dust inputs on bacterial activity and community composition in Mediterranean lakes and reservoirs, Limnol. Oceanogr., 54, 869–879, 2009.
Rivkin, R. B. and Anderson, M. R.: Inorganic nutrient limitation of oceanic bacterioplankton, Limnol. Oceanogr., 42, 730–740, 1997.
Robinson, C.: Heterotrophic bacterial respiration, in: Microbial Ecology of the Oceans (2nd edition), edited by: Kirchman, D. L., Wiley-Liss, New York, 299–336, 2008.
Saito, M. A., Goepfert, T. J., and Ritt, J. T.: Some thoughts on the concept of colimitation: three definitions and the importance of bioavailability, Limnol. Oceanogr., 53, 276–290, 2008.
Scheiner, S. M. and Gurevitch, J.: Design and Analysis of Ecological Experiments, Chapman and Hall, London, 1993.
Seitzinguer, S. P. and Sanders, R. W.: Atmospheric inputs of dissolved organic nitrogen stimulate estuarine bacteria and phytoplankton, Limnol. Oceanogr., 44, 721–730, 1999.
Smith, D. C. and Azam, F.: A simple, economical method for measuring bacterial protein synthesis rates in seawater using 3H-leucine, Mar. Microb. Food Webs, 6, 107–114, 1992.
Tanaka, T., Thingstad, T. F., Gasol, J. M., Cardelús, C., Jezberra, J., Sala, M. M., Simek, K., and Unrein, F.: Determining the availability of phosphate and glucose for bacteria in P-limited mesocosms of NW Mediterranean surface waters, Aquat. Microb. Ecol., 56, 81–91, 2009.
Thingstad, T. F. and Sakahaug, E.: Control of phytoplankton growth in nutrient recycling ecosystems, theory and terminology, Mar. Ecol.-Prog. Ser., 63, 261–272, 1990.
Thingstad, T. F. and Rassoulzadegan, F.: Nutrient limitations, microbial food webs, and "biological C-pumps": suggested interactions in a P-limited Mediterranean, Mar. Ecol.-Prog. Ser., 117, 299–306, 1995.
Thingstad, T. F., Hagström, A., and Rassoulzadegan, F.: Accumulation of degradable DOC in surface waters: is it caused by a malfunctioning microbial loop?, Limnol. Oceanogr., 42, 398–404, 1997.

Tréguer, P. and Le Corre, P.: Manuel d'analyse des sels nutritifs dans l'eau de mer. Utilisation de l'auto analyseur II, Technicon. L. O. C. Univ. Bretagne Occidentale, Brest, 1975.

Tyrrell, T.: The relative influences of nitrogen and phosphorus on oceanic primary production, Nature, 400, 525–531, 1999.

Van Wambeke, F., Obernosterer, I., Moutin, T., Duhamel, S., Ulloa, O., and Claustre, H.: Heterotrophic bacterial production in the eastern South Pacific: longitudinal trends and coupling with primary production, Biogeosciences, 5, 157–169, 2008, http://www.biogeosciences.net/5/157/2008/.

Weisse, T. and Scheffel-Möser, U.: Un coupling the microbial loop: grow and grazing loss rates of bacteria and heterotrophic nanoflagellates in the North Atlantic, Mar. Ecol.-Prog. Ser., 71, 195–205, 1991.

Williams, P. J. leB., and del Giorgio, P. A.: Respiration in aquatic ecosystems: history and background, in: Respiration in aquatic ecosystems, edited by: del Giorgio, P. A. and Williams P. J. leB., Oxford University Press, London, 1–18, 2005.

Worden, A. Z., Nolan, J. K., and Palenik, B.: Assessing the dynamics and ecology of marine picophytoplamkton: The importance of the eukaryotic component, Limnol. Oceanogr., 49, 168–179, 2009.

Wu, J., Sunda, W., Boyle, E. A., and Karl, D. M.: Phosphate depletion in Western Atlantic Ocean, Science, 289, 759–762, 2000.

Zubkov, M. V., Sleigh, M. A., Tarran, G. A., Burkill, P. H., and Leakey, R. J. G.: Picoplanktonic community structure on an Atlantic transect from 50° N to 50° S, Deep-Sea Res. Pt. I, 45, 1339–1355, 1998.

Zubkov, M. V., Sleigh, M. A., Burkill, P. H., and Leakey, R. J. G.: Bacterial growth and grazing loss in contrasting areas of North and South Atlantic, J. Plankton Res., 22, 685–711, 2000.

Zubkov, M. V., Fuchs, B. M., Tarran, G. A., Burkill, P. H., and Amann, R.: High rate of uptake of organic nitrogen compounds by *Prochlorococcus* Cyanobacteria as a key to their dominance in oligotrophic oceanic waters, Appl. Environ. Microb., 69, 1299–1304, 2003.

Zubkov, M. V., and Tarran, G. A.: Amino acid uptake of *Prochlorococcus* spp. in surface waters across the South Atlantic Subtropical Front, Aquat. Microb. Ecol., 40, 241–249, 2005.

Zweifel, U. L., Norrman, B., and Hagström, A.: Consumption of dissolved organic carbon by marine bacteria and demand for inorganic nutrients, Mar. Ecol.-Prog. Ser., 101, 23–32, 1993.

Table 1. Summary of initial conditions for each experiment. Sampling depth was 10 m excepting for experiment at 12° S 29° W (15 m). Nutricline depth was estimated as the first depth where nitrate concentration is >0.5 µM. DCM, deep chlorophyll maximum. N/A, not available.

Experiment	26° N 34° W	18° N 29° W	3° N 29° W	12° S 29° W	29° S 29° W
Surface temperature (°C)	24.6	25.8	27.9	25.6	22.0
Surface salinity	37.57	36.73	35.28	36.94	35.85
DCM depth (m)	120	100	75	140	100
Nutricline depth (m)	150	80	50	140	100
Surface nutrients					
NO_3^- (nmol l^{-1})	N/A	116	117	124	113
NH_4^+ (nmol l^{-1})	N/A	17	12	17	N/A
PO_4^{-3} (nmol l^{-1})	N/A	40	N/A	70	80

Table 2. Repeated measures ANOVA with one within subjects factor (sampling day, time), and two between subjects factor (experiment, exp; and treatment, treat). Chl-*a*, chlorophyll-*a* concentration, %chl-*a*<2 µm, percentage of chl-*a* in the <2 µm fraction, Prochl:Total Pico., *Prochlorococcus*:Total picophytoplankton biomass, BB, heterotrophic bacterial biomass, vHNA:BB, vHNA bacteria:Bacterial Biomass, PP, primary production, % PP<2 µm, percentage of primary production in the <2 µm fraction, PP/chl-*a*, primary production to chlorophyll-*a* ratio, BP, bacterial production, BR, bacterial respiration (estimated from in vivo ETS activity due to the fraction <0.8 µm), BGE, bacterial growth efficiency, CR, community respiration (estimated from total in vivo ETS activity). For each pair factor/factor combination-variable the significance (upper value) and the partial η^2, which reflects the proportion of variance associated with each factor or factor combination (lower value) is given. NS, no significant.

Factors	Chl-*a*	% Chl-*a*<2 µm	Prochl: TotalPico	BB	vHNA: BB	PP	% PP <2 µm	PP/chl-*a*	BP	BR	BGE	CR
Within subjects												
Time	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	0.466	0.528	0.803	0.644	0.921	0.283	0.343	0.283	0.850	0.432	0.749	0.880
Time×Exp	**<0.001**	**0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	NS	**<0.001**	**<0.001**	**<0.05**	**<0.05**	**<0.001**
	0.552	0.332	0.762	0.851	0.538	0.460		0.460	0.577	0.308	0.310	0.384
Time*Treat	NS	NS	NS	**<0.001**	**<0.001**	NS	NS	NS	**<0.001**	**<0.001**	**<0.05**	**<0.001**
				0.412	0.861				0.794	0.370	0.260	0.843
Between subjects												
Exp	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.01**	NS	**<0.001**
	0.757	0.769	0.774	0.856	0.807	0.786	0.968	0.663	0.805	0.513		0.781
Treat	NS	NS	NS	**<0.001**	**<0.001**	NS	**0.052**	NS	**<0.001**	**<0.001**	**<0.01**	**<0.001**
				0.794	0.985		0.315		0.964	0.832	0.485	0.958
Exp×Treat	NS	NS	NS	**<0.05**	**<0.05**	NS	NS	NS	**<0.001**	NS	NS	**<0.01**
				0.601	0.919				0.870			0.706

Table 3. Summary of the global effect of the different additions on biological variables (Bonferroni post hoc test): 0, no significant effect; +, significant effect $p<0.05$; ++, significant effect $p<0.01$; +++, significant effect $p<0.001$. +, stimulation, –, inhibition. Chl-*a*, chlorophyll-*a* concentration, % Chl-*a*<2 µm, percentage of total chl-*a* in the fraction <2 µm, Proch:Total Pico., *Prochlorococcus*:Total picophytoplankton biomass ratio, BB, heterotrophic bacterial biomass, vHNA:BB, vHNA:Bacterial Biomass ratio, PP, primary production, % PP<2 µm, percentage of total PP due to the fraction <2 µm, PP/chl-*a*, primary production to chlorophyll-*a* ratio, BP, bacterial production, BR, bacterial respiration (estimated from in vivo ETS activity due to the fraction <0.8 µm), BGE, bacterial growth efficiency, CR, community respiration (estimated from total in vivo ETS activity).

Variable	Inorganic	Organic	Mixed
Chl-*a*	0	0	0
% Chl-*a*<2 µm	0	0	0
Proch:Total Pico	0	0	0
BB	0	++	+++
vHNA:BB	0	+++	+++
PP	0	0	0
% PP<2 µm	–	0	0
PP/chl-*a*	0	0	0
BP	0	+++	+++
BR	0	+++	+++
BGE	0	++	++
CR	0	+++	+++

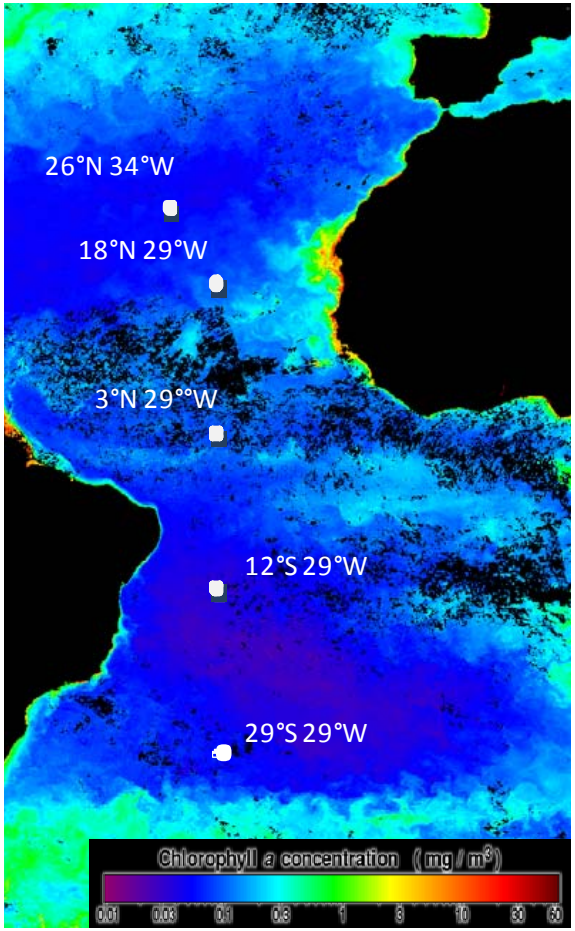

Fig. 1. Map of sampling stations superimposed on a SeaWifs chlorophyll-*a* monthly composite image (November 2007).

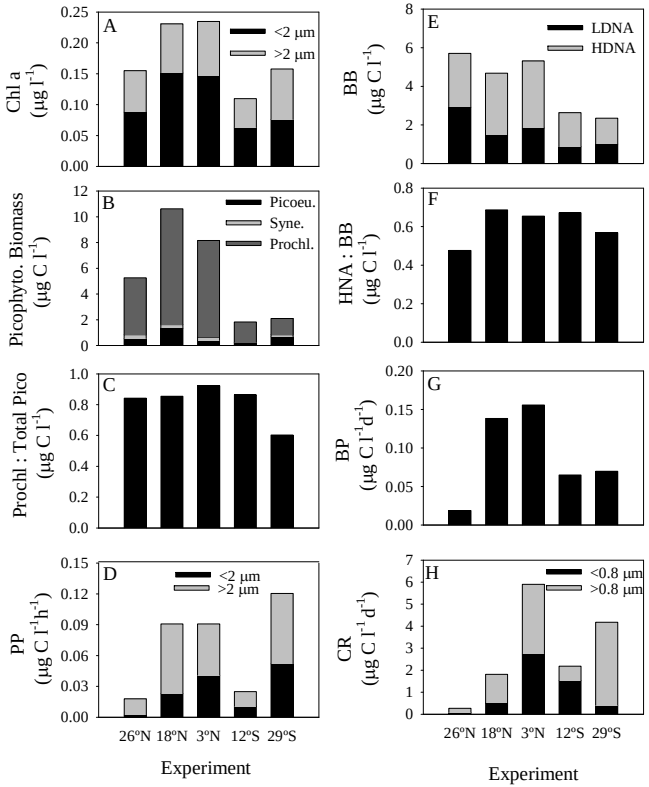

Fig. 2. Initial biological conditions at the sampling stations. **(A)**, Chl-*a*, size-fractionated chlorophyll-*a* ($\mu g\,l^{-1}$); **(B)**, Picophyto.Biomass, picophytoplankton biomass ($\mu g\,C\,l^{-1}$); **(C)**, Proch:Total Pico, *Prochlorococcus*:Total picophytoplankton biomass ratio; **(D)**, PP, size-fractionated primary production ($\mu g\,C\,l^{-1}\,h^{-1}$); **(E)**, BB, heterotrophic bacterial biomass ($\mu g\,C\,l^{-1}$); **(F)**, vHNA:BB, vHNA:Bacterial biomass; **(G)**, BP, bacterial production ($\mu g\,C\,l^{-1}\,d^{-1}$); **(H)**, CR, size-fractionated community respiration estimated from in vivo ETS activity ($\mu g\,C\,l^{-1}\,d^{-1}$).

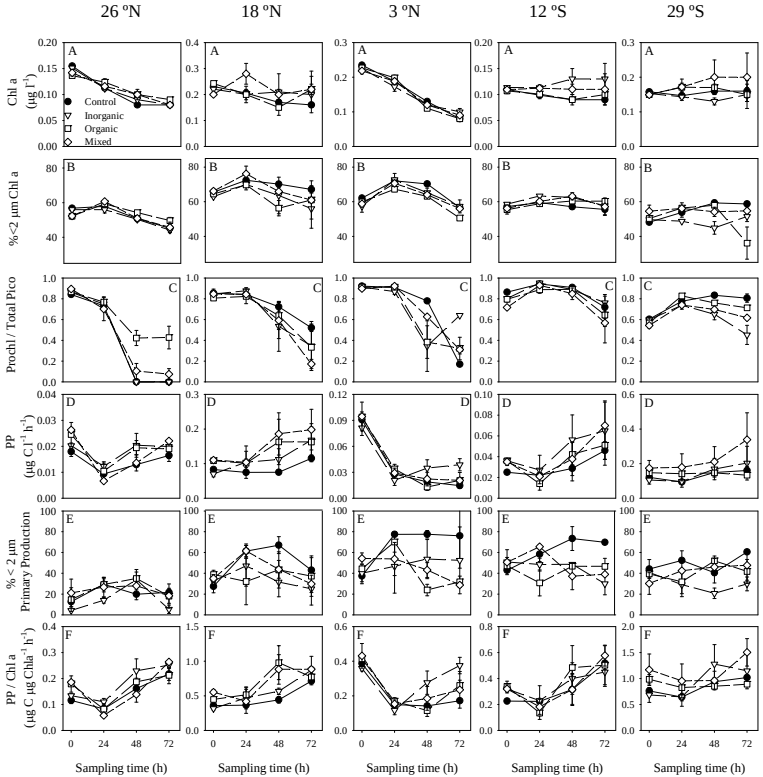

Fig. 3. Time course of the mean **(A)**, chl-*a*, chlorophyll-*a* (µg l^{-1}); **(B)**, %<2 µm chl-*a*, percentage of <2 µm chlorophyll-*a*; **(C)**, Prochl:Total Pico., *Prochlorococcus*:Total picophytoplankton biomass ratio; **(D)**, PP, total primary production (µg C l^{-1} h^{-1}); **(E)**, %<2 µm PP, percentage of <2 µm primary production; **(F)**, PP/chl-*a* , primary production to chl-*a* ratio, in the 5 experiments. Control, no addition, Inorganic, inorganic addition; Organic, organic addition; Mixed, mixed addition. Note that different scales were used. Error bars represent the standard error from two replicates; where error bars are not visible, they are smaller than the size of the symbol.

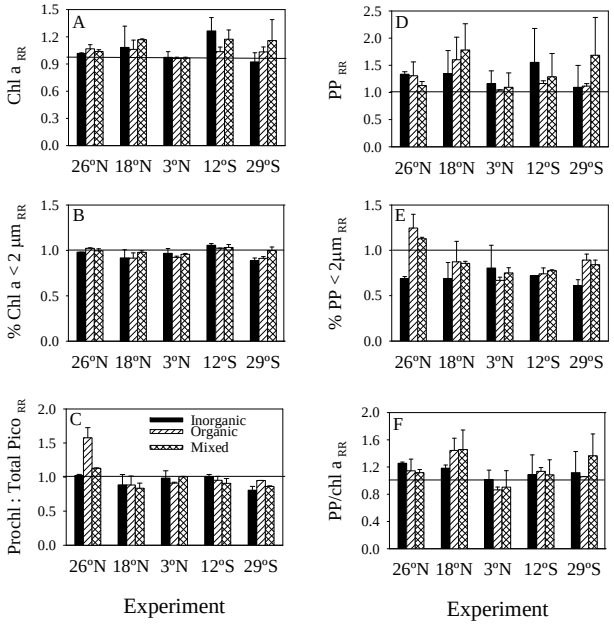

Fig. 4. Response ratios of **(A)**, total chlorophyll *a* concentration (Chl-a_{RR}); **(B)**, percentage of <2 µm chlorophyll-*a* (% Chl-*a*<2 μm_{RR}); **(C)**, *Prochlorococcus*:Total picophytoplankton biomass ratio (Proch:Total $pico_{RR}$); **(D)**, primary production (PP_{RR}); **(E)**, percentage of <2 µm primary production (% PP<2 μm_{RR}); **(F)**, primary production to chl-*a* ratio (PP/chl-a_{RR}), in microcosms amended with inorganic, organic and mixed nutrients, expressed as a ratio of the time-averaged value relative to the time-averaged value in the control microcosms. Inorganic, inorganic addition; Organic, organic addition; Mixed, mixed addition. Error bars represent the standard error from two replicates. The horizontal line in each graph represents 1 relative to 1 (no change) relative to control. Note that different scales were used.

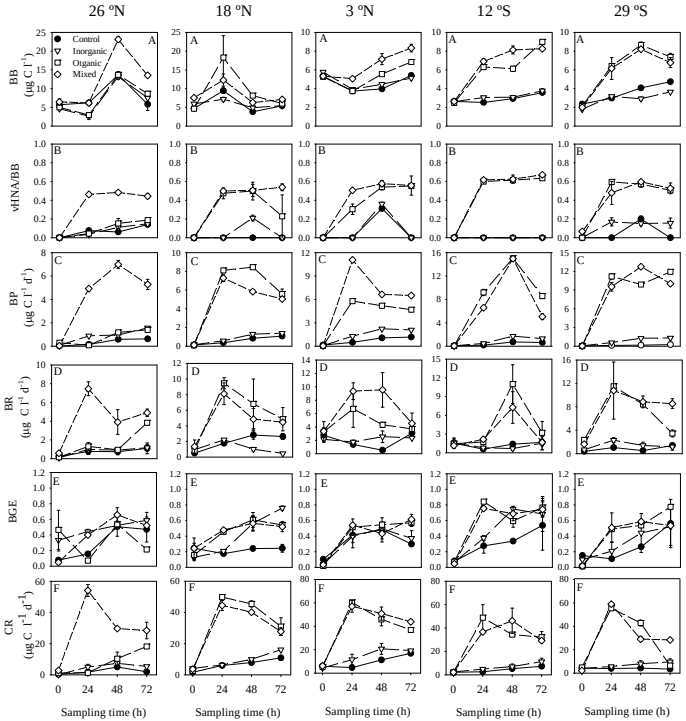

Fig. 5. Time course of the mean **(A)**, BB, bacterial biomass ($\mu g\,C\,l^{-1}$); **(B)**, vHNA:BB, vHNA:Bacterial Biomass ratio; **(C)**, BP, bacterial production ($\mu g\,C\,l^{-1}\,d^{-1}$); **(D)**, BR, bacterial respiration estimated from ETS activity in the fraction <0.8 µm ($\mu g\,C\,l^{-1}\,d^{-1}$); **(E)**, BGE, bacterial growth efficiency; **(F)** CR, community respiration estimated from total ETS activity ($\mu g\,C\,l^{-1}\,d^{-1}$), in the 5 experiments. Control, no addition; Inorganic, inorganic addition; Organic, organic addition; Mixed, mixed addition. Note that different scales were used. Error bars represent the standard error from two replicates; where error bars are not visible, they are smaller than the size of the symbol.

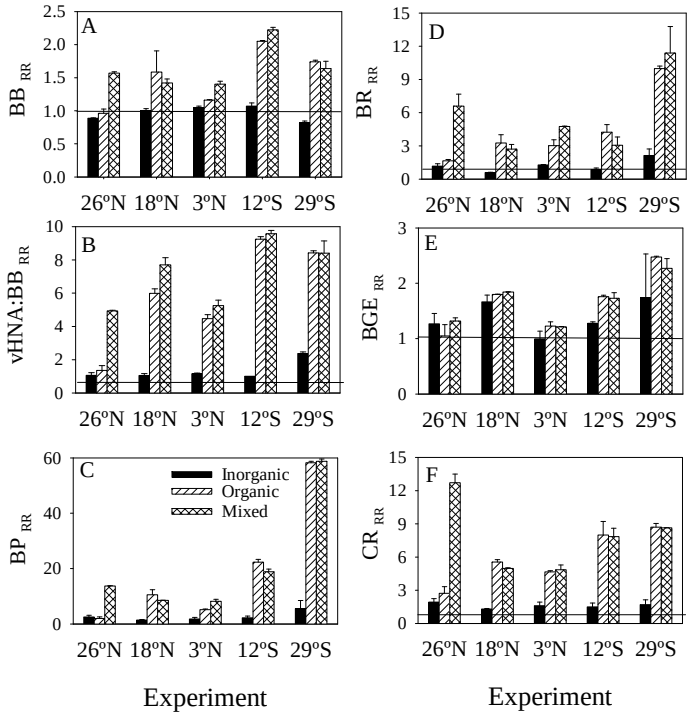

Fig. 6. Response ratios of **(A)**, total bacterial biomass (BB_{RR}); **(B)**, vHNA to Bacterial Biomass ratio (vHNA:BB_{RR}); **(C)**, bacterial production (BP_{RR}); **(D)**, bacterial respiration (BR_{RR}); **(E)**, bacterial growth efficiency (BGE_{RR}); **(F)** community respiration (CR_{RR}), in microcosms amended with inorganic, organic and mixed nutrients, expressed as a ratio of the time-integrated value relative to the time-integrated value in the control microcosms. Inorganic, inorganic addition; Organic, organic addition; Mixed, mixed addition. The horizontal line in each graph represents 1 relative to 1 (no change) relative to control. Note that different scales were used. Error bars represent the standard error from two replicates. The horizontal line in each graph represents 1 relative to 1 (no change) relative to control. Note that different scales were used.

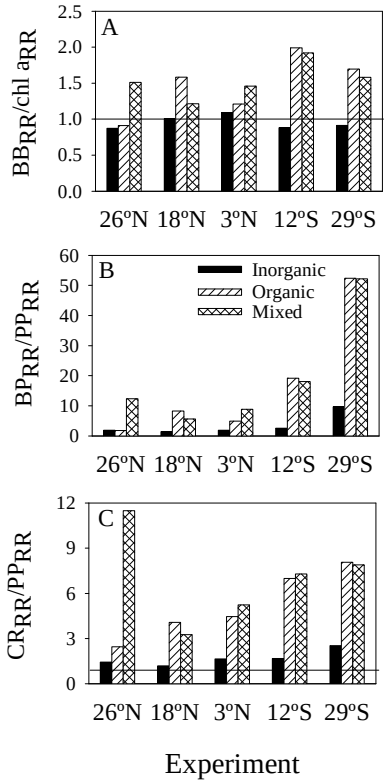

Fig. 7. Relationships between **(A)**, bacterial biomass response ratio and chlorophyll-*a* response ratio (BB_{RR}/chl-a_{RR}); **(B)**, bacterial production response ratio and primary production response ratio (BP_{RR}/PP_{RR}); **(C)**, community respiration response ratio and primary production response ratio (CR_{RR}/PP_{RR}); **(D)**, bacterial production response ratio and bacterial respiration response ratio (BP_{RR}/BR_{RR}), in the 5 experiments. Inorganic, inorganic addition; Organic, organic addition; Mixed, mixed addition. Note that different scales were used. Error bars represent the standard error from two replicates. The horizontal line in each graph represents 1 relative to 1.