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Dinitrogen fixation and dissolved organic nitrogen fueled primary production and particulate export during the VAHINE mesocosms experiment (New Caledonia lagoon)

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Abstract

In the oligotrophic ocean characterized by nitrate (NO_3^-) depletion in surface waters, dinitrogen (N_2) fixation and dissolved organic nitrogen (DON) can represent significant nitrogen (N) sources for the ecosystem. Here we deployed in New Caledonia large in situ mesocosms in order to investigate (1) the contribution of N_2 fixation and DON use to primary production (PP) and particle export and (2) the fate of the freshly produced particulate organic N (PON) i.e. whether it is preferentially accumulated and recycled in the water column or exported out of the system. The mesocosms were fertilized with phosphate (P) in order to prevent P-limitation and promote N_2 fixation. The diazotrophic community was dominated by diatoms-diazotrophs associations (DDAs) during the first part of the experiment for 10 days (P1) followed by the unicellular N_2-fixing cyanobacteria UCYN-C the 9 last days (P2) of the experiment. N_2 fixation rates averaged 9.8 ± 4.0 and $27.7 \pm 8.6\,nM\,d^{-1}$ during P1 and P2, respectively. NO_3^- concentrations ($< 40\,nM$) in the mesocosms were a negligible source of N indicating that N_2 fixation was the main driver of new production all along the experiment. The contribution of v fixation to PP was not significantly different ($p > 0.05$) during P1 ($9.0 \pm 3.3\,\%$) and P2 ($12.6 \pm 6.1\,\%$). However, the *e* ratio that quantifies the efficiency of a system to export particulate organic carbon (POC_{export}) compared to PP (*e* ratio = POC_{export}/PP) was significantly higher ($p < 0.05$) during P2 ($39.7 \pm 24.9\,\%$) than during P1 ($23.9 \pm 20.2\,\%$) indicating that the production sustained by UCYN-C was more efficient at promoting C export than the production sustained by DDAs. During P1, PON was stable and the total amount of N provided by N_2 fixation ($0.10 \pm 0.02\,\mu M$) was not significantly different ($p > 0.05$) from the total amount of PON exported ($0.10 \pm 0.04\,\mu M$), suggesting a rapid and probably direct export of the recently fixed N_2 by the DDAs. During P2, both PON concentrations and PON export increased in the mesocosms by a factor 1.5–2. Unlike in P1, this PON production was not totally explained by the new N provided by N_2 fixation. The use of DON, whose concentrations decreased significantly ($p < 0.05$) from $5.3 \pm 0.5\,\mu M$ to $4.4 \pm 0.5\,\mu M$, appeared to be the missing N source. The DON consumption of about

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0.9 µM during P2 is even higher than the total amount of new N brought by N_2 fixation (about 0.25 µM) during the same period. These results suggest that while DDAs mainly rely on N_2 fixation for their N requirement, both N_2 fixation and DON can be significant N-sources for primary production and particulate export following UCYN-C blooms in the New Caledonia lagoon and by extension in the N-limited Ocean where similar events are likely to occur.

1 Introduction

Nitrogen (N) availability constitutes one of the most limiting factors for marine primary production (PP) (Falkowski, 1997). About 80 % of the global ocean surface is depleted in dissolved inorganic N (nitrate (NO_3^-) and ammonium (NH_4^+) < 1 µM) and characterized by low PP, low biomass and low particulate matter export fluxes (Longhurst, 2007). In these Low Nitrate Low Chlorophyll (LNLC) ecosystems, the strong stratification of the alighted surface layer prevents the mixing with NO_3^--replete deep waters and imposes on phytoplanktonic communities to rely on alternative N sources for growth. These sources comprise the virtually inexhaustible dissolved dinitrogen (N_2) pool (~ 400 µM), and the large (~ 5 µM) but mainly refractory dissolved organic N (DON) pool.

The first pool (N_2) is only accessible to prokaryotic organisms possessing the nifH gene and able to reduce the N_2 gas molecule into bioavailable NH_4^+. This process called N_2 fixation (or diazotrophy) is responsible for the main external source of N for the upper ocean (Gruber and Galloway, 2008; Mahaffey, 2005) and fuels PP in LNLC ecosystems (e.g. Dugdale and Goering, 1967; Karl et al., 1997). However, the fate of recently fixed N_2 in the planktonic food web and its potential impact on carbon export are poorly understood. Moreover, this fate may differ according to the diazotrophic species involved in N_2 fixation. The widely distributed filamentous cyanobacterium *Trichodesmium*, one of the main contributors to global N_2 fixation (Capone et al., 1997), is rarely found in sediment traps (Chen et al., 2003; Walsby, 1992) indicating that *Trichodesmium* has a low direct export efficiency. However, a recent study performed in

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the South West Pacific indicates that N fixed by *Trichodesmium* is preferentially and rapidly (within few days) transferred to diatoms and bacteria (Bonnet et al., 2015b), potentially resulting in indirect carbon export. Conversely, diatoms-diazotrophs associations (DDAs) drive an efficient biological carbon pump in the Amazon River plume (Subramaniam et al., 2008) and in the North Pacific Gyre (Dore et al., 2008; Karl et al., 2012), indicating an efficient export of the N fixed by these organisms. Finally, unicellular N_2-fixing cyanobacteria (UCYN), are presumably the most abundant in the global ocean and are also major contributor to global N_2 fixation (Moisander et al., 2010; Montoya et al., 2004). However, little is known regarding the fate of the N fixed by UCYN, whether it is directly or indirectly exported out of the euphotic zone or recycled in surface waters (Thompson and Zehr, 2013).

The second N pool (DON) may constitute a significant N source for planktonic communities but remains poorly constrained (Bronk, 2002). The DON pool is a "Black box" composed of various chemical products more or less refractory with their own specific turnover time (Bronk et al., 2007). The persistence of high DON concentrations in surface oceanic waters has formerly led to consider that it is unavailable for the marine biota. However, the determination of DON concentrations is submitted to high analytical uncertainties (Czerny et al., 2013) that may hide low but ecologically relevant changes in concentration resulting from consumption of the labile or semi labile fraction of the DON pool. Furthermore, due to the heterogeneous composition of DON, isotopic labeling experiments using tracers are difficult to conduct, which explains the lack of information on the fluxes transiting in and out of the DON pool (Bronk, 2002; Bronk et al., 2007). If heterotrophic bacteria are presumably the main users of this organic pool, it has been shown that primary producers can also use it to meet their N requirements (Antia et al., 1991; Berman and Bronk, 2003). Similarly to N_2 fixed, the fate of DON assimilated by marine plankton will depend on the consumers, whether they would remineralize or export the particulate organic matter produced.

Studying the fate of N in the ocean is complex as it requires to follow the biogeochemical characteristics, the succession of planktonic species and the potential export

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from the same water mass for several weeks. In the open ocean, such studies are further complicated by physical processes (e.g. lateral advection) that spread the water masses. Here, we isolated a part of the water column from physical dispersion using in situ large mesocosms (52 m^3) equipped with sediment traps in order to overcome this issue. The objectives of this study were (1) to investigate the contribution of N_2 fixation and DON use on PP and particle export, (2) to trace the fate of these N sources in the ecosystem, i.e. whether the freshly produced particulate organic N (PON) is accumulated or exported out of the system.

The mesocosms were deployed in the subtropical New Caledonian lagoon (South West Pacific), characterized by LNLC conditions (Fichez et al., 2010), where high N_2 fixation rates and abundances of *Trichodesmium* and UCYN communities have been reported (Biegala and Raimbault, 2008; Garcia et al., 2007; Rodier and Le Borgne, 2008, 2010). Dissolved inorganic phosphate (DIP) availability has previously been reported to control N_2 fixation in the South West Pacific (Moutin et al., 2005, 2008). In order to avoid phosphate (P) limitation and to create favorable conditions for diazotrophs growth, the mesocosms were fertilized with DIP at the beginning of the experiment. Diazotrophs developed extensively in the mesocosms during the 23-days experiment (Turk et al., 2015). The diazotroph community was dominated by DDAs during the first half of the experiment (from day 5 to day 14, hereafter called P1), then shifted towards a large dominance of UCYN from group C (closely related to *Cyanothece* sp.) which developed extensively during the second half of the experiment (from day 15 to day 23, hereafter called P2). PP and N_2 fixation rates were monitored for the 23 days together with C, N and P pools dynamics in the water column and in export material. The results are discussed under the light of the shift of dominance between the two diazotrophic communities.

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2 Material and method

2.1 Study site and mesocosm description

Three mesocosms were deployed at the exit of the oligotrophic New Caledonian lagoon (22°29.1′ S–166°26.9′ E), 28 km off the coast of New Caledonia from 13 January 2013 (day 1) to 4 February 2013 (day 23). The site was 25 m depth on sandy bottom, protected from the dominant trade winds (southeast sector) and characterized by high influence of oceanic oligotrophic waters coming from outside the lagoon through the Boulari passage (Ouillon et al., 2010). The complete description of the mesocosms design is detailed in Bonnet et al. (2015c). Briefly, the enclosures were cylindrical bags 2.3 m in diameter and reaching about 15 m deep into the water. The bags were maintained 1 m above the surface to prevent external water inclusions. They were supported by a polyethylene frame and kept at the surface with floats. The bags were straightened by weights at the bottom of the mesocosms. After deployment, the mesocosms were left opened at the bottom for 24 h to insure a total homogeneity in the water column. On day 1, the bottom was closed with a sediment trap consisting in a funnel shape end fitted with a 3″ adapter for fastening a collection bottle for the daily sinking material.

The DIP fertilization was conducted in the evening of day 4. The fertilization consisted in an addition in each mesocosm of 20 L of a filtered seawater solution enriched with KH_2PO_4 (41.6 mM) leading to a final concentration of ~ 800 nM in the mesocosms. To insure homogenization, the solution was added to each mesocosm using a polyethylene tubing connected to a Teflon pump lifted regularly from the bottom to the surface of the mesocosms.

2.2 In situ monitoring and water sampling

CTD casts and water collection were conducted daily in each of the three replicate mesocosms (hereafter called M1, M2, and M3) and in surrounding waters. Seawater sampling was performed from a floating platform moved around the mesocosms. CTD

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casts were performed at 10 a.m. (local time) in each mesocosm and in surrounding waters using a memory probe SBE 911 plus (Sea-Bird Electronics, Inc.) equipped with conductivity, turbidity, fluorimetry, temperature and dissolved oxygen sensors. The CTD was handled with a speed of 0.2–0.3 m s^{-1}. The water was collected just after the CTD casts at three depths in each mesocosm (1, 6 and 12 m) using an air-compressed Teflon pump (AstiPure™) connected to a polyethylene tubing. Samples for particulate and dissolved matter (C, N and P) and PP determination were first collected in 50 L polypropylene carboys at the three depths and sub-sampled back on the R/V *Alis* moored 1 nautical mile away from the mesocosms site. Samples for N_2 fixation rate determination were directly collected from the pump in polycarbonate bottles (4.5 L) for each depth in each mesocosm and in surrounding waters. Sinking material was collected every day by divers from sediment traps.

2.3 Primary production rates and DIP turnover time

PP rates and DIP turnover time (T_{DIP} i.e. the ratio of DIP concentration and uptake), were measured using the $^{14}C/^{33}P$ dual labeling method (Duhamel et al., 2006). 60 mL bottles were amended with ^{33}P and ^{14}C and incubated for 3 to 4 h on a mooring line close to the mesocosms site at the sampling depths. After incubation, 50 µL of KH_2PO_4 solution (10 mM) was added in order to stop DIP assimilation and kept in the dark to stop the DIC uptake. Samples were then filtered on 0.2 µm polycarbonate membrane filters, and placed into scintillation vials with 250 µL of HCl 0.5 M. After 12 h, 5 mL of scintillation liquid (ULTIMA Gold MV, PerkinElmer Inc.) was added to each vial before the first count on a Packard Tri-Carb® 2100TR scintillation counter. The activity of ^{33}P and ^{14}C was separated using a second count made 5 months later taking into account the half-life of the two isotopes. PP and T_{DIP} were calculated according to Moutin et al. (2002).

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2.4 N_2 fixation rates

Samples for N_2 fixation incubations were collected in 4.5 L polycarbonate bottles. The latter were amended with $^{15}N_2$ enriched seawater according to the protocol developed by Mohr et al. (2010). Briefly, the $^{15}N_2$ enriched seawater was prepared daily from 0.2 µm filtered seawater collected from the same site in a 4.5 L polycarbonate bottle. Seawater was first degassed through a degassing membrane (Membrana, Minimodule®, flow rate fixed at 450 mL min^{-1}) connected to a vacuum pump (< 200 mbar absolute pressure) during at least 1 h. It was then tightly closed with no head space with a silicone septum cap and amended with 1 mL of $^{15}N_2$ (98.9 % Cambridge isotope) per 100 mL. The bottle was then shaken vigorously and incubated overnight at 3 bars (20 m depth) to promote $^{15}N_2$ dissolution. Incubation bottles were then amended with 5 % vol : vol $^{15}N_2$ enriched seawater and closed without headspace with silicone septum caps and incubated on an in situ mooring line close to the mesocosms at the appropriate sampling depths for 24 h. After of incubation, 12 mL of incubated water was sampled in Exetainers® on 10 replicate samples and analyzed using a Membrane Inlet Mass Spectrometer (Kana et al., 1994) to estimate the final enrichment of the $^{15}N_2$ pool during the incubation. The measured final $^{15}N/^{14}N$ ratio of the N_2 in the incubation bottles was found to be 2.4 ± 0.2 atom% (n = 10). Samples were then filtered on combusted (450 °C, 4 h) GF/F filters and stored at −20 °C for the duration of the cruise. Every day, samples were spiked with $^{15}N_2$ and immediately filtered in order to determine the initial background of $^{15}N/^{14}N$ ratio of PON for calculation of N_2 fixation rates. Filters were then dried at 60 °C during 24 h prior to analysis using a mass spectrometer (Delta plus, Thermo Fisher Scientific) coupled with an elemental analyzer (Flash EA, Thermo Fisher Scientific) for the concentration of PON concentrations and PON ^{15}N enrichment determination. Standard deviation was 0.004 µmol for PON and 0.0001 atom% for the $^{15}N/^{14}N$ isotopic ratio. The fluxes were defined as significant when ^{15}N enrichment was higher than three times the standard deviation obtained on initial samples. The fluxes were calculated according to the equation detailed in Mon-

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toya et al. (1996). A recent study (Dabundo et al., 2014) reports potential contamination of commercial $^{15}N_2$ gas stocks with ^{15}N-enriched NH_4^+, NO_3^- and/or nitrite (NO_2^-), and nitrous oxide. The $^{15}N_2$ Cambridge Isotopes stocks analyzed contained low concentrations of ^{15}N contaminants, and the potential overestimated N_2 fixation rates modeled using this contamination level would range from undetectable to 0.02 nmol N L^{-1} d^{-1}. These rates are in the lower end of the range of rates measured in this study and we thus considered that this issue did not affect the results reported here.

2.5 Chlorophyll *a*, inorganic and organic matter analyses

Samples for chlorophyll *a* (Chl *a*) concentrations determination were collected by filtering 550 mL of seawater on GF/F filters. Filters were directly stored in liquid nitrogen. Chl *a* was extracted in methanol and measured by fluorometry (Herbland et al., 1985).

Samples for total organic carbon (TOC) concentrations were collected in duplicate at only one depth (6 m) in each mesocosm and in surrounding waters in precombusted (450 °C, 4 h) 12 mL sealed glassware flasks, acidified with H_3PO_4 and stored in the dark at 4 °C until analysis. Samples were analyzed on a Shimadzu TOCV analyzer with a typical precision of 2 µM. Samples for particulate organic carbon (POC) concentrations were collected by filtering 2.3 L of seawater through precombusted (450 °C, 4 h) GF/F filter and determined using the combustion method (Strickland and Parsons, 1972) on an EA 2400 CHN analyzer. Filters were not acidified to remove inorganic carbon as it is assumed to be < 10 % of the total particulate C (Wangersky, 1994). Dissolved organic carbon (DOC) concentrations were calculated as the difference between TOC and POC concentrations. The DOC precision calculated from the analytical precision of each term according to the errors propagation law was 5 µM.

Samples for NH_4^+ were collected in 40 mL glass vials and analyzed by the fluorescence method according to Holmes et al. (1999) on a trilogy fluorometer (Turner Design). The detection limit was 0.01 µM. Samples for NO_3^-, NO_2^-, DIP, total N (TN) and total P (TP) concentrations determination were collected in 40 mL glass bottles and

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stored at −20 °C until analysis. NO_3^-, NO_2^- and DIP concentrations were determined on a segmented flow analyzer according to Aminot and Kérouel (2007). The detection limit was 0.01 and 0.005 µM for $NO_3^- + NO_2^-$ and DIP respectively. TN and TP concentrations were determined according to the wet oxidation procedure described in Pujo-Pay and Raimbault (1994). The precision was 0.5 µM and 0.02 µM for TN and TP, respectively. Samples for PON and particulate organic P (POP) concentrations were collected by filtering 1.2 L of water on precombusted (450 °C, 4 h) and acid washed (HCl, 10 %) GF/F filters and analyzed according to the wet oxidation protocol described in Pujo-Pay and Raimbault (1994) with a precision of 0.06 and 0.007 µM for PON and POP, respectively. DON concentrations were calculated from TN concentrations subtracted by PON, NO_3^-, NO_2^- and NH_4^+ concentrations. Dissolved organic P (DOP) concentrations were calculated from TP concentrations subtracted by POP concentrations and DIP concentrations. The precision calculated according the propagation law of analytical precision associated with each parameter was 0.5 and 0.03 µM for DON and DOP respectively.

Samples from sediment traps were collected daily and preserved in a 5 % buffered solution of formaldehyde and stored at 4 °C until analysis. All the swimmers were hand-picked from each sample, and were found to be negligible source particulate matter compared to the total particulate matter exported (< 5 %). Samples were then desalted using ultrapure water (Milli-Q grade) and frozen dried. The daily amount of POC exported (POC_{export}), and PON exported (PON_{export}) were measured using a CHN analyzer (Perkin Elmer 2400). The POP exported (POP_{export}) was measured after mineralization using nitric acid and further determination of mineralized P according to Pujo-Pay and Raimbault (1994).

2.6 Data presentation and statistical analyses

The build-up of an elemental mass balanced budget is theoretically accessible as all the stocks and fluxes were sampled in the mesocosms. However, the attempts of closing a elemental mass budget in similar mesocosms studies were limited by the large

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analytical uncertainties on the suspended organic pool determination (Czerny et al., 2013; Guieu et al., 2014). Nevertheless, as the only incoming (N_2 fixation) and export fluxes (PON_{export}) of N were characterized accurately, we were able to calculate the change in TN content (ΔTN_{calc}) of a mesocosm. It was defined as:

$$\Delta TN_{calc} = \Sigma N_{2,fix} + \Sigma PON_{export} \quad (1)$$

where $\Sigma N_{2,fix}$ and ΣPON_{export} are the cumulated average over depth N_2 fixation rates and PON_{export}. This approach does not discriminate the different N pools in the water column but allows a precise evaluation of the TN variation in the mesocosm and a direct comparison of the N_2 fixation and the PON_{export}.

Considering the absence of significant differences between the three depths sampled of most of the concentrations and fluxes measured (paired non parametric Friedman test, $\alpha = 0.05$), the values presented in the text are averaged over the three depths. Statistical differences between each mesocosm or between the mesocosms and surrounding waters were tested using the paired non parametric Wilcoxon signed-rank test ($\alpha = 0.05$) for each parameter presented. If no significant differences between the mesocoms were detected, the values were averaged between the mesocosms. The associated uncertainties were calculated as the analytical precision cumulated to the standard deviation of each term according the propagation of errors. Differences between P1 and P2 were tested using the non parametric Kruskal–Wallis test ($\alpha = 0.05$).

3 Results

3.1 Hydrological background

The detailed description of hydrological and inorganic nutrients conditions during the experiment is extensively presented in Bonnet et al. (2015c). Briefly, seawater temperature increased from 25.5 to 26.7 °C over the course of the experiment, similarly inside the mesocosms and in surrounding waters. The water column was well mixed

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in the mesocosms as temperature and salinity were homogeneous with depth over the course of the experiment. The sum of NO_3^- and NO_2^- concentrations averaged over depth in the mesocosms were below 0.04 µM the day before the DIP fertilization (day 4) and decreased to 0.01 µM toward the end of the experiment. NH_4^+ concentrations were close to the detection limit of 0.01 µM from day 1 to day 18 and increased in all the mesocosms up to 0.06 µM toward the end of the experiment. Prior to the DIP fertilization, DIP concentrations in the mesocosms ranged from 0.02 to 0.05 µM. The day after the fertilization, DIP concentrations reached ~ 0.8 µM in all mesocosms and decreased steadily during the course of the experiment and tended to initial concentrations (0.02–0.08 µM) at the end of the experiment. In surrounding waters, NO_3^- remained below 0.20 µM and DIP averaged 0.05 µM all along the experiment.

3.2 DIP turn over time

The evolution of T_{DIP} was closely related to the dynamics of DIP concentrations. Before the DIP fertilization, T_{DIP} decreased from 1.0 ± 0.1 d on day 3 to 0.4 ± 0.1 d on day 4 in all the mesocosms (Fig. 1a). At the start of P1, T_{DIP} dramatically increased in all mesocosms reaching 35.7 ± 15.7, 30.1 ± 8.6 and 35.8 ± 10.5 d in M1, M2 and M3 respectively. T_{DIP} then decreased steadily in all the mesocosms reaching 1 d on day 14, day 19 and day 21 for M1, M2 and M3, respectively. At the end of the experiment (day 23), T_{DIP} values were the lowest reached over the experiment in all the mesocosms with values below 0.2 d. In surrounding waters, T_{DIP} was stable around 1.8 ± 0.7 d from the start of the experiment to day 15 and then decreased to reach 0.5 ± 0.1 d on day 23 (Fig. 1a).

3.3 N_2 fixation rates and primary production

Before the DIP fertilization, N_2 fixation rates inside the mesocosms were 17.4 ± 7.3 nM d^{-1} and decreased the days after the fertilization (Fig. 1b). During P1, the average N_2 fixation rates in the mesocosms were 9.8 ± 4.0 nM d^{-1}. During P2, N_2 fixation

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rates in the mesocosms were significantly ($p < 0.05$) higher than during P1 averaging $27.7 \pm 8.6\,\mathrm{nM\,d^{-1}}$. N_2 fixation rates were not significantly different ($p > 0.05$) between the three mesocosms all along the experiment. In surrounding waters, N_2 fixation rates did not show any clear pattern along the experiment and averaged $9.2\,\mathrm{nM\,d^{-1}}$, ranging from 1.9 to $29.3\,\mathrm{nM\,d^{-1}}$ (Fig. 1b).

The day before the DIP fertilization, PP was not significantly different ($p > 0.05$) between the three mesocosms and averaged $0.4 \pm 0.1\,\mu\mathrm{M\,C\,d^{-1}}$ (Fig. 1c). During P1, PP increased steadily in the mesocosms to reach $0.9 \pm 0.1\,\mu\mathrm{M\ C\ d^{-1}}$ at the end of P1. During P2, while T_{DIP} was decreasing, PP increased faster than during P1 in the mesocosms with values generally exceeding $1.5\,\mu\mathrm{M\,C\,d^{-1}}$. During P2, PP was significantly higher in M3 than in M1 and M2 ($p < 0.05$). In surrounding waters, PP was stable before and during P1 at $0.9 \pm 0.3\,\mu\mathrm{M\,C\,d^{-1}}$ and increased during P2 reaching $1.5 \pm 0.2\,\mu\mathrm{M\,C\,d^{-1}}$ on day 23. Over the whole experiment, PP in the mesocosms was not significantly different from surrounding waters ($p > 0.05$) except for M3 during P2 ($p < 0.05$).

Assuming that all the diazotrophs are primary producers and have a C : N fixation ratio of 6.6 (Redfield, 1934), we calculated that N_2 fixation sustained 10.8 ± 5.0 % (range 3.7–32.2 %) of PP in the mesocosms after the DIP fertilization and 5.7 ± 2.0 % (range 2.2–9.1 %) in surrounding waters. The contribution of N_2 fixation to PP was not significantly different ($p > 0.05$) during P1 (9.0 ± 3.3 %) and P2 (12.6 ± 6.1 %) (Fig. 2).

3.4 Chl *a* and particulate organic matter dynamics

The day before the fertilization, Chl *a* concentrations in the mesocosms were $0.21 \pm 0.05\,\mu\mathrm{g\,L^{-1}}$ (Fig. 3). During P1, Chl *a* did not show any clear pattern; concentrations were in the 0.12 to $0.28\,\mu\mathrm{g\,L^{-1}}$ range. During P2, Chl *a* increased in all the mesocosms but to a greater extend in M3 compared to M1 and M2 and reached maximal depth-averaged concentrations of 0.55 ± 0.01, 0.47 ± 0.08 and $1.29 \pm 0.22\,\mu\mathrm{g\,L^{-1}}$ for M1, M2 and M3, respectively. Before and during P1, Chl *a* concentrations in surrounding waters were close to the concentrations in the mesocosms and ranged between 0.09 and

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0.28 µg L^{-1}. During P2, they increased but to a lower extent than in the mesocosms with daily averaged concentrations of 0.42 ± 0.03 µg L^{-1} on day 23.

The day before the DIP fertilization, POC concentrations ranged between 9 and 15 µM (Fig. 4a). During P1, POC concentrations did not show any clear pattern in the mesocosms and concentrations ranged between 6 and 13 µM. During P2, POC concentrations increased in M3 reaching 18 µM on day 21, whereas they remained stable in M1 and M2. POC concentrations in surrounding waters were stable all along the experiment and were significantly lower ($p < 0.05$) than in the mesocosms. Initial PON concentrations were about 0.9 µM and remained relatively stable during P1 (Fig. 4b). During P2, PON concentrations increased in all the mesocosms by a factor 1.5 in M1 and M2, and by a factor 2 for in M3 at day 23 reaching 2 µM. PON concentrations also increased outside but to a lesser extent with values remaining below 1 µM. POP showed the same pattern than PON. The day before the DIP fertilization, POP concentrations were not significantly different ($p > 0.05$) between the mesocosms and averaged 0.05 µM (Fig. 4c). During P1, the concentrations in the mesocosms remained relatively stable. During P2, POP concentrations increased in all the mesocosms but to a higher extent in M3, reaching 0.07, 0.07 and 0.12 µM in M1, M2 and M3 respectively. Particulate POC/PON ratio decreased during the experiment from the initial averaged ratio of 12 to 8 at the end of the experiment, but remained higher than the Redfield ratio (6.6).

3.5 Dissolved organic matter dynamics

DOC concentrations ranged from 50 to 74 µM (average value of 60 ± 4 µM) over the course of the experiment without any clear trend over the 23 days (Fig. 5a). Furthermore no significant differences were measured between the mesocosms and surrounding waters ($p > 0.05$). Before the DIP fertilization, DON concentrations averaged 5.2 ± 0.5 µM on day 4 (Fig. 5b). Concentrations remained stable during P1 in and out the mesocosms. In contrast during P2, DON concentrations decreased signifi-

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cantly ($p < 0.05$) in the three mesocosms. The decrease was of 0.7 ± 0.5, 0.8 ± 0.5 and 1.0 ± 0.5 µM between day 17 and day 23 in M1, M2 and M3, respectively, and was not significantly different between the mesocosms ($p > 0.05$). DON concentrations were not significantly different in surrounding waters and in the mesocoms up to day 17 ($p > 0.05$). From this day, even though a significant decrease ($p < 0.05$) in DON concentrations was also observed in surrounding waters, the resulting concentrations were significantly higher than in the mesocosms ($p < 0.05$).

The DOP dynamics was similar to the DON dynamic: during P1, DOP concentrations were on average 0.14 ± 0.03 µM and remained stable up to day 14, day 16 and day 17 for M1, M2 and M3, respectively (Fig. 5c). After these days, DOP concentrations significantly decreased ($p < 0.05$) of 0.10, 0.07 and 0.06 µM in M1, M2 and M3, respectively, which also occurred in a lower extent in surrounding waters from day 18.

3.6 Export fluxes and their coupling with PP and N_2 fixation

Before the DIP fertilization (day 4), the exported fluxes were not significantly different ($p > 0.05$) between the three mesocosms (104 ± 35, 6.5 ± 1.7 and 0.35 ± 0.09 nM d^{-1} in average for POC_{export}, PON_{export} and POP_{export}, respectively) (Fig. 6). The daily exported particulate matter remained relatively stable during P1 averaging at 164 ± 141, 10.2 ± 7.1 and 0.9 ± 1.3 nM d^{-1} for POC_{export}, PON_{export} and POP_{export} respectively. Fluxes in M1 were higher than in M2 and M3 during this period, which explains the large standard deviation of the averaged fluxes. During P2, the daily export fluxes increased continuously in all the mesocosms to a higher extent than during P1 for C and N, peaking at 1197 ± 257 and 106.1 ± 20.1 nM d^{-1}, respectively. The daily POP_{export} was much more stochastic ranging from 1.0 to 18.4 nM d^{-1}.

The *e* ratio is defined as the amount of exported carbon (POC_{export}) relative to the fixed carbon (PP). The box-plot of the daily *e* ratio data collected in the three mesocosms during P1 and P2 is shown in Fig. 7. The *e* ratio was significantly higher ($p < 0.05$) during P2 (39.7 ± 4.9 %) than during P1 (23.9 ± 20.2 %). N_2 fixation rates

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integrated over P1 was 0.10 ± 0.02 µM on average for all the mesocosms and was not significantly different from the integrated PON_{export} of 0.10 ± 0.04 µM (Fig. 8). The resulting change of the TN pool in the mesocosms remained between −0.01 and 0.01 µM and was not significantly different from 0 (sign test, $p > 0.05$). During P2, integrated N_2 fixation was 0.25 ± 0.06 µM and the PON_{export} was 0.45 ± 0.04 µM (Fig. 8). The resulting change of the TN_{calc} pool in the mesocosms remained not significantly different from 0 (sign test, $p > 0.05$) up to day 18 but deviated negatively from 0 (sign test, $p < 0.05$) on day 19 up to day 23 (Fig. 8). Thus, even though PON concentrations increased during P2, the TN_{calc} pool decreased of 0.20 ± 0.04 µM.

4 Discussion

4.1 DIP availability sustained N_2 fixation and in turn new PP

A widely accepted concept in marine biogeochemistry states that N_2 fixation is locally limited by micronutrient availability such as iron (Fe) (Dekaezemacker et al., 2013; Monteiro et al., 2011; Moore et al., 2009; Shiozaki et al., 2014), temperature (Breitbarth et al., 2007; Fu et al., 2014; Mulholland and Bernhardt, 2005) or light availability (Garcia et al., 2013; Kranz et al., 2010). However, N_2 fixation is ultimately driven by the DIP excess (Dore et al., 2008; Karl et al., 1997; Moutin et al., 2008), resulting from N loss through denitrification or anammox (Weber and Deutsch, 2014). During our mesocosms experiment where no P supply could be provided, the artificial DIP fertilization was performed in order to alleviate a limitation that would have prevented diazotrophs growth. This fertilization associated with the relatively high micronutrients (e.g. Fe) concentrations previously reported in the lagoon (Ambatsian et al., 1997), the seawater temperature above 25 °C and the maintenance of the water mass in the lighted upper layer are considered as ideal conditions for diazotrophs growth. As a result, diverse diazotroph phylotypes developed extensively in the mesocosms at abundances comprised between 1.10^5 and 5.10^5 nifH copies L^{-1} (Turk et al., 2015). Furthermore, N_2 fixation

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rates measured in the mesocosms were high (18.5 ± 13.1 nM d^{-1} in average) compared to those measured in surrounding waters (9.2 ± 4.8 nM d^{-1} in average) (Fig. 1b) and are among the highest previously reported in the literature (Luo et al., 2012).

The contribution of N_2 fixation to PP (10.8 ± 5.0 % on average) in the mesocosms and in surrounding waters (5.7 ± 2.0 % on average) was in the upper range reported in previous studies in the Pacific Ocean (Raimbault and Garcia, 2008; Shiozaki et al., 2013) and in the Mediterranean Sea (Bonnet et al., 2011; Ridame et al., 2013). Before the DIP fertilization, NO_3^- concentrations were below 40 nM. As no external supply of NO_3^- can be provided to the system and considering N inputs from atmospheric deposition as negligible in the studied region (Jickells et al., 2005), we estimated that the potential consumption of NO_3^- initially present in the mesocosms would have represented 11.5 % of the integrated N_2 fixation rates over P1 and P2 (0.35 ± 0.08 µM) (Fig. 7). Thus, N_2 fixation supplied nearly all the new production (sensu Dugdale and Goering, 1967) during P1 and P2. The mesocosms isolates only a part of the water column, which hinders any comparison with open ocean field studies. However, this experiment shows that in a N depleted system, diazotrophs can provide enough new N to sustain high PP (exceeding at times 2 µM C d^{-1}) and biomass (up to 1.42 µg L^{-1} of Chl *a*), as long as P does not limit N_2 fixation.

4.2 The relative efficiency of different diazotrophs to export particulate matter

Only few studies have focused on the direct coupling between N_2 fixation and particulate export (Dore et al., 2008; Karl et al., 2012; White et al., 2012). To our knowledge, the only study that has compared the export efficiency of different diazotrophs reports that in the North East Pacific DDAs blooms could contribute up to 44 % of the direct export, while UCYN (Group A) and *Trichodesmium* could account for only 0 to 10 % of the particulate export at the base of the euphotic layer (White et al., 2012). The scarcity of data is explained by methodological issues that are often encountered when using sediment traps to collect the sinking material in the open ocean. They include (1) the

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patchy geographical distribution of N_2 fixers that is not necessarily collected in sediment traps, (2) the temporal lag between production of N_2 fixers and export which is difficult to assess (Nodder and Waite, 2001). The mesocosms approach used here was designed to overcome these limitations. Thus, even if the shallow depth of the traps (~ 15 m) and the absence of NO_3^- supply trough the nitracline prevent any comparison with open ocean studies, it allows a comparison of the export efficiency under contrasted ecological situations, here between P1, the period dominated by DDAs, and P2, the period dominated by UCYN-C.

During P1, the biomass was stable and the amount of N_2 recently fixed was equal to the amount of N exported (Fig. 8). It has been shown that large aggregates of the diatom *Rhizosolenia* spp., that represented more than 80 % of the diatoms involved in DDAs during P1 (Turk et al., 2015), may directly sink at high rates (Villareal et al., 1996). *Rhizosolenia* spp. may also have been ingested by zooplankton producing fast sinking fecal pellets. However, the large size of this diatom limits its grazing by mesozooplankton (Perissinotto, 1992) and this species is generally poorly represented in copepod guts (Haq, 1967; Marshall and Orr, 1966). This suggests that during this experiment, the recently fixed N_2 by DDAs remained within the symbiotic association and was quickly exported in settling particles. This is in good agreement with Karl et al. (2012) findings who showed that DDAs support the pulses of particle export regularly observed in late summer in the tropical North Pacific Ocean.

The situation was contrasted during P2: the total amount of exported PON exceeded the total amount of N provided by N_2 fixation (Fig. 8) suggesting an additional N source. Furthermore, a part of the PON produced was accumulated in the water column increasing the N source deficit. The equilibrium can only be reached considering the DON pool as a source for the PON production (including PON_{export}), which is consistent with the significant DON concentrations decrease of 0.9 ± 0.7 µM in the mesocoms during P2 (see next section for further discussion on the DON consumers). Assuming a DON use of 0.9 µM and neglecting the NH_4^+ and NO_3^- sources, we calculated that the DON pool supported 78 % of the PON production during P2 and thus, potentially

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fueled the PON export in the same extent. Torres-Valdes et al. (2009) support the idea of a lateral transport of DON and DOP from the productive area toward the equatorial gyres of the Atlantic ocean were it can be assimilated and support up to 40 % of the vertical PON and POP export. Recently Letscher et al. (2013) confirmed the importance of the lateral advection of DON toward the Atlantic and Pacific gyres. The DON concentrations measured during this experiment (4.5–5.5 µM) are in the lower range of the reported values for the surface Pacific Ocean (Bronk, 2002). Together with low inorganic nutrient availability, low DON concentrations indicate that the studied water mass was characteristic of the open ocean. Thus, even in oligotrophic areas, DON pool appears as a dynamic contributor to the N cycle able to fuel particulate export.

Using our data only, it is difficult to assess the contribution of N_2 fixation and DON use to PON_{export} during P2. A quantification of diazotrophs in the sediment traps performed on day 19 shows that ~ 10 % of the UCYN-C biomass in the mesocosms was directly exported daily in the sediment traps and may explain ~ 7 % of the total export (Bonnet et al., 2015a). The latter paper suggests that this direct export may have been promoted by the formation of high sinking aggregates (~ 1 mm size) of UCYN-C observed in the mesocosms. The formation of these aggregates may have been enhanced by the production of extracellular polysaccharides (EPS) by UCYN, as described in culture by Sohm et al. (2011). However, the direct export of UCYN-C biomass does not completely explain the biomass exported. This suggests that a part of the recently fixed N_2 was accumulated in the water column and may have been recycled through the bacterial loop or directly released under dissolved inorganic or organic N compounds and potentially transferred to non-diazotrophic plankton cells during the experiment that in turn, were exported in the sediment traps. On day 17, Bonnet et al. (2015a) demonstrated that at ~ 20 % of the recently fixed N_2 by the diazotrophs dominated by UCYN-C was transferred toward non diazotrophic plankton i.e. in picoplankton and bacteria. This may explain the accumulation of picocyanobacteria observed during P2 in all the mesocosms (Leblanc et al., 2015). Zooplankton may have also played a role in the transfer of the recently fixed N by grazing on UCYN and may have potentially

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been quickly exported trough the production of rapid sinking fecal pellet (Hunt et al., 2015).

The contrasted pattern between P1 and P2 also appeared regarding the *e* ratio. Indeed the production driven by UCYN-C was more efficient to promote POC_{export} than the production driven by DDAs (Fig. 7). During P1, it is probable that the recently fixed C by DDAs remained within the symbiotic association and sunk together with the recently fixed N_2 constituting a direct and net C export. During P2, the higher efficiency of C export indicates that the use of the DON pool ultimately fueled PP which in turn enhanced the POC_{export}. Additionally, a preferential recycling of N compared to C when UCYN-C dominated, may have allowed more carbon to be fixed per unit of fixed N_2.

4.3 Who were the DON consumers?

The use of dissolved organic compounds and their implications on PP in the ocean has long been suggested (Antia et al., 1991). The use of DOP by plankton communities in the oligotrophic ocean has been observed in the North Pacific Ocean (Bjorkman and Karl, 2003) or in the Atlantic Ocean (Lomas et al., 2010; Mather et al., 2008) and generally occurs under DIP scarcity. In the present study, the decrease of DOP concentrations during P2 occurred when T_{DIP} reached the lowest values confirming the ability of the planktonic community to significantly use the DOP under low DIP availability. More surprisingly, the significant and rapid decrease of DON concentrations (0.9 ± 0.7 µM in average in the mesocoms) observed during the development of UCYN-C (P2) associated with a rapid increase in PP (Fig. 1c), biomass (Figs. 3 and 4) and bacterial production (BP) (Van Wambeke et al., 2015), suggests a considerable consumption of this organic N pool directly or indirectly by primary producers. In the open ocean, DON is considered as mainly refractory. Nevertheless, it is now recognized that a fraction of the DON is labile and can directly support phytoplankton growth, while a semi labile fraction can be mineralized by bacterioplankton (Antia et al., 1991; Bronk, 2002; Bronk et al., 2007). The large analytical uncertainties on DON determination (~ 0.5 µM) imply that small but relevant changes in concentrations in the open ocean are difficult to

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trace. Furthermore, DON is composed of a heterogenic assemblage of organic compounds such as urea, amino acid, nucleic acids, humic and fulvic substances. Due to this heterogeneous composition, experiments using isotopically labeled compounds are difficult to conduct to measure the DON uptake. As a result, it is challenging to identify the producers and consumers of the DON pool. In the present study, we propose three hypotheses that could explain in part or totally the observed DON concentrations decrease during P2: (1) a bacterial mineralization of DON triggered by high PP, (2) a direct uptake of DON by primary producers including UCYN-C and (3) an abiotic photo-degradation of DON into NH_4^+.

The increase in PP driven by high N_2 fixation rates during P2 has led to an increase of bacterial production (Van Wambeke et al., 2015). The significant negative correlation between BP and DON concentrations (Spearman rank correlation, $r = -0.35$; $p < 0.001$) would argue for a significant consumption of the DON by bacterial mineralization. Based on BP data and assuming a bacterial growth efficiency between 10 and 30 % (del Giorgio and Cole, 1998) and a C : N ratio of 6.6 (Fukuda et al., 1998), we calculated that bacterial respiration could have led to a DON consumption of 0.2 to 0.7 µM during P2, which could explain the DON removal reported here. Therefore, during P2, the increasing PP stimulated by the new N provided by UCYN-C may have stimulated in turn bacterial activity. Figuring that (1) the diazotrophs are known to over-fix C relative to N and (2) the POC : PON ratio was well above the Redfield one during the experiment, the N demand for bacterial mineralization may have been ultimately found in labile or semi labile DON. This hypothesis is supported by Van Wambeke et al. (2015) who showed that BP was limited by N availability. Furthermore, the increasing NH_4^+ concentrations suggest an increasing regenerated production potentially mediated by bacterial ammonification that support the hypothesis of a bacterial mediated DON consumption.

An alternative explanation for the DON decrease in concentration is a direct consumption by primary producers. Cyanobacteria are known to be able to use DON compounds as urea (Collier et al., 2009; Painter et al., 2008) in such extent that DON has

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been reported to be the main source of N fueling cyanobacterial blooms in coastal waters (Glibert et al., 2004). In our system, the DON decrease that occurred during the large development of the diazotrophic cyanobacteria UCYN-C, whose abundances reached 5.10^5 nifH copies L^{-1} (Turk et al., 2015), questions the ability of the latter to use DON to meet their N requirements. Direct uptake of glutamate and amino acid (constitutive components of the DON pool) has been reported in natural and laboratory populations of *Trichodesmium* (Mulholland and Capone, 1999; Mulholland et al., 1999). Furthermore, similarly to our results, Berman (1997) observed that large decrease in DON concentration were followed by blooms of the diazotroph *Aphanizomenon ovalisporum* in Lake Kinneret. Their hypothesis of a direct use of DON by the diazotroph was confirmed in culture experiment where *A. ovalisporum* development was stimulated by DON additions (Berman, 1997, 1999). To our knowledge, no direct uptake measurement of DON compounds has been performed on UCYN. However, the ureA gene implicated in the urea assimilation has recently been identified in the cyanobacterial diazotrophic strain *Cyanothece* PCC 7822 (Bandyopadhyay et al., 2011) that is related to the UCYN-C cluster. This would suggest that in addition to provide new N trough N_2 fixation, the UCYN-C present during P2 would have been able to use the DON pool to meet a large part of their N requirements, which may explain the observed significant decrease in DON concentrations.

Finally, photo-degradation has been pointed out as a possible sink of DON in surface waters (Bronk, 2002). Only few measurements have been performed in open ocean systems, with only one field study performed in the ultraoligotrophic eastern basin of the Mediterranean Sea indicating a production of NH_4^+ from DON of 0.2–2.9 nM d^{-1} in surface water (Kitidis et al., 2006). However, even taking into account the highest rates reported above, this process can only explain a small part of the DON removal observed here. Moreover, the DON decrease occurred only during P2 whereas photo-degradation was likely to occur continuously over the experiment. Consequently, the two first hypotheses are preferred to explain the DON decrease and the concomitant PON increase during P2. None of these two hypotheses can be excluded even though

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direct evidence of large uptake of DON by UCYN-C is lacking. Anyhow, in this study the DON use appears directly or indirectly triggered by the UCYN-C activity.

5 Conclusions

This study confirms that in the South West Pacific, N_2 fixation is a biogeochemically relevant process able to provide sufficient new N to drive new PP, biomass accumulation and organic matter export as long as P is not limiting. It appears that the fate of the recently fixed N is closely related to the diazotrophic community involved in N_2 fixation. Thus, a strong coupling of N_2 fixation and PON_{export} occurred when DDAs dominated the diazotrophic community suggesting their direct export. Conversely, when the community was dominated by UCYN-C, biomass accumulation was observed together with an efficient particulate export. Moreover, a significant decrease of DON concentrations was observed during the same period indicating a direct or indirect use of DON by UCYN-C. Thus, in addition to fuel primary production, UCYN-C appears able to enhance regenerated production based both on the transfer of recently fixed N_2 toward non fixing planktonic groups and on the use of the DON pool. This use of DON exceeded the new N provided by N_2 fixation even though the N_2 fixation rates were among the highest reported in literature for the global ocean. These results suggests that DON has to be considered as a dynamic pool even in LNLC area as it may provide significant amounts of N and contribute significantly to the particulate export.

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References

Ambatsian, P., Fernex, F., Bernat, M., Parron, C., and Lecolle, J.: High metal inputs to closed seas: the New Caledonian lagoon, J. Geochem. Explor., 59, 59–74, doi:10.1016/S0375-6742(96)00020-9, 1997.

Antia, N. J., Harrison, P. J., and Oliveira, L.: The role of dissolved organic nitrogen in phytoplankton nutrition, cell biology and ecology, Phycologia, 30, 1–89, doi:10.2216/i0031-8884-30-1-1.1, 1991.

Bandyopadhyay, A., Elvitigala, T., Welsh, E., Stöckel, J., Liberton, M., Min, H., Sherman, L. A., and Pakrasi, H. B.: Novel metabolic attributes of the genus cyanothece, comprising a group of unicellular nitrogen-fixing *Cyanothece*, MBio, 2, 5, doi:10.1128/mBio.00214-11, 2011.

Berman, T.: Dissolved organic nitrogen utilization by an *Aphanizomenon* bloom in Lake Kinneret, J. Plankton Res., 19, 577–586, doi:10.1093/plankt/19.5.577, 1997.

Berman, T.: Algal growth on organic compounds as nitrogen sources, J. Plankton Res., 21, 1423–1437, doi:10.1093/plankt/21.8.1423, 1999.

Berman, T. and Bronk, D. A.: Dissolved organic nitrogen: a dynamic participant in aquatic ecosystems, Aquat. Microb. Ecol., 31, 279–305, doi:10.3354/ame031279, 2003.

Biegala, I. and Raimbault, P.: High abundance of diazotrophic picocyanobacteria (< 3 µm) in a Southwest Pacific coral lagoon, Aquat. Microb. Ecol., 51, 45–53, doi:10.3354/ame01185, 2008.

Bjorkman, K. and Karl, D.: Bioavailability of dissolved organic phosphorus in the euphotic zone at Station ALOHA, North Pacific Subtropical Gyre, Limnol. Oceanogr., 48, 1049–1057, doi:10.4319/lo.2003.48.3.1049, 2003.

Bonnet, S., Grosso, O., and Moutin, T.: Planktonic dinitrogen fixation along a longitudinal gradient across the Mediterranean Sea during the stratified period (BOUM cruise), Biogeosciences, 8, 2257–2267, doi:10.5194/bg-8-2257-2011, 2011.

Bonnet, S., Berthelot, H., Grisoni, J.-M., Fawcett, S. E., Van Wambeke, F., Cornet-Bartaux, V., Helias, S., Grosso, O., Rahav, E., Berman-Frank, I., Leblond, N., Moutin, T., and L'Helguen, S.: Dinitrogen fixation and fate of diazotroph-derived New Nitrogen during the VAHINE mesocosms experiment, Biogeosciences Discuss., in prep., 2015a.

Bonnet, S., Berthelot, H., Turk-Kubo, K., Cornet-Bartaux, V., Fawcett, S. E., Berman-Frank, I., Barani, A., Dekaezemacker, J., Benavides, M., Charriere, B., and Capone, D. G.: Diazotroph

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12, 4273–4313, 2015

derived nitrogen supports diatoms growth in the South West Pacific: a quantitative study using nanoSIMS, ISME, in rev., 2015b.
Bonnet, S., Grisoni, J.-M., Moutin, T., Folcher, E., Bourgeois, B., and Renaud, A.: Introduction to the project VAHINE: VAriability of vertical and tropHIc transfer of fixed N_2 in the south wEst Pacific, Biogeosciences Discuss., in prep., 2015c.
Breitbarth, E., Oschlies, A., and LaRoche, J.: Physiological constraints on the global distribution of *Trichodesmium* – effect of temperature on diazotrophy, Biogeosciences, 4, 53–61, doi:10.5194/bg-4-53-2007, 2007.
Bronk, D. A.: Dynamics of DON, in: Biogeochemistry of Marine Dissolved Organic Matter, edited by: Hansell, D. A. and Carlson, C. A., Academic press, San Diego, 153–247, 2002.
Bronk, D. A., See, J. H., Bradley, P., and Killberg, L.: DON as a source of bioavailable nitrogen for phytoplankton, Biogeosciences, 4, 283–296, doi:10.5194/bg-4-283-2007, 2007.
Capone, D. G., Zehr, J. P., Paerl, H. W., Bergman, B., and Carpenter, E. J.: *Trichodesmium*, a globally significant marine cyanobacterium, Science, 276, 1221–1229, doi:10.1126/science.276.5316.1221, 1997.
Chen, Y., Chen, H., and Lin, Y.: Distribution and downward flux of *Trichodesmium* in the South China Sea as influenced by the transport from the Kuroshio Curren, Mar. Ecol.-Prog. Ser., 259, 47–57, doi:10.3354/meps259047, 2003.
Collier, J. L., Baker, K. M., and Bell, S. L.: Diversity of urea-degrading microorganisms in open-ocean and estuarine planktonic communities., Environ. Microbiol., 11, 3118–3131, doi:10.1111/j.1462-2920.2009.02016.x, 2009.
Czerny, J., Schulz, K. G., Boxhammer, T., Bellerby, R. G. J., Büdenbender, J., Engel, A., Krug, S. A., Ludwig, A., Nachtigall, K., Nondal, G., Niehoff, B., Silyakova, A., and Riebesell, U.: Implications of elevated CO_2 on pelagic carbon fluxes in an Arctic mesocosm study – an elemental mass balance approach, Biogeosciences, 10, 3109–3125, doi:10.5194/bg-10-3109-2013, 2013.
Dabundo, R., Lehmann, M. F., Treibergs, L., Tobias, C. R., Altabet, M. A., Moisander, P. H., and Granger, J.: The contamination of commercial $^{15}N_2$ gas stocks with ^{15}N-labeled nitrate and ammonium and consequences for nitrogen fixation measurements, PLoS One, 9, e110335, doi:10.1371/journal.pone.0110335, 2014.
Dekaezemacker, J., Bonnet, S., Grosso, O., Moutin, T., Bressac, M., and Capone, D. G.: Evidence of active dinitrogen fixation in surface waters of the eastern tropical South Pacific

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12, 4273–4313, 2015

during El Niño and La Niña events and evaluation of its potential nutrient controls, Global Biogeochem. Cy., 27, 768–779, doi:10.1002/gbc.20063, 2013.
Dore, J. E., Letelier, R. M., Church, M. J., Lukas, R., and Karl, D. M.: Summer phytoplankton blooms in the oligotrophic North Pacific Subtropical Gyre: historical perspective and recent observations, Prog. Oceanogr., 76, 2–38, doi:10.1016/j.pocean.2007.10.002, 2008.
Dugdale, R. C. and Goering, J. J.: Uptake of new and regenerated forms of nitrogen in primary productivity, Limnol. Oceanogr., 12, 196–206, doi:10.4319/lo.1967.12.2.0196, 1967.
Duhamel, S., Zeman, F., and Moutin, T.: A dual labelling method for the simultaneous measurement of dissolved inorganic carbon and phosphate uptake by marine planktonic species, Limnol. Oceanogr.-Meth., 4, 416–425, doi:10.4319/lom.2006.4.416, 2006.
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, doi:10.1038/246170a0, 1997.
Fichez, R., Chifflet, S., Douillet, P., Gérard, P., Gutierrez, F., Jouon, A., Ouillon, S., and Grenz, C.: Biogeochemical typology and temporal variability of lagoon waters in a coral reef ecosystem subject to terrigeneous and anthropogenic inputs (New Caledonia), Mar. Pollut. Bull., 61, 309–322, doi:10.1016/j.marpolbul.2010.06.021, 2010.
Fu, F., Yu, E., Garcia, N., Gale, J., Luo, Y., Webb, E., and Hutchins, D.: Differing responses of marine N_2 fixers to warming and consequences for future diazotroph community structure, Aquat. Microb. Ecol., 72, 33–46, doi:10.3354/ame01683, 2014.
Fukuda, R., Ogawa, H., Nagata, T., and Koike, I.: Direct determination of carbon and nitrogen contents of natural bacterial assemblages in marine environments, Appl. Environ. Microb., 64, 3352–3358, 1998.
Garcia, N., Raimbault, P., and Sandroni, V.: Seasonal nitrogen fixation and primary production in the Southwest Pacific: nanoplankton diazotrophy and transfer of nitrogen to picoplankton organisms, Mar. Ecol.-Prog. Ser., 343, 25–33, doi:10.3354/meps06882, 2007.
Garcia, N. S., Fua, F. X., Breene, C. L., Yu, E. K., Bernhardt, P. W., Mulholland, M. R., and Hutchins, D. A.: Combined effects of CO_2 and light on large and small isolates of the unicellular N_2-fixing cyanobacterium *Crocosphaera watsonii* from the western tropical Atlantic Ocean, Eur. J. Phycol., 48, 128–139, 2013.
Del Giorgio, P. A. and Cole, J. J.: Bacterial growth efficiency in natural aquatic systems, Annu. Rev. Ecol. Syst., 29, 503–541, doi:10.1146/annurev.ecolsys.29.1.503, 1998.

BGD
12, 4273–4313, 2015

Glibert, P. M., Heil, C. A., Hollander, D., Revilla, M., Hoare, A., Alexander, J., and Murasko, S.: Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay, Mar. Ecol.-Prog. Ser., 280, 73–83, doi:10.3354/meps280073, 2004.

Gruber, N. and Galloway, J. N.: An Earth-system perspective of the global nitrogen cycle, Nature, 451, 293–296, doi:10.1038/nature06592, 2008.

Guieu, C., Ridame, C., Pulido-Villena, E., Bressac, M., Desboeufs, K., and Dulac, F.: Impact of dust deposition on carbon budget: a tentative assessment from a mesocosm approach, Biogeosciences, 11, 5621–5635, doi:10.5194/bg-11-5621-2014, 2014.

Haq, S. M.: Nutritional physiology of *Metridia lucens* and *M. longa* from the Gulf of Maine, Limnol. Oceanogr., 12, 40–51, doi:10.4319/lo.1967.12.1.0040, 1967.

Herbland, A., Le Bouteiller, A., and Raimbault, P.: Size structure of phytoplankton biomass in the equatorial Atlantic Ocean, Deep-Sea Res., 32, 819–836, doi:10.1016/0198-0149(85)90118-9, 1985.

Holmes, R. M., Aminot, A., Kérouel, R., Hooker, B. and Peterson, B. J.: A simple and precise method for measuring ammonium in marine and freshwater ecosystems, Can. J. Fish. Aquat. Sci., 56, 1801–1808, doi:10.1139/f99-128, 1999.

Hunt, B. P. V., Conroy, B. J., Pagano, M., Rodier, M., Berthelot, H., Foster, R. A., and Bonnet, S.: Zooplankton trophic structure and nitrogen uptake pathways during the VAHINE mesocosms experiment (New Caledonia), Biogeosciences Discuss., in prep., 2015.

Jickells, T. D., An, Z. S., Andersen, K. K., Baker, A. R., Bergametti, G., Brooks, N., Cao, J. J., Boyd, P. W., Duce, R. A., Hunter, K. A., Kawahata, H., Kubilay, N., LaRoche, J., Liss, P. S., Mahowald, N., Prospero, J. M., Ridgwell, A. J., Tegen, I., and Torres, R.: Global iron connections between desert dust, ocean biogeochemistry, and climate, Science, 308, 67–71, doi:10.1126/science.1105959, 2005.

Kana, T. M., Darkangelo, C., Hunt, M. D., Oldham, J. B., Bennett, G. E., and Cornwell, J. C.: Membrane inlet mass spectrometer for rapid high-precision determination of N_2, O_2, and Ar in environmental water samples, Anal. Chem., 66, 4166–4170, doi:10.1021/ac00095a009, 1994.

Karl, D., Letelier, R., Tupas, L., Dore, J., Christian, J., and Hebel, D.: The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean, Nature, 388, 533–538, 1997.

BGD
12, 4273–4313, 2015

Karl, D. M., Church, M. J., Dore, J. E., Letelier, R. M., and Mahaffey, C.: Predictable and efficient carbon sequestration in the North Pacific Ocean supported by symbiotic nitrogen fixation., P. Natl. Acad. Sci. USA, 109, 1842–1849, doi:10.1073/pnas.1120312109, 2012.

Kitidis, V., Uher, G., Upstill-Goddard, R. C., Mantoura, R. F. C., Spyres, G., and Woodward, E. M. S.: Photochemical production of ammonium in the oligotrophic Cyprus Gyre (Eastern Mediterranean), Biogeosciences, 3, 439–449, doi:10.5194/bg-3-439-2006, 2006.

Kranz, S. A., Levitan, O., Richter, K.-U., Prásil, O., Berman-Frank, I., and Rost, B.: Combined effects of CO_2 and light on the N_2-fixing cyanobacterium *Trichodesmium* IMS101: physiological responses, Plant Physiol., 154, 334–345, 2010.

Leblanc, K., Cornet-Barthaux, V., Rodier, M., Desnues, A., Berthelot, H., Caffin, M., Héliou, J., and Moutin, T.: Response of phytoplanktonic community composition during a diazotroph bloom: a mesocoms approach, Biogeosciences Discuss., in prep., 2015.

Letscher, R. T., Hansell, D. A., Carlson, C. A., Lumpkin, R., and Knapp, A. N.: Dissolved organic nitrogen in the global surface ocean: distribution and fate, Global Biogeochem. Cy., 27, 141–153, doi:10.1029/2012GB004449, 2013.

Lomas, M. W., Burke, A. L., Lomas, D. A., Bell, D. W., Shen, C., Dyhrman, S. T., and Ammerman, J. W.: Sargasso Sea phosphorus biogeochemistry: an important role for dissolved organic phosphorus (DOP), Biogeosciences, 7, 695–710, doi:10.5194/bg-7-695-2010, 2010.

Longhurst, A. R.: Toward an ecological geography of the sea, in: Ecological Geography of the Sea, Academic Press, San Diego, 1–17, 2007.

Luo, Y.-W., Doney, S. C., Anderson, L. A., Benavides, M., Berman-Frank, I., Bode, A., Bonnet, S., Boström, K. H., Böttjer, D., Capone, D. G., Carpenter, E. J., Chen, Y. L., Church, M. J., Dore, J. E., Falcón, L. I., Fernández, A., Foster, R. A., Furuya, K., Gómez, F., Gundersen, K., Hynes, A. M., Karl, D. M., Kitajima, S., Langlois, R. J., LaRoche, J., Letelier, R. M., Marañón, E., McGillicuddy Jr., D. J., Moisander, P. H., Moore, C. M., Mouriño-Carballido, B., Mulholland, M. R., Needoba, J. A., Orcutt, K. M., Poulton, A. J., Rahav, E., Raimbault, P., Rees, A. P., Riemann, L., Shiozaki, T., Subramaniam, A., Tyrrell, T., Turk-Kubo, K. A., Varela, M., Villareal, T. A., Webb, E. A., White, A. E., Wu, J., and Zehr, J. P.: Database of diazotrophs in global ocean: abundance, biomass and nitrogen fixation rates, Earth Syst. Sci. Data, 4, 47–73, doi:10.5194/essd-4-47-2012, 2012.

Mahaffey, C.: The conundrum of marine N_2 fixation, Am. J. Sci., 305, 546–595, doi:10.2475/ajs.305.6-8.546, 2005.

BGD
12, 4273–4313, 2015

Marshall, S. M. and Orr, A. P.: Respiration and feeding in some small copepods, J. Mar. Biol. Assoc. UK, 46, 513, doi:10.1017/S0025315400033312, 1966.
Mather, R. L., Reynolds, S. E., Wolff, G. A., Williams, R. G., Torres-Valdes, 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, doi:10.1038/ngeo232, 2008.
Mohr, W., Großkopf, T., Wallace, D. W. R., Laroche, J., and Grosskopf, T.: Methodological underestimation of oceanic nitrogen fixation rates, PLoS One, 5, e12583, doi:10.1371/journal.pone.0012583, 2010.
Moisander, P. H., Beinart, R. A., Hewson, I., White, A. E., Johnson, K. S., Carlson, C. A., Montoya, J. P., and Zehr, J. P.: Unicellular cyanobacterial distributions broaden the oceanic N_2 fixation domain., Science, 327, 1512–1514, doi:10.1126/science.1185468, 2010.
Monteiro, F. M., Dutkiewicz, S., and Follows, M. J.: Biogeographical controls on the marine nitrogen fixers, Global Biogeochem. Cy., 25, 1–8, doi:10.1029/2010GB003902, 2011.
Montoya, J. P., Voss, M., Kahler, P., and Capone, D. G.: A simple, high-precision, high-sensitivity tracer assay for N_2 fixation, Appl. Environ. Microb., 62, 986–993, 1996.
Montoya, J. P., Holl, C. M., Zehr, J. P., Hansen, A., Villareal, T. A., and Capone, D. G.: High rates of N_2 fixation by unicellular diazotrophs in the oligotrophic Pacific Ocean., Nature, 430, 1027–1032, doi:10.1038/nature02824, 2004.
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, doi:10.1038/ngeo667, 2009.
Moutin, T., Thingstad, T. F., Van Wambeke, F., Marie, D., Slawyk, G., Raimbault, P., and Claustre, H.: Does competition for nanomolar phosphate supply explain the predominance of the cyanobacterium *Synechococcus*?, Limnol. Oceanogr., 47, 1562–1567, doi:10.4319/lo.2002.47.5.1562, 2002.
Moutin, T., Van Den B, B., Beker, B., Dupouy, C., Rimmelin, P., and Le Bouteiller, A.: Phosphate availability controls *Trichodesmium* spp. biomass in the SW Pacific Ocean, Mar. Ecol.-Prog. Ser., 297, 15–21, doi:10.3354/meps297015, 2005.
Moutin, T., Karl, D. M., Duhamel, S., Rimmelin, P., Raimbault, P., Van Mooy, B. A. S., and Claustre, H.: Phosphate availability and the ultimate control of new nitrogen input by nitrogen

BGD
12, 4273–4313, 2015

fixation in the tropical Pacific Ocean, Biogeosciences, 5, 95–109, doi:10.5194/bg-5-95-2008, 2008.
Mulholland, M. R. and Bernhardt, P. W.: The effect of growth rate, phosphorus concentration, and temperature on N_2 fixation, carbon fixation, and nitrogen release in continuous cultures of *Trichodesmium* IMS101, Limnol. Oceanogr., 50, 839–849, doi:10.4319/lo.2005.50.3.0839, 2005.
Mulholland, M. and Capone, D.: Nitrogen fixation, uptake and metabolism in natural and cultured populations of *Trichodesmium* spp., Mar. Ecol.-Prog. Ser., 188, 33–49, doi:10.3354/meps188033, 1999.
Mulholland, M. R., Ohki, K., and Capone, D. G.: Nitrogen utilization and metabolism relative to patterns of N_2 fixation in cultures of *Trichodesmium* NIBB1067, J. Phycol., 35, 977–988, doi:10.1046/j.1529-8817.1999.3550977.x, 1999.
Nodder, S. and Waite, A.: Is Southern Ocean organic carbon and biogenic silica export enhanced by iron-stimulated increases in biological production? Sediment trap results from SOIREE, Deep-Sea Res. Pt. II, 48, 2681–2701, doi:10.1016/S0967-0645(01)00014-5, 2001.
Ouillon, S., Douillet, P., Lefebvre, J. P., Le Gendre, R., Jouon, A., Bonneton, P., Fernandez, J. M., Chevillon, C., Magand, O., Lefèvre, J., Le Hir, P., Laganier, R., Dumas, F., Marchesiello, P., Bel Madani, A., Andréfouët, S., Panché, J. Y., and Fichez, R.: Circulation and suspended sediment transport in a coral reef lagoon: the south-west lagoon of New Caledonia, Mar. Pollut. Bull., 61, 269–296, doi:10.1016/j.marpolbul.2010.06.023, 2010.
Painter, S. C., Sanders, R., Waldron, H. N., Lucas, M. I., and Torres-Valdés, S.: Urea distribution and uptake in the Atlantic Ocean between 50° N and 50° S, Mar. Ecol.-Prog. Ser., 368, 53–63, doi:10.3354/meps07586, 2008.
Perissinotto, R.: Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edward Archipelago (Southern Ocean), Mar. Ecol.-Prog. Ser., 79, 243–258, doi:10.3354/meps079243, 1992.
Pujo-Pay, M. and Raimbault, P.: Improvement of the wet-oxidation procedure for simultaneous determination of particulate organic nitrogen and phosphorus collected on filters, Mar. Ecol.-Prog. Ser., 105, 203–207, doi:10.3354/meps105203, 1994.
Raimbault, P. and Garcia, N.: Evidence for efficient regenerated production and dinitrogen fixation in nitrogen-deficient waters of the South Pacific Ocean: impact on new and export production estimates, Biogeosciences, 5, 323–338, doi:10.5194/bg-5-323-2008, 2008.

BGD
12, 4273–4313, 2015

Redfield, A.: On the proportions of organic derivations in sea water and their relation to the composition of plankton, in: James Johnstone Memorial Volume, edited by: Daniel, R., University Press of Liverpool, Liverpool, 177–192, 1934.

Ridame, C., Guieu, C., and L'Helguen, S.: Strong stimulation of N_2 fixation in oligotrophic Mediterranean Sea: results from dust addition in large in situ mesocosms, Biogeosciences, 10, 7333–7346, doi:10.5194/bg-10-7333-2013, 2013.

Rodier, M. and Le Borgne, R.: Population dynamics and environmental conditions affecting *Trichodesmium* spp. (filamentous cyanobacteria) blooms in the south–west lagoon of New Caledonia, J. Exp. Mar. Biol. Ecol., 358, 20–32, doi:10.1016/j.jembe.2008.01.016, 2008.

Rodier, M. and Le Borgne, R.: Population and trophic dynamics of *Trichodesmium thiebautii* in the SE lagoon of New Caledonia. Comparison with *T. erythraeum* in the SW lagoon., Mar. Pollut. Bull., 61, 349–359, doi:10.1016/j.marpolbul.2010.06.018, 2010.

Shiozaki, T., Kodama, T., Kitajima, S., Sato, M., and Furuya, K.: Advective transport of diazotrophs and importance of their nitrogen fixation on new and primary production in the western Pacific warm pool, Limnol. Oceanogr., 58, 49–60, doi:10.4319/lo.2013.58.1.0049, 2013.

Shiozaki, T., Kodama, T., and Furuya, K.: Large-scale impact of the island mass effect through nitrogen fixation in the western South Pacific Ocean, Geophys. Res. Lett., 41, 2907–2913, doi:10.1002/2014GL059835, 2014.

Sohm, J. A., Edwards, B. R., Wilson, B. G., and Webb, E. A.: Constitutive extracellular eolysaccharide (EPS) production by specific isolates of *Crocosphaera watsonii*, Front. Microbiol., 2, 229, doi:10.3389/fmicb.2011.00229, 2011.

Strickland, J. D. H. and Parsons, T. R.: A Practical Handbook of Seawater Analysis, Fisheries Research Board of Canada, Ottawa, 1972.

Subramaniam, A., Yager, P. L., Carpenter, E. J., Mahaffey, C., Björkman, K. M., Cooley, S., Kustka, A. B., Montoya, J. P., Sañudo-Wilhelmy, S. A., Shipe, R., and Capone, D. G.: Amazon River enhances diazotrophy and carbon sequestration in the tropical North Atlantic Ocean, P. Natl. Acad. Sci. USA, 105, 10460–10465, doi:10.1073/pnas.0710279105, 2008.

Thompson, A. W. and Zehr, J. P.: Cellular interactions: lessons from the nitrogen-fixing cyanobacteria, J. Phycol., 49, 1024–1035, doi:10.1111/jpy.12117, 2013.

Torres-Valdés, S., Roussenov, V. M., Sanders, R., Reynolds, S., Pan, X., Mather, R., Landolfi, A., Wolff, G. A., Achterberg, E. P., and Williams, R. G.: Distribution of dissolved organic

BGD
12, 4273–4313, 2015

nutrients and their effect on export production over the Atlantic Ocean, Global Biogeochem. Cy., 23, GB4019, doi:10.1029/2008GB003389, 2009.
Turk, K. A., Berman-Frank, I., Hogan, M. E., Desnues, A., Bonnet, S., and Zehr, J. P.: Diazotroph community composition shifts from diatom-associated Richelia- to Cyanothece-dominated during the VAHINE mesocosms experiment, Biogeosciences Discuss., in prep., 2015.
Villareal, T. A., Woods, S., Moore, J. K., and CulverRymsza, K.: Vertical migration of *Rhizosolenia* mats and their significance to NO_3^- fluxes in the central North Pacific gyre, J. Plankton Res., 18, 1103–1121, doi:10.1093/plankt/18.7.1103, 1996.
Van Wambeke, F., Pfreundt, U., Moutin, T., Rodier, M., Berthelot, H., and Bonnet, S.: Dynamics of heterotrophic bacterial community during an experimental diazotrophic bloom in new Caledonia and links with transcriptional changes during the VAHINE mesocosms experiment, Biogeosciences Discuss., in prep., 2015.
Walsby, A. E.: The gas vesicles and buoyancy of *Trichodesmium*, in: Marine Pelagic Cyanobacteria: *Trichodesmium* and other Diazotrophs, vol. 362, edited by: Carpenter, E. J., Capone, D. G., and Rueter, J. G., Springer, Dordrecht, the Netherlands, 141–161, 1992.
Wangersky, P. J.: Sampling and analysis of particulate and dissolved matter, in: The Biology of Particules in Aquatic Systems, 2nd edn., edited by: Wotton, R. S., Lewis, CRC Press, 7–43, 1994.
Weber, T. and Deutsch, C.: Local versus basin-scale limitation of marine nitrogen fixation, P. Natl. Acad. Sci. USA, 111, 8741–8746, doi:10.1073/pnas.1317193111, 2014.
White, A. E., Foster, R. A., Benitez-Nelson, C. R., Masqué, P., Verdeny, E., Popp, B. N., Arthur, K. E., and Prahl, F. G.: Nitrogen fixation in the Gulf of California and the Eastern Tropical North Pacific, Prog. Oceanogr., 109, 1–17, doi:10.1016/j.pocean.2012.09.002, 2012.

BGD
12, 4273–4313, 2015

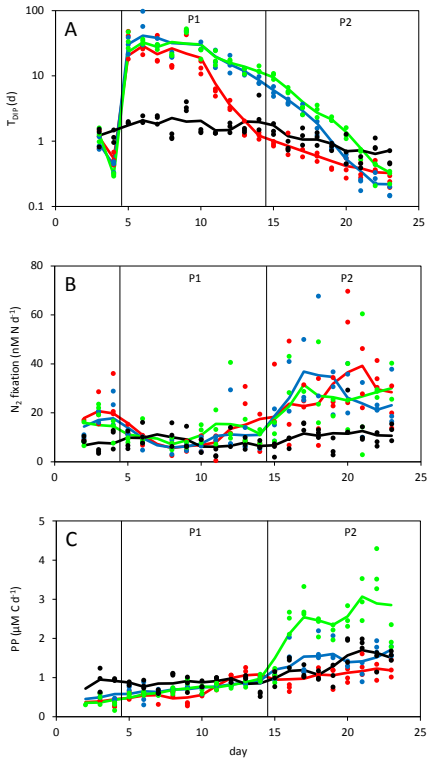

Figure 1. Temporal evolution of **(a)** dissolved inorganic phosphate turn over time (T_{DIP}, d), **(b)** N_2 fixation rates (nM N d^{-1}), **(c)** primary production (PP) rates (µM C d^{-1}) in the mesocosms M1 (red), M2 (blue) and M3 (green) and in surrounding waters (black). The three dots of each color represent the measured values on the three sampled depths. The solid lines are the three days running mean value. P1 and P2 denote the two phases of the experiment when the diazotrophic community was dominated by DDAs and UCYN-C, respectively.

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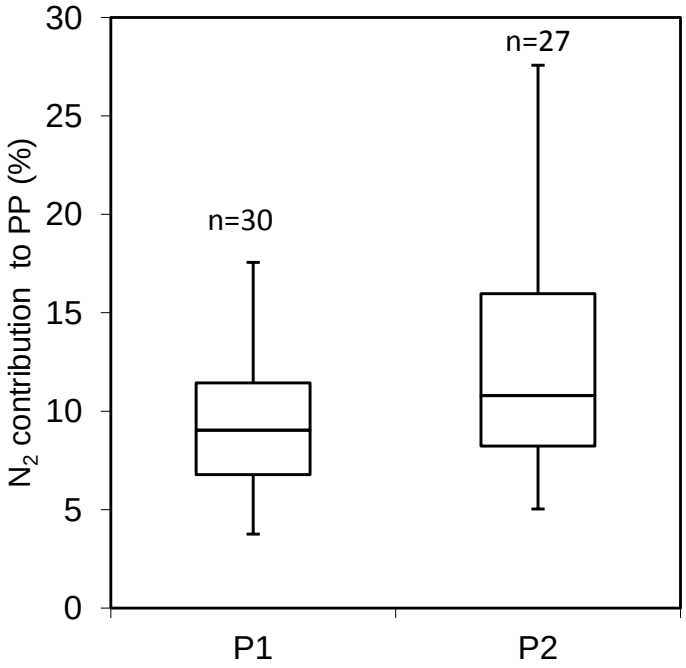

Figure 2. Boxplot of the contribution of N_2 fixation to PP during P1 (dominance of DDAs) and P2 (dominance of UCYN-C) in the mesocoms (see text for details). No significant differences were observed between the two phases (Krustal–Wallis test, $\alpha = 0.05$).

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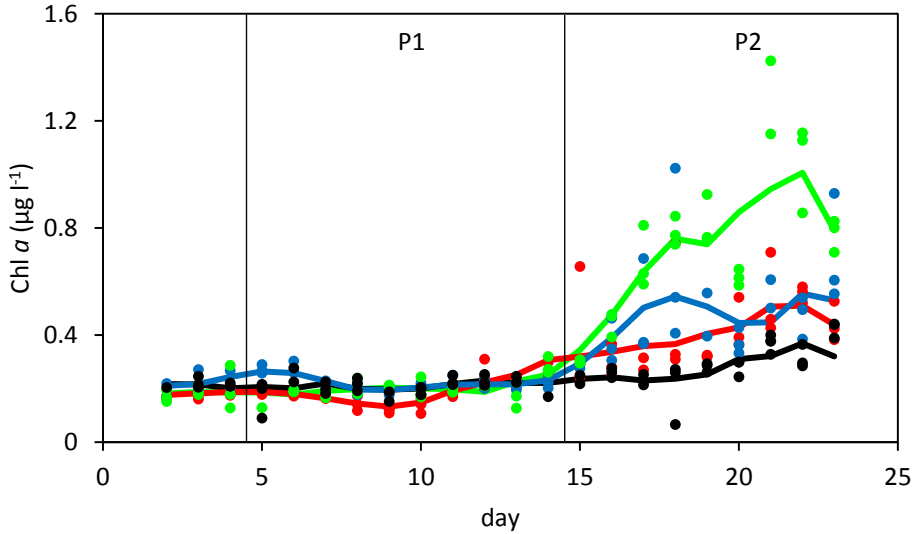

Figure 3. Temporal evolution of Chlorophyll *a* (Chl *a*) concentrations ($\mu g L^{-1}$) in the mesocosms and surrounding waters. The color code is identical to Fig. 1. The three dots of each color represent the measured values on the three sampled depths. The solid lines are the three days running mean value. P1 and P2 denote the two phases of the experiment when the diazotrophic community was dominated by DDAs and UCYN-C, respectively.

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12, 4273–4313, 2015

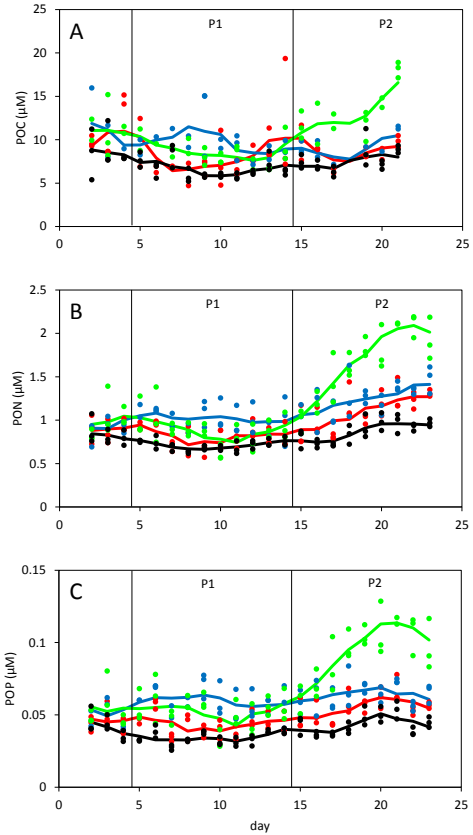

Figure 4. Temporal evolution of **(a)** particulate organic carbon (POC), **(b)** particulate organic nitrogen (PON), **(c)** particulate organic phosphorus (POP) concentrations (µM) in the mesocosms and surrounding waters. The color code as is identical to Fig. 1. The three dots of each color represent the measured values on the three sampled depths. The solid lines are the three days running mean value. P1 and P2 denote the two phases of the experiment when the diazotrophic community was dominated by DDAs and UCYN-C, respectively.

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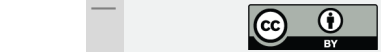
12, 4273–4313, 2015



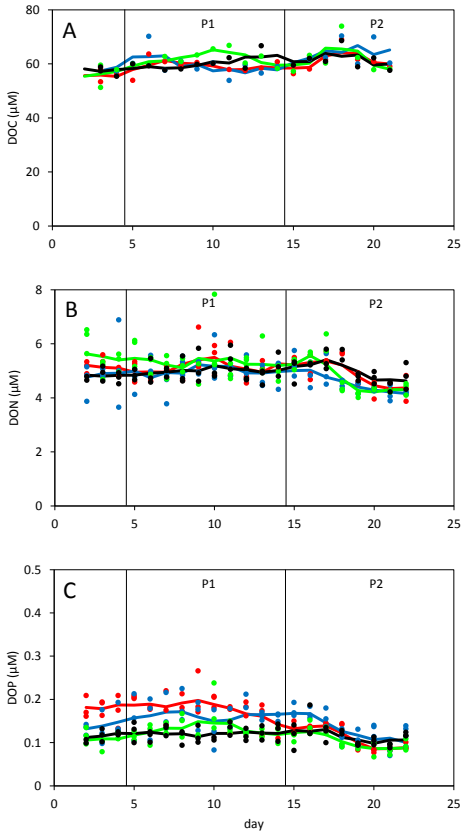


Figure 5. Temporal evolution of **(a)** dissolved organic carbon (DOC), **(b)** dissolved organic nitrogen (DON), **(c)** dissolved organic phosphorus (DOP) concentrations (µM) in the mesocosms and surrounding waters. The color code is identical to Fig. 1. The three dots of each color represent the measured values on the three sampled depths. The solid lines are the three days running mean value. P1 and P2 denote the two phases of the experiment when the diazotrophic community was dominated by DDAs and UCYN-C, respectively.

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12, 4273–4313, 2015

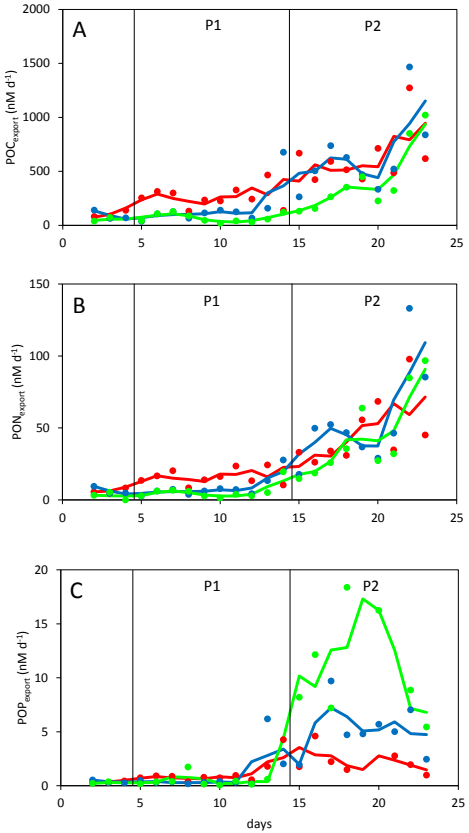

Figure 6. Temporal evolution of **(a)** POC_{export}, **(b)** PON_{export} and **(c)** POP_{export} fluxes ($nM\,d^{-1}$) in the mesocosms expressed in equivalent water volume. The color code is identical to Fig. 1. The solid lines are the three days running mean value. P1 and P2 denote the two phases of the experiment when the diazotrophic community was dominated by DDAs and UCYN-C, respectively.

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12, 4273–4313, 2015

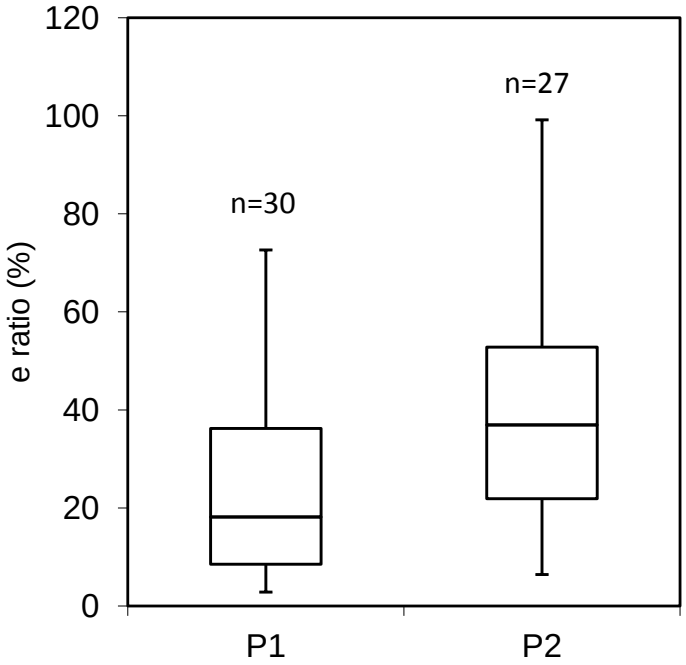

Figure 7. Boxplot of the *e* ratio (defined as POC_{export}/PP) during P1 (dominated by DDAs) and P2 (dominated by UCYN-C) in the mesocoms (see text for details). A significant difference were observed between the two phases (Krustal–Wallis test, $\alpha = 0.05$).

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12, 4273–4313, 2015

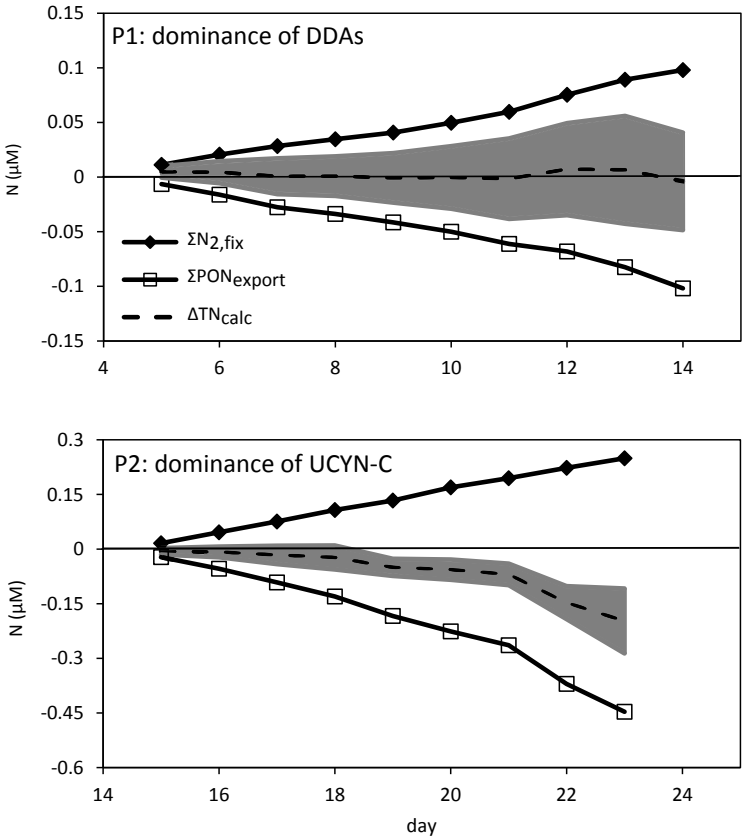

Figure 8. Integration of N_2 fixation rates ($\Sigma N_{2,fix}$) and PON exported (ΣPON_{export}) during P1 (dominance of DDAs) and P2 (dominance of UCYN-C) in the mesocosms together with the calculated change in Total N content (Δ TN_{calc}) defined as the difference between integrated N_2 fixation and PON exported. The shaded areas represent the uncertainty associated with the Δ TN change.

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