Author's response

We thank the two referees for their useful comments and address them below. The discussion has been modified according to their advices and corrected by an English native speaker. The full discussion is available on page 9.

In addition to the modifications proposed by the referees we have replaced the reference "Falkowski et al. 1997" by "Moore et al. 2013" as requested by the editor (*Moore, J. K., Geider, R. J., Guieu, C., Jaccard, S. L., Jickells, T. D., LaRoche, J., Lenton, T. M., Mahowald, N. M., Marañón, E., Marinov, I., Nakatsuka, T., Oschlies, A., Saito, M. A., Thingstad, T. F., Tsuda, A., Ulloa, O.: Processes and patterns of nutrient limitation, Nat. Geosci., 6, 701–710, 2013).*

Anonymous Referee #1:

Referee: If diazotrophs release almost nitrogen they fixed and primary production increased using the released nitrogen, f-ratio could decrease since regenerated production is likely to be enhanced. The decrease of f-ratio was observed in a time-series experiment in western Pacific warm pool when nitrogen fixation and primary production showed an increasing trend (Shiozaki et al., 2013, L&O). Please consider the difference between their results and your ones.

Response: We did not measure the f-ratio and thus we cannot compare directly our results with those presented in the Shiozaki et al. paper. However, an enhanced N remineralization under high PP and N_2 fixation rates may explain the higher efficiency of UCYN-C to promote C export. Therefore, we have added the reference at the end of section 4.2 to support the remineralization hypothesis: *"Additionally, when UCYN-C dominated, an enhanced N remineralization may have enabled more C to be fixed per unit of fixed N_2 leading to a higher e-ratio. A proportionally higher N remineralization following high PP and N_2 fixation rates is supported by similar findings in the western North Pacific warm pool (Shiozaki et al., 2013)."*

Referee: Recent study showed that DDA contributed to export production efficiently (Karl et al., 2012, PNAS). Meanwhile, the present study indicated that the production driven by UCYN-C was more efficient to promote export production than by DDA (P4293, L4-5). What environment makes UCYN-C flourish? Is this result consistent with the result of Karl et al. (2012)?

Response: Here we show a tight coupling between N_2 fixation and N export when DDAs dominated the diazotrophic community. This suggests a direct sink of the DDAs which is in good agreement with Karl et al. (2012) findings. Alternatively, when UCYN-C dominated, the use of DON and an enhanced remineralization of N led to a higher export production efficiency. We cannot conclude that UCYN-C are intrinsically more efficient to promote export production than DDAs. However, we propose that the flourishing of UCYN-C have triggered directly or indirectly the process that has enhanced the export. The ecology of UCYN-C is not well constrained and the factor controlling their development are poorly understood. This is discussed in a companion paper under submission in the VAHINE special issue (Turk et al, 2015).

Specific comment

Referee: P4275 L15 Correct to N2 fixation.

Response: It has been corrected in the new version.

Referee: P4290 L8 The unit of nitrate concentration is nM here. But that is µM in P4285 L2,3. The authors should use unit consistently.

Response: All the units of concentration are now expressed in µmol L^{-1}

Referee: P4290 L10 Jickells et al (2005) is not appropriate reference here.

Response: The reference has been deleted

Referee: P4292 L1-5 This discussion seems not to fit the context.

Response: The discussion has been modified as follows: "*Assuming that DON and N_2 fixation are the only possible sources of N in the mesocosms, we calculated that a DON use of 0.9 µmol L^{-1} would have supported up to 78 % of the PON production during P2, and potentially fueled the PON export to the same extent. This is in agreement with Torres-Valdes et al. (2009) and Letscher et al. (2013) who showed that DON pool is a dynamic contributor of the N cycle able to supports up to 40 % of the vertical PON export in the oligotrophic gyres of the Pacific and Atlantic Oceans.*"

Referee: P4294 "the diazotrophs are known to over-fix C relative to N" Need citation.

Response: The reference Mulholland et al. (2007) has been added (Mulholland, M.: The Fate of nitrogen fixed by diazotrophs in the ocean, Biogeosciences, 4, 37–51,doi:10.5194/bg-4-37-2007, 2007)

Anonymous Referee #2:

Specific comments

Referee: P4278, L13: do the authors mean phosphorous instead of phosphate? DIP is a commonly used abbreviation for dissolved inorganic phosphorous. Phosphate is in fact a form of this DIP, so this abbreviation seems redundant. If authors mean DIP in its original meaning please change phosphate by phosphorous. Otherwise, consider using PO4 instead. And apply these changes to the whole text.

Referee: P4278, L15: again, it is confusing that P is used for phosphate, as it is the name of the element. Please use PO4 or something similar instead.

Response: It is clear that phosphate (oxidation degree V) is by far the most important component of the "Phosphorous cycle" and that most of natural inorganic and organic compounds, in dissolved and particulate forms, contain phosphate group (H_3PO_4, ATP, ADP, Phospholipids, Glucose-6 phosphate…). It would be of great interest to speak about the Phosphate cycle and not the Phosphorous cycle. The Phosphorous in an element spontaneously oxidized which cannot exist in this elemental form in water. Nevertheless, we understand that it is confusing that P is used for phosphate, as it is the name of the element. We have replaced in the text DIP by phosphate* (PO_4^{3-}) and define DOP by dissolved organic phosphorous.

*Whatever the method currently used, the basis for phosphate measurements in seawater is the Murphy and Riley method (A modified single solution for the determination of phosphate in natural waters, Analytica Chimica Acta, Volume 27, Pages 31-36, 1962).

Referee: P4280, L13: please do not use unexplained abbreviations in section headers, write the complete term and add the acronym in parentheses, especially when it is not the commonly used one as DIP for dissolved inorganic phosphate. This helps the reader to skip through the sections without coming back to look for the meaning of the acronym. Do the same in the next headers whenever necessary.

Response: We deleted all the abbreviations in the headers

Referee: P4280, L17: Please could the authors explain why adding an excess of KH2PO4 stops PO4 assimilation? Is it an effect of dilution of the tracer?

Response: The addition of KH_2PO_4 is performed in order to dilute the tracer. The explanation has been added in the text as follow: "*Incubations were stopped by adding 50 µL of KH_2PO_4 solution (10 mmol L^{-1}) in order to reduce to a minimum the ^{33}P assimilation by dilution effect […]*".

Referee: P4286, L9: please explain what the authors mean with "increased faster". It is slightly ambiguous, it suggests a sharp change that it not so obvious looking at the graph.

Response: A sharp change occurred in M3 but is not obvious in M1, M2. The sentence has been modified by "*PP continued to increase*" in order to include the PP evolution in all mesocoms.

Referee: P4286, L19: the reviewer wonders if the authors consider that this figure is essential? Does it add to the information in the text? As most of the information of this figure is given or could be given in the text, is it essential to keep this fig 2 and the next fig 7?

Referee: P4288, L25-23: this sentence is unnecessary, the information is in the figure caption and the e ratio was defined in the previous sentence, simply add (Fig. 7) to the previous sentence, please. And again, is it essential to use this graph, given that more of its information is in the text?

Response: We agree that figures 2 and 7 do not add supplementary information and have thus been deleted. In the text, we added the size of the population after the p value when the statistical difference between P1 and P2 is tested *"(p<0.05, n=57)*".

Referee: P4290, L8: units of nitrate in nM, however, measurements were made in µM, as explained in the methods section (P4285) and in the results section (P4285). The authors should try to be consistent with units through the text.

Response: All the unit of concentrations are now expressed in µmol L^{-1}.

Referee: P4290, L10: Jickells et al (2005) does not apply here. Pathways of atmospheric nitrogen deposition are not only limited to dust, like Fe, which is exactly the scope of this study.

Response: The reference has been deleted.

Referee: P4291, L21 to P4292, L10: the argumentation of this part is difficult to follow. It is very difficult to grasp the different arguments supporting that the DON pool produced or maintained in the previous part of the experiment (P1) is now supporting part of the production of PON in addition to N2 fixation, and thus supporting the export of organic matter. Relating the effect of a lateral transport of DON to a close system seems difficult to fit in order to explain this argument.

Response: The conditions for the DON mobilization and the potential DON users are discussed in section 4.3. From P4291, L21 to P4292, L10 we showed the evidences of the DON consumption. As it was difficult to follow, we modified the paragraph as follows:" *During P2, the increase in PON concentrations (Fig. 3B) suggests that part of the freshly produced biomass remained in the water column. The accumulation of PON probably favored remineralization processes, explaining the increase in* NH_4^+ *concentrations. This may have enhanced the transfer of the recently fixed* N_2 *to the non diazotrophic plankton as demonstrated by Bonnet et al. (2015a) and explains the development of picocyanobacteria during P2 (Leblanc et al., 2015). Additionally, the total amount of N provided by* N_2 *fixation did not account for all the exported PON during P2 (Fig. 6), implying that an additional N source played a significant role in promoting the export. The only alternative N source is DON which, indeed, exhibited a significant decrease in concentration of 0.9 ± 0.7 µmol L-1 in the mesocosms during P2 (see section 4.3 for further discussion on DON consumption). Assuming that DON and* N_2 *fixation are the only possible sources of N in the mesocosms, we calculated that a DON use of 0.9 µmol* L^{-1} *would have supported ~78 % of the PON production during P2,* *and potentially fueled the PON export to the same extent. This is in agreement with Torres-Valdes et al. (2009) and Letscher et al. (2013) who showed that DON pool is a dynamic contributor of the N cycle able to supports up to 40 % of the vertical PON export in the oligotrophic gyres of the Pacific and Atlantic Oceans. A quantification of the diazotrophs in the sediment traps, performed on day 19, shows that ~10 % of the UCYN-C biomass in the mesocosms was exported this day, explaining ~ 7 % of the PON export (Bonnet et al., 2015a). Thus, the recently fixed N_2 by UCYN-C can directly be exported but is probably more efficiently transferred to non diazotrophic plankton through remineralization processes.*

Referee: P4292, L24-27: This sentence is incomplete or has some extra particles, probably it should say "at LEAST 20

Response: The sentence has been replaced by: "*Bonnet et al. (2015a) demonstrated that ~ 10% of the recently fixed N_2 during P2 was transferred toward non diazotrophic plankton i.e. in picoplankton and bacteria*".

Referee: P4294, L15: why do the authors relate a canonical Redfield ratio (6.6) with a cite of Fukuda et al (1998)?

Response: The Fukuda et al paper's show that the averaged C/N ratio was equal to the Redfield ratio in bacteria specifically. We modified the text as follow: "*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 <u>in bacteria cells (</u>*Fukuda et al. 1998*), we calculated that bacterial respiration would have led to a DON consumption of 0.2 to 0.7 µmol L-1 during P2.*"

Technical corrections

Referee: P4275, L15: please correct "v fixation".

Response: It has been replaced by "*N_2 fixation*".

Referee: P4276, L12: the term "alighted" is referred to fire, may the authours mean "lit up" instead?

Response: "Alighted" has been replaced by "photic"

Referee: P4277, L23: please change "If heterotrophic although…" by "Although heterotrophic bacteria…."

Response: The correction has been applied

Referee: P4278, L6: please add "export, AND (2) to trace…."

Response: The correction has been applied

Referee: P4280, L7: please add “organic” to “dissolved matter” to be consistent with other sections.

Response: The correction has been applied

Referee: P4281, L11-14: please re write the sentence “Incubation bottles…for 24h”. It is a bit too long and wordy sentence, difficult to understand.

Response: The sentence has been replaced by: “*Incubation bottles were then amended with 5 % (vol:vol) of* $^{15}N_2$ *enriched seawater and closed without headspace with silicone septum caps. The latter were incubated on an in situ mooring line close to the mesocosms at the appropriate sampling depths for 24 h.*”

Referee: P4281, L14: delete of in “After of incubation”. It should say, “after incubation”

Response: The correction has been applied

Referee: P4283, L14: correct “…DON and DOP, respectively”.

Response: The correction has been applied

Referee: P4283, L17: add “were found to be A negligible source OF particulate….”

Response: The correction has been applied

Referee: P4284, L10-13: please re write this sentence, it is slightly wordy and takes some readings to get through it.

Response: The sentence has been replaced by:” *The values of fluxes and concentrations presented in the text are averaged over the three depths (no significant differences between depths have been evidenced, paired Friedman test,* $\alpha=0.05$*).*”

Referee: P4284, L18: correct, “according TO the propagation of errors”.

Response: The correction has been applied

Referee: P4284, L24: please consider changing “similarly inside the mesocosms and in surrounding waters”. The sentence looks incomplete, awkward, as it needs a verb.

Response: The sentence has been replaced by:”*Briefly, seawater temperature increased inside the mesocosms and in surrounding waters from 25.5 to 26.7°C over the course of the experiment.*”

Referee: P4285, L8-10: another wordy sentence, too long, please try to re write.

Response: The sentence has been separated in two sentences: “*The day after the fertilization,* PO_4^{3-} *concentrations reached 0.08 µmol* L^{-1} *in all mesocosms. Then, the* *concentrations decreased steadily, tending to initial concentrations (0.02-0.08 µmol L^{-1}) at the end of the experiment."*

Referee: P4285, L15: try to keep consistency between figures and the mention in the text, change Fig. 1a. Use upper case for A in the text or change the A in the figure to a lower case. The same for the rest of figure mentions through the text.

Response: The upper case (Fig. 1A) is now used through the whole text

Referee: P4285, L23: add (PP) after primary production.

Response: The correction has been applied

Referee: P4285, L25: 7.3 nM d-1. This is an awkward way of expressing a rate, it might be confusing for many readers. It is commonly accepted to write all the units in rates, please change rates in the text to a format like nmol L-1 d-1 (as it was used in P4282,L5).

Response: The rates are now expressed in nmol L^{-1} d^{-1}.

Referee: P4288, L8: correct, "DON dynamicS".

Response: The correction has been applied

Referee: P4288, L10-12: wordy, please re write the sentence, "decreased of" in this context is confusing.

Response: The sentence has been separated in two sentences: "*After these days, DOP concentrations significantly decreased ($p< 0.05$) and reached 0.09 ± 0.01 µmol L^{-1} on average. DOP concentrations also decreased in surrounding waters from day 18 but to a lesser extent than in the mesocosms.*"

Referee: P4288, L17: delete at, "during P1 averaging at…"

Response: The correction has been applied

Referee: P4288, L18: comma before respectively. This happens through the text in several occasions, please, correct all of them.

Response: We added a comma before each "respectively".

Referee: P4288, L19: change to "M1 were higher than THOSE in…"

Response: The correction has been applied

Referee: P4288, L23: re write "much more stochastic", too informal and vague.

Response: The sentence has been replaced by:"*The daily POP_{export} ranged from 1.0 to 18.4 nmol L^{-1} d^{-1}."*

Referee: P4289, L1: "… integrated over P1 WERE…" (rates…were).

Response: The correction has been applied

Referee: P4289, L1: "… all the mesocosms, AND DID not significantly differ from"

Response: The correction has been applied

Referee: P4289, L3: "the resulting change ON the…"

Response: The correction has been applied

Referee: P4289, L7-8: "…but deviated negatively from 0… FROM day 19 TO day 23"

Response: The correction has been applied

Referee: P4289, L8: "Thus, even though…" Please re write this, too wordy.

Response: The sentence has been modified: *"At the end of P2, the decrease of the TN_{calc} pool was 0.20 ± 0.04 µmol L^{-1}."*

Referee: P4289, L9: delete of in "the TNcalc pool decreased of…."

Response: The sentence has been modified has suggested in the previous comment.

Referee: P4291, L5: change "trough" by "through". This is repeated through the discussion, please check all the misspellings and correct them.

Response: This change has been applied through the whole text.

Referee: P4294, L19-22: please, re write this sentence, wordy, difficult to understand. Add a cite to the first argument (diazotrophs over-fix C).

Response: The sentence has been modified as follow: "*Diazotrophs are known to over-fix C relative to N (Mulholland et al., 2007), which may explain why the POC:PON ratio was above the Redfield ratio during the experiment. The resulting N deficit for bacterial mineralization may have been found in the labile or semi labile DON pool. This hypothesis is supported by Van Wambeke et al. (2015) who showed that BP was limited by N availability."*

Referee: Figures. Please do not use unexplained acronyms and abbreviations in figures captions, do write the whole term before adding the acronym, e.g. DDAs, PP... Figures should be self-contained, so anyone looking at them without reading the text can understand them. Consider joining both boxplots in one figure.

Response: We remove (or define) all the acronyms and abbreviations in the figure captions. The two box plots have been deleted.

The discussion and the conclusions have been modified has follows:

4. Discussion

4.1. Phosphate availability sustained N_2 fixation and in turn new primary production

N_2 fixation is limited by micronutrients 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), light (Garcia et al., 2013; Kranz et al., 2010) and ultimately by PO_4^{3-} availability (Dore et al., 2008; Karl et al., 1997; Moutin et al., 2008). During this experiment, PO_4^{3-} fertilization was carried out as P limitation would have prevented diazotrophs growth. This fertilization associated with the relatively high micronutrient concentrations (e.g. Fe) (Ambatsian et al., 1997), high seawater temperature (>25 °C) and the maintenance of the water mass in the photic layer, provided optimal conditions for diazotrophs growth. As expected, diverse diazotroph phylotypes developed extensively in the mesocosms with abundances of 1.10^5 to 5.10^5 nifH copies L^{-1} (Turk et al., 2015). Furthermore, N_2 fixation rates in the mesocosms were high (18.5 ± 13.1 nmol N L^{-1} d^{-1}) compared to those in surrounding waters (9.2 ± 4.8 nmol N L^{-1} d^{-1}) (Fig. 1B) and are among the highest reported in the literature (Luo et al., 2012).

The contribution of N_2 fixation to PP (10.8 ± 5.0 %) in the mesocosms and in surrounding waters (5.7 ± 2.0 %) was in the upper range of previous studies in the Pacific Ocean (Raimbault and Garcia, 2008; Shiozaki et al., 2013) and the Mediterranean Sea (Bonnet et al., 2011; Ridame et al., 2013). Prior to PO_4^{3-} fertilization, NO_3^- concentrations were <0.04 µmol L^{-1}. As there was no external supply of NO_3^-, the potential consumption of the initial NO_3^- in the mesocosms represented <11.5 % of the integrated N_2 fixation rates over P1 and P2 (0.35 ± 0.08 µmol L^{-1}) (Fig. 6A). Thus, N_2 fixation supplied nearly all the new production during the experiment. These results indicate that in a N depleted system, diazotrophs can provide enough new N to sustain high PP (exceeding 2 µmol C L^{-1} d^{-1}) and biomass (up to 1.42 µg L^{-1} of Chl a*), as long as PO_4^{3-} 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 comparing the export efficiency of different diazotrophs reports that DDAs blooms could contribute up to 44 % of the direct export in the North East Pacific, while UCYN (Group A) and Trichodesmium *spp. could account for only 0 to 10 % of the export (White et al., 2012). The scarcity of data is due to methodological issues associated with the use of sediment traps in the open ocean due to (1) the patchy distribution of N_2 fixers that are not necessarily collected by the sediment traps, and (2) the temporal lag between the production and the export which is difficult to assess (Nodder and Waite, 2001). The mesocosm approach was designed to overcome these experimental limitations. The shallow depth of* *the traps (~15 m) and the absence of NO_3^- normally supplied via the nitracline prevent any comparison with open ocean studies. Nevertheless, the mesocosm approach enables a comparison of the export efficiency under contrasting ecological situations. In this case, the period dominated by DDAs (P1) is compared with the period dominated by UCYN-C (P2).*

During P1, the biomass was stable in the mesocosms and the amount of recently fixed N_2 was equal to the amount of exported PON, suggesting a tight coupling between the two processes (Fig. 6). It has been shown that large aggregates of the diatom Rhizosolenia *spp., representing the majority of DDAs during P1 (Turk et al., 2015), can sink at high rates (Villareal et al., 1996). This suggests that during this experiment, the recently fixed N_2 by DDAs remained within the symbiotic association and was quickly exported in the settling particles. This agrees with Karl et al. (2012) who showed that DDAs support the export pulses regularly observed in late summer in the tropical North Pacific Ocean.*

During P2, the increase in PON concentrations (Fig. 3B) suggests that part of the freshly produced biomass remained in the water column. The accumulation of PON probably favored remineralization processes, explaining the increase in NH_4^+ concentrations. This may have enhanced the transfer of the recently fixed N_2 to the non diazotrophic plankton as demonstrated by Bonnet et al. (2015a) and explains the development of picocyanobacteria (Leblanc et al., 2015). Additionally, the total amount of N provided by N_2 fixation did not account for all the exported PON during P2 (Fig. 6), implying that an additional N source played a significant role in promoting the export. The only alternative N source is DON which, indeed, exhibited a significant decrease in concentration of 0.9 ± 0.7 µmol L^{-1} in the mesocosms during P2 (see section 4.3 for further discussion on DON consumption). Assuming that DON and N_2 fixation are the only possible sources of N in the mesocosms, we calculated that a DON use of 0.9 µmol L^{-1} would have supported ~78 % of the PON production during P2, and potentially fueled the PON export to the same extent. This is in agreement with Torres-Valdes et al. (2009) and Letscher et al. (2013) who showed that DON pool is a dynamic contributor of the N cycle able to supports up to 40 % of the vertical PON export in the oligotrophic gyres of the Pacific and Atlantic Oceans. A quantification of the diazotrophs in the sediment traps, performed on day 19, shows that ~10 % of the UCYN-C biomass in the mesocosms was exported this day, explaining ~ 7 % of the PON export (Bonnet et al., 2015a). Thus, the recently fixed N_2 by UCYN-C can directly be exported but is probably more efficiently transferred to non diazotrophic plankton through remineralization processes.

The contrast between P1 and P2 is also observed using the e-ratio. The production driven by UCYN-C was more efficient in promoting POC export than the production driven by DDAs. During P1, it is probable that the recently fixed C by DDAs remained within the symbiotic association and sunk with the recently fixed N_2 constituting a direct and net C export. During P2, the higher efficiency of C export strongly suggests that the DON ultimately fueled PP which, in turn, increased POC export. Additionally, when UCYN-C dominated, an enhanced N *remineralization may have enabled more C to be fixed per unit of fixed N_2 leading to a higher e-ratio. A proportionally higher N remineralization following high PP and N_2 fixation rates is supported by similar findings in the western North Pacific warm pool (Shiozaki et al., 2013).*

4.3. The unexpected high dissolved organic matter consumption

The use of dissolved organic compounds and their implications on PP in the open ocean has long been demonstrated (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) and in the Atlantic Ocean (Lomas et al., 2010; Mather et al., 2008) and generally occurs under PO_4^{3-} limitation. In this study, the decrease in DOP concentrations during P2 occurred when T_{PO4} reached the lowest levels, confirming the ability of the planktonic community to use DOP under low PO_4^{3-} availability. More surprisingly, the significant and rapid decrease in DON concentrations (Fig. 4) observed during the development of UCYN-C (P2) in the mesocosms was associated with a rapid increase in PP (Fig. 1C), biomass (Figs. 2 and 3) and bacterial production (BP) (Van Wambeke et al., 2015), suggests high consumption of DON directly or indirectly by primary producers. In the open ocean, DON is 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). In this study, we propose three hypotheses that could explain the observed decrease in DON concentrations during P2: (i) bacterial mineralization of DON triggered by high PP, (ii) direct uptake of DON by primary producers including UCYN-C and (iii) abiotic photo-degradation of DON into NH_4^+.

(i) The increase in PP driven by high N_2 fixation rates during P2 led to an increase in bacterial production (Van Wambeke et al., 2015). The significant negative correlation between BP and DON concentrations (Spearman rank correlation, $r=-0.35$; $p< 0.001$) indicate significant consumption of DON by bacterial mineralization. Diazotrophs are known to over-fix C relative to N (Mulholland et al., 2007), which may explain why the POC:PON ratio was above the Redfield ratio during the experiment. The resulting N deficit for bacterial mineralization may have been found in the labile or semi labile DON pool. This hypothesis is supported by Van Wambeke et al. (2015) who showed that BP was limited by N availability in the mesocosms during the experiment. Based on BP data and assuming a bacterial growth efficiency of 10 to 30 % (del Giorgio and Cole, 1998) and a C:N ratio of 6.6 in bacteria cells (Fukuda et al., 1998), bacterial respiration would have led to a DON consumption of 0.2 to 0.7 µmol L^{-1} during P2, supporting at least part of the DON removal of ~0.9 µmol L^{-1} reported here.

(ii) An alternative explanation for the decrease in DON concentrations is direct consumption by primary producers. Cyanobacteria are known to use DON compounds such as urea (Collier et al., 2009; Painter et al., 2008) to such an extent that DON has been reported to be the main source of N fueling cyanobacterial blooms in coastal waters (Glibert et al., 2004). The DON decrease occurring during the development of UCYN-C, whose abundances reached

5.10^5 nifH copies L^{-1} (Turk et al., 2015), questions their ability to use DON to meet their N requirements. Direct uptake of glutamate and amino acids (constitutive components of the DON pool) has been reported in natural and laboratory populations of Trichodesmium *spp. (Mulholland and Capone, 1999; Mulholland et al., 1999). Furthermore, large decrease in DON concentrations were observed after blooms of the diazotroph* Aphanizomenon ovalisporum *in Lake Kinneret (Berman, 1997). The hypothesis of a direct use of DON by* A. ovalisporum *was confirmed in culture experiment where the development of this diazotroph was stimulated by DON additions (Berman, 1997, 1999). To our knowledge, no direct uptake measurements of DON compounds have been performed on UCYN. However, the ureA gene implicated in the urea assimilation has been identified in the cyanobacterial diazotrophic strain* Cyanothece *PCC 7822 (Bandyopadhyay et al., 2011) closely related to the UCYN-C cluster. These pieces of evidences suggest that in addition to N_2 fixation, UCYN-C might be able to use the DON pool to meet their N requirements.*

(iii) Finally, photo-degradation could be a possible sink of DON in surface waters (Bronk, 2002). A field study performed in the ultraoligotrophic eastern basin of the Mediterranean Sea indicates a production of NH_4^+ from DON of 0.2-2.9 nmol N L^{-1} d^{-1} in surface waters (Kitidis et al., 2006). Taking into account the highest rates reported above, this process cannot explain more than 10 % of the observed DON removal. Moreover, the DON decrease occurred only during P2 whereas photo-degradation would be occurring continuously over the experiment.

The first two hypotheses (i and ii) are more likely to explain the DON decrease during P2. None of these two hypotheses can be excluded even though direct proof of large uptake of DON by UCYN-C is lacking. Thus, in this study the DON use was directly or indirectly triggered by the UCYN-C activity.

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. The fate of the recently fixed N appears to be closely related to the diazotrophic community involved in N_2 fixation. A strong coupling of N_2 fixation and PON export occurred when DDAs dominated the diazotrophic community suggesting their direct export. When the community was dominated by UCYN-C, biomass accumulation was observed together with an efficient particulate export. A significant decrease in DON concentrations was observed during the same period indicating a direct or indirect use of DON by UCYN-C. Thus, in addition to fueling primary production, UCYN-C appear to be 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 suggest that

DON has to be considered as a dynamic pool in LNLC areas as it may provide significant amounts of N and contribute significantly to particulate export.