We greatly thank Referee #1 and #2 for their constructive comments and suggestions that we were pleased to answer during this revision process. All of them are detailed in the current .pdf file which contains :

1) **The response to the Referee 1 comments**

2) **The response to the Referee 2 comments**

3) **The revised manuscript with modifications highlighted in blue**

4) **The supplementary material added to the revised manuscript**

1 General comments

The authors compare two 1D simulations only differing in the presence of diazotrophy to examine the role of N fixation for plankton production and biogoechemical cycles in observations in the Western Tropical South Pacific. While this aim of the study is given at in the introduction and the simulations presented are well suited to address this aim, in their interpretation of the results the authors claim to show the control of preferential P regeneration (a model assumption that is not tested) on N fixation. In my opinion, the simulations necessary to justify this latter claim are not provided. The results are very interesting and relevant to the current discussion on N fixation, and the underlying processes identified seem reasonable, but either the interpretation needs rephrasing or additional simulations need to be presented to acknowledge the causality implied by the study setup. Affected sections are identified in detail below. Furthermore, some validation of the simulated physics (MLD) on the seasonal scale would be needed to give confidence in the validity of the results.

1. Does the paper address relevant scientific questions within the scope of BG? yes

2. Does the paper present novel concepts, ideas, tools, or data? yes

3. Are substantial conclusions reached? yes, but see below.

4. Are the scientific methods and assumptions valid and clearly outlined? partly. The design of the model study appears valid, but the way the interpretation of the results is phrased suggests a different cause and effect than the study design. Take, for example, the authors' claim in the abstract and the discussion that they "evidenced that the nitracline and phosphacline had to be respectively deeper and shallower than the Mixed-Layer Depth (MLD) .. [to create] ... favourable conditions for the development of diazotrophs" (p1,l8-11) and "concluded that a preferential regeneration of the detrital phosphorus (P) matter was necessary to obtain this gap between the nitracline and the phosphacline depths ..." (p1,l11-13). But neither the depth of the nutriclines nor the preferential P regeneration are manipulated in the simulations presented. Causality here goes the other way, in my opinion: the authors set up a system with preferential P regeneration and then show how N fixation creates different biogeochemical regimes.

The aim of our study was to investigate the role of nitrogen fixation in the biogeochemical contrast observed between the Western area (WMA) and the eastern area (WGY) of the WTSP by running two simulations, one representing WMA and the other WGY. For this, we first had to verify whether physical forcings were different in WMA and WGY and could explain part of this contrast between the two regions. When compared, atmospheric forcings and *in situ* mixed layer depths at WMA and WGY turned out to be very similar, which allowed us to use the same physical forcings for both simulations (we arbitrarily choose the forcings extracted at WMA). Furthermore, with the purpose of characterizing the role of diazotrophy in the contrast between WMA and WGY, the two simulations were designed so as to only differ by the presence or not of nitrogen fixers (present in WMA and absent in WGY). The two simulations simWMA and simWGY were run but they could not successfully represent WMA and WGY data unless modifying a feature of the biogeochemical model in order to reproduce the discrepancy between the nitracline and the phosphacline. In situ data indeed showed a nitracline deeper than the MLD (while the phosphacline is shallower) thereby allowing the input at the sea surface of P (but not N) from depth during winter mixing. To reproduce the nutriclines discrepancy, the only process-based lever in our model lied in the preferential regeneration of the P particulate matter, as this has already been measured in other regions. With this feature, the different biogeochemical fluxes and pools in WMA and WGY could have been well represented by the model, which allowed us to investigate the role of N2 fixation in the oligotrophy gradient observed in WTSP.

Nonetheless, we agree that more details and figures are necessary to illustrate the impact of this preferential P regeneration, and this point will be detailed in the specific comment "**causality between N fixation and preferential P regeneration".**

5. Are the results sufficient to support the interpretations and conclusions? no. The simulations required to show the control of P availability on N fixation as claimed (e.g., additional simulations without preferential P regeneration), are mentioned in the discussion as preliminary (p11,l34 - p12,l1), but are not shown. Either the interpretation needs to change from "control of P availability on N fixation" to "effects of N fixation on nutricline and seasonality", or additional simulations need to be provided.

We agree and decided for the sake of clarity to add the figures presenting the results from the simulation without preferential P regeneration, as detailed below in the specific comments "**causality between N fixation and preferential P regeneration".**

6. Is the description of experiments and calculations sufficiently complete and precise to allow their reproduction by fellow scientists (traceability of results)? no. The study refers to previous studies (Gimenez et al. 2016 - G2016, Alekseenko et al. 2014 - A2014) for all equations and parameter values, stating that "for all the non-diazotrophic features, TRI are parameterized as 100 PHYL cells ... and UCYN as PHYS." (p4, l20-21). Yet both references differ in some of the parameter values. Yet G2016 give specific mortality rates of UCYN as $1.16 \ 10^{-6} \ s^{-1}$ compared to $1.16 \ 10^{-7} \ s^{-1}$ for PHYS (A2014), and the max. growth rate of TRI as $2.08 \ 10^{-6} \ s^{-1}$ compared to $2.3 \ 10^{-5} \ s^{-1}$ for PHYL (A2014). This is confusing, although maybe not the fault of the authors: What is a typo, what is related to the conversion of values for TRI as 100 PHYL cells, which values are used in the present study?

Regarding the specific mortality rates, the value used for UCYN is the same as the one used for PHYS, namely $1.16 \ 10^{-6} \ s^{-1}$. We confirm that there is a typo error in A2014 which also used the same mortality rate for PHYS (i.e. $1.16 \ 10^{-6} \ s^{-1}$). Actually, the Eco3M-Med model firstly used and detailed in A2014 was then used by Guyennon et al. (2015)-G2015 and then used for our study. Obviously, during each of these works, additional reflexion and validation works led to some modifications and improvements regarding the model equations or parameters. For the sake of clarity, we propose here to provide our up-to-date complete set of parameter values in an additional table included in supplementary material (SM).

Regarding the TRI growth rate, we agree that the value reported in the manuscript is not well justified. In agreement with literature (e.g. Luo et al., 2012), we have considered in the model that a trichome of TRI was equivalent to 100 PHYL cells. This conversion factor between PHYL and TRI parameters was only applied for the "extensive parameters". Here extensive is used in the thermodynamic sense, and refers to the properties depending on the system size or the amount of material in the system. Since the specific growth rate is not an extensive property, this conversion factor was not applied to the specific growth rate of TRI, but we didn't use either the PHYL growth rate. Instead, we used a lower growth rate for TRI than for PHYL as suggested by experimental work: due to the filamentous shape of a trichome, a particular process for cell division is indeed observed in TRI. During their study on cell division in *Trichodesmium erythraeum* IMS101, Sandh et al. (2009) showed that "division never took place synchronously in the whole filament, but was restricted to small groups of cells that spread along the filaments" and that "the proportion of dividing cells, out of the total number of cells, varied from 5% to 20%". We therefore used the value of 0.17 d-1, which was averaged from values reported in the literature (Mulholland and Bernhardt, 2005, Hutchins et al., 2007).

We propose to clarify the part regarding the parameterization of diazotrophs (section 2.2.1) by adding :

"[..] For all the non-diazotrophic features and in agreement with literature (e.g. Luo et al., 2012), it has been considered that a Trichodesmium trichome was containing 100 PHYL cells and that a UCYN cell was equivalent to a PHYS cell. Yet, the conversion factor of 100 between TRI and PHYL was only applied for extensive parameters, i.e. those depending on biomass. Intensive parameters were set equal to those of PHYL, except for the specific growth rate which was instead averaged from literature since it has been experimentally demonstrated that it was lower than that of PHYL (Mulholland and Bernhardt, 2005, Hutchins et al., 2007). Parameter values, whether new or differing from those of Alekseenko et al. (2014), are given in SM: table 1."

7. Do the authors give proper credit to related work and clearly indicate their own new/original contribution? yes.

8. Does the title clearly reflect the contents of the paper? it reflects the study setup, but not the interpretation/conclusions drawn from it.

We propose to change the title by : "Diazotrophy as the main driver of the oligotrophic gradient in the Western Tropical South Pacific Ocean : results from a one-dimensional biogeochemical-physical coupled model".

9. Does the abstract provide a concise and complete summary? it needs rephrasing to fit the study design

The following sentence has been added to the abstract:

"Since physical forcings in both regions were very similar, it was considered that the oligotrophic gradient observed *in situ* between WMA and WGY was not explained by differences in physical processes but rather by differences in biogeochemical processes. A one-dimensional physical-biogeochemical coupled model was thus used to [...]»

10. Is the overall presentation well structured and clear? yes

11. Is the language fluent and precise? yes, only in few sections a bit redundant

12. Are mathematical formulae, symbols, abbreviations, and units correctly defined and used?

yes. some minor inconsistencies are pointed out below.

13. Should any parts of the paper (text, formulae, figures, tables) be clarified, reduced, combined, or eliminated? the abstract, discussion and conclusion should be brought in line with the simulations/results presented.

The different comments and questions raised during the revision process enabled us to improve the different sections of the paper in order to better present and highlight our main results and conclusion. All the modifications are presented in red in this current review response. They concern additional details on the nutriclines discrepancy due to a preferential regeneration of the P particulate matter : new figures have been added in the revised manuscript to better illustrate the model sensitivity (and especially on the N2 fixation rates) to this preferential P regeneration. The new figures and new sections associated are detailed in the specific concern "causality between N2 fixation and preferential P regeneration". We also improved the justification of our modeling strategy regarding the physical forcings implemented in the 1VD physical model by providing additional sections in the revised manuscript and figures in a supplementary material (details in the 1st specitic comment).

14. Are the number and quality of references appropriate? yes

15. Is the amount and quality of supplementary material appropriate? a supplement could clarify which parameter values were used (cf. no. 6 above)

We agree with Referee #1 and added a supplementary material to our article with the list of parameters used in our study and some additional figures.

2 Specific comments

1. p3, l24-27:

(a) you use two simulations identical in forcing and physics to simulate two locations about 40 deg. longitude apart with different biogeochemical characteristics. Is it justified to apply the same physics and forcing to both locations? If so, could you provide evidence for this, e.g. observations? It this choice compromising the fit between model and observations for station WGY?

As this point was also mentioned by Referee #2, the same answer is given to both of them as follows :

We will first detail our choice of using the same physic forcing and then propose some new sentences which will be added to the revised manuscript in order to better justify our strategy.

Our modeling strategy came from the observation that the WTSP was characterized by a significant biogeochemical gradient in terms of nutrient availability and planktonic production, which seemed to be directly related to the presence or not of nitrogen fixers inside this area (Moutin et al., 2018). In order to confirm or not this assumption through a modeling study, we designed two simulations only differing by the presence or not of diazotrophy. This was made possible only by the fact that, despite the large distance between WMA and WGY, the physical forcings were shown to be similar in the two regions. The question of whether the atmospheric forcings in WMA and WGY were similar enough to consider that their impact on the water column dynamics was the same arose very early in our reflexion. In that purpose, at the early stage of this study, we compared the atmospheric forcings calculated at WMA and WGY by the atmospheric model WRF (see figure below). This comparison shows that there is no significant difference between both forcings. To go further, we also compared two simulations only differing by the atmospheric forcing (respectively extracted in the two WMA and WGY regions) and did not observe differences nor in the water column dynamics, neither on biogeochemical cycles or on the trophic food web. Finally, in situ climatological data of MLD (Fig. 1) also indicate that there is no significant difference between the dynamics of these two regions despite their distance. We thereby decided to use the atmospheric forcing from the WMA region for both regions and the simulated MLD predicted by our model fits well with values obtained with climatology (Fig. 1). We acknowledge that this could have been further detailed in the submitted manuscript and propose to add the following text in the revised manuscript and the figure below in the supplementary material :

« The assumption made by using a unique set of atmospheric forcings for two regions significantly far away is first based on the *in situ* climatological data reported in Moutin et al. (2018). These authors showed that the vertical dynamics of the

water column, and especially the depths of the mixed layer were similar throughout the year in all the WTSP (see Figure SM1 in supplementary material). In addition, the atmospheric forcings calculated by the WRF atmospheric model at WMA and WGY were also very similar (see figure SM2 in supplementary material). Furthermore, we also compared two simulations ran with the respective atmospheric forcings calculated at WMA and WGY and did not observe any significant difference, nor in the water column dynamics, neither on the biogeochemical cycles. »
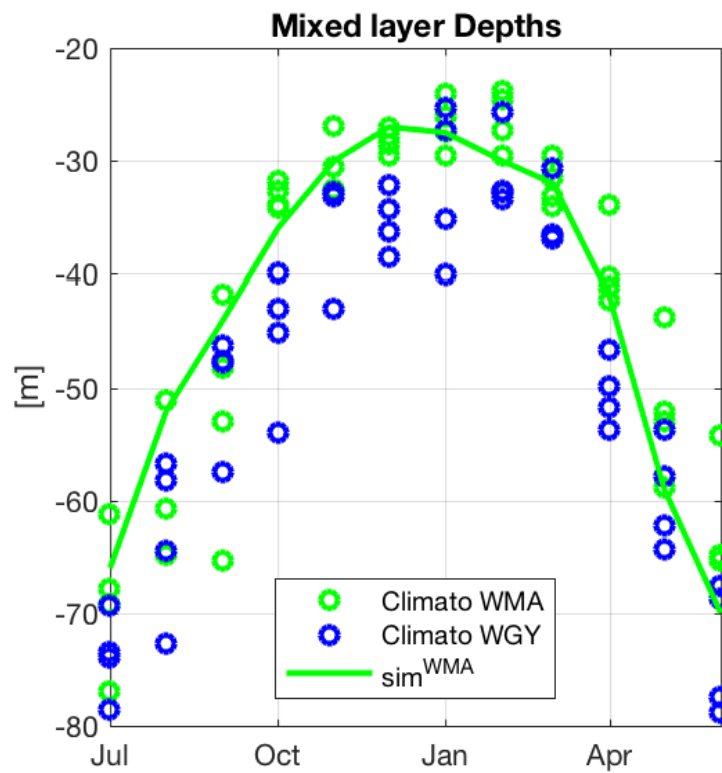

Figure 1 (in SM) Temporal dynamics of the *in situ* mixed layer depths estimated using a climatology (de Boyer Montégut et al., 2004) at WMA (green circles) and WGY (blue circles), and simulated by the model (green line)
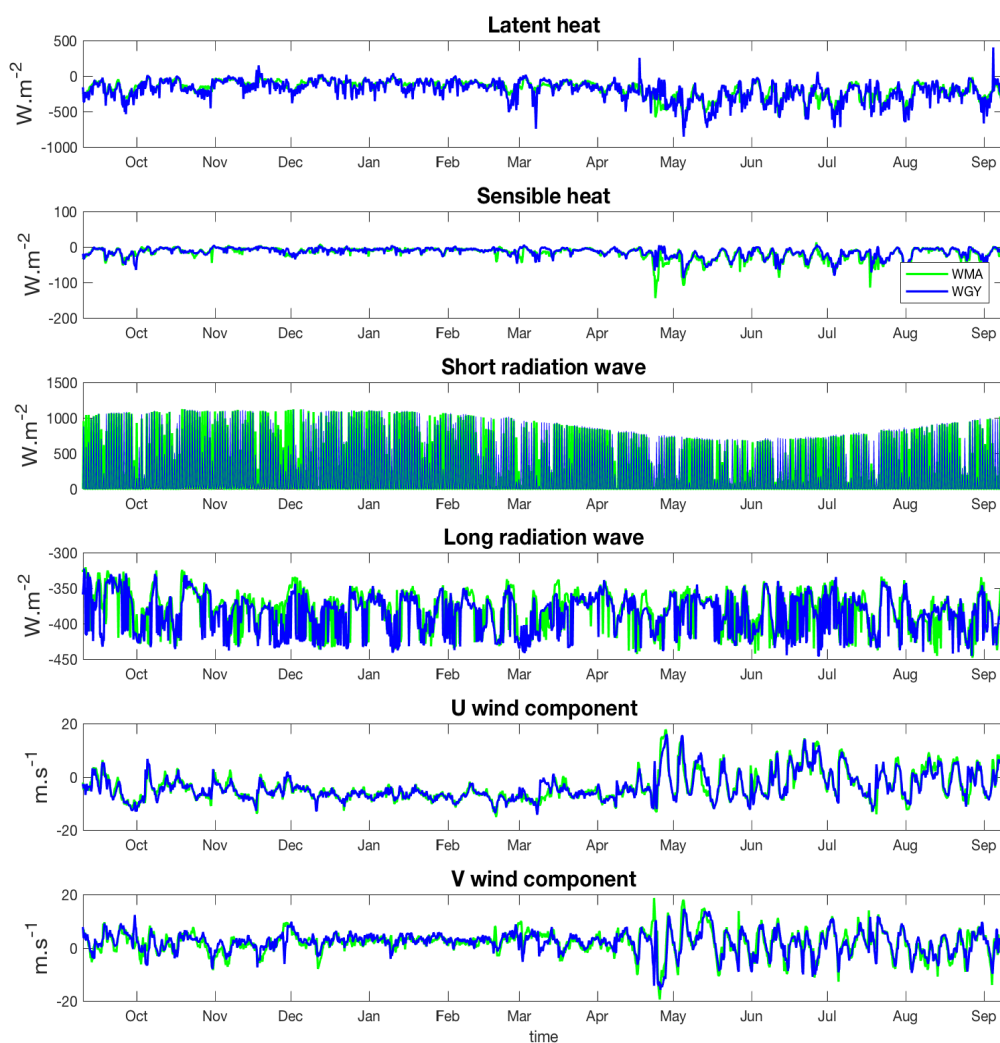
Figure 2 (in SM) Atmospheric forcings provided by the Weather Research Forecast model and extracted at the WMA (green) and WGY (blue) locations from September 2014 to September 2015

(b) it confused me that the simulations were named after the different locations, e.g. simWGA, while applying the same physics/forcing. I was expecting different physics. In my words, I would say you used an idealized environment representative of station WMA to test the effect of N fixation, and got results in good agreement with the other location in the case of no N fixation. To me it would thus be more intuitive to call the simulations Nfixation and no-Nfixation or something similar.

We acknowledge that using the same atmospheric forcings for both simulations while referring to them with the name of two distinct regions could be quite confusing. Nonetheless, we finally found it better to use the simWMA/simWGY nomenclature as the aim of our study was to try to find explanations for the biogeochemical differences observed *in situ* between WMA and WGY stations. Since these stations have similar atmospheric forcings (we could have used as well a mean forcing between WMA and WGY but the results would have been identical), the comparison of both regions boils down to the comparison between simulations including or not diazotrophy. Moreover, using the same nomenclature for the model outputs and the observations makes their comparison easier and adds clarity to the text. This choice also emphasizes our conclusion which showed that, without diazotrophy, our model predicted biogeochemical features close to those observed in the WGY, and that the differences observed between the West and the East of the sampled transect during the cruise was not due to physical forcing but rather to the presence or not of N fixers.

2

P4, l20-21. How does your parameterisation of the different PFTs compare to other parameterisations of diazotrophy in the literature?

Regarding the model parametrisation, our strategy was to try as far as possible to keep the same parameter values than those used in the other Eco3M-Med model versions. By adding the N2 fixation process, we aimed to implement two new PFTs, a large one to represent *Trichodesmium* sp (TRI). and a small one to represent the UCYN (UCYN). We assumed that regarding their size, UCYN would be parameterized as a cell of small phytoplankton (PHYS). Indeed, ranging from 3 to 10 µm diameter (Zehr et al., 2011), the UCYN parameterization similar to PHYS was realistic as the PHYS compartment includes autotrophs <10 µm. The maximum specific growth rate used in our model for UCYN is 2.7 d-1, in good agreement with results from Agawing et al. (2007) who found a maximum specific growth rate of 2.0 d-1 for *Cyanothece* (UCYN-C) during a chemostat experiment.

The parameterization regarding TRI was already explained above in the 6th general comments.

Regarding the diazotrophy process, our model, based on the Rabouille et al. (2006) work on Trichodesmium, represents N2 fixation using the nitrogenase activity as a state variable. Rabouille et al. (2006) conducted a chemostat experiment in order to calibrate the set of parameters used to model the nitrogenase activity in Trichodesmium. We thus used the same formulation which calculates the nitrogenase activity with our own quota functions regulating the increase or decay of the nitrogenase activity (detailed in Gimenez et al., 2016). If we compare the N2 fixation rates modelled and observed during the chemostat experiment in Rabouille et al. (2006), we find that their maximum specific N2 fixation rates (11 mmolN.molC-1.h-1) are 4 times higher than the ones simulated in our model (2.8 mmolN.molC-1.h-1). As the maximum specific growth rate depends on the N and C intracellular contents and on the NO3 availability in the field, it is not surprising to observe lower rates in our more complex NPZD biogeochemical model than in the chemostat model used in Rabouille et al. (2006), which does not take into account for instance the resource competition between *Trichodesmium* and other organisms. Hence, these results show that our model calculates N2 fixation rates in the same order of magnitude than N2 fixation rates provided by other models or measured during the OUTPACE cruise (Fig. 3, c) in the manuscript).

In a work that could be similar to the one of Rabouille et al. (2006), Grimaud et al. (2013) combined a chemostat experiment and modelling to assess the influence of light-dark regime on the UCYN-B *Crocosphaera watsonii* metabolism. However, they did not represent the N2 fixation as a function of the nitrogenase activity like in Rabouille et et al. (2006), but through the nitrogenase pool, in terms of concentration, which depends on a fixed nitrogenase synthesis rate. We therefore kept the formulation used in Rabouille et al. (2006) which was adapted for smaller nitrogen fixers implemented in our model supposed to represent the unicellular nitrogen fixers (UCYN). There is thus no similar parameters in the literature to compare with the ones used in our model, however, if we compare the C specific N2 fixation rates observed in UCYN-B culture reported for instance by Fu et al. (2008), our simulated C specific N2 fixation rates by UCYN (1.4 nmolN.µmolC-1.h-1 in average) is in good agreement with the ones measured in their study (from 1.2 to 3.2 nmolN.µmolC-1.h-1. For the same reasons as before, our model simulates N2 fixation rates close to the minimum range values observed in culture experiment, while the total N2 fixation rates simulated are consistent with the one measured during the OUTPACE cruise (Fig. 3, c) in the manuscript).

P4, l29-p5,l12: you modify the published biogeochemical model parameterization substantially. Why were those changes necessary? Did you perform any optimization or did you tune the model by hand? Was the model particularly sensitive to any of the parameters?

As this comment was also raised by Referee #2, we made the same response for both Referee #1 and Referee #2 :The biogeochemical model used in this study originates from a previous work as part of the VAHINE mesocosms experiment conducted in the Noumea Lagoon in New Caledonia, and published in Gimenez et al. (2016) - G2016. The model used in the G2016 study was run for 23 days and was not coupled to any physical model since it aimed at simulating a mesocosm experiment. Although G2016 and the present study use the same biogeochemical model and both aim to study the process of diazotrophy in the WTSP, the present work allowed to improve the first version of the biogeochemical model including nitrogen fixers and described in G2016. The entire year simulation run in this present study indeed revealed that some features of the model were not well represented, which led us to re-examine those features. The major problem we identified in the model results before its improvement was the replenishment in nitrate of the photic zone during the winter mixing which led to surface concentrations of nitrate largely higher than those measured *in situ*. This replenishment was due to a too shallow nitracline, itself controlled by the balance between uptake, sinking and mineralization of organic matter. In this regard, we studied the sensitivity of the model to those processes (without really performing an optimization) and found out that :

    i)   The sinking rates of organic matter was crucial in determining the depth of the nutriclines To better represent the fate of the detrital matter as a function of its size and its source (i.e. large detrital particles come from large organisms and the small ones come from smaller organisms), the detrital compartment has been splitted in two parts, each of them being associated with a different sinking rate.

The following paragraph has been added to the revised manuscript : « Since the Gimenez et al. (2016) modelling study was focusing on a mesocosm experiment, the assessment of the model skills was incomplete. With the new set of data

provided by the OUTPACE cruise, some features of the original model were improved and some new features were introduced to correct for the model major flaws or to add some realism in the model. To improve the representation of the nutricline depths which depend on the sinking of the detrital organic matter and its mineralization in the water column, we included two size classes of detrital matter associated with two different sinking rates, while the previous version (Gimenez et al., 2016) only included a single compartment of detrital material (see Table 1 in supplementary material). »

ii)   DOP availability has a crucial role in this P-depleted area for autotrophs. Since DOP mineralization by heterotrophic bacteria was likely underestimated by the model because it does not explicitly represent P mineralization by ectoenzymes produced by bacteria, DOP availability for organisms has been artificially increased to take this phenomenon into account. In practice, half-saturation constants Ks for DOP uptake were divided by 10 for all autotrophs.

iii) As suggested by recent studies, we decided to apply the same Redfield ratio , i.e. 106:16:1 to the C:N:P ratios of the upper and lower ranges of intracellular quotas for all the PFTs, including bacteria and HNF for which the C:N:P ratios of 50:10:1 were used so far. This change also brought a more consistent stoichiometry in ciliates (CIL) which were predating so far on organisms with very different stoichiometries. We propose to insert the following paragraph to justify this choice :

«While several studies have shown that the intracellular C:N:P ratios in heterotrophic bacteria tend to be below Redfield values as they were enriched in N and P (Bratbak, 1985, Goldman and Dennett, 2000, Vrede et al., 2002), more recent studies suggest that these ratios could be higher than 50:10:1 and highly variables in response to physical, chemical and physiological conditions (Cotner et al., 2010, Martiny et al., 2013 ; Zimmerman et al. 2014). This led us to replace the 50:10:1 ratios used so far in the model for bacteria and HNF by the Redfield 106:16:1 ratio as for the other PFTs represented in the model. It is reminded however that the PFT's stoichiometry is flexible in the model and that the Redfield ratios are only used to link together the limits of the ranges of C, N and P intracellular quotas, (i.e. $QC^{min} = 106 \ QP^{min}$, $QC^{max} = 106 \ QP^{max}$, see Table 1 in supplementary material) thereby allowing a large variety of possible C:N:P ratios in PFTs, and notably the 50:10:1 ratio in heterotrophic bacteria.»

P5, l22; p8,section 3.2.1.; Fig. 4: you mention winter and winter mixing. Is this appropriate for a tropical region at 17 deg S? As winter mixing I would understand much deeper and more rapid isolated mixing events as are characteristic for the temperate latitudes. Is the gradual deepening simulated for the MLD in Fig. 4 not mostly a result of increasing salinity in the dry season?

We thank Referee #1 for this relevant question regarding the cause of variations in the vertical density, and therefore in the vertical mixing observed during the austral winter (Moutin et al., 2018). Vertical mixing of the water column is induced by an increasing water density in the upper layer, which can either be due to a decreasing temperature or to an increasing salinity. A simple calculation of density variations using the equation of state of seawater, showed that temperature variations in the range of those measured in tropical regions ($\Delta T \sim 4,3$ °C) result in density variations (Δ rho $\sim 1,22$), whereas no density variations were induced by the salinity variations typical in this region ($\Delta S \sim 0,004$). This result shows therefore that, even in tropical waters, the vertical mixing is mostly due to a decreasing temperature in winter, though this decrease is not as important as in temperate latitudes. Moreover, around 22° N, Riser and Jonhson (2008) also observed « early winter mixing » which homogenized the upper water column at the HOT station, suggesting that a significant vertical mixing during the winter season can be observed even in tropical latitudes.

p6,l18: Could you mention here already that the shallower phosphacline than nitracline results from the model setup with preferential P regeneration? This aspect is not a result of the simulations presented here and would have made it significantly easier for me to understand this section. I acknowledge that there are different writing styles. In the case of this ms, readability of the results section would in my opinion be greatly improved if short explanations for the model data and the model-data discrepancies that follow directly from the model assumptions (i.e., the 1D model accumulating additional N due to missing advection; the shallower phosphacline compared to nitracline because of preferential P regeneration), were given already in the results section. The discussion section would then focus on putting the findings into context/analyzing more complex mechanisms.

We understand the point of Referee #1 although the Results sections aims to remain more descriptive than explanatory in our manuscript style. Nonetheless, we agree that the cause of the discrepancy between nitracline and phosphacline depths can be mentioned earlier than in the discussion, which is why we added the following sentence to introduce earlier the preferential P regeneration assumption.

« Note that to reproduce this discrepancy within the model, it has been necessary to introduce a preferential regeneration of the detrital matter in P compared to C and N in the biogeochemical model, a point thereafter detailed in Section 4.2.2. »

Fig. 2: could you add e.g. a small inset showing the location of this map on the globe?

Yes, the figure has been modified.

Fig. 3: you do not mention the identity of primary producers in the WMA simulation. With the confusing parameter value differences mentioned above I am not sure whether diazotrophs in these simulations only have net competitive advantages over the two other phyto types and would therefore be expected to dominate the WMA simulation?

We agree that giving the relative proportion of the different autotrophs to the total Chl a would have provided an evidence of the net competitive advantage of diazotrophs over the other non-diazotroph phytoplankton. Actually, in the photic layer, TRI represent 80% of the total Chl a, followed by PHYS (10%) and around 5 % each for UCYN and PHYL. The significant lower contribution of UCYN compared to TRI is due to the fact that UCYN are grazed by HNF and CIL while TRI has no predator in the model. In addition, the lower contribution of UCYN compared to PHYS seems counter-intuitive as we would think UCYN being advantaged by the N2 fixation compared to PHYS, but the energetic cost related to N2 fixation finally costs more to the cell than the advantage of fixing N2. These contributions were identical for PP. The following paragraph was added to the revised manuscript in order to give some details on the direct versus indirect impact of N2 fixation on other PFTs :

« In a previous study using nearly the same biogeochemical model including TRI and UCYN state variables in a one-dimensional configuration without physical coupling, Gimenez et al. (2016) highlighted the direct and indirect impact of the new N input provided by diazotrophs. By calculating the percentage of Diazotroph-Derived Nitrogen (DDN) in each model compartments, they followed the transfer of DDN throughout the entire trophic web as a function of time, and showed that after 25 days, 43% of the DDN fixed by diazotrophs were found in non-diazotroph organisms. These results clearly showed that N2 fixation had a significant indirect impact on the planktonic production by providing a new source of N for other organisms. DDN tracking inside the model compartments is associated with very high computational costs and could not be applied to the present study where simulations are run for several years (against 25 days for the previous study). However, it is worthwhile mentioning that the proportion of PFTs involved in total Chl a and PP was 80 % of TRI, 10 % of PHYS and 5% of PHYS and PHYL, suggesting that the impact of N2 fixation is rather direct (85% of PP is realized by diazotrophs) than indirect. In our model, diazotrophs have therefore net competitive advantage over the two other non-diazotrophic autotrophs. »

Moreover, instead of the fairly detailed description of the curves it might ease comprehension of the results to point out that in both simulations and observations the Chl a maximum is roughly located at the nutrient-limiting nutricline.

In response to this point, we will add the following sentence in the section 3.1.2 :

« In the model outputs, the location of the DCM is roughly located at the nutrient-limiting nutricline, i.e., at the phosphacline depth in WMA and simWMA, and at the nitracline depth in WGY and simWGY. »

Fig. 4: I guess the black line is the simulated MLD. You point out the connection between the MLD and the nutriclines on p11,l1-2. So how realistic is it compared to observations? Moutin et al. 2018 (BGD) present observation-based values from de Boyer Montegut et al. 2004 showing maximum MLD in August (here October) and high Chl from April to August (here October to April). What causes this discrepancy and how does it affect your results?

During the revision process and thanks to the reviewer's advice we spent a substantial time to figure out the time shift between the *in situ* MLD from the Deboyer Montegut climatology and the MLD predicted by the model. This allowed us to identify the source of the problem which was a technical error in the computer program used for the implementation of physical forcings in the model. The two simulations were then run again with the correction taken into account and, as expected, our main conclusions were not affected. The vertical profiles of Fig. 1 showed slight differences, but the corrected simulations fit better with observations than before (mostly the chlorophyll profiles in simWMA) and we are very grateful to the reviewer for his meticulous work. We revised the result section consequently by adding the new version of the figures, and removed the following sentence which mentioned the difference in the upper surface between the model and observations which is no more present with the corrected simulations :

« "[..] (around ~~17.0~~ 16.0 nmolN.L^{-1}.d^{-1} [..]~~»~~

~~« Another difference between the model outputs and the data lies in the higher surface values of Chl a^{simWMA} around 0.35 µgChl.L=1 whereas Chl a^{obsWMA} does not exceed 0.15 µgChl.L=1 from 0 to 50 m depth. »~~

« [..] a winter mixing beginning at the end of ~~August~~ May leading to a maximum MLD of 70 m in ~~October~~ August."

~~«We therefore observe surface seasonal variations in Chl a^{simWMA} and POC^{simWMA}, with maximum values from October July to the end of March January, and a [..] during the stratified period (from April February to August May). »~~

«They clearly indicate a winter mixing beginning at the end of ~~August~~ May leading to a maximum MLD of 70 m in ~~October~~ August, followed by a longer stratified period from ~~February~~ November to ~~July~~ April,[..] »

« [..]During winter mixing, surface DIP$^{simW M A}$ increases from 0.6 to 2 nM, then remains quite stable until the end of ~~January~~ February before regularly decreasing until ~~April~~ June down to 0.6 nM. DIP$^{simW M A}$ then remains low during the stratified period until the next winter mixing in August~~/September~~. »

« The total N$_2$ fixation at the surface varies from a minimum mean value of 15 nmol.L^{-1}.d^{-1} during the stratified period to a maximum mean value of 20 nmol.L^{-1}.d^{-1} reached between ~~September and January~~ July and August, i.e. during the winter mixing . »

«The newly available DIP in the surface layer is immediately followed by an increase in the N$_2$ fixation rates in ~~August~~ June (Figure 3, c)), which then remain quite stable until ~~January~~ October before slightly decreasing until the next winter mixing [..]»

« [..] and a less intense and deeper signal around 70 m (which corresponds to the nitracline depth~~) during the stratified period (~~from ~~January~~ April to the end of ~~August~~ May). »

causality between N fixation and preferential P regeneration:

- p9,l29-p10,l2: "The ... role of DIP availability in controlling N2 fixation ... has been highlighted over the last decade ..., and the consistent results between the OUTPACE data and our model outputs, comparing simWGA and simWGY, reinforces this view of the biogeochemical functioning in the region." - You do not test the effects of P availability in the simulations presented, you assume high/sufficient P availability and manipulate N fixation. Your simulations thus show the connection the other way round: without N fixation you have P left over.

- p11,l10-11: as above: the simulations presented do not show that a shallower phosphacline than nitracline was needed to observe N fixation rates in agreement with observations. they show that assuming N fixation leads to this gap between phospha- and nitracline. Could it be that you still had the simulations without preferential P regeneration in mind, that are mentioned on p11,l34-p12,l1?

- p11,l23-25: I have to admit during the first read it took me until here to realize how the difference in phospha- and nutricline depths came about. The preferential P regeneration is a model assumption. Why not mention it already when describing Fig. 3 in the results? If you want to keep it as a result, then simulations without preferential P regeneration might provide evidence for the causality you describe here. The same applies to p12,l10- 11.

As this point on the <u>causality between N fixation and preferential P regeneration</u> was mentioned by the two referees, we made the same answer :

As mentioned above, we agree with Referee #1 regarding the lack of proof in the previous version of the manuscript to support the assumption of the P availability controlling N2 fixation and the preferential P regeneration leading to a shallower phosphacline than the nitracline. To remedy it, we decided to add the results of the simulation without the preferential P regeneration which were compared to the simWMA, in order to clearly show that, without that preferential regeneration, the system did not provide the sufficient conditions to support N2 fixation as observed in the field in the WMA region.

The following figures have been added to the revised manuscript in addition with the following paragraph, inserted at in Section 4.2.2 :

« To illustrate how the discrepancy between nitracline and phosphacline depths can be attributed to preferential P regeneration, DIN and DIP concentrations and N2 fixation rates in simWMA calculated with and without preferential P regeneration (i.e. preferential hydrolysis of P particulate matter) have been compared (Fig. 5). This figure shows the deepening of the phosphacline in the simulation without preferential P regeneration. More importantly, without preferential P regeneration, the phosphacline depth is deeper than the MLD at 70m, which prevents DIP input in the surface layer during winter mixing, and leads to a strong limitation of diazotrophs by P. This stronger P-limitation without preferential P regeneration can also be observed at the cellular scale by analyzing the intracellular P quota of N2 fixers (Figure 6). In the simulation without preferential P regeneration, the relative intracellular quota of P in TRI and UCYN

are in average respectively 8 and 16 times lower than with preferential P regeneration, as shown in Figure 6. As N2 fixation alleviates N limitation for diazotrophs, their growth is thus limited by P availability. The significant decrease in relative intracellular P quotas has therefore a significant impact on their growth, and consequently explain the lower N2 fixation rates shown in Figure 5, c). »
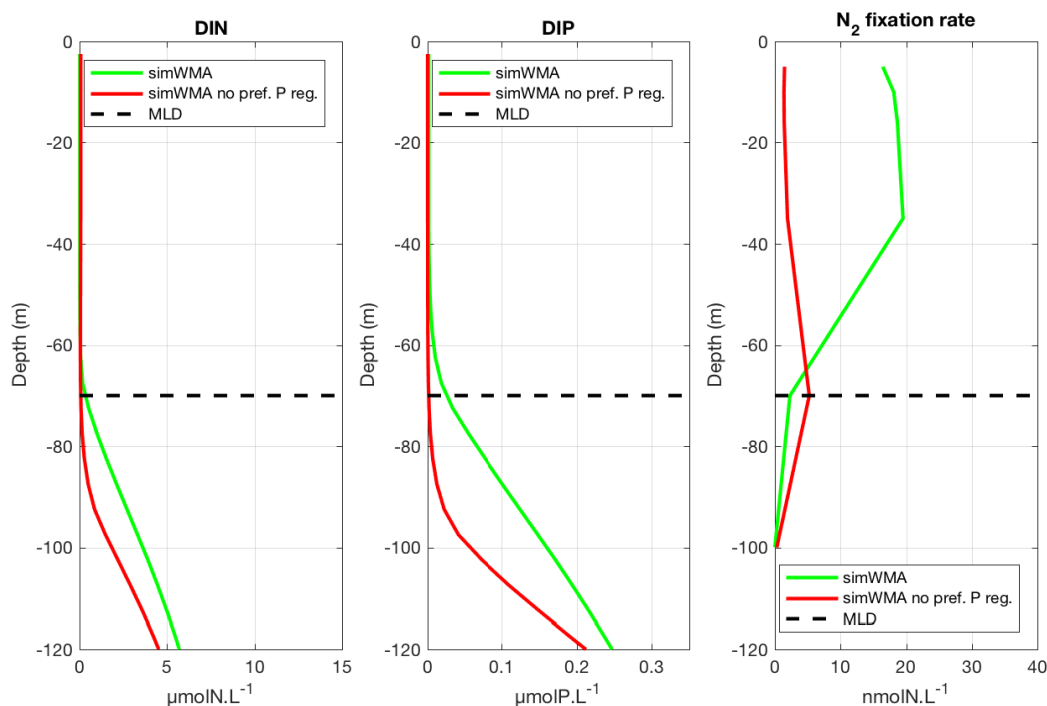

Figure 3 (inserted as Figure 5 in the revised manuscript) Vertical profiles of (a) dissolved inorganic nitrogen (DIN), (b) dissolved inorganic phosphorus (DIP), (c) N2 fixation rates for the simulation with diazotrophy, as a proxy of the WMA region (simWMA with the preferential P regeneration (in green) and without the preferential P regeneration (in red). The horizontal black dashed line represents the depth of the maximum mixing layer calculated at 70 m depth.

p12,l13-31: This section could be formulated a bit more concisely. Does the 1D model consider any N losses (at the bottom boundary, mimicked advection, ...)? If not I don't find it very surprising that newly fixed N accumulates in a 1D simulation - where else should it go - and would emphasize more the other aspects mentioned in this section.

As mentioned in this section, « [..] without any loss processes taken into account, the annual

N input by N2 fixation accumulates, as observed in simWMA. », there is no N losses in our model as it is totally conservative. Nonetheless, the main result pointed out in this section was not the accumulation of N, which is not surprising as mentioned by Referee #1 since N2 fixation brings new N in the system, but rather the location of this accumulation in the water column, namely around the main thermocline which seems on line with nitrate accumulation identified from N excess measurements (Fumenia et al., under rev.).

We propose to remove the following sentences which did not bring relevant information regarding the main result developed in this section, which is the location of the N accumulation in the water column : « The N* tracer is used to measure the N in excess with respect to the quantity expected from the thermocline N:P ratio (i.e., N:P of 16:1; Redfield et al. (1963); Takahashi et al. (1985); Anderson and Sarmiento (1994)), even if the relative contributions of the N-excess sources remain difficult to determine (Hansell et al., 2007). »

p12,l25: misleading wording: "Our ... results ... show an accumulation of N .. which can only be explained by the new N input ...". This to me suggests that you tested different mechanisms for N accumulation. maybe better: "... accumulation resultion from N fixation".

We agree with Referee #1 and propose the following rephrasing : « Our model […] in the 100-500 m layer which results from the new N input […].»

p13,l27: misleading wording: "DIP is never exhausted ... because the lack of iron is hypothesized to prevent N2 fixation."

maybe clearer: "DOP is never exhausted ... because the model implicitly assumes iron limitation to prevent N2 fixation."

We agree with Referee #1 for this rephrasing (assuming that DOP is a typo error instead of DIP), and the following sentence has been added to the revised manuscript.

« DIP is never exhausted [..] because the model implicitly assumes iron limitation to prevent N2 fixation ».

We thank the anonymous Referee #2 for the time and effort devoted to the review of the manuscript. Below, we reproduce the reviewer's comments and address their concerns point by point. The reviewer's comments are copied below in regular font with our responses in blue and the revised sections in the new manuscript version in red.

Just before answering, we would like to mention that during the revision process, we undertook some model technical check to answer a comment made by Referee #1. We thus noticed an error in the implementation of the physical forcings, which was responsible for a two-month shift between model results and data regarding the seasonal variations of the mixed-layer depth. We therefore ran again our two simulations with this error corrected. Corresponding results did not change at all our conclusion, and were even improved compared to observations. This point is more detailed in the specific comment regarding Fig. 4, and the figures 3 and 4 of the manuscript will be consequently updated in the revised version.

The study entitled "Diazotrophy as the main driver of planktonic production and bio- geochemical C, N, P cycles in theWestern Tropical South Pacific Ocean: results from a 1DV biogeochemical-physical coupled mode" by Gimenez et al. examines the role of diazotrophy in the western south Pacific ocean. The authors use a 1DV ecosystem model that is run in two different configurations at the same station that differ by the representation of diazotrophy. Their main conclusions are that nitrogen fixation sustains a significantly higher productivity, explains the consumption of DIP and induces significant seasonal variations. Furthermore, they claim that a decoupling between the depth of the phosphacline and nitracline is necessary to induce nitrogen fixation. This manuscript addresses a very important scientific question: The potentially critical role of nitrogen fixation in Low Nutrient-Low Chlorophyll areas. It is relatively well written, clear and thus it deserves publication in Biogeosciences. However, some important issues have to be addressed before. In particular, some of the major conclusions proposed in that study are not sufficiently demonstrated and thus, require more analysis.

A strong point is made on the decoupling between the phosphacline and nitracline to explain nitrogen fixation. In fact, this is not clearly demonstrated in the study. It only shows that nitrogen fixation explains the lack of DIP accumulation at the surface. However, the impact of this decoupling on nitrogen fixation is not analysed. This would require to manipulate the depths of the nitracline and phosphacline independently and to study the consequences on nitrogen fixation. In the discussion section, the authors mention that they have done some sensitivity tests by altering the degradation rates of P-rich organic matters (DOP, POP), but the results of these tests are not shown. Yet, this would support their conclusions.

We fully agree with Referee #2 and decided to add the results of the simulation without preferential P regeneration and to provide more details on this important point. This point is detailed below in the 10th specific concern.

My second concern is on the model setup. First, they use the same physical conditions and state that the differences between WMA and WGY are only explained by the presence or lack of diazotrophy. That's quite a strong assumption that should be better discussed.

We agree with Referee #2 and developed this point below in the 1st specific concern.

Furthermore, the physical setup is not sufficiently described. For instance, they explain that they used the output of a WRF configuration to force their 1D ocean model without clearly describing the atmospheric model setup, the region that has been selected in this atmospheric model, how they have averaged (or not) the atmospheric forcing fields, . . . I don't expect a full dynamical validation of the physical state predicted by the physical 1D ocean model but some additional information are necessary.

We agree with Referee #2 and developed this point below in the 3rd specific concern.

Finally, they have made some significant changes in their ocean biogeo- chemical models (two particles size classes, modified parameter values). They should explain why these changes have been made and how the parameter values have been chosen (fine tuning, assimilation, basic assumptions, . . .).

As this comment was also raised by Referee #1, we made the same response for both Referee #1 and Referee #2 :The biogeochemical model used in this study originates from a previous work as part of the VAHINE mesocosms experiment conducted in the Noumea Lagoon in New Caledonia, and published in Gimenez et al. (2016) - G2016. The model used in the G2016 study was run for 23 days and was not coupled to any physical model since it aimed at simulating a mesocosm experiment. Although G2016 and the present study use the same biogeochemical model and both aim to study the process of diazotrophy in the WTSP, the present work allowed to improve the first version of the biogeochemical model including nitrogen fixers and described in G2016. The entire year simulation run in this present study indeed revealed that some features of the model were not well represented, which led us to re-examine those features. The major problem we identified in the model results before its improvement was the replenishment in nitrate of the photic zone during the winter mixing which led to surface concentrations of nitrate largely higher than those measured *in situ*. This replenishment was due to a too shallow nitracline, itself controlled by the balance between the sinking and the mineralization rates of organic matter. In this regard, we studied the sensitivity of the model to those processes (without really performing an optimization) and found out that :

i) The sinking rates of organic matter was crucial in determining the depth of the nutriclines To better represent the fate of the detrital matter as a function of its size and its source (i.e. large detrital particles come from large organisms and the small ones come from smaller organisms), the detrital compartment has been splitted in two parts, each of them being associated with a different sinking rate.

The following paragraph has been added to the revised manuscript : « Since the Gimenez et al. (2016) modelling study was focusing on a ponctual mesocosm experiment, the assessment of the model skills was incomplete. With the new set of data provided by the OUTPACE cruise, some features of the original model were improved and some new features were introduced to correct the model major flaws or add some realism to the model. To improve the representation of the nutricline depths which depend on the sinking of the detrital organic matter and its mineralization in the water column, we included two size classes of detrital matter associated with two different sinking rates, while the previous version (Gimenez et al., 2016) only included a single compartment of detrital material (see Table 1 in supplementary material). »

ii) DOP availability has a crucial role in this P-depleted area for autotrophs. Since DOP mineralization by heterotrophic bacteria was likely underestimated by the model because it does not explicitly represent P mineralization by ectoenzymes produced by bacteria, DOP availability for organisms has been artificially increased to take this phenomenon into account. In practice, half-saturation constants Ks for DOP uptake were divided by 10 for all autotrophs.

iii) As suggested by recent studies, we decided to apply the same Redfield ratio , i.e. 106:16:1 to the C:N:P ratios of the upper and lower ranges of intracellular quotas for all the PFTs, including bacteria and HNF for which the C:N:P ratios of 50:10:1 were used so far. This change also brought a more consistent stoichiometry in ciliates (CIL) which were predating so far on organisms with very different stoichiometries. We propose to insert the following paragraph to justify this choice :

«While several studies have shown that the intracellular C:N:P ratios in heterotrophic bacteria tend to be below Redfield values as they were enriched in N and P (Bratbak, 1985, Goldman and Dennett, 2000, Vrede et al., 2002), more recent studies suggest that these ratios could be higher than 50:10:1 and highly variables in response to physical, chemical and physiological conditions (Cotner et al., 2010, Martiny et al., 2013 ; Zimmerman et al. 2014). This led us to replace the 50:10:1 ratios used so far in the model for bacteria and HNF by the Redfield 106:16:1 ratio as for the other PFTs represented in the model. It is reminded however that the PFT's stoichiometry is flexible in the model and that the Redfield ratios are only used to link together the limits of the ranges of C, N and P intracellular quotas, (i.e. $QC^{min} = 106\ QP^{min}$, $QC^{max} = 106\ QP^{max}$, see Table 1 in supplementary material) thereby allowing a large variety of possible C:N:P ratios in PFTs, and notably the 50:10:1 ratio in heterotrophic bacteria.»

My third concern is more subjective. I find the paper too descriptive and not quantitative enough. I would have liked to see a better quantification of the impact of nitrogen fixation on the system. Some budgets would have been interesting to present. For instance, how much of the PP is being sustained by nitrogen fixation directly (PP by UCYN and TRI) and indirectly (fresh input of N excreted by diazotrophs). How does N input from nitrogen fixation compare to export production? How sensitive are the model predictions to the parameter values, to UCYN and TRI descriptions, to DOP/POP dynamics? The latter question is partly related to my previous concerns.

We thank Referee #2 for this concern, even though we find that the different points raised are quite out of the scope of this paper which did not focus on the fate of fixed N2 fixation on the system, but rather on the interactions between nutrients availability and N2 fixation at a seasonal scale. Budgets, details on how new N influences other compartments, or to what extent N2 fixation impacts export production, could be the material for another article of interest. We however added in the revised manuscript more details regarding the contribution of diazotrophs in PP rates and Chl a biomass to better highlight the clear advantage of TRI in simWMA compared to other autotrophs. We also mentioned that in a previous study, we investigated the transfer of the Diazotroph-Derived-Nitrogen in a similar but non-coupled biogeochemical model, and explain why it was not used in the present study considering the special issue time schedule.

« In a previous study using nearly the same biogeochemical model including TRI and UCYN state variables in a one-dimensional configuration without physical coupling, Gimenez et al. (2016) highlighted the direct and indirect impact of the new N input provided by diazotrophs. By calculating the percentage of Diazotroph-Derived Nitrogen (DDN) in each model compartments, they followed the transfer of DDN throughout the entire trophic web as a function of time, and showed that after 25 days, 43% of the DDN fixed by diazotrophs were found in non-diazotroph organisms. These results clearly showed that N2 fixation had a significant indirect impact on the planktonic production by providing a new source of N for other organisms. DDN tracking inside the model compartments is associated with very high computational costs and could not be applied to the present study where simulations are run for several years (against 25 days for the previous study). However, it is worthwhile mentioning that the proportion of PFTs involved in total Chl a and PP was 80 % of TRI, 10 % of PHYS and 5% of PHYS and PHYL, suggesting that the impact of N2 fixation is rather direct (85% of PP is realized by diazotrophs) than indirect. In our model, diazotrophs have therefore net competitive advantage over the two other non-diazotrophic autotrophs. »

To conclude on my mains concerns, I think that the authors should improve the analysis, perform some sensitivity tests : and better justify their choices and conclusions before this manuscript becomes suitable for publication.

More details and proofs regarding our assumptions and strategy were added in the revised manuscript. They concern additional details on the nutriclines discrepancy due to a preferential regeneration of the P particulate matter: new figures have been added in the revised manuscript to better illustrate the model sensitivity (and especially on the N2 fixation rates) to this preferential P regeneration. The new figures and new sections associated are detailed in the 10th specific concern. We also improve the justification of our modeling strategy regarding the physical forcings implemented in the 1VD physical model by providing additional sections in the revised manuscript and figures in a supplementary material (details in the 1st specific concern).

Specific concerns:

1- P3, lines 24-27: This relates to one of my major concerns. The authors chose the same physical conditions to study two different sites. This is quite a strong assumption and this should be better justified. At present, I would consider that the study investigates the role of diazotrophy at a single location (which remains to be clearly stated, see below) rather than the differences between two sites.

As this point was also mentioned by Referee #1, the same answer is given to both of them as follows :

We will first detail our choice of using the same physic forcing and then propose some new sentences which will be added to the revised manuscript in order to better justify our strategy.

Our modeling strategy came from the observation that the WTSP was characterized by a significant biogeochemical gradient in terms of nutrient availability and planktonic production, which seemed to be directly related to the presence or not of nitrogen fixers inside this area (Moutin et al., 2018). In order to confirm or not this assumption through a modeling study, we designed two simulations only differing by the presence or not of diazotrophy. This was made possible only by the fact that, despite the large distance between WMA and WGY, the physical forcings were shown to be similar in the two regions. The question of whether the atmospheric forcings in WMA and WGY were similar enough to consider that their impact on the water column dynamics was the same arose very early in our reflection. In that purpose, at the early stage of this study, we compared the atmospheric forcings calculated at WMA and WGY by the atmospheric model WRF (see figure below). This comparison shows that there is no significant difference between both forcings. To go further, we also compared two simulations only differing by the atmospheric forcing (respectively using the to WMA and WGY forcings) and did not observe differences nor in the water column dynamics, neither on biogeochemical cycles or on the trophic web. Finally, in situ climatological data of MLD (Fig. 1) also indicate that there is not significant difference between the dynamics of these two regions despite their distance. We thereby decided to use the atmospheric forcing from the WMA region for both regions and the simulated MLD predicted by our model fits well with values obtained with climatology (Fig. 1). We acknowledge that this could have been further detailed in the submitted manuscript and we propose to add the following text in the revised manuscript and the figure below in the supplement material :

« The assumption made by using a unique set of atmospheric forcings for two regions significantly far away is first based on the in situ climatological data reported in Moutin et al. (2018). These authors indeed showed that the vertical dynamics of the water column, and especially the depths of the mixed layer were similar throughout the year in all the WTSP (see Figure SM1 in supplementary material). In addition, the atmospheric forcings calculated by the WRF atmospheric model at WMA and WGY were also very similar (see Figure SM2 in supplementary material). Furthermore, we also compared two simulations ran with the respective atmospheric forcings calculated at WMA and WGY and did not observe any significant difference, nor in the water column dynamics, neither on biogeochemical cycles. »
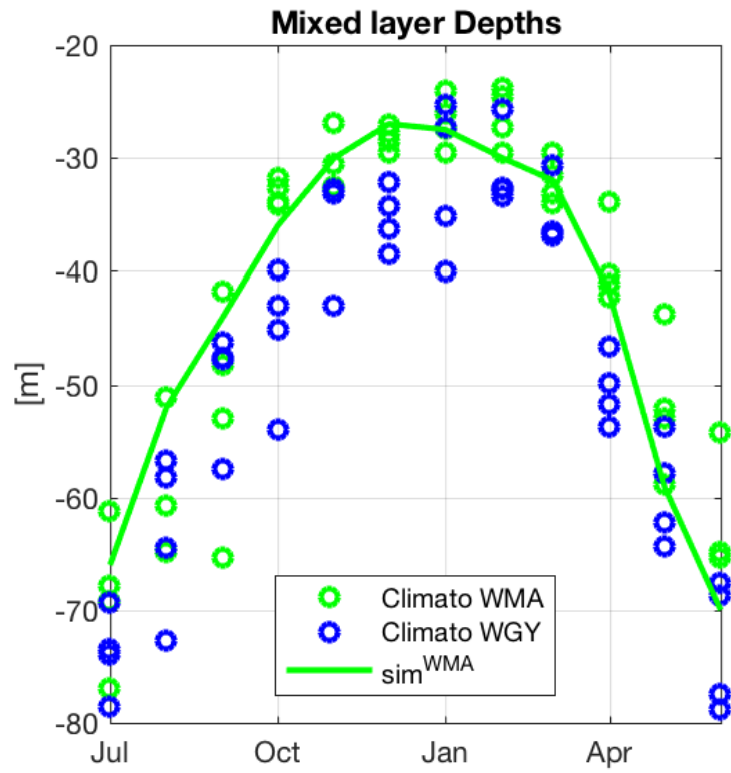
Figure 1 (in SM) Temporal dynamics of the *in situ* mixed layer depths estimated using a climatology (de Boyer Montégut et al., 2004) at WMA (green circles) and WGY (blue circles), and simulated by the model (green line)
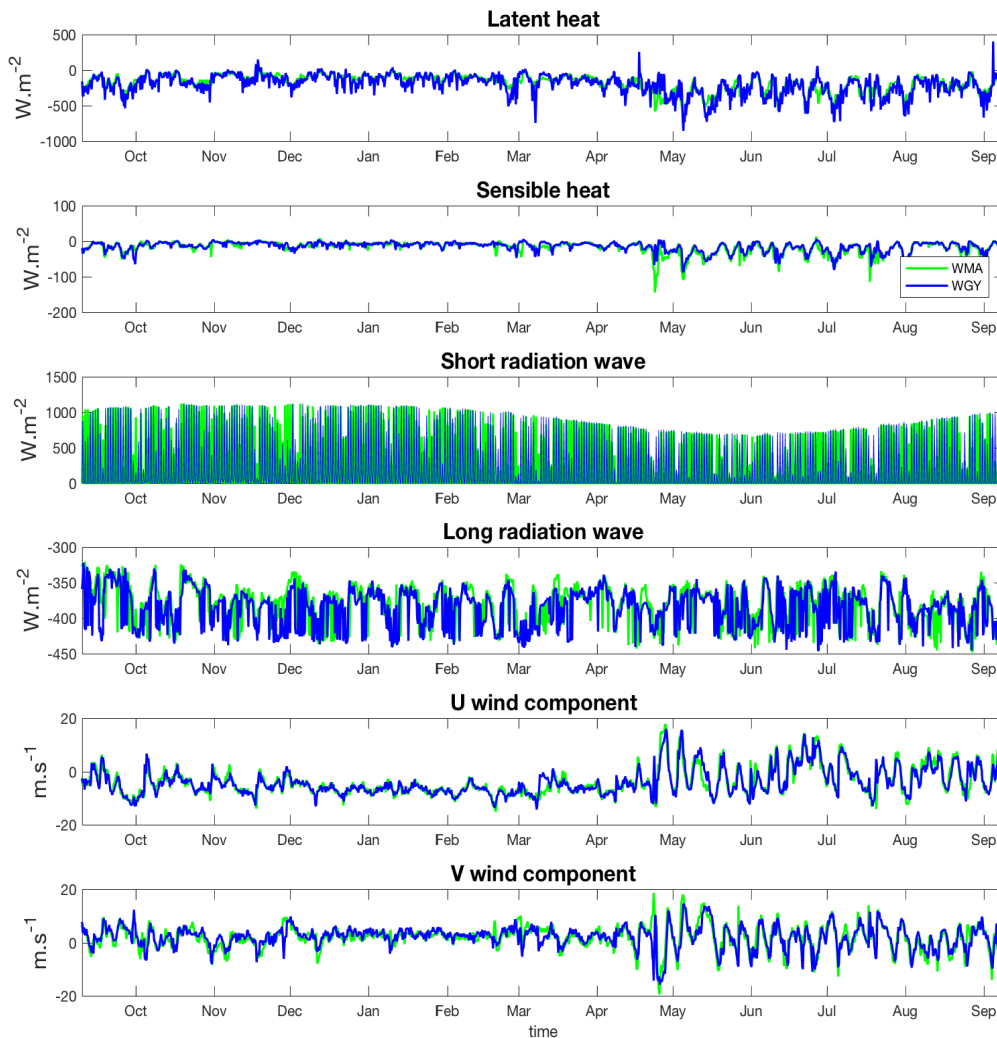
Figure 2 (in SM) Atmospheric forcings provided by the Weather Research Forecast model and extracted at the WMA (green) and WGY (blue) locations from September 2014 to September 2015

2 - P4, lines 20-21: I don't really understand what means TRI are equivalent to 100PHYL. I think that some more explanations in that paper would help the reader.

The following sentence has been modified in the revised manuscript to ease the comprehension:

"[..] For all the non-diazotrophic features and in agreement with literature (e.g. Luo et al., 2012), it has been considered that a Trichodesmium trichome was containing 100 PHYL cells and that a UCYN cell was equivalent to a PHYS cell. Yet, the conversion factor of 100 between TRI and PHYL was only applied for extensive parameters, i.e. those depending on biomass. Intensive parameters were set equal to those of PHYL, except for the specific growth rate which was instead averaged from literature since it has been experimentally demonstrated that it was lower than that of PHYL (Mulholland and Bernhardt, 2005, Hutchins et al., 2007). Parameter values, whether new or differing from those of Alekseenko et al. (2014), are given in SM: table 1."

3 - P5, lines 18-22: This is not clear enough. What is the model setup of WRF? Over which region and what time period have been averaged the atmospheric fields? How well does the physical model perform compared to actual in situ conditions?

As mentioned in the manuscript in section 2.3, the atmospheric forcings were provided by a run of the WRF model starting at the end of the winter mixing period preceding the OUTPACE cruise and lasting one year (i.e. Sept. 2014 – Sept. 2015)

. Concerning the location, the atmospheric forcings were extracted at the precise location of the long duration station sampled in the WMA region during the cruise, i.e. the LD A station, located at 19,2°S 164,7°E. There was thus no space or time average for the atmospheric forcings. Boundary conditions for the WRF model are provided by the American Global Forecast System (GFS) model (National Center for Environmental Prediction/National Center Environmental Prediction -NCAR / NCEP) analyzes. These analyzes correspond to a correction of the forecast using a larger number of observations during the data assimilation cycle. The WRF model is forced every 6 hours by analyzes during the processing.

The following paragraph has been added to the revised manuscript:

« [..15 km] and a time step of 6 hours. Boundary conditions for the WRF model are provided by the American Global Forecast System (GFS) model (National Center for Environmental Prediction/National Center Environmental Prediction - NCAR / NCEP) analyzes. These analyzes correspond to a correction of the forecast using a larger number of observations during the data assimilation cycle. The WRF model is forced every 6 hours by analyzes during the processing. »

Regarding the validation of the physical model, seasonal in situ data over the simulated period (Sept. 2014 – Sept. 2015) were not available to compare with the outputs of our physical model. However, we used climatology data to assess this model and found a good consistency between simulated and field-derived MLD in the WTSP (see Moutin et al. (2018)). The figures below represent the monthly-averaged surface temperature and density and the depth of the mixed layer provided by the physical model, compared to temperature and density data extracted from the WOA13 climatology (2005-2012) and MLD data from the de Boyer Montégut et al. (2004) climatology. We propose to join this figure to support the validation of our physical model and the following sentence has been added in Section 2.3 :

« The comparison between some physical outputs (i.e. surface temperature, surface density, mixed layer depth) and climatological *in situ* observations allowed to ensure that the one-dimensional physical model was relevant to address our scientific question (see Figure SM3 in supplementary material) .»
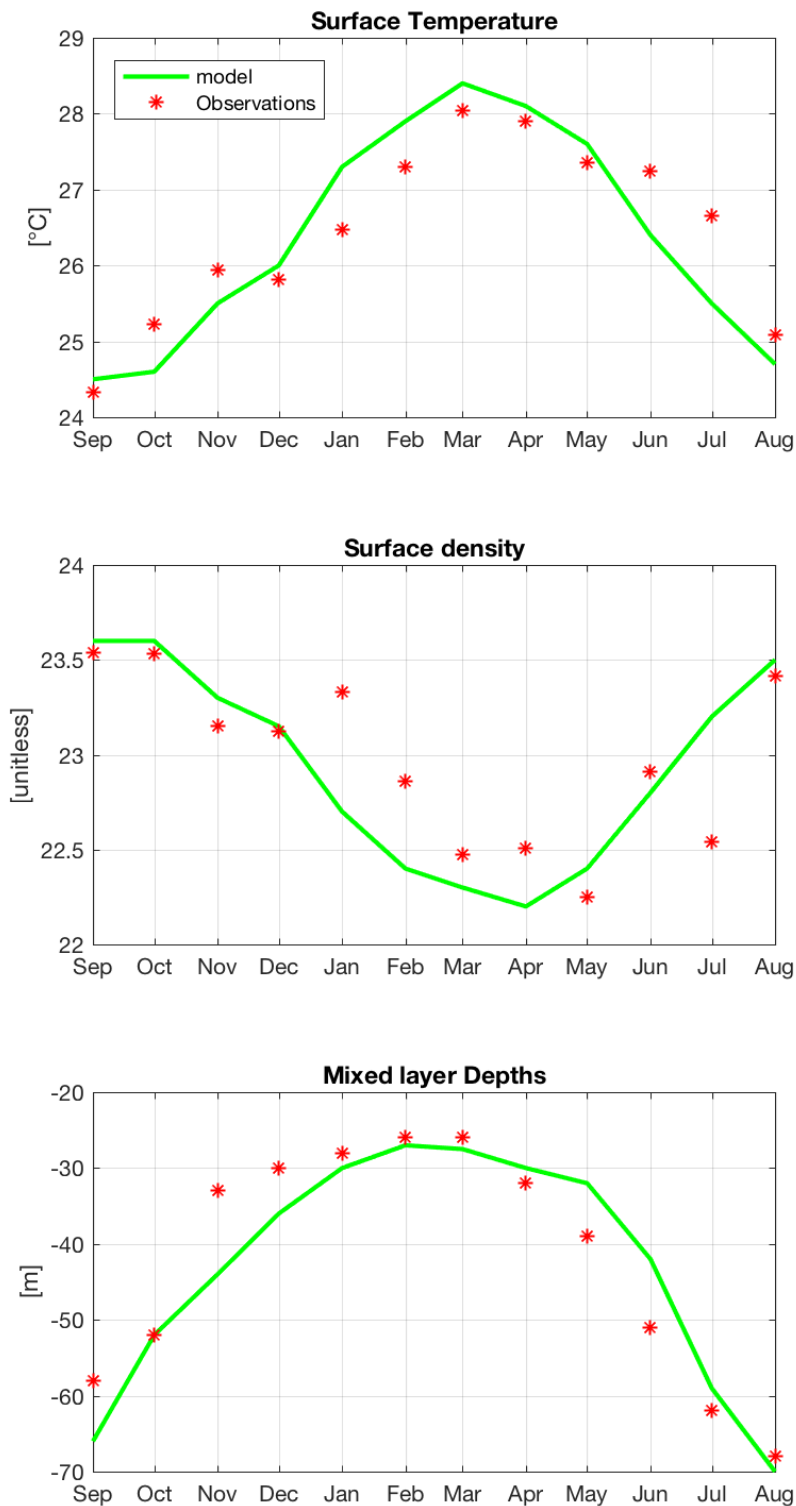
Figure 3 in SM Evolution of monthly averaged (a) sea surface temperature (SST), (b) surface density and (c) mixed layer depths (MLD) from September 2014 to August 2015 predicted by the model (green line) and calculated with climatologies (WOA13 for SST and Surface density, and de Boyer Montegut et al., 2004 for MLD)

4 - P6, section 3.1.1: A major difference between the two simulations is the lack of DIP accumulation in the top 200m or so of the water column when diazotrophy is activated. I understand that in the top 50 or 70m of the water column where

nitrogen fixation is significant. However, below that depth range, DIP consumption is being increased in WMA without any significant N fixation. This should be explained.

Section 3.1.1 describes Fig. 3 a)-b)-c) in order to correlate the vertical profiles of nutrients and that of N2 fixation. As mentioned by Referee #2, the main difference between simWMA and simWGY remains in the upper 0 to 70m layer, where N2 fixation is significant and DIP depleted in simWMA while a DIP accumulation is observed in simWGY without N2 fixation.

However, we are not sure to fully understand the second point mentioned by Referee #2 regarding DIP consumption. We can indeed notice in Fig. 3 b) that the phosphacline in simWMA starts at 70 m where the DIP concentration starts to increase gradually until 300 m depth. This means that below 70 m (which corresponds to the bottom of the photic zone), where there is indeed no more N2 fixation (Fig. 3 c)), DIP is less consumed by organisms and accumulates, and this is why we observe the beginning of the phosphacline at this depth. In simWGY, without N2 fixation, DIP concentrations are higher in the upper surface layer than in simWMA because the system is N-limited, thus preventing P consumption. This is why the organisms develop deeper, around the depth of the nitracline in simWGY.

5 - P7, section 3.1.2: In the WGY setup, a very deep but intense DCM is predicted which is as strong as in the WMA configuration. Yet PP (and thus phytoplankton growth rates) is very very small in the DCM. How can you explain that, since grazing rates should be similar?

As mentioned by Referee #2, grazing kinetics are the same in simWMA and simWGY but the effective grazing rates are not necessarily the same since they are also function of predator and preys concentrations. Moreover, though nitrogen fixation only occurs at simWMA, the DCM intensity is the same in both regions. The vertical profiles of PP and Chl a show that PP values are not proportional to the DCM concentration, and that the PP and Chla maxima do not necessarily match (it matches for WGY but not for WMA). For the same DCM intensity, PP values are indeed much lower in simWGY than in simWMA. A possible explanation for this lies in the fact that the composition of both DCM are quite different: the DCM in simWMA corresponds to high C biomass (i.e. the Chl:C ratios of autotrophs is quite low), while the DCM in simWGY is composed by less autotrophs which have higher Chl:C ratios (since they develop deeper where light is lower, they have to generate more Chl a pigments to increase their C fixation rate).

6 - P8, sections 3.2.1 and 3.2.2: I understand that the lack of data prevents a detailed and complete validation of the seasonal dynamics predicted by the model. However, is it really impossible to do some basic validation using for instance satellite data for Chl, historical data for nutrients averaged over a regional box which would be valid since the model setup is not representative of a specific station but rather of a broad region.

We agree with Referee #2 that such a validation would have potentially brought more confidence in the seasonal variations calculated by our model. However, in this oligotrophic to ultra-oligotrophic area, Chl a variations at the surface are very low and rarely observed in data, compared to other systems where large Chl a variations can be observed at the ocean surface. Moreover, the variations observed in the DIP concentrations in the model (Fig. 4, b)) remain in a range values below the quantification limit of the classical DIP measurements, meaning that this slight variations cannot commonly be observed *in situ.* Moreover, the complete list of previous cruises in this area is detailed in Fumenia et al. uner rev. showing that we are far to get an annual survey in this under sampled area. However, despite of the absence of possible validation, we considered that the results provided by the model were plausible and interesting enough to be analyzed and published in the present paper.

7 - P8, lines 16-18: I don't understand that statement. I don't understand why the vertical resolution of the fluxes is not the same as the vertical resolution of the state variables. It should be clarified.

The standard model outputs of the biogeochemical model consist in the vertical profiles of the different concentrations (pools) of all the state variables represented in the model, as a function of time. The dynamics of each state variable is calculated in the model thanks to a combination of several fluxes, which represent the different biological processes controlling the dynamics (growth, grazing, mortality, nutrients uptakes, exudation, etc..). However, the systematic storage of the numerical values of all these fluxes is impossible accounting for the computer memory this would require. Instead, we must select some fluxes and depths of interest to be saved. Since no significant N2 fixation or PP rates were measured below 100 m, we did not save the numerical values of these fluxes below 100 m.

The following sentence has been added in the revised manuscript at the end of section 3.2.1 :

«[..] Accounting for the huge computer memory this would require, the values of the different biogeochemical fluxes calculated by the model are not systematically saved. As a result, numerical values of fluxes are saved at a lower vertical resolution than concentrations (pools). For this reason why [..] »

8 - P 9, section 4.1.1: the study suggests that DIP accumulation might by explained by the lack of nitrogen fixation. However, it does not explain why there are small rates of nitrogen fixation at WGY.

We understand the point raised here by Referee #2 and acknowledge that the reason of the very low rates of N2 fixations observed in WGY are not detailed in this section. While this point is related to one of our main assumption, the scope of

this paper was not to provide explanations of the N2 fixation gradient observed during the cruise, as it was already described in Bonnet et al. (2017), Moutin et al. (2018) and Guieu et al. (2018). In order to bring some additional explanation to the reader, the following sentences have been added to the revised manuscript :

« Because of the high Fe requirement of diazotrophs (Paerl et al., 1987; Rueter et al., 1990), the low Fe availability in WGY is assumed to prevent or significantly limit N2 fixation in the South Pacific gyre (Moutin et al., 2008; Guieu et al., 2018, Moutin et al., 2018). By contrast, the high Fe availability in WMA is assumed to favor the growth of nitrogen fixers. Guieu et al. (2018) indeed measured high DFe concentrations in the photic layer in WMA provided by abnormally shallow hydrothermal sources (around 500 m deep) in the WTSP. Due to very low N2 fixation measured in WGY (Bonnet et al., 2018), autotrophs organisms are N-limited, leading to a lower PP than in WMA, which results in a higher DIP accumulation in the photic layer since DIP is less consumed by organisms. »

9 - P10, lines 21-26: The authors performed an additional sensitivity run in which they suppress TRI but not UCYN. In that case, the DCM is shallower and the model skill is improved. However, does that lead to a complete exhaustion in DIP at the surface? In that case, the conclusion of the paper would be quite different since it would mean that low rates of N fixation as observed in WGY do not explain the DIP accumulation. Results from that sensitivity test should be presented in the manuscript.

We thank Referee #2 for this interesting comment. This simulation led to the following conclusions:

-N2 fixation was significantly lower than the one in simWMA, but still 4 times higher than the rates calculated in simWGY.

- DIP concentrations were lower than in simWGY but still more than 10 times higher than in simWMA. In other words, this simulation did not lead to a complete exhaustion of available P in the upper surface layer.

We realize that the way this simulation is presented at the end of Section 4.1.2 might suggest that it is a better proxy of the ecosystem sampled in WGY than simWGY, but this is not the case. It is rather an intermediate system, with higher N2 fixation rates than those measured in WGY. We finally decided to rephrase the paragraph of interest without presenting the figures, as these figures would not contribute to illustrate one of our major result but concerns only a simulation used to argue the deeper DCM predicted in simWGY compared to the one measured in WGY. We reckon that presenting results from an additional simulation would confuse the guideline of the article.

« The results of this intermediate simulation (not shown) indicate low surface PP rates and POC concentrations, in agreement with those measured in WGY. Moreover, dissolved P is still available in the photic zone (though at concentrations lower than for simWGY) even if the calculated N2 fixation rates were slightly higher than the measured ones. In addition, the DCM (located around 150 m) and the nutriclines were shallower than in simWGY (i.e. without any diazotrophs). This simulation can thus be considered like an intermediate system between simWMA and simWGY, and confirms the close link between N2 fixation fluxes and P availability. »

10 - P11, lines 10-21: the results of the sensitivity experiment mentioned in that paragraph should be included in the study as they directly support one the main conclusions, i.e. the decoupling between the phosphacline and the nitracline explains the high N fixation rates at WMA.

As this point on the <u>causality between N fixation and preferential P regeneration</u> was mentioned by the two referees, we made the same answer :

As mentioned above, we agree with Referee #1 regarding the lack of proof in the previous version of the manuscript to support the assumption of the P availability controlling N2 fixation and the preferential P regeneration leading to a shallower phosphacline than the nitracline. To remedy it, we decided to add the results of the simulation without the preferential P regeneration which were compared to the simWMA, in order to clearly show that, without that preferential regeneration, the system did not provide the sufficient conditions to support N2 fixation as observed in the field in the WMA region.

The following figures have been added to the revised manuscript in addition with the following paragraph, inserted at the end of Section 4.2.2 :

« To illustrate how the discrepancy between nitracline and phosphacline depths can be attributed to preferential P regeneration, DIN and DIP concentrations and N2 fixation rates in simWMA calculated with and without preferential P regeneration (i.e. preferential hydrolysis of P particulate matter) have been compared (Fig. 5). This figure shows the deepening of the phosphacline in the simulation without preferential P regeneration. More importantly, without preferential P regeneration, the phosphacline depth is deeper than the MLD at 70m, which prevents DIP input in the surface layer during winter mixing, and leads to a strong limitation of diazotrophs by P. This stronger P-limitation without preferential P regeneration can also be observed at the cellular scale by analyzing the intracellular P quota of N2 fixers. In the simulation without preferential P regeneration, the relative intracellular quota of P in TRI and UCYN are in average respectively 8 and 16 times lower than with preferential P regeneration. As N2 fixation alleviates N limitation for diazotrophs, their growth is thus limited by P availability. The significant decrease in relative intracellular P quotas has

therefore a significant impact on their growth, and consequently explain the lower N2 fixation rates showed in Figure 5, c). »
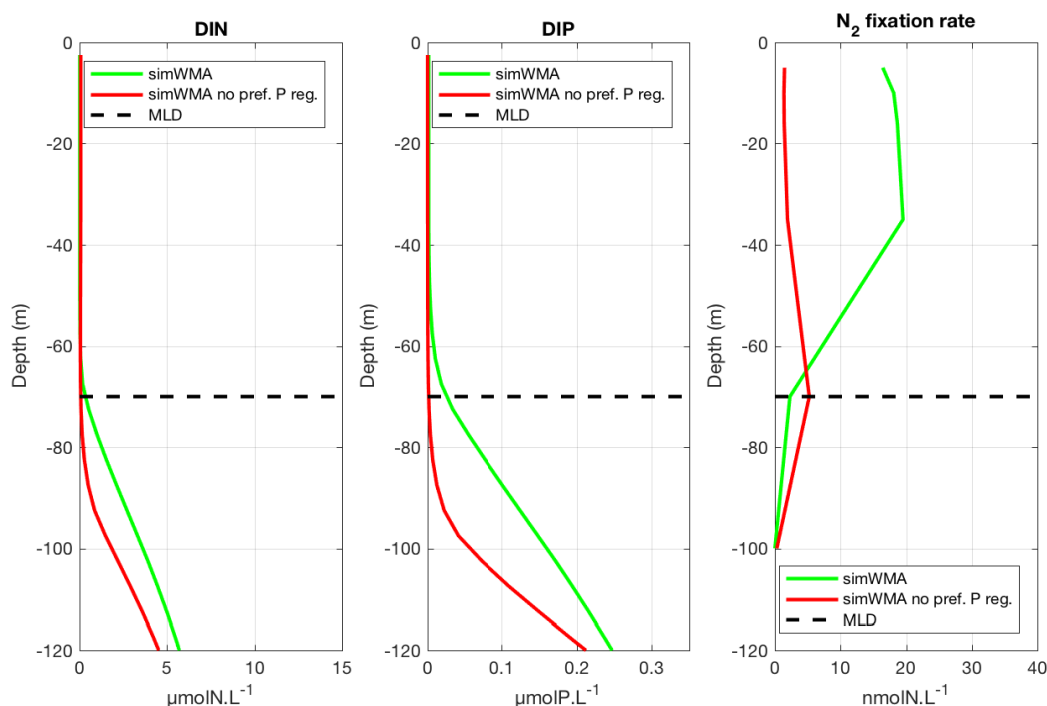

Figure 4 (inserted as Figure 5 in the revised manuscript) Vertical profiles of (a) dissolved inorganic nitrogen (DIN), (b) dissolved inorganic phosphorus (DIP), (c) N2 fixation rates for the simulation with diazotrophy, as a proxy of the WMA region (simWMA with the preferential P regeneration (in green) and without the preferential P regeneration (in red). The horizontal black dashed line represents the depth of the maximum mixing layer calculated at 70 m depth.

11 - P13, section 4.4: This section is a little bit too long and remains very descriptive.

We acknowledge that this section is quite long and it has been shortened and rewritten as follows in the revised manuscript:

To date, the WTSP, and more generally the South Pacific Ocean, is much less studied than the North Pacific Ocean which has been sampled since the late 1980s within the framework of the Long-term Oligotrophic Habitat Assessment (ALOHA) near the Hawaii islands. ~~The high frequency Hawaii Ocean Time- series (HOT) program provides a long-term database from the 1990s on oceanic variability regarding physical, biological and biogeochemical features in the North Pacific Ocean (Karl et al., 1996).~~ The South Pacific has been sampled from west to east during the BIOSOPE \citep{claustre_introduction_2008} and OUTPACE (Moutin et al., 2017, this issue) French oceanographic cruises and many other cruises (e.g. Moisander et al., 2012, and the cruises involved in the GLODAPv2 project (Olsen et al., 2016)) providing a spatial (Fumenia et al., under rev., this issue), but not a temporal overview of the south tropical Pacific. To date, the seasonal variations were only studied during the DIAPALIS cruises (http://www.obs-vlfr.fr/proof/vt/op/ec/diapazon/dia.htm) in several stations located in the MA close to New Caledonia. By means of our one-dimensional model, we can analyze the annual variability of the entire ecosystem implemented in the model in order to corroborate, or not, certain hypotheses raised from the OUTPACE data analysis. ~~Figure 4 shows the temporal variations of the [DIN, DIP,N2fix, Chl \underline{a} and POC]^{simWMA} over 3 years of simulation in the 0-200 m layer.~~

Seasonal variations obtained in simWMA (Figure 4) allow to trace the annual "history" of the WMA region: during the winter period, vertical mixing intensifies and replenishes the surface layer in DIP but not in DIN, as the nitracline is deeper than the MLD (70 m), whereas the phosphacline is shallower (Figures 3 a) and b)). [..]"

Diazotrophy as the main driver of ~~planktonic production and biogeochemical C, N, P cycles~~ the oligotrophy gradient in the Western Tropical South Pacific Ocean : results from a one-dimensional biogeochemical-physical coupled model

Audrey Gimenez[1], Melika Baklouti[1], and Thierry Moutin[1]

[1]Aix Marseille Université, CNRS/INSU, Université de Toulon, IRD, Mediterranean Institute of Oceanography (MIO) UM110, 13288, Marseille, France

Correspondence: A. Gimenez (audrey.gimenez@mio.osupytheas.fr)

Abstract. The Oligotrophy to UlTra-oligotrophy PACific Experiment (OUTPACE) cruise took place in the Western Tropical South Pacific (WTSP) during the austral summer (March-April 2015). The aim of the OUTPACE project ~~is~~ was to investigate a longitudinal gradient of biological and biogeochemical features in the WTSP, and especially the role of N_2 fixation on the C, N, P cycles. Two contrasted regions were considered in this study : the Western Melanesian Archipelago (WMA), characterized by high N_2 fixation rates, significant surface production and low dissolved inorganic phosphorus (DIP) concentrations, and the south Pacific gyre (WGY), characterized by very low N_2 fixation rates, surface production and high DIP concentrations. Since physical forcings and mixed layer dynamics in both regions were similar, it was considered that the gradient of oligotrophy observed *in situ* between WMA and WGY was not explained by differences in physical processes but rather by differences in biogeochemical processes. A one-dimensional ~~biogeochemical – physical~~ physical – biogeochemical coupled model was used to investigate the role of N_2 fixation in the WTSP by running two identical simulations, only differing by the presence (sim^{WMA}) or ~~not~~ absence (sim^{WGY}) of diazotrophs. We evidenced that the nitracline and the phosphacline had to be respectively deeper and shallower than the Mixed-layer Depth (MLD) to bring N-depleted and P-repleted waters to the surface during winter mixing, thereby creating favorable conditions for the development of diazotrophs. We also concluded that a preferential regeneration of the detrital phosphorus (P) matter was necessary to obtain this gap between the nitracline and the phosphacline depths, as the nutricline depths significantly depend on the regeneration of organic matter in the water column. Moreover, the model enabled us to highlight the presence of seasonal variations in primary production and P availability in the upper surface waters in simWMA, where diazotrophs provided a new source of nitrogen (N) to the ecosystem, whereas no seasonal variations were obtained in simWGY, in absence of diazotrophs. These main results emphasized the fact that surface production dynamics in the WTSP is based on a complex and sensitive system which depends on one hand on physical processes (vertical mixing, sinking of detrital particles), and on the other hand on biogeochemical processes (N_2 fixation, remineralization).

1 Introduction

The efficiency of the oceanic carbon (C) sequestration depends upon a complex balance between the organic matter production in the euphotic zone and its remineralization in both the epipelagic and mesopelagic zones. The growth of autotroph organisms, and therefore the assimilation of CO_2, is strongly linked to the nutrients' availability in the ocean surface layer (de Baar, 1994). Although nitrate (NO_3^-) and ammonium (NH_4^+) are the two main N sources taken up by autotrophs, their concentrations remain very low in the oligotrophic ocean and often growth-limiting in most of the open ocean euphotic layer (Falkowski et al., 1998). In contrast to NO_3^- and NH_4^+, the dissolved dinitrogen (N_2) gas in seawater is very abundant in the euphotic zone and could be considered as an inexhaustible N source for the marine ecosystems. Some prokaryotic organisms (Bacteria, Cyanobacteria, Archaea), commonly called diazotrophs or 'N$_2$-fixers', are able to use this gaseous N source by converting it into a usable form (i.e. NH_3) due to the nitrogenase enzyme system (Zehr and McReynolds, 1989; Zehr and Turner, 2001). In addition to providing a new source of nitrogen for themselves, diazotrophs release ~~dissolved N~~ a fraction of the fixed N in the dissolved pool under the form of NH_4^+ and dissolved organic N (DON) in the surface waters (Bronk and Ward, 2000; Mulholland et al., 2004, 2006; Benavides et al., 2013; Berthelot et al., 2015) and thus contribute to sustaining life and potentially ~~to~~ C export. This new N input would seem to bring a positive advantage to the C biological pump since it would reduce the ~~characteristic~~ N limitation ~~in the oligotrophic regions~~ for the phytoplankton and thus enhance primary production in oligotrophic regions. However, even if ~~the~~ diazotrophs are not limited by atmospheric N_2, their growth is controlled by other factors, including the availability of dissolved iron (DFe) and dissolved inorganic phosphate (DIP) (Moutin et al., 2005; Karl and Letelier, 2008). Moreover, chemostat experiments have highlighted that N_2 fixation activity was highly dependent on the circadian clock and that the success of non-diazotrophs and diazotrophs depend on the interplay between light intensity and DIN concentration, and the competition for those resources (Rabouille et al., 2006; Agawin et al., 2007). In a synthesis paper, Gruber (2004) reminds that over the last decades, the work on N_2 fixation and the diversity of diazotroph organisms has shown a significant contribution of N_2 fixation ~~in~~ to primary production in the global ocean (Falkowski, 1997; Gruber and Sarmiento, 1997; Capone et al., 1997; Karl et al., 2002), thereby calling into question the classical paradigm of the N limitation in the open ocean (Zehr and Kudela, 2011).

Furthermore, in the current context of climate change, Polovina et al. (2008) showed that global warming would intensify the stratification of surface waters in tropical and subtropical oceans, further reducing nutrient concentrations in the euphotic layer. It is therefore crucial to study in detail the coupling of the biogenic element cycles in the oligotrophic regions to better understand all the interactions between the processes involved in the surface production and therefore in the C biological pump. The Oligotrophy to UlTra-oligotrophy PACific Experiment (OUTPACE) cruise has as its main objective to study how production, mineralization and export of organic matter, and associated biogenic elements C, N, P biogeochemical cycles, depend on the N_2 fixation process. Along the transect covered during the OUTPACE cruise, a ~~biogeochemical and biodiversity gradient was observed from west to east in terms of surface productivity and nutrients availability. A~~ longitudinal gradient of DIP availability was ~~also~~ observed from low concentrations in the Melanesian Archipelago (MA) to higher concentrations in the South Pacific Gyre (SPG) (Moutin et al., 2018), closely related to an opposite gradient of primary production (Van Wambeke

et al., 2018) and N$_2$ fixation rates (Bonnet et al., 2017; Caffin et al., 2018). In the framework of the OUTPACE study, it appeared crucial to investigate in detail the role of N$_2$ fixation in the surface production, using a modeling approach combining a 3D modeling study at regional scale (Dutheil et al., 2018) and a process-focused study using a one-dimensional model (this work), with the aim of explaining the contrasted ecosystems and biogeochemical cycles observed in the WTSP. Since
5   experimental studies highlighted the significant contribution of N$_2$ fixation as a new source of N for planktonic ecosystems in the surface layer (Martínez et al., 1983; Karl et al., 1997; Capone et al., 2005), the process of diazotrophy associated (or not) with explicitly-represented diazotroph organisms has been implemented in numerous biogeochemical models in the last decades. As a result, more and more modeling studies have been investigating the role of diazotrophy at global scale (Moore et al., 2002, 2004; Monteiro et al., 2011), at regional scale (Coles and Hood, 2007; Zamora et al., 2010), at local scale (Fennel
10   et al., 2002; Gimenez et al., 2016) or more specifically at population scale~~, such as the work on *Trichodesmium* sp. by~~ (Rabouille et al., 2006; Grimaud et al., 2013). While three-dimensional (3D) models provide a general view of the studied ecosystems, computational costs often restrict the spatial and temporal resolutions and/or the complexity of the biogeochemical model. By contrast, one-dimensional models only provide a local view, but enable an accurate study of the biogeochemical processes deconvoluted from horizontal marine dynamics, at physiological (days) and ecological (months to years) time scales. In this
15   work, we used a one-dimensional physical-biogeochemical coupled model to simulate the dynamics of the complex ecosystems observed during the OUTPACE cruise, and built two simulations to represent each of two highly contrasted regions sampled during the OUTPACE cruise, namely the Western Melanesian Archipelago (WMA) and the Western South Pacific Gyre (WGY) (see Figure 2). One of these simulations was run with diazotrophy as a proxy of the WMA region, and the second without diazotrophy as a proxy of the WGY region, to implicitly take into account the role of DFe allowing N$_2$ fixation in the MA but
20   preventing it in the gyre (Moutin et al., 2008; Bonnet et al., 2017). The purpose of this study is to investigate the direct and/or indirect role of N$_2$ fixation in surface planktonic production and biogeochemical C, N, P cycles, with the aim of determining whether the main biogeochemical differences observed in the MA and in the SPG areas can be explained or not by diazotrophy.

2   Methods

2.1   Strategy of the OUTPACE cruise and of the modeling study

25   The OUTPACE cruise was carried out between 18 February and 3 April 2015 from Noumea (New Caledonia) to Papeete (French Polynesia) in the western tropical South Pacific (WTSP) (Figure 2). Two types of stations were sampled : fifteen short-duration (SD) stations dedicated to the study of the longitudinal variations of biodiversity and biogeochemistry~~cal gradient~~, and three long-duration (LD) stations where Lagrangian experiments and several additional measurements (such as measurements on the settling of organic matter using sediment traps) were carried out during 6 days. The details of all the operations conducted
30   at the different stations are summarized in Moutin et al. (2017), with a focus on the Lagrangian strategy followed at the LD stations in de Verneil et al. (2017). Along the eastward transect from the MA to the SPG, three areas were considered regarding ~~there~~ their different biogeochemical characteristics: the western MA (WMA), the eastern MA (EMA) and the western gyre (WGY) waters Moutin et al. (2018). In this study, we focused on the comparison of the two most ~~widely~~ contrasted areas,

3

namely the WMA and the WGY (Figure 2). While both WMA and WGY present extremely low nitrate concentrations in the photic layer, the WMA presents higher surface production, higher N_2 fixation rates and lower phosphate concentrations than WGY.

As already mentioned, in order to investigate the role of N_2 fixation in the WTSP, we ran two identical simulations, one including the process of diazotrophy, hereafter named 'simWMA', and the second without this process, hereafter named 'simWGY'. Except for the process of diazotrophy, the two simulations were strictly identical regarding the atmospheric forcings, the initial conditions, the model formulation and the parameter values. ~~Model outputs are compared to the observations gathered during the OUTPACE cruise at WMA and WGY.~~ The assumption made by using a unique set of atmospheric forcings for two regions significantly far away is first based on the *in situ* climatological data reported in Moutin et al. (2018). These authors showed that the vertical dynamics of the water column, and especially the depths of the mixed layer were similar throughout the year in all the WTSP (see Figure SM1 in supplementary material). In addition, the atmospheric forcings calculated by the WRF atmospheric model at WMA and WGY were also very similar (see Figure SM2 in supplementary material). Furthermore, we also compared two simulations ran with the respective atmospheric forcings calculated at WMA and WGY and did not observe any significant difference, nor in the water column dynamics, neither on the biogeochemical cycles.

The methods used to measure dissolved inorganic nitrogen (DIN), DIP, N_2 fixation (N_2 fix), Chlorophyll a (Chl a), Primary production (PP) and Particulate organic carbon (POC), as well as the corresponding data, are fully described in the companion paper by Moutin et al. (2018). For ease of reading, the following abbreviations will be used: for a given variable "X", abbreviations XsimWMA and XsimWGY will be used for the model outputs, respectively with and without diazotrophy, and XobsWMA and XobsWGY for the experimental data measured at WMA and WGY, respectively.

Model outputs were compared to the observations gathered during the OUTPACE cruise at WMA and WGY. For each profile presented in the Results section, we plotted the discrete values of the data collected at WMA and WGY (circles), and ~~an~~ the average over the respective sampling periods of WMA and WGY for the model results (~~simWMA,~~ from 02-21-2015 to 03-02-2015 for simWMA, and ~~simWGY,~~ from 03- 21-2015 to 03-31-2015 for simWGY). Both simulations were run over ten years, ~~as mentioned earlier~~. Since a cyclic steady-state was reached in the near-surface layer after three years, the vertical profiles of the third year of simulation (solid line) are presented for both simWMA and simWGY. Moreover, since the outputs of simWMA provided interesting information regarding the role of diazotrophs in fueling the system with new N inputs, the ten vertical profiles of the ten-year run are all presented in the Results section.

2.2 The biogeochemical model

The biogeochemical model implemented in this work is embedded in the modular numerical tool Eco3M (Baklouti et al., 2006). It was based on the Eco3M-MED model (Alekseenko et al., 2014) to which two diazotrophs were added for studying N_2 fixation fate in the frame of a mesocosm experiment in the Noumea lagoon (Gimenez et al., 2016). ~~and was first used during an in situ mesocosm experiment in the Noumea lagoon (Gimenez et al., 2016). To answer the questions raised during that project, we added two diazotroph organisms to the Eco3M-Med model (Alekseenko et al., 2014). For the present study,~~

4

and in order to improve the model, some features of the original model presented in Gimenez et al. (2016) were modified and some new features were introduced (see Section 2.2.2).

2.2.1 General backgrounds

~~To summarize, t~~The model includes eight Planktonic Functional Types (PFT): four autotrophs (a large and a small classic phytoplankton and a large and a small nitrogen fixer), three ~~consumers~~ grazers (zooplankton) and one decomposer (heterotrophic bacteria). ~~All~~ Each of them ~~are~~ is represented in terms of several concentrations (C, N, P and chlorophyll ~~concentrations~~ for phytoplankton) and an abundance~~s~~ (cells or individuals per liter) (Mauriac et al., 2011). Each PFT is ~~For ease of reading, the living compartments are abbreviated and populations are~~ represented by emblematic organisms indicated in brackets, and for ease of reading, living compartments are abbreviated as follows: TRI for the large diazotrophs (*Trichodesmium* sp.), UCYN for the small diazotrophs (unicellular nitrogen fixers), PHYS for the small autotrophs (pico- and nanoplankton), PHYL for the large autotrophs (diatoms), HNF for nanozooplankton (heteronanoflagellates), CIL for microzooplankton (cilliates) and COP for mesozooplankton (copepods). For all the non-diazotrophic features and in agreement with literature (e.g. Luo et al. (2012)), it has been considered that a Trichodesmium trichome was equivalent to 100 PHYL cells ~~TRI are parameterized as 100 PHYL cells (assuming that a trichome includes 100 cells; Luo et al., 2012), and UCYN as PHYS~~ and that a UCYN cell was equivalent to a PHYS cell. Yet, the conversion factor of 100 between TRI and PHYL was only applied for extensive parameters, i.e. those depending on biomass. Intensive parameters were set equal to those of PHYL, except for the specific growth rate which was instead averaged from literature since it has been experimentally demonstrated that it was lower than that of PHYL (Mulholland and Bernhardt, 2005; Hutchins et al., 2007). Parameter values, whether new or differing from those of Alekseenko et al. (2014), are given in SM: table 1.

In the model, N_2 fixation rates depend on the nitrogenase enzyme activity (Nase) (Rabouille et al., 2006; Gimenez et al., 2016); nitrogen fixation is the result of a balance between the increase and the decrease of the enzyme activity, which is controlled by the intracellular content ~~of~~ in C and N, and by the NO_3^- concentration. The more the cell is deprived of nitrogen, the more the nitrogenase activity is enhanced, but under the control of the intracellular C content which plays the role of "energy regulator", being itself tightly linked to the daily light cycle (Rabouille et al., 2006). Further details regarding the implementation of diazotrophy in the model are available in Gimenez et al. (2016). All the compartments and fluxes implemented in the model are summarized in Figure 1.

2.2.2 New features of the model

. ~~For the present study, and in order to improve our model, some features of the original model presented in (Gimenez et al., 2016) were modified and some new features were introduced : unlike the previous version (Gimenez et al., 2016) including only one compartment of detrital material (see Table 1 in supplementary material)~~ Since the Gimenez et al. (2016) modelling study was focusing on a mesocosm experiment, the assessment of the model skills was incomplete. With the new set of data provided by the OUTPACE cruise, some features of the original model were improved and some new features were introduced to correct the model major flaws or to add some realism in the model. To improve the representation of the nutricline depths

which depend on the sinking of the detrital organic matter and its mineralization in the water column, we included two size classes of detrital matter associated with two different sinking rates, while the previous version (Gimenez et al., 2016) only included a single compartment of detrital material (see Table 1 in supplementary material). The large detrital particles (DETL) are fueled by the death of COP, their fecal pellets and by the quadratic mortality of PHYL. The small detrital particles (DETS) are fueled by the hydrolysis of DETL and by the linear mortality of PHYL, TRI and CIL, whereas the mortality of PHYS, UCYN, HNF and BAC fills the compartment of dissolved organic matter (DOM). The sinking rates for DETS and DETL are 1 m.d^{-1} and 25.0 m.d^{-1}, respectively.

~~The intracellular C:N:P mean ratios of BAC and HNF, which were initially equal to 50:10:1 (Alekseenko et al., 2014), were finally set to the classical Redfield ratios of 106:16:1, like the other organisms.~~ While several studies have shown that the intracellular C:N:P ratios in heterotrophic bacteria tend to be below Redfield values as they were enriched in N and P (Bratbak, 1985, Goldman and Dennett, 2000, Vrede et al., 2002), more recent studies suggest that these ratios could be higher than 50:10:1 and highly variables in response to physical, chemical and physiological conditions (Cotner et al., 2010, Martiny et al., 2013 ; Zimmerman et al. 2014). This led us to replace the 50:10:1 ratios used so far in the model for bacteria and HNF by the Redfield 106:16:1 ratio as for the other PFTs represented in the model. It is reminded however that the PFT's stoichiometry is flexible in the model and that the Redfield ratios are only used to link together the limits of the ranges of C, N and P intracellular quotas, (i.e. $Q_C^{min} = 106\,Q_P^{min}$, $Q_C^{max} = 106\,Q_P^{max}$, see Table 1 in supplementary material) thereby allowing a large variety of possible C:N:P ratios in PFTs. Moreover, in this oligo – to ultraoligotrophic region, the regeneration of the organic matter is crucial ~~(specified in more detail in Sect. **4.2**~~ to maintain the ecosystem balance, and certain modifications have been made in this regard : 1) to indirectly take into account the enhanced consumption of organic P through the activity of extracellular alkaline phosphatase produced by bacteria in oligotrophic areas (Perry, 1972, 1976; Vidal et al., 2003), ~~production of the extracellular phosphatase alkaline occurring in such oligotrophic areas due to bacteria (enhancing the consumption of organic P, (perry et al., 1972; 1976; Vidal et al., 2003),~~ all the half-saturation constants (Ks) for the DOP uptake were divided by one order of magnitude, 2) the hydrolysis rate of the particulate organic P was modified (from 0.4 to 2.0 d^{-1}) to increase the regeneration of P compared to C and N in this P-depleted area (detailed in Section 4.2.2).

2.3 One-dimensional physical model and forcings

The biogeochemical model has been coupled with the one-dimensional physical model described in Gaspar (1988). Th~~e~~is model ~~considers the vertical discretization of the time evolution~~ solves the conservation equations for ~~temperature~~ heat, salinity, momentum and kinetic energy. The grid cell ~~size~~ is 5 m high from surface to 200 m, and 40 m high from 200 to 2000 m. It uses a simple eddy kinetic energy parametrization with a turbulence closure scheme, resolved by the turbulent kinetic energy (TKE) equation (Gaspar et al., 1990).

The atmospheric forcings (i.e. the sensible and latent heat fluxes, the short and long wave radiation and the wind stress) for the physical model were provided by the Weather Research Forecast (WRF) model (Shamarock et al., 2008), with a spatial resolution of 15 km and a time step of 6 hours. Boundary conditions for the WRF model are provided by the American Global Forecast System (GFS) model (National Center for Environmental Prediction/National Center Environmental Prediction -

NCAR / NCEP) analyzes. These analyzes correspond to a correction of the forecast using a larger number of observations during the data assimilation cycle. The WRF model is forced every 6 hours by analyzes during the processing. Only a single year of atmospheric forcing has been extracted (from September 2014 to August 2015), which was applied on a cyclical basis during the ten-year simulation. This one-year period has been arbitrarily chosen so as to cover the period from the winter mixing preceding the OUTPACE cruise to the next winter. The comparison between some physical outputs (i.e. surface temperature, surface density, mixed layer depth) and climatological *in situ* observations allowed to ensure that the one-dimensional physical model was relevant to address our scientific question (see Figure SM3 in supplementary material).

2.4 Initialization for the one-dimensional coupled physical-biogeochemical model

The initial profiles of temperature (T), salinity (S) T, S, DIN and DIP were constructed by interpolating mean field data from the WOA13 climatology database (Locarnini et al., 2013; Zweng et al., 2013) at the exact location of WMA (19° 13.00 S 164° 29.40 W). Initial dissolved organic matter concentrations, BAC and autotroph abundances were obtained from the vertical profiles measured in WMA: to represent due to the homogeneity of the surface layer due to winter mixing, the 0-70 m mean value was applied on the 0-70m layer of the initial vertical profiles. Below 70 m, initial concentrations were the same as data. Since the model includes variable stoichiometry for organisms, initial intracellular contents of non-diazotroph organisms were set up to 50 %, 25 % and 75 % for of their respective intracellular quota ranges of in C, N and P. While there was no difference for in initial C, N, P intracellular contents of C and P between diazotroph and non-diazotroph organisms, initial N intracellular contents of diazotrophs were set up to 50% to take into account their metabolic advantage of fixing N_2. Initial concentrations of detrital compartments are nil. Initial zooplankton abundances were obtained from the BAC abundances using a BAC:HNF:CIL = 1000:100:1 ratio. In simWGY where diazotrophs are removed, initial abundances and biomasses of TRI and UCYN were respectively transferred in PHYL and PHYS compartments, in order to strictly preserve the same initial biomasses and abundances in the two simulations.

3 Results

3.1 Vertical dynamics of the main biogeochemical stocks and flux

3.1.1 Nutrients availability and N_2 fixation

DIN and DIP concentrations are presented in Figure 3 a) and 3 b). Strictly, DIN is the sum of nitrate, nitrite and ammonium (DIN = $[NO_3^-]$ + $[NO_2^-]$ + $[NH_4^+]$). However, since $[NO_2^-]$ and $[NH_4^+]$ were negligible compared to $[NO_3^-]$, DIN was assimilated to $[NO_3^-]$. In the same way, DIP is strictly the sum of hydrogen phosphate and orthophosphates (i.e. DIP = $[HPO_4^{2-}]$ + $[PO_4^{3-}]$), but it is here assimilated to orthophosphates ($[PO_4^{3-}]$). From the surface to 70 m depth, DIN^{obsWMA} and DIN^{obsWGY} are below the quantification limit (i.e. 0.05 μM). DIN^{simWMA} and DIN^{simWGY} do not show any significant difference in the surface layer and range from 0.02 to 0.04 μM and from 0.03 to 0.04 μM for DIN^{simWMA} and DIN^{simWGY}, respectively. Even if the concentrations of DIP are low in the surface layer (below 0.2 μM), some differences can be seen between WMA and

WGY for both model outputs and data. Figure 3, b) shows a concentration around 0.2 μM for DIP^{obsWGY} from the surface to 120 m, whereas DIP^{obsWMA} is very low, with values below the quantification limit (0.02 μM) at the subsurface, with a steady increase up to 0.5 μM at 300 m depth. Regarding the model outputs, DIP^{simWMA} is close to zero from the surface to 60 m, and reaches a value of 0.70 μM at 300 m depth. DIP^{simWGY} is significantly higher than DIP^{simWMA}, with a homogeneous concentration of 0.16 μM from the surface to 175 m depth, and then increases slightly up to 0.7 μM at 300 m.

The vertical profiles of DIN^{simWMA} and DIP^{simWMA} show a deeper nitracline (around 75 m depth) than phosphacline (around 60 m depth), as observed with data. Note that to reproduce this discrepancy within the model, it has been necessary to introduce a preferential regeneration of the detrital matter in P compared to C and N in the biogeochemical model, a point thereafter detailed in Section 4.2.2. Regarding the WGY region, the observed and simulated nitracline and phosphacline are deeper than in the WMA region. The simulated nutriclines are however deeper than those measured (around 140 m and 125 m for the simWGY nitracline and phosphacline depths, respectively). While the simulated and the measured nitracline depths are both around 75 m at WMA, DIN^{simWMA} is higher than DIN^{obsWMA} below the nitracline. There is indeed a regular accumulation of DIN^{simWMA} below the photic zone during the ten-year simulation (Figure 3, a)), reaching at the end a high concentration of 17 μM that is not observed in DIN^{obsWMA}. Even if we may also note a slight variation in the phosphacline over time in simWMA, it is much less significant than the above-mentioned change in the simulated nitracline.

The N$_2$ fixation rates (N$_2$ fix) measured at WMA and WGY and the vertical profiles of N$_2$fix^{simWMA} are presented in Figure 3 c). At the surface, N$_2$ fix^{obsWMA} ranges from 9.0 to 30.0 nmolN.L^{-1}.d^{-1}, with a maximum rate of 35.0 nmolN.L^{-1}.d^{-1} near 10 m depth. N$_2$ fix^{obsWMA} then decreases gradually with depth to 9.0 nmolN.L^{-1}.d^{-1} at 40 m before reaching lower rates below 40 m with values less than 1.5 nmolN.L^{-1}.d^{-1} and a minimum of 0.1 nmolN.L^{-1}.d^{-1} at 100 m. Regarding the model results of the simulation with diazotrophy, N$_2$ fix^{simWMA} rates are consistent with data with a similar trend of higher rates (around ~~17.0~~ 16.0 nmolN.L^{-1}.d^{-1}) from the surface to 40 m depth, and decreasing values from 40 m to 70 m depth (down to 1.0 nmolN.L^{-1}.d^{-1} at 70 m). At WGY, very low N$_2$ fix^{obsWGY} were measured compared to N$_2$ fix^{obsWMA}, with a maximum rate of 2.0 nmolN.L^{-1}.d^{-1} observed at the surface. In the simulation without diazotrophy, N$_2$ fix^{simWGY} is nil (see Figure 3, c)).

3.1.2 Chlorophylle a, primary production and carbon biomass

Figure 3 shows the vertical profiles of d) primary production (PP), e) chlorophyll a concentration (Chl a) and f) particulate organic carbon (POC) from the surface to 300 m depth. PP is significantly higher in WMA than in WGY, in both the experimental data and the model results. At the surface, PP^{obsWMA} ranges from 4.0 to 16.0 mgC.m^{-3}.d^{-1} while PP^{obsWGY} never exceeds 1.5 mgC.m^{-3}.d^{-1}. PP^{simWGY} never exceeds 1.0 mgC.m^{-3}.d^{-1} and is in good agreement with PP^{obsWGY} in the whole photic layer. PP^{simWMA} is also in good agreement with PP^{obsWMA} ,even if PP^{simWMA} values are close to the upper limit of the PP^{obsWMA} range values. As for PP^{obsWMA}, PP^{simWMA} slightly decreases from the surface to the bottom of the photic layer, before reaching low rates below 70 m.

The main differences between Chl a^{obsWMA} and Chl a^{obsWGY} lies in the depth of the deep chlorophyll maximum (DCM), which is around 75 m for Chl a^{obsWMA} while the Chl a^{obsWGY} DCM is deeper at around 140 m. The deepening of the DCM

in WGY compared to WMA is a result also observed between simWGY and simWMA. This deepening is nevertheless higher in the model with a DCM for Chl $\underline{a}^{simWGY}$ located at 200 m, while the DCM for Chl $\underline{a}^{simWMA}$ is shallower (around 50 m). In the model outputs, the location of the DCM is roughly located at the nutrient-limiting nutricline, i.e., at the phosphacline depth in WMA and sim^{WMA}, and at the nitracline depth in WGY and sim^{WGY}. For both the data and the model outputs, we observe

5   a difference in the depth of the DCM between WMA and WGY, but no significant difference in the DCM intensity between the two regions. Nevertheless, there is a noticeable difference in the DCM intensity between observations and simulations: Chl $\underline{a}^{obsWMA}$ and Chl $\underline{a}^{obsWGY}$ maximum values are equal to 0.3 μgChl.L^{-1} while Chl $\underline{a}^{simWMA}$ and Chl $\underline{a}^{simWGY}$ maximum values are equal to 0.5 μgChl.L^{-1}. ~~Another difference between the model outputs and the data lies in the higher surface values of Chl $\underline{a}^{simWMA}$ around 0.35 μgChl.L^{-1} whereas Chl $\underline{a}^{obsWMA}$ does not exceed 0.15 μgChl.L^{-1} from 0 to 50 m depth.~~

10   The particulate carbon biomass (POC) presented in Figure 3, f) shows significant differences between WMA and WGY for both the data and the model results. First of all, there is a higher production of biomass at WMA close to the surface than at WGY. POC^{obsWMA} is, at the maximum, 5-fold higher than POC^{obsWGY} with maximum values at the surface reaching 5 μM. POC^{obsWMA} then slightly decreasing with depth to reach below 50 m values that are similar to those of POC^{obsWGY} (around 1.5 μM). Higher simulated than measured POC values are also observed close to the surface. A maximum value of

15   7.5 μM for POC^{simWMA} corresponding to the DCM is found at 65 m but is not observed in *in situ* data. A 2.5-fold lower and deeper maximum is also observed in POC^{simWGY} just above 200 m, with a maximum concentration of 3 μM. POC^{simWGY} concentrations remain very low between the surface and the deep maximum, while there is a significant ~~C biomass~~ POC production rate in simWMA with POC^{simWMA} concentrations higher than 6.5 μM at the surface.

3.2   Temporal seasonal variations

20   Unlike the available *in situ* data, the model can provide the time variations of all the above mentioned biogeochemical variables . The seasonal pattern of the nutrients pools, N$_2$ fixation, Chl $\underline{a}$ and POC is therefore shown over a 3-year period in order to focus on the seasonal variability. As already mentioned, the same atmospheric forcings are repeated every year, and they cover the period between the last winter mixing period before the OUTPACE cruise (September 2014) and the next winter in August 2015.

25   ### 3.2.1   Nutrients availability and N$_2$ fixation dynamics

The nutrients variation throughout the water column are in part related to the variations of the mixing layer depth (MLD) during the year. The seasonal variations of the MLD are plotted in Figure 4 a), b), d) and e). They clearly indicate a winter mixing beginning at the end of ~~August~~ May leading to a maximum MLD of 70 m in ~~October~~ August, followed by a longer stratified period from ~~February~~ November to ~~July~~ April, with a shallower MLD between 25 and 30 m compared to winter

30   mixing. Figure 4, a) shows the DIN concentrations for simWMA from the surface to 200 m on a logarithmic scale. There is a slight variation of the nitracline around 70 m, but the concentration in the near-surface layer always remains below 3 nmol.L^{-1} (nM), which is far below the quantification limit (50 nM).

Unlike DIN, DIP presents significant seasonal variations throughout the year (Figure 4, b). The concentrations are also presented on a logarithmic scale using the Redfield ratio (DIP x16) in order to easily compare DIN and DIP concentrations, with respect to the "classical" proportion of phytoplankton biological demand. During winter mixing, surface DIP^{simWMA} increases from 0.6 to 2 nM, then remains quite stable until the end of ~~January~~ February before regularly decreasing until ~~April~~ June down to 0.6 nM. DIP^{simWMA} then remains low during the stratified period until the next winter mixing in August~~/September~~. The phosphacline is always shallower than the nitracline in the simWMA and remains around 50 m depth.

Accounting for the huge computer memory this would require, the values of the different biogeochemical fluxes calculated by the model are not systematically saved. As a result, numerical values of fluxes are saved at a lower vertical resolution than concentrations (pools)., ~~The treatment applied to the model outputs is not the same for pools and flux: the vertical resolution for flux is lower than the one for pools. This is the~~ For this reason why we decided to represent the dynamics of N_2 fixation at the surface (averaged over the first 10 m) rather than as a function of depth, which would not have been as relevant as for the other variables. Figure 4 c) depicts the dynamics of the total N_2 fixation as well as the respective contributions of Trichodesimum sp. and UCYN to this flux. The total N_2 fixation at the surface varies from a minimum mean value of 15 $nmol.L^{-1}.d^{-1}$ during the stratified period to a maximum mean value of 20 $nmol.L^{-1}.d^{-1}$ reached between ~~September and January~~ July and August, i.e. during the winter mixing. The major contributor to the N_2 fixation in simWMA is Trichodesimum sp., with on average, a contribution of 80% of the total N_2 fixed against 20% for the UCYN.

3.2.2 Seasonal variations on surface chlorophyll a and carbon biomass production

Figure 4 d) presents the Chl a dynamics from the surface to 200 m depth, and shows clear seasonal variations in the photic layer throughout a year. Between October and April, the Chl a^{simWMA} is quite homogenous from surface to 70 m, with a DCM around 50 m reaching a maximum concentration of 0.5 $\mu gChl.L^{-1}$. From April and during the winter mixing, Chl a^{simWMA} at surface decreases rapidly, reaching concentrations below 0.15 $\mu gChl.L^{-1}$. During the same period, there is also a deepening of the DCM toward 80 m, with lower concentrations down to 0.4 $\mu gChl.L^{-1}$.

The production of C biomass in simWMA shows significant seasonal variations in the photic layer (Figure 4 e)). The period of maximum C production at surface lasts from October to February, with maximum concentrations of POC^{simWMA} around 8 μM. As shown in Figure 3 f), a deep maximum peak of biomass is at around 70 m, with concentrations close to 9 μM. Like for Chl a, from the end of March and during the winter period, the surface POC^{simWMA} decreases significantly to reach concentrations 2-fold lower than those obtained during the bloom (i.e. between November and February). While POC^{simWMA} in the 0-50 m layer decreases during the stratified period, the deep maximum remains at the same depth, even if its intensity decreases with POC^{simWMA} values at 70 m, reaching a minimum of 7 μM at the end of July.

4 Discussion

The Western Tropical South Pacific (WTSP) has been recently qualified as a hotspot of N_2 fixation (Bonnet et al., 2017). It is hypothesized that, while flowing westward following the South Equatorial Current (SEC), the N-depleted, P-enriched waters

from areas of denitrification located in the eastern Pacific meet in the western Pacific waters with sufficient iron to allow N_2 fixation to occur (Moutin et al., 2008; Bonnet et al., 2017). *In situ* data showed an ecosystem significantly more productive in WMA where N_2 fixation rates were higher than in WGY, where very low N_2 fixation rates were measured. These contrasted areas raised the question of whether the diazotrophy could be responsible for these differences observed between WMA and

5 WGY, which led us to run two simulations only differing by taking into account (i.e. simWMA), or not (i.e. simWGY), the process of diazotrophy. The results of these two simulations were compared to the observations collected at the WMA and WGY areas during the OUTPACE cruise (Figure 3) in order to study the role of N_2 fixation on surface planktonic production and biogeochemical C, N, P cycles.

4.1 N_2 fixation, closely linked to the DIP availability, enhances the surface production

10   ### 4.1.1   Concomitant low DIP concentrations and high N_2 fixation rates

While DIN concentration remains below the quantification limit (50 nM) everywhere in the surface layer, there is a significantly higher DIP concentration in the photic layer at WGY than at WMA in both the data and the model outputs (Figure 3, b). The relatively high DIP concentration in WGY may be associated ~~to~~ with inefficient or non-existent N_2 fixation in the gyre (Moutin et al., 2018). Because of the high Fe requirement of diazotrophs (Paerl et al., 1987; Rueter et al., 1990), the low Fe availability

15 in WGY is assumed to prevent or significantly limit N2 fixation in the South Pacific gyre (Moutin et al., 2008; Guieu et al., 2018; Moutin et al., 2018). By contrast, the high Fe availability in WMA is assumed to favor the growth of nitrogen fixers. Guieu et al. (2018) indeed measured high DFe concentrations in the photic layer in WMA provided by abnormally shallow hydrothermal sources (around 500 m deep) in the WTSP. Due to very low N_2 fixation measured in WGY (Bonnet et al., 2018), autotrophs organisms are N-limited, leading to a lower PP than in WMA, which results in a higher DIP accumulation in the

20 photic layer since DIP is less consumed by organisms. ~~Without N_2 fixation, DIP in the photic layer is less used in WGY than in WMA.~~ Associated with lower DIP concentrations, higher N_2 fixation rates are observed in WMA in both the data and the model results (Figure 3, c)). DIP depletion in simWMA is due to the presence of nitrogen fixers since the two simulations have exactly the same vertical dynamics and differ only by the presence/absence of nitrogen fixers.

Studies on the role of N_2 fixation in the biogeochemistry of the Pacific Ocean have increased in number over the last decades,

25 but the specific region of the WTSP remains patchily explored to date. Nevertheless, close to our studied area, Law et al. (2011) have observed a one-time DIP repletion in the surface layer due to a tropical cyclone which favored the upwelling of P-rich waters. On the basis of their Lagrangian strategy, they noticed a rapid consumption of this new ~~fresh~~ DIP in correlation with a significant increase in the N_2 fixation rates over the following 9 days. At a larger temporal scale, Karl et al. (1997) also observed a correlation between a decrease in DIP (about 50%) and a significant increase in N_2 fixation from 1989 to 1994, in

30 the oligotrophic region of the subtropical North Pacific. The significant role of DIP availability in controlling N_2 fixation in the oligotrophic iron repleted WTSP (Van Den Broeck et al., 2004; Moutin et al., 2018) has been highlighted over the last decade (e.g. Moutin et al. (2005, 2008)), and the consistent results between the OUTPACE data and our model outputs, comparing simWMA and simWGY, reinforces this view of the biogeochemical functioning in this region.

11

4.1.2 Surface plankton productivity mainly driven by N_2 fixation in the WSTP

SimWMA and simWGY present consistent patterns regarding surface production (Figure 3,d)): as for the *in situ* data, the model results show higher PP, POC and Chl <u>a</u> in simWMA (i.e. with diazotrophy) than in simWGY (i.e. without diazotrophy) in the first 0-50 m. PP^{simWMA} is 20-fold higher than PP^{simWGY} in the upper layer, in good agreement with PP^{obsWMA} which is 15-fold higher than PP^{obsWGY} (Figure 3, d)). Chl <u>a</u> concentrations never exceeding 0.5 μgChl.L^{-1} are representative of oligotrophic waters. Model outputs and observations both show significantly deeper DCMs at WGY than WMA. The deepening of the DCM characterizes the transition from oligo (WMA) to ultra-oligotrophic (WGY) conditions during the OUTPACE cruise (Moutin et al., 2018). In the model outputs, the difference between the DCM depth in simWMA and simWGY is greater than in the data : the DCM depth in simWGY is 150 m deeper than that of simWMA, whereas the observed DCM depth in WMA is only 50 m deeper than that measured in WMA. The simulation without diazotrophy presents therefore a deeper DCM around 200 m, on average 50 m deeper than that observed in the WGY region (Figure 3, e)). This deep DCM is consistent with the deep maximum of POC^{simWGY} just above 200 m depth (Figure 3, d)). Both deep maxima are related to the nutricline depths located at 195 m and 185 m for DIN^{simWGY} and DIP^{simWGY}, respectively.

As for the DCM, T~~t~~he nutriclines in simWGY are significantly deeper than those measured *in situ* in WGY. We assume that this gap is because N_2 fixation is totally removed in simWGY, whereas low but existing N_2 fixation still occurs *in situ* at WGY (Figure 3, c)). While the N_2 fixation rates reported in WGY were very low (Caffin et al., 2018), Stenegren et al. (2018) mention the presence of such diazotrophs from the UCYN group, whereas no Trichodesimum sp. were found in this region.The *in situ* planktonic ecosystem in the WGY might therefore be slightly fueled by weak N_2 fixation, which is not the case for simWGY since diazotrophy is not allowed. The above assumption concerning the gap between data and model outputs is consistent with the fact that the measured PP, POC and Chl <u>a</u> in WGY are always slightly higher than in the model outputs for the surface layer (Figure 3, d), e) and f)). To support this assumption, we ran another simulation considering only the presence of UCYN as diazotrophs in WGY. ~~While the N_2 fixation rates reported in WGY were very low (Caffin et al., 2018), (Stenegren et al., 2018) mention the presence of such diazotrophs from the UCYN group, whereas no Trichodesimum sp. were found in this region. The results of this last simulation (not shown) indicate low N_2 fixation rates, surface PP rates and POC concentration, in agreement with those measured in WGY. In addition, the DCM was shallower, around 150 m, than in simWGY (i.e. without any diazotrophs), in correlation with shallower nutriclines as well.~~ The results of this intermediate simulation (not shown) indicate low surface PP rates and POC concentrations, in agreement with those measured in WGY. Moreover, DIP is still available in the photic zone (though at concentrations lower than for simWGY) even if the calculated N_2 fixation rates were slightly higher than the measured ones. In addition, the DCM (located around 150 m) and the nutriclines were shallower than in simWGY (i.e. without any diazotrophs). This simulation can thus be considered like an intermediate system between simWMA and simWGY, and confirms the close link between N_2 fixation fluxes and DIP availability.

In a previous study using nearly the same biogeochemical model including TRI and UCYN state variables in a one-dimensional configuration without physical coupling, Gimenez et al. (2016) highlighted the direct and indirect impact of the new N input provided by diazotrophs. By calculating the percentage of Diazotroph-Derived Nitrogen (DDN) in each model

compartments, they followed the transfer of DDN throughout the entire trophic web as a function of time, and showed that after 25 days, 43 % of the DDN fixed by diazotrophs were found in non-diazotroph organisms. These results clearly showed that N_2 fixation had a significant indirect impact on the planktonic production by providing a new source of N for other organisms. DDN tracking inside the model compartments is associated with very high computational costs and could not be applied to the

5 present study where simulations are run for several years (against 25 days for the previous study). However, it is worthwhile mentioning that the proportion of PFTs involved in total Chl a and PP was 80 % of TRI, 10 % of PHYS and 5 % of PHYS and PHYL, suggesting that the impact of N_2 fixation is rather direct (85 % of PP is realized by diazotrophs) than indirect. In our model, diazotrophs have therefore a net competitive advantage over the two other non-diazotrophic autotrophs.

4.2 A close link between MLD, nutricline depth and N_2 fixation

10 ### 4.2.1 How can the nutricline depths influence N_2 fixation ?

In such oligotrophic areas, the positions of the nutriclines are crucial in controlling the surface production (Behrenfeld et al., 2006; Cermeño et al., 2008) as they provide nutrients from the bottom to the photic layer. The equatorial Pacific Ocean is known for its complex hydrodynamic circulation induced by constant trade-winds, leading to significant variations of the thermocline position between the east and the west of the basin (Meyers, 1979). ~~They also~~ Trade winds also have an influence on the

15 nutrient availability in the surface layer ~~throughout the nutricline positions which arepartly driven by the vertical dynamics in the water column which determine the MLD~~ since they determine the depth of the mixed layer (Radenac and Rodier, 1996; Zhang et al., 2007).

During OUTPACE, the phosphacline (above 50 m) appeared shallower than the nitracline (about 75 m) in the WMA region (Figure 3, a) and b)). A similar shift between nitracline and phosphacline depths was observed 10° further south than our studied

20 area, with a nitracline about 20 m deeper than the phosphacline (Law et al., 2011). In those N-depleted regions, diazotrophs may outcompete non-diazotroph organisms, using the unlimited atmospheric N_2 (Agawin et al., 2007; Dutkiewicz et al., 2014). However, their development also requires sufficient light intensity and other nutrients such as P and Fe, and the debate on their expected limitation or co-limitation is of great interest to the ocean biogeochemical community (Falkowski, 1997; Wu et al., 2000; Sañudo-Wilhelmy et al., 2001; Mills et al., 2004; Moutin et al., 2005; Monteiro et al., 2011).

25 On the basis of our model, we understood that it was crucial to take into account the nutricline depths, and that a shallower phosphacline than nitracline was needed to observe N_2 fixation rates in agreement with those measured *in situ* (Figure 3, c)). This led us to implement a preferential P regeneration in our model to reproduce the shift between the nitracline and the phosphacline (see Section 4.2.2 for more details). In our preliminary results (red lines in Figure 5), without this decoupling, the depths of the nitra- and phosphacline were the same and at around 80 m, below to the depth of the MLD (Figure 5, a)

30 and b)). Each winter, mixing brought low concentrations of DIN and DIP in the euphotic layer. Low DIN concentrations are favorable for the development of N_2 fixers (Holl and Montoya, 2008; Agawin et al., 2007) but they were rapidly limited by DIP availability as the winter mixing did not provide enough DIP in the photic layer, leading to very low N_2 fixation rates (Figure 5, c)). In this configuration, primary production was N-limited and low compared to what was observed in the WMA region. The

phosphacline had to be shallower (here about 25 m) than the nitracline, and above the winter MLD (70 m), to counteract DIP limitation. In this case, no DIN is brought by winter mixing in the photic layer, which favors N_2 fixers compared to non-fixer organisms, and sufficient DIP concentrations to support surface production until the next winter mixing. This simWMA configuration led to a significant development of N_2 fixers in the 0-50 m layer, dominated by *Trichodesmium* sp. (not shown),

5   with consistent rates of N_2 fixation and PP rates (Figure 3, c) and d)).

4.2.2   A preferential P regeneration needed to sustain N_2 fixation

To obtain with the model a phosphacline shallower than the nitracline, and thereby decrease DIP depletion in the surface layer, we had to decouple the regeneration of the detrital particulate N (DET-N) and the detrital particulate organic P (DET-P) by significantly increasing the remineralization rate of DET-P compared to that of DET-N and DET-C. The use of extracellular

10   phosphoenzymes (~~phosphatase alkaline or~~ e.g. alkaline phosphatase, nucleotidase, polyphosphatase or phosphodiesterase) by microorganisms to regenerate DIP from dissolved organic P when DIP is depleted is well known (Perry, 1972, 1976; Vidal et al., 2003). Our model does not include the explicit phosphatase alkaline activity, but it is represented indirectly by giving direct access to DOP by autotrophs. However, this advantage was not sufficient to decrease P limitation enough and allow the growth of N_2 fixers so as to calculate N_2 fixation rates consistent with those measured in WMA. A preferential P regeneration

15   of the particulate organic matter was required and obtained by increasing the DET-P hydrolysis compared to that of DET-C and DET-N. The location of the detrital matter regeneration in the water column is based on a balance between the sinking and the hydrolysis rates of the particulate organic matter. As mentioned in Section 4.2.2, the detrital matter is divided into two size fractions having two constant sinking rates of 1.0 and 25.0 m.d^{-1} for the small and the large detrital particulate matter, respectively. Initially, the hydrolysis rates for the detrital C, N and P particulate matter were the same, and equal to

20   0.05 d^{-1}. The preferential regeneration of P was a posteriori obtained by increasing the hydrolysis rate of particulate P to 2.0 d^{-1}, without any change in the sinking rates. To illustrate how the discrepancy between nitracline and phosphacline depths can be attributed to preferential P regeneration, DIN and DIP concentrations and N_2 fixation rates in simWMA calculated with and without preferential P regeneration (i.e. preferential hydrolysis of P particulate matter) have been compared (Fig. 5). This figure shows the deepening of the phosphacline in the simulation without preferential P regeneration. More importantly, without

25   preferential P regeneration, the phosphacline depth is deeper than the MLD at 70m, which prevents DIP input in the surface layer during winter mixing, and leads to a strong limitation of diazotrophs by P. This stronger P-limitation without preferential P regeneration can also be observed at the cellular scale by analyzing the intracellular P quota of N_2 fixers. In the simulation without preferential P regeneration, the relative intracellular quota of P in TRI and UCYN are in average respectively 8 and 16 times lower than with preferential P regeneration. As N_2 fixation alleviates N limitation for diazotrophs, their growth is thus

30   limited by P availability. The significant decrease in relative intracellular P quotas has therefore a significant impact on their growth, and consequently explain the lower N_2 fixation rates shown in Figure 5, c). This preferential P remineralization was also used by Zamora et al. (2010) who investigated different mechanisms that might be able to explain the N-excess observed in the North Atlantic main thermocline. Even if their model did not include N_2 fixation, they concluded that the N excess observed would be a consequence of a co-occurrence of a preferential P remineralization and a surface N input provided by

N$_2$ fixation. With the same aim of studying the N excess observed in the North Atlantic main thermocline, Coles and Hood (2007) implemented a more complex model including the N$_2$ fixation process and variable stoichiometry for the non-living compartments. They concluded that a preferential P regeneration was needed to generate the N excess anomalies observed in the subsurface North Atlantic, and the preferential P regeneration was obtained by increasing the P remineralization rates relative to N. In both their and our study, the change in P remineralization rate was necessary to reduce upper surface P limitation for diazotrophs and to obtain N$_2$ fixation rates consistent with observations.

4.3 N from N$_2$ fixation accumulates in the main thermocline

By running the model simulations over ten years, we observed the storage of the new N input by diazotrophy. The nitrate accumulation observed in simWMA from 70 m to 500 m (Figure 3, a)), reaching concentrations of 17.0 μM after a run of ten years, is obviously overestimated as we used a one-dimensional model, without any horizontal exchange. The horizontal advection which would occur in the field is not represented here, and without any loss processes taken into account, the annual N input by N$_2$ fixation accumulates, as observed in simWMA. The interesting point is the location of this accumulation around the first 400 m of the main thermocline between 100 and 500 m depth. This result is consistent with some studies which have investigated the N excess in the ocean, using for instance the N* tracer (N*= NO$_3^-$ - 16 x PO$_4^{3-}$, Gruber and Sarmiento (1997)) and the N$_2$ fixation contribution to this N-excess (Bates and Hansell, 2004; Hansell et al., 2004; Landolfi et al., 2008; Zamora et al., 2010). ~~The N* tracer is used to measure the N in excess with respect to the quantity expected from the thermocline N:P ratio (i.e., N:P of 16:1; Redfield et al., 1963, Takahasi et al., 1985, anderson et al., 1994), even if the relative contributions of the N-excess sources remain difficult to determine (Hansell et al., 2007).~~ A companion paper in this special issue investigates in detail the N excess observed in the WTSP in relation with N$_2$ fixation (Fumenia et al., *under rev.*, this issue). Our model results clearly show an accumulation of N in the 100-500 m layer which ~~can only be explained by~~ results from the new N input by diazotrophy, as this is the sole external N source implemented. This accumulation constantly increases every year by an average of 449.6 mmolN.m^{-2} while the annual integrated N$_2$ fixation provides 451.0 mmolN.m^{-2}. After benefiting the upper water ecosystem, more than 99.5% of new N derived from N$_2$ fixation ends in the DIN pool from the 100-500 m layer. We use a one-dimensional model which is not intended to provide any quantitative conclusion regarding this N accumulation, but these calculations explain the annual DIN accumulation observed in Figure 3 a). According to the model, N$_2$ fixation may explain the N excess observed *in situ* around the main thermocline in the WTSP, as reported by Fumenia et al. (*under rev.*, this issue).

4.4 N$_2$ fixation leading to seasonal variations in the WTSP

To date, the WTSP, and more generally the South Pacific Ocean, is much less studied than the North Pacific Ocean which has been sampled since the late 1980s within the framework of the Long-term Oligotrophic Habitat Assessment (ALOHA) near the Hawaii islands. ~~The high frequency Hawaii Ocean Time-series (HOT) program provides a long-term database from the 1990s on oceanic variability regarding physical, biological and biogeochemical features in the North Pacific ocean (Karl et al. 1996).~~ The South Pacific has been sampled from west to east during the BIOSOPE (Claustre et al., 2008) and OUTPACE (Moutin et al., 2017) French oceanographic cruises and many other cruises (e.g. Moisander et al. (2012), and the cruises

involved in the GLODAPv2 project, Olsen et al. (2016)) providing a spatial (Fumenia et al., *under rev.*, this issue), but not a temporal overview of the south tropical Pacific. To date, the seasonal variations were only studied during the DIAPALIS cruises (http://www.obs-vlfr.fr/proof/vt/op/ec/diapazon/dia.htm) in several stations located in the MA close to New Caledonia. By means of our one-dimensional model, we can analyze the annual variability of the entire ecosystem implemented in the

5   model in order to corroborate, or not, certain hypotheses raised from the OUTPACE data analysis. ~~Figure 4 shows the temporal variations of the [DIN, DIP, N₂fix, Chl a and POC]^{simWMA} over 3 years of simulation in the 0-200 m layer.~~

Seasonal variations obtained in sim^{WMA} (Figure 4) allow to trace the annual "history" of the WMA region : ~~The winter~~ During the winter period, vertical mixing intensifies and replenishes the surface layer in DIP but not in DIN, as the nitracline is deeper than the MLD (70 m), whereas the phosphacline is shallower (Figures 3 a) and b)). The newly available DIP in the

10   surface layer is immediately followed by an increase in ~~the~~ N₂ fixation rates in ~~August~~ June (Figure 3, c)), which then remain quite stable until ~~January~~ October before slightly decreasing until the next winter mixing. There is a close relationship between DIP availability and the N₂ fixation rates since N₂ fixation decreases as the DIP concentration decreases with the DIP gradual consumption after the mixing period. Because N₂ fixation provides a new source of N (characterized by a rapid turnover time, as it is immediately used and transferred into the ecosystem), the DIP is consumed, thereby generating seasonal variations in

15   the surface layer. Although autotrophs are dominated by N₂ fixers, N₂ fixation benefits the entire planktonic trophic web and enhances the surface production which is directly controlled by nutrient availability. We therefore observe surface seasonal variations in Chl a^{simWMA} and POC^{simWMA} , with maximum values from October to the end of March, and a less intense and deeper signal around 70 m (which corresponds to the nitracline depth~~) during the stratified period (~~from ~~January~~ April to the end of ~~August~~ May). During the stratified period, when N₂ fixation is the lowest, non-diazotroph organisms grow deeper

20   where DIN is available. The temporal evolution of simWGY is not shown here as there is no seasonal variations associated with N₂ fixation, which is the focus of the study presented here. The absence of diazotrophy leads to a deepening of the nitracline and available DIN is deeper. DIP is never exhausted in the surface layer because the ~~lack of iron is hypothesized~~ the model implicitly assumes iron limitation to prevent N₂ fixation. The maximum biomass and DCM are constant throughout the year, significantly less intense than in simWMA and located near the nitracline around 200 m.

25   ## 5   Conclusions

The purpose of this study was to investigate the direct and/or indirect role of N₂ fixation on surface planktonic production and biogeochemical C, N, P cycles, with the aim of determining whether the main biogeochemical differences observed in the MA and in the SPG areas could be explained or not by diazotrophy. For this purpose, a new coupled one-dimensional physical-biogeochemical model has been built based on the Eco3M-Med model. Two simulations were designed, only differing by

30   the presence/absence of diazotrophs. They enabled us to reasonably reproduce the main biogeochemical characteristics of the two biogeochemical areas (WMA and WGY). The model could also reproduce the high contrast between the two regions, such as (i) the high/low DIP availability respectively associated with significant/ negligible N₂ fixation and surface production, (ii) the higher/ lower depth of the nutriclines characteristic of oligotrophic (WMA)/ultra-oligotrophic (WGY) states, (iii) the

large/small gap between DIN and DIP nutriclines and the associated consequences in terms of nutrients input in the surface layer during winter mixing.

Winter mixing allows the annual replenishment of the surface layer in excess P, creating ideal conditions for diazotroph growth and intensive N_2 fixation, in the WTSP region where light intensity is high enough and not limiting the diazotrophs' growth. The development of diazotrophs can counteract DIN limitation for the entire planktonic trophic web in the photic layer in WMA, which leads to significant seasonal variations due to the progressive exhaustion of DIP after winter mixing. Throughout the year, we then evidenced a shift from N to P limitation of the planktonic community growth in MA. The strong influence of seasonal variations shown by the simulations in the WTSP, and generally not considered in tropical areas, needs to be further studied and backed up by *in situ* observations.

References

Agawin, N. S., Rabouille, S., Veldhuis, M. J., Servatius, L., Hol, S., van Overzee, H. M., and Huisman, J.: Competition and facilitation between unicellular nitrogen-fixing cyanobacteria and non—nitrogen-fixing phytoplankton species, Limnology and Oceanography, 52, 2233–2248, http://onlinelibrary.wiley.com/doi/10.4319/lo.2007.52.5.2233/abstract, 2007.

5 Alekseenko, E., Raybaud, V., Espinasse, B., Carlotti, F., Queguiner, B., Thouvenin, B., Garreau, P., and Baklouti, M.: Seasonal dynamics and stoichiometry of the planktonic community in the NW Mediterranean Sea; a 3D modeling approach, Ocean Dynamics, 64, 179–207, 2014.

Baklouti, M., Faure, V., Pawlowski, L., and Sciandra, A.: Investigation and sensitivity analysis of a mechanistic phytoplankton model implemented in a new modular numerical tool (Eco3M) dedicated to biogeochemical modelling, Progress in Oceanography, 71, 34–58, 10 https://doi.org/10.1016/j.pocean.2006.05.003, http://linkinghub.elsevier.com/retrieve/pii/S0079661106000772, 2006.

Bates, N. R. and Hansell, D. A.: Temporal variability of excess nitrate in the subtropical mode water of the North Atlantic Ocean, Marine Chemistry, 84, 225–241, https://doi.org/10.1016/j.marchem.2003.08.003, http://linkinghub.elsevier.com/retrieve/pii/S0304420303001415, 2004.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, 15 P. G., Letelier, R. M., and Boss, E. S.: Climate-driven trends in contemporary ocean productivity, Nature, 444, 752–755, https://doi.org/10.1038/nature05317, https://www.nature.com/articles/nature05317, 2006.

Benavides, M., Agawin, N., Aristegui, J., Penne, J., and Stal, L.: Dissolved organic nitrogen and carbon release by a marine unicellular diazotrophic cyanobacterium, Aquat Microb Ecol, 69, 2013.

Berthelot, H., Bonnet, S., Camps, M., Grosso, O., and Moutin, T.: Assessment of the dinitrogen released as ammonium and dissolved 20 organic nitrogen by unicellular and filamentous marine diazotrophic cyanobacteria grown in culture, Frontiers in Marine Science, 2, 80, https://doi.org/10.3389/fmars.2015.00080, https://www.frontiersin.org/articles/10.3389/fmars.2015.00080/full, 2015.

Bonnet, S., Caffin, M., Berthelot, H., and Moutin, T.: Hot spot of N2 fixation in the western tropical South Pacific pleads for a spatial decoupling between N2 fixation and denitrification, Proceedings of the National Academy of Sciences, 114, E2800–E2801, https://doi.org/10.1073/pnas.1619514114, http://www.pnas.org/content/114/14/E2800, 2017.

25 Bronk, D. A. and Ward, B. B.: Magnitude of dissolved organic nitrogen release relative to gross nitrogen uptake in marine systems, Limnology and Oceanography, 45, 1879–1883, https://doi.org/10.4319/lo.2000.45.8.1879, https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.2000.45.8.1879, 2000.

Caffin, M., Moutin, T., Foster, R. A., Bouruet-Aubertot, P., Doglioli, A. M., Berthelot, H., Guieu, C., Grosso, O., Helias-Nunige, S., Leblond, N., Gimenez, A., Petrenko, A. A., de Verneil, A., and Bonnet, S.: N2 fixation as a dominant new N source in the west- 30 ern tropical South Pacific Ocean (OUTPACE cruise), Biogeosciences, 15, 2565–2585, https://doi.org/10.5194/bg-15-2565-2018, https://www.biogeosciences.net/15/2565/2018/, 2018.

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, http://www.sciencemag.org/content/276/5316/1221.short, 1997.

Capone, D. G., Burns James A., Montoya Joseph P., Subramaniam Ajit, Mahaffey Claire, Gunderson Troy, Michaels Anthony F., and 35 Carpenter Edward J.: Nitrogen fixation by Trichodesmium spp.: An important source of new nitrogen to the tropical and subtropical North Atlantic Ocean, Global Biogeochemical Cycles, 19, https://doi.org/10.1029/2004GB002331, https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2004GB002331, 2005.

Cermeño, P., Dutkiewicz, S., Harris, R. P., Follows, M., Schofield, O., and Falkowski, P. G.: The role of nutricline depth in regulating the ocean carbon cycle, Proceedings of the National Academy of Sciences, 105, 20 344–20 349, https://doi.org/10.1073/pnas.0811302106, http://www.pnas.org/content/105/51/20344, 2008.

Claustre, H., Sciandra, A., and Vaulot, D.: Introduction to the special section bio-optical and biogeochemical conditions in the South East Pacific in late 2004: the BIOSOPE program, Biogeosciences, 5, 679–691, https://doi.org/10.5194/bg-5-679-2008, https://www.biogeosciences.net/5/679/2008/, 2008.

Coles, V. J. and Hood, R. R.: Modeling the impact of iron and phosphorus limitations on nitrogen fixation in the Atlantic Ocean, Biogeosciences, 4, 455–479, https://doi.org/10.5194/bg-4-455-2007, https://www.biogeosciences.net/4/455/2007/, 2007.

de Baar, H. J. W.: Von Liebig's law of the minimum and plankton ecology (1899–1991), Progress in Oceanography, 33, 347–386, https://doi.org/10.1016/0079-6611(94)90022-1, http://www.sciencedirect.com/science/article/pii/0079661194900221, 1994.

de Verneil, A., Rousselet, L., Doglioli, A. M., Petrenko, A. A., Maes, C., Bouruet-Aubertot, P., and Moutin, T.: OUTPACE long duration stations: physical variability, context of biogeochemical sampling, and evaluation of sampling strategy, Biogeosciences Discussions, pp. 1–33, https://doi.org/10.5194/bg-2017-455, https://www.biogeosciences-discuss.net/bg-2017-455/, 2017.

Dutheil, C., Aumont, O., Gorguès, T., Lorrain, A., Bonnet, S., Rodier, M., Dupouy, C., Shiozaki, T., and Menkes, C.: Modelling the processes driving *Trichodesmium* sp. spatial distribution and biogeochemical impact in the tropical Pacific Ocean, Biogeosciences Discussions, pp. 1–34, https://doi.org/https://doi.org/10.5194/bg-2017-559, https://www.biogeosciences-discuss.net/bg-2017-559/, 2018.

Dutkiewicz, S., Ward, B. A., Scott, J. R., and Follows, M. J.: Understanding predicted shifts in diazotroph biogeography using resource competition theory, Copernicus Publications, http://dspace.mit.edu/handle/1721.1/92505, 2014.

Falkowski, P. G.: Evolution of the nitrogen cycle and its influence on the biological sequestration of CO2 in the ocean, Nature, 387, 272–275, https://doi.org/10.1038/387272a0, http://www.nature.com/doifinder/10.1038/387272a0, 1997.

Falkowski, P. G., Barber, R. T., and Smetacek, V.: Biogeochemical controls and feedbacks on ocean primary production, Science, 281, 200–206, http://www.sciencemag.org/content/281/5374/200.short, 1998.

Fennel, K., Spitz, Y. H., Letelier, R. M., Abbott, M. R., and Karl, D. M.: A deterministic model for N_2 fixation at stn. ALOHA in the subtropical North Pacific Ocean, Deep Sea Research Part II: Topical Studies in Oceanography, 49, 149–174, http://www.sciencedirect.com/science/article/pii/S0967064501000984, 2002.

Fumenia, A., Moutin, T., Bonnet, S., Benavides, M., Petrenko, A., Helias Nunige, S., and Maes, C.: Excess nitrogen as a marker of intense dinitrogen fixation in the Western Tropical South Pacific Ocean: impact on the thermocline waters of the South Pacific, Biogeosciences Discuss., 2018, 1–33, https://doi.org/10.5194/bg-2017-557, https://www.biogeosciences-discuss.net/bg-2017-557/.

Gaspar, P.: Modeling the Seasonal Cycle of the Upper Ocean, Journal of Physical Oceanography, 18, 161–180, https://doi.org/10.1175/1520-0485(1988)018<0161:MTSCOT>2.0.CO;2, http://journals.ametsoc.org/doi/abs/10.1175/1520-0485(1988)018%3C0161:MTSCOT%3E2.0.CO%3B2, 1988.

Gaspar, P., Grégoris, Y., and Lefevre, J.-M.: A simple eddy kinetic energy model for simulations of the oceanic vertical mixing: Tests at station Papa and long-term upper ocean study site, Journal of Geophysical Research, 95, 16 179, https://doi.org/10.1029/JC095iC09p16179, http://doi.wiley.com/10.1029/JC095iC09p16179, 1990.

Gimenez, A., Baklouti, M., Bonnet, S., and Moutin, T.: Biogeochemical fluxes and fate of diazotroph-derived nitrogen in the food web after a phosphate enrichment: modeling of the VAHINE mesocosms experiment, Biogeosciences, 13, 5103–5120, https://doi.org/10.5194/bg-13-5103-2016, https://www.biogeosciences.net/13/5103/2016/, 2016.

Grimaud, G. M., Dron, A., Rabouille, S., Sciandra, A., Bernard, O., and others: Modelling light-dark regime influence on the carbon-nitrogen metabolism in a unicellular diazotrophic cyanobacterium, in: CAB, http://hal.upmc.fr/hal-00854479, 2013.

Gruber, N.: The dynamics of the marine nitrogen cycle and its influence on atmospheric CO_2 variations, in: The ocean carbon cycle and climate, pp. 97–148, Springer, 2004.

5   Gruber, N. and Sarmiento, J. L.: Global patterns of marine nitrogen fixation and denitrification, Global Biogeochemical Cycles, 11, 235–266, https://doi.org/10.1029/97GB00077, http://doi.wiley.com/10.1029/97GB00077, 1997.

Guieu, C., Bonnet, S., Petrenko, A., Menkes, C., Chavagnac, V., Desboeufs, K., Maes, C., and Moutin, T.: Iron from a submarine source impacts the productive layer of the Western Tropical South Pacific (WTSP), Scientific Reports, 8, https://doi.org/10.1038/s41598-018-27407-z, http://www.nature.com/articles/s41598-018-27407-z, 2018.

10   Hansell, D. A., Bates, N. R., and Olson, D. B.: Excess nitrate and nitrogen fixation in the North Atlantic Ocean, Marine Chemistry, 84, 243–265, https://doi.org/10.1016/j.marchem.2003.08.004, http://linkinghub.elsevier.com/retrieve/pii/S0304420303001427, 2004.

Holl, C. M. and Montoya, J. P.: Diazotrophic growth of the marine yanobacterium Trichodesmium Ims101 in continuous culture: effects of growth rate on N_2-fixation rate, biomass, and C:N:P stoichiometry, Journal of Phycology, 44, 929–937, https://doi.org/10.1111/j.1529-8817.2008.00534.x, http://onlinelibrary.wiley.com.lama.univ-amu.fr/doi/10.1111/j.1529-8817.2008.00534.x/abstract, 2008.

15   Hutchins, D. A., Fu, F.-X., Zhang, Y., Warner, M. E., Feng, Y., Portune, K., Bernhardt, P. W., and Mulholland, M. R.: CO2 control of Trichodesmium N2 fixation, photosynthesis, growth rates, and elemental ratios: Implications for past, present, and future ocean biogeochemistry, Limnology and Oceanography, 52, 1293–1304, https://doi.org/10.4319/lo.2007.52.4.1293, https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.2007.52.4.1293, 2007.

Karl, D. and Letelier, R.: Nitrogen fixation-enhanced carbon sequestration in low nitrate, low chlorophyll seascapes, Marine Ecology Progress Series, 364, 257–268, https://doi.org/10.3354/meps07547, http://www.int-res.com/abstracts/meps/v364/p257-268/, 2008.

20

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, https://doi.org/10.1038/41474, https://www.nature.com/articles/41474, 1997.

Karl, D., Michaels, A., Bergman, B., Capone, D., Carpenter, E., Letelier, R., Lipschultz, F., Paerl, H., Sigman, D., and Stal, L.: Dinitrogen fixation in the world's oceans, Biogeochemistry, 57-58, 47–98, https://doi.org/10.1023/A:1015798105851, https://link.springer.com/article/10.1023/A:1015798105851, 2002.

25

Landolfi, A., Oschlies, A., and Sanders, R.: Organic nutrients and excess nitrogen in the North Atlantic subtropical gyre, Biogeosciences, 5, 1199–1213, https://doi.org/10.5194/bg-5-1199-2008, https://www.biogeosciences.net/5/1199/2008/, 2008.

Law, C. S., Woodward, E. M. S., Ellwood, M. J., Marriner, A., Bury, S. J., and Safi, K. A.: Response of surface nutrient inventories and nitrogen fixation to a tropical cyclone in the southwest Pacific, Limnology and Oceanography, 56, 1372–1385,

30   https://doi.org/10.4319/lo.2011.56.4.1372, http://onlinelibrary.wiley.com/doi/10.4319/lo.2011.56.4.1372/abstract, 2011.

Locarnini, R. A., Mishonov, A. V., Antonov, J. I., Boyer, T. P., Garcia, H. E., Baranova, O. K., Zweng, M. M., Paver, C. R., Reagan, J. R., Johnson, D. R., Hamilton, M., and Seidov, D.: World ocean atlas 2013. Volume 1, Temperature, Tech. rep., NOAA Atlas NESDIS 73, https://doi.org/10.7289/V55X26VD, 2013.

Luo, Y.-W., Doney, S. C., Anderson, L. A., Benavides, M., Berman-Frank, I., Bode, A., Bonnet, S., Boström, K. H., Böttjer, D., Capone,

35   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, 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 System Science Data, 4, 47–73, https://doi.org/10.5194/essd-4-47-2012, http://www.earth-syst-sci-data.net/4/47/2012/, 2012.

Martínez, L., Silver, M. W., King, J. M., and Alldredge, A. L.: Nitrogen Fixation by Floating Diatom Mats: A Source of New Nitrogen to Oligotrophic Ocean Waters, Science, 221, 152–154, https://doi.org/10.1126/science.221.4606.152, http://science.sciencemag.org/content/221/4606/152, 1983.

Mauriac, R., Moutin, T., and Baklouti, M.: Accumulation of DOC in Low Phosphate Low Chlorophyll (LPLC) area: is it related to higher production under high N:P ratio?, Biogeosciences, 8, 933–950, https://doi.org/10.5194/bg-8-933-2011, http://www.biogeosciences.net/8/933/2011/, 2011.

Meyers, G.: On the Annual Rossby Wave in the Tropical North Pacific Ocean, Journal of Physical Oceanography, 9, 663–674, https://doi.org/10.1175/1520-0485(1979)009<0663:OTARWI>2.0.CO;2, https://journals.ametsoc.org/doi/abs/10.1175/1520-0485(1979)009%3C0663%3AOTARWI%3E2.0.CO%3B2, 1979.

Mills, M. M., Ridame, C., Davey, M., La Roche, J., and Geider, R. J.: Iron and phosphorus co-limit nitrogen fixation in the eastern tropical North Atlantic, Nature, 429, 292–294, http://www.nature.com/nature/journal/v429/n6989/abs/nature02550.html, 2004.

Moisander, P. H., Zhang, R., Boyle, E. A., Hewson, I., Montoya, J. P., and Zehr, J. P.: Analogous nutrient limitations in unicellular diazotrophs and Prochlorococcus in the South Pacific Ocean, The ISME journal, 6, 733–744, http://www.nature.com/ismej/journal/v6/n4/abs/ismej2011152a.html, 2012.

Monteiro, F. M., Dutkiewicz, S., and Follows, M. J.: Biogeographical controls on the marine nitrogen fixers: controls on marine nitrogen fixers, Global Biogeochemical Cycles, 25, n/a–n/a, https://doi.org/10.1029/2010GB003902, http://doi.wiley.com/10.1029/2010GB003902, 2011.

Moore, J. K., Doney, S. C., Glover, D. M., and Fung, I. Y.: Iron cycling and nutrient-limitation patterns in surface waters of the World Ocean, Deep Sea Research Part II: Topical Studies in Oceanography, 49, 463–507, https://doi.org/10.1016/S0967-0645(01)00109-6, http://www.sciencedirect.com/science/article/pii/S0967064501001096, 2002.

Moore, J. K., Doney, S. C., and Lindsay, K.: Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model: global ecosystem-biogeochemical model, Global Biogeochemical Cycles, 18, n/a–n/a, https://doi.org/10.1029/2004GB002220, http://doi.wiley.com/10.1029/2004GB002220, 2004.

Moutin, T., Van Den Broeck, N., Beker, B., Dupouy, C., Rimmelin, P., and Le Bouteiller, A.: Phosphate availability controls Trichodesmium spp. biomass in the SW Pacific Ocean, Marine Ecology Progress Series, 297, 15–21, https://www.com.univ-mrs.fr/~moutin/IMG/pdf/ArticlesPDF/Moutin_et_al_2005.pdf, 2005.

Moutin, T., Karl, D. M., Duhamel, S., Rimmelin, P., Raimbault, P., Van Mooy, B. A., and Claustre, H.: Phosphate availability and the ultimate control of new nitrogen input by nitrogen fixation in the tropical Pacific Ocean, https://darchive.mblwhoilibrary.org/handle/1912/2097, 2008.

Moutin, T., Doglioli, A. M., de Verneil, A., and Bonnet, S.: Preface: The Oligotrophy to the UlTra-oligotrophy PACific Experiment (OUTPACE cruise, 18 February to 3 April 2015), Biogeosciences, 14, 3207–3220, https://doi.org/10.5194/bg-14-3207-2017, https://www.biogeosciences.net/14/3207/2017/, 2017.

Moutin, T., Wagener, T., Caffin, M., Fumenia, A., Gimenez, A., Baklouti, M., Bouruet-Aubertot, P., Pujo-Pay, M., Leblanc, K., Lefevre, D., Helias Nunige, S., Leblond, N., Grosso, O., and de Verneil, A.: Nutrient availability and the ultimate control of the biological carbon pump in the western tropical South Pacific Ocean, Biogeosciences, 15, 2961–2989, https://doi.org/10.5194/bg-15-2961-2018, https://www.biogeosciences.net/15/2961/2018/, 2018.

Mulholland, M., Bronk, D., and Capone, D.: Dinitrogen fixation and release of ammonium and dissolved organic nitrogen by Trichodesmium IMS101, Aquatic Microbial Ecology, 37, 85–94, https://doi.org/10.3354/ame037085, http://www.int-res.com/abstracts/ame/v37/n1/p85-94/, 2004.

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, Limnology and oceanography, 50, 839–849, http://onlinelibrary.wiley.com/doi/10.4319/lo.2005.50.3.0839/abstract, 2005.

Mulholland, M. R., Bernhardt, P. W., Heil, C. A., Bronk, D. A., and O'Neil, J. M.: Nitrogen fixation and release of fixed nitrogen by Trichodesmium spp. in the Gulf of Mexico, Limnology and Oceanography, 51, 1762–1776, http://onlinelibrary.wiley.com/doi/10.4319/lo.2006.51.4.1762/abstract, 2006.

Olsen, A., Key, R. M., van Heuven, S., Lauvset, S. K., Velo, A., Lin, X., Schirnick, C., Kozyr, A., Tanhua, T., Hoppema, M., Jutterström, S., Steinfeldt, R., Jeansson, E., Ishii, M., Pérez, F. F., and Suzuki, T.: The Global Ocean Data Analysis Project version 2 (GLODAPv2) – an internally consistent data product for the world ocean, Earth System Science Data, 8, 297–323, https://doi.org/10.5194/essd-8-297-2016, http://www.earth-syst-sci-data.net/8/297/2016/, 2016.

Paerl, H. W., Crocker, K. M., and Prufert, L. E.: Limitation of N_2 fixation in coastal marine waters: Relative importance of molybdenum, iron, phosphorus, and organic matter availability1, Limnology and Oceanography, 32, 525–536, https://doi.org/10.4319/lo.1987.32.3.0525, https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.1987.32.3.0525, 1987.

Perry, M. J.: Alkaline phosphatase activity in subtropical Central North Pacific waters using a sensitive fluorometric method, Marine Biology, 15, 113–119, https://doi.org/10.1007/BF00353639, https://link.springer.com/article/10.1007/BF00353639, 1972.

Perry, M. J.: Phosphate utilization by an oceanic diatom in phosphorus-limited chemostat culture and in the oligotrophic waters of the central North Pacific1, Limnology and Oceanography, 21, 88–107, https://doi.org/10.4319/lo.1976.21.1.0088, http://onlinelibrary.wiley.com/doi/10.4319/lo.1976.21.1.0088/abstract, 1976.

Polovina, J. J., Howell, E. A., and Abecassis, M.: Ocean's least productive waters are expanding, Geophysical Research Letters, 35, L03 618, https://doi.org/10.1029/2007GL031745, http://onlinelibrary.wiley.com/doi/10.1029/2007GL031745/abstract, 2008.

Rabouille, S., Staal, M., Stal, L. J., and Soetaert, K.: Modeling the Dynamic Regulation of Nitrogen Fixation in the Cyanobacterium Trichodesmium sp., Applied and Environmental Microbiology, 72, 3217–3227, https://doi.org/10.1128/AEM.72.5.3217-3227.2006, http://aem.asm.org/cgi/doi/10.1128/AEM.72.5.3217-3227.2006, 2006.

Radenac, M.-H. and Rodier, M.: Nitrate and chlorophyll distributions in relation to thermohaline and current structures in the western tropical Pacific during 1985–1989, Deep Sea Research Part II: Topical Studies in Oceanography, 43, 725–752, https://doi.org/10.1016/0967-0645(96)00025-2, http://linkinghub.elsevier.com/retrieve/pii/0967064596000252, 1996.

Rueter, J. G., Ohki, K., and Fujita, Y.: The effect of iron nutrition on photosynthesis and nitrogen fixation in cultures of *Trichodesmium* (Cyanophyceae), Journal of Phycology, 26, 30–35, https://doi.org/10.1111/j.0022-3646.1990.00030.x, http://doi.wiley.com/10.1111/j.0022-3646.1990.00030.x, 1990.

Sañudo-Wilhelmy, S. A., Kustka, A. B., Gobler, C. J., Hutchins, D. A., Yang, M., Lwiza, K., Burns, J., Capone, D. G., Raven, J. A., and Carpenter, E. J.: Phosphorus limitation of nitrogen fixation by *Trichodesmium* in the central Atlantic Ocean, Nature, 411, 66–69, https://doi.org/10.1038/35075041, https://www.nature.com/articles/35075041, 2001.

Shamarock, W., Kemp, J. B., Dudhia, J., Gill, D., Barker, D., Duda, M., and Powers, J.: A Description of the Advanced Research WRF Version 3: NCAR Technical Note TN–475+ STR, Tech. rep., National Center for Atmospheric Research Boulder, Colorado, USA, 2008.

Stenegren, M., Caputo, A., Berg, C., Bonnet, S., and Foster, R. A.: Distribution and drivers of symbiotic and free-living diazotrophic cyanobacteria in the western tropical South Pacific, Biogeosciences, 15, 1559–1578, https://doi.org/10.5194/bg-15-1559-2018, https://www.biogeosciences.net/15/1559/2018/, 2018.

Van Den Broeck, N., Moutin, T., Rodier, M., and Le Bouteiller, A.: Seasonal variations of phosphate availability in the SW Pacific Ocean near New Caledonia, Marine Ecology Progress Series, 268, 1–12, http://www.int-res.com/abstracts/meps/v268/p1-12/, 2004.

Van Wambeke, F., Gimenez, A., Duhamel, S., Dupouy, C., Lefevre, D., Pujo-Pay, M., and Moutin, T.: Dynamics and controls of heterotrophic prokaryotic production in the western tropical South Pacific Ocean: links with diazotrophic and photosynthetic activity, Biogeosciences, 15, 2669–2689, https://doi.org/10.5194/bg-15-2669-2018, https://www.biogeosciences.net/15/2669/2018/, 2018.

Vidal, M., Duarte, C., Agustí, S., Gasol, J., and Vaqué, D.: Alkaline phosphatase activities in the central Atlantic Ocean indicate large areas with phosphorus deficiency, Marine Ecology Progress Series, 262, 43–53, https://doi.org/10.3354/meps262043, http://www.int-res.com/abstracts/meps/v262/p43-53/, 2003.

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

Zamora, L., Landolfi, A., Oschlies, A., Hansell, D., Dietze, H., and Dentener, F.: Atmospheric deposition of nutrients and excess N formation in the North Atlantic, Biogeosciences (BG), 7, 777–793, https://doi.org/Zamora, Lauren, Landolfi, Angela, Oschlies, Andreas, Hansell, D., Dietze, Heiner and Dentener, F. (2010) Atmospheric deposition of nutrients and excess N formation in the North Atlantic Biogeosciences (BG), 7 . pp. 777-793. DOI 10.5194/bg-7-777-2010 <http://dx.doi.org/10.5194/bg-7-777-2010>., http://www.biogeosciences.net/7/777/2010/, 2010.

Zehr, J. P. and Kudela, R. M.: Nitrogen Cycle of the Open Ocean: From Genes to Ecosystems, Annual Review of Marine Science, 3, 197–225, https://doi.org/10.1146/annurev-marine-120709-142819, http://www.annualreviews.org/doi/10.1146/annurev-marine-120709-142819, 2011.

Zehr, J. P. and McReynolds, L. A.: Use of degenerate oligonucleotides for amplification of the nifH gene from the marine cyanobacterium Trichodesmium thiebautii., Applied and Environmental Microbiology, 55, 2522–2526, http://aem.asm.org/content/55/10/2522.short, 1989.

Zehr, J. P. and Turner, P. J.: Nitrogen fixation: Nitrogenase genes and gene expression, in: Methods in Microbiology, vol. 30 of Marine Microbiology, pp. 271–286, Academic Press, https://doi.org/10.1016/S0580-9517(01)30049-1, http://www.sciencedirect.com/science/article/pii/S0580951701300491, 2001.

Zhang, R.-H., Busalacchi, A. J., and Xue, Y.: Decadal change in the relationship between the oceanic entrainment temperature and thermocline depth in the far western tropical Pacific, Geophysical Research Letters, 34, L23 612, https://doi.org/10.1029/2007GL032119, http://onlinelibrary.wiley.com/doi/10.1029/2007GL032119/abstract, 2007.

Zweng, M. M., Reagan, J. R., Antonov, J. I., Locarnini, R. A., Mishonov, A. V., Boyer, T. P., Garcia, H. E., Baranova, O. K., Johnson, D. R., Seidov, D., and Biddle, M. M.: World ocean atlas 2013. Volume 2, Salinity, Tech. rep., NOAA Atlas NESDIS 74, https://doi.org/10.7289/V5251G4D, 2013.
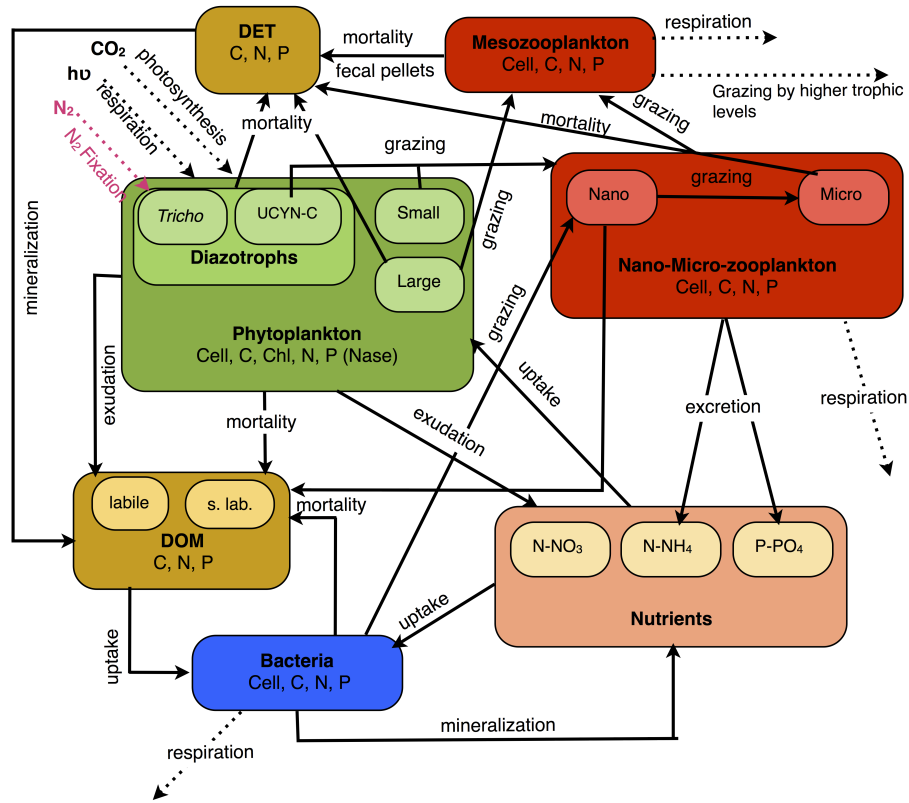
List of Figures

Figure 1. Conceptual diagram of the biogeochemical model for the physical-biogeochemical coupled 1D-vertical model used in the OUT-PACE project.
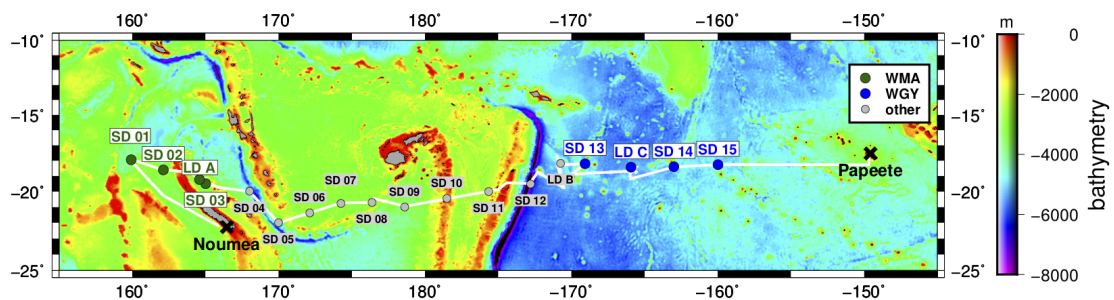

Figure 2. Transect of the OUTPACE cruise with the location of the short duration (SD) and long duration (LD) stations superimposed on a bathymetry map (GEBCO_2014 grid). The two main regions studied in this work are shown in green for WMA and in blue for the WGY.
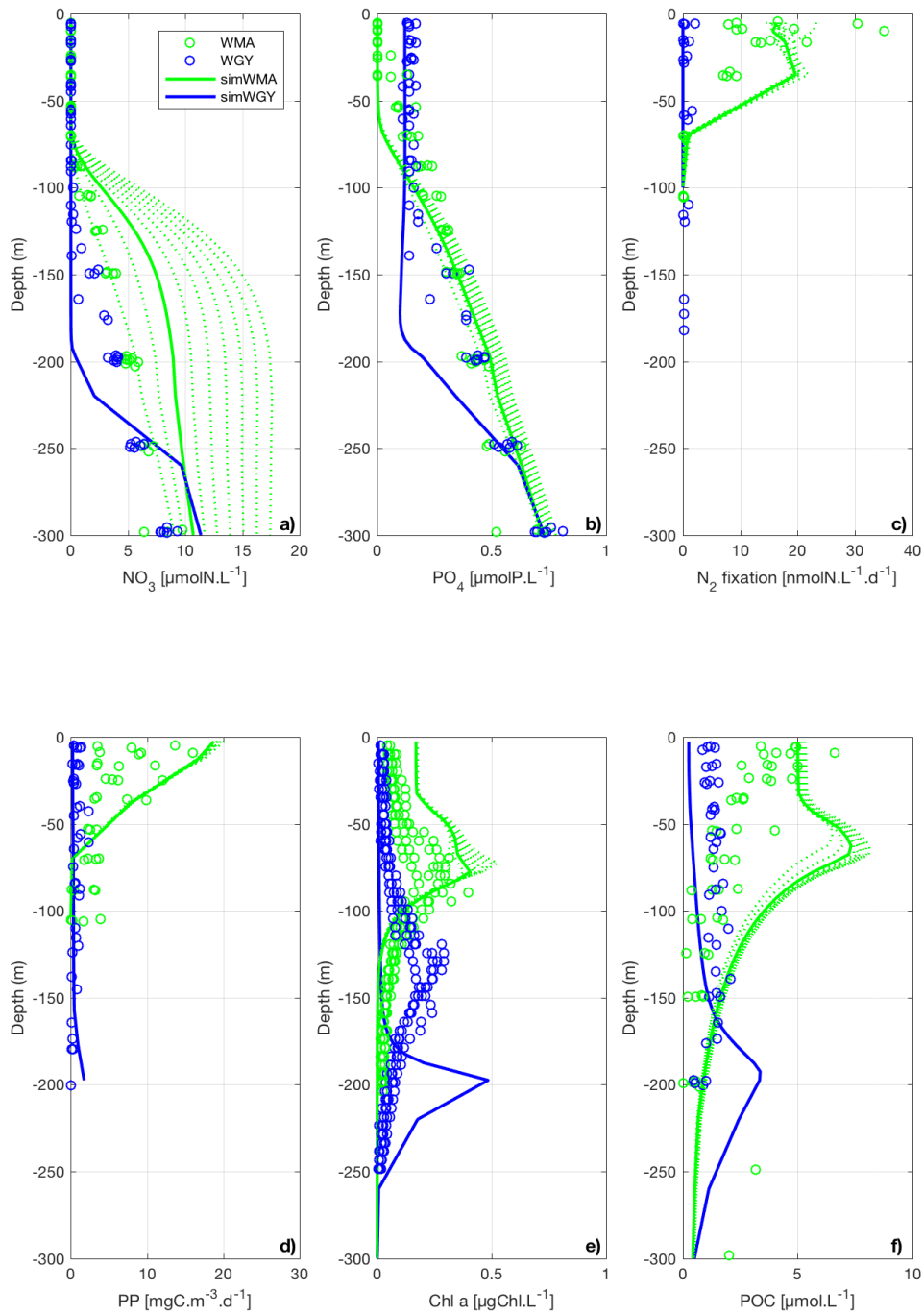
Figure 3. Vertical profiles of (a) dissolved inorganic nitrogen (DIN), (b) dissolved inorganic phosphorus (DIP), (c) N_2 fixation rates, (d) primary production (PP), (e) chlorophylle a (Chl a) and (f) particulate organic carbon (POC) during the OUTPACE cruise in the WMA region (green circles) and in the WGY region (blue circles), and from the model results of the simulation with diazotrophy as a proxy of the

Figure 4. Seasonal dynamics of (a) dissolved inorganic nitrogen (DIN) on a logarithmic scale in µM, (b) dissolved inorganic phosphorus

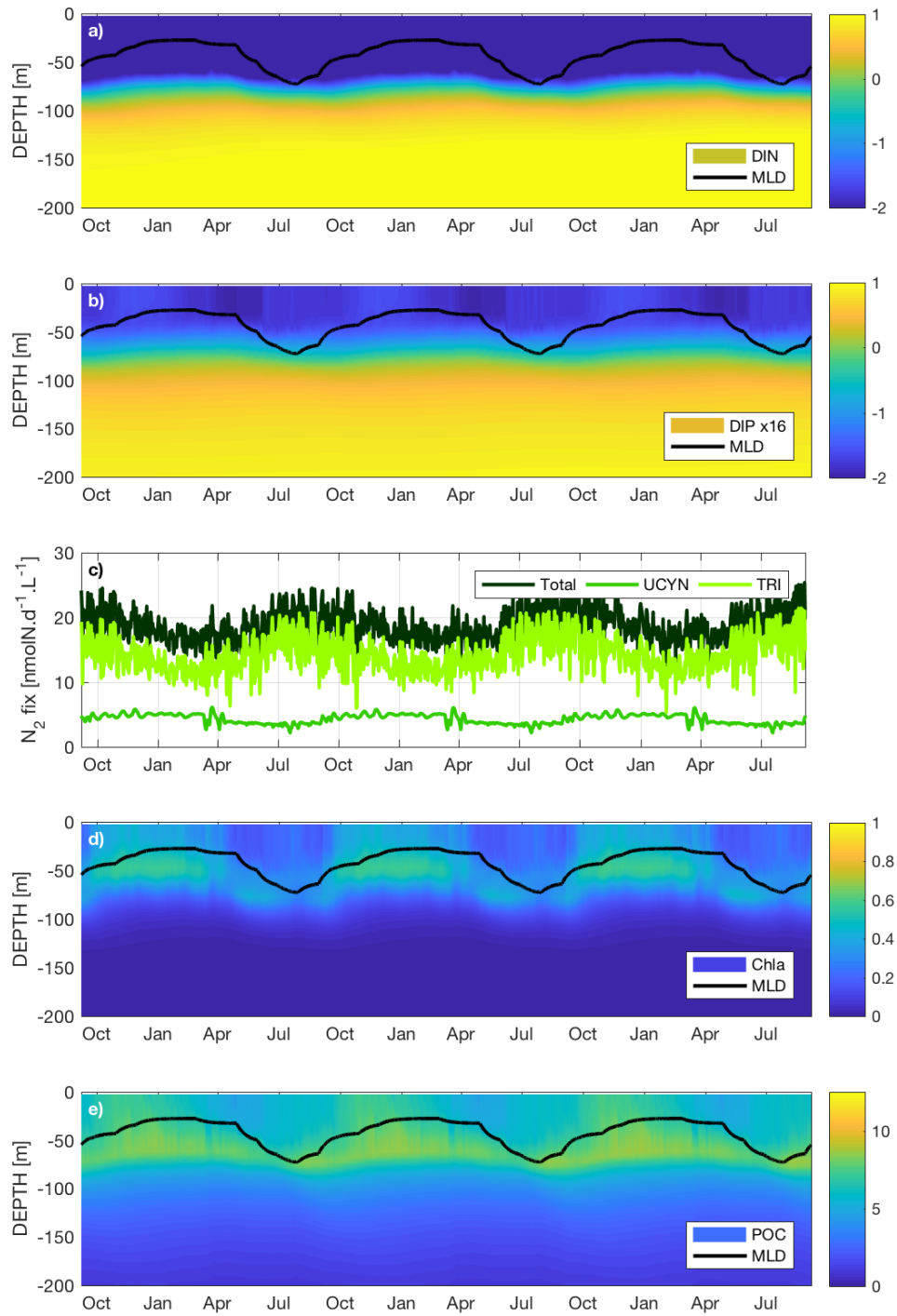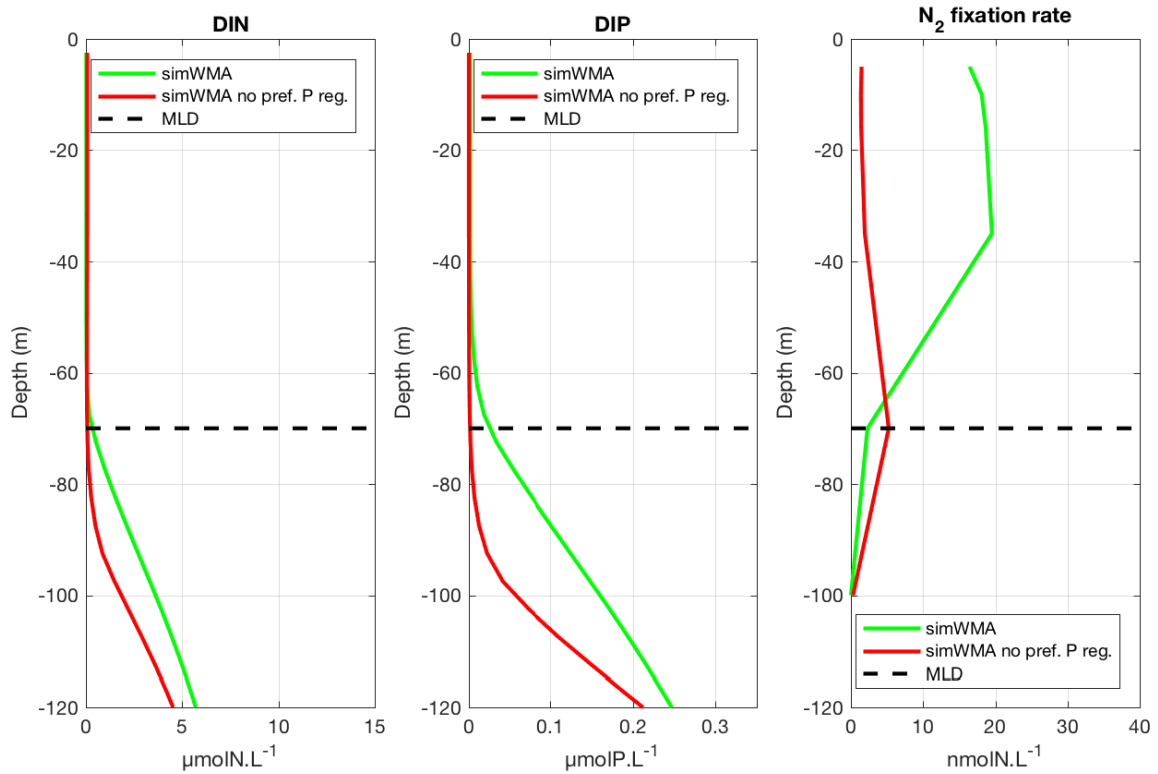**Figure 5.** Vertical profiles of (a) dissolved inorganic nitrogen (DIN), (b) dissolved inorganic phosphorus (DIP), (c) N_2 fixation rates for the simulation with diazotrophy, as a proxy of the WMA region (sim^{WMA}) with the preferential P regeneration (in green) and without the preferential P regeneration (in red). The horizontal black dashed line represents the depth of the maximum mixing layer calculated at 70 m depth.

Supplementary material

Symbol	Definition	Units	Value HNF	Value BAC	Value PHYS	Value UCYN	Value PHYL	Value TRI
				DOP assimilation				
K_{LDOP}	Half-saturation constant for LDOP	mol.L^{-1}	-	$6.62\,10^{-7}$	$6.57\,10^{-7}$	$6.57\,10^{-7}$	$5.66\,10^{-6}$	$5.66\,10^{-6}$
				Intracelullar contents				
Q_P^{min}	minimum phosphate content	mol.cell^{-1}	$1.27\,10^{-12}$	$1.15\,10^{-15}$	-	-	-	-
Q_P^{max}	maximum phosphate content	mol.cell^{-1}	$3\,Q_P^{min}$	$3\,Q_P^{min}$	-	-	-	-
Q_N^{min}	minimum nitrogen content	mol.cell^{-1}	$16\,Q_P^{min}$	$16\,Q_P^{min}$	-	-	-	-
Q_N^{max}	maximum nitrogen content	mol.cell^{-1}	$3\,Q_N^{min}$	$3\,Q_N^{min}$	-	-	-	-
Q_C^{min}	minimum carbon content	mol.cell^{-1}	$106\,Q_P^{min}$	$106\,Q_P^{min}$	-	-	-	-
Q_C^{max}	maximum carbon content	mol.cell^{-1}	$3\,Q_C^{min}$	$3\,Q_C^{min}$	-	-	-	-
				Nutrients assimilation				
V_{NO3}^{max}	Maximum uptake rate for NO$_3$	mol.cell^{-1}.s^{-1}	$\mu \cdot Q_N^{max}$	$\mu \cdot Q_N^{max}$	-	-	-	-
V_{NH3}^{max}	Maximum uptake rate for NH$_4$	mol.cell^{-1}.s^{-1}	$\mu \cdot Q_N^{max}$	$\mu \cdot Q_N^{max}$	-	-	-	-
V_{PO4}^{max}	Maximum uptake rate for PO$_4$	mol.cell^{-1}.s^{-1}	$\mu \cdot Q_P^{max}$	$\mu \cdot Q_P^{max}$	-	-	-	-
V_{DON}^{max}	Maximum uptake rate for DON	mol.cell^{-1}.s^{-1}	$\mu \cdot Q_N^{max}$	$\mu \cdot Q_N^{max}$	-	-	-	-
V_{DOP}^{max}	Maximum uptake rate for DOP	mol.cell^{-1}.s^{-1}	$\mu \cdot Q_N^{max}$	$\mu \cdot Q_P^{max}$	-	-	-	-

Symbol	Definition	Units	DETS-C	DETL-C	DETS-N	DETL-N	DETS-P	DETL-P
				Particulate matter hydrolysis and sink				
ω	sinking rate	m.d^{-1}	1.0	25.0	1.0	25.0	1.0	25.0
TT_{DET_P}	Turnover time for DET-P	d^{-1}					0.5	0.5

Table 1. Model parameters which differ from Alekseenko et al. (2014) mentioned in Section **2.2.2**, with μ = maximum growth rate

.

Symbol	Definition	Value TRI	Value UCYN	Units -
		Growth and Intracelullar contents		
μ_{max}	maximum growth rate	$2.08\ 10^{-6}$	$3.2\ 10^{-5}$	s^{-1}
k_m	specific natural mortality rate	$1.16\ 10^{-6}$	$1.16\ 10^{-6}$	s^{-1}
Q_C^{min}	minimum cell quota of C	$2.28\ 10^{-10}$	$6.84\ 10^{-15}$	$molC.Cell^{-1}$
Q_C^{max}	maximum cell quota of C	$6.84\ 10^{-15}$	$2.05\ 10^{-14}$	$molC.Cell^{-1}$
Q_N^{min}	minimum cell quota of N	$3.44\ 10^{-11}$	$1.03\ 10^{-15}$	$molN.Cell^{-1}$
Q_N^{max}	maximum cell quota of N	$1.03\ 10^{-10}$	$3.09\ 10^{-15}$	$molN.Cell^{-1}$
Q_P^{min}	minimum cell quota of P	$3.44\ 10^{-11}$	$1.03\ 10^{-15}$	$molN.Cell^{-1}$
Q_P^{max}	maximum cell quota of P	$1.03\ 10^{-10}$	$3.09\ 10^{-15}$	$molN.Cell^{-1}$
Q_{CN}^{min}	minimum cell C:N ratio	5.0	5.0	$molC.molN^{-1}$
Q_{CN}^{max}	maximum cell C:N ratio	19.8	19.8	$molC.molN^{-1}$
Q_{CP}^{min}	minimum cell C:P ratio	35.33	35.33	$molC.molP^{-1}$
Q_{CP}^{max}	maximum cell C:P ratio	318.0	318.0	$molC.molP^{-1}$
		Nutrients assimilation		
K_{NO3-}	Half-saturation constant for $_{NO3-}$	$1.85\ 10^{-6}$	$7.6\ 10^{-6}$	$mol.L^{-1}$
V_{NO3-}^{max}	Maximum uptake rate for $_{NO3-}$	$3.16\ 10^{-15}$	$9.91\ 10^{-20}$	$mol.cell^{-1}.s^{-1}$
K_{NH4+}	Half-saturation constant for $_{NH4+}$	$7.0\ 10^{-6}$	$1.69\ 10^{-6}$	$mol.L^{-1}$
V_{NH4+}^{max}	Maximum uptake rate for $_{NH4+}$	$3.16\ 10^{-15}$	$9.91\ 10^{-20}$	$mol.cell^{-1}.s^{-1}$
$K_{PO_4^{3-}}$	Half-saturation constant for $_{PO_4^{3-}}$	$1.4\ 10^{-6}$	$2.62\ 10^{-7}$	$mol.L^{-1}$
$V_{PO_4^{3-}}^{max}$	Maximum uptake rate for $_{PO_4^{3-}}$	$1.98\ 10^{-16}$	$6.19\ 10^{-21}$	$mol.cell^{-1}.s^{-1}$
K_{DON}	Half-saturation constant for $_{DON}$	$4.32\ 10^{-5}$	$1.05\ 10^{-5}$	$mol.L^{-1}$
V_{DON}^{max}	Maximum uptake rate for $_{DON}$	$3.16\ 10^{-15}$	$9.91\ 10^{-20}$	$mol.cell^{-1}.s^{-1}$
K_{DOP}	Half-saturation constant for $_{DOP}$	$3.4\ 10^{-6}$	$6.57\ 10^{-7}$	$mol.L^{-1}$
V_{DOP}^{max}	Maximum uptake rate for $_{DOP}$	$3.16\ 10^{-15}$	$6.19\ 10^{-21}$	$mol.cell^{-1}.s^{-1}$
		Diazotrophy process		
$Nase_{prod}^{max}$	Maximum rate of increase of nitrogenase activity	$1.17\ 10^{-21}$	$3.51\ 10^{-26}$	$mol.cell^{-1}.s^{-2}$
$Nase_{decr}^{max}$	Maximum rate of decay of nitrogenase activity	$9.36\ 10^{-22}$	$2.83\ 10^{-26}$	$mol.cell^{-1}.s^{-2}$
K_{Nase}	Coefficient of nitrogenase degradation	$9.44\ 10^{-16}$	$1.92\ 10^{-20}$	$mol.cell^{-1}.s^{-1}$
$COST_{DIAZO}$	Respiration cost for nitrogen fixation	1.5	1.5	$mol.mol^{-1}$
$EXUD_{DON}$	Exudation part of N$_2$ fixed towards $_{DON}$	0.5	0.5	
$EXUD_{NH_4}$	Exudation part of N$_2$ fixed towards $_{NH_4}$	0.5	0.5	

Table 2. Model Parameters relative to diazotroph organisms TRI and UCYN
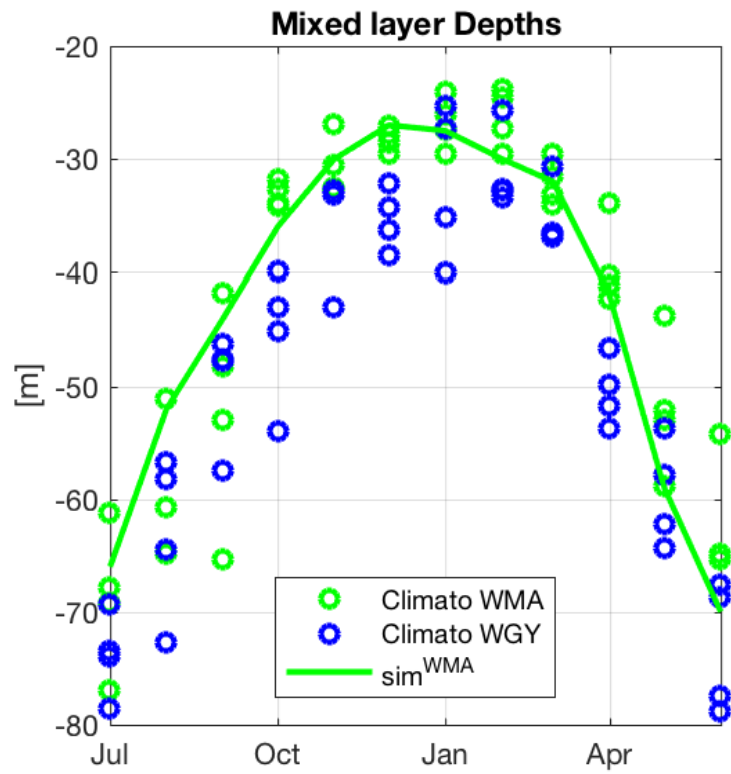
Figure SM 1 Temporal dynamics of the *in situ* mixed layer depths estimated using a climatology (de Boyer Montégut et al., 2004) at WMA (green circles) and WGY (blue circles), and simulated by the model (green line)
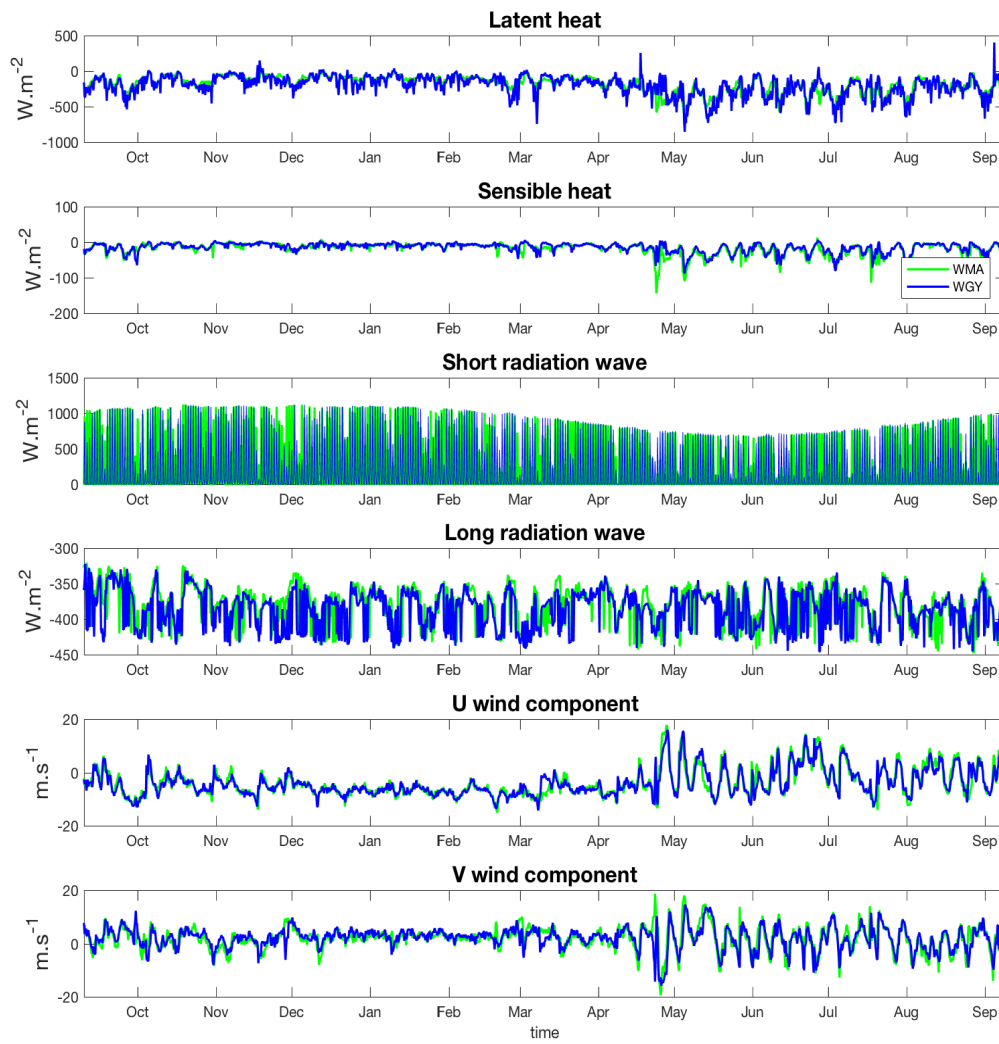
Figure SM 2 Atmospheric forcings provided by the Weather Research Forecast model and extracted at the WMA (green) and WGY (blue) locations from September 2014 to September 2015
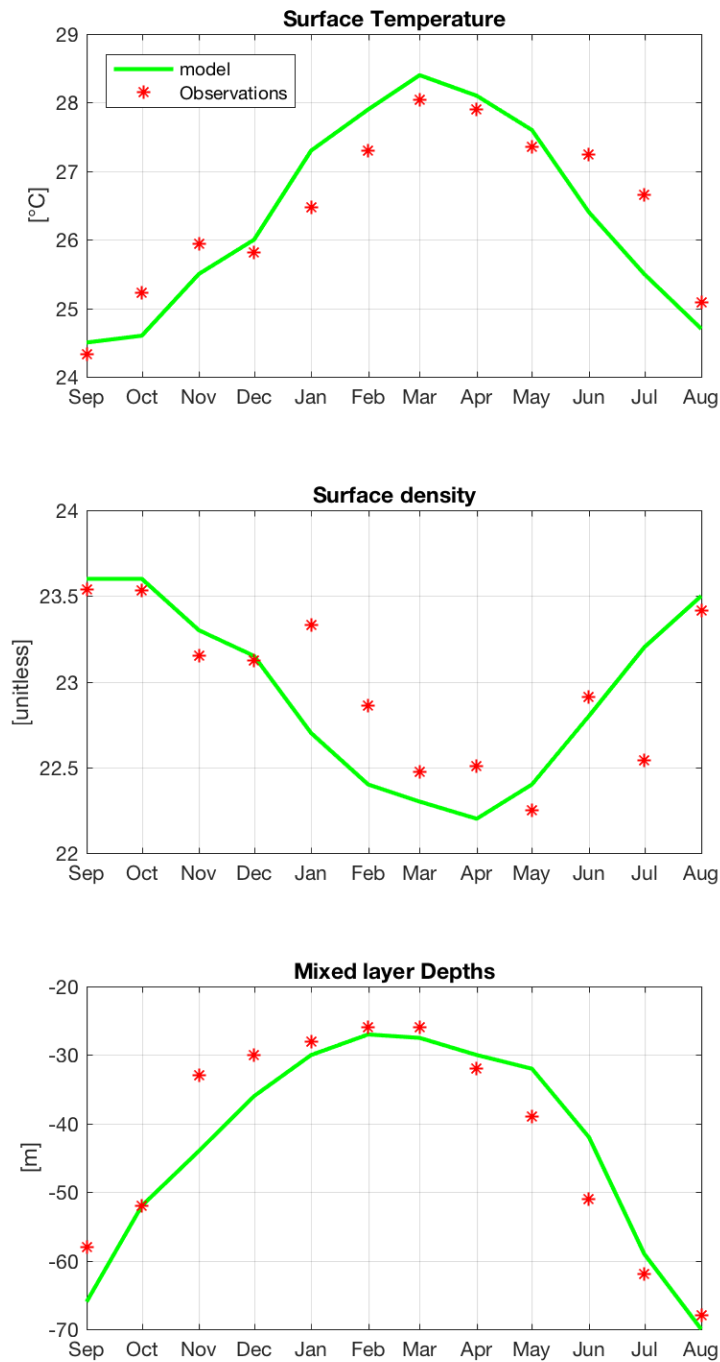
Figure SM 3 Evolution of monthly averaged (a) sea surface temperature (SST), (b) surface density and (c) mixed layer depths (MLD) from September 2014 to August 2015 predicted by the model (green line) and calculated with climatologies (WOA13 for SST and Surface density, and de Boyer Montegut et al., 2004 for MLD)