



Diazotrophy as the main driver of planktonic production and biogeochemical C, N, P cycles in the Western Tropical South Pacific Ocean: results from a 1DV biogeochemical-physical coupled model

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Abstract. The Oligotrophy to UItTra-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 to investigate a longitudinal gradient of biological and biogeochemical features in the WTSP, and especially the role of N₂ fixation on the C, N, P cycles. Two contrasted regions were considered : the Western Melanesian Archipelago (WMA), characterized by high N₂ fixation rates, significant surface production and low dissolved inorganic phosphorus (DIP) concentrations, and the Western south Pacific GYre (WGY), characterized by very low N₂ fixation rates, low surface production rates and high DIP concentrations. A one-dimensional biogeochemical – physical coupled model was used to investigate the role of N₂ fixation in the WTSP by running two identical simulations, only differing by the presence or not 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 upper surface waters in the simulation standing for WMA, where diazotrophs provided a new source of nitrogen (N) to their ecosystem, whereas no seasonal variations were obtained in the simulation standing for WGY, 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 N₂ fixation in a crucial way.

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 CO₂, is strongly linked to the nutrients' availability in the ocean surface layer (de Baar, 1994). Although nitrate (NO₃⁻) and ammonium (NH₄⁺) 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 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. However, even if the diazotrophs are not limited by atmospheric N_2 , their growth is controlled by other factors, including the availability of iron (Fe) and phosphate (P) (Moutin et al., 2005; Karl and Letelier, 2008). 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 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.

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 P availability was also observed from low concentrations in the Melanesian Archipelago (MA) to higher concentrations in the South Pacific Gyre (SPG) (Moutin et al., this issue), closely related to an opposite gradient of N_2 fixation rates (Bonnet et al., 2017, Caffin et al., this issue). 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., this issue) 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 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., 2001, 2004; Monteiro et al., 2011), at regional scale (Coles and Hood, 2007; Zamora et al., 2010), at local scale (Fennel et al., 2001; Gimenez et al., 2016) or more specifically at population scale, such as the work on *Trichodesmium* sp. by Rabouille et al. (2006). 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 work, we used a one-dimensional physical-biogeochemical coupled model to simulate the dynamics of the complex ecosystem 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 standing for WMA, and the second without diazotrophy standing for WGY, to implicitly take into account the role of Fe allowing N₂ fixation in the MA but 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 N₂ 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

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 biodiversity and biogeochemical 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 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 their different biogeochemical characteristics: the western MA (WMA), the eastern MA (EMA) and the western gyre (WGY) waters (Moutin et al., this issue). In this study, we focused on the comparison of the two most widely contrasted areas, 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 N₂ fixation rates and lower phosphate concentrations than WGY.

As already mentioned, in order to investigate the role of N₂ 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 methods used to measure dissolved inorganic nitrogen (DIN), dissolved inorganic phosphorus (DIP), N₂ fixation (N₂ 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., this issue). 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.



For each profile presented in the Results section, we plot the discrete values of the data collected at WMA and WGY (circles), and an average over the respective sampling periods of WMA and WGY for the model results (simWMA, from 02-21-2015 to 03-02-2015, and simWGY, from 03-21-2015 to 03-31-2015). 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) 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).

2.2.1 General backgrounds

To summarize, 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 (zooplankton) and one decomposer (heterotrophic bacteria). All of them are represented in terms of several concentrations (C, N, P and chlorophyll concentrations for phytoplankton) and abundances (cells or individuals per liter) (Mauriac et al., 2011). For ease of reading, the living compartments are abbreviated and populations are represented by emblematic organisms indicated in brackets, 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 (heteronano-flagellates), CIL for microzooplankton (ciliates) and COP for mesozooplankton (copepods). For all the non-diazotrophic features, TRI are parameterized as 100 PHYL cells (assuming that a trichome includes 100 cells; Luo et al. (2012)), and UCYN as PHYS. In the model, N_2 fixation rates depend on the nitrogenase enzyme activity (Nase) (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 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”. 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, this model includes two size classes of detrital matter associated with two different sinking



rates. 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.

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 production of the extracellular phosphatase alkaline occurring in such oligotrophic areas due to bacteria (enhancing the consumption of organic P, Perry (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 Sect. 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). The model considers the vertical discretization of the time evolution equations for temperature, salinity, momentum and kinetic energy. The grid cell size is 5 m from surface to 200 m, and 40 m 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. 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 chosen so as to cover the period from the winter mixing preceding the OUTPACE cruise to the next winter.

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

The initial profiles of 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 LD station located in WMA ($19^\circ 13.00 \text{ S } 164^\circ 29.40 \text{ W}$). Initial dissolved organic matter concentrations, BAC and autotroph abundances were obtained from the vertical profiles measured in WMA: to represent the homogeneity of the surface layer due to winter mixing, the 0-70 m mean value was applied on the 0-70 m layer of the initial vertical profiles. Below 70 m, initial concentrations were the same as data. Since the model includes variable stoichiometry for organisms, relative initial intracellular quota of non-diazotroph organisms were arbitrarily set to 50 %, 25 % and 75 % respectively for C, N and P. While there was no difference for relative initial intracellular quota of C and P between diazotroph and non-diazotrophs, relative initial N intracellular quota of diazotrophs were set 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

5 3.1.1 Nutrients availability and N₂ fixation

DIN and DIP concentrations are presented in Figure 3 a) and 3 b). Strictly, DIN is the sum of nitrate, nitrite and ammonium ($\text{DIN} = [\text{NO}_3^-] + [\text{NO}_2^-] + [\text{NH}_4^+]$). However, since $[\text{NO}_2^-]$ and $[\text{NH}_4^+]$ were negligible compared to $[\text{NO}_3^-]$, DIN was assimilated to $[\text{NO}_3^-]$. In the same way, DIP strictly equals orthophosphates (i.e. $\text{DIP} = [\text{HPO}_4^{2-}] + [\text{PO}_4^{3-}]$). From the surface to 70 m depth, $\text{DIN}^{\text{obsWMA}}$ and $\text{DIN}^{\text{obsWGY}}$ are below the quantification limit (i.e. $0.05 \mu\text{M}$). $\text{DIN}^{\text{simWMA}}$ and $\text{DIN}^{\text{simWGY}}$ do not show any significant difference in the surface layer and range from 0.02 to $0.04 \mu\text{M}$ and from 0.03 to $0.04 \mu\text{M}$ for $\text{DIN}^{\text{simWMA}}$ and $\text{DIN}^{\text{simWGY}}$, respectively. Even if the concentrations of DIP are low in the surface layer (below $0.2 \mu\text{M}$), some differences can be seen between WMA and WGY for both model outputs and data. Figure 3, b) shows a concentration around $0.2 \mu\text{M}$ for $\text{DIP}^{\text{obsWGY}}$ from the surface to 120 m, whereas $\text{DIP}^{\text{obsWMA}}$ is very low, with values below $0.05 \mu\text{M}$ at the subsurface, with a steady increase up to $0.5 \mu\text{M}$ at 300 m depth. Regarding the model outputs, $\text{DIP}^{\text{simWMA}}$ is close to zero from the surface to 60 m, and reaches a value of $0.70 \mu\text{M}$ at 300 m depth. $\text{DIP}^{\text{simWGY}}$ is significantly higher than $\text{DIP}^{\text{simWMA}}$, with a homogeneous concentration of $0.16 \mu\text{M}$ from the surface to 175 m depth, and then increases slightly up to $0.7 \mu\text{M}$ at 300 m.

The vertical profiles of $\text{DIN}^{\text{simWMA}}$ and $\text{DIP}^{\text{simWMA}}$ show a deeper nitracline (around 75 m depth) than phosphacline (around 60 m depth), as observed with data. 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, $\text{DIN}^{\text{simWMA}}$ is higher than $\text{DIN}^{\text{obsWMA}}$ below the nitracline. There is indeed a regular accumulation of DIN in simWMA below the photic zone during the ten-year simulation (Figure 3, a)), reaching at the end a high concentration of $17 \mu\text{M}$ that is not observed in $\text{DIN}^{\text{obsWMA}}$. 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 N₂ fixation rates (N₂ fix) measured at WMA and WGY and the vertical profiles of $\text{N}_2\text{fix}^{\text{simWMA}}$ are presented in Figure 3 c). At the surface, $\text{N}_2\text{fix}^{\text{obsWMA}}$ ranges from 9.0 to $30.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$, with a maximum rate of $35.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ near 10 m depth. $\text{N}_2\text{fix}^{\text{obsWMA}}$ then decreases gradually with depth to $9.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ at 40 m before reaching lower rates below 40 m with values less than $1.5 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ and a minimum of $0.1 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ at 100 m. Regarding the model results of the simulation with diazotrophy, $\text{N}_2\text{fix}^{\text{simWMA}}$ rates are consistent with data with a similar trend of higher rates (around $17.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$) from the surface to 40 m depth, and decreasing values from 40 m to 70 m depth (down to $1.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ at 70 m). At WGY, very low $\text{N}_2\text{fix}^{\text{obsWGY}}$ were measured compared to $\text{N}_2\text{fix}^{\text{obsWMA}}$, with a maximum



rate of $2.0 \text{ nmolN.L}^{-1}.\text{d}^{-1}$ observed at the surface. In the simulation without diazotrophy, $\text{N}_2 \text{ fix}^{\text{simWGY}}$ is nil (see Figure 3, c)).

3.1.2 chlorophyll a, primary production and carbon biomass

Figure 3 shows the vertical profiles of d) primary production (PP), e) chlorophyll a concentration (Chl \underline{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, $\text{PP}^{\text{obsWMA}}$ ranges from 4.0 to $16.0 \text{ mgC.m}^{-3}.\text{d}^{-1}$ while $\text{PP}^{\text{obsWGY}}$ never exceeds $1.5 \text{ mgC.m}^{-3}.\text{d}^{-1}$. $\text{PP}^{\text{simWGY}}$ never exceeds $1.0 \text{ mgC.m}^{-3}.\text{d}^{-1}$ and is in good agreement with $\text{PP}^{\text{obsWGY}}$ in the whole photic layer. $\text{PP}^{\text{simWMA}}$ is also in good agreement with $\text{PP}^{\text{obsWMA}}$, even if $\text{PP}^{\text{simWMA}}$ values are close to the upper limit of the $\text{PP}^{\text{obsWMA}}$ range values. As for $\text{PP}^{\text{obsWMA}}$, $\text{PP}^{\text{simWMA}}$ slightly decreases from the surface to the bottom of the photic layer, before reaching low rates below 70 m.

The main differences between $\text{Chl } \underline{a}^{\text{obsWMA}}$ and $\text{Chl } \underline{a}^{\text{obsWGY}}$ lies in the depth of the deep chlorophyll maximum (DCM), which is around 75 m for $\text{Chl } \underline{a}^{\text{obsWMA}}$ while the $\text{Chl } \underline{a}^{\text{obsWGY}}$ 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 $\text{Chl } \underline{a}^{\text{simWGY}}$ located at 200 m, while the DCM for $\text{Chl } \underline{a}^{\text{simWMA}}$ is shallower (around 50 m). For both the data and the model outputs, we observe 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: $\text{Chl } \underline{a}^{\text{obsWMA}}$ and $\text{Chl } \underline{a}^{\text{obsWGY}}$ maximum values are equal to $0.3 \text{ } \mu\text{gChl.L}^{-1}$ while $\text{Chl } \underline{a}^{\text{simWMA}}$ and $\text{Chl } \underline{a}^{\text{simWGY}}$ maximum values are equal to $0.5 \text{ } \mu\text{gChl.L}^{-1}$. Another difference between the model outputs and the data lies in the higher surface values of $\text{Chl } \underline{a}^{\text{simWMA}}$ around $0.35 \text{ } \mu\text{gChl.L}^{-1}$ whereas $\text{Chl } \underline{a}^{\text{obsWMA}}$ does not exceed $0.15 \text{ } \mu\text{gChl.L}^{-1}$ from 0 to 50 m depth.

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. $\text{POC}^{\text{obsWMA}}$ is, at the maximum, 5-fold higher than $\text{POC}^{\text{obsWGY}}$ with maximum values at the surface reaching $5 \text{ } \mu\text{M}$. $\text{POC}^{\text{obsWMA}}$ then slightly decreasing with depth to reach below 50 m values that are similar to those of $\text{POC}^{\text{obsWGY}}$ (around $1.5 \text{ } \mu\text{M}$). Higher simulated than measured POC values are also observed close to the surface. A maximum value of $7.5 \text{ } \mu\text{M}$ for $\text{POC}^{\text{simWMA}}$ 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 $\text{POC}^{\text{simWGY}}$ just above 200 m, with a maximum concentration of $3 \text{ } \mu\text{M}$. $\text{POC}^{\text{simWGY}}$ concentrations remain very low between the surface and the deep maximum, while there is a significant C biomass production rate in simWMA with $\text{POC}^{\text{simWMA}}$ concentrations higher than $6.5 \text{ } \mu\text{M}$ at the surface.

3.2 Temporal seasonal variations

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.

3.2.1 Nutrients availability and N₂ 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 leading to a maximum MLD of 70 m in October, followed by a longer stratified period from February to July, with a shallower MLD between 25 and 30 m. 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 before regularly decreasing until April down to 0.6 nM. DIP^{simWMA} then remains low during the stratified period until the next winter mixing in August/September. The phosphocline is always shallower than the nitracline in simWMA and remains around 50 m depth.

Since the vertical resolution for flux is lower than the one for pools, we represent the dynamics of N₂ 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 N₂ fixation as well as the respective contributions of *Trichodesimum* sp. and UCYN to this flux. The total N₂ 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, i.e. during the winter mixing. The major contributor to the N₂ fixation in simWMA is *Trichodesimum* sp., with on average, a contribution of 80% of the total N₂ 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. During winter mixing, 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 μgChl.L⁻¹. From April and during the stratified period, Chl *a*^{simWMA} at surface decreases rapidly, reaching concentrations below 0.15 μgChl.L⁻¹. During the same period, there is also a deepening of the DCM toward 80 m, with lower concentrations down to 0.4 μgChl.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 November 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 stratified 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 $\text{POC}^{\text{simWMA}}$ values at 70 m, reaching a minimum of $7 \mu\text{M}$ 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 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

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 inefficient or non-existent N_2 fixation in the gyre (Moutin et al., this issue). 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 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, 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 depletion 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 the oligotrophic region of the subtropical North Pacific. The significant role of DIP availability in controlling N_2 fixation in the oligotrophic iron depleted WTSP (Van Den Broeck et al. (2004); Moutin et al., *under rev.*, this issue) 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.

4.1.2 Surface plankton productivity mainly driven by N₂ 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 *a* 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 *a* 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., 2017). 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.

The nutriclines in simWGY are significantly deeper than those measured *in situ* in WGY. We assume that this gap is because N₂ fixation is totally removed in simWGY, whereas low but existing N₂ fixation still occurs *in situ* at WGY (Figure 3, c)). The *in situ* planktonic ecosystem in WGY might therefore be slightly fueled by weak N₂ 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 *a* 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 N₂ fixation rates reported in WGY were very low (Caffin et al., this issue), 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 N₂ 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.

4.2 A close link between MLD, nutricline depth and N₂ fixation

4.2.1 How can the nutricline depths influence N₂ 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 have an influence on the nutrient



availability in the surface layer throughout the nutricline positions, partly driven by the vertical dynamics in the water column which determine the MLD (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 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 N₂ (Agawin et al., 2007; Dutkiewicz et al., 2014). However, their development also requires 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, 2001; Mills et al., 2004; Moutin et al., 2005; Monteiro et al., 2011).

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 N₂ fixation rates in agreement with those measured *in situ* (Figure 3, c)). In our preliminary results (not shown), without this decoupling, the depths of the nitra- and phosphacline were the same and at around 70 m, close to the depth of the MLD. Each winter, mixing brought low concentrations of DIN and DIP in the euphotic layer. Low DIN concentrations are favorable for the development of N₂ 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 N₂ fixation rates. 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 N₂ 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 N₂ fixers in the 0-50 m layer, dominated by *Trichodesmium* sp. (not shown), with consistent rates of N₂ fixation and PP rates (Figure 3, c) and d)).

4.2.2 A preferential P regeneration needed to sustain N₂ 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 phosphoenzymes (phosphatase alkaline or nucleotidase) 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 N₂ fixers so as to calculate N₂ fixation rates consistent with those measured in WMA. A preferential P regeneration 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 Sect. 2.2.2, 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 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. 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 $17.0 \mu\text{M}$ 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 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 ($\text{N}^* = \text{NO}_3^- - 16 \times \text{PO}_4^{3-}$, 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); 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). 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 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 $449.6 \text{ mmolN.m}^{-2}$ while the annual integrated N_2 fixation provides $451.0 \text{ mmolN.m}^{-2}$. 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 N₂ 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 (Karl and Lukas, 1996; Campbell et al., 1997; Björkman Karin M. and Karl David M., 2003; Church et al., 2009). 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. Moisaner et al. (2012), and the cruises involved in the GLODAPv2 project Olsen et al. (2016)) providing a spatial (Fumenia et al., 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 *a* and POC]^{simWMA} over 3 years of simulation in the 0-200 m layer.

The winter mixing replenishes the surface layer in DIP but not in DIN, as the nitracline is deeper than 70 m, whereas the phosphacline is shallower (Figures 3 a) and b)). The newly available DIP in the surface layer is immediately followed by an increase in the N₂ fixation rates in August (Figure 3, c)), which then remain quite stable until January 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 the surface layer. 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 April to the end of August). During the stratified period, when N₂ fixation is the lowest, non-diazotroph organisms grow deeper 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 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 depth.

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 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 N_2 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. The development of diazotrophs can counteract DIN limitation for the entire planktonic food 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.

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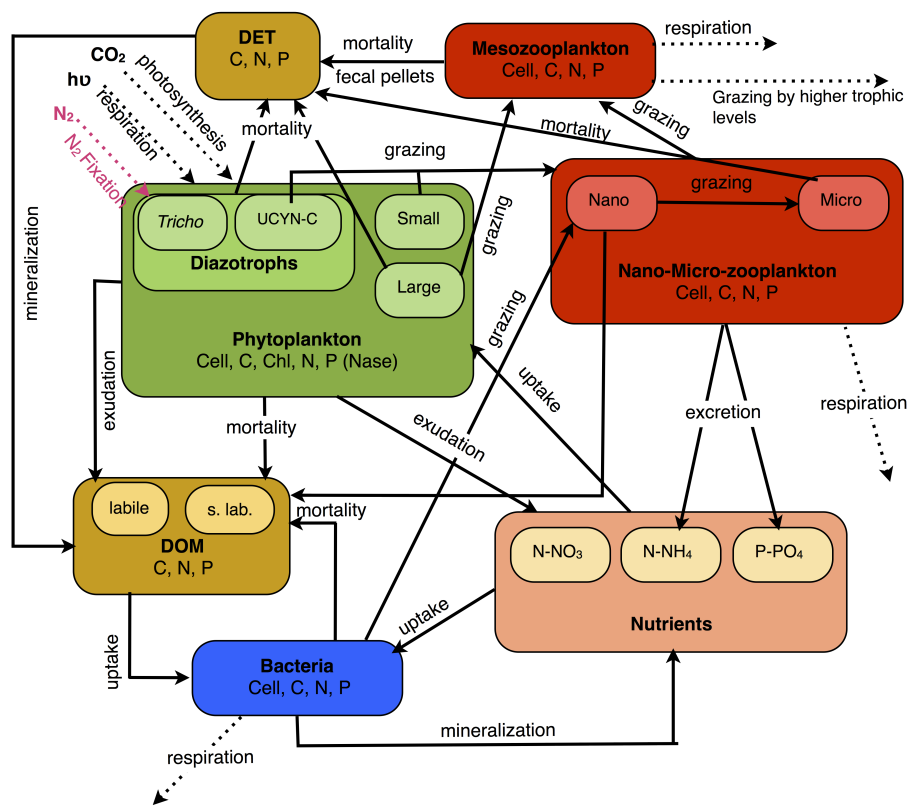


Figure 1.

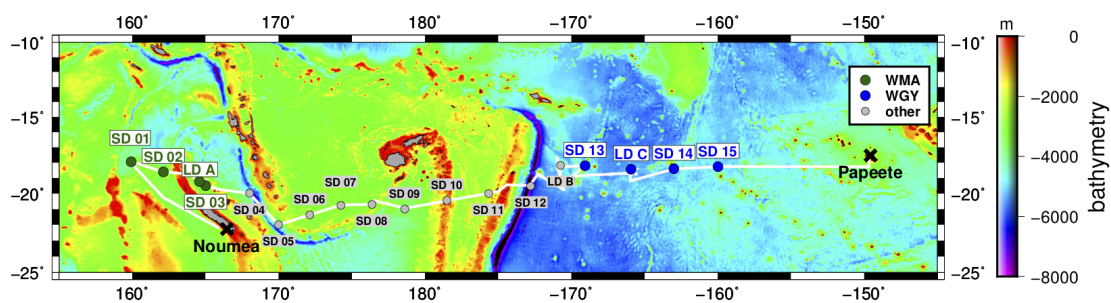


Figure 2.

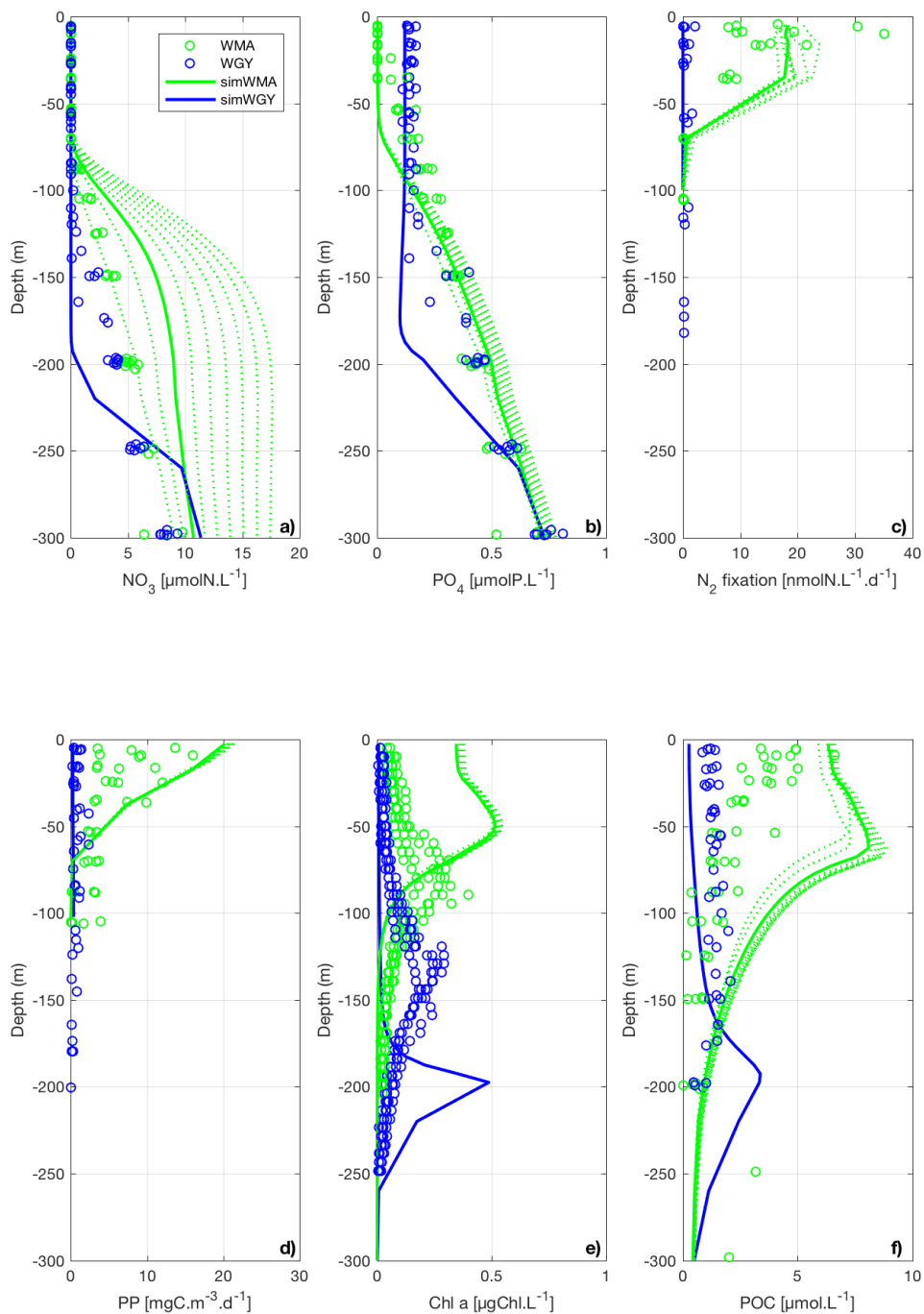


Figure 3.

