

1 Nitrogen isotope simulations show the importance of atmospheric 2 iron deposition for nitrogen fixation across the Pacific Ocean

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5 [1] Nitrogen (N) fixation by specialized microorganisms
6 (diazotrophs) influences global plankton productivity because
7 it provides the ocean with most of its bio-available N. How-
8 ever, its global rate and large-scale spatial distribution is still
9 regarded with considerable uncertainty. Here we use a global
10 ocean nitrogen isotope model, in comparison with $\delta^{15}\text{NO}_3^-$
11 observations, to constrain the pattern of N_2 fixation across
12 the Pacific Ocean. N_2 fixation introduces isotopically light
13 atmospheric N_2 from to the ocean ($\delta^{15}\text{N} = 0\text{‰}$) relative to
14 the oceanic average near 5‰, which makes nitrogen isotopes
15 suitable to infer patterns of N_2 fixation. Including atmo-
16 spheric iron limitation of diazotrophy in the model shifts
17 the pattern of simulated N_2 fixation from the South Pacific
18 to the North Pacific and from the East Pacific westward.
19 These changes considerably improve the agreement with
20 meridional transects of available $\delta^{15}\text{NO}_3^-$ observations, as
21 well as excess P ($\text{PO}_4^{3-} - \text{NO}_3^-/16$), confirming that atmo-
22 spheric iron deposition is indeed important for N fixation in
23 the Pacific Ocean. This study highlights the potential for
24 using $\delta^{15}\text{N}$ observations and model simulations to constrain
25 patterns and rates of N fixation in the ocean. **Citation:** Somes,
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30 1. Introduction

31 [2] Nitrogen (N) fixation is the dominant source of biolog-
32 ically available nitrogen (fixed-N) into the ocean [Codispoti,
33 2007], which is performed by specialized prokaryotes
34 (diazotrophs) that can reduce N_2 gas instead of oceanic fixed-N
35 (NO_3^- , NO_2^- , NH_4^+) during photosynthesis. Since diazotrophs
36 are not limited by fixed-N, they can grow in N-depleted sur-
37 face water provided other required nutrients (e.g., phosphorus
38 (P) and iron (Fe)) are available. Diazotrophs can have an
39 important influence on climate because fixed-N limits primary
40 production and biological sequestration of atmospheric CO_2 .
41 The efficiency, with which diazotrophs can balance the N-loss
42 from denitrification and anammox, the major sinks for fixed-N,
43 determines if the oceanic fixed-N inventory could fluctuate
44 significantly enough to affect atmospheric CO_2 .

45 [3] Throughout much of the contemporary ocean, biolog-
46 ical productivity is limited by fixed-N suggesting other factors,
47 such as light, temperature, P and Fe availability, and/or NO_3^-

inhibition, are preventing diazotrophs from fixing atmospheric
N. It has been observed that blooms of *Trichodesmium*, one of
the most important and best studied diazotrophs, occur more
frequently and are more extensive in warm ($>25^\circ\text{C}$) surface
water where fixed-N is depleted and rates of atmospheric Fe
deposition are high such as the North Atlantic, Indian, and
North Pacific compared to areas of low Fe deposition such as
the South Pacific where the abundance of *Trichodesmium*
appears to be much lower [Carpenter, 1983; Karl et al., 2002;
Carpenter and Capone, 2008]. This pattern of less N_2 fixation
in Fe-depleted waters is also consistent in the South Atlantic
[Moore et al., 2009]. This suggests that temperature and Fe
availability may be the most important factors that determine
where N_2 fixation is able to occur. However, other more
uncharacterized unicellular diazotrophs have been observed
to grow in cooler water near 20°C [Needoba et al., 2007], and
it has been suggested that they also may significantly con-
tribute to the global N_2 fixation rate [Zehr et al., 2001;
Montoya et al., 2004].

[4] The large spatial and temporal variability of diazotrophs
makes it difficult to constrain the global rate of N_2 fixation.
Recent estimates range widely between $\sim 100\text{--}200 \text{ Tg N yr}^{-1}$
and predict significantly different spatial patterns [Gruber and
Sarmiento, 1997; Karl et al., 2002; Deutsch et al., 2007;
Moore and Doney, 2007]. For example, a model using xSP
($\text{PO}_4^{3-} - \text{NO}_3^-/16$) observations within an ocean circulation
model estimates that N_2 fixation is tightly coupled with deni-
trification in the Pacific Ocean [Deutsch et al., 2007], but does
not explicitly account for Fe. In contrast, the Biogeochemical
Elemental Cycling model [Moore and Doney, 2007], which
explicitly includes the effects of Fe availability, predicts that
 N_2 fixation should be more abundant in the Western North
Pacific, where atmospheric Fe deposition is greater, and sug-
gests that the Pacific represents a fixed-N sink because the
absence of sufficient Fe prevents N_2 fixation from balancing
denitrification throughout much of the South Pacific.

[5] N_2 fixation introduces relatively isotopically light N
($\delta^{15}\text{N} = 0\text{‰}$) into the ocean compared to the global mean
 $\delta^{15}\text{NO}_3^-$ near 5‰. Therefore, the ratio of the two stable
nitrogen isotopes, represented in the $\delta^{15}\text{N}$ notation where
 $\delta^{15}\text{N} = [({}^{15}\text{N}/{}^{14}\text{N})_{\text{sample}}/({}^{15}\text{N}/{}^{14}\text{N})_{\text{atmosphere}} - 1] \cdot 1000$, may be
a powerful tool to trace patterns of N_2 fixation. Here we
compare a model of nitrogen isotopes, embedded within the
ocean component of a global Earth System Climate Model,
with $\delta^{15}\text{NO}_3^-$ measurements across the Pacific Ocean to
constrain N_2 fixation focusing on the effect of atmospheric Fe
limitation of diazotrophy.

2. Model Description

[6] The marine ecosystem/biogeochemical model includ-
ing N isotopes is the 2N2PZD (2 Nutrients, 2 Phytoplankton,

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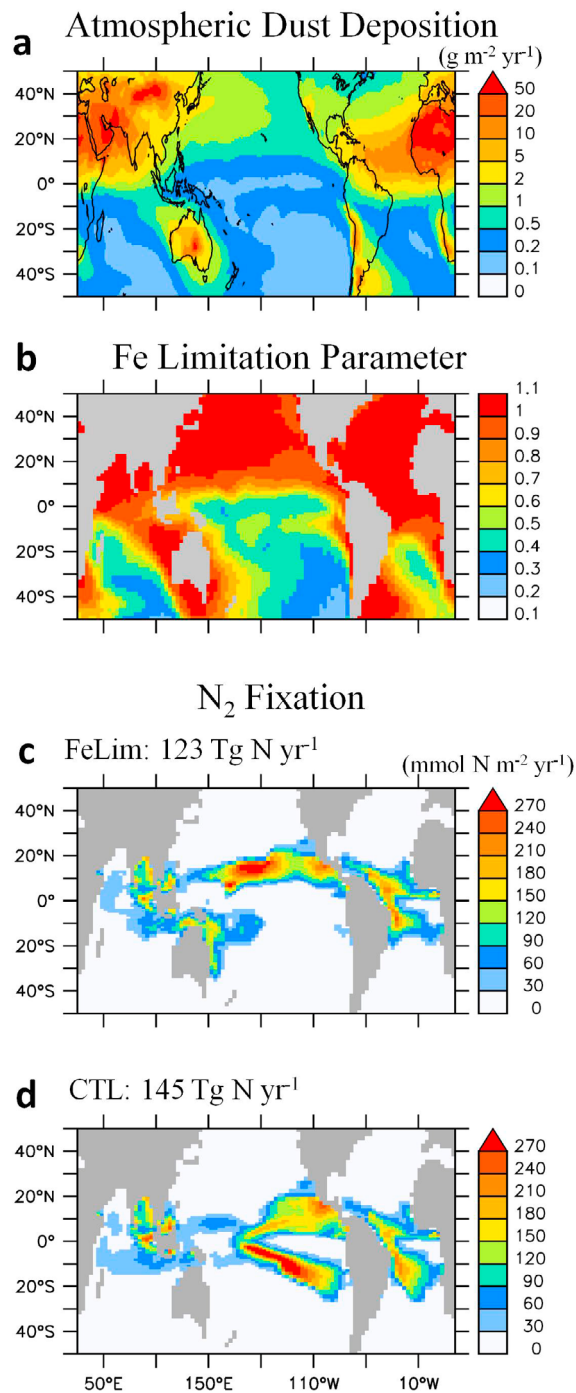


Figure 1. (a–b) Annual rates of dust deposition [Mahowald *et al.*, 2005] and FeLim parameter used to decrease the growth rate of diazotrophs. (c–d) Vertically integrated N₂ fixation in FeLim and CTL.

105 Zooplankton, Detritus) model of *Somes et al.* [2010] that
 106 includes N₂ fixation, water column denitrification, and ben-
 107 thic denitrification. It has run for over 1500 years as it ap-
 108 proaches equilibrium. Diazotrophs grow according to the
 109 same principles as the “general” phytoplankton class in the
 110 model, but we also account for some of their different char-
 111 acteristics. Since fixing dissolved N₂ is energetically
 112 more costly than assimilating fixed-N, the growth rate of

diazotrophs is lower than that of general phytoplankton in the
 113 model. It is zero in waters cooler than 15°C and increases 50%
 114 slower with temperature than the growth rate of general
 115 phytoplankton (note this value is increased from 40% in
 116 *Somes et al.* [2010], which results in an additional ~20 Tg N
 117 yr⁻¹ of N₂ fixation). Diazotrophs are not limited by NO₃⁻ and
 118 can out-compete general phytoplankton in surface waters that
 119 are depleted in fixed-N, but still contain sufficient P (i.e., high
 120 xsP water due to denitrification). However, diazotrophs will
 121 consume NO₃⁻ if it is available, consistent with culture
 122 experiments [Mulholland *et al.*, 2001; Holl and Montoya,
 123 2005], which is another factor that inhibits N₂ fixation in
 124 the model. Denitrification, and the propagation of N-deficient
 125 waters into the shallow thermocline by physical transport
 126 processes, creates an ecological niche for diazotrophs stim-
 127 ulating N₂ fixation [Tyrrell, 1999]. Fe is currently not
 128 included as a prognostic tracer in the model. However, we
 129 include a simple parameterization of atmospheric Fe limita-
 130 tion of diazotrophy as described in Section 3.
 131

[7] The nitrogen isotope model simulates the distribution of
 132 the two stable nitrogen isotopes, ¹⁴N and ¹⁵N, in all N species
 133 included in the marine ecosystem model. The processes in the
 134 model that fractionate nitrogen isotopes are algal NO₃⁻
 135 assimilation ($\epsilon_{\text{ASSIM}} = 5\%$), zooplankton excretion ($\epsilon_{\text{EXCR}} =$
 136 6%), water column denitrification ($\epsilon_{\text{WCD}} = 25\%$), and N₂
 137 fixation ($\epsilon_{\text{NFIX}} = 1.5\%$). Fractionation results in the iso-
 138 topic enrichment of the more reactive, thermodynamically
 139 preferred, light ¹⁴N into the product of each reaction by a
 140 process-specific fractionation factor [Mariotti *et al.*, 1981].
 141 Although little fractionation occurs during N₂ fixation in the
 142 model, it has an important effect on $\delta^{15}\text{N}$ by introducing
 143 isotopically light atmospheric N₂ ($\delta^{15}\text{N} = 0\%$) into the oce-
 144 anic fixed-N pool. Benthic denitrification has been observed
 145 to have little effect on the oceanic isotopic N pool because
 146 denitrifiers consume nearly all NO₃⁻ diffusing into the reactive
 147 zones within the sediments, leaving the oceanic N pool
 148 mostly unaltered [Brandes and Devol, 2002; Lehmann *et al.*,
 149 2007]. Therefore, in the model, there is no fractionation
 150 during benthic denitrification ($\epsilon_{\text{BD}} = 0\%$), although this is a
 151 simplification of observations [Lehmann *et al.*, 2007].
 152

3. Atmospheric Fe Limitation of Diazotrophy

[8] The nitrogenase enzyme, which fixes N₂ in diazotrophs,
 154 has a large structural iron (Fe) requirement [Raven, 1988;
 155 Sanudo-Wilhelmy *et al.*, 2001]. Diazotrophs may depend on
 156 Fe from atmospheric deposition in oligotrophic waters,
 157 where a deep pycnocline inhibits upward mixing of subsur-
 158 face Fe-replete waters into the euphotic zone. Therefore, we
 159 include an atmospheric Fe limitation of diazotrophy experi-
 160 ment (Figure 1, FeLim), where diazotrophs’ growth rate is
 161 further reduced by the Fe limitation parameter (FeL), which
 162 scales an estimate of monthly climatological atmospheric
 163 dust deposition [Mahowald *et al.*, 2005] between 0 and 1
 164 (Figure 1) by multiplying atmospheric dust deposition rate
 165 by a constant factor, and setting the maximum value to 1
 166 (i.e., maximum growth rate = $\mu_D \cdot \text{FeL}$). This parameteriza-
 167 tion does not account for any Fe that reaches the surface
 168 through vertical mixing or upwelling. Since this source of Fe
 169 will be accompanied by large concentrations of subsurface
 170 NO₃⁻ and PO₄³⁻, we assume that the faster-growing general
 171 phytoplankton class will consume all of this Fe along with the
 172

t1.1 **Table 1.** Global Measures of $\delta^{15}\text{NO}_3^-$ and Excess P Model
t1.2 Performance^a

Model	$\delta^{15}\text{NO}_3^-$			Excess P		
	<i>r</i>	STD	RMS	<i>r</i>	STD	RMS
CTL	0.668	1.76	1.33	0.520	1.30	1.27
FeLim	0.680	1.33	0.982	0.530	0.898	1.01

t1.7 ^aCorrelation coefficient (*r*), standard deviation (STD), and root mean
t1.8 squared (RMS) error. STD and RMS have been normalized by the standard
t1.9 deviation from the observations.

173 macronutrients. The model does not include Fe input from
174 rivers or shelf sediments.

175 4. Results

176 [9] The control (CTL) simulation does not include Fe
177 limitation of diazotrophs (i.e., maximum growth rate = μ_D)
178 and results in large N₂ fixation rates in the Central and Eastern
179 Tropical South Pacific (Figure 1). The only factor that pre-
180 vents N₂ fixation from occurring in the Eastern Tropical

Pacific of CTL is the presence of high surface NO₃⁻ in the core
181 of the HNLC region, where diazotrophs consume NO₃⁻
182 instead of fixing dissolved N₂ to meet their N requirement for
183 growth. This tight coupling of N₂ fixation and denitrification
184 in the Eastern Tropical South Pacific is consistent with the
185 model of *Deusch et al.* [2007], which does not explicitly
186 include Fe limitation or NO₃⁻ inhibition. However, we note
187 that the general pattern of N₂ fixation in the work of *Deusch*
188 *et al.* [2007] throughout the rest of the tropical/subtropical
189 Pacific is actually more consistent with the simulation
190 including Fe limitation of diazotrophs (FeLim) than CTL,
191 perhaps because atmospheric Fe deposition is greater there.

[10] Global patterns of N₂ fixation in FeLim—such as high
193 values in the tropical/subtropical North Pacific, the western
194 tropical/subtropical South Pacific, the western tropical/
195 subtropical South Atlantic, the tropical/subtropical North
196 Atlantic and the Indian Ocean—are more consistent with
197 direct observations [e.g., *Karl et al.*, 2002; *Carpenter and*
198 *Capone*, 2008] and with results from a more complex eco-
199 system/biogeochemical model [*Moore and Doney*, 2007].
200 Nevertheless, N₂ fixation in our model does not extend
201

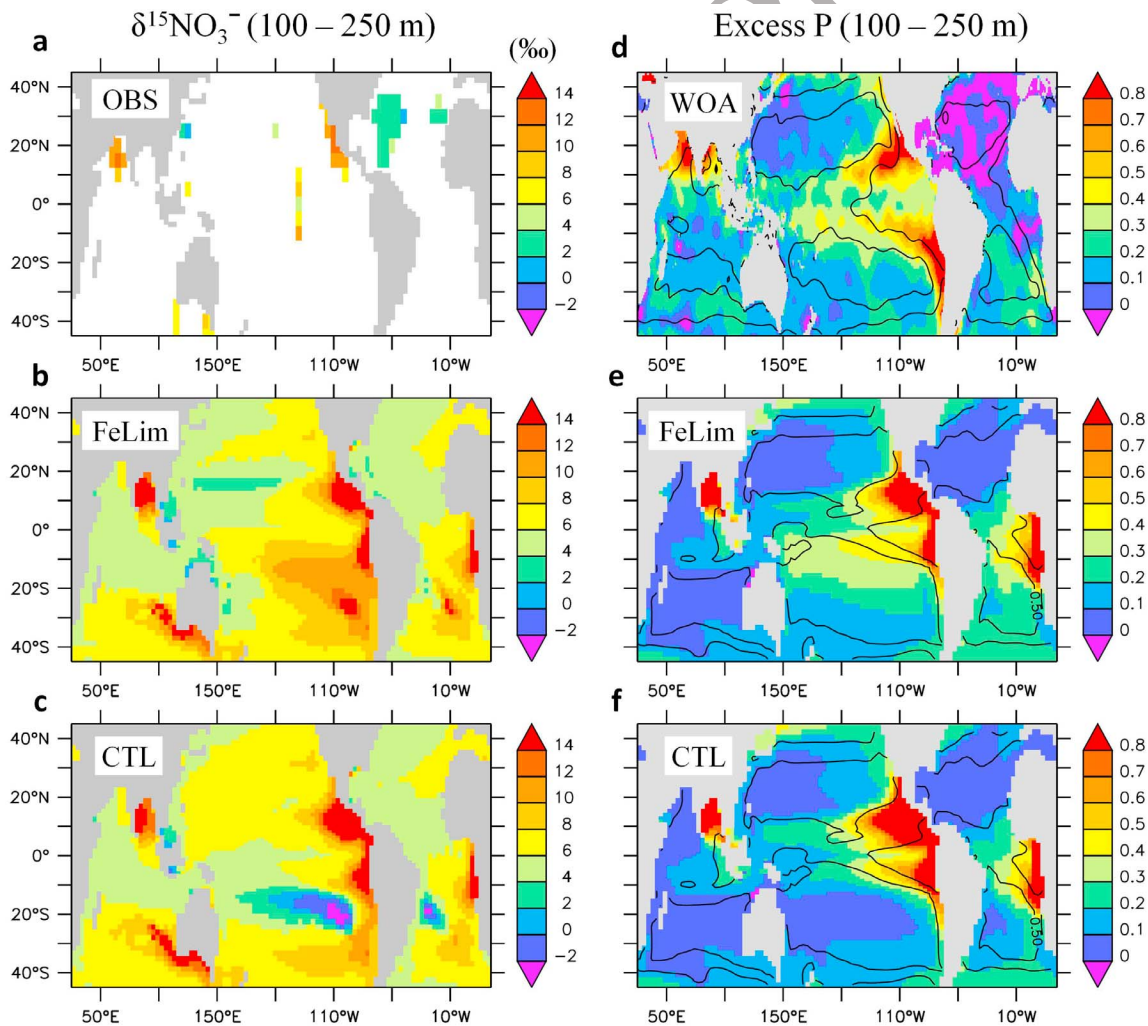


Figure 2. Comparison of (a–c) FeLim and CTL with $\delta^{15}\text{NO}_3^-$ observations [*Somes et al.*, 2010] and (d–f) World Ocean Atlas 2005: $\text{xsP} = \text{PO}_4^{3-} - \text{NO}_3^- / 16$ and near-surface (0–100m) NO_3^- contours of 5.0 and 0.5 μM . Note that due to the too low N:P for diazotrophs in the model (N:P = 16:1) compared to observations (N:P = ~50:1) [*Letelier and Karl*, 1996, 1998; *Krauk et al.*, 2006; *White et al.*, 2006], a slight overestimation of xsP is to be expected where N₂ fixation occurs.

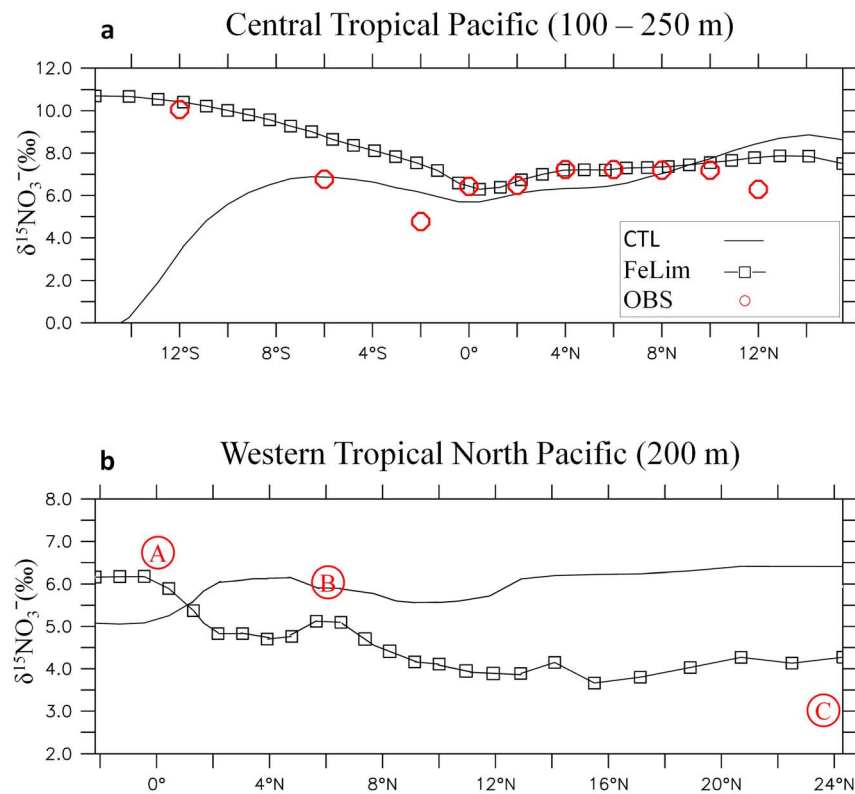


Figure 3. Comparison of FeLim and CTL $\delta^{15}\text{NO}_3^-$ with observations in the (a) Central Equatorial Pacific (140°W) (100–250 m) [Altabet, 2001] (reanalysis), and (b) Western North Pacific (100–250 m) (model transect connects through latitude/longitude of each data point): Location A, $\sim 6.75\%$ at 0°N/S, 140°E [Yoshikawa *et al.*, 2006]; location B, $\sim 6.0\%$ at 6°N, 125°E [Kienast *et al.*, 2008]; location C, $\sim 3.0\%$ at 25°N, 123°E [Liu *et al.*, 1996].

202 northward of $\sim 30^\circ\text{N}$ in the North Pacific, whereas some ob- 231
 203 servations show N₂ fixation as far north as 35–40°N 232
 204 [Needoba *et al.*, 2007; Kitajima *et al.*, 2009]. We hypothesize 233
 205 this discrepancy occurs due to the oversimplified fast-re- 234
 206 cycling microbial loop parameterization, which recycles 235
 207 organic matter to inorganic nutrients at N:P=16. It has been 236
 208 suggested that dissolved organic P recycles more efficiently 237
 209 relative to dissolved organic N and may also be directly 238
 210 consumed [Wu *et al.*, 2000], which is a mechanism that could 239
 211 help relieve diazotrophs of their P limitation throughout the 240
 212 tropical/subtropical oligotrophic ocean and stimulate addi- 241
 213 tional N₂ fixation. 242

214 [11] Global measures of $\delta^{15}\text{NO}_3^-$ and xsP improve in FeLim 243
 215 compared to CTL (Table 1). Generally lower $\delta^{15}\text{NO}_3^-$ and xsP 244
 216 in the Northern Hemisphere relative to the Southern Hemi- 245
 217 sphere in FeLim, due to more N₂ fixation occurring in the 246
 218 Northern Hemisphere where more atmospheric Fe deposition 247
 219 exists, result in a better match with observations than in CTL 248
 220 (Figure 2). The Central and Western Tropical Pacific repre- 249
 221 sent regions where N₂ fixation may occur as xsP flows 250
 222 westward “downstream” from the suboxic zones. Measured 251
 223 $\delta^{15}\text{NO}_3^-$ shows a decreasing trend northwards in the two 252
 224 transects across the Pacific (Figure 3), with a minimum near 253
 225 the equator in the Central Pacific. This equatorial minimum is 254
 226 reproduced in the model due to the low degree of surface NO₃⁻ 255
 227 utilization as a result of extensive NO₃⁻ supply to the surface 256
 228 from equatorial upwelling. The northward decreasing $\delta^{15}\text{NO}_3^-$ 257
 229 trend in FeLim in both transects is due to more N₂ fixation 258
 230 occurring north of the equator, where sufficient atmospheric 259

230 Fe deposition exists (Figure 1). When atmospheric Fe limi- 231
 232 tation of diazotrophy is not included in the model (CTL), the 233
 234 opposite $\delta^{15}\text{NO}_3^-$ trend is simulated because more N₂ fixation 235
 236 occurs south of the equator, in contrast to the observations. 237

238 [12] Global rates of N₂ fixation, water column denitrifica- 239
 240 tion, and benthic denitrification are smaller in FeLim (123, 241
 242 89.4, 35.3 Tg N yr⁻¹, respectively) compared to CTL (145, 243
 244 119, 34.6 Tg N yr⁻¹, respectively) because a tighter coupling 245
 246 of N₂ fixation and denitrification exists in CTL in the Eastern 246
 247 Pacific. More N₂ fixation occurring in and around denitrifi- 247
 248 cation zones leads to increased export production and re- 248
 249 mineralization of organic matter at depth, lower oxygen 249
 250 concentrations, and more denitrification. Since denitrification 250
 251 creates an ecological niche for diazotrophs, its increase will 251
 252 stimulate additional N₂ fixation, creating a positive feedback 252
 253 effect. This results in a bigger suboxic zone and more deni- 253
 254 trification in the Eastern Tropical South Pacific in CTL 254
 255 compared to FeLim. The amount of xsP water that commu- 255
 256 nicates with the Southern Ocean through the subsurface and 256
 257 then escapes the Pacific Ocean through the Antarctic Circu- 257
 258 mpolar Current makes the Pacific Ocean a fixed-N sink of 258
 259 10 Tg N yr⁻¹ in CTL. Since there is less xsP water south of the 259
 260 equator in FeLim (Figure 2), the Pacific Ocean is a nitrogen 260
 261 sink of only 4 Tg N yr⁻¹, even though Fe limits N₂ fixation 261
 262 throughout much of the South Pacific. Note that both model 262
 263 versions underestimate xsP off of Peru and Chile because the 263
 264 coarse-resolution model cannot capture suboxia there. In the 264
 265 real ocean, a part of this water may sustain high xsP until it 265
 266 reaches a region with sufficient Fe (e.g., North Atlantic or 266

260 North Indian Ocean), which could take hundreds of years, and
 261 result in a significant decoupling of N₂ fixation from deni-
 262 trification that occurs in the Fe-depleted Southern Hemi-
 263 sphere [see also *Falkowski*, 1997].

264 5. Conclusion

265 [13] Model simulations that include Fe limitation of dia-
 266 zotrophy show a much better agreement with $\delta^{15}\text{NO}_3^-$ and xsP
 267 observations compared to a model that neglects this effect
 268 (Table 1 and Figures 2 and 3). Nitrate isotope observations
 269 show a decreasing northward trend across two transects in the
 270 Central and Western Pacific (Figure 3). Comparisons with
 271 model results reveal that these trends can be best explained by
 272 the input of isotopically light N by N₂ fixation, where higher
 273 rates of atmospheric Fe deposition exist. This highlights
 274 the potential of $\delta^{15}\text{NO}_3^-$ as a tool to infer the spatial pattern
 275 of N₂ fixation. If no N₂ fixation was occurring, the $\delta^{15}\text{NO}_3^-$
 276 value would be expected to be very high ($\delta^{15}\text{NO}_3^- > 10\text{‰}$) due
 277 to the nearly complete utilization of surface NO₃⁻ in the oligo-
 278 trophic ocean [*Altabet and Francois*, 1994; *Somes et al.*, 2010],
 279 which is a drastically different $\delta^{15}\text{N}$ signature than what would
 280 be expected if N₂ fixation was significantly contributing to the
 281 local N pool ($\delta^{15}\text{N}_2 = 0\text{‰}$). Our results suggest that $\delta^{15}\text{N}$
 282 observations, in combination with models, can be used to
 283 constrain N₂ fixation patterns in present and past oceans.

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