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18	Improving simulated basin-scale and mesoscale distributions of <i>Trichodesmium</i> spp. in the
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34 Key points

35 1. Trichodesmium populations are simulated with an eddy resolving model of the Atlantic 2. Simulating the observed biomass and nitrogen fixation requires enhanced export 36 37 3. The model captures an observed association of *Trichodesmium* with anticyclonic eddies 38 39 40 Abstract 41 A new observational synthesis of diazotrophic biomass and nitrogen fixation provides the 42 opportunity for systematic quantitative evaluation of these aspects in biogeochemical models. We scrutinize one such model of the Atlantic Ocean, and find the simulated biomass to be an 43 44 order of magnitude too low. Initial attempts to increase biomass levels through decreasing 45 grazing and other loss terms caused an unrealistic buildup of nitrate in the upper ocean. Two key 46 changes to the model structure facilitated a closer match to the observed biomass and nitrogen 47 fixation rates: addition of a new pathway for export of diazotrophically-fixed organic material, 48 and uptake of inorganic nitrogen by the diazotroph population. These changes, along with a few 49 other revisions to existing model parameterizations, facilitate more accurate simulation of basin-50 scale distributions of diazotrophic biomass, as well as mesoscale variations contained therein. 51 Index terms: Biogeochemical cycles, processes, and modeling; ecosystems, structure, dynamics, 52

and modeling; eddies and mesoscale processes; nutrients and nutrient cycling; phytoplankton.
 Key Words: *Trichodesmium*, nitrogen fixation, North Atlantic, eddies, modeling, export.

55 1. Introduction

56 Nitrogen fixation by cyanobacteria of the genus Trichodesmium constitutes an important input into the global nitrogen cycle [Capone et al., 1997; Carpenter, 1983; Karl et al., 2002]. As 57 58 such, modeling the abundance, distribution, and productivity of these populations offers an 59 important tool for quantification of the associated fluxes of nitrogen and their impacts on 60 ecosystems and climate. A number of prior studies have documented realistic simulations of 61 diazotrophic biomass and nitrogen fixation on basin to global scales [Coles and Hood, 2007; 62 Coles et al., 2004; Dutkiewicz et al., 2012; Hood et al., 2004; Monteiro et al., 2011; Monteiro et 63 al., 2010; Moore and Doney, 2007]. However, a recent global compilation and synthesis of 64 observations [Luo et al., 2012] provides the opportunity for more thorough evaluation of models 65 of this type. Herein we make direct comparisons between one such model of the Atlantic Ocean 66 [Anderson et al., 2011] and the new observational synthesis. Although the large-scale simulated 67 patterns are similar to that described in Luo et al. [2012], diazotrophic biomass is underestimated 68 by an order of magnitude in the high-abundance region of the tropics and southern subtropical 69 gyre. Herein we describe revisions to the model that allow for closer agreement between 70 simulated and observed distributions of diazotrophs, both in terms of basin-scale biogeography 71 as well as mesoscale variations.

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73 **2. Model description**

The physical model is the Los Alamos Parallel Ocean Program "POP" [*Smith et al.*,
2000] Version 2.0.1. The spatial grid is an eddy-resolving (0.1° longitude × 0.1° cos(latitude))
North Atlantic domain (20 °S to 72 °N, 98 °W to 17 °E) with 42 z-coordinate levels.
Configuration of the physical simulation is identical to that of Anderson et al. [2011], as is the

coarse resolution implementation (1.6° longitude × 1.6° cos(latitude); 40 levels in the vertical)
used for parameter dependence and sensitivity analysis.

- 80 The biological/chemical component (Figure 1) is based on a 24-state variable version of 81 the "Biogeochemical Elemental Cycling" (BEC) model [Doney et al., 2009; Moore and Doney, 82 2007; Moore et al., 2002; Moore et al., 2004; Moore et al., 2006] as modified by Anderson et al. 83 [2011]. The model has three phytoplankton groups: diatoms (DIAT), small phytoplankton (SP) 84 and N₂-fixing diazotrophs (DIAZ). Although diazotrophic organisms in the ocean are comprised 85 by a diverse assemblage of taxa [LaRoche and Breitbarth, 2005; Zehr, 2011], the colonial 86 cyanobacteria *Trichodesmium* spp. tends to dominate in terms of biomass and nitrogen fixation 87 in the Atlantic region of primary interest in this study [Goebel et al., 2010]. Thus, for the present 88 purposes, we will use diazotroph and *Trichodesmium* spp. interchangeably. Model 89 phytoplankton, zooplankton and sinking POM have constant C/N/P ratios, but variable content of 90 Fe and Chl (for all phytoplankton), CaCO₃ (for small phytoplankton) and SiO₂ (for diatoms). 91 The limiting nutrients are NO₃, NH₄, PO₄, Fe and for diatoms SiO₃. The remaining biological 92 state variables are O₂, DIC, Alkalinity, DOC, DON, DOP and DOFe. The biological model is 93 coupled to and run concurrently with the physical model. The MPDCD advection scheme is 94 used for biological tracers [Oschlies and Garcon, 1999], and its implementation in the POP 95 model is described in McGillicuddy et al. [2003]. 96 In an attempt to better match the observations, the one-dimensional Regional Testbed 97 Model [Friedrichs et al., 2007] was set up at contrasting locations: the Bermuda Atlantic Time-
- 98 series (BATS) site where *Trichodesmium* spp. abundance is relatively low, and in the tropics
- 99 where it is much higher. The Regional Testbed software includes an optimization algorithm that
- 100 permits fitting parameters simultaneously amongst the selected sites. The optimized parameters

101 were then tested in coarse resolution (1.6°) three-dimensional simulations. Because optimal 102 parameters derived in a one-dimensional setting are not necessarily optimal in a three-103 dimensional environment, additional sensitivity experiments were carried out in the coarse 104 resolution model to improve upon the parameter choices derived from the Regional Testbed. 105 This was an iterative process that included not only refinements within the existing model 106 structure, but also revisions to the model structure itself (Figure 2; Table 1). Both aspects are 107 described in turn below.

108 Several parameterizations within the existing model structure were modified. First, the factor specifying temperature dependence on diazotroph growth rate was changed from a Q10-109 type relationship $T_{\text{func diaz}} = 2^{(T-30)/10}$ to a functional fit of laboratory experiments using an isolate 110 111 of *T. erythraeum* described in Breitbarth et al. [2007]. The data suggest a quasi-parabolic 112 dependence of growth rate on temperature within the interval between 18°C and 36°C, with 113 maximal growth at 26.9°C. To represent this, we define a temperature anomaly T_a relative to the 114 optimal temperature 115 $T_a = max(18, min(36, T))) - 26.9$

(1)

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118 to model the temperature dependence with

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120
$$T_{\text{func}_{\text{diaz}}} = \max(0, 1 - 0.0215*T_a^2 + 0.000109*T_a^4)$$
 (2)

such that T_{func_diaz} is zero outside the temperature window and rises to a value of one at the optimal temperature. Qualitatively this provides a good fit to the data presented in Figure 1 of Breitbarth et al. [2007].

125 Second, the parameterization of iron scavenging by adsorption onto particles was updated 126 from that described in Moore and Doney [2007] to Moore and Braucher [2008]. The primary 127 difference between them is that the definition of the sinking mass onto which scavenging occurs 128 is expanded from POC and mineral dust to include biogenic silica and calcium carbonate 129 components. In addition the scaling factor for scavenging at high iron concentrations 130 (fe max scale2; called Chigh in Eq. 2 of Moore and Braucher, 2008) was increased in order to 131 bring the near-surface iron concentrations into better agreement with observations. Half-132 saturation constants for iron uptake by small phytoplankton (sp kFe) and diatoms (diat kFe) 133 were updated to values used in version 1.0.4 of the Community Earth System Model (CESM; 134 http://www.cesm.ucar.edu). The half-saturation constant by iron uptake by diazotrophs 135 (diaz kFe) was increased to 0.8 nM. Although this value is a bit high relative to experimental 136 assays [Berman-Frank et al., 2001], it helps compensate for the continued overestimation of 137 near-surface iron concentrations despite the improved scavenging parameterization mentioned 138 above.

Third, the mortality and grazing losses of diazotrophs were modified in an attempt to rectify the systematic overestimation of *Trichodesmium* spp. biomass in the subtropics and underestimation in the tropics. In the Anderson et al. [2011] solution, diazotroph concentrations over most of the subtropical gyre were near their mortality threshold concentration (loss_thres_diaz), below which mortality and grazing losses do not occur. The threshold value used in that simulation was higher than observed concentrations of *Trichodesmium* spp. in the

subtropics (see Orcutt et al. [2001] and references therein), and was therefore lowered to the 145 146 same value used for small phytoplankton and diatoms. To ameliorate the underestimation of 147 biomass in the tropics, grazing and mortality rates (diaz umax 0 and diaz mort), which are 148 among the least constrained parameters, were lowered. Justification for the former lies in that 149 relatively few copepod species appears to graze *Trichodesmium* spp., most notably the 150 harpacticoid copepod Macrosetella gracilis [O'Neil and Roman, 1994]. As for the latter, the 151 mortality rate for *Trichodesmium* spp. probably should not be higher than that used for small 152 phytoplankton and diatoms (0.1 d^{-1}) .

153 Although these changes to the model resulted in improved simulations of *Trichodesmium* 154 spp. biomass and nitrogen fixation, there was an unintended consequence: unrealistic 155 accumulation of nitrate in near-surface waters of the high biomass regions. Increased abundance 156 and productivity of the *Trichodesmium* spp. population led to increased supply of biologically-157 fixed nitrogen, through remineralization of both particulate and dissolved organic material. This 158 in turn caused a regional shift from nitrogen to phosphorus limitation in the phytoplankton 159 community, resulting in buildup of nitrate in surface waters to unrealistic levels (>1 μ M) in those 160 areas. The only way we were able to simulate the high biomass and nitrogen fixation rates in the 161 tropics and southern subtropical gyre without building up excess nitrate in surface waters was to 162 introduce two structural changes to the model.

First, a separate parameterization for export of diazotrophically-derived particulate organic matter (POM) was added. The observational basis for this revision consists of isotopic data suggesting penetration of biologically-fixed light nitrogen into the main thermocline via sinking particles at station ALOHA in the Pacific [*Casciotti et al.*, 2008; *Dore et al.*, 2002; *Karl et al.*, 1997]. In the model, sources of diazotrophic POM include both grazing losses and

168 mortality; a quadratic term was added to the latter to create an aggregation term like those for 169 small phytoplankton and diatoms. All of the diazotroph mortality and 27.5% of diazotroph 170 grazing losses go to POM (f diaz loss poc=1.0 and f graze diaz poc=0.275). As in prior 171 implementations of the BEC model, the N/P ratio of diazotrophs is assumed to be 50:1 to reflect 172 the supra-Redfield ratio observed in natural populations of *Trichodesmium* spp. [Letelier and 173 *Karl*, 1998]. The C/N ratio in diazotrophs is close to Redfield, the same as that used for the 174 sinking flux of small phytoplankton, diatoms, and zooplankton. In contrast to the treatment of 175 other POM in the model, diazotrophic POM does not include ballasting by SiO₂, CaCO₃, or 176 lithogenic minerals. Thus the new sinking flux of diazotrophic carbon POCt_{flux} has only a single 177 unprotected, unballasted component:

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179
$$POCt_{flux}(z+dz) = POCt_{flux}(z) \exp(-dz/(POCt_diss/T_{funcP})) +$$

180
$$POCt_{prod} * (1 - exp(-dz/(POCt_diss/T_{funcP}))) POCt_diss/T_{funcP} (3)$$

181

182 where the remineralization length scale POCt_diss is distinct from that used for other "soft" 183 fractions of the export flux. Numerical experiments in the one-dimensional testbed framework 184 suggested a value of 300 m for POCt_diss provided the best fit to observations, although the 185 solutions were not particularly sensitive to that precise value.

A second change to the model structure allowed for uptake of inorganic nitrogen by diazotrophs. It has been known for some time that *Trichodesmium* spp. is capable of taking up both nitrate and ammonium [*Goering et al.*, 1966], yet the partitioning of uptake amongst the various forms of nitrogen is still not fully understood [*Mulholland et al.*, 2001]. Based on continuous culture experiments by Holl and Montoya [2005] that document preferential uptake

of nitrate over dinitrogen, the diazotrophs in our model first take up what they can in the form of
nitrate and ammonium and then meet any remaining need by fixing nitrogen. Values for the half
saturation constants for nitrate and ammonium uptake are specified from CESM version 1.0.4
[*Moore et al.*, submitted].

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196 **3. Experimental design**

197 The coupled physical-biological simulation was initialized with climatological 198 temperature, salinity and nutrients, and with previous model results for the rapidly-adjusting 199 biological variables, as described in Anderson et al. [2011]. The simulation was run for 14.5 200 years with a 6-h, repeating "normal year" atmospheric forcing [Large and Yeager, 2004], during 201 which time it reached quasi-equilibrium. The biological model changes mentioned above were 202 then made, the nutrients (NO₃, PO₄, SiO₃ and O₂) reinitialized with World Ocean Atlas 2005 July 203 distributions [Garcia et al., 2006a; b] and the coupled model run for 7 more years. Only the last 204 4 years of simulation are analyzed, after the biological fields (excluding DIC, Alkalinity and O₂, 205 which in this model do not affect the other biological variables) reached a new quasi-206 equilibrium. Model output was saved in 5 day averages.

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4. Basin-scale patterns in biomass and nitrogen fixation

The simulation of *Trichodesmium* spp. biomass is improved over the prior solution described in Anderson et al. [2011] (Fig. 3). In particular, near-surface biomass in the high abundance region of the tropics and southern subtropical gyre is much closer to observed concentrations. The model also predicts high concentrations in the Gulf Stream and its eastward

213	extension into the North Atlantic. Although this feature is not resolved by the <i>in situ</i> database,
214	its presence is evident in satellite observations [Westberry and Siegel, 2006].
215	Despite the overall improvement in the fidelity of the simulated biomass, some
216	discrepancies remain—such as overestimation east of South America at 10-15°S and in the 28-
217	32°N latitude band of the Sargasso Sea. Another area of apparent bias in the model is located
218	off west Africa in the latitude band 10-20°N, where the simulation seems to systematically
219	exceed the observations. Repeated transects in April/May and September/October reveal
220	consistently high biomass in this area from the equator to 15°N [Tyrrell et al., 2003], although
221	the binned annual averages computed by Luo et al. [2012] show considerable spatial variability
222	in that vicinity.
223	The large-scale patterns in nitrogen fixation (Figure 4) generally mimic those of biomass.
224	Differences between the revised and prior solutions are less dramatic than in the biomass fields,
225	but there are improvements. For example, the northern boundary of the high-fixation region in
226	the tropics (yellow-to-green transition in Figure 4) is shifted northward, bringing the simulated
227	rates into better agreement with the observations in the southern limb of the subtropical gyre.
228	Enhanced nitrogen fixation is also evident in the Gulf Stream region, bringing the simulation into
229	closer agreement with observations off the coast of northeastern North America.
230	We note that although the high biomass and rates of nitrogen fixation in the western
231	tropical Atlantic are relatively well captured in the model, the river plume dynamics thought to
232	be important to nitrogen fixation in that area [Borstad, 1982; Lenes et al., 2005] are not.
233	Specifically, Subramaniam et al. [2008] describe how the Amazon River outflow stimulates
234	nitrogen fixation both by diatom-diazotroph assemblages as well as Trichodesmium spp. in
235	different stoichiometric niches within the plume, which can extend more than 1000 km from the

river mouth. Neither of these two nitrogen-fixing regimes is represented in our model, insofar as
riverine influences are parameterized by restoring surface salinity to climatological values. As
such, freshwater fluxes are prescribed, but the associated nutrient and micronutrient inputs are
not.

240 Another important caveat with respect to assessment of the simulated rates arises from a 241 recently discovered bias in an established isotopic method for measure nitrogen fixation [Großkopf et al., 2012]. Typically ¹⁵N₂ tracer is introduced as a gas bubble which is assumed to 242 243 rapidly equilibrate with the liquid phase. Direct comparisons with a new approach using dissolved ${}^{15}N_2$ gas challenge that assumption, indicating the gas bubble method significantly 244 245 underestimates nitrogen fixation. Because this method is used in most of the data that comprise 246 the Luo et al. [2012] analysis, the observational estimates with which the model results are 247 compared (Figure 4) may have to be revised upward by as much as a factor of two.

248

249 5. Controls on the simulated diazotrophic populations

Over most of the high abundance region of the tropical and subtropical North Atlantic, diazotrophic populations are regulated by the availability of phosphorus (Figure 5), a pattern roughly consistent with predecessors of this model (Moore et al., 2004; cf. their Figure 7). North of that area, temperature exerts the primary control, although there is a narrow zonal band of iron limitation associated with the Gulf Stream and its extension (see section 7 below). From the equator south, iron generally limits diazotrophy in the model with the exception of a small region in the vicinity of 10°S 20°W.

257 Phosphorus limitation of diazotrophic populations of the North Atlantic is consistent with258 the notion of ample iron supply from aeolian deposition of dust particles originating from

African deserts [Berman-Frank et al., 2001; Fung et al., 2000; Mahowald et al., 2005].

260 Moreover, a wide variety of assays on natural populations from this region indicate phosphorus 261 stress, including cell quota measurements [Sañudo-Wilhelmy et al., 2001] and quantification of 262 alkaline phoshatase activity [Dyhrman et al., 2002; Hynes et al., 2009; Sohm et al., 2008; Webb 263 et al., 2007]. Experimental incubations with additions of inorganic phosphorus can stimulate 264 nitrogen fixation [Webb et al., 2007], although results from the eastern tropical North Atlantic 265 suggest co-limitation by phosphorus and iron [Mills et al., 2004]. Abundances of iron-binding 266 photosynthetic and nitrogen-fixing proteins in natural populations of Trichodesmium spp. in the 267 North Atlantic are also consistent with iron stress [Richier et al., 2012].

268

269 **6. Nitrogen fluxes**

270 Detailed nitrogen budgets for three of the most densely sampled sites (Figure 6) further 271 illustrate the improvement in simulated diazotrophic biomass. Whereas biomass was 272 underestimated by an order of magnitude in the Tropical West and Tropical East domains of the 273 Anderson et al. [2011] solution, biomass in the present simulation is much closer, albeit still 274 smaller, than observed. Diazotrophic biomass also increased at BATS, degrading the solution at 275 that location. However, biomass at BATS is still an order of magnitude smaller than in tropical 276 areas, and thus still qualitatively consistent with observed large-scale biogeography of 277 Trichodesmium spp. Nitrogen fixation also increased, eclipsing the observed means in all three 278 sites. However, given the high variability in the observations, the simulated rates at the tropical 279 sites are not unrealistic. Nitrogen fixation is no doubt overestimated at BATS, but again is an 280 order of magnitude less than in the high-abundance region.

281 Nitrogen fluxes are significantly re-organized in the new model (Figure 6). The most 282 significant change is the large amount of diazotrophic biomass that is converted into PON and 283 subsequently exported, a pathway not available in the prior model. This was a key addition to 284 the present formulation, allowing for higher standing stocks of diazotrophic biomass while 285 avoiding unrealistic buildup of inorganic nitrogen via remineralization within the euphotic zone. 286 Unrealistic buildup of inorganic nitrogen was also ameliorated by allowing for uptake of nitrate 287 and ammonium by diazotrophs, a pathway that supplies roughly one-fifth to one quarter of the 288 diazotrophic nitrogen demand at the tropical sites.

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290 **7. Mesoscale variations**

291 To assess eddy-driven fluctuations in the simulated populations of *Trichodesmium* spp., 292 mesoscale features were identified by local extrema in sea level anomaly (SLA) computed from 293 the five-day averages of model output. Model-based SLA was defined by the residual after 294 removing large-scale spatial trends by a symmetric two-dimensional Gaussian filter with a 3° 295 longitude e-folding scale and a 7.5° maximum radius. Following Anderson et al. [2011], each 296 eddy was classified as one of four types according to the sign of their SLA and the sense of the 297 isopycnal displacement at the base of the euphotic zone (taken to be 97 m): regular cyclones 298 ("C"; negative SLA and positive density anomaly at 97 m), regular anticyclone ("A"; positive 299 SLA and negative density anomaly), mode-water eddy ("M"; positive SLA and positive density 300 anomaly) and "thinny" ("T"; negative SLA and negative density anomaly). The term "thinny" 301 derives from the fact that in the Sargasso Sea these eddies have a relatively "thin" layer of 18° 302 mode water between the seasonal and main thermoclines, whereas in "mode-water" eddies that 303 layer is anomalously thick. In both cases, displacement of the main thermocline dominates the

SLA and associated surface geostrophic velocity, such that thinnies are cyclonic and mode-water
 eddies are anticyclonic.

306 The new model includes more realistic mesoscale variations in *Trichodesmium* spp. 307 populations. For example, Davis and McGillicuddy [2006] noted enhancements of 308 Trichodesmium spp. populations in anticyclones within the subtropical gyre, with local 309 abundance anomalies of up to an order of magnitude. This aspect was not captured in the 310 Anderson et al. [2011] solution, yet is clearly evident in the present simulation (Figure 7). 311 Because the observations were collected in the August-September time frame, we restricted our 312 analysis of the model solutions to that time interval. Of the four years we analyzed, the 313 association of positive biomass anomalies with anticyclones was most pronounced in year two 314 (not shown). A synoptic (5-day) snapshot during that time period illustrates the nature of the 315 association: anticyclonic eddy features derived from Gulf Stream extension region carry high 316 biomass into the north-northwestern region of the observational domain (Figure 8). 317 Based on this snapshot, it is clear that advection down the large-scale gradient of 318 *Trichodesmium* spp. biomass plays a role in generating the association with anticyclones. 319 However, that does not discount the possibility of local eddy-induced enhancement. To 320 investigate this, a composite anticyclone was created by averaging all such features within the 321 space/time domain of interest in eddy-centric coordinates. Indeed, there is a local enhancement 322 of growth rate within these anticyclones (Figure 9A). Analysis of the limitation terms in the 323 diazotrophic growth rate equation reveals they are limited by phosphate in the upper ocean and 324 temperature below (Figure 9B). The shallower temperature limitation horizon in the interior of 325 the eddies suggests relief from phosphorus limitation, and phosphate in the lower euphotic zone 326 (60-100 m) is on average higher in the interiors of anticyclones in this region (Figure 9C). In

fact, the phosphorus enhancement is sufficient to shift the population toward iron limitation in an
isolated area at 60 m depth at ca. 50 km radius (Figure 9B).

329 What is the source of the excess phosphate in these anticyclones? A transect from the 330 high abundance region in the Gulf Stream through the domain of interest (magenta line in Figure 331 8) reveals a gradient in phosphate with concentrations increasing to the northwest, particularly at 332 depth (Figure 10, lower panel). This large-scale gradient is consistent with the climatology used 333 to initialize the model nutrient fields. Detailed comparison of the vertical section with the 334 phenomenology in SLA and diazotrophic biomass in Figure 8 suggests eddy-driven transport of 335 phosphate which in turn drives local enhancement at the base of the euphotic zone (Figure 10, 336 upper panel). This finding is consistent with the suggestion by Palter et al. [2011] that excess 337 phosphate supplied from the Gulf Stream system is a key source of nutrition for nitrogen fixation 338 in the subtropics. Their study stressed the importance of wind-driven Ekman transport and 339 isopycnal mixing in phosphate transport, estimating the eddy-induced fluxes to be small and up-340 gradient via a parameterization derived from Gent et al. [1995]. Our eddy-resolving simulations 341 suggest down-gradient transport by the eddies provides an additional mechanism of phosphate 342 supply which would add to those described by Palter et al. [2011]. In the present simulation, 343 supply of phosphate from the Gulf Stream system is sufficient to transform the northern 344 periphery of the subtropical gyre from phosphorus limitation to iron limitation of diazotrophic 345 populations (Figure 5).

346

347 **8. Conclusions**

In our model, large export fluxes of diazotrophically-derived material are required to
 sustain observed nitrogen fixation rates while maintaining realistic nutrient gradients in the upper

350	ocean. Unfortunately, we are not aware of any direct measurements in the high-biomass region
351	of the North Atlantic that can be used to test this hypothesis. However, there is ample isotopic
352	evidence that this material does make its way into the food web [Montoya et al., 2002],
353	suspended particulate matter [Landrum et al., 2011], and deep water nitrate [Knapp et al., 2008].
354	Furthermore, supra-Redfield ratios of nitrate to phosphate in the main thermocline of the North
355	Atlantic imply substantial rates of nitrogen fixation and subsequent export of that material
356	[Gruber and Sarmiento, 1997; Hansell et al., 2004; Lipschultz and Owens, 1996; Michaels et al.,
357	1996]. Reconciliation of these various imprints of nitrogen fixation on near-surface and deep
358	ocean properties will require a mechanistic understanding of the nature of export flux of
359	diazotrophically-derived material, for which an expanded observational basis is essential.
360	Similarly, the effects of mesoscale ocean dynamics on diazotrophy are just beginning to
361	come into focus. Our simulations suggest that eddy-induced transport of Trichodesmium spp.
362	populations and excess phosphorus from the Gulf Stream region can potentially explain the
363	observed association with anticyclones in the northern subtropical gyre [Davis and
364	McGillicuddy, 2006]. However, this is also just a hypothesis that awaits evaluation with direct
365	observations of the nutrient environment in such features, as no such measurements were
366	available in the prior study. Enhancement of Trichodesmium spp. in anticyclones has also been
367	noted in other regions, such as the eastern North Atlantic [González Taboada et al., 2010] and
368	oligotrophic North Pacific [Church et al., 2009; Fong et al., 2008]. In both cases the mechanism
369	of enhancement is different than we describe herein, and we expect future studies of mesoscale
370	variations in such populations to reveal a wide variety of physical-biological interactions.
371	

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373

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598

599 Table 1: Model parameter changes.

600

Parameter	Definition	Anderson et al.	This model
		(2011)	
diaz_kNO3	Half saturation constant for	N/A	1.0 μM N
	nitrate uptake by diazotrophs		
diaz_kNH4	Half saturation constant for	N/A	0.1 μM N
	ammonium uptake by		
	diazotrophs		
fe_max_scale2	Iron scavenging coefficient	$4286 (\mu M Fe yr)^{-1}$	$20000 (\mu M \text{ Fe yr})^{-1}$
sp_kFe	Half saturation constant for iron	0.06 nM Fe	0.03 nM Fe
	uptake by small phytoplankton		
diat_kFe	Half saturation constant for iron	0.15 nM Fe	0.08 nM Fe
	uptake by diatoms		
diaz_kFe	Half saturation constant for iron	0.1 nM Fe	0.8 nM Fe
	uptake by diazotrophs		
loss_thres_diaz	Threshold for diazotrophic loss	0.01 µM C	0.001 µM C
	terms		
diaz_umax_0	Maximum growth rate of	$1.2 d^{-1}$	$0.1 \mathrm{d}^{-1}$
	diazotrophs		1
diaz_mort	Coefficient of linear	$0.16 \mathrm{d}^{-1}$	$0.02 \mathrm{d}^{-1}$
	diazotrophic mortality		
diaz_mort2	Coefficient of quadratic	0	0.0324 (µM C d) ⁻¹
	diazotrophic mortality		
r_Nfix_photo	Ratio of nitrogen fixation to	1.43	1.0*
	assimilation		
f_diaz_loss_poc	Fraction of linear diazotrophic	0	1.0
	mortality going to POCt		
f_graze_diaz_poc	Fraction of diazotrophic grazing	0	0.275
	loss going to POCt		
POCt_diss	Length scale for diazotroph POC	N/A	300 m
_	remineralization		

601

*The decrease in r Nfix photo from 1.43 to 1.0 was an attempt to alleviate the unrealistic

buildup of nitrate by eliminating the excess amount of fixed N₂ excreted as DON, which is in

604 turn remineralized to nitrate. This proved to have little impact on the solutions. Future versions

of the model should include DON excretion by diazotrophs, as there is ample evidence that

606 Trichodesmium spp. do just that [Glibert and Bronk, 1994; Mulholland et al., 2004].



- Figure 1. The BEC model as described by Moore and Doney [2007] and Moore et al. [2006].
- The dashed box for particulate organic matter reflects the fact that it is not a true state variable,
- insofar as that material is assumed to sink and remineralize instantly.



- 614

Figure 2. Schematic of the simulated diazotrophic nitrogen cycle. Fluxes added to the present model are indicated in bold, whereas thin lines indicate fluxes present in both prior and current versions. The dashed box for PON reflects the fact that it is not a true state variable, insofar as

- that material is assumed to sink and remineralize instantly.





Figure 3. Near-surface (0-10 m) diazotrophic biomass for the Anderson et al. (2011) solution
(top) and new biological model (bottom). Data from Luo et al. [2012], binned onto the 1.6°
model grid, are shown as colored circles. Outlined in black are the locations of BATS (circle
near 32°N 64°W), as well as Tropical West (rectangle centered at 10°N 54°W) and Tropical East
(rectangle centered at 6°N 28°W) domains, for which detailed flux diagnosis is presented in
Figure 6.



Figure 4. Near-surface (0-10 m) nitrogen fixation for the Anderson et al. (2011) solution (top)
and new biological model (bottom). Data from Luo et al. [2012], binned onto the 1.6° model
grid, are shown as colored circles. Outlined in black are the locations of BATS (circle near 32°N
64°W), as well as Tropical West (rectangle centered at 10°N 54°W) and Tropical East (rectangle
centered at 6°N 28°W) domains, for which detailed flux diagnosis is presented in Figure 6.





642 Figure 5. Most limiting factor for growth of the simulated diazotrophic population in near-

643 surface (0-10 m) waters, averaged over the final four years of the simulation: iron (Fe),

644 temperature (T), phosphate (PO₄), and light.





649 Figure 6. Annual mean surface (0-10 m) diazotroph-related nitrogen budget at the locations 650 shown in Fig 3. Fluxes between boxes are in μ mol N m⁻³ yr⁻¹. Diazotroph biomass values are 651 shown inside the DIAZ box. Observed values and standard deviations are in bold, the Anderson 652 et al. [2011] in italics, and the new model results shown in regular font.



Figure 7. Vertically integrated (0-104 m) diazotrophic biomass anomalies (mg C m⁻²), expressed as percent anomaly from the large-scale mean, binned according to SLA and in situ density anomaly at 97 m in the subdomain bordered by the white rectangle in Figure 8 (30-35°N, 30-48°W). The four quadrants correspond to anticyclones (A), mode-water eddies (M), thinnies (T) and cyclones (C). The background shading indicates the observed correlations in this region, which suggest enhancement of *Trichodesmium* spp. populations in anticyclones [Davis and McGillicuddy, 2006]. Left: the solution from Anderson et al. [2011]; right: the new model. For consistency with the observations, analysis of the model output is restricted to the August-September time frame.



Figure 8. Vertically-integrated (0-104 m) diazotrophic biomass (color) with isolines of sea level anomaly overlayed (contour interval of 6 cm; solid corresponds to +3 cm and above, dashed to -3

675 cm and below). Fields are averaged over the five-day period September 8-12 in year 18 of the

676 simulation. White rectangle indicates the area of comparison with observations from Davis and

677 McGillicuddy (2006). Magenta dots indicate two anticyclonic features with enhanced

diazotrophic biomass (see text). Location of the transect shown in Figure 10 is depicted as a

679 magenta line. Note that sea level anomaly has been smoothed with a Gaussian-weighted running

average with an e-folding scale of 4 grid points and a maximum cutoff of 10 points (1°

681 longitude).

682 683



Figure 9. Diazotrophic specific growth rate anomaly (A), limitation factors (B), and phosphate concentrations (C) in anticyclones with high diazotrophic biomass located within the white rectangle in Figure 8 (30-35°N, 30-48°W) during August-September. Two such features are identified by magenta dots in the snapshot shown in Figure 8. Radial averages were constructed from synoptic snapshots of model output, using local maxima in sea level anomaly to define the positions of eddy centers. In each panel, density (σ_{θ}) contours are overlayed in white.



692 693

Figure 10. Phosphate section (color) along the magenta line in Figure 8, averaged over the fiveday period September 8-12 of year 18 in the simulation, the year during which diazotrophic biomass anomalies were most pronounced in anticyclones. Density (σ_{θ}) contours are overlayed in white at intervals of 0.2 kg m⁻³. Top panel: 0-110 m concentrations plotted on a log scale; bottom panel: 0-320 m concentrations plotted on a linear scale.