

Dear reviewer,

Thank you for considering our manuscript important and valuable for publication in Biogeosciences. We are grateful for your comments and suggestions, which we addressed in the revised version, we believe they largely helped to improve our manuscript.

Response to reviewer comments:

Their hypothesis is that surface nutrient limitation restricts PP, the ensuing flux of sinking organic matter, and thereby oxygen removal at depth. However, the sampling focus is on N₂ fixation at greater depths than the euphotic zone, which will accordingly not fuel surface PP without upwelling. This is generally prohibited in this strongly stratified regime. It is the level of N₂ fixation in surface waters, not the OMZ, that will have the greatest impact on PP and therefore (potentially) organic matter supply and respiration in the OMZ. As cited in the manuscript there are some observations indicating likely high surface nitrogen fixation by *Trichodesmium* in the Bay of Bengal (e.g. Sahu et al. 2017). I think this discrepancy between the hypothesis and the observations should be made explicit through the paper, including the abstract. However, I do agree with the authors that the nitrate isotope data do seem to argue against this in the case of their observational time period.

Response: This is a generally agreeable point, and the observation of *Trichodesmium* during other cruises is not contradictory but rather in line with our hypothesis of a water mass dynamic-dependent on-set of N₂ fixation. For our cruise we were somewhat limited with regard to our coverage of the water column and thus we included isotope data which we read as an argument against N₂ fixation during the time of the cruise in surface waters. The manuscript of Sahu et al is now more thoroughly discussed in our revised version of the manuscript.

The authors summarize some of the very high variability in N₂ fixation in the Peruvian OMZ (i.e., detection limit to 840 $\mu\text{mol N m}^{-2} \text{d}^{-1}$); I think it could be useful to comment directly how this measured variability could provide relevant context to the BoB observations. i.e., how would this change the manuscripts conclusions? Indeed, that genomic signatures of diazotrophs were found suggests N₂ fixation does occur in this system at some time points, which would be in line with sediment trap isotopic compositions.

Response: The observations from the OMZ off Peru are in so far interesting to compare to the BoB as they demonstrate first how N₂ fixation in OMZs can vary, but also they show a potential of a very similar community of N₂ fixers to actively fix N₂ (as opposed to them being largely inactive). If we would assume rates in the same range for the BoB, an additional N input would be provided which would, according to our model, be enough to cause full anoxia. This is a helpful point and has now been included into the revised version of the manuscript.

I found a mixture of decimal points and commas (representing decimal points) in the text

Response: This has been cleaned up.

Lines 179-180: Please provide some value ranges for SST and salinity

Response: Ranges have been added.

Please provide a description in the Methods section about the remote sensing images: where did these data come from (sensor, database), and what exact dates were used to produce the images in Fig. 1 (can also go in figure caption if preferred). This also applies to the satellite-derived data in the SI, which includes phytoplankton types – it is important to know where this came from and the algorithms that were used to generate these.

Response: The information has been added to the figure captions as suggested.

Line 211: PP is a function of phytoplankton biomass and the biomass-normalized photosynthetic rate (depending on light availability, temperature etc), therefore lower POC biomass does not necessarily mean lower PP (as implied in the statement)

Response: I have some difficulties with this comment because it reads to me as some disconnect between primary production and POC. But I overall agree that POC is not necessarily an indicator for primary production. This point has been presented right above from line 202 on. I revised the sentence in question to make it clearer, it now reads 'While our POC concentrations from DCM are one order of magnitude higher than the satellite-derived POC estimates (Fig. S2) from surface waters indicating that POC and primary production in surface waters was not higher than in the DCM, it must be noted that our measurements did not cover the entire mixed layer and are thus likely a rather conservative minimum estimate.'

Line 217-218: But the N₂ fixation measurements were not performed at the surface, they were performed at depth (>=60 m), where fixed nitrogen concentrations were presumably higher and therefore potentially removing this niche for N₂ fixers.

Response: This is true, and this is also the reason for the parallel presentation of nutrient data showing N depletion in the surface and of $\delta^{15}\text{N}$ data showing no N₂ fixation signal, both of which are thus supporting this claim.

Paragraph starting line 252 and Figure 5: Would it not be meaningful to include one or more non-OMZ sites in this analysis? i.e., to both indicate if (i) the OMZ sites have similarity between each other and (ii) are unique from non-OMZ sites?

Response: It would indeed be meaningful and relevant for a global assessment; however, the limit of the Venn diagram has been reached by including six datasets. The purpose of this plot was to show that the non-cyanobacterial clades in different OMZs are similar, non-OMZ areas would show cyanobacterial N₂ fixers in combination with heterotrophs, however, it has been pointed out previously that those heterotrophs are not active in non-OMZ areas (e.g. Turk-Kubo et al. (2014)).

Lines 324-327: I do not understand this sentence – if the model includes the potential for Fe limitation of N₂ fixation, but the prescribed Fe concentrations are high, N₂ fixation should not be affected by the Fe limitation term?

Response: This is correct, I intended to say that the model only includes Fe as limiting nutrient and doesn't have any other possibly limiting nutrients such as molybdenum or Vitamin B12 included. The sentence has been revised.

Model equations lines 8–10 of the SI: equations do not balance? E.g. I count 42 oxygens on the left hand side of the second equation and 51 oxygens on the right?
Please check this and other equations!

Response: Yes, a number got lost, here. Thanks for the hint.

Some more details on the model would be useful – i.e., does the model have any time iteration, is it ran until steady state for each upwelling value?

Response: The model does not have any time iteration, which is certainly a weakness given different elemental recycling times and is run into steady state for upwelling rates. The information has been added to the supplementary material.

Figure 6: It is quite hard to see the different lines in the plot, e.g., I cannot see the blue oxygen line and whether it always stays at 0 for all upwelling values

Response: We adjusted the lines in figure 6.

Line 712: I don't understand the sentence: '...export to the productive surface if stratification becomes weaker'. Do you mean upwelling of ammonia to the surface, which then fuels more PP?

Response: It meant to say that a stock of nitrogen would be build up, which could eventually be upwelled into surface waters and fuel primary production, there. The Figure caption has been rephrased for better readability.

Lines 339-341: Regarding the sentence: 'However, the fact that N₂ fixation is limited by phosphorous supply via recycling in addition to upwelling and diffusive fluxes imposes an upper limit to O₂ depletion.'
But this cannot be the case in the actual BoB, as phosphate concentrations are in excess (not reported, but indicated by the negative intercept on the nitrate versus phosphate plot), yet there is still O₂ present in the OMZ? Therefore, the field data indicate P availability in surface waters is not the cap on O₂ depletion in the OMZ as suggested by the model?

Response: This is actually very true; the statement made no sense in the context it was presented and has been removed.

It would be useful to briefly comment on how the physics of increased upwelling (or reduced stratification) might or might not increase ventilation of the OMZ? Are they completely decoupled?

Response: This would largely depend on the source of upwelled water. Our model distinguishes between deep water upwelling (ventilated) and intermediate OMZ water upwelling (not ventilated). We added a statement on the source of upwelled water to line 340.

References:

Turk-Kubo, K. A., M. Karamchandani, D. G. Capone, and J. P. Zehr. 2014. 'The paradox of marine heterotrophic nitrogen fixation: abundances of heterotrophic diazotrophs do not account for nitrogen fixation rates in the Eastern Tropical South Pacific', *Environ Microbiol*, 16: 3095–114.

Response to referee 2

Dear reviewer,

Thanks for this positive evaluation of our manuscript and for considering it a valuable contribution. I included your suggestions as follows and I believe they helped to make the manuscript clearer and better readable.

Line 66: There seems to be an extra closing parenthesis:

Author's response: This has been removed.

Line 77: 2,25 should be replaced by 2.25:

Author's response: This has been replaced.

Line 96: Cruise number should also be mentioned.:

Author's response: The cruise number has been added.

Line 202: It reads a bit awkward. How can Chlorophyll be compared to POC and stated as high or low? Both have different units.

Author's response: As for the ratio both, chlorophyll and POC was converted to mg m^{-3} following a study by Geider et al, 1997 in MEPS. However, the wording of the sentence was modified for better readability. It was indeed not very clear.

Lines 215-217: "Based on thecruise". These data are mostly from the deeper waters, so nutrients are not limited for productivity. Moreover, concentrations of both nitrate and phosphate would be higher than required for any process. Not only that, nitrate is not needed for nitrogen fixation, so stating "BoB waters were nitrogen limited" is slightly misleading. I would suggest the authors to elaborate the significance of intercept, state limiting for which process, and also define the threshold limiting values for nutrients – for N₂ fixation/C uptake, if required.

Author's response: This is a valuable point, and supports the view of another limiting nutrient such as or the limitation of processes by oxygen iron as discussed later on in the manuscript. For better readability, we changed the sentence to 'Based on the dissolved inorganic nitrogen ($\text{NO}_3^- + \text{NO}_2^-$) to phosphate (PO_4^{3-}) ratio which has a negative intercept with the y-axis (Fig. 3; Benitez-Nelson (2000)), primary production in BoB waters appeared nitrogen limited during the cruise assuming Redfield stoichiometry.'

Line 248: It would be helpful to provide $\delta^{15}\text{N}$ range when denitrification or nitrogen fixation dominates.:

Author's response: The ranges have been added, however in an earlier place of the manuscript, where $\delta^{15}\text{N}$ signatures were presented first (l. 219): 'Consistent with this, $\delta^{15}\text{N}$ signatures of both the nitrate and the particulate organic nitrogen (PON) pool were only slightly decreased in the top 100 m of the water column

to 5-8‰ (Fig. S3), thus not clearly supporting active N₂ fixation which would be expected to create light δ¹⁵N signatures of -2- 2‰ (e.g. Dähnke and Thamdrup (2013)).’

Line 276 and 358: data are plural, so it should be “our data suggest”:

Author’s response: This is true, we changed this.

Line 382: RV should be ORV:

Author’s response: This has been changed as suggested.

References: Kumar, S.P. and Prasanna Kumar, S. is one (same) author so such references should be clubbed.:

Author’s response: Thanks for the hint, we changed this accordingly.

Fig. 3: Equation on the should have decimal instead of commas. More appropriate will be to write $y = 14.2x - 0.6$ as the data do not have precision of more than three significant figures.:

Author’s response: This has been changed as suggested.

Supplementary, Line 2 does not read well. Some grammatical mistake.:

Author’s response: The sentence has been modified to ‘The model framework is based on Canfield’s 5-box model (Boyle et al. 2013; Canfield 2006), using available measurements for the BoB from our cruise and other literature (Tab. M1, the complete code will be released on Pangaea).’

Fig. S3: 15N-NO₃ should be replaced by δ¹⁵N-NO₃⁻, and delta 15N-PON should also be replaced by δ¹⁵N-PON in the figure and caption both.:

Author’s response: Agreed and replaced.

1 **No nitrogen fixation in the Bay of Bengal?**

2 Carolin R. Löscher^{1,2}, Wiebke Mohr³, Hermann W. Bange⁴, Donald E. Canfield¹

3

4 ¹Nordcee, Department of Biology, University of Southern Denmark, Odense, Denmark

5 ²D-IAS, University of Southern Denmark, Odense, Denmark

6 ³Max Planck Institute for Marine Microbiology, Bremen, Germany

7 ⁴GEOMAR Helmholtz Center for Ocean Research Kiel, Kiel, Germany

8 Correspondence to cloescher@biology.sdu.dk

9

10 The Bay of Bengal (BoB) has long stood as a biogeochemical enigma with subsurface waters containing
11 extremely low, but persistent, concentrations of oxygen in the nanomolar range which -for some, yet
12 unconstrained reason- are prevented from becoming anoxic. One reason for this may be the low productivity
13 of the BoB waters due to nutrient limitation, and the resulting lack of respiration of organic material at
14 intermediate waters. Thus, the parameters determining primary production are key to understanding what
15 prevents the BoB from developing anoxia. Primary productivity in the sunlit surface layers of tropical oceans
16 is mostly limited by the supply of reactive nitrogen through upwelling, riverine flux, atmospheric deposition,
17 and biological dinitrogen (N₂) fixation. In the BoB, a stable stratification limits nutrient supply via upwelling
18 in the open waters, and riverine or atmospheric fluxes have been shown to support only less than one quarter
19 of the nitrogen for primary production. This leaves a large uncertainty for most of the BoB's nitrogen input,
20 suggesting a potential role of N₂ fixation in those waters.

21 Here, we present a survey of N₂ fixation and carbon fixation in the BoB during the winter monsoon season.
22 We detected a community of N₂ fixers comparable to other OMZ regions, with only a few cyanobacterial
23 clades and a broad diversity of non-phototrophic N₂ fixers present throughout the water column (samples
24 collected between 10 m and 560 m water depth). While similar communities of N₂ fixers were shown to
25 actively fix N₂ in other OMZs, N₂ fixation rates were below the detection limit in our samples covering the
26 water column between the deep chlorophyll maximum and the OMZ. Consistent with this, no N₂ fixation
27 signal was visible in $\delta^{15}\text{N}$ signatures. We suggest that the absence of N₂ fixation may be a consequence of a
28 micronutrient limitation or of an O₂ sensitivity of the OMZ diazotrophs in the BoB. To explore how the onset
29 of N₂ fixation by cyanobacteria compared to non-phototrophic N₂ fixers would impact on OMZ O₂
30 concentrations, a simple model exercise was carried out. We observed that both, photic zone-based and
31 OMZ-based N₂ fixation are very sensitive to even minimal changes in water column stratification, with

32 stronger mixing increasing organic matter production and export, which would exhaust remaining O₂ traces
33 in the BoB.

34 **Introduction**

35 Primary production in large areas of the surface ocean is limited by the availability of fixed nitrogen (Moore
36 et al., 2013). This deficiency in nitrogen creates a niche for dinitrogen (N₂) fixation, an energy-costly process
37 carried out only by certain prokaryotes, also referred to as diazotrophs, which are phylogenetically highly
38 diverse. N₂ fixation in the ocean has been described quantitatively as most important in the oligotrophic
39 surface waters of the subtropical gyres (Sohm et al., 2011;Luo et al., 2012;Wang et al., 2019) where
40 cyanobacterial N₂ fixers dominate. Over the last decade, the development of novel molecular tools revealed
41 that non-cyanobacterial N₂ fixers are widely distributed throughout ocean waters (Farnelid et al.,
42 2011;Farnelid et al., 2013;Fernandez et al., 2011;Luo et al., 2012;Riemann et al., 2010;Zehr et al., 1998) and
43 sediments (Fulweiler et al., 2007;Andersson et al., 2014;Bertics et al., 2013;Gier et al., 2017;Gier et al., 2016).
44 Their quantitative importance for global N₂ fixation, however, is not yet clear. In oxygen minimum zones
45 (OMZs) of the eastern tropical North and South Pacific Ocean, hypoxic basins in the Californian Bay and the
46 Arabian Sea, those N₂ fixers form a unique community consisting of different clades of proteobacteria,
47 clostridia, spirochaetes, chlorobia, and methanogenic archaea (Christiansen and Loescher,
48 2019;Dekaezemacker et al., 2013;Fernandez et al., 2011;Gaby et al., 2018;Gier et al., 2017;Goebel et al.,
49 2010;Halm et al., 2012;Hamersley et al., 2011;Jayakumar et al., 2012;Jayakumar et al., 2017;Löscher et al.,
50 2014). In contrast, cyanobacterial N₂ fixers and diatom-diazotroph-associations (DDAs), which are commonly
51 considered the most important N₂ fixers in the surface ocean, were either absent or were detected only in
52 low abundances in OMZs (Turk-Kubo et al., 2014;White et al., 2013;Jayakumar et al., 2012). Both, the
53 presence of diazotrophs clustering with proteobacteria, clostridia, spirochaetes, chlorobia, and
54 methanogenic archaea, and the underrepresentation of cyanobacterial and DDA N₂ fixers could thus be
55 considered characteristic for OMZ environments.

56 Nutrient stoichiometry and model predictions (Deutsch et al., 2007) suggest that oxygen-deficient waters are
57 a potentially important niche for N₂ fixation. Based on this suggestion, several studies have focused on N₂
58 fixation in the large and persistent OMZ of the eastern tropical South Pacific. In this region N₂ fixation rates
59 vary, however, with maximum rates of 840 μmol N m⁻²d⁻¹ detected in nitrogenous sulfidic waters off the
60 coast of Peru (Löscher et al., 2014), and 117 μmol N m⁻²d⁻¹ in the oxygen-depleted zone (Bonnet et al., 2013).
61 Low N₂ fixation rates close to the detection limit were reported from the same area (Chang et al., 2019),
62 another set of N₂ fixation rates estimated from sediment trap analyses were in the range of 0-23 μmol N
63 m⁻²d⁻¹ (Knapp et al., 2016). Taken together, these rates suggest either a strong temporal variation or spatial

64 patchiness. A similar variation in N₂ fixation rates was described for the eastern tropical North Pacific ranging
65 from close to the detection limit in the OMZ (Jayakumar et al., 2017) up to 795 μmol N m⁻²d⁻¹ in episodic
66 diazotroph blooms (White et al., 2013). This apparent temporal or spatial variation in N₂ fixation rates may
67 originate from unresolved environmental controls on N₂ fixation and makes it difficult to quantify N₂ fixation
68 in OMZ waters.

69 The Bay of Bengal (BoB) is a region with a strong seasonality driven by the Asian monsoon system. Massive
70 rainfall and river discharge with maximum freshwater inputs in September (e.g. Mahadevan (2016)) cause a
71 considerable lowering of surface water salinity during and after the monsoons throughout the whole basin
72 (Subramanian, 1993). This, together with increased surface water temperatures, leads to intensive and
73 persistent stratification of the water column (Kumar et al., 2004), restricting nutrient fluxes to the surface
74 from below and promoting a strong OMZ (McCreary et al., 2013;Paulmier and Ruiz-Pinto, 2009;Sarma, 2002)
75 with minimum oxygen (O₂) concentrations in the lower nanomolar range (Bristow et al., 2017).

76 The potential importance of N₂ fixation in the BoB can be derived from a simple N budget estimate with an
77 overall N loss of 7.9 ± 0.6 Tg N yr⁻¹ and N sources other than N₂ fixation of 3.15 ± 2.25 Tg N yr⁻¹ (Tab. 1, data
78 from (Naqvi, 2008;Naqvi et al., 2010;Bristow et al., 2017;Singh et al., 2012;Krishna et al., 2016;Srinivas and
79 Sarin, 2013;Suntharalingam et al., 2019)). This implies a deficit of 4.7 ± 2.4 Tg N yr⁻¹ within the given range of
80 uncertainty indicating the potential importance of N₂ fixation assuming a coupling of nitrogen loss and N₂
81 fixation as proposed by (Deutsch et al., 2007). Naqvi et al. (2010) proposed N₂ fixation to contribute 1 Tg N
82 yr⁻¹ in the BoB, while Srinivas and Sarin (2013) interpolated a contribution of 0.6- 4 Tg N yr⁻¹ from phosphate
83 availability. Measurements of N₂ fixation rates from the BoB are not available, isotope analysis of sediment
84 trap samples indeed suggests that the BoB is a site of active N₂ fixation. Indeed, the composition of the
85 organic material produced in BoB surface waters is characterized by a high portion of biogenic opal (20%)
86 and a low δ¹⁵N nitrate signal (3.2 - 5‰, Gaye-Haake et al. (2005)). This points towards a production of a
87 considerable part of organic matter produced by diatoms in symbiotic association with or in close proximity
88 to diazotrophs (Subramaniam et al., 2008). Only few studies report the presence of diazotrophs including
89 *Trichodesmium* in the BoB (Wu et al., 2019;Shetye et al., 2013;Sahu et al., 2017;Jyothibabu et al.,
90 2006;Mulholland and Capone, 2009), with only one of them using a functional gene approach.

91 To investigate the diazotrophic community and to quantify N₂ and carbon fixation in the BoB OMZ, we used
92 a combination of gene sequencing and quantification, rate measurements, isotope tracing and box modeling.

93

94 **Methods**

95 Geochemical sampling

96 Samples were collected from the top 500 m of the water column during the SK-308 cruise with the ORV *Sagar*
97 *Kanya* to the BoB during the winter monsoon between 24 January and 3 February 2014. Seawater samples
98 were collected using 5 L and 30 L-Niskin bottles on a CTD- rosette equipped with a Seabird SBE 43 oxygen
99 sensor and a WET Labs ECO-AFL/FL chlorophyll sensor as previously described in Bristow et al. (2017). To
100 resolve oxygen dynamics below the Seabird sensor's detection limit a STOX (Switchable Trace amount
101 OXYgen) amperometric oxygen sensor was used (Revsbech et al., 2009), which had a detection limit of 7 –
102 12 nmol L⁻¹ during this sampling campaign (Bristow et al., 2017). Nutrients, including nitrate, nitrite and
103 phosphate were determined according to Grasshoff (1999).

104

105 N₂/C-fixation rate measurements

106 Seawater was collected from the Niskin bottles and filled into 2.4-L glass bottles or 2.8-L polycarbonate
107 bottles for (near-) anoxic and all other (oxic) waters, respectively. Bottles were capped with black rubber
108 stoppers (anoxic waters) or Teflon-coated butyl rubber septa (oxic waters). Incubations were performed with
109 the method developed by Mohr et al. (2010) as described in (Grosskopf et al., 2012). Batches of ¹⁵N₂ gas
110 (Cambridge Isotopes, USA) –enriched water was prepared with degassed water from two – three of the six
111 sampling depths. Each incubation bottle was supplemented with 50 mL of the ¹⁵N₂-enriched seawater.
112 Discrete samples for the measurement of the ¹⁵N₂ concentration were taken from each incubation bottle and
113 were measured by membrane-inlet mass spectrometry (MIMS). Final ¹⁵N₂ enrichments were on average 1.65
114 atom % ¹⁵N. For carbon fixation measurements, NaH¹³CO₃ was dissolved in sterile MilliQ water (1g/117mL),
115 and 5 mL were added to each incubation (~8 atom% final, based on total DIC of 2.2 mM). Bottles with water
116 from the upper two depths were kept in surface seawater-cooled on-deck incubators. Bottles from the lower
117 depths were incubated at 13-15°C in the dark. Incubations were stopped after approximately 24 h (samples
118 with less than 20h incubation time were excluded from our analysis). Volumes between 2.1 and 2.7 L of
119 seawater were filtered onto pre-combusted (450°C, 4-6 hours) 25 mm diameter GF/F filters (Whatman, GE
120 Healthcare, Chalfont St Giles, UK) under gentle vacuum (200 mbar). Filters were either frozen at -20°C and
121 oven-dried prior to processing or oven-dried (50°C) directly for 24 h and stored dry until analysis. Untreated
122 seawater was filtered and prepared as described above to obtain background natural abundance values. For
123 elemental and isotopic analysis, GF/F filters were acidified over fuming HCl overnight in a desiccator to
124 remove inorganic C. Filters were then oven-dried for 2 hours at 50°C and pelletized in tin cups. Samples for
125 particulate organic carbon and nitrogen (POC and PON) and C and N isotopic composition were analyzed on

126 an Elemental Analyzer Flash EA 1112 series (Thermo Fisher) coupled to a continuous-flow isotope ratio mass
127 spectrometer (Finnigan Delta Plus XP, Thermo Fisher). A table of N₂ and C fixation rate measurements is given
128 in the supplementary material. Data sets were deposited on PANGAEA.

129

130 Molecular methods

131 Nucleic acid samples were collected at stations 1, 4 and 5 (Fig. 1). Between 5 and 27 L of seawater were
132 filtered in two size fractions (3 μm and 0.22 μm pore size, Supor PES membrane disc filters; Pall, Portsmouth,
133 UK), exact filtration volumes were recorded. Filters were stored in 2.7 mL sucrose lysis buffer at -20 °C.

134 DNA was extracted using an established protocol based on a phenol/chloroform extraction (Giovannoni et
135 al., 1996). The quality and concentration of the purified DNA was checked spectrophotometrically and using
136 the Quant-iT PicoGreen dsDNA kit (Invitrogen, Carlsbad, USA).

137 A metagenome from the deep chlorophyll maximum (DCM, 84m water depth) at station 4 was Illumina HiSeq-
138 sequenced using a 2x125bp read length on a NexteraXT library at the Institute for Clinical Microbiology
139 (IKMB) at Kiel University, Germany. Sequencing resulted in 321Mbp. Sequences were analyzed using the
140 MetPathways pipeline (Konwar et al., 2013), a modular annotation and analysis pipeline for predicting
141 diversity and metabolic interaction from environmental sequences consisting of a quality control, an open
142 reading frame prediction and annotation, diversity analysis, and environmental pathway reconstruction.
143 Phylogenetic identification of OTUs was derived via a comparison with the RefSeq and Greengenes databases
144 (DeSantis et al., 2006). After quality check, 6,454 sequences of ribosomal RNA were identified, 622,286
145 sequences (27.56%) of proteins with known functions, and 1,628,841 sequences (72.15%) were predicted
146 proteins with unknown function.

147 *nifH* gene amplification was performed using a nested PCR protocol (Zehr et al., 1998). PCRs were performed
148 using the GoTaq kit (Promega, Fitchburg, USA) adding one additional μL BSA (20 mg mL⁻¹ (Fermentas,
149 Waltham, USA). The TopoTA Cloning® Kit (Invitrogen, Carlsbad, USA) was used for cloning of PCR amplicons,
150 according to the manufacturer's protocol. Sanger sequencing (340 *nifH* sequences) was performed by the
151 Institute of Clinical Molecular Biology, Kiel, Germany. Negative controls were performed using the PCR
152 mixture as described without template DNA; no amplification was detected. Samples from the particulate
153 fraction >3 μm were consistently negative for *nifH* gene copies and were thus not further investigated.
154 Sequences were ClustalW aligned in MEGA 7 (Kumar et al., 2016) and a maximum likelihood tree was
155 constructed on a 321 base pair fragment. Reference sequences were obtained using BlastX on the NCBI

156 database. Sequences were submitted to Genbank, submission ID 2245434. The metagenome has been
157 submitted to the NCBI's sequence read archive, accession number SRR9696254.

158 Quantitative real time PCRs for *nifH* were performed using cluster specific TaqMan-probe qPCRS as described
159 in Löscher et al (2014), with primers, probes, environmental standards and PCR conditions as presented in
160 table S1. Samples were run in duplicates on a Biorad qPCR machine (Biorad, Hercules, USA).

161

162 Box model exercise

163 We used a simplistic five-box representation of an upwelling system with a deep and intermediate water iron
164 source, with primary and export production as well as respiration derived from the original models (Canfield,
165 2006;Boyle et al., 2013). The model was used to distinguish a N₂ fixation state of the BoB and a non-N₂ fixation
166 state with primary production driven by recycled dissolved nitrogen compounds. In contrast to the previous
167 model versions, we applied a non- Redfield-based N₂ fixation scenario. Ammonia concentrations were set to
168 zero in all boxes, in accordance with our direct measurements. Fe concentrations were set to 0.1 μmol L⁻¹ in
169 the deep and intermediate water boxes and 0.00044 μmol L⁻¹ in the productive zone (Grand et al.,
170 2015a;Grand et al., 2015b). Oxygen concentrations were adjusted to our measurements with 220, 0.02 and
171 50 μmol L⁻¹ in the surface, OMZ and deep water, respectively (Bristow et al., 2017). Phosphate and nitrate
172 concentrations were taken from our measurements with phosphate concentrations of 0, 2.7 and 2.5 μmol L⁻¹
173 in the surface, OMZ and deep boxes, respectively; and oxidized nitrogen compounds (nitrate+ nitrite) at a
174 concentration of 0, 38 and 35 μmol L⁻¹ in the surface, intermediate and deep boxes, respectively. Further
175 information on the model stoichiometry is given in the supplementary material.

176

177 **Results and discussion**

178 We explored the diversity, distribution and activity of N₂ fixing microbes and carbon fixers in the OMZ of the
179 northern BoB during the Northeast monsoon in January 2014. During the time of the cruise, low sea surface
180 temperatures (SST) and low surface water salinity reaching from the coasts of India, Bangladesh and
181 Myanmar southwards to approximately 16°N were present (Figure 1A, B). At the coast, this low salinity/low
182 SST plume co-occurred with increased chlorophyll concentrations (Fig 1C), thus suggesting a stimulation of
183 primary production by waters possibly of riverine origin (Fig 1C). This is in line with earlier suggestions of
184 riverine nutrient runoff promoting primary production close to the shelf, where nutrients are consumed
185 rapidly thus preventing their offshore transport (Kumar et al., 2004;Singh et al., 2012;Singh and Ramesh,
186 2011;Krishna et al., 2016). Chlorophyll concentrations in the BoB during the time of the cruise detected via
187 satellite monitoring ranged between 0.08 mg m⁻³ in open waters and 15 mg m⁻³ at the northern coast and

188 were consistent with previous in-situ measurements during low productivity periods in the BoB (Kumar et
189 al., 2010).

190 The sampling stations were located offshore in the central BoB (Fig. 1), where waters were strongly stratified
191 with low sea surface salinity, but warmer SST compared to the coast, and a steep oxycline reaching O₂
192 concentrations close to anoxia at around 100 m water depth. No in-situ chlorophyll measurements are
193 available from the cruise, but a fluorescence sensor attached to the CTD showed a maximum of up to 0.8 mg
194 m⁻³ between 32-90 m water depth (Fig. 2). Satellite derived chlorophyll concentrations in the coastal BoB
195 were in the range from 0.08 to 0.35 mg m⁻³, slightly higher than in a previous study of this region (0.06 mg m⁻³
196 ³, Kumar et al. (2002)). Carbon fixation rates ranged between 286-1855 nmol C L⁻¹ d⁻¹ at the depth of the DCM
197 (Fig. 2), however, our rate measurements did not cover the water column above 60 m water depth where
198 rates may have been higher. Consistent with previous descriptions of primary producers at our study site
199 (Loisel et al., 2013) and with satellite imaging (Fig. S1), we identified cyanobacteria related to *Synechococcus*
200 and *Prochlorococcus* as the most abundant primary producers in the in our metagenome from the BoB DCM,
201 accounting for 3.3% of OTUs while eukaryotic phytoplankton accounted for only 0.3% of OTUs (Table S2).

202 Similar to chlorophyll, particulate organic carbon (POC, Tab. S3; see also Fig. S2 for a distribution of POC in
203 the BoB) concentrations were low, ranging between 4.96 and 7.84 μmol C L⁻¹ in surface waters, and resulting
204 in an average POC:chlorophyll ratio of 68:1 to 115:1 at the depth of the DCM (Fig. 1). This ratio, is comparable
205 to POC:chlorophyll ratios reported from cyanobacteria-dominated communities (74:1–126:1; e.g., (Lorenzoni
206 et al., 2015; Sathyendranath et al., 2009)), but it is higher compared to other OMZ regions (e.g. 50:1 in the
207 eastern tropical South Pacific (Chavez and Messié, 2009; Chavez et al., 1996)). Similarly, carbon fixation rates
208 were 1-2 orders of magnitude lower compared to the Arabian Sea, the tropical South Pacific and tropical
209 Atlantic (e.g. Longhurst et al. (1995)). While our POC concentrations from DCM are one order of magnitude
210 higher than the satellite-derived POC estimates (Fig. S2) from surface waters indicating that POC and primary
211 production in surface waters was not higher than in the DCM, it must be noted that our measurements did
212 not cover the entire mixed layer and are thus likely a rather conservative minimum estimate.

213 N₂ fixation in the upper water column and the oxycline

214 Based on the dissolved inorganic nitrogen (NO₃⁻ + NO₂⁻) to phosphate (PO₄³⁻) ratio which has a negative
215 intercept with the y-axis (Fig. 3; Benitez-Nelson (2000)), primary production in BoB waters appeared nitrogen
216 limited during the cruise assuming Redfield stoichiometry. This nitrogen limitation would be expected to
217 create a niche for N₂ fixation, but except for two samples for which in both cases only one out of three

218 technical replicates showed an isotope enrichment, N₂ fixation rates were below the detection limit (Tab.
219 S1). Consistent with this, δ¹⁵N signatures of both the nitrate and the particulate organic nitrogen (PON) pool
220 were only slightly decreased in the top 100 m of the water column to 5-8‰ (Fig. S3), thus not clearly
221 supporting active N₂ fixation which would be expected to create light δ¹⁵N signatures of -2- 2‰ (e.g. Dähnke
222 and Thamdrup (2013)). Several clusters of N₂ fixing microbes were, however, identified by screening for the
223 key functional marker gene *nifH* (Fig. 4). Only a few *nifH* sequences were associated with cyanobacteria
224 commonly abundant in ocean surface waters. This pattern seems to be typical for OMZ areas (Fernandez et
225 al., 2011; Jayakumar et al., 2012; Löscher et al., 2014) and for the eastern Indian Ocean (Wu et al., 2019),
226 where cyanobacterial *nifH* sequences are also rare. Similar to earlier studies, which identified *Trichodesmium*
227 in BoB surface waters (Bhaskar et al., 2007; Hegde, 2010; Wu et al., 2019), we detected *nifH* copies related to
228 *Trichodesmium* in our samples, both by sequencing and by qPCR (Fig. 4, Tab. S4). These sequences clustered
229 closely to *Trichodesmium-nifH* previously recovered from the Arabian Sea (Jayakumar et al., 2012; Mazard et
230 al., 2004), where those N₂ fixers were found in low abundances, but possibly actively fixing N₂ as indicated
231 by *nifH* presence in a cDNA library. No sequences related to the different groups of unicellular cyanobacterial
232 diazotrophs (UCYN-A, -B, or -C; Zehr et al. (2001)) were present in our *nifH* dataset. UCYN-A and UCYN-B
233 have previously been found in the Arabian Sea, but only at oligotrophic stations with warm water
234 temperatures >30°C (Mazard et al., 2004). While UCYN-A may occur at temperatures below 25°C,
235 *Trichodesmium* and UCYN-B may be limited by the water temperatures at our sampling stations, which were
236 possibly too low with around 25°C. *Trichodesmium* is usually abundant in high-iron input regions such as the
237 tropical Atlantic Ocean (Martínez-Pérez et al., 2016). The absence of *Trichodesmium* and other cyanobacterial
238 N₂ fixers may thus also result from an insufficient iron source (Moore et al., 2013). Additionally, light
239 limitation due to severe atmospheric pollution (known as the ‘South Asian Brown Cloud’) which lasts over
240 the BoB from November to May (e.g. Ramanathan et al. (2007)) may influence the distribution of
241 cyanobacteria in the BoB (Kumar et al., 2010). While earlier studies also detected *Chaetoceros* (Bhaskar et
242 al., 2007; Hegde, 2010; Wu et al., 2019), a diatom known to live in association with diazotrophs, no diatom-
243 associated N₂ fixers could be identified from our sequences. Thus our data does not directly support previous
244 suggestions of those specific diazotrophs producing low δ¹⁵N nitrate signatures along with high opal
245 concentrations previously detected in sediment trap samples (Gaye-Haake et al., 2005).

246

247 N₂ fixation in the OMZ

248 In the OMZ, we detected again the genetic potential for N₂ fixation, but N₂ fixation rates were below the
249 detection limit and δ¹⁵N signatures of nitrate and PON indicated nitrogen loss instead of N₂ fixation (Fig. S3).
250 The community of N₂ fixers in the BoB consisted mostly of the non-phototrophic, proteobacterial
251 representatives of *nifH*- clusters I and III (Fig. 4), most of them related to previously identified OMZ
252 diazotrophs (Fernandez et al., 2011; Jayakumar et al., 2012; Löscher et al., 2014).

253 A statistical comparison of BoB *nifH* sequences with OMZ diazotroph communities from the Arabian Sea, the
254 ETSP, ETNP and hypoxic basins in California Bay revealed a strong similarity suggesting that certain
255 diazotrophs are characteristic for OMZs (Fig. 5). Those typical OMZ-clusters include uncultured γ-, δ- and ε-
256 proteobacteria and clostridia. Only one cluster was uniquely represented in the BoB and absent from the
257 other OMZ datasets, with only three individual sequences related to *Azotobacter chroococum*. Another
258 difference between the BoB and in the other OMZ diazotroph communities was the composition of Cluster
259 IV *nifH* sequences, which are present but cluster in different groups as compared to for instance the Arabian
260 Sea Cluster IV community. It is, however, unlikely that Cluster IV diazotrophs are important for N₂ fixation in
261 the BoB or other OMZs because they were never shown to be transcribed (Fernandez et al., 2011; Jayakumar
262 et al., 2012; Löscher et al., 2014) and Cluster IV-*nif* is generally considered to encode non-functional *nif* or
263 paralogous sequences (Gaby and Buckley, 2014; Angel et al., 2018). In addition, the presence of Cluster IV
264 *nifH* sequences has previously been ascribed to PCR-contamination (Zehr et al., 2003). Thus, the importance
265 of this cluster for N₂ fixation in OMZs is generally debatable and the different composition of the Cluster IV
266 diazotroph community does likely not explain the absence of N₂ fixation in the BoB.

267 While diazotroph communities highly similar to the identified BoB diazotrophs promote active N₂ fixation in
268 other OMZ waters, we have no consistent indication for N₂ fixation in the BoB (Table S1). One explanation
269 for the absence of N₂ fixation could be the sensitivity of the BoB OMZ diazotrophs to O₂ as opposed to the
270 relative O₂ tolerance of cyanobacterial N₂ fixers. We identified BoB diazotrophs closely related to cultivated
271 N₂ fixers, including *Vibrio diazotrophicus* and *Desulfonema limnicola*, which fix N₂ only under strictly
272 anaerobic conditions (Urdaci et al., 1988; Bertics et al., 2013; Gier et al., 2016). Further, communities of
273 diazotrophs from other OMZs highly similar to the BoB diazotroph community were described to transcribe
274 their *nifH* gene and to actively fix N₂ only under strictly anoxic or anoxic-sulfidic conditions (Löscher et al.,
275 2016; Löscher et al., 2014; Jayakumar et al., 2012; Jayakumar et al., 2017), and are unable to fix N₂ in the
276 presence of even minimal concentrations of O₂ (reviewed in Bombar et al. (2016)). N₂ fixation in our samples
277 (Tab. S1) may therefore be directly inhibited by the detected traces of O₂. Thus, our data suggest that even
278 only nanomolar O₂ concentrations such as present in the BoB may prevent non-phototrophic N₂ fixers from
279 actively fixing N₂, which could ultimately limit the supply of new nitrogen to the BoB.

280 Role of Fe and mesoscale activities (eddies)

281 The high iron (Fe) requirement of N₂ fixing microbes (60 times higher compared to other marine organisms,
282 Gruber and Galloway (2008)) limits N₂ fixation in large parts of the ocean (Moore et al., 2013). However,
283 aeolian Fe fluxes to surface waters of the southern BoB were estimated to be comparable to those detected
284 underneath Saharan dust plumes in the Atlantic ($290 \pm 70 \mu\text{mol m}^{-2} \text{yr}^{-1}$; Grand et al. (2015a)). Indeed,
285 dissolved Fe (dFe) accumulates in the BoB OMZ reaching comparably high concentrations of up to 1.5 nM
286 (Grand et al., 2015b;Chinni et al., 2019). In surface waters, dFe concentrations were described to range from
287 0.4 nM in the area of the cruise to up to 0.5 nM towards the north of the BoB, with increasing concentrations
288 coinciding with decreasing salinity north of 15°N (Grand et al., 2015a;Grand et al., 2015b;Chinni et al., 2019).
289 While the reported Fe concentrations do not indicate Fe limitation of N₂ fixation in the OMZ, surface primary
290 production and N₂ fixation may be limited by any other micro-nutrient. Indication for such a limitation can
291 be derived from eddy-induced Ekman pumping, mesoscale dynamics and the summer monsoon current have
292 been shown to trigger plankton blooms with high productivity (Jyothibabu et al., 2015;Vinayachandran and
293 Mathew, 2003;Chen et al., 2013;Fernandes et al., 2009) possibly induced by upwelling of certain nutrients to
294 surface waters. Besides locally increasing surface water chlorophyll concentrations, erosion of the strong
295 stratification and subsequent nutrient input to surface waters result in a change of phytoplankton size class
296 (Prasanna Kumar et al., 2004). While usually smaller phytoplankton dominate the primary producer pool (60
297 – 95 % of the total chlorophyll), the contribution of larger phytoplankton has been observed to double in the
298 regions influenced by the summer monsoon current and in mesoscale eddies, which impacts the vertical
299 organic carbon flux in the BoB temporally and locally (Jyothibabu et al., 2015;Prasanna Kumar et al.,
300 2004;Huete-Ortega et al., 2010;Gomes et al., 2016). The resulting increase of organic matter production, the
301 modified composition of organic matter (i.e. production fresh and labile POM), a faster export and
302 subsequent respiration could promote anoxic OMZ conditions in the BoB. This may subsequently allow for
303 O₂-sensitive processes to take place, which may include N₂ fixation and nitrogen loss processes (Johnson et
304 al., 2019), locally or regionally. Rapid changes in dissolved O₂ induced by increased surface productivity and
305 organic matter export were reported in the context of mesoscale water mass dynamics in the BoB (Johnson
306 et al., 2019), and also in other eddy systems in the Atlantic, which showed rapid O₂ exhaustion in otherwise
307 oxic waters (Fiedler et al., 2016;Löscher et al., 2015). Episodes of increased biological productivity have also
308 been reported from the BoB during both the pre-southwest monsoon and northeast monsoon (Kumar et al.,
309 2004). Under those scenarios, large parts of the BoB's surface waters exhibited a strong *p*CO₂ undersaturation
310 compared to the atmosphere (~350 μatm), resulting in an air-sea *p*CO₂ gradient sometimes exceeding 100
311 μatm . This gradient is explainable only by an increase in biological primary production fueled by temporal

312 external nutrient input (Kumar et al., 2004). As Singh et al. (2012) pointed out, these high productivity
313 episodes cannot be explained by riverine or atmospheric deposition of nutrients alone, but that upwelling or
314 N_2 fixation would be required to sustain the nitrogen demand.

315

316 Feedbacks between N_2 fixation and OMZ intensity

317 We used a simple model to test the conditions allowing for N_2 fixation in the surface waters and in the OMZ
318 of the BoB, and the interplay of N_2 fixation with primary production in response to changes in stratification
319 (i.e. upwelling). We further explored in how far N_2 fixation controls O_2 concentrations in the BoB OMZ. We
320 simulated a nitrate-driven primary production, and a N_2 fixation-dependent primary production, which is
321 representative of N_2 fixation in the photic zone and governed by excess phosphorus and Fe availability as
322 previously used in Canfield (2006) and Boyle et al. (2013). In addition, we simulated primary production that
323 is dependent on OMZ-associated N_2 fixation, which in contrast to the classical N_2 fixation scenario is
324 independent of a Redfield-based nitrogen deficit with N_2 fixation being active as long as phosphorus and Fe
325 are available in concentration > 0 (Bombar et al., 2016; Löscher et al., 2014). One weakness of this model
326 simulation is that it **only** includes Fe as potentially limiting nutrient for N_2 fixation, which is according to the
327 available datasets (Grand et al., 2015b; Chinni et al., 2019) not necessarily correct but may be valid as an
328 indicator for any other unrecognized micro-nutrient limitation. Consistent with the previous deep-time
329 models of Canfield (2006) and Boyle et al. (2013), our model exercise revealed that additional nitrogen supply
330 by N_2 fixation or other external nitrogen sources would generally exhaust the remaining traces of O_2 with
331 increasing upwelling (Fig. 6). According to our model, this would lead to denitrification, which is in line with
332 O_2 -manipulated experiments as presented in Bristow et al. (2017) and consistent with the available isotope
333 records from the OMZ (Fig. S3). A weaker stratification (in the model depicted as increased upwelling fluxes)
334 would have the strongest effect on oxygen exhaustion and the onset of denitrification if primary production
335 is dependent on N_2 fixation in the photic zone, followed by OMZ-located N_2 fixation, and last by nitrogen
336 recycling. Given that OMZ regions are sites of massive nitrogen loss characterized by a nitrogen deficit in the
337 water column (Deutsch et al., 2007), the similar diazotroph community in the OMZ paired with an absence
338 of N_2 fixation in the euphotic zone suggest that OMZ-associated N_2 fixation is the most likely scenario. Thus,
339 nitrogen limited primary production in the BoB and in OMZs in general would be susceptible to changes in
340 stratification, with increased upwelling of nutrient-rich waters causing O_2 exhaustion. Considering the
341 potential O_2 sensitivity of OMZ diazotrophs based on the comparison with other OMZs, the interplay between

342 O₂ concentrations, stratification and N₂ fixation may act as a stabilizing feedback on the BoB OMZ, preventing
343 full O₂ depletion.

344 One factor possibly disturbing a possible stabilizing feedback is the external anthropogenic supply of nitrogen
345 to the northern Indian Ocean. This additional nitrogen source is projected to increase over the next decades
346 (Duce et al., 2008) potentially accelerating primary production in the future ocean including the BoB. An
347 atmospheric input in the range of 1.1 (model-based) to 1.6 Tg N yr⁻¹ (observation based) has been reported,
348 which will likely increase in the future (Suntharalingam et al., 2019). This additional nitrogen fertilization
349 would cause the same effect as N₂ fixation in our model, thus exhausting the present traces of O₂ in the OMZ
350 rapidly. Until an increased supply of atmospheric or riverine nitrogen would become significant, changes in
351 water column stratification, however, likely impose the strongest control on N₂ fixation and primary
352 production, and thus on respiration, nitrogen loss processes and ultimately on the O₂ status of the OMZ in
353 the BoB.

354

355 **Conclusion**

356 We detected a diazotrophic community similar to those from other OMZ regions, however, we could not
357 obtain consistent evidence for active N₂ fixation in the BoB. Coming back to our original question ‘No N₂
358 fixation in the BoB?’ our data suggest ‘No.’. In other OMZs, N₂ fixation has been observed to largely vary
359 temporally and spatially but never reaching rates comparable to oligotrophic open ocean systems such as
360 the Pacific gyres. Episodes of N₂ fixation, however, could be induced by changes in water mass dynamics,
361 riverine or atmospheric nutrient input. Resulting increased N₂ fixation and primary production would possibly
362 lead to O₂ exhaustion in the BoB, which otherwise doesn’t become fully anoxic.

363 Previous observations describing the absence of nitrogen loss processes in the BoB were explained by the
364 remaining traces of O₂ (Bristow et al., 2017) and possibly by a nitrogen deficiency relative to carbon in the
365 organic matter pool. While we acknowledge that our dataset represents only a snapshot of the BoB’s
366 biogeochemical setting, our observations may help to predict the future development of N₂ fixation in the
367 BoB and of the BoB OMZ with regard to increasing atmospheric dust deposition and ocean fertilization (Duce
368 et al., 2008), altered ocean circulation patterns (Yeh et al., 2009), and deoxygenation of the ocean as a
369 consequence of global warming (Schmidtko et al., 2017;Stramma et al., 2008).

370

371 **Code/Data availability:** Sequence data is available from Genbank, submission ID 2245434 and from NCBI's
372 sequence read archive, accession number SRR9696254. The model code and other biogeochemical data are
373 available from the Pangaea database (<https://doi.pangaea.de/10.1594/PANGAEA.905498>,
374 <https://doi.pangaea.de/10.1594/PANGAEA.905496>).

375 **Author contribution:** CRL carried analyzed the data together with WM, CRL ran the model simulations and
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377 **Competing interests:** The authors declare no competing interests.

378

379

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672

673 **Tables:**

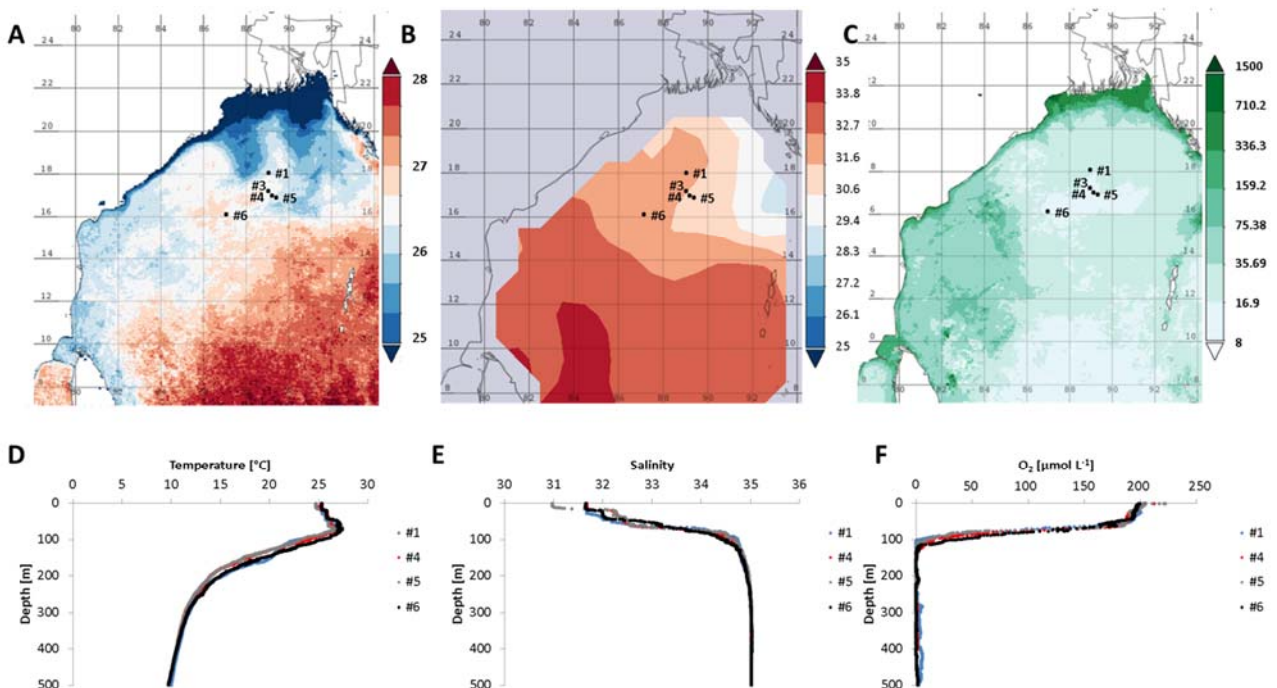
674 Table 1: Nitrogen fluxes in the BoB (Tg N yr^{-1}); N loss fluxes are given in black, N sources are given in gray;
675 DIN = dissolved inorganic nitrogen, PON = particulate organic nitrogen, IO = Indian Ocean. N_2 loss by
676 denitrification was excluded by Bristow et al. (2017). Naqvi et al. (2010) reported possible N loss to the
677 atmosphere in the form of N_2O .

	Flux [Tg N yr^{-1}]	reference
Net exchange with the IO	3.3	Naqvi , 2010
Sedimentary denitrification	3 - 4.1	Naqvi , 2008; Naqvi 2010
PON burial	1	Naqvi , 2010
Water column N loss to the atmosphere	0 - 0.07	Naqvi , 2010; Bristow, et al. 2017
Atmospheric deposition	0.5 - 1.6	Naqvi , 2010; Singh et al., 2012; Suntharalingam et al., 2019
Riverine/ land input	0.4 - 4	Naqvi , 2010; Singh et al., 2012; Krishna et al., 2016
N_2 fixation	0.6-11.3	Naqvi , 2010; Srinivas & Sarin, 2013

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680 **Figures:**

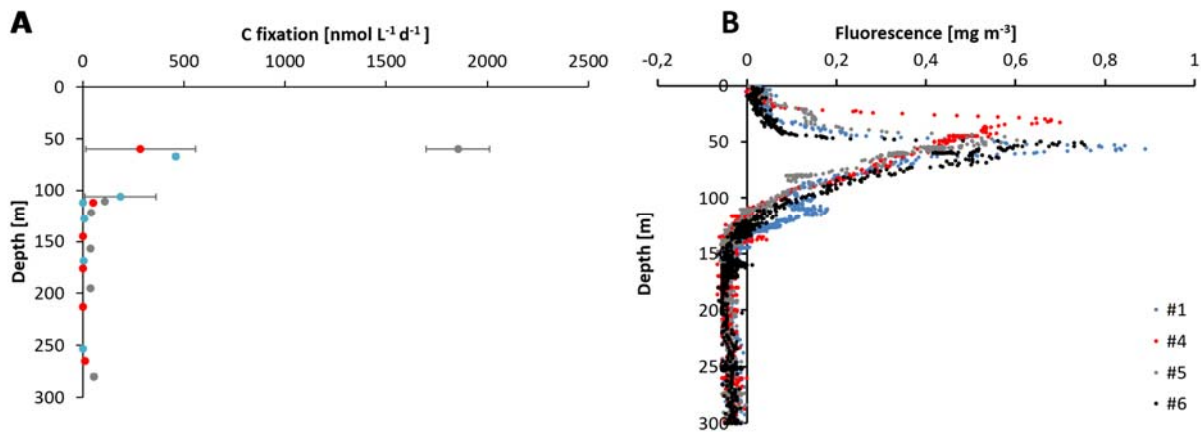


681

682 Fig. 1: Time-averaged maps from 15. Jan 2014 – 15. Feb 2014 of (A) sea surface temperature (SST in °C (night
683 only, 8-daily, 4 km resolution obtained from MODIS-Aqua, <https://giovanni.gsfc.nasa.gov>), (B) sea surface
684 salinity, (C) chlorophyll a concentration in $10^{-2} \text{ mg m}^{-3}$, note the log scale (8-daily, 4 km resolution obtained

685 from MODIS-Aqua, <https://giovanni.gsfc.nasa.gov>). (D) CTD data-based water temperature in °C, (E) salinity
 686 at the cruise stations. (F) O₂ (in μmol L⁻¹) over the top 500 m of the water column, data from Bristow et al.
 687 (2017)

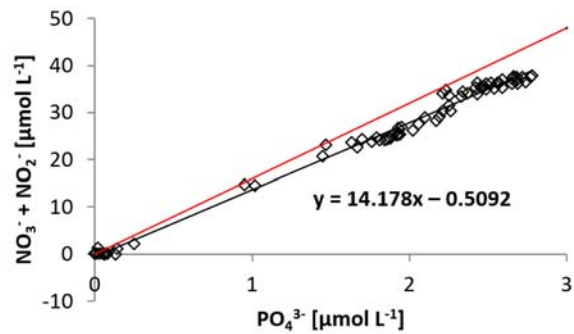
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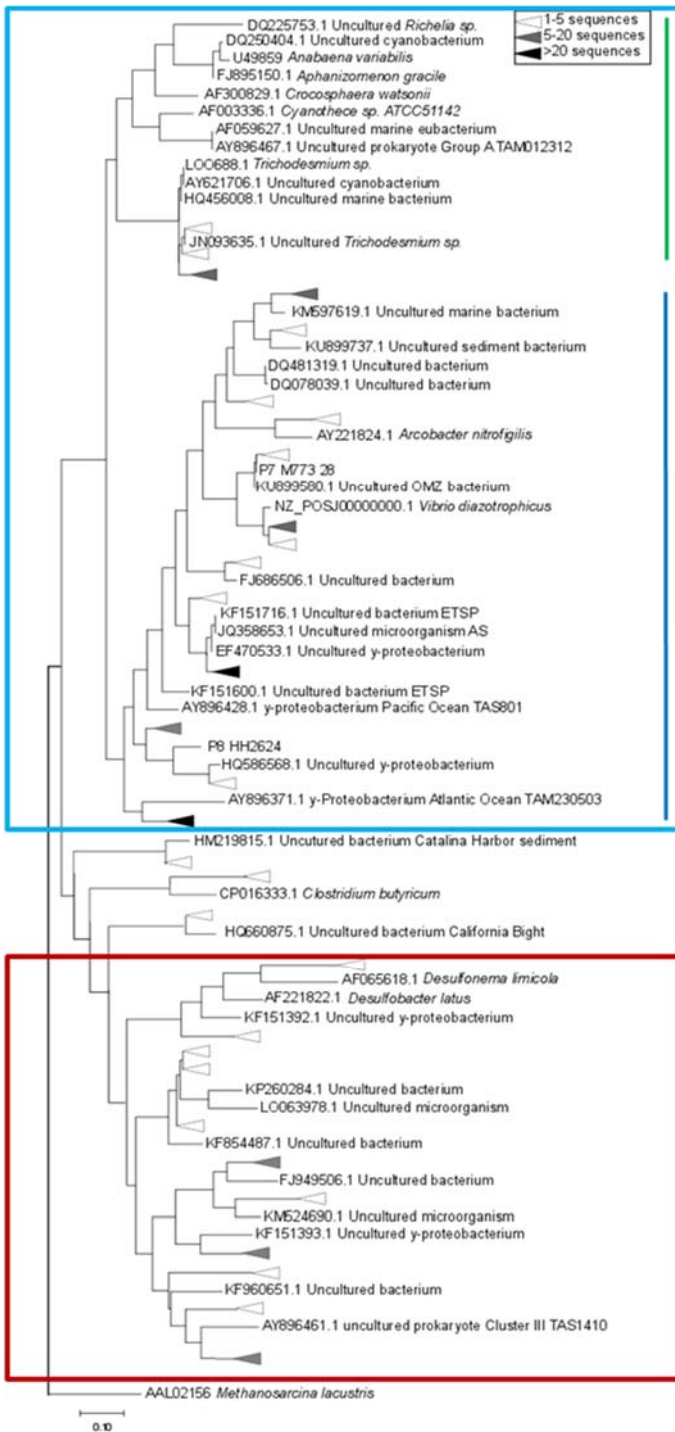
690 Fig. 2: (A) Carbon fixation rates at stations 1, 4 and 5, and (B) sensor-based fluorescence measurements from
 691 station 1, 4, 5 and 6.

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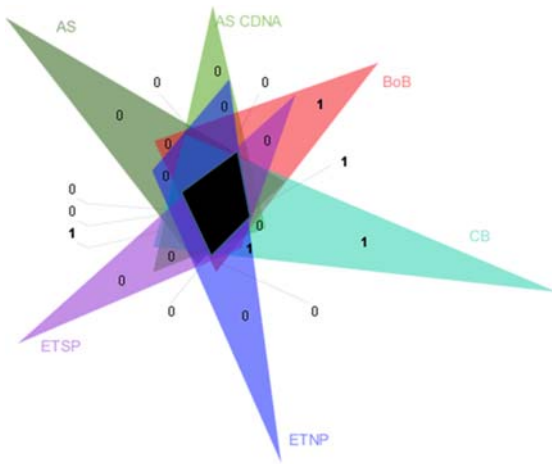
694 Fig. 3: N:P ratio at station 1, 4, 5 and 6, with the Redfield ratio of N:P = 16:1 indicated with a red line, the
 695 negative intercept of the trendline indicates a deficit in dissolved inorganic nitrogen.



696

697 Fig. 4: Maximum likelihood tree of a 321 bp fragment of the *nifH* gene. Clusters identified by Sanger
 698 sequencing are indicated with triangles with colors denoting the sequence abundances in our dataset. The
 699 light blue box indicates Cluster I sequences including cyanobacteria (green line) and proteobacteria (blue
 700 line). Cluster III sequences are indicated with a red box.

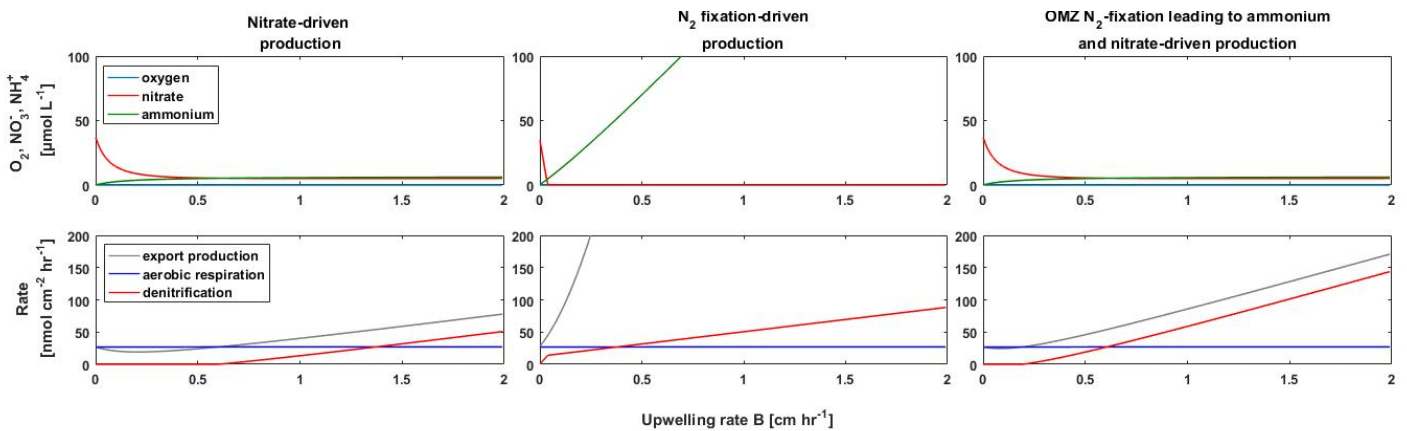
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702

703 Fig. 5: Venn diagram of *nifH* clusters present in Arabian Sea DNA libraries (AS), and in cDNA libraries (AS
 704 cDNA), clusters identified in the BoB, in O₂-depleted basins of the Californian Bay (CB), the eastern tropical
 705 North Pacific (ETNP) and the eastern tropical South Pacific (ETSP). Clusters as depicted by triangles in Fig. S
 706 6) were collapsed based on a 98% identity. The black area shows the clusters present in all OMZs. Numbers
 707 indicate the individual clusters in fields which would otherwise appear unproportionally large.

708



709 Fig. 6: Model of the response of the BoB OMZ to a weaker stratification corresponding to increased upwelling
 710 in this model, under a non-N₂ fixation scenario with nitrate driven production, a photic zone N₂ fixation-
 711 dependent primary production, and a scenario of N₂ fixation in the OMZ, which would result in built-up of a
 712 nitrogen stock and export to the productive surface if stratification becomes weaker.

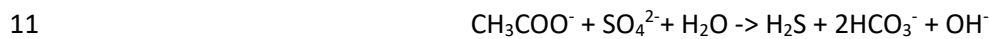
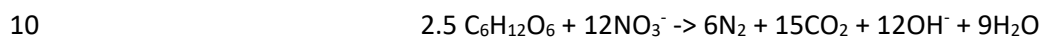
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1 **Supplementary material to Löscher et al. 'No nitrogen fixation in the Bay of Bengal?'**

2 Model experiment

3 The model framework is based on Canfield's 5-box model (Boyle et al. 2013; Canfield 2006), using available
4 measurements for the BoB from our cruise and other literature (Tab. M1, the complete code will be released
5 on Pangaea). The model is classically based on the identification of the limiting nutrient for euphotic primary
6 production under Redfield conditions. Primary production provides the basis for determination of export
7 fluxes under consideration of respiration first using oxygen, followed by nitrate and sulfate according to the
8 following stoichiometry:



12 Export production is estimated as the sum of organic carbon respiration (R) of the three above mentioned
13 processes:

14
$$EP = R_{aerobic} + R_{denitrification} + R_{sulfate_reduction}$$

15 For nitrate-based primary production, i.e. if nitrate is available above Redfield conditions, primary and
16 export production directly depend on upwelling of bioavailable nitrogen. Surface N₂ fixation is based on
17 Redfield stoichiometry and on Fe availability (Fe > 0). If

18
$$N_{ox} - \Gamma_{N:P} P < 0$$

19 is true, export production is proportional to phosphate upwelling to the euphotic zone.

20 The model was further modified to explore OMZ N₂ fixation, which we suggest adding a source of reduced N
21 (N_R) to the OMZ. This pool of N_R would upon mixing or upwelling to the oxic surface promote nitrification and
22 primary production.

23 OMZ N₂ fixation has been shown not to be limited by Redfield constraints Redfield stoichiometry as suggested
24 by Bombar, Paerl, and Riemann (2016). This leads to a modification of the previous OMZ model (Boyle et al,
25 2013) with the Redfield control of N₂ fixation being replaced by a phosphorous only control with P > 0
26 constantly allowing for N₂ fixation and export production scaling with phosphate and N_{ox} + N_R upwelling.

27

28 Tables

29 Tab M1: Concentrations used in the model experiment, data taken from Bristow et al. (2017), Grand et al.
30 (2015) and (Chinni et al. 2019)

Parameter	Description	Concentration [μM]	Reference
$\text{O}_{2\text{U}}$	Oxygen concentration in surface waters	220	Bristow et al., 2017
$\text{O}_{2\text{I}}$	Oxygen concentration in intermediate waters	0.05	Bristow et al., 2017
$\text{O}_{2\text{D}}$	Oxygen concentration in deep sea	50	Bristow et al., 2017
P_{U}	Phosphate concentration in surface	0	Bristow et al., 2017
P_{I}	Phosphate concentration in intermediate water depth	2.7	Bristow et al., 2017
P_{D}	Phosphate concentration in deep waters	2.5	Bristow et al., 2017
N_{oxU}	Nitrate concentration in surface	0	Bristow et al., 2017
N_{oxI}	Nitrate concentration in intermediate water depth	38	Bristow et al., 2017
N_{oxD}	Nitrate concentration in intermediate water depth	35	Bristow et al., 2017
N_{RU}	Ammonia concentration in surface	0	Bristow et al., 2017
N_{RI}	Ammonia concentration in intermediate water depth	0	Bristow et al., 2017
N_{RD}	Ammonia concentration in deep sea	0	Bristow et al., 2017
Fe_{RU}	Dissolved iron concentration in surface waters	0.0004	Chinni et al., 2019
Fe_{RI}	Dissolved iron concentration in intermediate waters	0.015	Grand et al., 2015
Fe_{RD}	Dissolved iron concentration in deep sea	0.01	Grand et al., 2015

31

32 Table S1: CO_2 and N_2 fixation rates based on triplicate measurements at stations 1 (17.9970°N, 88.9968°E),
33 4 (16.9828°N, 89.2063°E) and 5 (17.2075°N, 89.4282°E). N_2 fixation was only measurable in two individual
34 samples, but only in one out of three technical replicates.

station #	Incubation depth	CO ₂ fixation [nmol L ⁻¹ d ⁻¹]	SD	N ₂ fixation [nmol L ⁻¹ d ⁻¹]	SD
1	67	460.1	14.0	0.0	0.0
1	106	186.2	174.7	0.0	0.0
1	112	0.0	0.0	0.0	0.0
1	128	8.8	2.6	17.4	8.2
1	169	4.8	0.2	0.0	0.0
1	253	2.0	2.9	0.0	0.0
4	60	286.1	270.2	0.0	0.0
4	112	50.6	4.1	0.0	0.0
4	145	0.0	0.0	0.0	0.0
4	176	2.4	2.4	0.0	0.0
4	213	3.2	2.2	1.0	0.5
4	265	10.2	2.9	0.0	0.0
5	60	1855.0	157.6	0.0	0.0
5	111	109.3	5.8	0.0	0.0
5	122	41.7	1.2	0.0	0.0
5	157	37.8	3.8	0.0	0.0
5	195	37.7	4.5	0.0	0.0
5	280	56.1	12.4	0.0	0.0

35

36 Table S2: OTU counts of primary producers from a metagenome from station #4, 84m.

Class	% of OTUs in metagenome	Order	% of OTUs in class
Cyanobacteria	3,25%	Chroococcales	48%
		Prochlorales	41%
		Nostocales	5%
		Oscillatoriales	5%
		unclassified cyanobacteria	1%
Chlorophyta	0,33%	Mamiellales	75%
		Chlamydomonadales	21%
		Chlorellales	2%
		Ulvophyceae	0.4%
		unclassified chlorophta	1.6%

37

38 Table S3: POC and PON distribution at stations 1 (17.9970°N, 88.9968°E), 4 (16.9828°N, 89.2063°E) and 5
 39 (17.2075°N, 89.4282°E).

station #	Incubation depth	POC [$\mu\text{mol L}^{-1}$]	SD	PON [$\mu\text{mol L}^{-1}$]	SD	POC:PON
1	67	4.956	0.195	0.531	0.027	9.331
1	106	11.057	5.038	1.411	0.773	7.838
1	112	6.730	2.493	0.700	0.182	9.613
1	128	6.709	1.015	0.818	0.048	8.198
1	169	5.946	0.830	0.586	0.125	10.151
1	253	4.720	1.774	0.262	0.105	17.998
4	60	5.854	0.734	0.688	0.051	8.505
4	112	3.833	0.336	0.395	0.030	9.714
4	145	6.674	2.634	1.022	0.645	6.527
4	176	7.884	1.713	1.247	0.255	6.321
4	213	4.858	0.112	0.676	0.048	7.186
4	265	4.166	0.667	0.475	0.074	8.773
5	60	7.844	1.094	1.253	0.256	6.259
5	111	6.461	1.462	1.013	0.080	6.376
5	122	8.783	1.263	1.488	0.143	5.902
5	157	7.409	0.241	1.325	0.067	5.590
5	195	9.337	0.404	1.433	0.203	6.514
5	280	5.232	0.659	0.674	0.017	7.766

40

41

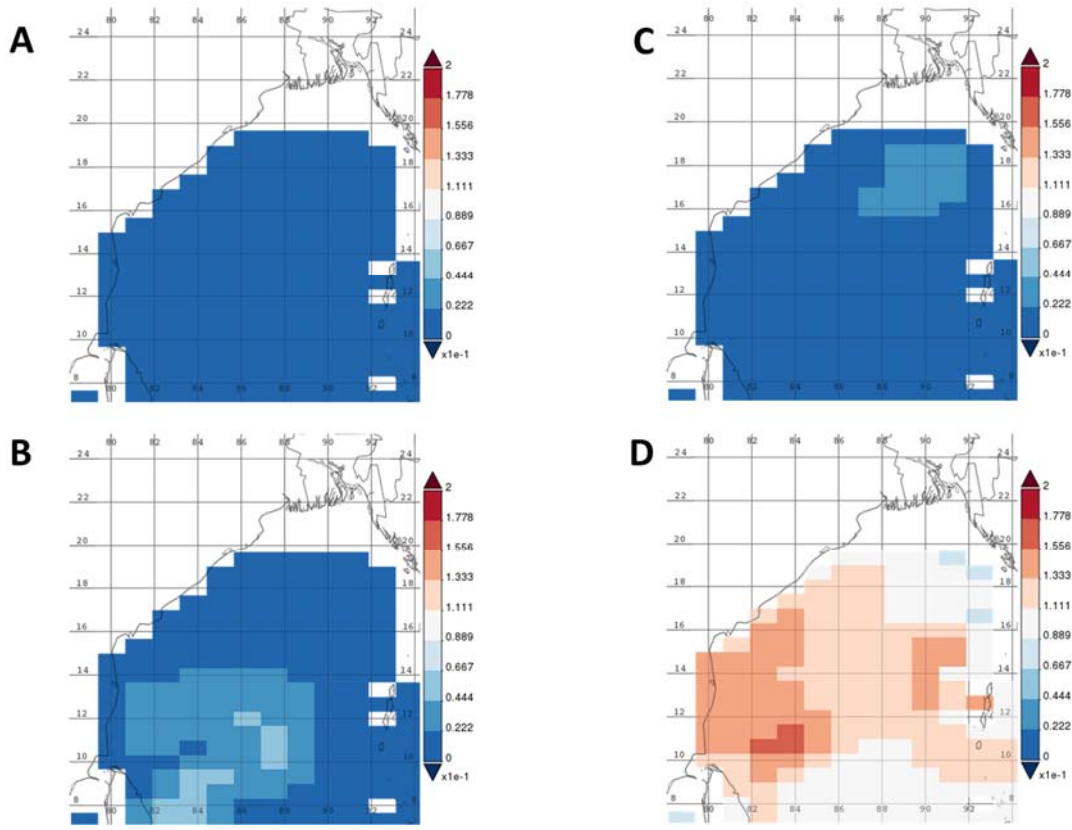
42 Table S4: *nifH* qPCR quantification [copies L^{-1}], clusters which did were detectable by PCR but not
 43 quantifiable (below the detection limit of 4 copies L^{-1}) are not shown.

station	depth [m]	filtration volume [L]	<i>nifH</i> [copies L^{-1}]					
			filamentous	SD	Gamma-PO	SD	Green sulfur	SD
1	10	10.2	8.2E+08	4.6E+03	1.5E+03	5.6E+02	6.4E+03	2.6E+03
1	68	10.3	1.4E+11	2.2E+06	1.2E+03	1.6E+02	1.1E+04	1.2E+03
1	80	16.2	2.4E+11	6.1E+10	5.4E+02	0.0E+00	1.8E+03	2.0E+03
1	115	12.7	0.0E+00	0.0E+00	2.2E+03	3.8E+02	3.0E+03	1.5E+03
1	130	14	0.0E+00	0.0E+00	4.3E+03	9.0E+02	1.6E+03	5.0E+02
1	140	20	0.0E+00	0.0E+00	1.7E+11	3.9E+10	4.5E+02	2.3E+02
1	160	20.2	0.0E+00	0.0E+00	5.1E+02	6.9E+01	3.4E+03	1.1E+03
1	256	21.5	0.0E+00	0.0E+00	1.7E+03	1.7E+02	3.8E+03	5.5E+02
1	500	16.3	0.0E+00	0.0E+00	7.5E+02	3.3E+01	1.6E+03	1.4E+02
2	61	14	6.7E+03	8.5E+03	1.7E+03	2.6E+02	1.9E+03	7.4E+02
2	120	10.7	8.3E+05	3.7E+05	0.0E+00	0.0E+00	1.5E+03	1.2E+03
4	60	8	0.0E+00	0.0E+00	5.1E+02	7.3E+01	1.7E+03	3.4E+01
4	84	7.6	0.0E+00	0.0E+00	4.4E+02	6.1E+01	1.6E+03	1.4E+02
4	112	9.2	0.0E+00	0.0E+00	1.0E+12	1.3E+12	2.9E+03	3.4E+02
4	154	11.7	0.0E+00	0.0E+00	1.6E+02	2.0E+01	1.5E+04	2.1E+03
4	179	19.1	0.0E+00	0.0E+00	1.8E+02	4.1E+01	3.9E+03	1.0E+03
4	211	20.1	0.0E+00	0.0E+00	1.1E+02	1.8E+01	7.7E+02	2.8E+02
4	265	22.9	5.4E+04	7.0E+04	4.7E+02	0.0E+00	2.0E+03	1.3E+03
4	321	23.2	3.0E+03	3.2E+03	0.0E+00	0.0E+00	7.3E+02	1.7E+02
5	60	7.6	5.8E+02	5.1E+02	7.5E+02	2.3E+02	1.8E+03	5.8E+02
5	80	12.6	8.9E+02	4.4E+02	0.0E+00	0.0E+00	8.1E+02	1.8E+02
5	127	14.3	0.0E+00	0.0E+00	2.4E+03	7.9E+02	2.5E+04	8.8E+03
5	156	6.4	0.0E+00	0.0E+00	0.0E+00	0.0E+00	9.8E+02	1.5E+02
5	560	15.4	8.2E+08	4.6E+03	1.5E+03	5.6E+02	6.4E+03	2.6E+03

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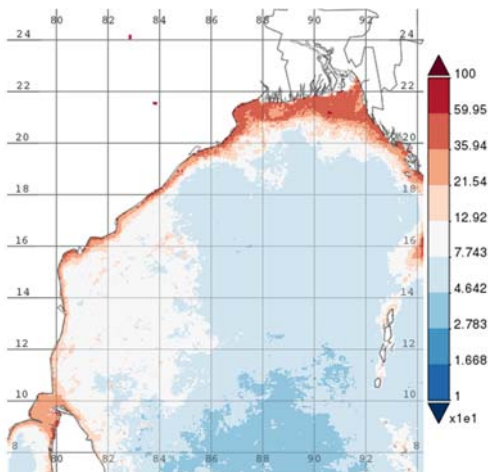
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46 **Figures**



47

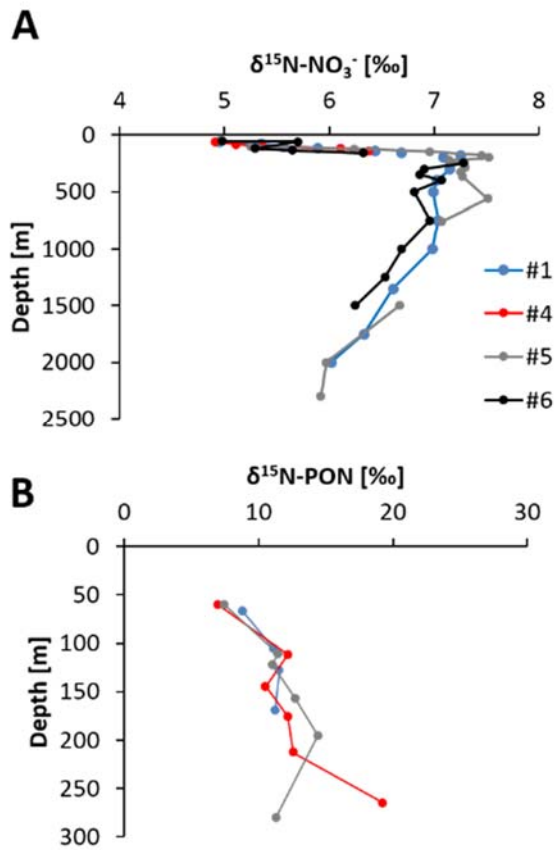
48 **Figure S1: Phytoplankton distribution in the BoB during the time of the cruise: (A) diatoms, (B) chlorophytes,**
49 **(C) coccolithophores, and (D) cyanobacteria in mg m^{-3} . Data has been averaged from 15 Jan to 15 Feb, 2019,**
50 **based on the MODIS-Aqua satellite product as available from <https://giovanni.gsfc.nasa.gov>.**



51

52 **Figure S2: Time-averaged (15 Jan to 15 Feb, 2019) POC distribution as monitored via MODIS-Aqua**
53 **(<https://giovanni.gsfc.nasa.gov>) on an 8-daily basis, with a 4km resolution, POC concentrations in mg m^{-3} ,**

54 concentrations in the cruise area were between 7.7 and 12.9 mg m⁻³ and are consistent with our in-situ
55 measurements.



56

57 Fig. S3: Both, (A) $\delta^{15}\text{N-NO}_3^-$ (data from Bristow et al., 2017) and (B) $\delta^{15}\text{N-PON}$ show slightly lighter isotope
58 signatures in the upper 100 m of the water column, however, this signal does not clearly indicate N₂ fixation.

59

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