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N₂ production in the Bay of Bengal Oxygen Minimum Zone

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A third or more of the fixed nitrogen lost from the oceans^{1,2} is removed by anaerobic microbial processes in pelagic oxygen minimum zones (OMZs). Regions of nitrogen loss associated with oxygen depletion are presently recognized in the Eastern Tropical Pacific Ocean, off the coast of Namibia, and in the Arabian Sea^{1,3,4}. OMZ waters have expanded over the past decades⁵, and further anthropogenically-induced expansion⁶ could accelerate nitrogen loss, thus impacting the marine nitrogen economy. In this regard, the Bay of Bengal (BoB) has proven an enigma; despite having oxygen levels below detection with conventional methods (1 to 2 μM)⁷ there have been no indications of nitrogen loss from the region⁷⁻⁹. Here we show that the BoB supports denitrifier and anammox microbial populations, mediating low, but significant N loss, but unlike other OMZs, the BoB has persistent concentrations of oxygen in the 10 to 200 nM range. We propose that this oxygen supports nitrite oxidation, thereby restricting the nitrite available for anammox or denitrification. If the last traces of oxygen were removed, nitrogen loss in the BoB OMZ waters could accelerate to global significance.

We sampled the BoB in January 2014 during the winter monsoon (Figure 1 and S1). At five stations we measured oxygen *in situ* with a highly sensitive STOX sensor (switchable trace oxygen)¹⁰, with a limit of detection (LOD) of 7 to 12 nM. We used Niskin bottles to collect samples for nutrients, dissolved gases, nitrate isotopic analyses, molecular characterization of microbial populations and for experiments exploring aerobic and anaerobic microbial nitrogen metabolism.

STOX oxygen data revealed sub-micromolar oxygen concentrations over a depth interval of about 200 meters throughout the study area (Figure 1). Only six single measurements were below the LOD, and these were confined to thin layers in the depth range between 280 and 360

m at Station 7 (Table S1). There was no evidence for distinct broad anoxic zones as seen in the
40 other OMZs at any station, even at Station 1, where a secondary nitrite maximum of up to 180
nM was observed in the depth range 115 m to 150 m (Figure 1; nitrite was at or below the LOD
of 10 nM at all other stations analyzed). At this station, the lowest oxygen concentration was 36
nM at ~150 m (Figure 1 and Table S1). Persistent oxygen and low nitrite in the BoB contrasts
with other major OMZs, which have anoxic cores (oxygen below STOX sensor detection) with >
45 500 nM nitrite^{11,12}. When calibrated to the STOX data (Figure S2), a Seabird oxygen sensor
revealed tremendous vertical structure in the oxygen profiles (Figure 1), indicating oxygen input
by lateral intrusions.

Despite the lack of evidence for anoxia in BoB OMZ waters, the vertical zonation of
microorganisms with nitrogen-metabolizing capabilities resembled typical OMZs supporting
50 active N₂ production as indicated by 16S rRNA and functional gene abundances (Figure 2).
Anammox bacteria, as quantified through their nitrite reductase gene (*Scalindua nirS*, or *Sc*
nirS), were present within the OMZ waters, peaking at the depth of 150 m with about 1300
copies mL⁻¹, some 40 to 60% of the maximal abundance found in other OMZs with active N₂
production^{13,14}. Nitrite reductase genes attributed to denitrifiers (Denitrifier *nirS*) were found at
55 similar distribution and abundance to the *Sc nirS*, and were even more abundant than in the
Eastern Tropical South Pacific (ETSP) OMZ^{13,15}. In addition, the distribution of functional genes
of aerobic ammonium and nitrite oxidizers, thaumarchaeotal *amoA* (*Th amoA*) and
Nitrospira/Nitrospina nxrB (*nxrB*) respectively, resembled the distributions in other OMZ
waters^{13,15-17}, where *Th amoA* abundance peaks in the upper oxycline, here at about 80 m, and
60 *nxrB* abundance peaks lower in the water column where *Sc nirS* is also most abundant. The
similarity with other OMZs was further supported by the presence of the SUP05 clade,

gammaproteobacterial sulfur oxidizers (GSO), and abundant adenylylsulfate (APS) reductase genes (*aprA*), suggesting a role for sulfur cycling in the BoB OMZ waters¹⁸ (Figure S3).

Thus, microbial populations in BoB OMZ waters are capable of both anaerobic and aerobic
65 nitrogen (and maybe sulfur) cycling as in other OMZs supporting N₂ production, despite a lack
of any prior evidence for N₂ production. We performed parallel experiments with ¹⁵N-labeling to
survey rates of microbial nitrate reduction and N₂ production in BoB OMZ waters (process rate
experiments). With additions of ¹⁵NH₄⁺ alone, anammox (NH₄⁺ + NO₂⁻ → N₂ + 2H₂O) rates were
below detection (LOD 1.3 nM N d⁻¹) at all stations. Anammox rates of up to 6.2 nM N d⁻¹,
70 however, were observed when NH₄⁺ and NO₂⁻ were added together, with labeling of either of the
substrates (Figure 3A and S4). These potential rates are comparable to off-shore locations in the
OMZs of the ETSP¹⁵ and Eastern Tropical North Pacific (ETNP)¹⁹.

Anammox was also detected at rates of up to 5.5 nM N d⁻¹ in separate experiments designed
to explore the oxygen regulation of nitrite transformations (oxygen regulation experiments)
75 where ¹⁵NO₂⁻ was added alone (Figure 3B). Anammox activity decreased with increasing oxygen
concentrations in three of the four experiments, but activity was observed up to our maximum
concentration of 9.5 μM, in line with a number of previous observations²⁰. Indeed, anammox
rates remained high across the oxygen concentrations of the BoB OMZ. Summarizing our
results, anammox was not measurable when ammonium was added alone, but was only detected
80 with added nitrite. Thus, there is a large potential for N-loss via anammox in the BoB, but *in situ*
anammox bacteria are likely nitrite-limited rather than being limited by ammonium or inhibited
by oxygen. Denitrification was below the LOD (2.7 nM N d⁻¹) in BoB OMZ waters in our
process rate experiments (Figure 3A). We did, however, detect denitrification (up to 0.9 nM N d⁻¹
1) with ¹⁵NO₂⁻ at Station 5 (but not Stations 1 or 4) in our oxygen regulation experiments with a

85 lower median detection limit of 0.4 nM N d⁻¹ (Figure 3B), suggesting a patchy distribution of denitrification in BoB OMZ waters. When present, denitrification exhibited higher oxygen sensitivity than anammox (Figure 3B), with complete inhibition at O₂ concentrations above 4-5 μM (except one outlier), consistent with observations from the ETSP OMZ²¹.

Despite the low rates of anammox and denitrification, and the general absence of nitrite in
90 BoB OMZ waters, we measured nitrite production rates from nitrate (¹⁵NO₃⁻) of up to 12.1 nM N d⁻¹ at Stations 4 and 5 (Figure 3A). We also measured potential nitrite oxidation rates of up to 52 nM N d⁻¹ in our oxygen regulation experiments (Figure 3B; Table S2). The presence of nitrite-oxidizing bacteria was confirmed by the detection of *Nitrospira/Nitrospina*-related *nxB* sequences (Figure 2). The rates of nitrite oxidation exceeded those of nitrite production even at
95 low oxygen concentrations, reaching maximum values at ~1 μM O₂, suggesting nitrite oxidizing bacteria have a high affinity for oxygen (Figure 3A). Our combined data indicate an active, coupled, anaerobic/aerobic nitrogen cycle where nitrate is reduced to nitrite and rapidly oxidized again to nitrate in the OMZ waters. A close coupling between nitrate reduction to nitrite and subsequent nitrite oxidation has also been described in the oxyclines of other OMZs, where
100 nitrite also fails to accumulate despite active nitrate reduction to nitrite^{20,22}.

Thus, based on our experimental data, we conclude that the BoB OMZ oxygen concentrations (10 to 200 nM) limit N₂ production through anammox indirectly, by enabling aerobic nitrite oxidizing bacteria to outcompete anammox bacteria for the available nitrite. Denitrification was also not inhibited by the oxygen levels of BoB OMZ waters, but was
105 generally low and only detected at two stations. Such patchiness may be related to the presence or absence of organic-matter rich aggregates in the incubations¹⁹.

Our molecular results and process rate measurements are supported by geochemical data that indicate a slow, but functioning, anaerobic nitrogen cycle in BoB OMZ waters. A small, albeit noisy, nitrogen deficit of 2 to 3 μM , indicative of net N loss, was calculated from our nutrient data (Figure 4 and SI). We also observed a maximum N_2 excess (calculated from N_2/Ar ratios) on the order of 2 to 3 μM N_2 in the OMZ waters (equivalent to 4 to 6 μM N). Throughout the sub-surface ocean, N_2 excess increases monotonically with depth due to abiotic factors²³ but a local maximum within OMZs is strongly indicative of biogenic N_2 production²⁴. The $\delta^{15}\text{N}$ of NO_3^- from the BoB OMZ showed small enrichments of up to 1.5 ‰ relative to deep-water values consistent with net nitrate reduction. The larger ^{18}O enrichment in NO_3^- of 3 ‰ is consistent with the coupled anaerobic/aerobic nitrogen cycle explored above, with nitrate reduction to nitrite followed by reoxidation back to nitrate²⁵ (see SI). These three geochemical indicators integrate over larger water volumes and over longer time scales than our rate measurements, and, therefore, imply that nitrogen cycling and N_2 production are persistent phenomena in the BoB, although these signals are smaller in magnitude than in other major OMZs^{24,25}.

Taken together, our nitrogen deficit and N_2 excess measurements point to $\sim 2 \mu\text{M}$ of biologically produced N_2 (4 μM $\text{N}_2\text{-N}$) in BoB OMZ waters. Previous studies have estimated annual water exchange of $18 \times 10^{12} \text{ m}^3 \text{ y}^{-1}$ in the depth interval from 150 to 250 meters, and $31 \times 10^{12} \text{ m}^3 \text{ y}^{-1}$ in the interval from 250 to 500 m²⁶. We take 40% of the later ($12 \times 10^{12} \text{ m}^3 \text{ y}^{-1}$) to estimate the exchange from 250 to 350 m, obtaining a total annual water exchange of $30 \times 10^{12} \text{ m}^3 \text{ y}^{-1}$ from 150 to 350 meters depth, and a turnover time of 12 years for the $372 \times 10^{12} \text{ m}^3$ volume of this interval²⁶. This exchange rate, combined with a biogenic N_2 excess of 2 μM , yields an annual production rate of $\sim 1.7 \text{ Tg N y}^{-1}$. This N_2 production is about 12% of the production rate

in the Arabian Sea, and some 2.5 % of the global water-column production in OMZ settings

130 $(66 \pm 6 \text{ Tg N y}^{-1})^2$.

This annual rate of N_2 production amounts to an average N_2 production rate of 0.88 nM-N d^{-1} for the volume between 150 to 350 m. As we were unable to measure N_2 production by anammox without added nitrite, and as denitrification rates were low when detected at all (Figure 3), there must be either seasonal or spatial variability in N_2 production that we have not captured
135 in our process rate experiments. Still, our process rate and oxygen regulation experiments (Figure 3) suggest a potential for N_2 production of about 3 nM-N d^{-1} under nitrite replete conditions, some 3.5 times greater than the average rate calculated from the N_2 excess.

Therefore, there is considerable potential for additional N_2 production in the BoB OMZ above that indicated from the geochemical indicators. As N_2 production, particularly through anammox,
140 is nitrite limited, the rates should increase if oxygen is depleted further, suppressing nitrite oxidation and allowing nitrite to accumulate¹¹ in BoB OMZ waters. An accumulation of nitrite in the sub-micromolar range may be sufficient to stimulate anammox substantially, judging from the independence of anammox rates on nitrite concentrations across OMZs²⁷. If N_2 production increased to an average of 3 nM-N d^{-1} (as our experiments suggest), then N_2 production rates
145 would increase to about 6 Tg N y^{-1} or about 40% of Arabian Sea rates and 9% of global water-column rates². Such an increase would make the BoB an important player in the global nitrogen cycle.

The stable accumulation of nitrite in BoB OMZ waters would require the removal of the last traces of oxygen. The oxygen concentration reflects the dynamic balance between the processes
150 mixing oxygen into the OMZ and the processes consuming it. An increase in the flux of organic matter to the OMZ waters would be one way to increase oxygen consumption, and an increase in

primary production could accomplish this. Possible vehicles for increased primary production include the accelerated input of anthropogenic nitrogen into the BoB, as projected for the coming decades⁶ and changing intensity of the summer monsoon. In particular, the high southwesterly summer monsoon winds generate coastal upwelling, producing high concentrations of chlorophyll *a*²⁸ and enhanced oxygen depletion in coastal waters²⁹. Therefore, accelerated summer monsoon intensity could potentially increase the flux of organic matter to OMZ waters, drawing down oxygen and accelerating N₂ production.

However, an enhanced summer monsoon would also increase river runoff and the flux of particulates to the BoB. Riverine particulates ballast sinking organic material resulting in rapid sedimentation of labile organics through the OMZ, reducing their decomposition in OMZ waters⁹. Thus, the main climate driver in the BoB, the summer monsoon, generates what appear to be opposing influences on the development of anoxia in the BoB OMZ waters. A test of summer monsoon intensity on N₂ loss in the BoB could come from current climate change as some climate models suggest future increases in the intensity of the Asian summer monsoon³⁰.

Historical evidence indeed suggests a potential relationship between climate change and an active anaerobic nitrogen cycle in the BoB³¹. Elevated sediment nitrogen isotope values are correlated with elevated concentrations of organic matter and organic nitrogen about 42,000 years ago. These results suggest that higher rates of organic matter productivity at that time enabled a nitrogen cycle with higher N loss rates, although the driver of this relationship is unclear.

Overall, we demonstrate that the BoB is like the other well known OMZs with microbial populations supporting N₂ production, although at low rates. The BoB OMZ also maintains

widespread nanomolar oxygen concentrations that inhibit the stable accumulation of nitrite, a
175 key substrate for N-loss. If these last traces of oxygen were removed, allowing nitrite to
accumulate, rates of N₂ production would increase considerably. Thus, the BoB OMZ sits at a
geochemical “tipping point” where any process removing the last of the oxygen, such as
anthropogenic nutrient input or climate change, would make the BoB a major player in the
marine nitrogen cycle.

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Figure Captions

Figure 1. Station locations and oxygen data for the Bay of Bengal.

Oxygen concentration profiles focus on the upper 500 m of the water column containing the oxygen minimum zone (OMZ). Black dots represent STOX oxygen data, while the blue line represents Seabird oxygen data, calibrated with the STOX data at the low oxygen levels. At Station 1, nitrite concentrations are indicated by the red line (a distinct primary nitrite maximum in the oxic upper 100m, and a secondary nitrite maximum under nanomolar oxygen concentrations). Nitrite was not detected at any of the other stations.

Figure 2. Abundance of bacterial 16S rRNA and selected functional genes in the Bay of

Bengal. Copy numbers were obtained with qPCR using primer sets as shown in Table S3. Shown are total copies of bacterial 16S rRNA (A), nitrite reductase genes attributed to denitrifiers (Denitrifier *nirS*; B) and to anammox bacteria (*Scalindua*, *Sc nirS*; C), thaumarchaeotal ammonia monooxygenase (Th *amoA*; D) and *Nitrospira/Nitrospina* nitrite oxidoreductase (*nxrB*; E). The dashed rectangle outlines the approximate depth interval where oxygen concentrations drop below 2.5 μM . Error bars represent the standard deviation. Note variability in x axes scales.

Figure 3. Depth profiles and regulation experiments of N transformations in the Bay of

Bengal A) Process rate experiments showing rates of anammox and nitrate reduction to nitrite using ^{15}N labeling experiments. Denitrification was below detection in these experiments: B) Experiments using ^{15}N -labeled substrates to explore the oxygen regulation of nitrogen transformations. The top panel shows the oxygen regulation of nitrite oxidation (note the use of both y axes), the middle panel shows the oxygen regulation of denitrification, while the bottom panel shows the oxygen regulation of anammox. Error bars represent the standard error.

Figure 4. Geochemical indicators of nitrogen cycling in the Bay of Bengal OMZ waters.

205 Depth profiles of excess N_2 (calculated from N_2/Ar ratios; A), and the N deficit (B; calculated as $[NO_3^- + NO_2^-] - (N/P_{bw} * [PO_4^{3-}])$, with N/P_{bw} being the average $NO_3^- + NO_2^-$, PO_4^{3-} ratio seen in bottom waters during this cruise, which was assigned a value of 14). The $\delta^{15}N$ of nitrate, along with a depth profile of average nitrate concentrations (solid black line; grey shading shows upper and lower bounds) from all stations (C), and the $\delta^{18}O$ of nitrate (D). The dashed rectangle

210 outlines the approximate depth interval where oxygen concentrations drop below $2.5 \mu M$.

Figure 1

Figure 2

Figure 3

Figure 4

225

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Additional information

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330 Author Contributions

L.A.B., M.L., M.G., R.N.G., M.M.M.K., G.L., S.W.A.N., N.P.R., B.T. and D.E.C. designed the study; L.A.B., C.M.C., M.L., J.D., M.F., G.L., J. M., D.E.C. performed experiments; L.A.B., C.M.C., M.L., M.A.A., M.F., G.L., B.T., A.H.T. and D.E.C. analyzed data; A.P. provided nutrient data; L.A.B., C.M.C., M.L., R.N.G., G.L., B.T. and D.E.C. wrote the manuscript with
335 input from all co-authors.