

# Microbial ecosystem dynamics drive fluctuating nitrogen loss in marine anoxic zones

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**The dynamics of nitrogen (N) loss in the ocean's oxygen-deficient zones (ODZs) are thought to be driven by climate impacts on ocean circulation and biological productivity. Here we analyze a data-constrained model of the microbial ecosystem in an ODZ and find that species interactions drive fluctuations in local- and regional-scale rates of N loss, even in the absence of climate variability. By consuming O<sub>2</sub> to nanomolar levels, aerobic nitrifying microbes cede their competitive advantage for scarce forms of N to anaerobic denitrifying bacteria. Because anaerobes cannot sustain their own low-O<sub>2</sub> niche, the physical O<sub>2</sub> supply restores competitive advantage to aerobic populations, resetting the cycle. The resulting ecosystem oscillations induce a unique geochemical signature within the ODZ—short-lived spikes of ammonium that are found in measured profiles. The microbial ecosystem dynamics also give rise to variable ratios of anammox to heterotrophic denitrification, providing a mechanism for the unexplained variability of these pathways observed in the ocean.**

microbial ecology | oxygen minimum zones | nitrogen cycle | species oscillations

**B**ioavailable nitrogen (N) is a key macronutrient that limits the rates of biological activity. In the ocean, the concentration of nitrate (NO<sub>3</sub><sup>-</sup>), the major form of bioavailable N, is reduced by anaerobic reduction to biologically inert N<sub>2</sub> gas within small subsurface O<sub>2</sub>-deficient zones (ODZs) (1). The volumetric rate of N removal within these zones is limited by the downward flux of organic matter from sinking particles (2). In turn, ODZ volumes are strongly dependent on the regional O<sub>2</sub> content of the thermocline in which they reside (3). Variations in climate have major impacts on the supply of O<sub>2</sub> and organic matter to the ODZ, driving changes in the magnitude of N removal across a wide spectrum of timescales, from months to millennia (4–6).

Microbial community structure also plays a major role in regulating N<sub>2</sub> gas production. Anaerobic processes, such as anammox and heterotrophic denitrification, can tolerate up to micromolar amounts of O<sub>2</sub>, allowing them to coexist with aerobic nitrifying microbes, which become limited by O<sub>2</sub> only at nanomolar concentrations (2, 7–14). Because both anaerobic and aerobic metabolisms utilize the key N-cycle intermediates ammonium (NH<sub>4</sub><sup>+</sup>) and nitrite (NO<sub>2</sub><sup>-</sup>) as substrates, their coexistence results in resource competition whose outcome is determined by nanomolar variations in O<sub>2</sub> (15). When nitrification is dominant, the reoxidation of partially denitrified NO<sub>2</sub><sup>-</sup> to nitrate (NO<sub>3</sub><sup>-</sup>) reduces the magnitude of N<sub>2</sub> production and increases O<sub>2</sub> consumption; when aerobic nitrifiers are excluded by O<sub>2</sub> scarcity, NO<sub>3</sub><sup>-</sup> is efficiently reduced all of the way to N<sub>2</sub> (15, 16). Here we demonstrate that resource competition between aerobic nitrifiers, anaerobic denitrifiers, and anammox bacteria can also lead to regional-scale temporal variability in the rates of N and O<sub>2</sub> cycling, even with constant physical fluxes of O<sub>2</sub> and organic matter into the ODZs.

To examine the role of microbial interactions in the dynamics of fixed N loss, we analyzed a microbial ecosystem model (15) embedded within an ocean general circulation model (17, 18). The

steady three-dimensional ocean circulation is optimized to fit tracer observations (temperature, salinity, radiocarbon, and CFC-11), implying realistic ventilation rates and pathways of the ODZs (19). We focus on the world's largest ODZ, in the eastern tropical North Pacific (ETNP) (20), by restricting the boundaries of the model from the equator to 35° N, the coast to 180° W, and the surface ocean to 2,000-m depth. Observed annual mean concentrations of O<sub>2</sub> and NO<sub>3</sub><sup>-</sup> (21) are transported into the domain at its open boundaries to ensure their realistic supply to the ODZ region. The circulation does not vary over time, leaving microbial ecosystem dynamics as the sole source of temporal variability.

The microbial ecosystem model simulates the biomass of four microbial functional groups and the biogeochemical cycles of N and O<sub>2</sub> (15). In the surface ocean, phytoplankton produce dissolved organic nitrogen (DON) and sinking organic particles from inorganic N (NH<sub>4</sub><sup>+</sup>, NO<sub>2</sub><sup>-</sup>, NO<sub>3</sub><sup>-</sup>). DON is remineralized by heterotrophic bacteria using O<sub>2</sub>, or multistep denitrification (reduction of NO<sub>3</sub><sup>-</sup> to NO<sub>2</sub><sup>-</sup>, then to N<sub>2</sub>) below a critical O<sub>2</sub> threshold (O<sub>2</sub><sup>crit</sup>). The NH<sub>4</sub><sup>+</sup> and NO<sub>2</sub><sup>-</sup> released by heterotrophs is used by autotrophs: slow growing and O<sub>2</sub>-inhibited anammox bacteria, or aerobic archaea and bacteria that either perform NH<sub>4</sub><sup>+</sup> or NO<sub>2</sub><sup>-</sup> oxidation with nanomolar O<sub>2</sub> sensitivities. Autotrophs assimilate NH<sub>4</sub><sup>+</sup> from seawater for growth. Because the

## Significance

**The removal of bioavailable nitrogen (N), a critical nutrient that limits marine primary production, is thought to vary due to climate forcing of the ocean's low oxygen zones. Here we demonstrate that competition between aerobic and anaerobic microbes for scarce resources drives fluctuations in the rate of marine N loss over time, even in a stable environment. Biological oscillations have been theorized for nearly a century in idealized models, but are shown here for the first time in a three-dimensional and data-constrained model of ocean circulation. A predicted geochemical signature of the oscillations is detected in environmental samples. This previously overlooked source of natural variability reconciles conflicting empirical evidence for the dominance of heterotrophic versus autotrophic pathways of N removal.**

Author contributions: J.L.P. and C.D. designed research; J.L.P. performed research; J.L.P., T.W., and C.D. analyzed model output; B.X.C. made NH<sub>4</sub><sup>+</sup> measurements; J.L.P. and C.D. wrote the paper; and T.W. and B.X.C. provided input on the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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Data deposition: Data related to this work have been deposited in [Figshare.com](#); doi: [10.6084/m9.figshare.7627439](#).

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1818014116/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1818014116/-DCSupplemental).

C:N ratio of bacterial biomass ( $6.8 \pm 1.2$ ) (22) matches that of organic matter within the ODZ (6.8) (2) heterotrophs satisfy their nutrient demand via  $\text{NH}_4^+$  remineralized from DON (23). DON is released by phytoplankton, sinking particles, and all microbial populations during mortality.

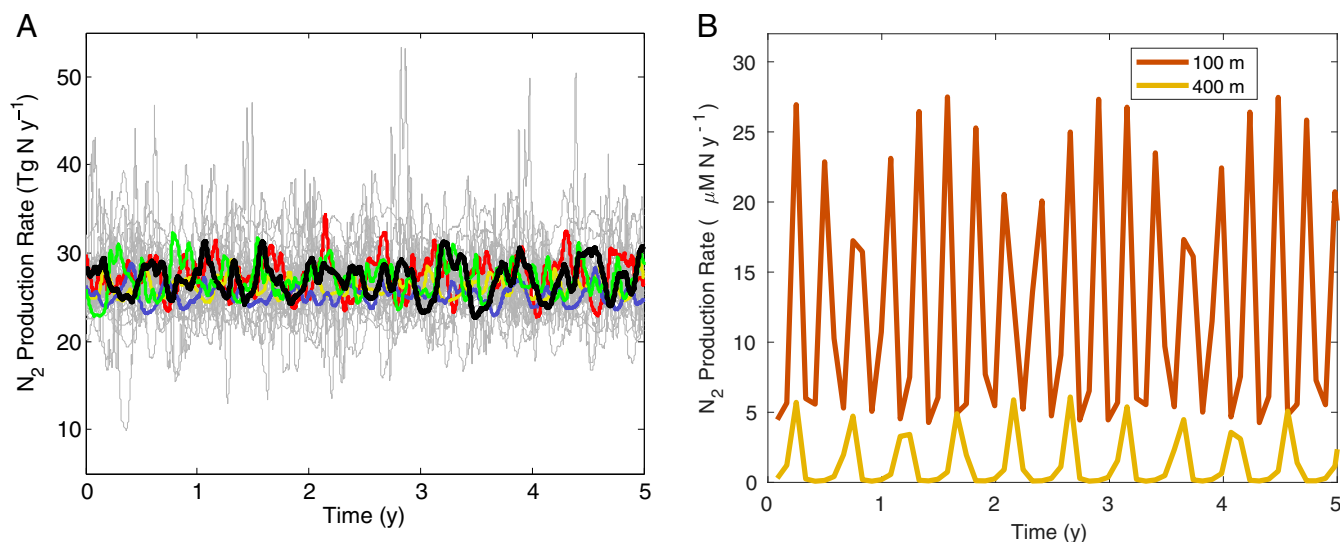
In previous work (15), we assessed the model fit to observed long-term mean (climatological) fields of  $\text{O}_2$  and  $\text{NO}_3^-$ , and profile compilations of  $\text{NH}_4^+$ ,  $\text{NO}_2^-$ , and biologically produced  $\text{N}_2$  gas ( $\text{N}_2^{\text{xs}}$ ) from within the ETNP. These data reflect the characteristic vertical profiles of key chemical indicators of the metabolic status of the ODZs: subsurface maxima in  $\text{NO}_2^-$  and  $\text{N}_2^{\text{xs}}$ , reduced accumulations of  $\text{NO}_3^-$ , and nanomolar levels of  $\text{NH}_4^+$  and  $\text{O}_2$  (SI Appendix, Fig. S1). To constrain uncertainty in model parameters, we varied microbial growth, mortality, and nutrient affinities over two orders of magnitude, spanning values observed in laboratory cultures and process studies (SI Appendix, Table S1), and compared the resulting simulated profiles to the observations (SI Appendix, Fig. S1). Of the 90 parameter combinations tested, half reproduce all observed chemical profiles simultaneously, implying a realistic balance of physical and biological fluxes of N and  $\text{O}_2$ . This ensemble of model simulations that reproduce the data are used for further analysis and to quantify the sensitivity of our main results.

The simulated rate of regional N loss aligns with geochemical estimates based on measurements of the accumulation of  $\text{N}_2^{\text{xs}}$ , the deficits of  $\text{NO}_3^-$ , and its isotopes (19, 24), but fluctuates strongly over time (Fig. 1A) despite the steady rates of ocean circulation. These fluctuations are not caused by changes in the flux of organic matter or the physical supply of  $\text{O}_2$  to the ODZ region, which are stable (SI Appendix, Fig. S2). The fluctuations persist across a wide range of physiological and ecological assumptions: regardless of the precise  $\text{O}_2$  sensitivities of the microbial populations (yellow, red, and green lines in Fig. 1A); with and without inclusion of dissimilatory  $\text{NO}_3^-$  reduction to  $\text{NH}_4^+$  (DNRA) (25) (blue line in Fig. 1A); whether heterotrophic denitrification is represented as a facultative or obligate process (1, 26) or if its steps are mediated by a single or multiple populations (27) (SI Appendix, Fig. S3). Fluctuations in N loss are found under all ecosystem model parameter combinations that satisfy

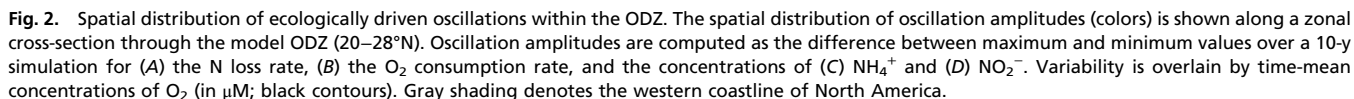
the available tracer data constraints (SI Appendix, Fig. S4). Their amplitude is large relative to time-mean rates, averaging  $43\% \pm 35\%$  (SD) on regional scales and  $233\% \pm 123\%$  (SD) at the locations where fluctuations occur. While the regionally integrated N-loss rate lacks a characteristic frequency, local rates of N loss vary through semiregular oscillations (Fig. 1B). The complex fluctuations in the regional-scale N loss (Fig. 1A) thus arise from the integration of the many localized oscillators with distinct periods, phasing, and amplitudes.

The oscillations are also evident in aerobic metabolic rates, which together with the changes in N loss, drive large-scale fluctuations in the concentrations of  $\text{O}_2$ ,  $\text{NH}_4^+$ , and  $\text{NO}_2^-$  (Fig. 2). Fluctuations are strongest at the edge of the ODZ's anoxic core, in a "suboxic" zone, where the full diversity of simulated microbial populations coexist— aerobic  $\text{NH}_4^+$  and  $\text{NO}_2^-$  oxidizers as well as autotrophic anammox bacteria and heterotrophic denitrifiers (15). In the anoxic core of the ODZ, where aerobic metabolisms are excluded, the chemical environment, the resident microbial populations, and their metabolic rates are relatively stable over time. The coincidence of variability in zones of long-term nitrifier–denitrifier coexistence implies that the oscillations are driven by interactions between these microbial groups. Indeed, if the nitrifiers are separated from autotrophic anammox and heterotrophic denitrifiers by imposing non-overlapping  $\text{O}_2$  thresholds, oscillations do not arise in the model simulations (SI Appendix, Fig. S5).

The mechanism of these oscillations derives from a fundamental ecosystem dynamic: consumption of  $\text{O}_2$  by aerobic microbes provides an advantage for anaerobes, but their niche cannot be sustained against the physical  $\text{O}_2$  supply without intermittent dominance of the aerobes. In the model ODZ, the consumption of  $\text{O}_2$  by  $\text{NO}_2^-$  oxidation ( $\sim 41 \text{ Tg O}_2 \text{ y}^{-1}$ ) vastly outweighs  $\text{NH}_4^+$  oxidation ( $\sim 4.9 \text{ Tg O}_2 \text{ y}^{-1}$ );  $\text{NH}_4^+$  oxidation thus plays little role in the oscillatory dynamic. The complete ecological sequence of the oscillation is illustrated by the phase diagram of  $\text{NH}_4^+$  and  $\text{O}_2$  at a single point in space (Fig. 3). When  $\text{O}_2$ ,  $\text{NH}_4^+$ , and  $\text{NO}_2^-$  are plentiful,  $\text{NO}_2^-$  oxidizing bacteria experience net population growth (location Fig. 3A and B, i). Their metabolic rate exceeds the physical  $\text{O}_2$  supply and depletes



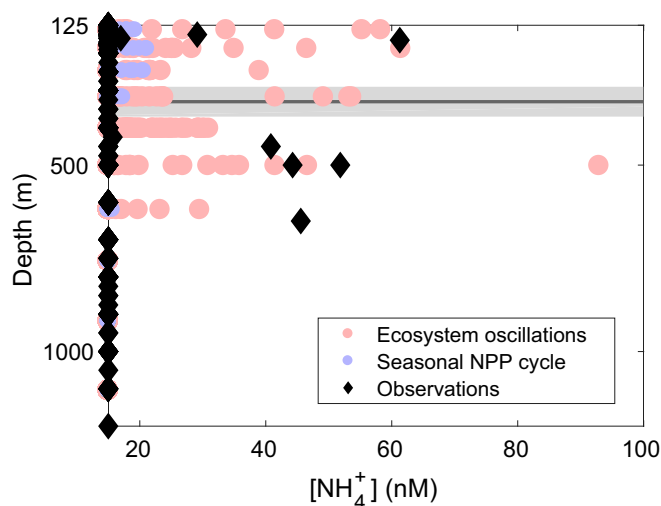
**Fig. 1.** Time series of unforced variability in the regional and local rates of N loss from the ODZ of the eastern tropical North Pacific. (A) Rates ( $1 \text{ Tg N y}^{-1} = 10^{12} \text{ g N y}^{-1}$ ) are spatially integrated across the ETNP in the standard model simulation (black) and sensitivity cases (gray and colors). Fluctuations occur regardless of physiological or ecological uncertainties (SI Appendix, Table S1): whether  $\text{O}_2$  tolerances of anaerobes are  $1 \mu\text{M}$  (yellow) or  $\geq 10 \mu\text{M}$  (red), if the two steps of nitrification ( $\text{NH}_4^+$  and  $\text{NO}_2^-$  oxidation) have different nanomolar  $\text{O}_2$  sensitivities (green), or if an additional metabolism [dissimilatory nitrate reduction to ammonium (DNRA)] is incorporated into the model (blue). They also hold across wide ranges in other microbial ecosystem parameters (gray, SI Appendix, Table S1). (B) Time series of local rates of N loss in locations with representative ecosystem oscillations ( $12^\circ\text{N}$ ,  $90^\circ\text{W}$  at 100 m and  $25^\circ\text{N}$ ,  $113^\circ\text{W}$  at 400 m).



Top-down ecological controls on microbial populations also have the potential to limit fluctuations caused by resource competition. We represented grazing losses in the model by applying a quadratic mortality term to all microbial populations, assuming predation is unselective (*SI Appendix*, Fig. S8). We varied the intrinsic grazing rate by an order of magnitude and find that while the variance in regional N loss is unchanged under weak grazing, under strong grazing the variance is decreased by an order of magnitude (*SI Appendix*, Fig. S8A). However, adding this strong grazing term causes an unrealistic build up of  $\text{NH}_4^+$  concentration in the anoxic core of the ODZ



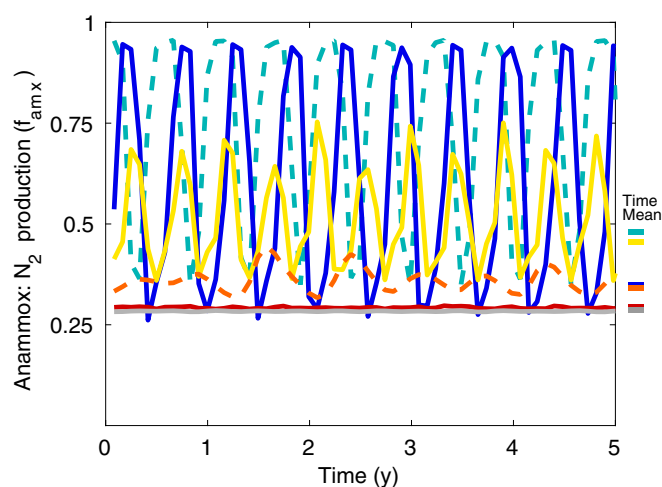




**Fig. 4.**  $\text{NH}_4^+$  depth profiles from the ODZ of the eastern tropical North Pacific in model simulations and observations. Depth profiles were sampled monthly over the course of a year in the standard model simulation (pink circles) and measured on a cruise to the ETNP in 2012 (black diamonds, [SI Appendix, Supplementary Information Text](#)).  $\text{NH}_4^+$  exceeds the detection limit ( $\sim 15 \text{ nM}$ )  $\sim 5\%$  of the time in the model simulation and in  $\sim 8\%$  of observations at  $\text{O}_2 < 5 \mu\text{M}$ , but on average is below detection in both. Model and observed  $\text{NH}_4^+$  values below  $15 \text{ nM}$  are set to this detection limit. Diel vertical migration depth for the ETNP is plotted (mean indicated by line, SD by shading) (32). The time-dependent  $\text{NH}_4^+$  profiles are also shown from a model simulation with a data derived seasonal cycle of net primary production (NPP), but weak internal oscillations (violet). Seasonal fluctuations in the supply of organic matter to the ODZ cannot produce the magnitude of  $\text{NH}_4^+$  spikes implied by the observations.

small pulses of  $\text{NH}_4^+$ . In this case, even with forced fluctuations in the supply of organic matter into the ODZ, the predicted time-varying concentrations of  $\text{NH}_4^+$  barely exceed the measured detection limit at any depth. The measured spikes in  $\text{NH}_4^+$  therefore support strong nonequilibrium ecosystem behavior.

Ecological oscillations within the ODZ have direct consequences for the fraction of total N loss that derives from anammox ( $f_{\text{amx}}$ ) as opposed to heterotrophic denitrification (Fig. 5). The contribution of these metabolic pathways to N loss has been observed to vary across and within the ODZs from direct rate measurements in the field, but the causes of these variations remain hotly debated (e.g., refs. 2, 4, and 32). During the course of the oscillation, when  $\text{NO}_2^-$  oxidizing bacteria are ascendant, the  $\text{NO}_2^-$  that would otherwise be reduced by heterotrophs is reoxidized to  $\text{NO}_3^-$ . The suppression of heterotrophic denitrification temporarily allows  $\text{NH}_4^+$ -limited anammox to contribute 100% of local  $\text{N}_2$  production. However, after  $\text{NO}_2^-$  accumulates, the rapid bursts of heterotrophic denitrification vastly exceed previous rates of anammox (Fig. 3 C and D) and thereby dominate total N loss over a complete oscillatory cycle (horizontal lines Fig. 5). These local variations in the balance of N loss processes can temporarily obscure the time-mean gradients in  $f_{\text{amx}}$  across the ODZ (15). Because they occur over an



**Fig. 5.** The contribution of anammox to total  $N_2$  production ( $f_{\text{anmx}}$ ) over time. Time series of  $f_{\text{anmx}}$  in representative locations across the ODZ, from 115 m to 450 m. At the oxic–anoxic interface (oxycline),  $f_{\text{anmx}}$  can vary over wide ranges that temporarily obscure its time-mean gradient (blue, cyan, and yellow lines). Within the secondary  $NO_2^-$  maximum,  $f_{\text{anmx}}$  approaches the value of 0.28 and oscillations are weak (orange, red, and gray lines). Solid lines are from the heart of the ODZ, whereas dashed lines are from its margins. Time-mean contributions of anammox to N loss are shown as colored horizontal lines on the *Right* axis.

extremely narrow range in the concentrations of  $\text{O}_2$ ,  $\text{NH}_4^+$ , and  $\text{NO}_2^-$ , evaluating this ecological contribution to observed variations in  $f_{\text{amx}}$  will require frequent and high-precision measurements of these chemical abundances and associated metabolic rates.

Oscillatory behavior is a common feature of idealized ecosystem models with multiple interacting populations (33, 34), but is rarely shown to persist in realistic representations of the environment such as a three-dimensional ocean circulation. Intrinsic ecosystem oscillations provide a mechanism to generate variations in marine microbial community structure and N and O<sub>2</sub> cycling, which are often ascribed to externally forced changes in physical and chemical conditions. Because these oscillations lack spatial coherence and power at decadal and longer timescales (Fig. 14), they are unlikely to explain large-scale decadal variations in N loss (5). However, dynamics such as these may be pervasive beyond the ODZs, occurring wherever the physical supply of resources selects for a microbial community that over time undermines its own ecological niche by shifting the chemical environment to temporarily favor the growth of its competitors or degrade the growth of its facilitators.

**ACKNOWLEDGMENTS.** We thank Tim DeVries for supplying the ocean circulation model, H. Frenzel for technical assistance, and C. Fuchsman and A. Santoro for insightful discussions. This work was made possible by grants from the Gordon and Betty Moore Foundation (GBMF 3775 to C.D.) and the Joint Institute for the Study of the Atmosphere and Ocean under NOAA Cooperative Agreement (NA15OAR4320063, contribution no. 2018-0141, to B.X.C.). This work is NOAA-Pacific Marine Environmental Laboratory contribution no. 4772.

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