

Enhancement of anammox by the excretion of diel vertical migrators

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Edited by David M. Karl, University of Hawaii, Honolulu, HI, and approved September 15, 2014 (received for review June 10, 2014)

Measurements show that anaerobic ammonium oxidation with nitrite (anammox) is a major pathway of fixed nitrogen removal in the anoxic zones of the open ocean. Anammox requires a source of ammonium, which under anoxic conditions could be supplied by the breakdown of sinking organic matter via heterotrophic denitrification. However, at many locations where anammox is measured, denitrification rates are small or undetectable. Alternative sources of ammonium have been proposed to explain this paradox, for example through dissimilatory reduction of nitrate to ammonium and transport from anoxic sediments. However, the relevance of these sources in open-ocean anoxic zones is debated. Here, we bring to attention an additional source of ammonium, namely, the daytime excretion by zooplankton and micronekton migrating from the surface to anoxic waters. We use a synthesis of acoustic data to show that, where anoxic waters occur within the water column, most migrators spend the daytime within them. Although migrators export only a small fraction of primary production from the surface, they focus excretion within a confined depth range of anoxic water where particle input is small. Using a simple biogeochemical model, we suggest that, at those depths, the source of ammonium from organisms undergoing diel vertical migrations could exceed the release from particle remineralization, enhancing in situ anammox rates. The contribution of this previously overlooked process, and the numerous uncertainties surrounding it, call for further efforts to evaluate the role of animals in oxygen minimum zone biogeochemistry.

anammox | denitrification | oxygen minimum zone | diel vertical migration

Water column oxygen minimum zones (OMZs), where oxygen concentrations plummet to submicromolar levels (1), are responsible for approximately one-third of the total removal of fixed nitrogen from the oceans (2, 3). Several processes mediated by specialized prokaryotes convert fixed inorganic nitrogen (NH_4^+ , NO_2^- , and NO_3^-) to N_2 in anoxic waters. Canonical denitrification, consisting of dissimilatory NO_3^- reduction to NO_2^- (DNRN) followed by the further oxidation of organic matter with NO_2^- (the denitrification step), was long considered the dominant fixed N removal pathway in anoxic waters. Over the last decade, anammox has gained attention as a major sink of fixed N in nearly anoxic waters ($\text{O}_2 < 10 \text{ mmol}\cdot\text{m}^{-3}$) (4, 5).

Stoichiometric considerations would suggest a close coupling between denitrification and anammox (6, 7). Under anoxic conditions, the NH_4^+ liberated by the remineralization of organic matter through DNRN and denitrification should accumulate in the water column because conventional (aerobic) nitrification cannot proceed. However, this accumulation is not observed in the cores of anoxic waters, where observed NH_4^+ concentrations are generally much less than $1 \text{ mmol}\cdot\text{m}^{-3}$ (8). In these regions, oxidation of NH_4^+ with NO_2^- by anammox is thought to be the major sink of NH_4^+ (9). Given that no significant NH_4^+ accumulation takes place in the cores of OMZs, the supply of NH_4^+ by denitrification must be completely consumed by its consumption via anammox. This would lead to $\sim 70\%$ of the total fixed nitrogen (N) removal occurring through denitrification, and about 30% from anammox, with some variability related to the stoichiometry of the organic matter respired (7, 10).

However, in situ measurements of denitrification and anammox in anoxic waters have in most cases failed to show a close coupling between these two biogeochemical pathways. While measurements of fixed N removal with isotopically labeled substrates show anammox occurring in many OMZs, denitrification appears to be patchier (11). In incubation experiments, anammox proceeds as soon as labeled NH_4^+ is added, while denitrification can sometimes lag by multiple days following the addition of organic matter (e.g., ref. 12). This suggests that anammox could proceed at low, uniform rates in anoxic waters, while denitrification could be intermittent in space and time, fueled by high organic matter input events (13). It is possible that, despite the local mismatch of observed rates, a stoichiometric balance between anammox and denitrification is realized as an average on large spatial and temporal scales (11). However, the current pool of measurements is not extensive enough to test this hypothesis by providing an integrated view of fixed N removal in the water column, and the observed decoupling between anammox and denitrification remains puzzling due to the cryptic ammonium source.

Alternative sources of NH_4^+ , other than the byproduct of DNRN and denitrification, could be responsible for some of this decoupling. Different biogeochemical pathways can supply NH_4^+ to anammox bacterial communities. These include dissimilatory nitrate reduction to ammonium (DNRA) (14), as well as diffusion and advection from sulfate-reducing sediments, or from microaerobic remineralization at the boundaries of anoxic waters. However, it is not clear whether DNRA, thermodynamically disfavored compared with DNRN and denitrification, is important in anoxic open waters, compared with sediments (15). Similarly, advection and diffusion of NH_4^+ can be relevant at the boundaries of anoxic layers, or where anoxic waters impinge on sulfidic sediments (8), but are of limited importance in the anoxic cores of

Significance

Nitrogen, the limiting nutrient for primary production across much of the ocean, is converted to biologically inactive N_2 by denitrification and anaerobic ammonium oxidation (anammox) in anoxic waters. Anammox requires an active source of ammonium, which can be provided by concurrent denitrification. However, anammox has been observed at high rates in the absence of denitrification, and the source of ammonium has remained cryptic. Using a combination of observations and models, we suggest that zooplankton and micronekton provide a missing source of ammonium to anoxic waters through diel vertical migrations, fueling anammox and decoupling it from denitrification. This previously overlooked mechanism can help to reconcile observations with theory and highlights the role of animals on ocean biogeochemistry.

Author contributions: D.B., A.R.B., and E.D.G. designed research; D.B., A.R.B., and E.D.G. performed research; D.B. analyzed data; and D.B., A.R.B., and E.D.G. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

See Commentary on page 15604.

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OMZs, which are characterized by weak circulation and mixing (16, 17), small NH_4^+ gradients (8), and undetectable oxygen concentrations over water layers hundreds of meters thick (1).

Here, we suggest that the excretion of NH_4^+ by diel vertically migrating animals could play an important role in the N cycle of OMZs, and contribute to the decoupling of anammox and denitrification. As shown in *DVM Association With Anoxic Waters*, diel vertical migrations (DVM) of zooplankton and micronekton commonly reach the anoxic layers of the major OMZs of the open ocean. Because animals excrete reduced N mostly as NH_4^+ , they can fuel anammox directly, and decouple it from denitrification. Here, we present a first assessment of this process.

The rest of the paper is organized as follows. In *DVM Association With Anoxic Waters*, we show the common occurrence of DVM across major OMZs by using acoustic data. In *DVM Effects on the N Cycle in Anoxic Waters*, we describe how the excretion of NH_4^+ by vertical migrators can alter the balance between fixed N removal pathways, enhancing anammox. In *Spatial Models of DVM Amplification of Anammox*, we outline the results of an idealized, spatially resolved model of the nitrogen cycle in anoxic waters, to estimate the potential for anammox amplification by DVM. Finally, in *Summary*, we discuss the implications for OMZ biogeochemistry.

DVM Association with Anoxic Waters

The balance of anammox and denitrification can be modified if vertically migrating organisms enter anoxic waters. Anaerobic reactions are generally thought to be inhibited in waters with more than 3–5 $\text{mmol}\cdot\text{m}^{-3}$ O_2 (7, 18). However, thresholds up to around 20 $\text{mmol}\cdot\text{m}^{-3}$ for anammox and DNRN (19) and around 40 $\text{mmol}\cdot\text{m}^{-3}$ for denitrification (20) have been reported, perhaps as a result of anoxic microenvironments within sinking aggregates. In the rest of the paper, we focus on waters with oxygen concentrations between 0 $\text{mmol}\cdot\text{m}^{-3}$ and 10 $\text{mmol}\cdot\text{m}^{-3}$, which are common in upper-ocean OMZs, and where DVM are observed.

We determined the depth of DVM by analyzing a global dataset of Acoustic Doppler Current Profiler (ADCP) measurements as described in ref. 21. ADCP data provide continuous, depth-resolved views of migrating sound-scattering layers, which can be integrated with in situ net data to obtain a comprehensive picture of migrating

animal communities (22–24). Our technique identifies the depth of the main DVM stationary depth, at which the strongest sub-ephotic sound scattering layer is centered during the daytime.

The data that we analyzed cover the three major open-ocean oxygen minima that host anoxic waters: the Northern Indian Ocean (Arabian Sea), the Eastern Tropical North Pacific (ETNP), and the Eastern Tropical South Pacific (ETSP) OMZs. When plotted against in situ oxygen profiles from these regions, the acoustic data show that migrators enter waters with the lowest measured oxygen concentrations (Fig. 1). This picture is broadly consistent with in situ net data, for example from the Arabian Sea and the ETNP, indicating diel migration of zooplankton and micronekton, including abundant euphausiids and myctophid fish, in and out of the oxygen-deficient layers (25–27).

We quantified the overlap of DVM and anoxic waters by mapping the minimum O_2 concentration observed at the depth of migration, as shown in Fig. 2. Where available, we used the direct DVM depth estimates from acoustic data from ref. 21. These regions are shown with dots in Fig. 2. In many areas where a direct estimate from acoustic data was not possible, we estimated the DVM depth using a multiple linear regression against hydrographic data (oxygen, surface chlorophyll, mixed layer depth, and temperature) as described in ref. 21. We used the O_2 data from the monthly World Ocean Atlas (WOA) climatology (28), after applying the correction of ref. 29 at low oxygen. Ideally, concurrent observations of O_2 and DVM depth should be used. However, the sparseness of synchronous O_2 profiles and acoustic ADCP data over the OMZs necessitates the use of climatological data. Because climatological data are likely to underestimate the extent of anoxic waters (29), the overlap of DVM and anoxic waters could be larger than shown in Fig. 2.

Little information is available on the distribution of migrators around their daytime migration depth. The DVM depths estimated in Fig. 2 (21) have an uncertainty of approximately ± 30 m over the regions considered. In addition, the acoustic data indicate thicknesses of the scattering layers of several tens of meters. To capture the potential for overlap between DVM and anoxia, in Fig. 2, we show the minimum O_2 concentrations found within a 50-m-thick layer centered at the migration depth.

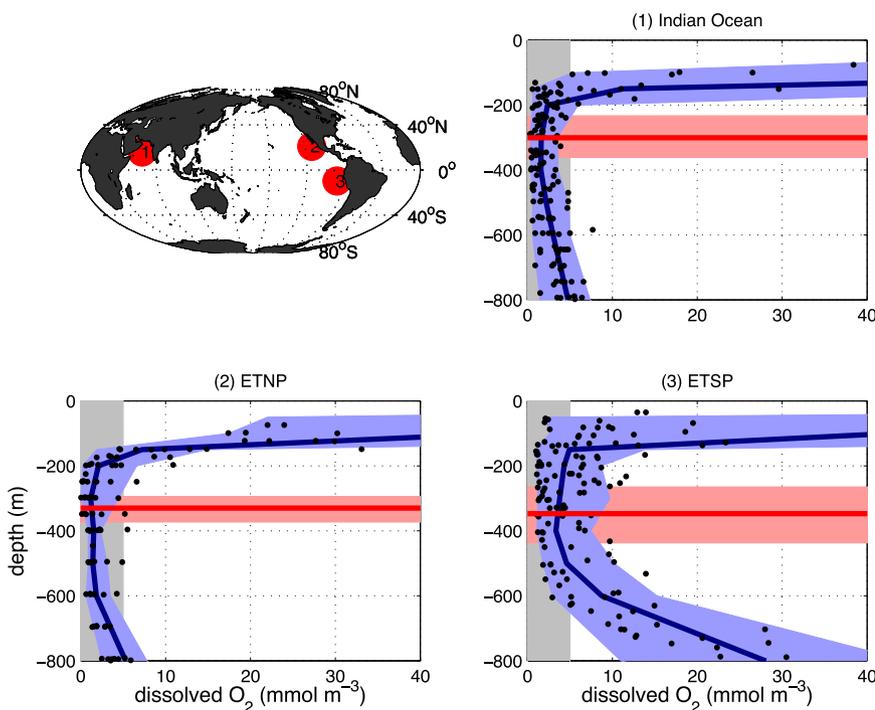


Fig. 1. Oxygen (millimoles per cubic meter) and DVM depths (meters) from the three major open-ocean anoxic zones shown in the map. The dots show in situ oxygen measurements from the Global Data Analysis Project dataset (45) sampled within 5×5 degree subregions (indicated in the map as red circles). For each region, the blue line shows the mean oxygen profile and the blue shadings show one SD around this mean. The red line shows the mean DVM depth and the red shading shows one SD around it. The gray shading indicates oxygen concentrations below $5 \text{ mmol}\cdot\text{m}^{-3}$.

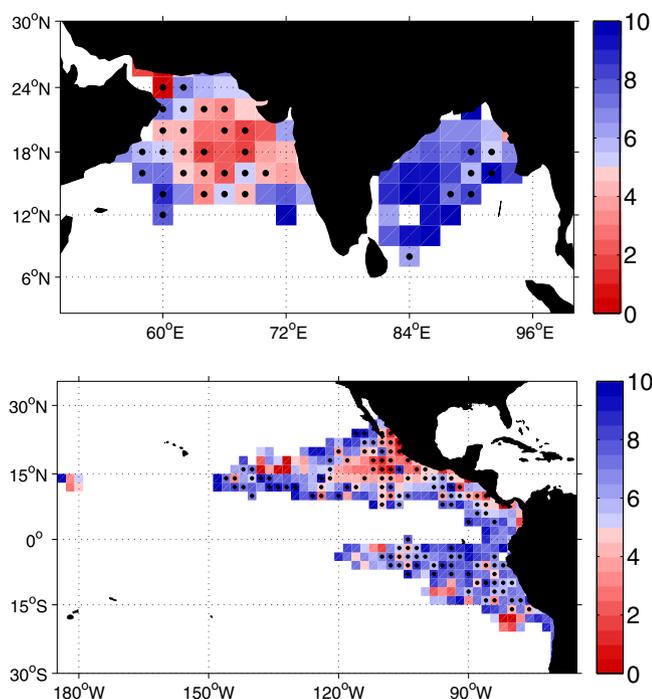


Fig. 2. Mean oxygen concentrations (millimoles per cubic meter) at the DVM depth in the cores of the oxygen minimum zones of (A) the Indian Ocean, and (B) the eastern tropical Pacific. OMZ cores are defined as $O_2 < 10 \text{ mmol m}^{-3}$. Averages over 2×2 degree areas are shown. Areas with and without dots show regions where the DVM depths were estimated from acoustic data and from the regression in ref. 21, respectively. Oxygen is from the monthly World Ocean Atlas climatology (28), corrected at low oxygen concentrations as in ref. 29.

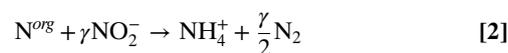
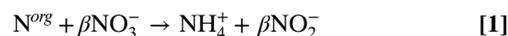
Fig. 2 suggests that over large swathes of the ocean's oxygen minima, migrators spend most of their time in anoxic or nearly anoxic waters. For example, in places where the local OMZ is $< 10 \text{ mmol m}^{-3}$, the average minimum O_2 within 50 m of the main DVM stationary depth is estimated as 5 mmol m^{-3} (Fig. 2). Given the uncertainties in the DVM depth estimate as determined by the acoustic method, and roundoff errors associated with the climatological O_2 concentrations, this is essentially consistent with the main DVM stationary depths lying within anoxic waters wherever they occur, consistent with observations (25–27). It is within these regions that an intensification of anammox by DVM could be anticipated.

DVM Effects on the N Cycle in Anoxic Waters

Typically, zooplankton and micronekton release fixed N mostly as NH_4^+ (70–80%), and the remaining (20–30%) as dissolved organic nitrogen, a combination of urea and primary amines (30). While urea may not be used directly for anammox, it is quickly converted to NH_4^+ by microbes (31, 32) and can thus fuel anammox indirectly. Primary amines, on the other hand, contain significant organic carbon and provide a substrate for heterotrophic processes, including denitrification and DNRN. For the purpose of anammox intensification, we consider in the model the additional input of NH_4^+ and urea by migrating animals, and express it in NH_4^+ units, noting that these compounds generally dominate N excretion (30).

We model the N cycle of anoxic waters using the set of equations for DNRN, denitrification, and anammox discussed, for example, in refs. 10 and 7. We focus on waters characterized by functional anoxia, which extend for hundred of meters in major OMZs (1). Thus, we ignore aerobic reactions, generally important only at the boundaries of anoxic waters. We further assume that

the nitrogen cycle of the OMZ is fueled by the remineralization of organic matter (Γ_{org}), for example, sinking particle aggregates, and by the local input of NH_4^+ by diel vertical migrations (Γ_{dvm}). The reactions can be described by the following equations:



Eq. 1 represents DNRN, Eq. 2 denitrification, and Eq. 3 anammox. The stoichiometric coefficients depend on the composition of organic matter. Following refs. 10 and 7, and adopting a bulk organic matter stoichiometry of C:H:O:N:P = 106:175:42:16:1, as in ref. 33, we use the approximate values $\beta = 14.8$, $\gamma = 9.8$, and $\chi = 1.3$.

We consider anammox in the water column to be limited by NH_4^+ availability, as generally observed in oceanic OMZs (34). We further assume that the system is in local steady state, with complete utilization of NH_4^+ and NO_2^- , and nonlimiting supply of NO_3^- . Partial utilization of NH_4^+ or NO_2^- could alter the balance of Eqs. 1–3, but this would not change the qualitative impacts of DVM. Furthermore, as discussed in previous studies, the effects of partial NO_2^- utilization are important only for large NO_2^- accumulation rates, which are not typical of OMZs (7, 10).

Under these assumptions, the fraction of fixed N removal that is due to anammox can be expressed as:

$$f^{\text{amx}} = \frac{1}{\left[1 + \frac{\gamma}{2} \frac{\beta - \chi}{\gamma + \beta}\right] (1 - r_{\text{dvm}}) + \left[1 - \frac{\gamma}{2} \frac{\chi}{\gamma + \beta}\right] r_{\text{dvm}}} \quad [4]$$

where

$$r_{\text{dvm}} = \frac{\Gamma_{\text{dvm}}}{\Gamma_{\text{org}} + \Gamma_{\text{dvm}}} \quad [5]$$

is the fraction of reduced N introduced by migrating organisms as NH_4^+ , relative to the total inputs of reduced N as NH_4^+ and organic nitrogen.

The equations show that the effect of the NH_4^+ injection by DVM raises the fraction of anammox above a baseline given by $r_{\text{dvm}} = 0$:

$$f^{\text{amx}} = \left[1 + \frac{\gamma}{2} \frac{\beta - \chi}{\gamma + \beta}\right]^{-1} \approx 0.27. \quad [6]$$

Thus, under steady-state conditions, with complete utilization of organic matter, NH_4^+ , and NO_3^- , $\sim 27\%$ of the N_2 produced would come from anammox, and 73% from denitrification. This is a well-known consequence of stoichiometry and is discussed among others in refs. 4, 7, 10, and 11.

In the presence of excretion by migrating organisms, the proportion of reduced N entering the system as NH_4^+ (r_{dvm}) is greater than zero, increasing the rate of anammox relative to denitrification, as shown in Fig. 3. For example, if the NH_4^+ input by DVM is comparable to the input by the breakdown of organic matter within anoxic waters ($r_{\text{dvm}} = 0.5$), the proportion of N_2 produced by anammox doubles from 27% to about 45%. If the NH_4^+ input is twice the organic N remineralization ($r_{\text{dvm}} = 0.66$), this proportion skews to about 60% anammox.

The NH_4^+ input by migrators is difficult to determine. One of the few studies that targeted N excretion by migrators (30) suggested that, at Bermuda Atlantic Time-Series Study in the subtropical North Atlantic, migrating organisms introduced a

combination of NH_4^+ and dissolved organic nitrogen into the mesopelagic zone (200–300 m depth) equivalent to 20–30% of the sinking flux of organic N. The maximum values of these inputs were much larger, and reached between 2 and 3.5 times the inputs by particles. Average active transports around 15–35% of the total organic matter input are commonly reported across the ocean (21). The inclusion of micronekton, in particular myctophid and other vertically migrating fish, which are abundant but often undersampled, would increase these fractions (21, 35).

Active transport studies focus on the total amount of organic matter exported to the ocean interior, and little information is available on the vertical profiles of respiration by migrators. While the attenuation of the particle flux is well described by a power-law decrease with depth, with a weaker attenuation in OMZs compared with well-oxygenated waters (36–38), the depths at which migrators respire are more uncertain. The simplest assumption is that NH_4^+ excretion peaks around the migration depth, and becomes quickly negligible below it. Therefore, the source of NH_4^+ by migrators could locally exceed particle remineralization, even if active export is much less than particle export at the surface (3). This can be illustrated by the following example. Consider the case in which DVM excretion is focused in a 100-m-thick layer between 200 and 300 m depth (a relatively shallow migration depth). Assuming a typical particle remineralization for the OMZ (e.g., an attenuation coefficient $b = -0.4$), about 10% of the particle flux from the surface will be remineralized in this layer. Thus, for DVM excretion to be as large as the breakdown of particles ($r_{dvm} = 0.5$), migrators only need to export the equivalent of about 10% of the particle flux. This would increase the local anammox fraction from 27% to about 45%. Larger DVM export fractions and deeper migrations would further enhance this effect. This example highlights the importance of the vertical distribution of remineralization and excretion, as well as the configuration of anoxic waters and the depths of migration. These effects are discussed in *Spatial Models of DVM Amplification of Anammox*.

Spatial Models of DVM Amplification of Anammox

Geometric factors should play an important role for the amplification of anammox by DVM excretion. The position of the upper boundary of anoxic waters and the depths of migration modulate the amount of export that reaches oxygen-deficient waters. Assuming that sinking particle fluxes decrease with depth due to respiration, deeper migrations would introduce NH_4^+ to

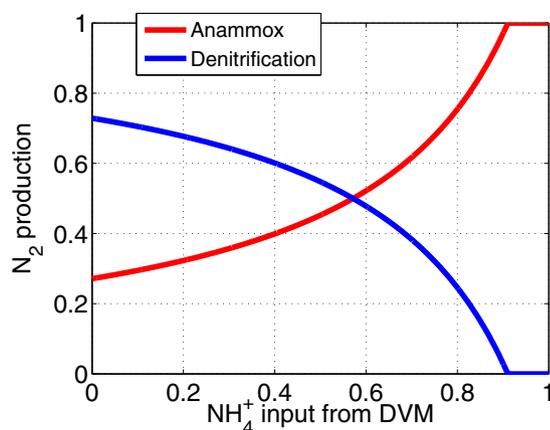


Fig. 3. Enhancement of anammox by NH_4^+ inputs from DVM. The y axis shows the fraction of N_2 production (fixed N removal) due to anammox (solid red line) and denitrification (solid blue line) relative to the total, as a function of the relative input of NH_4^+ by migrating organisms versus the total input of NH_4^+ from organic matter breakdown (e.g., sinking particles) plus NH_4^+ excretion. See Eq. 4.

waters with lower particle remineralization, resulting in a larger relative anammox amplification. Similarly, because of the stronger attenuation of particle fluxes by respiration in oxygenated waters compared with anoxic waters, for a given profile of DVM excretion, a deeper boundary of anoxic waters would reduce particle remineralization at depth, increasing the amplification of anammox.

To elucidate these effects, we combined them in an idealized, spatially resolved model of the N cycle in anoxic waters based on the steady-state equations of *DVM Effects on the N Cycle in Anoxic Waters*, and on a set of simple assumptions regarding the particle and DVM excretion fluxes. The role of this modeling exercise is not to provide a quantitative and detailed representation of the processes that take place in OMZs, but rather to (i) illustrate how the interplay between different aspects of particle and animal-mediated exports could alter the N cycle, enhancing anammox; (ii) indicate where we expect the amplification of anammox to be most important; and (iii) provide a first-order estimate of the magnitude of anammox amplification by DVM.

The model, similar to the one described in ref. 29, relies on the following assumptions. Particle export follows a power-law profile, with strong remineralization (exponent $b = -0.9$) in oxygenated waters, and weak remineralization ($b = -0.4$) in anoxic waters (36–38). The suboxic threshold is set at 5 $\text{mmol}\cdot\text{m}^{-3}$. We use the satellite-based monthly climatological particle export from ref. 39, and, for simplicity, we assume that active export due to DVM is a fixed proportion of it. In the following, we indicate the ratio between the active export and the particle flux with f_{dvm} , and we vary it across a range of values in line with observations.

The production of fecal pellets by migrating zooplankton above the euphotic zone is implicit in the particle flux used to force the model. For simplicity, the production of fecal pellets at depth is considered to be negligible. Fast gut clearing rates, on the order of less than a few hours (40), imply that fecal pellet production takes place mostly near the surface and during the downward migration, so that, at depth, excretion of dissolved N should dominate.

We assume that excretion takes place as NH_4^+ , and follows a profile consisting of a daytime excretion term, shaped as a Gaussian function centered at the migration depth, plus a migratory term uniformly distributed between the surface and the migration depth (21). The partitioning between the daytime and migratory terms is regulated by the depth of migration, and depends on the relative time spent by organisms at depth versus the time spent migrating (assuming a constant typical speed of 3 $\text{cm}\cdot\text{s}^{-1}$, and a day length of 12 h). The divergence of the particle and excretion fluxes (Γ_{org} and Γ_{dvm}) determines the local ratio (r_{dvm}) between the two NH_4^+ sources according to Eq. 5, which in turn determines the anammox fraction (f^{anm}) according to Eq. 4.

Because of its idealized nature, we use the model as an illustration and for scaling purposes. Nonetheless, as shown in Fig. 4, the model predicts anammox rates and vertical profiles that are similar to observations (8, 11). Many of the observed anammox rates can be reproduced by simulations with no DVM. However, including DVM increases the proportion of high anammox that can be reproduced. Other considerations, such as short-timescale variability not captured by our monthly climatologies, or increased organic matter cycling and additional processes at the oxic/anoxic interface (11), may contribute to the small number of very high observed anammox rates.

Without DVM, the model produces $\sim 60 \text{ TgN}\cdot\text{y}^{-1}$ of water column fixed N removal, partitioned as 73% denitrification and 27% anammox, consistent with previous results (2, 29), and with the expected stoichiometry of anaerobic reactions (10). As the proportion of active versus particle export (f_{dvm}) increases, anammox becomes more important, so that, for $f_{dvm} = 0.1, 0.2,$ and 0.5 , when averaged globally, anammox amounts to, respectively, 34%, 38%, and 51% of N_2 production. These proportions can be substantially higher (e.g., up to 75% for $f_{dvm} = 0.2$) in specific regions and at certain depth horizons.

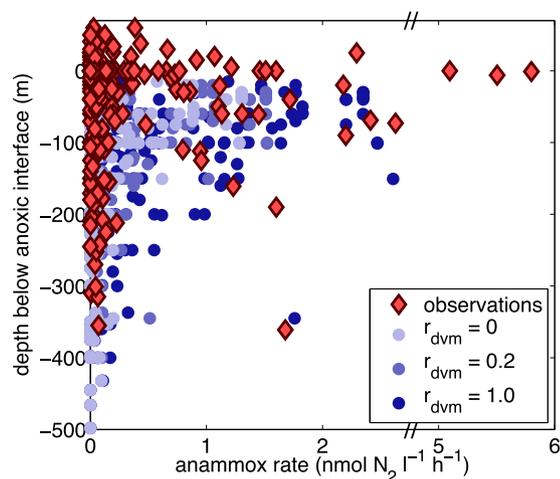


Fig. 4. Observed and modeled anammox rates in the Peru upwelling system. Observations (red diamonds) are from the data compilations described in refs. 8 and 11. Modeled rates (blue dots) are sampled at the same geographical locations as the observations. For the models, the shades of blue indicate the DVM export as a fraction of the particle export ($r_{dvm} = 0, 0.2$, and 1.0 , from light to dark blue, respectively). Note the break in the x axis.

Fig. 5C shows the expected amplification for DVM contributing 20% of particle export ($f_{dvm} = 0.2$), a typical if perhaps conservative value (21, 35). Rather than being equally distributed, the amplification is stronger in select areas of OMZs, including the northwestern margin of the ETNP, and the western margin of the ETSP. In these regions, the model predicts that anammox could be responsible on average for more than half of the N_2 production.

The geographical patterns of anammox amplification shown in Fig. 5C are due to the interplay of the anoxic waters distribution and the depths of migration (Fig. 5A and B). A stronger amplification is predicted in regions of deep DVM and deep anoxic waters, for example, the northern and northwestern boundaries of the anoxic zones in the ETNP and ETSP, respectively. Spatially varying fractions of export by DVM relative to sinking particles could also alter the patterns shown in Fig. 5C. While an average fraction of around 0.2–0.4 seems appropriate for eastern tropical and equatorial Pacific waters (3, 35, 41–43), little is known about its geographical and temporal variability, which could be influenced by, among other factors, the patterns of primary production and export, mesozooplankton and micronekton abundance, and the proportion of diel vertical migrators (3, 35).

Summary

The downward export of organic matter by migrating zooplankton and micronekton is generally smaller than that of particles at the base of the euphotic zone. However, sinking particles are rapidly consumed with depth, and the active transport by migrators can exceed particle remineralization in deeper layers where animals congregate during the daytime. As a result, inside anoxic waters, the excretion of NH_4^+ by vertically migrating animals could alter the balance between fixed N removal pathways, decoupling anammox and denitrification, and enhancing anammox above the values predicted by typical stoichiometry.

Based on an idealized biogeochemical model, for a typical mean active transport of about 20% of the particle fluxes, DVM could drive an increase of anammox from about 27% to about 40% when averaged over the entire anoxic domain. The models also suggest the effect may be larger in specific parts of the OMZ, depending on the magnitude of DVM export, the geometry of the anoxic zone, and the patterns of migration. In these regions, sustained by the direct NH_4^+ addition, anammox could become

even more important. This decoupling effect could help explain observed peaks in anammox with limited denitrification, patchiness in fixed N removal rates, and the rapid onset of anammox compared with denitrification in incubation experiments. In this respect, the introduction of NH_4^+ by vertical migrators adds to the complex series of concurrent N cycle processes, identified, for example, in shelf waters, that could decouple anammox and denitrification (8, 14).

Additional questions arise from the proposed amplification of anammox and, more generally, the impact of animals on subsurface water biogeochemistry. Despite decades of active research, the magnitude and spatial distribution of export by migrating animals are still very uncertain. In this study, we adopted constant global mean export fractions. However, it is clear that DVM-mediated fluxes vary regionally and temporally, and are modulated by a number of factors, including surface productivity and ecosystem composition. The vertical range over which this export is returned to the water column, a function of the distribution, behavior, and metabolism of animals within migrating layers, is an important albeit uncertain parameter that could affect the expression of animal-mediated processes.

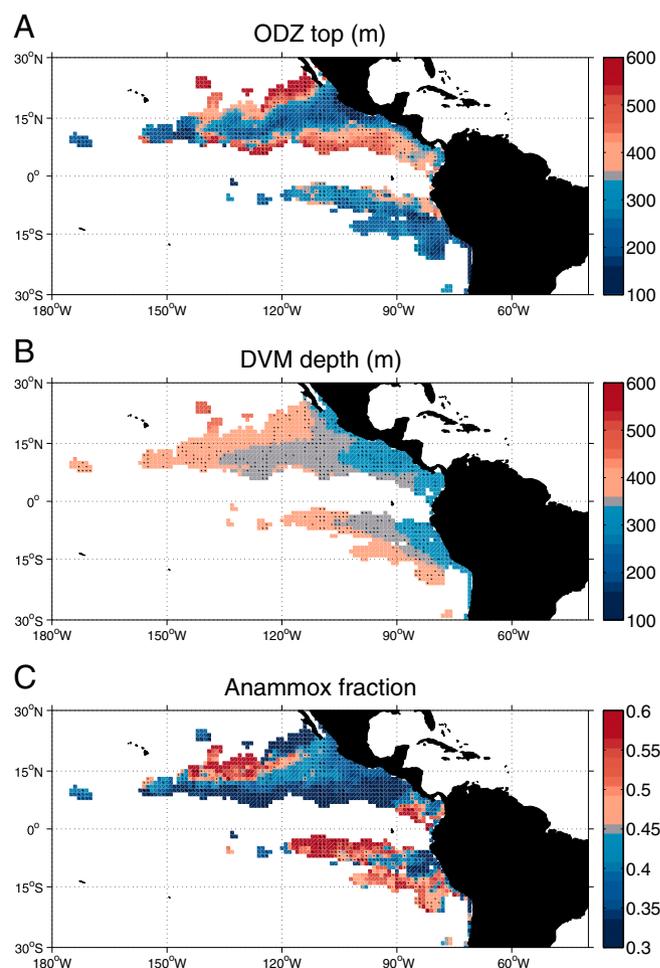


Fig. 5. Spatial distribution of anoxic depth, DVM depth, and anammox fraction from the eastern tropical Pacific. (A) Mean depth (meters) of the anoxic zone upper boundary, here defined with a $O_2 < 5 \text{ mmol} \cdot \text{m}^{-3}$ threshold; (B) mean DVM depth (meters) in the anoxic zone; and (C) mean modeled anammox fraction in the anoxic zone, for DVM export equal to 0.2 times the particle export. Oxygen is taken from WOA monthly climatologies (28), and corrected as in ref. 29. Areas with and without dots show regions where the DVM depths were estimated from acoustic data and from the regression in ref. 21, respectively.

Similarly, the production of fecal pellets at depth, and the dependence of metabolism and excretion on dissolved oxygen (44), should be further quantified.

Global models of the type described here and elsewhere (e.g., ref. 2) are useful in providing a synthesis of observations and in predicting N cycle changes due to natural and anthropogenic forcings. The possible impacts of animals on the N cycle of anoxic zones suggests that animal-mediated processes might be more important than appreciated for ocean biogeochemistry, and that they

should be given careful consideration in future generations of ocean biogeochemistry and Earth system models.

ACKNOWLEDGMENTS. The authors would like to thank Bess Ward for insightful comments, Rainer Kiko for discussing preliminary zooplankton observations from the Eastern Tropical South Pacific, and two anonymous reviewers for their thoughtful suggestions. D.B. was funded by the Canadian Institute for Advanced Research. Computational infrastructure was provided to E.D.G. by Compute Canada and the Canadian Foundation for Innovation. A.R.B. acknowledges funding from National Science Foundation Grant 1029951 awarded to Bess Ward.

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