

# A flux-based threshold for anaerobic activity in the ocean

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## Key Points:

- We show that a flux-based threshold for anaerobic activity in the ocean is consistent with observations at the global scale.
- Our diagnostic calculation uses global datasets to define the three major pelagic anoxic zones in a new way.
- The flux-based threshold is qualitatively different than a threshold based on the oxygen concentration.

## Abstract

Anaerobic microbial activity in the ocean causes losses of bioavailable nitrogen and emission of nitrous oxide to the atmosphere, but its predictability at global scales remains limited. Resource ratio theory suggests that anaerobic activity becomes sustainable when the ratio of oxygen to organic matter supply is below the ratio required by aerobic metabolisms. Here, we demonstrate the relevance of this framework at the global scale using three-dimensional ocean datasets, providing a new interpretation of existing observations. Evaluations of the location and extent of anoxic zones and a diagnostic rate of pelagic nitrogen loss are consistent with previous estimates. However, we demonstrate that the flux-based threshold is qualitatively different from a threshold based solely on the ambient oxygen concentration. Since the framework is feasible for application in global biogeochemical models, it represents a way forward for more dynamic, mechanistic predictions of anaerobic activity and nitrogen loss.

## Plain Language Summary

Where oxygen concentrations are sufficiently low in the ocean, nutrients are lost to the atmosphere because of specialized activity by microorganisms. Typically, biogeochemical models rely on the imposition of a threshold oxygen concentration to predict this activity. Here, we explain and demonstrate that an alternative threshold is more appropriate. The new threshold takes into account the flux of oxygen, rather than the concentration, as well as the flux of organic matter that is consumed by the microorganisms. We use global datasets to demonstrate that this threshold is relevant at the global scale. Since it is distinct from and more mechanistic than the typical oxygen concentration threshold, it may be used in global biogeochemical climate models to improve their ability to predict the loss of nutrients to the atmosphere and the impact on the climate system.

# 1 Introduction

Anaerobic activity in the pelagic ocean plays a critical role in global biogeochemical cycles. Denitrifying metabolisms remove bioavailable (“fixed”) nitrogen from the water column (Codispoti & Richards, 1976; Devol, 2008; B. B. Ward, 2013), potentially impacting rates of primary production (Oschlies et al., 2019). Some of this nitrogen is lost as nitrous oxide ( $\text{N}_2\text{O}$ ), a potent greenhouse gas with a warming potential 200x that of  $\text{CO}_2$  (Ciais et al., 2013). Deoxygenation of the oceans due to global warming may lead to expansion of the anoxic zones where these metabolisms occur, potentially providing feedbacks to climate change (Keeling et al., 2010; Ciais et al., 2013; Oschlies et al., 2018). Therefore, understanding and accurately predicting anaerobic microbial activity at global scales is important for understanding and predicting the evolution of the climate.

Both physical and microbial processes drive the formation of anoxic zones and rates of nitrogen loss. Permanently anoxic pelagic zones in the open ocean are characterized by the combination of high primary productivity at the surface from coastal upwelling and low ventilation of subsurface waters (Wyrski, 1962; Luyten et al., 1983; Paulmier & Ruiz-Pino, 2009). A portion of the organic matter produced at the surface sinks into these subsurface waters. Aerobic heterotrophic organisms of all sizes consume and respire this organic matter using oxygen. Because of the weak ventilation, the oxygen supply to these subsurface areas is less than that demanded by the organisms, and so oxygen is depleted to nanomolar or lower levels, excluding all but microorganisms. At some threshold, anaerobic activity becomes energetically favorable, and some microorganisms use nitrate, nitrite, or sulfate rather than oxygen as an electron acceptor to respire the residual organic matter (Zumft, 1997; Devol, 2008). A portion of this respiration transforms fixed nitrogen species into gaseous forms, some of which is lost to the atmosphere. Chemoautotrophic metabolisms, both aerobic and anaerobic, are also key players. In general, heterotrophs oxidize the carbon in organic substrates but release the nitrogen at the same oxidation state, which chemoautotrophs then oxidize. Chemoautotrophic anaerobic am-

monium oxidation (anammox) accounts for roughly a third of pelagic nitrogen loss (Koeve & Kähler, 2010; B. B. Ward, 2013; Babbín et al., 2014).

However, the thresholds that drive the transitions from aerobic to anaerobic metabolisms are not well understood. The lack of a theoretical underpinning inhibits the extrapolation of the dynamics driving the observed phenomena to diverse environments. A dynamical understanding of these thresholds is critical for accurate prediction of nitrogen loss because of the dynamic nature of the processes. Despite the persistence of some anoxic zones, microbial communities in or near anoxic zones experience frequent oscillations in oxygen supply because the supply is dominated by time-varying circulation (i.e. eddies and equatorial jets (Brandt et al., 2012; Pena-Izquierdo et al., 2015; Oschlies et al., 2018)). Observations and experimental evidence suggest that communities have likely adapted to this dynamic state with facultative capabilities, high oxygen affinity, and the ability to rapidly switch between aerobic and anaerobic respiration (F. J. Stewart et al., 2012; Kalvelage et al., 2015; Tiano et al., 2014; Bristow et al., 2016; Dalsgaard et al., 2014).

Resource ratio theory suggests that the transitions are controlled by the relative supply rates of oxygen to organic matter and other electron donors, and not strictly by the oxygen concentration (Tilman, 1982; Zakem et al., 2019). In previous work, we showed that for a given electron donor, the relevant threshold is the point where its supply rate relative to the oxygen supply rate meets the ratio required by aerobic metabolism (Zakem et al., 2019). Thus for the same low external oxygen concentration, respiration may be predominantly aerobic or predominantly anaerobic, depending on the supply rates. This provides a hypothetical explanation for why aerobic and anaerobic metabolism can apparently co-occur, in addition to within-particle anoxia and vertical mixing (Karl et al., 1984; Bianchi et al., 2018; Zakem et al., 2019). The framework applies to an aerobic and anaerobic pair competing for the same electron donor or to the activity of a facultatively aerobic population. In the complex microbial community, there are many competing metabolic demands for common substrates, such as the competition for ammonia by aerobic and

anaerobic ammonia oxidation, as well as potentially for each of the thousands of organic compounds. In principle, a different threshold of oxygen to electron donor supply characterizes each of these interactions (Dalsgaard et al., 2014). Though the community metabolism is more complex, we here use its simple, average stoichiometry to explore the first-order controls on anoxic zone formation.

With broad brush strokes, we aim to connect a recently proposed theoretical framework, developed with mechanistic descriptions of microbial metabolism (Zakem et al., 2019), to observations of the global ocean. We test the theory with a diagnostic approach, using data-based gridded estimates of the relevant fluxes. We calculate the threshold for anaerobic activity in three dimensions using a climatology of oxygen concentrations, an inverse model estimate of ocean circulation, and an inverse model estimate of the sinking particulate organic carbon (POC) flux. The results delineate the volume of the ocean in which anaerobic metabolism is ecologically sustainable. Although this allows us to quantify global nitrogen loss, the main goal here is not a new and improved map of anoxic zones or global denitrification rate estimate. Rather, our goal is to first demonstrate the broad consistency between theory and observations, and then to discuss how the flux-based threshold is qualitatively distinct from thresholds based on concentrations. We show that the framework may be utilized in dynamic global biogeochemical models to more mechanistically predict nitrogen loss.

## 2 Methods

### 2.1 Theory: The flux-based threshold for anaerobic activity in the ocean

Here, we derive an expression for the conditions that allow sustained anaerobic activity in the ocean. Previous work developed a theoretical model for the competition of aerobic and anaerobic metabolism (Zakem et al., 2019). The formulation accounts either for the literal competition between two obligate populations (one obligately aerobic, one obligately anaerobic), or for intracellular optimization for the more energetically favorable electron acceptor within one facultative population (Zakem et al., 2019). In

a chemostat environment, the outcome of the competition depends on the ratio of the supply rate of oxygen to the supply rate of a mutually required electron donor, such as an organic substrate or ammonium. The ratio of this supply relative the ratio demanded by the specified aerobic metabolism – a ratio of ratios, termed  $\phi$  (B. A. Ward et al., 2013; Dutkiewicz et al., 2014; Zakem et al., 2019) – determines whether a metabolism using an alternative electron acceptor can be sustained, even while the use of oxygen remains thermodynamically more efficient.

In the ocean environment, the physical transport of oxygen and organic substrate in three dimensions is relevant. The transports of each are decoupled because of the gravitational sinking of particulate organic matter. Using the metabolic descriptions in Zakem et al. (2019), we describe the rates of change of oxygen concentration ( $\text{mmol m}^{-3} \text{ O}_2$ ) and POC, defined as detritus  $D$  ( $\text{mmol m}^{-3} \text{ C}$ ), as:

$$\frac{\partial O_2}{\partial t} = \underbrace{-\rho_{O_2O} B_O}_{\text{microbial consumption}} - \underbrace{\nabla \cdot (\vec{u} O_2)}_{\text{advection}} + \underbrace{\nabla \cdot (\kappa \nabla O_2)}_{\text{diffusion}} \quad (1)$$

$$\frac{\partial D}{\partial t} = \underbrace{-\rho_{D_O} B_O - \rho_{D_N} B_N}_{\text{microbial consumption}} - \underbrace{\nabla \cdot (\vec{u} D)}_{\text{advection}} + \underbrace{\nabla \cdot (\kappa \nabla D)}_{\text{diffusion}} - \underbrace{\frac{\partial}{\partial z} w_s D}_{\text{sinking}} \quad (2)$$

where  $B_O$  and  $B_N$  ( $\text{mmol m}^{-3} \text{ C}$ ) are the biomasses of aggregate microheterotrophic aerobic and anaerobic functional type populations,  $\rho_{i_j}$  ( $\text{mol C mol C}^{-1} \text{ t}^{-1}$ ) is the specific uptake rate of substrate  $i$  by population  $j$ ,  $\vec{u}$  ( $\text{m t}^{-1}$ ) is the velocity,  $\kappa$  ( $\text{m}^2 \text{ t}^{-1}$ ) is the diffusion coefficient, and  $w_s$  ( $\text{m t}^{-1}$ ) is the sinking rate of POC. The microbial biomass may alternatively may be represented by one facultatively aerobic population (Zakem et al., 2019). For the pelagic subsurface, we assume that additional  $\text{O}_2$  consumed for the oxidation of dissolved organic matter, ammonia, and nitrite is implicitly represented in these two equations, because to first-order all key reductants are derived from the sinking flux of POC.

We are interested in evaluating the incoming (gross) flux of  $\text{O}_2$  to a water parcel. This is because it is possible for aerobic populations to deplete  $\text{O}_2$  to their limiting subsistence concentrations (Zakem et al., 2019), and thus the incoming supply is relevant

for the potential for anaerobic activity. Ultimately (below), we will neglect the outgoing oxygen flux from the water parcel. This is analogous to similar frameworks considering the depletion of inorganic nutrients by phytoplankton in the ocean surface (B. A. Ward et al., 2013; Dutkiewicz et al., 2014). Following Dutkiewicz et al. (2014), we approximate Eqns 1 and 2 by decomposing the physical transport into the three-dimensional gross incoming flux  $I$  ( $\text{mmol m}^{-3} \text{ t}^{-1}$ ) and the gross outgoing flux  $O$  ( $\text{mmol m}^{-3} \text{ t}^{-1}$ ) as

$$\frac{\partial O_2}{\partial t} = -\rho_{O_2O} B_O + \underbrace{I_{O_2}}_{\text{adv + diff in}} - \underbrace{O_{O_2}}_{\text{adv + diff out}} \quad (3)$$

$$\frac{\partial D}{\partial t} = -\rho_{D_O} B_O - \rho_{D_N} B_N + \underbrace{I_D}_{\text{adv + diff + sink in}} - \underbrace{O_D}_{\text{adv + diff + sink out}} \quad (4)$$

Assuming the steady state of Eqn. 3, which is a good first-order assumption for permanent anoxic zones (with additional complexity arising from time-varying circulation as we discuss below), we can approximate the biomass associated with aerobic metabolism as

$$B_O = \frac{1}{\rho_{O_2O}} (I_{O_2} - O_{O_2}) \quad (5)$$

Plugging Eqn. 5 into the steady state version of Eqn. 4 gives an expression for anaerobic consumption as

$$\rho_{D_N} B_N = -\frac{\rho_{D_O}}{\rho_{O_2O}} (I_{O_2} - O_{O_2}) + (I_D - O_D) \quad (6)$$

Therefore, for anaerobic biomass to be sustained ( $B_N > 0$ ), the right-hand-side of Eqn. 6 must be positive, and so

$$\frac{\rho_{D_O}}{\rho_{O_2O}} \frac{(I_{O_2} - O_{O_2})}{(I_D - O_D)} < 1 \quad (7)$$

for sustained anaerobic activity.

We label the left-hand-side of the conditional statement as  $\phi$ . Redox chemistry links the uptake rates of oxygen and organic carbon, and so we represent them with ratio  $r = \frac{\rho_{O_2O}}{\rho_{D_O}}$  (mol  $\text{O}_2$  consumed per mol C consumed). In the environment,  $r$  represents the requirements for aerobic oxidation by the aggregated heterotrophic microbial community, and is similar to the ‘respiratory quotient,’ the amount of  $\text{CO}_2$  produced per mol  $\text{O}_2$  respired (Williams & del Giorgio, 2005; Robinson, 2008).

We make two further simplifications. First, analogous to depleted inorganic nutrients in the surface (Dutkiewicz et al., 2014), we neglect the outgoing supply of  $O_2$  from the water parcel. This is because in regions of interest – at the boundary where anaerobic metabolism becomes viable – oxygen is relatively low and likely to be consumed locally. We cannot neglect the outgoing supply of POC because its sinking happens at timescales similar to or greater than the timescales of microbial growth, and thus sinking right through a water parcel of interest is likely, preventing its complete depletion at any one location. This gives  $\phi$  as

$$\phi = r^{-1} \frac{I_{O_2}}{I_D - O_D} \quad (8)$$

Second, we make the assumption that the three-dimensional divergence of the POC flux ( $I_D - O_D$ ) is dominated by the sinking flux  $F_{POC}$  ( $\text{mmol C m}^{-2} \text{ t}^{-1}$ ), and thus that

$$\phi = r^{-1} \frac{I_{O_2}}{\nabla \cdot F_{POC}} \quad (9)$$

144 where  $\nabla \cdot F_{POC}$  ( $\text{mmol C m}^{-3} \text{ t}^{-1}$ ) is the divergence of the sinking flux of POC.

145 The critical threshold is  $\phi = 1$ . When  $\phi < 1$ , the ratio of oxygen supply to avail-  
 146 able oxygen to organic matter is lower than the ratio of demand by the aerobic metabolism,  
 147 and the anaerobic metabolism is sustainable. When oxygen is supplied in abundance,  
 148 aerobic metabolism can competitively exclude the anaerobic metabolism, and only oxy-  
 149 gen will be used to oxidize the electron donor. When the oxygen supply drops below the  
 150 amount required for aerobic oxidation, the anaerobic metabolism can access a portion  
 151 of the electron donor. In this regime of sustained coexistence, the ratio of aerobic to anaer-  
 152 obic activity is proportional to the ratio of the supply of oxygen to electron donor. Be-  
 153 cause of this coexistence, the zone designated by the threshold  $\phi = 1$  represents an up-  
 154 per bound on the zone of anaerobic activity.



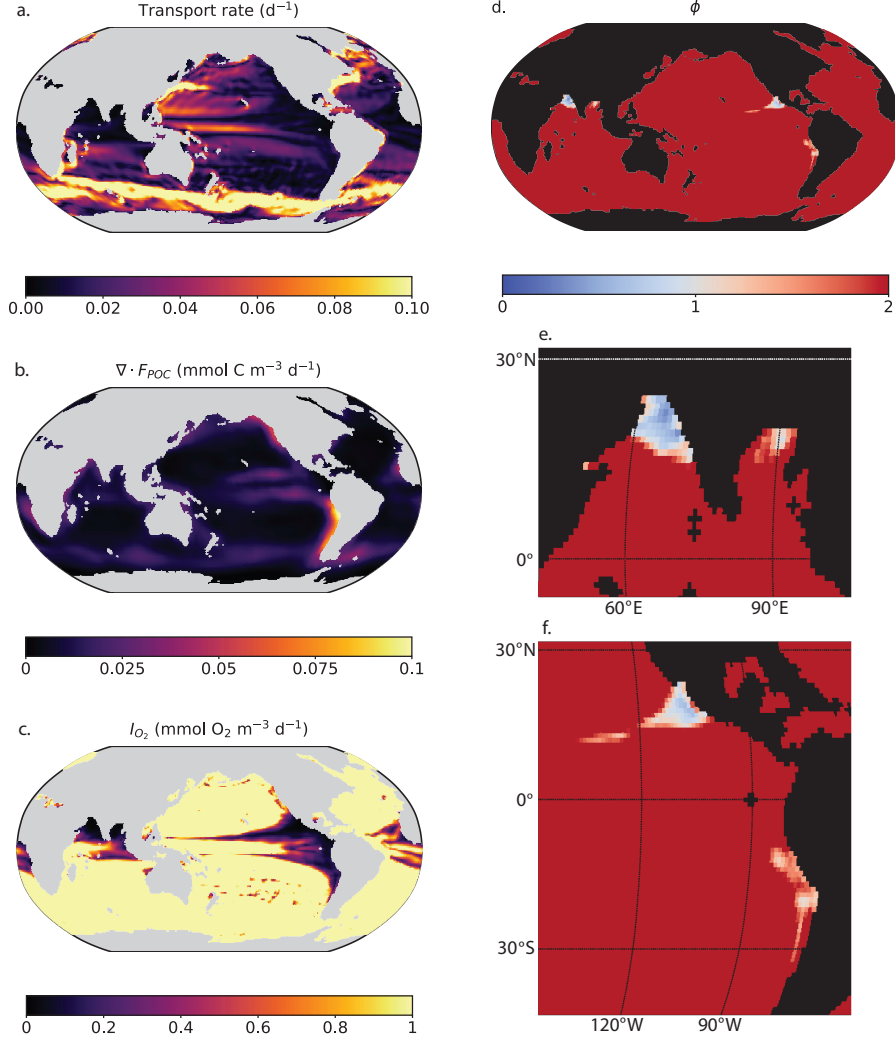
## 2.2 Data-based calculation of $\phi$

We use data-based estimates of oxygen supply, the particulate organic carbon flux, and the metabolic requirements of the bulk heterotrophic microbial community to evaluate  $\phi$  in three dimensions in the ocean (Fig. 1).

We calculate the incoming oxygen flux  $I_{O_2}$  ( $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ ) from ocean circulation and oxygen concentrations. For the circulation, we use the Ocean Comprehensible Atlas (OCCA) state estimate of the annual mean ocean circulation ( $1^\circ \times 1^\circ$  horizontal resolution with 50 depth levels; Forget (2010)) using routines similar to Lauderdale et al. (2016) (see code). OCCA provides a dynamically plausible inverse estimate of advective and diffusive flows using an adjoint method. We include the impact of along-isopycnal eddy transport and mixing in the calculation of gross (incoming) transport rates (Fig. 1a).

For oxygen concentrations, we use the World Ocean Atlas 2013 version 2 climatology of dissolved oxygen concentration (Garcia et al., 2013) ( $1^\circ \times 1^\circ$  horizontal resolution with 102 depth levels), incorporating the correction scheme of Bianchi et al. (2012) for the systematic overestimate of  $\text{O}_2$ . Global standard error is 2%, but error increases for lower oxygen concentrations. We account for the 12% error of the concentrations less than  $10 \mu\text{M}$ . This does not account for sampling bias that also contributes to a systematic overestimate of  $\text{O}_2$  in anoxic zones in particular. We interpolate the oxygen climatology to match the vertical resolution of the transport, and then compute  $I_{O_2}$  as the sum of all incoming fluxes of oxygen at the faces of each grid box (Fig. 1b).

We estimate the divergence of the organic matter flux  $\nabla \cdot F_{POC}$  ( $\text{mmol C m}^{-3} \text{ d}^{-1}$ ) using the three-dimensional gridded estimate of the POC flux from the inverse model of Schlitzer (2002) (experiment C). The model is on a non-uniform horizontal grid varying from  $1^\circ$  to  $3^\circ$  resolution with 21 depth levels (beginning at 133 m), and has a global export flux of about  $10 \text{ GtC yr}^{-1}$  (Schlitzer, 2002). We interpolate the values on the non-uniform horizontal grid to the uniform  $1^\circ \times 1^\circ$  grid of the oxygen flux, and retain the depth resolution. Uncertainty in the POC fluxes ranges from 20% to 35%, although the low-



**Figure 1.** The flux-based criteria for anaerobic activity  $\phi$  and its components at 270m depth: (a) the bulk gross (incoming) transport rate of oxygen, analogous to a chemostat dilution rate for each water parcel (calculated as  $I_{O_2}[O_2]^{-1}$ ) (b) the incoming flux of oxygen  $I_{O_2}$ , (c) the divergence of the sinking POC flux  $\nabla \cdot F_{POC}$  from the inverse model of Schlitzer (2002), and (d) resulting  $\phi$  (Eqn. 1), with the colorbar saturated at  $\phi = 2$  to emphasize the threshold  $\phi = 1$ . Panels (e) and (f) zoom in on the zones of viable anaerobic metabolism.

est uncertainties are associated with the depths relevant to our conclusions (200-800m) (Schlitzer, 2002). To overestimate the uncertainty at these depths, we incorporate the midpoint of 28% when propagating the errors. We consider the resulting divergence as a coarse estimate of the available organic carbon (Fig. 1c).

The ratio of demand  $r$  reflects the chemical composition and stoichiometry of the organic matter being respired as well as the bulk growth efficiency of the heterotrophic microbial community (Williams & del Giorgio, 2005; Robinson, 2008). We expect  $r$  to vary spatially and temporally with changes in community structure and function (Moreno et al., 2020), although  $r$  on average may be relatively stable (Tanioka & Matsumoto, 2020). Here, we use the respiratory quotient for average algal material of 0.9 mol CO<sub>2</sub> per mol O<sub>2</sub> (Williams & del Giorgio, 2005), and incorporate a 10% uncertainty.

We evaluate  $\phi$  in three dimensions using Eqn. 9. We interpolate the incoming oxygen supply to the depth resolution of the POC divergence. Our final calculation has a horizontal resolution of 1°x1° and 20 vertical levels, with resolution in depth increasing from about 100 m to 500 m. The shallowest resolved depth is 176 m. We calculate upper and lower bounds for  $\phi$  and N loss with propagation of error assuming linear (Taylor) expansion, incorporating an overall uncertainty of 32%.

### 3 Results and Discussion

Our data-based calculation of  $\phi$  allows us to identify zones favorable for anaerobic metabolism in the water column as a function of the relative supply rates of oxygen and organic matter. Locations where  $\phi < 1$  should coincide with anaerobic activity and N loss within limits of uncertainties.

#### 3.1 The 3D calculation identifies major anoxic zones

Fig. 1 shows  $\phi$  and its components in the global ocean at 270 m depth. The incoming transport rate (calculated as  $I_{O_2}[O_2]^{-1}$ ) is analogous to a chemostat dilution rate for each location, representing the rate of supply of oxygen (Fig. 1a). Transport is low

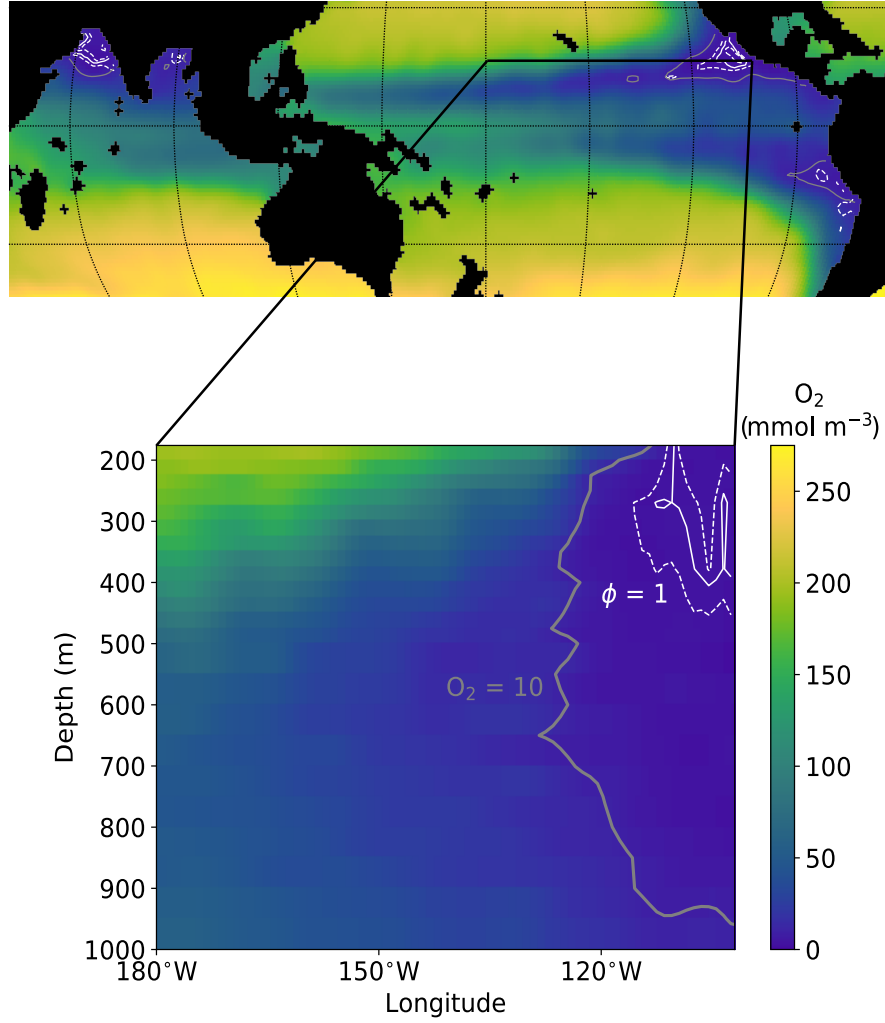
at low latitudes along the eastern continental boundaries. In idealized gyre circulation theory, these are the ‘shadow zones’ that are not ventilated by access to the nearby surface (Luyten et al., 1983). Thus the incoming flux of oxygen is minimal in these zones (Fig. 1b). Simultaneously, the POC flux and its divergence (i.e., the inferred consumption of POC at that location) is high in these areas because of the characteristic upwelling along eastern boundaries fuels surface production, subsequently fueling deep communities with abundant organic substrate (Fig. 1c).

Values of  $\phi$  reach one or below at the locations known to have permanent anoxia (Fig. 1d). Both the high values of the POC divergence and the low values of the incoming oxygen flux contribute to the low values of  $\phi$ . The contour  $\phi = 1$  (white line) in Fig. 2 identifies the three main pelagic anoxic zones: the Eastern Tropical North and South Pacific (ETNP and ETSP) zones, and the northern Arabian Sea (Devol, 2008; Ulloa et al., 2012). In these areas, POC availability exceeds the supply of oxygen necessary to oxidize all of it aerobically.

Thus, our  $\phi$ -based identification of the zones where anaerobic metabolism is viable coincides with those inferred from a threshold oxygen concentration. Empirical identification utilizes measurements of oxygen concentration, or more directly, anaerobic microbial activity. Nevertheless, the extent of the zones calculated with  $\phi = 1$  also reflects underlying uncertainties associated with the different components of our calculation. We discuss these uncertainties in the next section.

### 3.2 Estimation of global N loss

Using the resulting  $\phi$  and the POC divergence, we can estimate the amount of bioavailable nitrogen lost via anaerobic activity. If all of the organic matter consumed in the volume with  $\phi \leq 1$  were oxidized anaerobically, assuming the bulk estimate denitrification remineralization ratio  $r_{denitr}^{N:C}$  of 104:106 of Gruber and Sarmiento (1997), a calculated average of 42 Tg N yr<sup>-1</sup> would be lost from the ocean globally, with an uncertainty

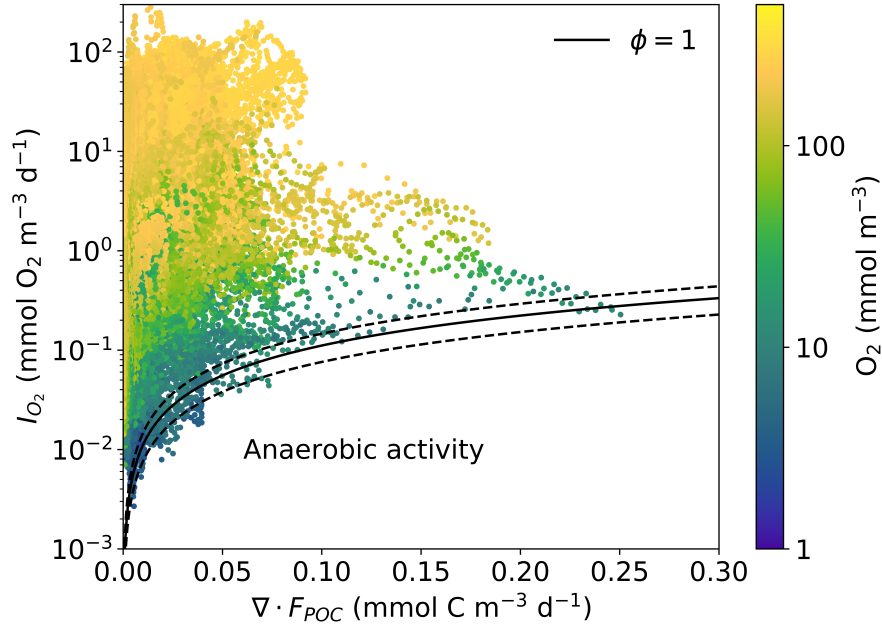


**Figure 2.** Data-based estimate of the zones of favorable anaerobic activity. The white line designates  $\phi = 1$  (with uncertainty bounded by dashed white lines), overlaid on a climatology of dissolved oxygen concentrations (Garcia et al., 2013). For comparison, the grey line designates the contour  $[O_2] = 10 \text{ mmol m}^{-3}$ . Top: At 270 m depth. Bottom: At 17°N in the eastern Pacific ocean.

range of 17–102 Tg N yr<sup>-1</sup>. The ratio  $r_{denitr}^{N:C}$  implicitly accounts for the amount of nitrogen that would be lost via the combination of heterotrophic denitrification and anammox, since it accounts for the complete oxidation of the organic carbon and nitrogen.

This estimate is consistent with, though at the lower end, of other estimates of global denitrification in the pelagic ocean, which range from 65–150 Tg N yr<sup>-1</sup> (Galloway, 2004; Codispoti, 2007; Gruber, 2008; Bianchi et al., 2012; DeVries et al., 2013; Somes et al., 2013; Martin et al., 2019). Recent estimates using global models show a narrower and lower range, from 50 to 80 Tg N yr<sup>-1</sup> (DeVries et al., 2013; Somes et al., 2013; Martin et al., 2019).

Our estimate is highly uncertain for multiple reasons. First, there are large, unquantified uncertainties in the underlying datasets: the oxygen climatology is most certainly an overestimate in low oxygen regions due to sampling bias and sparsity, contributing to higher  $\phi$  and lower N loss, and much of the time-varying circulation dominating the dynamics in the anoxic zones is not represented in the 1°x1° circulation climatology. Second,  $\phi = 1$  represents a threshold for the viable, stable co-existence of anaerobic metabolism, not necessarily the onset of dominant anaerobic activity. Where  $\phi \approx 1$  at the periphery of the zones, a significant fraction of organic carbon and reduced nitrogen may still oxidized aerobically. Thus, when calculated accurately,  $\phi = 1$  can be interpreted as an upper bound on the volume in which anaerobic activity is dominant. Third, the calculation does not account for any systematic changes in parameter  $r$  due to changes in the average heterotrophic growth efficiency. If the average growth efficiency decreases with depth, for example, as the quality of organic substrate decreases, then  $r$  will increase, and the anaerobic domain will be larger for the same nutrient fluxes. Fourth, the actual anaerobic domain is broader because of the persistence of anaerobic activity in unsustainable locations because of vertical mixing (such as in the oxycline (Zakem et al., 2019)) and within-particle anoxia (Karl et al., 1984; Bianchi et al., 2018). Indeed, Bianchi et al. (2018) estimated that particle anoxia amidst higher ambient oxygen con-



**Figure 3.** Resource ratio diagram of the delineation of favorable anaerobic activity in the ocean using  $\phi = 1$ . Incoming oxygen flux  $I_{O_2}$  is plotted against the divergence of the sinking POC flux  $\nabla \cdot F_{POC}$  for all grid points in the ocean at 176 m depth and below ( $1^\circ \times 1^\circ$  horizontal resolution with 20 depth levels). Color indicates the oxygen concentration.

centrations may double pelagic denitrification. However, the utility of our calculation is not providing a new number for global N loss, but rather, demonstration that the flux-based framework can identify regions of persistent anaerobic metabolism.

### 3.3 Organization of the ocean by resource supply ratios: a dynamic threshold

We use the components of  $\phi$  to assemble a resource ratio diagram for aerobic vs. anaerobic microbial metabolism in the ocean (Fig. 3) (Tilman, 1982). The incoming oxygen flux  $I_{O_2}$  is plotted against the divergence of the sinking POC flux  $\nabla \cdot F_{POC}$  at each of the grid points, with the color indicating the corresponding oxygen concentration. The line  $\phi = 1$  delineates the flux ratio space in which anaerobic activity is favorable.

This illustrates how the multifactorial flux-based threshold controls anaerobic activity. For a given rate of oxygen supply, anaerobic activity may or may not be favorable. As organic matter availability increases, more oxygen is required to maintain exclusively aerobic activity.

The overall pattern in Fig. 3 is similar to that of a prognostic biogeochemical model (Fig. A2 in Zakem et al. (2019)). However, for high POC divergences in Fig. 3, the supply ratios from low oxygen environments loosely track the  $\phi = 1$  line. This reflects in part that observed oxygen concentrations were used as one of the constraints in the adjoint method producing the POC flux (Schlitzer, 2000, 2002). Thus the POC flux and  $O_2$  climatology are not entirely independent, although  $O_2$  was only one of eight datasets used as a constraint (Schlitzer, 2002). Despite this correlation, our conclusions remain robust because we are showing that a novel arrangement of observed quantities is consistent with the theoretical framework, rather than making a quantitative prediction. Furthermore, in only a handful of locations does the oxygen concentration reach below 1  $\mu M$  in the climatology. If oxygen concentrations in the climatology reached the measured nanomolar concentrations (Revsbech et al., 2009), we would expect more points with  $\phi \ll 1$  to fill the bottom third of the diagram (as in Fig. A2 in Zakem et al. (2019)).

### 3.4 The flux-based threshold vs. oxygen concentrations

Though broadly consistent, the flux-based threshold for the onset of anaerobic microbial activity is qualitatively different from a threshold based on the external oxygen concentration. To demonstrate, we compare the  $\phi = 1$  contour (white line) to the  $[O_2] = 10 \mu M$  contour (grey line) along a transect through the Eastern Tropical North Pacific anoxic zone (Fig. 2). The shape of the two contours is different: the  $\phi = 1$  area sits higher up in the water column. Unfortunately, the resolution and lower limit of the oxygen climatology do not allow us to compare the contours using the nanomolar concentrations of oxygen known to designate anoxic zones (Revsbech et al., 2009).



The difference in the  $\phi = 1$  and  $[\text{O}_2] = 10 \mu\text{M}$  contours reflects that the flux-based threshold changes with depth despite consistently low ambient oxygen concentrations, according to the underlying data. This implies a possibility that in the real ocean, some deeper portions of pelagic anoxic zones may exhibit a higher frequency of aerobic activity amidst low oxygen concentrations. Higher in the water column, the POC flux (and divergence) is higher, and so anaerobic activity is favorable. Lower in the water column, where the POC flux has attenuated, anaerobic activity may be no longer favorable. Thus, some deep regions of anoxic zones may contain predominantly aerobic respiration of organic matter, ammonium, and nitrite.

## 4 Outlook

In the diagnostic calculation, microbial activity is implicitly represented. The divergence of the POC flux is due to heterotrophic microbial consumption, and the oxygen concentrations used to calculate the oxygen supply are low also because of heterotrophic consumption. Thus, the datasets contain correlations because these underlying processes are intertwined (i.e. the consumption of organic matter and oxygen). Here, we use resource ratio theory to reveal these correlations and consistencies through a new lens.

Technically, of course, it *is* the oxygen concentration that microorganisms detect. However, according to resource competition theory, the concentrations are set by the physiological traits and ecological characteristics of the microorganisms themselves (F. M. Stewart & Levin, 1973; Tilman, 1982; Zakem & Follows, 2016). These resource subsistence concentrations dictate the outcome of competition for substrate, while the substrate fluxes structure the community (B. B. Ward et al., 2008; Babbitt et al., 2014; Zakem et al., 2019).

Application of our framework to prognostic biogeochemical models is the ultimate goal. Why did we here opt for the diagnostic calculation instead of a prognostic ecosystem model to demonstrate the flux-based threshold? Presently, our biogeochemical models are riddled with many uncertainties in parameterizations to accurately estimate global N loss without tuning or incorporating data-based constraints. The parameterization of

the sinking organic matter flux in particular remains limited. In contrast, the diagnostic calculation allows us to demonstrate the relevance of the flux-based framework directly and transparently.

A fully prognostic ecosystem model resolves the consumption of substrate and subsequent growth and respiration by the heterotrophic populations. Consumption of oxygen by aerobic functional types depletes oxygen and creates the niche for the anaerobic types. A biogeochemical model that resolves the biomass of these functional types thus would allow quantification of the coexistence of aerobic and anaerobic activity (Zakem et al., 2019). Furthermore, such a model with a sufficiently high resolution circulation (eddy-permitting) would allow for the investigation of how time-varying circulation impacts the competitive outcomes. Specifically, competitive exclusion of anaerobic metabolisms when oxygen is replete requires a sufficient number of growth cycles. Therefore, intermittent supply of oxygen at timescales on par or shorter than microbial growth timescales may inhibit competitive exclusion and allow anaerobic metabolisms to persist in more oxygenated conditions, expanding the anaerobic domain.

Other studies have used the geochemical indicator  $N^*$  to estimate global pelagic nitrogen loss (Gruber & Sarmiento, 1997; Deutsch et al., 2001). Our estimate of 42 Tg N yr<sup>-1</sup> (range 17–102 Tg N yr<sup>-1</sup>) is somewhat quantitatively consistent with extrapolation using this method ( $65 \pm 20$  Tg N yr<sup>-1</sup>; Gruber (2008)). Each method has its advantage.  $N^*$  indicates where nitrate concentrations are lower than an assumed proportionality to phosphate concentrations, since nitrate and phosphate on average are coupled in the ocean due to universally similar biological requirements. Unlike  $\phi = 1$ ,  $N^*$  in principle represents the actual loss of fixed nitrogen without the implicit overestimate due to stable coexistence. Also, the climatologies of nitrate and phosphate concentrations are more accurate than that of oxygen in anoxic zones, and so  $N^*$  is not influenced by an oxygen sampling bias at low concentrations. However,  $N^*$  does not precisely estimate the locations of fixed N loss because physical transport disperses the waters with

depleted nitrate, and furthermore, N fixation confounds the signature. Thus  $\phi$  may more precisely identify the geography of N loss.

The flux-based threshold represents a mechanistic description of the transition from aerobic to anaerobic activity. Ultimately, accounting for anaerobic activity in this way in global biogeochemical models can improve our understanding and predictions of nitrogen loss. Coupled with accurate resolution of organic matter dynamics and physical transport, this can improve our understanding and predictions of anaerobic microbial feedbacks to changes in climate.

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