

Supplementary Information: Stable aerobic and anaerobic coexistence in anoxic marine zones

Zakem et al.

1 **Appendix 1: Derivation of ϕ**

2 The concentration of aerobic biomass from the steady state balance of Eqn. T4 ($\frac{dO_2}{dt} = 0$) is:

$$B_O = \frac{D}{\mu_O} (O_{2in} - O_2^*) y_{O_2} \quad (\text{A1})$$

3 Thus, for aerobic biomass to exist, $O_{2in} > O_2^*$.

4 The relationship of the steady state biomasses of both the aerobic and anaerobic populations from

5 Eqn. T3 ($\frac{dOM}{dt} = 0$) is:

$$0 = D(OM_{in} - OM_N^*) - \frac{1}{y_{OM_O}} \mu_O B_O - \frac{1}{y_{OM_N}} \mu_N B_N \quad (\text{A2})$$

6 The organic matter subsistence concentration for anaerobic biomass OM_N^* is the relevant subsistence

7 concentration for this expression, since we are working towards an expression for the coexistence

8 of both populations, and this is the larger. (If $OM_{in} < OM_N^*$ and $OM_{in} \geq OM_O^*$, aerobic but

9 not anaerobic biomass can accumulate.) Since $\mu = D$ at steady state in the chemostat, further

10 simplification can be made for the chemostat, but we retain these values in order to later extend the

11 expression to natural environments.

12 Plugging Eqn. A1 into Eqn. A2, rearranging gives an expression for anaerobic biomass:

$$B_N = y_{OM_N} D(OM_{in} - OM_N^*) - \frac{y_{OM_N}}{y_{OM_O}} D(O_{2in} - O_2^*) y_{O_2} \quad (\text{A3})$$

Thus, for anaerobic biomass to exist,

$$0 < D(OM_{in} - OM_N^*) - \frac{y_{O_2}}{y_{OM_O}} D(O_{2in} - O_2^*) \quad (\text{A4})$$

$$\frac{y_{O_2}}{y_{OM_O}} D(O_{2in} - O_2^*) < D(OM_{in} - OM_N^*) \quad (\text{A5})$$

$$\frac{y_{O_2}}{y_{OM_O}} \frac{D(O_{2in} - O_2^*)}{D(OM_{in} - OM_N^*)} < 1 \quad (\text{A6})$$

13 In the main text, we label the LHS expression as ϕ , and thus the threshold $\phi = 1$ is relevant for
 14 identifying the domain of coexistent aerobic and anaerobic biomass. We also use r to represent the
 15 ratio of oxygen to organic matter demand: $r = y_{OM_O} y_{O_2}^{-1}$ (mol O_2 utilized per mol OM utilized),
 16 and so:

$$\phi = \frac{D(O_{2in} - O_2^*)}{D(OM_{in} - OM_N^*)} r^{-1} \quad (\text{A7})$$

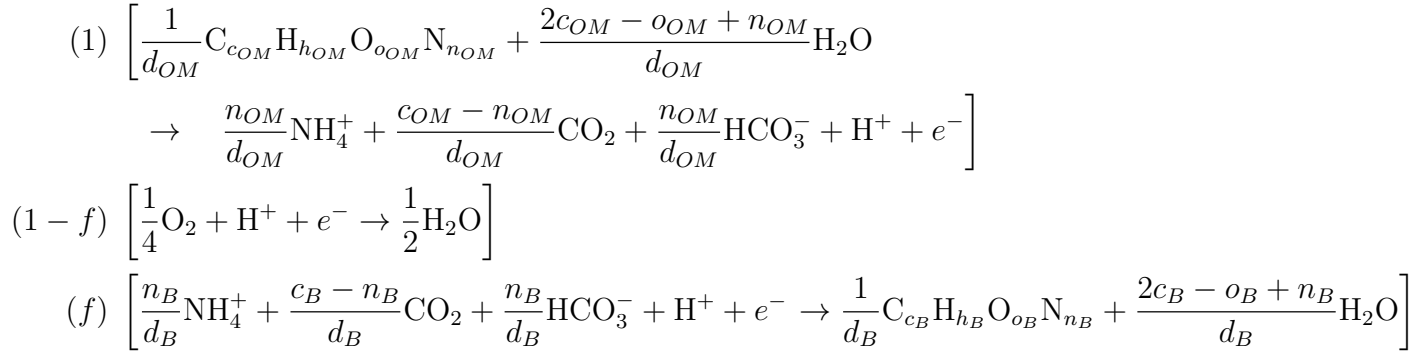
17 **Appendix 2: Redox-based descriptions of metabolisms**

18 Following the methodology of Rittman and McCarty (2001), three half-reactions combine to form
19 the catabolic and anabolic full reactions for each metabolism: 1. the oxidation of an electron
20 donor, 2. the reduction of oxygen or nitrogen as an electron acceptor, and 3. biomass synthesis.
21 Electron fraction parameter f partitions the electron flow towards biomass synthesis (f) vs. towards
22 respiration for energy ($1 - f$).

23 We describe the N-cycling in AMZs using a minimum set of metabolisms, described below. Though
24 natural assemblages may carry out a diversity of pathway lengths of the full denitrification reaction
25 (Zumft 1997), we here resolve the denitrification pathway with two discrete steps, as do other
26 modeling approaches (Penn et al. 2016; Babbin et al. 2017), because the intermediate NO_2^- is
27 critical to AMZ biogeochemistry. We do not resolve N_2O because the small amounts formed have
28 negligible impact on the stoichiometries of these metabolisms. We do not consider anaerobic nitrite
29 oxidation because our understanding the process is still emerging (Babbin et al. 2017), though we
30 provide the tools with which the traits and ecology of this (and other) metabolisms could also be
31 examined.

Aerobic heterotrophy For the aerobic heterotroph, organic matter (OM) provides the elements and electrons for both the synthesis of biomass (B) and energy production, and oxygen serves as the electron acceptor. The three half-reactions, with notation of the factor by which each is multiplied

before summing to give the whole metabolism, are:



32 Summing the above gives the balance for the whole metabolism, here substituting organic matter
 33 $OM = C_{c_{OM}} H_{h_{OM}} O_{o_{OM}} N_{n_{OM}}$ and biomass $B_{HetO} = C_{c_B} H_{h_B} O_{o_B} N_{n_B}$, and ignoring water and
 34 lumping bicarbonate into the CO_2 pool for brevity, as:

$$\frac{1}{d_{OM}} OM + \frac{1-f}{4} O_2 \rightarrow \frac{f}{d_B} B_{HetO} + \left(\frac{c_{OM}}{d_{OM}} - \frac{c_B f}{d_B} \right) CO_2 + \left(\frac{n_{OM}}{d_{OM}} - \frac{n_B f}{d_B} \right) NH_4^+ \quad (A8)$$

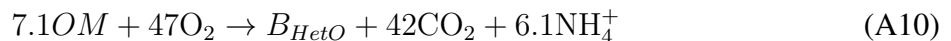
35 where d normalizes the organic reactions to one electron. In the half-reactions for organic matter
 36 decomposition or biomass synthesis, d represents the number of electron equivalents that correspond
 37 to the oxidation states of the inorganic constituents (Rittman and McCarty 2001). For generic
 38 organic composition $C_c H_h O_o N_n$, assuming that organic N is decomposed into or assimilated from
 39 N at oxidation state -3 gives $d = 4c + h - 2o - 3n$. (Different values of d may account for the
 40 assimilation of DIN species at higher oxidation states into biomass, following Rittman and McCarty
 41 (2001)). Here, we assume a microbial biomass composition of $C_5 H_7 O_2 N$ for all functional types, in
 42 accordance with the estimate of marine heterotrophic bacterial biomass C:N of 5 ± 1 (Zimmerman
 43 et al. 2014), giving $d_B = 20$. For the generic organic substrate, we assume an average Redfieldian
 44 composition of $OM = C_{6.6} H_{10.9} O_{2.6} N$ (Anderson 1995), giving $d_{OM} = 29.1$.

45 The organic matter yield (or growth efficiency; mol B synthesized per mol OM consumed) relates
 46 to f as:

$$y_{OM} = \frac{d_{OM}}{d_B} f \quad (A9)$$

47 and so $y_{OM} \approx f$ if the stoichiometries and redox states of the organic matter substrate and microbial
 48 biomass are similar, and $y_{OM} = 1.45f$ for our assumed Redfieldian organic substrate and microbial
 49 biomass stoichiometries.

50 For the aerobic heterotroph, we assign $y_{OM_{BhetO}} = 0.14$, the average marine growth efficiency in the
 51 open ocean compiled by Robinson (2008). This translates to $f = 0.096$, and gives a stoichiometry
 52 normalized to one mole of biomass as:



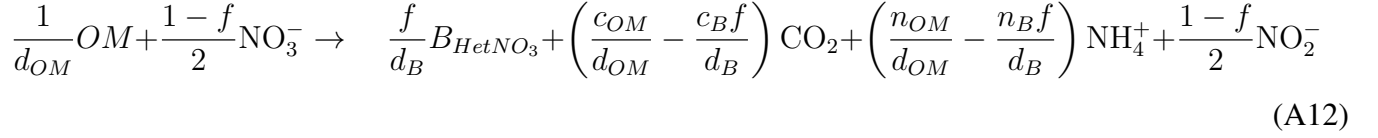
53 For the following anaerobic heterotrophic metabolisms, the above half-reactions are the same except
 54 for the electron acceptor half-reaction. For the anaerobic heterotrophs, we assign the same organic
 55 matter yield to all: $y_{OM_{Bhet_i}} = 0.9y_{OM_{BhetO}}$, giving $f = 0.087$, in accordance with our assumption
 56 that oxygen is a superior electron acceptor for the range of oxygen concentrations resolved for
 57 our generic organic substrate. LaRowe and Van Cappellen (2011) show that this may be so for
 58 a wide range of oxygen and DIN concentrations for the oxidation of glucose. This allows the
 59 anaerobic types to coexist in the steady state model. Further attention to time-varying states is
 60 needed to explain coexistences among anaerobic heterotrophic types if organic matter yields differ
 61 significantly.

62 We also note how ratio r in the equations for ϕ can be written in terms of f . Since $r = y_{OM_O}y_{O_2}^{-1}$
 63 (mol O_2 utilized per mol OM utilized),

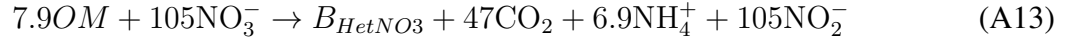
$$r = \frac{d_{OM}(1 - f)}{4} \quad (A11)$$

64 Thus r increases as f decreases, and converges to $d_{OM}/4$ at low efficiencies (Fig. A1). With our
 65 assumed organic matter stoichiometry, r is about 6.6 mol O_2 per mol organic N, or about 1 mol O_2
 66 per mol organic C, which is close to the inverse of the “respiratory quotient” for algal material of
 67 0.9 moles of CO_2 produced per mol O_2 consumed (Robinson 2008).

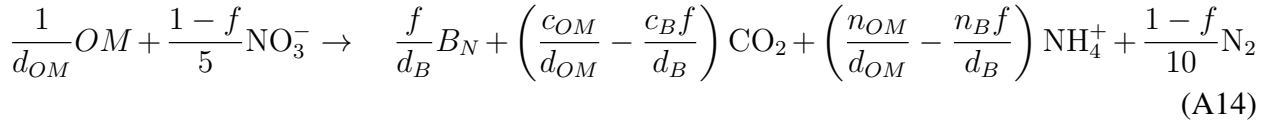
Nitrate-reducing heterotrophy For NO_3^- reduction to NO_2^- , organic matter (OM) provides the elements and electrons for both the synthesis of biomass (B) and energy production, and NO_3^- serves as the electron acceptor. The full metabolism forming biomass B_{HetNO_3} is:



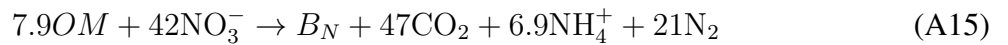
68 With $f = 0.087$, the stoichiometry normalized to one mole of biomass is:



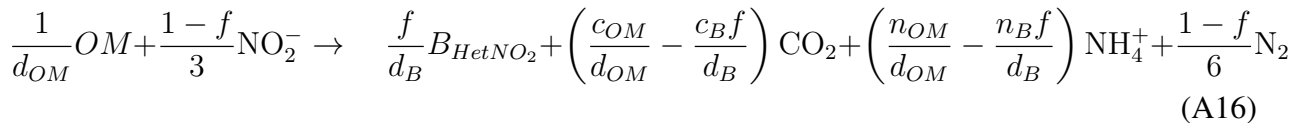
69 **Denitrifying heterotrophy** For the denitrification of NO_2^- to gaseous elemental form, organic
 70 matter (OM) provides the elements and electrons for both the synthesis of biomass (B) and energy
 71 production, and either NO_3^- or NO_2^- serves as the electron acceptor, which is then reduced to an
 72 unspecified combination of N_2 and N_2O . Using NO_3^- as an electron acceptor (as in Fig. 2 in main
 73 text), the full metabolism forming biomass B_N is:



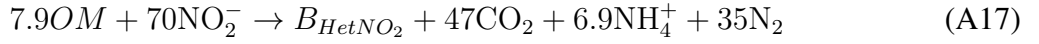
74 With $f = 0.087$, the stoichiometry normalized to one mole of biomass is:



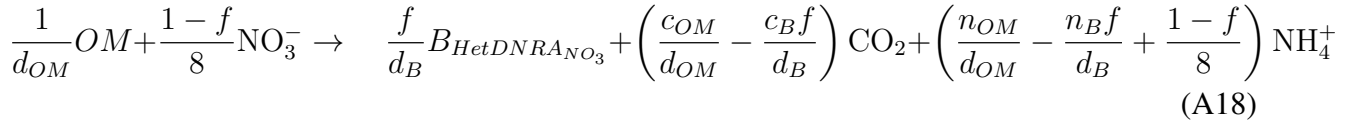
75 Using NO_2^- as an electron acceptor (all but Fig. 2 in main text), the full metabolism forming biomass
 76 B_{HetNO_2} is:



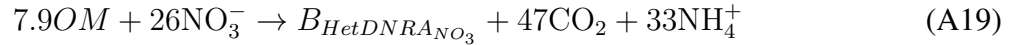
77 With $f = 0.087$, the stoichiometry normalized to one mole of biomass is:



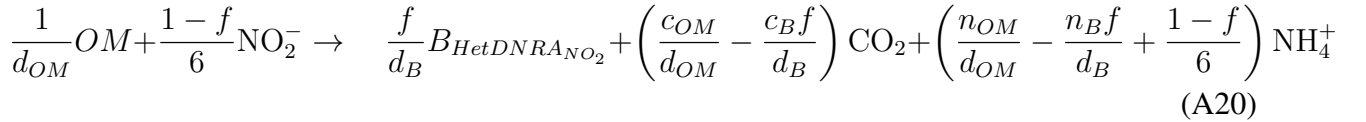
78 **DNRA** For organisms carrying out dissimilatory nitrate (or nitrite) reduction to ammonium
 79 (DNRA), organic matter (OM) provides the elements and electrons for both the synthesis of
 80 biomass (B) and energy production, and either NO_3^- or NO_2^- serves as the electron acceptor,
 81 which is reduced to NH_4^+ . When using NO_3^- as an electron acceptor, the full metabolism can be
 82 approximated as:



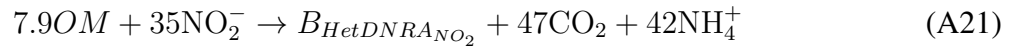
83 For the $f = 0.087$ assumed for all anaerobic heterotrophs, the stoichiometry normalized to one
 84 mole of biomass is:



85 When using NO_2^- as an electron acceptor for DNRA, the full metabolism can be approximated as:

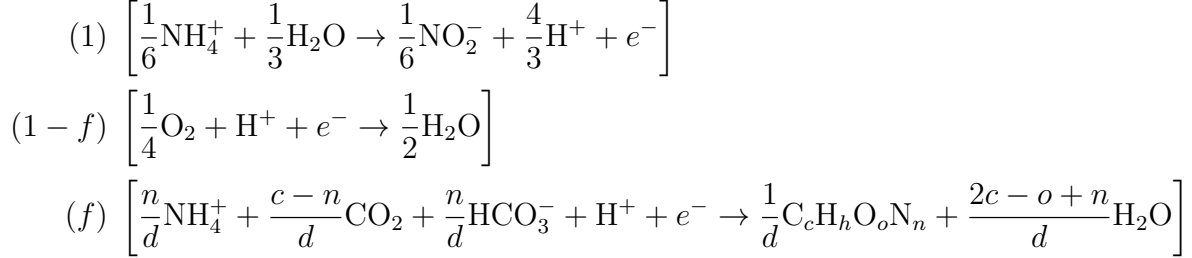


86 and with $f = 0.087$, the stoichiometry normalized to one mole of biomass is:

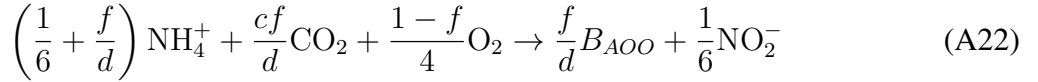


87 Solutions including both of these metabolisms as metabolic functional types in the chemostat are
 88 plotted in Fig. A3 and discussed in Appendix 3.

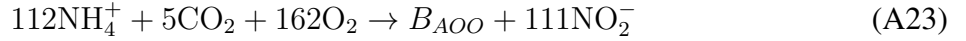
Chemoautotrophic aerobic NH_4^+ oxidation For the NH_4^+ oxidizer (here considering NH_4^+ and NH_3 interchangeably), as in Zakem et al. (2018), the three half-reactions, for generic biomass $\text{C}_c\text{H}_h\text{O}_o\text{N}_n$, and their electron-partitioning coefficients, are:



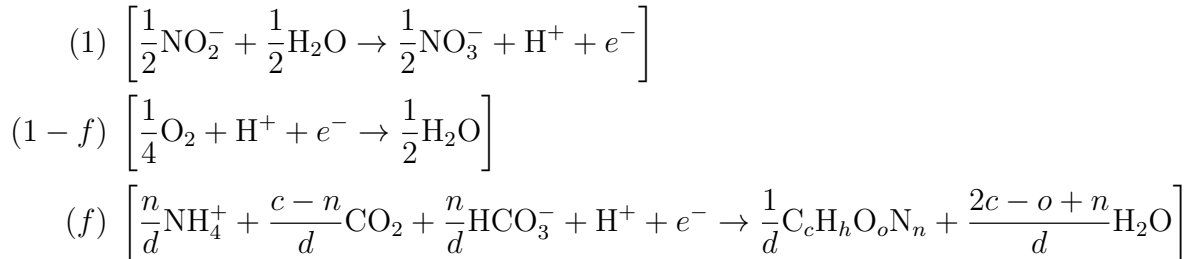
89 The sum gives the full metabolism for NH_4^+ -oxidizing biomass B_{AOO} , as a function of f :



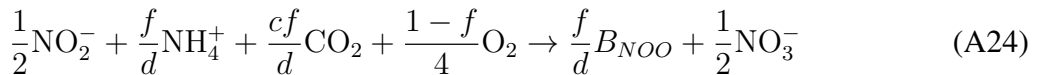
90 For $f = 0.03$, the stoichiometry normalized to one mole of biomass is:



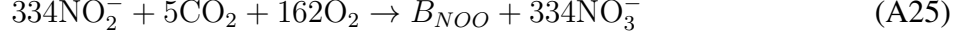
Chemoautotrophic aerobic NO_2^- oxidation For the NO_2^- oxidizer, as in Zakem et al. (2018), the three half-reactions are:



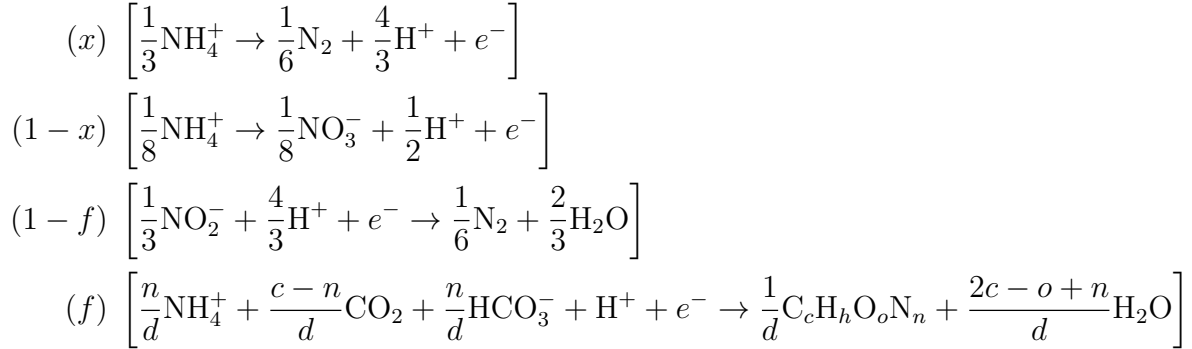
91 which when summed gives the full metabolism NO_2^- -oxidizing biomass B_{NOO} as:



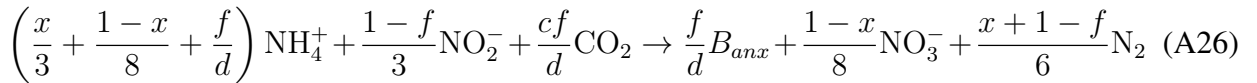
92 where the requirement of one mole of NH_4^+ per mole NOO biomass is effectively negligible in all
 93 model simulations. For $f = 0.03$, the stoichiometry normalized to one mole of biomass is:



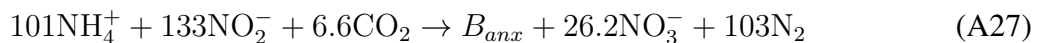
Chemoautotrophic anammox For chemoautotrophic anaerobic ammonium oxidation (anammox), NH_4^+ oxidation to elemental N provides electrons for energy that fuels cell synthesis (here considering NH_4^+ and NH_3 interchangeably), and NO_2^- serves as the electron acceptor, forming elemental N_2 . Anammox is observed to also excrete NO_3^- (Strous et al. 1998). Thus, the whole metabolism may be characterized by considering two electron donor half reactions for NH_4^+ : oxidation to NO_3^- and oxidation to N_2 . With this simplified form, the following four half-reactions can represent the anammox metabolism, with x dictating the weighting of the electron donor reaction:



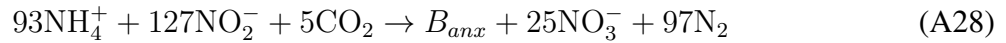
94 This gives the full metabolism forming anammox biomass B_{anx} as:



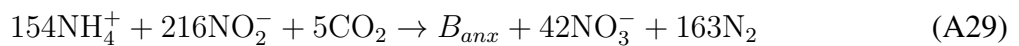
95 To estimate an appropriate value for x , we calibrate this with the stoichiometry of anammox in
 96 wastewater reported by Strous et al. (1998). Normalized to one mole of N-based biomass for
 97 comparison, this published stoichiometry is:



98 This shows that anammox produces NO_3^- to N_2 at a ratio of approximately 1:4. From this, we
 99 can solve for $x \approx 0.5$. With $x = 0.5$, we find that the stoichiometry of Strous et al. (1998) is
 100 approximated when the value of f is 0.05:



101 However, for all three chemoautotrophic metabolic functional types, we assume $f = 0.03$ in the
 102 illustrated solutions. This is because Zakem et al. (2018) used theoretical and empirical analysis to
 103 estimate that the electron fraction f for both steps of aerobic nitrification was significantly lower
 104 in marine environments ($f \approx 0.03$) than in wastewater ($f \approx 0.1$). Furthermore, the published
 105 stoichiometry for anammox in wastewater suggests value of f lower than those of aerobic ammonia
 106 oxidation in wastewater ($f \approx 0.05$) (Strous et al. 1998; Rittman and McCarty 2001). Thus if the
 107 degree to which anammox efficiency is lower than aerobic nitrifier efficiency in the ocean can be
 108 approximated by the ratio of anammox to nitrifier efficiency in wastewater (0.05:0.1), a value of
 109 $f \approx 0.03/2 \approx 0.015$ may be a justifiable estimate for anammox efficiency in the ocean. However,
 110 given the uncertainty, and to most robustly test the competition between them, we assigned the
 111 same value of $f = 0.03$ to anammox as well as to the nitrifiers. With $f = 0.03$ and $x = 0.5$, the
 112 anammox stoichiometry is:



113 **Appendix 3: Detail for the multiple redox-based metabolisms in the virtual**

114 **chemostat**

Equations Equations for the multiple metabolisms in the chemostat are similar in form to those in Table 1 in the main text. Organic matter, O_2 , and NO_3^- are supplied to chemostat. The biomass B_i ($\mu\text{M N}$) of each metabolic functional type i , organic matter ($\mu\text{M N}$), and all nutrients (μM) are resolved by solving their rates of change with time defined by incoming nutrient supply, nutrient uptake, growth rate, excretion of waste respiration products, and the chemostat dilution rate D as:

$$\frac{dB_i}{dt} = B_i(\mu_i - D) \quad (\text{A30})$$

$$\frac{dOM}{dt} = D(OM_{in} - OM) - \sum_i \frac{1}{y_{OM_i}} \mu_i B_i \quad (\text{A31})$$

$$\frac{d[NH_4^+]}{dt} = \sum_i e_{NH_{4i}} \mu_i B_i - \sum_i \frac{1}{y_{NH_{4i}}} \mu_i B_i - D[NH_4^+] \quad (\text{A32})$$

$$\frac{d[NO_2^-]}{dt} = \sum_i e_{NO_{2i}} \mu_i B_i - \sum_i \frac{1}{y_{NO_{2i}}} \mu_i B_i - D[NO_2^-] \quad (\text{A33})$$

$$\frac{d[NO_3^-]}{dt} = \sum_i e_{NO_{3i}} \mu_i B_i - \sum_i \frac{1}{y_{NO_{3i}}} \mu_i B_i - D[NO_3^-] \quad (\text{A34})$$

$$\frac{d[O_2]}{dt} = D([O_{2in}] - [O_2]) - \sum_i \frac{1}{y_{O_{2i}}} \mu_i B_i \quad (\text{A35})$$

115 where yields y and excretion ratios e are listed in Table A1. Each growth rate μ is calculated
 116 according to Eqn. 1 in the main text using the yields and uptake kinetic parameters in Tables A1
 117 and A2.

118 **Model ensemble** To consider uncertainty in the parameterizations, we computed an ensemble
 119 of 1000 model simulations for which parameters were randomly sampled from a distribution as
 120 follows. The efficiency of the heterotrophic metabolisms overall was varied, the degree to which
 121 anaerobic heterotrophy was less efficient than aerobic heterotrophy was varied, and the efficiencies

122 of the three chemoautotrophic metabolisms were independently varied. Since we expect variation in
123 these yields, but not the underlying energetic constraints, we vary the overall heterotrophic growth
124 efficiency but retain the lower efficiency of the anaerobic heterotrophs. The aerobic heterotrophic
125 yield $y_{OM_{BhetO}}$ was varied over a linear range from 0.1 to 0.3 (mol biomass synthesized per mol
126 OM utilized). The anaerobic heterotrophic yields were less this yield by a factor of 1% to 50%,
127 varying linearly over this range. The three chemoautotrophic yields were independently varied by
128 varying their electron fraction f over a linear range from $f = 0.02$ to $f = 0.04$. This allowed the
129 potential for cases in which the anammox NH_4^+ yield was higher than that of the aerobic NH_4^+
130 oxidizer, potentially resulting in sustainable anammox in the oxygenated state, but this case did not
131 occur in any of the 1000 solutions.

132 **An argument for low efficiency of DNRA** The model solutions without DNRA are illustrated
133 in the main text (Fig. 3), and with DNRA in Fig. A3. When the DNRA functional type is included,
134 NH_4^+ but not NO_2^- accumulates to micromolar concentrations in the anoxic state (Fig. A3). This is
135 consistent with some observations in the South Pacific oxygen minimum zone of Kalvelage et al.
136 (2013): at the few locations where measured DNRA rates were significantly high (10–1000 nM
137 d^{-1}), NH_4^+ concentrations were also significantly high (1–5 μM), and NO_2^- concentrations were low.
138 Since DNRA rates were low throughout the rest of the dataset (less than about 1 $nM d^{-1}$), and since
139 in general AMZs show characteristic accumulation of NO_2^- and not NH_4^+ , with an assessment of the
140 literature we agree with the speculation that DNRA operates sporadically in AMZs (Lam et al. 2009;
141 Jensen et al. 2011; Füssel et al. 2012; Kalvelage et al. 2013). The specific mechanism sustaining
142 DNRA remains unclear, but this does hypothesize that DNRA may be associated with a lower
143 efficiency than other anaerobic metabolisms. In the steady state solutions, DNRA is excluded if its
144 efficiency is lower, and so we further speculate that favorable DNRA may require a time-varying
145 environment to avoid competitive exclusion as an ‘r-selected’ vs. a ‘k-selected’ metabolism.

Table A1: Parameters for metabolic functional type yields y (inverse values listed) and excretions e from redox-based descriptions (see chemical equations in Appendix B). Units for y^{-1} and e are mol substrate per mol biomass N synthesized.

Type	Parameter	Symbol	Value (mol/mol)	Source
Two metabolisms (Fig. 2 case study):				
B_O	Organic matter demand	$y_{OM_{B_O}}^{-1}$	7.1	Robinson (2008)
	Oxygen demand	$y_{O_2}^{-1}$	47	Eqns. A8 and A9
B_N	Organic matter demand	$y_{OM_{B_N}}^{-1}$	7.9	$y_{OM_N} = 0.9 \cdot y_{OM_O}$
	DIN demand	y_N^{-1}	42	Eqns. A9 and A14
Multiple metabolisms (Fig. 3, for chemostat and 2D model):				
B_{HetO}	Organic matter demand	$y_{OM_{B_{HetO}}}^{-1}$	7.1	Robinson (2008)
	Oxygen demand	$y_{O_2_{B_{HetO}}}^{-1}$	47	Eqns. A8 and A9
	Ammonium excretion	$e_{NH_4_{B_{HetO}}}$	6.1	Eqns. A8 and A9
B_{HetNO_3}	Organic matter demand	$y_{OM_{B_{HetNO_3}}}^{-1}$	7.9	$y_{OM_{B_{Het_i}}} = 0.9 \cdot y_{OM_{B_{HetO}}}$
	Nitrate demand	$y_{NO_3_{B_{HetNO_3}}}^{-1}$	105	Eqns. A9 and A12
	Ammonium excretion	$e_{NH_4_{B_{HetNO_3}}}$	6.9	Eqns. A9 and A12
	Nitrite excretion	$e_{NO_2_{B_{HetNO_3}}}$	105	Eqns. A9 and A12
B_{HetNO_2}	Organic matter demand	$y_{OM_{B_{HetNO_2}}}^{-1}$	7.9	$y_{OM_{B_{Het_i}}} = 0.9 \cdot y_{OM_{B_{HetO}}}$
	Nitrite demand	$y_{NO_2_{B_{HetNO_2}}}^{-1}$	70	Eqns. A9 and A16
	Ammonium excretion	$e_{NH_4_{B_{HetNO_2}}}$	6.9	Eqns. A9 and A16
	N ₂ (or N ₂ O) excretion	$e_{N_2_{B_{HetNO_2}}}$	35	Eqns. A9 and A16
B_{AOO}	Ammonium demand	$y_{NH_4_{B_{AOO}}}^{-1}$	112	$f = 0.03$; Zakem et al. (2018)
	Oxygen demand	$y_{O_2_{B_{AOO}}}^{-1}$	162	Eqn. A22
	Nitrite excretion	$e_{NO_2_{B_{AOO}}}$	111	Eqn. A22
B_{NOO}	Nitrite demand	$y_{NO_2_{B_{NOO}}}^{-1}$	334	$f = 0.03$; Zakem et al. (2018)
	Oxygen demand	$y_{O_2_{B_{NOO}}}^{-1}$	162	Eqn. A24
	Nitrate excretion	$e_{NO_3_{B_{NOO}}}$	334	Eqn. A24
B_{anx}	Ammonium demand	$y_{NH_4_{B_{anx}}}^{-1}$	154	$f = 0.03$
	Nitrite demand	$y_{NO_2_{B_{anx}}}^{-1}$	216	Eqn. A26
	Nitrate excretion	$e_{NO_3_{B_{anx}}}$	42	Eqn. A26, $x = 0.5$
	N ₂ excretion	$e_{N_2_{B_{anx}}}$	163	Eqn. A26, $x = 0.5$
DNRA (included in Fig. A3 only):				
$B_{HetDNRA_{NO_3}}$	Organic matter demand	$y_{OM_{B_{HetDNRA-NO_3}}}^{-1}$	7.9	$y_{OM_{B_{Het_i}}} = 0.9 \cdot y_{OM_{B_{HetO}}}$
	Nitrate demand	$y_{NO_3_{B_{HetDNRA-NO_3}}}^{-1}$	26	Eqns. A9 and A18
	Ammonium excretion	$e_{NH_4_{B_{HetDNRA-NO_3}}}$	33	Eqns. A9 and A18
$B_{HetDNRA_{NO_2}}$	Organic matter demand	$y_{OM_{B_{HetDNRA-NO_2}}}^{-1}$	7.9	$y_{OM_{B_{Het_i}}} = 0.9 \cdot y_{OM_{B_{HetO}}}$
	Nitrite demand	$y_{NO_2_{B_{HetDNRA-NO_2}}}^{-1}$	35	Eqns. A9 and A20
	Ammonium excretion	$e_{NH_4_{B_{HetDNRA-NO_2}}}$	42	Eqns. A9 and A20

Table A2: Uptake kinetic parameters for metabolic functional types.

Substrate	Parameter	Symbol	Value (mol/mol B)	Units	Source
OM	Maximum uptake rate	V_{maxOM}	1 (0.5 in 2D)	mol OM mol B^{-1} d $^{-1}$	*
	Half-saturation conc.	K_{OM}	0.1 (0.01 in 2D)	μ M OM	
DIN	Maximum uptake rate	V_{maxN}	50.8	mol N mol B^{-1} d $^{-1}$	Martens-Habbena et al. (2009); Zakem et al. (2018)
	Half-saturation conc.	K_N	133	nM N	
O_2	Cell radius	r	0.25	μ m	Bratbak and Dundas (1984) Unisense Seawater and Gases
	Cell C quota**	q	18.3	fmol C μ m $^{-3}$	
	Diffusion coefficient for O_2 in seawater	\mathcal{D}	$1.5 \cdot 10^{-5}$	cm 2 s $^{-1}$	

*The kinetic parameters for organic matter uptake rate were estimated from the average marine bacterial growth efficiency of order 0.1 d $^{-1}$ with the estimate of the average bulk marine bacterial growth rate of order 0.1 d $^{-1}$. A maximum uptake rate of $V_{maxOM} \approx 1$ allows this growth rate when organic matter is abundant. The chosen half-saturation constant is arbitrarily chosen to allow for depletion of the average (non-recalcitrant) organic matter pool.

**A C:N of 5 for microbial biomass is used to express yields in units of biomass N.

146 **Appendix 4: 2D model detail**

147 **Flow field**

148 **Governing Equations** A two-dimensional, basin-wide closed flow field is developed (in the $x - z$
149 plane with no gradients in y) using the governing momentum equations:

$$\frac{\partial u}{\partial t} = -u \frac{\partial u}{\partial x} - w \frac{\partial u}{\partial z} - \frac{1}{\rho_0} \frac{\partial p}{\partial x} + fv + \nabla \cdot \kappa \nabla u \quad (\text{A36})$$

150

$$\frac{\partial v}{\partial t} = -u \frac{\partial v}{\partial x} - w \frac{\partial v}{\partial z} - fu + \nabla \cdot \kappa \nabla v \quad (\text{A37})$$

151 A wind stress in the y direction, $\tau = (0, \tau^y)$, is imposed by the surface boundary condition
152 $\kappa \frac{\partial v}{\partial z} = \tau^y / \rho$, where ρ is the density of seawater. With horizontal u computed, a non-divergent 2D
153 circulation field can be computed from continuity as:

$$\frac{\partial u}{\partial x} + \frac{\partial w}{\partial z} = 0 \quad (\text{A38})$$

154 and integrating downwards (or upwards) to solve for the vertical velocity field w , with $w = 0$ as the
155 top (or bottom) boundary condition.

156 **The Pressure Field** The wind-driven Ekman transport in the x -direction sets up an overturning
157 circulation through the horizontal pressure gradient. Assuming the pressure to be hydrostatic, the
158 horizontal pressure gradient can be decomposed into the baroclinic pressure gradient, calculated
159 from density anomalies, and the surface pressure gradient, arising from deviations in sea surface
160 height. In this 2D circulation model, temperature and salinity are not resolved, and density anomalies
161 are set to zero throughout the domain. Thus the horizontal pressure gradient is depth-independent

162 and consists of only the surface pressure gradient, as:

$$\frac{\partial p}{\partial x} = \frac{\partial p_{surf}}{\partial x} \quad (\text{A39})$$

163 Using the rigid lid approximation as a constraint, the total flux in and out of each water column
 164 must sum to zero, and can be expressed in discretized form as:

$$\sum_{j=1}^{n_j} (u_{j,i+1} - u_{j,i}) dz_j = 0, \quad (\text{A40})$$

165 where the grid cell index i refers to the x -direction, j to the z -direction, and dz is the height of the
 166 grid cell. Substituting Eqn. A39 into Eqn. A36 (momentum in the x -direction) and then inserting
 167 this into Eqn. A40 allows for solving the horizontal surface pressure derivative. For a boundary
 168 condition, $\frac{\partial p}{\partial x} = 0$ was imposed on the left (or right) boundary, and the pressure gradient was solved
 169 for at the face of each column by integrating from left to right (or right to left), which resulted
 170 in an analogous boundary pressure gradient of zero at the far boundary. The u velocity was then
 171 calculated with the newly updated pressure gradient at each time step, and checked for consistency
 172 with Eqn. A40.

173 **Wind Stress Forcing** The y -component of the wind stress was modeled to simulate the climato-
 174 logical mean from Hellerman and Rosenstein (1983) over the Pacific Basin at 10°S latitude (Fig.
 175 A4) as:

$$\tau_y(x) = 0.0125 \left(\sin\left(\frac{\pi x}{0.8L} - \frac{\pi}{2}\right) + 1 \right) \left(-\tanh\left(\frac{\pi x}{0.1L} - 9\pi\right) + 1 \right) \quad (\text{A41})$$

176 where L is the length of the domain (10,000 km).

177 **Mixing** A mixed layer was imposed by varying the vertical diffusion coefficient κ_Z with depth,
 178 from a maximum κ_{Zmax} at the surface to a minimum κ_{Zmin} with a length scale of z_{ML} . The fixed
 179 (no flux) boundary conditions result in some accumulation of POM at the bottom of the 2000 m

180 domain, conceptually representing a sediment layer. To diffuse this sediment layer, vertical mixing
 181 was increased within a bottom boundary mixed layer of depth scale 100 m. κ_Z ($\text{m}^2 \text{s}^{-1}$) is thus
 182 calculated at cell faces as:

$$\kappa_Z = \kappa_{Zmax} e^{-\frac{z}{z_{mld}}} + \kappa_{Zmin} + \kappa_{Zmax} e^{-\frac{z-H}{100}} \quad (\text{A42})$$

183 where z is in meters and H is the height of the domain (2000 m). A constant value of horizontal
 184 diffusion κ_X was prescribed to account for mixing by subgrid-scale processes.

185 **Numerical solution** The momentum equations were solved to calculate the flow field with 10
 186 m vertical resolution and 100 km horizontal resolution over a domain 2000 m in height and
 187 10,000 km in width. The choice to resolve the time step explicitly led to the need to resolve gravity
 188 waves, and so a 10^{-3} day time step was necessary. Equations were integrated forward in time
 189 using the 4th order Runge-Kutta method. Advection was carried out using the QUICK advection
 190 scheme, consisting of a linear interpolation between points weighted by an upstream 2nd order
 191 curvature, resulting in 3rd order accuracy. Fluxes were calculated at the faces of each grid cell, and
 192 concentrations at the centers. The resulting u and w fields used for the biogeochemistry model were
 193 saved after 100 years of spin up.

194 **Biogeochemistry**

195 The idealized AMZ biogeochemical model includes 17 state variables (11 populations and 6
 196 nutrients): the biomasses of the microbial metabolic functional type populations from the chemo-
 197 stat model (B_{HetO} , B_{AOO} , B_{NOO} , B_{HetNO_3} , B_{HetNO_2} , and B_{anx}), two phytoplankton populations
 198 (smaller P_S and larger P_L), three zooplankton grazer populations (microzooplankton microbial
 199 grazer Z_B , and one each preying on the phytoplankton populations, Z_{P_S} and Z_{P_L}), dissolved organic
 200 matter (DOM), sinking particulate organic matter (POM), three inorganic species of DIN (NH_4^+ ,
 201 NO_2^- , and NO_3^-), and oxygen (O_2). All are resolved in concentrations of nitrogen except for O_2 .

202 Total nitrogen (the sum of all nutrients, organic matter, and biomasses) is conserved. The DIN
 203 transformed to gaseous form (as N_2O or N_2) is balanced by immediately redistributing its sum
 204 evenly over the domain as nitrate, which simulates a distant source of nitrogen fixation. Oxygen
 205 fluxes across the air-sea interface according to transfer coefficient of κ_g over equilibration depth h_g
 206 according to a saturation concentration O_{2sat} . See Table A3 for parameter values.

207 Each tracer C is advected and diffused by the two-dimensional velocity field $\mathbf{u} = (u, w)$ and
 208 diffusion coefficients κ as:

$$\frac{\partial C}{\partial t} = -\nabla \cdot (\mathbf{u}C) + \nabla \cdot (\kappa \nabla C) + S_C \quad (\text{A43})$$

209 where S_C are additional sources and sinks. Growth rate μ_i for each microbial population is calculated
 210 with Eqn. 1, using the yields and uptake kinetic parameters in Tables A1 and A2, and modified by
 211 temperature by γ_T (Eqn. A60; Table A3). For each of the 17 tracers, the sources and sinks are as
 212 follows:

$$S_{B_i} = B_i(\mu_i - m_{lin} - m_q B_i - g Z_B) \quad (A44)$$

$$S_{P_i} = P_i(\mu_i - m_{lin} - m_q P_i - g Z_{P_i} \frac{O_2}{O_2 + K_{O_2}}) \quad (A45)$$

$$S_{Z_B} = Z_B(\zeta g \sum_i B_i - m_Z Z_B) \quad (A46)$$

$$S_{Z_{P_i}} = Z_{P_i}(\zeta g P_i \frac{O_2}{O_2 + K_{O_2}} - m_Z Z_{P_i}) \quad (A47)$$

$$S_{POM} = f_{mort} \left[m_{lin} \sum_i B_i + m_{lin} \sum_i P_i + m_q \sum_i B_i^2 + m_q \sum_i P_i^2 + m_Z \sum_i Z_i^2 \right] \\ - \sum_i \frac{1}{y_{OM_i}} \mu_i B_i \frac{POM}{POM + DOM} - \frac{\partial(w_s POM)}{\partial z} \quad (A48)$$

$$S_{DOM} = (1 - f_{mort}) \left[m_{lin} \sum_i B_i + m_{lin} \sum_i P_i + m_q \sum_i B_i^2 + m_q \sum_i P_i^2 + m_Z \sum_i Z_i^2 \right] \\ - \sum_i \frac{1}{y_{OM_i}} \mu_i B_i \frac{DOM}{POM + DOM} \quad (A49)$$

$$S_{NH_4^+} = \sum_i e_{NH_{4i}} \mu_i B_i - \sum_i \frac{1}{y_{NH_{4i}}} \mu_i B_i - \sum_i \mu_i P_i \frac{NH_4^+}{DIN} + (1 - \zeta)g \left[\sum_i B_i Z_B + \sum_i P_i Z_{P_i} \frac{O_2}{O_2 + K_{O_2}} \right] \quad (A50)$$

$$S_{NO_2^-} = \sum_i e_{NO_{2i}} \mu_i B_i - \sum_i \frac{1}{y_{NO_{2i}}} \mu_i B_i - \sum_i \mu_i P_i \frac{NO_2^-}{DIN} \quad (A51)$$

$$S_{NO_3^-} = \sum_i e_{NO_{3i}} \mu_i B_i - \sum_i \frac{1}{y_{NO_{3i}}} \mu_i B_i - \sum_i \mu_i P_i \frac{NO_3^-}{DIN} + \frac{\iint (\sum_i e_{N_{2i}} \mu_i B_i) dx dz}{\iint dx dz} \quad (A52)$$

$$S_{O_2} = \frac{\kappa_g}{h_g} (O_{2sat} - O_2)^* + R_{O_{2P}} \sum_i \mu_i P_i - \sum_i \frac{1}{y_{O_{2i}}} \mu_i B_i - f(O_2, Z_B) - R_{O_{2Z}} (1 - \zeta)g \sum_i P_i Z_{P_i} \frac{O_2}{O_2 + K_{O_2}} \quad (A53)$$

213 *over equilibration depth h_g

214 **Phytoplankton** Two oxygenic phytoplankton types are resolved: one representing a small, high-
 215 affinity *Prochlorococcus*-like population with a lower maximum growth rate and higher nutrient
 216 affinity, and one representing a larger, faster growing type with lower affinity. Following Dutkiewicz
 217 et al. (2015), light absorption for the smaller type is higher than that of the larger type, and so the
 218 smaller type is more fit at lower light levels deeper in the water column. Both types produce oxygen
 219 in relation to their growth with a Redfieldian O₂:N ratio (7.3:1). Phytoplankton grow as a function
 220 of a maximum growth rate μ_{max} (d⁻¹), with type-specific limitation by nutrients (γ_{N_i}), type-specific
 221 limitation by light (γ_{I_i}), and modification by temperature (γ_T) as:

$$\mu_{P_i} = \mu_{maxP_i} \gamma_{N_i} \gamma_{I_i} \gamma_T \quad (\text{A54})$$

222 Nutrient limitation is a function of the total concentration of all species of DIN:

$$\gamma_{N_i} = \min \left[1, \frac{\text{NH}_4^+}{\text{NH}_4^+ + K_{\text{NH}_4P_i}} + \frac{\text{NO}_2^-}{\text{NO}_2^- + K_{\text{NO}_xP_i}} + \frac{\text{NO}_3^-}{\text{NO}_3^- + K_{\text{NO}_xP_i}} \right] \quad (\text{A55})$$

223 The uptake of each DIN species by each phytoplankton type is weighted by the concentration
 224 of each substrate. The inhibition of NO₂⁻ and NO₃⁻ assimilation in the presence of NH₄⁺ had a
 225 negligible effect on the solutions and so was not included. Values for the maximum growth rate
 226 and the half-saturation constants were computed as functions of cell size following data-based
 227 allometric relationships in Litchman et al. (2007) as in Ward et al. (2012). The effective half-
 228 saturation constants for DIN uptake with respect to μ_{max} were calculated with respect to maximum
 229 uptake rate V_{max} and minimum cell quota Q_{min} from the relationships in Litchman et al. (2007),
 230 following Verdy et al. (2009) and Ward et al. (2012) (Table A3).

231 Light limitation was parameterized using an exponential form as a function of an instantaneous
 232 photosynthetic rate and the Chl *a* to Carbon ratio θ , following Geider et al. (1997) and Hickman
 233 et al. (2010):

$$\gamma_{I_i} = 1 - \exp \left(\frac{-\Gamma_i \theta_i}{\mu_{maxP_i} \gamma_{N_i} \gamma_T} \right) \quad (\text{A56})$$

234 Photosynthetic rate Γ_i for each type was computed as a function of photosynthetically active
 235 radiation $I(z)$, the maximum quantum yield of carbon fixation ϕ (mol C mol⁻¹ photons), and
 236 the absorption of light by phytoplankton $a_{P_i}^{\text{chl}}$ (m² (mgChl)⁻¹) representing a mean value over all
 237 wavelengths, as:

$$\Gamma_i = \phi a_{P_i}^{\text{chl}} I(z) \quad (\text{A57})$$

238 The Chl:C (θ) varies with photoacclimation, and is computed using a steady-state solution (Geider
 239 et al. 1997) with maximum ratio θ_{max} as:

$$\theta_i = \frac{\theta_{max}}{1 + \frac{\Gamma_i \theta_{max}}{2(\mu_{max} P_i \gamma_{N_i} \gamma_T)}} \quad (\text{A58})$$

240 **Grazing** Three grazer populations consume oxygen, contributing to the formation of the AMZ.
 241 One population represents microzooplankton bacteriovores and consumes all of the non-photosynthetic
 242 microbial functional types. A second consumes the small phytoplankton type, and a third consumes
 243 the large phytoplankton type. Each zooplankton population grows as a linear function of its prey
 244 biomass with grazing coefficient g and growth efficiency ζ (Armstrong 1994). NH₄⁺ is excreted as a
 245 waste product in proportion to $(1 - \zeta)$. Quadratic mortality rate m_Z represents predation by higher
 246 trophic levels.

247 Since the diffusive oxygen limitation assumed for the aerobic microbes should not apply to these
 248 larger organisms, further parameterization of oxygen limitations to zooplankton are required. For the
 249 population consuming the non-photosynthetic community (Z_B), we developed a parameterization
 250 of zooplankton oxygen consumption that implicitly simulates bacteriovore migration in and out of
 251 AMZs (Escribano et al. 2009; Wishner et al. 2013; Bianchi et al. 2014). Oxygen demand by the
 252 zooplankton at any given location is spread vertically above and below that location, and weighted
 253 by the oxygen concentration at that location, with zero weight if O₂ is below a critical oxygen
 254 concentration for zooplankton (here, 10 μM; see attached code). This mimicks zooplankton ability
 255 to breathe above or below the anoxic area, and swim into the area for grazing Escribano et al. (2009).

256 This loss is termed $f(O_2, Z_B)$ in the differential equation for oxygen for the 2D model (Eqn. A53).
 257 The two grazing types that consume phytoplankton are not allowed this capability, from the
 258 perspective that these grazers are adapted to oxygenated surface conditions, and are inhibited
 259 by oxygen using a saturating form in which their rate of grazing is halved at K_{O_2} . This oxygen
 260 inhibition of grazers consuming phytoplankton is a necessary (but not sufficient) condition for the
 261 formation of the secondary chlorophyll maximum in the model.

262 **Light** Light energy I decreases with depth according to the attenuation coefficients for water k_w :

$$I(z) = I_{in} e^{(-zk_w)} \quad (\text{A59})$$

263 **Temperature** All microbial growth, grazing, and mortality rates are represented as a function
 264 of temperature (non-dimensional γ_T) using a formulation that follows the Arrhenius equation
 265 (Dutkiewicz et al. 2015) as:

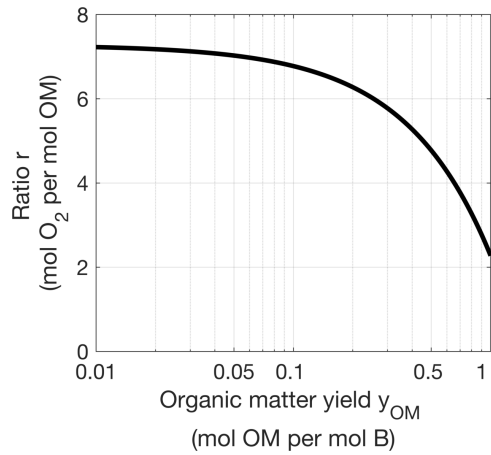
$$\gamma_T = \tau \exp\left(A_E \left(\frac{1}{T} - \frac{1}{T_0}\right)\right) \quad (\text{A60})$$

266 where T is the ambient temperature (K), T_0 is a reference temperature, A_E regulates the temperature
 267 modification, and τ normalizes the maximum value. The model assumes a constant temperature
 268 profile, an average of the 10°S Pacific Ocean transect from the WOA 2013 climatology. This
 269 temperature dependency increases microbial rates by a factor of three from the deep to the surface,
 270 but does not impact solutions qualitatively.

271 **Numerical solution** The biogeochemical model was run ‘offline’ using the above flow field
 272 with 10 m vertical resolution and 100 km horizontal resolution. Particulate organic matter was
 273 additionally advected by constant sinking velocity w_s . The air-sea flux of oxygen is resolved as an
 274 open boundary with a fixed equilibrium concentration as described above. Solutions were integrated
 275 until an equilibrium state was reached.

Table A3: Additional parameters for 2D idealized AMZ model.

Parameter	Symbol	Value	Units
Phytoplankton growth:			
Maximum growth rate, P_S	μ_{maxP_S}	0.5	d^{-1}
NO_x^- half-saturation, P_S	$K_{NO_xP_S}$	3.6	nM
NH_4^+ half-saturation, P_S	$K_{NH_4P_S}$	1.8	nM
Chl a -specific light absorption, P_S	$a_{P_S}^{chl}$	0.01	$m^2 (mgChl)^{-1}$
Maximum growth rate, P_L	μ_{maxP_L}	3	d^{-1}
NO_x^- half-saturation, P_L	$K_{NO_xP_L}$	327	nM
NH_4^+ half-saturation, P_L	$K_{NH_4P_L}$	164	nM
Chl a -specific light absorption, P_L	$a_{P_L}^{chl}$	0.04	$m^2 (mgChl)^{-1}$
Maximum quantum yield	ϕ	0.04	$mol\ C\ mol^{-1}\ photons$
Chl:C maximum	θ_{max}	0.2	$g\ Chl\ g^{-1}\ C$
Phytoplankton O_2 production	R_{O_2P}	7.3	$mol\ O_2: mol\ biomass\ N$
Grazing and mortality:			
Grazing coefficient	g	$2\gamma_T$	$\mu M\ N^{-1}\ d^{-1}$
Grazing efficiency	ζ	0.2	unitless
Grazer O_2 consumption	R_{O_2Z}	7.3	$mol\ O_2: mol\ biomass\ N$
Oxygen-limiting half-saturation conc. for Z_{P_i}	K_{O_2}	1	$\mu M\ O_2$
Linear mortality rate (B and P)	m_{lin}	$0.01\gamma_T$	d^{-1}
Quadratic mortality rate (B and P)	m_q	$0.1\gamma_T$	$\mu M\ N^{-1}\ d^{-1}$
Quadratic mortality rate (Z)	m_Z	$0.5\gamma_T$	$\mu M\ N^{-1}\ d^{-1}$
Fraction of mortality to POM vs. DOM	f_{mort}	0.5	unitless
Temperature dependence:			
Reference temperature	T_0	293.15	K
Temperature regulation	A_E	-4000	K
Temperature normalization	τ	0.8	unitless
Physical parameters:			
Saturated dissolved oxygen concentration	O_{2sat}	212	μM
Air-sea O_2 transfer coefficient	κ_g	$3 \cdot 10^{-5}$	$m\ s^{-1}$
Air-sea equilibration depth	h_g	100	m
Maximum incoming PAR flux	I_{max}	1000	$W\ m^{-2}$
PAR attenuation in water	k_w	0.04	m^{-1}
Mixed-layer attenuation depth	z_{ML}	20	m
Horizontal mixing coefficient	κ_X	10^3	$m^2\ s^{-1}$
Minimum vertical mixing coefficient	κ_{Zmin}	10^{-5}	$m^2\ s^{-1}$
Maximum vertical mixing coefficient	κ_{Zmax}	10^{-2}	$m^2\ s^{-1}$
POM sinking rate	w_s	10	$m\ d^{-1}$



276

277 **Figure A1:** Ratio r (mol O_2 consumed per mol OM consumed) as a function of the average aerobic
 278 heterotrophic organic matter yield $y_{OM_{B_{hetO}}}$ (mol B synthesized per mol OM consumed), for $d_{OM} = 29.1$,
 279 $d_B = 20$, and with biomass B and organic matter OM accounted for in moles of N. Here, $r \approx 6.6$ mol O_2
 280 per mol organic N, or $r \approx 1$ mol O_2 per mol organic C, reflecting our assumed organic matter stoichiometry.
 281 This value is close to the “respiratory quotient” for algal material of 0.9 mol CO_2 produced per mol O_2
 282 (Robinson 2008).

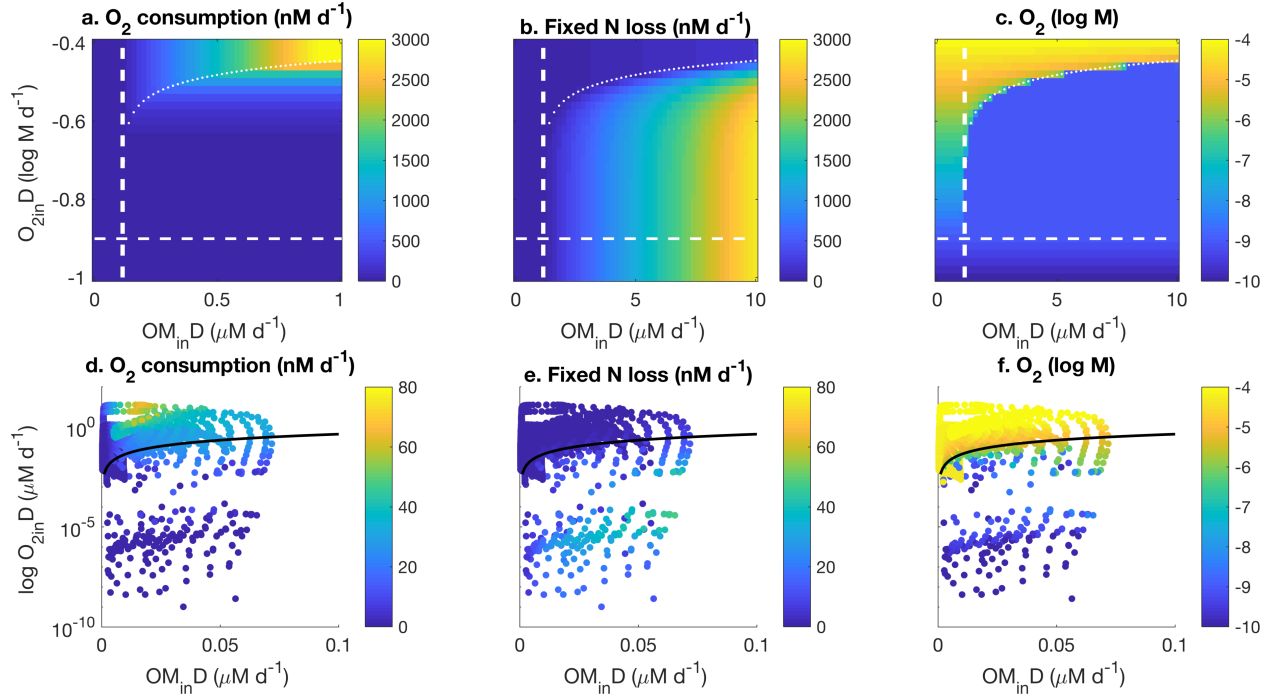


Figure A2: Top: Steady state solutions for varying ratios of oxygen and organic matter supply (incoming concentrations O_{2in} and OM_{in} and dilution rate D) in the virtual chemostat with two metabolisms (a-c), and in the 2D ecosystem model with multiple N-cycling metabolisms (d-f). The curved lines $\phi = 1$ (white lines in a-c, black lines in d-f) indicates the theoretically predicted onset of sustainable coexistence. The dashed, straight white lines in a-c correspond to the subsistence concentrations of oxygen (for the aerobic heterotrophic metabolism) and organic matter (for both aerobic and anaerobic metabolisms; the aerobic population has a slightly lower but visually indistinguishable subsistence concentration). For the 2D model solutions, the incoming oxygen and organic matter supply rates were calculated at each of the 20,000 grid points, and ϕ is calculated accounting for the divergence of the organic matter flux with ϕ_{ocean} .

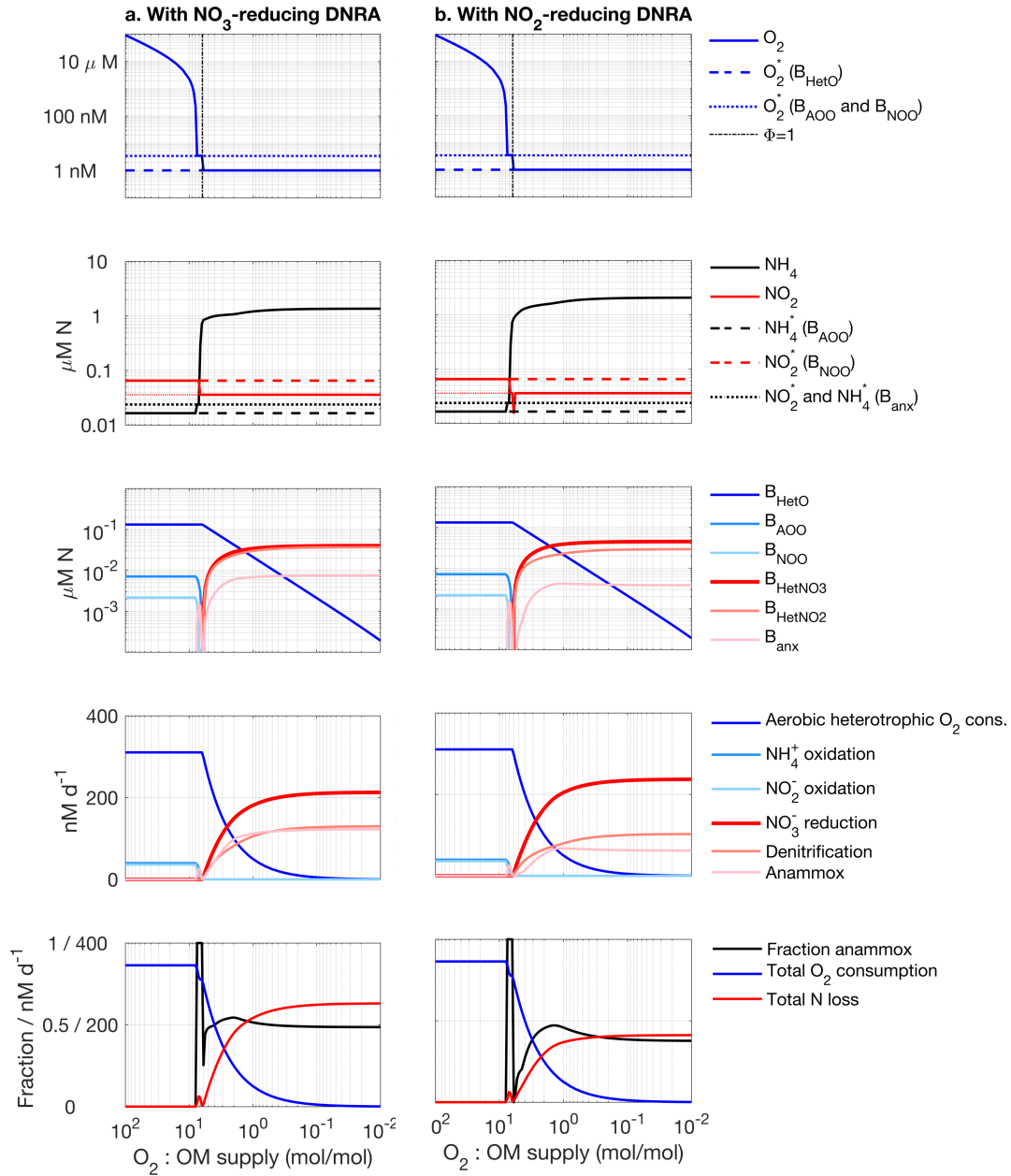


Figure A3: Chemostat model solutions when DNRA (dissimilatory nitrate or nitrite reduction to ammonium) is included as a metabolic functional type. We assumed that the organic matter yield for DNRA was equal to the other anaerobic heterotrophic functional types, allowing for its coexistence in the model with other anaerobic heterotrophs competing for organic substrate in the anoxic state. The type using NO_3^- as an electron acceptor (column a) competed against the NO_3^- -reducing heterotroph B_{HetNO_3} , and the type using NO_2^- as an electron acceptor (column b) competed against the denitrifying heterotroph B_{HetNO_2} .

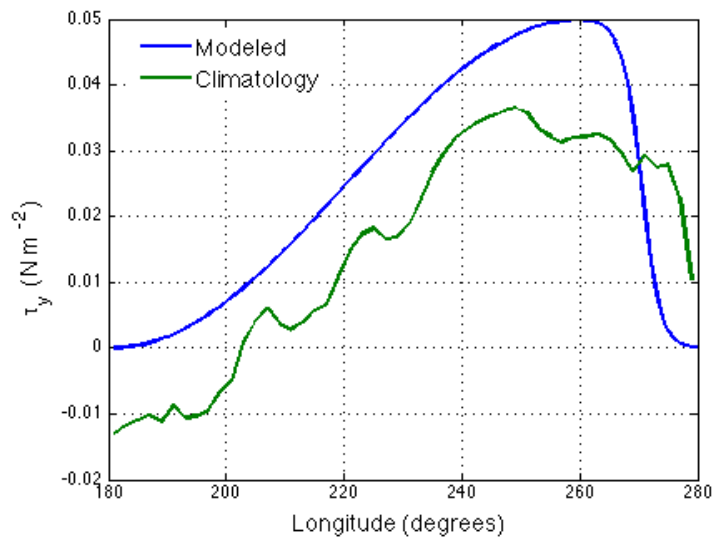


Figure A4: The modeled wind stress used as the forcing for the 2D circulation field against climatological mean. The y component of the annual mean wind stress was averaged meridionally, from the Hellerman and Rosenstein Global Wind Stress Climatology from 180°E to 80°W and 0°S to 10°S (Hellerman and Rosenstein 1983).

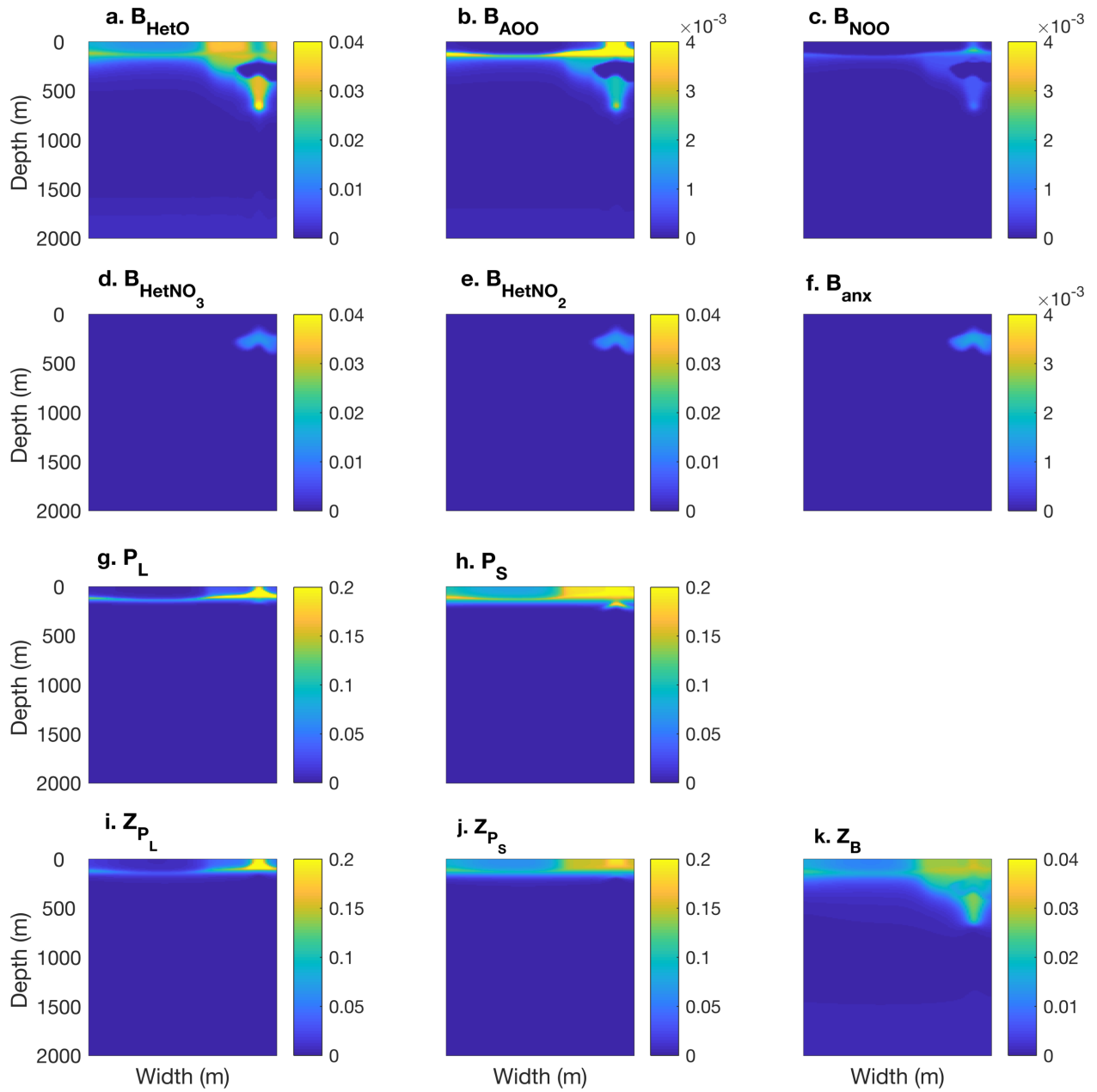


Figure A5: Steady state biomasses of the 11 functional type populations in the 2D model. Units for all: $\mu\text{M N}$.

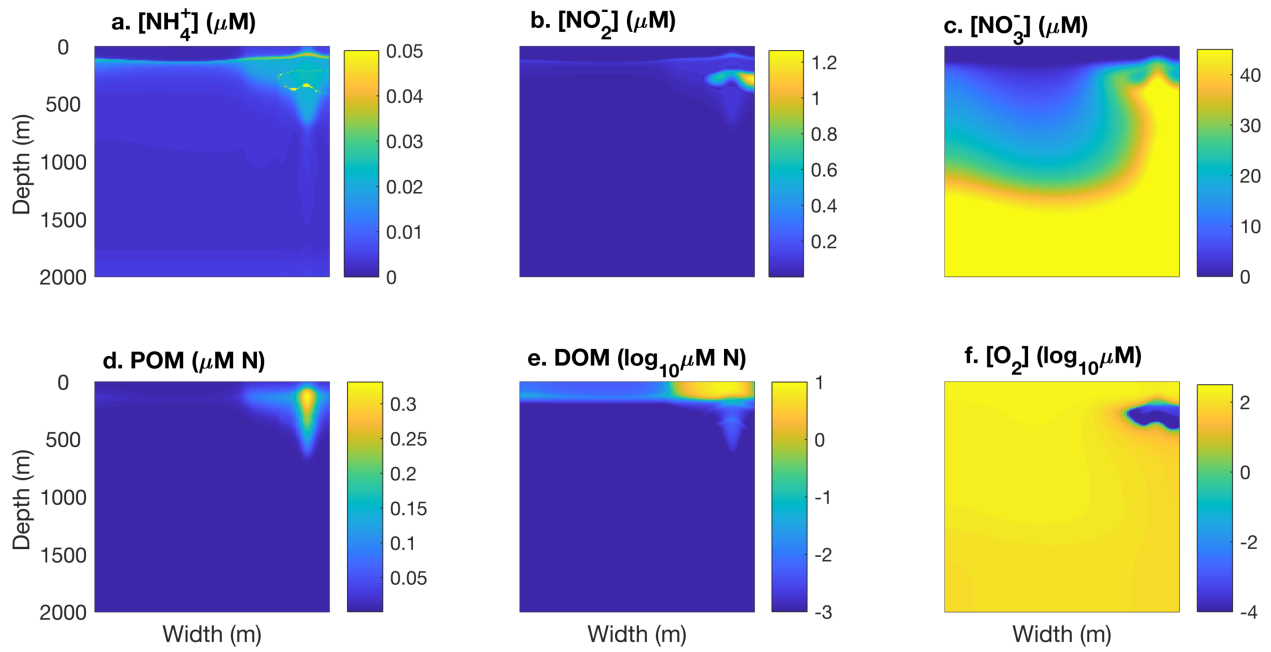


Figure A6: Steady state nutrient and oxygen concentrations in the 2D model.

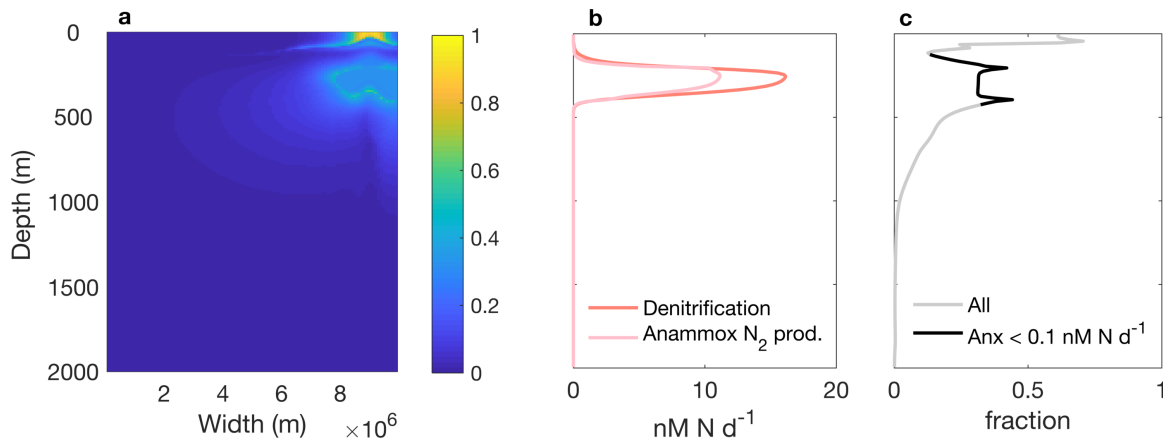


Figure A7: The fraction of anammox contribution to total fixed N loss in the 2D model. The fraction over the whole solution (a) decreases to zero (or increases in a few places) where anaerobic activity is insignificant in the aerobic domain, but this reflects the difference of small numbers. Vertical profiles of the rates of fixed nitrogen loss (b) and the fraction of anammox (c) are illustrated at the same location as in Fig. 5.

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