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Article

Keywords: DNRA, microbial processes, nitrogen cycle, oxygen, OMZ, biogeochemistry, ecosystem, coupled model, central Chile

Posted Date: September 11th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10820709/v1>

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Additional Declarations: There is **NO** Competing Interest.

DNRA stimulates aerobic microbial processes and restructures the surface planktonic community in the Chilean OMZ

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Abstract

Oxygen Minimum Zones (OMZs) are key components of the climate system, where uncertainties persist regarding the microbial processes controlling oxygen consumption and nitrogen cycling. The dynamics of the anaerobic remineralization process Dissimilatory Nitrate Reduction to Ammonium (DNRA) remain poorly understood in OMZs. Here, we implement DNRA in a simple biogeochemical model coupled to a 3 km resolution hydrodynamic model of the Chilean coastal OMZ. While the large-scale OMZ structure remains governed by physical processes, DNRA redistributes nitrogen toward recycling, away from pathways leading to fixed-N loss with negligible effects on mean oxygen. Unexpectedly, DNRA decreases nitrite and ammonium concentrations (by a factor of 5 and 2, respectively), due to a tight connection with nitrification oxidizing ammonium back to nitrate. This regenerated nitrate partly transported upward fosters growth of large phytoplankton and zooplankton. Results clarify DNRA contribution to both OMZ nitrogen cycling and surface ecosystem dynamics, and guide future observations.

Keywords: DNRA, microbial processes, nitrogen cycle, oxygen, OMZ, biogeochemistry, ecosystem, coupled model, central Chile

1 Introduction

Marine life fundamentally depends on primary production, which is itself mainly controlled by the principal limiting nutrient, most often dissolved inorganic nitrogen (nitrate essentially). To date, significant uncertainties still remain regarding the balance between nitrogen sources and sinks in the ocean. Sources include riverine inputs, atmospheric deposition, and biological nitrogen fixation (diazotrophy), whereas the dominant sinks are denitrification and anaerobic ammonium oxidation (anammox), resulting in an apparent imbalance in the nitrogen budget at basin scales that has further widened under Anthropocene conditions [1]. Approximately 30–50% of the total fixed nitrogen (N) loss in the ocean occurs within Oxygen Minimum Zones (OMZs) [1, 2]. Despite occupying about 0.1% only of the ocean volume, these regions account for a disproportionately large fraction of marine nitrogen loss. Consequently, even modest changes in OMZ extent under global warming could substantially alter the global N-cycle. Pioneering studies of N-loss processes, mainly canonical denitrification and anammox, in oxygen-deficient systems revealed a persistent imbalance between ammonium supply and demand, which might be adjusted by Dissimilatory Nitrate Reduction to Ammonium (DNRA) [3, 4], an anaerobic remineralization process that has been reported *in situ* within OMZs [5]. DNRA reduces nitrate (NO_3^-) to nitrite (NO_2^-) and subsequently to ammonium (NH_4^+), rather than to N_2 as in canonical denitrification, thereby retaining bioavailable N within the system instead of removing it [3, 6, 7]. Consequently, DNRA may represent an important source of NH_4^+ and has been proposed as one of the primary mechanism supplying the NH_4^+ required to sustain anammox where denitrification alone cannot account for the NH_4^+ demand [3, 4, 8]. Despite its potentially important role in the N cycle, the mechanisms that regulate DNRA, as well as its persistence and spatial extent, remain poorly understood.

DNRA is a two-step anaerobic respiratory process that competes with denitrification (Figure B1 in Supplemental material). The overall reaction reads : $(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 53 NO_3^- + 122 H^+ \rightarrow 106 CO_2 + 69 NH_4^+ + 53 H_2O + H_3PO_4$. The first step, the reduction of NO_3^- to NO_2^- , is shared with denitrification [3, 6, 9], whereas the second step reduces NO_2^- to NH_4^+ and so competes with denitrification for NO_2^- . In the marine environment, organic matter is the dominant electron donor supporting DNRA [10, 11]. Under oxygen-depleted conditions, NO_3^- serves as the most energetically favorable terminal electron acceptor for heterotrophic organic matter oxidation [12]. DNRA therefore represents an additional source of NH_4^+ in OMZs by coupling NO_3^- reduction to organic matter remineralization. Highly reducing conditions were thought to generally favor DNRA over denitrification because they increase the availability of electron donors, including organic carbon, sulfide, and ferrous iron, thereby promoting DNRA activity [13]. Consequently, DNRA is expected to become increasingly important toward the core of the OMZ, where reducing conditions are most pronounced [3].

The South East Pacific (SEP) OMZ was selected as the study region because DNRA activity has been quantified there using stable-isotope pairing experiments [4], corroborated by analysis of *nrfA* expression, the functional gene encoding cytochrome c nitrite reductase [3]. The SEP OMZ is one of the widest and most intense OMZs, extending offshore both Peru and Chile [14]. It is maintained by low ventilation rates and oxygen consumption associated with the decomposition of sinking organic matter from one of the most productive upwelling systems in the world’s ocean [15, 16]. The SEP OMZ experiences variability across multiple timescales. On the interannual scale, climate modes such as El Niño-Southern Oscillation (ENSO) modulate the depth of

109 its upper boundary through changes in coastal trapped waves and regional circula-
 110 tion, including the Peru-Chile Undercurrent (PCUC) [17]. On the seasonal scale, the
 111 volume of the OMZ fluctuates in response to changes in dissolved oxygen transport
 112 associated with the PCUC and alternating zonal jets [18–20]. At the mesoscale, anticy-
 113 clonic intrathermocline eddies generate pronounced vertical and horizontal variability
 114 in oxygen distribution and OMZ structure [21, 22]. In this study, we focus on mean
 115 state conditions during the 2007–2023 period, which is characterized by the occurrence
 116 of prolonged La Niña conditions conducive to the activation of anaerobic processes
 117 such as DNRA. In south-central Chile, particularly between 30°–38°S, the SEP OMZ
 118 reaches its shallowest coastal expression [19], with oxygen concentrations often falling
 119 below 1 μM in the OMZ core [23], creating favorable conditions for anaerobic nitrogen
 120 transformations such as DNRA. We therefore focused on the coastal upwelling system
 121 off Concepción (36.8°S) (Figure 1), where the seasonal intrusion of oxygen-depleted,
 122 nitrate-rich Equatorial Subsurface Waters (ESSW) fuels high primary production and
 123 intense organic matter remineralization [24–26], thereby reinforcing the reducing con-
 124 ditions ought to promote DNRA [4]. Together with the interannual ENSO variability
 125 described above, this seasonal forcing generates recurrent periods of intensified oxy-
 126 gen depletion, providing an ideal natural setting to investigate the role and dynamics
 127 of DNRA.

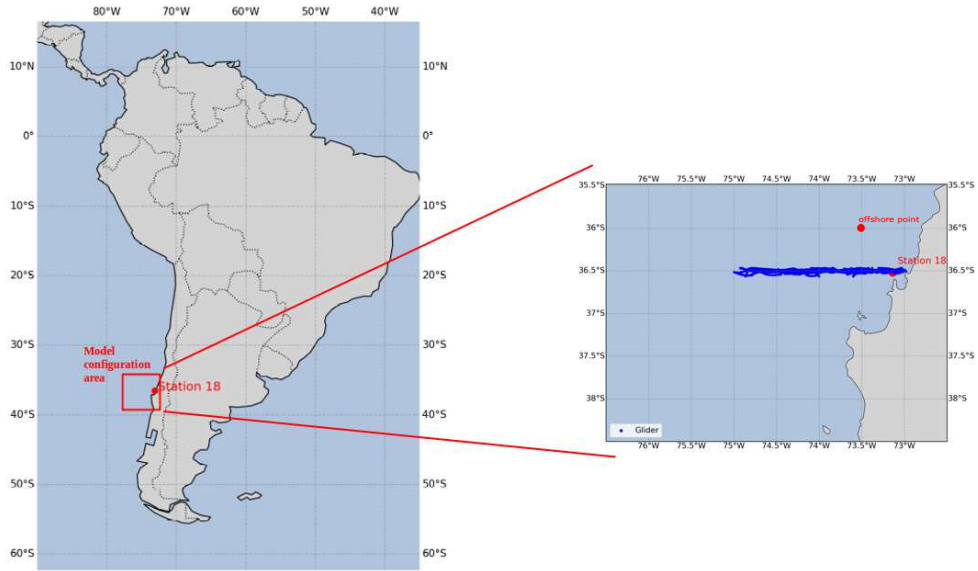


Fig. 1 Map of South America with the model domain framed in red and station 18 marked by the red dot (left). Model configuration area with station 18 and offshore point studied marked by the red dots and glider transects ([27]) available to date, marked by the blue dots (right).

128 The study region offers important observations and available measurements for
 129 both key Essential Ocean Variables (EOVs) and microbial rates. Since 2002, the Uni-
 130 versity of Concepcion has maintained an oceanographic time series at Station 18
 131 (Figure 1), located on the mid-continental shelf (36° 30', 80°S and 73° 7.75'W; 92 m
 132 water depth). The station provides continuous observations of temperature, salinity,
 133 dissolved oxygen (DO), nutrients, greenhouse gases (CH_4 and N_2O) and phyto-
 134 plankton pigments [26]. Furthermore, eight autonomous glider deployments conducted
 135 between 2010 and 2012 sampled the physical structure of the water column along a
 136 zonal transect extending from the coast to the open ocean (73°W to 75°W; [27]),
 137 providing an exceptional observational framework for model evaluation.

These long-term observations have been complemented by extensive ^{15}N tracer incubation experiments that have characterized the major nitrogen transformation pathways in the region. Although planktonic anammox, mostly performed by members of the *Candidatus Scalindua* clade, is widely distributed throughout the water column year-round [28], canonical denitrification has been identified as the dominant pathway of fixed nitrogen loss in bottom waters [29]. During summer, when oxygen depletion reaches its maximum and anoxic conditions develop near the seafloor, sulfur-driven autotrophic denitrification becomes the predominant N-loss pathway [29]. More recently, DNRA has also been quantified *in situ*, demonstrating that ammonium regeneration through nitrate reduction co-occurs with nitrogen-loss processes in the oxygen-deficient waters ($< 20 \mu\text{mol.L}^{-1}$) of the SEP OMZ [4]. Complementary benthic studies have further shown that nitrogen regeneration increases under low-oxygen conditions (about $2.68 \mu\text{M O}_2$), with enhanced ammonification and reduced denitrification in near-anoxic sediments [30], highlighting the importance of ammonium recycling across the coastal system. In addition, nitrogen fixation has been documented throughout the annual cycle, reaching maximum rates during late summer and autumn and being largely sustained by heterotrophic diazotrophs [31]. Collectively, these observations provide one of the most comprehensive characterizations of marine nitrogen cycling available for any eastern boundary upwelling system.

The limited measurements of total DNRA rates, as well as of the individual nitrate- and nitrite-reduction steps available for the SEP OMZ (Table B1 in Supplemental material), reveal pronounced spatiotemporal variability [3, 4, 9], while the environmental controls governing this variability remain poorly understood. Beyond the considerable challenges associated with measuring DNRA in the field, its role has also remained largely unexplored from a theoretical perspective because the process has not yet been incorporated into the coupled physical-biogeochemical models currently used to investigate N-cycling in OMZs (e.g. [32, 33]). Currently none of the global Earth System Models participating to the CMIP include this process.

In this study, we investigate how a more comprehensive representation of anaerobic biogeochemistry, through the incorporation of the DNRA pathway into a regional coupled physical-biogeochemical ocean model, alters nitrogen fluxes and organic matter transformations within the Chilean Oxygen Minimum Zone. Beyond the direct production of NH_4^+ , we demonstrate that DNRA modulates the availability of inorganic nitrogen species together with organic matter fluxes and stocks, generating cascading effects across the ecosystem. These effects extend from the reorganization of aerobic and anaerobic nitrogen cycling processes—including denitrification, anammox, and nitrification—to the restructuring of the surface planktonic community.

This paper is organized as follows. Section 2 presents the results, structured around three themes: the mean effect of DNRA on nitrogen fluxes, the interactions between aerobic and anaerobic layers, and the restructuring of flux contributions. Section 3 discusses these findings, first examining the reorganization of the nitrogen cycle induced by DNRA, then assessing the robustness of our results through a sensitivity analysis to a range of anaerobic thresholds and DNRA kinetics. Concluding remarks are provided in Section 4. Finally, Section 5 describes the model configuration and the experimental design, including the control and DNRA simulations.

2 Results

A sensitivity analysis was performed with respect to the DNRA kinetics and the anaerobic oxygen concentration threshold, as described in Section 5. Twelve configurations were tested (Table B2 in Supplemental material). For clarity we first focus here on the median configuration (i.e. V_{max} combined with an anaerobic threshold of $45 \mu M$) as it represents the central point of the explored parameter space. This choice allows us to interpret the main effects of DNRA under the same conditions as denitrification, before examining their sensitivity to parameter uncertainty in Section 3. Using this configuration, we compare the run incorporating DNRA to a control run without DNRA.

2.1 Overall impact of DNRA

In the following, to illustrate the cascading effects induced by DNRA, we focus on an offshore location ($36^\circ S$; $73.7^\circ W$) where the model simulates a particularly intense DNRA activity. Figure 2 shows the mean vertical profiles of the main biogeochemical fluxes and state variables for simulations with (solid lines) and without (control run, dashed lines) DNRA over the period 2008-2014. The gray shadow represents the depth where O_2 is less than $60 \mu M$. The simulated DNRA profiles show consistently higher rates of nitrite reduction than nitrate reduction. Maximum DNRA rates occur at approximately 100 m depth, near the upper OMZ boundary, where oxygen concentrations begin to decline into the hypoxic range. Counterintuitively, DNRA does not significantly modify vertical NO_3^- distribution, and does not increase NO_2^- and NH_4^+ stocks. Instead, the inclusion of DNRA led to a decrease of $0.3 \mu M$ (88%) in NO_2^- and $0.15 \mu M$ (55%) in NH_4^+ at their respective shallow peak (primary relative maxima), located in the middle of the oxycline at approximately 30 m depth. A secondary deeper relative NO_2^- and NH_4^+ maxima are also reported around the hypoxic-suboxic interface (≈ 100 m depth), which is consistent with DNRA occurrence and maxima at similar depth. For NO_2^- , this secondary maxima is around 50 m shallower compared to the control run, whereas for NH_4^+ , this secondary peak is new (no visible in the CTRL run). Similarly to the NO_3^- distribution, the O_2 profile appears mostly unchanged. Figure 2 also shows that DNRA activation differentially impacts phytoplankton and zooplankton according to their size. Specifically, within the upper 50 m, the nitrogen biomass of large phytoplankton (LPHY) and large zooplankton (LZOO) increases by nearly 0.55 and $0.45 \mu M$, respectively, corresponding to relative increases of 44% and 60%. In contrast, small phytoplankton (SPHY) and zooplankton (SZOO) decrease by 60% and 18%, respectively. Regarding organic matter pools, the inclusion of DNRA reduces the near-surface peak concentration of small detritus (SDET) by approximately 50% and that of dissolved organic nitrogen (DON) by 14%. In contrast, large detritus (LDET), which remained at low concentration and displayed a relative uniform vertical distribution with a deeper maximum (around 50 m), increased within the oxygenated layer before declining to nearly zero within the oxygen-deficient layer.

Figure 2 further shows that the addition of DNRA significantly impacts both anaerobic and aerobic processes in the nitrogen cycle. Maxima of both steps of denitrification are displaced upward toward the upper OMZ boundary from 150 to 100 m deep, near the $60 \mu M$ O_2 isopleth. Whereas the peak of the first step of denitrification (nitrate reduction) increases by 55% ($0.3 \cdot 10^{-7} \mu M.s^{-1}$) compared to the control run, the second step (nitrite reduction) undergoes a substantial reduction in its maximum activity (50%). The anammox peak also shifts upward from 150 m to 100 m, closer to the upper OMZ boundary, and is restricted to a narrow depth interval; its maximum

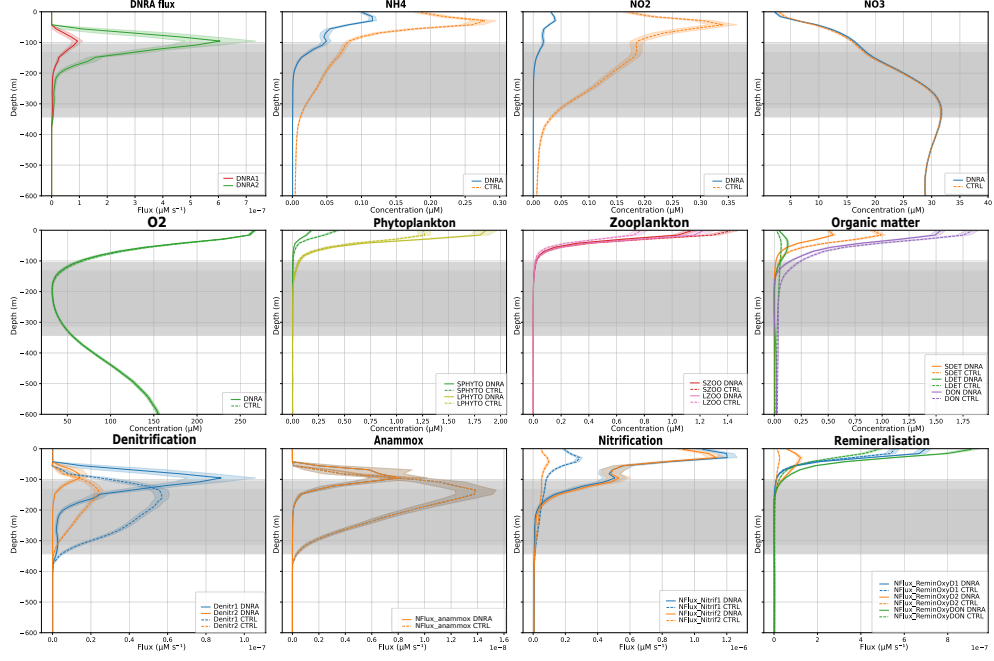


Fig. 2 Comparison between the DNRA (solid lines) and CR (dotted lines) runs at (36°S ; 73.7°W ; offshore point): Vertical profiles of nutrients, DO, phytoplankton, zooplankton, organic matter, remineralization, and the processes of nitrogen loss and nitrogen cycling from surface to 600m depth time-averaged on 2008-2014 period. The DNRA run uses an anaerobic threshold (O_{2dn}) at $45\mu\text{M}$ in the V_{max} formulation. The envelope around each profile corresponds to the temporal standard deviation obtained using a bootstrap method (see Method section 5.2). The dark gray horizontal band corresponds to depths where the time-averaged oxygen concentration is less than $60\mu\text{M}$, with the standard deviation of this average shown in light gray.

rate decreases by 43%, from approximately $1.4 \cdot 10^{-8} \mu\text{M.s}^{-1}$ to $0.8 \cdot 10^{-8} \mu\text{M.s}^{-1}$.

To quantify the net effect of DNRA on denitrification and anammox across the water column, vertical profiles were integrated over the 0–600 m depth interval. Despite the local increase in the maximum activity of the first step of denitrification, its depth-integrated value is reduced by 52% in the simulation including DNRA relative to the control (from $5.251 \cdot 10^{-6}$ to $2.498 \cdot 10^{-6} \mu\text{M.m}^{-2}.\text{s}^{-1}$). More notably, the depth-integrated anammox rate decreases by 80% (from $2.6 \cdot 10^{-7}$ to $1.3 \cdot 10^{-7} \mu\text{M.m}^{-2}.\text{s}^{-1}$), indicating that inclusion of DNRA substantially reduces the loss of total fixed-nitrogen through both denitrification and anammox across the water column.

The rates of both nitrification steps increase markedly within the upper 150 m of the water column. The maximum rate of the first step (ammonium oxidation) increases 5.5-fold, from $0.22 \cdot 10^{-6} \mu\text{M.s}^{-1}$ to $1.2 \cdot 10^{-6} \mu\text{M.s}^{-1}$, whereas the second step (nitrite oxidation) increases 11.5-fold, from $0.1 \cdot 10^{-6}$ to $1.15 \cdot 10^{-6} \mu\text{M.s}^{-1}$. In addition to the surface maximum at approximately 30–50 m depth, both nitrification steps develop a second, deeper maximum near 100 m, at the hypoxic-suboxic transition. This deep nitrification maximum occurs immediately above the depth of maximum DNRA rates and is approximately 50 times greater than the maximum anammox rate. Over the water column (0–600m depth), the integration of the vertical profiles of the total nitrification shows an increase of nearly 300% (from $3.98 \cdot 10^{-5}$ in the control simulation to $1.58 \cdot 10^{-4} \mu\text{M.m}^{-2}.\text{s}^{-1}$ in the DNRA simulation).

Remineralization rates also increase for all organic matter pools (DON, SDET, and LDET; Figure 2). Within the upper 50 m depth, remineralization rates increase by approximately 4, 1.2 and $0.6 \cdot 10^{-7} \mu M.s^{-1}$ for DON, SDET and LDET, respectively. These changes correspond to increases of approximately 100% for DON, 22% for SDET and 150% for LDET. The profiles integrated over 0-600m depth show an increase of 73% of the total remineralization over the water column. Overall, the inclusion of DNRA modifies not only inorganic nitrogen pools but also organic matter remineralization, affecting the intensity of both anaerobic and aerobic nitrogen transformation processes in the suboxic and oxic layers.

2.2 Oxic-suboxic layer exchanges

To further interpret the changes induced by DNRA activation, the temporal mean (2008-2014) vertical advective and diffusive fluxes of NO_3^- , NO_2^- and NH_4^+ are shown in Figure 3, for both simulations. The dominant vertical fluxes involve NO_3^- , which are significantly higher ($\times 10$) than those of NO_2^- and NH_4^+ .

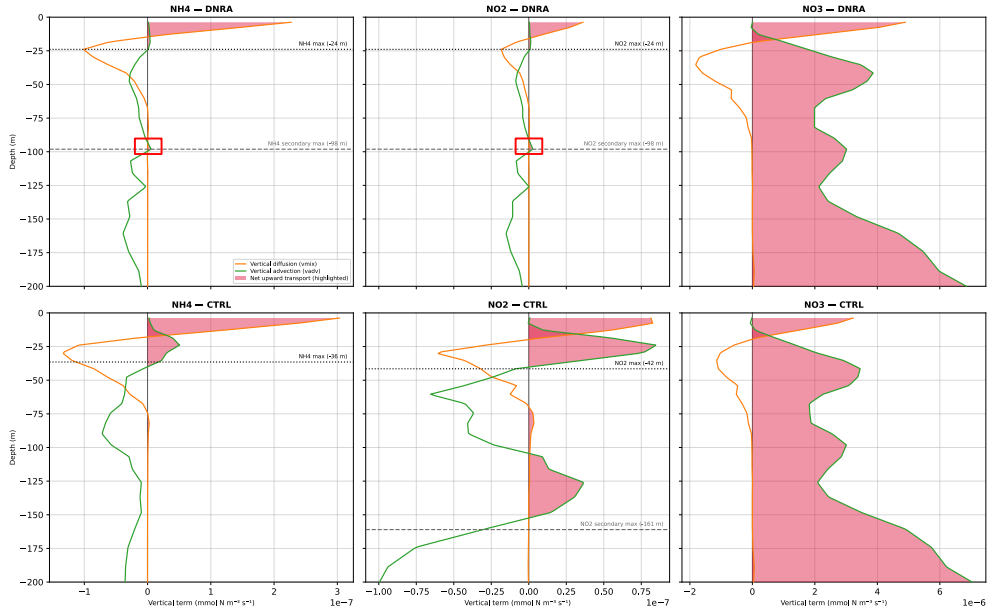


Fig. 3 Vertical profiles of the vertical advection (vadv, green) and diffusion (vmix, orange) tendency terms for NH_4^+ , NO_2^- and NO_3^- (columns) in the anaerobic-aerobic exchange layer (0–200 m) at the offshore station (36°S, 73.7°W), comparing the DNRA simulation (top row) and the CTRL simulation (bottom row). The red color filling part of the profile indicates upward flux for both advective and diffusive terms, including upward flux in thin layer (boxed in red) around 100 m for NH_4^+ and NO_2^- . Dotted horizontal lines with depth labels mark the mean depth of the relative primary and secondary NH_4^+ and NO_2^- concentration maxima for each simulation, since the magnitude of their advective and diffusive fluxes depends primarily on the vertical position of these peaks. Profiles are averaged over 2008–2014.

For NH_4^+ , the primary relative concentration maximum occurs at 24 m depth in the DNRA run (Figures 4 and 3), compared to 35 m depth in the control (CTRL) run, indicating that the peak shifts closer to the surface with DNRA. Moreover, a secondary relative maximum is observed at 98 m depth, signal of the DNRA activity. Diffusion is strongly positive near the surface (0 to ≈ 10 m depth; upward flux) and then becomes negative down to ≈ 90 m depth. In the surface layer between ≈ 0 m

and 30 m, the advective term is positive with an upward transport for the CTRL run only. On the contrary, in the subsurface around a secondary relative maximum at ≈ 100 m, near the anaerobic-aerobic interface (cf. shaded area in Figure 2), a minor upward transport occurs across a very thin layer, as indicated by the positive advective term. This feature is observed only in the DNRA run and coincides with the relative maxima of DNRA and nitrification.

For NO_2^- , the difference between the two simulations is the most pronounced. Although both runs have the same configuration with two relative maxima in NO_2^- concentrations (Figures 2 and 3), these maxima are more intense in the CTRL run. Furthermore, these two relative maxima are shallower (24 m and 98 m, respectively) in the DNRA run than in the CTRL run. Upward diffusive flux occurs mainly in surface (0-20 m) as well as upward advective flux (above the primary relative maximum) but much more intense in the CTRL. In subsurface, above the secondary relative maxima, both runs show upward transport, which is more intense in the CTRL run. In the DNRA run, this transport is correlated to the secondary maximum at ≈ 100 m, near the anaerobic-aerobic interface (cf. shaded area in Figure 2), where relative maxima in DNRA and nitrification are observed. In this run, the amplitude of advective and diffusive fluxes greatly reduced throughout the water column, becoming virtually zero beyond ≈ 100 m depth, in the suboxic zone. This marked attenuation of vertical NO_2^- transport with DNRA reflects local consumption (nitrification) that occurs faster than transport, thereby limiting its vertical redistribution on a very thin layer at the anaerobic-aerobic interface. Therefore, NH_4^+ and NO_2^- show a slight positive advective peak at a depth of about 100 m (red boxes in Figure 3), where the secondary maximum of NO_2^- and NH_4^+ is observed. This induces a very local upward advection of both NH_4^+ and NO_2^- to the aerobe boundary where the deep nitrification maxima occur.

For NO_3^- , the DNRA and CTRL profiles are very similar in shape: positive diffusion near the surface and positive advection that increases with depth, dominating all other fluxes (up to $6\text{--}7 \cdot 10^{-6} \mu M \cdot s^{-1}$ at 200 m depth). The upward advection of NO_3^- appears significantly more intense (+12.7%) in the DNRA run between 0 and 80 m, confirming a consistent effect of the production of NO_3^- at a substantial secondary relative nitrification maximum. To elucidate these dynamics and understand how DNRA modifies the balance among tendency terms, we examine the physical and biogeochemical source and sink terms governing each state variable.

2.3 Sensitivity of nitrogen-related tracer budgets to DNRA activation

To further understand how DNRA modulates nitrogen-related fluxes, we decompose the depth-integrated fluxes into their biological and physical advection+diffusion contributions for both the 0-150m and the 150-300m layers (Figure 4). Across almost all the biogeochemical variables, a consistent vertical pattern emerges over the upper 300 m, characterized by surface layer peak followed by a gradual decrease with depth. Vertical physical transport thus contributes to a sink (always negative) for all the variables in 0-300 m but NO_3^- and O_2 , for which there is a vertical physical gain in the 150-300 m layer. The vertical contribution is always compensated by an opposite horizontal contribution, generally a gain from the coastal shallower area in 0-300 m, from the South in the upper 0-100 m layer and from the North in the lower (100-300 m) layer associated with the PCUC, according to the mean latitudinal and longitudinal velocities (see Figure B3 in supplemental material). O_2 and NO_3^- are largely controlled by physical processes, especially in the OMZ core (cf 150-300 m), whereas

fluxes of the other variables result from relatively balanced influences of the physical and biogeochemical processes. In the DNRA run, the integrated fluxes of all variables decrease in the surface 0-150 m compared to the control run. This is most striking for NO_2^- , whose net biological production is divided by 10 in the aerobic layer and becomes near zero in the anaerobic layer, confirming that it is consumed *in situ* by nitrification rather than produced or exported at either depth; horizontal import and vertical export of NO_2^- are also strongly reduced (by up to two orders of magnitude) in the 150-300 m layer. Similarly, biological production of NH_4^+ is weaker in the DNRA run at both depths, consistent with enhanced consumption via nitrification rather than lateral export. The planktonic compartments confirm the size-structured response already seen in the concentration profiles (Figure 2): small phytoplankton and zooplankton show reduced biological, horizontal and vertical fluxes in the DNRA run, whereas large phytoplankton and zooplankton are sustained by intensified lateral (horizontal) and vertical transport despite stronger local biological losses, particularly in the aerobic layer. For NO_3^- in the 0-150 m layer, NO_3^- advective and diffusion upward flux is slightly higher in DNRA than CTRL run, with an increase of diffusive term mainly between 25 and 50 m, mitigating the effect of NO_3^- upward advection enhancement (Figure 4). In the deeper layer, O_2 shows a modest increase in supply (less negative biological flux, more positive vertical flux) in the DNRA run. Finally, on both layers (0-150 m and 150-300 m), large organic and planktonic compartments (LDET, LPHY, LZOO) show enhanced horizontal and vertical transport with little change in their biological fluxes, indicating that their dynamics at depth are primarily transport-driven.

To examine in detail the individual biogeochemical processes underlying this reorganization, we now turn to the full flux budget decomposition for each state variable (Figures 5, 6 and Figure B4 in Supplemental material). The biogeochemical budgets integrated over 0-150 m and 150-300 m layers provide a consistent picture of how DNRA reshapes nitrogen cycling and ecosystem functioning at this offshore location. Within the aerobic layer, the clearest fingerprint of DNRA activity, reaching $10^{-5} - 10^{-6} \mu M.m.s^{-1}$, is the appearance of substantial nitrogen fluxes through the increased consumption of LDET, SDET, DON and NO_3^- , and channeling NO_3^- toward NH_4^+ production. Despite an intensified nitrification in the DNRA run, NO_3^- is diverted away from phytoplankton assimilation and the resultant, increased competitive assimilation for the remaining NO_3^- appears to be in favor of large phytoplankton (Figure 5a, Figure B4 a in Supplemental material). Within the lower surface layer (75-150 m) (Figure 2) that shows suboxic conditions, DNRA efficiently competes with denitrification. But despite this additional NH_4^+ source, concentrations of NH_4^+ are paradoxically lower throughout the water column in the DNRA run (Figure 2). The budget analysis resolves this apparent contradiction by revealing that the produced NH_4^+ is rapidly re-oxidized through an intensified nitrification flux (Nitrif1 and 2, $\approx 10^{-4} \mu M.m.s^{-1}$), leaving little time for local accumulation of NH_4^+ or NO_2^- (Figure 6a). The secondary nitrite maximum at 100-150 m is also substantially reduced (-88%) in the DNRA run relative to the control run, (Figure 2), consistent with a faster downstream consumption of NO_2^- through the intensified nitrification pathway rather than its accumulation. Associated with an increase of the advective upward NO_3^- transport in 0-150 m layer (+6%), this $NO_3^- \rightarrow NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$ short circuit comes at a direct cost for primary producers with a response clearly size-structured. SPHY concentrations are visibly reduced throughout the aerobic zone in the DNRA run relative to the control (-67%) (Figure 2), consistent with reduced production in the budget differences (Figure 6a). In contrast, LPHY concentrations are higher (+52%) in the DNRA run (Figure 2). The budget analysis indicates that this increase is mainly driven by stronger local

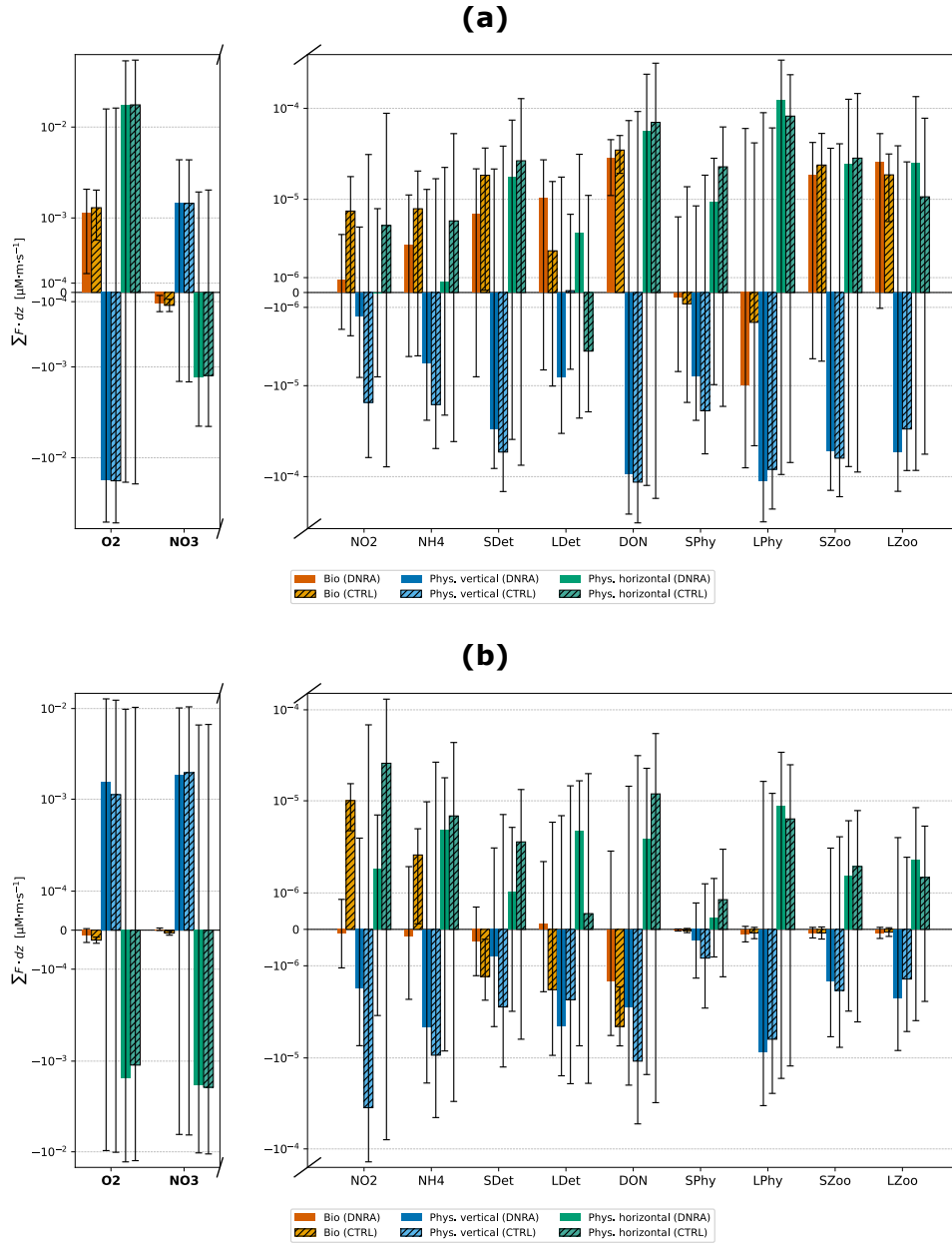


Fig. 4 Budgets of biogeochemical tracers at (36° S, 73.7° W): Total mean (2008-2014) biogeochemical and physical (advection + diffusion) contributions to the rate of change in tracers' concentration in the (solid bars) DNRA and (hatched bars) control simulations at (a) 0–150 m and (b) 150–300 m depth. Positive values represent net gains in the corresponding layer, and negative values indicate net losses. All y-axes are shown on a logarithmic scale. Vertical segments represent the RMSE about the mean, reflecting intra to inter-annual variability. Because O_2 and NO_3 flux magnitudes exceed those of the other variables by one to two orders of magnitude, they are plotted on a separate sub-panel with its own y-axis to preserve the resolution of the smaller fluxes.

production, complemented by enhanced horizontal advective import from the coast (Figure 6a).

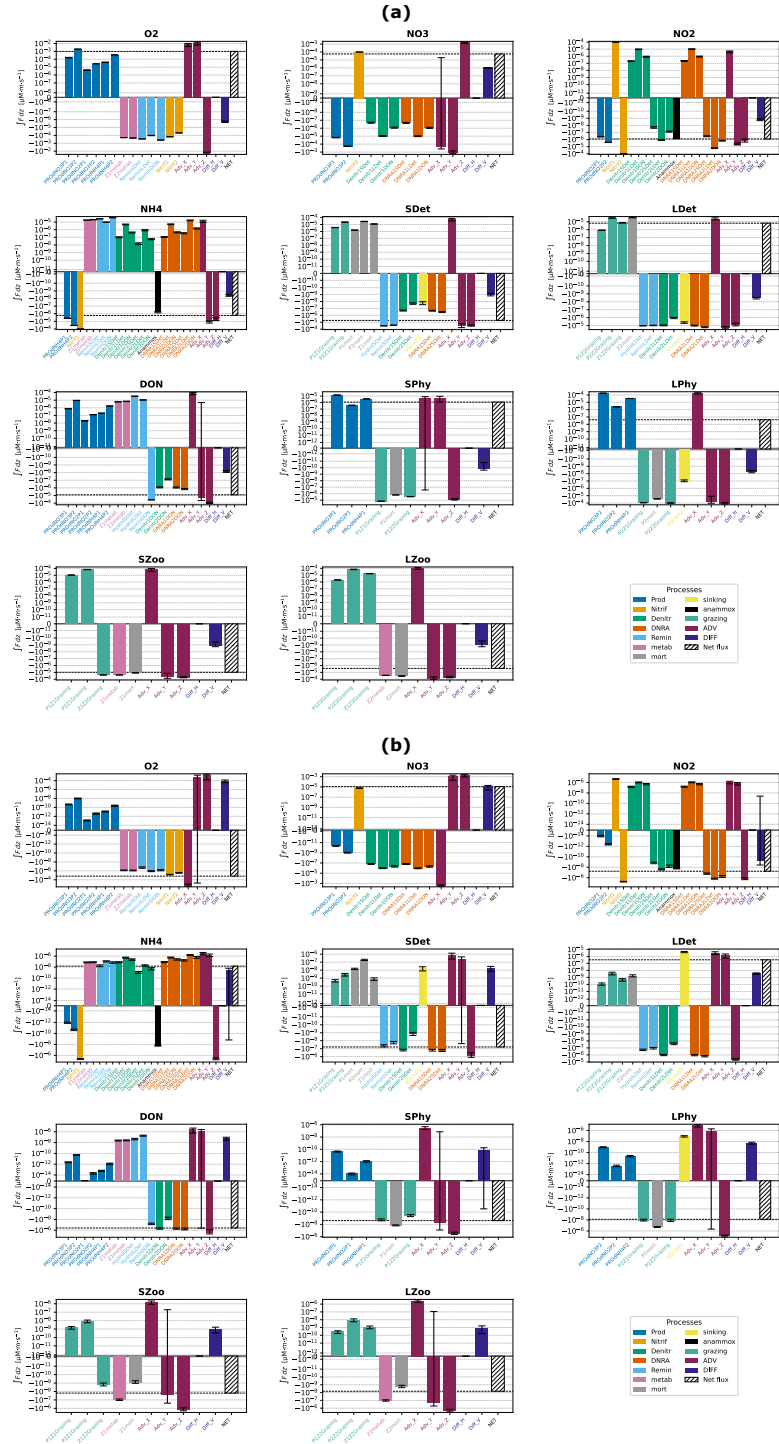


Fig. 5 Vertically integrated biogeochemical budgets at the offshore point (lat = 36.0°S, lon = 73.7°W). Contributions of individual processes to the net tendency of each tracer are shown for the DNRA run (V_{max} with anaerobic threshold (O_{2dn}) at 45 μ M) for the upper aerobic layer (0-150 m) (a) anaerobic layer (150-350 m) (b). Bars represent the mean integrated fluxes (μ M s $^{-1}$) computed over the 2008–2014 period, while error bars indicate the error in the mean estimated via bootstrap resampling. Colors denote process categories (i.e., biological production, nitrification, denitrification, DNRA, remineralization, metabolism (excretion), mortality, anammox, grazing, advection, and diffusion). Positive (negative) values indicate sources (sinks) of the considered tracer. The y-axis is displayed on a symmetric logarithmic scale to emphasize both small and large contributions.

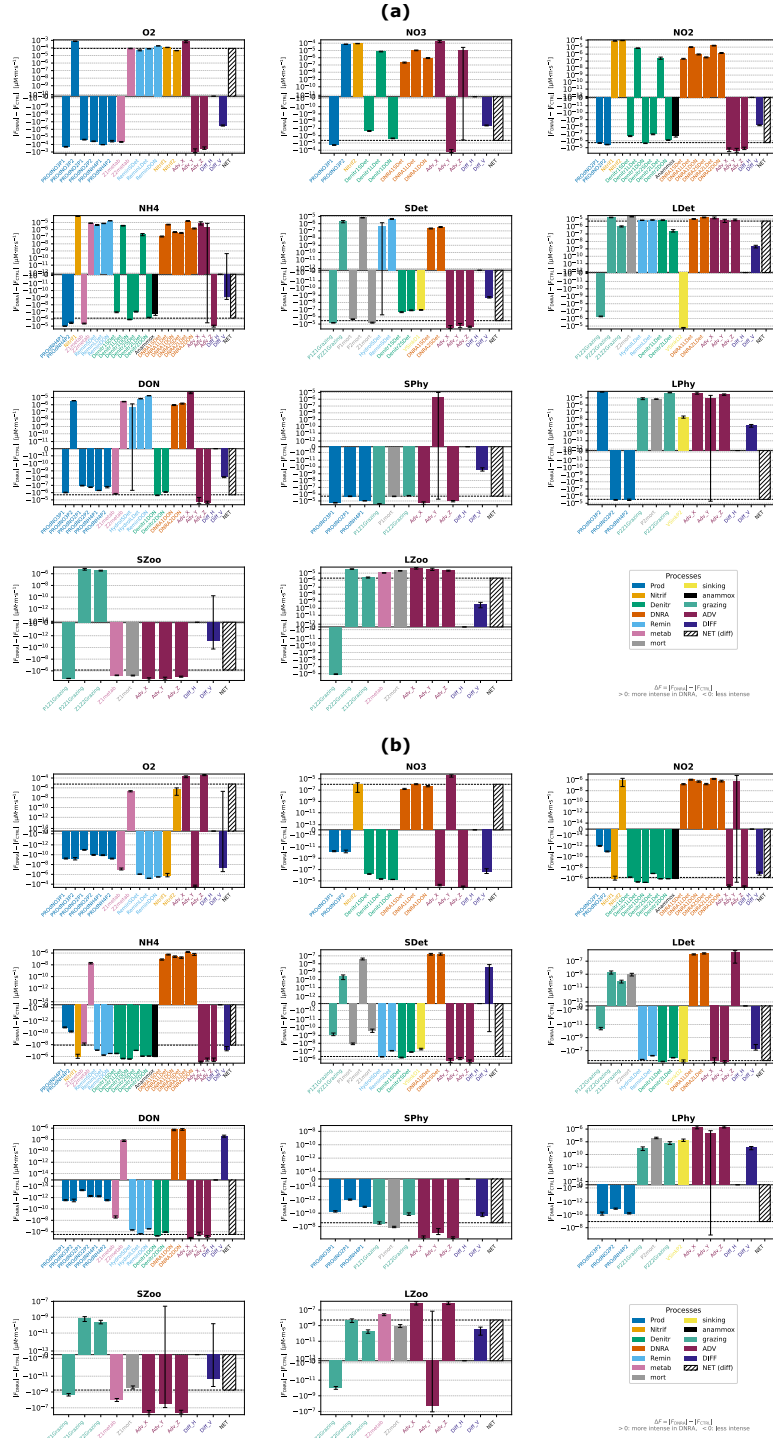


Fig. 6 Differences of vertically integrated biogeochemical budgets at the offshore point (lat = 36.0°S, lon = 73.7°W) between the DNRA run (V_{max} with anaerobic threshold (O_{2dn}) at 45 μM) and the control run. For each process term, the bar represents $\Delta F = |F_{DNRA}| - |F_{CTRL}|$ where F is the vertically integrated flux over the aerobic layer (0–150 m, panel a) and the anaerobic layer (150–350 m, panel b). A positive bar indicates that the process is more intense in the DNRA run, regardless of its sign (source or sink); a negative bar indicates a weaker process in the DNRA run. The hatched bar (NET) shows $|\Sigma F_{DNRA}| - |\Sigma F_{CTRL}|$ i.e. the difference in the amplitude of the total budget: positive when the net tendency is larger in magnitude in DNRA than in CTRL, negative otherwise.

This size-based reorganization extends consistently through the food web. SZOO biomass decreases together with SPHY, as shown by Figure 2. This pattern agrees with the reduced grazing fluxes identified in the budget analysis (Figure 6a). In contrast, LZOO biomass increases in the DNRA run (2), following the greater availability of LPHY. The organic matter pools show a differentiated response depending on particle size. While LDET shows higher net flux in the DNRA run than in CTRL, SDET and DON show lower net fluxes in the DNRA run than in CTRL (Figures 5a, Figure B4 a in Supplemental material, Figure 6a), consistent with the reduced solid-line profiles visible in Figure 2. This reduction reflects a weakening of their primary biological sources: lower SPHY mortality, reduced SZOO metabolic excretion, and diminished fecal pellet production collectively curtail the supply of both particulate and dissolved organic nitrogen across all size classes. Increased LDET production, resulting from LZOO and SZOO grazing, increased LZOO mortality, and horizontal advective import of LDET in the DNRA run (Figure 5a) are inducing higher hydrolysis as well as aerobic and anaerobic (denitrification and DNRA) remineralisation. These processes consume LDET and therefore mitigate its increase compared to the CTRL run. Anammox activity is also slightly reduced in the DNRA run (6a), consistent with the faster upstream consumption of NO_2^- through the intensified nitrification pathway, which limits NO_2^- availability for anammox bacteria.

Deeper in the water column, between 150 and 300m, DNRA fluxes are two orders of magnitude weaker (Figure 2) due to the organic substrate limitation; yet this layer is not left unaffected. A strengthened vertical oxygen advection (Adv_Z) emerges as the dominant difference between both runs at this depth (Figure 6 b), producing a slightly better-oxygenated mesopelagic environment in the DNRA run. This signal is too subtle to translate into a noticeable difference in oxygen concentration in the O_2 profiles (Figure 2) but is robustly captured by the integrated budget approach. The organic matter pools also show a consistent, though attenuated, response at this depth: SDET, LDET, and DON budgets remain slightly lower in the DNRA run compared to the CTRL (Figures 5b, 6b), consistent with the profiles of those pools in Figure 2. The modest improvement in oxygen conditions is associated with elevated metabolic and grazing fluxes of large zooplankton in the 150–300 m budget of the DNRA run (Figure 5b). However, given the small magnitude of the oxygen difference and the absence of an unambiguous signal in the concentration profiles (Figure 2), this potential ecological response should be interpreted with caution, and no direct causal link between the slight oxygen increase and the zooplankton response can be firmly established.

3 Discussion

The present study examines how incorporating DNRA into the BioEBUS ecosystem model reshapes the balance between nitrogen recycling and fixed-nitrogen loss. We first identify a bypass effect associated with DNRA, whereby nitrogen is diverted from pathways leading to permanent nitrogen loss and redirected toward recycling within the system. We also assess the sensitivity of this response to the oxygen threshold activating anaerobic processes and to DNRA kinetics parameters.

3.1 Revisiting the N cycle: strengthening anaerobic–aerobic microbial coupling within 75–200 m

3.1.1 DNRA-nitrification coupling

Although DNRA has long been suggested as an important player in the biogeochemistry of OMZs, its system-wide effects on the nitrogen budget have remained difficult to describe, quantify, and disentangle from other processes. Our simulations show that incorporating DNRA into the BioEBUS model shifts the balance between nitrogen retention and fixed-nitrogen loss, with effects that propagate throughout the system and extend to trophic interactions.

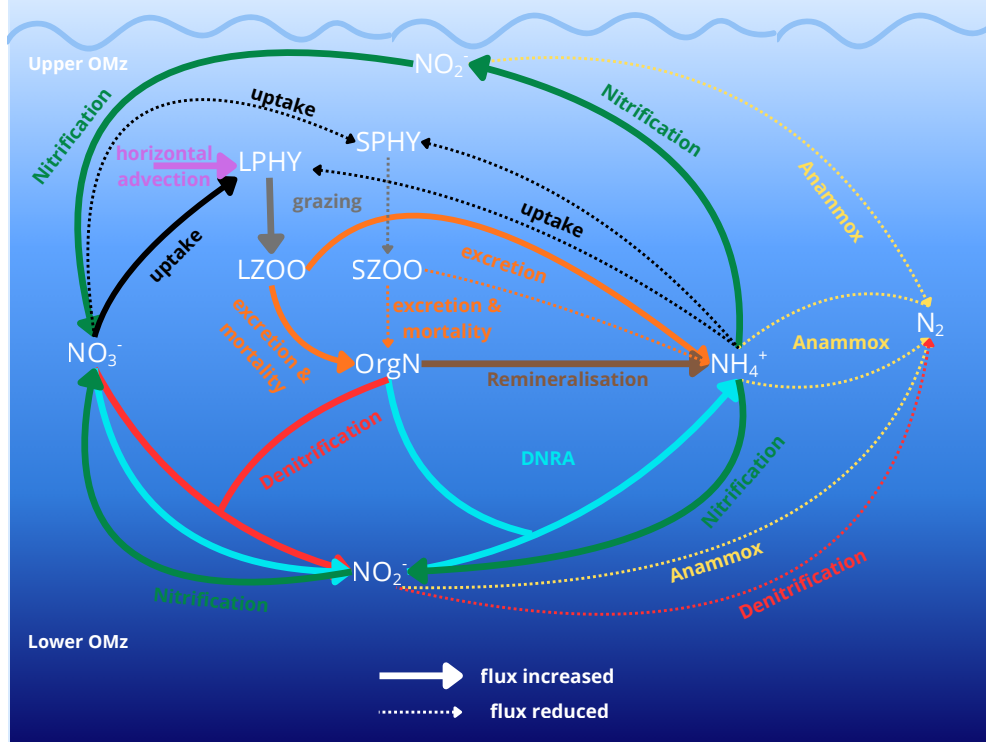


Fig. 7 Summary diagram of the impact of DNRA on the nitrogen cycle and the food chain. A color code is used to indicate the processes at work. Arrows shown as solid thick lines indicate an increase in the rate of change of the corresponding tracer, whereas dotted arrows indicate a decrease

The summary diagram (Figure 7) synthesizes the full architecture of the way DNRA reshapes nitrogen cycling across the OMZ, in both the aerobic and anaerobic layers. DNRA channels NO_3^- and NO_2^- reduction toward NH_4^+ rather than N_2 . Moreover, for simplicity, we use maps of mean gradient (Figure 8) of key state variables to interpret the results, assuming that non-linear advection has a secondary role. Those maps provide a clear and immediate signature of the competition on the nitrite field.

Horizontally, the control run displays intense and spatially heterogeneous NO_2^- gradients (Figure 8e), reaching up to $\approx 4\text{--}5 \cdot 10^{-6} \mu\text{M m}^{-1}$, with the strongest values concentrated along the northern and eastern boundaries, a pattern consistent with active nitrite accumulation driven by remineralisation and incomplete denitrification

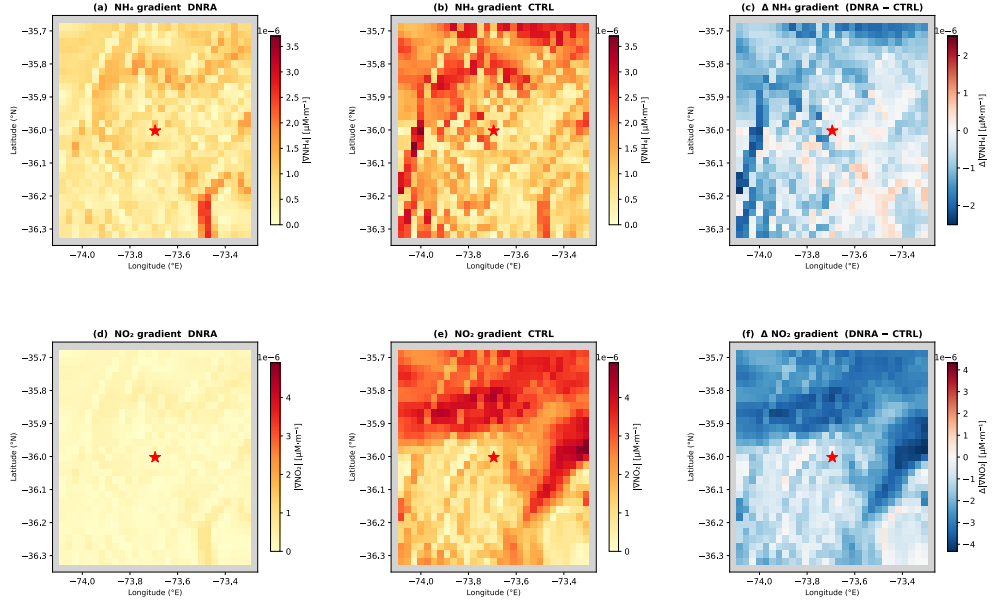


Fig. 8 Horizontal mean gradient magnitude $|\nabla C|$ of NH_4^+ (panels a to c) and NO_2^- (panels d to f) averaged over 2008–2014 within the 0–150 m layer, around the offshore point (36°S, 73.7°W). Panels (a, d) show the DNRA simulation (including the dissimilatory nitrate reduction to ammonium process), panels (b, e) the control run (CTRL), and panels (c, f) their difference (DNRA - CTRL); the red star marks the offshore point.

in the coastal upwelling system [34]. Vertically, this same accumulation manifests as a broad depth-concentration distribution, with NO_2^- extending up to $0.10\text{--}0.12 \mu M L^{-1}$ between approximately 100 and 400 m (Figure 9), consistent with the secondary nitrite maximum typically observed in OMZs [35]. DNRA suppresses both signatures at once: lateral gradients collapse and the depth-concentration distribution shifts toward negligible values throughout the water column, up to 88% lower than in the control run. Our budget analysis confirms that this depletion results from faster downstream consumption of NO_2^- through an intensified nitrification pathway, which limits the secondary maximum. This depth-persistent depletion results from active competition for NO_2^- among DNRA, denitrification, anammox and nitrification, in which DNRA and nitrification dominate.

The most counterintuitive result of this study is that while DNRA adds a source of NH_4^+ to the system, the model ultimately shows lower NH_4^+ concentrations throughout the water column, indicating that this additional production is rapidly reprocessed rather than accumulated. Three lines of evidence support this interpretation. First, the NH_4^+ gradient maps (Figure 8) show that intense and spatially structured gradients in the control run (exceeding $3 \times 10^{-6} \mu M \cdot s^{-1}$) become markedly attenuated and spatially smoothed in the DNRA run. Second, our budget analysis of NH_4^+ sources and sinks shows that the NH_4^+ produced by DNRA is almost immediately consumed through two competing pathways: rapid re-oxidation via an intensified nitrification flux, and lateral export driven by enhanced horizontal advection. Third, the density distributions (Figure 9) corroborate this pattern: in the DNRA run (Figure 9c), the NH_4^+ distribution is slightly more compressed than in the control run (Figure 9d), with the density peak shifting toward a shallower depth, consistent with faster consumption of NH_4^+ within the aerobic layer. Together, this fast reprocessing prevents any local accumulation of NH_4^+ , effectively masking its DNRA source. This rapid recycling, due to an intensified nitrification flux (represented by thick, solid arrows in

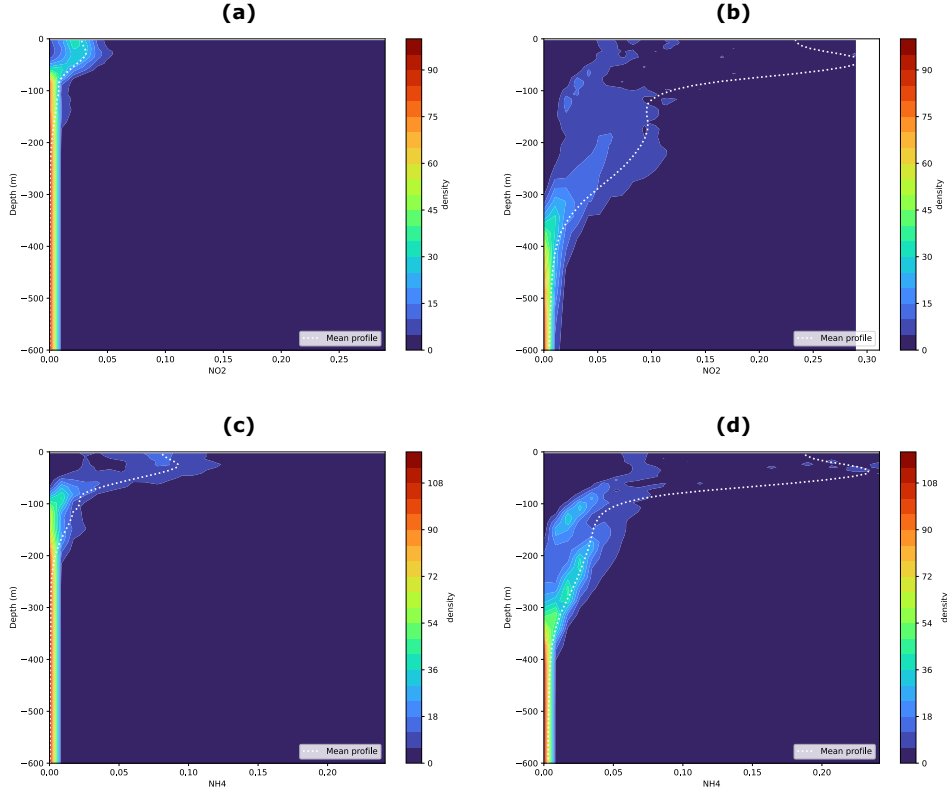


Fig. 9 Probability density function of NO_2^- (a, b) and NH_4^+ (c, d) concentration at (36°S, 73.7°W) as a function of depth for the DNRA run (a, c) and the control run (b, d) for the period 2008-2014. The average profile appears as a white dotted line

Figure 7), establishes a $NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$ short circuit.

3.1.2 From a nitrogen-losing toward a nitrogen-conserving regime

One direct consequence of the short circuit is a decline in anammox and denitrification (second step) activities, whose peaks also shift upward, from around 150 to 100 m. The starting point is the diversion of NO_3^- and NO_2^- away from denitrification and toward NH_4^+ production via DNRA. Indeed, in the 0-150m layer, the conversion of NO_3^- to N_2 (the ratio of N_2 produced by denitrification and anammox to NO_3^- reduced by the first stage of denitrification and DNRA in the simulation with DNRA) decreases by 81%. Furthermore, at these depths, the biogeochemical production of NH_4^+ increases from $8.35 \cdot 10^{-5} \mu M.m.s^{-1}$ in the control to $1.43 \cdot 10^{-4} \mu M.m.s^{-1}$ in the DNRA simulation, the DNRA flux accounting for 16.9 % of it. This contribution alone shifts the metabolic balance of the upper oxygen minimum zone, with the anaerobic fraction of NH_4^+ production fluxes rising from 5.5% in the control to 21.4% in the DNRA run. Deeper, between 150 and 300m, the conversion of NO_3^- to N_2 decreases even further, falling by 95%. Also in this layer, the biogeochemical production of NH_4^+ decreases from $9.52 \cdot 10^{-6} \mu M.m.s^{-1}$ in the control to $4.54 \cdot 10^{-6} \mu M.m.s^{-1}$ in the DNRA simulation, representing a 52% decrease. Nevertheless, DNRA becomes the dominant NH_4^+ source, accounting for 72.5% of ammonium production. At this depth, anaerobic processes already dominated in the control run (85.9%), but DNRA pushed further to 92.2%, consolidating the suboxic character of the mesopelagic OMZ

layer. Another important message of Figure 7 diagram however lies in what is negatively impacted. Anammox is not stimulated despite an increased NH_4^+ availability, contrary to what was proposed by Lam et al. 2009 [3]. Instead, the near-complete depletion of NO_2^- by DNRA, documented in Section 2, in the gradient map (Figure 8 d-f) and in the density distribution (Figure 9 a and b), imposes a strong substrate limitation to anammox bacteria that constrains their activity. Denitrification turns out to be similarly NO_2^- -limited. Nevertheless, despite this decrease in anammox and the second stage of denitrification, the contribution of anammox to nitrogen loss increased from 36% in the control run to 41% in the DNRA run. This is due to a greater decrease in denitrification than in anammox, and highlights the competition between the second stages of DNRA and denitrification.

3.1.3 Assessing the robustness of the results across parameter ranges: A sensitivity analysis

We investigated whether the nitrogen-conserving effect of DNRA and the consequent competitive reorganization of anaerobic pathways held across a range of anaerobic thresholds and DNRA kinetics within the studied spatial domain. The sensitivity analysis conducted over the whole study area is synthesized in Figure 10. Overall, model results when adding DNRA are sensibly equivalent across all combinations of oxygen threshold (24, 45 and 60 μM) and DNRA maximum rate ($V_{max}/2$, V_{max} and $V_{max}*2$), indicating model robustness with regard to these parameters.

It is important to note that the oxygen threshold is a model parameter that allows anaerobic processes to be triggered below a certain oxygen concentration. This threshold is the same for all anaerobic processes (anammox, denitrification, and DNRA). We had to make this approximation given the limited number of measurements available in the study area and the range of oxygen concentrations observed in those measurements [4, 30]. The decision to study the thresholds of 25, 40, and 60 μM also takes into account the positive bias of O_2 in the model described in the supplementary material, which also led us to limit the study period in order to encounter the lowest possible oxygen concentrations, conducive to the activation of the DNRA process.

Accounting for DNRA consistently reroutes NO_2^- fluxes across all threshold configurations, while denitrification and anammox rates decline in response, confirming that competition for NO_3^- and NO_2^- is a robust feature of the model rather than an artifact of a particular parameter choice. Nitrification and remineralisation rates remain broadly stable across the entire parameter space, indicating that these fundamental processes are modulated, but not fundamentally disrupted, by DNRA. The stock responses follow the same pattern, NH_4^+ and NO_2^- concentrations decline systematically as DNRA kinetics increase, regardless of the threshold applied, confirming our previous interpretation.

The anaerobic threshold modulates the absolute magnitude of anaerobic process rates, but leaves the competitive hierarchy between DNRA, denitrification and anammox unchanged. Indeed, higher thresholds expand the suboxic volume and produce stronger baseline anaerobic activities. At 25, 45, and 60 μM alike, the same dynamic appears: DNRA increases, while denitrification and anammox decrease, and the system shifts toward nitrogen conservation over nitrogen loss. This consistency across the parameter space strengthens the main conclusion of the study: the nitrogen-conserving signature of DNRA is not contingent on a specific parametric configuration, but reflects a fundamental reorganization of anaerobic nitrogen processing that any model incorporating DNRA is likely to capture.

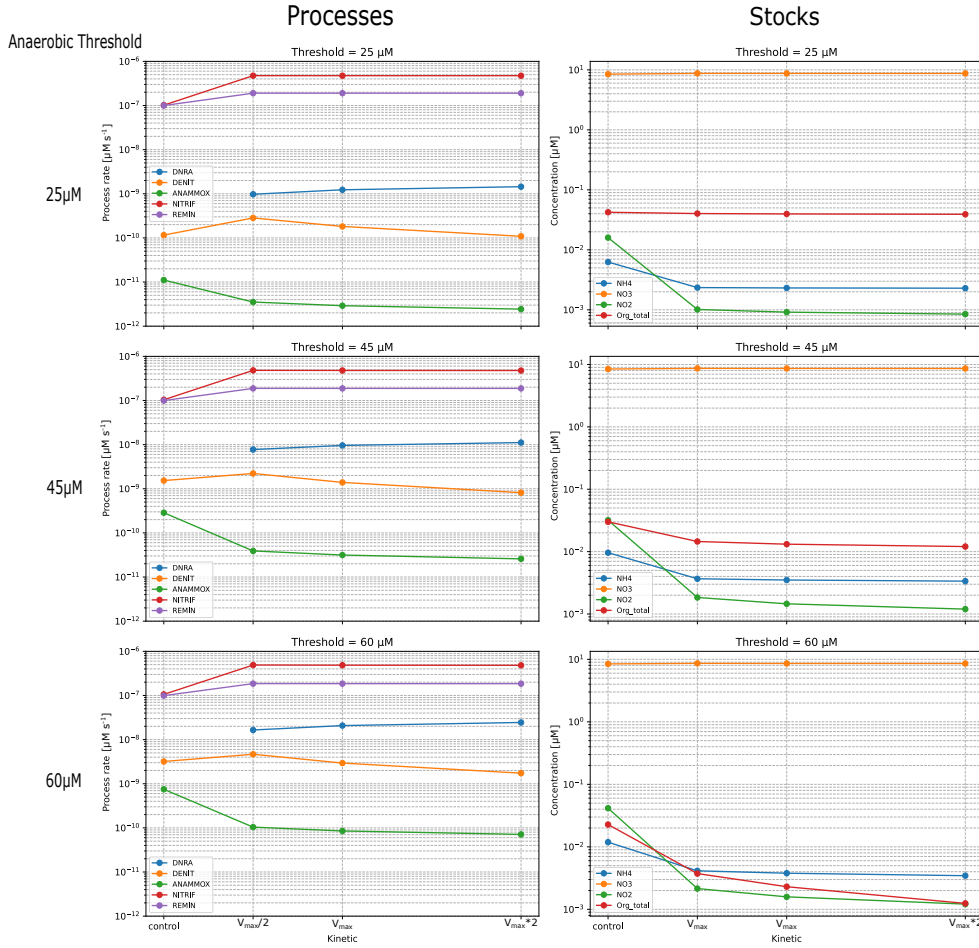


Fig. 10 Comparison of domain-averaged nitrogen fluxes (left panel) and stocks (right panel) across the full spatio-temporal domain, evaluated under a range of kinetic parameterizations (V_{max} , $V_{max}/2$ and $V_{max}*2$) and dissolved oxygen thresholds (O_{2dn}). Values represent the average rates and concentrations computed over all spatial locations and time steps (between 2008 and 2014) for each scenario.

This study does, however, have certain limitations. The modeling framework is based on a limited domain, exhibits a positive bias in the average oxygen concentration, and suffers from low resolution as well as the omission to account for riverine inputs, which limits its comparability with observed data. Furthermore, the lack of high-temporal-frequency observational data prevents a full assessment of the model realism.

3.2 Strengthened coupling with plankton dynamics in the surface layer (0–75 m)

The rapid $NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \rightarrow NO_2^- \rightarrow NO_3^-$ short circuit, combined with the vertical transport of NO_3^- , stimulates phytoplankton NO_3^- uptake. This reorganization of the inorganic nitrogen pool propagates through the food web in a clearly size-structured manner: the NO_3^- transported to the surface layer fertilizes large primary producers (diatoms, LPHY), which grow faster than SPHY despite their lower nitrate uptake efficiency, with corresponding repercussions on large versus small

grazers. Accordingly, LPHY and LZOO both increase in the DNRA run, sustained by both stronger local production and enhanced horizontal advection import. NH_4^+ produced by DNRA is converted into NO_3^- by nitrification. NO_3^- will then be transported into the productive surface layer, and fertilize large plankton communities, with NO_3^- uptake by LPHY increasing by 66% between the control run and the DNRA run. In return, the production of organic matter, especially large detritus, sinking in the lower layer, will stimulate a recycling into NH_4^+ by enhancing both aerobic and anaerobic remineralization processes. As a result, DNRA stimulates primary production. In fact, a 16% increase in total primary production was observed between the control run and the DNRA run (total uptake of NO_3^- , NO_2^- , and NH_4^+ by small and large plants). This increase is driven by LPHY, with total uptake of nitrogen species rising by 42% between the control run and the DNRA run, while that of SPHY decreases by 62%. Finally, primary production relies predominantly on NO_3^- uptake rather than on NO_2^- or NH_4^+ uptake. Indeed, NO_3^- uptake by total phytoplankton (SPHY+LPHY) increases by 37% between the control and DNRA runs, despite a decrease in SPHY NO_3^- uptake, whereas NO_2^- and NH_4^+ uptake decreases by 66% and 26%, respectively.

3.3 Role of the physical transport

Results highlight a close coupling between biogeochemical processes and physical transport, which shapes matter fluxes between the surface and the subsurface. Vertical fluxes are primarily controlled by the physical components (Figure 4), with advective transport contributing far more than diffusion, particularly for the upward transport of nitrate. This advective transport thus redistributes NO_3^- from subsurface waters to the surface, particularly around the thermocline/oxycline (≈ 30 – 50 m), but also between the anaerobic layers, where DNRA is active, and the aerobic layers, where nitrification dominates, around 100 m. A comparison between horizontal and vertical transport also highlights a compensatory effect linked to mass conservation, as both components jointly contribute to the redistribution of matter (Figure 4, Figure 8, and 9). At the same time, downward fluxes of organic matter—particularly LDET, SDET, and LPHYTO—close the loop between the surface and the subsurface by enabling the transfer of organic matter to deeper layers and its recycling. This transfer notably fuels NH_4^+ production through remineralization and can thus indirectly stimulate subsurface DNRA via the input of organic matter, particularly LDET. An increase in LDET (large particles) could potentially lead to greater bacterial activity within these particles (not accounted for in this model).

Some of this organic matter is transported into the subsurface and then stimulates heterotrophic activity in oxygen-poor waters, promoting anaerobic processes such as denitrification (Denit1) and DNRA (Figures 2 and 6). This suggests a possible positive feedback loop between surface biomass production and subsurface anaerobic recycling: the stimulation of DNRA promotes nitrate availability and primary production, which in turn increases the export of organic matter to the subsurface, fueling heterotrophic processes and potentially reinforcing DNRA in turn.

Thus, DNRA shifts the OMZ from a nitrogen-losing toward a nitrogen-conserving regime. While the control simulation channels reactive nitrogen toward N_2 via denitrification and anammox, the DNRA simulation retains it as NH_4^+ and recycles it internally through nitrification. A system where nearly 17% of surface-layer NH_4^+ production and over 72% of deep-layer NH_4^+ production originate from DNRA is a system where the classical picture of OMZ nitrogen loss needs to be revised. Models that omit this process will systematically overestimate denitrification and anammox rates,

underestimate internal recycling, and ultimately misrepresent the nitrogen balance of one of the ocean’s most biogeochemically active environments.

4 Conclusion

This study demonstrates that DNRA, once active, does not simply add an extra nitrogen pathway but changes the nitrogen cycle and OMZ paradigms, especially the fact that DNRA could stimulate anammox by providing additional NH_4^+ . On the contrary, by diverting NO_3^- and NO_2^- toward NH_4^+ production, DNRA activates coupling mechanisms leading to unexpected diagnostics and triggers a cascade that intensifies internal nitrogen recycling through nitrification, reduces substrate availability for denitrification and anammox, fertilizes the surface layer increasing the total primary production while restructuring the planktonic community toward larger size classes, and weakens the biological pump efficiency by increasing the organic matter aerobic remineralization. These effects are robust across a wide range of anaerobic threshold and kinetic configurations. Taken together, they suggest that oxygen minimum zones are not solely hotspots of nitrogen loss but also, when DNRA is locally active, sites where nitrogen conservation and internal recycling can dominate.

Despite its limitations, this study provides valuable insights into a process that remains poorly documented. These results open up new avenues for strategies to monitor oxygen minimum zones: higher-frequency measurements, particularly of NH_4^+ in both the surface and subsurface layers, appear necessary to confirm these results and better characterize the DNRA in situ dynamics.

The cumulative effects of DNRA need to be evaluated based on a tailored model setup, avoiding in particular excessive constraints of boundary conditions on the model solution, which is certainly the case here. As mesoscale eddies transport low-oxygen waters off-shore [22], our results call for investigating how DNRA modulates the nitrogen cycle from near-shore to off-shore, and rectify the mean state. Last, temporal intra- and inter-annual DNRA activation and coupling /decoupling mechanisms, and their propagation, time lag, or synchronicity with the surface planktonic dynamics are other issues for future studies.

5 Materials and Methods

5.1 Model Configuration

For this study, we used the Regional Ocean Modelling Systems (ROMS; [36, 37]), in its Coastal and Regional Ocean COmmunity (CROCO) version [38], coupled to the BioEBUS biogeochemical model [39, 40]. CROCO uses a terrain-following vertical coordinate to solve the primitive equations, applying the Boussinesq and hydrostatic approximations. BioEBUS is a biogeochemical model based on the nitrogen cycling. It derives from the N2P2Z2D2 (two compartments for Nutrients, Phytoplankton, Zooplankton and Detritus) model of Kone et al. 2005 [41] and was specifically developed for Eastern Boundary Upwelling Systems (EBUS) and OMZ systems [39, 40]. BioEBUS represents the ecosystem using ten nitrogen-based state variables, in which all living and detrital compartments are expressed in units of nitrogen. These include two size classes for phytoplankton (small flagellates, large diatoms), zooplankton (small ciliates, large copepods), and detritus (small and large). Additionally, four other compartments represent dissolved organic nitrogen (DON) and three pools of dissolved inorganic nitrogen (DIN): NO_3^- , NO_2^- and NH_4^+ . In addition to nitrification and remineralization, BioEBUS also explicitly accounts for specific microbial processes

in the OMZ that interact with the DIN pool, such as denitrification and anammox [40]. For this study, we used the version tuned for the Peru upwelling system [42], to which we first incorporated the DNRA process. A schematic representation of the BioEBUS model is shown in Figure 11). The domain extends from 35.5°S to 38.5°S and from the coast to 76.5°W with a 1/36° horizontal resolution.

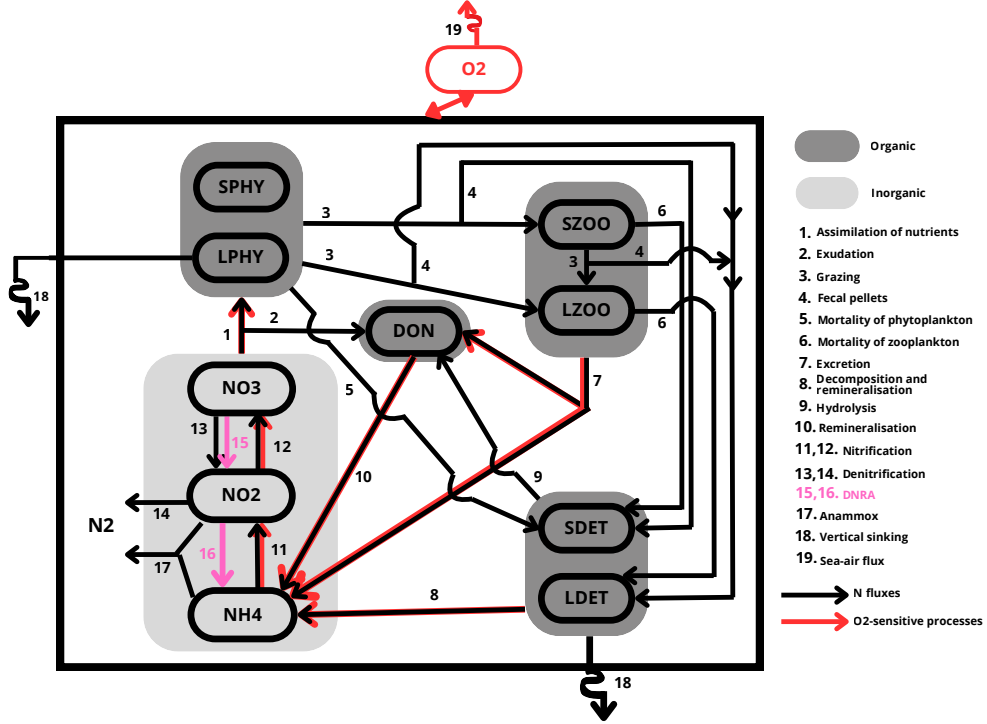


Fig. 11 Updated schematic representation of the BioEBUS model adapted from [40]

5.1.1 Control simulation

A control simulation was first run without the DNRA process, serving as a baseline to assess the effect of the DNRA process in a subsequent sensitivity experiment. This control run was performed on the configuration domain between 2007 and 2023. The model is forced at the surface using atmospheric fields from the ERA5 reanalysis [43–45], provided by the European Centre for Medium-Range Weather Forecasts (ECMWF). The applied forcing includes wind stress, surface heat fluxes, and freshwater fluxes. Open boundary conditions for the physical variables (temperature, salinity, sea level, and horizontal velocities) are obtained from a Mercator ocean reanalysis product [46]. Biogeochemical boundary conditions are prescribed using climatological fields from the CARS 2009 dataset [47] for NO_3^- and O_2 distributions, while surface chlorophyll concentrations are derived from SeaWiFS satellite observations to constrain the biological state at the open boundaries. The control run was validated from available observations, exhibiting reasonable skill in accounting for the main features of the circulation in this region. The validation procedure of this control run is detailed in the Supplemental material.

5.1.2 DNRA simulations

The nitrogen cycle in the model with DNRA is schematically shown in Figure 11. Both stages of DNRA are implemented in the model as follows:

$$\text{DNRA} = \text{DNRA}_1 + \text{DNRA}_2, \quad \text{DNRA}_i = \text{DNRA}_i(\text{DON}) + \text{DNRA}_i(D_s) + \text{DNRA}_i(D_l) \quad (1)$$

With DON being the dissolved organic matter (in $\text{mmol N } m^{-3}$), D_s (SDET) the small detritus pool and D_l (LDET) the large detritus pool corresponding to the particulate organic matter.

DNRA follows a Michaelis-Menten kinetics ([11]), which we chose to model like the denitrification parametrization in [48].

First step: NO_3^- reduction to NO_2^- :

$$\text{DNRA}_1 = K_{\text{DNRA1}} \times F_{\text{dnox}} \times \frac{\text{NO}_3^-}{\text{NO}_3^- + K_{m\text{NO}_3^-}} \times [\text{DET}] \quad (2)$$

Second step: NO_2^- reduction to NH_4^+ :

$$\text{DNRA}_2 = K_{\text{DNRA2}} \times F_{\text{dnox}} \times \frac{\text{NO}_2^-}{\text{NO}_2^- + K_{m\text{NO}_2^-}} \times [\text{DET}] \quad (3)$$

$K_{\text{DNRA}i}$ is the maximum, specific rate of DNRA step i expressed in day^{-1} . We initially assigned the denitrification values to $K_{\text{DNRA}i}$ and then adjusted them with a sensitivity analysis. $K_{m\text{NO}_i}$ is the half-saturation constant of NO_i use for DNRA, expressed in $\text{mmol N } m^{-3}$. DET represents all useable organic matter (LDET, SDET or DON). As stated in the introduction, few measurements of DNRA rates are available to date in the literature (Table B1 in Supplemental material). These measurements do not allow us to identify either the maximum rate for this activity or its oxygen sensitivity. However, they do provide information on the order of magnitude of the effective DNRA rate, which will be precious to assess how plausible simulations are. Without clearer knowledge on the oxygen sensitivity of the organisms that operate DNRA, we decided to attribute the same oxygen dependence to all anaerobic processes, not to introduce any a priori bias in the model that would favor one process over another. F_{dnox} is thus the same oxygen dependence as that in the denitrification equation (without units), and it is currently modeled as in [49]:

$$F_{\text{dnox}} = \begin{cases} 0, & \text{si } [\text{O}_2] > O_2dn, \\ 1 - \frac{[\text{O}_2]}{O_2dn \times (O_2dn + 1 - [\text{O}_2])}, & \text{si } [\text{O}_2] \leq O_2dn. \end{cases} \quad (4)$$

O_2dn is the oxygen threshold below which anaerobic processes are triggered.

We performed a sensitivity analysis on the oxygen threshold O_2dn and on the kinetic parameters for DNRA (K_{DNRA1} and K_{DNRA2} in equations 2 and 3). We chose the values 25, 45 and 60 μM (60 μM is the hypoxic threshold) for O_2dn . In the OMZs, anammox bacteria can remain active in an environment containing up to $\approx 20 \mu\text{M}$ of O_2 , and the NO_3^- to NO_2^- reduction can remain fully active until at least 25 μM . This provides an empirical basis for setting a model threshold of approximately 25 μM when seeking to allow for the coexistence of aerobic and anaerobic pathways

[50]. For kinetics with DNRA competing with denitrification, we initially started with K_{DNRA1} and K_{DNRA2} identical to denitrification $K_{Denitr1}=K_{DNRA1}=1.2\text{ d}^{-1}$ and $K_{Denitr2}=K_{DNRA2}=2\text{ d}^{-1}$ (we will refer to this configuration as V_{max}), then we also tested $V_{max}/2$ and $V_{max} * 2$ to explore non-linear behavior. We analyzed all state variables relevant for understanding the sensitivity of the OMZ dynamics to DNRA, as well as their physical and biogeochemical fluxes. For biogeochemical fluxes, a positive value corresponds to the production of the variable in question. For physical fluxes, zonal advection (u) is positive toward the east, meridional advection (v) is positive toward the north, and vertical advection is positive toward the surface.

The validation of our control run (see Supplemental material) shows that the model overestimates the mean oxygen concentration in the OMZ core by $\approx 20\text{ }\mu\text{M}$, thereby triggering an inactivation of DNRA since this process is bound to an oxygen threshold (Equation 2). To ensure that DNRA could be meaningfully activated across the different threshold configurations tested, we performed a temporal sub-sampling of our simulation period, selecting only the periods when modeled oxygen concentrations fall below each threshold (Figure B2 in supplemental material). This approach is preferable to running additional short sensitivity experiments, as it preserves the physical-biogeochemical coherence of the coupled model and exploits the natural variability of the system. We selected a study period spanning 2008–2014 for several reasons. First, it is the period during which oxygen concentrations fall below all three thresholds with frequency that allows robust statistics (Figure B2 in supplemental material). Indeed, while the $25\text{ }\mu\text{M}$ and $45\text{ }\mu\text{M}$ thresholds (Figure B2 in supplemental material (b) and (d), respectively) appear to show a period with a large number of occurrences of oxygen concentrations below the threshold between 2017 and 2023, this does not hold true for the $60\text{ }\mu\text{M}$ threshold. Second, this period coincides with strong to moderate La Niña events (2008, 2010–2012), which are characterized by enhanced coastal upwelling, a shallower oxycline, and a thicker OMZ core [51]. These conditions promote increased organic matter inputs and remineralization, driving enhanced oxygen consumption and lower O_2 concentrations — conditions particularly favorable for DNRA activity. Last, in situ observations are available over this period.

5.2 Statistical method: The bootstrap method

Uncertainties associated with the mean budgets calculated Figures 5, Figure B4 in Supplemental material and Figure 6 were quantified using a non-parametric bootstrap procedure [52]. The bootstrap method estimates the sampling variability of a statistic by repeatedly resampling values from the original model output with replacement. For each variable, missing values were first excluded, and 500 bootstrap sample of equal size to the original dataset were generated by random resampling with replacement. The mean was then calculated for each bootstrap replicate, yielding an empirical distribution of the mean. The standard deviation of this bootstrap distribution was used as an estimate of the uncertainty associated with the mean budget estimate.

Acknowledgements

This study was supported by a Sorbonne University French PhD. fellowship to M. Robo, by the action ECOS n°C22U02, by the project CLAP, COPAS COASTAL and the LIA MAST. This work was granted access to the HPC resources of CALMIP supercomputing center under the allocation 2016-P19024, "Intermittence multi-échelle de champs océaniques". We also thank the CROCO community for the use the model and its tools. Finally, we would like to thank LOMIC, LEGOS and CECI laboratories, and the Department of Oceanography at the University of Concepción for hosting M.R.

Authors contributions

Malaëka Robo, Aurélien Paulmier, Véronique Garçon, Boris Dewitte, Sophie Rabouille, Alexander Galán conceived this study and led the manuscript writing. Malaëka Robo wrote the first draft, implemented the model, performed the analysis and conducted the sensitivity experiments. Malaëka Robo and Boris Dewitte made the modelling setup. Oscar Pizarro and Laura Farias provided the data for the model validation. Diego A Narváez, Laura Farias, Oscar Pizarro, Camila Fernández reviewed and provided feedback on the manuscript. Malaëka Robo, Aurélien Paulmier, Véronique Garçon, Boris Dewitte, Sophie Rabouille, and Camila Fernández contributed to provide financial support for this study, with Malaëka Robo and Sophie Rabouille supported through a Sorbonne University fellowship and Camila Fernández. through the LIA MAST and COPAS COASTAL. Aurélien Paulmier provided computational CALMIP support. All authors contributed to improving the manuscript.

Competing interests

The authors declare no competing interests

Data availability

Atmospheric forcing data from ERA5 are available at: <https://cds.climate.copernicus.eu/datasets/reanalysis-era5-single-levels?tab=download>. Open boundary conditions for physical variables from the Mercator ocean reanalysis product are available at : <https://doi.org/10.5194/os-14-1093-2018>. Surface chlorophyll concentrations from SeaWiFS are available at: <https://www.earthdata.nasa.gov/data/catalog/ob-cloud-seawifs-l3m-chl-2022.0>. SST data from OSTIA are available at : https://data.marine.copernicus.eu/product/SST_GLO_SST_L4_REP_OBSERVATIONS_010_011/services. Data used from CARS2009 are available at: <https://catalogue-imos.aodn.org.au/geonetwork/srv/eng/catalog.search#/metadata/d9302a48-57b1-41c2-a0dc-78bd00dd5e4b>. Glider data are available upon request to Oscar Pizarro (oscar.pizarro@imo-chile.cl). Station 18 data are available upon request to Laura Farias (laura.farias@udec.cl). Regional model data that support the findings of this study are available from the corresponding author on reasonable request.

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