



The impact of primary and export production on the formation of the secondary nitrite maximum: A model study



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ABSTRACT

The so-called secondary nitrite maximum (SNM) is a pronounced subsurface feature in many oxygen deficient zones of the ocean. A nitrite layer of up to several hundred meters thickness indicates high microbial activity and nitrogen loss from the system. To study the effects of primary and export production on the SNM, we have developed a one-dimensional ecosystem model for oxygen deficient zones. Our model couples the marine nitrogen and oxygen cycles with physical water column processes, includes euphotic, aphotic, aerobic and anaerobic processes and thereby dynamically describes source and sink processes for nitrite. The model is able to reproduce a number of typical SNM features found in observations from several oxygen deficient zones. Sensitivity experiments indicate that the SNM is particularly sensitive to the amount of labile dead organic matter sinking out of the euphotic zone but rather insensitive to the strength of regenerated primary production. The absence or presence of SNMs in oxygen deficient zones may be explained by the (non-)availability of labile detritus. Our model is applicable to different ocean regions and can be used to quantify sinks of bioavailable nitrogen due to potential changes in oxygen levels and/or detritus composition.

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1. Introduction

The secondary nitrite maximum (SNM) in the subsurface ocean occurs under low oxygen conditions and is an indicator for potential nitrogen loss. Since nitrogen is the most limiting element for primary productivity, the processes governing the nitrogen cycling and loss are of interest. However, the role of ecosystem processes on nitrogen cycling, particularly primary and export production which strongly influence the oxygen dynamics in the water column is not well understood.

Pronounced nitrite maxima can be found in the so-called oxygen minimum zones (OMZs) or oxygen deficient zones (ODZs), see, e.g. Goering (1968); Naqvi et al. (2006); Ulloa et al. (2012); the term ODZ is used hereafter. The most prominent ODZs are the northern and southern Eastern Tropical Pacific, the Arabian Sea and to a smaller extent the South-Eastern Tropical Atlantic (e.g. Karstensen et al., 2008; Paulmier and Ruiz-Pino, 2009; Ulloa et al., 2012). Reactive

nitrogen is lost from all these regions via microbially mediated processes.

Driven by a diverse microbial community, there are a number of different transformation processes of nitrogen (see, e.g., reviews by Arrigo, 2005; Lam and Kuypers, 2011; Zehr and Kudela, 2011): Under oxic conditions ammonium, the compound produced during decomposition of dead organic matter, is oxidized to nitrite and eventually nitrate; this microbial process is called nitrification. Under suboxic conditions the balance between the reactive nitrogen compounds, i.e., ammonium, nitrite and nitrate, changes. Nitrate and nitrite are converted by microbes through dissimilatory nitrate reduction to nitrite (DNRN) or ammonium (DNRA). In addition, two microbial processes eventually lead to the formation of dinitrogen gas N_2 – denitrification as well as anaerobic ammonium oxidation (anammox). They are assumed to be the main mechanisms responsible for the loss of reactive nitrogen from the system. During the heterotrophic degradation process (denitrification), a significant amount of nitrite can be formed as an intermediate product and subsequently reduced to N_2 . Autotrophic anammox microbes reduce nitrite to oxidize ammonium while N_2 is released directly. Although nitrite is formed during both oxic and suboxic conditions (via nitrification and denitrification, respectively), high nitrite concentrations only occur in suboxic layers. The layer con-

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taining nitrite may be up to several hundred meters thick (see, e.g. Naqvi, 2008).

Interestingly, not all regions with low oxygen concentrations feature a secondary nitrite maximum. For example, oxygen concentrations in the Bay of Bengal are similar to those in the Arabian Sea but an SNM is absent (see, e.g. Naqvi, 2008). The reasons are not understood yet. Likewise, it is unclear which processes are particularly important leading to the formation and maintenance of the nitrite maximum. Among the ecosystem processes, primary and export production are crucial, because the two processes lead to a spatial separation of oxygen sources and sinks. The higher the primary production, the more oxygen can be produced and potentially diffuses to the deeper low oxygenated zone. However, the more detritus is formed as a result of higher primary production, the more oxygen is consumed during its remineralization. In fact, the availability of labile organic matter is assumed to govern the nitrogen loss processes (e.g. Lam et al., 2011).

The amount of nitrogen lost from the system may change in future. Global warming may lead to a significant expansion of ocean oxygen deficient zones (Shaffer et al., 2009) and it has been speculated (Gruber, 2011) that this will increase the global nitrogen loss significantly. In addition, any change in the composition of dead organic matter will also affect the microbial activity and thus the amount of nitrogen being lost from the system. To study the sensitivity of the system, a model that couples both nitrogen and oxygen dynamics by including the most important microbial pathways is needed.

Here, we investigate the sensitivity of the nitrogen cycling in a suboxic environment with respect to primary and export production. We develop a model that includes all major nitrogen cycling pathways and study the sensitivity of the system towards oxygen production and oxygen consumption as well as organic matter production. The model can be applied to different oxygen deficient zones to investigate sensitivities and to quantify the loss of nitrogen today and in future scenarios.

2. Model description

To study the dynamics in ODZs, we use an ecosystem model coupled to a one-dimensional water column model.

2.1. Ecosystem model

The ecosystem model considers the different marine nitrogen pathways and uses stoichiometric ratios as specified in the reaction equations (see Appendix A). It uses seven prognostic variables: phytoplankton (P), nitrate (NO_3^- , called NO_3), ammonium (NH_4^+ , called NH_4), nitrite (NO_2^- , called NO_2), two (labile and refractory) detritus pools (D_L , D_R) and oxygen (O_2). Fig. 1 shows the coupled nitrogen and oxygen fluxes between the different model compartments.

The different groups of aerobic and anaerobic microbes are not explicitly included as prognostic variables. Instead, we assume these organisms are generally abundant in their respective niches. Thus, “only” the microbial activities, i.e., the nitrogen transformation processes are considered through reaction rates. The model describes three basic loops. The first loop comprises cycling in the *euphotic* zone (EZ). The loop starts with the light-limited growth of phytoplankton based on nitrate or ammonium (PPROD-N, PPROD-A). The growth rate for ammonium based growth is assumed to be higher than nitrate based growth, because the former requires less energy (see Appendix A). The loss of phytoplankton through mortality (PMORT) is the source for the two detritus pools that differ in lability and sinking velocities. During remineralization (REMIN-L, REMIN-R) nitrogen is transferred from the detritus

compartments to the ammonium pool. The second loop includes processes which take place under oxic conditions in the *aphotic* zone. In low light, ammonium oxidation (AMMOX) leads to nitrite which is further oxidized (NITOX) to nitrate. Finally, the third loop encompasses all anaerobic processes in the *suboxic* zone. In this regime, nitrate reduction to nitrite (DNRN) or ammonium (DNRA), anammox (ANAMMOX) and nitrite reduction to N_2 (NRN2) take place; to avoid confusion we have introduced the term NRN2, because the widely-used alternative “(heterotrophic) denitrification” includes the two-step process DNRN and NRN2. The latter two processes constitute the internal sink terms for nitrogen in our model. The coupled oxygen cycle considers the following processes: production through PPROD and consumption by REMIN, NITOX and AMMOX. Note that the oxygen balance is not formally closed, as water (H_2O) represents both the unlimited source for O_2 production during photosynthesis and the ultimate fate of oxygen in several aerobic and anaerobic processes.

The functional dependencies and parameters to describe the processes PPROD, PMORT and REMIN are those commonly used in ecosystem models (see, e.g., Anderson et al., 2007; Beckmann and Hense, 2007). The maximum phytoplankton growth rate is chosen smaller than usual, because we do not explicitly consider the diurnal and seasonal cycle of light because we are mainly interested in the steady state of the system. Light and nutrient limitation of phytoplankton growth are described by Monod kinetics with typical values for the half saturation constants. Mortality is modelled as a linear term; the mortality rate includes natural as well as grazing losses, in accordance with other model approaches (e.g., Beckmann and Hense, 2007). For the two detritus species, different remineralization rates and sinking velocities are applied, resulting in different remineralization length scales (the ratio of sinking speed and remineralization rate) of 100 m and 3000 m, respectively. This is necessary to account for the fast turnover of part of the biogenic material in the upper layers of the ocean and the simultaneous deep penetration of part of the detritus (see also Lutz et al., 2002; Lamborg et al., 2008). Refractory detritus is assumed to be resistant to denitrification; this is motivated by the fact that decomposition of refractory organic matter is hampered under anaerobic conditions (e.g., Kristensen et al., 1995).

Only few estimates of metabolic rates and half saturation constants for microbial processes are available. The diversity of microbes (generally and also in the ocean) is large and their metabolic pathways (e.g., anammox) and characteristics (e.g., growth rates) vary considerably. Proper description of specific processes like anammox requires the determination of all participating microbes and the derivation of a suitably weighted average of metabolic rates and half saturation constants. This task is non-trivial and has not been done yet. We therefore rely on what we consider reasonable assumptions for all values to describe the microbial processes: In particular, we assume that the rates of aerobic autotrophic processes are generally higher than those of aerobic heterotrophic processes and of anaerobic autotrophic processes (e.g. Kirchman, 2012). Aerobic and anaerobic heterotrophic processes are assumed to be of the same order of magnitude (e.g. Kristensen et al., 1995). Finally, we adopt the general notion that the rate for ANAMMOX is lower than for NRN2 (see, e.g., Dalsgaard et al., 2012, and references therein). Rate limitations for microbial processes are again described by the Monod kinetics: AMMOX and NITOX are both suppressed under light. The heterotrophic processes DNRN, DNRA and NRN2 are limited by detritus, ANAMMOX by nitrite. In addition, aerobic processes depend on an oxygen limitation function; anaerobic processes depend on the same relationship in complementary form. A temperature dependence of all these rates is not considered because the temperature variability in the subsurface layers is small and microbes are able to adapt.

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