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Microbial uptake and regeneration of inorganic nitrogen off the coastal Namibian upwelling system

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ABSTRACT

We used ^{15}N-labeled substrates to measure microbial nitrate (NO_3^-) and ammonium (NH_4^+) uptake, regeneration and associated dissolved organic nitrogen (DON) release in a coastal upwelling system off Namibia (Benguela Current) in the austral winter of 2011 with the aim of quantifying rates of new production (Pnew) and regenerated production (Preg). These measurements were made during four consecutive coastal-offshore transects. The water parcels sampled at the different stations over the transect were classified into three groups according to the time passed from the first contact of the water with the surface during coastal upwelling ('pseudo-age'). The average Pnew was high in freshly upwelled waters with a pseudo-age <13 d (17.8 mmol N m^{-2} h^{-1}), and decreased abruptly towards older waters (3.9 and 2.3 mmol N m^{-2} h^{-1} in waters with a pseudo-age of 13 to 55 d, and >55 d, respectively). Preg rates were similar in <13 d and 13–55 d waters (10.9 and 11.1 mmol N m^{-2} h^{-1}, respectively), and decreased to 6.24 mmol N m^{-2} h^{-1} in waters with a pseudo-age >55 d. Measuring nitrogen regeneration and DON release fluxes allowed us to correct Pnew and Preg rates. NO_3^- regeneration rates were low (<0.5 mmol N m^{-2} h^{-1}), while NH_4^+ regeneration rates were in the range of NH_4^+ uptake rates (~2 to 5 mmol N m^{-2} h^{-1}), thus influencing significantly Preg rates. Parallel studies presented in this volume indicate a relatively high abundance of dinoflagellates and mixotrophic microflagellates, which may be partly responsible for the high Preg rates observed. Our results suggest that nitrogen regeneration plays an important role in sustaining primary production in this upwelling system.

1. Introduction

Eastern boundary upwelling systems (EBUS) are very productive areas created by the combined effect of equatorward wind stress and the Coriolis effect which give rise to Ekman offshore transport and the subsequent upwelling of nutrient-rich deep waters. Despite comprising a small percentage of the oceans' total surface (<1%), EBUS provide ~2% of global ocean primary production, producing abundant fish landings (Carr and Kearns, 2003). This primary production is supported by dissolved inorganic nitrogen availability. This nitrogen may become from the deep upwelled waters which are rich in nitrate (NO_3^-), which is considered 'new' nitrogen (Dugdale and Goering, 1967), or it can be recycled and reused within the lit water column — such as ammonium (NH_4^+), which is considered 'regenerated' nitrogen.

The degree to which a system depends on new or regenerated nitrogen is estimated through the f-ratio, which measures the proportion of total production (new + regenerated production, i.e. NO_3^- uptake + NH_4^+ uptake) attributable to new nitrogen uptake (Eppley and Peterson, 1979). The f-ratio is a proxy of the fraction of the total production that can be exported to the deep ocean or consumed by higher trophic levels, i.e. the more productive a given system is the higher f-ratio it will have and vice versa. This ratio has been amended in recent years by including other nitrogen fluxes such as NO_3^- and NH_4^+ regeneration, dissolved organic nitrogen release (DONr), and atmospheric nitrogen (N_2) fixation. Excluding these fluxes may under or overestimate f-ratio values substantially (e.g. Fernández and Raimbault, 2007). New production (Pnew) rates are overestimated when NO_3^- regeneration (i.e. nitrification) is not taken into account. The regeneration of NO_3^- was thought to be inhibited by light, but it has been demonstrated that this process contributes importantly to NO_3^- availability in well-lit surface waters of the ocean (Yool et al., 2007). Similarly, regenerated production (Preg) rates are underestimated when NH_4^+ regeneration is not measured, as this flux has been proven to occur at high rates in many marine systems (see review by Bronk and Steinberg, 2008). DONr resulting from either NO_3^- or NH_4^+ uptake may also represent a considerable percentage of gross uptake (e.g. 30–40% in the central

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North and South Atlantic; Varela et al., 2005), therefore obviating these fluxes underestimates Pnew and Preg rates. Measuring DONr is also important given the recognized role of DON as a substrate for primary producers (Bronk et al., 2007) and as a promoter of export production in the open ocean (Letscher et al., 2013). Finally, N_2 fixation – which is thought to maintain ~50% of primary production in the oligotrophic open ocean (Capone et al., 2005) – can also contribute substantially to Pnew in coastal margins and other upwelling sites (Fernández et al., 2011; Raimbault and Garcia, 2008; Subramaniam et al., 2013). For example, Fernández et al. (2011) measured N_2 fixation rates generally <1 nmol L^{-1} d^{-1} in the Humboldt Current System, although values up to 14 nmol N L^{-1} d^{-1} were measured at specific locations. Similarly, Sohm et al. (2011) reported N_2 fixation rates up to 8 nmol L^{-1} d^{-1} in the Benguela Current System. These rates are comparable to those measured in the open ocean. Altogether, the accuracy of Pnew and Preg estimates depends on the inclusion of all these nitrogen fluxes in their calculation.

The MSM18/5 'Succession' cruise was designed to track the evolution of physical, chemical and biological parameters along three stages of upwelled waters in the northern Benguela upwelling system off Namibia as proposed by Barlow (1982): (1) newly upwelled water, (2) maturing upwelled water, and (3) aged upwelled water. In our cruise, these three stages were established by grouping stations according to their 'pseudo-age', an indicator of the time passed since a water parcel first reached the surface when it upwelled near the coast (see Materials and methods). As in other companion papers of this volume, we use this classification to study the variability of Pnew and Preg rates along the above described water parcel continuum according to the in situ phytoplanktonic community and inorganic nutrient distributions.

2. Materials and methods

2.1. Sampling and hydrographic measurements

The MSM18/5 'Succession' cruise was performed onboard the R/V *Maria S. Merian* from 23 August to 20 September 2011. The cruise consisted in a coastal to open ocean waters transect (perpendicular to the coast), which was repeated four times (transects 1, 2, 3 and 4 — T1, T2, T3 and T4, respectively; see Fig. 1). T1 took place from 27 to 30 August, T2 from 30 August to 2 September, T3 from 8 to 11 September, and T4 from 11 to 15 September 2011. Water samples were collected from the surface (2 m), 20 and 40 m depths with 10 L free flow bottles mounted in a Rosette sampler equipped with a SBE911 + conductivity–temperature–depth (CTD) probe with attached fluorescence (WETlab FLRT-1754) oxygen (SBE43) and photosynthetic active radiance (PAR) sensors (QSP 2350 by biospherical Instruments Inc.).

2.2. Station clustering approach

The objective of the 'Succession' cruise was to track changes in biological, physical and chemical parameters as waters separate from the coastal upwelling towards the open ocean. However, the intense mesoscale variability observed during our cruise (Mohrholz et al., 2014–in this volume) made it difficult to establish clear coast to open ocean gradients of chemical and biological variables. For example, freshly upwelled waters may be found further offshore than it would be expected, transported from the coastal upwelling center through the filament. In order to classify the sampled water parcels according to the time passed from their first contact with the surface at the coastal upwelling until they reached oceanic waters further offshore, we use the 'pseudo-age' proxy. Related to the three stages of aging water described by Barlow (1982), the pseudo-age proxy is computed using temperature, oxygen and salinity data. The reader is referred to Mohrholz et al. (2014–in this volume) for further details on the calculation of the pseudo-age.

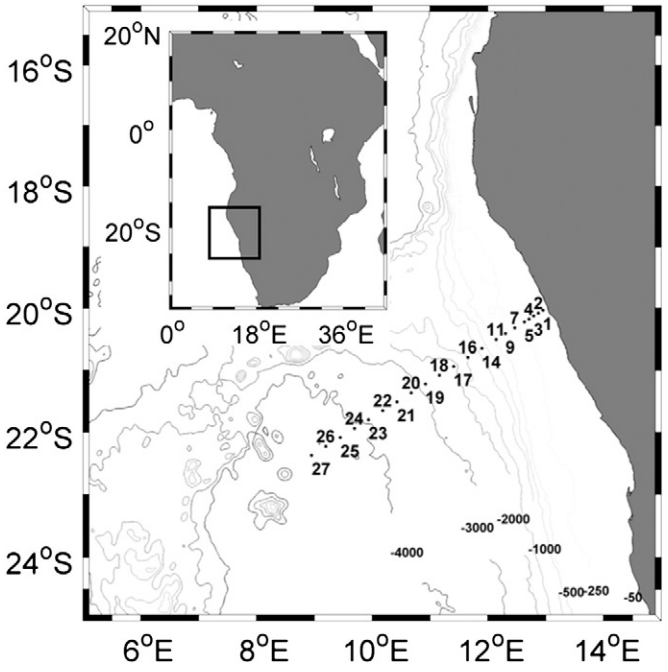

Fig. 1. Map of stations visited during the MSM18/5 'Succession' cruise.

To summarize our nitrogen fluxes data, all stations were then operationally defined into three groups according to their pseudo-age and their biological and chemical properties (chlorophyll *a*— Chl *a*— and nutrient concentrations). These three groups are detailed in Table 1 of Hansen et al. (2014–in this volume): Stage 1 — waters with a pseudo-age <13 d, 13.5 ± 0.4 °C, 35.17 ± 0.02 salinity, 20.36 ± 2.35 μM NO_3^-, and 0.5–3.5 mg m^{-3} Chl *a*—, Stage 2 — waters with pseudo-age 13–55 d, 14.5 ± 0.5 °C, 35.27 ± 0.06 salinity, 14.85 ± 2.58 μM NO_3^-, and 1.5–7 mg m^{-3} Chl *a*—, and finally Stage 3 — waters with pseudo-age >55 d, 16.2 ± 0.3 °C, 35.48 ± 0.05 salinity, 7.75 ± 4.03 μM NO_3^-, and <1 mg m^{-3} Chl *a*—.

2.3. Incubations with ^{15}N-labeled substrates

Water for $^{15}NO_3^-$ and $^{15}NH_4^+$ uptake, regeneration and release experiments was collected at 3 stations during T1 (stations 1, 14 and 18), 2 stations during T2 (stations 4 and 14), 3 stations during T3 (stations 1, 7 and 17), and 5 stations during T4 (stations 1, 7, 17, 21 and 25), at the surface (2 m), 20 m and 40 m depth, making a total of 39 samples for each type of nitrogen flux measurement (i.e. for each uptake, release or regeneration flux). Seawater was directly transferred from the sampling bottles of the Rosette into acid-cleaned 2 L transparent polycarbonate bottles (Nalgene) using silicone tubing. Trace additions of ^{15}N-labeled substrates were added to the incubation bottles as 1 mL of $K^{15}NO_3$ (200 μM; 99 at.%; 0.1 μM ^{15}N final concentration), or 1 mL of $^{15}NH_4Cl$ (20 μM; 99 at.%; 0.01 μM ^{15}N final concentration) (Sigma-Aldrich). Two bottles were used per each type of isotope addition. One of the two bottles was immediately filtered onto precombusted (6 h, 450 °C) 25 mm Whatman GF/F filters after substrate addition to determine the initial ^{15}N at.% enrichment of particulate organic nitrogen (PON) in the samples. All other bottles were incubated for 3–4 h in on-deck incubators cooled with surface seawater and shaded with mesh to mimic in situ photosynthetic active radiation (PAR) levels at the relevant depths. The light intensity of on-deck incubators was checked with a PAR sensor. The resulting PAR attenuation was 5–10% for 2 m, 15–20% for 20 m and 25% for 40 m. The incubations were usually were performed between 10:00 and 13:00 UTC, coinciding with the local solar zenith, which occurs around 11:00 UTC at this time of the year. Isotope