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Rates of nitrification and ammonium dynamics in northeastern Chukchi Sea shelf waters



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ABSTRACT

Nutrient concentrations are often depleted in surface waters during the late summer open-water period in the northern Chukchi Sea. Yet the rate of re-supply of nutrients to the pelagic environment controls phytoplankton community abundance and productivity, which in turn influences the benthic components of this relatively shallow ecosystem. We measured nitrogen cycling rates at four experimental stations on the northeastern Chukchi Sea shelf in the western arctic. At each station, rates for net NH_4^+ regeneration, actual NH_4^+ uptake, and nitrification were measured using ^{15}N isotope enrichment methods with 24-h bottle incubations under both light and dark conditions. Net NH_4^+ regeneration rates throughout the water column ranged between -0.25 and $0.23 \mu\text{mol N L}^{-1} \text{h}^{-1}$, with highest net positive regeneration occurring under light exposure in surface waters. Actual uptake rates ranged between -0.41 and $-0.01 \mu\text{mol N L}^{-1} \text{h}^{-1}$. Nitrification rates (measured at two stations) were generally highest in the sediment overlying waters, ranging between 0.14 and $0.67 \mu\text{mol N L}^{-1} \text{h}^{-1}$, and appear to account for most NH_4^+ uptake. Calculations of turnover time indicate that N is recycled within one day throughout the water column under natural conditions in the northern Chukchi Sea. Our findings confirm the results of previous studies that suggest a significant portion of surface nutrients on the Chukchi Shelf are products of horizontal advection through the Anadyr Current but also highlight the role of sediment regenerated N in supporting water-column primary production.

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1. Introduction

Water-column ammonium (NH_4^+) regeneration in aquatic ecosystems reflects the combined nitrogen (N) dynamics of eukaryotic and microbial organisms. Variability in the supply of nutrients to the pelagic environment controls phytoplankton community abundance and productivity, which in turn, influences the benthic ecosystem (Egge, 1998; Dunton et al., 2005; Walsh et al., 2005; Popova et al., 2010). In addition to autochthonous N sources, nutrients are advected into the Chukchi Sea by three main water masses (Anadyr, Alaska Coastal and Bering Shelf) flowing northward through the Bering Strait (Coachman and Aagaard, 1988). The Alaska Coastal Water and intermediate Bering Shelf Water are considered nutrient poor, while the Anadyr Water is characterized by high nutrient concentrations (Springer and McRoy, 1993). The Anadyr Water replenishes the Chukchi shelf with nutrients that fuel primary production (Mathis et al., 2009).

Nutrient concentrations vary seasonally within the Chukchi Sea region. Nitrate (NO_3^-) is often depleted in surface waters during the late summer open-water period due to heterotrophic and

photoautotrophic activity (Cota et al., 1996). The relative importance of microbial remineralization of organic matter (OM) in producing NH_4^+ , as a N source for the pelagic community, increases with the depletion of external sources of N. Heterotrophic bacterial regeneration of NH_4^+ is significant when labile organic substrates are available (Allen et al., 2002). However, heterotrophic competition with phytoplankton for N increases as nutrient concentrations decrease to levels below phytoplankton uptake capacity (Smith and Harrison, 1991). Thus, the depletion of nutrients leads to decreased primary production, changes in phytoplankton community structure, and an increased reliance on regenerated N for phytoplankton growth (Cota et al., 1996; Sukhanova et al., 2009).

Regeneration and uptake of NH_4^+ are important to benthic food web studies. Stable carbon and nitrogen isotopes are commonly used to categorize a benthic consumer's trophic position and define its food sources (Fry and Sherr, 1984; Post, 2002). The broad range of sediment OM isotope values in the Chukchi Sea shelf complicates this process because the source signal of inorganic N used by autotrophs affects the N-isotopic composition of the organic matter synthesized in the water column (Sigman et al., 1999; Naidu et al., 2000). The isotopic signature of phytoplankton, for example, varies according to the isotopic value of the NO_3^- and NH_4^+ pools (Doi et al., 2004; Needoba et al., 2004), which are

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not conservative. In particular, isotope fractionation is introduced by nitrification, in which preferential uptake of $^{14}\text{NH}_4^+$ leaves the nutrient pool relatively enriched in $^{15}\text{NH}_4^+$ and produces ^{15}N depleted nitrification products (Sigman et al., 2008). The increasing use of regenerated NH_4^+ by phytoplankton, as nitrate becomes depleted in surface waters during the late spring and summer, may result in a mixture of phytodetritus with different isotopic signatures.

The availability of nitrogen often controls primary productivity in surface ocean waters. High primary production is often linked to the supply of NO_3^- and NH_4^+ . Estimates of ‘new’ and ‘regenerated’ production rely on the knowledge of source and fraction that these forms of inorganic-N are taken up by phytoplankton. For example, phytoplankton production derived from the uptake of allochthonous NO_3^- is referred as ‘new’ production (Dugdale and Goering, 1967; Hansell et al., 1993). Estimates of production are therefore compromised by microbial processes that produce NO_3^- . Nitrification, for example, transforms regenerated NH_4^+ into NO_3^- and consumes oxygen. Consequently, nitrification influences the supply of NO_3^- to phytoplankton in the euphotic zone.

Inaccuracy of new and regenerated production occurs when a portion of NO_3^- phytoplankton uptake is produced by nitrification within the euphotic zone (Wankel et al., 2007). Knowledge of the NH_4^+ turnover time can help to describe the contributions of autochthonous NH_4^+ assimilated by phytoplankton, which is estimated from total NH_4^+ production rates. Furthermore, establishing the role of microbial activity on the regeneration and distribution of nutrients in the mixed layer negates the commonly-used assumption that regeneration of nutrients in nutrient depleted waters is insignificant (Cota et al., 1996). Therefore, if total NH_4^+ production rates are not measured, net NH_4^+ production plus nitrification rates must be considered together to estimate ‘new’ production rates (Wassmann, 1990).

Primary production is a crucial component of the benthic ecosystem in the Chukchi Sea. The coupling between water column primary production and secondary production of benthic fauna and its relationship to the surrounding environmental conditions is well understood in the region (Bates et al., 2005). However, the role of prokaryotes on inorganic nitrogen regeneration and utilization is still under-studied in the Arctic, and our understanding of nitrification in the offshore waters of the Chukchi Sea is very limited.

The purpose of this work was to quantify actual NH_4^+ production and uptake rates in addition to nitrification rates in the water column and sediment overlying water (OLW) during late summer. We consider that net NH_4^+ regeneration measurements underestimate actual rates because NH_4^+ production and uptake processes occur simultaneously (Tupas et al., 1994). The hypotheses tested are that (1) light favors rates of NH_4^+ uptake but not regeneration, (2) regeneration rates are higher than uptake rates in the water immediately overlying the sediments because of potentially lower photosynthetic rates and the effects of additional microbial activity fueled by organic matter associated with suspended sediments, and (3) nitrification accounts for most of the NH_4^+ uptake in subsurface waters. Additionally, measurements of NH_4^+ demand (AD), estimated from the difference between potential and actual uptake rates (Lin et al., 2011), provided insights into the degree of potential N limitation within the water column for both microbial and phytoplankton communities.

2. Materials and methods

Water-column N cycling rates were measured during a cruise to the northeastern Chukchi Sea in summer 2010 as part of the ‘Chukchi Sea Offshore Monitoring in Drilling Area: Chemical and

Benthos (COMIDA CAB) project. The objectives of this study were to measure under natural light and dark conditions ‘actual’ regeneration and ‘potential’ uptake rates for NH_4^+ by measuring the dilution rates of added ^{15}N isotopes. We also compared regeneration and uptake rates to ‘net’ production rates of NH_4^+ without isotope addition at four water depths at four stations. Nitrification rates were measured at two sites, and the rates of these processes were determined in bottle experiments by measuring the dilution rates of added ^{15}N isotopes, including $^{15}\text{NH}_4^+$ for ammonium cycling experiments (Blackburn, 1979) and $^{15}\text{NO}_3^-$ for nitrification experiments (Carini et al., 2010).

2.1. Sampling stations and field measurements

Temperature, salinity, water column background concentrations of NO_3^- , PO_4^{3-} and NH_4^+ , and rates of NH_4^+ regeneration, NH_4^+ uptake, and nitrification were examined at four depths (4 m, 20–30 m, 1 m over the sediment surface, and sediment overlying water) at four stations (Station 103, 65.724°N, 168.957°W; Station 9, 70.671°N, 167.083°W; Station 1015, 70.840°N, 163.291°W and Station 48, 71.377°N, 159.468°W) distributed longitudinally within the COMIDA CAB region during the summer field season aboard the *R/V Moana Wave* (July–August 2010; Fig. 1).

Temperature (T) and salinity (S) were measured using a YSI-650-MDS Sonde (YSI Inc, Yellow Springs, OH), resolving at 0.01 parameter units and an accuracy of ± 0.15 °C and ± 0.001 milli S cm^{-1} , for T and S respectively. The salinity probe was calibrated with conductivity/TDS 50,000 micromhos cm^{-1} (30.300 ppm as NaCl) standard solution (Ricca Chemical Co. part# 2248-32).

Water column samples were collected at three different depths (4 m, 20–30 m, and 1 m above sediment) with a peristaltic pump and transferred to respective 1-L bottles. Sediment overlying water (OLW) was collected into a 1-L bottle by siphoning overlying water from relatively undisturbed sediment cores collected using a HYPOX coring device (Gardner et al., 2009).

Background NO_3^- and PO_4^{3-} concentrations were measured in water samples collected at each depth. Samples were filtered (nylon syringe filter, 0.2 μm pore size) and filtrates transferred into one 15-mL centrifuge tube per nutrient ($n=1$) and frozen until later analysis with a Lachat Quikchem 8000 Flow injection analysis system. Each sample was analyzed twice. The coefficients of variation for replicate NO_3^- and PO_4^{3-} standard solutions were less than 1%.

Net NH_4^+ regeneration was determined from the change in background NH_4^+ concentration in bottle-enclosed unamended

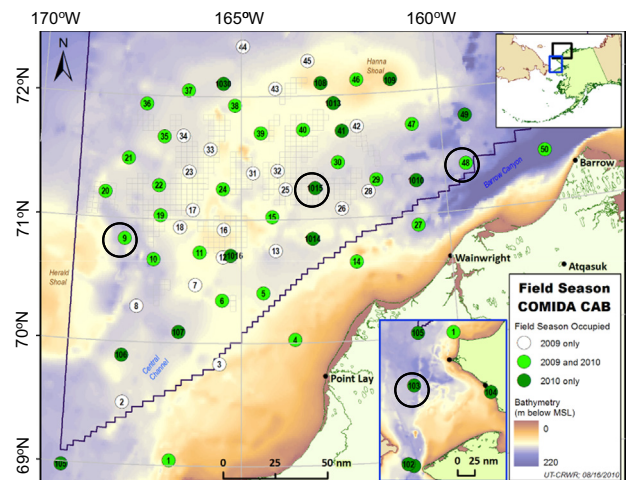


Fig. 1. Location of the four sampling stations (encircled) occupied in the northeastern Chukchi Sea.

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