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Elevated $^{15}N/^{14}N$ in particulate organic matter, zooplankton, and diatom frustule-bound nitrogen in the ice-covered water column of the Bering Sea eastern shelf

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ABSTRACT

We conducted a survey of the natural abundance $^{15}N/^{14}N$ ratio ($\delta^{15}N$) of particulate organic matter (POM), diatom frustule-bound nitrogen ($\delta^{15}N_{DB}$), and zooplankton from water column material collected with net tows across the eastern Bering Sea shelf in late winter of 2007 and 2008, to investigate the N dynamics of primary and secondary production in relation to the presence of seasonal sea ice. The data reveal a pattern of increasing $\delta^{15}N$ northward and eastward (POM: 2.1–14.7‰; frustule-bound N: 4.9–20.7‰; zooplankton: 6.4–18.0‰), with POM $\delta^{15}N$ reaching ~9‰ higher than that of water-column nitrate. Higher $\delta^{15}N$ in each of these plankton fractions was largely associated with stations covered by sea ice. POM $\delta^{15}N$ collected concurrently from within sea ice was not sufficiently ^{15}N-enriched to explain the elevated water-column values. Rather, the $\delta^{15}N$ of water-column POM under sea ice appears to derive from the assimilation of ammonium released from shelf sediments. Water-column ammonium $\delta^{15}N$ was between 28‰ and 63‰, most likely due to partial nitrification in the sediment and overlying water column. The high $\delta^{15}N$ of this ammonium is effectively transmitted to phytoplankton under sea ice because light limitation from the ice cover delays the springtime nitrate assimilation that yields algal biomass with a lower $\delta^{15}N$. Despite this seasonal explanation, published $\delta^{15}N$ data from sediment traps, summertime zooplankton, and surface sediment indicate that a shoreward and northward $\delta^{15}N$ increase – albeit of a weaker magnitude – is perennial, suggesting that the $\delta^{15}N$ of the total annual fixed N supply (including both ammonium and nitrate) also increases shoreward and northward. This requires that the partial nitrification of ammonium underlying the spatial pattern in $\delta^{15}N$ is at least partly coupled to denitrification in the sediments that preferentially removes ^{14}N, causing the total fixed N reservoir on the shelf to evolve toward higher $\delta^{15}N$. Shelf geometry and the consequent benthic–pelagic coupling of N cycling thus seem to underlie the spatial pattern in the mean annual $\delta^{15}N$ of plankton, while sea-ice cover causes the high $\delta^{15}N$ of ammonium on the shelf to be most strongly reflected by the production occurring in the winter and early spring. Our results provide a basis for tracing the geographic and seasonal origins and trophic transfer of N in the Bering shelf ecosystem.

1. Introduction

The continental shelf region accounts for 50% of the Bering Sea's area and an even greater proportion of the region's annual primary production (Springer et al., 1996; Rho and Whitledge, 2007). Phytoplankton blooms occurring in late spring/early summer under open water conditions comprise the bulk of primary production over the eastern shelf region (Rho and Whitledge, 2007). This springtime production is dependent on an annual cycle of consumption and subsequent replenishment of nutrients available in the shelf water column.

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Nitrate is the dominant N species in winter shelf waters (e.g., Granger et al., 2011), and is responsible for fueling most of the spring production. Spring phytoplankton growth depletes nitrate from the mixed layer of the eastern Bering shelf, and new inorganic nitrogen is only occasionally brought to the surface by rare summer storms (Sambrotto et al., 1986; Walsh and McRoy, 1986; Whitledge et al., 1986). Nutrient recharge of surface shelf waters starts in fall and peaks in winter (Whitledge et al., 1986), when effective horizontal and vertical transport of nutrients across the southeastern shelf is possible due to the weakening of hydrographic fronts, elimination of vertical stratification of the water column, and increasing wind strength (Coachman, 1986; Stabeno et al., 2002).

Two sources resupply inorganic nitrogen to the shelf surface waters: (1) nitrate-rich waters from the open Bering basin and (2) nitrogen (ammonia and nitrate) remobilized from shelf sediments. Nitrate-laden water from the Bering basin is transported shoreward across the shelf break along the base of the water column (Coachman and Walsh, 1981; Coachman, 1986; Stabeno et al., 2002). Wind and tidal mixing vertically redistribute this nutrient-rich water to the surface. Although off-shelf exchange appears to be the main form of nutrient recharge on the shelf, it is believed that the influence of this horizontal nutrient transport diminishes rapidly away from the shelf break (Coachman and Walsh, 1981; Coachman, 1986). Instead, nitrogen remobilized (both as nitrate and ammonium) and vertically redistributed directly from the shelf sediments appears to be more important for nutrient recharge on the inner and middle shelf areas (Whitledge et al., 1986; Rowe and Phoel, 1992; Granger et al., 2011, 2013).

Although the bulk of primary production occurs in spring, algae remain active on the shelf during winter. However, we know little about the nutrient consumption of primary producers outside of the late spring and summer productive seasons. Conditions for algal growth in winter are very different from those in other seasons, not only because nutrients are more abundant and light is less available but also because a large expanse of the inner (depth: 0–50 m) and middle (depth: 50–100 m) shelf and parts of the outer (depth: $100-\sim200$ m) shelf experience ice cover for a significant time period. Starting in fall, ice moves from the northern shelf polynyas and accumulates as far south as 54–56°N in February–March before starting its northward retreat (Stabeno et al., 2007a). The sea ice cover alters the salinity, temperature, nutrient distribution (Stabeno et al., 2010, 2012) and availability of light to primary producers (Gradinger, 2009; Lee et al., 2010), creating a growth environment for phytoplankton distinct from that of open water regions of the shelf.

The sea ice environment provides three potential habitats for winter algal growth: (1) the under-ice water column, (2) the bottom surface of the ice floes (Horner, 1985; Sukhanova et al., 1999), and (3) the interstitial spaces and brine channels within the ice column (Gradinger, 1999; Mock and Gradinger, 1999). Access to nutrients and light varies among these three habitats, best summarized as a gradient of potentially reduced nutrient availability but increased light levels upwards from the water column to the ice surface. Phytoplankton growing in the ice-covered water column have access to ambient inorganic water column nutrient pools, but experience significantly lower light levels than those in open-water conditions (Gradinger, 2009). Algae using the bottom of the ice as a growth substrate are protected from being mixed out of the euphotic zone and can benefit from increased light exposure while still accessing water column nutrients. However, boundary layer conditions at the ice surface potentially restrict access to nutrients by bottom-ice algae. Algae growing within the interstitial spaces of the ice column may benefit from the greatest light exposure, but they depend on nutrients incorporated during ice formation and occasionally imported from the water column such as during brine convective events (Notz and Worster, 2009).

The unique growth environments created by the sea ice are likely to have notable effects on the nutrient consumption dynamics and, consequently, on the C and N isotopic composition of organic matter originating from algal production on the ice-covered shelf. Studies in both the Arctic and Antarctic have shown that C and N isotope ratios (δ^{13}C and δ^{15}N) of ice-associated algal material can be very elevated relative to particulate organic matter (POM) from the ice-free water column (Rau et al., 1991; Hobson et al., 1995). Elevated δ^{13}C and δ^{15}N of ice-derived POM likely derive from the semi-closed environment within the ice and its effects on the physical and biological dynamics of both C and N pools (Rau et al., 1991; Rysgaard and Glud, 2004; Rysgaard et al., 2008; Munro et al., 2010; Cozzi and Cantoni, 2011). Such findings suggest that the δ^{13}C and δ^{15}N of organic material on the ice-covered Bering shelf could provide a tracer of the relative contribution of ice-derived organic matter to shelf production. Additionally, the decreased light availability in the water column due to sea ice cover also curtails metabolic rates of phytoplankton C and N assimilation (Lee et al., 2010; Yun et al., 2012). This energetic restriction may be manifested as an increased reliance on ammonium relative to nitrate for N nutrition (e.g., Lee et al., 2010; Yun et al., 2012). A recent study suggested that on the eastern Bering shelf, ammonium and nitrate have substantially different δ^{15}N, with ammonium enriched in ^{15}N relative to nitrate (Granger et al., 2011). Hence, the δ^{15}N of organic material on the shelf may also provide an indicator that sea ice cover affects which form of nitrogen is primarily consumed by phytoplankton in the water column.

To elucidate the N dynamics of production on the ice-covered shelf, we surveyed the δ^{15}N of three fractions of organic matter (phytoplankton-$\delta^{15}N_{POM}$; diatom frustule-bound N-$\delta^{15}N_{DB}$; zooplankton-$\delta^{15}N_{Zoo}$) isolated from net tows in the late winter to early spring over the eastern Bering Sea shelf. We investigated the regional distribution of organic matter δ^{15}N with a focus on identifying geographic patterns and the potential influence of sea ice on the δ^{15}N signal of primary ($\delta^{15}N_{POM}$ and $\delta^{15}N_{DB}$) and secondary production ($\delta^{15}N_{Zoo}$). Specifically, we investigated whether: 1) the δ^{15}N of POM produced under ice cover differs from that produced in open water conditions and 2) if the characteristic δ^{15}N signal of ice-associated production is transmitted to zooplankton consumers ($\delta^{15}N_{Zoo}$). Having identified a spatial pattern in organic matter δ^{15}N, we sought to distinguish whether it was caused by the contribution of within-ice algal production to water column POM, or by differences in phytoplankton consumption of isotopically distinct inorganic N sources across the shelf. We additionally measured the δ^{13}C of zooplankton as a supplementary way of assessing the importance of ice productivity as a zooplankton food source. Our interpretation of the distribution of δ^{15}N of organic matter is discussed in the context of the N and C isotopes of within-ice algal production and the δ^{15}N of the inorganic nitrogen sources (nitrate and ammonium) available on the shelf.

2. Materials and methods

2.1. Study area and data sources

We collected samples and data over the eastern Bering shelf aboard the USCG Healy during spring 2007 (April 10–May 12, *HLY-07-01*) and 2008 (March 31–May 6, *HLY-08-02*) as part of the Bering Sea Ecosystem Study (BEST) (Fig. 1). Sea ice was present over the shelf during both sampling seasons and ice extent differed between years, with ice covering most of the shelf region in 2008 (Fig. S1).