Vertical distribution of prokaryote production and abundance in the mesopelagic and bathypelagic layers of the Canada Basin, western Arctic: Implications for the mode and extent of organic carbon delivery

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ABSTRACT

The vertical distributions of prokaryote heterotrophic production (^{3}H-leucine incorporation rate) and abundance were investigated in the meso- and bathy-pelagic layers of the Canada Basin, western Arctic Ocean, during September 2009. Prokaryote production and abundance were high in the Pacific-origin water mass located in the upper mesopelagic layer (depth, 100–200 m). Below the halocline layer (depth, 300–3000 m), both the production and abundance decreased with depth, with log–log regression slopes of -1.33 and -0.77, respectively. Depth-integrated production and biomass in the meso- and bathy-pelagic layers was three- to five-fold lower than the corresponding values reported in the subpolar regions, whereas they were close to or lower than the corresponding values in oligotrophic subtropical regions. Prokaryote turnover times were estimated to be 1.1 and 6.1 years for meso- and bathy-pelagic layers, respectively, with the latter being among the longest turnover times reported for oceanic basins. We estimated prokaryote carbon demand in the water column (100–3000 m) to be on the order of 11 mg C m^{-2} d^{-1}, which largely exceeds (by 38-fold) the sinking particulate organic carbon flux at depths of 120–200 m reported in the literature. This large carbon imbalance may be partly explained by organic carbon delivery by lateral intrusion of the Pacific-origin water mass into the upper mesopelagic layer.

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1. Introduction

The estimated global vertical delivery of organic carbon from the ocean's sunlit layer to its deep layers is in the order of 4–11 Pg C y^{-1} (Laws et al., 2000). This carbon delivery is mediated by multiple processes, including the sinking of particulate organic carbon (POC; Honjo et al., 2008), advective and convective transport of dissolved organic carbon (DOC; Hansell, 2002), and zooplankton migration (Steinberg et al., 2008). The vertical delivery of organic carbon, followed by remineralization by microbes in the mesopelagic (100–1000 m) and bathypelagic (> 1000 m) layers, constitutes an important element of oceanic biogeochemical cycles, markedly influencing the extent and patterns of carbon sequestration in the oceans (Sarmiento and Gruber, 2006). Over the past three decades, studies have

evaluated the regional variability in the extent of the vertical carbon fluxes and depth-dependent patterns in carbon remineralization in various oceanic regions (reviewed by Honjo et al., 2008). General empirical models have been proposed to relate the vertical carbon fluxes to depth (Martin et al., 1987) or a combination of depth and primary production (Suess, 1980; Betzer et al., 1984; Pace et al., 1987). Increasingly, however, evidence has indicated that the carbon delivery and remineralization patterns in the deep ocean are more complex and variable than previously thought (Buesseler et al., 2007b; Steinberg et al., 2008; Baltar et al., 2010b; Yokokawa et al., in press), underscoring the importance of a detailed evaluation of the variation, mechanisms, and control of carbon cycling in the mesopelagic and bathypelagic oceans (Aristegui et al., 2009; Nagata et al., 2010; Robinson et al., 2010).

The Arctic Ocean is an important, yet largely understudied, oceanic biogeochemical province that is experiencing large and rapid changes in hydrographic and ecological conditions as a consequence of climate change (Steele et al., 2008; Richter-Menge and Overland, 2010). Changes in primary productivity, food web

structure, and hydrography could have a large, intricate effect on the extent of and patterns in the vertical delivery of organic carbon in the Arctic (Honjo et al., 2010; Nishino et al., 2011b), although little is known about the supply and consumption of organic carbon in the interior of the Arctic basins (Macdonald et al., 1993; Honjo et al., 2010). Recently, Honjo et al. (2010) found that the sinking POC flux, as shown by sediment traps deployed at depths of 120–200 m in the Canada Basin, was low relative to that in other oceanic regions, presumably because of a lack of ballast particles in the region investigated. Other lines of evidence indicate that water mass intrusion from adjacent seas, a characteristic physical feature of the Arctic basins (Macdonald et al., 2004), can result in DOC delivery into the upper mesopelagic layer. In the Canada Basin, the intrusion of Pacific Winter Water (PWW; Coachman and Barnes, 1961) is evident just above the depth of Lower Halocline Water (LHW; Jones and Anderson, 1986; Rudels et al., 1996), producing a strong halocline between the core depths of the PWW and LHW. PWW is modified during its passage through the Bering Strait and Chukchi Shelves via interaction with seafloor sediment (Mathis et al., 2005, 2007). Davis and Benner (2007) suggested that the DOC in the PWW contained large quantities of labile components. However, it is unclear if the intrusion of DOC-rich Pacific-origin water results in enhanced carbon consumption and remineralization in the interior of the Canada Basin.

Studies conducted in lower latitude regions of various oceans have suggested that the prokaryote production and biomass in the mesopelagic and bathypelagic layers reflect the extent of and vertical patterns in the supply of organic matter available for prokaryote consumption at depth (Nagata et al., 2000, 2010; Hansell and Ducklow 2003; Reinthaler et al., 2006; Yokokawa et al., in press). Prokaryote production can be coupled with the sinking POC fluxes because of the active conversion of sinking POC into DOC, presumably due to the physical fragmentation and ectoenzymatic hydrolysis of POC, followed by the prokaryote consumption of DOC (Smith et al., 1992; Nagata, 2008). In oceanic regions where the transport of semi-labile DOC during the formation of intermediate and deep water masses occurs, the distribution of prokaryote production could reflect the water mass distributions (Moriarty et al., 1997; Teira et al., 2006). Studies have also suggested that inputs of organic matter from bathyal sediments might result in high prokaryote production in bathypelagic layers (Nagata et al., 2000; Yokokawa et al., in

press). Consequently, prokaryote production distribution patterns provide useful information on how organic carbon is delivered vertically and laterally in oceanic water columns.

Here, we collected data on the vertical distributions of prokaryote production and abundance at six stations in the Canada Basin during September 2009 to examine the mode and extent of organic carbon delivery and consumption in the interior of the Canada Basin.

2. Material and methods

2.1. Sample collection

Samples were collected at six stations along a nearshore-to-offshore transect in the Canada Basin during the cruise of the R/V Mirai (MR09-03) conducted between September 9 and October 15, 2009 (Fig. 1). Seawater samples were collected at 16 predetermined depths in the mesopelagic and bathypelagic layers using acid-washed 12-L Niskin bottles mounted on a conductivity–temperature-depth (CTD) system (SBE9Plus, Sea-Bird Electronics). Samples for prokaryote production and abundance were collected in acid-washed 1-L polycarbonate bottles (Nalgene) and transferred to an onboard laboratory for further processing. Care was taken and gloves were worn to minimize contamination.

2.2. Prokaryote production, abundance, and turnover time

Heterotrophic prokaryote production was estimated from the rate of ^{3}H-leucine incorporation according to Kirchman (2001). A 1.5-mL seawater sample was put in a 2-mL sterile tube (SSI) and 10 μL of ^{3}H-leucine (TRK510, Amersham; specific activity 5.14 TBq mmol^{-1}, final concentration 10 nmol L^{-1}) were added. This mixture was incubated in the dark at *in situ* temperature (± 0.5 °C) for 2 or 24 h for shallower (100–200 m) and deeper (>200 m) samples, respectively. The time course of the incorporation in bathypelagic waters is generally linear during incubation for 24 h (Nagata et al., 2000; Uchimiya, unpublished data). Incubation was stopped by adding 80 μL of 100 w/v% trichloroacetic acid (TCA) and then the sample was centrifuged at 14,000 rpm for 10 min using a microcentrifuge (Kubota 1130, Kubota). The precipitate was extracted with 1 mL of 5% TCA and
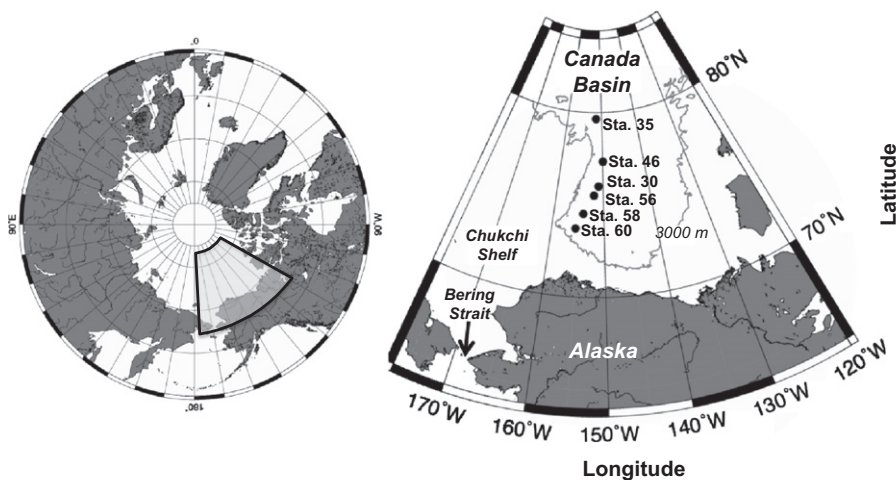
Fig. 1. Locations of the sampling stations during the MR09-03 cruise. The respective position, bottom depth, and sampling date (dd/mm/yy) at each station are as follows: Sta. 35 (79.0°N, 151.6°W; 3800 m; 20/09/09); Sta. 46 (77.2°N, 149.9°W; 3813 m; 22/09/09); Sta. 30 (76.0°N, 151.0°W; 3842 m; 18/09/09); Sta. 56 (75.5°N, 152.0°W; 3820 m; 24/09/09); Sta. 58 (74.5°N, 154.1°W; 3850 m; 26/09/09); Sta. 60 (73.7°N, 155.5°W; 3836 m; 27/09/09). The maps were created using The Generic Mapping Tools (⟨http://gmt.soest.hawaii.edu⟩).