THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

Abundance and Production Rates

of # Heterotrophic Bacterioplankton

in the Context of Sediment and Water Column Processes in the Chukchi Sea

By Lee W. Cooper, Alexander S. Savvichev,
and Jacqueline M. Grebmeier

Photo credit: Marshall Swartz, Woods Hole Oceanographic Institution

ABSTRACT. Bacterial production and abundance are linked to areas of high biological production in the water column and in the underlying benthos in the Chukchi Sea. Process measurements taken during the Russian American Long-term Census of the Arctic (RUSALCA) program, such as the carbon isotope composition of sinking particulate organic matter and sediment organic matter, are used to put bacterial production and abundance in context. These measurements show that there are vertical gradients in the water column and that the stable carbon isotope composition of organic materials in the sediments is significantly different from sedimenting materials in the overlying water column. Differences within the water column likely reflect late summer declines in productivity that increase discrimination against ^{13}C and also provide indications of carbon metabolism in the water column and underlying sediments. Temporal changes in the stable carbon isotope composition of organic matter in surface sediments, as well as C/N ratios in organic matter during the RUSALCA program, are also being observed, specifically higher ratios of $^{13}C/^{12}C$ at some stations near the Chukotka coast, and lower ratios of $^{13}C/^{12}C$ near Point Hope, Alaska. C/N ratios have increased since 2004 at productive sites in the south central Chukchi Sea, suggesting changes in organic material deposition. Other parameters studied on some or all of the decadal series of joint Russia-US cruises include sediment oxygen demand, the nitrogen isotopic composition of organic matter, sediment grain size, chlorophyll content in surface sediments, and elemental ratios of carbon and nitrogen in surface sediments. These process measurements support interpretations that the ecosystem shows strong coupling between bacterial and primary production and the underlying benthos.

INTRODUCTION

One of the key strengths of the Russian-US Long-term Census of the Arctic (RUSALCA) program in the Chukchi Sea is the capability to cross the international frontier between Russia and the United States and to assess the Chukchi Sea from an integrated ecosystem perspective. Another strength is the capability to assess the relationship between water column and sediment processes on a shallow, productive, polar continental shelf where water column production affects the benthos and where sedimentary processes, including mineralization, can in turn influence water chemistry as waters flow across the shallow shelf and into the deep Arctic basin (e.g., Jones et al., 1998; Codispoti et al., 2005; Mathis et al., 2014). In this overview of selected results from the RUSALCA program, we focus on tying bacterial production and abundance in the water column to related processes in the sediments by presenting data on water column primary production, sediment oxygen respiration, and chlorophyll deposited to the sediments. We estimate bacterial production using

rate measurements of dark CO_2 assimilation in water samples by $NaH^{14}CO_3$, while recognizing the limitations of such incubations as an index of bacterial productivity and in comparison to other techniques such as ^3H labeled thymidine incorporation (Riemann and Søndergaard, 1984).

Bacterial communities and processes are best understood in an environmental context, so we also present data on the elemental and isotopic ratios of carbon and nitrogen in the sediments as indicators of regional-scale deposition and productivity processes, and data on the distribution of sediment characteristics such as sediment grain size and the total organic content of surface sediments. These environmental data are directly related to physical flow fields and deposition of organic materials to the biologically productive benthic microbial and macrofaunal communities on this polar continental shelf.

Together with primary productivity of phytoplankton and chlorophyll *a* content, abundance and productivity of bacterioplankton are key parameters characterizing the state of marine ecosystems (Ducklow, 2000). Qualitative

characteristics of phyto- and bacterioplankton communities of the Arctic seas have also been the subject of prior experimental study (e.g., Kirchman et al., 2009b). Much attention has also been recently paid to microbial transformation of organic matter (OM) delivered to the Arctic shelf seas with the inflow of major rivers such as the Ob, the Yenisei, and the Mackenzie (Amon and Meon, 2004; Vallières et al., 2008). Heterotrophic bacterioplankton (consisting of both *Bacteria* and *Archaea*) play a major role in OM decomposition, with the degree of decomposition depending significantly on the qualitative composition of organic matter (del Giorgio and Davis, 2003).

Significant changes in seasonal ice cover in the Arctic Basin resulting from recent climatic warming (Moritz et al., 2002; Stroeve et al., 2012) have also attracted much attention. The quantity and quality of organic matter in the water column is also potentially changing. Runoff increases and permafrost thaw associated with climate change are likely to change the concentrations and lability of organic carbon released into the Arctic Ocean (Benner et al., 2004; Guo et al. 2007; Perminova et al. 2014). The abundance and productivity of the heterotrophic bacterioplankton community in turn depends upon the composition of organic matter (Kirchman et al., 2009b), and serves as the main component of the microbial loop that returns inaccessible organic matter into the planktonic trophic network (Pomeroy et al., 2007).

We use here the stable carbon isotopic composition of particulate organic material (SCIC POM) as an important indicator of the state and genesis of plankton, including heterotrophic bacterioplankton. This indicator can be used with care to separate the two major sources of organic matter—the isotopically light ($\delta^{13}C < -25‰$) OM produced by terrestrial plants, which arrives from continental sources, while isotopically heavier POM (in the Arctic $\delta^{13}C > -22‰$; Stein and Macdonald, 2004) is produced autochthonously by marine phytoplankton. The
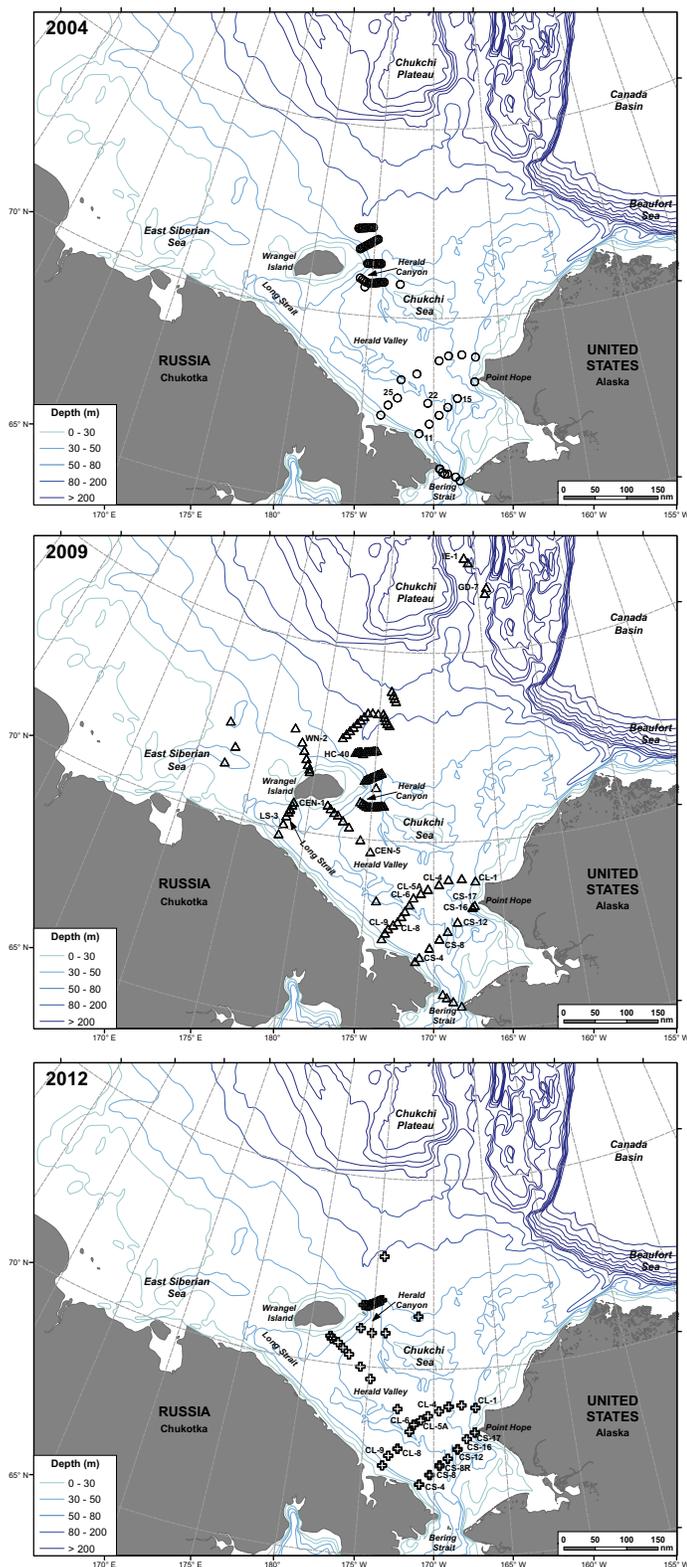
FIGURE 1. Locations of RUSALCA sampling in (a) 2004, (b) 2009, and (c) 2012.

SCIC of allochthonous POM varies depending on the biochemical characteristics of photosynthesis by terrestrial plants (e.g., the ratio between the C_3 and C_4 types of photosynthesis, which is not a major factor in the Arctic, as well as water use efficiency in C_3 plants). It can also vary for aquatic plants depending upon the isotopic composition of dissolved carbon dioxide and bicarbonate in freshwater, which is typically more depleted in ^{13}C than bicarbonate of seawater. This difference results in significantly more depleted $\delta^{13}C$ values for POM produced by freshwater photosynthetic organisms, but can lead to complexities in interpretation (Marty and Planas, 2008).

During the last two decades, in the course of a number of research efforts, the $\delta^{13}C$ values of OM in the surface sediments of much of the East Arctic shelf seas (Chukchi, East Siberian, Laptev, as well as the Beaufort Sea) have been determined and extensive maps produced (e.g. Fahl et al., 1999; Dunton et al., 2012, and references therein). Unlike other Arctic coastal seas, the Chukchi Sea and the eastern part of the East Siberian Sea are not dominated by river runoff but rather by Pacific water inflow via the Bering Strait. However, changing seasonal sea ice conditions in the Chukchi Sea have resulted in a considerable increase in freshwater derived from melted sea ice because the Chukchi has been impacted by dramatic decreases in seasonal sea ice extent (Cooper et al., 2005).

Joint Russian-US research as part of RUSALCA began in September 2004 (Figure 1) and provided data of relevance on the concentrations of macronutrients and primary production in various areas of the Chukchi Sea (Lee et al., 2007, 2014; Yun et al., 2014), on methane concentrations in the water column and bottom sediments, and on the total microbial abundance and the rates of the key microbial processes (Lein et al., 2007; Savvichev et al., 2007). High rates of biological processes are associated with an area of organic accumulation that has been termed a "hotspot" in the southern part of the sea (Grebmeier et al., 2006, 2015a; Sirenko and Gagaev, 2007). The highest rates of microbial processes were associated with surface sediments (Savvichev et al., 2007). In general, bacterial productivity in the northern parts of the Chukchi Sea sampled as part of RUSALCA was lower by an order of magnitude than observations made in the southern Chukchi Sea (Savvichev et al., 2007). Particularly during the second process cruise in September 2009, favorable ice coverage conditions facilitated the expansion of sampling areas to sites in Long Strait, in the eastern part of the East Siberian Sea, and to sub-oceanic ridges along the northern edge of the Chukchi Plateau. The third RUSALCA expedition was carried out in September 2012 (Figure 1) and also investigated both the southern and the northern parts of the Chukchi Sea, but was not spatially as extensive as the cruise in 2009 (Figure 1).

MATERIALS AND METHODS

Water and sediment samples were obtained in August/September 2004, September 2009, and September 2012 during RUSALCA expeditions on board R/V *Professor Khromov* (Figure 1). Sampling was carried out along two parallel sections in the southern part of the Chukchi Sea (CS) between the coasts of Alaska and the Chukchi Peninsula (CL) and in the central part of the Chukchi Sea (CEN) along four short sections: through Herald Canyon in the northwestern part of the Chukchi Sea (HC), in Long Strait (LS), in an area with pockmark-like structures over the Chukchi Plateau (GD), and at the northernmost edge of the Chukchi Sea (IE). Water and bottom sediments were also sampled along two short sections (SS and WN) during 2009 in the eastern part of the East Siberian Sea.

On each cruise, water samples were collected at most continental shelf stations from three depths (surface, near bottom, and chlorophyll maximum) using 10 L Niskin bottles mounted on a Sea-Bird 911+ conductivity-temperature-depth (CTD) instrument equipped with additional sensors for turbidity, fluorescence, and oxygen concentration. For productivity measurements, water from the bottles was dispensed by overflowing water into glass vials, which were then sealed with gas-tight stoppers in order to avoid contact with atmospheric oxygen. Data reported correspond to the average of surface, near-bottom, and chlorophyll maxima measurements.

Bottom sediments were collected using a HAPS benthic corer and a van Veen grab. The sediment samples were placed in cut-off 5 mL plastic syringes and sealed with gas-tight rubber stoppers. All experiments with the water and sediment samples were carried out at in situ temperatures (+1° to +6°C) within several hours after sampling.

Sediment pore waters were analyzed for C_{org} and C_{HCO3^-} content in surface sediments (0–5 cm) using a total organic carbon (TOC) analyzer (Shimadzu, Japan) equipped with a Model SSM 5000A solid sample combustion system. For dissolved organic carbon, the calibrated range of the measurable concentrations was from 0.05 to 25,000 mg C L^{-1} in a sample of 100 μL volume. For the bottom sediments, the calibrated range of the organic carbon (% of the dry mass) was from 0.05 to 30 mass % in a sample of 100 μg mass (Belyaev et al., 2010). Eh measurements of fresh sediment samples were carried out using a portable WTW Model 320 pH/mV meter (Germany) with a SenTix ORP ceramic electrode.

Bacterial abundance was determined from water samples in glass vials that were fixed with glutaraldehyde (final concentration 2%). The fixed material (5–10 mL) was filtered through black polycarbonate membranes with nominal 0.2 μm pore diameters (Millipore). The filters were stained with acridine orange (2 μg mL^{-1}; Hobbie et al., 1977) and examined under a Lumam-I microscope (LOMO, Russia) at 1000X. Cells were counted in 20 microscope fields. Cell volumes of the cocci and rods were calculated by approximating them as geometric spheres and cylinders, respectively. An average of ~200 cells was counted for each sample.

Dark CO_2 assimilation in water samples was determined using NaH^{14}CO$_3$. A 0.2 mL aliquot of sterile water containing NaH^{14}CO$_3$ (Amersham CFA3) was added to seawater samples in 35 mL dark glass vials with a final radioactivity of 0.15 μCi mL^{-1}. For each sample, two replicates and one control were analyzed. The controls were fixed with 1 mL 0.2 N HCl prior to bicarbonate addition. The samples were incubated for 20 to 26 hours in a refrigerator at close to in situ temperatures. After incubation, the samples were filtered through nylon membranes (Millipore 0.2 μm pore diameter). Residual carbonates were removed by washing with large amounts of filtered, slightly acidified seawater. Separation of the ^{14}C products and radioactivity measurements (Rack-Betta Model 1219 scintillation counter, LKB, Sweden) were carried out as described previously (Rusanov et al., 1998). Dark CO_2 assimilation rates were calculated after accounting for the overall alkalinity (*Alk*) in the water samples. Bacterial production was calculated using the dark CO_2 assimilation rates for the cells (neglecting extracellular exometabolites). We used the assumptions of Sorokin (1998) that the ratio of production of marine heterotrophic bacterioplankton to heterotrophic CO_2 assimilation is ~20 (heterotrophic production only). The *P/B* coefficient (the ratio of net productivity to biomass), or growth rate, was also calculated assuming that carbon content is 10% of the biomass wet weight (Sorokin, 1998).

The carbon isotope ratio for organic matter ($\delta^{13}C_{Corg}$) in suspension was determined from water samples (4–12 L) filtered through pre-combusted 47 mm GF/F glass fiber filters. The amount of suspended matter was determined gravimetrically after washing the filters to remove salt and drying at 60°C. The carbon isotope composition of the organic matter, whether filtered or derived from dried surface sediments, was determined by incineration of the samples after pretreatment with HCl to remove carbonates. The $\delta^{13}C_{Corg}$ values for POC and surface sediments in 2009 were determined on a ThermoFisher Delta Plus stable isotope mass spectrometer (Germany) at the Winogradsky Institute of Microbiology using a standard calibrated to the international Vienna-PDB standard. Another ThermoFisher Delta Plus stable isotope mass spectrometer and similar procedures were used at the Chesapeake Biological Laboratory to determine carbon (and nitrogen) isotope and elemental compositions of the organic fractions of surface sediments in 2004 and 2012 (sediment samples from 2009 were analyzed using the Winogradsky Institute instrument). International standards were used to ensure that data from each lab was comparable; analytical precision using both instruments was ±0.1‰. Studies of the stable carbon isotope composition of carbonates in pore waters were also determined using standard phosphoric acid dissolution following removal of all
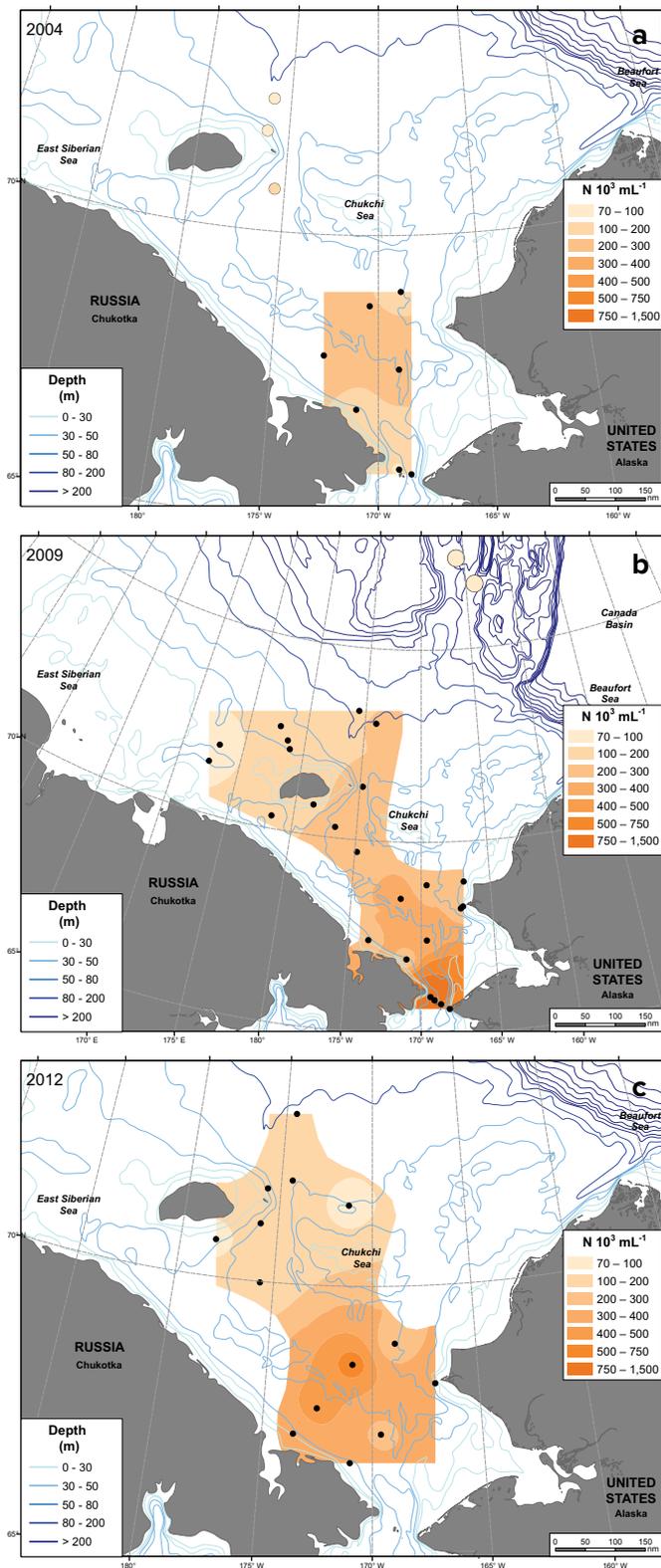
FIGURE 2. (a) Bacterial abundance in (a) 2004, (b) 2009, and (c) 2012. All data are expressed as numbers of cells per mL.

water traces from the phosphoric acid.

Surface sediment subsamples (0–1 cm) were also collected from a single 0.1 m² van Veen grab, packaged in Whirl-Pak bags, and frozen for post-cruise grain size determinations and organic carbon and nitrogen content following standard sampling methods (Cooper et al., 1998; Grebmeier, 2012). Syringe subsamples (1.54 cm²) of surface sediments were collected from the top 0–1 cm of the grab before it was opened for determination of chlorophyll *a* content. Following dark storage for 12 hours in 90% acetone at 0–2°C, chlorophyll *a* concentrations from these sediment aliquots were determined using a Turner Designs 10-AU fluorometer aboard the ship (Cooper et al., 2002). The mean of two chlorophyll *a* concentration measurements for each station were converted to chlorophyll *a* per m² of surface sediments.

Sediment community oxygen consumption (SCOC) was measured using duplicate benthic cores collected at all process stations using the single HAPS benthic corer. Removable plastic inserts to the HAPS corer are designed for rapid replacement and have specialized beveled chamber lids and bases for incubation setup immediately after core collection, and with minimal disturbance. Oxygen uptake was measured using micro-Winkler methodologies, and nutrient fluxes were also determined shipboard (with samples collected and frozen at the start and end of the experiment for post-cruise processing) on sediment cores maintained at in situ bottom water temperatures for 18 to 24 h, depending on macroinfaunal biomass density (see Grebmeier et al., 1988, for further details).

RESULTS

Bacteria Abundance and Size

In all three sampling years, certain consistent patterns were observed. For example, in all three years, bacterial abundance was highest at the "hotspot" to the north of the Bering Strait, where strait inflow slows down and particle deposition increases (2.8×10^5 cells mL^{-1} in 2004; 3.9×10^5 cells mL^{-1} in 2009; Figure 2a,b). Overall, bacterial abundance was low, for example, varying in 2004, depending on the sampling area, from 0.7×10^5 to 2.8×10^5 cells mL^{-1}, with an average value of 1.64×10^5 cells mL^{-1} (Figure 2a). The lowest abundances were observed in Herald Canyon (0.1×10^5 to 1.0×10^5 cells mL^{-1}, in 2004 and 2009), but higher bacterial abundances were found in zones of active sea ice melt in the melt lens in the upper water layer. Absolute bacterial abundance at productive stations were, however, higher in 2012 than in the previous sampling years (4.5×10^5 to 5.5×10^5 cells mL^{-1}), and the average number of bacterial cells (2.4×10^5 cells mL^{-1}) was also higher in 2012 than in 2004 and 2009 (Figure 2c).

Microscopic observations showed a predominance of large rods associated with detritus particles in the samples

collected near the Alaskan coast and in the Bering Strait. The average cell volume was 0.104 ± 0.06 μm^3. In Long Strait and in the East Siberian Sea, bacterial abundances were considerably lower than in the Chukchi Sea (from 0.76×10^5 to 1.8×10^5 cells mL^{-1}), although the average cell volume was similar to observations in the Chukchi Sea (0.12 ± 0.05 μm^3). While almost all of the stations sampled during RUSALCA are on the continental shelf (depth <100 m), the lowest bacterial abundances were observed at the sole northern station (GD-7) sampled off the continental shelf (depth 604 m) at intermediate and deep water depths in 2009 (0.36×10^5 cells mL^{-1}). By comparison, the average bacterial abundance for the Chukchi and East Siberian Seas (not including the Bering Strait data) was 1.9×10^5 cells mL^{-1}. At most of the Chukchi Sea shelf stations (40–60 m), higher bacterial numbers (up to 8.0×10^5 cells mL^{-1}) were observed. Bacteria attached to suspended particles constituted 20% to 30% of the total cell number in the upper water layers throughout the study area. Also in general, the numbers of single (unattached) cells decreased significantly with depth over the shelf. The numbers of bacteria attached to suspended particles either did not change, or increased with depth, reaching up to 80% of the total cell number in near-bottom water depths. In the easternmost American sector of the Bering Strait (BS stations), bacterial numbers were unusually high (14.0×10^5 cells mL^{-1}), while bacterial abundances decreased in the direction of the Chukchi Peninsula, reaching 5.5×10^5 cells mL^{-1} at the westernmost station. However, the average size of bacterial cells increased from Alaska to the Chukchi Peninsula (from 0.071 to 0.139 μm^3).

Bacterial Production

Highest levels of bacterial production were observed at stations in the southeastern Chukchi Sea (from 0.78 to 1.0 μg C L^{-1} day^{-1} in 2004 and 2009 and from 1.2 to 1.7 μg C L^{-1} day^{-1} in 2012; Figure 3a,b,c). Bacterial production decreased gradually in a south-north direction, with the lowest values observed in the northern part of the sea with 0.08 to 0.14 μg C L^{-1} day^{-1}. Bacterial production both in the water column of the East Siberian Sea (sampled only in 2009) and in the northern part of the Chukchi Sea was similarly low (<0.32 μg C L^{-1} day^{-1}). At most stations, bacterial production in the water column generally decreased with depth (data not shown). The lowest value (0.04 μg C L^{-1} day^{-1}) was observed at 200 m depth at station GD-7 (2009). In August 2009, the highest average bacterial production was found in well-mixed waters in the Bering Strait (up to 3.3 μg C L^{-1} day^{-1}). In 2012, elevated levels of bacterial production were again observed in the "hotspot" area and in the southeastern part of the Chukchi Sea, and bacterial production in the northern part of the Chukchi Sea did not differ significantly from observations for 2004 and
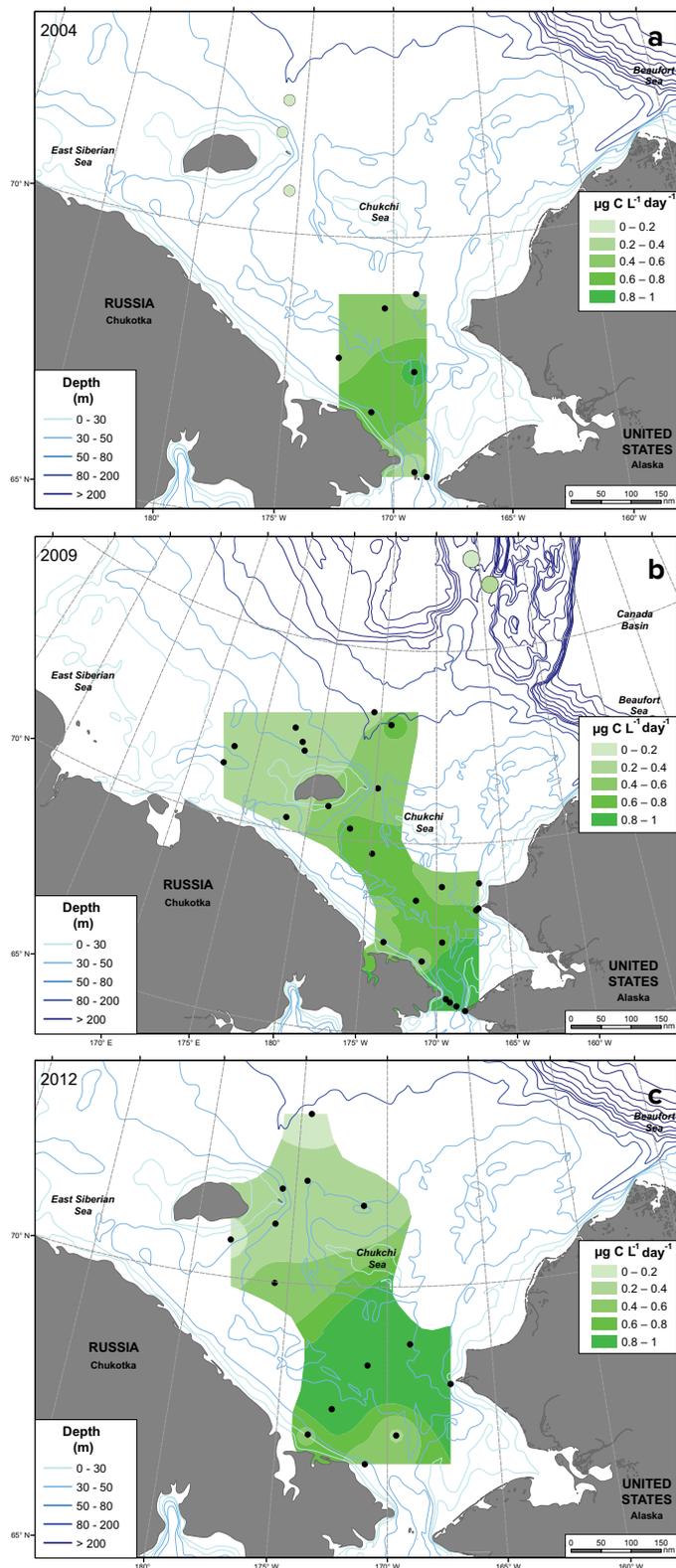

FIGURE 3. Bacterial production in (a) September 2004, (b) September 2009, and (c) September 2012. Data are expressed in units of μg C per liter per day.
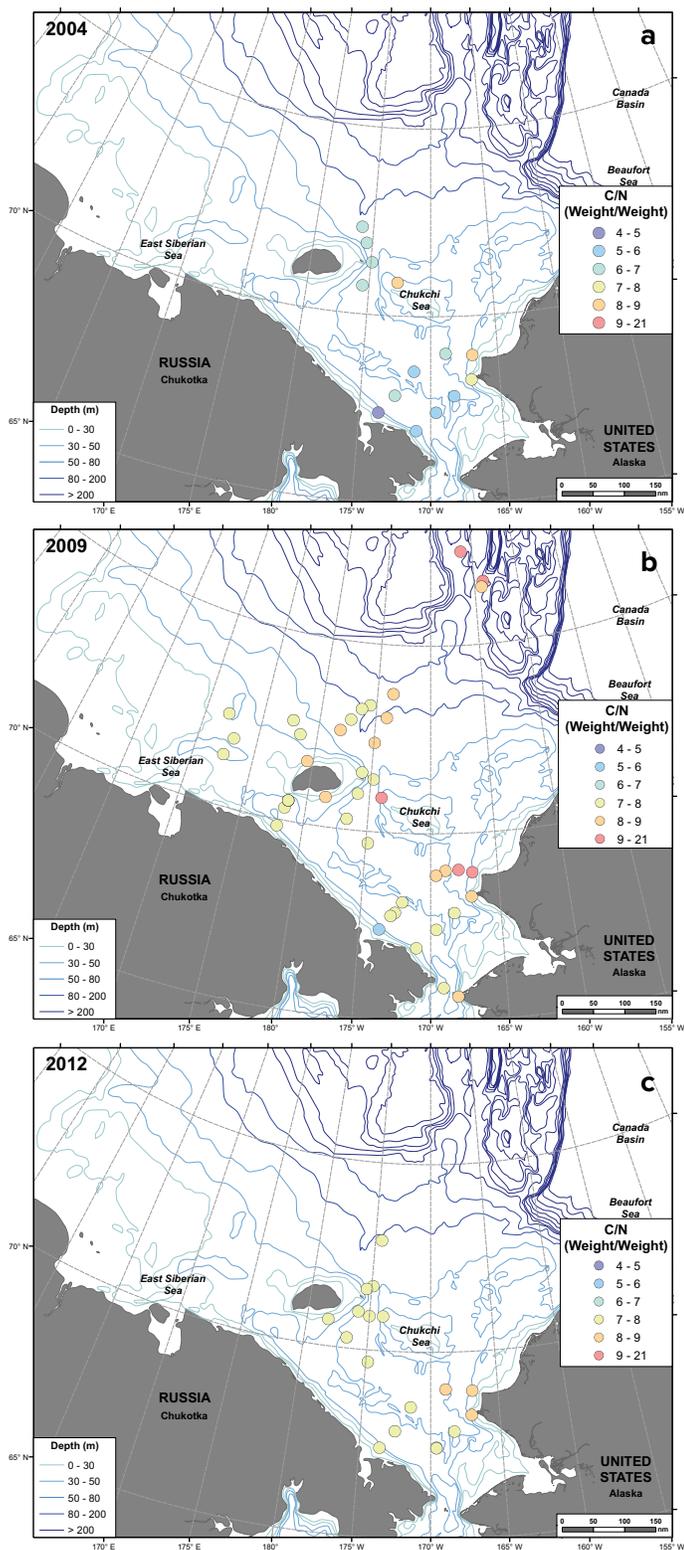
FIGURE 4. Carbon/nitrogen ratios (weight/weight) for organic matter in surface sediments, in (a) 2004, (b) 2009, and (c) 2012.

2009 (on average 0.27 µg C L^{-1} day^{-1}).

In the upper water column, the average growth rates associated with specific bacterial production varied from 0.10 to 0.53 day^{-1} (average = 0.29 day^{-1}) in 2004, from 0.12 to 0.43 day^{-1} (average = 0.23 day^{-1}) in 2009, and from 0.09 to 0.74 day^{-1} (average = 0.33 day^{-1}) in 2012. The growth rates in the near-bottom water depths for all three study years were lower, from 0.04 to 0.23 day^{-1} (average = 0.18 day^{-1}). The lowest values were recorded in the cold bottom waters of the East Siberian Sea and the intermediate depths at the northern stations of the Chukchi Sea. Analyses of bacterial abundance and production data revealed steady decreases in these values from south to north, as well as similar gradients from the southern Chukchi "hotspot" to Long Strait and further into the East Siberian Sea. On the other hand, the distribution of the growth rate values could also be described as a fractal distribution with no tendency for increase or decrease in latitudinal and longitudinal directions (according to the 2009 data, the average growth rate was 0.22 day^{-1} for the northern stations and 0.25 day^{-1} for the southern and central stations).

General Sediment Organic Matter Characteristics

C/N ratios in the RUSALCA study area were lower downstream of the Bering Strait and in Herald Canyon (i.e., spatial variation), but there are also indications that ratios have increased at individual locations since the first RUSALCA cruise (Figure 4a,b,c).

Sediment grain size in turn also exerts controls on organic matter composition. Generally, sediment samples collected during RUSALCA cruises were primarily semi-liquid oxidized or reduced pelite-aleurite silts. Eh values for the upper sediment horizon (0–5 cm) were usually positive, varying from +200 mV (station CS-16) to –145 mV (station CS-8). The content of dissolved organic material in pore waters of the upper sediments varied from 20 mg C L^{-1} (station GD-7) to 80–90 mg C L^{-1} (stations CS-8, HC-40).

There was higher silt and clay (%) in the upper/central Herald Valley and on the western side of Herald Canyon as well as around Wrangel Island. Sandy sediments (low % silt/clay) occurred along the Alaskan and Chukotka coastlines (Figure 5a,b,c). Sandy and sandy-aleurite sediments as well as rocky substrates predominated in the Bering Strait.

The percentages of total organic carbon had similar patterns to the silt and clay content. Sediment TOC (%) in surface sediments can be an indicator of current speed and material deposition zones, and TOC is directly related to the silt/clay fraction of organic carbon. Higher TOC occurred in deposition zones in the central Herald Valley, with lower TOC along the coasts of the United States and Russia (Figure 6a,b,c). Sediments within Herald Canyon and downstream of the Bering Strait inflow had higher TOC.

Overall, TOC varied from 0.3‰ to 2.3% (wt/wt) of dry sediment, and averaged 1.16%. The C-CO$_3^{2-}$ isotopic composition varied within a narrow range, from –1.56‰ to +1.95‰, indicating a marine origin of the carbonates present.

Sediment chlorophyll inventories in surface sediments were consistent with the distribution of TOC and grain size, with finer-grained sediments having higher inventories of sediment chlorophyll. Such higher inventories of sediment chlorophyll were observed underlying areas of high productivity in the central southern Chukchi Sea and downstream into Herald Canyon, where deposition is locally high (Figure 7a,b,c).

Stable Carbon Isotopic Composition of Suspended Particulate Organic Material (δ^{13}C$_{Corg}$)

The Chukchi Sea and the eastern East Siberian Sea have relatively low and localized inflows of river water and, therefore, only contribute small amounts of terrigenous POM to suspended matter. The 2004, 2009, and 2012 data, as well as data from prior international cruises in 1988, 1993, and 1995, indicate that organic matter in suspension was mainly of phytoplankton origin (Figure 8a,b,c). This conclusion is based upon the relatively isotopically heavy carbon composition of POM, which was, on average, –22.1‰ for surface waters in 2004 (Savvichev et al., 2007). In near-bottom waters, the POM isotopic composition was typically even less depleted in ^{13}C (average –21.8‰ in 2004). The difference in δ^{13}C$_{Corg}$ for POM between the surface and near-bottom waters varied from –0.3‰ (close to analytical uncertainty) and up to +3.1‰ in 2004. The δ^{13}C values for POM in 2009 also increased with depth throughout the central Chukchi Sea. In 2009, at 19 stations, δ^{13}C values of POM were also higher in the near-bottom waters than in the surface layer, and at some stations (e.g., CS-17, CL-1, CL-4, and GD-7), this difference was 3‰ or more, although the average difference in the POM δ^{13}C values for the 22 stations sampled in 2009 was 1.5‰. This pattern of less heavy isotope-depleted POM near the bottom was also observed in 2012, with differences of –1.1‰ to 4.9‰ (average of 1.4‰). On a geographical basis, stations in the central part of the Chukchi Sea were associated with high production rates, based upon relatively positive δ^{13}C values (~ –21‰), but in 2009 at stations such as CS-16 and CS-17 adjacent to Alaska and stations CL-9 and CEN-1 adjacent to Chukotka, somewhat more negative δ^{13}C values were observed, which is consistent with coastal current influence (Cooper et al., 2009). The average δ^{13}C value for POM from near-bottom water in 2009 was –20.4‰ for the open sea and –21.4‰ for the coastal stations. The δ^{13}C values for Chukchi Sea POM in surface waters were similar in 2012 and ranged from –19.3‰ (station CL-5A) to –25.7‰ at station CS-8R, which is coastally influenced.

In the East Siberian Sea and Long Strait, δ^{13}C values for
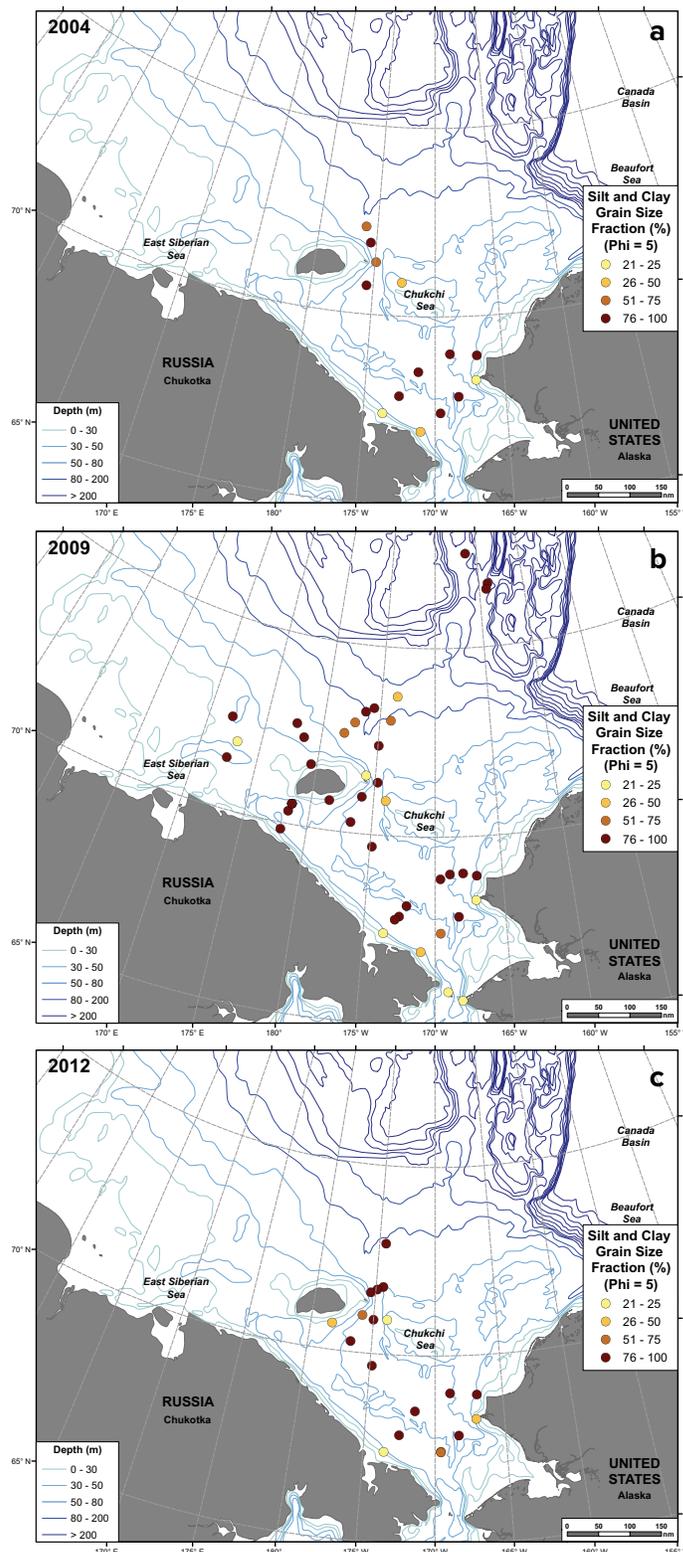

FIGURE 5. Silt and clay content (percentage) in surface sediments in (a) 2004, (b) 2009, and (c) 2012.
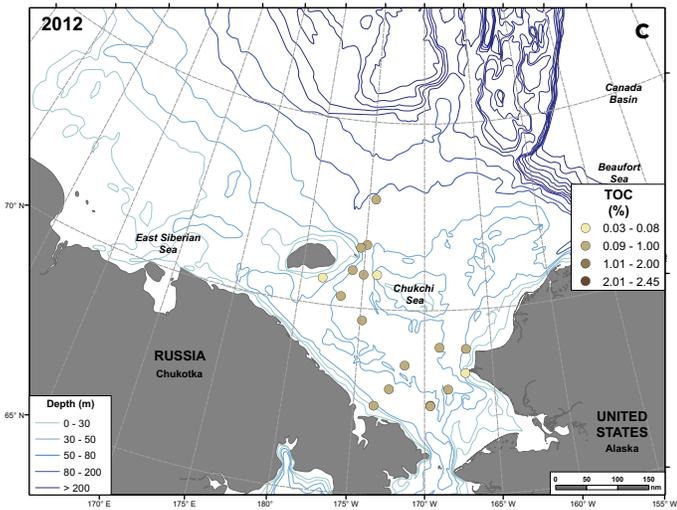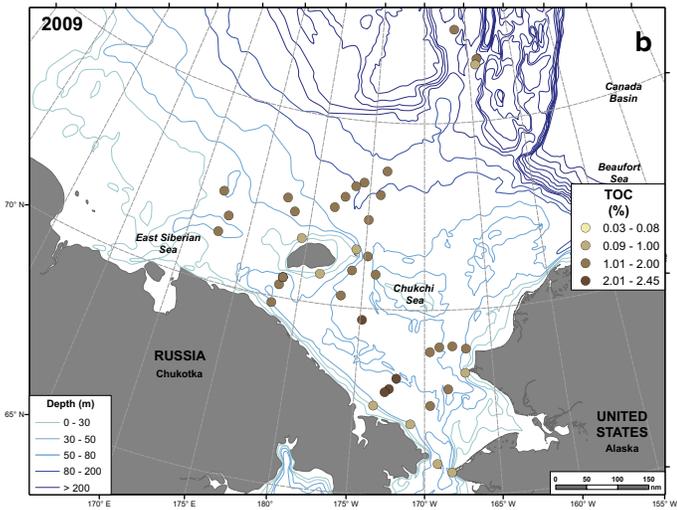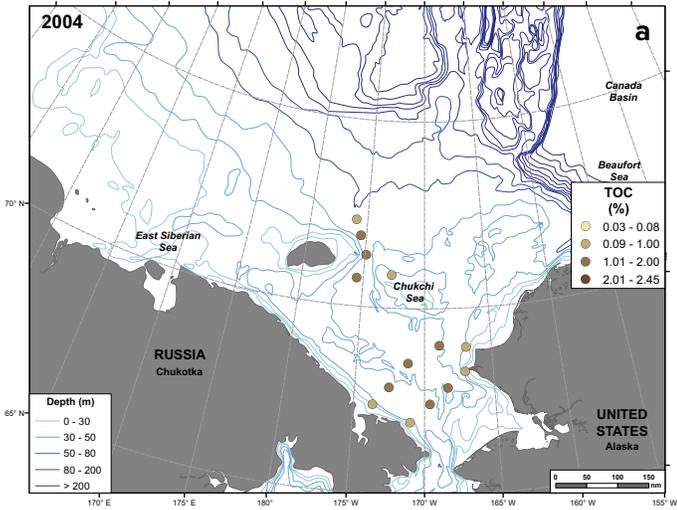
FIGURE 6. Total organic carbon (TOC, %) in surface sediments in the RUSALCA study area in (a) 2004, (b) 2009, and (c) 2012.
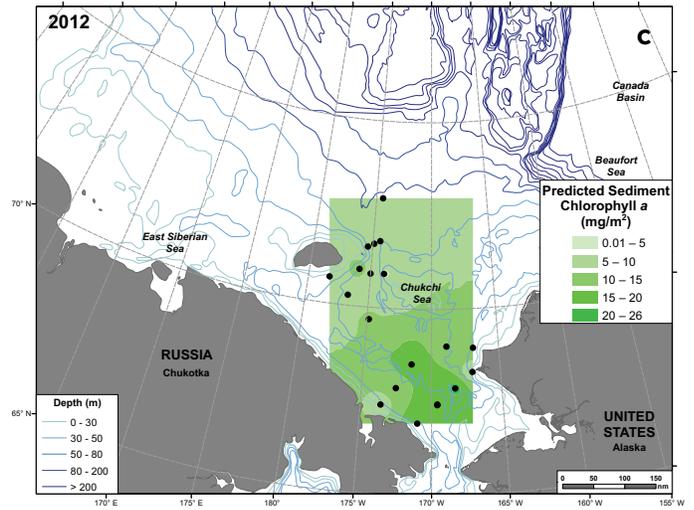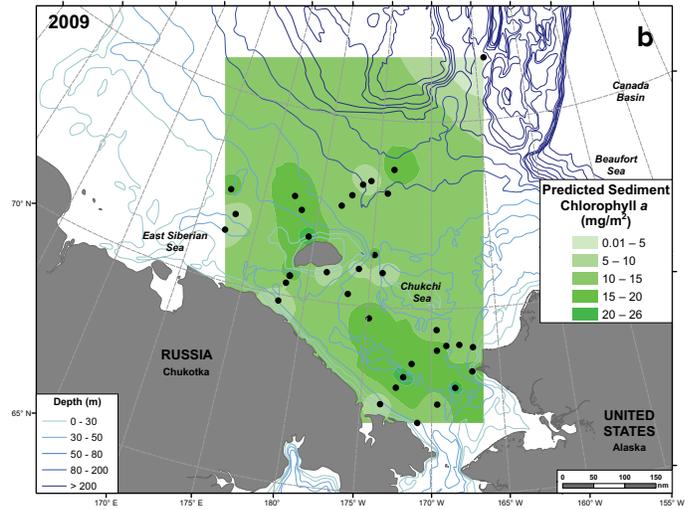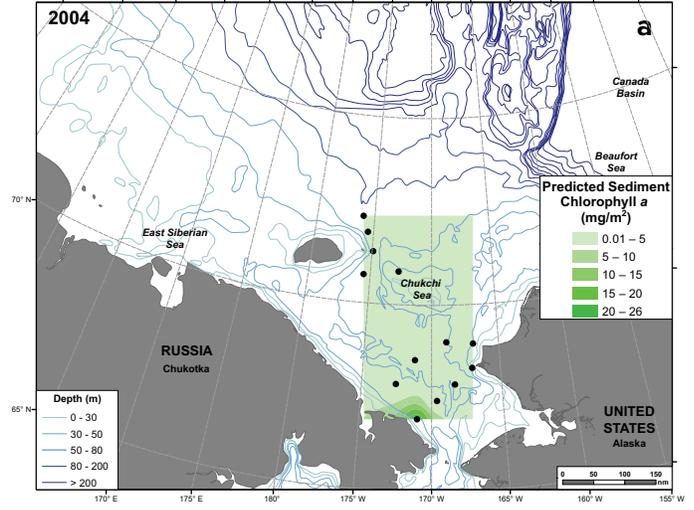
FIGURE 7. Sediment chlorophyll *a* present in surface sediments in the RUSALCA study area in (a) 2004, (b) 2009, and (c) 2012.

POM of surface waters varied from –24.0‰ at station WN-2 to –25.3‰ at station LS-3, with an overall average value of –24.5‰. The difference between the δ¹³C values for POM of surface and near-bottom waters varied from –0.7‰ to 2.8‰, with an average difference of –1.7‰. At three stations in the eastern and central parts of the Chukchi shelf, δ¹³C of near-bottom water varied within a narrow range from 19.0‰ to 20.6‰ (Figure 8b); surface POM was more depleted in δ¹³C by 2‰ to 4‰. Overall, the observed isotopic ratios are consistent with a phytoplanktonic origin of POM in surface waters of these stations. POM from surface waters was most depleted in ¹³C (the average δ¹³C value for the four stations was –23.0‰), but POM from near-bottom waters and OM of the sediments were typically enriched with ¹³C (average δ¹³C = –22.2‰ and –21.0‰, respectively).

The δ¹³C values for organic materials in surface sediments also differed from the values for POM from surface waters in 2004, 2009, and 2012. While at a few stations in 2009, δ¹³C values of C_{org} in the sediments were more depleted in ¹³C than POM in overlying water (stations CS-4, CS-16, and CS-17), for the most part, sedimentary organic matter was usually more enriched in ¹³C than in POM from surface water. For example, at four stations in the northern Chukchi Sea in 2009, δ¹³C values were determined for POM from the surface and near-bottom water depths and for organic carbon from surface sediments (Figure 8b).

At the Bering Strait stations (BS) closest to the Chukchi Peninsula coast, the δ¹³C value of sediment OM was –23.2‰, indicating an admixture of terrigenous OM in this coastal region. Overall, the new observations provided here are consistent with prior observations (Cooper et al., 2009) showing temporal variability in OM in sediments, with less negative δ¹³C values close to Chukotka and more negative δ¹³C values in Alaskan Coastal Waters in more recent years (Figure 9).

Sediment Oxygen Metabolism, Carbon Uptake, and Sediment Nutrient Exchange

Sediment community oxygen respiration rates indicate that the highest rates of oxygen utilization (and related organic carbon export to the benthos) consistently occurred in the Southeast Chukchi Sea "hotspot" site where we also have observed high biomasses of bivalves and polychaetes (Figure 10; see also Grebmeier, 2012). Consistent with these observations, effluxes of nutrients during sediment incubations (RUSALCA09 and 12) were highest in samples from the Southeast Chukchi Sea "hotspot" (data shown for ammonium and silica in 2009; Figure 11a,b). The lowest outflux of nutrients was observed in samples from the offshore East Siberian Sea and north of Pt. Hope off Alaska (Figure 11a,b). The rate of dark CO_2 assimilation integrates microbial activity (autotrophic and heterotrophic, aerobic and anaerobic). Dark CO_2 assimilation rates in the sediment samples varied
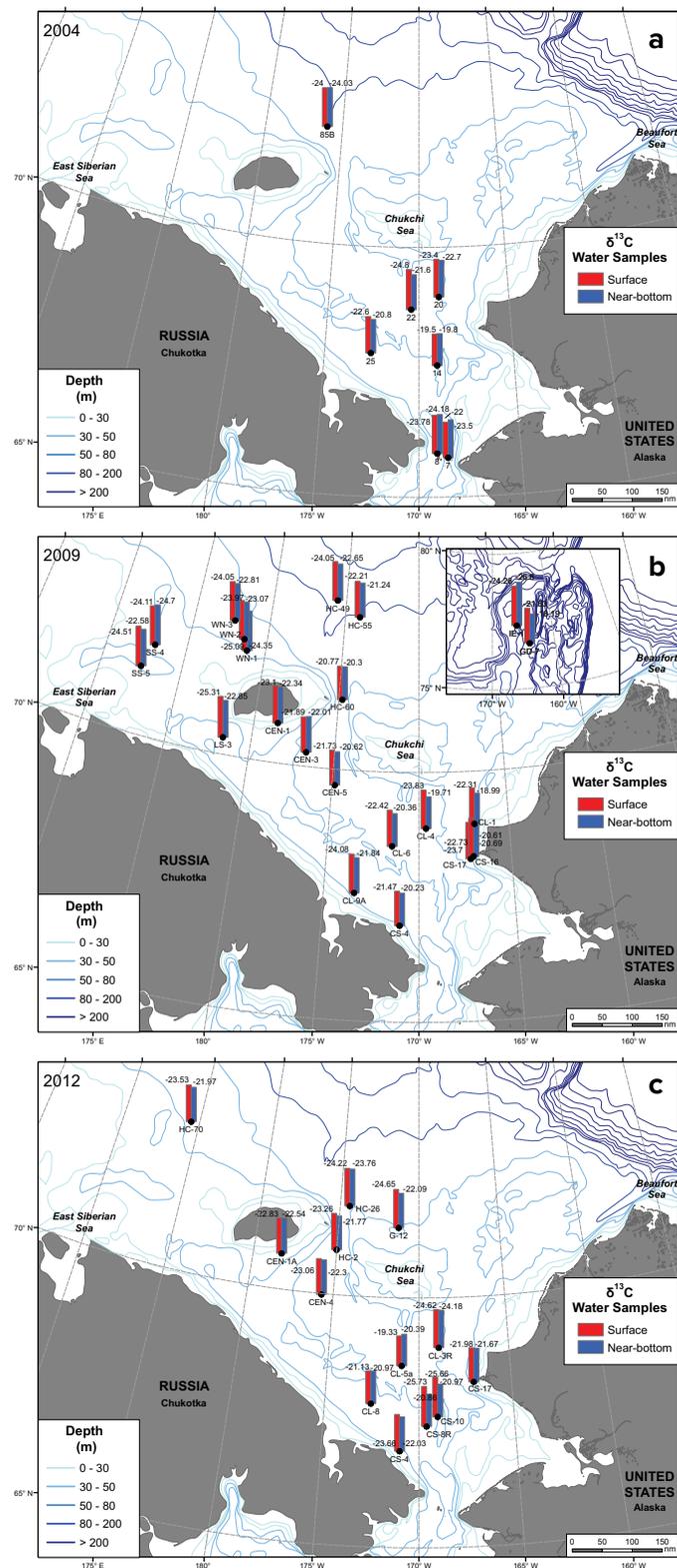

FIGURE 8. Surface water versus near-bottom water particulate organic carbon stable isotope compositions in (a) 2004, (b) 2009, and (c) 2012. Red columns reflect surface water particulate organic carbon (POC), and blue columns correspond to near-bottom POC.

from 0.26 to 10.3 mM C m^{-3} day^{-1}, with an average of 2.21 mM C m^{-3} day^{-1}. The lowest microbial activity was observed in the sediments of the northern, deepwater part of the Chukchi Sea (stations GD-7 to IE-1). The highest dark carbon assimilation rates occurred in the sediments of the "hotspot," the most productive part of the Chukchi Sea (station CS-4, CS-8, and CL-6; 5.7–10.3 mM C m^{-3} day^{-1}). On a molar basis, dark CO_2 assimilation in the sediments was lower than oxygen uptake (Figure 10), but was of the same approximate order of magnitude.

The δ^{15}N values of sediment OM, including samples from 1988, 1993 (Joint US-Soviet/Russian Expeditions), and 1995 (*Alpha Helix* cruise 189) as well as the 2004 and 2012 RUSALCA cruises, tended to increase south to north, with some exceptions (Figure 12). Nevertheless, the δ^{15}N values (~0) observed, even in coastal areas, are consistent with a marine origin. Other processes may result in trends toward higher δ^{15}N values in downcurrent locations, such as Herald Canyon, that are remote from terrestrial sources that would also increase δ^{15}N values. These sediment-based processes are likely to include denitrification, which would tend to enrich remaining pools of inorganic nitrogen as nitrate is consumed.

DISCUSSION
Bacterial Abundance and Productivity

Analysis of the quantitative results on bacterioplankton abundance and productivity requires assessment of primary production. Labile and easily available OM of phytoplankton origin is the base for the functioning of the carbon cycle, including the microbial loop. During RUSALCA expeditions in 2004, 2009, and 2012, phytoplankton production was measured (Lee et al., 2007; Yun et al., 2014) using the ^{13}C–^{15}N-dual isotope tracer technique. In 2004, measurement of phytoplankton production by the classical radioisotope method was also carried out (Savvichev et al., 2007). The summarized existing primary production data for all RUSALCA cruises differed 18- to 100-fold (Table 1). Comparison of the average values indicates similar productivity in 2004 and 2012 (404–426 mg C m^{-2} day), while in 2009 it was 1.5 times lower. Although comparing primary production measurements is often problematic, consistent rates were obtained in 2004 using two independent methods (Table 1). The "hotspot" zone is easily isolated because it is identified by the maximum values of the parameters (at stations 11 and 15 in 2004, stations CL-6 and CS-12 in 2009, and stations

CL-5A and CL-8 in 2012), but extrapolating these data to a wider area would likely result in unjustified overestimates of the average primary production values for the relatively oligotrophic East Siberian and Chukchi Seas. Neglecting the data from the "hotspot" results in considerably lower values of Chukchi Sea average production (163–263 mg C m^{-2} day^{-1}), with the 2009 average production no longer minimal. Production rates in the East Siberian Sea (2009) are consistently lower than in the Chukchi Sea, with a range of 17 to 130 mg C m^{-2} day.

Data obtained on the abundance of bacteria during the three expeditions, each at a similar time of year, is generally similar to that found in the literature (Table 2). While high bacterioplankton abundance in the southern part of the sea and in the "hotspot" area are within the upper range of the known values for Arctic seas (4.3 × 10^5 cells mL^{-1}), bacterioplankton numbers in the northern Chukchi Sea are lower (1.1–1.5 × 10^5 cells mL^{-1}), consistent with central Arctic areas (Table 2).

Our bacterial abundances are lower than results obtained during the 2002 and 2004 USCGC *Healy* expeditions to the Chukchi Sea (Shelf-Basin Interactions Project; Kirchman et al., 2009a). At depths below 100 m, bacteria abundance in summer was 9–12 × 10^5 cells mL^{-1} (the
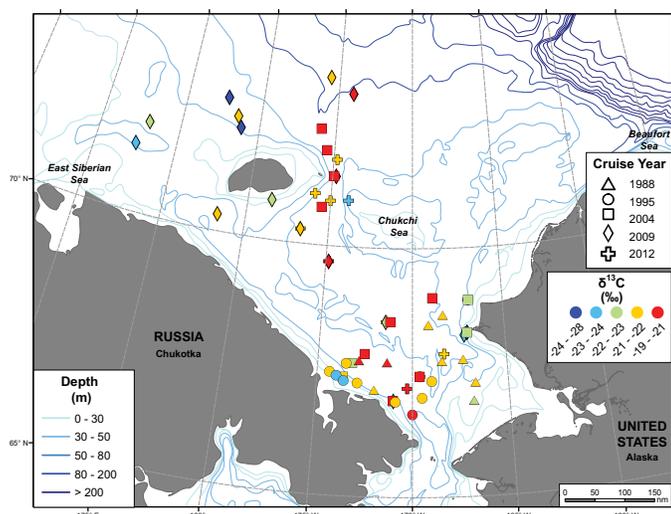

**FIGURE 9.** Stable carbon isotope composition of organic carbon in surface sediments, 1988–2012.
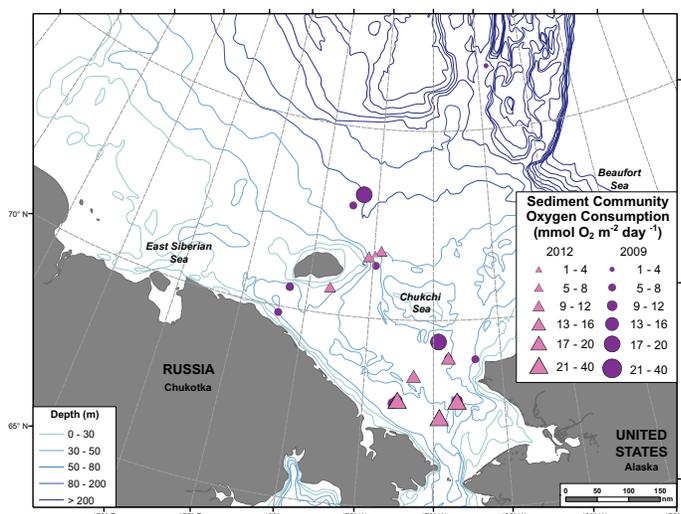
FIGURE 10. Rates of sediment oxygen consumption (mmol O$_2$ m^{-2} day^{-1}).

values were obtained by microscopy of DAPI-stained preparations versus our use of acridine orange). However, this previous study was undertaken during or immediately after the summer phytoplankton bloom, so the abundances observed cannot be compared entirely with our late summer sampling. Primary production values determined by the same authors in 2002 and 2004 (averaged for the area) also varied widely (1,581 and 458 mg C m^{-2} day^{-1}), although the variation observed is not as great as that discussed above during the RUSALCA measurements, 18- to 100-fold (Table 1). Bacterioplankton production during the western Arctic Shelf Basin Interactions (SBI) study was also somewhat higher (30–60 mg C m^{-2} day^{-1}) than our observations (Table 2).

Our data on daily bacterioplankton production for 2009 stations with depths <100 m show production variation from 9.0 mg C m^{-2} day^{-1} (station WN-2) to 44 mg C m^{-2} day^{-1} (station CS-8). The ratio of bacterioplankton production to phytoplankton production (BP/PP) varied from 0.049 to 0.67, with the highest values found at stations with the lowest production. This pattern may indicate active consumption of newly synthesized autochthonous OM by heterotrophic bacterioplankton in low-production waters, which would enhance the secondary component of the carbon cycle. By contrast, in areas of high phytoplankton production (e.g., "hotspot" area), heterotrophic bacterioplankton consume an insignificant fraction of phytoplankton-produced OM (BP/PP <0.1). By comparison, the ratio of bacterioplankton production to phytoplankton production in the prior SBI study (Kirchman et al., 2009a) varied from 0.06 to 0.79, with an average of 0.34. Overall, the growth rates we observed suggest an absence of spatial synchronization in the state of the heterotrophic bacterioplanktonic community; its growth and development are determined by the quality and quantity of organic matter available.

The patterns of highest microbial activity observed in surface sediments are also associated with high biomass of benthic animals (discussed by Grebmeier et al., 2015b, in this issue). Functionally, the model for processes within sediments in the Chukchi Sea are consistent with phytoplankton blooms providing fresh organic carbon to the bottom sediments and thus enhancing rates of microbial processes. These surface sediments are characterized by high biomass of benthic animals actively consuming OM (Grebmeier et al., 2006, 2015a). Activity of these animals results in constant mixing and aeration of the semiliquid sediment. Below this thin "bioreactor" layer, the rates of microbial processes decrease, and anaerobic degradation of unconsumed OM predominates (Savvichev et al., 2007). These patterns may be considered a special type of detrital trophic chain, in which bacterial degraders and animal detritovores are the key components.

Sediment Organic Matter Characteristics

The characteristics of the sediments sampled during the three process cruises of the RUSALCA program (2004, 2009, 2012) are consistent with prior findings (e.g., Grebmeier et al., 2006), which show that organic matter content, sediment chlorophyll, grain size, and C/N ratios of organic matter in surface sediments are all interrelated. The organic matter composition of Chukchi Sea bottom sediments is determined by autochthonous contributions to the sediments, products of coastal erosion, runoff, and ice transfer. Areas with high particle deposition in the Chukchi "hotspot" region downstream of the Bering Strait typically have higher organic matter content, fine-grained sediments, high sediment chlorophyll content, and lower C/N ratios. In areas with higher current flow, such as close to the Alaskan or Russian coasts, grain size is coarser,
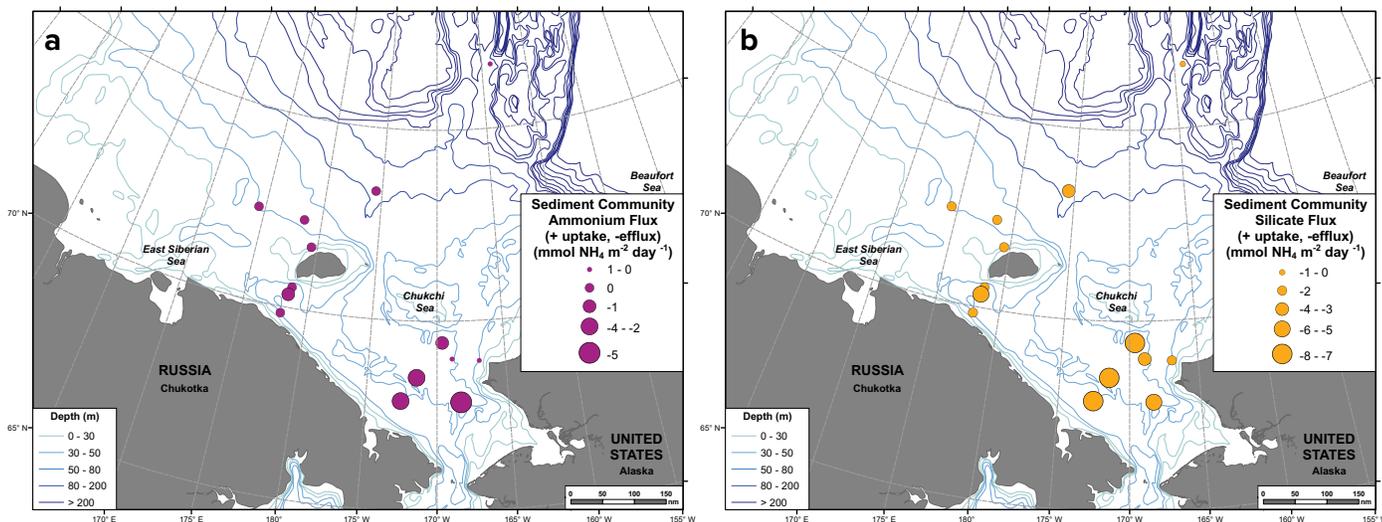

FIGURE 11. Nutrient effluxes of (a) ammonium, and (b) silica from sediments in regions of high organic carbon deposition during RUSALCA 2009.
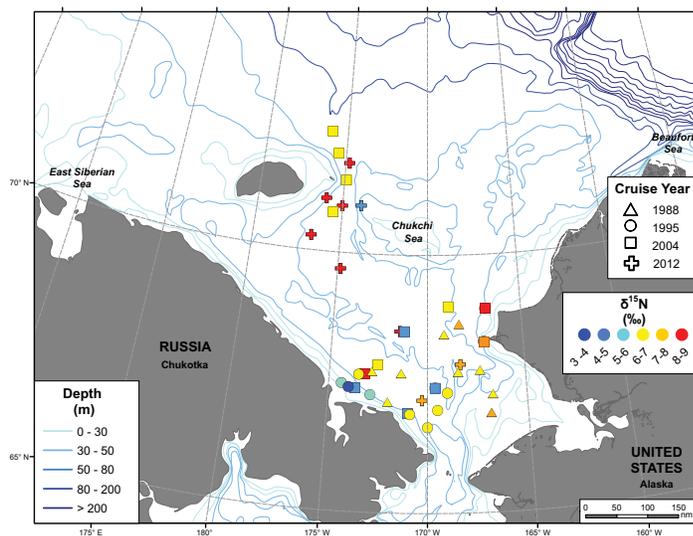
FIGURE 12. Stable nitrogen isotope composition of organic matter in surface sediments. Data for 1988 and 1995 are from samples archived prior to the RUSALCA program.

organic carbon content decreases while C/N ratios of organic matter increase, and sediment chlorophyll declines, indicating lower particle deposition. The potential additional contribution available from this study is the variability in these characteristics apparent over the decade-long period of the study. For example, TOC was in many cases higher at stations sampled in 2009 than in 2004 and 2012 (Figure 6), and C/N ratios of organic matter were lowest (highest food quality) in 2004 and have declined since then (Figure 4). Stable carbon isotope ratios have also changed during the decade of sampling (see discussion below). However, a limitation with all sediment characteristic data that have been collected is that sampling density and points of repeated sampling varied each year. There are probably not enough data to definitely state how the

sediment characteristics are changing, but it is clear that deposition patterns and sediment characteristics of organic matter are not static and must be more systematically sampled in the future to understand how and if the ecosystem is changing.

Stable Carbon Isotopic Composition of Suspended Particulate Organic Material

Investigation of the isotopic composition of suspended organic matter ($\delta^{13}C_{Corg}$) in the water column of the East Siberian and Chukchi Seas revealed a persistent tendency for isotopically heavier OM to occur in near-bottom waters compared with the surface (Figure 8a,b,c). Observations of shifts to higher $\delta^{13}C$ values in suspended organic matter at similar depths (~50 m) were also observed in sampling on the Bering Sea shelf

(Lovvorn et al., 2005) and in floating sediment trap collections on the Chukchi shelf (Lalande et al., 2007), although this trend did not continue at depths (~100 m) greater than we sampled here. We consider here four possible explanations for this phenomenon.

First, organic matter may be transformed in the course of sedimentation (e.g., see reviews by Blair and Aller, 2012; Bauer et al., 2013). However, this explanation is inconsistent with the often analytically identical SCIC of POM from intermediate water depths, as compared to surface samples (intermediate-depth samples were collected in 2012, but the data are not shown here). Second, the difference in the origin of the surface and near-bottom suspensions may be a function of horizontal transport, with different sources of organic matter at the surface and near the bottom. This is clearly true for deepwater station IE-1 (665 m) in the northernmost part of the Chukchi Sea, which had different water masses throughout the water column, including Atlantic water at depth. But this explanation is insufficient for the shallow stations of most of the Chukchi Sea area, because the surface and near-bottom waters in most cases have a common Pacific water mass origin (e.g., the simultaneous presence of Alaska Coastal Water on the surface and Bering Winter Water in bottom waters does not occur over large areas). Third, the isotopic ratio of organic carbon in near-bottom water may also change due to activity of microorganisms transforming reduced organic material from the bottom sediments. Although this process certainly occurs, and enhanced

TABLE 1. Comparison of daily minimum, mean (bold), and maximum primary productivity measured in Chukchi and East Siberian Sea samples collected on RUSALCA cruises in 2004, 2009, and 2012.

	2004[a] (mg C m^{-2} day^{-1})	2004[b] (mg C m^{-2} day^{-1})	2009[a] (mg C m^{-2} day^{-1})	2012[a] (mg C m^{-2} day^{-1})
All areas	45 – **406** – 1,487	80 – **426** – 1,400	9 – **268** – 889	18 – **419** – 1,609
Chukchi Sea without the "hot spot"	45 – **163** – 432	80 – **170** – 270	9 – **214** – 555	18 – **192** – 407
East Siberian Sea			17 – **66** – 130	

[a] Lee et al., 2007, 2010; Yun et al., 2014 ($^{13}C-^{15}N$-dual isotope tracer technique)
[b] Savvichev et al., 2007 (^{14}C uptake method)

heterotrophic bacterioplankton activity is observed in the near-bottom layer, the biogeochemical scale of this activity is insufficient to shift the carbon isotopic ration by 1‰ or more (Ivanov et al., 2012; Lein et al., 2012).

The final explanation, the one we consider most likely, is that all three expeditions were carried out in late August and September, so that the sampling period did not coincide with the summer phytoplankton bloom. Thus, the near-bottom SOM retained the isotopically heavy OM of phytoplanktonic origin, which was initially synthesized during the brief bloom period when nutrients remain in the surface waters. A subsurface chlorophyll maximum is commonly observed in the Chukchi Sea (reviewed by Brown et al., 2015) and represents the residual of the phytoplankton bloom that sinks to near bottom waters where low light and nutrient availability sustain some productivity.

During intense photosynthesis, discrimination against ^{13}C diminishes, so POM synthesized early in the season, prior to our sampling of surface waters, would likely have been isotopically enriched in ^{13}C relative to POM synthesized later during the RUSALCA expeditions. Also, the isotopically lighter surface suspension is low in bacterioplankton and is diluted by allochthonous matter later in the season (Figure 8a,b,c). Assuming this scenario, the most productive blooms probably occurred at stations 22 and 25 in 2004, at CS-4, CS-16, and CS-17 in 2009,

and at CS-4 and CS-8 in 2012 (assuming no horizontal transport of bloom materials). Resuspension from the sediments into bottom waters of any organic materials that have been acted upon by sedimentary bacteria (increasing δ^{13}C values; Lovvorn et al., 2005) would also have the same effect, although we observe a difference between near-bottom water OM and sediment OM at most stations. This explanation is thus only sufficient for a portion of the observed difference between OM in the sediments and that within the water column.

It should be noted that the relatively heavy isotopic composition of suspended organic matter is common at all stations in productive areas, which indicates predominance of autochthonous photosynthesis (including from ice algae) in replenishing POM in near-bottom water (e.g. δ^{13}C = –19.8‰ to –22.0‰ for the "hotspot" area) and in surface sediments. Active bacterial degradation and transformation of this relatively labile POM is linked to high benthic biomass, as bacterial transformations in the sediments result in production of food for deposit feeders (Lovvorn et al., 2005; North et al., 2014). In the Arctic seas that are supplemented with considerable river inflow, allochthonous organic carbon is comparatively more important. For example, the carbon isotopic ratio for organic matter from the Ob river arriving to the Kara Sea is δ^{13}C = –29.4‰ to –30.7‰ (Savvichev et al., 2010; Ivanov et al.,

2013). It is only in the northeast part of the Kara Sea, which is remote from the influence of river water, that δ^{13}C values of organic matter in near-bottom waters are –24.7‰. The abundance of allochthonous organic material, which is not that easily available to deposit feeders, cannot support the benthic trophic chain typical of the Chukchi Sea's productive areas.

The carbon isotope composition of sediment OM confirms recent compilations (e.g., Dunton et al., 2012) that have combined numerous data sets collected over the past several decades from the East Siberian Sea east through the Chukchi and Beaufort Seas. The general pattern confirmed is of terrestrial organic carbon in regions close to river mouths, and variation in OM that reflects general patterns of productivity, with less negative δ^{13}C values in areas of high production, such as the Southeast Chukchi Sea under nutrient-rich water masses. However, the growing temporal record indicates that caution is advised before assuming that the stable carbon isotope composition of OM is static. The RUSALCA data collected in 2004, 2009, and 2012, as well as data from previous joint US-Russian projects in 1988, 1993, and 1995, confirm indications in Cooper et al. (2009) of shifts to less negative δ^{13}C sedimentary OM values at certain locations near Chukotka. The new data presented here also indicate more negative δ^{13}C values along the Alaskan coast near Point Hope in the most recent sampling. The causes

TABLE 2. Measured minimum, mean (bold), and maximum bacterial abundance (BA) and production rates (BP) in polar seas.

Study Area	Sampling Period	BA Depth (m)	BA (10⁵ cells mL⁻¹)	BP Depth (m)	BP (mg C m⁻² day⁻¹)	References
Central Arctic Ocean	June–Sept	Z_{eu}: ≤ 40	1.9 – **3.2** – 6.7	50	1 – **4** – 15	Sherr and Sherr, 2003
Kara Sea	Aug–Sept	1–2	2.3 – **3.5** – 4.7	25	12 – **43** – 79	Meon and Amon, 2004
Kara Sea	Sept 2007	1–20	1.2 – **5.6** – 10.8	25–100	2 – **26** – 185	Savvichev et al., 2010
Greenland Sea	end of July	≤50	0.97 – **11** – 28	50	12 – **157** – 634	Börsheim, 2000
Franklin Bay	Nov–Aug	≤10	0.87 – **3.2** – 11	200	1 – **8** – 80	Garneau et al., 2008
Chukchi Sea	mid-Aug to mid-Sept	≤10	2.1 – 21	50	152 – **227** – 301	Steward et al., 1996
Chukchi Sea	Aug–Sept 2004	1–20	0.77 – **1.7** – 2.8	20–50	4.6 – **16** – 19.5	Savvichev et al., 2007
Chukchi Sea	Aug–Sept 2009	1–20	0.78 – **3.8** – 7.2	20–50	6.5 – **18** – 65	This study
Chukchi Sea	Aug–Sept 2012	1–20	0.7 – **2.4** – 4.5	20–50	3.0 – **28** – 44	This study

of these changes could be due to increases in terrestrial runoff near Point Hope and alterations of marine productivity and/or decreases in freshwater runoff at affected regions along the Chukotka coast.

Sediment Oxygen Metabolism and Sediment Nutrient Exchange

High rates of sediment oxygen metabolism are consistent with the sediment organic matter characteristics, discussed above, and are located in the high productivity region to the north of the Bering Strait, in the south central Chukchi Sea. This site is recognized as ecologically important and is part of the time series Distributed Biological Observatory (DBO) effort. The Herald Canyon stations to the northwest indicate a down-canyon decline in oxygen utilization and carbon export, with highest rates observed in the upper canyon near Wrangel Island and decreasing rates as water deepens. Macroinfaunal community collections indicate that the highest biomass is also in the Southeast Chukchi Sea in the region of the hotspot of fresh phytodetrital deposition (Grebmeier et al., 2015a and 2015b, in this issue). The lowest infaunal biomass areas studied during RUSALCA are downstream in Herald Valley, which is to the northwest of the hotspot site, and deeper in Herald Canyon (Grebmeier et al., 2015a and 2015b, in this issue). Again, as with sediment characteristic data, more sampling over time should provide insights on changes in sediment metabolism, but the RUSALCA sediment data are limited to 2009 and 2012. Additional sampling is needed to resolve whether the oxygen utilization rates in these sediments are changing over time. Higher nutrient efflux rates appear well associated with higher oxygen utilization rates (Figure 10) that are in turn controlled by benthic biomass (Grebmeier et al., 2015a).

The data available for the stable nitrogen isotope composition of sediment OM (Figure 11) are not as extensive as those available for carbon isotopes, but they still reveal some interesting patterns that suggest transformations of inorganic

nitrogen during the transit of water across the Chukchi Shelf. The $\delta^{15}N$ values of sediment OM tend to increase to the north, which is consistent with evidence for significant denitrification of nitrate within sediments as northward-flowing water passes over the Chukchi Shelf (Jones and Anderson, 1986; Devol et al., 1997; Cooper et al., 1999; Chang and Devol, 2009). This would lead to increasingly more positive $\delta^{15}N$ OM values in sediments (e.g., Altabet and François, 1994; Piccolo et al., 1994; Emmer and Thunell, 2000). There are also some indications that $\delta^{15}N$ values may become more positive, particularly in Herald Canyon from 2004 to 2012 (Figure 12). 🌀

REFERENCES

Altabet, M.A., and R. François. 1994. Sedimentary nitrogen isotope ratio as a recorder for surface ocean nitrate utilization. *Global Biogeochemical Cycles* 8:103–116, http://dx.doi.org/10.1029/93GB03396.

Amon, R.M.W., and B. Meon. 2004. The biogeochemistry of dissolved organic matter and nutrients in two large Arctic estuaries and potential implications for our understanding of the Arctic Ocean system. *Marine Chemistry* 92:311–330, http://dx.doi.org/10.1016/j.marchem.2004.06.034.

Bauer, J.E., W.-J. Cai, P.A. Raymond, T.S. Bianchi, C.S. Hopkinson, and P.A.G. Regnier. 2013. The changing carbon cycle of the coastal ocean. *Nature* 504:61–70, http://dx.doi.org/10.1038/nature12857.

Belyaev, N.A., V.I. Peresypkin, and M.S. Ponyaev. 2010. The organic carbon in the water, the particulate matter, and the upper layer of the bottom sediments of the west Kara Sea. *Oceanology* 50(5):706–715, http://dx.doi.org/10.1134/S0001437010050085.

Benner, R., B. Benitez-Nelson, K. Kaiser, and R.M.W. Amon. 2004. Export of young terrigenous dissolved organic carbon from rivers to the Arctic Ocean. *Geophysical Research Letters* 31, L05305, http://dx.doi.org/10.1029/2003GL019251.

Blair, N.E., and R.C. Aller. 2012. The fate of terrestrial organic carbon in the marine environment. *Annual Review of Marine Science* 4:401–423, http://dx.doi.org/10.1146/annurev-marine-120709-142717.

Børsheim, K.Y. 2000. Bacterial production rates and concentrations of organic carbon at the end of the growing season in the Greenland Sea. *Aquatic Microbial Ecology* 21:116–123, http://dx.doi.org/10.3354/ame021115.

Brown, Z.W., K.E. Lowry, M.A. Palmer, G.L. van Dijken, M.M. Mills, R.S. Pickart, and K.R. Arrigo. 2015. Characterizing the subsurface chlorophyll a maximum in the Chukchi Sea and Canada Basin. *Deep Sea Research Part II* 118:88–104, http://dx.doi.org/10.1016/j.dsr2.2015.02.010.

Chang, B.X., and A.H. Devol. 2009. Seasonal and spatial patterns of sedimentary denitrification rates in the Chukchi Sea. *Deep Sea Research Part II* 56(17):1,339–1,350, http://dx.doi.org/10.1016/j.dsr2.2008.10.024.

Codispoti, L.A., C. Flagg, V. Kelly, and J.H. Swift. 2005. Hydrographic conditions during the 2002 SBI process experiments. *Deep Sea Research Part II* 52:3,199–3,226, http://dx.doi.org/10.1016/j.dsr2.2005.10.007.

Cooper, L.W., R. Benner, L.A. Codispoti, V. Kelly, J.W. McClelland, B.J. Peterson, R. Holmes, and J.M. Grebmeier. 2005. Linkages among runoff,

dissolved organic carbon, and the stable oxygen isotope composition of seawater and other water mass indicators in the Arctic Ocean. *Journal of Geophysical Research* 110, G02013, http://dx.doi.org/10.1029/2005JG000031.

Cooper, L.W., G.F. Cota, L.R. Pomeroy, J.M. Grebmeier, and T.E. Whitledge. 1999. Modification of NO, PO, and NO/PO during flow across the Bering and Chukchi shelves: Implications for use as Arctic water mass tracers. *Journal of Geophysical Research* 104(C4):7,827–7,836, http://dx.doi.org/10.1029/1999JC900010.

Cooper, L.W., J.M. Grebmeier, I.L. Larsen, V.G. Egorov, C. Theodorakis, H.P. Kelly, and J.R. Lovvorn. 2002. Seasonal variation in sedimentation of organic materials in the St. Lawrence Island polynya region, Bering Sea. *Marine Ecology Progress Series* 226:13–26, http://dx.doi.org/10.3354/meps226013.

Cooper, L.W., C. Lalande, R.S. Pirtle-Levy, I.L. Larsen, and J.M. Grebmeier. 2009. Seasonal and decadal shifts in particulate organic matter processing and sedimentation in the Bering Strait shelf region. *Deep Sea Research, Part II* 56:1,316–1,325, http://dx.doi.org/10.1016/j.dsr2.2008.10.025.

Cooper, L.W., I.L. Larsen, T.M. Beasley, S.S. Dolvin, J.M. Grebmeier, J.M. Kelley, M. Scott, and A. Johnson-Pyrtle. 1998. The distribution of radiocesium and plutonium in sea ice-entrained Arctic sediments in relation to potential sources and sinks. *Journal of Environmental Radioactivity* 39(3):279–303, http://dx.doi.org/10.1016/S0265-931X(97)00058-1.

del Giorgio, P.A., and J. Davis. 2003. Patterns in dissolved organic matter lability and consumption across aquatic ecosystems. Pp. 399–424 in *Aquatic Ecosystems: Interactivity of Dissolved Organic Matter.* S.E.G. Findlay and R.L. Sinsabaugh, eds, Academic Press, Burlington.

Devol, A.H., L.A. Codispoti, and J.P. Christensen. 1997. Summer and winter denitrification rates in western Arctic shelf sediments. *Continental Shelf Research* 17(9):1,029–1,050, http://dx.doi.org/10.1016/S0278-4343(97)00003-4.

Ducklow, H. 2000. Bacterial production and biomass in the oceans. Pp. 85–120 in *Microbial Ecology of the Oceans.* D. Kirchman, ed., Wiley-Liss, New York.

Dunton, K.H., S.V. Schonberg, and L.W. Cooper. 2012. Food web structure of the Alaskan nearshore shelf and estuarine lagoons of the Beaufort Sea. *Estuaries and Coasts* 35(2):416–435, http://dx.doi.org/10.1007/s12237-012-9475-1.

Emmer, E., and R.C. Thunell. 2000. Nitrogen isotope variations in Santa Barbara Basin Sediments: Implications for denitrification in the eastern tropical North Pacific during the last 50,000 years. *Paleoceanography* 15(4):377–387, http://dx.doi.org/10.1029/1999PA000417.

Fahl, K., H. Cremer, H. Erlenkeuser, H. Hansserr, J. Hölemann, H. Kassens, K. Knickmeier, K. Kosobokova, M. Kunz-Pirrung, F. Lindemann, and others. 1999. Sources and pathways of organic carbon in the modern Laptev Sea (Arctic Ocean): Implications from biological, geochemical and geological data. *Polarforschung* 69:193–205, http://epic.awi.de/28470/1/Polarforsch1999_24.pdf.

Garneau, M.-E., S. Roy, C. Lovejoy, Y. Gratton, and W. Vincent. 2008. Seasonal dynamics of bacterial biomass and production in a coastal Arctic ecosystem: Franklin Bay, western Canadian Arctic. *Journal of Geophysical Research* 113, C07S91, http://dx.doi.org/10.1029/2007JC004281.

Grebmeier, J.M. 2012. Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. *Annual Review of Marine Science* 4:63–78, http://dx.doi.org/10.1146/annurev-marine-120710-100926.

Grebmeier, J.M., B.A. Bluhm, L.W. Cooper, S. Danielson, K.R. Arrigo, A.L. Blanchard, J.T. Clark, R.H. Day, K.E. Frey, R.R. Gradinger, and others. 2015a. Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Progress In Oceanography* 136:92–114, http://dx.doi.org/10.1016/j.pocean.2015.05.006.

Grebmeier, J.M., B.A. Bluhm, L.W. Cooper, S.G. Denisenko, K. Iken, M. Kędra, and C. Serratos. 2015. Time-series benthic community composition and biomass and associated environmental

characteristics in the Chukchi Sea during the RUSALCA 2004–2012 Program. *Oceanography* 28(3):116–133, http://dx.doi.org/10.5670/oceanog.2015.61.

Grebmeier, J.M., L.W. Cooper, H.M. Feder, and B.I. Sirenko. 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Progress in Oceanography* 71:331–361, http://dx.doi.org/10.1016/j.pocean.2006.10.001.

Grebmeier, J.M., C.P. McRoy, and H.M. Feder. 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas: Part I. Food supply source and benthic biomass. *Marine Ecology Progress Series* 48:57–67, http://dx.doi.org/10.3354/meps051253.

Guo, L., C.-L. Ping, and R.W. Macdonald. 2007. Mobilization pathways of organic carbon from permafrost to arctic rivers in a changing climate. *Geophysical Research Letters* 34, L13603, http://dx.doi.org/10.1029/2007GL030689.

Hobbie, J.E., R.J. Daley, and S. Jasper. 1977. Use of nucleopore filters for counting bacteria by fluorescence microscopy. *Applied and Environmental Microbiology* 33(5):1,225–1,228.

Ivanov, M.V., A.Yu. Lein, A.S. Savvichev, I.I. Rusanov, E.F. Weslopolova, E.E. Zakcharova, and T.S. Prusakova. 2013. Abundance and activity of microorganisms at the water-sediment interface and their effect on the carbon isotopic composition of suspended organic matter and sediments of the Kara Sea. *Microbiology* 82(6):723–730, http://dx.doi.org/10.1134/S0026261713060064.

Ivanov, M.V., A.Yu. Lein, E.E. Zakharova, and A.S. Savvichev. 2012. Carbon isotopic composition in suspended organic matter and bottom sediments of the east Arctic seas. *Microbiology* 81(5):596–605, http://dx.doi.org/10.1134/S0026261712050086.

Jones, E.P., and L.G. Anderson. 1986. On the origin of the chemical properties of the Arctic Ocean halocline. *Journal of Geophysical Research* 91(C9):759–767, http://dx.doi.org/10.1029/JC091iC09p10759.

Jones, E.P., L.G. Anderson, and J.H. Swift. 1998. Distribution of Atlantic and Pacific waters in the upper Arctic Ocean: Implications for circulation. *Geophysical Research Letters* 25(6):765–768, http://dx.doi.org/10.1029/98GL00464.

Kirchman, D.L., V. Hill, M.T. Cottrell, R. Gradinger, R.R. Malmstrom, and A. Parker. 2009a. Standing stocks, production, and respiration of phytoplankton and heterotrophic bacteria in the western Arctic Ocean. *Deep Sea Research Part II* 56(17):1,237–1,248, http://dx.doi.org/10.1016/j.dsr2.2008.10.018.

Kirchman, D.L., X.A.G. Morán, and H. Ducklow. 2009b. Microbial growth in the polar oceans: Role of temperature and potential impact of climate change. *Nature Reviews Microbiology* 7:451–459, http://dx.doi.org/10.1038/nrmicro2115.

Lalande, C., J.M. Grebmeier, P. Wassmann, L.W. Cooper, M.V. Flint, and V.M. Sergeeva. 2007. Export fluxes of biogenic matter in the presence and absence of seasonal sea ice cover in the Chukchi Sea. *Continental Shelf Research* 27:2,051–2,065, http://dx.doi.org/10.1016/j.csr.2007.05.005.

Lee, S.H., H.-U. Dahms, Y. Kim, E.J. Choy, S.-H. Kang, and C.-K. Kang. 2014. Spatial distribution of small phytoplankton composition in the Chukchi Sea. *Polar Biology* 37(1):99–109, http://dx.doi.org/10.1007/s00300-013-1413-6.

Lee, S.H., D. Stockwell, and T.E. Whitledge. 2010. Uptake rates of dissolved inorganic carbon and nitrogen by under-ice phytoplankton in the Canada Basin in summer 2005. *Polar Biology* 33(8):1,027–1,036, http://dx.doi.org/10.1007/s00300-010-0781-4.

Lee, S.H., T.E. Whitledge, and S.-H. Kang. 2007. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Continental Shelf Research* 27(17):2,231–2,249, http://dx.doi.org/10.1016/j.csr.2007.05.009.

Lein, A.Yu., M.D. Kravchishina, N.V. Politova, A.S. Savvichev, E.F. Veslopolova, I.N. Mitskevich, N.V. Ul'yanova, V.P. Shevchenko, and M.V. Ivanov.

2012. Transformation of particulate organic matter at the water-bottom boundary in the Russian Arctic seas: Evidence from isotope and radioisotope data. *Lithology and Mineral Resources* 47(2):99–128, http://dx.doi.org/10.1134/S0024490212020034.

Lein, A.Yu., A.S. Savvichev, I.I. Rusanov, G.A. Pavlova, N.A. Belyaev, K. Crane, N.V. Pimenov, and M.V. Ivanov. 2007. Biogeochemical processes in the Chukchi Sea. *Lithology and Mineral Resources* 42(3):221–239, http://dx.doi.org/10.1134/S0024490207030029.

Lovvorn, J.R., L.W. Cooper, M.L. Brooks, C.C. De Ruyck, J.K. Bump, and J.M. Grebmeier. 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Marine Ecology Progress Series* 291:135–150, http://dx.doi.org/10.3354/meps291135.

Marty, J., and D. Planas. 2008. Comparison of methods to determine algal $\delta^{13}C$ in freshwater. *Limnology and Oceanography: Methods* 6:51–63, http://dx.doi.org/10.4319/lom.2008.6.51.

Mathis, J.T., J.M. Grebmeier, D.A. Hansell, R.R. Hopcroft, D. Kirchman, S.H. Lee, and S.B. Moran. 2014. Carbon biogeochemistry of the Western Arctic: Production, export and ocean acidification. Pp. 223–268 in *The Pacific Arctic Region: Ecosystem Status and Trends in a Rapidly Changing Environment*. J. Grebmeier and W. Maslowski, eds, Springer, Dordrecht.

Meon, B., and R.M. Amon. 2004. Heterotrophic bacterial activity and fluxes of dissolved free amino acids and glucose in the Arctic rivers Ob, Yenisei and the adjacent Kara Sea. *Aquatic Microbial Ecology* 37(2):121–135, http://dx.doi.org/10.3354/ame037121.

Moritz, R.E., C.M. Bitz, and E.J. Steig. 2002. Dynamics of recent climate change in the Arctic. *Science* 297:1,497–1,502, http://dx.doi.org/10.1126/science.1076522.

North, C.A., J.R. Lovvorn, J.M. Kolts, M.L. Brooks, L.W. Cooper, and J.M. Grebmeier. 2014. Deposit-feeder diets in the Bering Sea: Potential effects of climatic loss of sea ice-related microalgal blooms. *Ecological Applications* 24(6):1,525–1,542, http://dx.doi.org/10.1890/13-0486.1.

Perminova, I.V., I.V. Dubinenkov, A.S. Kononikhin, A.I. Konstantinov, A.Y. Zherebker, M.A. Andzhushev, V.A. Lebedev, E. Bulygina, R.M. Holmes, Y.I. Kostyukevich, and others. 2014. Molecular mapping of sorbent selectivities with respect to isolation of Arctic dissolved organic matter as measured by Fourier transform mass spectrometry. *Environmental Science & Technology* 48(13):7,461–7,468, http://dx.doi.org/10.1021/es5015423.

Piccolo, M.C., C. Neill, and C.C. Cerri. 1994. Natural abundance of ^{15}N in soils along forest-to-pasture chronosequences in the western Brazilian Amazon Basin. *Oecologia* 99(1–2):112–117, http://dx.doi.org/10.1007/BF00317090.

Pomeroy, L.R., P.J.leB. Williams, F. Azam, and J.E. Hobbie. 2007. The microbial loop. *Oceanography* 20(2):28–33, http://dx.doi.org/10.5670/oceanog.2007.45.

Riemann, B., and M. Søndergaard. 1984. Measurements of diel rates of bacterial secondary production in aquatic environments. *Applied and Environmental Microbiology* 47(4):632–638.

Rusanov, I.I., A.S. Savvichev, S.K. Yusupov, N.V. Pimenov, and M.V. Ivanov. 1998. Production of exometabolites in the microbial oxidation of methane in marine ecosystems. *Microbiology* 67(5):590–596.

Savvichev, A.S., I.I. Rusanov, N.V. Pimenov, E.E. Zakharova, E.F. Veslopolova, A.Yu. Lein, K. Crane, and M.V. Ivanov. 2007. Microbial processes of the carbon and sulfur cycles in the Chukchi Sea. *Microbiology* 76(5):603–613, http://dx.doi.org/10.1134/S0026261707050141.

Savvichev, A.S., E.E. Zakcharova, E.F. Weslopolova, I.I. Rusanov, A.Yu. Lein, and M.V. Ivanov. 2010. Microbial processes of the carbon and sulfur cycles in the Kara Sea. *Oceanology* 50(6):893–906, http://dx.doi.org/10.1134/S0001437010060093.

Sherr, B.F., and E.B. Sherr. 2003. Community respiration/production and bacterial activity in the upper water column of the central Arctic Ocean. *Deep Sea Research Part I* 50(4):529–542, http://dx.doi.org/10.1016/S0967-0637(03)00030-X.

Sirenko, B.I., and S.Y. Gagaev. 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. *Russian Journal of Marine Biology* 33(6):355–364, http://dx.doi.org/10.1134/S1063074007060016.

Sorokin, Y.I. 1998. *Radioisotopic Methods in Hydrobiology*. Springer-Verlag, Berlin Heidelberg New York, 321 pp.

Stein, R., and R.W. Macdonald, eds. 2004. *The Organic Carbon Cycle in the Arctic Ocean*. Springer-Verlag, Heidelberg, 349 pp.

Steward, G.F., D.C. Smith, and F. Azam. 1996. Abundance and production of bacteria and viruses in the Bering and Chukchi Seas. *Marine Ecology Progress Series* 131:287–300, http://dx.doi.org/10.3354/meps131287.

Stroeve, J.C., M.C. Serreze, M.M. Holland, J.E. Kay, J. Malanik, and A.P. Barrett. 2012. The Arctic's rapidly shrinking sea ice cover: A research synthesis. *Climatic Change* 110:1,005–1,027, http://dx.doi.org/10.1007/s10584-011-0101-1.

Vallières, C., L. Retamal, P. Ramlal, C.L. Osburn, and W.F. Vincent. 2008. Bacterial production and microbial food web structure in a large arctic river and the coastal Arctic Ocean. *Journal of Marine Systems* 74:756–773, http://dx.doi.org/10.1016/j.jmarsys.2007.12.002.

Yun, M.S., T.E. Whitledge, M. Kong, and S.H. Lee. 2014. Low primary production in the Chukchi Sea shelf, 2009. *Continental Shelf Research* 76:1–11, http://dx.doi.org/10.1016/j.csr.2014.01.001.

AUTHORS

Lee W. Cooper (cooper@umces.edu) is Research Professor, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD, USA. **Alexander S. Savvichev** is a researcher at the Winogradsky Institute of Microbiology, Russian Academy of Sciences, Moscow, Russia. **Jacqueline M. Grebmeier** is Research Professor, Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD, USA.