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Seasonal dynamics of bacterial biomass and production in a coastal arctic ecosystem: Franklin Bay, western Canadian Arctic

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[1] The Canadian Arctic Shelf Exchange Study (CASES) included the overwintering deployment of a research platform in Franklin Bay (70°N, 126°W) and provided a unique seasonal record of bacterial dynamics in a coastal region of the Arctic Ocean. Our objectives were (1) to relate seasonal bacterial abundance (BA) and production (BP) to physico-chemical characteristics and (2) to quantify the annual bacterial carbon flux. BA was estimated by epifluorescence microscopy and BP was estimated from ^{3}H-leucine and ^{3}H-thymidine assays. Mean BA values for the water column ranged from 1.0 (December) to 6.8×10^5 cells mL^{-1} (July). Integral BP varied from 1 (February) to 80 mg C m^{-2} d^{-1} (July). During winter-spring, BP was uncorrelated with chlorophyll *a* (Chl *a*), but these variables were significantly correlated during summer-autumn ($r_s = 0.68$, $p < 0.001$, $N = 38$), suggesting that BP was subject to bottom-up control by carbon supply. Integrated BP data showed three distinct periods: fall-winter, late winter–late spring, and summer. A baseline level of BB and BP was maintained throughout late winter–late spring despite the persistent cold and darkness, with irregular fluctuations that may be related to hydrodynamic events. During this period, BP rates were correlated with colored dissolved organic matter (CDOM) but not Chl *a* ($r_{s\ \mathrm{BP.CDOM|Chl\ a}} = 0.20$, $p < 0.05$, $N = 176$). Annual BP was estimated as 6 g C m^{-2} a^{-1}, implying a total BP of 4.8×10^{10} g C a^{-1} for the Franklin Bay region. These results show that bacterial processes continue throughout all seasons and make a large contribution to the total biological carbon flux in this coastal arctic ecosystem.

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1. Introduction

[2] Prokaryotic heterotrophs play a key role in marine global carbon fluxes by way of their production and consumption of dissolved organic matter, respiratory CO_2 production and nutrient recycling activities [*Arrigo*, 2005; *Kirchman*, 2000]. In oligotrophic parts of the ocean they can even be the dominant component of total planktonic biomass [*Biddanda et al.*, 2001; *Cole*, 1999; *Cotner and Biddanda*, 2002]. Yet despite the abundance and pivotal function of bacteria in marine ecosystems, few open-water studies have addressed their seasonal variations in biomass and production [*Carlson et al.*, 1996; *Hoch and Kirchman*, 1993]. Increasing attention has been given to seasonal changes in bacterial community structure in the sea [*Bano and Hollibaugh*, 2002; *Murray et al.*, 1998; *Pinhassi and Hagström*, 2000; *Schauer et al.*, 2003], and evidence has begun to emerge of repeated patterns over time [*Fuhrman et al.*, 2006]. In general, however, bacterial studies are typically restricted to a single oceanic cruise to a region, generally focusing on the spring bloom and subsequent summer period when primary and bacterial production rates are usually maximal. This seasonal bias is particularly striking for cold arctic ecosystems owing to the logistic difficulties of sampling such remote and inaccessible environments, especially during the ice-covered period over much of the year. However, bacterial heterotrophy may persist throughout all seasons, and several studies indicate that bacteria can be a major component of total community biomass and productivity even in cold polar waters [*Rivkin et al.*, 1996; *Vincent and Hobbie*, 2000].

[3] The Arctic is characterized by strong seasonality, and prokaryotes that grow in its coastal shelf environment must contend with pronounced fluctuations in photosynthetic production, ice cover, riverine discharge and temperature. Seasonal studies of bacterial abundance and production in

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polar marine waters are limited to a few areas, notably the Ross Sea, Antarctica, which focused mainly on the daylight period [*Ducklow*, 2003] and the upper water column of the Central Arctic Ocean during the SHEBA/JOIS study [*Sherr and Sherr*, 2003; *Sherr et al.*, 2003]. Overall, however, the composition, physiology and function of prokaryotic heterotrophs in the marine Arctic are poorly understood, both in terms of spatial variations as well as temporal dynamics [*Amon*, 2004; *Loeng et al.*, 2005].

[4] Our central aim in the present study was to determine the seasonal dynamics of biomass stocks and productivity of the prokaryotes (Archaea and Bacteria, subsequently referred to here as bacteria, since they are the dominant prokaryotes) in an arctic shelf environment over an annual cycle, and to relate these to variations in the physico-chemical environment. We hypothesized that bacterial biomass and productivity would be closely coupled to the primary production cycle, which in turn is dependent on incident solar irradiance and ice cover. A secondary aim was to quantify the annual bacterial carbon fluxes in terms of production and respiration. We undertook this study within the program Canadian Arctic Shelf Exchange Study (CASES) in which our research platform was frozen into the ice at a station in Franklin Bay, at the edge of Amundsen Gulf, Beaufort Sea.

2. Methods

2.1. Study Site and Sampling

[5] The study was carried out from 4 November 2003 to 6 August 2004 in Franklin Bay, western Canadian Arctic, onboard the icebreaker CCGS *Amundsen*. Microbial variables were collected from the surface to bottom of the water column, on 33 occasions covering almost a complete year. From 5 December 2003 to 1 June 2004, the ship was frozen into first-year pack ice at station 200 (70°02′N, 126°18′W). Deepwater sampling and profiling throughout this period was performed through the ship's internal moon pool. Conductivity, temperature and depth were measured using a Seabird 911+ CTD which was also equipped with a chlorophyll fluorescence probe, transmissometer, pH, oxygen and PAR (photosynthetically active radiation; 400–700 nm) probes. The CTD system was mounted on a Seabird Carousel rosette equipped with 24 12-L PVC Niskin type bottles. Throughout the winter period, water samples were taken from six fixed depths: 20, 50, 100, and 150 m, and near the bottom at approximately 220 m. Surface samples were taken from a site located 450 m up current from the ship to any avoid contamination. A 5-L Go-Flo bottle was deployed on a wire through an ice hole at 3 m (to avoid frazil ice) and at 10 m from the top of the ice. Salinity and temperature were measured with a SBE-19 CTD profiler. The maximum ice thickness during the study was 1.8 m.

[6] During the open water sampling (4 November to 4 December 2003 and 2 June to 6 August 2004), all the samples were collected using the rosette deployed from the ship's A frame. At this time samples were taken at 4 photic depths (100%, 10%, 1%, 0.1% of surface PAR) and near bottom. The photic depths were determined using a Secchi disk as an approximate guide to the diffuse light attenuation coefficient (K_d). The 0.1% depth measured on 16 July, 6 August and 4 November ranged from 33 to 65 m.

2.2. Environmental Variables

[7] Incident PAR was measured at 10-min intervals over the entire sampling period with a GUV-510 surface radiometer (Biospherical Instruments, Inc.) mounted at the top of the ship's wheelhouse. The data, provided by T. Papakyriakou (University of Manitoba) and S. Brugel (Université du Québec à Rimouski), were first integrated over 24 h for each day. Running means computed for 7-day intervals were plotted against time, expressed in Julian days, with day zero set at 1 January 2004.

[8] CDOM (colored dissolved organic matter) absorption, used as a potential index of terrigenous inputs from the river [see *Retamal et al.*, 2007], was measured in acid-cleaned 10-cm quartz cells using a Varian Cary Bio 300 scanning spectrophotometer. Samples were scanned at 1 nm intervals between 200 and 850 nm against MilliQ pure water. The spectrum was corrected for the absorption offset using the mean value for wavelengths greater than 800 nm.

[9] The absorption coefficient at 320 nm was calculated as

$$a_{320} = 2.303 \times A(320)/L, \quad (1)$$

where $A(320)$ is the optical density for wavelength 320 nm and L is the cell path length in meters.

2.3. Biological Variables

[10] Phytoplankton biomass was estimated from chlorophyll *a* (Chl *a*) analysis of the total community. Samples were filtered onto 25 mm diameter Whatman GF/F glass fiber filters and stored frozen (−80°C) until pigment extraction in ethanol [*Nusch*, 1980]. Concentrations were determined by fluorometry before and after acidification [*Strickland and Parsons*, 1972] using a Cary Eclipse spectrofluorometer standardized with *Anacystis* Chl *a*. Chl *a* data were compared to estimates from the CTD fluorometer and showed a significant relationship ($r = 0.75$, $p < 0.001$, $N = 198$).

[11] Bacterial abundance was estimated from formalin fixed samples (2% final conc.) filtered within 24 h through 0.2 μm black polycarbonate membranes and stained with 4′,6-diamidino-2-phenylindole (DAPI). A minimum of 400 DAPI stained cells were counted on each slide by epifluorescence microscopy using an Olympus BX51 microscope on board the ship. Bacterial biomass was estimated using the bacterial cellular biomass of 10 fg C cell^{-1} as suggested for oligotrophic marine systems [*Bell*, 1993] (see below).

[12] Bacterial production (BP) was estimated using the centrifugation method of *Smith and Azam* [1992] from measurement of the incorporation rates of two tritiated substrates. Incorporation rates of the amino acid [4,5-^{3}H]-leucine (Leu; specific activity: 159 Ci mmol^{-1}) provided an estimate of protein production while incorporation rates of the nucleoside [methyl-^{3}H]-thymidine (TdR; specific activity: 88 Ci mmol^{-1}) provided an estimate of DNA synthesis. The final concentration of radiolabeled substrate in each sample was 10–15 nM. Triplicate samples were incubated

in the dark at temperature in close agreement to in situ conditions (from −1.4 to 4°C) for 4 h.

[13] Bacterial production rates were estimated from leucine incorporation using a conservative carbon conversion factor of 1.5 kg C mol^{-1} of ^{3}H-leucine incorporation, as used in the Ross Sea [*Ducklow*, 2003]. Our leucine-based bacterial production rates provided the primary estimate of bacterial production. Leucine incorporation measurements were not performed on four sampling dates (11, 16, 23 and 28 January) and bacterial production was estimated from ^{3}H-thymidine incorporation measurements. This was possible because there was a close, linear relationship between the ^{3}H-leucine and ^{3}H-thymidine incorporation rates (r = 0.89, $p < 0.001$, $N = 92$). To convert thymidine incorporation into bacterial production, we used (1) a common empirical carbon conversion factor for marine waters of 2.0×10^{18} cells mol^{-1} of ^{3}H-thymidine incorporated and (2) the bacterial cellular biomass of 10 fg C $cell^{-1}$. The latter is based on what is recommended for oligotrophic marine systems, based on 97 experimental studies in the open ocean [*Bell*, 1993]. This value is consistent with the 11.5 fg C $cell^{-1}$ used in the Greenland Sea [*Börsheim*, 2000] and is within the range of 7–15 fg C $cell^{-1}$ estimated for oceanic regions [*Ducklow*, 2000]. The Beaufort Sea region, specifically the Mackenzie Shelf, is an oligotrophic system [*Carmack et al.*, 2004], and thus the conservative value of 10 fg C $cell^{-1}$ used in the present study was deemed appropriate.

[14] The incubation time for ^{3}H-leucine and ^{3}H-thymidine was determined from experiments using surface samples on 30 October 2003 and using surface and the near-bottom depth samples on 26 June 2004. Samples inoculated with ^{3}H-leucine or ^{3}H-thymidine (10 nM final conc.) were incubated for 120, 240, 360 to 480 min. Regressions between the DPM incorporated against time were linear for up to 480 min for ^{3}H-leucine uptake at surface in October and in June ($r = 94$, $p < 0.05$, $N = 4$), but at the near-bottom depth, incorporation decreased after 360 min. Regressions were linear for up to 480 min for ^{3}H-thymidine uptake at surface in June ($r = 85$, $p < 0.05$, $N = 4$), and for up to 360 min at surface in October ($r = 65$, $p < 0.05$, $N = 3$) and at depth in June ($r = 90$, $p < 0.05$, $N = 3$). Our uptake measurements from 4-h incubations were thus made on the linear section of the uptake curves. Saturation curve experiments were conducted in parallel to determine the appropriate radioisotope concentrations. The ^{3}H-leucine and ^{3}H-thymidine were added to samples at final concentrations of 15, 20, 25, 30, 40, 60 and 80 nM and incubated 4 h at the simulated in situ temperature. The use of a substrate concentration between 10 and 20 nM was confirmed to be appropriate for both radioisotopes, and is within the range recommended for oligotrophic environments [*Simon and Azam*, 1989].

2.4. Statistics

[15] Statistical analyses were performed over the entire annual data set and also for each season separately: autumn (21 September to 20 December), winter (21 December to 20 March), spring (21 March to 20 June) and summer (21 June to 20 September). Associations between pairs of variables were tested with the Pearson correlation (r coefficient), or Spearman rank correlation (r_s coefficient) when large deviations from normality were found [*Zar*, 1999]. Partial correlations were run to examine the interactions between three variables order to remove spurious correlations, and significance tests were made with Student's t test with df = n − 3 [*Myers and Well*, 2003]. Kruskal-Wallis analysis was used to test differences of the median values between sampling seasons since the data failed the normality and homogeneity of variance tests.

3. Results

3.1. Upper Water Column Characteristics

[16] PAR ranged from continuous darkness during the polar night to continuous sunlight in summer (Figure 1a). There were large variations in cloud cover in summer resulting in substantial day-to-day fluctuations in daily PAR, from a minimum of 25 mol photons m^{-2} on 8 July to 55 mol photons m^{-2} on 14 June. The seawater temperature at 10 m depth was relatively constant at around −1.7°C over much of the year, rising to 3.3°C in summer (Figure 1b). The summer warming was accompanied by a freshening of the surface layer, to a minimum of 28.5 on 6 August (Figure 1b), likely caused by freshwater river inflows and ice melt. There was a significant inverse relationship between temperature and salinity ($r_s = -0.91$, $p < 0.0001$, $N = 33$). Salinities increased during ice formation in fall, followed by large fluctuations in salinity (of amplitude 5 units) in mid to late December 2004, implying upwelling and horizontal advection of water masses at that time.

[17] The a_{320} measurements showed low to moderate CDOM concentrations with minor fluctuations most of the year (Figure 1c). A maximum of 1.43 m^{-1} was recorded in autumn on 19 November and a minimum of 0.40 in summer. Chl *a* concentrations in the surface mixed layer were consistently low throughout the year, varying from 0.01 mg m^{-3} on 4 January to 0.36 mg m^{-3} on 16 May (Figure 1c), with an annual mean of 0.12 mg m^{-3}. Chl *a* concentrations were significantly higher in spring (median of 0.22 mg m^{-3}; Kruskal-Wallis, $p < 0.05$) compared to winter and autumn concentrations (0.04 and 0.05 mg m^{-3}, respectively). The summer median (0.12 mg m^{-3}) was not statistically different from the other seasons, in part reflecting the small number of estimates and the large variability between summer sampling dates. Chl *a* concentrations were significantly correlated with the daily integrated PAR ($r_{s\ \mathrm{Chl\ }a.\mathrm{PAR|T°C}} = 0.80$, $p < 0.001$, $N = 29$), but not with temperature when the effect of incident light was controlled ($r_{s\ \mathrm{Chl\ }a.\mathrm{T°C|PAR}} = -0.23$, $p = 0.2$, $N = 29$).

[18] Bacterial abundance in the upper 10 m of the water column varied over 2 orders of magnitude during the sampling period, from 8.73×10^4 cells mL^{-1} on 16 December to 1.07×10^6 cells mL^{-1} on 16 July (Figure 1d and Table 1). There were irregular variations through time possibly reflecting sampling error and different water masses, as well as fluctuations in growth and loss processes. However, there was a clear increase during the summer months. Bacterial production rates were similarly variable, ranging from 6.6 μg C m^{-3} d^{-1} on 4 April to 163 μg C m^{-3} d^{-1} on 9 May. In winter, a peak of 53 μg C m^{-3} d^{-1} was recorded on 22 December, coincident with an increase in salinity (Figures 1b and 1d) that was suggestive of an

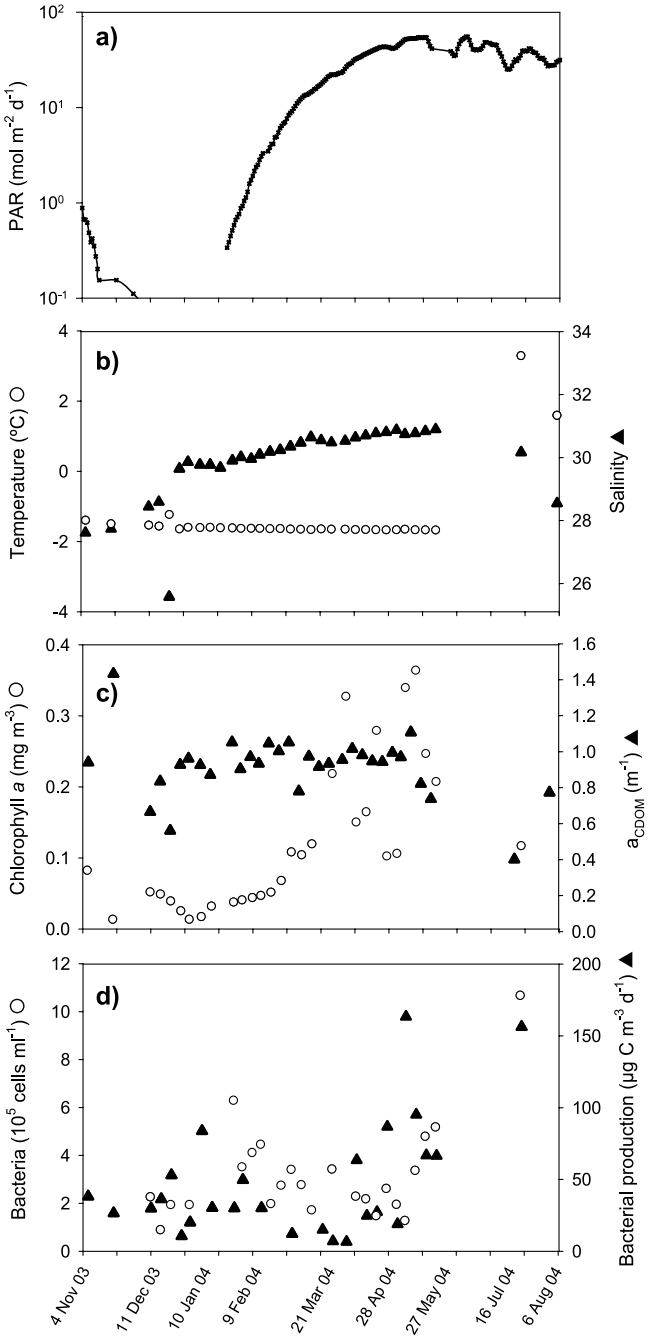

Figure 1. Seasonal variation in environmental variables in the surface waters (10 m) of Franklin Bay from 4 November 2003 to 6 August 2004. (a) Seven-day running means of daily integrated incident irradiance expressed as PAR (note log scale); (b) temperature and salinity; (c) chlorophyll *a* (Chl *a*) and CDOM absorption coefficient at 320 nm (a_{320}); and (d) bacterial abundance and leucine-based bacterial production.

upwelling event. There was no correlation between bacterial production and abundance ($r_s = 0.18$, $p = 0.5$, $N = 19$) and no significant difference was observed between seasons in mean values of both bacterial abundance and production in the upper 10 m. This is likely an effect of the small number of estimates for the upper water column.

3.2. Vertical Structure of the Water Column and Biological Variables

[19] The Franklin Bay water column was strongly stratified throughout the year of sampling (Figures 2 and 3) and had profiles that are typical of much of the Arctic Ocean [*Dittmar and Kattner*, 2003]. A shallow (<30 m) Polar Mixed Layer (PML) of cold (<−1.5°C), relatively fresh (<30) water overlay higher-salinity, Pacific-derived water. The transition to the latter was characterized by a sharp temperature maximum in the halocline at 30–40 m depth, with the Halocline Arctic Layer (HAL) grading into the Deep Atlantic Layer (DAW) of saline (34.5) and warmer (>0°C) water at 200 m. The profiles during two sampling periods showed a deviation from this pattern. In December 2003, there was a hydrodynamic event that pushed DAW higher up the water column, and resulted in temporarily warmer, much more saline water at the surface (Figure 2c). In summer, the water column was stratified even within the PML depth range, with high surface water temperatures (>2°C) and minimum salinities (Figures 2m and 2n).

[20] Chl *a* concentrations were usually greatest in the near surface waters, decreased sharply below 20 m and maintained low values from the pycnocline to the bottom of the water column (Figure 3). In July and August, a deep Chl *a* maximum developed at around 50 m (Figures 3m and 3n). There was a significant inverse relationship ($r_{s\ \mathrm{Chl}\ a.\mathrm{NO3|Sal}} = -0.39$, $p < 0.001$, $N = 168$) between Chl *a* and nitrate concentrations (the latter from J.-É. Tremblay et al., unpublished data, 2004) consistent with nutrient drawdown by the phytoplankton. Chl *a* concentrations were significantly higher (Kruskal-Wallis, $p < 0.05$) in summer (median of 0.19 mg m^{-3}) than in spring (0.02 mg m^{-3}), winter (0.03 mg m^{-3}) and autumn (0.04 mg m^{-3}).

[21] CDOM concentrations, as estimated by a_{320}, had maximum values at the surface, and typically declined by a factor of two down the water column (Figure 4). The highest value of 2.24 m^{-1} was recorded in the warm, freshwater-influenced surface layer in July, with values declining to $\leq$0.6 m^{-1} deeper in the water column (Figure 4m). However, the mean water column concentrations of CDOM (Table 2) did not significantly differ among seasons (Kruskal-Wallis, $p = 0.06$). During part of the winter (10 December–22 January) when concurrent measurements were made of DOC [*Roy*, 2006] and CDOM, there was a highly significant linear relationship between the two variables ($r = 0.80$, $p < 0.0001$, $N = 35$).

[22] The vertical distribution of bacteria was similar to that for Chl *a*, with values that were often highest at the surface and much lower throughout most of the rest of the water column (Figure 4). However, on several occasions in winter, maximum abundance values were found at 100 m or deeper (Figures 4d and 4e). Overall, there was a strong positive correlation between bacterial and Chl *a* concentrations (Table 3). As observed in the first 10 m, bacterial abundance in the water column varied over 2 orders of magnitude during the sampling year. The lowest bacterial abundance was 1.5×10^4 cells mL^{-1} measured on 20 February at the bottom depth, and the highest bacterial abundance was 1.7×10^6 cells mL^{-1}, on 16 July at 22 m. On average, bacteria were significantly (Kruskal-Wallis, $p <$ 0.05) more abundant in summer (median of 1.1×10^6 cells

Table 1. Bacterial Abundance and Production Rates in Polar and Atlantic Seas[a]

Study Area	Sampling Period	BA Depth, m	BA, 10^5 cells mL^{-1}	BP Depth, m	BP, mg C m^{-2} d^{-1}	CF, kg C mol^{-1}	References
			Arctic Ocean				
Central Arctic Ocean	June–Sept	Z_{eu}: ≤40	1.9–**3.2**–6.7	50	1–**4**–15	3.1	*Sherr and Sherr* [2003]
	Nov/Feb–May	≤40	1.3–**1.8**–2.9	50	**0.9**	3.1	and *Sherr et al.* [2003]
	late July to late Aug	<30	3–15[b]	Z_{eu}: 40–100[c]	32–**73**–100	2.3	*Rich et al.* [1997]
Chukchi Sea	mid-Aug to mid-Sept	≤10	2.1–21	50	152–**227**–301	nd	*Steward et al.* [1996]
Greenland Sea	end July	≤50	0.97–**11**–28	50	12–**157**–634[d]	23[d]	*Börsheim* [2000]
Franklin Bay	Nov–Aug	≤10	0.87–**3.2**–11	200	1–**8**–80	1.5	This study
		≤200	1.0–**2.6**–6.8				
Kara Sea	Aug–Sept	1–2	2.3–**3.5**–4.7	25	12–**43**–79	2.3	*Meon and Amon* [2004]
			Southern Ocean				
Bransfield Strait	Dec–Jan	≤100	4.2	100	**25**	0.81	*Pedrós-Alió et al.* [2002]
	Jan–Feb		3.0		**8**		
Eastern Atlantic sector	Dec–Jan	2–10	<1–15	150	40–**76**–100	Nd	*Granéli et al.* [2004]
Gerlache Strait	Dec–Jan	≤100	2.6–4.6	100	42–48	0.81	*Pedrós-Alió et al.* [2002]
	Jan–Feb		4.9–5.8		10–23		
Ross Sea	Oct–April	Z_{eu}	∼1[e]–30	150	39–**54**–72	1.5	*Ducklow* [2003]
			Others				
North Atlantic Ocean	mid-May	≤50	2–20	50	**293**	nd	*Ducklow et al.* [1993]
Sargasso Sea (BATS)	Composite annual cycle (1991–1994)	≤100	3–7	Z_{eu}: ∼140 m	11–**22**–36	0.2–1.3	*Carlson et al.* [1996]

[a]Bacterial abundance (BA) values are averages from the surface to the BA depth, and bacterial production rate (BP) values are leucine-based estimates that have been integrated over the upper water column, from the surface to the BP depth. Minimum, mean (in bold) and maximum values are shown. CF: carbon conversion factor; nd: not determined; Z_{eu}: euphotic zone.
[b]Value estimated from Figure 2b of *Rich et al.* [1997].
[c]Values estimated from Figures 3 and 4 of *Rich et al.* [1997].
[d]Thymidine-based bacterial production; conversion factors used were 2.65×10^{18} cells mol^{-1} and 2×10^4 g C cell^{-1}.
[e]Value estimated from Figure 1a of *Ducklow* [2003].

mL^{-1}) than in spring (2.0×10^5 cells mL^{-1}), winter (2.8×10^5 cells mL^{-1}) and autumn (1.3×10^5 cells mL^{-1}).

[23] Bacterial production rates, like Chl *a* and bacterial abundance, were generally highest at the surface and often declined exponentially with depth (Figure 4). However, bacterial productivity was relatively high below 100 m on several occasions during winter and spring, with peak activity around 100–150 m in December–January (Figures 4c, 4d, and 4e) and at the bottom depth on three other occasions in March (Figure 4i). For the overall data set, there was a significant correlation between bacterial production rates and Chl *a* concentration (Table 3). Partial correlations showed that the latter correlation was independent of CDOM concentration effect ($r_{s\ \mathrm{BP.Chl\ }a|\mathrm{CDOM}} = 0.44$, $p < 0.001$, $N = 214$) over the year. There was also a significant relationship between bacterial abundance and bacterial production rates, but no significant relationship with temperature (Table 3) nor with CDOM when Chl *a* concentration effect was removed ($r_{s\ \mathrm{BP.CDOM|Chla}} = -0.04$, $p = 0.5$, $N = 214$). Maximum bacterial productivity was measured in the upper 10 m from early spring until the 6 August (Figures 4j–4m). The highest bacterial production rate of the year was 1121 μg C m^{-3} d^{-1}, from the surface waters on 16 July (Figure 4m), and the lowest rate of 0.61 μg C m^{-3} d^{-1} was measured on 9 February at 50 m (Figure 4f).

3.3. Integrated Microbial Stocks and Bacterial Production

[24] Integrated Chl *a* values for the entire water column varied from 1.8 mg m^{-2} on 3 January to 36.6 mg m^{-2} on 6 August, with an annual mean of 7.7 mg m^{-2} (Table 2). The integrated Chl *a* was higher in summer than in the other seasons, with a mean value that was 4–7 times higher than during autumn, winter or spring (Table 2). However, results were not significant, again likely reflecting the small number of estimates and the large variability between summer sampling dates.

[25] Mean bacterial concentrations for the water column varied greatly throughout the sampling year, from a minimum mean value of 1.0×10^5 cells mL^{-1} in late autumn on 16 December to a maximum mean value of 6.8×10^5 cells mL^{-1} in summer, with an annual average of 2.6×10^5 cells mL^{-1} (Table 2). There was no significant difference between depth-integrated seasonal means (Table 2). There was a significant correlation between integrated values of bacterial numbers and Chl *a* in the water column ($r_s = 0.44$, $p < 0.05$, $N = 24$), but no significant correlation was found between bacteria abundance and bacterial production rates ($r_s = -0.02$, $p = 0.9$, $N = 22$).

[26] Integrated bacterial production varied by almost 2 orders of magnitude over the year, with an annual mean value of 7.6 mg C m^{-2} d^{-1} (Tables 1 and 2). The lowest rate was 1.3 mg C m^{-2} d^{-1} in late winter (26 February) and the maximum rate was 80 mg C m^{-2} d^{-1} in summer (16 July). Seasonal integrated bacterial production rates (Table 2) in summer and autumn were both significantly greater than winter rates (Kruskal-Walis, $p < 0.05$). On average, 50% (range 29–66%) of total bacterial production for the water column was between 100 m and the bottom. The highest proportion of total bacterial activity in this lower 100 m was in winter (mean of 54%), followed by autumn (49%) and finally spring (46%).

[27] There was a striking correspondence between the seasonal changes in integral bacterial production and integral Chl *a* (Figure 5; for the log transformed data, $r_s = 0.50$,

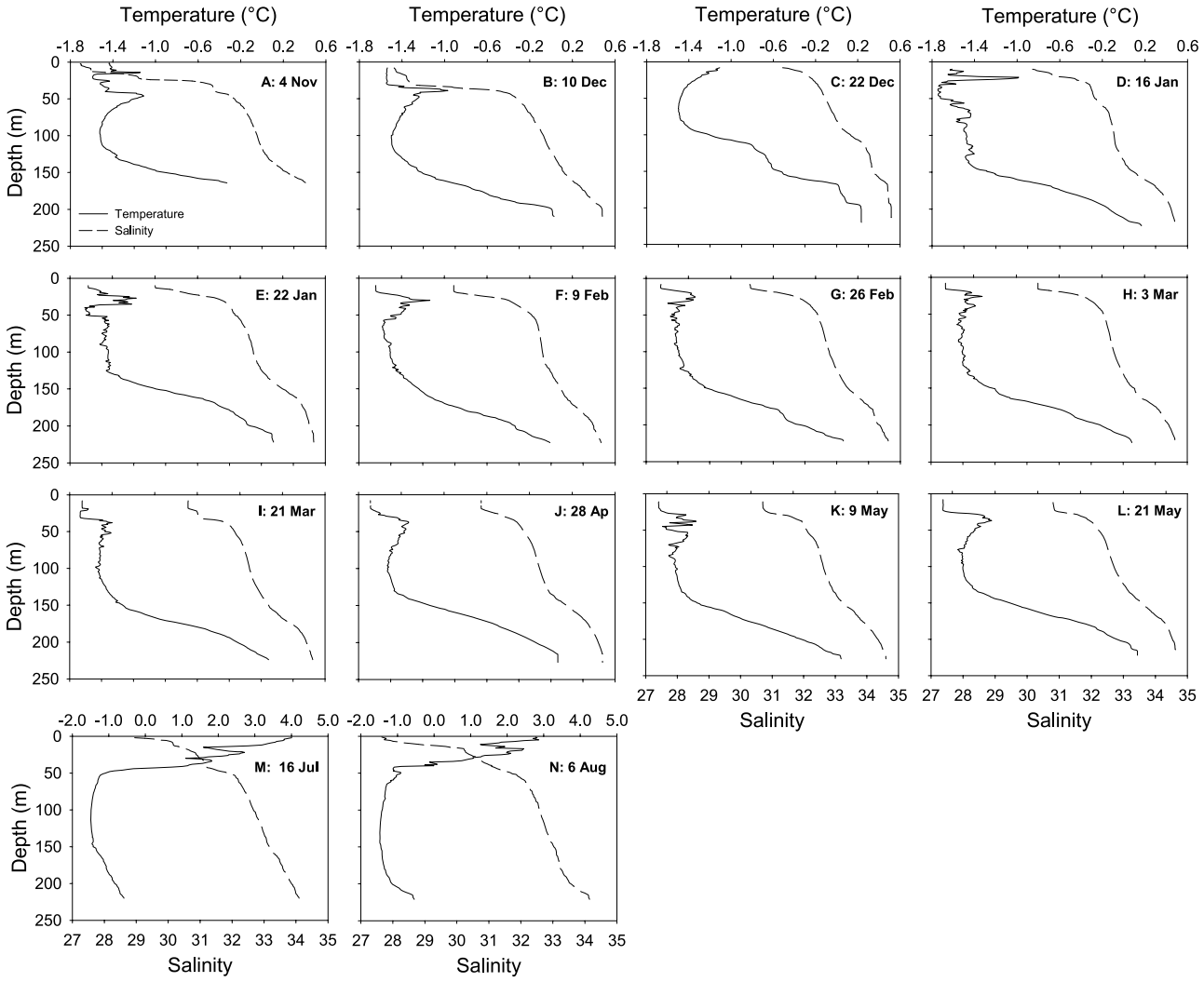

Figure 2. Selected profiles of temperature (line) and salinity (dashed line) at station 200 in Franklin Bay, from 4 November 2003 to 6 August 2004.

$p = 0.005$, $N = 30$). This bacterial production curve shows three periods: a variable period during fall and winter (fall–winter); a long period of relatively constant activity during late winter and spring (late winter–late spring); and a major rise in activity to peak values in summer at the same time as peak phytoplankton stocks.

3.4. Seasonal Controls on Bacterial Production

[28] The bacterial production rates in the water column were highest in summer (median of 274 μg C m^{-3} d^{-1}) and significantly greater than in winter (16 μg C m^{-3} d^{-1}) and spring (15 μg C m $^{-3}$ d^{-1}; Kruskal-Wallis, $p < 0.05$), but not autumn. Bacterial production in autumn (45 μg C m^{-3} d^{-1}) was significantly higher than estimated in winter and spring (Kruskal-Wallis, $p < 0.05$). Thus we regrouped the winter and spring data sets (Figures 6a and 6b) and the summer and autumn data sets (Figures 6c and 6d) to test relationships with environmental variables. First-order partial correlations revealed that CDOM and Chl *a* concentrations ($r_{s\ \mathrm{CDOM.Chl\ }a|\mathrm{BP}} = 0.64$, $p < 0.0001$, $N = 176$) were correlated, but that bacterial production rates were correlated only with CDOM ($r_{s\ \mathrm{BP.CDOM|Chla}} = 0.20$, $p < 0.05$, $N = 176$) in winter-spring. There was no correlation between bacterial production rates and temperature for this period.

[29] In summer and autumn there was a significant positive correlation between average bacterial production rates in the water column and temperature ($r = 0.74$, $p < 0.001$, $N = 37$). A simple linear model II regression calculated by the ordinary least square method (OLS) [*Legendre and Legendre*, 1998] gave the equation

$$\mathrm{BP} = (0.12 \times \mathrm{Temperature}) + 0.24, \qquad (2)$$

where BP is in mg C m^{-3} d^{-1} and temperature in °C. However, this relationship was slightly below the 5% significance level ($r = 0.73$; $p = 0.08$, $N = 37$).

[30] There was also a significant positive correlation between bacterial production and Chl *a* concentrations ($r_s = 0.68$, $p < 0.001$, $N = 38$; Figure 6c). First-order partial correlations revealed that both temperature and Chl *a* concentration significantly affected bacterial production ($r_{s\ \mathrm{BP.Chl\ }a|\mathrm{T°C}} = 0.63$, $p < 0.0001$ and $r_{s\ \mathrm{BP.T°C|Chl\ }a} = 0.51$, $p < 0.005$, $N = 37$). Multiple linear regression analysis with standardized coefficients (dimensionless values) showed

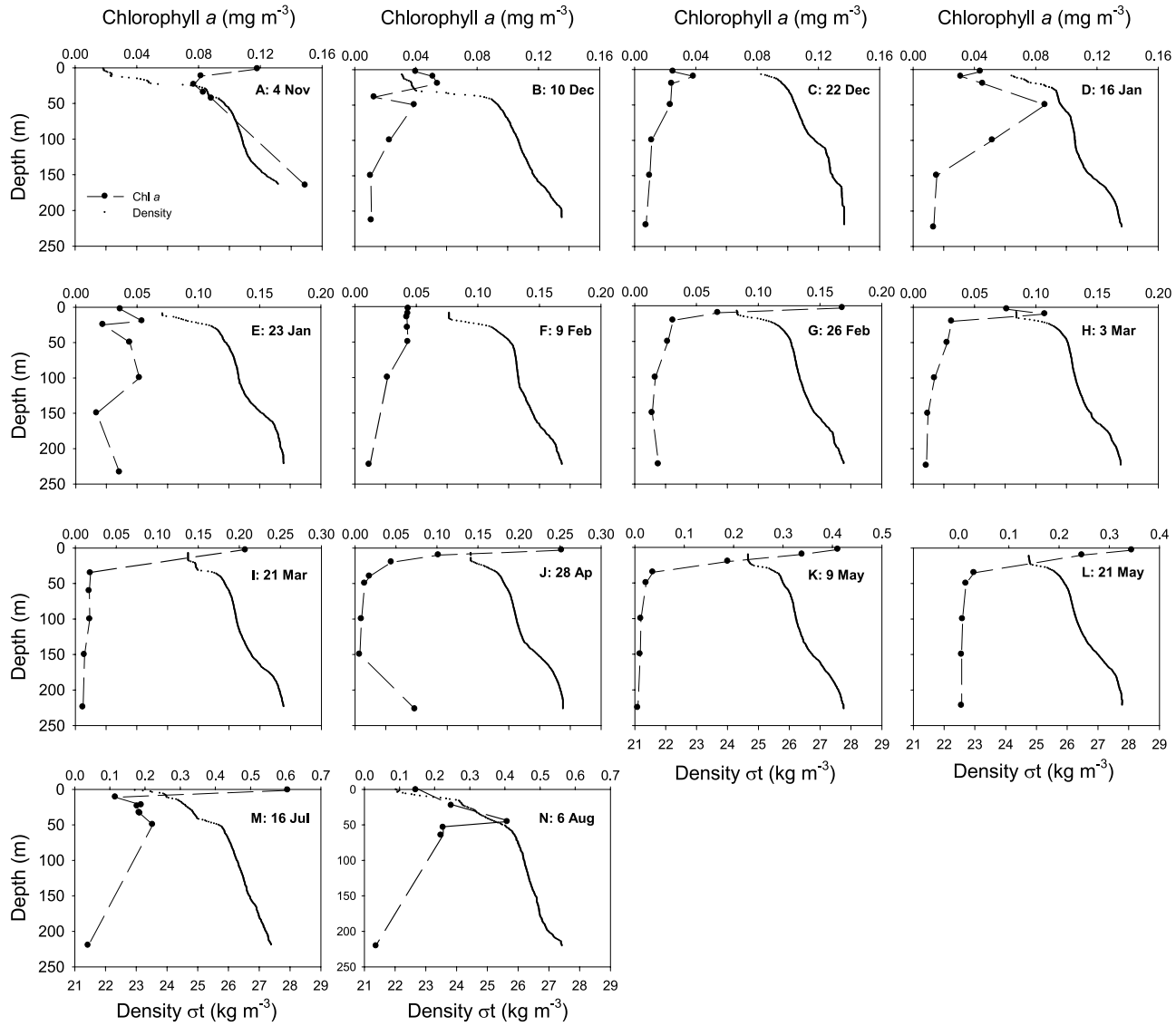

Figure 3. Selected profiles of seawater density (small dots) and chlorophyll *a* concentration (filled symbols) illustrating the seasonal variation in the water column at station 200 in Franklin Bay, from 4 November 2003 to 6 August 2004. Note changes in scales for chlorophyll *a* over time.

that bacterial production in the summer-autumn period was well described ($r = 0.80$, $p < 0.001$, $N = 37$) by the equation

$$\mathrm{BP} = (0.39 \times \mathrm{Chl}\,a) + (0.52 \times \mathrm{Temperature}) + 0.11. \quad (3)$$

For each coefficient, the variance inflation factor (a measure of multicolinearity) was 1.4 indicating that there was no redundant information among the independent variables. The summer-autumn data set also showed a significant linear relationship between bacterial production rates and bacterial cell abundance ($r = 0.81$, $p < 0.0001$, $N = 26$; Figure 6d). The slope of regression equation was 0.80, with a probability that the slope is not zero of $p < 0.0001$.

3.5. Bacterial Production Estimates From Leucine Versus Thymidine Assays

[31] Bacteria incorporate ^{3}H-leucine into proteins and ^{3}H-thymidine into DNA, and the ratio between the two incorporation rates expressed in mol h^{-1} (Leu:TdR) is an indicator of the metabolic status of prokaryotes [*Shiah and Ducklow*, 1997]. Overall, there was a close, linear relationship between the ^{3}H-leucine and ^{3}H-thymidine incorporation rates ($r = 0.89$, $p < 0.001$, $N = 95$). Leu:TdR ranged from 0.6 and 158, with an average of 20 for all depths combined (Table 2). There was a seasonal trend, with Leu:TdR that were significantly lower in summer (6) relative to autumn (27) and winter (17) (Kruskal-Wallis, $p < 0.05$), but not significantly different from spring (14). There was an inverse relationship between Leu:TdR and Chl *a* concentrations ($r_s = -0.33$, $p < 0.0001$, $N = 89$) and with bacterial abundance ($r_s = -0.37$, $p < 0.001$, $N = 72$).

4. Discussion

4.1. Comparisons With Other Sites

[32] The overwintering deployment of our research platform allowed the multiseasonal sampling of bacterial and environmental variables, and provided a unique record for

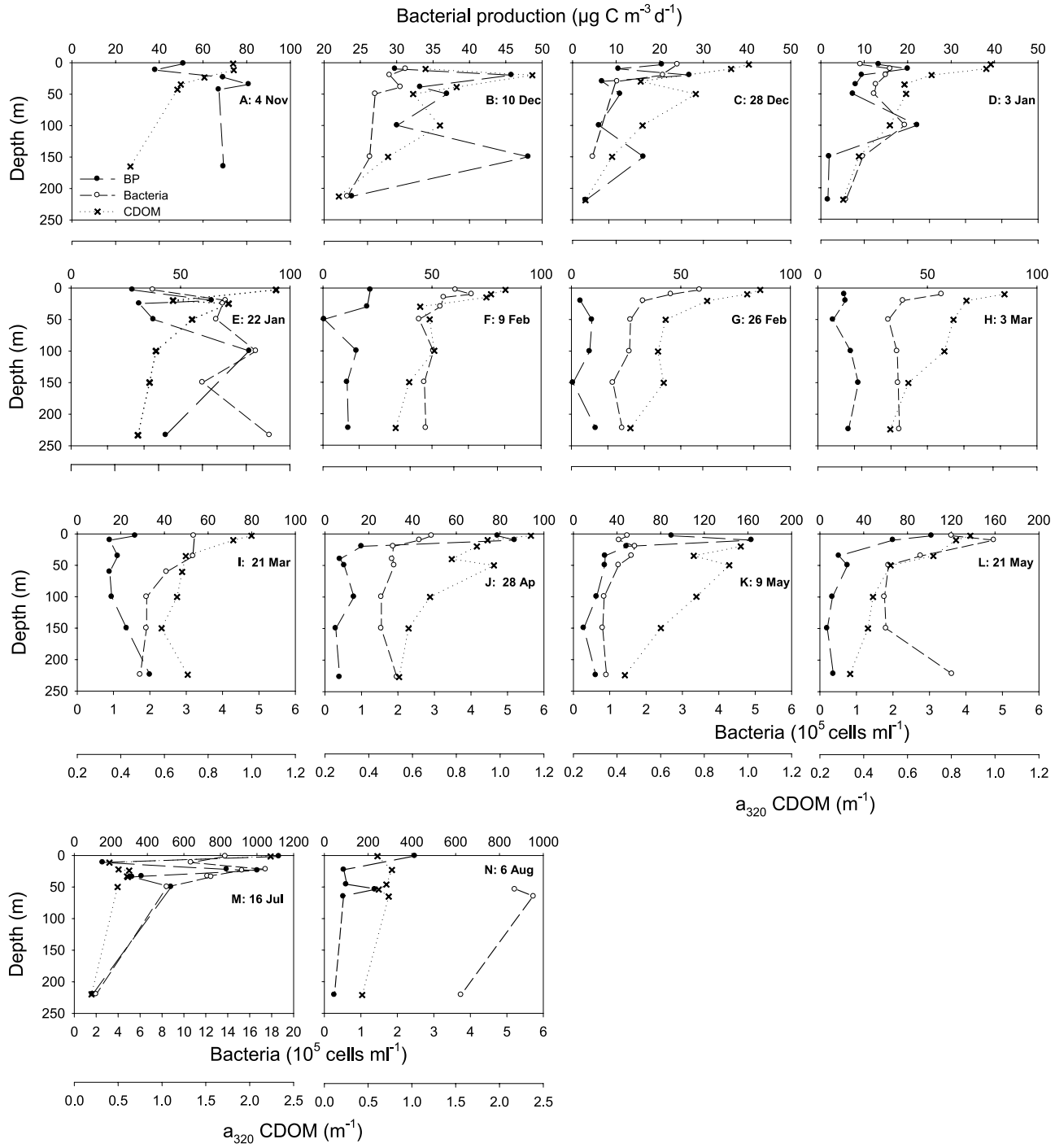

Figure 4. Selected profiles of CDOM absorption at 320 nm (a_{320}; crosses), bacterial abundance (open symbols) and bacterial production (BP; filled symbols) illustrating the seasonal variation in the water column at station 200 in Franklin Bay, from 4 November 2003 to 6 August 2004. On 22 January, bacterial production was estimated from thymidine incorporation rates instead of leucine incorporation. Note changes in scales for bacterial production and abundance over time.

the coastal Arctic Ocean. Our estimates of bacterial abundance fall within the ranges reported from other time series studies in polar and Atlantic seas (Table 1). However, most of these studies are for spring and/or summer, and they differ in depth of averaging and integration, which complicates comparisons. The most comparable Arctic data set to our own is the yearlong series from the offshore Arctic Ocean [*Sherr and Sherr*, 2003; *Sherr et al.*, 2003], and this shows bacterial fluctuations within a similar range to that reported here. The maximum concentrations were low, however, by comparison with maxima at several other polar sites including the Chukchi Sea, Greenland Sea and Ross

Table 2. Seasonal Means of Variables Measured in Franklin Bay[a]

Season	PAR, mol m^{-2}	CDOM, m^{-1}	Chl *a*, mg m^{-2}	BA, 10^5 cells mL^{-1}	BP, mg C m^{-2} d^{-1}	Leu:TdR, mol:mol
Autumn	1.3	0.82	7.9	1.2	8.8	27
SD	*1.4*	*0.29*	*6.8*	*1.1*	*4.3*	*18*
N	*42*	*4*	*4*	*2*	*4*	*20*
Winter	4.9	0.66	5.3	3.1	4.0	17
SD	*5.5*	*0.12*	*1.9*	*1.4*	*3.3*	*27*
N	*54*	*15*	*15*	*11*	*13*	*34*
Spring	41.3	0.62	6.1	2.0	3.5	14
SD	*10.8*	*0.10*	*1.7*	*0.48*	*1.2*	*14*
N	*82*	*12*	*12*	*10*	*11*	*(21)*
Summer	33.0	0.52	34.7	6.8	50.7	6
SD	*6.8*	*0.14*	*2.7*	–	*41.6*	*8*
N	*53*	*2*	*2*	*1*	*2*	*14*
Annual mean	**27.5**	**0.66**	**7.7**	**2.6**	**7.6**	**20**
SD	***18.3***	***0.15***	***7.5***	***1.4***	***14.4***	***21***
N	***231***	***33***	***33***	***24***	***30***	***90***

[a]PAR (photosynthetically active radiation) values are the medians of running means; CDOM (colored dissolved organic matter) absorbance at 320 nm and bacterial abundance (BA) are mean values over the water column; chlorophyll *a* concentration (Chl *a*) and bacterial production rates (BP) are integrated values for the water column; and the Leu:TdR ratios (see text) are median values from all values at all depths for a given season. *N*, number of samples; *SD*, standard deviation.

Sea. The low bacterial concentrations in Franklin Bay are consistent with the highly stratified nature of this environment throughout the year (Figures 2 and 3), and its resultant low nutrient availability [*Carmack et al.*, 2004] and low phytoplankton stocks.

[33] Bacterial production rates in Franklin Bay were also low by comparison with sites elsewhere (Table 1). The maximum rates of bacterial production were similar to peak activities recorded in the Kara Sea and Southern Ocean, but less than 30% of maximum activities in the Chukchi Sea and Greenland Sea where Chl *a* concentrations were also much higher. The maximum production rates were comparable with the central Arctic Ocean, despite much lower maximum Chl *a* values in the Beaufort Sea (generally <0.5 mg m^{-3}, but up to 4.3 mg m^{-3} in the Arctic Ocean [*Sherr et al.*, 2003]), implying a subsidy by allochthonous carbon sources in the coastal ocean.

[34] The magnitude of seasonal variation in bacterial abundance was at or below that at many sites elsewhere (Table 1). Surface water concentrations of bacteria varied seasonally by about a factor of 10 in Franklin Bay, 10 in the North Atlantic Ocean and by more than 30 in the Ross Sea. Much lower variation was recorded in the central Arctic Ocean (factor of 2 from November to May) suggesting more variable conditions at our coastal arctic site. There is also lower seasonal variation in bacterial abundance and production in the subtropical Sargasso Sea (factor of 3 variation in the upper water column; Table 1), where environmental conditions are more stable relative to the strongly seasonal polar environment. Polar ecosystems experience a wide span of environmental conditions over a year, notably in incident light regime [*Smith and Sakshaug*, 1990], that in turn affect the ice and snow cover, water temperature, mixed layer depth and nutrient supply. Additionally, Franklin Bay receives terrestrial inputs of riverine freshwater, nutrients and organic carbon. The latter, highly variable external forcing may explain why despite relatively low seasonal variations in bacterial abundance (factor 10), our annual survey revealed a large variability in bacterial production (factor 80) in Franklin Bay, which largely exceeded sites elsewhere in the polar regions including the central Arctic Ocean (factor 15) as well as the North Atlantic (factor 3) (Table 1).

4.2. Seasonal Controls

[35] The integrated bacterial production data showed three distinct periods: fall-winter; late winter–late spring and summer (Figure 5). Contrary to our expectation, bacterial biomass and activity did not continue to decline during fall-winter. Instead, a baseline level of bacterial concentrations and productivity was maintained throughout the late winter–late spring period despite the persistent cold and darkness, with irregular fluctuations that may be related to hydrodynamic events. The pronounced change in water column properties on 22 December followed a period of ice formation and apparent thermohaline convection [*Forest et al.*, 2007], and was accompanied by major shifts in temperature and salinity (Figure 2c), Chl *a* (Figure 3c),

Table 3. Spearman Correlation Coefficients With Corresponding *p* Values and Number of Samples for Environmental Parameters Compared to Bacterial Abundance and Production for the Entire Annual Data Set at All Depths[a]

	Temp	CDOM	Chl *a*	BP
		BA		
r_s	−0.001	0.11	0.45	0.22
p	*0.9*	*0.1*	*<0.0001*	*<0.005*
N	*169*	*185*	*187*	*169*
		BP		
r_s	−0.03	0.24	0.49	
p	*0.6*	*<0.001*	*<0.001*	
N	*200*	*214*	*216*	

[a]Spearman correlation coefficients, r_s; *p* values, *p*; number of samples, *N*; bacterial abundance, BA; bacterial production, BP; CDOM, colored dissolved organic matter; Chl *a*, chlorophyll *a* concentration; Temp, temperature.

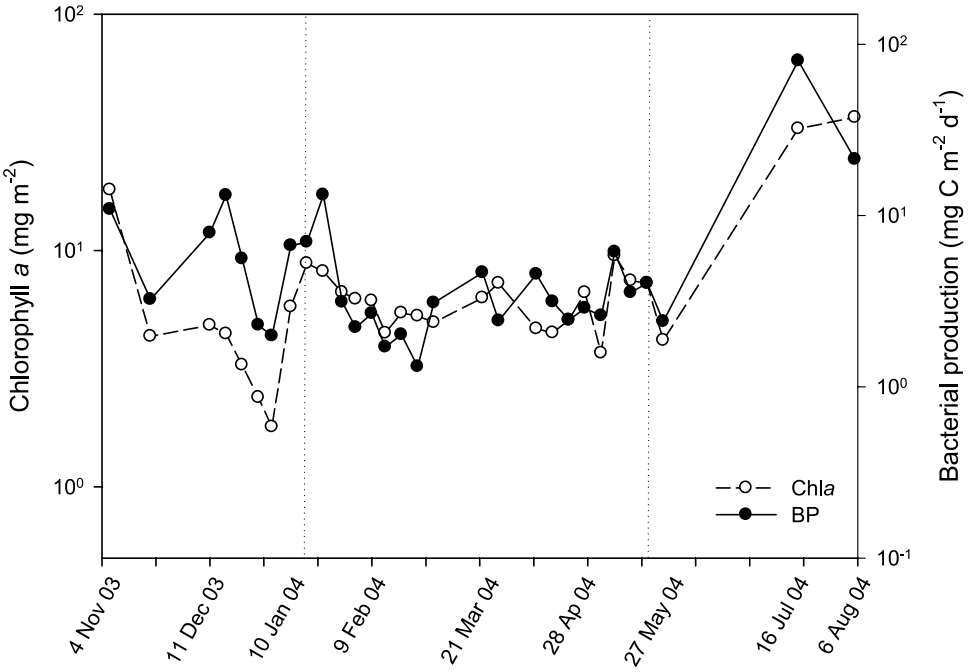

Figure 5. Seasonal variations in integrated chlorophyll *a* concentration (open symbols) and bacterial production (filled symbols) on log scales in the water column of Franklin Bay, from 4 November 2003 to 6 August 2004.

nitrate (J.-É. Tremblay et al., unpublished data, 2004) and an enhancement of bacterial production (Figures 4c and 5). A similar event occurred in March, and was again accompanied by a shift in bacterial production. Thus winter is not a quiescent period of stable conditions beneath the ice, but instead can have episodes of advection and mixing that import nutrients, organic material and maybe bacterial cells, thereby affecting the distribution and activity of microbial communities.

[36] Light availability (Figure 1a) and photosynthesis (S. Brugel et al., unpublished data, 2004) were undetectable to extremely low during the winter months and the bacterial community likely depends on prior inputs of organic carbon into the system, including the slow breakdown of larger molecular weight DOC into more biolabile constituents. In the Greenland Sea, sustained bacterial production has similarly been attributed to the consumption of accumulated organic material during the preceding productive months [*Börsheim*, 2000]. In the coastal Arctic Ocean, advection and upwelling of resuspended sediments as well as nutrients may also be a factor contributing to the observed rises in production. Bioassays conducted during winter showed that bacterial abundances were strongly stimulated by the addition of low molecular weight DOC substrates, and additionally by inorganic nitrogen [*Roy*, 2006], indicating that bacterial production would be highly responsive to such inputs.

[37] Throughout more than 100 days from late winter to late spring, bacterial production was remarkably constant (Figure 5), suggesting a low but continuous supply of organic substrates. As in winter, the production rates were likely to be strongly limited by organic carbon supply during this time of year. Detailed pigment records have shown the continuous net growth of phytoplankton beneath the sea ice during this time, with low standing stocks and dominance by picoprasinophytes [*Lovejoy et al.*, 2007]. The bacterial communities at this time were likely to be fueled by this low input of autochthonous carbon, as well as slow degradation of less labile, allochthonous DOC. It is likely that bacteria in winter-spring rely strongly on DOC previously derived from river inputs, as indicated by the significant correlation between bacterial production and CDOM.

[38] During the open water conditions, bacterial biomass and activity increased substantially (Figures 1 and 5), commensurate with the increase in surface water temperatures, phytoplankton abundance and organic carbon and nutrient input from rivers. Could top-down control by grazing and viral parasitism be a more important determinant of bacterial abundance and production at this time of year? One approach toward addressing this question is an analysis of the log BP versus log BB (bacterial biomass) relationship, which for the summer-autumn data set gave a highly significant positive regression (Figure 6d). *Billen et al.* [1990] showed how this simple graphical representation may provide information about bacterial controls given that bacterial production is equal to the product of the specific growth rate and the bacterial biomass. Growth rate is affected by food availability (bottom-up control) whereas biomass is governed by predatory and viral pressure (top-down control). The slope for summer-autumn in Franklin Bay was 0.80, well above the threshold of 0.60 and implying strong bottom-up control [*Ducklow*, 1992]. The close statistical dependence of bacterial production on Chl *a* and temperature for this period of the year (equation (3)) also implies bottom-up control via the chemical and phys-

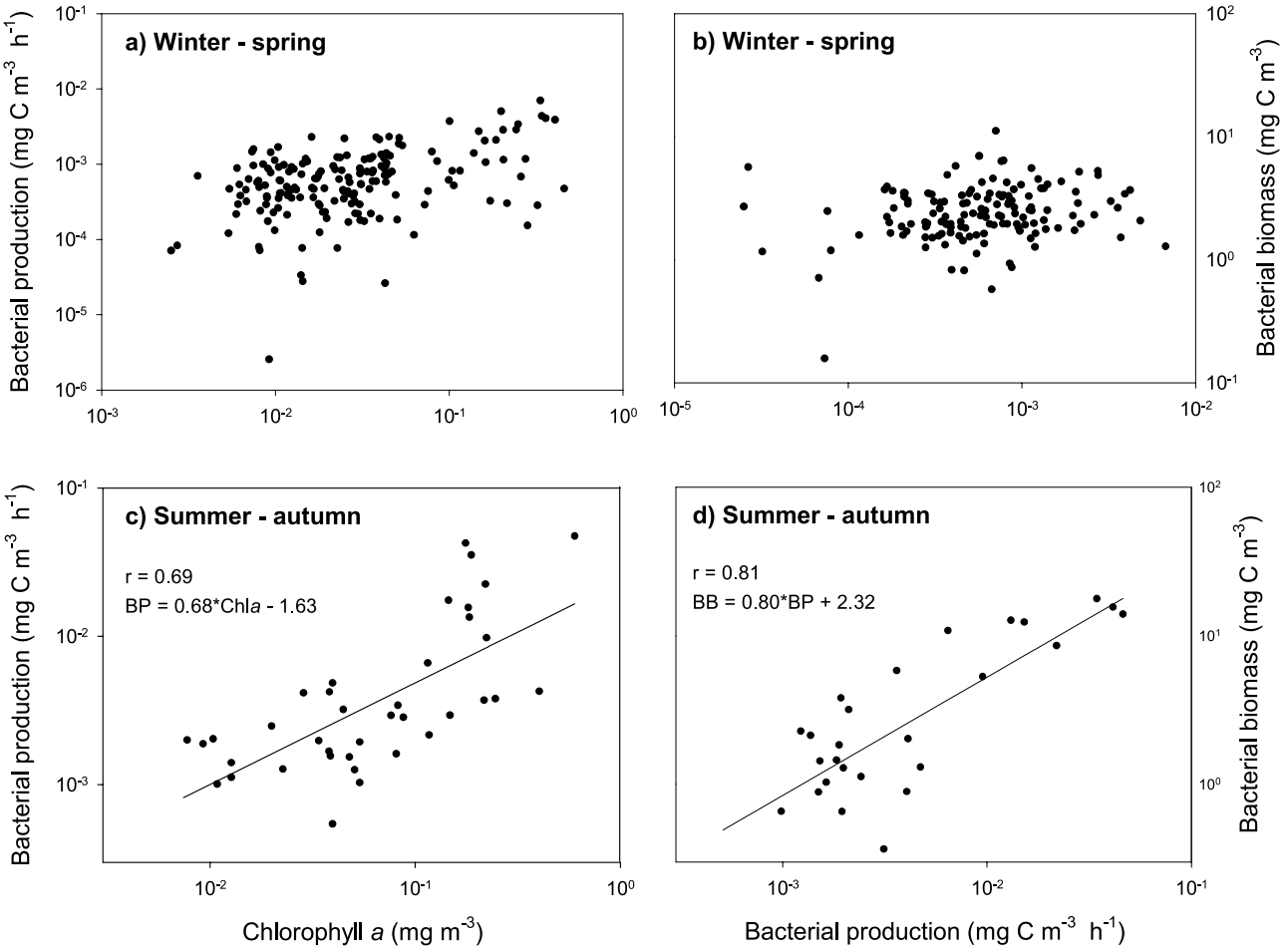

Figure 6. Relationships between (a, c) bacterial abundance and chlorophyll *a* concentration and (b, d) bacterial biomass and bacterial production for winter and spring (Figures 6a and 6b) and summer and autumn (Figures 6c and 6d). Values are presented on a log scale.

ical environment, rather than top-down control by biological processes such as grazing or viral attack.

[39] Further information about the environmental control of bacterial production and biomass is given by the Leu:TdR molar ratio as a measure of protein synthesis versus cell division. Low ratios suggest favorable environmental conditions for population growth, while high ratios imply that the bacteria are in a state of biomass accumulation to maximize survival [*Chin-Leo and Kirchman*, 1990; *Shiah and Ducklow*, 1997]. This ratio is known to be affected by substrate supply [*Chin-Leo and Kirchman*, 1990], temperature [*Longnecker et al.*, 2006; *Shiah and Ducklow*, 1997; *Tibbles*, 1996], taxonomic composition [*Cottrell and Kirchman*, 2003] and metabolic activity of bacterial assemblage [*Longnecker et al.*, 2006]. Our data show a significant correlation between Leu and TdR indicating continuous bacterial protein production coupled to cell division throughout the year. On average, however, the values are high, implying strong resource limitation at most times (Table 2). The significantly lower ratio in summer implies improved conditions for cell division at that time, and is consistent with the significant inverse correlation of the Leu:TdR ratio with Chl *a* and with bacterial biomass.

4.3. Coastal Shelf Effects

[40] One of the distinguishing features of the shelf environment in this region of the coastal Arctic Ocean is the presence of high concentrations of Archaea [*Garneau et al.*, 2006; *Wells et al.*, 2006] of diverse lineages [*Galand et al.*, 2008]. Their abundance is correlated with suspended particulate material and they contribute to 6.0–15.5% of total prokaryotes on the Mackenzie Shelf [*Garneau et al.*, 2006; *Wells et al.*, 2006]. More detailed analyses elsewhere in the western Arctic Ocean have shown that Crenarcheota contribute to 10% of prokaryotes in the surface waters, rising to 40% in deeper samples [*Kirchman et al.*, 2007]. Archaea are able to take up amino acids, including leucine, at ambient concentrations [*Ouverney and Fuhrman*, 2000] and their contribution to total 'bacterial production' was likely to have been adequately assayed and included within our measurements.

[41] Several other features of the coastal environment may affect bacterial production in this region. The high CDOM values in the surface waters in summer (Figure 1c) are consistent with large allochthonous inputs of organic carbon to this system [*Retamal et al.*, 2007]. The presence of freshwater picocyanobacteria across the shelf [*Waleron et*

al., 2007] is also indicative of this effect. A variety of sources may provide dissolved and particulate carbon substrates to the bacterial community in Franklin Bay including coastal erosion, the melting of landfast ice [*Rachold et al.*, 2004; *Wassmann et al.*, 2004] and the resuspension of bottom particles into a benthic nepheloid layer [*Forest et al.*, 2007; *O'Brien et al.*, 2006]. The significant dependence of bacterial production on Chl *a* and temperature (in part the result of heat and buoyancy fluxes associated with the river inputs) but not CDOM suggest that the effects of allochthonous carbon input are secondary relative to autochthonous sources and the effects of warming during the summer period. However, the low percent variance in bacterial production attributable to Chl *a* (20%) is consistent with these other variables playing a role in the bacterial productivity of this coastal environment. In the North Atlantic, slowly degradable DOC may contribute more to bacterioplankton metabolism relative to labile DOC produced by phytoplankton [*Ducklow et al.*, 1993]. In the Sargasso Sea, reliance on refractory DOC was considered as a factor explaining the weak bacterial response to a phytoplankton bloom [*Carlson et al.*, 1996]. In Franklin Bay uncoupling between Chl *a* and bacterial production was seen in winter-spring, when bacteria may rely more on terrigenous carbon, as indicated by CDOM, than on Chl *a*, possibly because the allochthonous carbon source was sufficiently available to sustain the community demand. The winter-spring bacterial assemblage might be distinctive in including numerous efficient users of CDOM, such as Cytophaga-Flavobacterium cluster representatives [*Kirchman*, 2002]. CARD-FISH analysis in autumn has shown the widespread distribution of this group over the Mackenzie Shelf [*Garneau et al.*, 2006].

4.4. Carbon Fluxes

[42] The results obtained in the present study allow a first-order estimate of bacterial carbon fluxes for this region of the coastal Arctic Ocean. For this calculation, integrated daily water column values of bacterial production were averaged for each 3-month season, multiplied by 90 days and then summed, giving an annual estimate of 6.0 g C m^{-2} a^{-1}.

[43] Bacterial growth efficiency (BGE), the ratio of biomass produced to substrate assimilated, can used to estimate of the total bacterial carbon demand. BGE is computed as [*del Giorgio et al.*, 1997]

$$\mathrm{BGE} = \mathrm{BP}/(\mathrm{BP} + \mathrm{BR}), \tag{4}$$

where BP is bacterial production and BR is the bacterial respiration. Rearrangement of the equation provides an estimate of bacterial respiration,

$$\mathrm{BR} = (\mathrm{BP}/\mathrm{BGE}) - \mathrm{BP}. \tag{5}$$

BGE values are known to be a function of nutrient status and bacterial production rates. Average values range from 0.15 in low productivity, open ocean systems (~370 μg C m^{-3} d^{-1}) to 0.27 in productive coastal environments (~2410 μg C m^{-3} d^{-1}) [*del Giorgio and Cole*, 2000]. For the following analysis, we therefore used a BGE of 0.15 for winter, spring and autumn periods and a value of 0.27 for summer.

[44] The application of bacterial growth efficiencies to our annual bacterial production of 6.0 g C m^{-2} a^{-1} gives an estimate of the total bacterial carbon demand of 26.7 g C m^{-2} a^{-1}. This value is greater than other carbon flux components, including annual primary production by phytoplankton (12–16 g C m^{-2} a^{-1} for April to September 1987 [*Carmack et al.*, 2004]) and primary production by sea ice algae (0.64 g C m^{-2} a^{-1} for the 49-day period of maximum of ice algal bloom development (A. Riedel et al., Winter-spring dynamics in sea-ice carbon cycling on the Mackenzie shelf, Canadian Arctic, submitted to *Journal of Marine Systems*, 2008)). This again implies the importance of allochthonous inputs to this coastal region and suggests that this ecosystem is net heterotrophic, as for many coastal marine [*Smith and Hollibaugh*, 1993] and oligotrophic [*del Giorgio et al.*, 1997] ecosystems elsewhere. However, the difference between autotrophic and heterotrophic C fluxes in Franklin Bay is not large and the system could readily fluctuate across the equilibrium of CO_2 production and loss over seasonal or shorter timescales (see for example CO_2 measurements for the nearby Mackenzie Shelf from *Vallières et al.* [2008]). In part, the heterotrophic nature of Franklin Bay is dictated by the low primary production, in turn a consequence of its highly stratified, low-nutrient regime.

[45] The CO_2 production rate by bacteria as estimated above greatly exceeds the rates of photomineralization of dissolved organic carbon of 0.31 g C m^{-2} a^{-1} [*Bélanger et al.*, 2006]. Assuming an area of 87,000 km^2 for the Amundsen Gulf region, the DIC production rate for photomineralization would be 0.014 Tg a^{-1} per year [*Bélanger et al.*, 2006] while the total bacterial CO_2 production for this area would be 1.8 Tg a^{-1}. The latter is of a similar order to terrestrial DOC fluxes by the Mackenzie River to the Canadian Shelf of the Beaufort Sea of ~1.3 Tg a^{-1} [*Telang et al.*, 1991]. The same calculation for Franklin Bay (8003 km^2) gives an estimate of bacterial CO_2 production of 0.17 Tg C a^{-1}, equivalent to 13% of the Mackenzie River inputs of terrestrial DOC to the Beaufort Sea Shelf [*Telang et al.*, 1991]. Such comparisons should be made with caution in the absence of any assessment of spatial variability across this region of the shelf, however they imply that neither photochemical nor bacterial processes can account for most of the annual loss of DOC from this coastal environment. It is therefore likely that much of this allochthonous carbon is exported by advection, including via density currents to the deep ocean as described by *Dittmar* [2004].

[46] Given the large year-to-year variations in summer ice cover [*Bélanger et al.*, 2006] affecting primary production, and irregular hydrodynamic events in this region of the coastal Arctic Ocean, there are likely to be large interannual variations in bacterial production rates. A 2 order-of-magnitude change in bacterial abundance ($0.1-10 \times 10^5$ cells mL^{-1}) between consecutive summers has been reported for the Mackenzie River estuary, and attributed to differences in onshore winds and advection [*Parsons et al.*, 1988, 1989]. A large difference in bacterial production was also recorded between these two summers (5 and 20 mg C

m^{-3} d^{-1}, respectively [*Parsons et al.*, 1988, 1989]) consistent with large variations in environmental forcing.

[47] Our annual bacterial production estimate of 6.0 g C m^{-2} a^{-1} will require close comparison with other estimates of carbon fluxes during the CASES study period. For example, early estimates of phytoplankton production over this period provide values of 40, 0.05, 26 and 114 mg C m^{-2} d^{-1} for fall, winter, spring and summer, respectively (S. Brugel et al., unpublished data, 2004, in the CASES database; accessible via www.polardata.ca). Multiplying these seasonal means by 90 and then summing them, would give an annual primary production estimate of 16.2 g C m^{-2} a^{-1}. Thus, the annual bacterial production would be equivalent to 37% of this estimate of phytoplankton production, which is a large percentage compared with marine systems in general where BP:PP is usually about 10–20% [*Ducklow*, 2000]. This analysis requires corroboration, but such a high value for Franklin Bay would be consistent with a large subsidy to bacterial production from riverine carbon inputs.

5. Conclusions

[48] Our observations in Franklin Bay showed that bacterial activity continued throughout the year, albeit at slow rates, which reflect the low primary production and inorganic nutrient supplies in this highly stratified environment. As seen in other oligotrophic systems [*Ducklow*, 1999; *Sanders et al.*, 1992], bacterial production in this region is probably controlled by bottom-up processes rather than by grazers. Although strongly resource limited, bacterial carbon fluxes appear to be large relative to other processes, and are likely supplemented by allochthonous inputs, specifically less labile organic carbon from rivers, coastal erosion, landfast ice and bottom sediments. The relationship between bacterial production and Chl *a* in summer-autumn but not in winter-spring implies that bacterial production is coupled to autochthonous production for only part of the year, and is supported for many months by slow breakdown of less labile substrates. Future analysis and biophysical models of the carbon flows for the coastal Arctic Ocean will need to pay close attention to the balance between autochthonous and allochthonous sources.

[49] The fastest rates of global warming are currently observed in the Arctic [*Christy et al.*, 2001; *Huntington et al.*, 2005], and there has been an accelerated reduction in arctic sea-ice extent and thickness during spring and summer [*Cavalieri et al.*, 2003; *Christy et al.*, 2001]. The lengthening of the open-water period as seen in the Beaufort Sea off the Mackenzie River Shelf [*Smith*, 1998], is likely to stimulate primary production via increased light availability, which in turn would enhance bacterial production. Such effects may be amplified by increased wind-induced mixing and upwelling during late season storms, which would likely entrain additional organic carbon and nutrients into the surface waters [*Loeng et al.*, 2005; *Walsh et al.*, 2005]. Climate forcing will also augment terrestrial nutrient and organic carbon loads [*Frey and Smith*, 2005; *Wrona et al.*, 2005] through increasing riverine discharge [*Peterson et al.*, 2002]. Such changes are likely to stimulate bacterial production and respiration, which in turn will modify net carbon fluxes in this coastal arctic system.

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