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Bacterial production and microbial food web structure in a large arctic river and the coastal Arctic Ocean

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Abstract

Globally significant quantities of organic carbon are stored in northern permafrost soils, but little is known about how this carbon is processed by microbial communities once it enters rivers and is transported to the coastal Arctic Ocean. As part of the Arctic River-Delta Experiment (ARDEX), we measured environmental and microbiological variables along a 300 km transect in the Mackenzie River and coastal Beaufort Sea, in July–August 2004. Surface bacterial concentrations averaged 6.7×10^5 cells mL^{-1} with no significant differences between sampling zones. Picocyanobacteria were abundant in the river, and mostly observed as cell colonies. Their concentrations in the surface waters decreased across the salinity gradient, dropping from 51,000 (river) to 30 (sea) cells mL^{-1}. There were accompanying shifts in protist community structure, from diatoms, cryptophytes, heterotrophic protists and chrysophytes in the river, to dinoflagellates, prymnesiophytes, chrysophytes, prasinophytes, diatoms and heterotrophic protists in the Beaufort Sea.

Size-fractionated bacterial production, as measured by ^{3}H–leucine uptake, varied from 76 to 416 ng C L^{-1} h^{-1}. The contribution of particle-attached bacteria (>3 μm fraction) to total bacterial production decreased from >90% at the Mackenzie River stations to <20% at an offshore marine site, and the relative importance of this particle-based fraction was inversely correlated with salinity and positively correlated with particulate organic carbon concentrations. Glucose enrichment experiments indicated that bacterial metabolism was carbon limited in the Mackenzie River but not in the coastal ocean. Prior exposure of water samples to full sunlight increased the biolability of dissolved organic carbon (DOC) in the Mackenzie River but decreased it in the Beaufort Sea.

Estimated depth-integrated bacterial respiration rates in the Mackenzie River were higher than depth-integrated primary production rates, while at the marine stations bacterial respiration rates were near or below the integrated primary production rates. Consistent with these results, P_{CO2} measurements showed surface water supersaturation in the river (mean of 146% of air equilibrium values) and subsaturation or near-saturation in the coastal sea. These results show a well-developed microbial food web in the Mackenzie River system that will likely convert tundra carbon to atmospheric CO_2 at increasing rates as the arctic climate continues to warm.

1. Introduction

Global climate change is predicted to have its greatest effects at high latitudes, and there is increasing evidence

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of the onset of rapid environmental change in the Arctic (Moritz et al., 2002; ACIA, 2005). Many marine and freshwater ecosystems in the Arctic depend on ice cover and are vulnerable to even small shifts in the ambient temperature regime (Serreze et al., 2000; Mueller et al., 2003). The predicted changes in precipitation and runoff (ACIA, 2005) are also likely to have major impacts on arctic rivers and coastal seas. Additionally, it is estimated that more than half of the global organic carbon pool is stocked in the catchments that surround the Arctic Ocean (Dixon et al., 1994). Permafrost melting will potentially liberate this organic carbon in the watershed of lakes and rivers, and make it available for microbial breakdown to CO_2 (Kling et al., 1991). Arctic rivers discharge annually 3299 km^3 $year^{-1}$ of freshwater in the Arctic Ocean or approximately 11% of the global river discharge (Rachold et al., 2004). There is therefore great interest in identifying the role of large arctic rivers in greenhouse gas production, and their influence on arctic coastal ecosystems.

Over the past 100 years within Canada, the greatest warming has been observed in the Mackenzie Basin (Macdonald and Yu, 2006). The Mackenzie River drains the largest catchment in Canada, with a total area of 1.8×10^6 km^2 (Macdonald et al., 1998), and it is the fourth largest arctic river in terms of freshwater discharge (330 km^3 y^{-1}). Microbial dynamics in floodplain lakes of the Mackenzie River have been studied (Spears and Lesack, 2006), however little is known about the microbial processes that operate in the main body of the river.

Freshwater–saltwater transition zones lie at the interface between rivers and the sea. They integrate upstream and downstream processes and are often the most biologically productive sections of the river (Vincent and Dodson, 1999). They are also regions of complex biogeochemical transformations of dissolved and particulate materials (Dagg et al., 2004), including the flocculation of particles of different sizes (Eisma and Cadée, 1991). The microbial community structure also undergoes pronounced changes along the salinity gradient with major shifts in bacterioplankton (Bouvier and del Giorgio, 2002; Selje and Simon, 2003; Crump et al., 2004) and protists (Frenette et al., 1995). There is some evidence of changes in the Bacteria (Garneau et al., 2006) and Archaea (Galand et al., 2006) communities across the transition zone of the Mackenzie River, however little is known about the overall microbial food web in this or other high latitude estuaries.

The Mackenzie River contains high concentrations of particulate matter that may provide substrates for microbial colonization and growth. It is the largest arctic river in terms of sediment discharge (124 MT per year; Rachold et al., 2004) and deposits 65 MT of sediments onto its delta annually (Macdonald et al., 1998). Contrary to other large arctic rivers, the Mackenzie carries annually more particulate organic carbon (POC) than dissolved organic carbon (DOC) (Rachold et al., 2004), and these carbon pools differ in age and origin. Mackenzie River POC appears to be dominated by old soil organic carbon derived from permafrost thawing and river-bank erosion, while the DOC is much younger and largely derived from modern terrestrial vegetation (Guo et al., 2007). In temperate latitude waters, aggregates constitute important microhabitats for microorganisms (Logan and Hunt, 1987; Azam et al., 1993) and the proportion of particle-bound bacteria generally increases with increasing suspended particle concentration (Fletcher, 1991). In the Columbia River Estuary, 90% of the bacterial activity was associated with particles larger than 3 μm (Crump et al., 1998), and in the St. Lawrence River transition zone, particle-attached bacteria also dominate total bacterial production (Vincent et al., 1996). Studies by Wells et al. (2006) have also drawn attention to the relationship between archaeal abundance and particles in the Mackenzie River and coastal Arctic Ocean (see also Galand et al., 2008). We therefore surmised that particles would play a key role in the bacterial production dynamics of the Mackenzie River and estuary.

Heterotrophic picoplankton (Bacteria and Archaea) play the dominant role in the degradation of organic matter and several intrinsic and extrinsic factors limit their efficiency in aquatic ecosystems (del Giorgio and Davis, 2003). Intrinsic factors include the chemical characteristics of the organic matter affecting its bioavailability, such as the molecular weight distribution and the nutrient content, which are determined by the source and the diagenetic state of the matter. Extrinsic factors are those regulating bacterial metabolism and their utilization of organic matter. These include temperature, the availability of inorganic and trace nutrients, trophic interactions within microbial food webs, and the phylogenetic composition of the bacterial assemblage.

Another factor that influences carbon cycling in the aquatic environment is the photodegradation of chromophoric dissolved organic matter (CDOM). Photochemical transformations of CDOM by solar radiation have been revealed by the photobleaching of CDOM and the appearance of photoproducts including dissolved inorganic carbon (Bertilsson and Tranvik, 2000). The photodegradation of CDOM affects its biolability and can increase or decrease its degradation by the bacterial community (Obernosterer et al., 1999; Tranvik and

Bertilsson, 2001). Studies on the Mackenzie Shelf and coastal Beaufort Sea have shown that photochemical breakdown of CDOM can account for a substantial carbon flux under ice-free conditions (Bélanger et al., 2006).

Our aim in the present study was to define the gradients in bacterial activity and in microbial community structure across the freshwater–saltwater transition zone from the Mackenzie River to the Arctic Ocean. We hypothesized that there would be major changes in the microbial community structure across this interface: from a heterotrophic community in the river and the estuary where the turbidity is high, to an autotrophic community dominated by the picophytoplankton and nanophytoplankton in the marine zone. We surmised that bacterial metabolism would be likely to increase towards the marine stations due to the increasing autochthonous origin and lability of the dissolved organic carbon (DOC) in the ocean, and that particle-attached bacteria (relative to free-living cells) would account for a large fraction of total bacterial production. An additional objective was to evaluate the limitation of bacterial metabolism by organic carbon availability, and the effect of UV-photochemical reactions on DOC lability. We hypothesized that the bacterial metabolism was carbon limited, and that the exposure of DOC to UV radiation would increase the bioavailability or terrigenous carbon and thus stimulate bacterial metabolism. The final goal of this study was to integrate our measurements with data from other observations during the ARDEX cruise in order to address the question of whether northern waters are a source or a sink of greenhouse gases (Vincent and Hobbie, 2000).

2. Materials and methods

2.1. Sampling

Sampling was carried out from 26 July to 2 August 2004 aboard the shallow-draft research vessel CCGS Nahidik within the program ARDEX (Arctic River-Delta Experiment), a satellite program of CASES (Canadian Arctic Shelf Exchange Study). Water samples were collected along a 300 km transect from Inuvik, NWT, Canada, to a station 50 km offshore in the Beaufort Sea across the freshwater–saltwater transition zone (TZ) (Fig. 1). Surface samples were collected using a clean, sample-washed, plastic bucket and deeper samples were obtained with a 6.2 L Kemmerer sampler or a peristaltic pump. We sampled eight stations at the surface and near the bottom (except at R9 where the deepest sample was at 21 m in the deep chlorophyll maximum), and two additional stations at the surface only (R1 and R5b).

Mid-channel depths in the Mackenzie River varied greatly among the stations from 2.7 m at R1 to 29.6 m at R3. In the transition zone, the water column was shallow with 3.7 m at R5d and 2.9 m at R5a. In the coastal Beaufort Sea, the maximum water column depth increased offshore, from 7.5 m at R7, to 16 m at R8 and 32 m at R9. The stations were separated into three

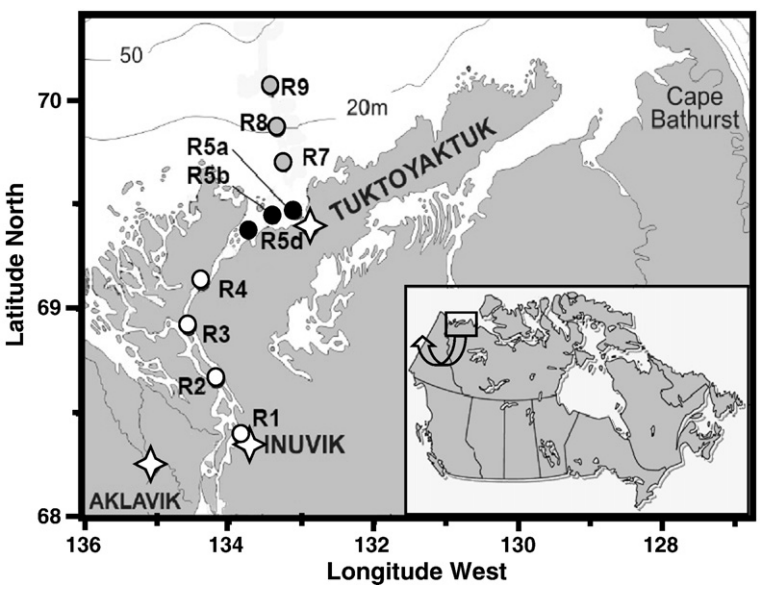

Fig. 1. Sampling site and stations. White circles: Mackenzie River stations. Black circles: transition zone stations. Grey circles: Coastal Beaufort Sea stations. The figure shows the 20 m and 50 m isobaths.

categories according to their surface salinities in order to evaluate general trends in the data set: river (R1 to R4; salinity 0 to 1 psu), transition zone (TZ) (R5d to R5a; salinity 1 to 10 psu) and sea (R7 to R9; salinity >20 psu).

2.2. Physical characteristics of the water column

An RBR CTD logger (RBR Inc., Canada) was used to profile the water column. The logger was equipped with standard temperature, conductivity (salinity) and pressure (depth) sensors.

2.3. Particulate and dissolved matter

Samples for suspended particulate matter (SPM) were filtered in duplicate onto pre-combusted and pre-weighed glass fiber GF/F filters (0.7 μm, 47 mm) and stored in aluminum foil at −80 °C. Filters were subsequently dried at 60 °C for 24 h and re-weighed for determination of SPM mass. Particulate organic carbon (POC) samples were filtered in duplicate onto pre-ashed glass fiber GF/C (1.2 μm, 25 mm) which were frozen at −80 °C in aluminum foil until further processing. POC concentration was analyzed by high temperature oxidation using an elemental analyzer LECO CHNS-932 with a detection limit of 0.03 mg L^{-1}. Filters were acidified with HCl fumes overnight and allowed to dry at 65 °C prior to analysis in tin or silver sleeves. Dissolved organic carbon (DOC) samples were obtained by filtering water through 0.2 μm cellulose acetate filters (47 mm). The filtrate was stored in acid-washed brown glass bottles at 4 °C. Before analysis, samples were bubbled with CO_2-free nitrogen for 7 min to ensure complete removal of dissolved inorganic carbon. DOC concentrations were measured by high combustion, direct injection in a Shimadzu TOC Analyzer 5000A (detection limits of 0.05 mg L^{-1}).

2.4. Microbial community structure

Picophytoplankton (picocyanobacteria and picoeukaryotes) samples were filtered onto Anodisk filters (0.2 μm, 25 mm) under gentle pressure and mounted between slides and cover slips with Aquapoly/Mount (Polyscience, Inc.). The slides were stored at −20 °C for up to 20 months before analysis. The samples were counted under a Zeiss Axioskop 2 epifluorescence microscope using green and blue excitation at 1000× magnification with immersion oil. Picocyanobacteria fluoresce bright orange or red under green light and yellow or pale red under blue light contrary to photosynthetic picoeukaryotes that fluoresce deep red in both cases (MacIsaac and Stockner, 1993). A minimum of 15 fields and 400 cells were counted wherever possible.

Heterotrophic picoplankton samples (Bacteria and Archaea) were preserved with formaldehyde (2%, final concentration) in acid-washed clear glass bottles previously rinsed with the sample and stored in the dark at 4 °C (for up to 10 months). Due to the presence of large amount of sediments, the samples from the river and estuarine stations were sonicated for 15 s in acid-washed glass test tubes using an ultrasonic bath (Bransonic 220, 117 V, 50–60 Hz, 125 W). Samples were then filtered onto Nuclepore black polycarbonate membranes (0.22 μm, 25 mm) placed on cellulose acetate backing filters (0.8 μm, 25 mm) under low pressure. DAPI was added at 5 μg L^{-1} final concentration (Porter and Feig, 1980) when 2 mL of sample were remaining and left to stain for 15 min before the final filtration to dryness. Filters were mounted on slides with cover slips and non fluorescent immersion oil and stored at −20 °C until counting on a Zeiss Axioskop 2 epifluorescence microscope, under UV light and 1000× magnification with immersion oil. A minimum of 15 fields and 400 cells were counted wherever possible.

Protist samples were preserved with paraformaldehyde (0.5 g L^{-1} final concentration) and glutaraldehyde (0.5% final concentration; Tsuji and Yanagita, 1981) in HDPE Nalgene bottles and stored in the dark at 4 °C for up to 18 months. Flagellates and protozoa were counted, measured and identified using a combined system of fluorescence, Nomarski interference and Utermöhl sedimentation (FNU; Lovejoy et al., 1993) for the riverine stations R3 and R4, the TZ stations R5d and R5a and the coastal stations R8 and R9. Between 3.6 mL and 100 mL of samples were concentrated in Utermöhl sedimentation chambers, depending on the concentration of cells and sediments. Sedimentation duration varied from 12 to 48 h depending on the sedimentation column volume. After the sedimentation, DAPI was gently added (0.1 μg mL^{-1} final concentration) and left to stain for a minimum of 2 h. The enumerations were made with a Zeiss Axiovert 100 inverted epifluorescence microscope under 1000× magnification using immersion oil. Counts and identification of riverine and estuarine samples were difficult due to the high sediment load and sparse cell concentrations. For stations R3, R4 and R5d, more than 250 fields and less than 100 cells were observed. At other stations, counts were easier with fewer fields and more cells observed. Cells were separated in size classes as nanoplankton (2 to 20 μm) and microplankton (>20 μm), heterotrophs and autotrophs (pigment fluorescence), and to genus wherever possible.

Plankton biovolumes were calculated as in Hillebrand et al. (1999), with biovolume estimates calculated for each protist taxon. Because many protist species could only be measured once, missing dimensions were estimated from identification guides, if possible, or from similar organisms observed during counting. For picophytoplankton, dimensions used were from Bertrand and Vincent (1994) who studied the picophytoplankton community in another large river, the St. Lawrence. Picocyanobacteria and picoeukaryotes biovolumes were calculated as spheres with diameters of 1.25 μm and 1.5 μm respectively. Protist and picophytoplankton carbon biomass was estimated for each group with the equations given in Menden-Deuer and Lessard (2000): pg C $cell^{-1} = 0.216 \times V^{0.939}$ for non-diatom cells and pg C $cell^{-1} = 0.288 \times V^{0.811}$ for diatoms, where V is the mean cell biovolume of a group. Heterotrophic picoplankton carbon biomass was estimated with the widely used value of 20 fg C per cell (Lee and Fuhrman, 1987).

2.5. Bacterial production

The ^{3}H–leucine (^{3}H–Leu) incorporation method was used to measure protein synthesis by the heterotrophic picoplankton (Bacteria and Archaea), which we refer to subsequently as "bacterial production". Bacterial production was measured on the total bacterial community (unfiltered water sample) and on the free-living bacterial community, defined as single cells or cells associated with aggregates <3 μm in diameter. For the free-living fraction, water samples were prefiltered through Poretics 3 μm polycarbonate filters. Prior tests had shown that this gave a good separation of the community in coastal waters (Garneau et al., 2006). The filters were initially washed with sample water and changed whenever clogging was apparent. Particle-attached bacterial production was extrapolated by subtracting the free-living fraction from total bacterial production.

For each site and sample fraction (total and <3 μm), five sterile microvials (2 mL) were filled with 1.25 mL of sample water. Two of these samples were killed with trichloroacetic acid (TCA; 5% final concentration) to serve as controls, and all five microvials were then inoculated with ^{3}H–Leu (specific activity: 152 Ci $mmol^{-1}$, Amersham Biosciences). It was not possible to obtain the results of our saturation curve experiments while on the ship, and we therefore used a standard final concentration of 10 nM as proposed by Simon and Azam (1989). Microvials were incubated in the dark at the simulated *in situ* temperature for 2 h. Difference from true *in situ* temperature was usually very small (<2 °C). Protein synthesis was stopped by the addition of TCA (5% final concentration). The microvials were then stored at 4 °C to be processed in the next 24 h or frozen (−20 °C) to be processed later. Unincorporated ^{3}H–Leu was eliminated using a microcentrifugation protocol modified from Smith and Azam (1992) and the microvials were then stored at −20 °C. Microvials received 1 mL of scintillation liquid (OptiPhase 'HiSafe' 2; Wallac Scintillation products) and were subsequently vortexed. After 24 h at room temperature, the samples were radio-assayed in a Beckman LS 6500 scintillation counter.

At station R3, a time series and a saturation curve experiment were performed on the total bacterial community (unfiltered water). For the time series, the tubes received 10 nM of ^{3}H–Leu and were incubated for 70, 130, 200, 250 or 335 min. This experiment showed that ^{3}H–Leu uptake was linear for at least 350 min. For the saturation curves, the tubes received 6.25, 10, 15, 20 or 25 nM of ^{3}H–Leu and were incubated for 2 h. These measurements demonstrated that the concentration of 10 nM was below saturation, at least in the river stations. Thus, the bacterial production rates reported here should be considered as conservative estimates.

Net bacterial C production was estimated using the conversion factor of 3.1 kg C per mol of ^{3}H–Leu incorporated (Simon and Azam, 1989). We also calculated depth-integrated net C production for each station by using a trapezoidal integration formula. To convert net bacterial C production rates into bacterial respiration rates, we used the bacterial growth efficiency (BGE) values from Meon and Amon (2004) who calculated BGEs of 25% in another large arctic river, the Ob, and 27% in its estuary and the adjacent coastal Arctic Ocean (Kara Sea).

2.6. Carbon limitation of bacterial production

At stations R4, R5b and R9, three 1-L polypropylene bottles were filled with unfiltered surface water. Two bottles received 5 μM of glucose (final concentration) as a labile carbon source and one was kept unamended to serve as a control. The bottles were incubated on deck for 24 h in the dark at the *in situ* water temperature. At the end of incubation, subsamples from each bottle were filtered through 3 μm polycarbonate filters and bacterial production was measured for the total and <3 μm bacterial communities.

2.7. UV radiation effects on carbon biolability

At stations R4 and R9, water sterilized by filtration through 0.2 μm Gelman PALL filters was exposed to

sunlight for 3 days in quartz bottles on the deck of the ship, and a duplicate sample was maintained in the dark. At the end of these incubations, 90 mL subsamples from each bottle were inoculated with 10 mL of the original bacterial inoculum (water from R4 or R9 that was filtered through 0.8 μm polycarbonate membrane filters, stored in the dark in acid-washed clear glass bottles) and then incubated in acid-washed 125 mL clear glass bottles. Bacteria were allowed to grow for 24 h in the dark at simulated *in situ* temperatures. Bacterial production was then measured for each bottle without fractionation.

2.8. Surface water and atmospheric P_{CO2}

The partial pressure of CO_2 (P_{CO2}) was measured in the surface waters (0.3 m depth) using a continuous flow of water pumped through a gas permeable, water impermeable exchanger that allowed a gas filled loop to come to equilibrium with the gases in the water. The gases in the loop were circulated past a non-dispersive IRGA to detect the CO_2 (LiCor-800). The gas loop was equipped with two three-way solenoid driven valves. When actuated, these valves bypassed the equilibrator so that outside air could be drawn directly through the detectors. This allowed carbon dioxide in the air above the water to be measured. The IRGA was calibrated with CO_2 gas standards before and after the cruise, and showed no significant drift during this time.

3. Results

3.1. Sampling and meteorological conditions

During the week prior to sampling, the Mackenzie watershed received a moderate amount of precipitation. However, during the sampling cruise, a large amount of rain occurred over the basin causing an increase in the river discharge between the beginning and the end of the sampling. During the sampling of R1 (July 26th) and R4 (July 27th), the Mackenzie River discharge at Inuvik (East Channel) was 176 and 170 $m^3\ s^{-1}$ respectively. On August 1st (sampling at R3 and R4) it increased by 25% to 214 $m^3\ s^{-1}$ (see Emmerton et al., 2008).

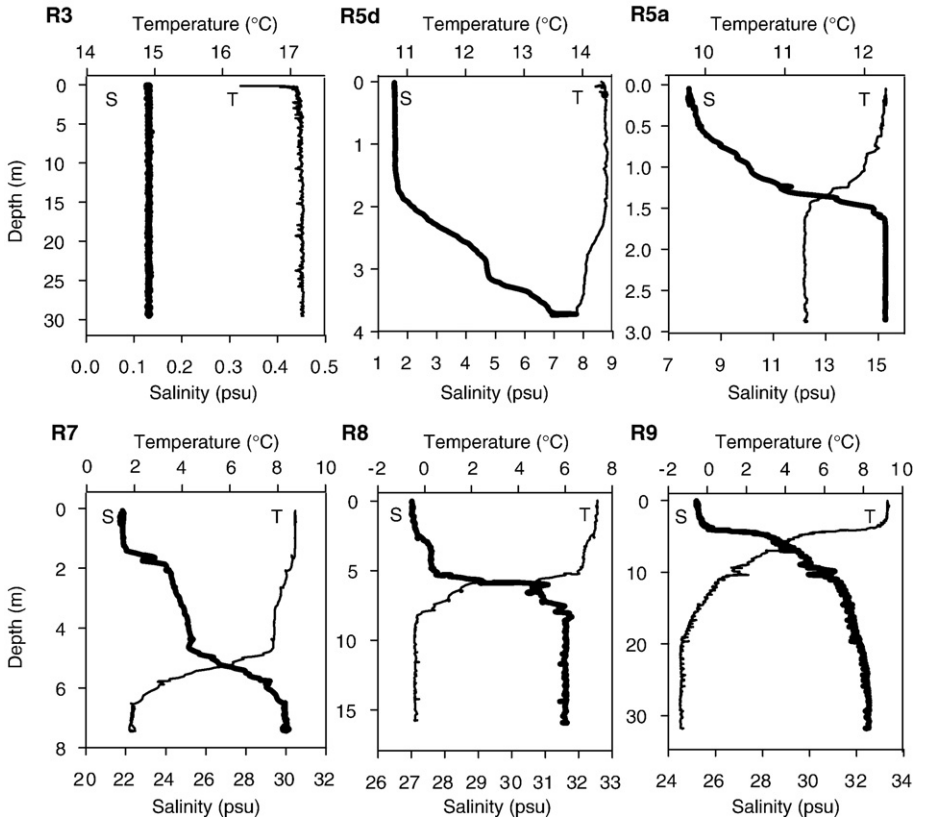

Fig. 2. Water column structure at 6 stations measured by CTD profiling. S: Salinity. T: temperature. Only one set of profiles is presented for the river because the structure of the water column was similar at each freshwater station.

3.2. Hydrographic and environmental gradients

Large changes in water column structure occurred across the freshwater–saltwater transition zone (TZ) of the Mackenzie River and the Beaufort Sea (Figs. 2 and 3). In the river, the water column was well mixed with no variations with depth in salinity or temperature. In the TZ, an intrusion of slightly more saline and colder sea waters was evident at the bottom of the water column in the CTD profiles. The stratification of the water column increased offshore and the thickness of the warm, brackish river plume diminished with increasing distance from the coast (Fig. 2). In the coastal zone, the salinity of the surface waters of the buoyant plume was significantly lower than in the bottom waters ($t=-3.8$, $P=0.018$; Fig. 3). The three zones differed significantly in their surface (ANOVA, $F=86.3$, $P<0.001$; Fisher-LSD, $P<0.001$) and bottom (ANOVA, $F=119.5$, $P<0.001$) water temperatures (Fig. 3).

The Mackenzie River carried a high load of suspended particulate matter (SPM; Fig. 3) which averaged 54±14- mg L^{-1} across the sampled freshwater stations. Even though mean surface SPM concentrations were not significantly different among the three zones (ANOVA, $F=3.5$, $P=0.088$), a trend could be observed along the transect, with a pronounced decrease of SPM load in the surface waters between the Mackenzie River and the Beaufort Sea, and the sharpest decrease across the TZ. The highest SPM concentration (167 mg L^{-1}) was observed at the bottom of R7 and was probably associated with bottom sediment resuspension. The difference between the mean SPM concentrations of coastal zone surface and bottom layers was not significant, but a pattern of increasing SPM concentration towards the bottom was apparent. SPM load in the bottom waters did not significantly differ among the three zones (ANOVA, $F=0.4$, $P=0.70$).

Particulate organic carbon (POC; Fig. 3) was also high and averaged 1.4±0.3 mg L^{-1} across the riverine stations. Maximum POC concentration in surface waters occurred in the TZ at R5d. It was followed by a large drop towards R5b and, subsequently, by an almost linear decrease to a minimum at R9 that was below the detection limit of the analyzer (0.05 mg L^{-1}). POC concentrations were not significantly different between the surface and the bottom waters in any of the three zones. However, surface POC concentrations were significantly different between the river and the TZ (ANOVA, $F=7.7$, $P=0.017$; Fischer-LSD, $P=0.025$), and between the river and the sea (ANOVA, $F=7.8$, $P=0.017$; Fischer-LSD, $P=0.007$).

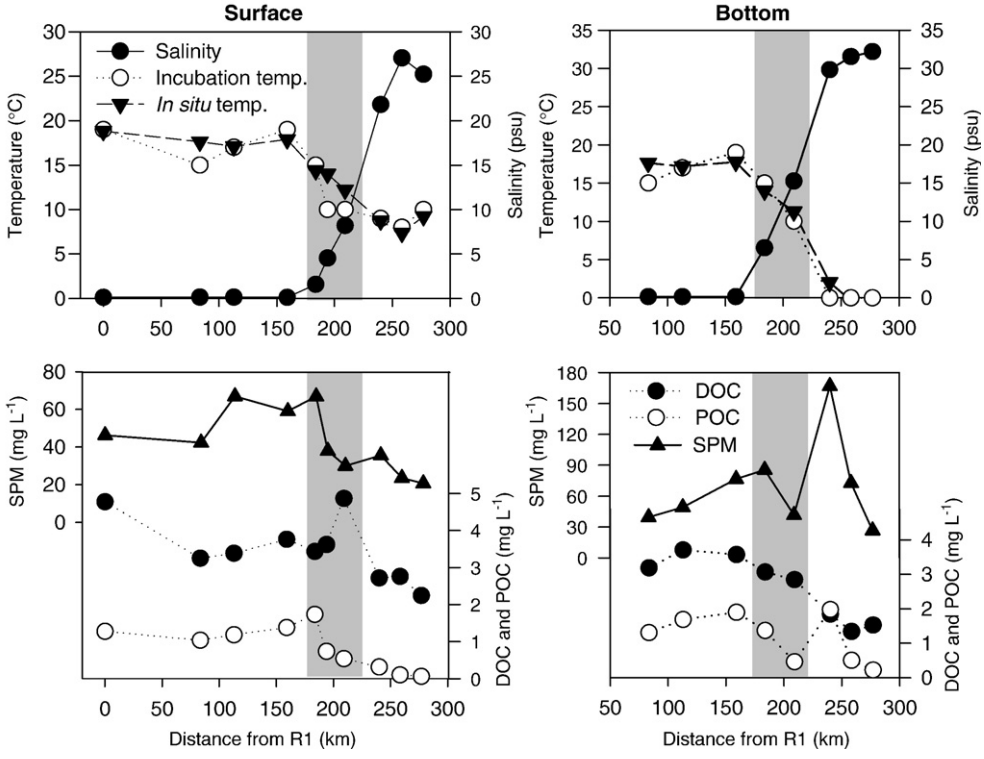

Fig. 3. Surface and bottom water properties at each station along the ARDEX transect. *In situ* and incubation temperatures are presented to show the general correspondence.

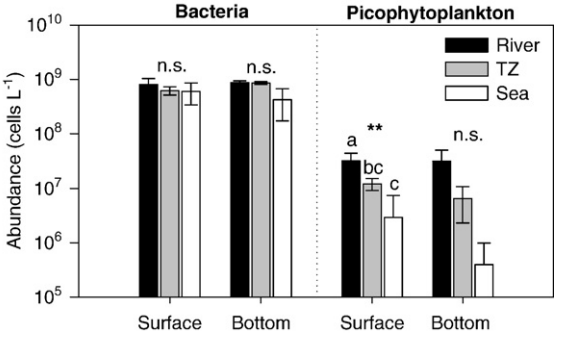

Fig. 4. Surface and bottom bacterial and picophytoplankton mean abundance in each zone. The error bars are ±SD. The results of variance analyses between the zones are shown above each bar group (n.s. = no significant difference, ** = highly significant difference ($P \leq 0.01$)). The letters show the results of multiple comparison tests. Note the logarithmic scale.

Dissolved organic carbon (DOC; Fig. 3) was highly variable in the river and in the TZ. In the river, it averaged 3.7±0.5 mg L^{-1}, and in the TZ, 3.6±0.8 mg L^{-1}. In the coastal zone, DOC concentrations dropped to a mean value of 2.6±0.3 mg L^{-1} at the surface. In this zone, DOC concentrations decreased significantly towards the bottom layer with a mean of 1.6±0.3 mg L^{-1} (t=4.5, P=0.01). At the surface, there was no significant difference between the three zones, (ANOVA, F=4.5, P=0.056), but the power of the test (0.46) was well below the desired level of 0.8. For the bottom, the river and the sea (ANOVA, F=48.2, P<0.001; Fischer-LSD, P<0.001) were significantly different from each other, as were the TZ and the offshore ocean (ANOVA, F=48.2, P<0.001; Fischer-LSD, P=0.002).

3.3. Microbial gradients

In terms of cell concentrations, heterotrophic picoplankton (Bacteria and Archaea) dominated the picoplankton community by 1 to 4 orders of magnitude over the picophytoplankton community (picocyanobacteria and picoeukaryotes). There was no significant difference in heterotrophic picoplankton abundance among the three zones (ANOVA, Surface: F=0.54, P=0.62; Bottom: F=5.126, P=0.079), nor between the surface and the bottom of each zone (Fig. 4).

Surface autotrophic picoplankton abundance (Figs. 4 and 5) decreased along the transect towards the marine stations from 45.1×10^3 cells mL^{-1} in the river (R2) to 0.03×10^3 cells mL^{-1} in the sea (R9). Between R7 and R9, picophytoplankton abundance dropped by two orders of magnitude. Autotrophic picoplankton abundance was significantly different between the river and the sea (ANOVA, F=10.4, P=0.008; LSD, P=0.003), and between the river and the transition zone (ANOVA, F=10.4, P=0.008; LSD, P=0.021; Fig. 4). The picophytoplankton community in the bottom waters (Figs. 4 and 5) showed a similar pattern of decrease towards the coastal zone, but concentrations were not significantly different among the three zones (ANOVA, F=5.6, P=0.053; Fig. 4). The difference between the surface and the bottom for the picophytoplankton abundance was not significant in the river, in the TZ and in the sea. The relative contribution of picocyanobacteria and picoeukaryotes to total autotrophic picoplankton differed among sites, with an increasing contribution of picoeukaryotes in the sea (Fig. 5). The largest contribution of picoeukaryotes to autotrophic picoplankton abundance was at the bottom of R9 where it reached 58%. At the same location, picoeukaryotes composed 70% of the carbon biomass of the total picoplankton community. Surface picophytoplankton abundance showed a strong negative correlation with salinity (r_s=−0.87, P<0.001) and (given the inverse relationship between salinity and temperature) a strong positive relationship with temperature (r_s=0.87, P<0.001). It was correlated with SPM (r_s=0.66, P=0.03) and POC (r_s=0.64, P=0.04), and with bacterial abundance (r_s=0.75, P=0.04).

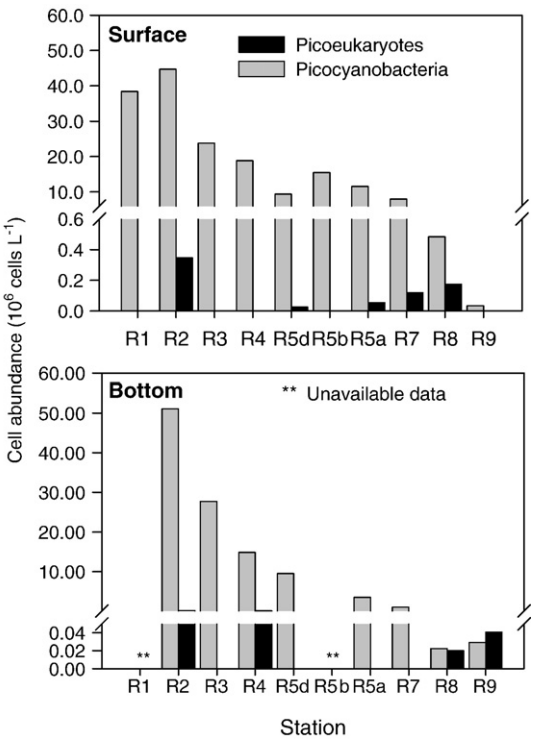

Fig. 5. Abundance of picocyanobacteria and picoeukaryotes along the ARDEX transect in the Mackenzie River and coastal Beaufort Sea.

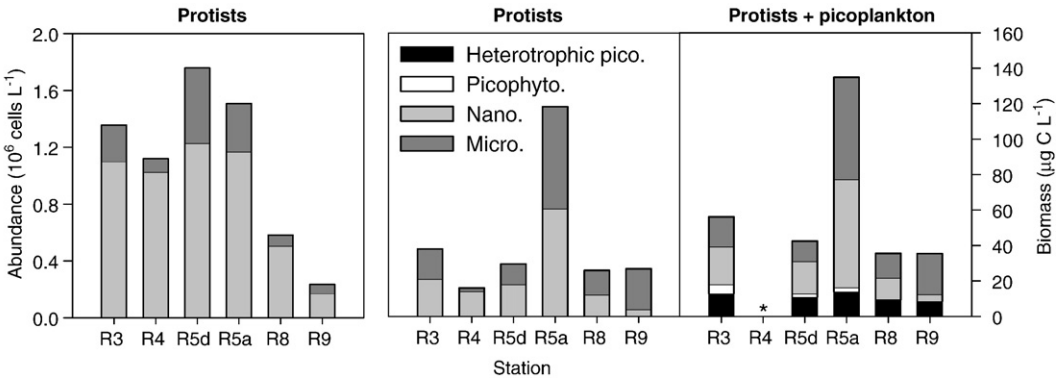

Fig. 6. Nanoplanktonic and microplanktonic protist abundance and biomass along the ARDEX transect, and comparison with autotrophic and heterotrophic picoplankton biomass.

Protist community structure showed large changes across the transect both in terms of cell concentration (Fig. 6) and dominant taxa (Tables 1 and 2). Protists were significantly more abundant in the TZ and in the river than in the sea where their concentration dropped by an order of magnitude (Table 1; R+TZ vs S, $t=4.52$, $P=0.011$). At each station, many organisms could not be classified in a specific taxonomic or trophic group due in part to the usual difficulties of preservation. In terms of carbon biomass and percent contribution of heterotrophs (Table 2 and Fig. 6), the protist community showed no significant differences among the three zones (Kruskal–Wallis, $H=2.0$, $P=0.53$). However, a biomass peak was evident at R5a with 118.3 ng C mL^{-1}, which was 3 (R3) to 7 (R4) times higher than the biomass found at other stations.

Heterotrophic picoplankton was the most abundant component of the microbial community, constituting 96 (R3) to almost 100% (R9) of total cell abundance. However, it contributed only 10 (R5a) to 26% (R8) of total carbon biomass (Fig. 6). The largest percentage of carbon biomass was due to nanoplanktonic and microplanktonic protists (Fig. 6). The highest carbon biomass of around 135 ng C mL^{-1} was found in the TZ at R5a.

Table 1
Abundance of protists (in 10^3 cells L^{-1}) observed along the ARDEX transect

	River				Transition zone				Coastal zone			
	R3	R4	Mean	%	R5d	R5a	Mean	%	R8	R9	Mean	%
Bacillariophyceae	530	76	303	24	302	215	259	16	48	12	30	7
Bacillariophyceae (hypn.)	0	0	0	0	0	10	5	0	6	2	4	1
Chlorophyceae	118	0	59	5	435	174	305	19	4	2	3	1
Chrysophyceae	79	114	96	8	170	0	85	5	36	47	41	10
Cryptophyceae	20	228	124	10	95	451	273	17	20	6	13	3
Dinophyceae (auto.)	20	0	10	1	0	72	36	2	80	47	63	16
Dinophyceae (hetero.)	0	0	0	0	19	0	9	1	4	0	2	0
Dinophyceae (UTS)	0	0	0	0	0	0	0	0	10	0	5	1
Euglenophyceae	0	0	0	0	0	0	0	0	0	2	1	0
Prasinophyceae	0	0	0	0	0	0	0	0	62	8	35	9
Prymnesiophyceae	0	0	0	0	0	0	0	0	100	18	59	14
Raphidophyceae	0	0	0	0	0	62	31	2	2	0	1	0
Ciliates (hetero.)	0	19	9	1	0	10	5	0	8	10	9	2
Unidentified auto. cells	177	304	240	19	529	287	408	25	121	65	93	23
Other hetero. cells	393	323	358	29	113	51	82	5	60	14	37	9
Unidentified cells (UTS)	20	57	38	3	95	174	134	8	22	0	11	3
TOTAL	1356	1120	1238	100	1758	1508	1633	100	581	234	408	100

Abundances are given for each station, in addition to the mean abundance and the percentage of each group in each zone. The organisms are classified by taxon except for heterotrophic cells, other than Dinophyceae and ciliates, which are pooled in one category (other heterotrophic cells) including identified and unidentified cells. (auto.: autotrophic; hetero.: heterotrophic; hypn.: hypnospores; and UTS: unknown trophic status).

Table 2
Biomass of protists (in ng C L^{-1}) observed along the ARDEX transect

	River				Transition zone				Coastal zone			
	R3	R4	Mean	%	R5d	R5a	Mean	%	R8	R9	Mean	%
Bacillariophyceae	22.2	0.4	11.3	42	8.0	15.6	11.8	16	3.0	2.3	2.7	10
Bacillariophyceae (hypn.)	0	0	0	0	0	0.5	0.3	0	0.2	0.1	0.2	1
Chlorophyceae	2.8	0	1.4	5	3.6	2.2	2.9	4	0.1	0.1	0.1	0
Chrysophyceae	1.1	1.9	1.5	6	3.5	0	1.7	2	0.1	0.2	0.2	1
Cryptophyceae	0.4	4.2	2.3	8	3.2	14.0	8.6	12	0.4	0.3	0.3	1
Dinophyceae (auto.)	2.7	0	1.4	5	0	1.8	0.9	1	3.7	19.9	11.8	45
Dinophyceae (hetero.)	0	0	0	0	2.6	0	1.3	2	0.1	0	0	0
Dinophyceae (UTS)	0	0	0	0	0	0	0	0	3.8	0	1.9	7
Euglenophyceae	0	0	0	0	0	0	0	0	0.0	0.2	0.1	0
Prasinophyceae	0	0	0	0	0	0	0	0	0.4	0.03	0.2	1
Prymnesiophyceae	0	0	0	0	0	0	0	0	9.2	0.3	4.8	18
Raphidophyceae	0	0	0	0	0	41.1	20.5	28	0.3	0	0.1	1
Ciliates (hetero.)	0	3.6	1.8	7	0	0.1	0.1	0	2.7	2.2	2.5	9
Unidentified auto. cells	1.0	1.3	1.1	4	4.3	8.1	6.2	8	1.4	0.6	1.0	4
Other hetero. cells	7.6	4.3	5.9	22	3.9	31.9	17.9	24	0.4	0.5	0.5	2
Unidentified cells (UTS)	0.2	0.5	0.4	1	0.6	3.1	1.8	2	0.2	0	0.1	0
TOTAL	38.0	16.1	27.0	100	29.6	118.3	74.0	100	25.9	26.9	26.4	100

The values are given for each station, in addition to mean abundance and the percentage of each group in each zone. Organisms are classified by taxon except for heterotrophic cells, other than Dinophyceae and ciliates, which are pooled in one category (other heterotrophic cells) including identified and unidentified cells. (auto.: autotrophic; hetero.: heterotrophic; hypn.: hypnospores; and UTS: unknown trophic status).

The percentage contribution of heterotrophs to total microbial community carbon biomass did not vary greatly among the zones and ranged from 32 (R9) to 41% (R5d).

3.4. Bacterial production gradients

Surface measurements of total bacterial carbon production (BCP; Fig. 7) showed two levels of activity in the Mackenzie River. Stations R1 and R4 showed elevated activities (mean of 390±36 ng C L^{-1} h^{-1}) that were more than three times higher than R2 and R3 (mean of 119±10 ng C L^{-1} h^{-1}). The first two stations of the TZ showed an activity level similar to R2 and R3, but production rates rose downstream to reach 329 ng C L^{-1} h^{-1} at R5a. In the sea, the total BCP rates averaged 178±48 ng C L^{-1} h^{-1}. In the surface water of the Mackenzie River, particle-attached bacteria (>3 μm; Fig. 7) were responsible for the largest fraction of total BCP, accounting for 94±5% of the activity. In the TZ, the importance of the particle-bound bacteria in the BCP decreased to 73±2%. BCP in the Beaufort Sea was dominated by the free-living fraction, and particle-attached bacteria accounted for only 31±16% of the activity. The three zones did not significantly differ in their surface total BCP (ANOVA, $F=0.44$, $P=0.66$; Fig. 7), however there were significant differences between the river and the sea surface for the contribution of particle-bound bacteria to total heterotrophic activity (Kruskal–Wallis, $H=7.0$, $P=0.005$; Dunn's test, $P<0.05$).

In the river and the TZ, there was no significant difference between the surface and the bottom values for the heterotrophic microbial activity data. In the sea, particle-attached bacteria accounted for a higher fraction of the total BCP at the bottom (almost 3 times higher) than at the surface ($t=-6.3$, $P=0.003$). The bottom waters of the TZ had significantly higher BCP rates relative to the sea (ANOVA, $F=12.4$, $P=0.012$; LSD,

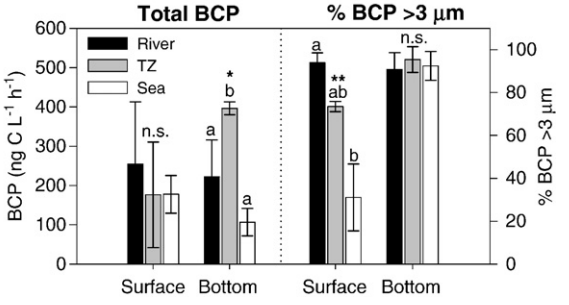

Fig. 7. Total bacterial carbon production (BCP) and percentage of BCP due to particle-attached bacteria (>3 μm). The values are means (±SD) at the surface and the bottom of each zone. The results of variance analyses between the zones are shown above each bar group (n.s. = no significant difference, * = significant difference ($P\leq0.05$), ** = highly significant difference ($P\leq0.01$)). The letters show the results of multiple comparison tests.

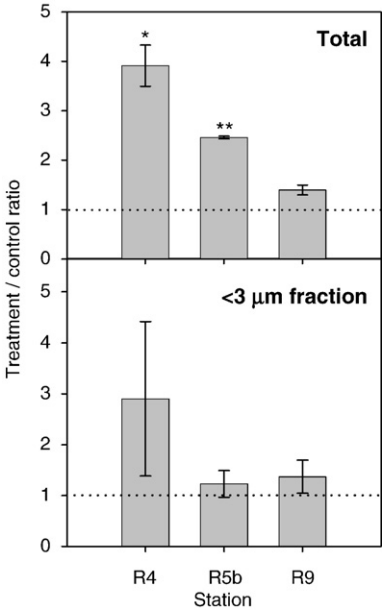

Fig. 8. Response of bacterial activity to glucose addition as the ratio of treatment ^{3}H–Leu uptake to control in the Mackenzie River, transition zone and coastal Beaufort Sea. The error bars represent the range of the two ratios. * = significantly >1 ($P<0.05$) and ** = significantly >1 ($P<0.01$).

$P=0.004$) and the river (ANOVA, $F=12.4$, $P=0.012$; LSD, $P=0.03$; Fig. 7).

Total BCP was not correlated with any of the measured environmental or microbial variables. However, the percentage of BCP due to attached bacteria was positively correlated with temperature ($r_s=0.93$, $P<0.001$), DOC ($r_s=0.72$, $P=0.03$), POC ($r_s=0.67$, $P=0.04$), % POC/SPM ($r_s=0.75$; $P=0.02$) and picophytoplankton abundance ($r_s=0.87$, $P<0.001$). It was negatively correlated with salinity ($r_s=-0.90$, $P<0.001$). Depth integrated BCP varied from 1.12 (R1) to 6.33 mg C m^{-2} h^{-1} (R4) in the Mackenzie River, from 0.67 (R5d) and 1.06 mg C m^{-2} h^{-1} (R5a) in the transition zone, and from 1.60 (R7) to 2.83 mg C m^{-2} h^{-1} (R9) in the coastal Beaufort Sea.

3.5. Response of bacterial activity to carbon addition

The bacterial community responded differently among sites to glucose addition, with greater stimulation in the river than in the sea, and an intermediate effect in the TZ (Fig. 8). However, there was no statistically significant difference between the three stations in terms of response to glucose addition (ratio of the two treatment bottles to the control) (Kruskal–Wallis, $H=4.6$, $P=0.067$). This lack of significance is likely due to the low power of the statistical test due to the small sample size for each treatment ($n=2$). In the river station R4, bacterial activity increased almost fourfold in the glucose enriched bottles compared to the control (Fig. 8) (ratio = 3.9 ± 0.4, significantly different from 1, $t=9.8$, $P<0.05$). This glucose-induced stimulation decreased in the TZ to reach 2.5 times the control level ($t=80.9$, $P<0.01$). In the sea, bacterial production responded slightly to glucose addition, but the ratio was not significantly different from 1 ($t=5.8$, $P>0.05$).

The free-living heterotrophic picoplankton fraction (<3 µm) showed no clear response to glucose addition (Fig. 8), with no significant differences among stations (Kruskal–Wallis, $H=3.7$, $P=0.20$). In the river, the range of responses in the two treatment bottles was too large to allow an interpretation of the results. In the TZ and in the coastal zone, there was only a weak stimulation of the <3 µm fraction induced by the addition of glucose.

3.6. Response of bacterial activity to sunlight-exposed DOC

After the sunlight exposure, 36% of the CDOM (a_{350}) had been lost in the river sample (station R4), but there was only 1% decrease in CDOM absorption in the marine sample (station R9). The pre-exposure of the riverine CDOM to sunlight induced an almost twofold increase in bacterial metabolic rates (Fig. 9). However, at the coastal station, the inverse response was observed: the sunlight treated DOC showed an activity level that was only one third of that in the dark pre-incubated control (Fig. 9).

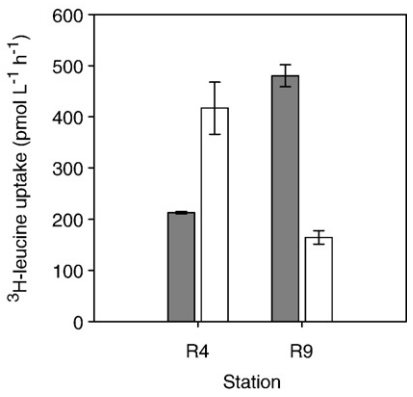

Fig. 9. Effect of sunlight exposure on DOC lability in river water (R4) and offshore sea water (R9). The values (±SD for triplicate assays) are for bacterial ^{3}H–Leu uptake in filtered water (0.2 µm) that was pre-incubated in a quartz bottle for 3 days under sunlight (white bars) or in darkness (black bars) and then re-inoculated with bacteria from the respective site.

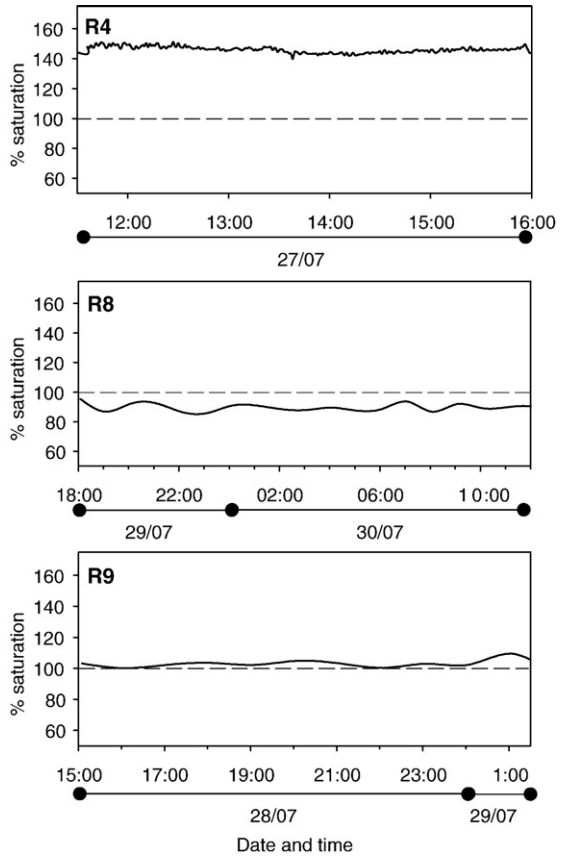

Fig. 10. Percent saturation of surface water CO_2 concentrations compared with mean values in the overlying atmosphere at each site.

3.7. Percentage saturation of CO_2

At station R4 in the Mackenzie River, the surface waters were supersaturated in CO_2 at 146.0±2.0% of the measured air value (475.5±0.0 ppm; Fig. 10), indicating a net efflux from the river to the atmosphere. In contrast, CO_2 concentrations in the surface waters at offshore site R8 were 89.5±2.6% that of overlying atmosphere (400.8±5.9 ppm; Fig.10). At the most offshore station, R9, surface waters showed CO_2 concentrations that were 103.1±2.5% of measured air values (405.7±2.4 ppm; Fig. 10), indicating near-equilibrium conditions.

4. Discussion

4.1. Microbial community structure

Microbial community structure across the freshwater–saltwater transition zone showed marked changes in terms of picophytoplankton, and in protist abundance and species. Contrary to our hypothesis, picophytoplankton (specifically picocyanobacteria, but commonly in colonial forms) were more abundant in the river and the TZ than in the coastal Beaufort Sea, and autotrophs dominated the protist community in the three zones. Heterotrophs were an important fraction of total microbial biomass at all sites and did not change significantly along the transect, contrary to our predictions.

Surface heterotrophic picoplankton abundances measured in the Mackenzie River during the ARDEX cruise were an order of magnitude smaller than those measured by Garneau et al. (2006) in September–October 2002 which varied from 1.4 to 1.8×10^6 cells mL^{-1}. This may reflect real seasonal differences. However, sediments can interfere in the evaluation of cell concentration (Kepner and Pratt, 1993), and this difference could in part be due to differences in counting efficiency because there were lower sediment concentrations in September–October (35.2 mg L^{-1}) relative to July–August (53.6 mg L^{-1}). Bacterial concentrations measured in other arctic rivers are also higher than our values. For example, Meon and Amon (2004) measured bacterial concentrations of 1.2 to 2.5×10^6 cells mL^{-1} in the Ob and Yenisei Rivers and estuaries, and, in the Lena River and delta, heterotrophic picoplankton abundance ranged between 6.0×10^5 and 8.3×10^6 cells mL^{-1} (Saliot et al., 1996). In the Mackenzie River transition zone, Garneau et al. (2006) found heterotrophic prokaryote concentrations of 3.9 to 5.7×10^5 cells mL^{-1} and of 3.6×10^5 cells mL^{-1} in the coastal zone which are consistent with our measurements in these zones. Meon and Amon (2004) evaluated bacterial concentrations of 2.3 to 4.7×10^5 cells mL^{-1} in the Kara Sea, and Saliot et al. (1996) found in the Laptev Sea bacterial abundance varying from 2 to 20×10^5 cells mL^{-1}. Compared to our TZ data, Parsons et al. (1988; 1989) found lower concentrations of heterotrophic picoplankton concentration in summer 1986 (10^4 cells mL^{-1}), and higher concentrations in 1987 ($>10^6$ cells mL^{-1}) that were attributed to advection caused by on-shore winds.

Cyanobacteria are a major component of the microbiota in arctic lakes, ponds and rivers (Vincent and Hobbie, 2000). In our study, we considered picoplankton as both single and colonial cyanobacteria that had individual cells of diameter 2 μm and less. Picophytoplankton abundance dropped by two orders of magnitude between R7 and R9 and was strongly negatively correlated with salinity. In autumn 2002, sampling in the Mackenzie River showed that picocyanobacteria populations passing through 3-μm pore size filters (thus excluding colonial forms) were one order of magnitude more abundant in the Mackenzie River and estuary than in the Beaufort Sea (Garneau et al., 2006; Waleron et al., 2007). Picophytoplankton concentrations

in the surface waters of the Mackenzie River in the 2002 studies were much lower than in the present study, possibly due to seasonal effects and perhaps also to the exclusion of colonies larger than 3 μm. Rae and Vincent (1998) measured concentrations of photosynthetic picoplankton in the Great Whale River (August 1995) of 10^3 cells mL^{-1} with a dominance of picocyanobacteria and a very small representation of picoeukaryotes (<1% total picophytoplankton abundance). Sorokin and Sorokin (1996) observed the presence of picocyanobacteria in the freshwater part of the Lena River and their complete disappearance in the mixing zone of the river with the Laptev Sea. A study by Bertrand and Vincent (1994) across the St. Lawrence River estuary also showed higher picophytoplankton concentrations in the freshwater section of the estuary than in the more saline downstream waters.

Few studies have examined protist community structure in large arctic rivers. In the freshwater zone of the Great Whale River, in August 1995, the cell abundance of protists >2 μm was 977 cells mL^{-1}. The most abundant protist taxa were Chlorophyceae, Bacillariophyceae (diatoms) and Chrysophyceae (Rae and Vincent, 1998). We found protist cell abundance an order of magnitude higher in the Mackenzie River dominated by Bacillariophyceae, Cryptophyceae, heterotrophic organisms and Chrysophyceae. In the Lena River, the major phytoplanktonic groups observed by Sorokin and Sorokin (1996) were diatoms, nanoplanktonic phytoflagellates and coenobial cyanobacteria. This latter group may include the colonial picocyanobacteria observed in our study in the Mackenzie River.

Consistent with our analyses in the Beaufort Sea, Sakshaug (2004) concluded that the most common algal groups in the arctic and subarctic seas are Bacillariophyceae, Chrysophyceae, Dinophyceae, Prymnesiophyceae and green flagellates. HPLC analysis in the Chukchi and eastern Beaufort Seas showed that low productivity and biomass are observed at the surface and that Prasinophyceae, Haptophyceae (syn. Prymnesiophyceae) and Bacillariophyceae are identified as major contributors to the shelf community (Hill et al., 2005). A detailed seasonal record of the coastal Beaufort Sea has shown the persistence, and often dominance, of picoprasinophytes through most of the year (Lovejoy et al., 2007), consistent with our observation of picoeukaryotes offshore.

4.2. Bacterial production

Heterotrophic picoplankton metabolism did not increase towards the coastal zone nor did it vary significantly among zones. Consistent with our hypothesis, particle-attached bacteria were a major component of total bacterial metabolism accounting for 16 to almost 100% of total production. The importance of this fraction was a function of the degree of influence of the river water, as measured by temperature, salinity, POC and POC as a percentage of total SPM.

The marked difference in the bacterial production rates between riverine stations R1–R4 and R3–R4 is likely due to changes in the water mass characteristics between the sampling periods (almost 6 days). There was a large amount of precipitation in the watershed during the sampling cruise that induced a significant increase in the Mackenzie River discharge. Heavy rains bring large quantities of water that may cause an increase in DOC concentrations at the beginning of the flood, followed by a decrease due to dilution in the second part of the flood (Cauwet, 2002).

Bacterial production rates in the surface waters of the Mackenzie River were less than 50% of the rates measured by Meon and Amon (2004) in two large Siberian Rivers, the Lena and Yenisei, in September 2001. They also reported almost twofold higher production rates in the estuaries of these rivers. These large differences may reflect the low phosphorus availability in the Mackenzie River (Emmerton et al., 2008) and the higher phytoplankton biomass concentrations in the large Siberian rivers (see Retamal et al., 2008; and references therein). They might also be explained in part by our use of subsaturating concentrations of ^{3}H–Leu, although Meon and Amon (2004) found production rates in the surface Kara Sea similar to our estimates in the surface Beaufort Sea.

Attached bacteria (>3 μm) were a major component of total bacterial production in the Mackenzie River and its estuarine freshwater–saltwater TZ. Previous sampling in October 2002 in the TZ of the Mackenzie River and the Beaufort Sea showed that 68% of surface ^{3}H–Leu uptake was due to particle-bound bacteria (>3 μm; Garneau et al., 2006), a value very similar to those measured in the present study. Droppo et al. (1998) found that bacteria were an important constituent of Mackenzie River delta flocs. This is consistent with studies on turbid rivers and estuaries elsewhere. In the Columbia River and estuary, particle-attached bacterial carbon production (>3 μm) represented on average 90% of total bacterial production and was positively correlated with SPM and POC, while free-living bacterial production was not (Crump et al., 1998). Vincent et al. (1996) found that there was a large increase in the contribution of bacteria attached to particles >2 μm in the frontal zone of increasing salinity and turbidity in the St. Lawrence River estuary, passing from a non-significant contribution to 46% (range 40–

60%) of the total activity. In the Tamar estuary, the activity of the attached bacteria fraction followed the concentration of suspended particles and contributed a major proportion of total bacterial production in the maximum turbidity zone (Plummer et al., 1987). The relative proportion of aggregate-associated bacteria to total bacterial numbers appears to vary greatly, from 14 to 90% depending on the abundance of aggregates (Zimmermann-Timm, 2002). Our results show that the Mackenzie River falls at and above the high end of this range, reflecting its particle-rich conditions.

The contribution of particle-bound bacteria to total bacterial production was significantly higher in the bottom waters of the coastal zone than in the surface waters. This difference may be due to the higher concentration of particles in the bottom waters of the Beaufort Sea, although this difference was not statistically significant. SPM, POC and DOC were higher at the bottom, with only DOC showing a significant difference. A study on fine particles (<2 to 10 μm) in the Lena River–Laptev Sea system showed that bottom samples of coastal waters yielded higher particle concentrations than surface samples due to particle resuspension and the presence of a marked halocline, which prevented entrainment of particles into the surface waters (Moreira-Turcq and Martin, 1998).

4.3. Carbon limitation of bacterial production

In the Mackenzie River, glucose addition increased total bacterial production, suggesting that bacterial metabolism was limited by the lability of available organic carbon despite the high ambient DOC concentrations. The strong response of the riverine bacteria was specifically due to the dominant, particle-associated fraction, and this may reflect the substantial age (>6000 years; Guo et al., 2007) and refractory nature of the POC particles entering the river from terrigenous sources. The stimulation of total bacterial production by the addition of glucose diminished towards the coastal zone, with no significant stimulation at the station R9, suggesting other factors limited bacterial production. Dissolved inorganic nitrogen is in particularly low concentration over the Mackenzie Shelf relative to the Siberian shelves (see Table 3 in Emmerton et al., 2008), and nitrogen availability could be a greater constraint on bacterial production than organic carbon supply. Addition of glucose as a carbon source in the Ob and Yenisei rivers, their estuaries, and in the Kara Sea significantly increased bacterial production relative to control treatments indicating a carbon limitation of bacterial growth in the rivers and throughout the Kara Sea (Meon and Amon, 2004). Similarly, bacterial respiration and production in the Amazon River were carbon limited, indicating that the bulk of the relatively abundant particulate and dissolved organic matter was of limited bioavailability (Benner et al., 1995; Amon and Benner, 1996). In Raunefjorden on the western coast of Norway, bacterial production was carbon limited and this response was consistent with low phytoplankton growth, low light conditions and high nutrient availability occurring in November at this latitude (Flaten et al., 2003).

4.4. Effect of photochemical conditioning of DOC on bacterial production

The pre-exposure of DOC to sunlight induced contrasting responses of bacterial production in the Mackenzie River and in the Beaufort Sea. In the Mackenzie River, sunlight-exposed DOC stimulated bacterial production. However, Beaufort Sea DOC decreased bacterial metabolism after being exposed to sunlight. Photochemical reactions are of special interest in the context of climate warming, because UV-dependent processes are likely to accelerate as a result

Table 3
Comparisons between bacterial metabolism (net bacterial production plus bacterial respiration, BR) and net primary production (PP; from Retamal et al., 2008)

Station	Integration depths (m)	BGE used (%)	Bacterial production (mg C m^{-2} d^{-1})	Bacterial respiration (mg C m^{-2} d^{-1})	Primary production (mg C m^{-2} d^{-1})	BR vs PP
R1	0–3	25	27.0±1.3	81.0±3.9	12.0	BR ≫ PP
R2	0–21	25	70.9±5.4	212.7±16.2	143.1	BR ≫ PP
R3	0–30	25	110.5±7.8	331.5±23.4	59.0	BR ≫ PP
R4	0–19	25	152.0±2.9	456.0±8.7	20.6	BR ≫ PP
R5d	0–4	27	16.0±1.5	43.1±3.9	36.3	BR ≅ PP
R8	0–16	27	44.2±4.5	119.5±12.2	466.8	BR ≪ PP
R9	0–32	27	68.0±5.9	183.7±16.0	144.7	BR ≅ PP

Metabolic rates are presented as daily, depth-integrated rates. Bacterial growth efficiencies were from Meon and Amon (2004).

of shrinking sea ice and decreasing ice thickness. Under an ice-free scenario in southeastern Beaufort Sea, the photodegradation of DOC to DIC could pass from the present value of 2.8 to 6.2% of the DOC input from the Mackenzie (Bélanger et al., 2006).

In the York River estuary, photobleaching increased bacterial DOC decomposition by 27 to 200% (McCallister et al., 2005). Exposure of surface water DOC to sunlight in the Gulf of Mexico resulted in a 75% reduction in bacterial production (Benner and Biddanda, 1998). These contrasting effects of solar UV radiation on dissolved organic sources for bacterial growth have been ascribed to qualitatively different photoreactions of autochthonous DOC versus older humic material. Recently produced algal DOC may be transformed into compounds of lower microbial substrate quality by condensation reactions, while old humic material is converted into lower molecular weight, biologically labile products (Tranvik and Bertilsson, 2001), including nitrogenous nutrients (Bushaw-Newton and Moran, 1999). Consistent with our results for the Mackenzie River, DOM in the Yenisei and Ob Rivers is also known to be photoreactive, as demonstrated by photooxidation assays (Amon and Meon, 2004). In all of these arctic systems, the strong attenuation of UV irradiance by CDOM (Retamal et al., 2008) will restrict these effects to the very surface waters.

4.5. Metabolic balance

To address the overall question of whether northern waters are a source or a sink of greenhouse gases requires an assessment of net ecosystem production (NEP), the balance between gross primary production (GPP) and total respiration (R) of the ecosystem. Net heterotrophic aquatic communities (R>GPP) are net producers of CO_2 to the atmosphere whereas net autotrophic communities (GPP>R) act as net CO_2 sinks (Duarte and Prairie, 2005). During the ARDEX cruise, Retamal et al. (2008) measured net algal primary production (NPP) in parallel with our bacterial production (BP) measurements. Thus, we can combine our data to estimate the metabolic balance of the system.

In the Mackenzie River, depth-integrated BR was 1.5 (R2) to 22 (R4) times higher than depth-integrated NPP which implies that the river is a strongly net heterotrophic ecosystem (Table 3). Given that our measurements likely underestimated BP, the net respiratory production of CO_2 by the river ecosystem may be even higher. In contrast, the transition zone and coastal Beaufort Sea stations had estimated respiration rates that were near or below the NPP values, indicating near-equilibrium or slight undersaturation conditions (Table 3). These estimates of bacterial respiration depend on conversion factors from other environments, and these can vary greatly. For the range of literature BGE values reviewed in del Giorgio and Cole (1998), the river bacterial respiration rates could vary (on average) from 106 to 2913 mg C m^{-2} d^{-1}, which greatly exceeds the average measured photosynthetic rate of 59 mg C m^{-2} d^{-1}.

An additional, independent measure of metabolic balance is provided by our measurements of CO_2 concentrations in the surface waters and the overlying atmosphere. Unbalanced aquatic metabolic processes will generate gaseous disequilibria with respect to the atmosphere, which can therefore indicate the prevalence of auto- or heterotrophy (Duarte and Prairie, 2005). Our P_{CO2} results are consistent with the biological data (Table 3), with supersaturation in the river and subsaturation or near-saturation in the sea. The high atmospheric values of P_{CO2} in Mackenzie River region also indicate that its floodplain delta was a net source of CO_2 to the atmosphere at the time of sampling. These results are limited to one time of year, but they are consistent with measurements from other freshwater ecosystems showing that the vast majority of streams, lake and rivers are net heterotrophic ecosystems that emit CO_2 to the atmosphere (Duarte and Prairie, 2005). For example, Raymond et al. (1997) showed that in the Hudson River throughout the year, water P_{CO2} was always supersaturated (mean 1147 μatm) relative to the atmospheric mean of 416 μatm. Similarly, in arctic Alaska, measurements of P_{CO2} in 29 aquatic ecosystems showed that in most cases (27 of 29) CO_2 was released to the atmosphere (Kling et al., 1991).

5. Implications of climate change

The circumpolar Arctic has begun to experience warming temperatures and this trend is likely to accelerate in the future. Global circulation models for this region predict ongoing decreases in sea ice and terrestrial snow extent during the 21st century, increased precipitation minus evaporation, and increased river discharge to the Arctic Ocean (ACIA, 2005). Also, permafrost temperatures have increased markedly since the mid-20th and this trend also appears to be accelerating (Nelson, 2003). Given that more than half of global soil organic carbon is stored in the Arctic Ocean basin (Dixon et al., 1994), large quantities of organic carbon may be released in the future by this melting. A warming arctic climate could lead to increased release of old, sequestered peat carbon through permafrost degradation (Frey and Smith, 2005), as well as new inputs of

dissolved organic carbon associated with vegetation shifts (Guo et al., 2007). Climate model simulations predict a major northward advance of the −2 °C annual isotherm by 2100 that would nearly double the west Siberian land surface with air temperatures exceeding this threshold (Frey and Smith, 2005). The sediment load of arctic rivers is predicted to increase by 22% for every 2 °C warming of the averaged drainage basin temperature and by 32% if this warming is combined with a 20% increase in runoff (Syvitski, 2002). Some studies have shown that old organic matter can support a significant fraction of bacterial metabolism. For example, bacterial production in the Hudson River is partly (up to 25%) supported by old (24 ka BP), soil-derived allochthonous organic matter (McCallister et al., 2004). Similarly in northeastern Siberia, CO_2 with radiocarbon ages ranging from 21 to 24 ka BP was respired when permafrost soils from tundra and boreal forest locations that have been continuously frozen since Pleistocene were thawed (Dutta et al., 2006).

Our study has shown that the Mackenzie River, its estuary and adjacent coastal Beaufort Sea support a well-developed microbial food web with a high percentage of heterotrophic organisms. Heterotrophic prokaryote activity was high across the system with most of the river bacteria associated with particles. Our evaluations of the metabolic state of the system reveal that net heterotrophy occurs in the Mackenzie River, implying that heterotrophic processes are fueled by allochthonous organic carbon from the watershed in addition to autochthonous organic carbon. Bacterial community metabolism was limited by the availability of carbon in the Mackenzie River, indicating that bacterial production will be stimulated by new organic carbon input, with the amplitude of this response dependent on the lability of the new carbon inputs. Considering the large amount of organic carbon stored in the Arctic Ocean catchment area and the predicted warming of the Arctic, future climate change is likely to increase the net heterotrophy of this large river ecosystem, with a positive feedback effect on greenhouse gas production and warming.

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