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Nutrient dynamics in the western Canadian Arctic. II. Estimates of new and regenerated production over the Mackenzie Shelf and Cape Bathurst Polynya

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ABSTRACT: Uptake of ^{15}N-labelled nitrate, ammonium, and urea was measured over a quasi-annual cycle in the Cape Bathurst Polynya in the Amundsen Gulf and on the Mackenzie Shelf, during the Canadian Arctic Shelf Exchange Study (CASES) in 2003 and 2004. Before the phytoplankton bloom and in autumn, nitrogen uptake was slow, representing less than 5% of annual consumption. Uptake rates increased exponentially after ice retreat and within 3 wk reached a maximum of 38.6 mmol N m^{-2} d^{-1}. During spring, NO_3^- uptake supported new production of 166 mmol N m^{-2} and *f*-ratios rose from 0.1–0.2 to 0.6–0.9. Filter fractionation showed that GF/F filters retained 93.1 ± 1.3% of the ^{15}N incorporated into particulate matter, suggesting that phytoplankton were responsible for the majority of the N uptake. Although free-living bacteria took up relatively more ^{15}N in autumn and in the lower part of the euphotic zone than phytoplankton, their assimilation of inorganic N had little effect on water column integrated *f*-ratios or new production. Urea supplied almost half the N assimilated by phytoplankton annually and about 80% of the regenerated production during the spring bloom. Total new production, estimated from water column integrated ^{15}N-nitrogen uptake rates and linear models that interpolated rates over unsampled periods, was 342–415 mmol N m^{-2} yr^{-1}. Total annual N production for the region was 1.24–1.48 mol N m^{-2} yr^{-1}.

KEY WORDS: Nitrogen uptake ^{15}N isotopes · ^{15}N uptake · Phytoplankton · Bacteria · Amundsen Gulf · Arctic Ocean · New production · Primary production · Polynya

INTRODUCTION

Seasonal variation in photosynthetically active radiation (PAR) exerts principal control over the amount and rate of primary production in the Arctic Ocean. Ice cover and snow pack further reduces light input to these waters and in conjunction with a low angle of the sun during spring greatly limits the optimal period for phytoplankton growth. Recent studies show that in spite of reduced light, some regions of the Arctic are among the most productive in the sea (Smith et al. 1997, Gosselin et al. 1997, Olsson et al. 1999, Luchetta et al. 2000, Klein et al. 2002). These areas are generally characterized by early ice retreat, as in polynyas, where phytoplankton are exposed to an increased supply of PAR as the sun rises above the horizon after polar night (Tremblay et al. 2006).

Nutrient availability also regulates the amount of phytoplankton production during the growing season. Low concentrations of nitrate (NO_3^-) in Arctic surface waters (Simpson et al. 2008) are maintained by biological consumption, particulate N (PON)

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export and by a strong halocline that resists wind-mixing and convection. Recharging the surface waters with nutrients in autumn can be impeded by early ice cover that prevents mixing. As a consequence, nutrient concentrations at the sea surface in spring may be only a small fraction of their concentration at depth. All available evidence points to nitrogen (N) as the primary limiting nutrient for phytoplankton growth in the Arctic, thus the size of the NO_3^- inventory established in autumn prior to ice formation affects the biomass and extent of new production. River runoff and precipitation contribute some N to these waters, but the impact of these inputs is localized (Simpson et al. 2008). Regenerated nutrients (i.e. ammonium [NH_4^+] and urea) are consequently the most important sources for phytoplankton growth in the Arctic Ocean.

The importance of regenerated N in the Arctic is illustrated by low *f*-ratios that characterize the Canadian Basin and are observed in summer under ice (f = 0.1–0.25; Cota et al. 1996, Lee & Whitledge 2005). High rates of NO_3^- consumption primarily coincide with phytoplankton production during the spring and autumn blooms. Tremblay et al. (2006), for example, noted that *f*-ratios in the highly productive North Water (NOW) Polynya increased rapidly during spring and reached a maximum of 0.96. Similar results were obtained for the Northeast Water (NEW) Polynya (*f*-ratio ~0.69; Smith et al. 1997).

Urea, one of the 2 major regenerated forms of N, is unusually abundant in the Arctic (Conover & Gustavson 1999, Simpson et al. 2008) and an important N source for phytoplankton growth. In Baffin Bay, Harrison et al. (1985) calculated it provided as much as 30% of the phytoplankton N requirements, while in the NEW Polynya it supplied as much N as NH_4^+ (Smith et al. 1997). Kinetic experiments showed similar half-saturation constants for urea and NH_4^+ uptake, but faster maximum rates for urea uptake in the eastern Canadian Arctic (Smith & Harrison 1991).

Utilization of inorganic nutrients is generally attributed to phytoplankton uptake with bacteria playing only a minor role. Indeed, estimating new and regenerated production by measuring N uptake (Dugdale & Goering 1967) depends critically on this assumption. But a number of ocean experiments have identified bacteria as consumers of NO_3^-, NH_4^+ and urea (Kirchman 2000). Wheeler & Kirchman (1986) first recognized the importance of bacteria to NH_4^+ uptake, and since then others have confirmed these results and established that NO_3^- uptake by bacteria may be significant (up to 50% of total uptake; Kristiansen et al. 1994, Kirchman 2000). The proportion of total N assimilated by bacteria in Arctic waters has recently been reported to vary widely depending on environmental conditions (Allen et al. 2002, Fouilland et al. 2007). Allen et al. (2002) showed that bacteria assimilated both NH_4^+ and NO_3^- in the Barents Sea, but that the amount depended on depth and proximity to the marginal ice zone. The relative amount of total N used by bacteria was greater at depth and under ice cover where phytoplankton uptake was likely light-limited. Fouilland et al. (2007) also found that bacteria could account for a large proportion (> 50%) of total NO_3^- uptake and suggested that this could greatly affect the *f*-ratio and measurement of phytoplankton new production.

Simpson et al. (2013, this volume) measured NO_3^- draw-down to estimate new production during spring in the Cape Bathurst Polynya. Here, we report the results of short-term N uptake rate experiments conducted in the same region using stable isotope tracers. Size fractionation was used to evaluate the amount of dissolved inorganic N and urea assimilated by phytoplankton and bacteria to estimate new, regenerated and total production over a quasi-annual cycle.

MATERIALS AND METHODS

Sampling was conducted onboard the icebreaker, CCGS 'Amundsen' during the Canadian Arctic Shelf Exchange Study (CASES) in the Mackenzie Shelf and Amundsen Gulf in the southeastern Beaufort Sea (Fig. 1). Rates of N uptake were measured at 28 stations between 30 Sep 2003 (day of year [DOY] 273) and 25 Jul 2004 (DOY 207), using standard ^{15}N enrichment techniques (Collos 1987). Location of the sampling stations and time of occupancy are shown in Fig. 1. The stations were in ice-free zones in the polynya or near the ice edge, except in spring (17 May–28 May 2004; DOY 137–148) where 3 vertical profiles were obtained under ice at the overwintering station in Franklin Bay (Simpson et al. 2013). Additional information about sampling logistics and the study area is reported in Simpson et al. (2013).

Biological-physical-chemical measurements

Vertical profiles of temperature, salinity, and chlorophyll *a* (chl *a*) fluorescence were obtained using a Sea-Bird 911 CTD equipped with a Seapoint fluorometer. Sampling depths corresponded to 100, 50, 10 and 1% of sea surface irradiance

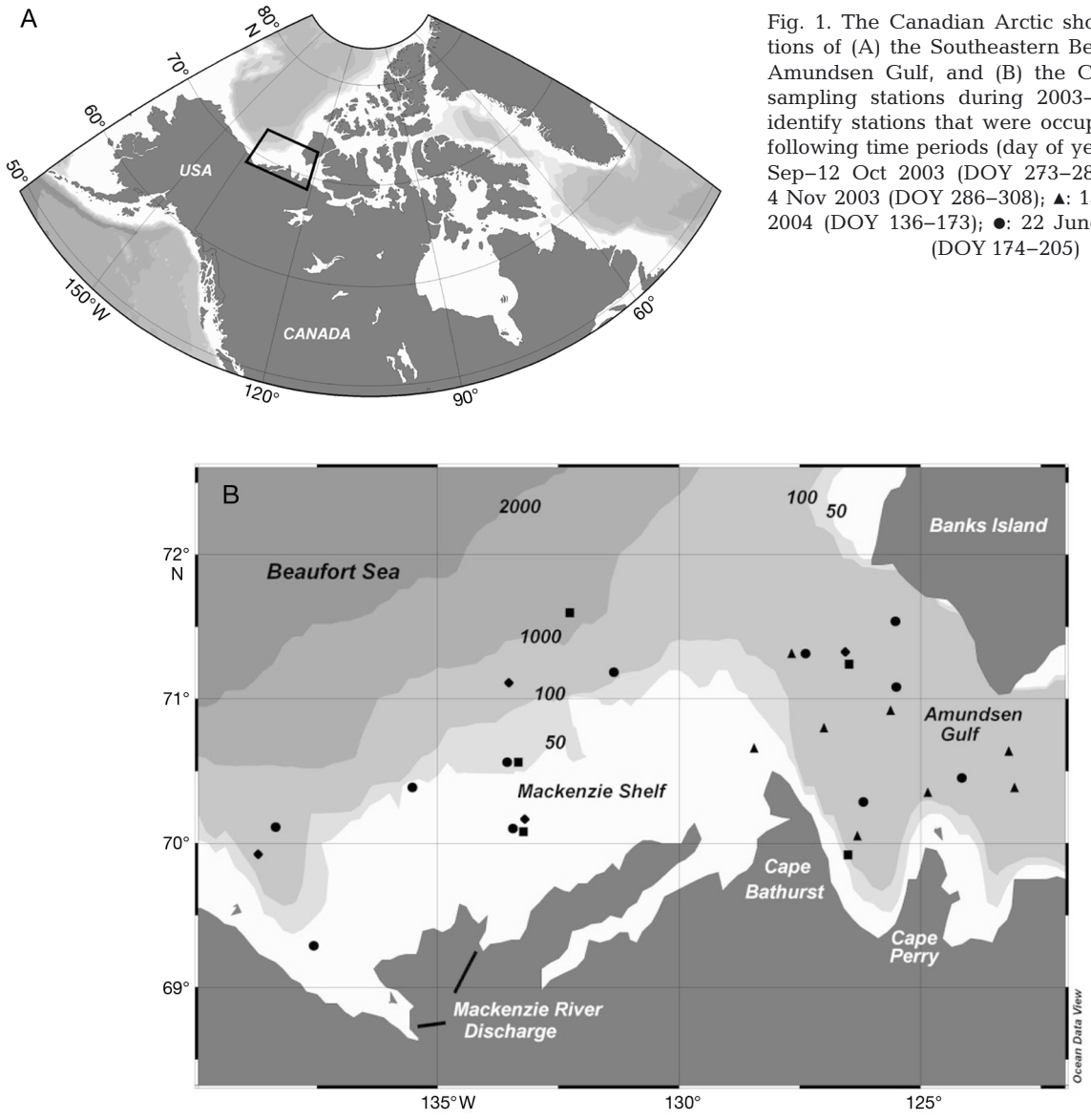

Fig. 1. The Canadian Arctic showing the locations of (A) the Southeastern Beaufort Sea and Amundsen Gulf, and (B) the CASES site and sampling stations during 2003–2004. Symbols identify stations that were occupied during the following time periods (day of year, DOY). ◆: 30 Sep–12 Oct 2003 (DOY 273–285); ■: 13 Oct–4 Nov 2003 (DOY 286–308); ▲: 15 May–21 June 2004 (DOY 136–173); ●: 22 June–23 July 2004 (DOY 174–205)

and were determined by Secchi disc and/or a PUV Profiling Ultraviolett Radiometer (Biospherical Instruments). Beginning at sunrise or when the sun started climbing from its lowest angle, water was collected with 12 l Niskin bottles attached to a rosette sampler (Seabird Carousel rosette). These samples were then used for ^{15}N uptake experiments and analyzed for chl *a* (Parsons et al. 1984), NO_3^- plus NO_2^-, NH_4^+, and urea concentrations (Simpson et al. 2008).

Nitrogen uptake and standing stock

Water from each Niskin bottle was passed through a 300 µm Nitex mesh filter to remove large zooplankton and then dispensed into duplicate 500 or 1000 ml polycarbonate bottles. Each sample was enriched with potassium nitrate [$K^{15}NO_3$ 98%+], ammonium chloride [$^{15}NH_4Cl$ 98%+] or urea [$(^{15}NH_2)_2CO$ 98%+] (Cambridge Isotope Labs) at a concentration of ~10% of ambient. In some cases a 10% enrichment of the substrate was not possible and 0.05 µmol N l^{-1} was added. Because urea concentrations were not measured immediately, all urea uptake samples were enriched with 0.1 µmol urea-N l^{-1}. This enrichment was about 11% of the sea surface concentration (Simpson et al. 2008), but in 25% of the samples it increased the substrate concentration by about 20–50%. Addition of 0.05 µmol ^{15}N-NH_4^+ l^{-1} also increased the ambient NH_4^+ concentration by a similar percentage in 1/3 of our incubation bottles. The ^{15}N-NO_3^- additions were typically 10% of the ambient concentra-

tion except during the post-bloom period where the ambient NO_3^- concentrations were lowest. Samples were incubated for 24 h on deck in Plexiglas tubes and maintained at *in situ* temperatures with water pumped from the upper mixed layer. The irradiance in the incubators was adjusted with neutral density filters to simulate *in situ* levels.

^{15}N uptake experiments were terminated by filtering the samples under low-vacuum pressure (<100 mm Hg) onto combusted (500°C, 24 h) 25 mm Whatman GF/F filters (0.7 µm median particle retention size reported by manufacturer). All filtrations were performed under reduced light. The filters were rinsed with 0.2 µm filtered sea water, dried at 50°C for 48 h, and stored in cryovials until analysis. Adsorption of the ^{15}N isotope to the filters was assessed by filtering samples immediately after adding the ^{15}N enrichment, and was insignificant. The ^{15}N content of the particulate matter and mass of particulate N on the filters were determined with a Europa Scientific Integra isotope ratio mass spectrometer (UC Davis Stable Isotope Facility). Particulate N concentrations are reported in Simpson et al. (2013). Absolute N uptake rates (ρ; µmol N l^{-1} h^{-1}) were calculated according to Eq. 6 of Collos (1987). Isotope exhaustion was evaluated by comparing the amount of ^{15}N collected on the filters to the amount of ^{15}N added in the incubation.

At 12 stations, the GF/F filtrate from the ^{15}N uptake experiments was collected in a side-arm flask and then re-filtered through a 0.2 µm pore size silver (Ag) filter (Sterlitech membrane filters # 45336). The side-arm flask was carefully rinsed before use with particle-free (0.2 µm filtered) seawater. The Ag filters were processed as described above and the amounts of PON and ^{15}N in the small particles (ca. <0.7 µm) were determined. Bacteria and Archaea (hereafter referred to as bacteria) were enumerated in the GF/F filtrate and in unfiltered seawater samples by epifluorescence microscopy according to Turley (1993). A minimum of 400 cells was counted for each sample. ^{15}N collected on the Ag filters was assumed to represent uptake by bacteria and the accumulation of ^{15}N-labelled fragments of phytoplankton that were not retained by the GF/F filters (see 'Discussion').

Isotope dilution was not measured explicitly, but post hoc calculations were used to evaluate its potential impact on the uptake rates (Kanda et al. 1987). The results showed that during the bloom and post-bloom phases, NH_4^+ uptake rates may have been underestimated by as much as 40 ± 33% and 27 ± 25%, respectively. We have not corrected the uptake rates to account for this effect, but acknowledge its potential significance.

Statistics and calculations

Statistical analyses were performed using Systat v11.00.01 and curve fits were made using SigmaPlot v10. Euphotic zone N uptake (mmol N m^{-2}) was calculated by common trapezoidal integration to the 1% isolume. Seasonal estimates of primary N production were calculated by summing the daily rates of N uptake (see below) during each growth phase. Four growth phases were operationally-defined based on nutrient and chlorophyll concentrations (Simpson et al. 2008). These phases, delineated by day of year (DOY) were identified as pre-bloom (DOY 136–156; 16 May–4 Jun 2004), bloom (DOY 157–182; 5–30 Jun 2004), post-bloom (DOY 183–205; 1–23 Jul 2004), and autumnal (DOY 273–308; 30 Sep–4 Nov 2003). The post-bloom and autumnal phases defined here were 15 and 18 d shorter than reported by Simpson et al. (2008) because ^{15}N uptake experiments ended earlier during these cruises. Seasonal and depth dependent differences in nutrient utilization were assessed using ANOVA and Tukey post hoc comparison at $p \leq 0.05$. Mean values of quantities, rates and percentages are reported ±1 SD.

RESULTS

Pelagic nitrogen consumption

Vertical profiles of dissolved N species showed a gradual increase in upper water column NO_3^- inventory in late autumn and high but variable concentrations of NH_4^+ and urea (Fig. 2). Rates of N uptake measured at this time differed significantly (Fig. 3) depending on N substrate ($p < 0.0001$), sampling station ($p < 0.001$) and quantity of phytoplankton biomass as chl *a* concentration ($p < 0.0001$). The mean rates for NH_4^+ were 38.5 ± 44.6 nmol N l^{-1} d^{-1} (n = 35), roughly 5–10 times faster than for NO_3^- (4.24 ± 3.97 nmol N l^{-1} d^{-1}, n = 37) and urea (8.61 ± 7.97 nmol N l^{-1} d^{-1}, n = 27) ($F = 19.4$, Tukey post hoc test $p < 0.05$). Towards the end of the autumn cruise, day length declined from 11.2 to 6 h with the approach of polar night and significantly affected sea-surface uptake of NO_3^- and NH_4^+ ($p < 0.05$), but not urea ($p = 0.14$) (Fig. 4).

Successive sampling in spring revealed a rapid increase in N transport during a span of 2 wk following ice retreat and the onset of the phytoplankton bloom (Fig. 5). Initially, uptake of NO_3^-, NH_4^+ and urea was slow and fairly uniform with depth. The rates then increased by as much as 40- to 250-fold by the middle of June to about 1 µmol N l^{-1} d^{-1} for

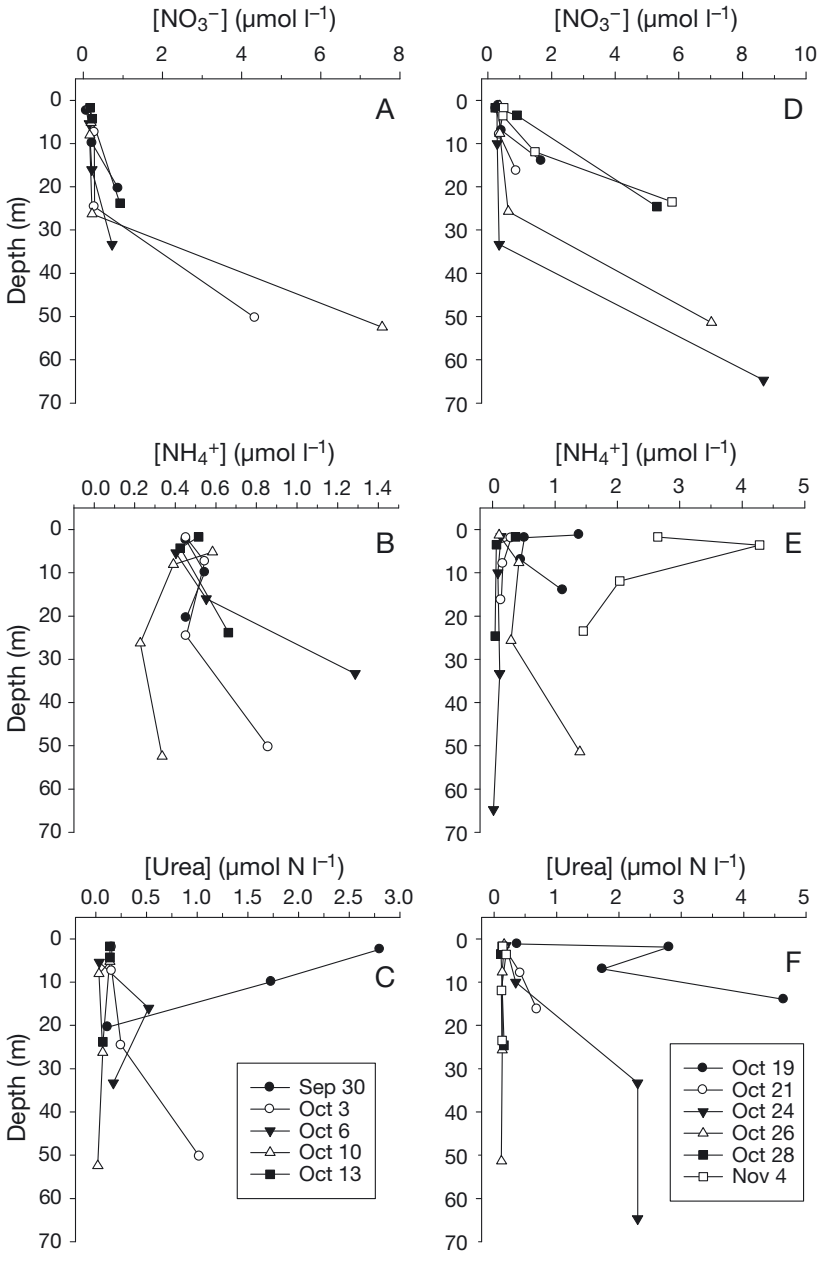

Fig. 2. Vertical profiles of dissolved (A,D) nitrate, (B,E) ammonium and (C,F) urea concentrations in autumn 2003. Data are grouped chronologically: (A,B,C) 30 Sep to 13 Oct (day of year [DOY] 273–286); (D,E,F) 19 Oct to 4 Nov (DOY 292–308)

urea and NO_3^-, respectively. Mass balance calculations showed that N concentration was not exhausted in the incubation bottles during these experiments except in 2 surface samples obtained on 19 June when phytoplankton biomass was at its highest. For those samples, we calculated that 95% of the added $^{15}NO_3^-$ was consumed so that the uptake rates were likely underestimates. Average NH_4^+ uptake rates were significantly faster in spring than in autumn ($p = 0.027$) although the mean seasonal difference was much less than observed for NO_3^- and urea (cf. Figs. 3 & 5). Nutrient draw-down data showed that surface NO_3^- had been greatly reduced (~0.3 µmol l^{-1}) by 19 June (DOY 171), near the end of the spring bloom (Simpson et al. 2013).

Bacteria and phytoplankton N uptake

To assess the role of bacteria in ^{15}N uptake we used post incubation filter fractionation with GF/F and Ag filters. The Ag filters collected particles approxi-

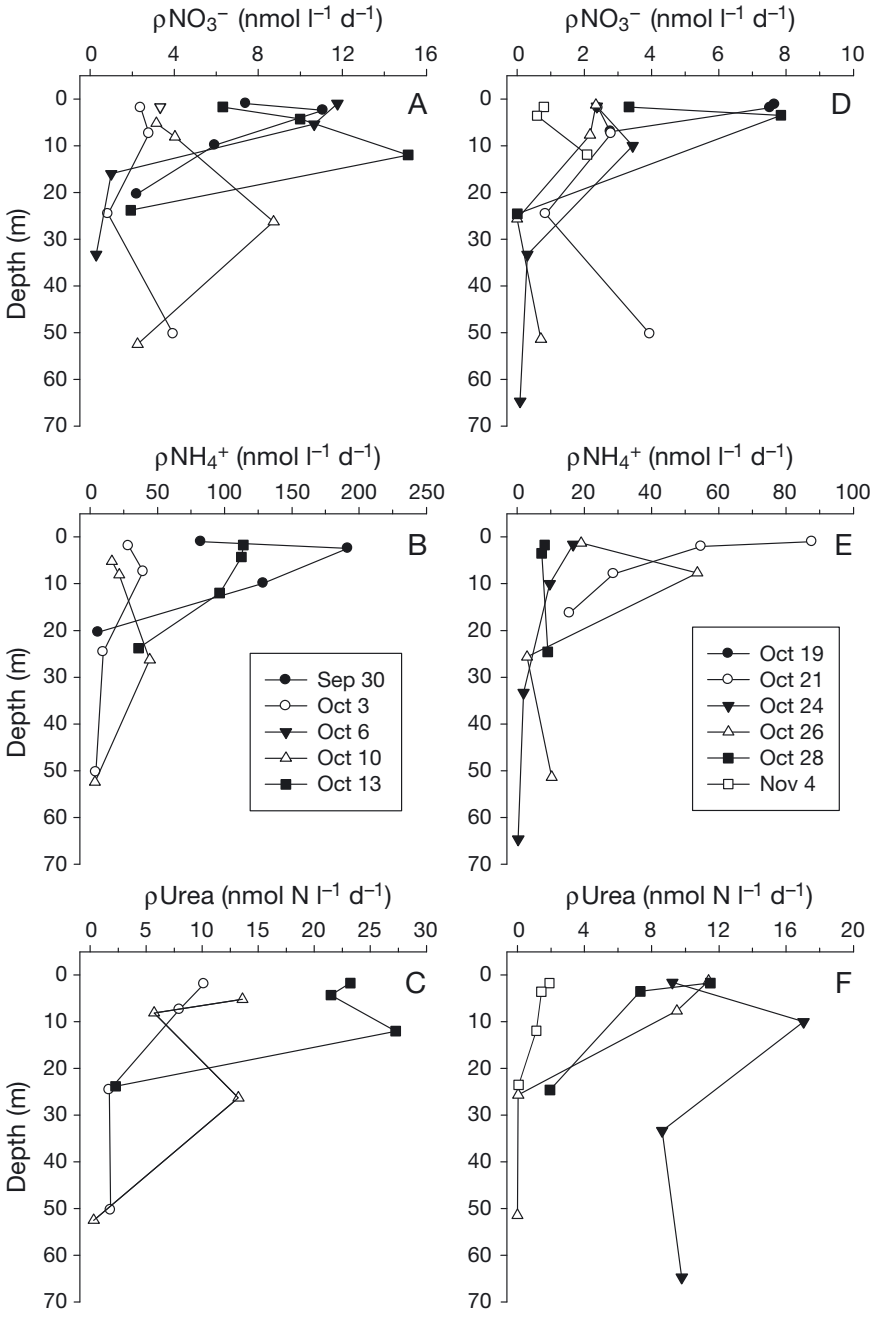

Fig. 3. Vertical profiles of (A,D) nitrate, (B,E) ammonium, and (C,F) urea uptake (ρ) rates in autumn 2003

mately 0.2–0.7 µm in size that included bacteria that passed through the GF/F filters. The GF/F filters had a median retention size of 0.7 µm (as reported by the manufacturer) and so captured phytoplankton and larger bacteria. Prior to analysis, a logarithm transformation was used to normalize the data and reduce heteroscedasticity. Linear regression analysis revealed a highly significant relationship ($p < 0.001$, $F = 203.7$) between log N uptake of particles collected on Ag and GF/F filters, considering all stations, depths and N substrates (Fig. 6a). The equation of the model II regression was: log Ag filter N uptake rate = 0.763 × log GF/F filter N uptake rate – 0.8499; $r^2 = 0.7205$, n = 81, where uptake rates were expressed as nmol N l^{-1} d^{-1}. On average, GF/F filters captured 93.1 ± 0.14 % of the total particulate ^{15}N. Because the slope of the linear regression (0.763 ± 0.046) was significantly less than 1 (*t*-test, $p < 0.001$), the relative amount of ^{15}N retained by the Ag filters increased as the amount on GF/F filters decreased and vice versa.

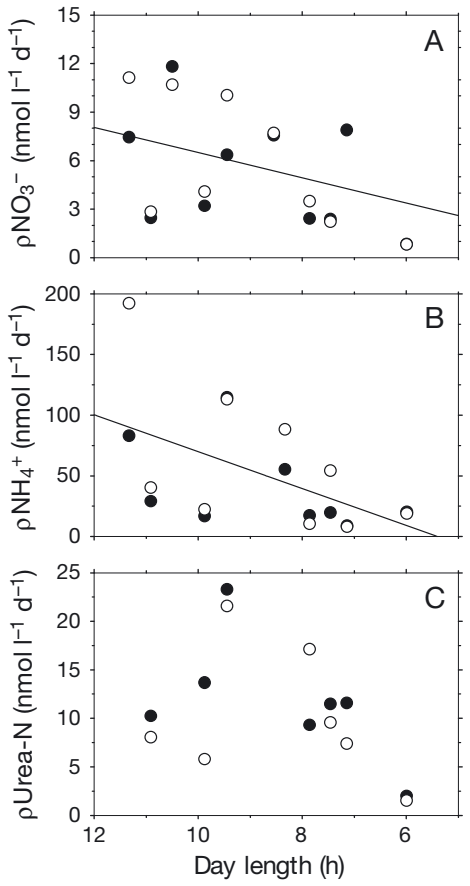

Fig. 4. Nitrogen uptake rates (ρ) as a function of day length during autumn 2003: (A) nitrate, (B) ammonium, and (C) urea. Data are from samples collected from the sea surface (○) and 50% isolume (●). The lines in each panel are linear regressions fitted using a least squares procedure. Nitrate and ammonium uptake rates declined significantly ($p < 0.05$) with day length ($r^2 = 0.2837$ and $r^2 = 0.2874$, respectively), but urea uptake rates did not ($p = 0.141$)

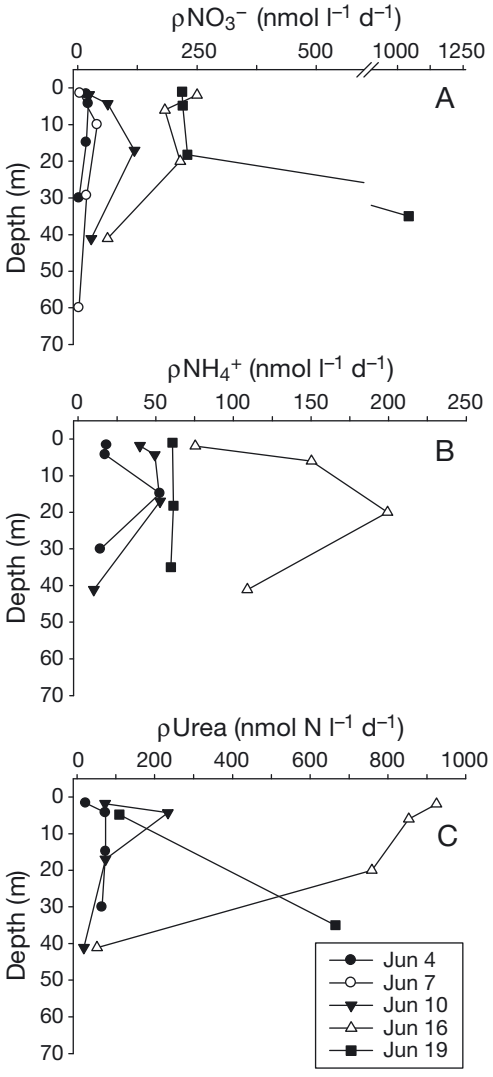

Fig. 5. Vertical profiles of (A) nitrate, (B) ammonium, and (C) urea uptake rates (ρ) measured after ice retreat in the Cape Bathurst polynya, Amundsen Gulf, between 4 and 19 June 2004 (DOY 156–171). The phytoplankton bloom started in late May and ended in mid June 2004 (Simpson et al. 2013). Nitrate uptake rates in the 2 near-surface samples on 19 June are likely underestimates because of near substrate exhaustion during the incubation. Note the axis break in the nitrate plot

Direct counts showed 45.6 ± 16.5% (n = 67) of the unicellular bacteria passed through the GF/F filters at the CASES study site. We assumed (see 'Discussion') that these bacteria (which were retained by the Ag filters) took up ^{15}N, and then calculated the cell specific uptake rate. Total bacteria uptake of N was computed by multiplying the bacteria cellular rate measured on the Ag filters by total bacteria density. ^{15}N retained by the GF/F filters was corrected for bacteria uptake by subtraction so the phytoplankton contribution to N uptake could be determined (Fig. 6b). Overall, bacteria were responsible for 14.1 ± 21.4% (CI of the mean = 5.3%, n = 66) of the total N uptake. The model II regression equation describing the relationship between bacteria and phytoplankton N uptake was highly significant: log bacteria N uptake rate = 0.813 ± 0.055 × (log phytoplankton N uptake rate) − 0.5510 ± 0.025; $F = 174.8$, $p < 0.0001$, $r^2 = 0.735$, with a slope significantly less than 1 (*t*-test, $p < 0.001$). Thus, bacteria assimilated relatively more N when phytoplankton uptake was slow and relatively less N when phytoplankton N uptake was fast. In a few cases, bacteria took up as much as 50% of the N at the sea surface and at depth, but averaged over all the stations only contributed substantially to N assimilation at the 1% isolume where they took up 22 ± 16% of the NO_3^- (n = 7) and 18 ± 17% of the NH_4^+ (n = 10). The absolute rates of

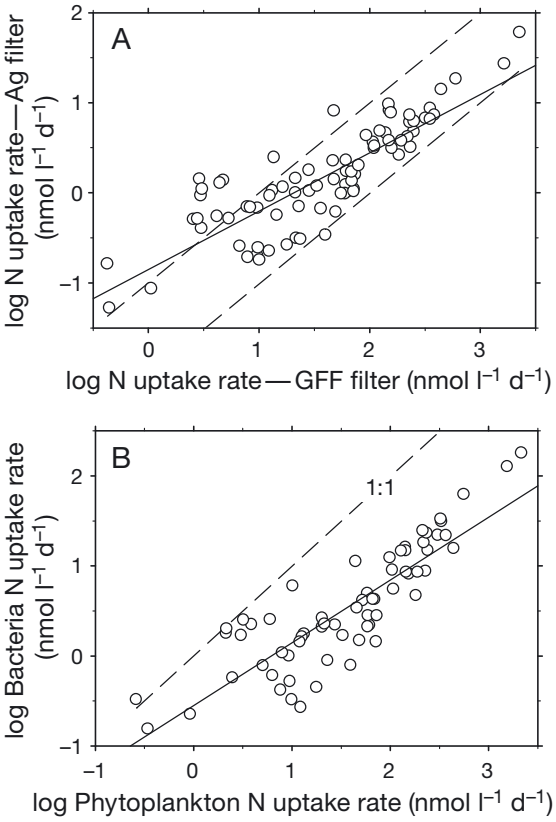

Fig. 6. Log-transformed nitrogen uptake rates. The solid line through the data is the least-squares linear regression. (A) Daily nitrogen uptake rates of particulate matter retained by silver (Ag) (<0.7 and >0.2 µm in size) compared to GF/F filters (>0.7 µm in size). The dashed lines represent 10% and 1% of the GF/F N uptake rate. (B) Bacteria nitrogen uptake rate plotted as a function of phytoplankton nitrogen uptake rate. Nitrogen uptake rates of free-living bacteria and phytoplankton were calculated as outlined in 'Materials and methods'. The dashed line represents the 1:1 relationship

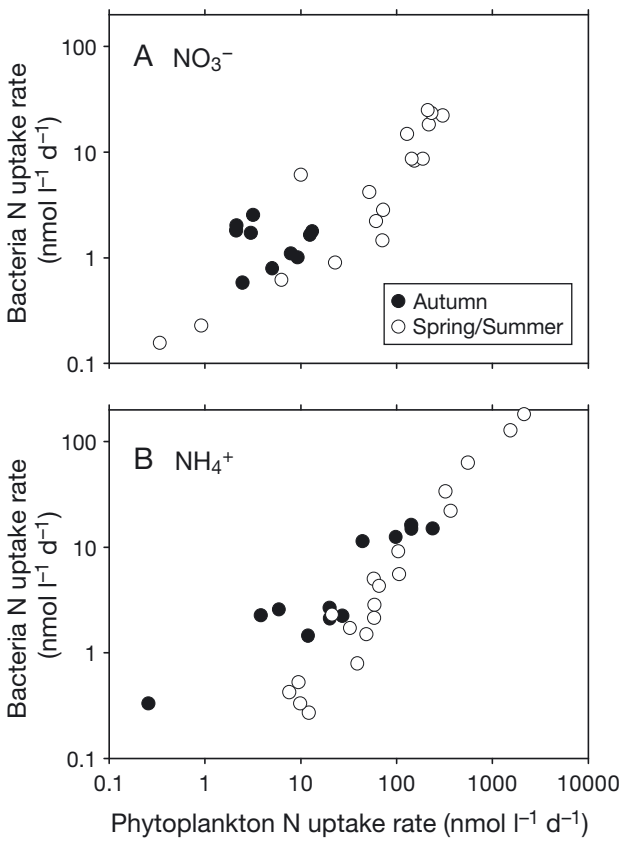

Fig. 7. Bacteria nitrogen uptake rate (nmol l^{-1} d^{-1}) as a function of phytoplankton nitrogen uptake rate (nmol l^{-1} d^{-1}) during autumn and spring/summer: (A) nitrate uptake, (B) ammonium uptake

N uptake at the 1% isolume were a small fraction of the rates in the upper water column, so at the community level, phytoplankton were responsible for virtually all of the N uptake. Too few data were available to confidently estimate bacteria contribution to urea uptake at each isolume, but they were responsible for 5.2 ± 2.6% of the total urea uptake at the 3 stations we sampled.

The relationship between bacteria and phytoplankton N uptake was examined as a function of N substrate and season (Fig. 7). Logarithm-transformed data were analyzed using the general linear model of Systat 11.0. The analysis showed that log phytoplankton uptake rate was a significant predictor of log bacteria N uptake rate for both NO_3^- and NH_4^+ ($p = 0.040$ and $p < 0.0001$, respectively), and that these relationships (slopes) were seasonally dependent ($p = 0.021$ and $p < 0.0001$, respectively).

Phytoplankton N uptake was expressed as a water-column integrated rate and analyzed according to the time of sampling defined by the onset and decline of the spring bloom (Simpson et al. 2008). We took this approach to condense the data and to account for seasonal changes in phytoplankton activity and both light and nutrient availability. Significant differences in the average uptake rates of all N substrates were observed depending on growth phase (Table 1). Generally, the rates were 1 to 2 orders of magnitude faster during the bloom and post-bloom periods compared to the pre-bloom period and autumn. Average NH_4^+ uptake rates showed the least amount of seasonal variation.

The pre-bloom and autumnal periods exhibited fast rates of reduced N uptake compared to NO_3^-, resulting in low *f*-ratios (Fig. 8). Nitrogen uptake on the GF/F filters were used to compute the ratios reported here. The *f*-ratio followed a similar pattern to the N uptake dynamics increasing substantially from 0.1–0.2 to 0.4–0.6 as spring phytoplankton growth commenced. During the peak period of production *f*-ratios

Table 1. Mean (±SD) water-column integrated uptake rates (ρ, mmol N m^{-2} d^{-1}) of NO_3^-, NH_4^+, and urea during different phytoplankton growth phases. The start and duration of each phase is specified as day of year (DOY). Different superscripts denote significant differences (ANOVA) between growth phases for each substrate: ρNO_3^-, $p < 0.001$; ρNH_4^+, $p < 0.07$; ρUrea, $p < 0.001$

Growth phase	DOY	ρNO_3^-	ρNH_4^+	ρUrea
Pre-bloom	136–156	0.04 ± 0.01^a	0.50 ± 0.43^a	1.99 (n = 1)
Bloom	157–182	5.71 ± 5.52^b	3.07 ± 2.18^{ab}	12.84 ± 9.12^a
Post-bloom	183–205	2.76 ± 3.84^{ab}	4.08 ± 3.31^b	4.22 ± 0.10^b
Autumnal	273–308	0.13 ± 0.09^a	1.04 ± 0.69^a	0.30 ± 0.24^b

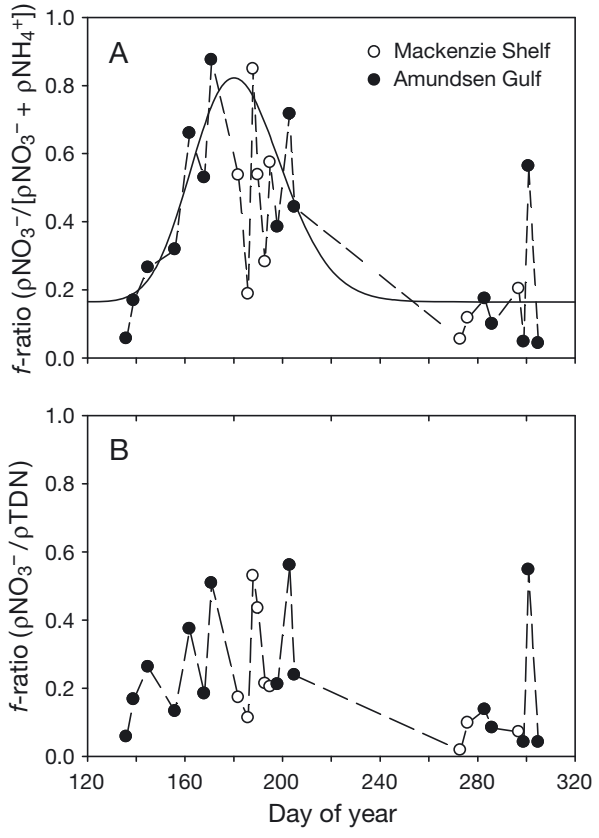

Fig. 8. Temporal variation in water-column integrated *f*-ratio during CASES 2003–2004 calculated (A) without, and (B) with urea uptake rate (ρ) $\rho TDN = \rho NO_3^- + \rho NH_4^+ + \rho Urea$. Time on the *x*-axes is measured as day of year irrespective of year. The temporal change in *f*-ratio reported in (A) was well described by a log-normal curve (solid line, $r^2 = 0.52$, $p < 0.001$)

were between 0.6 and 0.9, depending on whether or not urea uptake was considered. The temporal change in *f*-ratio (excluding urea) was well described by a log normal curve ($r^2 = 0.52$, $p < 0.002$). Including urea uptake in the calculation made the curve fit insignificant, although an increase from the late winter to mid July was still apparent in the data (Fig. 8b).

The influence of bacteria uptake on the *f*-ratio calculation was evaluated by comparing ^{15}N uptake rates measured with GF/F filters with and without correction for bacteria N consumption. We calculated water column integrated rates of N transport and computed the corresponding *f*-ratio for each of the stations where we had concurrent measurements of bacteria and phytoplankton NO_3^- and NH_4^+ uptake at all light depths. Too few data were available to include urea uptake in this calculation. The mean percent error in the *f*-ratio due to bacteria N uptake was 3.7 ± 8.7%, min. = −1, max. = 25, n = 9. The largest effect of bacteria was observed at a station near the shelf break in late autumn (23 Oct, DOY 297) where total N uptake rates were the slowest. During the spring and summer periods the *f*-ratios were not affected by bacteria N consumption (percent difference = −0.14 ± 0.5%, n = 5). The mean euphotic zone *f*-ratios with and without bacteria N uptake were 0.35 ± 0.24 and 0.34 ± 0.24, respectively.

Seasonal new and regenerated production

A quasi-annual sequence of pelagic phytoplankton N utilization was constructed for the CASES study region beginning on 15 May (DOY 136) by including the samples taken from the Mackenzie shelf and the Amundsen Gulf and by using the autumn data from 2003 (Fig. 9). Sea surface NO_3^-concentration decreased sharply from about 2 to <0.3 µmol l^{-1} as the phytoplankton bloom developed. The amount of N taken up was computed by integrating the area under the curve of each N substrate: similar calculations were made for the total dissolved N uptake (TDN; sum of NO_3^- + NH_4^+ + urea). As expected, a large amount of N assimilation occurred in the bloom period despite its short duration (Table 2). The maximum rate of TDN uptake during this time was 38.6 mmol N m^{-2} d^{-1}. TDN uptake rate declined steadily thereafter into the post-bloom phase, except for a high rate of uptake at one station on 18 July (DOY 200). As shown in Table 2, regenerated N production was dominant throughout all sampling periods. Urea uptake was responsible for 81% of regenerated production in spring and played a significant, but diminishing, role during the post-bloom (54%) and autumnal (35%) phases.

Because a substantial portion of the annual cycle was not sampled, we took a variety of approaches to

estimate the amount of N taken up during that time. Two of these used a straight line extrapolation from mean values measured during the post-bloom and autumnal periods. In one case, the means were calculated using all the available data from the post-bloom and autumnal periods and in the other, the means were calculated from the last 3 and first 3 measurements, respectively. A third approach used a linear model relating TDN uptake in the autumn samples (29 Sep–3 Nov, DOY 273–308) with day length. A regression of integrated TDN uptake on day length was significant at $p \leq 0.06$ level, whereas no relationship was apparent between TDN uptake rate and integrated N concentration ($p = 0.523$). Thus, during the period of declining light, N production was largely controlled by the amount of available energy, as illustrated in Fig. 4. We extrapolated the regression to predict TDN uptake at longer day lengths over the unsampled part of the

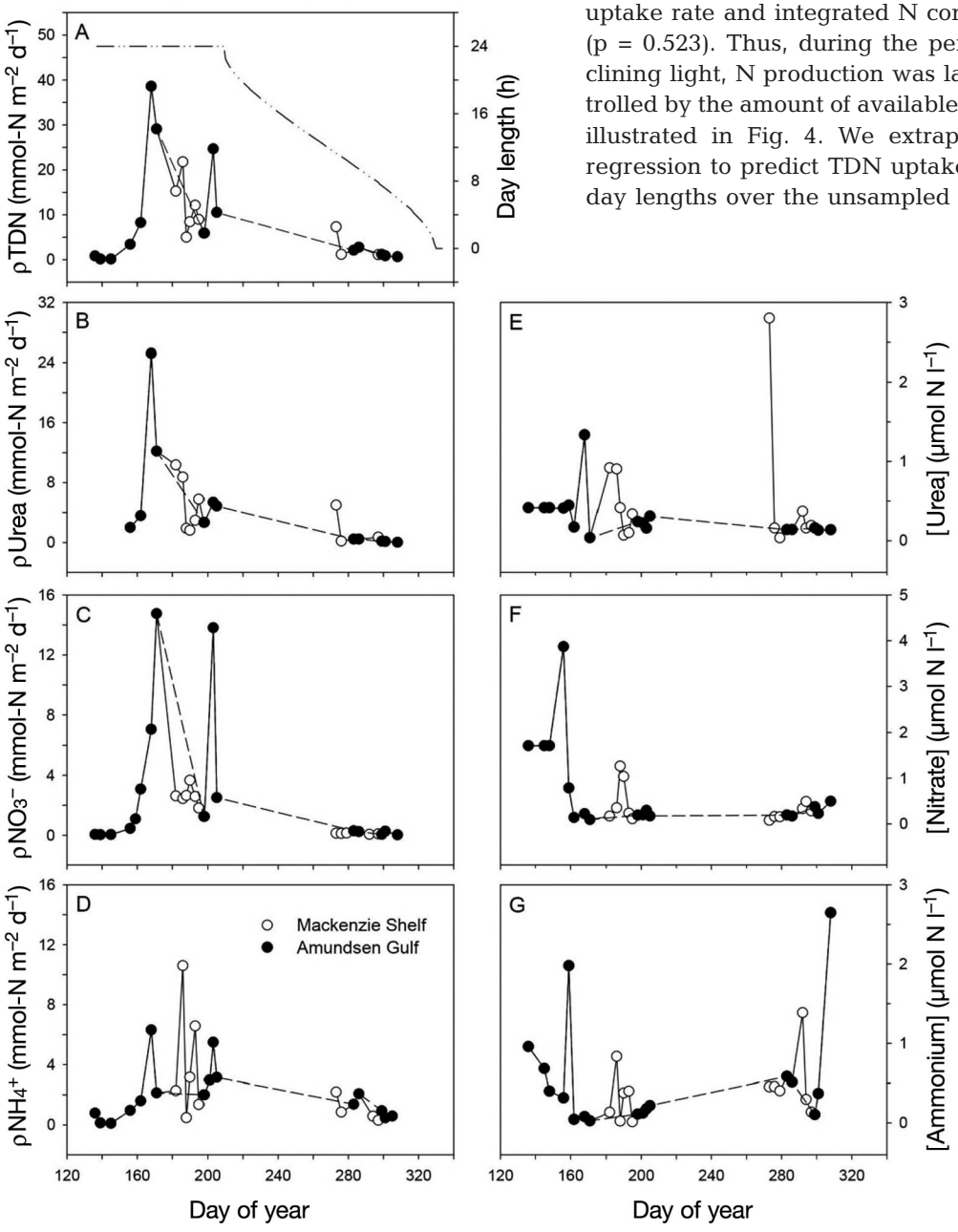

Fig. 9. Temporal variation in water-column integrated nitrogen uptake rate (ρ) of phytoplankton and sea surface nutrient concentration. Total dissolved nitrogen uptake (ρTDN) is the sum of the individual nitrogen uptake rates. Left-hand panels show (A) ρTDN, (B) urea, (C) nitrate, and (D) ammonium uptake; right-hand panels show the concentrations of (E) urea, (F) nitrate and (G) ammonium. Time on the *x*-axes is measured as day of year irrespective of year. The dot-dashed line in (A) represents approximate day length according to data from the US Naval Observatory for Franklin Bay, NWT. The dashed line in all plots connects samples taken exclusively from the Amundsen Gulf (●); the solid line connects samples taken from all stations including those on the Mackenzie Shelf (○)

Table 2. New, regenerated, and total phytoplankton N production measured throughout the growth season in the Cape Bathurst polynya in 2003 and 2004. Nitrogen uptake for each time interval was calculated by integrating the area under the curve from the data presented in Fig. 9. Time interval is measured in day of year (DOY). Multiple estimates of production are provided for some time periods as described in the footnotes. NS: not sampled (no measurements of ^{15}N uptake were made during this time period so production was estimated indirectly by 3 alternative methods; see 'Results: Seasonal new and regenerated production)

Growth phase	DOY	Phytoplankton production (mmol N m^{-2}) New	Regenerated	Total
Pre-bloom	136–156	2.90	7.95	10.9
Bloom	157–182	167	350	517
		210 ± 19[a]		
Post-bloom	183–205	90.9	187	278
NS	206–272	106[b]	376[b]	482[b]
		84.6 ± 23[c]	294 ± 117[c]	379 ± 120[c]
		75.8[d]	465[d]	541[d]
Autumnal	273–308	4.92	55.6	60.5
Annual	136–308	342–415	895–1070	1240–1480

[a]Average estimate derived from spring draw-down of nitrate (Simpson et al. 2013)
[b]Estimate derived from an average of the last 3 samples in the post-bloom and first 3 samples in the autumnal phase (see dashed line, Fig. 9)
[c]Estimate derived from the average of all post-bloom and all autumnal samples
[d]Estimate derived from a linear regression model of integrated TDN uptake and day length: ρTDN = 0.78 × day length − 4.66 (r^2 = 0.38, p = 0.06) and an average *f*-ratio of 0.14 calculated from Fig. 9

annual cycle. An average *f*-ratio of 0.14 between 24 Jul and 28 Sep (DOY 206 and 272) was applied to compute new and regenerated production. All 3 methods produced similar estimates of total production: 379–541 mmol N m^{-2}. The annual rate of phytoplankton production ranged from 1240–1480 mmol N m^{-2} and new production was 342–415 mmol N m^{-2}, or roughly 30% of the total (Table 2).

DISCUSSION

Our attention to the role of bacteria in dissolved inorganic N (DIN) uptake addresses recent observations of their importance in Arctic waters (Allen et al. 2002, Fouilland et al. 2007) and their potential to bias estimates of phytoplankton new production. Since Wheeler & Kirchman (1986) first reported bacteria assimilate and compete with phytoplankton for DIN, numerous reports have evaluated the types and amounts of N they consume throughout the world's oceans. These studies show bacteria are responsible for about 20 and 40% (median values) of total NO_3^- and NH_4^+ uptake, respectively (Kirchman 2000, Cochlan 2008). Our results also show that bacteria take up N, but the rates of uptake were slow compared to phytoplankton over an annual cycle and had little impact on estimates of new, regenerated and total production.

Measurement of bacteria nitrogen utilization

A major obstacle in assessing uptake of N by different functional groups of plankton is that size overlap prevents them from being physically separated. We used filter fractionation to obtain a relatively pure subsample of free-living bacteria on Ag filters by first removing phytoplankton and larger bacteria on GF/F filters. The initial filtration step captured roughly half (54.4 ± 16.5%) of the bacteria and the remaining cells were collected on Ag filters. Particulate matter on the Ag filters was assumed to be essentially free of photosynthetic picoplankton because of their low abundance in the high Arctic and large size. In the Beaufort Sea, for example, cyanobacteria and picoeucaryotic phytoplankton were ≥0.8 µm (Waleron et al. 2007, Lovejoy et al. 2007) and densities varied between 1–120 cells ml^{-1} and 100–20 000 cells ml^{-1}, respectively (Tremblay et al. 2009), which are low compared to the density of bacteria (1.2 ± 0.9 × 10^6 cells ml^{-1}).

Although the filtration method produced a clean bacteria sample, it may have introduced artifacts that could affect the measurement of bacteria DIN uptake. For example, assimilation of ^{15}N-DON (dissolved organic nitrogen) produced by phytoplankton or lysis of phytoplankton and retention of ^{15}N-labelled fragments on the Ag filters would cause the amount of DIN uptake by bacteria to be overestimated. We were careful to ensure that filtration pressures were always <100 mm Hg to minimize phytoplankton lysis, but cannot completely rule it out. Even if these artifacts were present, the rates of bacteria N uptake reported here were only a small fraction of the N uptake by phytoplankton. Conversely, bacteria associated with particles might not easily be counted so their contribution to N uptake would be overlooked. Although most bacteria exist as single cells in oceanic waters (Azam & Hodson 1977, Iriberri et al. 1987), a substantial number can be found associated with detrital and mineral surfaces near the

coast (Yoon & Rosson 1990), particularly those influenced by rivers and shelf sediments. Garneau et al. (2009) found that much of the heterotrophic activity assessed by leucine uptake was due to bacteria >3 µm in the Mackenzie River confluence, but in the marine dominated stations, particulate activity only amounted to 26% of the total, and all of the thymidine incorporation was associated with the small particles (<3 µm). Thus, particle associated bacteria were likely rare in our samples because the vast majority of sites we occupied were outside the Mackenzie shelf area and in areas of high salinity.

A related concern is whether the bacteria populations collected on Ag and GF/F filters were equally active. Bacteria N uptake was calculated by multiplying the cellular rate from the Ag samples by total bacteria density so the estimate would be biased if cellular rates differed in the bacteria removed by the GF/F filter. Bacteria on GF/F filters would be larger and contain more N than bacteria on Ag filters but would be expected to have slower biomass-specific rates of metabolism. Although the net effect of these 2 traits might cancel each other out, some measurements actually show greater activity in the large compared to small bacteria (Gasol et al. 1995) and in attached compared to free-living ones (Kirchman & Mitchell 1982), which would increase further their uptake of N for growth.

The reliability of the bacteria N uptake rates reported here can be assessed by comparing these rates to N uptake rates predicted from *in situ* measurements of bacteria production. If bacteria are in balanced growth, the N demand is equal to the product of bacteria production and the C:N ratio, assumed to be 3.4 (Fagerbakke et al. 1996). A compilation of data obtained from a variety of sources (Steward et al. 1996, Rich et al. 1997, Middelboe et al. 2002, Sherr & Sherr 2003, Garneau et al. 2006, 2009, Kirchman et al. 2007, Vallieres et al. 2008) yields an average N production rate of 2.2 ± 3.3 amol N bacterium^{-1} h^{-1}. This rate is based primarily on measurements made in spring and summer in pelagic waters of the Arctic Ocean. Using estimates of bacteria N uptake from Fig. 6b we calculate that the sum of the average rate of uptake of all 3 forms of N was 1.3 ± 1.3 amol N bacterium^{-1} h^{-1}. This rate is about 60% of the bacteria N demand calculated above and in keeping with other estimates of the contribution of DIN to bacterial N requirements. For example, Kirchman reported that NH_4^+ uptake provided from 19–75% of the N ration of bacteria in coastal and oceanic waters of the North Atlantic Ocean (Keil & Kirchman 1991, Kirchman 2000) and Allen et al. (2002) calculated that about 50% of the bacteria requirement was derived from DIN uptake in the Barents Sea. The remainder presumably is obtained from amino acids and other organic N compounds. These calculations show the measured rate of N uptake by bacteria agrees well with values predicted from bacteria growth, giving us confidence that our approach had no systematic bias.

Consequences of bacteria DIN uptake

The implications of the bacteria uptake results are 2-fold. First, we find no evidence for a serious impact of bacteria N uptake on calculated *f*-ratios and estimates of new production in the Cape Bathurst Polynya. This was true regardless of whether we compared *f*-ratios for individual samples or for the entire water column. Our results are in contrast to Fouilland et al. (2007) who reported fast rates of DIN use by bacteria in the NOW Polynya that had a large effect on *f*-ratio. This could simply be due to interannual variability that is well documented in Arctic waters (Sherr & Sherr 2003) or to differences in the location of the study sites. Indeed, the rates of N uptake measured in the NOW Polynya (57 ± 63 amol N bacterium^{-1} h^{-1}; Fouilland et al. 2007) were remarkably fast, well above the upper 95% confidence limit (6.6 amol N bacterium^{-1} h^{-1}) for cellular transport we computed from the literature. More surprising was that volumetric rates of bacteria N transport in the NOW Polynya were at times similar to the phytoplankton N uptake rates we measured during the spring and early summer. High rates of bacteria N uptake have been measured before and are not unique to the Fouilland study. Kristiansen et al. (1994), for example, reported NO_3^-, NH_4^+ and urea uptake rates by bacteria of 1.7, 5.4 and 2.2 nmol l^{-1} h^{-1}, respectively. Assuming a bacteria density of 5–10 × 10^8 l^{-1}, this is roughly equivalent to 9.5–19 amol N bacterium^{-1} h^{-1}. We note that these rates were also measured in the autumn when net phytoplankton uptake was reduced.

The data set also provides evidence for a greater role of bacteria in N uptake during autumn (Fig. 7), although the absolute rates of bacteria N uptake we measured were much slower than in the 2 studies reported above. In general, the proportion of bacteria to total N uptake was higher in autumn than in spring and summer (21 ± 3.4%, n = 23 vs. 7 ± 0.9%, n = 43) and at the bottom than at the top of the euphotic zone (Autumn data: 1% isolume depth, 35.5 ± 6.8%, n = 7 vs. 50–100% isolume depth, 15.0 ± 2.9%, n = 15). Allen et al. (2002) found consistently higher relative

uptake by bacteria for both NH_4^+ and NO_3^- (12–40 % and 16–40 %, respectively) and higher relative bacteria uptake in the marginal ice zone where extensive ice cover (80 %) likely limited light availability and slowed phytoplankton rates. These results are similar to our own at the 1 % isolume in showing bacteria can consume relatively large amounts of DIN when light is limiting phytoplankton production. In the Cape Bathurst Polynya, however, the absolute amount of N bacteria take up is so small that its impact on total annual N flux is minor.

Bacteria and phytoplankton N uptake

The second observation we can make regarding bacteria DIN uptake is that it co-varies with phytoplankton N uptake rate (Fig. 6). The relationship is consistent with the tight coupling that exists between bacteria and phytoplankton production in aquatic systems. Regression analysis, for example, shows bacteria production and phytoplankton production are highly correlated with model II regression slopes indistinguishable from 1 (Cole et al. 1988), a pattern also observed in the western and central Arctic in spring and summer (Rich et al. 1997, Kirchman et al. 2009). Mechanistically, the coupling is thought to arise from the dependence of heterotrophic microbial growth on organic C produced by photosynthesis of phytoplankton. Chemoautotrophic bacteria and Archaea would not have the same dependence on phytoplankton, but likely represent a small fraction of the microbial community in these waters (Kirchman et al. 2007). Because relative uptake of DIN by bacteria increased with a decrease in phytoplankton consumption and vice versa (Fig. 6), some environmental variable may alter the way DIN uptake is partitioned by the community. Although it is tempting to suggest that greater relative uptake by bacteria at low phytoplankton uptake rates was due to reduced N substrate availability, this does not seem to be a complete explanation because slow rates of phytoplankton uptake were caused by low light availability in autumn and at the base of the mixed layer where N concentrations were high (Simpson et al. 2008). Instead, we hypothesize that the relationship between bacteria and phytoplankton DIN uptake may be related to the amount of labile dissolved organic N that is available. In this scenario, high rates of phytoplankton DIN uptake fuel production of amino acids and other organic N substrates that are made available to the bacteria by lysis, excretion and grazing thereby reducing their reliance on DIN. Slow rates of DIN uptake by phytoplankton reduce the production and supply of DON to bacteria which consequently make use of larger amounts of DIN to meet N requirements for growth. Such a feedback system is consistent with the results of shipboard experiments (Kirchman et al. 1989, Kirchman 1990) that showed reduced bacteria NH_4^+ uptake in the subarctic Pacific following the addition of amino acids.

Bloom dynamics: seasonal new and regenerated production

The stable isotope uptake results allowed us to compute phytoplankton N consumption at the CASES study site to derive an annual estimate of production. Our focus here was exclusively on pelagic phytoplankton but we recognize that ice algae can contribute significantly to primary production and NO_3^- consumption shortly before ice breakup (Gosselin et al. 1997). The measured rates of N uptake (ρ^*) could be slightly faster than *in situ* (ρ) because adding the ^{15}N-labelled substrate increased the ambient concentration. To evaluate how this might have affected our results, we computed ρ^*/ρ assuming uptake followed Michaelis-Menten kinetics and the half saturation constants reported by Smith & Harrison (1991). Addition of the ^{15}N tracer had little effect on the NO_3^- data, as ρ^*/ρ averaged 1.12 ± 0.14 (n = 150) for the entire study. In spring and in autumn, similar results were obtained for NH_4^+ and urea uptake (ρ^*/ρ = 1.09 ± 0.15, n = 71; and 1.13 ± 0.16, n = 47, respectively), but during the post-bloom period, when ambient concentrations were lowest, ^{15}N addition may have stimulated uptake relative to *in situ* rates (ρ^*/ρ NH_4^+ = 1.24 ± 0.22, n = 42; ρ^*/ρ urea = 1.21 ± 0.11, n = 34). Thus, the effect of ^{15}N enrichment was small but likely increased the measured rates of regenerated N uptake by 20–25 %.

We can compare the amount of spring new production based on ^{15}N uptake and NO_3^-disappearance to assess the accuracy of the tracer measurement. During the spring bloom, the net decrease in NO_3^- concentration was 209.6 ± 19 mmol m^{-2} (Simpson et al. 2013). Water-column integrated measurements of $^{15}NO_3^-$ uptake (Table 2) showed that 167 mmol NO_3^- m^{-2} was taken up by phytoplankton at the same time, corresponding to about 80 % of the amount estimated by NO_3^- disappearance. Maximum rates of new production from NO_3^- draw-down (11.8 mmol m^{-2} d^{-1}; Simpson et al. 2013) and from ^{15}N-NO_3^- assimilation (14.7 mmol m^{-2} d^{-1}; Fig. 9) were also in close agreement during the spring bloom. Thus, extrapolation

of short-term measurements of NO_3^- consumption using stable isotope tracers in small bottles provides an excellent estimate of NO_3^- consumption at the regional scale.

Primary N production during autumn was minor compared to spring and summer (Table 2), as phytoplankton growth began to slow with the approach of polar night and increasing ice cover. We inferred that slow rates of pelagic production occurred from this time until May because of a lack of light. Indeed, the negative correlation between uptake of NO_3^- and NH_4^+ and day length (Fig. 4) illustrated the important control of light on phytoplankton surface production during the autumn sampling period. Garneau et al. (2009) also demonstrated a strong effect of light in the NOW Polynya with N uptake rates declining by 3-fold during the transition from summer to autumn. Light is known to control the rate and type of N uptake in polar regions (Kristiansen & Lund 1989, Smith & Harrison 1991, Klein et al. 2002) and to greatly increase transport rates compared to rates in the dark. Uptake rates of all N substrates increased rapidly after ice retreat resulting in depletion of NO_3^- from the surface waters and build-up of particulate N (Simpson et al. 2013). This rapid response of phytoplankton to favourable conditions is similar to what has been shown in other Arctic polynyas (Tremblay et al. 2006).

Sampling in 2003 only began in October, so a 2 mo period during the open water season from late July to late September was un-sampled during the CASES study. We used a variety of methods to interpolate phytoplankton uptake rates during this time based on regression analysis of decreasing day length against total uptake rate, and by using averages from post-bloom and autumnal phases. These simple linear models indicated that N-based production after the post-bloom period could contribute very significantly to the annual estimate (Table 2). This gap in sampling represents a major limitation in our attempt to obtain an annual measurement of phytoplankton N uptake and suggests that additional data are required to validate the production estimates we report for this period. Satellite images, for example, observe an autumn phytoplankton bloom in the Cape Bathurst region (Arrigo & van Dijken 2004), but its occurrence and size varies from year to year. We are not able to assess its potential importance to N fluxes in the polynya but recognize that our estimates are likely too low as a consequence. New production in the NOW Polynya during the autumn bloom is about 1/10th of the amount of new production during the spring, which would suggest a small correction to our annual estimate if the same pattern holds true for the Amundsen Gulf.

In summary, annual new production in the Cape Bathurst Polynya ranged from 342–415 mmol N m^{-2} and a large proportion of this (40–61%) occurred over an ~18 d period during spring. Total N production during 2003–2004 was between 1.24 and 1.48 mol N m^{-2} (Table 2), supported primarily by urea and nitrate uptake. If we assume that the phytoplankton consume C in a Redfield proportion (Simpson et al. 2013), then this uptake of N translates into a particulate C production of between 91–110 g C m^{-2} yr^{-1}. Estimates of primary production derived from remote sensing (135 ± 35 g C m^{-2}) are remarkably similar to this rate (Arrigo & van Dijken 2004).

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LITERATURE CITED

Allen AE, Howard-Jones MH, Booth MG, Frischer ME, Verity PG, Bronk DA, Sanderson MP (2002) Importance of bacterial assimilation of ammonium and nitrate in the Barents Sea during summer. J Mar Syst 38:93–108

Arrigo KR, van Dijken GL (2004) Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. Geophys Res Lett 31:L08304, doi:10.1029/2003GL018978

Azam F, Hodson RE (1977) Size distribution and activity of marine microheterotrophs. Limnol Oceanogr 22:492–501

Cochlan WP (2008) Nitrogen uptake in the Southern Ocean. In: Capone DG, Bronk DA, Mulholland MR, Carpenter EJ (eds) Nitrogen in the marine environment, 2nd edn. Academic Press, Burlington, MA, p 569–596

Cole JJ, Findlay S, Pace ML (1988) Bacteria production in fresh and saltwater ecosystems: a cross-system overview. Mar Ecol Prog Ser 43:1–10

Collos Y (1987) Calculation of ^{15}N uptake rates by phytoplankton assimilating one or several nitrogen sources. Appl Radiat Isot 38:275–282

Conover RJ, Gustavson KR (1999) Sources of urea in Arctic seas: zooplankton metabolism. Mar Ecol Prog Ser 179: 41–54

Cota GF, Pomeroy LR, Harrison WG, Jones EP, Peters F, Sheldon WM Jr, Weingartner TJ (1996) Nutrients, primary production and microbial heterotrophy in the southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy. Mar Ecol Prog Ser 135: 247–258

Dugdale RC, Goering JJ (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol Oceanogr 12:196–206

Fagerbakke KM, Heldal M, Norland S (1996) Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria. Aquat Microb Ecol 10: 15–27

Fouilland E, Gosselin M, Rivkin RB, Vasseur C, Mostajir B (2007) Nitrogen uptake by heterotrophic bacteria and phytoplankton in Arctic surface waters. J Plankton Res 29:369–376

Garneau ME, Vincent WF, Alonso-Sáez L, Gratton Y, Lovejoy C (2006) Prokaryotic community structure and heterotrophic production in a river-influenced coastal arctic ecosystem. Aquat Microb Ecol 42:27–40

Garneau ME, Vincent WF, Terrado R, Lovejoy C (2009) Importance of particle-associated bacterial heterotrophy in a coastal Arctic ecosystem. J Mar Syst 75:185–197

Gasol JM, del Giorgio PA, Massana R, Duarte CM (1995) Active versus inactive bacteria: size-dependence in a coastal marine plankton community. Mar Ecol Prog Ser 128:91–97

Gosselin M, Levasseur M, Wheeler PA, Horner RA, Booth BC (1997) New measurements of phytoplankton and ice algal production in the Arctic Ocean. Deep-Sea Res II 44: 1623–1644

Harrison WG, Head EJ, Conover RJ, Longhurst AR, Sameoto DD (1985) The distribution and metabolism of urea in the eastern Canadian Arctic. Deep-Sea Res A 32:23–42

Iriberri J, Unanue M, Bacina I, Egea L (1987) Seasonal variation in population density and heterotrophic activity of attached and free-living bacteria in coastal waters. Appl Environ Microbiol 53:2308–2314

Kanda J, Laws EA, Saino T, Hattori A (1987) An evaluation of isotope dilution effect from conventional data sets of ^{15}N uptake experiments. J Plankton Res 9:79–90

Keil RG, Kirchman DL (1991) Contribution of dissolved free amino acids and ammonium to the nitrogen requirements of heterotrophic bacterioplankton. Mar Ecol Prog Ser 73:1–10

Kirchman DL (1990) Limitation of bacterial growth by dissolved organic matter in the subarctic Pacific. Mar Ecol Prog Ser 62:47–54

Kirchman DL (2000) Uptake and regeneration of inorganic nutrients by marine heterotrophic bacteria. In: Kirchman DL (ed) Microbial ecology of the oceans. Wiley-Liss, New York, NY, p 261–288

Kirchman D, Mitchell R (1982) Contribution of particle-bound bacteria to total microheterotrophic activity in five ponds and two marshes. Appl Environ Microbiol 43: 200–209

Kirchman DL, Keil RG, Wheeler PA (1989) The effect of amino acids on ammonium utilization and regeneration by heterotrophic bacteria. Deep-Sea Res A 36:1763–1776

Kirchman DL, Elifantz H, Ditell AI, Malmstrom RR, Cottrell MT (2007) Standing stocks and activity of Archaea and Bacteria in the western Arctic Ocean. Limnol Oceanogr 52:495–507

Kirchman DL, Hill V, Cottrell MT, Gradinger R, Malstrom RR, Parker A (2009) Standing stocks, production, and respiration of phytoplankton and heterotrophic bacteria in the western Arctic Ocean. Deep-Sea Res II 56: 1237–1248

Klein B, LeBlanc B, Mei ZP, Beret R and others (2002) Phytoplankton biomass, production and potential export in the North Water. Deep-Sea Res II 49:4983–5002

Kristiansen S, Lund BA (1989) Nitrogen cycling in the Barents Sea—I. Uptake of nitrogen in the water column. Deep-Sea Res A 36:255–268

Kristiansen S, Farbrot T, Wheeler PA (1994) Nitrogen cycling in the Barents Sea—seasonal dynamics of new and regenerated production in the marginal ice zone. Limnol Oceanogr 39:1630–1642

Lee SH, Whitledge TE (2005) Primary and new production in the deep Canada Basin during summer 2002. Polar Biol 28:190–197

Lovejoy C, Vincent WF, Bonilla S, Roy S and others (2007) Distribution, phylogeny and growth of cold-adapted picoprasinophytes in Arctic seas. J Phycol 43:78–89

Luchetta A, Lipizer M, Socal G (2000) Temporal evolution of primary production in the central Barents Sea. J Mar Syst 27:177–193

Middelboe M, Nielsen TG, Bjørnsen PK (2002) Viral and bacterial production in the North Water: *in situ* measurements, batch-culture experiments and characterization and distribution of a virus–host system. Deep-Sea Res II 49:5063–5079

Olsson K, Anderson LG, Frank M, Luchetta A, Smethie W (1999) Carbon utilization in the Eurasian sector of the Arctic Ocean. Limnol Oceanogr 44:95–105

Parsons TR, Maita Y, Lalli CM (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Elmsford, NY

Rich J, Gosselin M, Sherr B, Sherr E, Kirchman DL (1997) High bacterial production, uptake and concentrations of dissolved organic matter in the Central Arctic Ocean. Deep-Sea Res II 44:1645–1663

Sherr BF, Sherr EB (2003) Community respiration/production and bacteria activity in the upper water column of the central Arctic Ocean. Deep-Sea Res I 50:529–542

Simpson KG, Tremblay JE, Gratton Y, Price NM (2008) An annual study of inorganic and organic nitrogen and phosphorus and silicate in southeastern Beaufort Sea. J Geophys Res 113:C07016, doi:10.1029/2007JC004462

Simpson KG, Tremblay JE, Price NM (2013) Nutrient dynamics in the western Canadian Arctic. I. New production in spring inferred from nutrient draw-down in the Cape Bathurst Polynya. Mar Ecol Prog Ser 484:33–45

Smith WO Jr, Harrison WG (1991) New production in polar regions. The role of environmental controls. Deep-Sea Res A 38:1463–1479

Smith W, Gosselin M, Legendre L, Wallace DWR, Daly K, Kattner G (1997) New production in the Northeast Water Polynya: 1993. J Mar Syst 10:199–209

Steward GF, Smith DC, Azam F (1996) Abundance and production of bacteria and viruses in the Bering and Chukchi Seas. Mar Ecol Prog Ser 131:287–300

Tremblay JE, Michel C, Hobson KA, Gosselin M, Price NM (2006) Bloom dynamics in early opening waters of the Arctic Ocean. Limnol Oceanogr 51:900–912

Tremblay G, Belzile C, Gosselin M, Poulin M, Roy S, Tremblay JE (2009) Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: strong numerical dominance by picoeukaryotes. Aquat Microb Ecol 54:55–70

Turley CM (1993) Direct estimates of bacterial numbers in seawater samples without incurring cell loss due to sample storage. In: Kemp PF, Sherr BF, Sherr EB, Cole JJ (eds) Handbook of methods in aquatic microbial ecology. Lewis Publishers, Boca Raton, FL, p 143–147

Vallieres C, Retamal L, Ramlal P, Osburn CL, Vincent WF (2008) Bacterial production and microbial food web structure in a large arctic river and the coastal Arctic Ocean. J Mar Syst 74:756–773

Waleron M, Waleron K, Vincent WF, Wilmotte A (2007) Allochthonous inputs of riverine picocyanobacteria to coastal waters in the Arctic Ocean. FEMS Microbiol Ecol 59:356–365

Wheeler PA, Kirchman DL (1986) Utilization of inorganic and organic nitrogen by bacteria in marine systems. Limnol Oceanogr 31:998–1009

Yoon WB, Rosson RA (1990) Improved method of enumeration of attached bacteria for study of fluctuation in the abundance of attached and free-living bacteria in response to diel variation in seawater turbidity. Appl Environ Microbiol 56:595–600

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