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Nutritive and photosynthetic ecology of subsurface chlorophyll maxima in the Canadian Arctic waters

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Abstract

Assessments of carbon and nitrogen (N) assimilation in Canadian Arctic waters confirmed the large contribution of subsurface chlorophyll maxima (SCM) to total water-column production from spring to late fall. Although SCM communities showed acclimation to low irradiance and greater nitrate (NO_3^-) availability, their productivity was generally limited by light and temperature. During spring-early summer, most of the primary production at the SCM was sustained by NO_3^- , with a f -ratio (i.e. relative contribution of NO_3^- uptake to total N uptake) of 0.74 ± 0.26 on average. The seasonal decrease in NO_3^- availability and irradiance, coupled to the build up of ammonium (NH_4^+), favoured a transition toward a predominantly regenerative system (f -ratio = 0.37 ± 0.20). Results emphasize the need to include SCM in remote-sensing algorithms and to revisit ecosystem model parameters in highly stratified environments such as the Canadian Arctic waters.

1 Introduction

In the Arctic Ocean, the extreme solar cycle and the formation, ablation and motion of sea ice exert a major influence on light availability in the water column (Smith and Harrison, 1991; Sakshaug, 2004). While these processes constrain the timing of algal production and impose large, short-term light fluctuations during the growth period, first-order differences in the annual primary production of seasonally-open waters ultimately depend on mixing regime, which modulates the supply of nitrogen (N) to the upper euphotic zone (Tremblay and Gagnon, 2009; Ardyna et al., 2011).

In peripheral Arctic seas (e.g. Bering Sea, Barents Sea, eastern Baffin Bay) the relatively weak vertical stratification allows for vertical mixing that recharges the euphotic zone with nutrients at least once a year (Tremblay et al., 2002). In the interior (e.g. Chuckchi and Beaufort seas), however, low-salinity waters entering through Bering Strait and the freshwater supplied by river discharge impart strong vertical stratification.

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Although large quantities of nutrients are supplied by the Bering Sea, N is depleted in the productive Chukchi Sea and weakly replenished downstream in the Beaufort Sea (Tremblay et al., 2008).

Recent work showed that strongly opposing vertical gradients of irradiance and inorganic N in the Canadian Arctic result in the widespread occurrence of subsurface chlorophyll maxima (SCM; Martin et al., 2010). Because SCMs are seasonally persistent and composed of photosynthetically-active phytoplanktonic population, Martin et al. (2010) hypothesized that SCMs mediate a large share of new production, i.e. the portion of total primary production based on the uptake of allochthonous N (e.g. nitrate, NO_3^-). Due to their positioning in the water column, SCMs probably act as a “nutrient trap” that further weakens N renewal in the upper euphotic zone (see also Harrison, 1990). Primary production can be partly decoupled from N uptake in the short term, especially at low irradiances such as observed at the SCM (Price et al., 1985; Cochlan et al., 1991; Smith and Harrison, 1991). This decoupling can be caused by luxury uptake, whereby NO_3^- is stored or released as NO_2^- after incomplete reduction, or differential adaptation/acclimation of carbon (C) and N uptake systems to irradiance (e.g. greater capacity to assimilate N in the dark or at low irradiance; Smith and Harrison, 1991; Probyn et al., 1996). However, the extent to which SCM productivity responds to the availability of light and N in the Arctic Ocean is not known.

In the study of Martin et al. (2010), the combination of low levels of ammonium (NH_4^+) at and above the SCM with rapidly increasing concentrations underneath suggested that local N recycling is important for SCM communities. Such regenerated production possibly fuels a substantial part of total primary production on a daily basis. When abundant, reduced N (i.e. NH_4^+ and urea) is generally preferred over NO_3^- , whereas all N forms tend to be used in proportion to their availability when total N is lower than phytoplankton demand (McCarthy et al., 1977; Harrison et al., 1982). Whether SCM communities are predominantly regenerative or efficient vectors of export toward the food web or the deep ocean remains to be assessed.

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Here we report the results of a comprehensive investigation of the nutritive and photosynthetic ecology of SCM communities in different regions and seasons in the coastal Canadian Arctic. We measured the simultaneous uptake of C and N in light-gradient incubators to determine the relative influence of light and N availability on total, new and regenerated production by SCM communities. Nitrogen was added in trace or enriched amounts in the form of NO_3^- , NH_4^+ , urea, or nitrite (NO_2^-). These results were compared to those of surface samples to reveal the unique physiological properties of the phytoplankton in the SCM. Practical objectives were to assess the contribution of the SCM layer to water-column rates of total, new and regenerated production as well as to establish contemporary parameters for use in ecosystem models and remote-sensing algorithms.

2 Materials and methods

2.1 Sampling

During 2005 (16 August to 16 October), 2006 (4 September to 4 November), 2007 (28 September to 6 November) and 2008 (26 April to 13 July) expeditions of the *CCGS Amundsen*, 983 vertical profiles were obtained with a CTD-Rosette equipped with sensors to measure in vivo fluorescence (SeaPoint Chlorophyll Fluorometer), transmissivity (WET Labs CST-671DR), dissolved oxygen (Sea-Bird SBE43), NO_3^- (SATLANTIC ISUS V1), photosynthetically active radiation (PAR; Biospherical QCP-2300), temperature and salinity (Sea-Bird SBE-911*plus*). Our sampling covered the entire latitudinal and longitudinal swath of the Canadian Archipelago, including Baffin Bay, the Northwest Passage, the Beaufort Sea, Foxe Basin, Hudson Bay and three Labrador fjords (Fig. 1).

Nutrient concentrations were measured at a subset of 265 stations (55 in 2005, 85 in 2006, 52 in 2007 and 73 in 2008). Samples for $\text{NO}_3^- + \text{NO}_2^-$ and NO_2^- were taken at standard depths (see Martin et al., 2010 for detailed protocol). Chlorophyll *a* (chl *a*)

concentrations, photosynthetic competency (F_v/F_m) and NH_4^+ were analysed at 129 stations (35 in 2005, 29 in 2006, 22 in 2007 and 43 in 2008). Of the 129 stations, 59 were selected for light-gradient incubations with water collected at SCM depth (11 in 2005, 12 in 2006, 10 in 2007 and 26 in 2008). In 2006, 9 of the 12 incubations examined NO_3^- uptake simultaneously by the surface (5 m) and SCM communities (Table 1).

2.2 Nutrients

Samples for nutrient analyses were collected in acid-cleaned tubes (stored with 10% HCl) and stored in the dark at 4 °C. Concentrations of $\text{NO}_3^- + \text{NO}_2^-$ and NO_2^- were determined within a few hours using standard colorimetric methods (Grasshoff et al., 1999) adapted for the AutoAnalyzer 3 (Bran + Luebbe) and NH_4^+ was measured manually with the sensitive fluorometric method (Holmes et al., 1999). For the latter, reagents were added within minutes of sample collection. Urea samples were either frozen or analyzed fresh using the method of Mulveena and Savidge (1992) and Goeyens et al. (1998). The analytical detection limits for NH_4^+ and urea were 0.02 μM and 0.1 μM , respectively.

2.3 Chlorophyll and F_v/F_m

Samples for chl *a* and F_v/F_m were collected at surface (5 m) and SCM depths. Concentrations of chl *a* were determined using the fluorescence method (Parsons et al., 1984) and F_v/F_m by Pulse-Amplitude-Modulated fluorometry (WALZ Phyto-PAM; see details in Martin et al., 2010). F_v/F_m measurements have also been used to assess the response of SCM and surface communities to experimental treatment. Samples were obtained from bottles after their incubation and dark adapted for 30 min before analysis.

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2.4 Incubations

Relationships between irradiance (E ; estimated with a Biospherical QSL-2101 light sensor) and the uptake of C and N by phytoplankton from the SCM was assessed with four light-gradient incubators (400 W Optimarc metal-halide lamps used in combination with optical filters to obtain 10 light intensities). In order to reproduce the light environment at the SCM, the irradiances selected for our incubations covered the low range (from 664.2 to $0.3 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$ in 2005 (6 of the 10 light intensities were lower than $100 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$), from 309.1 to $1.8 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$ in 2006, from 358.0 to $3.0 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$ in 2007 and from 281.0 to $1.8 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$ in 2008; 8 to 9 of 10 light intensities lower than $100 \mu\text{mol quanta}^{-1} \text{m}^{-2} \text{s}^{-1}$ between 2006 and 2008). Temperature was maintained at in situ levels with a chilling circulator. Samples from all incubators were spiked with ^{13}C -bicarbonate; one incubator was enriched with $^{15}\text{NO}_3^-$ ($10 \mu\text{M}$) and another with either $^{15}\text{NH}_4^+$ ($4 \mu\text{M}$) or $^{15}\text{NO}_2^-$ ($2 \mu\text{M}$). The other two incubators received trace additions (10% of ambient concentrations) of the same N substrates. Experiments that compared surface and SCM communities were performed with enriched and trace additions of $^{15}\text{NO}_3^-$ only. Incubations were kept short (5–6 h) to minimize isotopic dilution and were terminated by filtration onto 24-mm glass microfibre filters (Whatman GF/F). All filters were desiccated at 60°C and stored dry for post-cruise analysis. An elemental analyzer (ECS 4010, Costech Analytical Technologies Inc.) coupled to a mass spectrometer (Delta V Advantage, Thermo-Finnigan) was used to determine isotopic enrichment and particulate organic carbon and nitrogen using a modified Dumas method (Fiedler and Proksch, 1975). Specific C and N uptake was calculated according to Collos (1987) equation.

2.5 Sensor calibrations and data transformations

Detail vertical profiles were obtained with a CTD and attached sensors (see Martin et al., 2010 for detailed post-calibration procedures). The depths (Z) of the SCM,

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pycnocline and nitracline were identified as those where the vertical gradients of in vivo fluorescence, N^2 and NO_3^- had the highest values, respectively. Daily-averaged irradiance at the SCM (E_{SCM}) and at other sampling depths was calculated using the coefficient of diffuse light attenuation (k ; see Martin et al., 2010 for calculation method) and a continuous record of incident PAR above the sea surface (Kipp & Zonen; PAR-Lite) to estimate E_0 .

Chl *a* normalized (superscript *B*) photosynthesis-irradiance parameters were calculated using the empirical exponential models that provided the best fit to the data. The model of Platt et al. (1980) was used when photoinhibition occurred:

$$P^B = P_s^B [1 - \exp(-\alpha E / P_s^B)] [\exp(-\beta E / P_s^B)] \quad (1)$$

where

$$P_m^B = P_s^B [\alpha / (\alpha + \beta)] [\beta / (\alpha + \beta)]^{\beta / \alpha} \quad (2)$$

and the model of Webb et al. (1974) when photoinhibition was not apparent

$$P^B = P_m^B [1 - \exp(-\alpha E / P_m^B)], \quad (3)$$

where P_m^B is the maximum observed uptake rate [$\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$], E is the incubation irradiance ($\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$), and α and β in units of [$\mu\text{g C } (\mu\text{g chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$] are the photosynthetic efficiency at low irradiance (initial slope of the relationship) and the photoinhibition parameter, respectively. The models of Platt et al. (1980) and Webb et al. (1974) were previously shown to give similar results (Frenette et al., 1993). The photoacclimation index (E_k ; $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$) was calculated as:

$$E_k = P_m^B / \alpha \quad (4)$$

The same model parameters were estimated for nitrogen uptake (in which case the letter *N* substitutes for *P* in Eqs. (1) to (3), with the inclusion of a term for dark uptake (D^B in [$\mu\text{g N } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$]) on the right hand side of Eqs. (1) and (3) (Priscu, 1989).

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A more robust estimation of D^B was done a posteriori by taking the y-intercept ($E = 0$) of the linear portion of the relationship at low irradiance. On average, standard errors were $8 \pm 7\%$, $11 \pm 8\%$ and $15 \pm 9\%$ for the photosynthetic parameters P_m^B , α and E_k , respectively, and $21 \pm 36\%$, $31 \pm 27\%$, $54 \pm 70\%$ and $41 \pm 44\%$ for the N uptake parameters N_m^B , α , D^B and E_k , respectively.

Since irradiance varied between incubators, the f -ratio ($N_{NO_3^-}^B / (N_{NO_3^-}^B + N_{NH_4^+}^B)$) at a given irradiance was calculated using uptake values predicted from individual $N^B - E$ curves for NO_3^- and NH_4^+ . The resulting f -ratio $-E$ curves were used to assess the f -ratio and the relative preference index (RPI) for NO_3^- uptake at E_{SCM} . The RPI was calculated by dividing the f -ratio by the relative contribution of NO_3^- to total inorganic N concentration ($NO_3^- + NH_4^+$) and represented the degree to which NO_3^- was selected (RPI > 1) or discriminated (RPI < 1) over NH_4^+ (McCarthy et al., 1977).

2.6 Statistical analyses

The geometric mean regression (model II linear regression; considering error on both variables) was used to assess functional relationships between variables. Relationships between environmental variables and uptake-irradiance parameters for C and N were determined with the Pearson's product moment correlation (PPMC) and differences between treatments were evaluated with a paired t-test when data were distributed normally or the Wilcoxon's signed-rank test otherwise. When relevant, descriptive statistics were calculated separately for the spring-early summer period and late summer-fall period (see Table 1).

3 Results

3.1 General conditions in the sampling area

Unless stated otherwise, the descriptions below refer to all data from 2005 to 2008. When appropriate, separate results are reported for the subset of stations where C and N uptake rates were measured (hereafter termed “experimental stations”). Distinct SCM were present at 81 % of the 465 stations analyzed (Fig. 1; see Martin et al. (2010) for a discussion of the other stations where chl *a* was maximum at the surface or vertically homogenous). The depth of the SCM ranged from 4 to 114 m with a mean of 35 ± 16 m (at experimental stations the range was 11–75 m and the mean 36 ± 15 m). The vertical position of the SCM matched the depth of the nitracline (mean = 38 ± 16 m for all stations and 40 ± 17 m for experimental ones) within ± 10 m in 79 % (67 % for experimental stations) of the cases and within ± 20 m in 89 % (88 % for experimental stations) of cases ($Z_{\text{SCM}} = 1.00 \times Z_{\text{nitracline}} - 2.57$, $r^2 = 0.46$ for all stations; $Z_{\text{SCM}} = 1.12 \times Z_{\text{nitracline}} - 9.24$, $r^2 = 0.41$ for experimental stations). Primary maxima of NO_2^- (PNM) and NH_4^+ (PAMM) were widespread (not shown but see Martin et al., 2010) and their vertical positions were significantly correlated with the SCM ($Z_{\text{PNM}} = 0.50 \times Z_{\text{SCM}} + 39.23$, $r^2 = 0.12$, $n = 201$; $Z_{\text{PAMM}} = 0.72 \times Z_{\text{SCM}} + 25.75$, $r^2 = 0.20$, $n = 96$).

F_v/F_m was generally high at the surface and the SCM (not shown), with median values of 0.55 and 0.58, respectively (see Martin et al., 2010). Although the overall data distribution was similar for the two sampling depths, a comparison of locally paired samples showed F_v/F_m to be significantly higher at the SCM during spring-early summer (2008 expedition; Wilcoxon’s signed-rank test, $p < 0.001$). This difference was not apparent during late summer-fall (2005, 2006 and 2007 expeditions; $p = 0.76$).

Table 1 provides the details of physical and chemical properties at Z_{SCM} for experimental stations. Temperature ranged from -1.7 to 5.1 °C and exceeded 0 °C in only 17 % of cases. Daily averaged irradiance varied between 0.1 and

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67 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ across stations (overall mean of $13 \pm 14 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$), representing 0.001 to 47% of incident irradiance at the surface (mode in the 1–10% range for 68% of stations). Concentrations of NO_3^- ranged from the limit of detection to 10.6 μM but were generally lower than 2 μM (47% of stations), whereas NH_4^+ concentrations ranged from the limit of detection to 1.0 μM , with values below 0.2 μM at 55% of stations. The concentrations of NO_2^- and urea were relatively low with mean values of $0.13 \pm 0.09 \mu\text{M}$ (max = 0.47 μM) and below the limit of detection ($0.05 \pm 0.07 \mu\text{M}$; max = 0.2 μM), respectively. Overall, 99% of the variability in the concentration and 78 \pm 24% of the total amount of inorganic N (i.e. $\text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) at the SCM were due to NO_3^- .

3.2 Difference in uptake-irradiance parameters between surface and SCM communities

At stations where incubations were performed simultaneously (see Table 1) with surface and SCM samples, P_m^B did not differ significantly between the two communities (Fig. 2; $n = 9$, paired t-test $p = 0.212$), whose mean values were 0.82 ± 0.35 and $0.64 \pm 0.46 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{h}^{-1}$, respectively. However, α was significantly lower at surface than at the SCM (Fig. 2; mean of 0.026 ± 0.013 versus $0.033 \pm 0.015 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$; Wilcoxon's signed-rank test $p = 0.004$), driving a decrease in E_k with depth (Fig. 2; mean of $33 \pm 7 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at the surface and $19 \pm 9 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ at the SCM; paired t-test $p = 0.005$). Photoinhibition was observed only at the SCM, for which β varied between 0 and $0.0006 \mu\text{g C} (\mu\text{g chl } a)^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$ (data not shown).

The N_m^B for NO_3^- uptake (not shown) was clearly lower at the surface than at the SCM (mean of 0.018 ± 0.022 and $0.031 \pm 0.021 \mu\text{g N} (\mu\text{g chl } a)^{-1} \text{h}^{-1}$, respectively; $n = 8$; paired t-test $p = 0.017$). However, α (mean of 0.001 ± 0.002 versus $0.003 \pm 0.003 \mu\text{g N} (\mu\text{g chl } a)^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$) and E_k (mean of 18 ± 14 versus

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$15 \pm 9 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) were not significantly different (Wilcoxon's signed-rank test $p = 0.578$ and 0.844 , respectively).

In order to assess the contribution of the SCM layer to daily primary production and NO_3^- uptake during 2006, we combined uptake-irradiance parameters with measurements of daily mean irradiance and detailed vertical profiles of chl *a* (Fig. 3). We observed that the SCM layer mediated 43 to 76 % of C uptake (mean = 62 ± 11 %) and 64 to 98 % of NO_3^- uptake (mean = 80 ± 12 %) in the euphotic zone (defined as 0.1 % of surface irradiance). For instance, at station 303 (a station representative of mean conditions for the entire data set; yellow arrow in Fig. 1), we prescribed the uptake-irradiance parameters of the surface community between 0 and 14 m (depth of the pycnocline and top of the SCM) and those of the SCM community from 14 to 71 m (bottom of the euphotic zone). Maximum primary production ($15.67 \mu\text{g C l}^{-1} \text{d}^{-1}$) and NO_3^- uptake ($1.55 \mu\text{g N l}^{-1} \text{d}^{-1}$) occurred at 20 m and coincided with the SCM ($1.64 \mu\text{g chl } a \text{ l}^{-1}$; Fig. 3). Vertical integration over the two vertical horizons gave a production of $36.35 \mu\text{g C l}^{-1} \text{d}^{-1}$ and a NO_3^- uptake of $2.00 \mu\text{g N l}^{-1} \text{d}^{-1}$ above the pycnocline (representing 24 % and 13 % of the total, respectively). Below the pycnocline, C production and NO_3^- uptake were $112.40 \mu\text{g C l}^{-1} \text{d}^{-1}$ (76 % of the total) and $13.44 \mu\text{g N l}^{-1} \text{d}^{-1}$ (87 % of the total).

3.3 Photosynthetic parameters at the SCM under trace ^{15}N additions

A larger set of experiments was performed with water from the SCM only (excluding results obtained from incubations performed simultaneously with surface and SCM; see Table 1) collected during late summer-fall (2005 to 2007) and spring-early summer (2008). For a given station, photosynthetic parameters were derived using data from all incubators since no significant effect of N substrate on C uptake was observed. The P_m^B in units of $\mu\text{g C} (\mu\text{g chl } a)^{-1} \text{h}^{-1}$ ranged from 0.07 to 2.77 (mean = 0.65 ± 0.45 ; Fig. 4). The parameter α in units of $\mu\text{g C} (\mu\text{g chl } a)^{-1} \text{h}^{-1} (\mu\text{mol quanta m}^{-2} \text{s}^{-1})^{-1}$ ranged from 0.006 to 0.078 (mean = 0.027 ± 0.014 ; Fig. 4). Corresponding E_k values in units of

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$\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ varied between 7 and 97 (mean = 24 ± 13 ; Fig. 4). The β parameter (same units as α) was significant at only 12% of the station, with values ranging from 0.00002 to 0.0032 (mean = 0.0010 ± 0.0008 ; data not shown).

3.4 Nitrogen uptake by SCM communities under trace ^{15}N additions

5 Nitrate uptake was highly variable among stations ($n = 53$; Appendix A). The mean values for uptake-irradiance parameters was $0.042 \pm 0.043 \mu\text{g N } (\mu\text{g chl } a)^{-1} \text{ h}^{-1}$ for N_m^B , $0.004 \pm 0.007 (\mu\text{g N } (\mu\text{g chl } a)^{-1} \text{ h}^{-1} (\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1})$ for α , $18 \pm 12 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ for E_k and 0.010 ± 0.030 for D^B (same unit as N_m^B) representing $14 \pm 17\%$ of the total uptake ($N_m^B + D^B$). Nitrite uptake was an order of magnitude lower (mean $N_m^B = 0.005$; mean $\alpha = 0.0007$; mean $E_k = 11$; mean $D^B = 0.001$;
10 $n = 3$). For NH_4^+ uptake ($n = 32$; Appendix A), $N_m^B = 0.016 \pm 0.017$, $\alpha = 0.005 \pm 0.008$ and $E_k = 7 \pm 8$. Dark uptake = 0.008 ± 0.009 and accounted for $26 \pm 24\%$ of the total uptake. Urea uptake-irradiance incubations was also performed, but data will not be shown here since only 2 out of 8 stations had detectable responses and in situ urea concentrations were most often below the limit of detection.
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3.5 Relationships between environmental factors and uptake-irradiance parameters under trace ^{15}N additions

The PPMC analysis showed a strong correlation between P_m^B , E_k and in situ temperature (correlation coefficient for P_m^B between 0.62 and 0.97 across incubation sets, $p < 0.0001$ and for E_k between 0.72 and 0.88, $p < 0.0001$; Appendix B). Note that for the SCM this correlation was strongly influenced by station NR24, which was near the Nelson River and showed anomalously high temperature (5.1°C). The day of year (DY) was significantly related to N_m^B for NO_3^- uptake. No correlation was observed between E_k and daily-averaged irradiance at the SCM (E_{SCM} ; for surface samples, the E_k and α for C and N uptake showed a strong correlation with both NH_4^+ and total inorganic
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N concentrations (Table B2). A weak negative correlation was observed between α of C uptake and NO_2^- concentrations and positive between α and NH_4^+ concentrations. At the SCM, strong positive relationships were observed between N_m^B , α and the concentrations of NO_3^- and total dissolved N (Table B1). The only relationship observed with dark uptake (not shown) was a weak positive correlation between E_{SCM} and D^B for NO_3^- uptake (0.40, $p = 0.03$).

When excluding outlying station NR24 (see above), a detailed analysis of P_m^B versus in situ temperature (T) showed a significant, positive linear relationship during late summer-fall (Fig. 5; $P_m^B = 0.178T + 0.538$, $r^2 = 0.64$, $p < 0.0001$). No significant relationship with temperature was observed during spring-early summer when the temperature range was very narrow at the SCM (between -1.7 and -1.0 °C). The predictive power of the relationship for the spring-early summer was increased by including both T and DY in a multiple linear regression ($P_m^B = 8.417 - 0.0229 DY + 2.742T$, $r^2 = 0.77$, $p < 0.001$; not shown).

Estimates of E_{SCM} were lower than E_k for C uptake at 47% of the experimental stations during spring-early summer and 85% of the stations during late summer-fall (Fig. 6). The same percentage (85%) was observed for NO_3^- uptake during late summer-fall, but not during spring-early summer when only 21% of E_{SCM} were lower than E_k . For NH_4^+ uptake, E_{SCM} was lower than E_k in only 11% and 29% of cases during the spring-early summer and late summer-fall periods, respectively.

3.6 Contribution of NO_3^- uptake to inorganic N uptake (f -ratio) at the SCM

When excluding dark uptake (D^B) from calculations, the average f -ratio estimated for the mean E_{SCM} during spring-early summer ($23 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) was 0.74 ± 0.26 (Fig. 7). During late summer-fall, the average f -ratio estimate was 0.37 ± 0.20 for a mean E_{SCM} of $7 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Fig. 7). Despite the wide range of observed E_{SCM} during spring-early summer (0.3 to $67 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) the mean f -ratio estimated from individual f -ratio-irradiance curves for all stations only varies from

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uptake (except for P_m^B in the enriched NH_4^+ treatment; Table B1). Positive correlations were observed between P_m^B , E_k and in situ temperature at the surface and the SCM (Table B2). Finally, we observed positive relationships between chl *a* concentration and N_m^B and α (for N only) and between E_{SCM} and P_m^B , N_m^B and E_k in the enriched NH_4^+ treatment (Table B1).

3.8 C:N stoichiometry at the SCM

The C:N uptake ratios (where N is the sum of NH_4^+ and NO_3^- uptake) showed a general decrease with increasing inorganic N concentration (Fig. 10). The ratios at E_{SCM} ($P^B:N^B$) were lower than at light-saturation ($P_m^B:N_m^B$) and generally close to the Redfield value. The negative effect of N enrichment on C:N uptake ratios was strongest under experimental light saturation and rapidly disappeared when N concentrations rose above 2 μM (Fig. 10).

3.9 Post-incubation F_v/F_m

A significant negative correlation was observed between F_v/F_m of SCM phytoplankton and irradiance following the incubation (Fig. 11; $r = -0.64$, $p < 0.0001$, $n = 553$). F_v/F_m was stable (mean = 0.62) up to ca. 30 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ and then declined with irradiance. All extreme low values (F_v/F_m below 0.3) were measured in samples exposed to irradiance greater than 85 $\mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (representing on average 27 % of incident irradiance at the surface). Post-incubation F_v/F_m of surface phytoplankton (5 m; mean of 62 % of incident irradiance measured at surface) also showed a significant negative correlation (Fig. 11; $r = -0.73$, $p < 0.0001$, $n = 48$), but extremely low values were not observed in the range of simulated irradiance.

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This study provides the first assessment of combined C and N uptake by SCM communities over the entire swath of the Canadian Arctic and the full extent of the growth season (April to early November). It also extends recent observations showing that SCM are major, photosynthetically-active features of the water column in the Arctic Ocean (Martin et al., 2010) and provides contemporary uptake-irradiance parameters to better tune models and remote-sensing algorithms of primary production. By distinguishing between the new and regenerated components of total primary production, our study addressed the biogeochemical significance of SCM communities for the food web and the biological CO₂ pump.

Martin et al. (2010) hypothesized that the primary productivity of SCM communities was limited by irradiance due to their position in the lower euphotic zone near the nitracline. As a corollary, they further hypothesized that SCM depend principally on NO₃⁻ and mediate a large share of water-column new production. Here we examine these hypotheses through a discussion of (1) the relative importance of dark versus light-dependent uptake for different N sources, (2) the photo-acclimation and stoichiometry of C and N uptake at low irradiance, and (3) the response of C and N uptake to environmental conditions. The discussion ends with a strategy for selecting uptake-irradiance parameters for models and remote-sensing algorithms.

4.1 N nutrition and the significance of dark versus light-driven N uptake

Dark N uptake is known to occur at night and/or during daytime when samples taken in the euphotic zone are placed in the dark or at very low irradiance. Since the midnight sun precluded “true nighttime” uptake in our study, only the light-independent component of uptake (D^B) was assessed from the y-intercept of $N - E$ curves. The nature of D^B must be considered when estimating new production from short-term N uptake rates because it can be mediated by heterotrophic bacteria and the portion taken up by phytoplankton is not necessarily constitutive (i.e. not assimilated or, more precisely,

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not leading to amino acid synthesis) since photosynthesis does not occur in the dark (e.g. N maybe be stored in cell vacuoles). In this study, however, adding D^B to N_m^B generally had a modest impact on the f -ratio, translating in potential errors of only 4–17% (9% on average) in new production estimates. A decision must nevertheless be made to include D^B or not in calculations and, since it represented a variable and sometime high proportion of total N uptake, the role of D^B in N cycling needs to be assessed.

Using antibiotics and 0.2 μm filters, Berrouard (2011) estimated absolute bacterial uptake rates in our study area to be $0.0017 \pm 0.0019 \mu\text{g N l}^{-1} \text{h}^{-1}$ for NO_3^- and $0.0032 \pm 0.0061 \mu\text{g N l}^{-1} \text{h}^{-1}$ for NH_4^+ , on average. Those numbers are close to the median absolute dark uptake ($D^B \times \text{chl } a$) values obtained here using GF/F filters ($0.0014 \mu\text{g N l}^{-1} \text{h}^{-1}$ for NO_3^- ; $0.0029 \mu\text{g N l}^{-1} \text{h}^{-1}$ for NH_4^+). Since over half the bacteria present in the water are retained by GF/F filters in the coastal Beaufort Sea (Simpson et al., 2012), we estimate that up to 39 and 45% of D^B for NO_3^- and NH_4^+ , respectively, was attributable to assimilation or non-constitutive uptake by autotrophs.

Assimilatory algal D^B requires excess C and energy previously acquired in the light, which is likely to be near the surface but is unlikely to occur under low light at the SCM, where biomass is generated primarily by local growth instead of the accumulation of cells sinking from above (Martin et al., 2010). The low occurrence of assimilatory uptake by the phytoplankton in the dark could explain the absence of correlation between D^B for NH_4^+ uptake and E_{SCM} . Since NH_4^+ is a N form favoured by bacteria, their contribution probably masks the low assimilatory rate of the phytoplankton in the dark. It would also explain why the ratio of D^B to total N uptake at light saturation was low in our study compared to previous ones (Price et al., 1985; Cochlan et al., 1991; Smith and Harrison, 1991; Probyn et al., 1996). This ratio was also much lower for NO_3^- than other N sources, as expected from the relatively high energy cost of NO_3^- reduction (Behrenfeld et al., 2008). Unlike NH_4^+ , the positive correlation between D^B for NO_3^- uptake and E_{SCM} suggest the presence of assimilatory uptake. Nevertheless, algae seem to lack energy to perform both photosynthesis and the full assimilation of NO_3^- at low

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light, leading to the release of NO_2^- (Kiefer et al., 1976; Lomas et al., 2006) and presence of a PNM near or at the SCM (see also Tremblay et al., 2008 and Martin et al., 2010). It is advantageous to use reduced N in this situation, which explains the negligible contribution of NO_2^- to total N uptake and the positive effects of NH_4^+ enrichment on NH_4^+ uptake (Fig. 9) and incubation irradiance on the f -ratio (Fig. 7).

Since N enrichment or elevated ambient N concentrations did not stimulate P_m^B in our study, we surmise that D^B was mediated mostly by bacteria, with a secondary contribution of non-constitutive uptake by phytoplankton. Without D^B , $P_m^B:N_m^B$ ratios at E_{SCM} hovered near the Redfield ratio, implying that phytoplankton did not need D^B to fulfill their N demand (Fig. 10). If anything, the autotrophic component of D^B could result from the storage of inorganic N in the vacuoles of diatoms, which are numerically important at the SCM (Martin et al., 2010), and would explain decreasing $P_m^B:N_m^B$ ratios under N enrichment (Fig. 10). Whether this storage actually occurs or eventually fuels PON synthesis before the cells sink or die is unknown. For these reasons, only the light-driven component of N uptake will be considered for further analysis.

Based on the above considerations, our working hypothesis that NO_3^- was the main form of N consumed by phytoplankton at the SCM is supported during spring-early summer (the mean f -ratio estimated for this period = 0.74 ± 0.26). However, our hypothesis is not supported for later summer and fall, when the mean f -ratio declined to 0.37 ± 0.20 due to decreasing NO_3^- availability and irradiance at the SCM, which was then often lower than the E_k for NO_3^- uptake.

4.2 Acclimation and vertical coupling of C and N uptake

SCM communities located within a strong halocline would benefit by acclimating to low irradiance. For C uptake, this expectation is consistent with the contrast between the data of Platt et al. (1982), who found no vertical differences in uptake-irradiance parameters in weakly-stratified waters (Baffin Bay), and our data set, where α was higher at the SCM than at the surface. Here, uncoupled changes in P_m^B and α resulted in

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lower E_k values for SCM communities, which maintained very high photosynthetic performance (F_v/F_m). This pattern is entirely consistent with photochemical acclimation to low light instead of a physiological response to nutrient stress, senescence or the influence of taxonomic composition (i.e. E_k -independency, sensu Behrenfeld et al., 2008).

5 The low E_k values ($24 \pm 13 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) observed during all years and seasons at the SCM imply widespread and persistent shade acclimation and generalize similar observations made during the ice-open water transition in the coastal Beaufort Sea (Palmer et al., 2011). This interpretation is supported by the sharp drop (photoinhibition) in post-incubatory F_v/F_m for SCM phytoplankton exposed to irradiances greater
10 than $70 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$ (Fig. 11) irrespective of season or region.

The photochemical acclimation observed for C uptake was not observed for NO_3^- uptake, for which N_m^B but not α was significantly higher at the SCM than at the surface (E_k -independency). Since N_m^B was also positively related to ambient NO_3^- concentration (Table B1), SCM communities near the nitracline physiologically adjusted to higher
15 N concentrations presumably by increasing their enzymatic capacity to reduce NO_3^- .

The general lack of increase in N_m^B with experimental NO_3^- enrichment suggests that acclimation occurred on time scales of days rather than hours. The inhibition of NO_3^- uptake by NH_4^+ observed in other regions (e.g. Glibert et al., 1982; Price et al., 1985; Cochlan, 1986) was not manifest in the Canadian Arctic (no significant negative correlation between the f -ratio and NH_4^+ concentration as observed by Smith and Harrison
20 1991 nor between the N_m^B for NO_3^- uptake and in situ NH_4^+ concentration), probably due to the fact that ambient NH_4^+ concentrations were generally low. Inhibition is typically observed at concentration exceeding $0.5\text{--}1.0 \mu\text{M}$ (McCarthy et al., 1977).

For NH_4^+ , the absence of correlation between N_m^B and ambient concentration was
25 probably due to the highly dynamic nature of this N pool, which defeats the purpose of acclimation. However, the clear response of N_m^B to experimental NH_4^+ enrichment indicates that phytoplankton can exploit sudden inputs, in accord with the minimal energy and enzymatic requirements of NH_4^+ assimilation. Despite this advantage, low ambient

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NH_4^+ availability forced the phytoplankton to rely strongly on NO_3^- to fulfill their N demand when irradiance and NO_3^- concentrations at the SCM were relatively high during spring-early summer (Fig. 7). This reliance decreased toward late summer-fall with declining irradiance and NO_3^- availability (SCM is likely to act like a “trap” for NO_3^- flux from deep waters; Harrison et al., 1982; Harrison, 1990; Weston et al., 2005) (Fig. 7). The synoptic manifestation of this phenomenon is well rendered by the RPI for NO_3^- uptake and the relationship between the f -ratio and NO_3^- concentrations, which indicated strong “discrimination” against this N source at relatively low ambient concentrations (Fig. 8).

Overall, the acclimation of C uptake to low light and of NO_3^- uptake to high concentrations, as well as the low cost of NH_4^+ uptake, favoured efficient C and N nutrition at the SCM. However, the different E_k values ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) obtained for C (24 ± 13), NO_3^- (18 ± 12), and NH_4^+ (7 ± 8) uptake imply a measure of vertical decoupling between total, new and regenerated production. For example, using these mean E_k values with the irradiance data of station 303 (Table 1) yields the onset of light-saturation at depths of 34, 24 and 21 m, for NH_4^+ , NO_3^- and C uptake, respectively. However, the maxima in absolute total and new production both occurred at 22 m because the strong SCM there abolished the separation that different E_k values would otherwise impart (Fig. 3). This was primarily a biomass effect, reinforced by the fact that N_m^B was twice as high for NO_3^- than NH_4^+ uptake at the SCM (see Methods; Fig. 3).

In the reconstructed profiles (Fig. 3), the depth of maximum productivity occurred at the SCM and the “classical” decrease in primary productivity with depth was not observed (Cullen, 1982; Harrison, 1990). The SCM layer thus mediated the larger part (up to 76%; close of the value of 72% estimated in the same region by Arrigo et al., 2011) of total water-column production and NO_3^- uptake (up to 98%), which underscores the need to consider this structure in remote-sensing estimations of productivity in the Arctic. This is especially true in regions where strong vertical stratification prevails (e.g. the Chuckchi Sea; Arrigo et al., 2011) and/or where NO_3^- is perennially low at the surface (e.g. the Beaufort Sea), but less so in areas characterized by strong vertical or

advective NO_3^- supply and high overall productivity (where SCM represent <10% of the annual primary production; Arrigo et al., 2011).

4.3 Environmental control of SCM productivity

Although SCM communities were shade-adapted, several if not most (47% for spring-early summer and 85% for late summer-fall) were exposed to E_{SCM} lower than the E_k for C uptake (Fig. 6). Light conditions were more favorable at the remaining stations where irradiance equaled or slightly exceeded E_k (mostly during spring-early summer) but even if E_{SCM} was 2 times higher than E_k (a condition met at only 2 out of 48 stations), P^B would not exceed 87% of P_m^B (based on Eq. 3). Primary production in the SCM layer thus operated at sub-optimal irradiance throughout most of the growth period.

Despite sub-optimal irradiance at the SCM, P_m^B may have been constrained by nutrient availability or temperature, which would negatively affect P^B when E_{SCM} exceeds E_k . Because the E_k for N uptake was lower than for C uptake, we surmise that low light levels had a much lower impact on nutrition than on photosynthesis. The independency of P_m^B from ambient N concentrations further suggests that total primary production was not nutrient-limited at the SCM and the C:N uptake ratios at E_{SCM} ($P^B:N^B$) showed no clear sign of N stress under trace additions, except perhaps when ambient N reached the lowest values (Fig. 10). This pattern is expected in a situation where SCM communities push the nitracline downward or benefit from upward N fluxes in its vicinity, as long as E_{SCM} remains above the compensation depth (e.g. ca. $0.16 \pm 0.02 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$; Tremblay et al., 2006). The much greater uptake ratios at light saturation ($P_m^B:N_m^B$; Fig. 10) suggest the possibility of N stress at light levels greatly exceeding what is realistic for the SCM, consistent with the effect of NH_4^+ enrichment on $P_m^B:N_m^B$.

In polar regions, phytoplankton experience low temperatures throughout the year but uptake-irradiance parameters do not reveal specific adaptations to this condition (Platt

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et al., 1982; Smith and Harrison, 1991). Given that optimum temperatures ($>10^{\circ}\text{C}$; Li, 1985) are greater than those observed during our study, the positive correlation between P_m^B and temperature in late summer-fall (Fig. 5) is expected and consistent with previous Arctic data sets (Harrison et al., 1982; Harrison and Platt, 1986; Harrison and Cota, 1991) and experimental studies (Subba Rao and Platt, 1984; Smith and Harrison, 1991). Despite the absence of a similar correlation at the SCM early in the season, data in the lower range of P_m^B (<1.0) were consistent with the relationship for late summer-fall (Fig. 5). Cold stations with high P_m^B values at the SCM were probably associated with fast-growing, blooming diatoms.

4.4 Strategy and rationale for the selection of uptake-irradiance parameters

The extensive spatial and regional coverage of our data set allows us to derive realistic and relevant parameters for models use in Arctic and remote sensing algorithms. Although uptake-irradiance parameters do not appear to follow regional or seasonal patterns, the typical P_m^B constant of $2\ \mu\text{g C}(\mu\text{g chl } a)^{-1}\ \text{h}^{-1}$ based on previous studies (Harrison and Platt, 1980; Subba Rao and Platt, 1984; Harrison and Cota, 1991; Smith and Harrison, 1991; Weston et al., 2005) clearly needs to be revised. In a companion study of Franklin Bay and Darnley Bay (Beaufort Sea; Palmer et al., 2011), mean P_m^B was respectively 1.25 and 0.82 during spring, similar to values reported here ($P_m^B = 0.65 \pm 0.45$). When considering spring-early summer only, P_m^B can be approximated as a function of day of the year and temperature (e.g. $P_m^B = 8.417 - 0.0229\ \text{DY} + 2.742\ T$). Otherwise P_m^B can be estimated as a function of temperature only (e.g. $P_m^B = 0.178\ T + 0.538$; Fig. 5) for post-bloom situations spanning spring, summer and fall (since P_m^B after the spring bloom apparently obeys the relationship obtained for late summer and fall). The difference in photosynthetic parameters observed between the upper mixed layer and the SCM suggests that algorithms should consider acclimation of the phytoplankton to the vertical light gradient in strongly stratified Arctic waters (e.g. implement models with at least 2 sets of parameters). At the

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very beginning of the season, the phytoplankton seems to show a continuous and rapid acclimation (within 4 to 10 days) to changing conditions at the time of the SCM development (Palmer et al., 2011). In this specific case, the E_k values used by algorithms below the upper mixed layer should be lower (e.g. $E_k = 24 \pm 13 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$) than those prescribed for surface waters (e.g. E_k of ca. $60 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$; Arrigo et al., 2011; Palmer et al., 2011).

By contrast with C uptake, the f -ratio showed a relatively weak dependence on irradiance during spring-early summer. A vertically constant value of 0.74 could thus be assumed for this period. The situation was different in late summer-fall, where the f -ratio was relatively low even at light saturation. Considering that the SCM acts as a “nutrient trap”, limiting upward NO_3^- diffusion to the surface, we would advocate using a maximum f -ratio of 0.3 in the upper mixed layer (derived from the relationship observed at SCM where f -ratio = $0.1 \text{NO}_3^- + 0.3$; see also Harrison, 1990). In the SCM layer, a f -ratio of 0.37 could be used to convert remote sensing estimations of total P into new production. In models using N as a currency (Fasham et al., 1990; Kuhn and Radach, 1997), a more dynamic parameterization of N_m^B according to the day of year could be achieved (e.g. N_m^B for $\text{NO}_3^- = -0.0005 \text{DY} + 0.16$).

5 Conclusions

Data collected over the full extent of the growth season in the Canadian Arctic revealed that primary production at the SCM is generally co-limited by light and temperature. Nevertheless, SCM communities (1) show high photosynthetic competence, (2) are well acclimated to low light conditions and (3) can be photoinhibited by irradiance levels typical of those prevailing in the upper mixed layer. These communities consume predominately NO_3^- during spring-early summer but their reliance on NO_3^- decreases seasonally as the algae eventually discriminate against this N source and use mostly NH_4^+ . The low concentrations of NH_4^+ in the water column could explain the association

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observed between the SCM and the nitracline, where the phytoplankton can meet their N demand.

The importance and dynamic nature of phytoplankton communities at the SCM demonstrate the imperative need to adapt ecosystem models and remote sensing algorithm to the strong temporal and vertical gradients of temperature, irradiance and nutrient concentrations that prevail in strongly stratified Arctic waters. A more effective parameterization could consider the vertical and seasonal dynamism of N uptake parameters observed for different N forms and the change observed in the ratio of new to regenerated production ratio throughout the growth season.

Tremblay and Gagnon (2009) showed that the major differences in productivity and trophic status at the pan-Arctic scale are controlled by nutrient supply to the surface, which is typically greater in polynyas or peripheral areas with a short ice-covered season. Within a given region, productivity can increase with the duration of the ice-free season (Pabi et al., 2008; Arrigo et al., 2011) but the relative role of nutrient re-supply versus greater exposure to irradiance on this trend is unknown. Here, we showed how the later may act in synergy with rising temperature and lead to greater productivity by SCM layers, either through more complete NO_3^- usage or by deepening of the nitracline.

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Table 1. Characteristics of the SCM at experimental stations located in the coastal Beaufort Sea (CBS), offshore Beaufort Sea (OBS), North-West Passage (NWP), Western, Central and Eastern Baffin Bay (WBB, CBB and EBB, respectively) for spring–early summer and late summer–fall. Stations where incubations were also performed with surface samples are marked with an asterisk and “–” indicates values below the limit of detection.

| Region | Station | Date | Day of year | Depth (m) | [chl <i>a</i>] ($\mu\text{g L}^{-1}$) | [NO ₃ ⁻] (μM) | [NO ₂ ⁻] (μM) | [NH ₄ ⁺] (μM) | [Urea] (μM) | Total N (μM) | <i>T</i> (°C) | % of <i>E</i> at surface | <i>E</i> _{SCM} ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) |
|--------|-------------------|------------|-------------|-----------|--|---|---|---|--------------------------|---------------------------|---------------|--------------------------|---|
| CBS | D43 ¹ | 28-04-2008 | 119 | 30 | 0.73 | 3.63 | 0.09 | 0.02 | – | 3.77 | -1.7 | 6.4 | 0.3 |
| CBS | 1020A | 06-05-2008 | 127 | 44 | 0.46 | 6.21 | 0.26 | 0.02 | – | 6.54 | -1.7 | 8.8 | 48 |
| CBS | 405b | 19-05-2008 | 140 | 16 | 8.31 | 0.00 | 0.10 | 0.05 | – | 0.15 | -1.0 | 16 | 67 |
| CBS | 1011 | 21-05-2008 | 142 | 63 | 0.88 | 6.53 | 0.11 | 1.01 | – | 7.66 | -1.5 | 1.7 | 6.3 |
| CBS | 1806 | 23-05-2008 | 144 | 50 | 4.47 | 7.53 | 0.11 | – | – | 7.65 | -1.4 | 4.3 | 19 |
| CBS | 9008 | 27-05-2008 | 148 | 37 | 12.10 | 1.34 | 0.08 | – | – | 1.42 | -1.2 | 6.8 | 34 |
| CBS | 405 | 01-06-2008 | 153 | 37 | 0.53 | 4.02 | 0.16 | 0.20 | – | 4.38 | -1.7 | 11 | 39 |
| CBS | F7 ¹ | 08-06-2008 | 160 | 12 | 2.98 | 1.87 | 0.18 | 0.25 | 0.1 | 2.42 | -1.4 | 44 | 32 |
| CBS | 405b | 10-06-2008 | 162 | 37 | 0.84 | 2.32 | 0.19 | 0.10 | 0.1 | 2.75 | -1.2 | 4.8 | 32 |
| CBS | F7 ¹ | 19-06-2008 | 171 | 33 | 9.57 | 5.00 | 0.16 | 0.35 | – | 5.52 | -1.4 | 4.7 | 1.7 |
| CBS | FB07 ¹ | 21-06-2008 | 173 | 37 | 4.42 | 1.16 | 0.14 | 0.16 | – | 1.53 | -1.3 | 2.7 | 10 |
| CBS | 1216 | 23-06-2008 | 175 | 33 | 1.27 | 3.44 | 0.12 | 0.18 | – | 3.74 | -1.4 | 2.2 | 16 |
| CBS | F7 ¹ | 24-06-2008 | 176 | 33 | 4.80 | 1.61 | 0.08 | 0.63 | – | 2.34 | -1.3 | 6.7 | 27 |
| CBS | 1200 | 27-06-2008 | 179 | 36 | 1.52 | 0.80 | 0.16 | 0.09 | 0.1 | 1.18 | -1.2 | 2.7 | 18 |
| CBS | 1208 | 28-06-2008 | 180 | 35 | 1.64 | 0.10 | 0.00 | – | 0.2 | 0.27 | -1.1 | 1.7 | 12 |
| OBS | 421 | 01-07-2008 | 183 | 62 | 3.55 | 0.79 | 0.08 | 0.08 | – | 0.96 | -1.2 | 2.8 | 21 |
| CBS | 6006 | 04-07-2008 | 186 | 54 | 7.55 | 4.55 | 0.20 | 0.06 | 0.2 | 5.05 | -1.3 | 2.0 | 13 |
| CBS | 2010 | 06-07-2008 | 188 | 29 | 0.37 | 3.89 | 0.14 | 0.04 | 0.2 | 4.25 | -1.5 | 5.9 | 32 |
| CBS | 410 | 08-07-2008 | 190 | 54 | 1.25 | 3.54 | n/d | 0.26 | – | 3.80 | -1.5 | 4.6 | 30 |
| CBS | 416 | 10-07-2008 | 192 | 73 | 4.52 | 6.77 | 0.14 | 0.19 | – | 7.10 | -1.4 | 0.9 | 5.8 |
| | | | Mean (SD) | 40 (15) | 3.59 (3.42) | 3.26 (2.32) | 0.13 (0.06) | 0.22 (0.25) | 0.15 (0.05) | 3.62 (2.40) | -1.4 (0.2) | 7.0 (9.3) | 23 (17) |

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Table 1. Continued.

| Region | Station | Date | Day of year | Depth (m) | [chl <i>a</i>] ($\mu\text{g L}^{-1}$) | [NO ₃ ⁻] (μM) | [NO ₂ ⁻] (μM) | [NH ₄ ⁺] (μM) | [Urea] (μM) | Total N (μM) | <i>T</i> (°C) | % of <i>E</i> at surface | <i>E</i> _{SCM} ($\mu\text{mol quanta m}^{-2} \text{s}^{-1}$) |
|--------|-----------|------------|-------------|-----------|--|---|---|---|--------------------------|---------------------------|---------------|--------------------------|---|
| EBB | BA01-05 | 16-08-2005 | 228 | 24 | 0.88 | 0.28 | 0.08 | 0.05 | n/d | 0.41 | 0.0 | 9.2 | 13 |
| WBB | BA03-05 | 18-08-2005 | 230 | 42 | 2.14 | 0.07 | 0.06 | – | n/d | 0.13 | 1.9 | 0.5 | 1.4 |
| CBB | BA04-05 | 22-08-2005 | 234 | 25 | 1.05 | 5.34 | 0.30 | – | n/d | 5.64 | -1.4 | 10 | 26 |
| NWP | S3 | 23-08-2005 | 235 | 33 | 3.45 | 2.73 | 0.12 | 0.33 | n/d | 3.18 | -0.7 | 4.8 | 4.4 |
| NWP | S4 | 24-08-2005 | 236 | 29 | 6.38 | 0.49 | 0.09 | 0.39 | n/d | 0.97 | -1.1 | 4.4 | 8.5 |
| CBS | S201 | 02-09-2005 | 245 | 19 | 0.79 | 1.13 | 0.10 | 0.41 | n/d | 1.64 | 0.4 | 3.6 | 8.5 |
| OBS | S10 | 05-09-2005 | 248 | 52 | 0.41 | 2.34 | 0.12 | 0.14 | n/d | 2.60 | -1.0 | 9.3 | 23 |
| CBS | CA08-05 | 09-09-2005 | 252 | 43 | 0.41 | 0.70 | 0.10 | – | n/d | 0.80 | -0.2 | 8.1 | 13 |
| CBS | CA18-05 | 12-09-2005 | 255 | 30 | 2.70 | 4.82 | 0.22 | 0.11 | n/d | 5.15 | -1.1 | 4.4 | 8.6 |
| HB | S22 | 06-10-2005 | 279 | 35 | 0.83 | 0.70 | 0.09 | 0.04 | n/d | 0.83 | -1.4 | 2.5 | 1.4 |
| HB | NR24 | 10-10-2005 | 283 | 17 | 1.35 | 1.03 | 0.08 | 0.25 | n/d | 1.36 | 5.1 | 0.8 | 2.0 |
| CBB | 132* | 09-09-2006 | 252 | 34 | 0.32 | 4.03 | 0.09 | 0.34 | n/d | 4.46 | -1.4 | 2.4 | 1.3 |
| EBB | 131* | 11-09-2006 | 254 | 35 | 0.62 | 4.84 | 0.23 | 0.47 | n/d | 5.54 | -0.2 | 1.3 | 2.6 |
| WBB | 118 | 14-09-2006 | 257 | 50 | 1.84 | 1.23 | 0.07 | 0.12 | n/d | 1.42 | -1.2 | 0.1 | 0.1 |
| CBB | 108* | 17-09-2006 | 260 | 40 | 1.50 | 2.32 | 0.11 | 0.34 | n/d | 2.77 | 0.7 | 0.9 | 1.5 |
| NWP | 303* | 21-09-2006 | 264 | 22 | 1.36 | 2.34 | 0.06 | 0.64 | n/d | 3.04 | 0.2 | 12 | 22 |
| NWP | 307* | 23-09-2006 | 266 | 31 | 0.16 | 5.47 | 0.12 | 0.63 | n/d | 6.22 | -1.3 | 9.1 | 13 |
| CBS | 405* | 01-10-2006 | 274 | 48 | 0.67 | 8.30 | 0.47 | 0.30 | n/d | 9.07 | -1.3 | 0.8 | 0.9 |
| CBS | 408* | 03-10-2006 | 276 | 67 | 0.32 | 7.13 | 0.27 | 0.09 | n/d | 7.49 | -1.3 | 2.1 | 2.3 |
| CBS | SH (409)* | 04-10-2006 | 277 | 35 | 0.47 | 0.19 | 0.09 | 0.25 | n/d | 0.53 | 0.4 | 2.2 | 2.6 |
| CBS | 436 | 09-10-2006 | 282 | 18 | 0.65 | 0.03 | 0.07 | 0.04 | n/d | 0.14 | 0.4 | 11 | 3.2 |
| CBS | 435* | 12-10-2006 | 285 | 55 | 0.16 | 3.69 | 0.20 | 0.03 | n/d | 3.92 | -1.2 | 3.3 | 1.6 |
| CBS | 407 | 18-10-2006 | 291 | 30 | 0.70 | 0.88 | 0.15 | 0.13 | n/d | 1.16 | -0.5 | 2.6 | 1.0 |
| WBB | 101 | 29-09-2007 | 272 | 41 | 0.31 | 1.66 | 0.00 | 0.79 | n/d | 2.45 | -1.6 | 1.4 | n/d |
| EBB | 115 | 01-10-2007 | 274 | 80 | 0.13 | 10.6 | 0.12 | – | – | 10.73 | -0.8 | 0.001 | n/d |
| CBB | 108 | 03-10-2007 | 276 | 30 | 5.62 | 2.22 | 0.03 | 0.35 | – | 2.61 | -0.6 | 3.4 | n/d |
| NWP | 302 | 07-10-2007 | 280 | 37 | 0.24 | 0.63 | 0.03 | 0.51 | – | 1.17 | 0.4 | 6.1 | n/d |
| CBS | 435 | 17-10-2007 | 290 | 16 | 0.24 | 1.85 | 0.02 | 0.29 | – | 2.16 | -0.9 | 24 | 6.6 |
| CBS | 1806 | 19-10-2007 | 292 | 22 | 0.33 | 0.00 | 0.02 | 0.02 | – | 0.04 | -0.8 | 17 | 1.8 |
| CBS | 408 | 22-10-2007 | 295 | 12 | 0.65 | 0.51 | 0.15 | 0.32 | n/d | 0.98 | -1.1 | 22 | 3.6 |
| CBS | 407 | 23-10-2007 | 296 | 34 | 0.70 | 2.28 | 0.14 | 0.34 | n/d | 2.76 | -1.3 | 4.1 | 0.4 |
| CBS | 405 | 25-10-2007 | 298 | 31 | 0.23 | 0.47 | 0.06 | 0.17 | n/d | 0.70 | -0.7 | 6.0 | 0.9 |
| CBS | 1116 | 28-10-2007 | 301 | 7 | 0.23 | 7.10 | 0.31 | 0.46 | – | 7.89 | -1.5 | 47 | 13 |
| | | | Mean | 34 | 1.15 | 2.65 | 0.13 | 0.29 | – | 3.03 | -0.5 | 7.2 | 6.5 |
| | | | (SD) | (15) | (1.47) | (2.70) | (0.10) | (0.20) | (–) | (2.79) | (1.3) | (9.3) | (7.3) |

¹ *E*_{SCM} corrected for the presence of ice-covered.

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Table A1. Summary of uptake-irradiance parameters for N uptake by at SCM.

| NO_3^- | | | | | | |
|------------------|---|--|--|---|--------------------|--|
| | N_m^β $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | α $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | E_k $(\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$ | D^β $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | Relative D^β | |
| Mean (\pm SD) | 0.042 ± 0.043 | 0.004 ± 0.003 | 18 ± 12 | 0.010 ± 0.030 | 14 ± 17 | |
| Minimum | 0.001 | 0 | 1 | 0 | 0 | |
| Maximum | 0.210 | 0.040 | 57 | 0.210 | 64 | |
| NH_4^+ | | | | | | |
| | N_m^β $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | α $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | E_k $(\mu\text{mol quanta m}^{-2} \text{ s}^{-1})^{-1}$ | D^β $\mu\text{g N } (\mu\text{g chl a})^{-1} \text{ h}^{-1}$ | Relative D^β | |
| Mean (\pm SD) | 0.016 ± 0.017 | 0.005 ± 0.008 | 7 ± 8 | 0.008 ± 0.009 | 26 ± 24 | |
| Minimum | 0 | 0 | 1 | 0 | 0 | |
| Maximum | 0.070 | 0.039 | 43 | 0.030 | 80 | |

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Table B1. Significant correlations between water-column variables and uptake-irradiance parameters for the data set where SCM communities were incubated with trace (*T*) or enriched (*E*) N additions.

| | Carbon | | | | | | | | | | | |
|--|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|-------------------|
| | P_m^B | | | | E_k | | | | α | | | |
| | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ |
| Temperature (°C) | 0.85*** | 0.73*** | – | 0.86*** | 0.88*** | 0.79*** | – | 0.88*** | – | – | – | – |
| Day of the year | – | – | –0.53** | – | – | – | – | – | – | – | – | – |
| [chl <i>a</i>] ($\mu\text{g l}^{-1}$) | – | – | 0.51** | – | – | – | 0.43* | – | – | – | – | – |
| [NO_3^-] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| [NO_2^-] (μM) | – | – | – | – | – | – | – | – | –0.39* | – | – | – |
| [NH_4^+] (μM) | – | – | – | – | – | – | – | – | – | 0.46* | – | – |
| Total [N] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| E_{SCM} | – | – | 0.49* | – | – | – | 0.48* | – | – | – | – | – |
| | Nitrogen | | | | | | | | | | | |
| | N_m^B | | | | E_k | | | | α | | | |
| | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ | $\text{NH}_4^+ T$ | $\text{NO}_3^- T$ | $\text{NH}_4^+ E$ | $\text{NO}_3^- E$ |
| Temperature (°C) | – | – | – | – | – | – | – | – | – | – | – | – |
| Day of the year | – | –0.36* | –0.50** | –0.60*** | – | – | – | – | – | –0.44* | –0.61*** | – |
| [chl <i>a</i>] ($\mu\text{g l}^{-1}$) | – | – | 0.53** | 0.58*** | – | – | – | – | 0.36* | 0.37* | 0.54** | – |
| [NO_3^-] (μM) | – | 0.52** | – | – | – | – | – | – | 0.35* | – | 0.35* | – |
| [NO_2^-] (μM) | – | 0.53** | – | – | – | – | – | – | – | – | – | – |
| [NH_4^+] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| Total [N] (μM) | – | 0.52** | – | – | – | – | – | – | 0.36* | – | – | – |
| E_{SCM} | – | – | 0.67*** | 0.62*** | – | – | 0.44* | – | – | – | – | – |

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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Table B2. Significant correlations between water-column variables and uptake-irradiance parameters for the data set where surface and SCM communities were incubated with trace (*T*) or enriched (*E*) NO_3^- additions.

| | Carbon | | | | | | | | | | | |
|--|----------------------------|------------------------|----------------------------|------------------------|----------------------------|------------------------|----------------------------|------------------------|----------------------------|------------------------|----------------------------|------------------------|
| | P_m^β | | | | E_k | | | | α | | | |
| | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM |
| Temperature (°C) | 0.93*** | – | 0.97*** | – | – | 0.72* | 0.74* | – | 0.76* | – | 0.81* | – |
| Day of the year | – | – | – | – | – | – | – | – | – | 0.68* | – | 0.78* |
| [chl <i>a</i>] ($\mu\text{g l}^{-1}$) | – | – | – | – | – | 0.68* | – | – | – | – | – | – |
| [NO_3^-] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| [NO_2^-] (μM) | – | – | – | – | – | –0.69* | – | – | – | – | – | – |
| [NH_4^+] (μM) | – | – | – | 0.72* | – | 0.74* | – | 0.82* | – | – | – | – |
| Total [N] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| E_{SCM} | – | – | – | 0.90** | – | – | – | 0.95*** | – | – | – | – |
| | Nitrogen | | | | | | | | | | | |
| | N_m^β | | | | E_k | | | | α | | | |
| | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM | NO_3^- Surface | NO_3^- SCM |
| Temperature (°C) | – | – | – | – | 0.71* | 0.82** | – | 0.94*** | – | – | – | – |
| Day of the year | – | – | –0.84** | – | – | – | – | – | – | 0.70* | – | – |
| [chl <i>a</i>] ($\mu\text{g l}^{-1}$) | – | – | – | – | – | 0.87** | 0.86** | 0.82* | – | – | – | – |
| [NO_3^-] (μM) | – | – | – | – | – | – | 0.81* | – | – | – | – | – |
| [NO_2^-] (μM) | – | – | – | – | – | – | – | – | – | – | – | – |
| [NH_4^+] (μM) | – | – | – | 0.85** | 0.93*** | – | – | – | 0.95** | 0.72* | – | – |
| Total [N] (μM) | – | – | – | – | 0.94*** | – | – | – | 0.90** | – | – | – |
| E_{SCM} | – | – | – | 0.86** | – | – | 0.77* | – | – | – | – | 0.73* |

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

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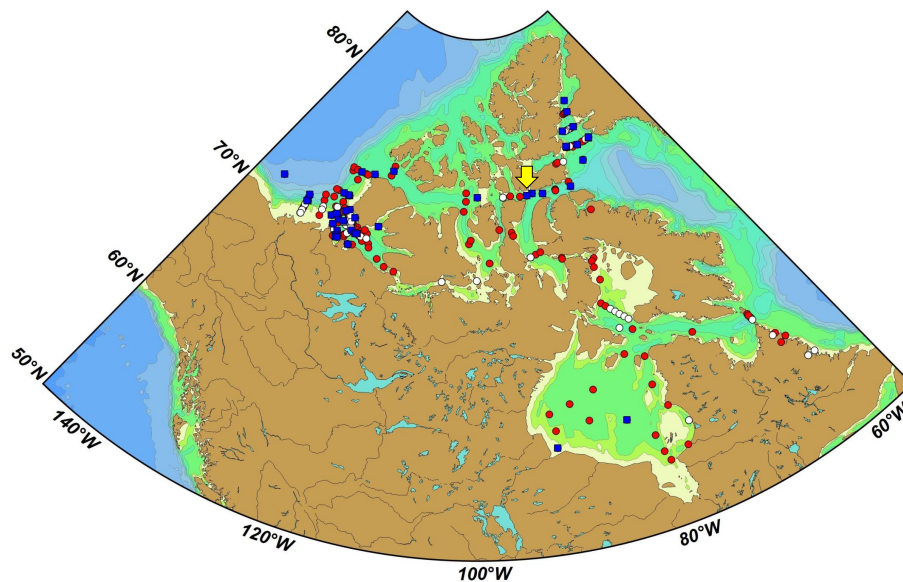


Fig. 1. Location of all sampling stations (red circles) and those where incubation were performed (blue squares). Open symbols represent stations with no visible SCM and the yellow arrow points to station 303, which is analyzed separately in the text.

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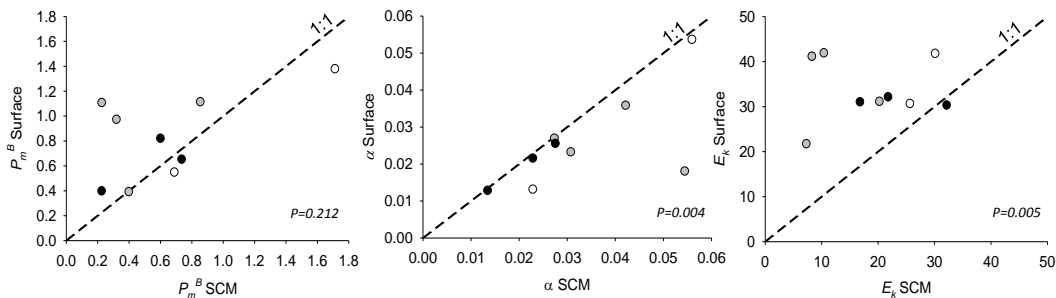


Fig. 2. Comparison of photosynthesis-irradiance parameters (P_m^B , α and E_k) between the surface and the SCM in Baffin Bay (black), the Canadian Archipelago (white) and the Beaufort Sea (gray). The level of significance (p) for the difference between paired samples is given in each panel.

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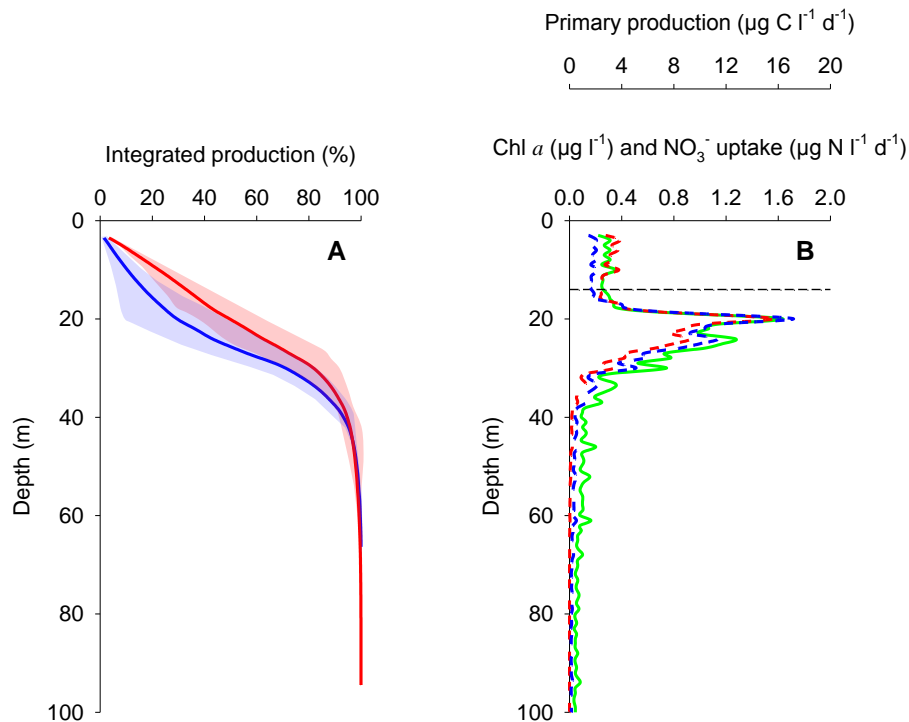


Fig. 3. Reconstructed profiles of **(A)** averaged integrated production (% of total water-column production; standard deviation delimited by the shaded areas) for C uptake (red) and N uptake (blue) for incubations performed simultaneously with surface and SCM samples and **(B)** chl *a* concentration estimated from post-calibrated *in vivo* fluorescence ($\mu\text{g l}^{-1}$; solid green line) and primary production ($\mu\text{g C l}^{-1} \text{d}^{-1}$; red dashed line) and NO_3^- uptake ($\mu\text{g N l}^{-1} \text{d}^{-1}$; blue dashed line) estimated from uptake-irradiance parameters for station 303 in 2006 (yellow arrow in Fig. 1; left-hand side). The black dashed line marks the depth of the pycnocline (14 m).

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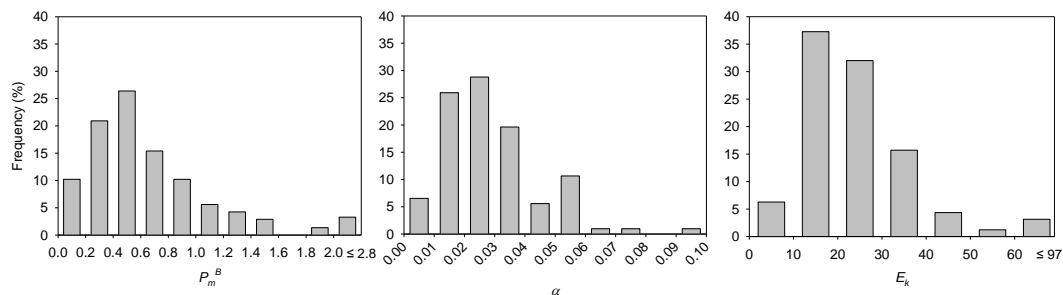


Fig. 4. Relative frequency distribution of photosynthesis-irradiance parameters at the SCM.

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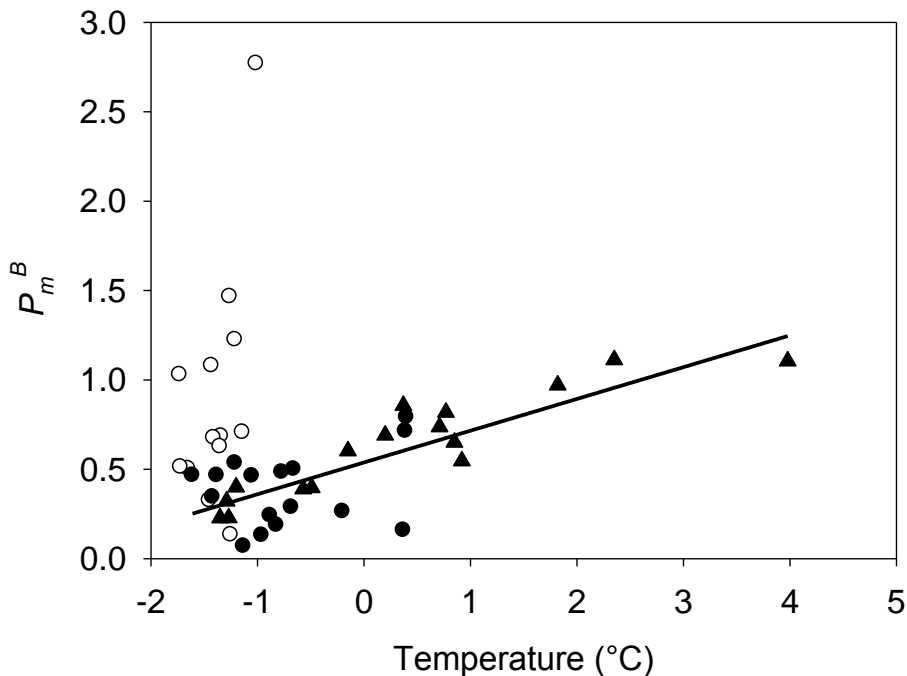


Fig. 5. Relationships between P_m^B and in situ temperature for spring-early summer (open symbols) and late summer-fall (solid symbols) for surface (triangles) and SCM (circles) communities. The line represents the linear regression for late summer-fall dataset.

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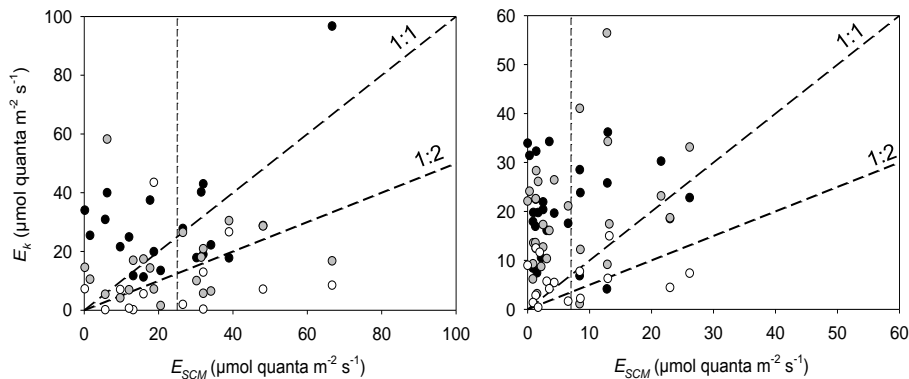


Fig. 6. Relationship between E_k and E_{SCM} for photosynthesis (black circles) and the uptake of NO_3^- (gray circles) and NH_4^+ (white circles) during spring-early summer (left-hand side) and late summer-fall (right-hand side). The dashed vertical lines represent the mean E_{SCM} for each season and the dashed lines provide visual reference for 1:1 and 1:2 ratios.

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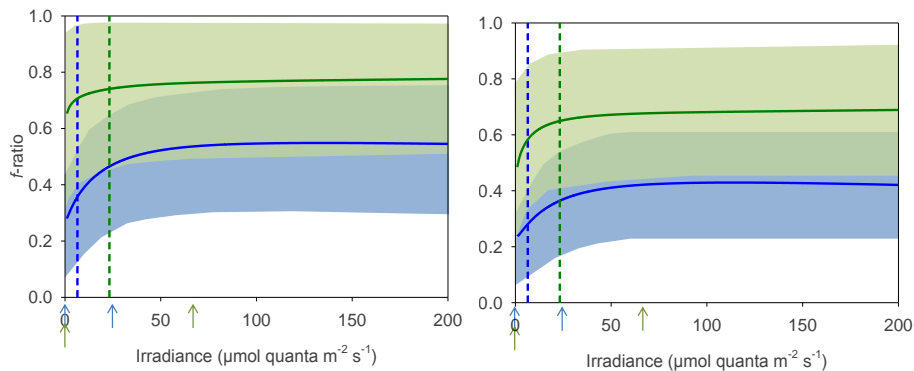


Fig. 7. Averages (solid lines) and ranges (shaded areas) of the f -ratio at the SCM as a function of incubation irradiance during spring-early summer (green) and late summer and fall (blue), calculated with (right-hand side) or without (left-hand side) dark uptake (D^B). Arrows and dashed lines give the range and mean of E_{SCM} , respectively.

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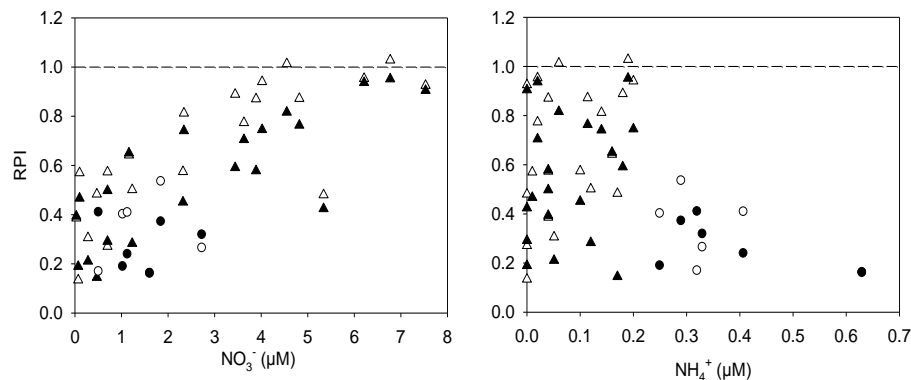


Fig. 8. Relationships between the ambient concentrations of NO_3^- (left-hand side) or NH_4^+ (right-hand side) and the relative preference index (RPI) for NO_3^- calculated with D^B included (solid symbols) or not (open symbols) for NH_4^+ concentrations above (circles) and below or equal to (triangles) 0.2 μM .

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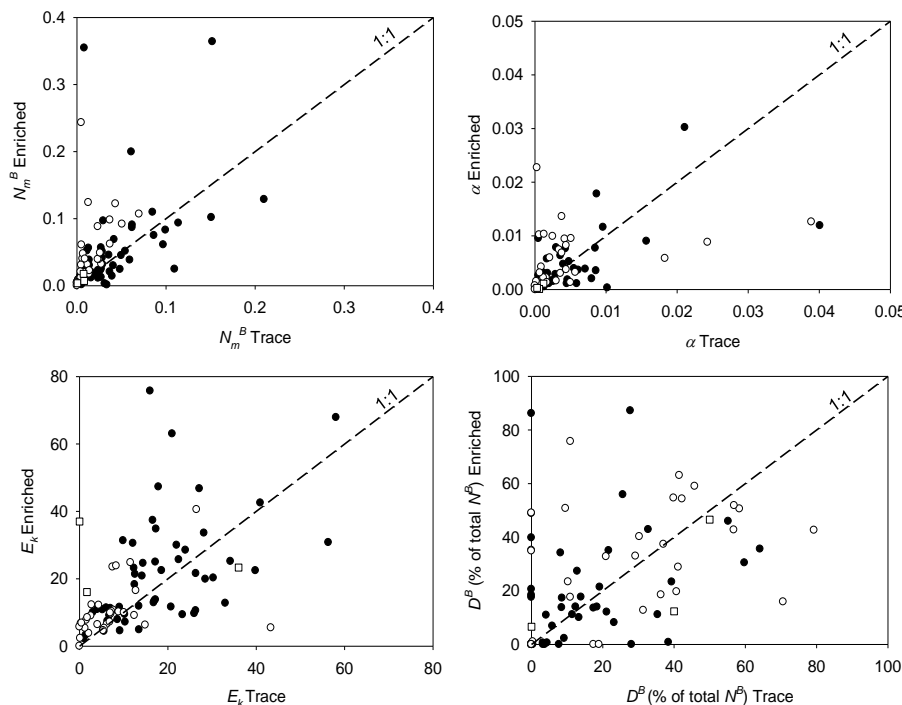


Fig. 9. Response of N_m^B , α , E_k and D^B for NO_3^- (solid circles), NH_4^+ (open circles), and NO_2^- (open squares) uptake to experimental N enrichment during incubations (see Methods). The dashed 1:1 line represents a lack of response and is provided for visual reference. To ease the comprehension, the standard error is not presented in the graph (refer to “Sensor calibrations and data transformations” section).

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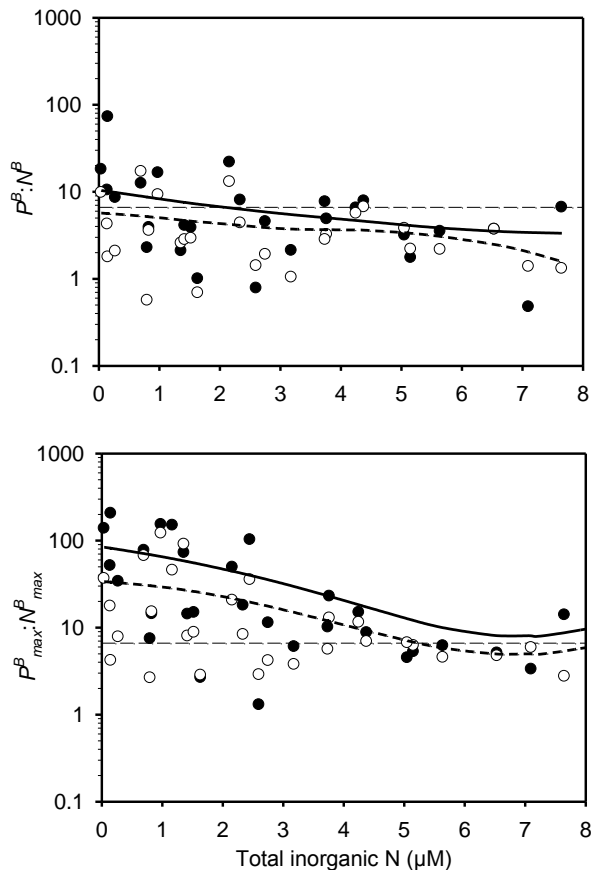


Fig. 10. Relationships between total inorganic N and C:N uptake ratios under trace (closed symbols) and enriched (open symbols) N additions at E_{SCM} (upper panel) and under saturating light conditions (bottom panel). Lines indicate the Redfield ratio (fine dashed) and moving averages for trace (solid) and enriched (dashed) conditions.

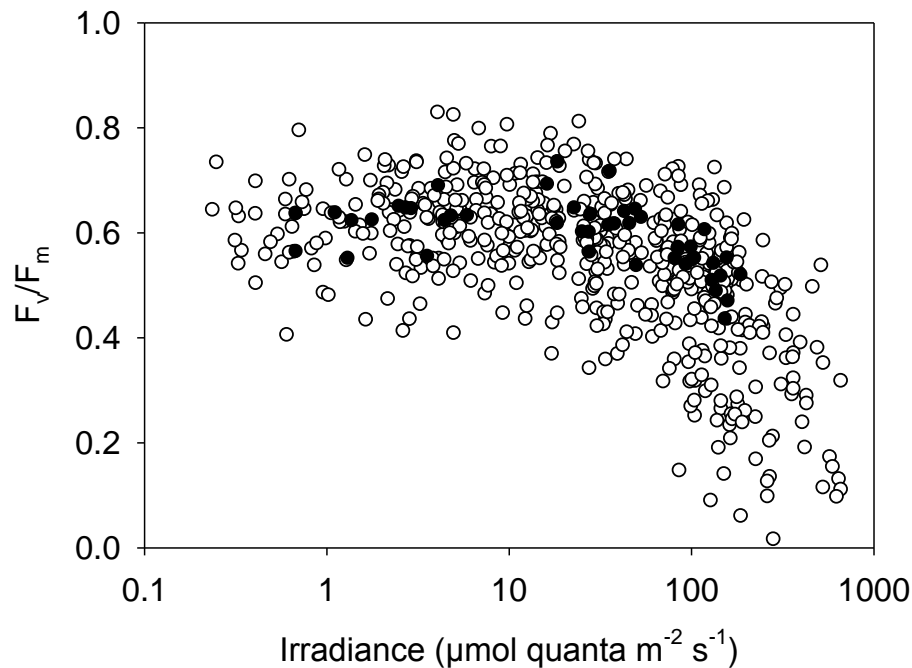


Fig. 11. Changes in F_v/F_m after light-gradient incubations of SCM algae (open symbols) and surface algae (solid symbols).

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