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SHORT NOTE

Short note: extracellular export and consumption of glucose in Antarctic sea ice

Fraser Kennedy[1] · **Andrew McMinn**[1,2] · **Andrew Martin**[1]

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Abstract

Extracellular carbohydrate production is widespread in sea ice microbial communities, being produced by both algae and bacteria. Under stressful conditions, including nutrient limitation and high light, cells may export excess fixed carbon as glucose. Glucose microsensors were used to measure extracellular glucose exudation and consumption in a sea ice algal community. Glucose export increased with increasing irradiance between 15 and 512 µmol photons m^{-2} s^{-1}. This export correlated with declining F_vF_m values and increasing NPQ values, implying that glucose export resulted from exposure to above optimal irradiances. Glucose concentrations in samples treated with DCMU to block photosynthesis, declined at all irradiances. Bacterial consumption of glucose was between 6 and 34% of extracellular export per hour. There have been very few measurements of DOC/glucose in sea ice and the data presented here make an important contribution to our understanding of sea ice microbial processes.

Keywords Glucose · Antarctic microsensor · Sea ice algae

Introduction

Polar sea ice contains high biomass, specifically diverse microbial communities that make a major contribution to the annual primary productivity of perennially ice-covered polar seas (Arrigo 2014). Biomass is typically dominated by diatom communities although other protists, bacteria, Archea and viruses are also abundant (McMinn et al. 2020). Even though temperatures and under-ice irradiances are low, productivity rates are often high and comparable to productive communities elsewhere (Lizotte 2001; McMinn et al. 2012; van Leeuwe et al. 2018).

Extracellular carbohydrate production is widespread in sea ice microbial communities, being produced by both algae and bacteria (Ugalde et al. 2014). One class of carbohydrates, extracellular polymeric substances (EPS), has been shown to have multiple roles that include cell motility, substrate attachment and protection from grazing (Underwood and Kromkamp 1999; Staats et al. 2000; Cook et al. 2007). Much of this EPS is composed of polysaccharides, uronic acids, and sulphated sugars (Underwood and Paterson 2003; Bellinger et al. 2009; Oakes et al. 2010; Rivaro et al. 2021). Microalgal dissolved organic carbon (DOC) production and export are fundamental characteristics that underpin the functioning of microbial food webs (Martin et al. 2011, 2012). After export from the microalgae, the DOC is rapidly taken up by both heterotrophic bacteria and the microalgae. It has been shown that most microalgae have the ability to directly take up glucose (Leles et al. 2019). Extracellular release of DOC from microalgae is mostly by either cell lysis, resulting from grazing or viral attack, or photosynthetic overflow, i.e. where photosynthetic carbon fixation exceeds that required for balanced macromolecular synthesis and the resulting excess photosynthate is released directly into the water column (Smith and Underwood 2000). The availability of an organic substrate is essential for heterotrophic bacterial growth and the effective functioning of the microbial loop (Azam et al. 1983). There is consequently often a close and coupled association between autotrophic producers, such as diatoms, and bacterial consumers (Fenchel 2008; Martin et al. 2012). The composition of DOC exudates from microalgae is dominated by glucose, which often comprises more than 70% of the total (Hama and Yanagi 2001; Haas

✉ Andrew McMinn
Andrew.mcminn@utas.edu.au

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag129, Hobart, TAS 7001, Australia

[2] College of Marine Life Sciences, Ocean University of China, Qingdao 266003, China

and Wild 2010; Underwood et al. 2010). The causes and drivers of extracellular DOC export (through photosynthetic overflow) are not well understood, but any process that leads to a reduction in growth, such as nutrient limitation or excessive light (Staats et al. 1999; Underwood and Paterson 2003; Cook et al. 2004, 2007), is likely to contribute. Extracellular DOC exudation in culture, for instance, is mostly associated with the low nutrient, stationary phase of growth rather the exponential phase (Myklesstad 1977). Under ice nutrients are usually abundant and non-limiting during spring in McMurdo Sound (McMinn et al. 1999) and so growth limitation is most likely to result from insufficient light.

Whilst a range of organic carbon compound categories (e.g. lipids, proteins and carbohydrates) have previously been quantified in the EPS of sea ice (Palmisano and Sullivan 1985; Aslam et al. 2012; Ugalde et al. 2014), glucose itself was first identified as an important component of sea ice habitats by Underwood et al. (2010). Extracellular glucose production has since been documented by Aslam et al. (2016). Here we examine extracellular glucose exudation and consumption in sea ice exposed to a light gradient. We hypothesise that excessive irradiance, i.e. light levels high enough to cause photoinhibition, will lead to an increase in glucose exudation.

Materials and methods

Three replicate sea ice cores, within one metre of each other, were collected from Cape Evans, Antarctica (77° 37′ 99″ S, 166° 23′ 99″ E), by SIPRE corer on 12 November 2019.

The bottom 5 mm of each core was shaved into 500 ml of pre-chilled filtered sea water and stored in the dark at ~ 0 °C for 20 min for the cells to acclimate. This approach resulted in a drop in salinity of less than 2%. Chlorophyll *a* analysis of the sea ice community followed McMinn et al. (2007). Relative species analysis was based on a count of 400 cells using a Zeiss Axioskop microscope at 400×.

Subsamples (5 ml) from each ice core were placed in 3 ml cuvettes and exposed to light levels of 15, 68, 227, and 512 µmol photons m^{-2} s^{-1} for four minutes for the glucose concentrations to be measured. This time period was considered sufficient to measure the change in glucose concentration over time (i.e. extracellular glucose production/consumption) but insufficient for algal and bacterial biomass to change. Glucose measurements were made every 1 s. The control sample, which contained the same samples but with the sea ice algae removed, was also measured at each irradiance. DCMU (concentration 20 mM) was added to an additional set of samples from the same cores and measured at the same range of irradiances. All incubations and measurements occurred at 0 °C.

Glucose measurements

A glucose biosensor (Pinnacle Technology Lawrence KS, USA) was used to measure net glucose exudation following McMinn and Lee (2018). This biosensor uses the oxidase enzyme to reduce the glucose molecules and produce hydrogen peroxide as a by-product. The hydrogen peroxide is reduced on a platinum electrode to produce electrons that are then detected on an Ag/AgCl reference electrode (McMinn and Lee 2018). As relatively high glucose concentrations are required for detection (> 2–5 µM L^{-1}), it was important to use relatively high biomass sea ice samples. The output of each biosensor (picoamps) was calibrated against a standard curve (D-glucose standard, Sigma Aldrich, St. Louis, MO, USA), composed of glucose solutions at concentrations of 0.125, 0.25, 0.375, 1.375 and 2.375 mM L^{-1}. This standard curve was used to convert the raw millivolt signal of the biosensors to actual glucose concentrations. The biosensors have a 90% response time of ~ 4 s (McMinn and Lee 2018).

The glucose biosensor was mounted onto a motorized micromanipulator (Unisense A/S, Aarhus, Denmark) and connected to a field multimeter (Unisense, A/S, Aarhus, Denmark); the raw data were converted into mg glucose L^{-1} using the relationship from the standard curve.

To obtain total glucose exudation, the glucose consumption in the dark (the control) was added to the glucose production in the light. Glucose consumption in the dark represents heterotrophic uptake of glucose by both algae and bacteria. The exudation rate was measured by determining the change in glucose concentration over two minutes.

Exudation rates were normalized to chlorophyll *a* (chl *a*) concentrations and time [µM glucose (mg chl *a*)$^{-1}$ h^{-1}]. Chlorophyll *a* concentration of each replicate was measured by fluorometer (Turner 10AU, KA), using the acidification method, noting that the sea ice algal community was the same in each replicate.

Pulse amplification-modulated fluorometry (PAM)

Chlorophyll *a* fluorescence of photosystem II was measured using a pulse amplitude-modulated fluorometer (Water-PAM, Walz, Effeltrich, Germany) with an internal actinic light source centred on 660 nm. All samples were dark acclimated for 30 min prior to measurement.

A more complete description of the PAM methods used is described in Kennedy et al. (2020). Fluorescence induction curves, which were used to examine the effect of increasing irradiance on PSII reaction centre kinetics and energy dissipation mechanisms, were obtained under

software control (WinControl 3; Walz). Cells were first dark adapted for 30 min and then exposed to a brief pulse of far-red illumination (wavelength > 680 nm) for 5 s to oxidize PSI and the electron transport chain to gain an estimate of F_0. Induction curves were initiated by first determining F_v/F_m by a saturation pulse, followed by a delay of 30 s before actinic illumination (either 15, 68, 227 or 516 µmol photons m^{-2} s^{-1}) was turned on. Additional saturation pulses were performed at the onset of actinic illumination and every 20 s thereafter until the cessation of actinic light four minutes later. The final saturation pulse at four minutes, with actinic light turned off, was used to determine the final F_v/F_m value and non-photochemical quenching (NPQ). NPQ represents the fraction of heat that is dissipated via regulated photoprotective mechanisms such as the xanthophyll cycle and is derived from:

$$\mathrm{NPQ} = \left(F_m - F'_m\right)/F'_m \text{ (Genty et al. 1989)}$$

Statistics

Pearson correlations were performed to observe relationships between glucose exudation, F_v/F_m and NPQ using the software package Rstudio [RStudio team (2021), version 1.4.1106]. Data were checked for normality using the Shapiro–Wilk test.

Results

Sea ice at Cape Evans on 12 November 2019 was 1.25 m thick without a snow cover. Chlorophyll *a* concentration was 74.9 ± 6.9 mg chl*a* m^{-2} and the ice algal community was dominated by *Nitzschia stellata* (52%), *Berkelaya adeliense* (36%) and *Navicula glaciei* (7%). Diatoms comprised > 99% of the protists.

Glucose measurements

Independent glucose measurements were made at each of the four light treatments (15, 68, 227, 512 µmol photons m^{-2} s^{-1}). At each irradiance, additional samples were used to measure a control (no added sea ice algae) and samples treated with DCMU, to inhibit photosynthetic activity. At all light levels, glucose concentrations in the control samples were beneath the level of detection. Glucose concentrations across all other samples ranged from 0.012 to 0.167 mg L^{-1}. Net extracellular glucose export rates were 0.638 ± 1.062, 0.844 ± 0.022, 13.472 ± 11.374 and 9.942 ± 1.282 µM glucose (mg chl *a*)$^{-1}$ h^{-1} at 15, 68, 227 and 512 µmol photons m^{-2} s^{-1}, respectively (Table 1). Samples treated with DCMU experienced a drop in glucose concentrations, presumably mostly due to bacterial consumption. Glucose consumption rates were 0.283 ± 0.112, 0.799 ± 0.325 and 0.766 ± 0.0005 µM glucose (mg chl *a*)$^{-1}$ h^{-1} at 68, 227 and 512 µmol photons m^{-2} s^{-1}, respectively (Table 1). Electrode response in the 15 µmol photons m^{-2} s^{-1} sample was unstable and so no consumption rate could be measured. Drop in glucose concentrations in the dark (bacterial consumption) was equivalent to ~ 34, 6 and 8% of extracellular glucose production per hour in the light; these are equivalent to glucose pool turnover times of 2.9, 17 and 13 h^{-1} at 68, 227 and 512 µmol photons m^{-2} s^{-1}, respectively, although the large standard deviations for some of the measurements means these values are indicative only. There was a moderate negative correlation between extracellular glucose export and bacterial uptake ($r^2 = 0.68$, $p = 0.001$).

Pulse-amplitude modulation (PAM) measurements

F_v/F_m values at the beginning of the inductions curves at the four irradiances were between 0.331 ± 0.156 and 0.476 ± 0.019 (Table 1). However, at the end, after four minutes of actinic light exposure these had dropped from 0.303 ± 0.082 at 15 µmol photons m^{-2} s^{-1} to 0.206 ± 0.120,

Table 1 Extracellular glucose export and consumption

Irradiance	Glucose export rate	Glucose consumption rate	Turnover time	F_vF_m (start)	F_vF_m (end)	% decline	NPQ
15	0.115 ± 0.193			0.476 ± 0.019	0.303 ± 0.082	36	0.253 ± 0.027
68	0.152 ± 0.004	0.051 ± 0.021	2.9	0.331 ± 0.156	0.206 ± 0.120	38	0.355 ± 0.248
227	2.427 ± 2.068	0.144 ± 0.059	17	0.371 ± 0.077	0.025 ± 0.031	93	0.432 ± 0.020
512	1.791 ± 0.233	0.138 ± 0.0001	13	0.471 ± 0.035	0.019 ± 0.018	96	0.779 ± 0.293

Irradiance (µmol photons m^{-2} s^{-1}); glucose export rate [i.e. net extracellular glucose export rate, mg glucose (mg chl *a*)$^{-1}$ h^{-1}]; glucose consumption rate (i.e. net reduction in the amount of exuded algal glucose by bacterial/algal glucose consumption) [mg glucose (mg chl *a*)$^{-1}$ h^{-1}]; turnover time (time to consume glucose pool h^{-1};); F_v/F_m (start) is the F_v/F_m value (dimensionless ratio) at the start of the induction curve after 30-min dark acclimation. F_v/F_m (end) is the F_v/F_m value (dimensionless ratio) at the end of the 4-min induction curve; % decline is the percentage drop in F_v/F_m values between the beginning and end of the induction curve

NPQ non-photosynthetic quenching (dimensionless)

Errors are standard deviations based on three replicates

0.025 ± 0.031 and 0.019 ± 0.018 at 68, 227 and 512 µmol photons m^{-2} s^{-1}, respectively. Over the same time interval, NPQ values increased from 0.253 ± 0.027 at 15 µmol photons m^{-2} s^{-1} to 0.430 ± 0.298, 0.696 ± 0.432 and 0.779 ± 0.293 at 68, 227 and 512 µmol photons m^{-2} s^{-1}, respectively (Table 1). There was a moderate correlation between extracellular glucose export and % decline in F_v/F_m ($r^2 = 0.75$, $p = 0.00026$) and a weak correlation between extracellular glucose export and maximum NPQ ($r^2 = 0.39$, $p = 0.031$).

Discussion

In this study, net extracellular glucose export in a sea ice community from McMurdo Sound increased with increasing irradiance, with a major increase between 68 and 227 µmol photons m^{-2} s^{-1}. DOC production and exudation in marine biofilms, including sea ice, have been well documented and has usually been found to be associated with high light levels and/or nutrient limitation (Staats et al. 1999; Underwood and Paterson 2003; Cook et al. 2004, 2007; Underwood et al. 2013; Ugalde et al. 2014). Although nutrient levels were not measured, other studies have found Antarctic under-ice nutrient concentrations during spring to be high and non-limiting (McMinn et al. 1995, 1999; Cummings et al. 2019). Most studies have shown that sea ice communities reach light saturation, i.e. have E_k values, at irradiances of less than 200 µmol photons m^{-2} s^{-1}, with inhibition starting at < 300 µmol photons m^{-2} s^{-1} (McMinn et al. 2012; Sorrell et al. 2021). Similarly, in situ communities exposed to ambient irradiances have $F'_v/F_{m'}$ values of < 0.1, compared with night-time values of > 0.4 (McMinn et al. 2003). Most studies actually show E_k values less than 100 µmol photons m^{-2} s^{-1} (McMinn et al. 2003, 2007, 2010; Sorrell et al. 2021). In this study also, there was a sharp drop in final F_v/F_m and an increase in NPQ values, between irradiances of 68 and 227 µmol photons m^{-2} s^{-1}. NPQ is a protective mechanism that is upregulated to divert energy from excess irradiance to prevent cellular damage. In this study NPQ increased at all irradiances but was much greater after exposure to higher irradiances. There is a weak correlation between these increased NPQ values and glucose export ($r^2 = 0.370$). As under-ice inorganic nutrient levels in spring in McMurdo Sound are consistently high (Arrigo 2014; Cummings et al. 2019), this relationship implies that it is likely that the above optimal irradiances alone caused the increase in DOC exudation (glucose) in the sea ice community.

The addition of DCMU to the samples inhibited electron flow between PSII and PSI, thus preventing carbon fixation and the production of glucose. The subsequent drop in dissolved glucose concentrations thus potentially resulted from both biotic and abiotic processes. However, in similar experiments with benthic microalgae, McMinn and Lee (2018) treated samples in the dark with antibiotics to inhibit bacterial activity. These samples showed no significant decline in glucose concentrations with time, indicating that abiotic breakdown of glucose was occurring at a much slower rate. Thus, bacterial consumption was responsible for most of the drop in glucose concentrations in the ice algae samples treated with DCMU. Glucose turnover times were between 2.9 and 17 h, rates consistent with open marine and freshwater turnover times elsewhere (Bunte and Simon 1999; Skoog et al. 2002; Alonso-Saez et al. 2012).

This study, together with that of McMinn and Lee (2018), has demonstrated that microsensors can be reliably used to measure microalgal exudation and bacterial uptake rates of glucose in these communities. Microsensors are well suited to these systems as biomass levels and DOC concentrations are often many times higher than in open water, which overcomes microsensor sensitivity issues.

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Author contributions AMcM conceived the research, AM and FK conducted the field work, FK conducted the experiments, AMcM wrote the manuscript and all authors read and improved the manuscript.

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Data availability The authors declare that all data used in the production of this manuscript are presented in incorporated tables and also that all data support the claims made herein.

Declarations

Conflict of interest The authors are unaware of any conflicting interests. The authors have no relevant financial or non-financial interests to disclose.

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