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NOTE

Polar marine diatoms likely take up a small fraction of dissolved dimethylsulfoniopropionate relative to bacteria in oligotrophic environments

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ABSTRACT: Dimethylsulfoniopropionate (DMSP) constitutes a major compound in the global sulfur cycle. A few studies over the last decade have revealed that not only bacteria but also eukaryotic phytoplankton may take up DMSP from the dissolved pool, although the mechanisms and quantitative importance of this undefined DMSP uptake pathway, particularly by polar phytoplankton, remain poorly known. To fill this gap, we undertook short-term ^{35}S-DMSP uptake kinetic experiments in axenic laboratory batch cultures of 3 polar marine diatoms (*Thalassiosira gravida*, *Chaetoceros neogracilis*, and *Chaetoceros gelidus*). DMSP uptake by *C. neogracilis* and *C. gelidus* was below the detection limit, but significant DMSP uptake by *T. gravida* was observed. These differences might be explained by the presence of a putative OpuD/DddT-like DMSP transporter in various *Thalassiosira* spp., which is absent in the transcriptomes of *Chaetoceros* spp. Based on conservative extrapolation of DMSP uptake kinetics measured in *T. gravida* cultures to the complex consortium of diatoms found in oligotrophic Arctic environments, the fraction of dissolved DMSP taken up by polar diatoms is probably small compared to that taken up by bacteria and (perhaps) other eukaryotic algae.

KEY WORDS: DMSP · Osmotrophy · Chaetoceros · Thalassiosira · Transporters · Arctic · Marine bacteria

INTRODUCTION

More than 10^{15} g of dimethylsulfoniopropionate (DMSP) are produced annually in the marine environment, making it a major compound in the global sulfur cycle (Johnston et al. 2012). This tertiary sulfonium compound is the main precursor of the climate-active gas dimethylsulfide (DMS), which may contribute to cloud condensation nuclei production and climate cooling, particularly in an aerosol-poor atmosphere such as that in polar regions (Mungall et al. 2016). DMSP also supplies a major fraction of the sulfur and carbon required for growth of heterotrophic bacteria in surface ocean water (Kiene et al. 2000, Ruiz-González et al. 2012).

One relatively new and currently evolving idea regarding the DMS(P) cycle concerns the uptake of dissolved DMSP ($DMSP_d$) by eukaryotic phytoplankton. Even though dissolved organic matter

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uptake by eukaryotic autotrophic microalgae was traditionally thought to be of minor importance compared to that of heterotrophic bacteria, new studies challenge this old paradigm. Indeed, Spielmeyer et al. (2011) found that cells in axenic laboratory cultures of the coccolithophore *Emiliania huxleyi* and the diatom *Thalassiosira weissflogii* were able to rapidly take up $DMSP_d$ when present at 125 nM. In addition, field experiments in the Sargasso Sea involving size-fractionation showed that phototrophic prokaryotes and eukaryotes >0.6 µm were responsible for up to 70% of the total assimilated ^{35}S (ultimately coming from ^{35}S-$DMSP_d$ added at tracer levels) (Vila-Costa et al. 2006). Subsequent results of Ruiz-González et al. (2012) using microautoradiography were even more surprising; they showed that >80% of ^{35}S from labelled $DMSP_d$ (at tracer levels) accumulated by microorganisms from the Arctic and Antarctic was mediated by eukaryotic phytoplankton (>5 µm) devoid of attached bacteria, and particularly by diatoms. The results from these pioneer studies should be taken with caution since they did not distinguish between uptake of DMSP per se and/or sulfur compounds derived from DMSP. Indeed, in the field, co-existing bacteria can also metabolize DMSP and release other sulfur compounds, which could then be taken up by the algal community. Due to the lack of well-controlled studies of DMSP uptake kinetics in polar phytoplankton, the quantitative importance of DMSP uptake in polar phytoplankton remains unknown. However, a better understanding of this largely undefined organic sulfur assimilatory pathway is needed for the development of accurate mechanistic DMS-DMSP models (Le Clainche et al. 2010, Gypens et al. 2014), particularly in polar regions where global climate change is occurring at a fast pace and where the summer aerosol-poor atmosphere favors the cloud formation effect of DMS and associated climate feedback (Quinn & Bates 2011, Mungall et al. 2016).

In the present study, we quantified DMSP uptake in 3 common polar diatoms (*Chaeotoceros gelidus*, *Thalassiosira gravida*, *Chaetoceros neogracilis*) using axenic laboratory batch cultures. The species *T. gravida* is one of the most frequently recorded diatoms at the pan-Arctic scale (Poulin et al. 2011) and both *Chaetoceros* species are dominant in polar environments (Balzano et al. 2012, 2017, Chamnansinp et al. 2013). We chose to focus on diatoms in the present study because diatoms are a dominant algal group accounting for >50% of annual primary production in the Arctic (Uitz et al. 2010).

MATERIALS AND METHODS

Algal culturing technique

Non-axenic algae cultures of *Thalassiosira gravida* (CCMP 986), *Chaetoceros neogracilis* (RCC2278) and *Chaetoceros gelidus* (RCC2046) were treated with antibiotics to produce axenic cultures (see Section 1 on 'Details of the methodology' in the Supplement at www.int-res.com/articles/suppl/a081p213_supp.pdf). Preliminary analysis of DMSP in cultures by gas chromatography using the methodology of Michaud et al. (2007) indicated that *T. gravida* produces 24 ± 3 mmol, mean ± SD, of DMSP per liter of cell volume, based on measurements conducted during algal acclimation and at the beginning of the DMSP uptake experiments. By contrast the 2 other species did not synthesize measurable amounts of DMSP, i.e. <0.4 mmol DMSP per liter of cell volume for *C. neogracilis* and <0.3 nM in total (particulate + dissolved) DMSP for *C. gelidus*.

Axenic cultures of the 3 polar diatoms were maintained in batch cultures using enriched artificial seawater medium (ESAW) and sterile techniques and acclimated for more than 7 growth cycles (Berges et al. 2001). *T. gravida* and *C. neogracilis* were kept in exponential growth phase (cell density $<2 \times 10^6$ cells ml^{-1}) for acclimation under their optimal light and temperature growth conditions (when specific growth rates were 0.72 ± 0.07 d^{-1} and 0.54 ± 0.04 d^{-1} for *T. gravida* and *C. neogracilis*, respectively). *C. gelidus*, on the other hand, was maintained by allowing it to grow through full growth cycles. However, all uptake experiments were performed with exponentially growing algae. For both the acclimation periods and the experiments themselves, cultures (100 ml) were grown in 250 ml glass Erlenmeyer flasks under continuous fluorescent light at 30 µE m^{-2} s^{-1} at 4°C (for *T. gravida*) and at 150 µE m^{-2} s^{-1} at 4°C (for *C. neogracilis*). Cultures (30 ml) of *C. gelidus* were grown in 100 ml glass vials during the acclimation period and in Erlenmeyer flasks during the experiments under continuous fluorescent light at 30 µE m^{-2} s^{-1} at 0°C. Cultures were placed in incubators within the refrigerated laboratory of the Takuvik research unit at Laval University.

For *T. gravida*, one set of algal cultures (n = 3) inoculated at around 7000 to 10 000 cells ml^{-1} were also pre-exposed to the ESAW medium supplemented with cysteine (1 mM initial cysteine concentration) for 5 d before DMSP uptake experiments in fresh ESAW medium with 1 mM cysteine; while the other set of algal cultures (n = 3) was grown in the absence

of cysteine. The objective of the pre-exposure to cysteine was to determine whether the uptake of DMSP could be regulated by the presence of added organic sulfur. The cysteine pre-exposure experiment was done only with *T. gravida* because this species was the only one taking up significant amount of DMSP. Cell growth was monitored using a Coulter counter.

DMSP uptake experiments

Carrier-free ^{35}S-DMSP (~ 1019 nCi pmol^{-1}, >97% radiochemical purity) was used to measure DMSP uptake rates (See Section 1 in the Supplement for further details about the synthesis of the radiotracer). Aliquots of algal cultures (n = 3, cell density = 70 000 to 110 000 cells ml^{-1} for *T. gravida* and *C. neogracilis*; but 30 000 cells ml^{-1} for *C. gelidus*) acclimated to the ESAW medium were exposed to 1.5 (*T. gravida*), 2.6 (*C. neogracilis*), and 2.5 (*C. gelidus*) pM ^{35}S-DMSP in glass Erlenmeyers for 5.5 h. For the *C. neogracilis* and the *C. gelidus* cultures, unlabeled DMSP was added so that the final total concentration of $DMSP_d$ was 1 nM, i.e. representative of the $DMSP_d$ concentration range measured in polar environments (Luce et al. 2011). For *T. gravida* cultures, $DMSP_d$ was measured before and after the 5.5 h experiments and was equal to 69 ± 7 nM due to exudation by *T. gravida* of cellular DMSP in the culture medium and, possibly, carry-over of degraded cells. Since the cells were not filtered or centrifuged prior to the experiments to minimize handling stress to the algae, the presence of this $DMSP_d$ concentration was unavoidable. For the *T. gravida* cultures pre-exposed to cysteine, DMSP uptake was measured in the presence of 1 mM cysteine as in the pre-cultures. Cell-free culture media spiked with ^{35}S-DMSP served as a negative control. The pH of all cultures was affected by less than 0.1% due to cysteine and/or DMSP addition based on calculations of proton additions from acidified stock solutions. Aliquots of 400 µl of algal cultures were pipetted at the beginning and at the end of the DMSP uptake experiments and confirmed that no significant decrease (e.g. by adsorption on the Erlenmeyer flasks or volatilization of DMS) in total added ^{35}S-DMSP occurred during the experiments.

After a given exposure time to ^{35}S-DMSP, algal cultures and culture medium without algal cells were filtered through 25 mm GF/F filters using low vacuum (<5 cm Hg). The filters were rinsed 4 times with 10 ml fresh ESAW containing no added DMSP to remove passively adsorbed DMSP in the filter and were subsequently placed in Ecolume and analyzed by liquid scintillation counting (counting efficiency = 95%). This washing step removed most of the $DMSP_d$ that had been passively retained in the filters, but did not specifically desorb DMSP adsorbed onto the algal cells. To correct for the remaining labeled $DMSP_d$ passively embedded in the filters, the amount of labeled $DMSP_d$ in the blank filter was subtracted from that measured on the filter with algal cells. This procedure yielded the 'total cell-associated DMSP', comprising the DMSP internalized in the cells and the DMSP adsorbed onto the cells.

RESULTS AND DISCUSSION

For *Thalassiosira gravida* cultures grown in either ESAW medium alone or ESAW plus 1 mM cysteine, cell associated ^{35}S rapidly increased after the first 5 min of exposure relative to the beginning of the experiment and then slowly continued to increase over the 5.5 h exposure period (Fig. 1), but at a slower rate in cultures containing cysteine. We suggest that the initial high DMSP uptake rate may be due to a fast initial adsorption phase of DMSP on algal cells (limited by diffusion of DMSP toward the cells) followed by a slow internalization phase limited by the kinetics of a putative membrane-bound DMSP transporter. Note that DMSP adsorption onto the cells should be achieved rapidly; the time required for diffusion of DMSP through the unstirred boundary layer of a 5 µm radius spherical phytoplanktonic cell is on the order of seconds (Wilkinson & Buffle 2004). The linear uptake phase of DMSP took place over a much longer period than necessary for adsorption processes, thus indicating that DMSP is not just adsorbed onto the cells, but also internalized into the algal cells.

Exposure to cysteine decreased the internalization rate by almost 4 times (from 4.8 to 1.2 amol DMSP cell^{-1} h^{-1}), measured between 5 min and 5.5 h, relative to that measured for algal cells acclimated to the ESAW medium without cysteine (see the slope of linear regressions shown in Fig. 1). However, cysteine exposure did not significantly decrease the amount of DMSP adsorbed onto the algal cells (*y*-axis intercept in Fig. 1); the initial amount of cell-associated DMSP after 5 min of exposure was 7.08 ± 0.65, mean ± SE, and 7.53 ± 0.57 amol DMSP cell^{-1} without or with pre-exposure to cysteine, respectively (Fig. 1). These results suggest that cysteine, which was present at much higher concentration than $DMSP_d$, either decreased the sulfur requirement of *T. gravida* or it competed with DMSP for uptake by a common membrane transporter. This is the first demonstration that

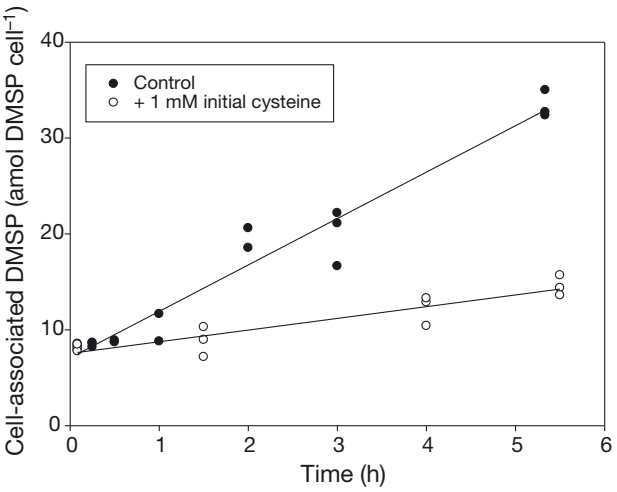

Fig. 1. Total cell-associated DMSP (labeled and unlabeled ^{35}S-DMSP, amol DMSP cell^{-1}) as a function of the exposure time in cultures of the polar diatom *Thalassiosira gravida* acclimated to the enriched artificial seawater medium (ESAW) medium (control) or exposed to 1 mM initial cysteine. Totals comprise DMSP internalized in the cells plus DMSP adsorbed onto the cells. The dissolved DMSP concentration measured during the experiment was 69 ± 7 nM, mean ± SD. DMSP uptake in similar experiments performed on the diatoms *Chaetoceros neogracilis* and *Chaeotoceros gelidus* was undetectable

DMSP uptake in phytoplankton is affected by the presence of other organic sulfur compounds. Although the initial cysteine concentration used in our experiments (1 millimolar) is much higher than cysteine concentrations found in the marine environment (in the nanomolar range), our results contribute to a better understanding of the regulatory mechanisms of DMSP uptake and provided additional evidence that DMSP uptake was mediated by sensitive physiological processes such as via a putative DMSP membrane-bound transporter.

What are the costs and purpose of DMSP uptake in *T. gravida*? Calculations in Section 2 of the Supplement indicate that for *T. gravida,* DMSP uptake would only save a small fraction of the total cellular energy required for DMSP synthesis. Indeed, the measured DMSP uptake rate in *T. gravida* represents only around 2% of the net DMSP production rate. Note that the benefits of DMSP uptake will also depend on the mechanistic and resource cost associated with the synthesis of the membrane DMSP transport system. Our bioinformatic analyses failed to identify DMSP-specific catabolism enzymes (DddA, DddC, DddD, DddK, DddL, DddP, DddQ, DddW, Alma 1-7, and DmdA-D) in the *Thalassiosira* transcriptomes (Fig. S1B in the Supplement), suggesting that the DMSP taken up may not be degraded, but only utilized as algal osmolyte.

In contrast with *T. gravida*, the 2 other diatoms tested did not take up measurable amount of DMSP during the 5.5 h exposure to 1 nM $DMSP_d$ (See Section 3 in the Supplement for an estimation of the DMSP uptake rate detection limit). To identify putative homologues of DMSP transport systems in *Thalassiosira* species, but absent in the *Chaetoceros* genus, the protein sequences for 9 different known DMSP transport systems were looked for in the Phylo-MetaRep databases (See Section 3 in the Supplement for further details on the bioinformatic analyses). One putative DMSP transporter was found in the 3 available *Thalassiosira* transcriptomes most closely related to *T. gravida* CCMP 986, as well as in 7 other *Thalassiosira* species (Figs. S1 & S2 in the Supplement). This putative DMSP transporter is a homologue to the betaine/carnitine/choline transporter (BCCT) family glycine betaine transporter OpuD from *Bacillus subtillis* (Broy et al. 2015) and the DMSP transporter DddT from *Halomonas* (Todd et al. 2010). Highly similar OpuD/DddT-like sequences were found in other marine eukaryotic phytoplankton species as well (data not shown), but were absent from species of the *Chaetoceros* genus (Section 4 in the Supplement). Although the presence of incomplete sequences in the investigated transcriptomes could have biased our results, this OpuD/DddT-like putative DMSP transporter could be a good candidate to explain the ability of *T. gravida* to take up DMSP. Interestingly, 2 *Thalassiosira* species with sequenced transcriptome, i.e. *T. pseudonana* CCMP1335 and *T. oceanica* CCMP1005, were previously reported to take up DMSP (Vila-Costa et al. 2006).

Although we have data from only a single diatom species which showed uptake activity, we used these data to make a preliminary estimate of the potential relative importance of bacteria and algae in $DMSP_d$ turnover in polar environments, using reported algal and bacterial cell density as well as DMSP turnover rate in the Arctic. At a low diatom cell density of 1×10^4 cells l^{-1}, even assuming that all diatom species take up DMSP at a rate similar to that measured for *T. gravida* exposed to 69 nM $DMSP_d$ (i.e. 1.16 pmol DMSP l^{-1} d^{-1}), this would translate into a turnover rate of 1 nM $DMSP_d$ in 860 d. This rate is much slower than the turnover rates of around 1 nM d^{-1} previously reported at several Arctic stations with low diatom cell density (Luce et al. 2011). The contribution of diatoms to DMSP turnover rate could be higher under the bloom conditions encountered at the marginal ice zone. However, they could also represent an upper limit considering that primary production in the Arctic is often dominated by species of the

Chaetoceros genus (Booth et al. 2002, Martin et al. 2010), and that the 2 *Chaetoceros* species investigated in the present study did not take up measurable amount of DMSP.

Although our laboratory investigation was limited to 3 diatom species and ignored the DMSP uptake potential of several other non-diatom algal species, our study of the DMSP uptake potential of 3 polar diatoms, which are common or dominant primary producers in the Arctic, shows that DMSP uptake by arctic diatoms is likely of minor quantitative importance when conditions are not favorable for diatom blooms. We note however that extrapolation of the results obtained in axenic laboratory cultures to field situations is difficult since the complex environmental and biological factors in the field cannot be reproduced in the laboratory; hence, further studies should be done in the field to determine whether our laboratory findings are representative of processes actually occurring in the Arctic.

Our laboratory results with bacteria-free algal cultures contrast with those of Ruiz-González et al. (2012) who showed, using autoradiography, that >80% of ^{35}S from labelled $DMSP_d$ accumulated by micro-organisms assemblages from the Arctic and Antarctic is mediated by eukaryotic phytoplankton (>5 µm). This apparent discrepancy could be due to different algal community composition, and hence DMSP uptake capacity. It could also result from bacterial uptake of the ^{35}S DMSP and its subsequent rapid conversion into ^{35}S-labelled molecules such as methanethiol (CH_3SH), which could in turn be taken up by eukaryotic algae. If true, phytoplankton in the field might take up DMSP metabolites produced by bacteria rather than DMSP. Clearly, more laboratory and field studies are needed to test this hypothesis.

CONCLUSIONS

So far, existing models of the DMS(P) cycle ignore algal DMSP uptake and assume that all the dissolved DMSP pool is metabolised by heterotrophic bacteria. Our results suggest that this assumption may be justified when diatoms are found in low abundance. However, non-diatom algal groups (including autotrophic, heterotrophic and mixotrophic species) in the Arctic such as Dinophyceae, Prymnesiophycea, Cryptophyceae, Chrysophyceae, Chlorophyceae and Prasinophyceae could also divert a significant fraction of $DMSP_d$ away from bacteria. Hence, additional laboratory studies on the DMSP uptake potential of other key algal species are needed to better assess the quantitative importance of all eukaryotic algal species on DMSP uptake compared to that of bacteria. Studies on the expression and role of the putative *Thalassiosira* OpuD/DddT-like transporter are also needed to further improve our understanding of DMSP uptake in phytoplankton and potentially develop biomarkers of algal DMSP uptake in the field. This study enhances our current knowledge on DMSP uptake in one dominant algal group in the Arctic, i.e. diatoms, and helps better understand the biogeochemical sulfur cycle and climate at high latitudes.

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