Release and consumption of DMSP from Emiliania huxleyi during grazing by Oxyrrhis marina

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ABSTRACT: Degradation and release to solution of intracellular dimethylsulfoniopropionate (DMSP) from Emiliania huxleyi 370 was observed during grazing by the heterotrophic dinoflagellate Oxyrrhis marina in 24 h bottle incubations. Between 30 and 70% of the lost algal DMSP was metabolized by the grazers without production of dimethylsulfide (DMS) when grazer densities were 150 to 450 ml−1. The rest was released to solution and about 30% was converted to DMS by bacteria associated with the grazer culture. These experiments demonstrate that grazing by herbivorous protists may be an important sink for DMSP in marine waters, removing a potential source of DMS. Microzooplankton grazing may also indirectly increase the production of DMS by transferring algal DMSP to the dissolved pool, making it available for bacterial metabolism.

KEY WORDS: DMSP - DMS - Flagellate - Herbivory - Microbial loop

INTRODUCTION

Dimethylsulfide (DMS), a climatically active trace gas (Charlson et al. 1987), is thought to be formed in the marine environment primarily from algal dimethylsulfoniopropionate (DMSP). DMSP may function as a 'compatible solute' in some phytoplankton (Dickson & Kirst 1986) and can reach intracellular concentrations of hundreds of millimolar (Keller et al. 1989). Bulk DMSP abundances in seawater are usually 10 to 100 nM, much greater than typical DMS concentrations < 10 nM (Cooper & Matrai 1989, Belviso et al. 1990, 1993). There is therefore a large potential for DMS production, and its regulation in part determines how much DMS is available for outgassing to the atmosphere.

Dissolved DMSP is consumed rapidly (hours) in natural seawater samples, with partial conversion to DMS and partial metabolism to other products such as 3-methylpropionate (Kiene & Service 1991, Kiene 1992, Taylor 1993). Bacteria which mediate these transformations have been enumerated, isolated, and characterized (Taylor & Gilchrist 1991, Ledyard et al. 1993, Visscher et al. 1993), and it is likely that DMSP-degrading bacteria are ubiquitous in surface waters.

Furthermore, at least 1 marine phytoplankter, Phaeocystis pouchetti, can also transform dissolved DMSP to DMS (Stefels & van Boekel 1993).

However, the majority of DMSP is usually associated with particulate material. Although most studies have not identified the exact source, it is usually assumed to be synthesized and stored inside living phytoplankton. Therefore, processes which release algal DMSP, such as grazing, may be critical to DMS production since they will influence the amount of dissolved DMSP available to bacteria which can transform it to DMS. Several field observations have shown correlations between zooplankton abundances and DMS concentrations (Nguyen et al. 1988, Leck et al. 1989, Belviso et al. 1990, 1993, Holligan et al. 1993), and bottle grazing experiments with 30 to 40 copepods 1−1 (Dacey & Wakeham 1986) increased DMS production by about 3-fold. At least some heterotrophic dinoflagellates may consume or convert DMSP, and Ishida & Kadota (1967) showed that the osmotroph Gyrodinium colonii could synthesize DMSP and enzymatically convert it to DMS. However, the role of heterotrophic protists in the consumption and release of DMSP and the production of DMS is poorly understood, despite their importance as herbivores (Capriulo et al. 1991, Sherr & Sherr 1992),
and study of these processes has been limited to size-fractionation of natural water samples (Belviso et al. 1990).

Here we present results from batch culture experiments where we examined the role of the heterotrophic dinoflagellate Oxyrrhis marina in the consumption of algal DMSP from the coccolithophore Emiliania huxleyi, and the subsequent release of DMSP to solution followed by production of DMS. Our objective was to work with a highly simplified system, a monospecific, axenic, high-DMSP-titer prey and a monospecific (though non-axenic), low-DMSP-titer predator, at densities roughly comparable to those in natural waters.

**METHODS**

**Bottle incubations.** Incubations were carried out with 500 ml or 1000 ml polycarbonate bottles (Nalgene), acid-washed and autoclaved, filled completely with glass-fiber (0.7 μm) filtered, autoclaved seawater (FASW). Oxyrrhis marina (originally isolated from Danish coastal waters by H. Havskum) was grown in the light at 16 °C on Dunaliella tertiolecta to densities of approximately 10⁴ cells ml⁻¹, then transferred to the dark at 16 °C on Dunaliella tertiolecta to densities of approximately 10⁴ cells ml⁻¹. Any chemical amendments, such as glycine betaine, were added and the bottles were allowed to sit at least 1 h before addition of prey.

Axenic Emiliania huxleyi 370 (Bigelow culture collection, West Boothbay Harbor, ME, USA) was maintained on f/2 medium at 16 °C in a 14:10 h light:dark cycle, and was added from log growth cultures to initial densities of 3000 ml⁻¹. Algal cultures were examined microscopically and periodically plated on rich heterotrophic marine agar plates to insure against contamination.

Duplicate bottles of Emiliania huxleyi only, E. huxleyi with Oxyrrhis marina, and O. marina only were prepared. Bottles were incubated in the dark at 16 °C without agitation, and were sampled for DMS, DMSP (particulate and dissolved), and prey and predator densities over 24 h. We found that bottles without grazers showed stable cell and sulfur pools over this period (see 'Results'), but not during longer incubations, where 'bottle effects' became important.

**Cell enumeration.** Prey cells were enumerated by epifluorescence microscopy after preservation (sodium tetaborate-buffered formalin, 4% final concentration) and staining with acridine orange (AO). Actively swimming Oxyrrhis marina cells were enumerated with a dissecting microscope (Wild M3Z, Leica, Inc.) in replicate 5 or 10 μl drops. Grazer cell numbers were also enumerated by epifluorescence microscopy after preservation and staining using AO or DAPI (4,6-diamidino-2-phenylindole). Samples (5 ml) were preserved with Lugol’s (10 μl ml⁻¹ sample) to prevent ejection of grazer food vacuoles, and cleared with 3% sodium thiosulfate (Rassoulzadegan 1991, Sherr & Sherr 1993), then preserved with formalin. Samples were stained and filtered onto black 0.2 or 0.8 μm membrane filters (Poretics, Livermore, CA, USA; #11053, 11031) immediately after preservation. Samples stained with DAPI were used to examine prey inside grazer food vacuoles by observing algal chlorophyll autofluorescence under blue light, and samples stained with AO were used to count prey and grazer numbers.

**Sulfur analyses.** Sulfur analyses were made by gas chromatography (GC) using a Shimadzu GC-14 chromatograph equipped with a flame photometric detector. The column packing was Chromosil 330 (Supelco, Bellefonte, PA, USA), operated isothermally at 60 °C. Helium was the carrier gas, and was also used for sample sparging.

Because DMS was frequently lost during filtration, whole-water samples (3 to 5 ml) were first pipetted directly into sparge tubes and stripped to remove DMS. A second 3 ml aliquot was then filtered gently using a syringe and 25 mm GF/C or GF/F glass-fiber filters into 3 ml of 10 N NaOH in a separate sparge tube, and stripped to measure DMS + dissolved DMSP (DMSPₐ). DMSPₐ was then calculated by difference. The filter was placed in 8 ml of 2 N NaOH, allowed to sit at room temperature for 6 to 12 h, and 1 to 2 ml sub-samples were sparged for particulate DMSP (DMSPₚ). Filtration was performed as slowly as possible, and injection into the sparge tube was done through a 1 mm Teflon tube rather than with a needle in order to minimize pressure across the filter.

Samples were sparged with helium at 85 to 90 ml min⁻¹ for 3 to 6 min and cryotrapped on liquid nitrogen in Teflon traps, which were then heated to >80 °C and injected onto the column. Nafion dryer tubes (#MD-050-72F, Permapure, Toms River, NJ, USA) were used to remove water vapor. DMSP-HCl standards were prepared in deionized water acidified to prevent microbial degradation, and were injected into sparge tubes pre-filled with NaOH. Detection limit was about 20 pg S, or approximately 0.1 nM DMS in a 5 ml sample. Sample-to-sample precision was typically 10 to 15%.

**Size-fractionated production of DMS from DMSP.** In 1 grazing experiment with 100 Oxyrrhis marina ml⁻¹, 50 ml subsamples taken at time zero and after 14 h of grazing were filtered sequentially by gentle positive pressure (syringe) through 25 mm filters to remove grazers (Whatman 540 qualitative filters), prey (Milli-
pore 3 μm membrane), and most bacteria (Millipore 0.45 μm membrane). Samples were examined microscopically before and after filtration to insure that qualitative removal of selected organisms took place. Subsamples (5 ml) of whole water, water without grazers but with prey and bacteria (‘<10 μm’), water without grazers or prey but with bacteria (‘<3 μm’), and water without all organisms (‘<0.45 μm’) were assayed for comparative DMS production rates from 50 μM DMSPd additions.

Isolation of DMSP-lysing bacteria. A culture containing Oxyrrhis marina grown on Dunaliella tertiolecta was streaked onto plates made with FASW amended with 10 mM Tris, pH 7.4, and 0.1% DMSP-Cl, and incubated at room temperature in the dark. After 4 to 5 d, small colonies were visible and DMS odor was noted. Colonies were restreaked onto marine heterotrophic plates (1% glucose, peptone, 0.5% yeast extract). After several days, numerous uniform colonies formed. A large motile rod (~1 x 2 μm) forming pale white colonies was the main strain found, and the only one which produced DMS from DMSP. The ability of this culture to degrade DMSP was studied by dispersing a loopful (ca 50 μl) of the plate culture in several ml ASW with 50 mM DMSPd additions. After incubations, 1 ml 10 N NaOH was added and sparged periodically for DMS and DMSP over 24 h. Control samples contained 8 ml seawater buffer with no cells.

Chemicals. DMSP-HCl was obtained from Research Plus (Bayonne, NJ, USA) and glycine betaine HCl from Aldrich (#14,793-1, Milwaukee, WI, USA). Stocks for bacterial growth were kept frozen until use. Stocks for GC standards were acidified with 10% HCl to prevent bacterial growth and stored at room temperature.

RESULTS

Removal of algal DMSP, and production of DMSPd during grazing

Four experiments employed similar prey densities (ca 3000 ml⁻¹), but initial grazer numbers varied from about 150 to 450 ml⁻¹. In bottles without grazers, Emilianha huxleyi numbers and DMSP and DMS pools were unchanged over the 24 h experiment periods (Figs. 1 & 2a). They showed little or no release of DMSP from the particulate to the dissolved pool, and little or no production of DMS, indicating low or no endogenous production of DMS from E. huxleyi. In 1 experiment, the bottles without grazers showed conversion of dissolved DMSP to DMS after about 12 h, apparently due to bacteria from the grazed bottles introduced during non-sterile sampling (see 'Discussion'). Internal E. huxleyi DMSP concentrations per cell were ca 30 to 100 mM, based on a cell diameter of 4 μm and assuming no vacuole space. DMSPd and DMS in the algal culture were low. Oxyrrhis marina cultures raised on low-DMSP-titer prey (Dunaliella tertiolecta) contributed <5% of the total DMSP and DMS in the experiments.

The presence of Oxyrrhis marina caused a decline in the number of Emilianha huxleyi, but this did not result in any appreciable increase of O. marina cell numbers over 24 h (Fig. 1). Grazer numbers enumerated by epifluorescent microscopy were consistently lower than when enumerated by dissecting microscope, indicating lysis of protist cells during preservation, staining, and/or filtration. Prey were visible inside protist vacuoles within minutes of adding the prey and throughout the experiments.
In the predator + prey bottles, coincident with the decrease in prey, particulate DMSP also disappeared, and dissolved DMSP and DMS increased in the grazed bottles compared to those with out grazers (Fig. 2, Table 1). However, in all cases the decrease in DMSP$_p$ was greater than the increase in DMS and DMSP$_d$. DMSP$_p$ decreased more slowly than prey numbers (Fig. 3), suggesting that a portion of DMSP$_p$ during the experiment was contained inside grazers, and this fraction increased as grazing continued. It is possible that part of the increase in DMSP$_d$ observed was due to breakup of O. marina cells during filtration and release of undigested DMSP; this was not quantified but likely due to the fragility of the flagellates. The rate of fractional loss of DMSP$_p$ [(change in DMSP$_p$)/(initial DMSP$_p$)/time] increased with increasing grazer density (data not shown).

### Bacterial production of DMS from DMSP

The increase in DMS observed in all experiments coincided with an increase in bacterial numbers as determined by acridine orange direct count (AODC). These bacteria were probably introduced with the Oxyrrhis marina culture, since the other components of the experimental system were bacteria-free. Conversion of DMSP to DMS and consumption of DMS in prey and predator cultures was tested by addition of either compound to concentrated cultures used for the experiments. The O. marina culture, including Dunaliella tertiolecta prey and associated bacteria, showed rapid and linear conversion of DMSP to DMS, but no consumption of DMS (Fig. 4). The axenic Emiliania huxleyi culture showed little if any activity (data not shown). A sample of the O. marina culture was plated onto DMSP-FASW agar and a bacterium was isolated

### Table 1. Oxyrrhis marina grazing on Emiliania huxleyi. Summary of DMSP and DMS pool changes in 3 grazing experiments

<table>
<thead>
<tr>
<th>Experiment period (h)</th>
<th>22.5</th>
<th>22.0</th>
<th>20.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grazing density (cells ml$^{-1}$)</td>
<td>159</td>
<td>366</td>
<td>476</td>
</tr>
<tr>
<td>Initial pools (nM)$^a$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DMS</td>
<td>1.1 (0.2)</td>
<td>1.7 (0.1)</td>
<td>0.5 (0.1)</td>
</tr>
<tr>
<td>DMSP$_d$</td>
<td>5.7 (1.5)</td>
<td>2.4 (0.2)</td>
<td>3.8 (0.1)</td>
</tr>
<tr>
<td>DMSP$_p$</td>
<td>32.1 (5.2)</td>
<td>17.2 (2.5)</td>
<td>41.1 (2.7)</td>
</tr>
<tr>
<td>Change (nM)$^b$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DMS</td>
<td>+3.4</td>
<td>+0.7</td>
<td>+2.2</td>
</tr>
<tr>
<td>DMSP$_d$</td>
<td>+6.0</td>
<td>+1.5</td>
<td>+7.6</td>
</tr>
<tr>
<td>DMSP$_p$</td>
<td>-12.4</td>
<td>-9.0</td>
<td>-28.0</td>
</tr>
<tr>
<td>Net change in $\Sigma$DMS (nM)$^b$</td>
<td>-3.0</td>
<td>-6.8</td>
<td>-18.2</td>
</tr>
</tbody>
</table>

$^a$Average with range in parentheses

$^b$$\Sigma$DMS = DMS + DMSP$_d$ + DMSP$_p$
that lysed DMSP to DMS. After growth on rich heterotrophic-marine agar plates, this organism showed a lag of about 1 to 3 h at room temperature before converting 20 μM DMSP (Fig. 5), and this lag period was greatly extended by 400 μg ml⁻¹ chloramphenicol, suggesting an inducible DMSP lyase enzyme. Addition of 100 mM glycine betaine had no effect on DMS production (Fig. 5). No other DMS-producing strains from the O. marina culture were isolated, although the presence of other strains with different DMSP metabolism (e.g. demethylation) cannot be ruled out. Addition of 100 μM glycine betaine in 1 grazing experiment with 150 O. marina ml⁻¹ did not result in any significant changes in DMS or DMSP concentra-
ations in any bottles, with or without grazers (data not shown).

Degradation of DMSP without production of DMS by lysed Oxyrrhis marina cells

The lysed Oxyrrhis marina samples removed approximately 80% of the DMS during the incubation without significant production of DMS while controls without cells were stable except for slight DMS production after 18 h (Fig. 6). Unlysed O. marina samples showed approximately 10% removal of DMSP with production of DMS (data not shown). After 24 h, unlysed samples were examined by dissecting microscope and motile O. marina were observed. AODC slides of the lysed samples showed concentrated cell debris as well as bacteria.

Size-fractionated production of DMS from DMSP in grazing experiments

At both time zero and after 14 h of grazing, the sample fractions from bottles without grazers did not show significant activity, consistent with the results of the Emiliania huxleyi culture alone. With addition of Oxyrrhis marina and associated bacteria, DMSP conversion activity was found at time zero in samples including grazers and prey and prey alone (Fig. 7a), while after 14 h activity was found in the bacterial fraction as well (Fig. 7b). The production of DMS in these bottles was initially weak and was noticeably greater after incubation for 6 h, suggesting bacterial growth.
DISCUSSION

These experiments show that protist grazing may be a sink for algal DMSP and may also convert it to dissolved or submicron form, making it available for metabolism by bacteria. Therefore, herbivorous protists may be a key in situ link between the production of algal DMSP and its conversion to climatically active DMS.

Although we employed an artificially simple system of a single prey and predator, cell densities were reasonably realistic and therefore the results may serve as a model for natural situations. We attempted to use the simplest possible system of a monospecific, axenic prey and a monospecific grazer. Because we did not have *Oxyrrhis marina* in axenic culture, we performed additional tests to determine whether removal and/or conversion of DMSP was due to the grazers or associated bacteria.

A key to understanding the production of DMS from DMSP lies in determining which organisms have the ability to express DMSP-lyase enzyme(s), and under what conditions these are activated. Although marine phytoplankton produce a large fraction of DMSP, it is not obvious that they are all capable of converting it to DMS, or that they do so under natural growth conditions. Reports of DMS production by living phytoplankton cultures are limited (Andreae et al. 1983, Vairavamurthy et al. 1985, Vetter & Sharp 1993) and it is not always clear that these were axenic cultures. Our observations that many phytoplankton cultures are easily contaminated by DMSP-consuming bacteria, and the reports of ubiquitous bacteria which either demethylate or cleave DMSP (Taylor & Gilchrist 1991, Ledyard et al. 1993, Taylor 1993, Visscher et al. 1993), indicate that DMSP released from algal cells may be the most likely to be a source of DMS.

In our experiments, several observations indicate that the actual production of DMS was due to bacteria associated with the grazer cultures. In all cases, the major production of DMS in grazed bottles coincided with increase in bacterial numbers, and in one experiment, we observed this in non-grazed bottles after 12 h, which we believe was due to bacteria accidentally introduced from the grazer bottles during non-sterile sampling. In all experiments DMS rose by similar amounts (0.7 to 3.4 nM) over 21 to 23 h despite widely varying decreases in DMSP (9 to 28 nM; Table 1), suggesting a possible decoupling of DMSP-to-DMS conversion from DMSP consumption by grazers.

As grazing progressed, both prey and DMSP declined, and only a fraction of the lost DMSP appeared as DMSP or DMS (Figs. 1 & 2, Table 1). This suggests that *Oxyrrhis marina* may have metabolized a large fraction of the algal DMSP without production of DMS. The removal of DMSP in lysed *O. marina* samples
without production of DMS over 24 h also suggests this dinoflagellate may metabolize DMSP, possibly employing it as a methyl donor. Several studies have implicated DMSP in transmethylation reactions in a wide variety of marine heterotrophs (Ishida & Kadota 1968, Nakajima 1993), and this may be a common metabolic fate in many herbivores. The relatively slow removal of DMSP in the lysed samples may also have been due to the growth of DMSP-demethylating bacteria (Taylor & Gilchrist 1991, Visscher et al. 1993), although unlysed cells did not show significant DMSP degradation. However, the grazing experiments also suggested that DMSP may be degraded relatively slowly by *O. marina*. During grazing, phytoplankton prey numbers declined more rapidly than particulate DMSP (Fig. 3). We believe that DMSP production by the prey was low or zero during these unlit experiments; DMSP$_p$ did not increase in samples without grazers (Fig. 2a) and there is some evidence that DMSP production by phytoplankton may be light-dependent (Karsten et al. 1991, Kiene pers. comm.). If prey DMSP$_p$ were degraded rapidly in grazer guts, we would expect both prey numbers and DMSP$_p$ to decline at the same rate. The more rapid removal of prey indicates the accumulation of unmetabolized prey DMSP either in protist food vacuoles or in feeding-associated detritus captured on our filters. By 21 h, this represented nearly 50% of the total DMSP$_p$, suggesting that turnover of DMSP$_p$ inside grazer vacuoles may have been relatively slow.

Although microbial consumption of DMS is rapid in some marine environments (Kiene & Bates 1990, Kiene & Service 1991, Wolfe & Kiene 1993b), we have found no evidence to date for this process in our culture experiments. Additions of DMS to a concentrated *Oxyrrhis marina*/bacterial assemblage resulted in stable elevated DMS concentrations (Fig. 4), and in additional experiments with inhibitors of DMS consumption such as dimethyl ether (Wolfe & Kiene 1993a) or chloroform, DMS did not accumulate to any degree in incubations with amendments (data not shown). Therefore, we believe that DMS loss was probably dominated by outgassing, which was minimized by low headspace volumes and careful sampling handling. It is possible that microbial DMS consumption at 16°C is slower than in warmer waters where it has been frequently measured, or it may be that our simplified experimental system simply did not have sufficient microbial diversity to include DMS-consuming bacteria.

If DMS loss were near zero, the accumulation of DMS observed in the grazed samples gives some indication of the rate of DMS production from either dissolved DMSP released during grazing or from the protists or prey themselves, and allows us to assemble a budget of DMSP consumption and conversion (Fig. 8). Although our results do not exclude the possibility that *Oxyrrhis marina* might be able to take up and lyse dissolved DMSP, the production of DMS in the size-fractionated prey fraction taken from the grazing bottles suggests possible bacterial association with predator and prey (Fig. 7), and we assume that bacteria were the main utilizers of DMSP$_d$ in our experiments.

We do not directly know the fraction of DMSP$_d$ which was demethylated or metabolized to non-DMS products, but we believe it was low in these cultures since the only bacterial isolate which metabolized DMSP$_d$ did not appear to form products other than DMS. Furthermore, addition of glycine betaine, which has been suggested to block transport of DMS into bacterial cells (Kiene & Service 1993), did not inhibit DMS production in our bacterial isolate, nor did it affect DMSP$_d$ pools in the grazing experiments. This suggests that organisms similar to our isolate may possibly have been the dominant sink for dissolved DMS in these experiments.

If we assume that demethylation or other metabolism of DMSP$_d$ was negligible, then the combined accumulation of DMSP$_d$ and DMS gives the total DMSP$_d$ produced during grazing. When grazer densities were high (>300 ml$^{-1}$), the majority of prey DMSP$_p$ (about 70%; Fig. 8a) was consumed by grazers while only

![Fig. 8. *Oxyrrhis marina* grazing on *Emiliania huxleyi*. Effect of grazers on DMSP cycling for *O. marina* densities of (a) 350 to 450 ml$^{-1}$ and (b) 150 ml$^{-1}$. Percentages next to arrows are fractions of total change in DMSP$_p$ or DMSP$_d$ over 20 to 22 h incubation periods](image-url)
about 30% was released to the dissolved pool. In the experiment where grazer density was lower, this pattern was reversed (Fig. 8b). In all cases, bacteria converted approximately 25 to 35% of the newly produced DMSP to DMS.

Although our evidence suggests that *Oxyrrhis marina* may metabolize DMSP without direct production of DMS, other heterotrophic flagellates and other microherbivores likely have different abilities. DMSP clearly accumulates to some degree in larger predators such as shellfish and fish (Motohiro 1962, Ackman et al. 1966, Ackman & Hingley 1968, Iida & Tokunaga 1986) and may bioconcentrate within marine food webs (Sieburth 1960). Measurements of DMSP in the >240 μm fraction in the NE Pacific showed approximately 10% of total DMSP associated with copepods and other metazoan grazers (Wolfe 1992). Therefore some heterotrophs probably do not rapidly metabolize DMSP. On the other hand, one of the few studies of a DMSP lyase enzyme was in a heterotrophic dinoflagellate, the osmotroph *Gyrodi-rium cohnii*, which synthesized and lysed DMSP when grown on acetate (Ishida & Kadota 1967). Additionally, Antarctic krill *Euphausia superba* accumulated DMSP from its prey and could enzymatically convert it to DMS (Tokunaga et al. 1977). These reports suggest that various marine heterotrophs probably can cleave, metabolize, and/or accumulate DMSP.

Because micrograzers comprise such a large fraction of marine herbivores and process a large fraction of primary production (Capriulo et al. 1991, Sherr & Sherr 1992), they are likely to be important to DMSP cycling regardless of their biochemical abilities. Only those predators which can lyse DMSP will form DMS directly, but those which excrete ingested DMSP in dissolved or submicron form may be more important to DMS production in the sea because they make it available to bacterial action. It is also possible that grazing stimulates associated bacterial activity by increasing availability of low molecular weight compounds like DMSP associated with egested detritus or dissolved waste. Furthermore, predators which metabolize algal DMSP in other ways, such as via transmethylation reactions, may remove a large fraction of ‘potential DMS’ and thereby limit the amount of DMS produced. The fraction of grazed DMSP that is metabolized by microzooplankton, or made available to water column bacteria, may be critical to regulating DMS production from marine microbial communities.

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