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- Latitude drives global-scale spatial variation
- Temperature drives local-scale temporal variation

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Coralline algae as a globally significant pool of marine dimethylated sulfur

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Abstract Marine algae are key sources of the biogenic sulfur compound dimethylsulphoniopropionate (DMSP), a vital component of the marine sulfur cycle. Autotrophic ecosystem engineers such as red coralline algae support highly diverse and biogeochemically active ecosystems and are known to be high DMSP producers, but their importance in the global marine sulfur cycle has not yet been appreciated. Using a global sampling approach, we show that red coralline algae are a globally significant pool of DMSP in the oceans, estimated to be ~110×10^{12} moles worldwide during the summer months. Latitude was a major driver of observed regional-scale variations, with peaks in polar and tropical climate regimes, reflecting the varied cellular functions for DMSP (e.g., as a cryoprotectant and antioxidant). A temperate coralline algal bed was investigated in more detail to also identify local-scale temporal variations. Here, water column DMSP was driven by water temperature, and to a lesser extent, cloud cover; two factors which are also vital in controlling coralline algal growth. This study demonstrates that coralline algae harbor a large pool of dimethylated sulfur, thereby playing a significant role in both the sulfur and carbon marine biogeochemical cycles. However, coralline algal habitats are severely threatened by projected climate change; a loss of this habitat may thus detrimentally impact oceanic sulfur and carbon biogeochemical cycling.

1. Introduction

Dimethylsulphoniopropionate (DMSP) and its breakdown product DMS (collectively DMS/P) have been linked to global climate regulation via the formation of atmospheric aerosols [*Charlson et al.*, 1987]. DMS/P are also critical to the healthy functioning of pelagic and benthic marine ecosystems [*Exton et al.*, 2014], through their range of functions in algal cells [*Stefels*, 2000; *Sunda et al.*, 2002] and their role in maintaining trophic interactions, such as invertebrate grazing [*Van Alstyne and Houser*, 2003] and vertebrate foraging [*De Bose et al.*, 2008; *Kowalewsky et al.*, 2006; *Nevitt*, 2011]. Our current understanding of spatiotemporal changes in DMS/P is limited to relatively few studies, causing large uncertainties in models [*Halloran et al.*, 2010]. Observed patterns in the open ocean have been attributed to the development of spring/summer phytoplankton blooms [*Lana et al.*, 2011] and sea ice melt [*Carnat et al.*, 2014] at high latitudes, irradiance "stress" in low latitudes [*Vogt et al.*, 2010] or year-round productivity in upwelling regions [*Kloster et al.*, 2006].

In coastal benthic systems, spatiotemporal patterns appear to reflect the proposed cellular functions of DMSP. In tropical coral reef ecosystems, peaks in coral and water column DMS/P are observed in the summer months [*Broadbent and Jones*, 2006; *Jones et al.*, 2007], supporting the antioxidant function hypothesis [*Sunda et al.*, 2002]. In contrast, peak concentrations in intracellular DMSP in the invasive macroalga *Codium fragile* are observed in late winter, supporting the proposed cryoprotective function [*Lyons et al.*, 2007, 2010]. Similarly, intracellular DMSP concentrations in nongeniculate red coralline algae are known to respond to local environmental change including pH [*Burdett et al.*, 2012], light [*Burdett et al.*, 2014; *Rix et al.*, 2012], and salinity [*Burdett et al.*, 2015]. However, regional-scale spatiotemporal variations in benthic ecosystem DMS/P are yet to be determined.

Red coralline algae can encrust rocks or grow as free-living thalli (known as maerl or rhodoliths) from the intertidal zone to depths of >300 m [*Friedlander et al.*, 2014], with an estimated global coverage of ~2.24 million km^2 [*van der Heijden and Kamenos*, 2015]. The growth of coralline algae is known to be extremely sensitive to water temperature [e.g., *Adey*, 1970; *Kamenos and Law*, 2010] and light [*Burdett et al.*, 2011], permitting their use as a high-resolution palaeoclimatic proxy [*Burdett*, 2014]. From a biogeochemical perspective,

coralline algal habitats are known to be important in the coastal carbon cycle, for example, acting as a major blue carbon repository [*van der Heijden and Kamenos*, 2015]. Since red coralline algae are globally ubiquitous and are high macroalgal producers of DMSP [*Burdett et al*., 2015], they are thought to be an important benthic component of the marine sulfur cycle [*Kamenos et al*., 2008b], but this has yet to be determined on a regional/global scale.

Here, we present a global study of DMS/P associated with coralline algal beds and identify the environmental drivers at local and regional spatiotemporal scales, reflecting processes at the ecosystem (e.g., seasonal changes in the ecosystem) and suborganism (e.g., physiological response to environmental change) level.

2. Methods

2.1. Quantifying the Global Coralline Algal Pool of DMSP

Coralline algal intracellular DMSP was determined from 10 sites across a 124° latitudinal range, considering seven genera with both encrusting and free-living growth forms (Table 1). All samples were collected during the summer months of the respective hemisphere in 2010–2012 and were hand collected using SCUBA. Branch fragments (~0.1 g) were stored in 10 M sodium hydroxide in gas-tight glass vials (Wheaton) sealed with Pharma-Fix septa (Grace Alltech) to convert intracellular DMSP into DMS. Samples were stored in the dark until DMS determination (within 3 months of collection) by gas chromatography (Shimadzu GC2014) using direct injection of the vial headspace (injector temperature: 45°C). The gas chromatograph (GC) was equipped with a 25 m capillary column (Restek RTx-5MS, 45°C, nitrogen carrier gas) and sulfur-specific flame photometric detector (200°C). Sample concentrations were calculated from DMSP standard calibration curves (DMSP standard from Research Plus Inc.). The detection limit for direct injection was 30 nmol per injection; analytical precision was within 1%.

2.2. Identifying Local-Scale Temporal Variation

To investigate local-scale temporal variations in more detail, a 2 year temporal investigation was conducted at Loch Sween, on the west coast of Scotland, UK, where the coralline algal bed is dominated by *Lithothamnion glaciale* (Table 1). All samples were collected at slack tide using SCUBA, from March 2010 to February 2012 (~10 week sampling frequency). At each timepoint, intracellular DMSP concentrations were determined to complement the regional-scale spatial investigation, as well as water samples to identify the impact of the coralline algal ecosystem on dimethylated sulfur concentrations in the overlying water column. Four stations around the coralline algal bed were sampled: (1) at the seafloor at the coralline algae bed (depth: 6 m), (2) at the seafloor to the side of the bed (mud/sand substrate, depth: 6 m), (3) midwater above the coralline algae bed (depth: 3 m), and (4) midwater above the bed side (depth: 3 m).

Water samples ($n = 5$ per station, per time point) were taken for dissolved DMS (DMSd), dissolved DMSP (DMSPd), and particulate DMSP (DMSPp) determination, following protocols in *Kiene and Slezak* [2006]. Water samples were hand collected in syringes using SCUBA and processed immediately on return to the shore. Water samples were drip filtered through a GF/F 0.7 μm depth filter (Millipore). Half of the filtrate was bubbled with oxygen-free nitrogen gas to purge the sample of DMS (thus representing dissolved DMSP; prior tests showed that this was an effective and reliable method); the unpurged half represented dissolved DMS + DMSP. Dissolved DMS concentrations were determined by taking the concentration difference between dissolved DMS + DMSP and dissolved DMSP samples. Particulate DMSP was determined from the difference between dissolved DMSP + DMS and unfiltered (= dissolved + particulate DMSP + DMS) samples, since particulate DMS is assumed to be negligible [*Kiene and Slezak*, 2006]. All samples were stored at 0.33 M NaOH final concentration in gas-tight glass vials (Wheaton) sealed with Pharma-Fix septa (Grace Alltech) to hydrolyze DMSP in the sample to volatile DMS. No DMS samples were taken in March and April 2010, samples from above the bed side were not available in March 2011, and particulate DMSP samples could not be collected in November 2011. All water samples were analyzed for DMS using the purge-cryotrap-GC method using sodium hydroxide to hydrolyze DMSP in the sample to volatile DMS [*Turner et al*., 1990]. The detection limit for direct injection was 30 nmol per injection and 0.02 nmol for the purge-cryotrap method; analytical precision was within 1%.

2.3. Abiotic Variables

In situ water temperature (°C) at each of the 10 sites was monitored using Gemini TinyTag TGI-3080 data loggers (no difference was observed between the four stations at Loch Sween). For statistical modeling

Table 1. Details of the Sample Sites for Coralline Algal Intracellular DMSP Quantification

Species	Location	Latitude, Longitude	Depth (m)	Water Temperature (°C)[a]
Lithothamnion glaciale[b]	Loch Torridon, Scotland	57°32.09′N 05°32.34′W	7	7
Phymatolithon calcareum[b]	Loch Carron, Scotland	57°19.78′N 05°40.89′W	0.1	7
P. calcareum[b]	Loch Ailort, Scotland	56°50.98′N 05°44.58′W	3	7
L. glaciale[b]	Loch Sween, Scotland	56°01.99′N, 05°36.13′W	6	3.5–17.3[c]
L. glaciale[b]	Nova Scotia, Canada	44°04.11′N 64°36.71′W	4	14
Mesophyllum alternans[d]	Banuyls-sur-Mer, France	42°30.03′N 03°08.28′E	17	14
Lithophyllum kotschyanum[b]	Dahab, Egypt	28°28.79′N 34°30.83′E	1	28
Porolithon sp.[b]	Dahab, Egypt	28°28.79′N 34°30.83′E	1	28
Mesophyllum sp.[b]	Punta del Tralca, Chile	33°25.33′S 71°42.24′W	15	18
Lithothamnion sp.[b]	Las Cruces, Chile	33°30.01′S 71°37.93′W	0.2	18
Clathromorphum sp.[e]	Adelaide Island, Antarctica	67°36.71′S 68°12.57′W	9	−1
Mesophyllum sp.[e]	Adelaide Island, Antarctica	67°36.71′S 68°12.57′W	9	−1
Spongites sp.[e]	Adelaide Island, Antarctica	67°36.71′S 68°12.57′W	9	−1

[a]Water temperature is at time of collection.
[b]Free-living growth form.
[c]Multiple samples taken over a two-year period, see text and Figure 2.
[d]Crustose growth form as part of a coralligenous framework (coralligène).
[e]Crustose growth form.

(see below), the average in situ temperature for the week prior to each sampling timepoint was used. Light availability for the global-scale investigation was taken into account by using latitude as a proxy. Light availability for the local-scale temporal investigation utilized cloud cover and daylength. Cloud cover (oktas) for the local-scale temporal investigation was obtained from the ICOADS database as a monthly average, at a 1° × 1° spatial resolution [*Woodruff et al*., 2011]; mean cloud cover in the month prior to sampling was used in the modeling. This is the best estimate available for the sampling period; data were available for all timepoints. Daylength (hours) was taken as the time between sunrise and sunset in Glasgow, UK (85 km east of the study site), on the day of sampling. Data were obtained from the *Astronomical Almanac*, published annually by the UK Hydrographic Office and the United States Naval Observatory.

2.4. Statistical Analyses

Correlations between environmental factors (latitude, longitude, in situ water temperature, and depth) and coralline algal intracellular DMSP concentrations were determined using Spearman's rank correlation analyses for all 10 sites (data could not be transformed to meet normality assumptions of parametric testing), conducted in Minitab V14.1. Generalized Additive Models (GAMs) were used to assess the relationship between the abiotic variables and the DMS/P measurements from the Loch Sween time series (all $\log_{10}$ transformed). GAMs were conducted in R (V2.14.2) using the "mgcv" package [*Wood*, 2006]. Thin plate regression splines were used as the smoothing basis, allowing multiple predictors to be considered and reducing subjectivity as knot locations (i.e., where splines join) were not manually specified [*Wood*, 2003]. The "ccf" function was used to identify significant (95%) correlations. Where a lagged correlation was identified, only positive lags were considered as negative lags were not ecologically relevant; no autocorrelation in the data sets was identified. No interactions between the abiotic variables were identified ("coplot" function). The most parsimonious GAM for each DMS/P data set was determined using generalized cross-validation techniques (GCV) [*Wood*, 2006]. Annual averages of DMSd, DMSPd, and DMSPp were compared between sites using a one-way ANOVA with $\log_{10}$ transformation, conducted in Minitab V14.1.

3. Results

3.1. Regional-Scale Spatial Variations in DMSP

The concentration of coralline algal intracellular DMSP ranged from 13.1 ± 2.10 to 430.4 ± 39.44 μmol g^{-1} (mean ± standard error) between global sites (Figure 1) and was strongly correlated to latitude ($r_s = -0.607$,

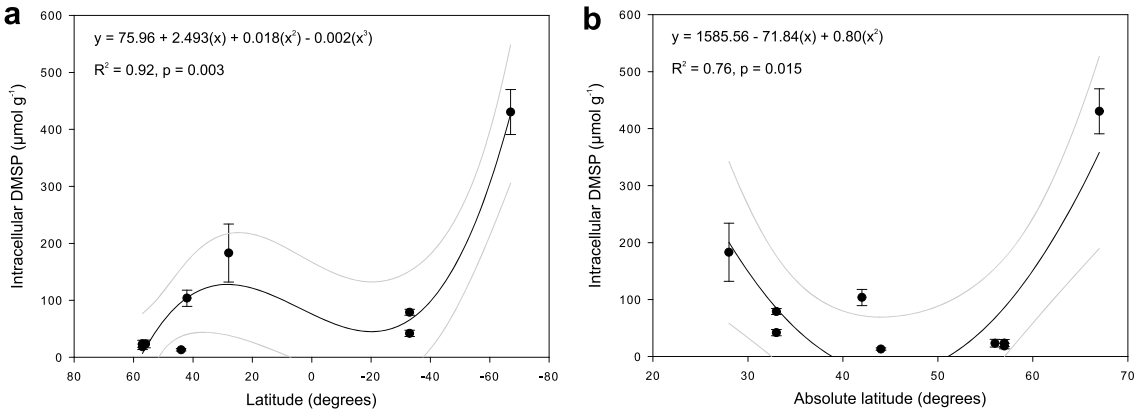

Figure 1. Relationship between coralline algal intracellular DMSP and (a) latitude and (b) absolute latitude (i.e., regardless of Northern/Southern Hemisphere). Data presented as mean ± SE. Black line represents (Figure 1a) cubic or (Figure 1b) quadratic relationship; grey lines represent 95% confidence intervals.

$p < 0.001$), but only weakly correlated to longitude ($r_s = -0.224$, $p < 0.001$) and in situ water temperature ($r_s = -0.211$, $p < 0.001$). Intracellular DMSP concentrations were not significantly correlated to water depth ($r_s = 0.098$, $p = 0.06$).

Intracellular DMSP concentration was highest at both high and low latitudes; a cubic function of latitude explained up to 92% of the observed variation in intracellular DMSP, although this projects intracellular DMSP to be zero >60°N (Figure 1a); this is unlikely to be the case. When absolute latitude was considered (i.e., disregarding Northern/Southern Hemisphere), a clear pattern of elevated DMSP at both high and low latitudes was observed ($R^2 = 0.76$, $p = 0.01$; Figure 1b).

3.2. Global-Scale Estimation of Coralline Algal DMSP Pool

Regression models of intracellular DMSP (Figure 1) were used to estimate the size of the pool of DMSP harbored by coralline algae based on recent estimates of global coralline algal distribution. The areal mass of a live coralline algal bed is ~86 kg m^{-2} [*Burrows et al.*, 2014]. The total area of coralline algal beds in Scotland is ~7.02 km^2 [*Burrows et al.*, 2014] and 3 million km^2 globally [*van der Heijden and Kamenos*, 2015]. Using these data, the summertime coralline algal pool of DMSP was estimated to be ~1.1×10^7 moles in Scotland, ~1.5×10^{13} mol across the 124° latitudinal range covered by this study, and extrapolated to ~1.1×10^{14} mol globally.

3.3. Local-Scale Temporal Variations

At a local scale, temporal variations in intracellular DMSP concentrations were significantly explained by daylength (Table 2), which ranged from 6.9 to 17.5 h (Figure 2a): intracellular DMSP was ~15 µmol g^{-1} for most of the year (Figure 2b), with small peaks in April 2010 and May 2011, and a larger peak in September 2010 (Figure 2b).

Dissolved DMS concentrations were highest above the maerl bed (15.4 ± 3.63 nmol L^{-1}; mean ± SE); average concentrations in the other three locations were lower (10.4 ± 1.51 nmol L^{-1}, Figure 2c). Maximum dissolved DMS concentration was observed in July 2010 (51.9 ± 14.69 nmol L^{-1} at the bed side), followed by a decline to a winter minimum of 1–2 nmol L^{-1} at all locations; this decline was most rapid at the coralline algal bed (Figure 2c). Dissolved DMSP concentrations were lower at the seafloor to the side of the coralline algal bed (18.0 ± 2.99 nmol L^{-1}), compared to the other locations (21.7 ± 2.14 nmol L^{-1}) (Figure 2d). Maximum dissolved DMSP concentrations at, and above, the bed side were later in the year than the maerl bed locations, peaking in September 2010; a distinct peak above the coralline algal bed in August 2011 was not observed in the other locations (Figure 2d). Dissolved DMSP concentrations during the winter November 2010 to January 2011 were higher at the coralline algal bed than the other three locations (Figure 2d). Particulate DMSP concentrations followed a similar pattern to dissolved DMSP, but with more pronounced summer peaks (Figure 2e). Particulate DMSP concentrations at the seafloor to the side of the bed had the lowest overall average (46.4 ± 7.76 nmol L^{-1}), followed by above the bed side (51.6 ± 9.63 nmol L^{-1}), at the maerl bed (55.8 ± 11.73 nmol L^{-1}) and above the maerl bed (60.7 ± 9.69 nmol L^{-1}) (Figure 2e). Water column

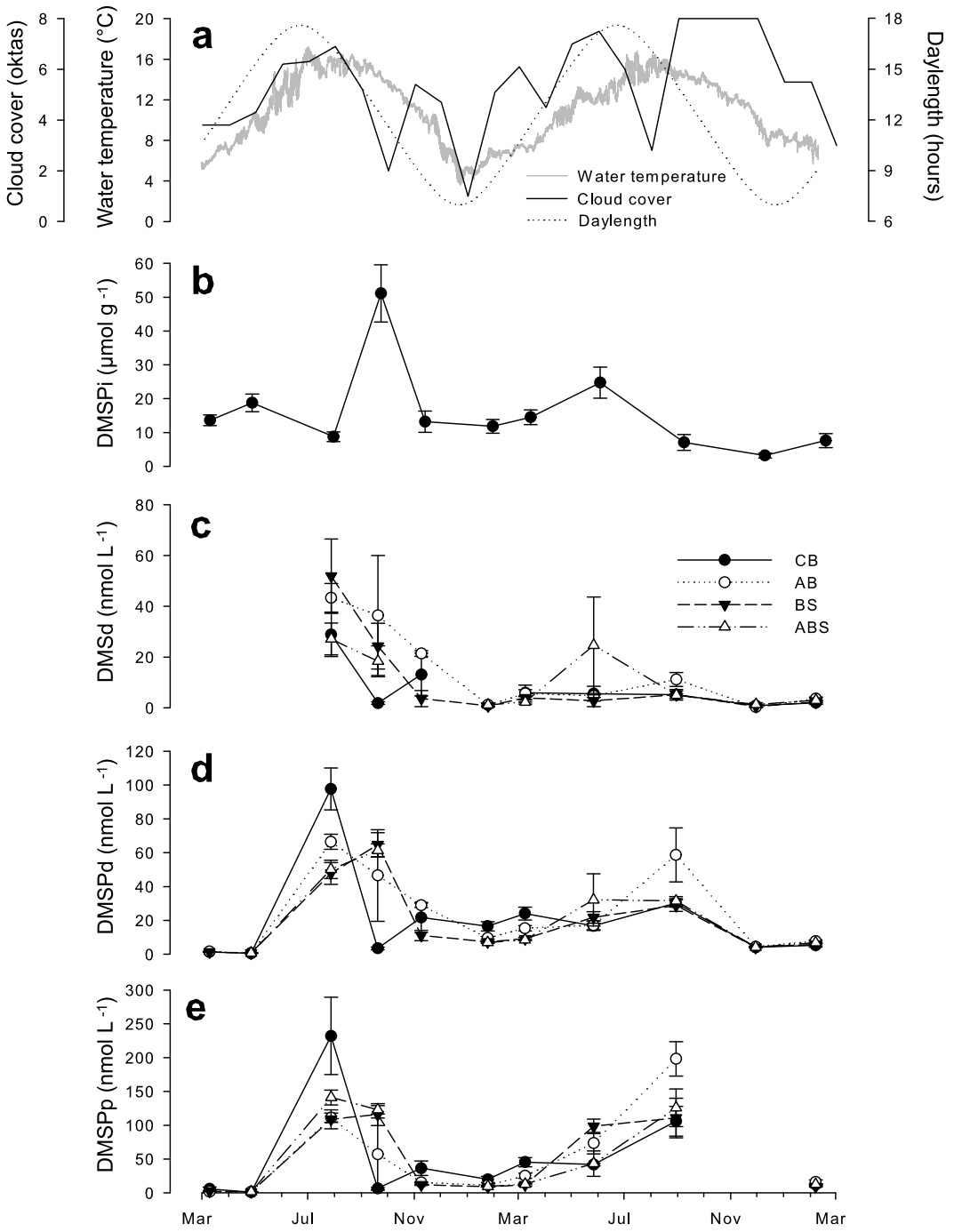

Figure 2. Abiotic and DMS/P measurements from Loch Sween, March 2010 to February 2012: (a) hourly water temperature (°C, grey line), monthly cloud cover (oktas, black line), and daylength (hours, dotted line), (b) intracellular DMSP (DMSPi, µmol g^{-1}) of *Lithothamnion glaciale*, (c) dissolved DMS (DMSd, nmol L^{-1}), (d) dissolved DMSP (DMSPd, nmol L^{-1}), and (e) particulate DMSP (DMSPp, nmol L^{-1}) from four locations within Loch Sween: at the coralline algal bed (CB, black circles), above the coralline algal bed (AB, open circles), at the bed side (BS, black triangles), and above the bed side (ABS, open triangles). DMS/P data presented as mean ± SE.

DMSP and DMS concentrations were primarily explained by water temperature (which ranged from 3.5 to 17.3°C, Figure 2a and Table 2) and cloud cover (which ranged from 1 to 8 oktas; Figure 2a and Table 2); like intracellular DMSP, dissolved DMS over the bed side was best explained by daylength (Table 2).

Table 2. Most Parsimonious GAM Models for DMS/P Measurements at Loch Sween[a]

Location	GAM Formula	Est. df	GCV Score	Adjusted R^2	Dev. Exp. (%)	*n*
Maerl	DMSPi ~ s(DL + 1)	8.97	0.179	0.403	42.5	217
Maerl bed	DMSd ~ s(CC)	9.46	0.251	0.604	68.6	42
	DMSPd ~ s(T) + s(CC)	10.92	0.031	0.942	95.3	52
	DMSPp ~ s(T) + s(CC)	10.92	0.053	0.913	93.1	47
Above maerl bed	DMSd ~ s(CC)	9.77	0.224	0.617	70.1	41
	DMSPd ~ s(T) + s(CC)	8.79	0.097	0.802	83.0	56
	DMSPp ~ s(T) + s(CC)	10.39	0.103	0.861	88.9	49
Bed side	DMSd ~ s(DL)	4.56	0.348	0.417	47.5	37
	DMSPd ~ s(T) + s(CC)	10.55	0.017	0.966	97.2	53
	DMSPp ~ s(T)	9.84	0.020	0.968	97.4	50
Above bed side	DMSd ~ s(CC)	9.77	0.224	0.617	70.1	41
	DMSPd ~ s(T) + s(CC)	8.79	0.097	0.802	83.0	56
	DMSPp ~ s(T) + s(CC)	10.39	0.103	0.861	88.9	49

[a]Modeled measurements include intracellular DMSP (DMSPi) of *Lithothamnion glaciale* and water samples from four locations in Loch Sween: at the maerl bed, above the maerl bed, at the bed side, and above the bed side, split into dissolved DMS (DMSd), dissolved DMSP (DMSPd), and particulate DMSP (DMSPp). GAMs were constructed using the abiotic variables water temperature (T), cloud cover (CC), and daylength (DL). DL + 1 indicates a one timepoint (= 10 weeks) lag in daylength correlation. Estimated degrees of freedom (Est. df), GCV score, adjusted R^2, % deviance explained (Dev. Exp.), and the number of observations (n) are presented. Models were run for all measurements with all abiotic variables; only the most parsimonious GAM for each DMS/P measurement is presented.

Despite the observed seasonal patterns and identified environmental drivers, no significant difference between sampling locations in Loch Sween was observed (dissolved DMS: $F_{3,\ 157} = 0.77$, $p = 0.512$, dissolved DMSP: $F_{3,\ 205} = 0.31$, $p = 0.818$, particulate DMSP: $F_{3,\ 186} = 0.38$, $p = 0.769$; Figure 3). However, average water column DMS and DMSP concentrations were considerably higher than global open-ocean estimates (Figure 3), and regional averages for the North Atlantic ($3.65 \pm 6.35/1.77$ nmol L^{-1}) and UK shelf ($5.4 \pm 10.3/2.3$ nmol L^{-1}, mean ± SD/median) (derived from the DMS database) [*National Oceanic and Atmospheric Administration-Pacific Marine Environmental Laboratory*, 2004].

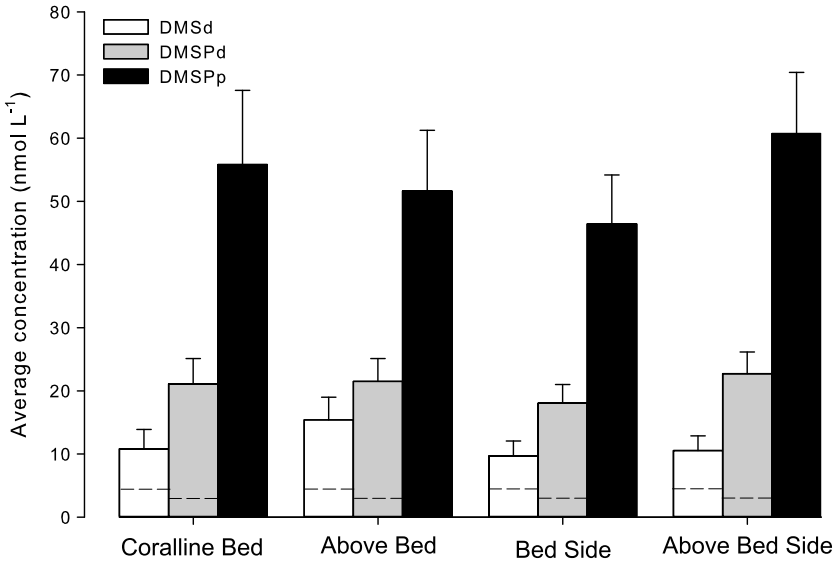

Figure 3. Average water column DMS/P in Loch Sween, Scotland, March 2010 to February 2012: Averaged dissolved DMS (white bars), dissolved DMSP (grey bars), and particulate DMSP (black bars) at a maerl bed in Loch Sween at four sampling sites: at the maerl bed, above the maerl bed, at the bed side, and above the bed side. Data presented as mean ± SE. Dotted lines represent the global estimate for annual averages of dissolved DMS (up to 5 nmol L^{-1}) [*Lana et al.*, 2011] and dissolved DMSP (2.8 nmol L^{-1}) [*Kiene and Slezak*, 2006].

4. Discussion

There is a current paucity of dimethylated sulfur data from coastal oceans, preventing their inclusion in global climatologies [*Lana et al*., 2011]. Here we have demonstrated that coralline algae, globally important autotrophic ecosystem engineers, harbor a large pool of marine dimethylated sulfur. Elevated intracellular DMSP concentrations at high and low latitudes likely reflect the proposed cellular functions of DMSP in macrophytes as a cryoprotectant [*Lyons et al*., 2007] and as an antioxidant [*Broadbent and Jones*, 2006; *Jones et al*., 2007]. This study also presents the longest time series of coastal DMS/P to date, showing that DMS/P concentrations in the water surrounding coralline algal beds are considerably higher than global and regional annual averages (Figure 3).

From a holistic perspective, this study actually represents an underestimate of the size of the DMSP pool harbored by coralline algal ecosystems. The framework engineered by coralline algae provides a structurally and functionally complex habitat that can support a very rich biodiversity, including a wide range of macroalgae and microalgae [*Barbera et al*., 2003]. These other algae represent additional DMSP producers that will add to the total coralline algal ecosystem pool. Associated invertebrates may also bioaccumulate DMSP [*Van Alstyne and Puglisi*, 2007], further contributing to the overall DMSP pool. Unlike some marine ecosystems (e.g., phytoplankton blooms), coralline algae thalli, and their associated beds are spatially stable over long time periods [*Kamenos*, 2010], thereby representing a large, and long-term, DMSP pool in the coastal zone.

Interannual variability is an important, but poorly understood, aspect of global DMS dynamics [*Halloran et al*., 2010]. In line with other ecosystems, coralline algal habitats appear to exhibit significant interannual variability in DMS/P concentrations. Summer DMS/P peaks are likely to have been caused by (1) increased coralline algal ecosystem production in the warmer temperatures, (2) a breakdown in water column stratification as autumn approached, and/or (3) a degradation of seasonal macroalgae (e.g., *Corda filum*) as irradiance began to decrease from the summer maximum. Other DMS/P peaks (e.g., in the spring) may have been missed by the sampling regime. Interestingly, water temperature and cloud cover (which best explained local-scale temporal variability, Table 2) are also important in driving the growth and calcification of coralline algae [*Burdett et al*., 2011; *Kamenos et al*., 2008a; *Kamenos and Law*, 2010]. This supports previous suggestions of a link between macroalgal calcification and DMSP production [*Burdett et al*., 2012, 2013], warranting further investigations at the suborganism level. Water temperature has also been described as an important driver in coral reef DMS/P concentrations [*Broadbent and Jones*, 2006; *Jones et al*., 2007], highlighting a similarity between temperate and tropical DMS/P regimes.

Evidence that coralline algal habitats also exert a direct seasonal influence on water column DMS/P pools was also observed. During the winter months, dissolved and particulate DMSP concentrations were highest at the maerl bed site, suggesting that the maerl bed ecosystem acts as a winter source of DMSP. The origin of this is likely to be from sloughing of the *L. glaciale* thalli and the continued degradation of summer macroalgal detritus. Peak summer DMSP concentrations at the coralline algal bed sites occurred 1–2 months before the bed side maximum, suggesting that the coralline algal habitat may be more responsive to environmental change (e.g., rising water temperatures), acting as a source of DMSP in the early summer and creating fine-scale heterogeneity in the water column.

This study demonstrates that coralline algal habitats are a previously overlooked, yet globally important, pool of dimethylated sulfur in the marine environment. Coralline algae are therefore likely to play crucial roles in both the sulfur and carbon cycles. Interaction with the overlying water column also results in localized elevations in water column DMS/P concentrations far higher than global and regional averages for pelagic systems. At the global scale, latitude drives the regional magnitude of the coralline algal DMSP pool. At the local scale, water temperature and cloud cover drive temporal variations in DMS/P—two factors which also affect coralline algal growth and calcification. At first glance, one may envisage that projected ocean warming will thus increase the global coralline algal DMSP pool. However, coralline algal survival is severely threatened by projected ocean warming and acidification [*McCoy and Kamenos*, 2015], especially at high latitudes where the coralline algal DMSP pool may be highest. Thus, while the amount of DMSP per unit area may increase under projected climate change, habitat loss may offset this effect in terms of the global pool of coralline algal-derived DMSP. This change in DMSP provision may severely affect both the carbon and sulfur biogeochemical cycles and may impact the healthy functioning of coastal ecosystems.

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