RESEARCH ARTICLE

Coral reef aerosol emissions in response to irradiance stress in the Great Barrier Reef, Australia

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Abstract We investigate the correlation between stress-related compounds produced by corals of the Great Barrier Reef (GBR) and local atmospheric properties—an issue that goes to the core of the coral ecosystem’s ability to survive climate change. We relate the variability in a satellite decadal time series of fine-mode aerosol optical depth (AOD) to a coral stress metric, formulated as a function of irradiance, water clarity, and tide, at Heron Island in the southern GBR. We found that AOD was correlated with the coral stress metric, and the correlation increased at low wind speeds, when horizontal advection of air masses was low and the production of non-biogenic aerosols was minimal. We posit that coral reefs may be able to protect themselves from irradiance stress during calm weather by affecting the optical properties of the atmosphere and local incident solar radiation.

Keywords Aerosols · Coral bleaching · Corals · GBR · Irradiance stress

INTRODUCTION

This study investigates the hypothesis that the emission of biogenic gases that contribute to aerosol production by coral reefs may regulate their local climate—an issue that goes to the core of the coral’s ability to adapt to changes associated with enhanced greenhouse conditions. The Great Barrier Reef (GBR) lies off the coast of Queensland in northeastern Australia and is the largest complex of coral reefs in the world. It is a long, narrow system stretching 2300 km along the coast from 10.5°S at Cape York to 24.5°S near Bundaberg. It ranges in width from 60 km in the north to 250 km in the south and is bounded by the Queensland coast on the west and the Coral Sea on the east.

The climate of the GBR ranges from subequatorial in the north to subtropical in the south. South-east trade winds dominate during the dry months of May to October, and northeast winds dominate the wetter, summer months of November to April (Lough 1998).

The GBR has long been recognized as a strong source of aerosol particles, dominated by sulfates and organics (Bigg and Turvey 1978; Leck and Bigg 2008; Modini et al. 2009); however, the full characterization of these aerosols is as yet incomplete. It is thought that coral reef emissions of aerosol precursor compounds may be an important contributor to the overall atmospheric aerosol burden over the GBR, determining cloud properties and hence impacting the regional radiation budget (Fischer and Jones 2012; Deschaseaux et al. 2013, 2016; Leahy et al. 2013; Jones 2015). This may provide a natural defense mechanism against bleaching for corals locally through the regulation of incident solar radiation. Solar radiation management (SRM) or solar geo-engineering has been suggested as one approach to alleviating warming (Caldeira et al. 2013), and although a complete analysis of the implications is pending (Irvine et al. 2017), serious attention is now being given to this technique to alleviate increasingly frequent bleaching episodes in coral reefs (Kwiatkowski et al. 2015).

There is also the possibility that the global decline in coral cover associated with multiple anthropogenic stressors, such as deteriorating water quality, overfishing, and ocean acidification, will accelerate the deterioration of this habitat and its associated ecological and economical value. Further, the very high sulfate aerosol emissions associated with extant coral reefs (Jones et al. 1994; Hill et al. 1995) suggest that the widespread loss of coral reefs could potentially lead to further destabilization of the global and regional climate.

Dimethylsulfoniopropionate (DMSP) is an organic sulfur compound, that is synthesized by a range of phytoplankton (Keller et al. 1989; Curson et al. 2017) and has a number of key roles in marine ecological processes and biogeochemistry, including cell protection from oxidative stressors such as intense solar radiation (Sunda et al. 2002). This remarkable compound is ubiquitous in the sunlit upper layer of the oceans and seems to play a major role in interactions across trophic levels: from microbial plankton (Simó 2001) to organisms such as sea-birds at the highest food web level (Savoca and Nevitt 2014). DMSP degradation produces the volatile compound dimethylsulfide (DMS), whose global oceanic emission is currently estimated to be around 20–28 TgSy⁻¹ thus representing the main natural source of sulfur to the atmosphere (Lana et al. 2011; Land et al. 2014).

Once emitted to the atmosphere DMS is oxidized to sulfate aerosols, which can contribute to cloud condensation nuclei (CCN), impacting cloud microphysical properties such as cloud reflectivity and lifetime. This could potentially provide a negative feedback effect on increasing sea surface temperature (SST) and incident solar radiation—as described by the so-called ‘CLAW hypothesis’ (Charlson et al. 1987). However, after three decades of research, we now recognize that the proposed feedback cycle is much more complex and nuanced than first described (Ayers and Cainey 2007; Quinn and Bates 2011; Green and Hatton 2014). Although there is substantial evidence for a connection between marine biogenic aerosols and climate, with DMS potentially being one of the key players in this feedback cycle (Gabric et al. 2004, 2013; Rap et al. 2013), many other volatile organic compounds (VOCs) synthesized by the marine ecosystem are thought to have similar effects (Bigg et al. 2004; Meskhidze and Nenes 2010; Orellana et al. 2011), with some such as isoprene, shown to be sensitive to irradiance or temperature stress (Meskhidze et al. 2015).

Reef-building corals are prolific producers of DMSP, a central molecule in the marine sulfur cycle and precursor of DMS (Broadbent et al. 2002; Broadbent and Jones 2004). Both DMS and DMSP are particularly abundant in coral reef ecosystems (Jones et al. 1994; Hill et al. 1995), present in macroalgae (Broadbent et al. 2002), coralline algae (Burdett et al. 2015), and have also been detected in coral polyps themselves (Raina et al. 2013). Importantly, in strongly illuminated coral reef environments solar irradiance is a key determinant of DMS water concentration (Jones et al. 2007; Vallina and Simo 2007), with the photo-response of gross DMS production in most cases strong enough to (at least) compensate for the photochemical DMS loss at the water subsurface (Galí et al. 2013). Also of note is the observation that exposure of corals to air at low tides causes a significant increase of DMS to the

atmosphere (Hopkins et al. 2016; Swan et al. 2017) and elevated concentrations of intracellular DMSP in both coral tissue and symbiotic zooxanthellae (Deschaseaux et al. 2014; Jones et al. 2014; Frade et al. 2015; Hopkins et al. 2016).

There is some evidence to suggest that a coral reef–climate feedback that regulates SSTs does exist (Leahy et al. 2013; Jones 2015). Monitoring of SST in coral reefs worldwide has shown that pristine reefs within or near the western Pacific warm pool (north-east of Australia) have had fewer reported coral bleaching events relative to reefs in other regions of the world, possibly because of an “ocean thermostat” mechanism that acts to depress warming beyond certain SST thresholds (Kleypas et al. 2008). The exact physical nature of this mechanism is yet to be determined, although increased cloudiness has been hypothesized as a possible factor (Kleypas et al. 2015). DMS could be involved in local climate regulation over coral reefs through its oxidation into sulfate aerosol particles (Modini et al. 2009) that are known to produce condensation nuclei (CN) (Bigg and Turvey 1978), precursors of low-level cloud formation, increasing cloud reflectivity, thereby reducing light levels and water temperatures in the marine environment (Ayers and Gras 1991; Vallina and Simo 2007; Swan et al. 2017).

The GBR could be a significant hotspot for the emission of sulfate aerosol particles (Modini et al. 2009). The release of these particles along the 2300 km length of the GBR, the largest biological structure on the planet, could constitute a major source of CN. Indeed, Bigg and Turvey (1978) report median particle concentrations in Australian maritime air masses below the lowest temperature inversion averaged about 220 cm⁻³ except in the vicinity of extensive coral reefs where the median concentration increased to 1590 cm⁻³. Sulfate aerosol emissions from coral reefs might therefore have a central role in cloud formation in areas of the world with high coral densities, in particular the GBR, the Coral Triangle, and the western Pacific warm pool where the bulk of the earth’s coral reefs occur (Fischer and Jones 2012; Leahy et al. 2013). Declining trends in coral cover and predicted increases in coral mortality worldwide caused by anthropogenic stressors (De’ath et al. 2012) suggest that an associated decline in biogenic aerosol production from coral reefs may destabilize local climate regulation and accelerate degradation of these globally important and diverse ecosystems.

Enhanced DMS production occurs when corals experience high levels of thermal, radiative, and osmotic stress (Fischer and Jones 2012; Deschaseaux et al. 2014; Hopkins et al. 2016). However, when SST in the GBR exceed coral thermal tolerance thresholds (~ 29–30 °C), atmospheric DMS emissions are significantly reduced as corals instead utilize it intracellularly to cope with the oxidative stress

(Fischer and Jones 2012; Leahy et al. 2013). Such a reduction in DMS emissions to the atmosphere may potentially increase solar radiation levels over the reefs, thus exacerbating coral bleaching (Jones et al. 2017). A tidal effect on elevated levels of atmospheric DMS over coral reefs has been reported for the wider western Pacific (Andreae et al. 2005), suggesting a stress-related mechanism. Elevated dissolved and atmospheric DMS concentrations have been found to occur during very low spring tides and on rising tides at coral reefs in the GBR (Broadbent and Jones 2006; Jones et al. 2007; Swan et al. 2016). Further, atmospheric DMS concentrations often increase in the day after low tides and are positively correlated with tidal height, although the correlation is a polynomial relationship, possibly reflecting high concentrations of atmospheric DMS that occur during low tides and on rising tides over the reefs (Jones and Trevena 2005).

A study of seasonal variability of atmospheric DMS at Heron Island in the southern GBR by Swan et al. (2016) reported concentrations that ranged from 3 to 562 ppt (mean 159 ppt), with the highest levels detected during the summer months. Atmospheric DMS concentrations were highly variable, and occasional large pulses of DMS were observed and linked to low tides and low wind speeds. Samples of DMS collected at Heron Island for the period 30 May to 8 June 2011 were also highly variable, ranging from non-detectable (less than 3 ppt) to 320 ppt. The two largest pulses of DMS were detected on flooding tides shortly after low tides during sunny and calm conditions (Swan et al. 2016), suggesting a relationship between tide and enhanced emissions of atmospheric DMS.

The broad aim of this study is to evaluate the ability of corals to regulate their local radiative environment through the synthesis and emission of marine biogenic aerosol precursors. Specifically, we examine the hypothesis that the production of aerosol precursors by corals is due to irradiance stress, which is enhanced during low tides. We used hourly tidal height data obtained from the Australian Bureau of Meteorology (BOM) in conjunction with MODIS satellite-derived data measuring the properties of the atmosphere and ocean to examine the relationship between coral irradiance stress, tide, the optical properties of the atmosphere and relevant water column parameters.

MATERIALS AND METHODS

Heron Island in the southern GBR (23.4°S, 151.9°E) was chosen for this analysis. Daily measurements of atmospheric optical depth for fine-mode aerosols [0.1–0.25 μm radius, aerosol optical depth (AOD)], diffuse water column attenuation coefficient (k_{490}), and cloud-corrected photosynthetically available radiation (PAR) for the 16-year

period (2000–2015) collected by the moderate resolution imaging spectroradiometer (MODIS) sensor aboard the Terra and Aqua satellites were obtained from NASA's OceanColor DAAC (<https://oceancolor.gsfc.nasa.gov>). Data from both morning (Terra) and afternoon (Aqua) satellite overpasses were composited to produce the daily MODIS-derived AOD time series. Hourly tidal height data for the same period were obtained from the Australian BOM and sea surface wind data were acquired from NOAA Blended Ocean Winds Six Hour Aggregation available from, <http://www.ncdc.noaa.gov/thredds/OceanWinds.html?dataset=oceanwinds6hr>.

Mineral dust aerosol loading over the GBR was estimated using an integrated wind erosion and dust transport model (CEMSYS) to simulate atmospheric dust transport over the GBR for the component of the study period for which CEMSIS data were available (January 2003–December 2012). CEMSIS is a process-based model which couples an atmospheric sub-model, a wind erosion sub-model, and a dust transport and deposition sub-model. These sub-models utilize a GIS database of vegetation and terrain over Australia. The structure and details of the various sub-models are outlined in Shao and Leslie (1997) and Lu and Shao (2001). CEMSIS takes into account the atmospheric conditions (wind speed, rainfall and temperature), soil conditions (soil texture and soil water), and surface vegetation and has been used for modeling several major dust storms in Australia (Shao and Leslie 1997; Lu and Shao 2001). The model has been validated with measured dust concentration data for a major dust storm event that moved north-east over the continent during October 2002 (McTainsh et al. 2005).

At low tide during the day, corals generally experience high temperatures (Jones and Trevena 2005) and high light levels, possible air exposure, desiccation, and hypoxia (Deschaseaux et al. 2014). Such conditions are likely to induce stress-related production of DMSP by the coral, resulting in elevated DMS concentrations in the overlying water that is available to exchange with the atmosphere. A daily coral stress index (CSI) metric was formulated to estimate the stress that very low tides and high irradiances exert on corals. The light field, and potential irradiance stress, that the coral experience during each day depends on the sea surface irradiance, the depth of water overlying the coral at any time, and the clarity of the water. In lieu of measurements of the actual irradiance experienced by the coral, we estimated the relative radiance and used that to develop a metric of relative stress [Eq. (1)]. Here, the sea surface irradiance each day (PAR) is modified by a term that estimates the irradiance that reaches the coral between 9:00 a.m. and 1:00 p.m. local time each day from the relative depth of water overlying the coral (from the tide heights during that period) and an estimate of the clarity of

the water (from k_{490}). The instantaneous irradiance experienced by the coral is integrated over the period 9:00 a.m. to 1:00 p.m. and provides a metric of coral stress relative to other days.

The daily mean CSI used in the analysis is

$$\text{CSI}(t_d) = \text{PAR}(t_d) \times \int_{0900}^{1300} e^{-2 \times k_{490} \times \text{TIDE}(t)} dt, \quad (1)$$

where PAR is the cloud-corrected average daily photo-synthetically active radiation; TIDE is the hourly tidal height (m), and k_{490} is the daily water column diffuse attenuation coefficient [per metre, a function of suspended sediment and chlorophyll (CHL) concentration], t_d the day of the year, and t the hour of the day. PAR and k_{490} are the daily measurements from MODIS. The stress index is computed daily using the tide height over a 4-h period in the late morning, overlapping data acquisition by MODIS Terra, and just before MODIS Aqua local overpass times. For a given solar irradiance, the stress index will be maximal when $k_{490} \times \text{TIDE} \approx 0$, viz., at low tide or for very clear waters when light penetration is high. We doubled the satellite measured value of k_{490} to reflect that in situ measurements of k_{490} made inside the lagoon at Heron Island were approximately twice that of contemporaneous in situ measurements made outside the lagoon (Michael et al. 2012).

We used Pearson's correlation analysis, as the data were in general not normally distributed, to examine the relationship between the CSI [Eq. (1)] and daily satellite-derived fine-mode AOD as well as other potentially confounding ocean and atmospheric parameters, including: SST, cloud optical thickness (COT), cloud fraction (CLF), and cloud effective radius (CER). These secondary parameters were also measured by MODIS and were obtained from the Oceancolor site and the MODIS Atmosphere DAAC (<https://modis-atmos.gsfc.nasa.gov/products>).

RESULTS AND DISCUSSION

Time series of the key data describing the properties of the water and atmosphere at Heron Island during the study period are shown in Fig. 1. Pearson correlation coefficients calculated from these time series, and those of the supplementary parameters, are presented in Table 1. The correlation coefficients reveal that the clarity of the water surrounding Heron Island coral cay during the study period was primarily determined by phytoplankton, with a correlation coefficient of $r = 0.98$ between k_{490} and CHL. The data also reveal PAR to be the primary driver of CSI, with

a correlation coefficient of $r = 0.97$ between these two. SST was also correlated with CSI ($r = 0.57$) but much of this is due to the correlation between SST and PAR ($r = 0.65$). Other potentially confounding correlations, between PAR and TIDE, and SST and TIDE, are also evident in Table 1.

These data, however, eliminate continental dust as a primary determinant of the optical properties of the atmosphere during the study, with a correlation coefficient of $r = 0.17$ between AOD and CEMSYS simulated atmospheric dust load. Figure 1c shows the time series of simulated dust loading averaged over a $1 \times 1^\circ$ area centered at Heron Island as simulated by the CEMSYS dust transport model for the time period January 2003–December 2012. Apart from the large spike in dust loading during the spring of 2009, corresponding to one of the largest recorded dust storm events to cross the eastern Australian coastline (Gabric et al. 2016), the simulated atmospheric dust loading at Heron Island is generally low ($< 25 \text{ mg m}^{-2}$) and suggests that AOD at Heron Island is not often affected by continental dust aerosol. This result is consistent with a previous analysis of the likelihood of dust storms impacting the GBR region (Cropp et al. 2013). Furthermore, air parcel back trajectories from Heron Island computed during March 2012 and July 2013 show mainly marine-derived air flows (Swan et al. 2016), consistent with the predominance of east to southeast winds evident in the NOAA data used in this analysis (Fig. 2b).

The correlation results (Table 1) reveal strong positive correlations between the CSI, PAR, TIDE, and SST, as expected, but little correlation between k_{490} and CSI, suggesting that water clarity was a minor contributor to coral stress, as might be expected from the shallow depths of water involved. Due to bio-pigment effects on water color, k_{490} was strongly positively correlated with CHL, and to a lesser extent with SST and WIND. Positive correlations between PAR and TIDE, both at noon and low height are also evident. The strongest correlations involving AOD over Heron Island were with PAR ($r = 0.40$), morning TIDE low height ($r = 0.22$) and CSI ($r = 0.39$). We note that correlations were calculated for days when every parameter had a valid measurement, not when each pair had a valid measurement. Consequently, the correlation coefficients in Table 1 were calculated for only 874 or 20% of days in the 4380-day study period. The correlation coefficient between AOD and CSI increased to 0.44 for the 2137 days (about 50% of the days considered) when measurements of these two parameters were available.

VOCs such as DMS are known to contribute to the fine-mode aerosol burden (Cavalli et al. 2004; Swan et al. 2016). The AOD climatology in Fig. 1a displays a pronounced seasonal pattern with higher concentrations during spring (September–November), although high frequency

Fig. 1 Daily time series of measured (**a**, **b**, **d**) and modeled (**c**) environmental data at Heron Island 2000–2015. **a** MODIS chlorophyll *a*. Solid line is the 7-day moving average. **b** MODIS diffuse water column attenuation coefficient (k_{490}). Solid line is the 7-day moving average, **c** CEMSYS modeled vertically averaged atmospheric dust loading (mg m^{-2}) for the period 2003–2012, and **d** MODIS fine-mode AOD, for the period 2003–2015. Solid line is the 7-day moving average

Table 1 Pearson correlation coefficients for Heron Island (period 2003–2014, $n = 874$, data for all 14 parameters were available on about 20% of days). Correlation coefficients with an absolute magnitude greater than 0.116 are statistically significant at the $p = 0.001$ level

<i>r</i>	AOD	PAR	SST	k_{490}	COT	CHL	CLF	CER	WIND	TIDE noon ht	TIDE low ht	CSI	DUST
AOD	1.00	0.40	0.13	0.03	0.00	0.08	0.12	0.02	− 0.07	0.18	0.22	0.39	0.17
PAR		1.00	0.65	0.14	− 0.16	0.16	− 0.19	0.05	− 0.08	0.39	0.45	0.97	0.09
SST			1.00	0.38	− 0.11	0.35	− 0.07	0.19	− 0.02	0.27	0.43	0.57	− 0.01
k_{490}				1.00	0.00	0.98	0.07	0.06	0.33	0.13	0.22	− 0.05	0.00
COT					1.00	0.04	0.04	0.29	0.22	− 0.07	− 0.09	− 0.16	− 0.02
CHL						1.00	0.17	0.20	0.27	0.13	0.20	− 0.03	0.00
CLF							1.00	0.05	− 0.10	− 0.12	− 0.10	− 0.20	− 0.09
CER								1.00	0.07	0.00	0.02	0.04	0.00
WIND									1.00	− 0.05	− 0.04	− 0.13	− 0.09
TIDE noon ht										1.00	0.60	0.30	0.07
TIDE low ht											1.00	0.31	0.07
CSI												1.00	0.08
DUST													1.00

CSI calculated from Eq. (1)

COT cloud optical thickness, CLF cloud fraction, CER cloud effective radius, DUST modeled dust loading

Fig. 2 Measured (a–c) and modeled (d) data at Heron Island for 2000–2015. **a** Tide height and AOD. **b** Wind rose of daily wind direction and strength. Arrows point in direction wind is blowing. **c** Coral stress index time series [computed from Eq. (1)]. **d** Pearson correlation coefficient between CSI and AOD as a function of wind speed

variability is evident. There is a marked contrast in high frequency AOD variability between the winter and spring periods, with quite low variability during winter and much higher fluctuations seen during spring–summer. This may be a result of seasonal changes in biological activity or atmospheric mixing or lower tides not captured in our data retrieval methods and which increase the flux of DMS from the local coral reefs thus affecting the aerosol source strength.

Our satellite data analysis points to a regular seasonal cycle in CHL-*a*, with peaks normally occurring in the summer or early autumn often driven by fluvial discharge of nutrients during the wet season (Brodie et al. 2010), and a strong seasonal cycle in AOD with regular winter minima (early July) and spring or early summer maxima (Fig. 1a,

d). The water column light attenuation closely mirrors the cycle in CHL, with an annual minimum during spring (Fig. 1b). Water column transparency decreases during summer as the phytoplankton bloom reaches its annual peak. The AOD cycle is similar to the only seasonal DMS data for the GBR measured at a fringing coral reef at Orpheus Island in the central GBR (Jones et al. 2007). The timing of AOD peaks is consistent with reports of increased coral reef DMS(P) production in early summer in the southern GBR (Fischer and Jones 2012; Jones et al. 2014). The lack of synchronicity between AOD and CHL annual cycles at Heron Island (Table 1) argues against a simple relationship between phytoplankton and DMS-derived aerosols.

Figure 2a shows the climatology for noon tidal height and AOD at Heron Island. The seasonal variability in tidal height was less than 1 m at Heron Island, and it is interesting to note that the lowest mean midday tides occur during the winter months and early spring when the coral is likely to experience low water column light attenuation, but lower PAR and cooler SST. The time series of CSI shown in Fig. 2c displays a regular seasonal cycle with minima in July and maxima in late November, and is driven largely by the annual cycle in PAR (Table 1); however, the variability in the stress index around the time period of maximal stress and the variability in AOD (Figs. 1c, 2a) suggest that subtle relationships might be involved.

Wind conditions during the study period were predominantly from the southeast, with wind speeds up to 15 knots common (Fig. 2b). When the data are filtered according to wind speed, the correlation between AOD and CSI increased substantially (Fig. 2d), with the correlation peaking at low wind speeds ($< 4 \text{ m s}^{-1}$), when advection of air masses into and out of the study region is minimal. As the maximum included wind speeds reduce the AOD above Heron Island is more strongly influenced by local processes, and Fig. 2d suggests that in periods of calm weather, CSI and AOD are highly correlated. Sea-salt particles are generated via a bubble-bursting process, with a higher production rate associated with strong wind speeds (Shinozuka et al. 2004), suggesting the impact of sea-salt-derived aerosols on AOD will be low during periods of light winds. This is also consistent with local (biogenic) sources of aerosols being the dominant determinant of AOD during periods of low winds. The correlation decreases to background levels at higher wind speeds, when the irradiance stress, CSI, which is weakly sensitive to water clarity, may be reduced due to bottom sediment resuspension in shallower lagoonal waters, and when sea-salt spray particles will make up a larger component of the overall marine aerosol.

The CSI–AOD correlation was further investigated with the data set segmented according to wind direction. The correlation and the dependence on wind speed were similar for all wind directions, confirming a low influence of aerosols sourced from continental dust and the dominance of local effects. Finally, to test the apparent lack of influence of SST on DMS emissions, we computed a daily “temperature stress metric” for the coral—commonly considered to be when the water column temperature exceeds the long-term average (LTA) by more than 1° (Berkelmans 2002). This is defined as the difference between the climatological mean daily SST and the observed SST minus one. A temperature stress of zero thus implies a daily SST less than 1°C above the LTA. As suggested by the lack of correlation between SST and AOD in Table 1, there was no correlation between AOD and the

temperature stress metric at Heron Island for the period 2003–2014. However, we note that there were very few days during the study period when coral at Heron Island could have been considered temperature-stressed. We also note that our time period excludes the mass bleaching event in 2002 which did impact Heron Island (Berkelmans et al. 2004).

Although we have focused on a single GBR site, corals commonly occurring in the GBR such as *Acropora* spp. have been shown to contain DMS concentrations as high as $25.4 \mu\text{mol L}^{-1}$ (Broadbent and Jones 2004). Since *Acropora* constitutes the largest aerial extent of hard coral cover on the GBR (Osborne et al. 2011), it is likely a significant source of DMS to the atmosphere over the entire GBR. While our emphasis has been on DMS and related compounds (for which local measurements exist), laboratory studies by Swan et al. (2016) identified a range of other VOCs that were produced from *Acropora* coral collected from the GBR. These included isoprene, as well as several other reduced sulfur compounds such as dimethyldisulfide (DMDS), methylmercaptan (CH_3SH), and carbon disulfide (CS_2). These other sulfur volatiles emitted from *Acropora* can also be oxidized to SO_2 , methanesulfonic acid, and other aerosols (Pitts and Pitts 2000), providing evidence that this coral produces VOCs that are capable of producing new atmospheric particles $< 15 \text{ nm}$ diameter as observed at Heron Island coral reef. DMS and isoprene are known to play a role in low-level cloud formation, so aerosol precursors such as these could influence regional climate through a SST regulation mechanism hypothesized to operate over the GBR (Swan et al. 2016).

It is worth noting that the reaction of OH with DMDS and CH_3SH is significantly faster than its reaction with DMS (see Swan et al. 2016), and these compounds may provide relatively important precursors such as H_2SO_4 needed to initiate nucleation of new particles. The oxidation products from the sulfur VOCs produced by coral can potentially form secondary organic aerosol (SOA) which may grow to larger sizes with other VOC oxidation products, primary organic material, and ultra-fine sea-salt to produce climatically active CCN (Vaattovaara et al. 2006).

Isoprene is an important coral emission product because it has been demonstrated that gas phase OH oxidation of isoprene in the presence of NO_x and $(\text{NH}_4)_2\text{SO}_4$ seed can form SOA (Kroll et al. 2006). A study conducted at Lizard Island (14.7° , 145.4°E) identified new particle production during each observation over 10 days. These events occurred during the daytime where $> 10\text{--}20 \text{ nm}$ diameter particle number concentrations reached $40\,000 \text{ cm}^{-3}$ (Leck and Bigg 2008). Three quarters of the aerosol particles from Lizard Island were composed of $(\text{NH}_4)_2\text{SO}_4$ containing marine aggregates, which were concluded to have acted as centers for condensation of oxidized VOCs, such

as DMS and isoprene (Leck and Bigg 2008). These airborne gels and aggregates, which could be derived from coral mucus (since hard coral exude up to 4.8-L coral mucus $\text{m}^{-2} \text{day}^{-1}$) and microbial debris, may act as an immediate source of CCN (Bigg 2007; Leck and Bigg 2007). The decomposition of coral mucus may also provide a source of dimethylamine and other light alkyl-amines to react on surfaces producing alkyl-ammonium salts, which are abundant organic species in submicron marine aerosol (Facchini et al. 2008). A month-long continuous aerosol study from March to April 2007 at Agnes Water (24.2°S) on the Queensland coast opposite the southern GBR identified nucleation events during 65% of the study period. Analysis of particle composition consisted of ~ 40% organics and ~ 60% sulfates, in the form of $(\text{NH}_4)_2\text{SO}_4$ (Modini et al. 2009).

CONCLUSION

This analysis reveals that coral reefs may be able to influence the properties of the atmosphere above them during calm weather, through a mechanism where increasing irradiance stress and low tides causes the coral reef community to emit increasing quantities of aerosol precursor compounds that over time may increase particle nucleation events leading to CCN and low-level cloud formation reducing SSTs. Our quantitative measure of coral irradiance stress, a function of sea surface irradiance, tide height and water clarity, was positively correlated with fine-mode AOD, and the correlation was consistently greater during periods of calm weather and low wind stress. The atmosphere above the reef is less affected by distant processes during low wind conditions due to reduced air mass advection. Low winds reduce local sea-salt aerosol production, and consequently the influence of ocean physical processes on AOD is low. We were able to eliminate the confounding influence of aeolian dust on our analysis as the modeled atmospheric dust load at Heron Island is low and intermittent and uncorrelated with AOD, confirming that the contribution of terrestrial physical processes to the correlation is small. The lack of a correlation between AOD and WIND or PAR and WIND tends to suggest that potentially confounding factors such as enhanced atmospheric photochemistry due to increased light producing more aerosol gas precursors (Ayers and Gillett 2000) are not affecting the relationship between CSI, AOD, and WIND. Our analysis suggests that the correlation between the fine-mode aerosol concentration in the atmosphere and the irradiance stress experienced by the corals is at least to some extent the result of an in situ biological process.

Empirical evidence and recent laboratory studies point to corals as substantial sources of DMS-derived aerosols in coral reef ecosystems, especially when the corals are irradiance stressed, for example during aerial exposure or very low tides. Heron Island is the only GBR site where atmospheric DMS has been measured using a continuous sampler, for 15 days in March 2012 (wet season) and 18 days in July/August 2013 (dry season) (Swan et al. 2017). The field data collected at Heron Island demonstrated that spikes in atmospheric DMS (above background oceanic values) often occurred at low tide and during low wind speeds (Swan et al. 2017). By increasing the long time series of atmospheric DMS measurements by Swan et al. (2017) over coral reefs in the GBR the robustness of the relationship between coral stress and DMS will be improved.

Our results suggest that coral reefs may be a significant source of marine biogenic aerosol emissions during periods of high irradiance stress, and could potentially influence the properties of the atmosphere above them through biogenic aerosol formation that form low-level clouds. These do not influence the coral's local environment during windy periods, as the products are transported and dispersed by the wind. However, our analysis suggests that during calm periods of high irradiance, when the corals become susceptible to irradiance and thermal stress during low tides, the enhanced emission of volatile aerosol compounds could alter the properties of the local atmosphere, reduce the sea surface irradiance and seawater temperature and provide protection from irradiance stress, and perhaps potential bleaching. While our results are consistent with in situ measurements of DMS emissions at coral reefs in the GBR, we are not able to differentiate the potential contribution of other biogenic gases such as isoprene or monoterpenes to AOD, although chemical characterisation studies by Swan et al. (2016) suggest that it could be significant.

Whether emissions from upwind corals during windy conditions might help protect downwind corals, and how that might influence the survival of the upwind corals, remains an unresolved but intriguing question. However, the large extent of the GBR, which stretches for 2300 km along the direction of the summer prevailing wind, suggests such a mechanism could be possible. Whether this process is sufficient to affect regional climate over coral reefs in general also remains an open question, but in light of the increasing anthropogenic threats to coral reef survival, it is an important one to investigate further.

It is clear that the role of biogenic aerosols in tropical marine ecosystems is potentially of great significance, but as yet under-evaluated (Exton et al. 2015). In the context of mitigating the impacts of climate change, our results

suggest that SRM through the artificial injection of salt or sulfate aerosols into the overlying atmosphere may mimic the natural defense mechanisms that coral reefs already possess. Although much of the literature on SRM concerns the injection of particles to the stratosphere, there is a growing body of work that has examined other methods of ocean albedo modification including the potential for brightening of lower level clouds by injection of sea-salt spray (Niemeier et al. 2013; Maalick et al. 2014). Given the dire predictions for coral reef survival under current global warming trajectories (Frieler et al. 2013), the use of SRM to protect corals is being increasingly discussed and investigated (Kwiatkowski et al. 2015), and may prove to be an effective stop gap measure.

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