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The effect of coral bleaching on the cellular concentration of dimethylsulphoniopropionate in reef corals

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ABSTRACT

Measurements of DMSP production from *Acropora intermedia* collected from Heron Island, in the southern Great Barrier Reef (GBR) from 2001 to 2003, show a distinct seasonal cycle of increased production in summer, and lower production in winter, despite severe coral bleaching in 2002. Increasing seawater temperatures by +2 °C in summer and winter increased DMSP production from *A. intermedia* by approximately 45%. Compared with winter 2001 and summer 2002, marked increases in cellular DMSP occurred in *A. intermedia* in the winter of 2002 and summer 2003, five to six months after coral bleaching, and seemed to be related to high seawater temperatures and high rainfall. In contrast to these results cellular Chl *a* concentrations in *A. intermedia* decreased from 2001 to 2002 and then increased in summer 2003 as the coral slowly recovered. A parallel study conducted on *Pocillopera damicornis* from a fringing reef off Magnetic Island in the central GBR, highlighted marked variation in cellular concentrations of Chl *a*, DMSP, and algal symbionts, in colonies that were collected five months after a severe bleaching event. The increases in cellular DMSP at both low and high symbiont concentrations, and the highly significant correlation between cellular DMSP and Chl *a*, could reflect an adaptive response to enhanced levels of reduced oxygen species produced during the bleaching event, and may have aided the coral's recovery. The increases in cellular DMSP could also be explained by a change in the symbiont community. Comparison with measurements made mainly on *Acropora* coral from different locations in the GBR over different years, suggests that changes in the cellular or tissue concentration of DMSP are a sensitive indicator of coral stress.

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1. Introduction

Corals contain relatively high concentrations of dimethylsulphoniopropionate (DMSP), an organic sulphur substance that seems to have many biological roles such as osmoregulation in various species of phytoplankton (Stefels, 2000; Vairavamurthy et al., 1985), an antioxidant response in phytoplankton and coral (Deschaseaux et al., 2014a; Jones et al., 2007; Sunda et al., 2002), anti-predation (Otte and Morris, 1994; Van Alstyne and Houser, 2003; Van Alstyne et al., 2001; Wolfe et al., 1997), anti-bacterial activity (Sieburth, 1960, 1961), and as a methyl donor in the synthesis of nitrogen based metabolites (Chillemi et al., 1990). It also functions as a chemo-attractant for a whole range of marine species (DeBose et al., 2008; Knight, 2012; Savoca and Nevitt, 2014; Seymour et al., 2010), and as a chemical cue for bacteria (Garren et al., 2013; Seymour et al., 2010) including coral-associated bacterial communities, with important consequences for coral health and the resilience of coral reefs (Raina et al., 2009, 2010).

DMSP can be enzymatically cleaved by DMSP lyase to produce dimethylsulphide (DMS), acrylate, and acrylic acid. DMSP-lyases are encoded by different genes so far identified as dddL and dddP (Kirkwood et al., 2010; Todd et al., 2009). These genes could be widespread among marine organisms as DMSP-lyase activity has been found in phytoplankton (Niki et al., 2000; Stefels and Dijkhuizen, 1996), macroalgae (Malin and Kirst, 1997; Steinke and Kirst, 1996), bacteria (Desouza and Yoch, 1995a,1995b) and fungi (Bacic and Yoch, 1998; Bacic et al., 1998). Whilst DMSP lyase activity has been measured in symbiotic *Symbiodinium* from coral, not all strains of these dinoflagellates contain DMSP lyase activity (Yost and Mitchelmore, 2009). The gastrodermis of zooxanthellate corals normally contain high densities (~2×10^6 cm^{-2} coral tissue) of symbiotic dinoflagellates of the genus *Symbiodinium* (Harrison and Booth, 2007), which contain high concentrations of DMSP (Broadbent et al., 2002; Deschaseaux et al., 2012, 2014a; Hill et al., 1995; Jones et al., 1994; Keller et al., 1989; Steinke et al., 2011; Van Alstyne et al., 2006; Yost et al., 2010). Nuclear ribosomal and chloroplast DNA markers show that the genus *Symbiodinium* is highly diverse with nine distinct clades (A-I), each containing multiple

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subclades, strains or types (Pochon and Gates, 2010). Different clades exhibit varying tolerance to heat and light stress during coral bleaching (Berkelmans and van Oppen, 2006) and contain different concentrations of DMSP (Steinke et al., 2011).

Symbiodinium C is the most common symbiont type in *Acropora* corals on the Great Barrier Reef (Van Oppen et al., 2001). In one of the first field studies of its type, Jones et al. (2008) found evidence of a dramatic change in the symbiont community of *Acropora millepora*, a common and widespread Indo-Pacific scleractinian coral species, after a natural bleaching event in early 2006 in the Keppel Islands (Great Barrier Reef). After bleaching, 71% of the surviving tagged colonies that were initially predominantly hosting the thermally sensitive C2 clade changed to D or C1 predominance and significantly increased their thermal tolerance six months after the bleaching event (Baker, 2003; Jones et al., 2008).

Coral reefs are significant sources of DMSP and DMS to reef waters (Broadbent and Jones, 2004, 2006; Fischer and Jones, 2012; Jones et al., 2007) and contribute significantly to regional biogeochemical sulphur cycles (Andreae, 1990; Andreae et al., 1983). The expulsion of coral symbionts and coral mucous to reef waters raises DMS and DMSP concentrations (Broadbent and Jones, 2004) making coral reefs potential "hotspots" of atmospheric DMS production (Swan et al., 2012). Photochemical and bacterial oxidation of dissolved DMS produces dimethylsulphoxide (DMSO), a substance that may have a significant role in the corals antioxidant system (Deschaseaux et al., 2014a). These researchers found significant changes in the cellular concentrations of DMSP in *Acropora aspera* from Heron Island when this coral was subjected to temperature, light, tidal and salinity stress, compared with unstressed controls. It is now realised that some of this variation reflects production from the coral endosymbionts and the coral host (see Raina et al., 2013), and that during stress increased levels of reduced oxygen species (ROS) in *Symbiodinium* are accompanied by increased DMSP production (McLenon and DiTullio, 2012).

DMS oxidises in the atmosphere to produce sulphate aerosols, precursors of cloud condensation nuclei (CCN), which have a major effect on cloud albedo of marine stratiform or low level cloud. This in turn can significantly affect solar radiation over the ocean (Charlson et al., 1987). These authors hypothesised that as DMS is produced by phytoplankton in the world's oceans changes in phytoplankton activity can be mediated by changes in low level cloud cover and sunlight, which regulate sea surface temperatures. The CLAW hypothesis (named after the first letter of each authors surname) suggests that as temperatures increase due to GHG warming, greater amounts of DMS would be emitted into the atmosphere to produce more low level cloud cover, which would in turn lower SSTs, a type of ocean thermostat or climate feedback. It is now recognised that substances other than DMS, such as non-DMS volatile organic substances may also be involved in secondary aerosol and CCN formation (Deschaseaux et al., 2012; Modini et al., 2009; Vaattovaara et al., 2013), and that these atmospheric oxidation processes may be more complex than first described in the CLAW hypothesis (Quinn and Bates, 2011). As atmospheric DMS emissions from reefs contribute to the formation of sulphate aerosols over reefs (Deschaseaux et al., 2012; Modini et al., 2009; Vaattovaara et al., 2013), precursors of CCN, this may explain enhanced levels of low-level cloud over coral reefs in the Western Pacific Warm Pool (WPWP) (Kleypas et al., 2008; Ramanathan and Collins, 1991; Takahashi et al., 2010), central Pacific (Mumby et al., 2011), Coral Triangle and Great Barrier Reef (GBR) regions (Fischer and Jones, 2012; Leahy et al., 2013), where the majority of the Earth's coral reefs occur. Interestingly, evidence of a SST-low level cloud climate feedback or ocean thermostat has been described for the NE Pacific (Clement et al., 2009) and the western Pacific (Kleypas et al., 2008), and may significantly affect solar radiation (Masiri et al., 2008).

The first direct measurements of the concentrations of DMSP in the staghorn coral *Acropora formosa* were published by Jones et al. (1994), who found levels of 150–270 fmol cell^{-1} (Table 1). These concentrations were slightly higher than 140 fmol cell^{-1} recorded for a culture of the dinoflagellate, referred to as *Symbiodinium microadriaticum*, recognised to be present in coral (Keller et al., 1989). An axenic culture of zooxanthellae or coral symbionts isolated from the giant clam *Tridacna gigas*, also exhibited a high level of DMSP at 310 fmol cell^{-1} (Jones et al., 1994). Hill et al. (1995) measured much lower concentrations of DMSP in *Montipora verrucosa*, *Pocillopora damicornis* and *Porites compressa* (73–117 fmol cell^{-1}), three species of corals from Kaneohe Bay, Hawaii. Comparison with five other coral species from the GBR indicated that *Acropora* spp. contain the highest intracellular concentrations of DMSP of any coral (Broadbent et al., 2002) (Table 1) which has been confirmed recently by Tapiolas et al. (2013). However, it is now clear that cellular levels of DMSP in *Acropora* corals can vary markedly.

Climate change is now affecting the viability and sustainability of coral reefs as elevated SSTs cause increased coral bleaching, resulting in the mass exodus of the symbiotic algae from the coral polyp and/or a loss of photosynthetic pigments, so that the corals appear white or pale yellow, depending on the severity of stress (Brown, 1997; Hoegh-Guldberg, 1999). Coral bleaching has also been shown to be a result of oxidative stress (Lesser, 1997). Coral bleaching episodes have become more common in the GBR since the mid-1980s (Fisk and Done, 1985; Harriott, 1985; Hoegh-Guldberg et al., 1997; Jones et al., 1997; Oliver, 1985), culminating in two extreme mass coral bleaching episodes in 1998 and 2002, severely affecting hundreds of inshore coral reefs (Berkelmans and Oliver, 1999; Berkelmans et al., 2004). In 2002 nearly twice as many offshore reefs in the GBR bleached compared to the 1998 bleaching episode (41% vs 21%), making the January to March 2002 event the worst bleaching event on record for the GBR (Berkelmans et al., 2004).

The aims of this research were to (1) Measure the seasonal variation of DMSP, Chl *a*, and zooxanthellae concentrations in *Acropora intermedia* in seawater chamber experiments over two winter and two summer seasons at Heron Island from 2001 to 2003, which included the mass coral bleaching episode in the summer of 2002. (2) Measure the production of DMSP in chamber seawater from temperature stressed and non-stressed *A. intermedia* coral. (3) Measure DMSP in *P. damicornis* in the field during the recovery period six months after a severe bleaching event at Nelly Bay reef (central GBR), Magnetic Island. (4) Compare cellular concentrations of DMSP in stressed (e.g. bleached corals) and unstressed corals from different locations in the GBR.

2. Methods

2.1. Heron Island study site

Field work was carried out at the research station located on Heron Island reef in the southern GBR region (Fig. 1). Located 72 km northeast of Gladstone (23° 25′S 151° 55′E) and 539 km north of Brisbane, Heron Island is an 18-hectare coral cay, surrounded by a large platform reef, which drains at low tide and encompasses a substantial lagoon area (Scopelitis et al., 2011). It has a tropical climate, with an average year-round temperature of approximately 27 °C (Heron Island weather station). Substantial areas of the coral communities on Heron Island reef are dominated by *Acropora* coral species (Scopelitis et al., 2011), and the reef supports extensive colonies of *A. intermedia*. The Heron Island Research Station has a large aquarium complex supplied with flow-through seawater drawn directly from the reef slope, providing excellent conditions for conducting experiments with sensitive staghorn corals. Studies on *A. intermedia* were carried out in September 2001, February 2002, September 2002, and February 2003, which in the Southern Hemisphere essentially corresponds to a succession of winters (September) and summers (February).

2.2. Nelly Bay study site

Nelly Bay is one of the larger embayments on the eastern coast of Magnetic Island, which is approximately 7 km offshore from Townsville

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