Soft corals are significant DMSP producers in tropical and temperate reefs

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Abstract

Corals synthesise large quantities of the sulphur metabolite dimethylsulphoniopropionate (DMSP), which contributes to key roles in coral reef ecology including the capacity of corals to withstand various stressors. While closely related to scleractinian corals and often occupying similar ecological niche space, it is currently poorly defined to what extent soft corals produce DMSP. We therefore examined DMSP content within four key species of soft coral in February and July-August of 2017, including two temperate species from Sydney Harbour (*Erythropodium hicksoni*, *Capnella gaboensis*) and two tropical species from the Great Barrier Reef (*Sinularia* sp., *Sarcophyton* sp.). We compared DMSP content of these soft coral species to that of commonly occurring temperate (*Plesiastrea versipora*) and tropical (*Acropora aspera*) scleractinian coral species. DMSP content was normalised to coral protein content, with soft coral DMSP content highly variable across species and locations (56 - 539 nmol (mg protein)$^{-1}$), and lower than for the tropical (1242 – 4710 nmol (mg protein)$^{-1}$), but not temperate (465 – 1984 nmol (mg protein)$^{-1}$) scleractinian species. Further comparison with previously published values demonstrated that soft coral DMSP content falls within the “low-mid range” of scleractinian corals. Notably, DMSP content was also higher in summer samples than winter samples for the scleractinian corals, but did not differ between seasons for soft corals. Such contrasting dynamics of DMSP production by soft corals compared to scleractinian corals indicates that the regulation of DMSP content differs between these two important benthic cnidairian groups, potentially as a consequence of dissimilar ecophysiological roles for this compound.

Introduction

Dimethylsulphoniopropionate (DMSP) is a key sulphur containing metabolite produced in high quantities by marine organisms (10^9 tonnes year^{-1}) (Howard et al. 2006). DMSP is considered to not only provide a suite of important physiological roles (Sunda et al. 2002; Gardner et al. 2016; Hopkins et al. 2016), but is also important from a biogeochemical perspective as it is the precursor for the volatile gas dimethylsulphide (DMS) (Stefels and Van Boekel 1993). Emerging evidence suggests that this molecule may play a particularly critical role within coral reef ecosystems by maintaining coral health under stress conditions (Exton et al. 2015; Gardner et al. 2016; Hopkins et al. 2016).

DMSP is predominately produced by a wide range of marine phytoplankton (Keller and Korjeff-Bellows 1996), including the dinoflagellate endosymbionts (*Symbiodinium* sp.) of corals (Yost and Mitchelmore 2009). Reef-building corals are therefore amongst some of the largest producers of DMSP and DMS in marine ecosystems (Broadbent and Jones 2004; Hopkins et al. 2016) as they harbour high concentrations of *Symbiodinium* (10^5- 10^6 cm^{-2}). However, both the coral host (Raina et al. 2013) and its associated bacteria (Curson et al. 2017) can also produce DMSP. In scleractinian corals (Class: Anthozoa, Subclass: hexacorallia), there is evidence that DMSP plays an important role in alleviating intracellular oxidative stress (McLenon and DiTullio 2012; Deschaseaux et al. 2014a; Gardner et al. 2016), the process considered to initiate bleaching induced mortality (Downs et al. 2013). DMSP also provides coral-associated bacteria with an important source of nutrients and likely helps structure coral-bacterial interactions that appear critical to sustaining coral health (Raina et al. 2009). It is possible that the production of this compound will also influence the biochemistry and microbial interactions for other reef benthic taxa, such as soft corals. However, this notion so far remains relatively unexplored.

Octocorals (cnidarian subclass: Octocorallia) are a discrete and taxonomically diverse (> 3000 species) subclass of anthozoa (Daly et al. 2007), which comprise key benthic groups within reef environments, including soft corals and gorgonians. Soft coral species, which like hard corals form symbiotic associations with *Symbiodinium* sp., are widely dispersed across temperate to tropical reef systems (Fabricius and De'Ath 2008). Notably, these species often dramatically increase in abundance on coral reefs following disturbance events, e.g. blast fishing, Crown-of-Thorns starfish (*Acanthaster planci*) outbreaks, and eutrophication (Fabricius 1998), and thus can be considered 'opportunistic colonisers'. Evidence in fact suggests that under persistently disturbed habitats (CO_2 vents, coastal inlets), soft corals can become the dominant species within an alternate ecological state (Inoue et al. 2013), implying that reef communities may become increasingly dominated by soft corals in the future as anthropogenic pressures continue to accelerate (e.g. Suggett et al. 2012; Tsounis and Edmunds 2017).

Despite their ecological importance and capacity to harbour high densities of *Symbiodinium spp*., including clades reported to produce DMSP in scleractinian corals (Yost and Mitchelmore 2009; Steinke et al. 2011), only two studies have investigated DMSP production by soft corals. Specifically, DMSP was quantified within broadly distributed tropical species at single locations (*Lobophyton* sp.; Broadbent et al. 2002; *Sinularia* sp. and *Sarcophyton* sp.; Van Alstyne et al. 2006). Both studies reported uniformly low concentrations of DMSP present in the genera tested, raising questions about the likely physiological role of DMSP in these organisms and whether it has the same importance as in scleractinian corals. To date, the capacity of soft corals to produce this compound under varying environmental conditions has not yet been addressed, nor has it been elucidated whether such low concentrations are a common feature among other species of soft coral.

DMSP concentrations for scleractinian corals are highly variable (21-3831 fmol cell^{-1}) across species and environmental growth conditions (Broadbent et al. 2002; Van Alstyne et al. 2006; Jones et al. 2014). Much of this variability appears to reflect taxonomic or morphological (i.e. branching vs massive) differences between corals, or differences in the types of *Symbiodinium* hosted by the corals (Van alstyne et al. 2006). Additionally, changes in environmental conditions such as, temperature, light intensity and tidal height, have also been shown to influence DMSP upregulation (Deschaseaux et al. 2014a). Therefore, in order to resolve whether soft corals similarly exhibit a broad dynamic range of DMSP content, we conducted an assessment of DMSP content for commonly occurring tropical (Heron Island, southern Great Barrier Reef, GBR) and temperate (Sydney Harbour) soft corals at the seasonal extremes of summer and winter in 2017. We benchmarked DMSP content for soft corals against those from commonly co-occurring scleractinian corals to show that soft coral DMSP content varies within the low-mid range characteristic for scleractinian species. In contrast to scleractinian corals, soft corals did not exhibit seasonal variation in DMSP content, potentially suggesting that the regulatory mechanisms for production in soft corals differs to that described for scleractinian corals.

Materials and methods

Coral collection and preparation

Each species of coral was collected in triplicate (from separate colonies) during February 2017 (summer) and July-August 2017 (winter). “Tropical” soft coral species, including *Sinularia* sp., *Sarcophyton* sp., along with a common scleractinian species, *Acropora aspera* (Table 1) were collected from Heron Island (23°26’46.19”S, 151°54’46.35”E), on the southern GBR. Coral samples were collected from the reef flat at a depth of 1-3 m (low-tide) via snorkeling, with all samples collected prior to noon. “Temperate” soft corals, including *Erythropodium hicksoni*, *Capnella gaboensis*, and the common scleractinian species *Plesiastrea versipora* (Table 1), were collected from Bare Island, Botany Bay, New South Wales (33°59’31.0”S, 151°13’55.5”E). At this site, corals were collected at depths of 5-7 m from the rocky reef substrate. For both encrusting soft corals and all scleractinians, 5 cm diameter fragments were removed via hammer and chisel, whereas all other soft coral sample fragments were removed with a sharp knife. All samples were placed into falcon tubes filled with surrounding seawater (15 mL) and returned to shore, where the seawater was discarded and the fragments snap-frozen in liquid N_2. All fragments were stored at -80ºC for subsequent analysis.

Prior to DMSP analysis, soft coral fragments (~ 200 mg), were initially placed into 1.5 mL of autoclaved Phosphate Buffered Saline (PBS) (pH of 7.4), for full homogenisation using a TissueRuptor® with autoclaved and disposable probes at full speed (33,000 rpm) for 1 min. Individual aliquots (200 μL) were then sampled for DMSP quantification and protein assays. This procedure was also used for the scleractinian corals, with the exception of frozen tissue being initially extracted by air-blasting in 5 mL of PBS buffer using an air gun into a small zip lock bag for homogenisation (ultra-turrax®, T25, SIGMA).

Gas Chromatography (GC) analysis

For detection and quantification of DMSP in coral samples, aliquots of total homogenate were diluted into 5.8 mL of milliQ water and re-homogenised. Technical triplicates were then produced by subsampling 2 mL of the diluted homogenate in separate 14 mL GC headspace vials. All samples were hydrolysed with a 1 g pellet of 5 M NaOH to convert DMSP to DMS for detection, immediately capped with a butyl rubber septa (Sigma Aldrich, St Louis, USA) and crimped with an aluminium seal cap to minimise volatile DMS loss. All samples were covered with foil and stored in the dark at room temperature for 24 h prior to analysis. Following this equilibration period, the headspace gas was analysed using direct injection with a 100 µl gas tight syringe into a gas chromatographer (GC-2010, Shimadzu) fitted with a flame photometric detector (FPD) configured for analysis at 180°C. During this procedure, DMS was carried towards the FPD through a dimethylpolysiloxane capillary column (30 m x 0.32 mm x 5 µm, DB-1, Agilent Technologies, Delaware, USA) set at 120°C by a carrier gas, hydrogen. Peak area was recorded for DMS and the concentration of DMS was quantified against a standard curve generated for DMS using stock DMSP standards (National Measurement Institute, NSW, Australia). Concentrations of DMSP were then calculated from the sulphur mass detected and the volume injected.

DMSP normalisation

Soft coral DMSP concentrations were initially normalised by tissue fresh weight. However, to ensure a more accurate comparison to DMSP content in scleractinian corals, all measured DMSP concentrations were also normalised to total protein content present in coral tissue. To quantify total protein, coral homogenate underwent bead-beating with 425-600 µm sterile glass beads at 50 Hz with a Tissue Lyser II, (QUIGEN, Valencia, CA) for 5 min to lyse cells. The samples were then centrifuged at 10,000 g for 10 min to separate the total soluble protein content from the tissue before the supernatant was removed. This step was repeated three times until all host tissue was removed. Protein was extracted from the supernatant as total soluble protein from the coral holobiont (host and microbial fractions; Knowlton and Rohwer 2003) using the Pierce^{TM} BCA Protein assay kit (Thermo Scientific, USA). Bovine serum albumin standards ranging from 20 μg mL^{-1} – 2000 μg mL^{-1} were used for calibration curves and then incubated at 39°C for 30 min along with the samples, before total soluble protein concentrations were analysed using an Infinite 200 PRO microplate reader (Tecan, Switzerland).

Data analysis

DMSP concentrations were compared between coral species and between seasons by a two-way permutation ANOVA (PERMANOVA) using PRIMER v6 and PERMANOVA+ software following square root transformations to all data and using Euclidean distance. PERMANOVA pairwise comparisons, corresponding to t-statistics, were performed where significant differences were obtained within factors (species and seasons). Concentrations of DMSP were compared between individual coral species within each of the 2 sites (temperate and tropical), but also between seasons (summer and winter) for the same species. Significant differences were set at $\alpha < 0.05$ level.

Results & Discussion

DMSP production by soft and scleractinian corals

Scleractinian corals are prolific producers of DMSP and major contributors to biogenic sulphur emissions from reef systems (Swan et al. 2012). However, comparatively little is known of DSMP production by closely related soft corals, and thus how reef biogenic emissions may potentially change under scenarios where soft corals increasingly dominate reef assemblages (Ruzicka et al. 2013; Tsounis and Edmunds 2017). Here, DMSP concentrations measured from four soft corals during both summer and winter periods were found to be constantly measurable, but to vary by an order of magnitude, from 56 to 539 nmol (mg protein)$^{-1}$ (Fig. 1). These values were an order of magnitude lower than those recorded in the common tropical scleractinian coral *A. aspera* (1242 ± 308 – 4710 ± 516 nmol (mg protein)$^{-1}$ (Fig 1a), but of similar magnitude to that observed in the common temperate scleractinian coral *P. versipora* (465 ± 117 - 1984 ± 191 nmol (mg protein)$^{-1}$) (Fig. 1b). Notably, the difference in DMSP concentrations observed between the two scleractinian corals may reflect fundamental physiological differences between species rather than a difference between “tropical” vs “temperate” corals. The DMSP concentrations recorded in *A. aspera* samples are similar to values previously recorded for this species (Deschaseaux et al. 2014a), which has been shown to harbour DMSP concentrations that far exceed those in other massive and sub-massive growth forms (Yost and Mitchelmore 2010; Tapiolas et al. 2013; Swan et al. 2017; Table 2).

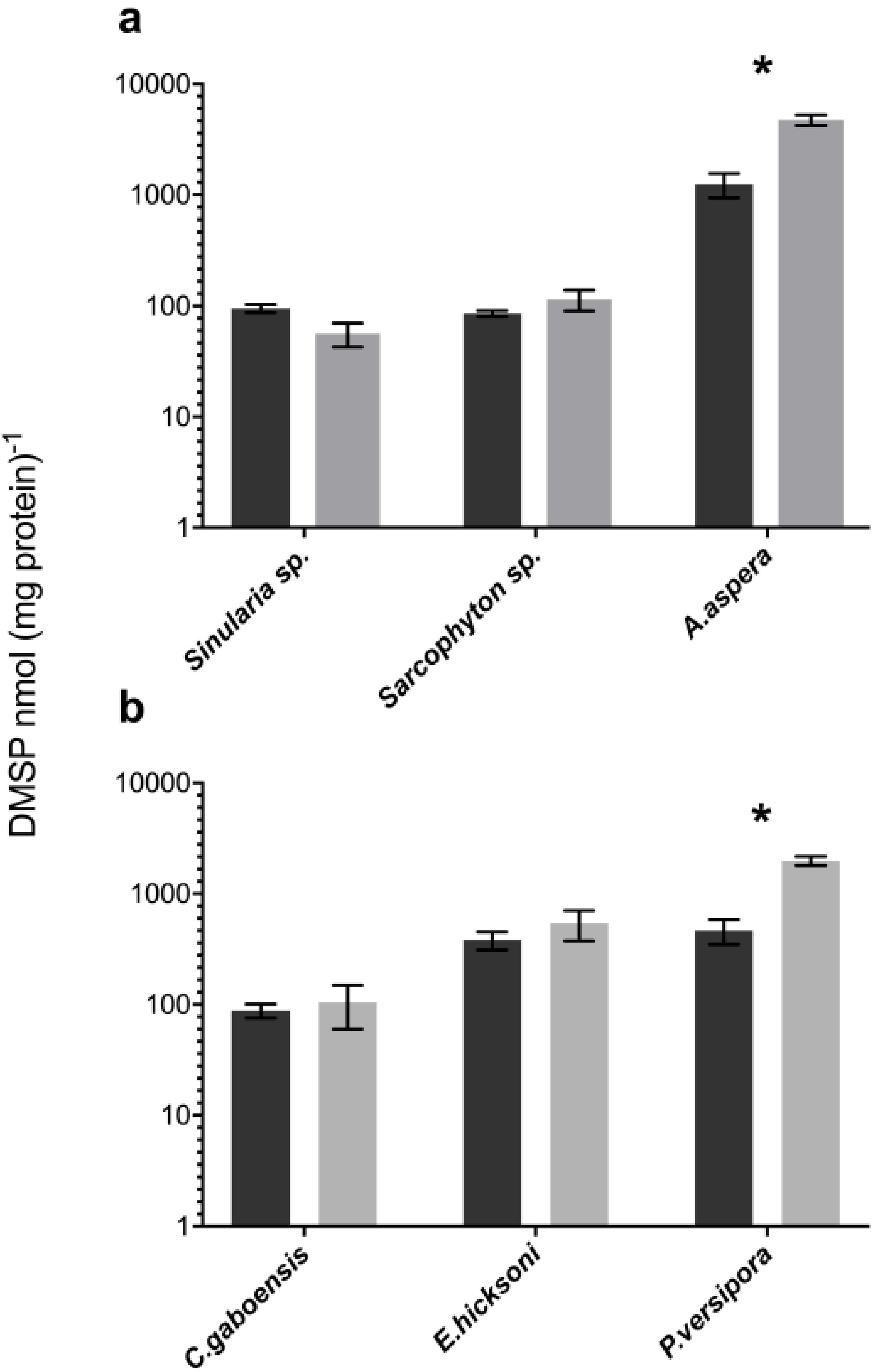
a
b
DMSP nmol (mg protein)-1
10000
1000
100
10
1
*
Sinularia sp.
Sarcophyton sp.
A.aspera
10000
1000
100
10
1
*
C.gaboensis
E.hicksoni
P.versipora

Fig. 1 Average concentrations of DMSP (nmol) normalised to (mg protein)$^{-1}$ of soft coral and scleractinian species from both the tropical (a) (*Sinularia* sp., *Sarcophyton* sp. and *Acropora aspera*) and temperate (b) (*Capnella gaboensis*, *Erythropodium hicksoni*, *Plesiastrea versipora*) environments, over summer (light bars) and winter (dark bars). Note – y-axis is presented in log scale due to the order of magnitude differences between coral species. Error bars represent ± SE, (n = 3). * represent significant differences temporally of DMSP production. Further statistical results can be found in (Table ESM 1)

Overall, the DMSP concentrations for the tropical soft corals (*Sinularia* sp. and *Sarcophyton* sp.) were > 2 fold higher than previous reports from the same genera when collected from a lagoon in summer (Guam; Van Alstyne et al. 2006). This variability in observed DMSP concentrations could be a consequence of localised environmental or taxonomic differences (e.g. Deschaseaux et al. 2014a; Swan et al. 2017), or the nature of normalisation approaches used in previous studies of soft coral DMSP content. We quantified DMSP normalised per milligram of coral protein, to enable inter-comparison with hard corals (Deschaseaux et al. 2014a). However, previous observations have normalised DMSP content to soft coral fresh weight (as per Van Alstyne et al. 2006; Table 2), which we argue might amplify variance across measurements since soft corals, unlike scleractinian corals, constantly change their biomass by upregulation of water depending on environmental conditions (Hellström and Benzie 2011). The resultant regular shift in biomass also eliminates the possibility of accurately normalising to surface area when quantifying DMSP concentration or *Symbiodinium* cell density.

In addition to providing new insights into the production of DMSP by soft corals, we also quantified DMSP concentrations in temperate species of scleractinian and soft coral for the first time. The two temperate soft coral species produced DMSP concentrations (88 - 581 nmol (mg protein)$^{-1}$) as high as the tropical soft corals, implying DMSP is an equally important metabolite for temperate soft corals as for tropical taxa. In fact, it is notable that the temperate encrusting soft coral *E. hicksoni*, produced higher DMSP concentrations than previously reported for many other species of scleractinian corals 381 ± 70 winter - 539 ± 163 nmol (mg protein)$^{-1}$ in summer (Yost and Mitchelmore 2010; Yost et al. 2012; Deschaseaux et al. 2014a). The high concentrations of DMSP measured in *E. hicksoni* are possibly a consequence of the specific *Symbiodinium* genotype harboured by the coral, which is currently unknown (Table 1). Alternatively, such relatively high values for *E. hicksoni* may provide evidence for potentially enhanced physiological importance of DMSP in temperate compared to tropical soft coral species. Our measurements of DMSP in temperate corals further highlights the diverse number of coral habitats in which this compound has been detected, and reveals a topic that warrants further investigation.

Temporal dynamics in DMSP production

DMSP content in the tested scleractinian corals differed significantly between summer and winter, for both the tropical and temperate species (Fig. 1, Table ESM 1). Specifically, the summer DMSP content in the temperate scleractinian *P. versipora* (1,984 nmol (mg protein)$^{-1}$) was 4-fold higher than was observed in winter (465 nmol (mg protein)$^{-1}$) (Fig. 1b). Similarly, for the tropical scleractinian *A. aspera*, summer concentrations (4,710 nmol (mg protein)$^{-1}$) were 4-fold higher than in winter (1,242 nmol (mg protein)$^{-1}$) (Fig. 1a). The summer value for *A. aspera* is amongst some of the highest protein normalised values reported for this species (Table 2). These temporal shifts in coral DMSP concentrations could be indicative of a short-term stress response as a consequence of elevated sea surface temperatures (SST) at both our study sites during summer. Swan et al. (2017) recently suggested that DMSP content generally remains stable in scleractinians unless exposed to anomalous environmental conditions. Indeed, SSTs were anomalously high in February 2017 for our study sites (Heron Island: 27.8℃, Botany Bay: 24.7℃, Fig. ESM 1), which may have amplified the seasonal dynamic range in DMSP content observed through stress towards upper thermal thresholds (Raina et al. 2013). However, without longer term temporal dynamics of DMSP content spanning both typical and atypical seasonal environmental conditions, it is not possible to fully baseline the responses we observed for these tropical and temperate scleractinians.

In contrast to the scleractinian corals, we did not observe temporal changes in DMSP content among the soft corals, with concentrations remaining relatively consistent between summer and winter (Fig. 1). Variation in DMSP content over space and time in scleractinian corals appears driven by a complex interplay of environmental exposure (Deschaseaux et al. 2014a) relative to the intrinsic coral physiological environmental thresholds (Gardner et al. 2016), which in part can be influenced by re-organisation of microbial-coral interactions (Raina et al. 2010). For example, shuffling of the dominant *Symbiodinium* sp. to one that is more capable of producing DMSP (Chen et al. 2005; Deschaseaux et al. 2014b), or higher DMSP lyase activity among coral-associated bacteria may conceal net DMSP upregulation (Frade et al. 2016). The lack of temporal changes in soft coral DMSP content may, therefore, indicate that the intrinsic mechanisms primarily regulating DMSP content ultimately differs for soft corals compared to scleractinian corals. Alternatively, the soft corals may have exhibited a higher tolerance to elevated SST or ultra violet light at each respective site. Clearly, identifying the functional roles, along with the environmental conditions that regulate DMSP production, warrants further targeted investigation in soft corals.

Conclusions

We have demonstrated that soft corals inhabiting both temperate and tropical reef systems produce significant quantities of DMSP, in concentrations that are within the (low-mid) range described for many scleractinian corals. Studies examining the physiological and microbial regulation of DMSP production in corals to date have almost exclusively focused on scleractinian species (e.g. Raina et al. 2013; Hopkins et al. 2016). However, given the increasing dominance of soft corals within anthropogenically disturbed reef systems (Norström et al. 2009), often as a consequence of climate change driven environmental conditions (Inoue et al. 2013), it is imperative to focus targeted investigation on this key benthic group to resolve the mechanisms responsible for how they produce DMSP over space and time. Therefore, we suggest further evaluation on the effects of environmental stressors on DMSP production to help elucidate the functional roles of this compound, and also to uncover the contribution of soft corals in the critical role of sulphur cycling in reef ecosystems.

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Conflict of interest: The authors declare that they have no conflict of interest

Compliance with ethical standards: All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained.

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Tables

Table 1 Details of coral species examined in this study: *Capnella gaboensis*, *Erythropodium hicksoni*, *Plesiastrea versipora*, *Sinularia* sp., *Sarcophyton* sp. and *Acropora aspera*, including taxonomic information, growth morphology and broad geographic location and conserved ITS2 clades defined from previous studies

Genus/Species	Order	Family	Morphology	ITS2 Clade	Location	Author
Sinularia sp.	Alcyonacea	Alcyoniidae	Soft branching	C3J	Tropical	(LaJeunesse et al. 2003)
Sarcophyton sp.	Alcyonacea	Alcyoniidae	Soft branching	C	Tropical	(Van Oppen et al. 2005)
A. aspera	Scleractinia	Acroporidae	Hard branching	C3	Tropical	(Fisher et al. 2012)
C. gaboensis	Alcyonacea	Nephtheidae	Soft branching	A1	Temperate	(Fujise) (unpubl data)
E. hicksoni	Alcyonacea	Alcyoniidae	Soft encrusting	Unknown	Temperate	
P. versipora	Scleractinia	Faviidae	Hard encrusting	B18	Temperate	(Davy et al. 2006)

Table 2 DMSP concentrations previously reported for species of soft corals and scleractinian corals from various regions. Values are given in different units where available to enable comparisons between this study and the literature. DMSP nmol per milligram of protein (mg protein)$^{-1}$ and DMSP µmol per gram of fresh weight (g FW)$^{-1}$. Values are given as Mean ± Standard deviation (SD) or Standard Error (SE)

Species	Season	Region	DMSP nmol (mg protein)$^{-1}$	DMSP µmol (g FW)$^{-1}$	Author
Soft corals					
Sarcophyton trocheliophorum		Guam		8 ± 1 (SD)	Van alstyne et al. (2006)
Sinularia maxima		Guam		6 ± 2 (SD)	Van alstyne et al. (2006)
Sinularia pauli		Guam		5 ± 0.7 (SD)	Van alstyne et al. (2006)
Sinularia polydactyla		Guam		6 ± 0.8 (SD)	Van alstyne et al. (2006)
Sinularia macropodia		Guam		2 ± 0.4 (SD)	Van alstyne et al. (2006)
Sarcophyton sp.	winter	GBR	85.6 ± 5.2 (SE)	11.7 ± 1.5 (SE)	Current study
	summer	GBR	114.1 ± 24 (SE)	20.6 ± 3.2 (SE)	
Sinularia sp.	winter	GBR	95.3 ± 8 (SE)	6.8 ± 1 (SE)	Current study
	summer	GBR	56.1 ± 13.6 (SE)	9.6 ± 1.8 (SE)	
Capnella gaboensis	winter	Botany Bay	88.2 ± 12.5 (SE)	5.9 ± 2.1 (SE)	Current study
	summer	Botany Bay	104.7 ± 44.6 (SE)	11.2 ± 4.4 (SE)	
Erythropodium hicksoni	winter	Botany Bay	381.5 ± 70 (SE)	8.8 ± 3.8 (SE)	Current study
	summer	Botany Bay	539.5 ± 165.3 (SE)	16.4 ± 8.1 (SE)	
Scleractinian corals					
Montastraea cavernosa	autumn	Bermuda	114.2 ± 9.8 (SE)		Yost et al. (2010)
Madracis mirabilis	autumn	Bermuda	62 ± 3.5 (SE)		Yost et al. (2010)
Porites asteroides	autumn	Bermuda	55.7 ± 8.8 (SE)		Yost et al. (2010)
Montastraea franksi	autumn	Bermuda	103 ± 8.8 (SE)		Yost et al. (2010)
Acropora aspera	summer	GBR	78.5 ± 10.9 (SE)		Deschaseaux et al. (2014a)
Acropora aspera (heat stress)	summer	GBR	1250 ± 219 (SE)		Deschaseaux et al. (2014a)
Acropora aspera (high light)	summer	GBR	2330 ± 168 (SE)		Deschaseaux et al. (2014a)
Acropora aspera	winter	GBR	1242 ± 308 (SE)		Current study
	summer	GBR	4710 ± 516 (SE)		

Pleisiastera versipora	winter	Botany Bay	465.5 ± 117 (SE)	Current study
	summer	Botany Bay	1984 ± 191 (SE)	