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## The distribution of dimethylsulfoniopropionate in tropical Pacific coral reef invertebrates

Received: 23 August 2005 / Accepted: 24 March 2006 / Published online: 27 April 2006  
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**Abstract** Dimethylsulfoniopropionate (DMSP) is an important component of the global sulfur cycle and may be involved, via its cleavage product dimethylsulfide, in climate regulation. Although it is common in many algae, reports of DMSP in animals, particularly tropical invertebrates, are limited. This study examined the distribution of DMSP in a diverse group of coral reef invertebrates. DMSP was present in all 22 species of cnidarians and ranged from 9 to 723  $\mu\text{mol g}^{-1}$  of dry mass (DM) with a mean ( $\pm$  1SD) of  $110 \pm 180 \mu\text{mol g}^{-1}$  DM. It was not detected in a flatworm and an ascidian or in two of five sponges. Concentrations in sponges ranged from undetectable to  $16 \mu\text{mol g}^{-1}$  DM with a mean of  $4 \pm 7 \mu\text{mol g}^{-1}$  DM. Within the cnidarians, DMSP concentrations did not differ among orders. Among cnidarian species, DMSP concentrations were correlated with symbiotic zooxanthellae densities. Within cnidarian species, DMSP concentrations of individuals were positively correlated with zooxanthellae densities in three of the four species examined. We speculate that DMSP is dietarily derived in sponges and derived from zooxanthellae in the cnidarians. The functions of DMSP in coral reef invertebrates are not known.

**Keywords** Cnidaria · DMSP · Invertebrates · Natural products · Porifera

Communicated by Environment Editor K. Fabricius

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### Introduction

Dimethylsulfoniopropionate (DMSP) is a tertiary sulphonium compound that is thought to be an important component of the global sulfur cycle and has been suggested to be involved, via its cleavage product dimethylsulfide (DMS), in climate regulation (Charlson et al. 1987; Malin et al. 1992; Malin and Kirst 1997 and references therein). In marine plants and algae, it has been reported from rhodophytes (red algae), chlorophytes (green algae), phaeophytes (brown algae), dinoflagellates, prymnesiophytes, diatoms, and salt marsh vascular plants (Kiene et al. 1996 and references therein).

Reports of DMSP in animals are less common and tend to be linked to dietary uptake or symbiosis. For example, the strong smell of DMS in Atlantic cod (*Gadus morhua*) has been correlated with high densities of DMSP-producing microalgae (Levasseur et al. 1994). Cod obtain DMSP by consuming pteropods (*Limacina helicina*), which in turn obtain DMSP from plankton. Sulfurous odors from Atlantic mackerel (*Scomber retroversa*) have also been associated with pteropod consumption (Ackman et al. 1972). Marine molluscs that consume DMSP-containing algae often accumulate it in their bodies. DMSP concentrations in the salt marsh mussel *Geukensia demissa* were higher in three sites where mussels fed primarily on phytoplankton, which contain DMSP, than at a single site where their diet was dominated by decomposed salt marsh grasses, which should have low DMSP concentrations (White et al. 1995).

Dimethylsulfoniopropionate has also been reported from animals that harbor symbiotic algae, including scleractinian corals, giant clams, and benthic flatworms (Table 1). In corals and clams, symbiotic dinoflagellates (zooxanthellae) are thought to be the source of the compound (Jones et al. 1994; Hill et al. 1995, 2000; Broadbent et al. 2002). The reason for the production of DMSP in benthic invertebrates is not known.

**Table 1** Published dimethylsulfoniopropionate (DMSP) concentrations of benthic coral reef invertebrates and their symbionts

Species	Location	[DMSP] $\mu\text{mol g}^{-1}$ FM	[DMSP] $\text{fmol cell}^{-1}$
Phylum Cnidaria			
<i>Acropora formosa</i> <sup>a</sup>	Magnetic Island, QLD, Australia	–	150–270
<i>Acropora formosa</i> <sup>b</sup>	Various locations, GBR, Australia	–	171–641
<i>Acropora palifera</i> <sup>b</sup>	Various locations, GBR, Australia	–	2,831–3,831
<i>Acropora pulchra</i> <sup>b</sup>	One Tree Reef, GBR, Australia	–	40
<i>Favites</i> sp. <sup>b</sup>	One Tree Reef, GBR, Australia	–	21
<i>Lobophytum</i> sp. <sup>b</sup>	Orpheus Island, GBR, Australia	–	43
<i>Montipora verrucosa</i> <sup>c</sup>	Kaneohe Bay, Oahu, HI, USA	–	47–86
<i>Pocillopora damicornis</i> <sup>c</sup>	Kaneohe Bay, Oahu, HI, USA	–	90–177
<i>Pocillopora damicornis</i> <sup>b</sup>	Various locations, GBR, Australia	–	89–99
<i>Porites compressa</i> <sup>c</sup>	Kaneohe Bay, Oahu, HI, USA	–	65–103
Zooxanthellae from <i>Lobophytum compactum</i> <sup>b</sup>	Cell culture	–	285
Zooxanthellae from <i>Montipora verrucosa</i> <sup>c</sup>	Cell culture	–	61–66
Zooxanthellae from <i>Porites compressa</i> <sup>c</sup>	Cell culture	–	48
Zooxanthellae from <i>Zoanthus</i> sp. <sup>b</sup>	Cell culture	–	164
Phylum Mollusca			
<i>Tridacna maxima</i> siphonal mantle <sup>d</sup>	Pohnpei, Federated States of Micronesia	21–47	–
<i>Tridacna squamosa</i> siphonal mantle <sup>d</sup>	Pohnpei, Federated States of Micronesia	18–40	–
Zooxanthellae from <i>Tridacna gigas</i> <sup>a</sup>	Cell culture	–	310
Zooxanthellae from <i>Tridacna squamosa</i> <sup>b</sup>	Cell culture	–	116
Phylum Platyhelminthes			
<i>Tetraselmis</i> from <i>Convoluta roscoffensis</i> <sup>e</sup>	Bay of Marennes-Oléron, Charente-Maritime, France	–	45

FM Fresh Mass; GBR Great Barrier Reef

<sup>a</sup>Jones et al. (1994)

<sup>b</sup>Broadbent et al. (2002)

<sup>c</sup>Hill et al. (1995)

<sup>d</sup>Hill et al. (2000)

<sup>e</sup>Van Bergeijk and Stal (2001)

The purpose of this study was to examine the distribution of DMSP concentrations in a broad range of tropical coral reef invertebrates. DMSP is known to be present in a variety of coral reef invertebrates (Table 1) and high concentrations of DMS and DMSP have been reported from coral mucus and ‘mucus ropes’ (Broadbent and Jones 2004). Elevated levels of DMS also occur in waters near reefs and in the air above them (Andreae et al. 1983; Jones et al. 1994; Jones and Trevena 2005). Because previous studies (Jones et al. 1994; Hill et al. 1995, 2000; Broadbent et al. 2002) have linked the presence of DMSP to algal symbionts, we focused much of our effort on quantifying DMSP in species known to contain zooxanthellae: anemones (Order Actiniaria), soft corals (Order Alcyonaria), corallimorphs (Order Corallimorpharia), and scleractinian corals (Order Scleractinia). In algae, the methods used to measure DMSP differ among algal groups (Karsten et al. 1994); therefore, we also conducted an experiment to examine several methods for storing and preparing tissues for analysis. We show here that DMSP is widespread within coral reef invertebrates and that the concentrations among species are highly variable.

## Methods

Marine invertebrates were collected by snorkeling from several shallow reefs around Guam, USA including

Cocos Lagoon (13°15'N, 144°41'E), Gab Gab Reef (13°26'N, 144°38'E), Luminao Reef (13°28'N, 144°39'E), and the Piti Bomb Holes (13°28'N, 144°42'E) (see Table 2 for species collected at specific locations). Additional analyses were conducted on anemones and corallimorphs that were inhabiting the seawater tables at the University of Guam Marine Laboratory (UOGML; 13°25'N, 144°48'E) in Mangilao, GU, USA (Table 2).

To explore the effects of several potential methods of storing and preparing samples for analysis, we conducted an experiment to determine whether DMSP would be lost during handling. The handling methods included drying the tissues prior to analysis, freezing tissues to either  $-4^{\circ}\text{C}$  or  $-80^{\circ}\text{C}$ , and storing the tissues in methanol (MeOH). To examine the effects of each of these methods, we collected apical tissues from 20 *Simularia polydactyla* from the Piti Bomb Holes, Asan, GU, USA. The tissues were transported to the UOGML and processed within 4 h of collection. Five distal tips were cut off each individual, weighed, and distributed among the following treatments: (1) conducting DMSP analyses on freshly collected material, (2) drying the material in an oven overnight at  $60^{\circ}\text{C}$  prior to conducting DMSP measurements, (3) freezing the material in darkness at  $-20^{\circ}\text{C}$  for a week prior to conducting DMSP measurements, (4) freezing the material in darkness at  $-80^{\circ}\text{C}$  for a week prior to conducting DMSP measurements, and (5) placing the tissue in 100% MeOH for a week prior to conducting DMSP

**Table 2** Dimethylsulfoniopropionate (DMSP) concentrations in benthic invertebrates of Guam

Species	N	[DMSP]		
		Mean $\pm$ SD ( $\mu\text{mol g}^{-1}$ FM)	Mean $\pm$ SD ( $\mu\text{mol g}^{-1}$ DM)	Mean $\pm$ SD (fmol cell $^{-1}$ )
<b>Phylum Porifera</b>				
<i>Axinella</i> sp. (GG)	5	3 $\pm$ 1	16 $\pm$ 6	–
<i>Plakina</i> sp. (GG)	5	ND	ND	–
<i>Stylissa massa</i>	4	0.7 $\pm$ 0.6	3 $\pm$ 3	–
<i>Tethys</i> sp. (GG)	5, 4	0.2 $\pm$ 0.1	1 $\pm$ 0.9	–
<i>Xestospongia carbonifera</i> (GG)	5	ND	ND	–
<b>Phylum Cnidaria</b>				
<b>Anemones (Order Actiniaria)</b>				
<i>Aiptasia pulchella</i> (UOGML)	13, 12, 12	15 $\pm$ 8	79 $\pm$ 8	161 $\pm$ 67
<i>Bolocerooides mcmurrichii</i> (UOGML)	6	36 $\pm$ 13	330 $\pm$ 139	1,598 $\pm$ 711
<i>Eutacmaea quadricolor</i> (GG)	5	5 $\pm$ 3	43 $\pm$ 23	194 $\pm$ 61
<b>Soft Corals (Order Alcyonacea)</b>				
<i>Sarcophyton trocheliophorum</i> (PBH)	10	8 $\pm$ 1	37 $\pm$ 8	149 $\pm$ 28
<i>Sinularia maxima</i> (PBH)	5	6 $\pm$ 2	35 $\pm$ 6	247 $\pm$ 61
<i>Sinularia maxima</i> x <i>polydactyla</i> (PBH)	4	5 $\pm$ 0.7	27 $\pm$ 5	178 $\pm$ 23
<i>Sinularia pauli</i> (CL)	3	2 $\pm$ 1	11 $\pm$ 9	106 $\pm$ 20
<i>Sinularia polydactyla</i> (PBH)	9, 8, 8	6 $\pm$ 0.8	26 $\pm$ 5	231 $\pm$ 31
<i>Sinularia macropodia</i> (CL)	3	2 $\pm$ 0.4	12 $\pm$ 1	193 $\pm$ 36
<b>Corallimorphs (Order Corallimorpharia)</b>				
<i>Discosoma nummiforme</i> (UOGML)	15, 14, 12	12 $\pm$ 8	70 $\pm$ 39	179 $\pm$ 45
<i>Rhodopsis</i> sp. (UOGML)	6	153 $\pm$ 23	723 $\pm$ 44	1,958 $\pm$ 207
<i>Ricordea yuma</i> (UOGML)	5	8 $\pm$ 2	55 $\pm$ 8	209 $\pm$ 44
<b>Stony Corals (Order Scleractinia)</b>				
<i>Acropora cerealis</i> (GG)	5	47 $\pm$ 6	236 $\pm$ 99	950 $\pm$ 615
<i>Acropora digitifera</i> (GG)	4	33 $\pm$ 8	127 $\pm$ 41	417 $\pm$ 162
<i>Acropora valida</i> (GG)	5	59 $\pm$ 16	467 $\pm$ 127	425 $\pm$ 132
<i>Heliopora coerulea</i> (LR)	4	1 $\pm$ 0.1	9 $\pm$ 2	310 $\pm$ 119
<i>Leptastrea purpurea</i> (CL)	4	3 $\pm$ 1	12 $\pm$ 3	211 $\pm$ 230
<i>Pavona decusata</i> (GG)	5	10 $\pm$ 48	48 $\pm$ 19	43 $\pm$ 19
<i>Pocillopora meandrina</i> (GG)	4	3 $\pm$ 1	10 $\pm$ 2	80 $\pm$ 22
<i>Porites cylindrica</i> (GG)	4	3 $\pm$ 0.7	18 $\pm$ 7	107 $\pm$ 39
<i>Porites rus</i> , decumbent (GG)	5	3 $\pm$ 0.7	18 $\pm$ 4	88 $\pm$ 28
<i>Porites rus</i> , upright (GG)	4	2 $\pm$ 0.4	14 $\pm$ 4	69 $\pm$ 24
<i>Psammocora digitata</i> (GG)	4	7 $\pm$ 6	22 $\pm$ 4	49 $\pm$ 19
<b>Phylum Platyhelminthes</b>				
<i>Pseudoceros indicus</i> (GG)	3	ND	–	–
<b>Phylum Chordata</b>				
<i>Didemnum</i> sp. (CL)	3	ND	–	–

Values are given in different units to facilitate comparisons with the literature (Table 1). Fresh mass (FM) and dry mass (DM) values are for tissues minus the mass of the skeletal components (sclerites in soft corals and skeleton in stony corals). Values per cell are amounts of DMSP per zooxanthella. The collection site is given parenthetically after each species name. Where columns have different sample numbers (N) these are shown as e.g., 14, 14, 12, respectively

CL Cocos Lagoon, GG Gab Gab Beach, LR Luminao Reef, PBH Piti Bomb Holes, UOGML seawater tanks at the University of Guam Marine Laboratory, ND not detectable

measurements. To measure the concentration of DMSP in *S. polydactyla* apices, tissues were placed in 4 N NaOH in 30 ml gastight vials. DMSP was measured as DMS after 24 h from the headspaces of the vials by direct injection into an SRI gas chromatograph (Chromosil 330 column, flame photometric detector; lower detection limit: 5  $\mu\text{g}$  DMS). DMSP standard additions using commercially obtained DMSP (Center for Analysis, Spectroscopy and Synthesis, University of Groningen; purity > 98%) added to equal volumes of NaOH were used to generate standard curves. The resulting data were compared with a repeated measures

analysis of variance (ANOVA, SPSS version 11.0). DMSP concentrations were based on fresh tissue masses that were not corrected for the mass of sclerites.

All additional analyses were conducted on material that was freshly collected and immediately analyzed at the UOGML. Whenever possible, individuals or individual tissues were divided in half. One half was weighed and dried overnight at 60°C to determine a dry-to-wet-weight ratio for that individual. In alcyonarians and scleractinian corals, the dried tissues were soaked overnight twice in 50% bleach (5% sodium hypochlorite) and once in acetone to remove organic matter as

described in Van Alstyne et al. (1992). The remaining sclerites or  $\text{CaCO}_3$  skeleton were then rinsed in acetone, dried, and weighed to determine the percentages of the original pieces that were composed of skeletal elements. These percentages were then used to estimate the non-skeletal fresh masses (FM) and dry masses (DM) of the tissues. The other half of the sample was weighed and placed in 4 N NaOH in a 30 ml gas-tight vial for measurements of DMSP, which were conducted as described above.

After the DMSP measurements were made, the vials containing tissues known to harbor zooxanthellae were shaken vigorously to further dissolve any intact tissues. Zooxanthellae were then concentrated by centrifugation and the NaOH was poured off. The samples were suspended in 4% formalin:96% seawater and shipped to the Shannon Point Marine Center in Anacortes, WA, USA where zooxanthellae numbers were determined with a hemocytometer. Pearson's correlation coefficients were calculated (Minitab 12.0) to compare DMSP concentrations as a percent of the DM versus zooxanthellae concentrations (as cells  $\text{DM}^{-1}$ ) among individuals in the four species of the zooxanthellate cnidarians (*Aiptasia pulchella*, *Discosoma nummiforme*, *Sarcophyton trocheliophorum*, and *Simularia polydactyla*) that had sample sizes of at least eight individuals.

Dimethylsulfoniopropionate was measured in the zooxanthellate larvae of *Leptastrea purpurea* from Cocos Lagoon, GU. Sixty larvae were collected from laboratory cultures by pipetting them individually into three containers ( $N = 20$  per container) and adjusting the volume to 5 ml with seawater. The seawater and larvae were added to 4 ml of 4 N NaOH in gas-tight containers ( $N = 3$ ). Seawater alone (5 ml) was added to three gas-tight containers with NaOH to confirm that there was no detectable DMSP or DMS in the seawater. Additional containers with known amounts of DMSP in equal volumes of seawater were used to generate standard curves. DMSP was measured as headspace DMS using solid phase microextraction (SPME) as described in Van Alstyne and Houser (2003).

## Results

The methods used to prepare samples had a significant impact on the outcome of the analyses (repeated measures ANOVA: Pillai's trace = 0.428,  $F = 6.735$ ,  $P = 0.007$ ). DMSP was not detectable in *Simularia polydactyla* tissues that were dried or stored in methanol. Concentrations of DMSP in tissues stored at  $-80^\circ\text{C}$  (mean [DMSP]  $\pm$  1 SE:  $18 \pm 2 \mu\text{mol g}^{-1}$  DM) were not statistically distinguishable from tissues that were extracted from freshly collected soft corals (mean [DMSP]  $\pm$  1 SE:  $19 \pm 1 \mu\text{mol g}^{-1}$  DM; Tukey's *post hoc* test:  $P > 0.05$ ); however, tissues that were stored at  $-20^\circ\text{C}$  lost about 22% of their DMSP (mean [DMSP]  $\pm$  1 SE:  $15 \pm 1 \mu\text{mol g}^{-1}$  DM).

In general, DMSP was present in the cnidarians but was absent or in low concentrations from the other phyla examined (Table 2). It was not detectable in the flatworm and ascidian or in two of the five sponges. The remaining sponges had measurable amounts of DMSP, but, with the exception of *Axinella* sp., the concentrations were lower than any of the cnidarians. Concentrations in *Axinella* were comparable to some of the lower concentrations in the soft and scleractinian corals.

In the cnidarians, DMSP concentrations ranged from a high value of  $723 \mu\text{mol g}^{-1}$  of the non-skeletal DM in the corallimorph *Rhodopsis* sp. to a low of  $9 \mu\text{mol g}^{-1}$  DM in the scleractinian coral *Heliopora coerulea* (Table 2). There were no significant differences in mean DMSP concentrations at a species level among the anemones (mean [DMSP]  $\pm$  1 SD:  $150 \pm 156 \mu\text{mol g}^{-1}$  DM) corallimorphs (mean [DMSP]  $\pm$  1 SD:  $282 \pm 381 \mu\text{mol g}^{-1}$  DM), soft corals (mean [DMSP]  $\pm$  1 SD:  $25 \pm 11 \mu\text{mol g}^{-1}$  DM), and scleractinian corals (mean [DMSP]  $\pm$  1 SD:  $89 \pm 144 \mu\text{mol g}^{-1}$  DM); one-way analysis of variance,  $F = 1.65$ ,  $P = 0.212$ ).

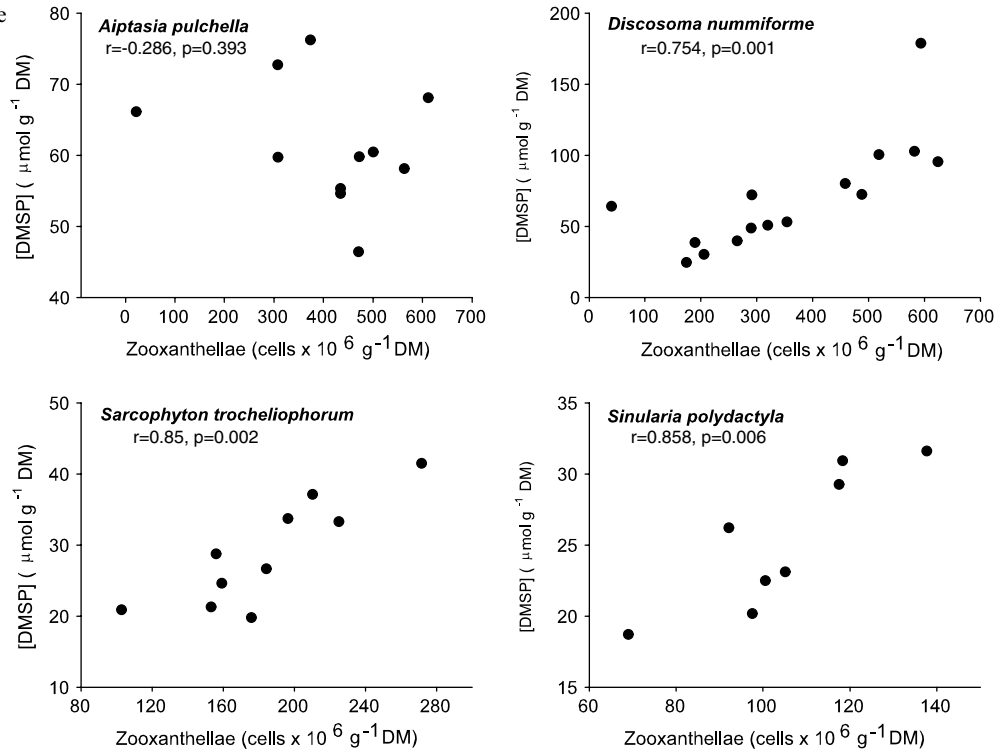
Concentrations of DMSP in the soft corals were uniformly low (Table 2) and ranged from 11 to  $37 \mu\text{mol g}^{-1}$ . However, they were in the same range as some species from the other cnidarian groups. Within the scleractinian corals, DMSP concentrations were highly variable, ranging from  $467 \mu\text{mol g}^{-1}$  DM in *Acropora valida* to  $9 \mu\text{mol g}^{-1}$  DM in *H. coerulea*. Concentrations were consistently higher in *Acropora* than in other genera, which were typically in the same range as the concentrations in the soft corals. There was no difference in mean DMSP concentrations in the decumbent and upright forms of *Porites rus* (Table 2; Student's *t*-test:  $T = 1.65$ ,  $P = 0.15$ ,  $DF = 6$ ). DMSP was consistently detectable in larvae of *L. purpurea* and occurred, on average, at a concentration of about 72 ng per larva. These values were very close to the lower limits of detection for the instrumentation used, so they may not be highly accurate. No DMSP was detected in the seawater controls.

The mean DMSP concentrations (as  $\mu\text{mol g}^{-1}$  DM) were correlated with the mean concentrations of zooxanthellae (as cells  $\text{g}^{-1}$  DM) across the 22 species of cnidarians (Pearson's correlation coefficient: 0.569,  $P = 0.006$ ). Within species, DMSP concentrations were highly correlated with zooxanthellae densities among individuals of *D. nummiforme*, *S. trocheliophorum*, and *Simularia polydactyla* (Fig. 1). However, they were not significantly correlated ( $P > 0.05$ ) within the anemone *A. pulchella*.

## Discussion

Our experimental evaluation of DMSP loss from different methods of storing tissues indicates that drying tissues before conducting measurements, a method commonly used for measuring DMSP in chlorophyte

**Fig. 1** Dimethylsulfoniopropionate (DMSP) concentration versus zooxanthellae density from individuals of four cnidarians. Pearson's correlation coefficient and *P* values are shown for each species



algal tissues, should not be used for invertebrate tissues without further evaluation. In soft corals, drying the tissues resulted in such a large loss of DMSP that it could no longer be detected. DMSP losses also occur after drying some red algae, possibly because structural properties of the cell walls make them more resistant to drying (Karsten et al. 1994). Our results indicate that freezing and maintaining tissues at very cold temperatures ( $-80^{\circ}\text{C}$ ) may be an acceptable way to store or transport invertebrate tissues prior to measurement of DMSP concentrations. The results of storing the samples in methanol were not unexpected because DMSP is methanol-soluble and most of the compound probably remained in solution rather than cleaving and causing DMS to enter the headspace of the vials.

Dimethylsulfoniopropionate was detectable in all of the cnidarians we sampled, but it was only present in some of the sponges and it was not found in the ascidian or the flatworm. The distribution of the compound supports the hypothesis that animals acquire DMSP either from their diet or from endosymbiotic zooxanthellae. In sponges, the variable occurrence and low concentrations of DMSP and lack of zooxanthellae suggest that DMSP is derived from the animals' diets, which generally consist of plankton obtained by filter-feeding (Kozloff 1990). The specific diets of the species examined in this study are not known. The zooxanthellate origin of DMSP in the cnidarians was supported by the trend for DMSP concentrations to be correlated with zooxanthellae densities both across and within species.

The amounts of DMSP found in cnidarians were generally 50–400 fmol per cell (mean  $\pm$  1 SD:  $367 \pm 498$ ,  $N = 22$ ), which is similar to the range of values previously reported for these taxa (Table 1). There were, however, some notable exceptions. The anemone *Bolocerooides mcMurrichii*, the corallimorph *Rhodopsis* sp., and corals in the genus *Acropora* all contained DMSP concentrations that were several-fold to an order of magnitude higher, on a per-cell basis. The concentrations of DMSP that we found in *Acropora* spp. were similar to those reported in other *Acropora* spp. from the Great Barrier Reef (Broadbent et al. 2002). The higher DMSP concentrations may be due to environmental induction of DMSP production. In some ulvoid macroalgae, DMSP concentrations vary in response to changes in light intensity (Karsten 1991, 1992) and salinity (Edwards et al. 1987, 1988; Karsten et al. 1992); however, in other species and locations they appear to be constitutive (Van Alstyne et al. 2003). Alternatively, differences in DMSP concentrations could be caused by genetic differences that result from localized selection or differences in the types of *Symbiodinium* harbored by the animals. There is considerable genetic diversity in symbiotic zooxanthellae hosted by cnidarians (Rowan 1998; Baker 2003). Even within species, animals can harbor multiple symbionts whose abundances can change over time (Rowan et al. 1997; Knowlton and Rohwer 2003).

In *Leptastrea purpurea*, DMSP was present in both the mobile larval and sessile adult stages. The presence of DMSP in larval stages is not surprising given that these larvae harbor zooxanthellae and the likelihood that DMSP is being produced by the symbionts.

The timing of symbiont acquisition varies among cnidarians. In some species they are obtained maternally, whereas in others they are acquired in later free-living planktonic or sessile stages (e.g., Hirose et al. 2000; Coffroth et al. 2001; Weis et al. 2001; Schwarz et al. 2002; Pasternak et al. 2004). We predict that DMSP concentrations in larvae will depend on the timing and mode of the acquisition of symbionts.

The reasons for the production and accumulation of DMSP by zooxanthellate cnidarians are unclear. The proposed functions of DMSP are diverse, and include physiological as well as allelopathic roles. DMSP was initially described as playing a role in osmoregulation or cryoprotection in macroalgae (Reed 1983a, b; Edwards et al. 1987, 1988; Kirst et al. 1991; Karsten et al. 1992; Stefels and Dijkhuizen 1996), functions that are unlikely to be important in subtidal coral reef invertebrates. It has also been suggested to be part of an activated defense system in microalgae (Wolfe and Steinke 1996; Wolfe et al. 1997) and macroalgae (Van Alstyne et al. 2001; Van Alstyne and Houser 2003).

Another likely function of DMSP in tropical reef invertebrates is protecting the host and/or symbionts from oxidative damage. Reactive oxygen species (ROS), which can cause molecular, cellular, and physiological damage, are produced in response to a variety of stressors, including elevated photosynthetically active radiation and temperature (Lesser et al. 1990), and ultraviolet radiation (Vincent and Neale 2000). In phytoplankton, DMSP, DMS, acrylate and acrylic acid can all scavenge ROS, but DMS and acrylic acid are the most effective scavengers (Sunda et al. 2002). Microalgae cleave DMSP into DMS and acrylic acid or acrylate in the presence of ROS, presumably to generate the more efficient ROS scavengers. Although it is not known whether a similar mechanism exists in tropical cnidarians, the high-light environments of tropical reefs make an antioxidant function for DMSP and its breakdown products a reasonable possibility. Colonies of *Acropora formosa* that have bleached have a higher concentration of DMSP on a per cell (zooxanthella) basis than unbleached colonies (Broadbent et al. 2002), suggesting that DMSP concentrations may increase in response to the stresses that cause bleaching or that symbionts containing low concentrations of DMSP either die or leave the colonies more quickly than cells with higher concentrations.

Dramatic changes in zooxanthellae densities and symbiont composition are seen during coral bleaching events and in recovery periods following these events (e.g., Rowan et al. 1997; Fagoonee et al. 1999; Baker 2003; Lewis and Coffroth 2004). If DMSP is involved in antipredator defense or in the removal of ROS, then decreases in DMSP associated with the loss of zooxanthellae during bleaching events could contribute to increases in physiological stresses experienced by the animals and possibly increased rates of mortality.

In summary, DMSP is found in a variety of animal taxa inhabiting tropical waters. Its origin is likely to be from dietary sources and endosymbiotic microalgae,

although we cannot yet rule out the possibility that some animals are producing the compound themselves. The function of DMSP is also unclear, but given the multiple uses of the compound in other taxa, it is likely that the compound has several roles in coral reef invertebrates, ranging from being an incidental result of ingesting plankton that contain it to functioning as an antipredator defense or an ROS scavenger.

**Acknowledgments** We thank University of Guam Marine Laboratory (UOGML) students for assistance in the field and for their efforts to locate trucks for the Cocos Lagoon trips, T. Rongo and M. McCormick for identifying corals, M. McCormick for providing *Leptastrea* larvae and G. Jones, and an anonymous reviewer for their many helpful comments on this manuscript. We are also grateful to the staff at the UOGML for the logistical support that they provided for this project. This work was funded by National Science Foundation grants IBN-0090825 and DBI-9877129 to K. Van Alstyne and National Oceanic and Atmospheric Administration NURP/NIUST NA 16RU1496 to M. Slattery. P. Schupp acknowledges support by the National Institutes of Health MBRS SCORE S06-GM44796-15 for ongoing support and laboratory infrastructure.

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