

Dimethylsulfoniopropionate is linked to coral spawning, fish abundance and squid aggregations over a coral reef

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Coral reefs are frequently used as transient aggregation sites for foraging and spawning by marine fishes. These fishes may use predictable changes in chemical cues associated with reefs as signals to coordinate their aggregations. Dimethyl sulfide (DMS) and its precursor, dimethylsulfoniopropionate (DMSP), are ubiquitous compounds associated with productive areas, preferred sites for foraging and spawning of pelagic species. It is possible that species may recruit to DMS or DMSP (DMS/P) signatures associated with these areas. Here we investigate how temporal variation in the abundance of reef fishes and squid related to changes in DMS/P during a coral spawning event. During 2003, we recorded significant increases in water column DMS/P during a coral spawning event and found that an elevation in DMS/P was paralleled by a surge in numbers of pelagic fishes, *Caranx* spp., and squid, *Loligo roperi*, over the reef. The changes in pelagic fish and squid abundance were positively correlated with DMS/P, suggesting that these animals may cue to the release of specific compounds during spawning. These results, coupled with other recent studies, provide further evidence that DMS/P may be used by fishes and squid to coordinate their aggregations over reefs.

Key Words: DMSP, pelagic fish, squid, aggregation, coral spawning

Introduction

Dimethyl sulfide (DMS) has been studied intensively by atmospheric and process-oriented oceanographers for its role in global climate, marine sulfur cycles and phytoplankton physiology (e.g., Curran and Jones 2000; Kiene *et al.* 2000). Dimethylsulfoniopropionate (DMSP) is a water-soluble osmolyte produced by species of marine phototrophic algae and is the major precursor of the volatile compound, dimethyl sulfide (DMS). DMSP is converted to DMS and acrylic acid by bacterial and algal enzymatic degradation (Kiene *et al.* 2000) and this metabolic conversion is accelerated during grazing by zooplankton (Dacey and Wakeham 1986; Daly and DiTullio 1996). Since the release of DMS and DMSP can be a by-product of zooplankton feeding (Cantin *et al.* 1996), its patchy distribution in the marine environment may reflect grazing rate (Kwint and Kramer 1996; Wolfe and Steinke 1996). Further, Hill and Dacey (2006) found that dissolved DMSP is released into the water immediately after foraging by planktivorous fishes.

Coral reefs are significant production sites for DMS and DMSP (Broadbent and Jones 2004). Reefs appear to produce DMSP in part through interactions between coral and their symbiotic zooxanthellae (Hill *et al.* 1995; Van Alstyne *et al.* 2006). Zooxanthellae taken from *Acropora* coral tissues from the Great Barrier Reef produce up to 285 fmol DMSP per

cultured cell and up to 3831 fmol per cell in corals (Broadbent *et al.* 2002). Further, Broadbent (1997) reported an increase in water column DMS and DMSP the day after a mass coral spawning and attributed it to the corals' release of mucus and eggs containing zooxanthellae.

We are only beginning to understand the roles of DMSP and DMS as signal molecules in marine and terrestrial ecosystems (see Nevitt *et al.* 1995; Zimmer-Faust *et al.* 1996; Steinke *et al.* 2006; DeBose *et al.* 2006, 2007, 2008). High DMS and DMSP concentrations over productive marine areas can be long-lasting (hours to days; Ledyard and Dacey 1996) and thus, provide predictable cues that may be used by organisms to locate habitat. For instance, frontal zones are productive areas where seabirds (Nevitt 2000), Humboldt penguins (see Culik 2001), and basking sharks (Sims and Quayle 1998) forage on dense plankton patches. Nevitt (2000) has implicated air-borne DMS as part of an 'olfactory landscape', which can be detected by pelagic Procellariiform seabirds in search of productive areas for foraging. Humboldt penguins increase their anticipatory activity in the presence of DMS, suggesting that penguins could use DMS as a foraging cue as well (Culik 2001). Similarly, Sims and Quayle (1998) suggest that basking sharks might use DMS to locate dense patches of plankton along frontal zones.

There are many other examples of pelagic fish and other organisms that aggregate over particular sites in the marine environment. Many of these known aggregation sites are highly productive areas, such as frontal zones (Sims and Quayle 1998), seamounts (reviewed by Genin 2004), and coral reefs (reviewed by Domeier and Colin 1997). Could scented compounds associated with plankton-rich frontal zones and coral reefs, including DMS and DMSP, represent an aquatic counterpart to the olfactory landscape used by foraging seabirds?

Whether marine organisms use variations in DMS/P as habitat cues has never been explicitly tested, but there is evidence that they can detect DMSP at biologically appropriate concentrations. Nakajima and coworkers (1989, 1996) have shown through electrophysiological and behavioral trials that several species of fresh- and saltwater fish respond to DMSP (see DeBose et al. 2006). Initial field studies have also suggested that fish may be able to use DMSP as an aggregation cue in their natural environments (DeBose and Nevitt 2007; DeBose et al. 2008). Predictable temporal or spatial DMS/P signatures, such as those produced during coral spawning, might thus provide an 'olfactory landscape' which pelagic animals may use to locate particular habitat (see Nevitt 2000).

Here we explore whether fish and squid aggregations are correlated to fluctuations of DMS/P in a natural coral reef system. We investigated this idea by quantifying whether DMS/P levels over an offshore coral reef change during a coral spawning event and examining whether these changes in DMS/P are associated with temporal changes in the abundance of pelagic fishes and squid over the same period.

Materials and Methods

Study site

The Flower Garden Banks (FGB) consist of two upraised salt domes in the northwestern Gulf of Mexico, approximately 200 km off the Texas and Louisiana coasts (USA). The reef crests of the East and West banks peak at 22-28 m and 21-27 m depths, respectively, and are topped by a thriving coral reef with over 50% coral cover (Rezak et al. 1985).

Total DMS and DMSP measurements

Water collection

Seawater samples were collected in Corning 50 mL plastic centrifuge tubes. Samples were taken by scuba divers, along 100 m transects at approximately 12 m depth (mid-water above the coral reef). Results of a preliminary study showed mid-water collections to represent the highest concentrations of total DMS+DMSP (DMS/P) (see DeBose 2008). Samples

for total DMS/P were collected using scuba on August 4, 5, 18-21, 2003. Six samples were taken per dive and samples were collected on August 4-5 during the morning between the hours of 06:54-07:18 and 10:58-11:24 local time (Central Standard Time). On August 18-21 both day and night samples were taken for comparison between the hours of 16:30-17:18 and 21:10-21:35. The timing of night sampling was based on a historical record of coral spawning events and estimated from the previous years' spawning times (Gittings et al. 1992; Vize et al. 2005). Sample times were consistent over nights, so even though samples may not have been collected during peak spawning activity, the samples reflect day to day changes in DMS/P. Samples were collected prior to the coral spawning on the night of August 18, so these samples were classified, along with samples collected on August 4-5, as within the "Pre-Spawn" period. Water samples collected on August 19-21 were classified as within the "Spawn" period. After surfacing from each dive, we pipetted 20 mL of the seawater samples into '20 mL' vials and added 1 mL of 1 N sodium hydroxide (NaOH). Vials were then sealed with Teflon-coated, butyl rubber septa and aluminum caps, crimped, and stored upside down in the dark.

Water chemistry analysis

Whole water samples were preserved with 1 N NaOH, which cleaves DMSP (particulate and dissolved) into DMS, so that the two sources of DMS could not be differentiated in this study. All concentrations are therefore reported as DMS/P.

Total DMS+DMSP was quantified using a gas chromatograph (GC; Shimadzu GC-14A equipped with a FPD-14) at the Dauphin Island Sea Lab, Alabama, USA. Samples were analyzed January 26-28, 2004. Our results can be considered conservative estimates of total DMS/P, since some loss of DMS from samples might have occurred during storage.

Each 20 mL sample was vortexed, and 1 mL of the sample was then combined with 1 mL of 5 N NaOH in a 5 mL serum vial. Headspace gas in the vial was captured using a modified cryotrapping method adapted from Kiene and Service (1991). The oven temperature was maintained at 70°C to adequately separate sulfur compounds. Standard preparation is described elsewhere (Kiene and Service 1991).

Coral Spawning Behavior

Seven to ten days after the first full moon in August, seven species of hermatypic corals of the Flower Garden Banks undergo their annual spawning (Gittings et al. 1992). Scuba dives to observe coral spawning were made from the diving vessel M/V Spree (Gulf Diving LLC) at the West Flower Garden Bank from August 18-20 and at the East Bank on

August 21. Observations were made by two teams of scuba divers (six total divers) for approximately 500.5 min per diver, at depths ranging between 18 and 30 m. Divers monitored coral spawning behavior every night between the hours of 20:30 and 24:00 from August 18-21. Each night, divers entered the water for consecutive, overlapping time periods in order to continuously monitor the onset and completion of coral spawning within 100 m radius of the boat. Divers quantified the number and species of coral heads spawning, and the times of spawning activity for each species.

Quantification of Fish and Squid Abundance

We used Reef Environmental Education Foundation (REEF) Roving Diver Technique surveys to quantify the abundance of reef fishes (see Pattengill-Semmens and Semmens 1998). REEF surveys were conducted between 07:00 and 22:00 and individual survey times lasted approximately 42 ± 8 min ($n=72$). Fish abundances were scored as: 0 (Absent), 1 (Single), 2 (Few, 2-10 individuals), 3 (Many, 11-100), 4 (Abundant, >100). Abundance scores were interpreted using a Density Index score: $DI = \{(S*1) + (F*2) + (M*3) + (A*4)\} / (\text{number of surveys in which species was observed})$ (REEF 2004).

Squid counts were recorded by instantaneous point sampling throughout the dive, using a remotely operated vehicle (ROV; Phantom, operated by National Undersea Research Center/UNCW) on August 5, and by scuba on August 4, 18-21. On August 4, dive time was 46 min (from 20:50 to 21:36). ROV dive time was 152 min (from 18:15 to 20:47). During the spawning week, scuba dives were made between the hours of 20:32-00:07. The observation time by any one dive team ranged from 443-586 minutes over four nights, with the average nightly dive lasting 110-146 min.

Statistical Analyses

A mixed, nested ANOVA was used to analyze the effects of several factors on water column DMS/P: Date, Period (Pre-Spawning or Coral Spawning), Bank (East or West Flower Garden Bank), and Day/Night collection. Date was nested within Period and Bank. The final ANOVA model was obtained by backwards elimination (eliminating factors with $F < 1$). Fish DI scores and squid counts failed to conform to normality and could not be transformed. Therefore, DI scores and squid numbers were analyzed using non-parametric Spearman's Rho Correlation. All statistical tests were two-tailed and performed using Statistica (StatSoft, Inc., Tulsa, OK).

Results

Total DMS+DMSP

The August 2003 spawning event (Table 1) occurred within the predicted time period (see Vize *et al.* 2005). Associated with this period of coral spawning, we observed a significant increase in water column DMS/P (Fig. 1; $F_{1,55} = 23.17$, $P = 0.0172$). DMS/P levels varied among days, and showed a significant increase beginning on the first day after the initial coral spawning ($F_{3,55} = 3.717$, $P = 0.0166$). DMS/P did not vary between day and night samples ($F_{1,53} = 0.0127$, $P = 0.9106$). Neither did DMS/P vary between the East and West Flower Garden Bank ($F_{1,55} = 1.125$, $P = 0.3695$).

Species	18-Aug-03	19-Aug-03	20-Aug-03	21-Aug-03
<i>Montastraea cavernosa</i> Great star coral	2030–2138 (10)	--	--	--
<i>Montastraea franksii</i> Mountainous star coral	2140–2214 (50)	2212–2230 (20)	--	--
<i>Diploria strigosa</i> Symmetrical brain coral	2200 (2)	2130–2230 (15)	--	--
<i>Stephanocoenia intersepta</i> Blushing star coral	2250 (2)	2250–2257 (2)	--	--
<i>Montastraea faveolata</i> Mountainous star coral	--	--	2300–2330 (5)	--
<i>Colpophyllia natans</i> Large-grooved brain coral	--	--	2040–2110 (3)	2045–2105 (17)

Table 1: Spawning times for each broadcast spawning coral species during August 2003. The number of coral heads observed spawning is in parentheses next to time frames detailing when the first and last coral head of each species released spawn.

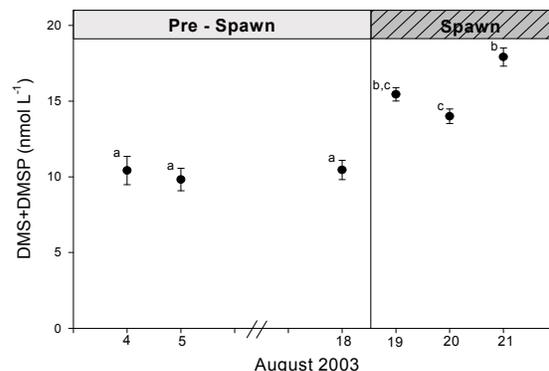


Figure 1: Total DMS+DMSP (nmol L^{-1}) in the water column increased significantly during coral spawning. Letters indicate a significant difference between days (see text).

Fish and Squid Abundance

Divers counted 133 fish species over the six days of sampling, with a maximum of 96 species on August 20-21. We found significant positive relationships between density scores for *Caranx hippos* (Fig. 2; $(r_s)_{0.05(2),6} = 0.8971$, $P = 0.0153$) and *C. latus* ($(r_s)_{0.05(2),6} = 0.9095$, $P = 0.0119$) and DMS/P. There was also a significant correlation between numbers of *Loligo roperi* ($(r_s)_{0.05(2),6} = 0.8971$, $P = 0.0153$) and DMS/P. The abundances of *Caranx* fishes and

number of squid were not significantly related to the number of corals reported spawning (*C. hippos* ($r_{s,0.05(2),6} = 0.6470$, $P = 0.1649$; *C. latus* ($r_{s,0.05(2),6} = 0.7276$, $P = 0.1012$; *L. roperi* ($r_{s,0.05(2),6} = 0.4706$, $P = 0.3462$).

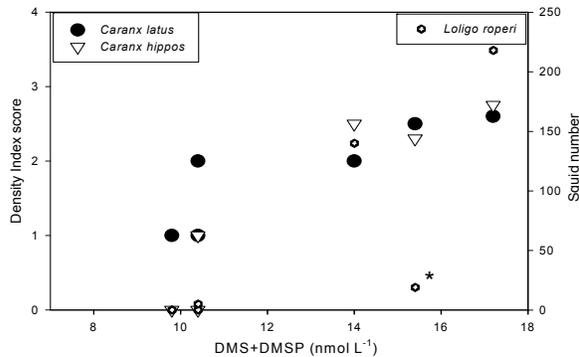


Figure 2: The density index scores for pelagic jacks (circles and triangles) and numbers of *Loligo roperi* (starred hexagons), showed positive correlations with temporal changes in DMS/P over the coral spawning period. DI scores and squid numbers are plotted against the average daily DMS/P. Asterisk denotes delay in squid numbers until after the first peak of DMS/P, which occurred on the first night of the coral spawning.

Discussion

Water column DMS/P increased significantly over the coral spawning period as compared to pre-spawning dates. The higher DMS/P concentrations were accompanied by increased abundances of pelagic fishes (*Caranx hippos* and *C. latus*) and squid (*Loligo roperi*) during the spawning period. These increases in fish and squid were associated with temporal variations in water column DMS/P rather than with the number of corals spawning.

Our data indicate that fish and squid are attracted to the coral spawning event, as evidenced by the increase in their abundances that we documented here (see also Westneat and Resing 1988; Pratchett et al. 2001). More specifically, we found the abundances of fish and squid were correlated with water column levels of DMS/P, suggesting that fish and squid may be using chemical DMS/P signatures as part of an olfactory landscape to time behaviors leading to aggregations. Based on this correlation, and similar behaviors elicited by an experimental release of DMSP (DeBose et al. 2008), we hypothesize that this attraction is mediated by temporally distinct elevations in DMS/P, or associated compounds in the water column, which serve as cues to help coordinate these behaviors. Additional chemical cues released either during spawning or by acts of predation, coupled with a changing visual landscape as fish recruit to the area, may draw in additional predatory, pelagic fishes. While in the present study we discuss this hypothesis over reef habitats, similar scenarios

might also occur in upwelling areas, where primary productivity is elevated and zooplankton grazing on plankton releases substantial amounts of DMS/P and other chemicals (see Steinke et al. 2002).

Loligo roperi numbers were also significantly correlated with high levels of DMS/P. An apparent delay in the increase in squid number (shown in Figure 2) suggests squid might be using DMS/P to coordinate their activity on the reef. The schools of *Loligo roperi* recorded over the Flower Garden Banks consist of mated/mating adults and reproductively immature juveniles; the Flower Garden Banks are the only known mating grounds for this elusive squid (DeBose and Vecchione 2005).

The proximate causes for the increase in DMS/P are still undetermined. Zooxanthellae harbor high amounts of DMSP ($73\text{--}117\text{ fmol cell}^{-1}$; Hill et al. 1995; $48\text{--}285\text{ fmol cell}^{-1}$; Broadbent et al. 2002), and the amount of zooxanthellae within coral spawn, including eggs and mucus (Muller-Parker and D'Elia 1997; Broadbent and Jones 2004) could produce a substantial release of DMSP. The highest levels of DMS and DMSP ever recorded in the marine environment were found within coral mucous ropes (DMS: $17.9\text{ }\mu\text{M}$; DMSP: $44.9\text{ }\mu\text{M}$) and surface waters (DMS: 219 nM ; DMSPd: 630 nM) of the Great Barrier Reef (Broadbent and Jones 2004). Peak DMS/P concentrations over the FGB (2002-2003: $9.8\text{--}49.4\text{ nM}$) did not reach the levels found by Broadbent and Jones (2004), however, the FGB are offshore reefs with notably different current regimes and tidal influences: corals do not breach the sea-surface, and mucous ropes do not appear to get trapped and aggregated within the area. Also, due to our whole-water sampling technique, the DMS/P totals could be considered averaged whereas odor plumes tend to have a filamentous structure containing high-concentration eddies (reviewed by DeBose and Nevitt 2008). This means that organisms perceiving DMS/P on finer scales would sense a higher concentration than we could capture in our samples (see Moore and Crimaldi 2004). Though the mechanism of DMSP release is still largely unknown, the evidence presented here suggests that coral spawning behavior of an off-shore reef is directly associated with increases in DMS/P over the reef.

In summary, we found an increase in water column DMS/P associated with a coral spawning event in the northwestern Gulf of Mexico. This increase was correlated with changes in pelagic fish and squid abundance. Our observations suggest that a natural increase in DMS/P might serve as a cue for foraging and/or spawning of pelagic fishes and squid. This idea provides a specific, testable hypothesis for examining how the sensory ecology of marine fishes and squid may be responsive to chemicals that originate from

the behaviors of other species (i.e., coral spawning, zooplankton foraging). Still, our explorations into this area are only beginning (see DeBose and Nevitt 2007; DeBose et al. 2008), and future work is needed to investigate DMS and DMSP as signal molecules in the marine environment.

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