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Investigating the association between pelagic fish and dimethylsulfoniopropionate in a natural coral reef system

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Abstract. Dimethylsulfoniopropionate (DMSP) is a biogenic chemical produced by marine algae that is associated with areas of high primary and secondary productivity in the ocean. In laboratory experiments, DMSP has been shown to be an effective feeding attractant for a variety of fresh and saltwater fishes, suggesting that it might also function as a foraging cue in the natural environment. Here we explore whether free-roaming pelagic fishes associate with periodic elevations of DMSP in their natural foraging habitat. Working in the vicinity of the coral reefs of the Flower Garden Banks in the Gulf of Mexico, we found that daily changes in the number of pelagic jack fishes (Carangidae) were significantly correlated with natural changes in concentrations of DMSP in the water column. These results provide the first evidence of a correlation between variation in the number of pelagic fishes and a specific habitat-associated chemical cue in the ocean.

Introduction

Pelagic fishes often form large aggregations over coral reefs (Domeier and Colin 1997) and other productive areas (Taylor 1996; Gende and Sigler 2006; Zainuddin *et al*. 2006), but how these fish coordinate the location and timing of their aggregations is not understood. One possibility is that some pelagic fishes may recruit to chemical signatures associated with areas of high primary and secondary production. However, whether fish are attracted to or associate with such biogenic chemical cues typically associated with these areas is unknown.

Recently, Broadbent and Jones (2004) found high dimethylsulfoniopropionate (DMSP) concentrations in surface and sediment waters of coral reefs. DMSP is produced by species of phytoplankton (Keller *et al*. 1989), algal symbionts (Hill *et al*. 1995), and macroalgae (Dacey *et al*. 1994). DMSP can also be found in a variety of organisms including tropical reef invertebrates (Van Alstyne *et al*. 2006), copepods (Dacey and Wakeham 1986), krill, shrimp, shellfish and fish (Iida 1988; Dacey *et al*. 1994; Hill and Dacey 2006) that ingest DMSP-producing plankton and algae, or harbour algal symbionts, such as corals and cnidarians. Dissolved DMSP (DMSPd) commonly results from the release of DMSP as protozoans and other microzooplankton graze on marine algae (Simo 2004). Areas of the ocean with elevated productivity therefore may have high concentrations of both dissolved and particulate DMSP (Curran *et al*. 1998), which could provide a predictable cue for pelagic ranging fishes to locate productive marine areas.

Several characteristics of DMSP make it an especially promising candidate for a signal molecule in the marine environment (see Kiene *et al*. 2000; Zimmer and Butman 2000). DMSP generally persists longer in the ocean than many free amino acids, which are rapidly taken up by bacteria (Ledyard and Dacey 1996; Decho *et al*. 1998). Moreover, laboratory experiments already provide evidence that some fish species detect DMSP and respond to it as a foraging cue. For example, DMSP evokes electrical potentials from the olfactory tract of carp (*Cyprinus carpio*: Nakajima *et al*. 1989) and, in behavioural tests, stimulates increases in biting activity in goldfish (*Carassius auratus*: Nakajima *et al*. 1989), red sea bream (*Pagrus major*) and yellowtail (*Seriola quinqueradiata*: Nakajima *et al*. 1990). Here, we show pelagic fish counts (family Carangidae) increase with natural elevations in total DMSP over coral reefs in the Gulf of Mexico. The present study is the first to demonstrate an association between changes in carangid numbers and variation in a specific habitat-associated chemical in the ocean.

Materials and methods

Study site

The study was carried out at the Flower Garden Banks, ~200 km off the coasts of Texas and Louisiana (USA) in the Gulf of Mexico. The East and West Flower Garden Banks are formed from two upraised salt domes that peak at depths of 22–28 m and 21–27 m, respectively, and are surrounded by oligotrophic waters. A thriving coral community covers more than 50% of both banks (Rezak *et al*. 1985).

Seawater collection

Our goal was to sample total DMSP (DMSPt: dissolved + particulate) in the water column while simultaneously sampling the number of carangids in the area. We chose to measure DMSPt as opposed to DMSPd because we could sample it more accurately for year-to-year comparisons (Kiene and Slezak 2006). We also reasoned that DMSPd might underestimate the total pool

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of DMSP in the water column available as a cue for fishes, as DMSPd has been shown to be released rapidly and intermittently from the particulate DMSP pool (Ledyard and Dacey 1996). DMSPt was estimated using the methods of Kiene and Slezak (2006). Seawater samples were collected from July through August 2004 ($n = 10$) and June through August 2005 ($n = 14$) in Corning 50-mL plastic centrifuge tubes at a mid-water depth (~12 m), where we had previously found DMSPt concentrations to be highest (J. DeBose, unpubl. data). On each dive, we opportunistically collected samples from at least five locations. Collections were made from 5 m to 100 m apart over a 1.85 km^2 area spanning the two reefs of the Flower Garden Banks. On two different days, sea conditions prevented divers from entering the water, thus six samples were collected using a Niskin bottle dropped six times from the side of the ship. Although we did not conduct corresponding fish surveys on these two days, we included these water sample measurements in our analysis of variation in DMSPt; these extra samples help provide a more complete picture of how DMSPt varied temporally over the reef. To our knowledge, this type of temporal variation in DMSPt has not been studied previously in deep, oligotrophic reefs.

DMSP preservation and analysis

Once onboard the research vessel, DMSPt was immediately preserved in unfiltered water samples by adding 50% sulphuric acid (50 μL) to 10 mL of each sample (Kiene and Slezak 2006). Vials were quickly crimped with butyl rubber septa and aluminium caps, and stored in the dark.

Samples were analysed for DMSPt 1–2 months later (see Curran *et al*. 1998). After vortexing, 10 N NaOH (1 mL) was added to the sample (1 mL) to cleave DMS from DMSPt (Kiene and Slezak 2006). Vials were then stored in the dark for 24 h to allow the headspace to equilibrate. Headspace DMS was captured using a cryogenic-trapping method and analysed using a gas chromatograph. Measurements were calibrated using DMSP standards (Chemische Laboratoria, Netherlands) prepared identically to the samples (for methods, see Wolfe *et al*. 2000).

Fish surveys

Carangids were counted over the reef using a variation of the roving-diver method (Schmitt *et al*. 2002; average dive = 22.2 ± 1.1 min; total dive time = 8.5 h; 2004: $n = 10$; 2005: $n = 12$). This general method provided us with the best relative estimate of the number of carangid fishes on the reef for each day, because, like other pelagic fishes, carangids tend to be too transient to accurately sample using alternative approaches (e.g. stationary sampling or belt transects; see discussion in Schmitt *et al*. 2002). Two divers entered the water; one diver surveyed fish while the other diver collected water samples. To control for inter-observer reliability or other potential biases, the same two divers conducted surveys throughout the study; divers were likewise unaware of DMSPt concentration in the water column at the time that surveys were conducted. Carangids were identified to species (see Table 1) and numbers of individuals present per species group were counted in the mid-water column. Fish surveys were conducted at both banks and coincided with water collections when sea and weather conditions permitted.

Statistical analyses

We first examined whether DMSPt varied among sampling dates using a one-factor ANOVA (Zar 1996). Next, we examined whether there was a significant association between DMSPt and the total number of carangids observed during a dive by a single diver. For our correlation analysis, we only used DMSPt measurements which coincided with fish surveys ($n = 22$). We combined individual species counts into a 'total carangid count' because more than 50% of our observations were zero for individual species (Table 1), and species that were present tended to co-occur with other jack species in mixed-species groups. Because total carangid counts were distributed non-normally, we used non-parametric Spearman's Rho Correlation to test whether variation in total number of carangids was related to variation in DMSPt over the sampling dates. All tests were two-tailed and carried out using STATISTICA™ software (Statsoft® Inc., Tulsa, OK, USA).

Results

Mean daily DMSPt concentrations varied over sampling dates (ANOVA; 2004–2005: $F_{17,157} = 18.53$, $P < 0.001$). Mean daily DMSPt concentrations also varied within years (ANOVA; Fig. 1*a*, 2004: $F_{6,50} = 6.88$, $P < 0.001$; Fig. 1*b*, 2005: $F_{10,107} = 5.72$, $P < 0.001$) and were lower in 2004 than 2005 ($F_{1,173} = 164.51$, $P < 0.001$). There was no difference between the east and west banks (ANOVA; 2004–2005: $F_{1,173} = 1.04$, $P = 0.310$; 2004: $F_{1,55} = 0.51$, $P = 0.479$; 2005: $F_{1,116} = 1.18$, $P = 0.279$). Water temperatures were similar between years, ranging from 27.2°C to 29.4°C in 2004 and from 25.0°C to 30.0°C in 2005 at 12 m depth.

The number of carangids (Table 1) showed a significant positive relationship with mean daily DMSPt concentration when data from both years were considered together (Fig. 2*a*; Spearman Rho; $n = 22$, $r_s = 0.731$, $P < 0.001$). We found a positive association between carangid number and DMSPt concentration for the 2005 season (Fig. 2*b*, 2005: $n = 12$, $r_s = 0.706$, $P = 0.010$) but not the 2004 season (Fig. 2*c*, 2004: $n = 10$, $r_s = 0.050$, $P = 0.890$), when years were analysed independently.

Discussion

Here we provide evidence that changes in the numbers of transient carangid fishes over a coral reef mirror the variation in background DMSPt concentration. DMSP has been shown to be an effective feeding stimulant for some marine fishes, including one carangid species (yellowtail, *Seriola quinqueradiata*), and a potent olfactory stimulant in carp (*Cyprinus carpio*) (Nakajima 1996). Our data show that total DMSP in the water column over an isolated reef can vary considerably among days and between years, and provide new evidence that numbers of pelagic fishes correlate with these fluctuations in a natural reef system.

Carangids may use DMSP as a cue to locate productive areas for foraging. Carangids generally feed on smaller fish, shrimps, and other invertebrates (Böhlke and Chaplin 1993). DMSP is likely to be released when these prey species either forage (Hill and Dacey 2006) or are consumed by carangids or other predators (Iida 1988). DMSP may thus serve as an indicator of both elevated primary productivity and associated foraging

Table 1. Counts from fish surveys from the East and West Flower Garden Banks during the summers of 2004 and 2005

Year	Date	Bank	Carangid species						
			Seriola rivoliana Almaco jack	*Seriola dumerili* Greater amberjack	*Carangoides ruber* Bar jack	*Caranx lugubris* Black jack	*Caranx hippos* Crevalle jack	*Caranx latus* Horse-eye jack	*Elagatis bipinnulata* Rainbow runner
2004	21 Jul	West	0	1	0	0	72	53	0
	22 Jul	East	0	0	1	1	0	22	0
	29 Jul	West	0	0	2	0	0	1	0
		East	0	0	3	0	0	10	0
	2 Aug	West	0	0	0	1	0	1	0
		East	0	0	2	0	1	5	0
	6 Aug	West	0	0	0	0	0	2	0
	7 Aug	East	0	0	24	2	6	1	0
	8 Aug	East	0	0	3	6	0	0	0
	9 Aug	West	0	0	2	0	1	0	30
2005	6 Jun	West	0	2	2	3	203	6	0
	7 Jun	West	0	0	4	0	210	5	0
	8 Jun	East	0	0	4	11	140	2	0
	9 Jun	East	1	0	8	6	65	21	0
	26 Jul	West	0	0	30	0	0	0	0
	27 Jul	West	0	0	21	1	23	1	0
		East	0	0	115	2	0	50	0
	28 Jul	East	0	0	97	1	0	7	0
	24 Aug	East	0	0	41	1	0	1	0
	25 Aug	West	0	0	200	2	1	17	0
		East	0	0	102	0	1	3	0
	26 Aug	East	0	0	14	0	0	1	0

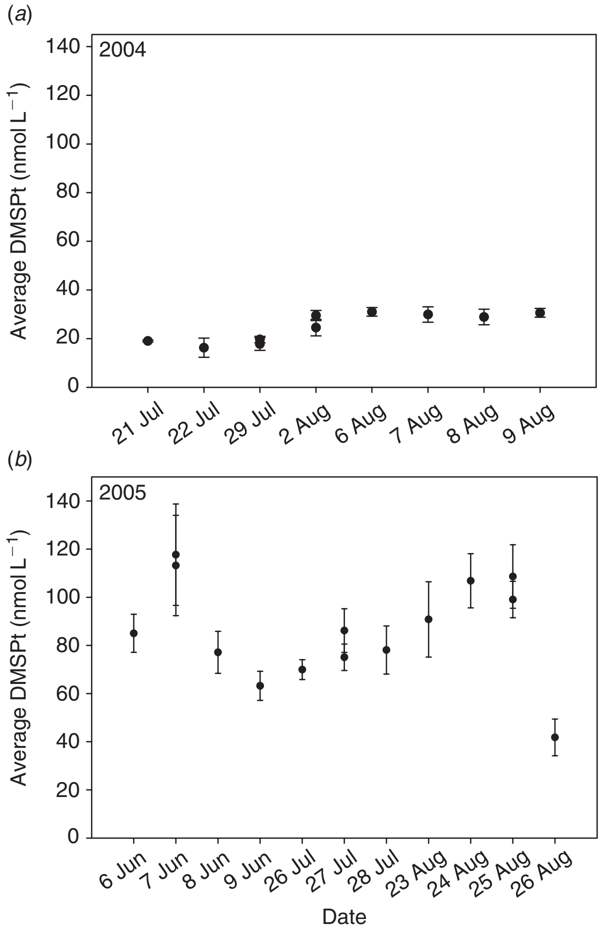

Fig. 1. Mean total dimethylsulfoniopropionate (DMSPt) concentration (nmol L^{-1}) varied significantly over the reefs during the summers of (*a*) 2004 and (*b*) 2005. Two means are shown for dates where water samples were collected from both the East and West Flower Garden Banks. Data are plotted as mean ± s.e.

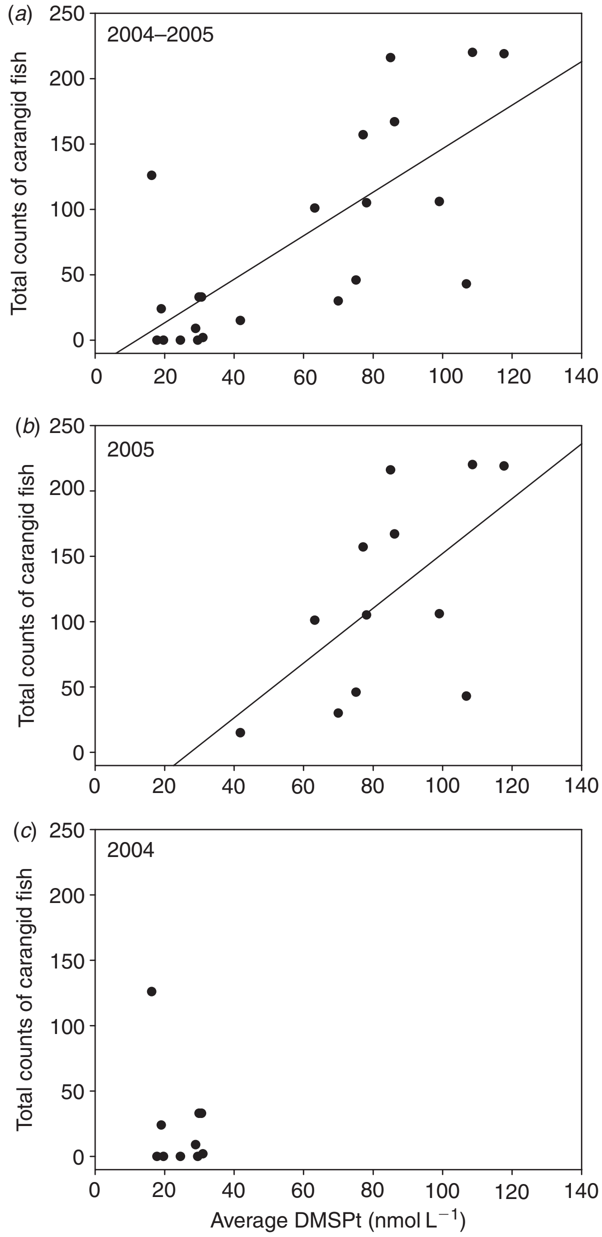

Fig. 2. Total counts of carangid fish correlated with mean total dimethylsulfoniopropionate (DMSPt) concentrations (nmol L^{-1}). (*a*) The relationship between numbers of individuals and DMSPt where data were combined for both years ($r_s = 0.731$). The relationship between carangid numbers and DMSPt during (*b*) 2005 ($r_s = 0.706$) and (*c*) 2004 ($r_s = 0.050$) respectively. Each point represents the total number of individuals observed per survey plotted against mean daily DMSPt concentration (nmol L^{-1}) at the survey site.

opportunities. In the present study, we found a significant association between carangids and DMSP when we considered data from either both years together or from 2005 alone. However, in 2004, the average daily DMSP concentrations were only 28% of 2005 levels, and similarly, average daily fish counts were just 19% of 2005 counts. Here we found no association between carangids and DMSP. Although other factors likely contribute to this lack of association, it is possible that DMSP concentrations were too low to cue pelagic fishes into the area during 2004.

In the present study, we specifically chose to test for an association between carangid fish and DMSPt because the connection between this potential cue (see Nakajima 1996) and primary and secondary production has been well established (see review by Simo 2004). Although zooplankton and phytoplankton release other potential feeding attractants or aggregation cues (e.g. dissolved organic carbon, nitrogen and free amino acids; see Steinke *et al.* 2002), these compounds are taken up more rapidly than DMSP by marine bacteria (Coffin 1989; Ledyard and Dacey 1996; Cherrier and Bauer 1998; Decho *et al.* 1998; Zimmer *et al.* 1999) and may be less persistent than DMSP in natural systems over the spatial and temporal scales pertinent to the present study (see Decho *et al.* 1998; Davis *et al.* 2006).

In summary, our data provide the first evidence for an association between pelagic fishes (carangids) and fluctuations in DMSP in a natural system. It is important to note, however, that these results are correlative, and further work is needed to establish whether carangid fishes are detecting DMSP and using it as an aggregation cue, or if they are using other compounds associated with elevations in DMSP, primary production or foraging activity (e.g. see Nevitt *et al*. 2004). Many species of pelagic fish aggregate at specific locations and times of year for foraging or spawning, but almost nothing is known about the sensory cues used to coordinate such behaviours. Given that we found a pattern of association between DMSP and pelagic fish, and no other environmental chemicals have been implicated thus far, our results identify DMSP as a potential signal molecule that needs to be further explored.

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