CHEMICAL ECOLOGY

Marine plastic debris emits a keystone infochemical for olfactory foraging seabirds

Matthew S. Savoca,[1,2]* Martha E. Wohlfeil,[1,2] Susan E. Ebeler,[3] Gabrielle A. Nevitt[1,2]*

Plastic debris is ingested by hundreds of species of organisms, from zooplankton to baleen whales, but how such a diversity of consumers can mistake plastic for their natural prey is largely unknown. The sensory mechanisms underlying plastic detection and consumption have rarely been examined within the context of sensory signals driving marine food web dynamics. We demonstrate experimentally that marine-seasoned microplastics produce a dimethyl sulfide (DMS) signature that is also a keystone odorant for natural trophic interactions. We further demonstrate a positive relationship between DMS responsiveness and plastic ingestion frequency using procellariiform seabirds as a model taxonomic group. Together, these results suggest that plastic debris emits the scent of a marine infochemical, creating an olfactory trap for susceptible marine wildlife.

INTRODUCTION

Trophic interactions in the pelagic marine environment are mediated, in part, by infochemicals, including dimethyl sulfide (DMS). DMS and its chemical precursor, dimethylsulfoniopropionate (DMSP), are ideal candidate molecules for this investigation in that they serve as infochemicals for microfauna to macrofauna in foraging cascades (*1*–*3*) and have also received considerable attention as a potential contributor to global climate regulation (*4*). In pelagic ecosystems, DMS is produced by the enzymatic breakdown of DMSP in marine phytoplankton, which increases during zooplankton grazing (*5*), thus triggering foraging activity in a variety of marine organisms, including tube-nosed seabirds (order: Procellariiformes) (*6*). The procellariiform seabirds include the albatrosses, petrels, and shearwaters; members of this order are highly olfactory, pelagic, and wide-ranging, foraging over vast expanses of open ocean (*7*). Results from controlled experimental studies performed at sea have demonstrated that some procellariiform species respond to DMS and use it as a cue to localize prey, whereas other species are more responsive to odors associated with higher trophic interactions (*6*, *8*–*10*). Recently, it has been further established that behavioral attraction to DMS is an adaptation for locating zooplankton grazers on phytoplankton (*2*), suggesting that DMS serves as a "keystone" infochemical in marine trophic interactions (*11*, *12*).

Plastic debris may provide a substrate for biota that produce infochemicals, such as DMS or DMSP, because floating plastic debris is known to be an excellent substrate for biofouling (*13*–*16*). If plastic floating on the ocean surface is easily fouled by DMS-producing biota, then plastic debris might also acquire a chemical profile that attracts DMS-responsive species, eventually leading them to consume it. To test this hypothesis, we examined whether preproduction plastic beads experimentally deployed within the photic zone acquire a biologically relevant DMS signature. We then investigated whether plastic ingestion can be explained by behavioral attraction to DMS using the procellariiform seabirds as a model group. We chose this group because species within this order are severely affected by plastic consumption (*17*–*20*), and sufficient data are already in place to test hypotheses about whether plastic ingestion may be linked to olfactory foraging across this phylogenetic group (*6*, *9*, *21*–*23*). Moreover, because DMS sensitivity is likely an ancestral trait that coevolved with burrow-nesting behavior (*24*), this relationship allows us to extend our hypothesis to test whether burrow-nesting procellariiforms have a higher incidence of plastic ingestion than surface-nesting species. Our final aim was to use the results of this mechanistic investigation to predict how different species are being negatively affected while accounting for unequal sampling effort to inform future monitoring and conservation efforts.

RESULTS

We first examined whether exposure to the photic zone changes the sulfur signature of plastic beads (diameter, 4 to 6 mm) made from the three most common types of microplastic and mesoplastic debris: high-density polyethylene (HDPE), low-density polyethylene (LDPE), and polypropylene (PP). These polymers are buoyant and make up more than 60% of global plastic production (*25*). We tested for a sulfur signature on clean beads that were never exposed to marine conditions (that is, virgin plastic; $n = 10$ for each plastic type) and also deployed replicate 3-g samples of microbeads contained in Nitex mesh bags ($n = 12$ bags of each plastic type) at two oceanographic buoys in the California current [Bodega Marine Laboratory (BML) and Hopkins Marine Station (HMS)] for approximately 3 weeks during the upwelling season (fig. S1). On dates when plastics were deployed at and retrieved from the buoys, we also collected replicate samples of seawater ($n = 20$ samples per site) within 10 m of the buoys. To measure headspace sulfur volatiles, we used solid-phase microextraction (SPME). After odor extraction via SPME, samples were manually injected into a gas chromatograph (GC) coupled to a sulfur chemiluminescence detector (SCD).

We did not find a DMS signature on any virgin plastic samples (Fig. 1A). In contrast, we detected DMS in the headspace of every plastic sample from both sites after marine exposure (concentration range, 0.6 to 28 μg of DMS per gram of plastic; Fig. 1B). These results confirm that three common varieties of plastic acquire a DMS signature after less than a month of marine exposure at concentrations that procellariiform seabirds can detect (*26*) (see figs. S2 and S3 for calibration curves).

DMS serves as a foraging cue for many pelagic marine organisms, including the highly olfactory procellariiform seabirds. Among procellariiform seabirds, a variety of experimental evidence suggests that DMS tracking is limited to a subset of species that specialize on phytoplankton grazers (for example, krill) (*2*) and that these seabird species also share certain life history traits, such as burrow-nesting (*24*). Behavioral detection

[1]Department of Neurobiology, Physiology, and Behavior, University of California, Davis, Davis, CA 95616, USA. [2]Graduate Group in Ecology, University of California, Davis, Davis, CA 95616, USA. [3]Department of Viticulture and Enology, University of California, Davis, Davis, CA 95616, USA.
*Corresponding author. Email: msavoca13@gmail.com (M.S.S.); ganevitt@ucdavis.edu (G.A.N.)

of DMS has been demonstrated to be as low as 10^{-12} M in laboratory studies, suggesting that these birds should be able to use natural biogenic emissions of DMS to locate zooplankton grazers (*27*). Therefore, we could use this species-specific response to test whether DMS behavioral sensitivity (that is, DMS responsiveness) can be used to predict plastic ingestion within the procellariiform order.

We analyzed plastic ingestion data from 55 studies that sampled a total of 13,350 individuals among 25 procellariiform species (fig. S4 and database S1). For our analyses, we used generalized linear mixed models (GLMMs) with a binomial distribution (binomial GLMMs) where the original sample size of each study was preserved to account for uneven sampling effort between species and between studies (*28*, *29*). We first used Akaike Information Criterion corrected for sample size (AIC_c) to rank models [see Materials and Methods (*30*)]. Models with DMS responsiveness as a predictor received >99% of the total AIC_c weight and offered the most explanatory power of any predictor we considered (see Materials and Methods and table S1). We next confirmed that DMS responsiveness had a significant effect on the frequency of plastic ingestion in the top-ranked model (binomial GLMM, $z_{1,139} = 3.891$, $P < 0.0001$; table S1). When we further examined the strength and direction of this effect while controlling for collection location and sampling effort (see Materials and Methods), we found that DMS responsiveness had a significant positive effect on the frequency of plastic ingestion (48.05% for DMS responders as compared to 7.52% for non–DMS responders; binomial GLMM, $z_{1,139} = 3.897$, $P < 0.0001$; Fig. 2A). We used "leave-one-out" cross-validation, which confirmed a high predictive performance of the model ($r = 0.86$, $r^2 = 0.73$; fig. S5).

Our next step was to use a Bayesian approach to generate predictions of plastic ingestion patterns to inform future research (see Materials and Methods). Parameter estimates were used to generate predictions for both group-level (DMS-responsive or non–DMS-responsive) and

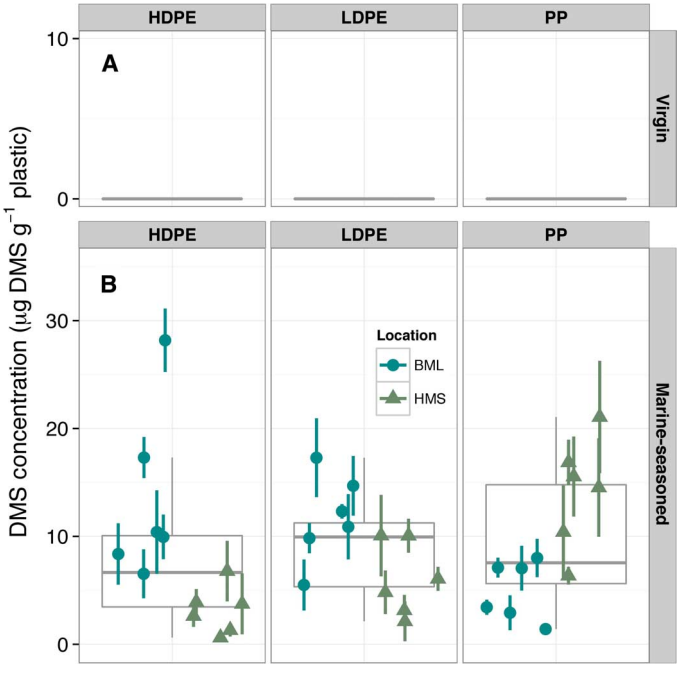

Fig. 1. DMS concentration in plastic debris headspace. (**A**) DMS was not detected on any of the virgin plastic samples tested ($n = 10$ samples each for HDPE, LDPE, and PP, $N = 30$ total). (**B**) DMS was detected on every plastic sample after marine exposure ($n = 12$ bags of each plastic type; each bag subsampled five times). Box plots illustrate DMS concentrations on marine-seasoned plastic of each plastic type across sites (HPDE = 8.31 ± 2.25 µg of DMS per gram of plastic; LDPE = 8.90 ± 1.34 µg of DMS per gram of plastic; PP = 9.56 ± 2.33 µg of DMS per gram of plastic). Points represent each bag's average DMS quantification; the error bars represent the SE of the five subsamples of each bag. Site averages by plastic type are as follows: for BML, $\overline{x}_{HDPE} = 13.45 \pm 2.41$ µg g^{-1}, $\overline{x}_{LDPE} = 11.76 \pm 1.65$ µg g^{-1}, and $\overline{x}_{PP} = 4.99 \pm 0.98$ µg g^{-1}; for HMS, $\overline{x}_{HDPE} = 3.16 \pm 1.07$ µg g^{-1}, $\overline{x}_{LDPE} = 6.05 \pm 1.39$ µg g^{-1}, and $\overline{x}_{PP} = 14.13 \pm 2.33$ µg g^{-1}.

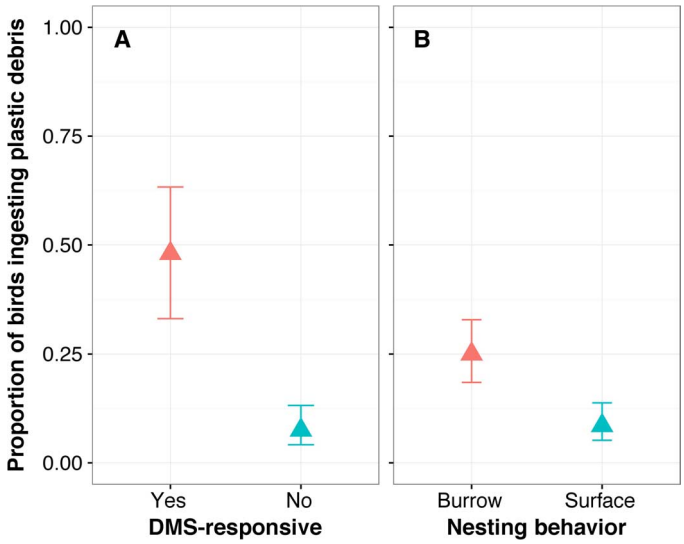

Fig. 2. Effects of DMS responsiveness and nesting behavior on plastic ingestion in procellariiform seabirds. (**A**) Maximum likelihood estimate (±SEM) of the DMS-responsive and non–DMS-responsive species groups, illustrating a significantly higher frequency of plastic debris ingestion in DMS-responsive species (binomial GLMM, $P < 0.0001$). (**B**) Maximum likelihood estimate (±SEM) of burrow- and surface-nesting species groups, illustrating a significantly higher frequency of plastic ingestion in burrow-nesting species (binomial GLMM, $P < 0.05$). Burrow-nesting behavior is used here as a proxy for DMS responsiveness.

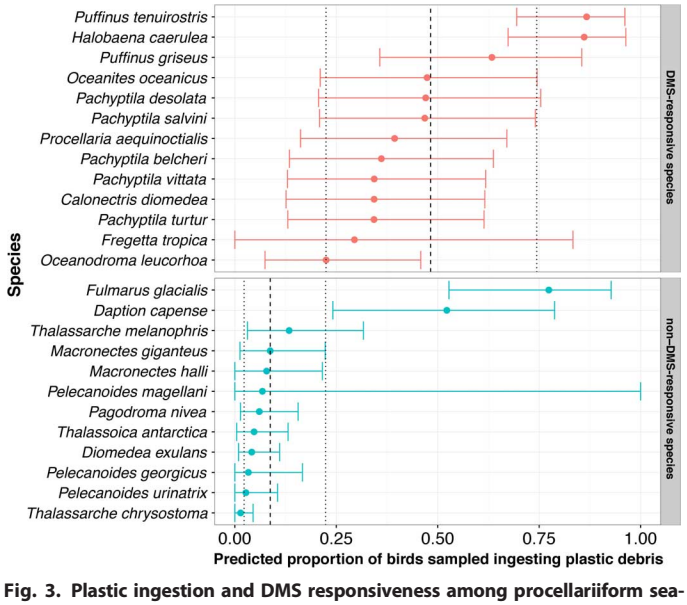

Fig. 3. Plastic ingestion and DMS responsiveness among procellariiform seabirds. Colored circles and horizontal lines represent the mean and 95% CIs for each species' model-predicted plastic ingestion prevalence. Vertical dashed lines are model-predicted mean plastic ingestion frequency for each group (DMS-responsive and non–DMS-responsive). Vertical dotted lines represent the 95% CIs of the plastic ingestion frequency for each group.

species-level plastic ingestion frequencies (Fig. 3). The group-level result suggests that DMS-responsive species ingest plastic five times as frequently as non–DMS-responsive species [48.40%; 95% confidence interval (CI), 23.04 to 74.51% versus 8.73%; 95% CI, 2.78 to 21.53%, respectively; Fig. 3].

We then extended our approach to examine our hypothesis on a much larger data set by using burrow-nesting behavior as a proxy for DMS responsiveness. This expanded our analysis to 20,852 individuals from 62 procellariiform species [fig. S6 and database S1; diving petrels (*Pelecanoides* sp.) were excluded from this analysis because they are the only burrow-nesting group that is not behaviorally responsive to DMS (*8*, *31*)].

Multimodel selection on this larger data set found that nesting behavior was the best predictor of plastic ingestion across the procellariiform order. To examine the effect of nesting behavior on plastic ingestion, we analyzed the top-ranked model (table S2). When controlling for sampling effort, the frequency of plastic ingestion in burrow-nesting species was 25.01%, compared to 8.56% for surface-nesting species (binomial GLMM, $z_{1,247} = -2.37$, $P < 0.05$; Fig. 2B). Assessment of the predictive performance of the model using leave-one-out cross-validation was $r = 0.86$ ($r^2 = 0.74$; fig. S7). To generate out-of-sample predictions, we used the same framework as that described for the DMS analysis. These findings suggest that burrow-nesting species ingest plastic nearly three times as frequently (25.64%; 95% CI, 13.49 to 41.19%) as surface-nesting species (9.20%; 95% CI, 3.58 to 18.26%) (Fig. 4).

DISCUSSION

We show first that three different types of plastic (HDPE, LDPE, and PP) take on the odor signature of DMS at concentrations of 10^{-5} to 10^{-8} M. This process can occur in less than 1 month of exposure at the offshore sites we tested (Fig. 1 and fig. S1). The DMS headspace concentrations we measured were higher than those that have been reported in association with frontal zones where DMS-responsive procellariiform species have been reported to aggregate (10^{-11} M) (*8*)

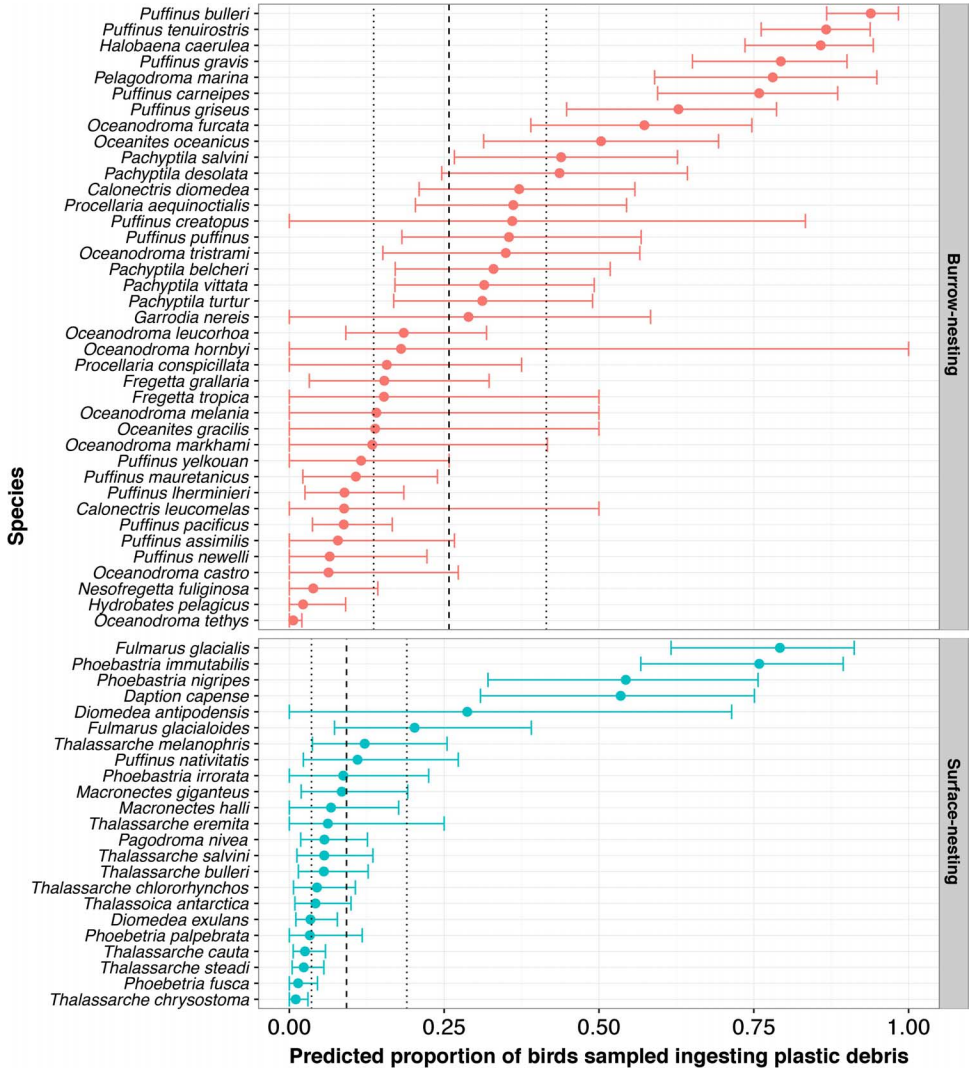

Fig. 4. Relationship of plastic ingestion and nesting behavior. Colored circles and horizontal lines represent the mean and 95% CIs for each species' model-predicted plastic ingestion frequency. Vertical dashed lines are model-predicted mean plastic ingestion frequency for each group (burrow- and surface-nesting). Vertical dotted lines represent the 95% CIs of the plastic ingestion frequency for each group.

and are at least four orders of magnitude above the behavioral detection threshold for Antarctic prions (*Pachyptila desolata*; 10^{-12} M) (*26*). The DMS concentrations we measured also overlap with values reported by classic laboratory studies that measured DMS emitted during phytoplankton grazing by zooplankton (10^{-7} to 10^{-9} M) (*5*). These laboratory measurements also served as a basis for identifying DMS as a keystone odorant in marine ecosystems (*3*, *11*).

We next demonstrate the idea that behavioral attraction to DMS is a strong predictor of plastic ingestion within the procellariiform seabirds ($n = 25$ species; Fig. 2A). This result is further supported in a more comprehensive analysis using burrow-nesting behavior as a proxy for DMS responsiveness ($n = 62$ species; Fig. 2B). Although it is frequently assumed that marine organisms consume plastic debris because it is visually mistaken for prey (*18*, *19*, *32*, *33*), our results suggest that chemical cues may also be mediating this maladaptive foraging behavior. The implication is that the odor signature plastic debris acquires in the photic zone hijacks a foraging response to a keystone marine infochemical. Thus, in addition to presenting a visual stimulus, our results provide evidence that marine plastic also presents an olfactory stimulus for species that have evolved to use DMS as a foraging cue. Our results (Figs. 3 and 4) suggest that many species that are predicted to be most vulnerable to this sensory trap may be overlooked and understudied in this regard.

DMS attraction is highly correlated to those species with diets rich in pelagic crustaceans (for example, krill), suggesting that behavioral sensitivity to DMS is an adaptation for locating nutrient-rich prey patches (*2*). This relationship presents the interesting possibility that the presence of a keystone infochemical on biofouled plastic may, in some cases, enhance attraction to an otherwise lower-quality foraging patch, creating an olfactory trap. This situation may be particularly problematic for species [such as prions (*Pachyptila* sp.)] that are highly sensitive to DMS and forage primarily by straining water through modified lamellae rather than by visual detection of individual prey items (*34*). Our analysis further indicates that some of the most affected species (for example, *Puffinus griseus* and *Puffinus tenuirostris*) migrate between the Southern Hemisphere and the Northern Hemisphere on a semiannual basis, suggesting that movement patterns may encourage contact with plastic debris on a global rather than a strictly regional basis.

Plastic debris has been found in pelagic environments worldwide (*35*, *36*) and is rapidly increasing in marine ecosystems (*37*). As of 2014, a global analysis reported a quarter of a billion metric tons of plastic suspended in the global oceans (*36*). More than 200 species of marine fish (*38*–*40*), marine mammals (*41*, *42*), sea turtles (*43*, *44*), and seabirds (*18*–*20*) have been found to consume plastic at sea. Seabirds are especially at risk; a recent projection model concluded that greater than 99% of all seabird ($n > 300$) species will have ingested plastic debris by 2050 (*17*). The negative consequences of plastic ingestion have received considerable study and range from physical obstruction to chemical toxicity (*45*–*48*).

Therefore, elucidating the mechanisms that drive plastic consumption by marine fauna is urgently needed to help direct mitigation efforts. With limited resources, studies of plastic ingestion routinely focus on those species that are most common, charismatic, or frequently monitored because of interactions with fisheries. In contrast, our analysis incorporates plastic debris into the marine food web, suggests that procellariiform species that are adapted to locate prey by tracking DMS might be especially predisposed to consume plastic debris, and points to the need for a more focused monitoring effort informed by sensory foraging theory.

Globally, DMS and DMSP have been implicated as infochemicals across a wide range of marine biota, from zooplankton (*1*) to baleen whales (*49*). The explanation we provide for plastic ingestion patterns seen in procellariiform seabirds should be explored in other groups, including sea turtles (*50*), penguins (*51*), various species of marine fishes (*52*, *53*), and even marine mammals (*54*), all of which have been shown to either detect or use these compounds in foraging contexts. Our results propose a novel mechanism for why plastic ingestion is becoming so prevalent among marine fauna and point to remediation strategies (including increasing antifouling properties of consumer plastics and using sensory ecology to identify at-risk species) that may aid future mitigation efforts.

MATERIALS AND METHODS

Field methods

Preproduction plastic beads of HDPE, LDPE, and PP (hereafter beads), 4 to 6 mm in diameter, were donated by SABIC Innovative Plastics (Saudi Basic Industries Corp.). Plastic beads (3 g) of each plastic type (HDPE, LDPE, and PP) were separately enclosed inside Nitex bags (1020-μm mesh size). Nine such Nitex bags (three of each plastic type) were zip-tied to a PP rope. We made four ropes, two for each of the two deployment sites, each with nine Nitex bags (each bag containing one type of plastic bead for ocean deployment). The ropes ($n = 2$ ropes per site, $n = 18$ Nitex bags per site; fig. S1) were attached to an oceanographic monitoring buoy located approximately 1 km offshore at two locations along the central California coast (fig. S1). One buoy was in the Bodega Marine Reserve maintained by the University of California's BML (38°18′58″N 123°04′29″W). The other buoy was in the Monterey Bay National Marine Sanctuary, maintained by the Monterey Bay Aquarium Research Institute, located offshore from the HMS of Stanford University (36°37′19″N 121°54′06″W).

Beads were deployed for 19 to 21 days (19 days at BML: 24 April 2014 to 13 May 2014; 21 days at HMS: 14 May 2014 to 4 June 2014). The beads from each bag were subsampled by weight into five 10-ml silanized headspace vials (Restek Co.) and sealed with a polytetrafluoroethylene (PTFE; Teflon) septum screw cap (18 mm thread; Restek Co.). Each vial was then wrapped externally in Parafilm M (Bemis Co. Inc.) to prevent gas exchange and stored frozen (−20°C) until analysis.

To check whether local seawater did not contain unusually high levels of DMS-producing algal or bacterial cells that might have affected our results, seawater samples were collected within 10 m of the buoys at the same time that beads were deployed (BML: 24 April 2014; HMS: 14 May 2014) and retrieved (BML: 13 May 2014; HMS: 4 June 2014) from the ocean. Surface seawater was collected in two 1-liter glass bottles that were washed three times with 95% ethanol and rinsed with ultrapure water (type 1, EMD Millipore) subsampled into 1-ml samples in 10-ml silanized headspace vials, sealed with an 18-mm-thread screw cap with a PTFE septum, wrapped externally in Parafilm M to prevent exchange, and stored frozen (−20°C) until analysis.

Analytical chemistry procedures

SPME description.

SPME was used for odor extractions using a 50/30-μm Divinylbenzene/Carboxen/Polydimethylsiloxane-coated fiber (Sigma-Aldrich). SPME has been shown to be an ideal method to sample volatiles from a polymer matrix (*55*). Fibers were conditioned according to the manufacturer's instruction before use.

GC-SCD methods.

After odor extraction, the SPME fiber was manually injected into a 5890 Hewlett Packard GC (Hewlett Packard/Agilent), equipped with a J&W

GS-GasPro PLOT (60 m × 0.32 mm) column (Agilent), connected to a Sievers 355 SCD (Agilent). The GC was set for splitless injection, with an inlet temperature of 250°C and using a deactivated glass SPME injection liner (Sigma-Aldrich) with a diameter of 0.7 mm. The split flow was opened at 3 min following the injection and closed again at 13 min after injection. The carrier gas was helium at a volumetric flow of 2.8 ml min^{-1} with a constant column head pressure of 20 psi (~140 kPa). The oven temperature program started with an initial setting of 40°C followed by an immediate ramp of 10°C min^{-1} to 260°C, followed by a hold of 3 min. The SCD burner temperature was 800°C with a hydrogen flow rate of 100 ml min^{-1} and an air flow rate of 40 ml min^{-1}. The SCD pressure was 6 torr, with the controller at 190 torr. The SPME fiber was left in the inlet for at least 10 min, retrieved, and exposed to the headspace of the following sample. These methods were adapted from previous studies of sulfur headspace compounds in food products (*56*, *57*).

Solution procedures.

To quantify the concentration of DMS in our plastic and seawater samples, we used ≥99% anhydrous diethyl sulfide (DES; Sigma-Aldrich) to generate an internal calibration standard. We performed a two-step serial dilution of DES to achieve a standard solution with a concentration of 10 parts per million (ppm) DES by volume (μl $liter^{-1}$). First, we made a 1:100 dilution of neat DES in anhydrous (200 proof) ethanol (EtOH; Koptec) to yield a solution with a concentration of 1×10^4 μl of DES per liter. Ethanol was chosen as a solvent for the first dilution because DES is more soluble in EtOH than in water. Then, we made a 1:1000 dilution in ultrapure water of the first dilution to create a solution with a concentration of 10 μl of DES per liter. Corrected for the density of DES (0.837 g ml^{-1}), this solution has a DES concentration of 8.37 mg $liter^{-1}$.

Similarly, for DMS, our analyte of interest, we performed two-step serial dilutions of ≥99% anhydrous DMS (Sigma-Aldrich) to achieve a standard solution with a concentration of 10 ppm (μl $liter^{-1}$) DMS by volume. First, we made a 1:100 dilution of neat DMS in anhydrous EtOH to yield 1×10^4 μl of DMS per liter of solution. Ethanol was chosen as a solvent for the first dilution because DMS is more soluble in EtOH than in water. Then, we made a 1:1000 dilution in ultrapure water of the first dilution to create a solution with a concentration of 10 μl of DMS per liter. Corrected for the density of DMS (0.846 g ml^{-1}), this has a DMS concentration of 8.46 mg $liter^{-1}$.

DMS standard solutions of differing concentrations were created via the same serial dilution method (varying the dilution in the second step according to the final DMS concentration desired) used to create the DES dilutions described above. The final concentration of a solution of DMS (10 μl $liter^{-1}$) is slightly different from the same concentration by volume of DES because of the difference in density between DES and DMS.

External calibration curve procedures.

To obtain the most accurate quantitative estimate of DMS dissipating from the bead samples, we generated two different external calibration curves. The first calibration curve was generated with lower concentrations of DMS (fig. S2A). We added 10 μl of DMS (Sigma-Aldrich) at one of five known concentrations—1, 2, 5, 10, and 20 μl $liter^{-1}$ (corresponding concentrations corrected for density: 0.85, 1.69, 4.23, 8.46, and 16.92 mg $liter^{-1}$)—to 0.5 g of clean beads contained in a headspace vial. We also added 10 μl of DES solution (10 μl $liter^{-1}$) (corresponding concentration corrected for density: 8.37 mg $liter^{-1}$) as an internal calibration standard. The second calibration curve was generated with higher concentrations of DMS (fig. S2B). We added 10 μl of DMS at one of six known concentrations—5, 10, 100, 200, 400, and 800 μl $liter^{-1}$ (corresponding concentrations corrected for density: 4.23, 8.46, 84.60, 169.20, 338.40, and 676.80 mg $liter^{-1}$)—to 0.5 g of clean beads contained in a headspace vial. We also added 10 μl of DES (10 μl $liter^{-1}$) (corresponding concentration corrected for density: 8.37 mg $liter^{-1}$) solution as an internal calibration standard. We chose this DMS concentration range because it encompasses the typical DMS concentrations we expected from our samples based on preliminary trials from summer 2013. Each DMS concentration was replicated four times to verify the precision of the GC-SCD.

Using peak area ratio calculations (DMS-integrated peak area/DES-integrated peak area) from these standard runs, we were able to generate a linear regression model with which unknown DMS concentrations from our plastic samples could be estimated from the formula of the regression line (fig. S2).

To produce an external calibration curve for seawater, we needed to use a matrix that closely resembled our seawater samples. To do so, we obtained filtered (25-μm filter size) seawater from BML. To ensure that all biological activity that might produce a DMS signature was eliminated, the seawater was heated to 60°C, well above the boiling point of DMS (35°C), in a precision economy oven (Thermo Fisher Scientific Inc.) for 12 hours. We then analyzed six samples of that water and confirmed that there was no detectable DMS in its headspace.

Because we expected the DMS in the headspace of a seawater sample to be at extremely low concentrations, we needed to determine the GC-SCD's sensitivity thresholds to DMS. A 3:1 signal-to-noise ratio was deemed to be the GC-SCD's limit of detection (LOD), whereas a 6:1 signal-to-noise ratio was considered to be the limit of quantitation (LOQ). Through repeated trials, we determined that the instrument's LOD for DMS in a seawater matrix was 0.5 μl $liter^{-1}$ (4.23 ng of DMS per gram of seawater; maximum concentration in headspace, 7×10^{-10} M), with an LOQ of 0.75 μl $liter^{-1}$ (5.29 ng of DMS per gram of seawater; maximum concentration in headspace, 1×10^{-9} M).

To create a standard curve, we added 10 μl of DMS at one of four known concentrations—0.75, 1, 2.5, and 5 μl $liter^{-1}$ (corresponding concentrations corrected for density: 0.423, 0.529, 0.846, 2.115, and 4.230 mg $liter^{-1}$)—to 1 g of seawater contained in a headspace vial. We also added 10 μl of solution of DES (10 μl $liter^{-1}$) (corresponding concentration corrected for density: 8.37 mg $liter^{-1}$) as an internal calibration standard. Each DMS concentration was measured no fewer than six times to verify the repeatability of the GC-SCD measurement. Using peak area ratio calculations from these standard runs of varying DMS concentrations while holding the internal calibration standard (DES) constant, we were able to generate a linear regression model with which unknown DMS concentrations from our seawater samples could be estimated from the formula of our regression line (fig. S3).

Plastic and seawater sample GC-SCD procedures.

We used GC-SCD to analyze 10 virgin samples of each plastic type (PP, HDPE, and LDPE) to confirm that there were no sulfur-based compounds in the headspace of the plastic beads before marine exposure. We placed 0.5 g of HDPE, LDPE, or PP beads in a 10-ml silanized headspace vial (Restek Co.) with 10 μl of 10 ppm DES solution (internal standard) and sampled volatiles for 30 min at room temperature (20°C).

On the day of analysis, a bead or seawater sample was removed from the freezer and allowed to thaw for 30 min. This allowed the sample to reach a temperature of 12° ± 5°C, approximately the temperature of the water at the time the beads were floating in the ocean (fig. S8). Then, 10 μl of 10 ppm DES solution (internal standard) was added to each sample. An additional 30 min was given to allow for volatile compounds to come to equilibrium within the headspace vial. Then, the SPME fiber

was injected into the closed 10-ml vial through the PTFE septa, and volatiles were extracted for 30 min at 15°C. Finally, the SPME fiber was removed from the headspace vial and manually injected into the GC-SCD.

Statistical analyses and results of plastic sulfur chemistry

To determine whether there was a significant difference in the DMS signature from the beads of different plastic types or at different sites, we ran GLMMs and performed analyses of variance (ANOVAs) on the fit models. To fit the GLMMs, we used the package nlme in R version 3.1. Our sampling unit was the bag of plastic beads ($N = 36$ total, $n = 18$ per site). The response variable for each bag was the average headspace concentration of DMS measured from the five subsamples within each bag ($N = 180$ samples total, $n = 60$ each for HDPE, LPDE, and PP). The DMS headspace concentration was reported as micrograms of DMS per gram of plastic.

For our exploratory model, the main effect predictors were plastic type (HDPE, LDPE, and PP), site (BML and HMS), an interactive effect of plastic type by site, and a nested effect of bag, within rope, within site. This nested effect was included to test for systematic differences between the two ropes at each site. If the nested effect was significant, then it would be included as a random effect in the final model.

After evaluating the factorial ANOVA, we ran a Tukey's post hoc test to investigate differences between groups. This analysis showed that there was a difference in DMS response between ropes at the BML site; thus, the final model included plastic type, site, an interactive effect of plastic type by site, and the random nested effect of bag, within rope, within site.

At the HMS site, PP exhibited a significantly higher DMS concentration than HDPE (Tukey's post hoc test, $P < 0.01$) and LDPE, although this difference was not significant (Tukey's post hoc test, $P = 0.06$). However, at the BML site, PP exhibited significantly lower DMS concentrations than HDPE (Tukey's post hoc test, $P = 0.04$).

DMS was only detectable in seawater samples in one instance (at HMS on 4 June 2014; 12.95 ± 1.60 ng of DMS per gram of seawater; $n = 10$). Headspace concentrations of DMS from all other seawater samples analyzed ($n = 30$) were below our instrument's LOQ. These DMS concentrations associated with seawater samples were one to three orders of magnitude lower than the DMS concentrations from every marine-seasoned plastic sample analyzed (Fisher's exact test, $P < 0.0001$).

Seabird plastic ingestion analyses

Plastic ingestion database.

We used Web of Science to search the scientific literature for publications from 1960 to 2014 using the keywords "procellariiform," "plastic," and "ingestion" found anywhere in the publication. We retained publications that reported original plastic ingestion data and any referenced publications. We did not include gadfly petrels (*Pterodroma* spp.) in our analysis because of insufficient behavioral and plastic ingestion data available for this clade. This resulted in a total of 73 studies containing data on 20,922 individuals representing 65 procellariiform species (database S1). Although probably not exhaustive, we believe to have collected most of the studies documenting plastic ingestion in procellariiform seabird species.

Statistical methods.

To analyze the effect of DMS responsiveness on plastic ingestion, we filtered our database to include only species groups where DMS responsiveness has been tested experimentally (*6*, *26*, *58*–*60*). Applying this filter left a total of 55 studies containing data on 13,350 individuals representing 25 procellariiform species. There were plastic ingestion records for 13 species of DMS-responsive procellariiform species (8485 total individuals) and 12 non–DMS-responsive procellariiform species (4865 total individuals). To examine the effect of nesting behavior on plastic ingestion, we analyzed the entire database excluding only diving petrels (*Pelecanoides* sp.) because diving petrels are burrow-nesting but not DMS-responsive (*8*, *31*). The resulting data set contained data from 73 studies, which included 20,852 individuals from 62 procellariiform species. There were ingestion records for 39 burrow-nesting procellariiform species (8157 total individuals) and 23 surface-nesting procellariiform species (12,695 total individuals).

For the analyses of DMS responsiveness and nesting behavior on plastic ingestion, all individuals of the same species within the same study were combined for analysis. Frequency of occurrence (FO) of plastic ingestion was reported for every study; therefore, the response variable for all analyses was FO of plastic ingestion (n ingesting plastic debris/total N studied) for each species within each study. Candidate models were GLMMs with a binomial distribution where the response variable's sample size is preserved. We performed multimodel selection using AIC_c to rank models (*30*). Our model set included models with every additive combination of DMS responsiveness, collection location [wrecked (that is, dead or moribund) on beach, sampled at sea, and sampled at breeding colony], breeding phenology (breeding versus nonbreeding), study region (Arctic, North Pacific, South Pacific, Equatorial Pacific, North Atlantic, South Atlantic, Equatorial Atlantic, Indian, and Southern oceans), and decade of study (1960s, 1970s, 1980s, 1990s, 2000s, and 2010s) as main effect predictor variables. This design allowed us to determine whether there were other ecologically relevant predictors that could explain the variability in the data better than DMS responsiveness. Other studies have shown that plastic ingestion within seabirds is correlated to capture strategy (termed "foraging behavior," for example, pursuit diving, surface seizing, etc.) and "diet" (*18*). We did not include these predictors in our analyses because capture strategy does not align with "species" among seabirds (*61*), and we have previously demonstrated that DMS tracking is an adaptation for foraging on crustaceans (*2*). Consequently, "DMS responsiveness" and "diet" are highly correlated and cannot be disentangled in our model.

Further, to account for uneven sampling effort, we included "species" and "study" as random effects. To control for the effect of phylogeny on the response variable, we also included a set of models with "family" as a random effect. To test for the effect of nesting behavior on plastic ingestion prevalence, we used the same procedure described above, except here, we replaced "DMS responsiveness" with "nesting behavior." We also removed "family" as a random effect because of issues of multicollinearity with nesting behavior. All models were analyzed using package lme4 in R version 3.1. The full model included DMS responsiveness (species level binary: yes or no), collection location, breeding status, study region, and decade of study as main effects. Random effects, controlling for phylogeny and unbalanced sampling effort by species and study, were also included.

Of the 14 models that received AIC_c weight, 13 contained DMS responsiveness as a significant predictor of plastic ingestion. Even more powerfully, these 13 models received >99% of total AIC_c weight (table S1). To examine the sole effect of DMS responsiveness on plastic ingestion, we used the top-ranked model and removed "collection location" as a main effect predictor while retaining it as a random effect. We then preformed a second multimodel selection between this model and a "control" null model. The model that included DMS responsiveness as a

predictor received 99% of AIC_c support (table S3). To derive Bayesian predictions from the model with DMS responsiveness as a predictor, we generated 10,000 sample parameters from the posterior of the model using a random binomial distribution, which accounts not only for the mean and variance of the parameters but also for sample size differences in the observed data. This Bayesian framework allowed us to account for uncertainty in parameter estimates and covariance among parameters (*29*). These parameter estimates were then used to generate predictions for both group-level (DMS-responsive or non–DMS-responsive) and species-level plastic ingestion occurrence.

For the analysis of the effect of nesting behavior on plastic ingestion, we used burrow-nesting behavior as a proxy for DMS responsiveness (*24*). In this more comprehensive analysis, 13 of the 19 models that received AIC_c weight contained "nesting behavior" as a predictor of plastic ingestion (table S2). These 13 models received 84% of total AIC_c weight (table S2). The top model included only "nesting behavior" as a significant main effect and "species" and "study" as random effects (table S2).

Here, again, we performed a second multimodel selection between the top model and a "control" null model. The model that included "nesting behavior" as a predictor received 82% of AIC_c weight as compared to only 18% support for the null model (table S4). Using the same methods described above, parameter estimates from the model that included "nesting behavior" were then used to generate predictions for both group-level (burrow- or surface-nesting) and species-level plastic ingestion prevalence.

To assess model performance, we conducted leave-one-out cross-validation (*62*). In this method, the data set was iteratively spilt into "1 to $n - 1$" observations, holding back one observation and generating a prediction for the omitted observation based on the "1 to $n - 1$" data set. Once an independent prediction has been made for the iteratively omitted observation, the predicted versus observed values are compared using Spearman's correlation coefficient (r).

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/2/11/e1600395/DC1

fig. S1. Field sites and experimental design for plastic deployments.
fig. S2. DMS standard curves with a plastic bead matrix.
fig. S3. DMS standard curves with a seawater matrix.
fig. S4. Plastic ingestion and DMS responsiveness among procellariiform species in the database.
fig. S5. Cross-validation results for the DMS responsiveness model.
fig. S6. Plastic ingestion and nesting behavior among procellariiform species in the database.
fig. S7. Cross-validation results for the nesting behavior model.
fig. S8. Data from oceanographic monitoring buoys.
table S1. Model selection table for the plastic ingestion meta-analysis in relation to DMS responsiveness.
table S2. Model selection table for the plastic ingestion meta-analysis in relation to nesting behavior.
table S3. Model selection table testing only DMS responsiveness as predictor against the null model.
table S4. Model selection table testing only nesting behavior as predictor against the null model.
database S1. Procellariiform plastic ingestion database (.xlsx).

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Acknowledgments: We are indebted to K. Van Alstyne for conducting preliminary experiments to establish feasibility at the Shannon Point Marine Center of Western Washington University. We thank G. Susner and D. Dann of the BML and K. Nickols and P. Leary at HMS for technical support, G. Humphries for assistance with fig. S1, N. Willits and G. Humphries for statistical consultation, and M. Losekoot for editorial assistance. We also appreciate comments from two anonymous reviewers; their feedback improved the manuscript. **Funding:** This work was supported by the University of California, Davis (CA-D-NPB-3509-H to G.A.N.) and the NSF (GRF 1148897 to M.S.S. and PLR 1142084 to G.A.N.).
Author contributions: M.S.S. conceived and designed the study, compiled and analyzed data, interpreted results, and drafted the manuscript. M.E.W. compiled and analyzed data and edited the manuscript. S.E.E. analyzed and interpreted chemical data and edited the manuscript. G.A.N. conceived and designed the study, interpreted data, and helped write the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 23 February 2016
Accepted 6 October 2016
Published 9 November 2016
10.1126/sciadv.1600395

Citation: M. S. Savoca, M. E. Wohlfeil, S. E. Ebeler, G. A. Nevitt, Marine plastic debris emits a keystone infochemical for olfactory foraging seabirds. *Sci. Adv.* **2**, e1600395 (2016).

ScienceAdvances

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Matthew S. Savoca, Martha E. Wohlfeil, Susan E. Ebeler and Gabrielle A. Nevitt

Sci Adv **2** (11), e1600395.
DOI: 10.1126/sciadv.1600395