

RESEARCH ARTICLE

Olfactory foraging in temperate waters: sensitivity to dimethylsulphide of shearwaters in the Atlantic Ocean and Mediterranean Sea

Gaia Dell'Arciccia^{1,*}, Aurélie Célérier¹, Marianne Gabriot¹, Pauline Palmas¹, Bruno Massa² and Francesco Bonadonna¹

ABSTRACT

Many procellariiforms use olfactory cues to locate food patches over the seemingly featureless ocean surface. In particular, some of them are able to detect and are attracted by dimethylsulphide (DMS), a volatile compound naturally occurring over worldwide oceans in correspondence with productive feeding areas. However, current knowledge is restricted to sub-Antarctic species and to only one study realized under natural conditions at sea. Here, for the first time, we investigated the response to DMS in parallel in two different environments in temperate waters, the Atlantic Ocean and the Mediterranean Sea, employing Cory's (*Calonectris borealis*) and Scopoli's (*Calonectris diomedea*) shearwaters as models. To test whether these birds can detect and respond to DMS, we presented them with this substance in a Y-maze. Then, to determine whether they use this molecule in natural conditions, we tested the response to DMS at sea. The number of birds that chose DMS in the Y-maze and that were recruited at DMS-scented slicks at sea suggests that these shearwaters are attracted to DMS in both non-foraging and natural contexts. Our findings show that the use of DMS as a foraging cue may be a strategy adopted by procellariiforms across oceans but that regional differences may exist, giving a worldwide perspective to previous hypotheses concerning the use of DMS as a chemical cue.

KEY WORDS: DMS, Foraging, Odour cues, Olfaction, Petrels, Procellariiform seabirds

INTRODUCTION

The first report of olfactory guidance in procellariiform foraging is more than a century old. In 1882, Collins reported that storm petrels and shearwaters were attracted by cod liver at sea under conditions of dense fog and 'when not a bird of any kind had been seen for hours'. Subsequent controlled observations and more extensive studies under natural conditions at sea provided support for Collins' and other early field reports, confirming the attraction of procellariiforms to different odours directly linked to food, such as cod liver oil, krill and squid homogenates (Grubb, 1972; Hutchison and Wenzel, 1980; Hutchison et al., 1984; Jouventin and Robin, 1984; Lequette et al., 1989; Nevitt, 1999b; Nevitt et al., 2004; Verheyden and Jouventin, 1994). The use of olfaction to locate food has also been revealed in terrestrial environments by turkey vultures, kiwis, magpies and honeyguides (Buitron and Nuechterlein, 1985;

Stager, 1964; Stager, 1967; Wenzel, 1971). More generally, odours are an essential component of navigation over land in homing pigeons, starlings, swifts and catbirds (Fiaschi et al., 1974; Holland et al., 2009; Papi, 1989; Wallraff et al., 1995). Very recently, the 'olfactory spatial' hypothesis has been proposed, which states that the primary function of olfaction in animals is navigation. According to this hypothesis, decoding and mapping patterns of odorants in the environment maximizes fitness by allowing animals to acquire resources and avoid competition and predation (Jacobs, 2012).

In 1995, Nevitt and collaborators (Nevitt et al., 1995) revealed that dimethylsulphide (DMS), a volatile compound that occurs naturally in worldwide oceans, is a strong attractant for some Antarctic procellariiforms at sea, making it the perfect candidate olfactory cue for locating foraging grounds and for navigation. DMS is a by-product of the metabolic decomposition of dimethylsulphoniopropionate (DMSP), produced during phytoplankton grazing; its production is often associated with zooplankton feeding and areas with high primary productivity, i.e. high phytoplankton concentration (Cantin et al., 1996; Dacey and Wakeham, 1986; Jean et al., 2009; Simó, 2001). DMSP may be a particularly strong source of chemical signal for zooplankton predators, and *in situ* observations indicate that schools of small fish aggregate along the periphery of plankton blooming areas (DeBose et al., 2008; DeBose and Nevitt, 2007). Eventually, local elevation in DMS on the sea surface may, opportunistically, alert higher order predators of rapidly accumulating aggregations of zooplankton and zooplankton predators, i.e. fish and squid that are among the main prey for many petrel species (del Hoyo et al., 1992; Hay and Kubanek, 2002; Warham, 1996). Indeed, satellite telemetry revealed an association between areas with high DMS emissions, prey aggregations and foraging grounds of different petrel species in the Antarctic and sub-Antarctic region (reviewed by Nevitt, 2000).

Following the identification of DMS as an attractant and possible chemical cue (Nevitt et al., 1995), the sensitivity to this odorant has been evidenced for a number of petrel and non-petrel species of the Southern oceans through physiological and behavioural tests carried out at the colony (Bonadonna et al., 2006; Cunningham et al., 2008; Nevitt and Bonadonna, 2005b). No other tests, however, were performed under natural conditions at sea, except for one study on African penguins (Wright et al., 2011), nor under different ecological conditions. With the aim of drawing attention to the current state of knowledge, Table 1 reviews all studies performed, to date, testing the response to different odours linked to foraging. It details the odorants tested, the species attracted and not attracted to these cues, the experimental conditions and the location of testing. The table emphasizes that not all species are equally sensitive to all odorants, and species responding to one odorant do not necessarily respond to another. For example, prions (*Pachyptila* spp.) did not

¹CEFE-CNRS, Behavioural Ecology Group – 1919, Route de Mende, 34293 Montpellier, France. ²Department of Agricultural and Forest Sciences, University of Palermo, Viale delle Scienze, 90128 Palermo, Italy.

*Author for correspondence (gaiadellarciccia@gmail.com)

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Table 1. Review of all publications dealing with the response to different odours linked to foraging

Reference	Article type	Odorant tested	Test conditions	Responder species	Non-responder species	Location
Miller, 1942 ¹		Bacon fat	Sea	<i>Diomedea nigripes</i>		
Kritzler, 1948 ¹		Melted pork fat	Sea	<i>Fulmarus glacialis rogersii</i>		
Grubb, 1972	Research article	Cod liver oil	Sea	<i>Oceanites oceanicus</i> , <i>Oceanodroma leucorhoa</i> ² , <i>Puffinus gravis</i>	<i>Puffinus griseus</i>	Bay of Fundy
Jouventin, 1977	Research article	Fish	Captivity	<i>Pagodroma nivea</i>		Terre Adélie; Antarctica
Hutchison and Wenzel, 1980	Research article	Fish oil, squid homogenate	Sea	Procellariiforms	Non-procellariiforms	California coast
Hutchison et al., 1984	Research article	Cod liver oil, squid homogenate, krill homogenate	Sea	<i>Fulmarus glacialis</i> , <i>Puffinus griseus</i>	Non-procellariiforms	Estero Bay off Morro Bay, California
Jouventin and Robin, 1984	Research article	Cod liver oil	Sea	<i>Daption capense</i> , <i>Macronectes giganteus</i> ² , <i>Oceanites oceanicus</i> , <i>Pagodroma nivea</i>	<i>Fulmarus glacialis</i>	Terre Adélie; Antarctica
Wenzel, 1985 ³	Research article	Cod liver oil	Sea at night	<i>Oceanodroma homochroa</i>		Pacific
Wenzel, 1986	Review					
Lequette et al., 1989	Research article	Cod liver oil	Sea	<i>Daption capense</i> , <i>Fregatta tropica</i> , <i>Fulmarus glacialis</i> ² , <i>Macronectes sp.</i> , <i>Oceanites oceanicus</i> , <i>Procellaria aequinoctialis</i>	<i>Diomedea exulans</i> , <i>Pachyptila sp.</i> , <i>Pelecanoides sp.</i> , <i>Phoebastria palpebrata</i> , non-procellariiforms	Possession Island, Crozet archipelago; Southern Indian Ocean
Clark and Shah, 1992	Research article	Odours from krill	Colony, also at night	<i>Oceanodroma leucorhoa</i>		Kent Island, New Brunswick
Nevitt, 1994	Short report	Krill extract, pyrazine and trimethylamine, rose scent	Sea	<i>Aphrodroma brevirostris</i> , <i>Daption capense</i> , <i>Diomedea melanophrys</i> , <i>Halobaena caerulea</i> , <i>Macronectes giganteus</i> , <i>Macronectes halli</i> , <i>Thalassoica antarctica</i>		Elephant Island, South Georgia; Antarctic waters
		Cod liver oil	Sea	<i>Halobaena caerulea</i>		Elephant Island, South Georgia; Antarctic waters
Verheyden and Jouventin, 1994	Research article	Cod liver oil	Sea	<i>Daption capense</i> , <i>Diomedea melanophrys</i> , <i>Fregatta gallaria</i> , <i>Fregatta tropica</i> , <i>Fulmarus glacialis</i> ² , <i>Garrodia nereis</i> , <i>Macronectes giganteus</i> , <i>Oceanites oceanicus</i> , <i>Pelagodroma marina</i> , <i>Procellaria aequinoctialis</i> , <i>Pterodroma incerta</i> , <i>Pterodroma mollis</i> , <i>Puffinus gravis</i> , <i>Puffinus griseus</i>	<i>Calonectris diomedea</i> , <i>Procellaria cinerea</i> , non-procellariiforms*	Southern Ocean
Nevitt et al., 1995	Research article	DMS	Sea	<i>Fregatta tropica</i> , <i>Oceanites oceanicus</i> , <i>Pachyptila sp.</i> , <i>Procellaria aequinoctialis</i>	<i>Daption capense</i> , <i>Diomedea chrysostoma</i> , <i>Diomedea exulans</i> , <i>Diomedea melanophrys</i>	South Georgia; Sub-Antarctic waters
Nevitt and Hunt, 1996	Meeting abstract	Fish oil, ammonia	Sea	<i>Fulmarus glacialis</i> , <i>Puffinus griseus</i> , <i>Puffinus tenuirostris</i>	NA	Bering Sea
		DMS, pyrazene	Sea	NA		Bering Sea
Nevitt, 1999a	Review	No new data			<i>Fulmarus glacialis</i> , <i>Puffinus griseus</i> , <i>Puffinus tenuirostris</i>	Bering Sea

Reference	Article type	Odorant tested	Test conditions	Responder species	Non-responder species	Location
Nevitt, 1999b	Research article	Krill extract	Sea	<i>Daption capense</i> , <i>Diomedea melanophrys</i> ² , <i>Macronectes giganteus</i> ²	<i>Fregatta tropica</i> , <i>Fulmarus glacialis</i> , <i>Oceanites oceanicus</i>	Elephant Island, South Georgia; Antarctic waters
Nevitt and Veit, 1999	Proceedings	No new data				
Roper, 1999	Review	No new data				
Nevitt, 2000	Review	DMS ⁴		<i>Halobaena caerulea</i> , <i>Pachyptilia sp.</i>		Southern and Pacific Oceans, 66°S–30°S
Cunningham et al., 2003	Research article	DMS	Colony/chicks	<i>Halobaena caerulea</i>	<i>Pachyptilia belcheri</i> , <i>Pelecanoides urinatrix</i>	Kerguelen archipelago; Antarctic waters
		Rose scent	Colony/chicks	<i>Halobaena caerulea</i> , <i>Pachyptilia belcheri</i>	<i>Pelecanoides urinatrix</i>	Kerguelen archipelago; Antarctic waters
Nevitt and Haberman, 2003	Research article	DMS	Colony	<i>Oceanodroma leucorhoa</i>		Kent Island, New Brunswick
Nevitt et al., 2004	Research article	Pyrazine	Sea	<i>Daption capense</i> , <i>Diomedea melanophrys</i> , <i>Macronectes sp.</i> , <i>Procellaria aequinoctialis</i>	<i>Diomedea chrysostoma</i> , <i>Diomedea epomophora</i> , <i>Diomedea exulans</i> , <i>Fregatta tropica</i> , <i>Halobaena caerulea</i> , <i>Oceanites oceanicus</i> , <i>Pachyptilia sp.</i> , <i>Pelecanoides urinatrix</i> , <i>Phoebastria fusca</i> , <i>Phoebastria palpebrata</i> , <i>Pterodroma lessonae</i> , <i>Pterodroma mollis</i> , <i>Puffinus gravis</i> , <i>Puffinus griseus</i>	Maurice Ewing bank; Sub-Antarctic front
		Herring oil	Sea	<i>Daption capense</i> , <i>Diomedea exulans</i> , <i>Diomedea melanophrys</i> , <i>Fregatta tropica</i> , <i>Macronectes sp.</i> , <i>Oceanites oceanicus</i> , <i>Pachyptilia sp.</i> , <i>Procellaria aequinoctialis</i>	<i>Diomedea chrysostoma</i> , <i>Diomedea epomophora</i> , <i>Halobaena caerulea</i> , <i>Pelecanoides urinatrix</i> , <i>Phoebastria palpebrata</i> , <i>Pterodroma lessonae</i> , <i>Pterodroma mollis</i> , <i>Puffinus gravis</i> , <i>Puffinus griseus</i>	Maurice Ewing bank; Sub-Antarctic front
Cunningham and Nevitt, 2005	Proceedings	No new data				
Nevitt and Bonadonna, 2005a	Review	No new data				
Nevitt and Bonadonna, 2005b	Research article	DMS	Colony	<i>Pachyptilia desolata</i>		Kerguelen archipelago; Antarctic waters
Bonadonna et al., 2006	Research article	DMS	Colony/chicks	<i>Halobaena caerulea</i>		Kerguelen archipelago; Antarctic waters
Cunningham et al., 2006	Research article	Cod liver oil	Colony/chicks	<i>Halobaena caerulea</i>		Kerguelen archipelago; Antarctic waters
Nevitt et al., 2006	Research article	Rose scent	Colony/chicks		<i>Halobaena caerulea</i>	Kerguelen archipelago; Antarctic waters
Nevitt et al., 2006	Research article	Ammonia	Colony	<i>Halobaena caerulea</i>		Kerguelen archipelago; Antarctic waters
Nevitt, 2008	Review	No new data				
Nevitt, 2011	Review	No new data				

For each reference, the odorants tested, responder and non-responder species, experimental conditions and location of experiments are highlighted.

¹Roper 1999; ²only at scented slicks but low numbers for statistics; ³Wenzel, 1986; ⁴this was not a specific test but only a count of birds at sea in relation to natural surface concentrations of DMS.

*A number of species showed a non-homogeneous response in different tests: *Diomedea chlororhynchos*, *Diomedea chrysostoma*, *Diomedea epomophora*, *Diomedea exulans*, *Halobaena caerulea*, *Pachyptilia belcheri*, *Pachyptilia desolata* and *Pachyptilia vittata*. DMS, dimethylsulphide; NA, not available.

respond to cod liver oil (Lequette et al., 1989) but were attracted by DMS (Nevitt et al., 1995); in contrast, cape petrels (*Daption capense*) were not attracted by DMS (Nevitt et al., 1995) but responded to krill odours (Nevitt, 1999b) and cod liver oil (Verheyden and Jouventin, 1994). Thus, lifestyle and foraging strategy probably modulate which kind of odorant constitutes a cue and elicits a behavioural response, and which does not (Nevitt and Bonadonna, 2005a). In the light of these variable results, there is no evidence that findings from a unique study on attraction to DMS at sea, though a valuable reference, apply to all petrels. In addition, even though the investigation of olfactory foraging began in the North Atlantic (Grubb, 1972) and North Pacific (Hutchison and Wenzel, 1980; Hutchison et al., 1984), all subsequent studies, and all studies investigating the response to DMS, were carried out in southern oceans (Table 1). The only exception is reported in a meeting abstract in which the response to different odorants was tested in the Bering Sea. Unfortunately, the methods and data of this experiment are not available, but it appears that northern petrel species are indifferent to DMS (Nevitt and Hunt, 1996). This result suggests that the response to DMS might be a local phenomenon. The marine environment is not homogeneous and oceanographic conditions in the two hemispheres are dramatically different as are the concentration and distribution of surface DMS. Antarctic waters, where the response to DMS by procellariiforms has only been tested so far, are the richest both in terms of primary production and DMS emissions. DMS emissions are greater near the poles and decrease by some order of magnitude towards sub-polar and temperate regions. Such reduction is more abrupt in the northern hemisphere than in southern oceans (Belviso et al., 2004; Kettle and Andreae, 2000). Therefore, DMS might be a strong signal only in the southern waters and responses recorded there cannot be directly transposed to other marine environments and feeding assemblages, i.e. temperate waters of the northern oceans where DMS emissions are dramatically lower and the diversity and abundance of procellariiform species is poorer. Moreover, in the northern hemisphere, a number of closed seas and basins are present. Seabirds living and foraging in these basins have to cope with extremely different habitat conditions compared with open oceans, including much lower DMS emissions (Belviso et al., 2003; Simó and Grimalt, 1998; Simó et al., 1997).

In order to increase knowledge concerning the response to DMS and to provide experimental support for generalizations of DMS-driven foraging behaviour, we investigated the response of Cory's and Scopoli's shearwaters to this compound, in relation to different environmental and ecological settings in the northern hemisphere. These are two closely related medium-sized petrel species that breed in the northern hemisphere waters during summer and migrate south for wintering (Dias et al., 2011; Ristow et al., 2000). Until 2012, they were considered a single species (Sangster et al., 2012), so their employment as model species allows a direct comparison of the response to DMS in different habitats. Cory's shearwater (*Calonectris borealis* Cory 1881), breeds in north Atlantic islands and migrates to different areas of both hemispheres of the Atlantic Ocean (Dias et al., 2011), while the Scopoli's shearwater (*Calonectris diomedea* Scopoli, 1769) breeds in the Mediterranean Sea and migrates to the Atlantic Ocean during winter (Brooke, 2004; Ristow et al., 2000). As with all procellariiforms, during breeding they are central place foragers: they must return to the colony either to retrieve a mate or to provision the chick while the foraging grounds remain pelagic (Stephens and Krebs, 1986). This ecological strategy requires high efficiency in locating productive food sources to ensure effective foraging and breeding success. As for the other procellariiforms, olfactory guidance may be

advantageous as odour emissions extend the prey patch detectability (Clark and Shah, 1992). Feeding habits are well known for Cory's shearwaters breeding in the Atlantic, where foraging behaviour exhibits great plasticity depending on the characteristics of the foraging grounds (Paiva et al., 2010). In contrast, very little is known about the habits and feeding grounds of Scopoli's shearwaters in the Mediterranean, which are mainly restricted to coastal areas, and foraging trips appear to be shorter, in terms of both duration and distance travelled (Cecere et al., 2013; Dell'Aricecia et al., 2010). These differences and the known foraging plasticity suggest that foraging strategies to locate productive areas could also be different; Mediterranean shearwaters, for example, may not rely on DMS to find food but could employ other cues, possibly taking advantage of coastlines as visual landmarks. The employment of these species as models allows us to address two main points. First, to explore the response to DMS in the northern hemisphere, where emissions are dramatically lower than in previously explored areas, in order to understand whether the attraction to DMS is widespread in oceans worldwide. Second, to directly compare the response by sister species in different marine environments so as to detail how the responses vary in relation to different ecological niches, an approach not previously used.

RESULTS

Two different experiments, at different spatial scales, were designed to determine whether these shearwaters would be attracted by DMS. To test whether the birds are able to detect and respond to DMS, we presented them with a binary choice between DMS and a control odour in a Y-maze at the colony, as other burrow-nesting petrel species significantly prefer the DMS arm in Y-mazes (Bonadonna et al., 2006; Nevitt and Bonadonna, 2005b). Then, to determine whether Cory's and Scopoli's shearwaters actually use this molecule in natural conditions, we also tested their response to DMS at sea.

Y-maze choice test

We tested 52 shearwaters in the Atlantic colony and 29 in the Mediterranean colony, of which 23 (44%) and 16 (55%),

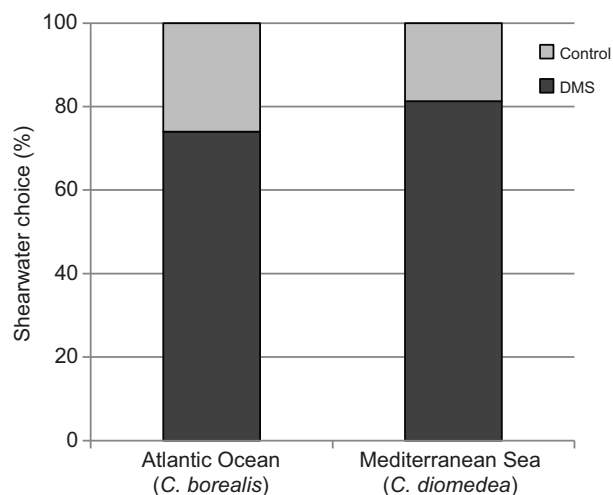


Fig. 1. Preference for dimethylsulphide in a Y-maze. The histogram shows the greater percentage of shearwaters that chose the dimethylsulphide (DMS, $1 \mu\text{mol l}^{-1}$) arm in preference to the control arm in the Y-maze in both the Atlantic (*Calonectris borealis*; binomial test, $P=0.03$) and Mediterranean (*Calonectris diomedea*; binomial test, $P=0.02$) colonies. The proportion of birds choosing DMS or control in the two colonies was not different (Fisher's exact test: $P=0.7$).

Table 2. Number of petrels recruited at DMS-scented and control slicks and wind conditions at the five Atlantic (A1–5) and Mediterranean (M1–5) sea sites

Sea site	DMS		Control		Mean wind speed
	Upwind	Downwind	Upwind	Downwind	
A1	4Cb + 1Bb	1Cb	1Cb	–	Gentle breeze (7–10 knots)
A2	14Cb	8Cb	3Cb	7Cb	Gentle breeze (7–10 knots)
A3	17Cb + 1Bb	–	2Bb	6Cb	Gentle breeze (7–10 knots)
A4	9Cb + 2Bb	11Cb + 5Bb	3Cb + 1Bb	13Cb + 3Bb + 1Pt	Breeze (11–15 knots)
A5	1Cb + 1Bb	–	1Bb	–	Light air (1–3 knots)*
M1	3Cd	–	–	–	Light air (1–3 knots)*
M2	1Cd	–	–	–	Light air (1–3 knots)*
M3	–	1Cd	–	–	Light air (1–3 knots)*
M4	1Cd	–	–	–	Light breeze (4–6 knots)*
M5	3Cd + 2Hp	–	–	2Cd	Light air (1–3 knots)*

Scores are depicted according to the flight direction with respect to the wind direction: upwind, birds flying against the wind; downwind, birds flying in the same direction as the wind. Cb, Cory's shearwater; Cd, Scopoli's shearwater; Bb, Bulwer's petrel; Pt, *Pterodroma* spp.; Hp, Mediterranean storm petrel.

*Calm sea with no waves.

respectively, entered one arm successfully, thereby making a choice. In the Atlantic colony, 17 chose the DMS arm whereas six entered the control arm (two-tailed binomial test: 23, $P=0.03$; Fig. 1). In the Mediterranean colony, 13 chose the DMS arm whereas three preferred the control arm (two-tailed binomial test: 16, $P=0.02$; Fig. 1). The proportion of birds choosing DMS or control was not different in the two colonies (Fisher's exact test: $P=0.7$). Choice time (the time that the bird took to walk halfway down the arm) was similar for DMS and control. In the Atlantic colony, the median choice time for DMS was 4.1 min (range 7 s to 10 min) and the median choice time for control was 2.4 min (range 11 s to 6.7 min) (Wilcoxon–Mann–Whitney for independent samples: $W=62.5$, $P=0.4$). In the Mediterranean colony, the median choice time for DMS was 2.8 min (range 9 s to 12.8 min) and the median choice time for control was 7.7 min (range 10 s to 11.5 min) (Wilcoxon–Mann–Whitney for independent samples: $W=16$, $P=0.7$). Overall, birds showed no lateral preference (Atlantic: DMS, 8 right and 9 left arm; control, 4 right and 2 left arm; Mediterranean: DMS, 6 right and 7 left arm; control, 2 right and 1 left arm; Fisher's exact test: $P=0.6$ and $P=1$, respectively). In both colonies, the no-choice birds were mainly inactive after removal of the divider, remaining immobile inside the entry arm throughout the experiment. Body mass did not have an influence on the choice or on the absence of choice; all pairwise comparisons of body mass among birds choosing DMS and control and making no choice in the two colonies were not significant (Wilcoxon–Mann–Whitney for independent samples, P range=0.2–0.9).

Attractiveness of DMS at sea

The scores of petrels observed at slicks at sea are summarized in Table 2. The majority of recruited birds were Cory's shearwaters (84.5%) in the Atlantic and Scopoli's shearwaters (84.6%) in the Mediterranean. But other petrel species were also observed: Bulwer's petrel (*Bulweria bulwerii*) and *Pterodroma* spp. in the Atlantic; Mediterranean storm petrel (*Hydrobates pelagicus melitensis*) in the Mediterranean. In both seas, the number of shearwaters flying upwind to DMS slicks was consistently greater than the number flying to control slicks (Fig. 2. G -test: $G=31.0$, $P=2.6 \times 10^{-8}$ in the Atlantic; $G=11.09$, $P=0.0009$ in the Mediterranean). Over the DMS scented slicks, some shearwater also exhibited an explorative behaviour, making one or two loops before flying away. In the Atlantic Ocean, we counted several Cory's

shearwaters flying downwind over both kinds of slicks. In this case, there were no differences between DMS and control slicks (G -test: $G=0.79$, $P=0.38$). Moreover, when deploying DMS-scented slicks, Cory's shearwaters approached significantly more frequently moving upwind (Chi-square test: $\chi^2=4.99$, $P=0.025$). In contrast, downwind flights were the most frequent approach to control slicks (Chi-square test: $\chi^2=5.96$, $P=0.015$, Fig. 3). In the Mediterranean Sea, only three birds flew over the slicks downwind, eliminating the

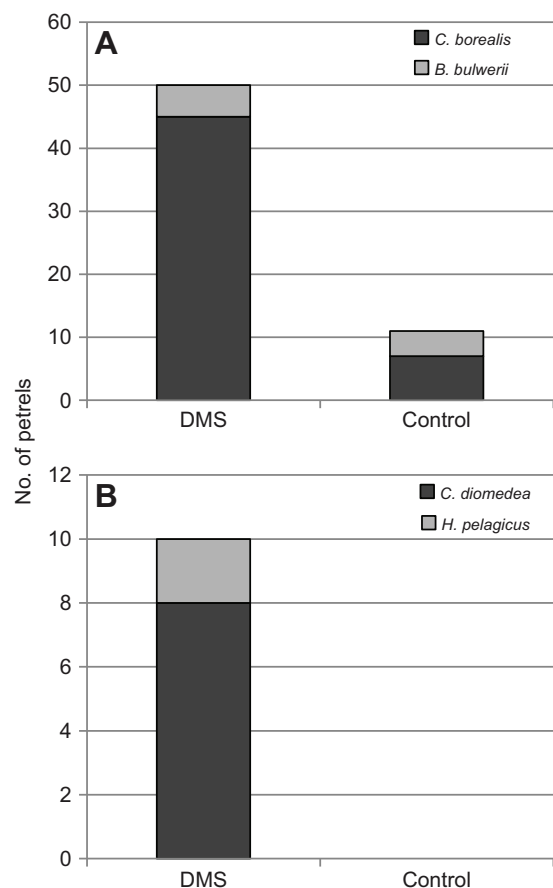


Fig. 2. Number of petrels recruited at DMS-scented and control slicks at sea. (A) Atlantic Ocean (*C. borealis*, G -test, $P=2.6 \times 10^{-8}$). (B) Mediterranean Sea (*C. diomedea*, G -test, $P=0.0009$).

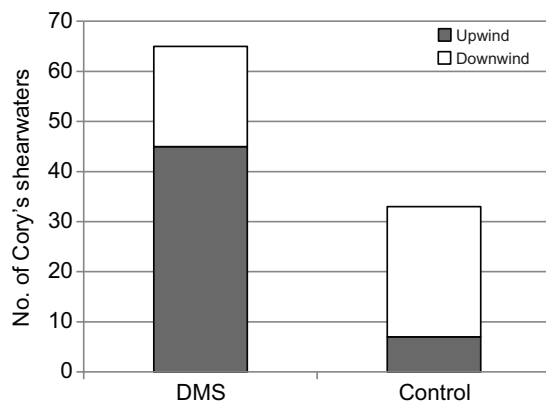


Fig. 3. Number of Cory's shearwaters that approached the DMS-scented and control slicks downwind and upwind in the Atlantic Ocean. At DMS-scented slicks, Cory's shearwaters approached significantly more frequently moving upwind (Chi-square test: $\chi^2=4.99$, $P=0.025$). In contrast, downwind flights were the most frequent approach to control slicks (Chi-square test: $\chi^2=5.96$, $P=0.015$).

possibility of performing the same analysis. No bird landed or pattered on any of the slicks.

DISCUSSION

This comprehensive study is the first to simultaneously and specifically explore the response to DMS of closely related species in two different marine environments and in both natural and non-foraging controlled conditions. In addition, this is the first test of attraction to DMS in temperate waters and in the northern hemisphere. Previous studies investigating the attractiveness of DMS either were carried out at the colony, specifically testing the response of only one species (Bonadonna et al., 2006; Nevitt and Bonadonna, 2005b; Nevitt and Haberman, 2003), or tested the attraction of procellariiforms at sea, with no particular target species (Nevitt et al., 1995). All of them were carried out in the procellariiform assemblage in the Antarctic and sub-Antarctic waters, where DMS emissions are particularly high. There, several different species are present that may be in competition for food resources, and bigger and more aggressive species (e.g. albatrosses and giant petrels) may force smaller species (e.g. prions and storm petrels) out of prey patches (Nevitt, 2008; Nevitt and Bonadonna, 2005a). In these petrels, which feed in mixed-species aggregations, specific adaptations may have evolved, potentially preventing conclusions from studies on the olfactory senses of these birds from being transposed directly to other procellariiforms. However, our findings seem to justify such generalization to other marine habitats, including closed basins where coastlines may provide profitable and alternative sources of spatial information. We show here that species of shearwaters that occupy different ecological niches also can detect and are attracted to DMS at concentrations similar to those that they would naturally encounter at sea (Belviso et al., 2003; Simó et al., 1997). The number of birds that chose the DMS in the Y-maze and that were recruited at DMS-scented slicks at sea in our experiments suggests that both Cory's and Scopoli's shearwaters respond to DMS, in both non-foraging and natural contexts. The attraction to DMS by procellariiform seabirds is thus not limited to Antarctic waters.

In both the Atlantic and Mediterranean colonies, under controlled experimental conditions, tested birds significantly preferred the arm of the maze that contained the DMS solution, providing evidence that these shearwaters are able to smell this compound and have a

tendency to head towards it. The preference for the DMS arm suggests that they recognize this odour as familiar and so they are motivated to move towards it, probably to find a possible exit out of the maze (Nevitt and Bonadonna, 2005b). Unfortunately, once in the maze, a large number of birds made no choice (56% in the Atlantic and 45% in the Mediterranean colonies). In all previous experiments performed on other petrel species with T- or Y-mazes, no-choice percentages ranged from 5% in Antarctic prions (*Pachyptila desolata*; mean no-choice in four published experiments was 19%) to 60% in common diving petrels (*Pelecanoides urinatrix*) probably because of the shy personality of some individuals (reviewed by Bonadonna and Sanz-Aguilar, 2012).

At sea, DMS-scented slicks systematically attracted more birds than control slicks, confirming that the tendency of both Cory's and Scopoli's shearwaters to head for this compound extends to a natural foraging context. Shearwaters flew upwind to the DMS-scented slick and often made one or two loops over it before flying away, suggesting either an interest in the slick or an attempt to scan the slick for prey. In contrast to upwind flights, the number of shearwaters overflying downwind over the slick was the same over DMS and control slicks. This equal number of downwind flights indicates that an equal number of birds was present in the area under the two experimental conditions and that other non-directional stimuli may have attracted birds to the slicks, i.e. visual stimuli provided by the glare of the slick over the water surface or by the boat. Moreover, it is not surprising that, over control slicks, a greater number of birds flew downwind because this is the preferred behaviour by flying petrels, linked to their particular flying strategy (Warham, 1996). The reversal of the distribution of upwind and downwind sightings over DMS and control slicks confirms that airborne stimuli were used for guidance and attraction by shearwaters.

Other petrel species were also sighted at slicks, but never non-procellariiforms. In the Mediterranean Sea, in addition to the Scopoli's shearwater, DMS-scented slicks also attracted the Mediterranean storm petrel. These birds are rarely observed at sea, and almost never during daylight, because of their very low abundance and nocturnal feeding habits (Brooke, 2004; del Hoyo et al., 1992; Warham, 1990). Their presence at DMS-scented slicks suggests that other Mediterranean petrel species may be attracted by this molecule and further studies would be necessary to confirm this. Other species attended the slicks in the Atlantic Ocean as well. In particular, Bulwer's petrels were often observed on both DMS and control slicks, flying very low over the water surface. Even if Bulwer's petrels did not show any preference for DMS or control slicks, their behaviour emphasizes the importance and the necessity of additional investigations.

Our results show that the attraction to DMS is not restricted to southern seabirds or those living exclusively in open oceans. At first glance, it may seem that the overall response in the Northern Hemisphere was much less important than in the southern one, where a previous study reported that several hundred petrels of different species were attracted by both DMS-scented and control slicks (Nevitt et al., 1995). However, these higher numbers were probably due to the greater abundance of petrels in the Southern Ocean compared with the Northern Hemisphere. To compare our results with those of Nevitt et al. (Nevitt et al., 1995), we calculated an index of response to DMS (ior, ranging from 0 to 1), corrected for the relative abundance of birds in the different experimental areas, from our current and previous results: we divided the number of birds attracted to DMS-scented slicks by the total number of birds attracted to both kinds of slick, and we corrected for the duration of

slick presentation. This index of the intensity of the response to DMS had the highest value in the Mediterranean Sea ($\text{ior}=1$), where petrels flew over only DMS slicks and never showed up over control slicks, while it was lower in the Southern Ocean ($\text{ior}=0.7$; Atlantic Ocean, $\text{ior}=0.9$). This finding highlights the fact that the smaller number of birds attracted in the Mediterranean and in the North Atlantic compared with the Southern Ocean was not due to a lower attractiveness to DMS but rather to a lower abundance of petrels. However, it would be important to confirm whether the different number of birds attending the slicks at sea in our and previous experiments is driven only by bird density or whether other factors also have a role. For example, higher wind speeds, as often observed in the Southern Ocean, increase the distance over which the DMS can be dispersed, thus increasing the detectability of the slicks. In addition, high winds and large swells have been shown to enhance the wandering behaviour of petrels at sea and, thus, their presence at slicks (Hutchison and Wenzel, 1980). A similar phenomenon was also observed in our study and probably accounts for the different number of birds in the Mediterranean and Atlantic. In fact, we observed that when the Atlantic conditions at sea were similar to those in the Mediterranean, with no or low wind speed and no waves, the bird count was similarly low and restricted to DMS-scented slicks. Finally, recent research on carbon and nitrogen stable isotope signature in feathers during the summer suggests that Scopoli's shearwater may include krill in their diet during the breeding season (Peron and Gremillet, 2014), implying that DMS might be a direct foraging cue in the Mediterranean rather than an indirect cue of foraging aggregations. This hypothesis deserves further investigation.

Our finding that petrel species foraging in closed basins may use olfactory cues to locate productive areas at sea opens new interesting perspectives. It would be of great interest to investigate whether visual cues are also employed to locate foraging spots in littoral and shelf waters, how petrels integrate the information coming from different kinds of cues and how they modulate their response to olfactory and visual cues according to circumstances (i.e. during the breeding season in the Mediterranean and during migration in the open Atlantic Ocean).

In addition to its role as foraging cue, DMS has also been proposed in numerous reviews as a chemosignal for navigation in open waters (Nevitt, 1999a; Nevitt, 2000; Nevitt, 2008; Nevitt, 2011; Nevitt and Bonadonna, 2005a; Nevitt and Bonadonna, 2005b). However, this idea lacks empirical validation and the potential role of DMS in seabird navigation beyond foraging remains unknown. Recently, it has been experimentally shown that Cory's shearwaters need olfaction to navigate over long distances (Gagliardo et al., 2013), but the chemical cues used in this navigation process have not yet been elucidated. Experiments that directly test the use of DMS as a cue for long distance navigation are therefore crucial.

In conclusion, our data provide new essential elements to understand the role of DMS in environments other than sub-Antarctic waters. We show that Cory's and Scopoli's shearwaters are sensitive and attracted to DMS, indicating that the sensitivity and attraction to DMS are actually widespread among petrel species and different marine environments, including temperate waters. Our study opens a worldwide perspective to previous hypotheses concerning the use of DMS as a cue for foraging, providing an experimental basis to theoretical work.

MATERIALS AND METHODS

The study was carried out on shearwaters breeding in two different colonies. The Mediterranean Scopoli's shearwater colony was on Linosa island

(Sicilian Channel, Italy: 35°52'N, 12°52'E), where ~10,000 pairs breed (Massa and Lo Valvo, 1986). In the Atlantic Ocean, we selected the Cory's shearwater colony on Selvagem Grande (Macaronesia, Portugal: 30°09'N, 15°52'W), where the breeding population is estimated to be 30,000 pairs (Granadeiro et al., 2006). In both colonies, we repeated the same protocols during incubation in June–July 2011 and 2012 in the Mediterranean and Atlantic, respectively.

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Y-maze choice test

The Y-maze was similar to the maze used in previous experiments (Bonadonna et al., 2006; Bonadonna and Nevitt, 2004; Nevitt and Bonadonna, 2005b). In Linosa, it was made of opaque PVC wire housing (three symmetrical arms: 100×23×19 cm L×W×H, angled at 120 deg), while in Selvagem Grande we were constrained for logistic reasons to use a smaller one made of stainless steel (three symmetrical arms: 65×17×17 cm L×W×H, angled at 120 deg). In both cases one arm, used as the starting point, was fitted with two trapdoors that formed a temporary holding compartment for the bird. Because Mediterranean shearwaters are nocturnal at the colony, and nest in dark burrows, the PVC maze was covered with a thick blanket to darken the goal arms and thus increase the motivation of birds to leave the clear starting point and move towards one of the dark arms. The end of each goal arm was equipped with a CPU cooling fan (DC Pico Ace 25, Sanyo Denki Co. Ltd, Tokyo, Japan) mounted on a partition to provide a low-noise controlled airflow (13 CFM). In the compartment behind the fan, a Petri dish (5.5 cm diameter) containing either DMS or control solution provided the stimulus. DMS solution was prepared in propylene glycol (4 ml; 1 $\mu\text{mol l}^{-1}$); the control solution contained propylene glycol only (4 ml) (Bonadonna et al., 2006). To eliminate any physical or positional bias, odour stimuli were alternated between arms at each trial and frequently exchanged (each 1–3 trials) with fresh solutions. In addition, the maze was washed with ethanol (70%) to remove any odour residue after each trial.

All experiments were performed during daylight, when there were no free-flying birds at the colony. For each experimental trial, one shearwater at a time was captured at the nest, transported in a cotton bag to the maze and then placed in the temporary holding compartment for a 3 min acclimation period. The inner trap door was then lifted for the bird to make a choice. Birds tended to stay in the intersection prior to making a choice, and could be heard sweeping their heads back and forth, presumably sampling each arm. The sounds of the bird walking in the maze allowed us to easily assess arm choice without disturbing the bird. A positive choice was scored if the bird travelled at least halfway down an arm and stopped for at least 30 s. Almost all birds stopped at the end of the arm and remained there. No-choice birds tended to sit quietly in the entryway, some facing away from the maze arms, and were removed from the maze after 15 min. Choice time was calculated as the time that a bird took to walk halfway down each maze arm. After the Y-maze test, birds were immediately returned to the nest burrow, where they promptly resumed warming the egg in a normal behaviour. Each bird was tested only once and was away from its nest for a maximum of 30 min. We noted no deleterious effects on breeding success.

Open sea test

To test the responsiveness of Cory's and Scopoli's shearwaters to DMS in natural foraging conditions, i.e. in the open sea, we compared the number of birds attracted by DMS-scented and non-scented vegetable oil slicks deployed on the water surface (Nevitt et al., 1995; Wright et al., 2011). Slicks were released upwind from a small boat at five different locations around Linosa island (mean \pm s.e.m. distance from coast: 7.5 \pm 0.7 km; maximum 10.8 km; minimum 4.3 km) and five around Madeira island (8.7 \pm 0.5 km; maximum 9.9 km; minimum 7.5 km). At each location, DMS-scented slicks (0.2 mol l⁻¹ DMS concentration in 2 l of vegetable oil) were coupled with non-scented slicks (consisting of 2 l of vegetable oil only) to control for any visual attraction that the slick could present to foraging birds. The DMS-scented and control slicks were presented consecutively, in a

random order, separated by a 45–60 min interval (after complete dissipation; see below) and by 1 km distance to ensure roughly similar experimental conditions within slick pairs but with no cross-contamination. Slicks were deployed only when no birds were in sight in any direction. Slicks drifted away from the release point during trials as a result of marine currents and wind (0–6 knots around Linosa; 0–18 knots around Madeira) and dissipated within 20–30 min. One person with binoculars made observations and recorded data starting from 2 min before the deployment of the oil by a second person. Birds were counted if they (1) flew upwind (against the current) over the slick within ~1 m of the surface (continuous sampling) and (2) landed or (3) pattered on the slick (instantaneous sampling at 1 min intervals). We also separately counted the birds that flew downwind over the slick (continuous sampling).

Statistical analyses

Statistical analyses were performed using R (R Development Core Team, 2011). Y-maze preferences were analysed using binomial tests (Zar, 1996). We then used the Wilcoxon–Mann–Whitney test for independent samples to check for differences in choice time and body mass of birds expressing different preferences in the maze, and the Fisher exact test to check for lateral choice and to compare Atlantic and Mediterranean choices. We compared the ratios of birds overflying DMS and control slicks at sea with the *G*-test for pooled data (McDonald, 2009), with an expected ratio of 1:1 in the case of no attraction by DMS-scented slicks, as in previous studies (Nevitt, 1994; Nevitt, 1999b; Nevitt et al., 2004; Nevitt et al., 1995). Finally, we compared the proportion of birds flying over the slicks upwind and downwind using the Chi-square test (Hutchison et al., 1984).

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Competing interests

The authors declare no competing financial interests.

Author contributions

G.D.A. and F.B. conceived and designed the experiments. G.D.A., A.C., M.G. and P.P. collected the data and G.D.A. analysed them. G.D.A., A.C., B.M. and F.B. interpreted findings. G.D.A. drafted the manuscript and all authors revised it.

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