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A field study of chemical senses in bottlenose dolphins and pilot whales

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Abstract

For most marine vertebrates, chemical cues provide crucial information during navigation and foraging, but their use by cetaceans is still poorly understood. In contrast to baleen whales, toothed whales (odontocetes) are scarcely equipped for chemoreception: they lack the conventional anatomical structures (*i.e.*, olfactory epithelium, nerves and bulbs) involved in olfaction and have reduced taste buds on the tongue. Several behavioral studies have however shown that captive dolphins can perceive chemical solutions, including odorants, in their oral cavity. To investigate whether odontocetes could use infochemicals in their foraging ecology, we implemented a behavioral response experiment in wild bottlenose dolphins and long-finned pilot whales. We tested dimethyl sulfide (DMS) as a potentially attractive stimulus since it is a chemical signature of highly productive marine areas, known to attract several marine predators including fishes and seabirds. We assessed cetacean responses to DMS exposure by analyzing their movements and surface behaviors recorded by onboard observers. In both species, results did not reveal any significant attraction or behavioral reaction toward DMS when compared to a control chemical stimulus, apart from a short-distance response in bottlenose dolphins. These results suggest that while odontocetes may perceive DMS in water, it apparently does not play a significant role in their foraging ecology. Testing potentially more attractive compounds such as prey extracts with the present method and analyzing surface, underwater and acoustic responses would provide further insights on odontocete feeding behavior. It would also provide valuable clues to studies on the anatomical structures involved in their chemosenses.

KEYWORDS

behavior, cetaceans, chemical sense, dimethyl sulfide, odontocetes

1 | INTRODUCTION

Chemical interactions determine many aspects of the life of marine organisms including their breeding, orientation, and foraging strategies (for a review, see Hay, 2009). In the open ocean, a visually featureless environment where food is patchily distributed, chemosenses (*i.e.*, senses of smell, taste,

and trigeminal perception) allow marine top predators to detect environmental compounds that provide them with crucial information for foraging. Fishes, especially sharks, can detect their prey metabolites hundreds of meters away, mainly using their highly sensitive olfactory and lateral line systems (Gardiner & Atema, 2007; Hara, 1994). At a larger scale, marine predators might also find their foraging

grounds in the open ocean by following chemical indicators of highly productive zones such as dimethyl sulfide (DMS), a molecule produced by phytoplankton when grazed by zooplankton (Cantin, Levasseur, Gosselin, & Michaud, 1996; Dacey & Wakeham, 1986). DMS, both in the air (DMS_g) and seawater (DMS_{aq}), is spatially correlated to zooplankton biomass (Owen et al., 2021). Several experimental studies have shown that DMS_g attracts seabirds and turtles and that DMS_{aq} attracts whale sharks (Dove, 2015; Endres & Lohmann, 2012; Nevitt & Bonadonna, 2005). This infochemical is therefore emerging as a key player in the foraging ecology of open ocean communities, attracting predators from multiple taxa (Savoca, 2018).

In cetaceans, however, the use of chemical cues such as DMS remains unclear and has seldom been studied. Baleen whales (mysticetes) possess the anatomical structures involved in olfaction, that is, a complete main olfactory system (olfactory epithelium, nerve and bulb, Breathnach, 1960; Oelschläger, 1992; Thewissen, George, Rosa, & Kishida, 2011; Hirose, Kishida, & Nakamura, 2018). However, they lack the dorsal domain of the olfactory bulb, an area known to induce innate avoidance behavior against odors of predators and spoiled foods (Kishida, Thewissen, Hayakawa, Imai, & Agata, 2015). The number of genes coding for the olfactory receptors (OR), i.e., the sensory receptors of the main olfactory system, is low in this taxonomic group compared to their close terrestrial relatives (Kishida et al., 2015; Liu et al., 2019). However, the proportion of OR pseudogenes varies greatly among different species, with some having about 65% of their OR genes still functional (Liu et al., 2019). Several authors have thus suggested they could use chemicals such as DMS as long-distance cues while foraging or navigating in the pelagic environment (Drake et al., 2015; Hagelin, Straley, Nielson, & Szabo, 2012; Thewissen et al., 2011; Torres, 2017). In a recent behavioral response experiment, humpback whales (*Megaptera novaeangliae*) were exposed to a prey extract (krill hydrolysate) and to DMS hundreds of meters away (Bouchard et al., 2019). Results showed that the whales changed their vocal activities when exposed to both chemicals. The whale trajectory analysis however suggested they were attracted toward the source of krill extract but not toward the source of DMS, which may not be a relevant cue at a fine scale (hundreds of meters) but over long distances (kilometers). These results suggest that while the number of functional OR is reduced in mysticetes, chemoreception plays a significant role in their foraging ecology. The use of this sense in the other suborder of cetaceans, the odontocetes (toothed whales), is however still unclear.

In contrast to mysticetes, anatomical and archeological studies revealed that odontocetes lost their main olfactory system during their adaptation to an aquatic lifestyle (reviewed in Kremers et al., 2016). As a result, toothed whales lack the main and accessory olfactory

tracts, as well as the cribriform plate and ethmoturbinals (Oelschläger & Buhl, 2008; Pihlström, 2008). While Behrmann (1989) described putative chemoreceptive cells in the nasal cavity of harbor porpoise (*Phocoena phocoena*), a recent histological study failed to find olfactory cells in common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), and long-finned pilot whale (*Globicephala melas*) (García de los Ríos y Loshuertos et al., 2021). Genetic data also show that a large proportion of their OR genes are pseudogenized (74%–100%, Kishida, Kubota, Shirayama, & Fukami, 2007, McGowen, Clark, & Gatesy, 2008, Liu et al., 2019), suggesting their function has been lost during evolution. Like mysticetes, odontocetes lack the vomeronasal organ (VR), part of the accessory olfactory system. This chemosensory organ exhibits two types of vomeronasal receptors (VR1 and VR2) involved in pheromone detection in terrestrial mammals. Only one intact VR1 gene is present in the bottlenose dolphin (*Tursiops truncatus*, Kishida et al., 2015).

Regarding the gustatory system, a reduction is also observed both anatomically and genetically in cetaceans. While baleen whales exhibit structures similar to taste buds in neonates (Kienle, Ekdale, Reidenberg, & Deméré, 2015), a genetic study has shown that they have lost three of the basic taste modalities, that is, sour, sweet, and umami (Kishida et al., 2015). The perception of salty is thought to be intact, but the ability to taste bitter is strongly reduced as only one gene (TASR16) was found intact in the common minke whale (*Balaenoptera acutorostrata*) genome (Jiang et al., 2012; Zhu et al., 2014) and possibly in two other mysticetes species, based on partial sequencing of coding regions (Feng, Zheng, Rossiter, Wang, & Zhao, 2014). Odontocetes also exhibit a reduced gustatory system and only maintained the ability to taste salt (Feng et al., 2014; Kishida et al., 2015). Additionally, the taste buds observed in juveniles tend to degenerate in adults (Komatsu & Yamasaki, 1980; Yamasaki, Komatsu, & Kamiya, 1978).

Although anatomical and genetic evidence shows that odontocetes have reduced chemosensory abilities, experiments and empirical observations suggest that odontocetes perceive various odorants in air or water. For example, several species of dolphins were reported to react to their congeners' secretions including blood, urine, and feces (Dudzinski, Thomas, & Gregg, 2009; Gubbins, 2002; Muraco & Kuczaj, 2015; Norris, Wursig, Wells, & Wursig, 1994). Kuznetsov (1990) showed that bottlenose dolphins display autonomous reactions, such as increased heart and respiratory rates, when exposed through their oral cavity to their congeners' excreta (i.e., urine and feces) or to odorants (i.e., trimethylamine, indole, camphor and valeric acid), usually perceived through the olfactory epithelium. He thus proposed a

new term for this perception: “quasi-olfaction” instead of gustation (Kuznetsov, 1990). More recently, spontaneous behavioral experiments using food-related chemicals indicated that captive bottlenose dolphins were able to detect odors from decomposing fish (Kremers et al., 2016) and to discriminate fish taste (Bouchard et al., 2017). However, to date, no experiments have been carried out on wild odontocetes to evaluate their potential use of chemical senses in natural settings.

In the present study, we tested DMS as a potential attractive chemical cue for wild odontocetes. We targeted resident groups of bottlenose dolphins and long-finned pilot whales (thereafter pilot whales) in the western Mediterranean Sea and exposed them to a chemical stimulation using DMS slicks. We focused on these two species because they can be found in similar areas but show very distinct feeding ecologies: while bottlenose dolphins mainly hunt teleost fish within the first 100 m under the surface, pilot whales almost exclusively feed on cephalopods during dives reaching more than 800 m (Blanco, Raga, & Salomón, 2001; Canadas & Sagarminaga, 2000; De Stephanis et al., 2008; Giménez et al., 2018; Heide-Jørgensen et al., 2002). As DMS is a marker of surface productivity (produced within the oceanic mixed layer at a depth less than 50–100 m, Royer et al., 2016) correlated with higher surface prey biomass (Owen et al., 2021), we can expect that it would be more attractive for bottlenose dolphins than pilot whales. This first behavioral exposure experiment in odontocetes thus allowed us to test whether chemical cues could play a role in their foraging ecology.

2 | MATERIALS AND METHODS

2.1 | Study site and cetacean groups targeted

The experiments were carried out during two surveys in the western Mediterranean Sea. The first took place in the Strait of Gibraltar in April and May 2015. This area hosts resident populations of bottlenose dolphins and long-finned pilot whales that share the same habitat in the narrowest part of the Strait, South of Tarifa, Spain (35°56'40" N - 35°53'51" N and 5°31'30" W - 5°40'26" W) (De Stephanis et al., 2008; Giménez et al., 2018; Verborgh et al., 2009). The second survey took place in April 2016 in the Gulf of Vera, South of Cartagena, Spain. This area allows frequent observations of bottlenose dolphins on the narrow continental shelf as well as of pilot whale groups found mostly on the steep slopes of the shelf edge relatively close to the coast (12–15 km south from the port of Cartagena) (Gómez De Segura, Crespo, Pedraza, Hammond, & Raga, 2006).

The experiments were set up during days of favorable sea conditions (wind force less than four on the Beaufort scale and a swell less than one m), maximizing the chances to detect cetacean groups from the research vessel. The vessel navigated to the known distribution area of the resident pilot whale and bottlenose dolphin populations until we spotted a group opportunistically. The animals were then approached at minimal speed (3–5 knots) to a distance of about 300 m to assess the group size and observe their activity for a minimum of ten minutes. These initial activities included traveling (moving toward one main direction), feeding (diving repeatedly and surfacing facing in varying directions), resting (floating at the surface or moving very slowly), and milling (moving in varying directions and remaining near the surface) (Shane, 1995; Shane, Wells, & Wursig, 1986). A trial was started when no other vessel was present in the area since this could have influenced cetacean behavior and group cohesion (Senigaglia, de Stephanis, Verborgh, & Lusseau, 2012).

2.2 | Exposure stimuli and protocol

We used a randomized controlled experimental design to analyze the effect of DMS on cetacean behaviors. We exposed bottlenose dolphin and/or pilot whale to a chemical stimulus using a scented slick (or unscented control slick) deployed in the vicinity of cetacean groups. This methodology was successfully applied to chemosensory research in mysticete whales (Bouchard et al., 2019) and seabirds (Nevitt, Veit, & Kareiva, 1995). A DMS solution was freshly prepared every day by dissolving DMS (Purity $\geq 99\%$, Sigma-Aldrich, Germany) in commercial sunflower oil at a final concentration of 0.2 M. The control (CTL) trials consisted of sunflower oil only. We built two identical devices of 80 cm in diameter using stainless steel-reinforced orange Styrofoam™ tubes (Figure 1a). Each device was used either for DMS or for CTL trials exclusively. A polyvinyl chloride membrane of 30 cm height was hung below the tubes to partly retain the oily solutions during each trial. Excessive drifting due to wind was reduced by hanging a one-kg weight of about 40 cm under the device using four polyester straps, which worked as an anchor. The use of this bright-colored, round floating device allowed a progressive release of the olfactory stimulus during the trial and created a focal point of concentrated solution that the observers used as a reference.

Before starting a trial, the vessel stopped 300 m upwind (*i.e.*, into the wind) from the cetacean group. An experimenter quickly deployed the chemical stimulus by pouring three liters of the test solution in the floating device at the

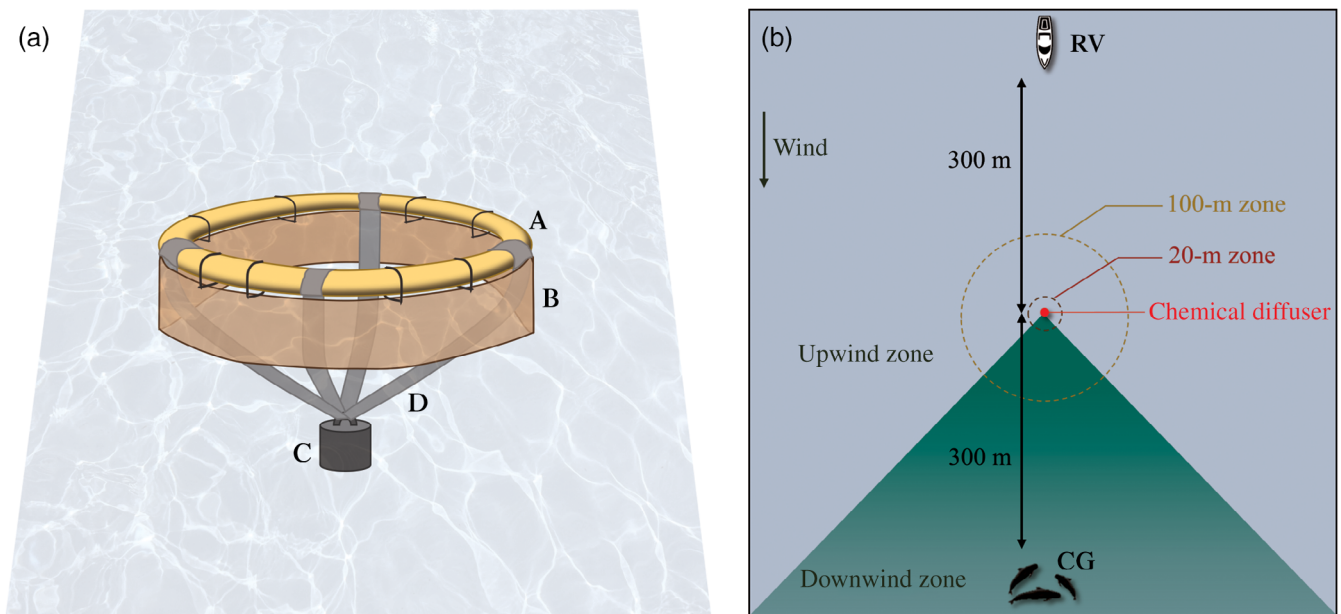


FIGURE 1 (a) Schematic presentation of the floating device used for the diffusion of test chemicals at sea. The floating part had a diameter of 80 cm and was made of one stainless steel-reinforced orange Styrofoam™ tube (A). A 30-cm-high polyvinyl chloride membrane (B) was hung below the tubes in order to partly retain the oily solutions during the trial. A weight of 1 kg of lead (C) was tied 40 cm under the device by four polyester straps (D), and worked as an anchor in order to prevent excessive drifting due to wind. (b) Schematic presentation of the exposure trial initial conditions. The floating chemical diffuser (red point) is placed 300 m upwind from the cetacean groups (CG). Two exposure zones are considered in the behavioral analyses: a close exposure zone with a 20-m radius, “contact zone” (dark red) and a medium exposure zone with a 100-m radius, “approach zone” (orange). The research vessel (RV) is placed another 300 m upwind from the floater. Vessel and cetacean dimensions are not at scale

stern of the vessel, out of sight of the observers and the rest of the crew (blinded experimental design). The vessel then immediately moved 300 m upwind from the floater (and therefore about 600 m from the target cetacean group) before the observation started (Figure 1b). The stimulus and control solutions were deployed in a randomized order. The skipper kept the vessel engine on neutral during the whole trial session, except for small adjustments in order to keep the position of 300 m upwind from the floater.

During 20 min, the position and behavior of each cetacean group were recorded by two experienced cetacean observers equipped with binoculars (7 x 50 magnification) placed on a 4-m-high chair. When additional cetacean groups appeared during the course of a trial, their position and behavior were also recorded. A group was defined as all individuals separated by less than 10 m (Smolker, Richards, Connor, & Pepper, 1992). We took the group as a unit based on preliminary observations indicating that it was not possible to follow each individual within the group separately, and because the individual movement and surface behavior are highly dependent on the other members of the group (Connor, Smolker, & Bejder, 2006; Smolker et al., 1992). When several groups of the same species were present at the same time in the observation area, we gave each group a

unique code and monitored it based on its size (number of individuals) and the presence of highly recognizable animals (e.g., individual size and/or dorsal fin shape and markings). We defined two exposure zones: a “contact zone” and an “approach zone” with a radius of 20 and 100 m around the diffuser, respectively (Figure 1b). The observers used the 300-m distance between the vessel and the diffuser (kept constant by the skipper) as a reference to estimate the borders of the 100-m zone. The 20-m zone was outlined using the length of mature animals as reference (5 and 3 m for large adult pilot whales and bottlenose dolphins, respectively). The entry of cetaceans in these exposure zones was recorded only if at least half of the group members passed within its border. Other observations included any inconspicuous surface behaviors such as spyhopping (raising the head vertically out of the water), breaching (jumping completely or partially out of the water), and slowing down (a marked decrease in navigation speed) (Perrin, Wursig, & Thewissen, 2009). Control and DMS trials only differed by the absence or presence of DMS in the sunflower oil solution. This protocol was designed to control for possible experimental biases such as the floater and the boat, which may be detected visually and/or acoustically by the animals and affect their approach or surface behaviors.

In order to validate the accuracy of the observers' visual estimates of cetacean group size and distance to the floater, we performed five trials using aerial images simultaneously collected by a drone (Phantom 3 advanced, DJI, Shenzhen, China). Drone images taken 150 m above water enabled us to count each group individual (including underwater animals) and precisely measure the distance between the group and the floating diffuser. The comparison of 13 measurements recorded by drone and cetacean observers allowed validating the observers' estimates, as the average errors for group-to-diffuser distances (1.8 ± 0.5 m in the 20-m zone and 9.1 ± 7.8 m in the 100-m zone) and group size (0.57 ± 0.53 individual) were considered negligible.

For each trial, the experimenter recorded the stimulus type (CTL or DMS), GPS position as well as environmental conditions (wind and sea forces, current speed, swell height and visibility). A trained ornithologist equipped with binoculars also recorded the presence of seabirds in sight from the vessel. Bird counts and flight behaviors (landing on water or flying in circles above the exposure zone) were included in the study since seabirds might be attracted by DMS (Nevitt & Bonadonna, 2005) and cetaceans could, in turn, be attracted to the same area by the presence of the birds (Evans, 1982).

After the 20-min trial was completed, the experimenter retrieved the floating diffuser. Another experiment was then started, but only after the boat moved at least five miles away and upwind from the stimulus zone, with an interval of at least one hour between the two trials, to avoid any disturbance from the previous stimulation.

2.3 | Data analysis

We considered cetacean groups as our statistical unit for all statistical analyses. A total of 100 cetacean groups were observed during 28 trials, including 37 groups of bottlenose dolphins and 63 groups of pilot whales (Table 1). Twenty-four groups (16 pilot whale and eight bottlenose dolphin groups) appeared during the course of a trial.

We first tested whether group sizes differed between the two cetacean species or the type of chemical stimulation (DMS vs. CTL solution), using Student's two-sided *t*-test on log-transformed data.

Then we examined the influence of stimulus (DMS/CTL) on the probability for each species to enter the approach zone (100-m radius around the chemical diffuser) or the contact zone (20-m radius). We modeled the response variable (binary: whether a group enters the exposure zone or not) as a binomial generalized linear model (GLM). First, we built a binomial GLM for entering the approach zone with stimulus (DMS/CTL), wind speed, initial activity, bird counts and

TABLE 1 Results of all trials

Cetacean species	Variable	Stimulus	
		CTL	DMS
Pilot whales	<i>Number of groups</i>	41	22
	Enter 20-m zone	9	8
	Enter 100-m zone	21	16
	Stopping	4	6
	Spyhopping	1	4
	Breaching	1	3
	Dive under	2	3
Bottlenose dolphins	<i>Number of groups</i>	22	15
	Enter 20-m zone	4	8
	Enter 100-m zone	13	10
	Stopping	1	1
	Spyhopping	0	1
	Breaching	4	3
	Dive under	1	2

Note: Occurrence of surface behaviors and entrance in exposure zones for pilot whales and bottlenose dolphin groups were shown. Abbreviations: CTL, control trials; DMS, chemical stimulus trials.

group size as covariates. The effect of the stimulus condition was compared to the control by post-hoc multiple comparisons using the *glt* function (multcomp R package) (Hothorn et al., 2015). We then restricted our analysis to the groups that entered the approach zone and analyzed the effect of the chemical stimulus on the probability to enter the contact zone. We used a similar GLM analysis with the chemical stimulus (CTL/DMS), wind speed, initial activity, and group size as covariates.

Then, we tested the influence of the stimulus on cetacean surface behaviors. We built a series of four 2×2 contingency tables for each species, with one variable being stimulus or control, and the other being the number of groups that displayed or did not display each of the four surface behaviors (stopping, breaching, spyhopping and diving under the diffuser). The differences between proportions were tested using a two-tailed Fisher's exact test.

Finally, as an additional analysis, we investigated whether the birds observed in the stimulation zone responded to the chemical stimulation and/or the cetacean behavior. We modeled the bird counts in each study zone with a GLM with a Poisson distribution using the chemical stimulus, wind speed, and cetacean counts as independent variables. While landing behavior was too rare to allow any statistical analysis (it occurred only three times over the course of all trials), we modeled the proportion of birds displaying a circling flight pattern with a binomial GLM using the same independent variables as for bird counts.

All analyses were performed in R v.4.0.3 (R Core Team, 2017).

3 | RESULTS

Both cetacean species were present in half of the trials (14/28), while only bottlenose dolphins were observed in six trials and only pilot whales in eight trials. The average target group size was slightly higher in bottlenose dolphins (mean = 8.0, SD = 10.9, range = 1–50) than in pilot whales (mean = 6.9, SD = 5.9, range = 1–30) but this difference was not statistically significant ($t = -0.59$, $df = 48.6$, $p = .56$, Student's two-sided t -test on log-transformed data). We also found no difference in cetacean group size between stimulus and control experiments for both species (difference = 0.554, IC95 = $-3.756 - 2.645$, $t = -0.350$, $df = 41.90$, $p = .650$ for pilot whales and difference = 1.782, IC95 = $-9.785 - 6.221$, $t = -0.459$, $df = 24.71$, $p = .728$ for bottlenose dolphins, Student's two-sided t -test on log-transformed data). Traveling and milling were both common initial activities in bottlenose dolphin groups (46 and 43% of the groups, respectively) while feeding was observed in only 11% of the groups and no resting was observed in this species. Most of the pilot whales (65%) were found traveling before the start of the trial while resting, milling, and feeding were seen less frequently (16, 13, and 6% of the groups, respectively).

3.1 | Pilot whales

The proportion of pilot whale groups entering the approach zone was higher during DMS trials than during CTL trials (72.7 vs. 51.2%) but the effect was not significant (estimate = 1.391, 95% CI = $-0.07-3.082$, $p = .0692$, Figure 2a). None of the covariates included in the model had a significant effect on this response variable and this GLM explained 9.96% of the deviance. The groups showing a feeding activity entered the approach zone less often than groups with other initial activity, but this difference was not significant and this was based on only four groups (estimate = 3.578, 95% CI = $0.231-7.61$, $p = .0529$, Figure 2b). Among the pilot whales that entered the approach zone, the proportion that entered the 20-m zone was not significantly different between DMS and CTL trials (50 vs. 42%, respectively, estimate = 0.623, 95% CI = $-1.02-2.38$, $p = .463$, Figure 3a).

We counted all surface behaviors because they could potentially be triggered by the animal perception of the chemical stimulus (Figure 4a). These behaviors occurred rarely, that is, mostly stopping in 15.9% of the groups, then breaching (7.9%), spyhopping (7.9%) and diving

under the diffuser (6.3%). The only significant difference between DMS and CTL trials was observed in spyhopping, which occurred in four of 22 groups during DMS trials and in one of 41 groups during CTL trials (18.2 vs 2.4%, $n = 63$, $p = .046$).

3.2 | Bottlenose dolphins

The entrance of bottlenose dolphin groups in the approach zone was not influenced by the type of chemical stimulus (estimate = 0.213, 95% CI = $-1.624-2.077$, $p = .818$, Figure 2c). The GLM for this response variable explained 16.7% of the variance, and none of the covariates had any significant effect (Figure 2d).

When considering only the dolphins that entered the approach zone, the proportion of groups that went into the 20-m zone was significantly higher during DMS trials than during CTL trials (80 vs. 31%, respectively, estimate = 3.121, 95% CI = $0.630-7.023$, $p = .042$, Figure 3b).

Bottlenose dolphins exhibited fewer surface behaviors than pilot whales and no significant difference was found between DMS and CTL trials (Figure 4b).

3.3 | Bird response

Bird numbers were significantly higher in the Strait of Gibraltar than in the Gulf of Vera (mean \pm SD = 10.1 ± 4.9 vs. 1.3 ± 1.4 birds per trials, $p < .0001$, Mann-Whitney U test). The GLM on bird counts explained 47.2% of the deviance. Most of the seabirds ($n = 212$, 82.6%) observed during the trials were yellow-legged gulls (*Larus michahellis*). We therefore focused on that species for the subsequent bird response analyses. Gull counts were significantly higher during DMS trials than CTL trials (estimate = 0.569, 95% CI = $0.269-0.874$, $p < .001$, Figure S1a). Gull counts were also slightly higher when cetaceans were more numerous (estimate = 0.008, 95% CI = $0.0001-0.016$, $p = .043$, Figure S1b). Circle flight increased in the presence of DMS but was not influenced by cetacean counts (estimate = 2.17, 95% CI = $1.19-3.43$, $p < .001$ and estimate = -0.007 , 95% CI = $-0.03-0.01$, $p = .49$, respectively, Figure S1c).

4 | DISCUSSION

Cetacean chemosensory abilities are still mostly unknown, and we describe here the first field behavioral response experiments on odontocetes in their natural habitat. The objective was to test whether the animals would react to DMS, a marker of highly productive marine areas. As

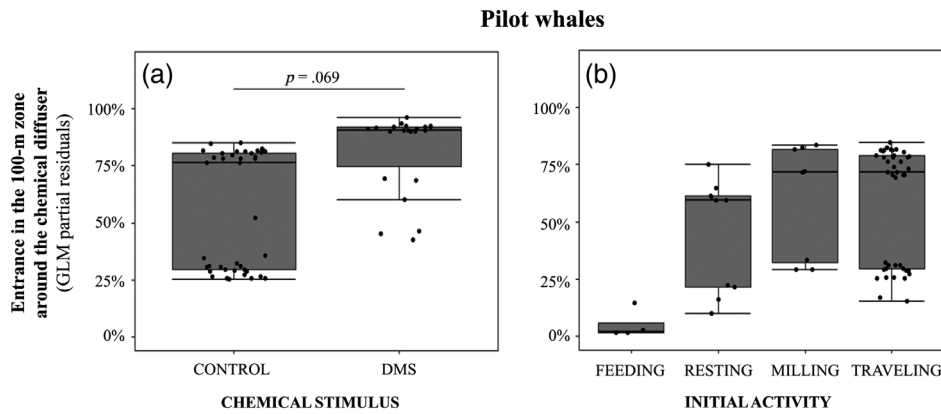


FIGURE 2 Partial regression plots showing the relationship between the cetacean group entrance in the approach zone (100-m zone around the chemical diffuser) and the type of chemical stimulation (a and c) or the group initial activity (b and d)

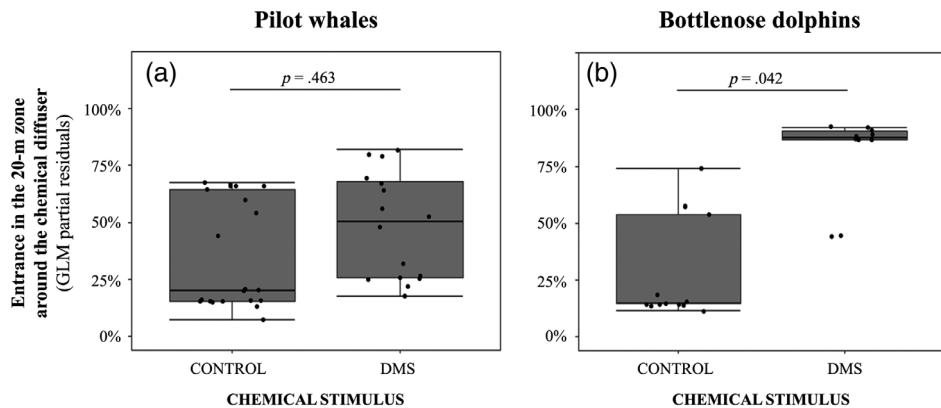
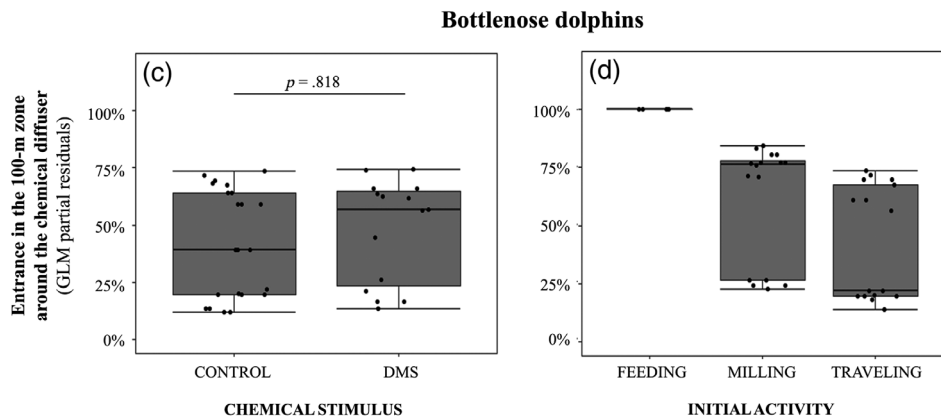


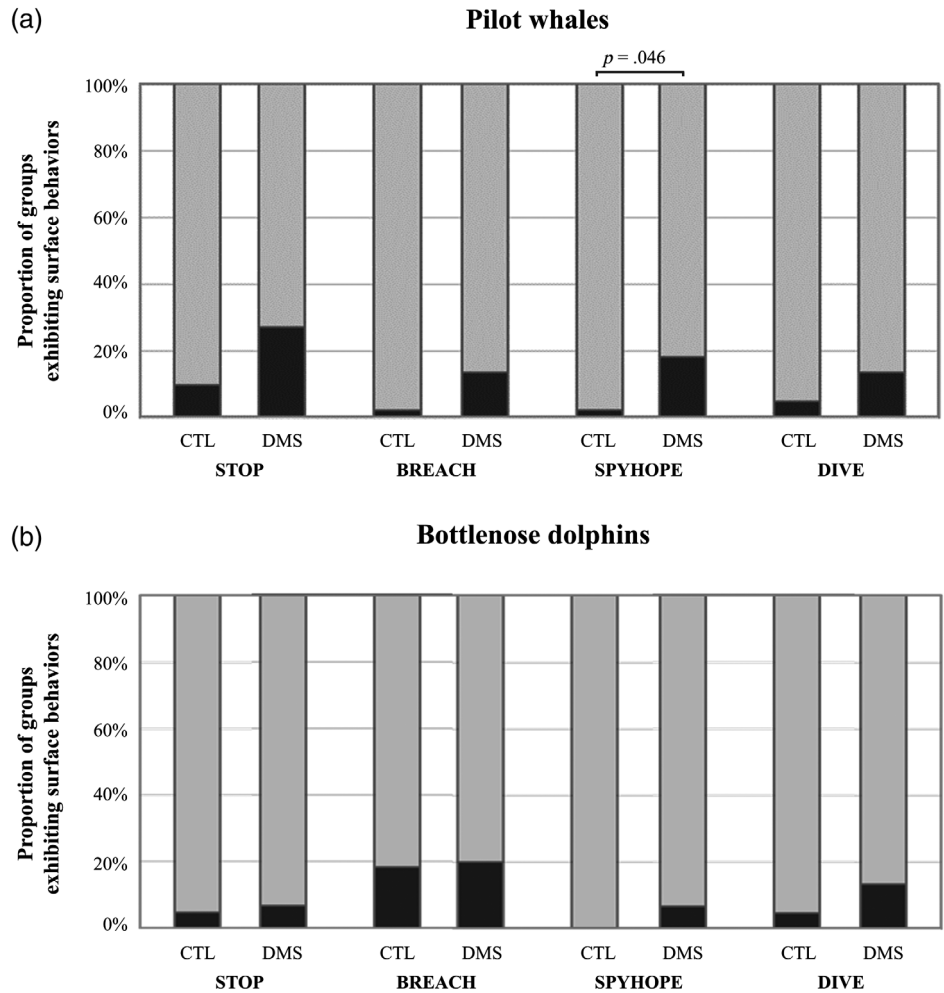
FIGURE 3 Partial regression plots showing the relationship between the entrance in the contact zone (20-m zone around the chemical diffuser) and the type of chemical stimulation for pilot whales (a) and bottlenose dolphins (b) groups that had already entered the 100-m zone

attraction to DMS may vary between species according to their foraging strategies, we analyzed the behavioral response of bottlenose dolphins (shallow divers) and pilot whales (deep divers). Our results did not reveal any significant attraction towards DMS compared to a control chemical stimulus, apart from a short distance response in bottlenose dolphins. This suggests DMS might not be an ecologically relevant foraging chemical cue for odontocetes.

In pilot whales, we observed a higher proportion of groups approaching the chemical diffuser (entering the 100- and 20-m radius zones) during DMS trials than during CTL trials but this difference was not statistically significant. This result was expected, as this species feeds at

depths of several hundreds of meters on cephalopods whose distribution mostly depends on bathymetry (De Stephanis, Cornulier, et al., 2008). Therefore, a high abundance of their prey is not necessarily related to high surface productivity where DMS is produced. Also, as deep divers do not usually move over large distances for foraging and show high foraging site fidelity (Bräger & Bräger, 2019), they are less likely to use long-range cues to find their prey. No significant difference was observed in pilot whale surface behaviors between DMS and CTL trials, except for a small increase in the occurrence of spyhopping with DMS. This behavior however occurred rarely (only five occurrences in total), so

FIGURE 4 Occurrence of surface behaviors (stopping, breaching, spyhopping and diving under the chemical diffuser) in cetacean groups exposed to DMS or a control solution for pilot whales (a) and bottlenose dolphins (b)



this difference may be a random effect due to a small sample size. Moreover, all groups that displayed spyhopping approached within 100 m from the chemical diffuser, so that could be a way to visually inspect this unknown floating object.

In bottlenose dolphins, the type of stimulus had no effect on the proportion of groups entering the approach zone (100-m radius around the chemical diffuser) or the occurrence of specific surface behaviors. However, dolphins present in the approach zone entered the contact zone (20-m radius) in higher proportions when DMS was diffused than during CTL trials, suggesting a short-range attraction toward the source of chemical. Dolphins may thus have perceived DMS only at a very short distance (micro scale), but not further away. One possible explanation may be that dolphins did not perceive the gaseous DMS (DMS_g) carried long distances by wind. They may only have detected the aqueous DMS (DMS_{aq}) carried by surface current moving much slower than the wind (at approximately 2% of wind speed, Chang, Chen, Tseng, Centurioni, & Chu, 2012), that remained close to the floating diffuser during the 20-min trials.

These behavioral observations are consistent with previous knowledge on odontocete chemosenses: an ability to perceive chemicals in water and a regression of their sense of smell in the air. It is possible that “quasi-olfaction” (detection of odorant compounds as defined by Kuznetsov, 1990) may therefore have contributed to the detection of DMS_{aq} (also an odorant) in water through receptors in their oral cavity. The presumed short-scale attraction of the dolphins toward the DMS diffuser would however more likely be a curiosity response than a foraging behavior. The DMS test solution was much more concentrated than natural seawater (0.2 M vs. less than 20 nM, Turner, Malin, Nightingale, & Liss, 1996; Owen et al., 2021). We chose this concentration as it was previously shown to attract seabirds in the wild (Dell’Ariccia et al., 2014; Nevitt et al., 1995; Wright, Pichegru, & Ryan, 2011) and to induce an acoustic reaction in humpback whales (Bouchard et al., 2019). Dolphins may however have perceived it as an unusually strong chemical stimulus. Combined with a novel visual cue (the floating chemical diffuser), this chemical stimulus may have induced curiosity, which resulted in an exploratory

approach towards the source of the chemical possibly as part of an object play behavior (Greene, Project, Melillo-sweeting, & Dudzinski, 2011; Janik, 2015). Future experiments could be conducted using DMS concentrations closer to those found in the environment. A more natural cue could perhaps trigger foraging responses in dolphins instead of plain curiosity toward an unusual stimulus.

Odontocetes lack the canonical olfactory structures that allow the perception of airborne chemicals in terrestrial mammals such as the olfactory mucosa, nerve and bulb (Breathnach, 1960; Oelschläger & Buhl, 2008). They also lost most of the vertebrate genes involved in olfaction (Kishida et al., 2007; McGowen et al., 2008; Thewissen et al., 2011). These results support the hypothesis that the conventional sense of smell is inexistent or strongly reduced in odontocetes and would explain the absence of significant behavioral response toward DMS at medium range (hundreds of meters) in the present experiment. In contrast, mysticetes have a high proportion of function OR genes and a functional olfactory system (Kishida et al., 2015; McGowen et al., 2008; Thewissen et al., 2011). Field exposure experiments in humpback whales showed they are attracted to krill extract at a short scale. They spent longer time near the stimulus area, stopping and diving more often around the chemical diffuser than during control tests (Bouchard et al., 2019). In that study, trials with DMS did not show a similar attraction towards the chemical cue. When exposed to DMS or krill extract, whales however showed a different vocal activity than during the control trials. This suggests whales reacted at least acoustically to both chemical stimuli. There is a growing body of evidence that the olfactory sense is still functional in mysticetes but that it has partly been lost in odontocetes. A recent oceanographic survey in North Atlantic waters interestingly confirmed that DMS_a and DMS_g would accurately lead zooplankton predators such as mysticetes towards prey aggregations over long distances (Owen et al., 2021). The authors of the study however found no correlation between DMS (in air or in seawater) and fish biomass, possibly due to time lags between DMS production and the buildup of fish biomass. This lack of correlation suggests that DMS may be a less valuable foraging chemical cue for higher trophic predators such as odontocetes. This is consistent with the hypothesis that the feeding behavior of toothed whales may have contributed to the relaxation of the selective constraints on the genes involved in olfaction and the reduction of their sense of smell.

Our study only included cetacean surface behaviors observed from a survey vessel as response variables. Specific responses may however have occurred underwater and therefore could have been missed. The observation of

open-mouth behavior near the diffuser during DMS experiments would have supported the hypothesis of perception of DMS_{aq} . Interestingly, such reactions have recently been reported in river dolphins during baited remote underwater video (BRUV) experiments, suggesting they used their sense of taste to find the source of a prey extract (Schmid & Giarrizzo, 2020). BRUV offers great potential as a tool for chemosensory experimentation in wild odontocetes (e.g., choice experiments). Our study could well have benefited from the use of underwater cameras to detect the behaviors around the diffuser. Aerial images from drones, which are now widely used for cetacean research (Torres, Nieu Kirk, Lemos, & Chandler, 2018), could substantially improve the range and accuracy of data collected during behavioral experiments when compared to distant boat-based observations. They could allow the accurate measurement of various response variables such as cetacean trajectories, swimming speed, distance to the chemical diffuser, surfacing times and respiratory rates as well as more subtle surface behaviors (e.g., social interactions, group cohesion). Other data collected from aerial images may be relevant explanatory variables (e.g., body length in relation to age class, group size) that could significantly improve the model explained variance. Finally, since cetaceans primarily use their sense of hearing for foraging and communicating (Nummela & Yamato, 2018), another way to improve the sensitivity of the protocol would be to analyze cetacean acoustic behavior during the experiments with a hydrophone attached to the diffuser. As shown in humpback whales exposed to DMS, a chemical stimulus could trigger specific acoustic responses without inducing other detectable changes in their behavior (Bouchard et al., 2019).

During the exposure trials, we recorded the number of birds flying in the study zone since it could be a visual cue for cetaceans. Results however showed that this variable did not significantly influence cetacean behaviors or their approach toward the chemical diffuser. Interestingly, an additional analysis suggested that yellow-legged gulls responded to DMS. Gulls came in higher numbers during DMS trials, showing they were attracted by this chemical cue. Once above the exposure area, gulls also displayed more circling flights in the presence of DMS. Circling behavior is associated with the detection of a visual cue during area-restricted search in various seabird species (Bairos-Novak, Crook, & Davoren, 2015; Nevitt, Losekoot, & Weimerskirch, 2008). In our study, gulls are likely to have used this behavior to inspect visual cues on the water surface (e.g., floating diffuser, boat, oil slick, and cetaceans). The increase in circling observed during trials with DMS could mean that this olfactory cue not only attracted them to the study zone, but also boosted their interest in exploring the area to detect prey aggregations. To our knowledge, the use of smell in gull foraging

ecology has never been reported before, and previous DMS experiments in the Mediterranean Sea did not report any attraction of gull species (Dell'Araccia et al., 2014). Our data also show that the presence of cetaceans had a slightly positive effect on gull approach towards the study area. Gulls may thus use cetaceans as a visual cue to find their foraging grounds, as it was shown in other seabird species (Camphuysen & Webb, 1999; Evans, 1982; Hawke & Dobinson, 2001; Veit & Harrison, 2017). Additional studies would however be required in order to confirm this hypothesis, using control trials in the absence of cetaceans.

Finally, this first response experiment suggests odontocetes do not react to airborne DMS at long distances, and that it is not an ecologically relevant infochemical for them. Short-range chemoreception in water may however be functional and its potential role in their foraging ecology could further be studied using chemical stimuli more directly associated with the presence of prey such as fish, squid, or shrimp extract. Futures experiments on toothed whale chemosensory abilities may thus yield interesting insights about the role of chemicals in their feeding, mating and social behaviors.

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AUTHOR CONTRIBUTIONS

Bertrand Bouchard: Conceptualization; data curation; formal analysis; investigation; methodology; validation; visualization; writing - original draft. **Jean-Yves Barnagaud:** Data curation; formal analysis; methodology; supervision; writing-review & editing. **Philippe Verborgh:** Investigation; methodology; validation; writing-review & editing.

Pauline Gauffier: Investigation; methodology; validation; writing-review & editing. **Sylvie Campagna:** Conceptualization; funding acquisition; investigation; methodology; writing-review & editing. **Aurélien Célérier:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-review & editing.

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